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ESTUARIES

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ESTUARIES

Introduction

Estuaries are significant to human welfare through their role in transportation, production of food, waste disposal, and various recreational pursuits. Many of the world's largest metropolitan areas have developed near estuaries and these waters have become adversely affected by human activities. Important fisheries may exist in estuarine and inshore waters as a result of generally high biological productivity and there is clear evidence that the influence of estuaries may extend well into ocean basins. Detailed information concerning such matters as estuarine circulation patterns, rates of exchange of materials with coastal and marine waters, and the ecology of estuarine organisms will afford opportunity for realistic and essential management of estuaries in the future.

The development of coastal areas has been very rapid in recent years, but knowledge of estuarine environments has not kept pace with the necessity to resolve problems arising from their intensive use. Need for a more comprehensive understanding of estuaries and their surroundings and the lack of an adequate means to exchange information concerning estuarine research stimulated the organization of the Conference on Estuaries, held at Jekyll Island, Georgia, from March 31 to April 3, 1964. The objectives were to provide an opportunity for the exchange of ideas between the various disciplines and individuals interested in estuarine research, to summarize the present knowledge of the natural characteristics of estuaries, and to delineate the direction of current research efforts.

The Sapelo Island Research Foundation, Inc., through funds provided by the late Richard J. Reynolds, Jr., supported initial planning for the Conference. Sponsors also included the University of Georgia Marine Institute; the U.S. Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia; the Atlantic Estuarine Research Society; and the American Society of Limnology and Oceanography, Inc. The U.S. Atomic Energy Commission, the U.S. National Science Foundation, the U.S. Office of Naval Research, and the Sport Fishing Institute supplied financial support. William W. Anderson, James H. Carpenter, John D. Costlow, Vernon J. Henry, and Bernard C. Patten assisted me in organizing the Conference program and in selecting participants. The session chairmen and participants contributed greatly to its success and Barbara Salter and Nadine Watson were most helpful.

This book is an outcome of the Conference. The subject matter is broad, and includes aspects of biology, chemistry, geography, geology, and physics. There is as yet no name like oceanography or limnology for estuarine research and its future strength lies, perhaps, in the diversity of disciplines which can contribute to it without the hindrance of established patterns and procedures.

The sequence of the papers is, for me, a logical one, though others might have arranged them differently. The term, estuary, has been defined numerous times beyond the initial chapter, as authors sought to establish a frame of reference for their presentations; other areas of overlap could not be completely avoided. But readers will not necessarily read the papers in sequence, and I hope that each paper can stand by itself. The Supplemental Bibliography includes pertinent papers published since the Conference and earlier ones not cited in the text.

I am particularly grateful to the American Association for the Advancement of Science, who by publishing this book have made it available to a far wider audience than it might have had. The Association's recognition of the multidisciplinary scope of estuarine research and the value of gathering the accumulated knowledge of the subject into one volume is heartening to workers in the field.

Bernard C. Patten, William W. Anderson, and other members of the program committee of the Conference reviewed the manuscripts. Jack W. Gehringer, Peter A. Hyppio, James W. McGary, and Don L. McGregor assisted in resolving editorial questions. Marion Blevins and Eleanor McAllister were most helpful in preparing and indexing the papers. I am especially grateful to Dolores Johnson for her dedication to all manner of clerical and editorial chores. *Estuaries*, however, might still be little more than a large number of manuscripts except for the cooperation and skillful work of Horace D. Porter, who, with the help of his wife, Mary, produced this book. It is with heartfelt thanks that I acknowledge their contribution to this volume.

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I. BASIC CONSIDERATIONS

What is an Estuary: Physical Viewpoint

DONALD W. PRITCHARD

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The problem of defining an estuary and delineating the area of estuarine oceanography has concerned me since I first started to study these bodies of water fifteen years ago. It is difficult to develop a definition that will include all the bodies of water one wishes to talk about and exclude all the others.

Historically, the term estuary has been applied primarily to the lower tidal reaches of a river. A review of some of the dictionary definitions is appropriate as a starting point. The Concise Oxford Dictionary gives, simply: "Tidal mouth of a large river." Webster's New 20th Century Dictionary states: "An arm of the sea; a frith or firth; a narrow passage, or the mouth of a river or lake, where the tide meets the current." Webster's New International Dictionary has: "1(a) A passage, as the mouth of a river or lake where the tide meets the river current; more commonly, an arm of the sea at the lower end of a river; a firth. (b) In physical geography, a drowned river mouth, caused by the sinking of land near the coast."

The French dictionary, Larousse, brings in a somewhat different concept, giving as a definition of an estuary: "Sinuosité du littoral, qui n'est couverte d'eau qu'à marée haute. Golfe formé par l'embouchure d'un fleuve." ("A coastline bight which is covered with water only at high tide. A gulf formed by the mouth of a river.") The second sentence refers to a drowned river mouth. However, the first part of this definition seems peculiar to the French. It describes, for example, the region near Mont St. Michel where a curving region of the coast is covered at high tide and bare at low tide. This area cannot be described as a coastal embayment, and there is no dilution of sea water—features which are important in defining an estuary.

From a physical standpoint, the definition of an estuary should recognize certain basic similarities in the distribution of salinity and density, as well as the circulation pattern and the mixing processes; it should point out also the importance of the boundaries which control the distribution of properties and the movement and mixing of waters.

A DEFINITION

Taking these features into account, I have defined an estuary as follows: *An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage.*

First, consider the requirement that an estuary be "a semi-enclosed coastal body of water". The circulation pattern in an estuary is influenced to a considerable degree by its lateral boundaries. This control of the water movements by the lateral boundaries is an important feature of an estuary and should be taken into account in the definition.

Further, the definition states that the estuary is a coastal feature and hence limits to some extent the size of the bodies of water under consideration. The intent here is that the estuary be a part of the coast and not form the coast. Admittedly, the application of this restriction involves somewhat arbitrary decisions. By this part of my definition I would exclude the Baltic Sea, the adjacent Gulf of Bothnia, and the Gulf of Finland from being designated as estuaries, despite other similarities. To me, the Baltic Sea and the adjacent Gulf of Bothnia and Gulf of Finland form the coastline rather than being a feature of the coastline. The physical significance of this restriction is that the lateral boundaries of such relatively large bodies of water are less important to the kinematics and dynamics of water movement than they are in a true estuary.

The next requirement of the definition, that of "a free connection with the open sea", is included to indicate that communication between the ocean and the estuary must be adequate to transmit tidal energy and sea salts. The free connection must allow an essentially continuous exchange of water between the estuary and the ocean. Again, it must be admitted that the definition does not perfectly delimit the character of the connection between the ocean and the coastal indenture required for the body of water to be classed as an estuary. In the great majority of cases, however, there should be no problem in concluding whether the connection is, in fact, "free".

Bar-built estuaries, as a class, come closest to the borderline of the definition with regard to free connection with the open sea; Pamlico Sound is an example. Normally the width of the inlet to such embayments is small compared to the horizontal dimensions of the estuary. If the inlet allows free passage of the ebb and flood flows at all stages of the tide, however, then the connection should be considered adequate. If the barrier bar has no fully open inlet at all stages of the tide, with water passages between the embayment and the ocean occurring through a shallow depression in the barrier beach only at high tide, then the connection is not adequate from the

standpoint of this definition. Such embayments are often referred to as lagoons, although this term also has other connotations.

We come finally to the phrase in the definition requiring that, within the estuary, sea water be "measurably diluted with fresh water derived from land drainage". This dilution of sea water provides the density gradients which drive the characteristic estuarine circulation patterns. In an early attempt to define an estuary, I did not include this feature in the primary definition. Instead, I considered three sub-groups of embayments under the general definition of an estuary. I then called "positive estuaries" those semi-enclosed coastal bodies of water having a free connection with the open sea, within which runoff plus direct precipitation exceeds evaporation, and hence within which sea water is diluted by fresh water. I called the embayment an "inverse estuary" if evaporation exceeds runoff plus precipitation, since the characteristic circulation pattern in such a hypersaline body is inverse to that found in a positive estuary. For those embayments in which there was near balance between freshwater supply and evaporation, I employed the term "neutral estuary". I now prefer to reserve the term "estuary", without any qualifying adjective, for those bodies I previously called "positive estuaries".

FOUR CLASSIFICATIONS

Having now defined an estuary, we should consider some possible subclassifications based on physical characteristics. From a geomorphological standpoint, there are four primary subdivisions of estuaries: (1) drowned river valleys, (2) fjord-type estuaries, (3) bar-built estuaries, and (4) estuaries produced by tectonic processes.

Drowned river valleys—These are the classical estuaries of the physical geographer. Because they are most commonly found along a coastline with a relatively wide coastal plain, and are generally confined to that geological regime, I have called these waterways coastal plain estuaries. This designation has received relatively wide use in the United States.

The Chesapeake Bay is a prime example of this type of estuary. During the last glacial period, the Susquehanna River reached the ocean about 180 km seawards of the present shoreline; the York River and the other rivers now entering the Bay to the north of the York were then tributaries of the Susquehanna. The James River probably reached the sea separately. The rise in sea level by about 100 m following the glacial period, roughly 10 thousand years ago, flooded the valleys of these rivers to form the Chesapeake Bay system.

Drowned river valleys are not only typical of the eastern seaboard of the United States, but are widespread throughout the world. It should be pointed out, with respect to coastal plain estuaries, that by the definition given here not all the length of the drowned river valley would be classified as an estuary. The

phrase "within which sea water is measurably diluted by fresh water" implies not only that there must be a supply of fresh water to mix with the sea water, but conversely that the estuary proper extends up the drowned river valley only so far as there is a measurable amount of sea salts. In most coastal plain estuaries the river bottom does not rise above sea level for a considerable distance landward from the point at which the last vestiges of sea-derived salt can be measured. The "fresh" water of the river of course has some dissolved solids, and therefore has a salt content. Even so, the upper limit of the estuary, as defined by the most landward intrusion of sea-derived salt, can be quite sharply delineated, because the ionic ratios of the major constituents in the river water are quite different from those in sea water. For example, the ratio of chloride ion to total dissolved solids in the sea is about 1:1.8, while this ratio in "freshwater" rivers is more characteristically 1:10 or 1:20.

As one proceeds from the mouth of a coastal plain estuary toward the head, the salinity (defined either in terms of chlorinity or of conductivity) usually decreases steadily from a value of about 30‰ to about 0.1‰. In the rivers along the east coast of the United States, the salt content of the fresh water is generally less than 100 ppm, or 0.1‰. However, since typically for these rivers the ratio of chlorinity to total dissolved solids is about 1:18, then even when the salinity, as defined by the classical seawater relationship to chlorinity, is 0.1‰, the salt content of the water is about 90% derived from sea salt. Beyond the point where the chlorinity is about 0.06‰ (salinity approximately 0.1‰) there will usually occur a short transitional region in which the chlorinity will continue to drop to about 0.01‰, and the ratios of the major dissolved constituents will undergo a rapid change. The point at which this occurs marks the upper limit of the estuary. Upriver from this point the chlorinity and conductivity will remain relatively constant.

Above this upper limit of the estuary there is usually a stretch of the freshwater river which is still subject to the oscillation of the tidal currents. The duration of the flood period compared to the ebb period will decrease until a point is reached where the downriver flow just ceases at what would be maximum flood. There then occurs a further stretch of the river which is subject to a tidal variation in water elevation, and within which there is a time variation in the downstream velocity, but without any flood flow. The tidal effect on surface elevation frequently can be traced, under certain flow conditions, to the point where the river bed rises above sea level. The stretch of the fresh river above the upper limit of intrusion of sea-derived salt which is still subject to tidal action is called the tidal section of the river.

Fjords—Generally U-shaped in cross section, these coastal indentures have been gouged out by glaciers. They frequently have a shallow sill formed by terminal glacial deposits at their mouths. The basins inside the sills are often quite deep: 300 or 400 m. Most fjords have rivers entering at the head and exhibit

estuarine features in the upper layers. The sill depths in Norwegian fjords are often so shallow that the estuarine features develop from the surface to the sill depth, while the deeper basin waters remain stagnant for prolonged periods. Some fjords along the British Columbia coast have greater sill depths, and the estuarine layers do not extend down to the sill. In this case the basin waters are subjected to a slow but steady exchange with the adjacent open sea waters.

Bar-built estuaries—When offshore barrier sand islands and sand spits build above sea level and extend between headlands in a chain, broken by one or more inlets, bar-built estuaries are formed. The area enclosed by the barrier beaches is generally elongated parallel to the coastline. Frequently more than one river enters into the estuary, though the total drainage area feeding a bar-built estuary is seldom large. The lower valleys of such rivers have frequently been drowned by the rising sea level, and hence the bar-built estuary might be considered as a composite system, part being an outer embayment partially enclosed by the barrier beaches, and part being a drowned river valley or valleys. Because the inlets connecting the bar-built estuary with the ocean are usually relatively small compared to the dimensions of the sound within the barrier, tidal action is considerably reduced in such estuaries. These systems are usually shallow, and the wind provides the important mixing mechanism. Albemarle Sound and Pamlico Sound in North Carolina are examples of bar-built estuaries.

Estuaries produced by tectonic processes—This fourth category is a catch-all classification for estu-

aries not clearly included in the other three divisions. Coast: I indentures formed by faulting or by local subsidence, and having an excess supply of freshwater inflow, are covered by this category. San Francisco Bay is an example of this group of estuaries.

Another approach to the classification of estuaries is to consider the dominant physical processes associated with movement and mixing in the estuary. There are three basic processes which produce motion and mixing in an estuary: the wind, the tide, and the inflow of river water. In an estuary dominated by the wind (for example, a bar-built estuary), wind provides most of the energy for moving and mixing the water. In a tide-dominated estuary, turbulence associated with the tidal currents results in mixing between the salt and fresh water, which in turn produces the density gradients associated with the non-tidal circulation pattern. In a river-dominated estuary such as the Mississippi, the mixing is caused mostly by the breaking of unstable interfacial waves at the upper boundary of the saltwater wedge.

The coastal plain estuary is the most common type of estuary and probably has been studied most completely. I have worked out a classification of coastal plain estuaries based on a consideration of the various terms which dominate the salt balance equation. This classification is discussed in another article in this book.

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Estuaries: Analysis of Definitions and Biological Considerations

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Dictionary and encyclopedia definitions of the word "estuary" seem comparatively clear, but general acceptance is not evident in the descriptions given in scientific publications. A precise definition seems even more difficult after a thorough study of estuarine animals and an attempt to characterize brackish-water fauna. Brackish water is typical of many, but not all, estuaries and it seems improbable that all characteristics of these bodies of water are determined by brackish-water conditions. Further, the use of the terms "estuary" and "estuarine" is often confused in biological studies.

ANALYSIS OF DEFINITIONS

The papers of Emery and Stevenson (1957) and Hedgpeth (1957) are helpful in discussing definitions. Emery and Stevenson consider an estuary as the wide mouth of a river, or arm of the sea, where the tide meets the river currents; they agree with the common dictionary definition, and they add that the tide is the principal cause of special conditions at the river mouth. Real estuaries, accordingly, are restricted to the outflow of rivers in a tidal sea, and, therefore, rivers flowing into a non-tidal sea, such as the Mediterranean, Black Sea, or the Baltic do not form estuaries. Their definition includes the supposition that the river has a wide mouth, but there is a variety of special situations ranging from those continually open to seasonally closed estuaries, or river mouths with a barrier separating them from the sea.

In 1951, Ketchum presented this definition: "An estuary may be defined as a body of water in which the river water mixes with and measurably dilutes sea water." This allows the inclusion of brackish water areas at the river outflows in non-tidal seas, which is a contradiction of the classical understanding of estuaries. It poses a difficulty in differentiating an estuary from a lagoon, which is described as "a shallow lake or sheet of water connected with the sea or a river". Emery and Stevenson (1957) also pointed out "these dictionary definitions are not mutually exclusive, since a lagoon connected with the sea may also be affected by the tide". I agree that it would be impractical to accept salinity as the only factor, because the most characteristic aspect of the estuarine environment—a region of steep and variable gradient in environmental conditions—is not recognized. Nevertheless, there is no sharp separation between estuaries

and lagoons, because gradients (mainly in salinity) are to be found in lagoons and even in whole sea basins, as in the Baltic.

Estuaries are sometimes defined from a physiographic viewpoint as bodies of water bordered by land masses and occupying the mouths of stream valleys. The condition of a drowned river valley does not seem appropriate, as an estuary may be built by the river itself through formation of a delta, and sedimentation, together with erosion, has often developed a system of typical estuaries in the lower part of the river. It is equally inexact to specify them as distinct hydrobiological types when the delta is built at the entrance of a tidal sea. As a result of sedimentation the river mouth is usually separated into different arms which can result in small estuaries with the same hydrographic and biological characteristics of those corresponding to the classical description. The definition of estuaries based on their physiography does not correspond to Pritchard (1952): "An estuary is a semi-enclosed coastal body of water having a free connection with the open sea and containing a measurable quantity of seawater." This description could also apply to most of the marine lagoons, and explains the confusion often found in American biological publications on the subject of "estuarine waters" and "estuarine communities".

Scientific investigations usually compare individual characteristics of one system with those of other systems to determine common features—a dangerous approach if we forget that reality in nature is individuality. Local geographic, hydrographic, and climatic conditions decisively determine the biological features of river mouths. In order to establish the common characteristics of all estuaries by combining the individual features of nature to a category, we must have a clear definition. For example, it is possible to describe the biology of one river mouth giving the name of the river, but if we speak of an estuary we must indicate what an estuary is and what it is not.

In considering the mouth of a river in a tidal sea, assuming that it is a river bed or a system of river beds that carry fresh water to the sea, one may ask what boundaries might be selected to determine the estuarine region of such a river. In most definitions, the hydrographic point of view is expressed; the estuary includes the region where river water mixes with sea water. This would mean that the estuary is confined to the area of brackish water. In nature, how-

ever, it is difficult to limit the estuarine region in this way. Perhaps this can be illustrated by the extreme case of the Amazon which is influenced some hundreds of miles up the river by the rise and fall of tides. The phenomenon is a result of the periodic restriction of freshwater outflow by the tides; all brackish water regions are limited to the mouth of the river. The freshwater flows are so large that tidal forces are inadequate to cause movement of marine waters into the river, except in the dry seasons. However, the pressure of the tides influences the development of tidal currents up and down the river over a considerable distance. This phenomenon occurs commonly in all open estuaries. The steepness of the salinity gradient and the distance of penetration of marine water depend upon the pressure of the tides entering the estuary. Upstream from the end of the mixo-oligohaline region, the fresh water is still influenced by the tidal rise and fall. In the Elbe Estuary, brackish water is present only in the lower quarter of that portion of the river influenced by the ebb and flow of tidal currents (Lucht, 1964); this means that the upper limit of the estuary is determined not by salinity, but by tidal forces. In other words, it is determined hydrodynamically rather than hydrochemically.

The lower limit of the estuary is fixed by geomorphological features. On rocky shores the opening of the river into the sea may be sudden; in flatland areas extensive sedimentation may occur; in extreme cases, a wide delta region develops, or the river may pass through a tidal marsh (for example, the Elbe). A line usually separates the river bed from the sea floor, but this line defines the limit of undiluted sea water and brackish water may occur a great distance beyond this point of separation.

Emery and Stevenson (1957) note that "most lagoons are elongate parallel to shore and lie athwart the mouths of one or more streams"—a description that does not clarify the character of lagoons and estuaries. Lagoons without tidal change can be deleted from consideration here, but it is sometimes difficult to determine if a tidally influenced area at the border of the sea having a freshwater inflow is a lagoon or part of an estuary. As Rochford (1951a, b) has shown in Australian estuarine systems, and Day (1951) in South Africa, a river often builds a barrier that separates its mouth from the open sea; and Johnson (1919) described the sequence of estuaries and lagoons by the influence of geological submergence and the formation of shore lines. But these descriptions do not provide a clear separation of estuaries and lagoons.

It may be possible to distinguish between lagoons and estuaries by analyzing another hydrological feature, the instability of salinity. When the inflow of fresh water in a separated basin develops a stable body of brackish water, it may be considered a lagoon. If the mixing of fresh and marine waters is not stable but shows periodic changes, the basin may be considered an estuary.

BIOLOGICAL CONSIDERATIONS

The unstable conditions of estuaries determine their principal biological features. In brackish water lagoons, the environmental conditions, expressed by the salinity, are relatively stable. In estuaries, however, poikilohaline conditions influence the whole biocoenosis; Day (1951) has emphasized that the distribution of animals in estuaries cannot be based on a single factor of the environment, but that a complex of periodically changing parameters limits the colonization to a restricted number of organisms with a wide range of ecological adaptations.

The bottom communities are most important, because the flora and fauna must survive extreme hydrographic changes, sometimes in a period of one tide. If extreme variation occurs in different seasons, the faunal composition may be significantly changed. Day (1951) has given many examples of "blind estuaries" in South Africa, and he noted that the distribution of organisms may be controlled by any of several factors: a wide variation in salinity, temperature, or turbidity often destroys the faunal populations. Some animals have become adapted to the environmental fluctuations in estuaries and represent a comparatively stable biotope, but this group does not contain a large variety of species (Caspers, 1948, 1951, 1954, 1955, 1958, 1959, 1960). Typically, brackish water lagoons or seas show a richer spectrum of species which adapt to reduced salinity. In contrast, it seems doubtful that estuaries develop a clearly specialized brackish water bottom fauna.

A somewhat different situation is evident in plankton communities. It is difficult to define typical potamoplankton communities in rivers because the plankton floats downstream too quickly, but in estuaries, because of the periodic change in current direction, the plankton remains in the same water mass for a long enough period to develop populations of various organisms (Schulz, 1960).

It is impractical to describe in this paper all the different types of estuaries, but some of their main features are:

1. Estuaries are limited to river mouths in tidal seas.
2. Estuaries often show saline areas, but the extent of these areas differs, depending on the amount of freshwater inflow.
3. In extended estuaries, tide-induced currents reach upstream into freshwater zones; in these cases, the upper limit of the estuary corresponds to the upper limit of tidal influence.
4. Estuaries, in contrast to lagoons, are characterized by poikilohalinity and the instability of environmental factors.

Hedgpeth (1957) discusses the monotony of estuarine populations as compared to those of the sea. Estuarine organisms are mainly euryhaline marine forms which are able to penetrate and exist in an unstable biotope. One does not find specialized organisms in the upper portion of an estuary, but only

those eurytopic elements of the freshwater biota which are able to survive. These organisms can usually be found in the tidal flats on the muddy borders of the river; in addition, some marine immigrants cross the salinity barrier. Anadromous and catadromous animals periodically migrate through the estuary or, like *Eriocheir*, select the brackish-water part of the estuary as a breeding place.

It has been suggested that estuaries may be invaded more easily in warm waters. This theory has developed primarily from observations of the richness of the fauna of tropical and subtropical estuarine waters as compared with those of higher latitudes. Hedgpeth (1957) attributed the difference to an increased osmoregulatory ability at higher temperatures. It seems to me, however, that it is a matter of statistics; the greater variety of species in tropical seas accounts for more ecological types which can penetrate unstable environs. A large number of marine microfaunal species exists in the upper regions of estuaries in non-tropical areas, as illustrated by the Elbe Estuary (Riemann, 1966).

The above examples have been mentioned to demonstrate that the flora and fauna of an estuary cannot be described merely as a brackish water community. The assemblage consists not only of brackish water elements but many other organisms able to resist the unstable conditions. Typical brackish water organisms are adapted to a more or less stable salinity, while estuarine brackish water organisms must be able to adapt to greater environmental changes. Should typical brackish water organisms be found in estuaries, their preadaptation to persist in unstable biotopes has probably permitted them to colonize. A distinction between estuaries as poikilohaline biotopes and lagoons as more or less stable brackish water areas should be made. The variety of estuarine organisms has developed by a selection quite different from that in lagoons and larger brackish water areas. Biological analyses will demonstrate the principal difference between estuaries and lagoons.

LITERATURE CITED

- CASPERS, H., 1948. Ökologische Untersuchungen über die Warentierwelt im Elbe-Aestuar. *Verhandl. Deut. Zool. Ges. Wilhelmshaven*, 1948; pp. 350-359.
- CASPERS, H., 1951. Bodengreiferuntersuchungen über die Tierwelt in der Fahrinne der Unterelbe und im Mündungsgebiet der Nordsee. *Verhandl. Deut. Zool. Ges. Wilhelmshaven*, 1951; pp. 404-418.
- CASPERS, H., 1954. Biologische Untersuchungen über die Lebensräume der Unterelbe und des Mündungsgebietes der Nordsee. *Mitt. Geol. Staatsinst. Hamburg*, 23:78-85.
- CASPERS, H., 1955. Limnologie des Elbeästuars. *Verhandl. Intern. Ver. Limnol.*, 12:613-619.
- CASPERS, H., 1958. Biologie der Brackwasser-Zonen des Elbeästuars. *Verhandl. Intern. Ver. Limnol.*, 13: 687-689.
- CASPERS, H., 1959. Die Einteilung der Brackwasser-Regionen in einem Aestuar. *Arch. Oceanogr. Limnol.*, Suppl. 11:155-169.
- CASPERS, H., 1960. Biologie des Elbe-Aestuar. Vorwort zum Band I "Elbe-Aestuar". *Arch. Hydrobiol.* Suppl. 26:1-4.
- DAY, J. H., 1951. The ecology of South African estuaries. I. A review of estuarine conditions in general. *Trans. Roy. Soc. S. Africa*, 33:53-91.
- EMERY, K. O., and R. E. STEVENSON, 1957. Estuaries and lagoons. I. Physical and chemical characteristics. In *Treatise on Marine Ecology and Paleoecology I.*, edited by J. W. Hedgpeth. *Geol. Soc. Am., Mem.* 67:673-693.
- HEDGPETH, J. W., 1957. Estuaries and lagoons. II. Biological aspects. In *Treatise on Marine Ecology and Paleoecology I.*, edited by J. W. Hedgpeth. *Geol. Soc. Am., Mem.* 67:693-729.
- JOHNSON, D. W., 1919. *Shore Processes and Shoreline Development*. John Wiley and Sons, New York.
- KETCHUM, B. H., 1951. The flushing of tidal estuaries. *Science Ind. Wastes*, 23:198-209.
- LUCHT, E., 1964. Hydrographie des Elbe-Aestuars. Hydrographische und hydrochemische Verhältnisse im Mündungsgebiet der Elbe mit Einschluss des angrenzenden Oberlaufes. *Arch. Hydrobiol., Suppl. 29 (Elbe-Aestuar II)*:1-96.
- PRITCHARD, D. W., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Mar. Res.*, 11:106-123.
- RIEMANN, F., 1966. Die interstitielle Fauna im Elbe-Aestuar. Verbreitung und Systematik. *Arch. Hydrobiol. Suppl. XXI*, 1:21-279.
- ROCHFORD, D. J., 1951a. Hydrology of the estuarine environment. *Proc. Indo-Pacific Fisheries Council*, 3: 157-168.
- ROCHFORD, D. J., 1951b. Studies in Australian estuarine hydrology. I. Introduction and comparative features. *Australian J. Marine Freshwater Res.*, 2:1-116.
- SCHULZ, H., 1960. Qualitative und quantitative Planktonuntersuchungen im Elbe-Aestuar. *Arch. Hydrobiol.* Suppl. 26 (Elbe-Aestuar I): 5-105.

Estuaries and Lagoons in Relation to Continental Shelves

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Many of the papers in this symposium volume describe the characteristics of estuaries and lagoons and outline the physical, biological, and chemical processes which are responsible for these characteristics. Others, for example, Klein, identify and describe Mesozoic and Paleozoic strata containing evidence of estuarine deposition. (All literature citations in this article refer to contributions contained elsewhere in this volume.) It may be useful to partly link the modern and the very ancient estuaries and lagoons by tracing the development of these features throughout the transgressions and regressions of the shoreline across the continental shelves during the Pleistocene epoch.

The groundwork for this discussion consists of a brief comparison of regional aspects of estuaries and lagoons, a general description of continental shelves, and an examination of the varying position of sea level during the Pleistocene epoch.

REGIONAL ASPECTS OF ESTUARIES AND LAGOONS

Estuaries and lagoons with their marsh or mud-flat fillings constitute a much higher percentage of the world's coasts than is generally recognized. In fact, many of the largest cities have been built on the marshes or on "made" ground adjacent to them. Around the United States 80 to 90 percent of the Atlantic and Gulf of Mexico Coasts and 10 to 20 percent of the Pacific Coast consist of estuaries and lagoons. Even a brief examination of a topographic chart of the United States reveals a dominance of lagoons from Mexico along the Gulf Coast and northward along the Atlantic Coast to Cape Hatteras. Between Cape Hatteras and New York lagoons are present, but they are compounded with much larger estuaries. From New York to Canada small but only slightly filled estuaries are common. Throughout most of the Pacific Coast small estuaries again dominate and many, especially those toward the south, are filled to overflowing with sediment. A similar pattern is outlined by Gossline.

A little reflection indicates that the regional distribution of estuaries and lagoons corresponds to the regional characteristics of continental shelves and their land continuations—the coastal plains. In other words, lagoons are typical where continental shelves and coastal plains are wide and nearly flat. Small estuaries occur where the shelves and coastal plains are narrow and have high relief. This distribution coincides with the long-established concept that lagoons are caused by the marine deposition of offshore

bars in areas of low relief, and estuaries are drowned valleys cut by streams or glaciers (fjords). Locally, embayments similar to estuaries have been formed by faulting and by volcanism.

Once formed, estuaries and lagoons tend to become destroyed by deposition of fresh- or brackish-water marshes at their heads, by deposition of marine marshes and sand islands and bars nearer their mouths, and by general coastal retreat by marine erosion. Stages in the filling of one estuary are well illustrated by Redfield. In the long run it is obvious that most sediments deposited within estuaries and lagoons must be derived from the land because of the dominance of erosion on land and of deposition on the sea floor. When first formed, however, estuaries or lagoons have some of the attributes of a vacuum because they attract clastic sediment from all directions: tributary streams or sheet wash (Jennings; Redfield), bordering cliffs (Guilcher; Klein), and the adjacent sea floor (Guilcher; Kulm; Postma; Steers). Biogenic materials, such as grasses of marshes (Redfield) and mangroves, aid in trapping these sediments and they themselves add to the deposits. In the early stages only very fine-grained sediment is capable of transitioning an estuary or lagoon and reaching the open sea. Because of the greater turbulence generally found in the open sea, most of these sediments continue in suspension to sites of deposition beyond the continental shelf. In some areas of quiet water off certain lagoons (Gossline), in large protected areas such as the Gulf of Maine, or behind associated deltaic (Morgan) or man-made barriers some of the fine-grained sediments may be deposited, but these are unusual.

The movements of coarse-grained sediments are not well known because of the difficulties in measuring the bed load of streams, but general reasoning indicates that only minor discharges of sands reach the continental shelf from estuaries and lagoons until the latter become largely filled; during early stages, in fact, sand is drawn into the estuaries and lagoons from the shores and sea floor adjacent to tidal inlets. Eventually, the features become so filled that alluvial fans develop on top of estuaries and then, of course, most sediments brought by the streams cross and are deposited on the continental shelf at the mouth of the estuary.

CONTINENTAL SHELVES

Sounding profiles generally reveal the continental shelf to be concave upward, steeper near shore and flat on the outer half. The shelf-break mostly ranges

between 60 and 150 m, with local wide variations due to isostatic or diastrophic movements or to rapid deposition of sediments. The worldwide average, about 130 m, is close to the figure for the maximum lowering of sea level during Pleistocene glaciations, according to recent estimates. Probably more than 90 percent of the continental shelf is deeper than the effective wave base, about 20 m, estimated from the position where waves begin to refract and thus to transfer energy to the sea floor.

Minor topographic features on continental shelves are significant indicators of origin. Most carefully surveyed shelves have a sequence of small terraces each with its own flat area fronted and backed by steeper zones. Samples indicate that coarse-grained sediments cover the flats and usually the steeper zones, but rock outcrops may be present along both seaward and landward margins of the terraces. In other places the shelf is covered by parallel sand waves or ridges, some of which have trends, shapes, and sizes analogous to the sand bars and sand islands which separate lagoons from the open sea.

Transverse to the continental shelf are drowned river valleys or submarine channels which were eroded by streams during low stages of sea level. They appear to have been cut deepest below their surroundings in the nearshore part of the shelf where seaward slopes are steepest. In some instances the channels extend beyond the shelf to join submarine canyons, but most of these shallow features are not well known because they are almost completely filled with sediments. Better known are the submarine canyons whose heads indent wide continental shelves or even extend completely across narrow ones.

Sediments on most parts of the continental shelf are sands that commonly are coarser grained than those nearer shore and are iron-stained as though they had lain on the sea floor for a long time with little movement. Associated with some of the sands are tests of foraminifera and shells of molluscs different from those living in the same areas today. An interesting example is the presence of dead shells of the oyster, *Crassostrea virginica*, in two parallel bands about 70 and 50 m deep along most of the Atlantic continental shelf off the United States, although the species is found alive only in estuarine or lagoonal waters shallower than 10 m.

Explored at depth chiefly by seismic profiling methods, the sediments of continental shelves are found to vary from a thickness of zero to about 100 m, usually, but not always, thicker on the nearshore half than farther offshore. Locally the sediments form prisms having shapes corresponding to the terraces on the shelves. In most profiles several strata of sediments are present. At the base of the sequence in some areas and most commonly on the outer part of the continental shelf these sediments lie above a nonconformity, below which older strata dip seaward more steeply than the overlying sediments.

All of these observations (depths, topographic details, relict sediments and fauna, internal structures,

and underlying rocks) closely support the concept that the wide continental shelves of today were cut by waves during glacial times of low sea level and that subsequently they have received repeated and irregular veneers of interglacial and post-glacial sediments. This concept is further supported by the presence of similar marine terraces, sand bars, lagoon fillings, and estuary deposits at positions higher than present sea level. In this sense estuaries and lagoons of today are only transitory representatives of many earlier ones now found both below and above the present sea level.

SEA LEVEL

When glaciation of the continents began about a million years ago sea level dropped from its pre-glacial position at about 50 m above the present level to about 160 m below it. Subsequent fluctuations occurred in response to alternating glacial and interglacial stages, but the details of timing and the elevations of maximum and minimum levels are highly speculative. Data for part of the rise from the level of the latest glacial minimum are provided by radiocarbon dating of shallow-water shells or of intertidal marsh deposits now found at abnormally deep positions. The best of these dates indicate a rise of sea level from about minus 100 m 18,000 years ago to minus 20 m 9,000 years ago (a rate of about 9 m per thousand years). Subsequently, more numerous measurements show that the rate decreased steadily so that about 3,000 years ago the level was 3 m or less below present sea level (Redfield). Since then the rise has been even slower and at a rate (relative to the land bench marks) which appears to be influenced by local isostatic or diastrophic movements of the coast, but which averages less than one m per thousand years.

CONCLUSIONS

During each crossing of the continental margin by the shore zone, the continental shelf was modified by erosion and deposition. Topographic details of the erosional and depositional features remain chiefly from the latest rise of sea level, which still continues. Speculation about the relationship of estuaries and lagoons to rising sea level and to position on the continental shelf may be interesting (Fig. 1).

When the sea level was lowest, at the shelf-break or beyond, the heads of earlier submarine canyons should have produced an irregular and even a steep coastal zone. Estuaries should have been common shore features, but the steep axes of the canyons should have prevented the accumulation of thick sedimentary fillings or marshes, and, in fact, none is known from the limited number of dredgings that have been made in these canyon heads. As sea level rose, the shore zone crossed the flat outer half of the continental shelf. The rise probably was slow at this stage and most likely the coast was one of long lagoons like those of the present Gulf and Atlantic Coasts of the southern United States. As the sea level continued to rise it drowned the shelf channels and formed estuaries, which probably at first were com-

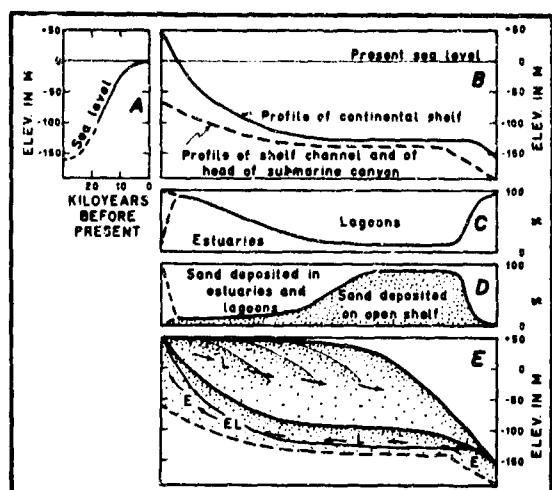


Fig. 1. Some relationships of the post-glacial rise of sea level, A, and the profile of the continental shelf, B, believed to be typical throughout the world. C shows the changing importance of estuaries versus lagoons as the shoreline crossed the continental shelf and intruded the channels previously cut into the shelf. D indicates the probable places of deposition of sand within estuaries and lagoons versus deposition on the open shelf after transitioning largely filled estuaries and lagoons. At the bottom, E suggests the order of deposition of sediments during a single epoch of rising sea level, first as estuaries, as lagoons, then as combined estuaries and lagoons, and finally as estuaries; a final stillstand of the sea level should allow the sediments to prograde seaward; arrows indicate the direction of sand deposition from oldest to youngest; E denotes estuary and L, lagoon. Vertical exaggeration of the profiles is about 1:150.

pounded with lagoons which lay across their mouths, such as those north and west of Cape Hatteras today. Further rise brought the shore zone to the steeper nearshore part of the continental shelf, so that estuaries became more common than lagoons, as is the present situation for the northern Atlantic and the Pacific coasts. As shown by Figure 1A, until the last few thousand years the rise of sea level was relatively fast, possibly faster than the estuaries could be filled with sediment. Subsequently, the rise appears to have been sufficiently slow for sedimentation to be keeping up (Rusnak; Morgan) and to be beginning to make up the deficit left in estuaries and lagoons by the previous rapid rise. Thus we can surmise that the post-glacial rise of sea level developed estuaries near the shelf-break, lagoons on the outer half, lagoons and estuaries near the middle, and estuaries on the nearshore part of many continental shelves. Where shelves are especially flat the later stages have not yet been reached. A further rise should tend toward producing more estuaries on most coasts of the world. With a long stillstand at maximum sea level, we

should expect the shore to prograde seaward as a succession of narrow lagoons or as beach ridges.

It is evident that the present estuaries are features that have a past and a future, but that the age of the present ones is only about one percent of the age of the shelf and its continuous sequence of estuaries and lagoons. The only evidence of this sequence to be found consists of their deposits. Much of the fine-grained sediment which reached the estuaries and lagoons from land may still be present at depth, as submerged marsh deposits buried under coarser sediments. As suggested by Figure 1, when sea level was lowest, most of the sands which reached the estuaries and lagoons from streams were discharged through the shelf channels, to be deposited in the heads of submarine canyons and thence to make their way farther seaward by mass movements and turbidity currents.

At this stage, sands were deposited in quantity neither on top of the continental shelves nor within the estuaries. As the sea level rose, the shore slowly crossed the flat part of the shelf, and offshore bars and barrier islands separated lagoons from the open sea. Widespread sands on the shelves indicate that the rise was slow enough so that many of the lagoons became filled, and a great quantity of sand was deposited above the shelf in the form of a succession of sand ridges, as well as blankets of sand between the ridges. With the faster rise across the steeper nearshore parts of the shelf, the sands may largely have been restricted to the filling of estuaries. If the present slow rise of sea level continues, the estuaries should become filled, and sand then will be discharged onto the shelf; but if the rate of rise again increases, we should expect that most sand will be deposited within the estuaries until the maximum level is reached and the sea level remains stationary.

In cross section, a simplified view may be drawn of the sites of deposition of sands on the continental shelf during a single epoch of rising sea level (Fig. 1E). The first deposits of the cycle are at the outer edge. Continued rise of sea level allowed the sands progressively to cover the shelf to the highest level reached by the sea. From then on we would expect sands to prograde back across the shelf as a succession of seaward-growing sand ridges, and perhaps offshore bars and barrier islands of lagoons. Thus, rising sea level followed by a stationary one would be revealed by landward deposition followed by seaward deposition. A future glaciation which causes a renewed lowering of the sea level would interrupt this sequence, erode part or all of the sediments, and finally deposit a new sequence of estuarine and lagoonal sediments.

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II. PHYSICAL FACTORS

Circulation and Diffusion

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An estuary may be defined as a partially enclosed body of water which receives an inflow of fresh water from land drainage and which has a free connection with the open sea. The water within the estuary consists of a mixture of fresh water and sea water in proportions which vary from place to place. This definition, which follows that used by Cameron and Pritchard (1963), covers coastal plain estuaries and fjords, as well as certain gulfs, sounds, and inlets. It also includes embayments formed behind offshore bars, provided they have a salinity significantly lower than the open sea.

The main physical problems to be investigated in an estuary are the water movements, the mixing processes, and the distribution of salinity which results from their combined action. The distribution of temperature is usually of secondary interest in an estuary, since, although it undergoes considerable variation, it has a less important effect on the density of the water. Another type of problem is concerned with the effect of the circulation and mixing processes on the movement and dispersion of other substances introduced into the estuary in various ways. Fresh water can often be used as an indicator; it provides information on the mixing processes which can then be used in calculating the effect on an effluent introduced at a particular location in the estuary. In some cases, special experiments with artificial tracers, such as fluorescent dye, may be needed to obtain a more detailed knowledge of the processes involved.

The rate of influx of fresh water from rivers varies greatly and the conditions in an estuary change with the variations in the volume of water discharged by the rivers flowing into it. A time lag of greater or less extent is involved, and usually there is a "buffering" effect, the estuarine processes reacting in such a way that the proportionate change in the salinity distribution is less than that in the river flow. A study of changing conditions is, therefore, important.

A comparison of the data obtained from a number of estuaries leads to a recognition of various types of circulation and salinity patterns and to a classification of estuaries based on the physical conditions in them. A logical development is the derivation of general principles, so that when an estuary not previously studied is encountered one may be in a position to predict the circulation and diffusion in it from a limited number of parameters. These include its physical dimensions, the river flow, and tidal conditions.

While important steps have been taken in this direction, the complete objective has not yet been achieved.

METHODS OF OBSERVATION

A survey of an estuary must include observations of the salinity distribution in horizontal position and depth, and these are usually combined with temperature observations. The traditional sampling methods with insulating or reversing bottles have been widely used. Such samples may also be analyzed for oxygen content and for other chemical constituents. For an adequate coverage of the region in a limited time, however, the introduction of *in situ* methods has proved to be very practical. The sufficiently accurate measurement of temperature is now comparatively easy by using the bathythermograph, platinum resistance thermometer, or thermistor probes. The determination of salinity *in situ* is more difficult, but satisfactory instruments measuring electrical conductivity have been devised, such as those described by Ketchum (1950), Pritchard (1952a), and Williams (1960). Because of the larger variations in salinity occurring in an estuary, such instruments do not need to have so high an accuracy as those designed for deep sea work.

While certain inferences as to the nature of the circulation can be drawn from salinity observations alone, direct measurements of currents are essential for a full and quantitative understanding of the processes involved. Both flow methods and drift methods are used. The flow methods comprise measurements by current meters of a variety of types, used either from an anchored vessel or from a moored buoy. Instruments used from a moored buoy either store the measurements in the form of photographic records or on tape, or they may transmit the data by radio to a receiver on board ship or on shore. Westbrook (1962) described an investigation in New York Harbor in which the measurements from four radio buoys, each with three Roberts current meters, were received on board the same vessel.

Drogues of various types have been used for drift experiments. A drogue has a large surface area and can be suspended at the desired depth below a surface buoy. The buoy offers only a small resistance to the flow and serves simply as an indicator of the position of the drogue. Surface currents have been studied also by photographing the drift of dye patches from the shore.

Descriptions of the measuring instruments and of the techniques employed in using them for estuarine investigations have been given by several authors, including studies of the Chesapeake Bay system by Pritchard (1952a), and Pickard's (1955) studies of the British Columbia Inlets.

The total flow across the section of a channel may be measured by the electromagnetic effect, using a pair of electrodes connected by cable to a recorder ashore. This method, used by Trites and McGregor (1962) across passages at the entrance to Passamaquoddy Bay, is useful for determining the tidal flow, but does not detect the differential flow between the upper and lower layers which is a characteristic feature of estuarine circulation.

In addition to observations within the estuary itself, a knowledge of the freshwater inflow is necessary for any physical study. This should preferably be based on actual gauge measurements on the rivers flowing into the estuary. In some cases such measurements are not available or cover only a fraction of the total drainage area. The inflow from the ungauged areas must then be estimated, either by comparison with adjacent gauged areas, or from rainfall data over the area, corrected for loss because of evaporation and other causes. Allowance should be made for the net gain of fresh water resulting from precipitation and evaporation over the estuary itself. Meteorological data are also required in order to take into account, for example, the effect of wind on the circulation. Pickard and Trites (1957) used data on the flow of heat through the surface of the water passing along an estuary to determine the rate of flow in the upper layer.

Although scale models have not been used for estuarine investigations to the same extent as they have in hydraulics and coastal engineering, there are a number of examples of very useful results being obtained from them. The model of Delaware Bay, described by Pritchard (1954a), has been used in a series of studies of circulation and diffusion. Similar use has been made of the Puget Sound model, described by Rattray and Lincoln (1955). The model of the Thames Estuary, described by Inglis and Allen (1957), showed the importance of density current flow on the transport of bottom material. Simmons (1960) has discussed the principles on which such models are designed, the scaling laws to be applied, and their limitations. Some degree of vertical distortion is unavoidable. The river flow and tidal movements are represented on length, velocity, and time scales which are related because the Froude number is constant. The salinity is reproduced on the natural scale, since, if fresh water is used for the river inflow, and the seaward end of the estuary is kept at the salinity of sea water, then the salinity distribution is modeled satisfactorily throughout the estuary. In such models it is possible to study the effects of changes in river flow on the circulation, and to study the movement and dispersion of tracers introduced at any desired point. A wide variety of conditions can be studied

in a comparatively short time. It is also possible to investigate the effect of any artificial changes in the estuary, such as those of proposed engineering works.

TYPES OF ESTUARINE CIRCULATION

A scheme for the classification of estuaries based on the physical character of the circulation was proposed by Stommel (1951, unpublished; 1953a) and its main features were adopted by Pritchard (1952b, 1955) and Ketchum (1953) in reviews they made of the knowledge available at that time. Later work has confirmed the usefulness of this method of classification which is essentially that followed in this paper. The basic factor in determining the type of circulation is the role played by tidal currents relative to that of river flow in the estuary in question. In the absence of other influences, the river water will tend to flow seawards as a layer of fresh water, separated by a fairly distinct interface from the salt water below.

Tidal currents, which alone do not result in any net transport of water over a complete tidal period, exert a profound influence through the turbulent mixing they produce. This tends to break down the interface between the river water and salt water and produce a mixing of the two waters through a part or whole of a vertical column. In an extreme case, the vertical mixing may be so thorough that there is no measurable variation of salinity from surface to bottom. A part of the tidal energy is converted into kinetic energy of turbulence, some of which is used to increase the potential energy of the water by vertical mixing. A part of this potential energy then reappears as kinetic energy in the mean estuarine circulation.

The interaction between the river flow and the tidal currents is influenced by two other factors: the physical dimensions of the estuary, and the effect of the earth's rotation represented by the Coriolis force. If the estuary is narrow the effect of the Coriolis force may be negligible, but in a wide estuary the lateral variation in properties because of this effect can be considerable. The influence of depth is seen in the difference between circulation in a shallow estuary and in an otherwise similar fjord. The main types and their characteristics are listed in Table 1.

SALT WEDGE ESTUARY

The best known example of a salt wedge estuary is the Mississippi, where the river flow almost completely dominates the circulation. In an estuary of this type, shown schematically in Figure 1, the salt water extends as a wedge into the river and if friction were completely absent the interface would remain horizontal and extend upriver to the point where the bed was at sea level. In fact there is a small amount of friction between the layers, and the interface slopes slightly downwards in the upstream direction. The steep density gradient at the interface, amounting to a discontinuity, reduces the turbulence and mixing to a very low level. The effect of the Coriolis force causes the

Table 1. Types of estuarine circulation.

Type	Physical processes	Forces
1. Salt wedge	River-flow dominant	Pressure gradients, field accelerations, Coriolis effect, interfacial friction
2. Two-layer flow with entrainment, including fjords	River-flow, modified by tidal currents	Pressure gradients, field accelerations, Coriolis effect, entrainment
3. Two-layer flow with vertical mixing	River-flow and tidal mixing	Pressure gradients, field accelerations, Coriolis effect, turbulent shear stresses
4. Vertically homogeneous (a) with lateral variation (b) laterally homogeneous	Tidal currents predominating	Pressure gradients, field accelerations, turbulent shear stresses, Coriolis effect in (a)
5. Exceptional cases: intensive mixing in restricted sections, tributary estuaries, sounds, straits, etc.	—	—

interface to slope downwards to the right in the northern hemisphere, looking towards the sea.

TWO-LAYER FLOW WITH ENTRAINMENT

If the velocity of the seaward-moving layer of fresh water exceeds a certain value, internal waves formed at the interface will tend to break at the crests, resulting in an entrainment of salt water into the upper layer. Entrainment is a one-way process, causing a movement of salt water upwards without a corresponding downward movement of fresh water. A number of theoretical studies and model investigations have been made on the conditions under which entrainment occurs in a two-layer flow. The application of these to estuarine circulation is discussed later. The salinity of the water in the upper layer is increased by entrainment and its volume also increases as it moves seaward. This usually results in an increased velocity of flow rather than an increase in the depth of the layer. The salinity of the deeper layer is almost unchanged, but there is a slow movement of water upstream from the sea to compensate for the water lost by entrainment. The conditions in such an estuary are represented in Figure 2.

Many fjords have essentially this type of circula-

tion. However, it is unusual for the interface to remain so sharp that the process is purely one of entrainment. There is often a certain amount of mixing, with a small proportion of low-salinity water from the upper layer entering the layer below. The interface is then replaced by an intermediate layer of steep salinity gradient, known as the halocline. This type of salinity structure was described for the Alberni Inlet, British Columbia, by Tully (1949), who regarded the base of the halocline as a level across which transfer of water was by entrainment only. Mixing takes place within the halocline. Most of the upstream flow occurs in the intermediate layer, the bottom layer acting mainly as a reservoir of sea water because movements in it are very slow. Other students of the flow in fjord-type estuaries, for instance Pickard and Rodgers (1959), have shown that in the deeper parts a three- or four-layer structure is present in the circulation.

TWO-LAYER FLOW WITH VERTICAL MIXING

In comparatively shallow estuaries, the vertical mixing, because of tidal currents of increasing ampli-

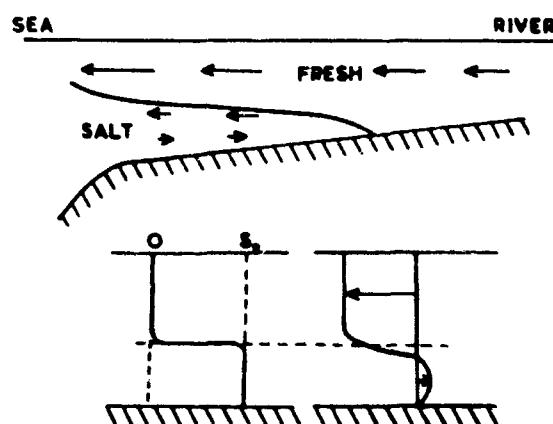


Fig. 1. Salt wedge estuary: above—section along estuary; below—typical salinity and velocity profiles.

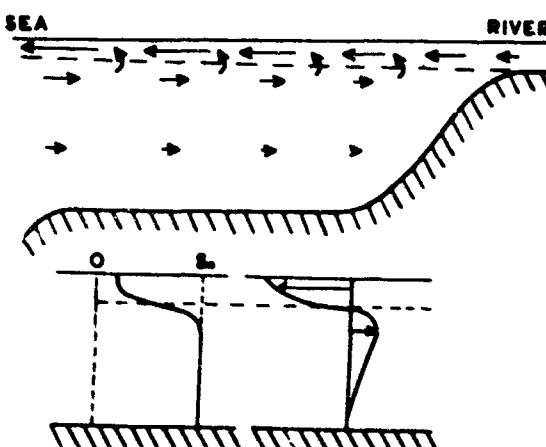


Fig. 2. Two-layer flow with entrainment: above—section along estuary; below—typical salinity and velocity profiles.

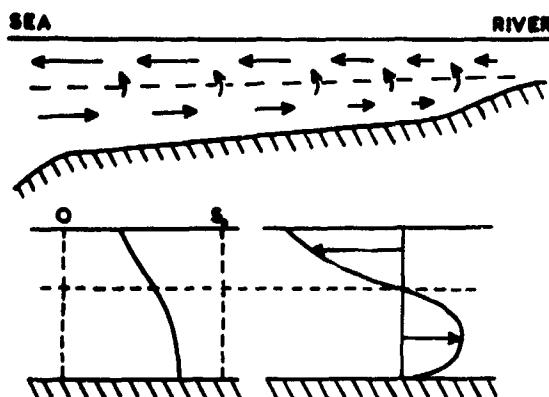


Fig. 3. Partially mixed estuary with entrainment and mixing: above—section along estuary; below—typical salinity and velocity profiles.

tude, extends throughout the depth, mixing the fresher water downwards and the more saline water upwards. There are still two layers as far as the flow is concerned; the surface of no motion which separates the seaward-flowing upper layer from the landward-flowing lower layer usually occurs somewhat above mid-depth, as in Figure 3. There is no marked interface, but the salinity profile shows a continuous increase in salinity from surface to bottom, the maximum gradient occurring near the level of no net motion. The estuaries of the Chesapeake Bay system are of this type, and one of them, the James River, has provided the data for estuarine studies by Pritchard (1952a, 1954b, 1956). The estuaries of the River Tees (Alexander *et al.*, 1931, 1935) and the Thames River (Inglis and Allen, 1957) are other examples of this type.

Since the main parameter is the ratio of the amplitude of tidal currents to the river flow, there is a wide range in the degree of stratification occurring in this type of estuary. In some the total increase in salinity from surface to bottom may be as much as 10‰ while in others it is less than 1‰. In a given estuary there may be large variations in conditions with changes in river flow, and smaller, but significant, differences between periods of spring and neap tides. The volume of water concerned in this type of circulation may be many times that of the river discharge. Thus the seaward transport in the upper layer might be 20 times the river flow, while the upstream transport in the lower layer is 19 times the river flow.

VERTICALLY HOMOGENEOUS ESTUARIES

If the tidal currents are very strong in relation to the river flow the vertical mixing becomes so intense that there is no measurable variation in salinity from surface to bottom. There is, of course, still a horizontal gradient of salinity, increasing from the head to the mouth. Estuaries of this type may be subdivided into two categories:

With Lateral Variation—If the ratio of width to depth is sufficiently large, the Coriolis force gives rise

to a lateral variation of salinity, the lower-salinity water occurring on the right-hand side, looking towards the sea. Associated with this, there is a net seaward flow of lower-salinity water on the right hand of the estuary and a compensating flow of higher-salinity water on the left.

Laterally Homogeneous—In estuaries where the ratio of width to depth is relatively small, there is frequently no appreciable variation in properties across the channel. Stommel (1953a) suggested that in this case there is no lateral or vertical variation in the net flow, which is therefore uniform over a cross section. He postulated that the upstream transport of salt, which is necessary to compensate for the seaward transport due to the river flow, must take place entirely by horizontal turbulent diffusion. As Cameron and Pritchard (1963) pointed out, however, the continuing existence of a horizontal density gradient implies that the horizontal pressure gradients vary with depth. It would seem, therefore, that a variation of net flow velocity with depth should not be excluded and, in that case, even a slight degree of salinity stratification might enable a significant transport of salt to be produced. It is possible that earlier investigators have regarded as insignificant salinity differences of the order of 0.1‰. The Severn Estuary has been treated as a completely mixed estuary, although observations have shown that vertical differences of salinity up to 0.5‰ can occur (Bassindale, 1943a, b).

EXCEPTIONAL CASES

It will be recognized that there is an almost continuous spectrum of estuarine circulation patterns and that there are gradual transitions between the types listed above. Some estuaries, however, have exceptional features which do not allow them to be fitted into the general scheme. In some estuaries nearly all the mixing occurs in a very limited section. Hachey (1935) described the intensive mixing occurring in the "reversing falls" in the gorge of the St. John River, New Brunswick. The investigations of Stommel on the controlling action of a restriction in an estuary are mentioned later in this paper. Stommel (1953a) has also described the effect of a promontory in promoting horizontal mixing by producing an eddy, first on one side and then on the other, in the alternating tidal flow. Such geomorphological features must frequently affect the mixing processes in an estuary, and if not taken into account specifically they may give rise to abnormal values of an effective coefficient of horizontal diffusion.

Other complex cases may occur where a number of estuaries are tributaries to a large estuarine system, as in the Chesapeake Bay area. Carpenter (1960) has described the condition in Baltimore Harbor and the exchange flow with the adjacent Chesapeake Bay. Owing to effective vertical mixing, the vertical salinity gradient is low in the harbor, and the salinity decreases towards the bay near the surface and increases towards the bay near the bottom. A three-layer pattern of flow results, with water moving to-

wards the harbor in both the surface and bottom layers and outwards at mid-depth. The whole of the Bay of Fundy was considered as one estuary by Ketchum and Keen (1953).

The conditions in certain straits and sounds communicating with the sea by two or more separate channels also resemble those in an estuary, with some complicating features. In Long Island Sound the communication with the sea is predominantly through one channel (Riley, 1952). In Georgia Strait (Pickard, 1956) and the Strait of Juan de Fuca (Herlinveaux and Tully, 1961) the communication with the ocean is more complicated and irregular depth and topography add to the complexity.

BASIC PRINCIPLES OF CIRCULATION AND MIXING

Before going on to a quantitative discussion of circulation and mixing problems, it is convenient to consider the basic principles controlling them. These are expressed by the equations of motion of the water and the equations of continuity of volume of water and mass of salt. Let rectangular axes be taken with OX and OY in a horizontal plane, near the free surface, OX being along the axis of the estuary, positive seawards, OY across the estuary and OZ vertically downwards. Let u, v, w be the components of mean velocity at the point (x, y, z) at time t . Then the equations of motion may be written:

$$\frac{Du}{Dt} - fv = -\alpha \left\{ \frac{\partial p}{\partial x} + \frac{\partial \tau_{zz}}{\partial x} + \frac{\partial \tau_{yy}}{\partial y} + \frac{\partial \tau_{xx}}{\partial z} \right\}, \quad (1)$$

$$\frac{Dv}{Dt} + fu = -\alpha \left\{ \frac{\partial p}{\partial y} + \frac{\partial \tau_{yy}}{\partial x} + \frac{\partial \tau_{vv}}{\partial y} + \frac{\partial \tau_{yy}}{\partial z} \right\}, \quad (2)$$

$$0 = -\alpha \frac{\partial p}{\partial z} + g, \quad (3)$$

where $(D/Dt) = (\partial/\partial t) + [u(\partial/\partial x)] + [v(\partial/\partial y)] + [w(\partial/\partial z)]$, $f = 2\omega \sin \phi$ is the Coriolis parameter, p is the pressure, α is the specific volume ($\alpha = 1/\rho$, where ρ is the density), g is the acceleration due to gravity and τ_{yy} is the stress on a plane perpendicular to OX acting in the OY direction. In these equations the stress components τ_{zz} , etc., are nearly always entirely a result of the turbulent stresses, since, except very near the boundaries, the stresses due to molecular viscosity are several orders of magnitude smaller. Then, if u', v', w' are the components of turbulent velocity at any instant, $\tau_{zz} = \rho \langle u'^2 \rangle$, $\tau_{yy} = \rho \langle v'^2 \rangle$, etc. where $\langle \rangle$ denotes an average over the time taken for computing the mean velocity. The remaining Coriolis terms and the vertical accelerations may be shown to be negligible and have been omitted.

The equation of continuity of volume is

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0. \quad (4)$$

The equation of conservation of salt may be written

$$\frac{DS}{Dt} = \frac{\partial}{\partial x} \left(K_x \frac{\partial S}{\partial x} \right) + \frac{\partial}{\partial y} \left(K_y \frac{\partial S}{\partial y} \right) + \frac{\partial}{\partial z} \left(K_z \frac{\partial S}{\partial z} \right). \quad (5)$$

where K_x, K_y , and K_z are the coefficients of eddy diffusion in the x, y, z directions respectively. As in the case of viscosity, the molecular diffusivity can nearly always be neglected.

In an estuary it is often assumed that the transverse velocities are very small compared with those along the estuary, so that the terms involving v in the above equation may be neglected.

From equation (3), the hydrostatic equation, the pressure at depth z is given by

$$p = p_0 + g \int_{-z}^0 \rho ds, \quad (6)$$

when p_0 is the atmospheric pressure and ζ is the elevation of the free surface above the level surface taken as reference. It will be assumed that p_0 is uniform, so that

$$\frac{\partial p}{\partial x} = \rho_0 \frac{\partial \zeta}{\partial x} + g \int_0^z \frac{\partial \rho}{\partial x} ds, \quad (7)$$

where ρ_0 is the density at the surface, and there is a similar equation for $\partial p/\partial y$.

The density ρ is a function of salinity S , temperature θ , and pressure, thus

$$\rho = \rho(S, \theta, p). \quad (8)$$

In an estuary, the variation of ρ with p may be neglected, and very often the dependence on θ is of little importance compared with that on S . In that case it is sufficient to take ρ as being a linear function of S , that is

$$\rho = \rho_0 + aS, \quad (9)$$

where a is a constant.

The complete solution of the estuarine circulation problem would involve solving equations (1) to (5) with (7) and (8) or (9). The velocity components depend on the pressure gradients, which are functions of the density distribution. The density is a function of salinity and the distribution of salinity depends on the velocities, thus completing the system. Very few attempts have been made to present a theory of estuarine circulation treating it as a closed system. In some methods the density distribution is assumed to be given by observations, and the circulation is derived from it. In others the circulation is regarded as given, and its effect on the distribution of salinity is calculated.

OVERALL ANALYSIS OF MIXING

Methods have been devised for computing the rate at which river water is flushed out of an estuary, and thereby estimating the rate of removal of a pollutant introduced into it. Fresh water usually is used as a tracer. No attempt is made in these methods to understand the dynamics of the circulation or the details of the diffusion processes.

FLUSHING TIME

Let the rate of influx of fresh water be R and let F be the total volume of fresh water accumulated in

the estuary. If S_0 is the salinity of the water outside the estuary which is available for mixing and S is the salinity at any point inside, the freshwater content at that point is given by

$$f = \frac{S_0 - S}{S_0}. \quad (10)$$

The accumulated volume of fresh water is then given by

$$F = \int_{vol}^0 f d(vol), \quad (11)$$

where the integration is carried out over the total volume. A steady state is assumed, so that R represents also the rate at which fresh water is being removed from the estuary. Then the flushing time t is the time taken to remove the accumulated volume of fresh water present at a given instant at this rate. Thus t is given by

$$t = \frac{F}{R}. \quad (12)$$

Half this time is sometimes referred to as the mixing half-life of the estuary. An estimation of the flushing time therefore requires a knowledge of the river flow and of the salinity as a function of depth at a sufficient number of positions within the estuary.

The flushing time as calculated in this way may be applied rigorously to a pollutant only if it is introduced into the estuary in the same way as the fresh water. Thus if practically all the fresh water enters by a river at the head of the estuary and the pollutant is also introduced at this point, the flushing time so calculated should apply closely to the pollutant. If, however, the pollutant is introduced into another part of the estuary, the flushing time for it may be different.

The length of the flushing time depends on the river discharge. The salinity distribution usually adjusts itself in such a way, however, that F increases to some extent with increasing R , and the proportionate decrease in the flushing time is less than the increase in the river discharge. For New York Bight, Ketchum (1950) found that the flushing time varied only between 6 and 11 days while the river discharge varied from 0.5 to 4×10^6 ft³ day.

TWO-LAYER MODEL

If it is assumed that the exchange of water between the estuary and the sea takes place entirely by advection, horizontal diffusion being negligible, then the rate of flow can be calculated from a knowledge of the mean salinity of the inflowing and outflowing layers and the freshwater influx. In Figure 4, let T_1 be the volume transport and S_1 the salinity in the outflowing water and T_2, S_2 the corresponding quantities for the inflowing water.

Then expressing the conditions for continuity of water and of salt respectively,

$$\begin{aligned} T_1 - T_2 &= R, \\ T_1 S_1 - T_2 S_0 &= 0. \end{aligned}$$

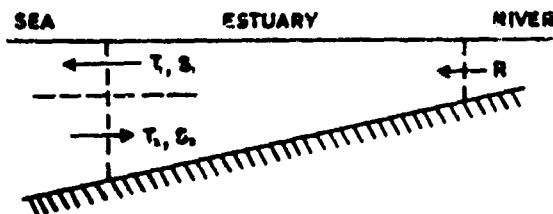


Fig. 4. Two-layer exchange of water between an estuary and the sea.

Then

$$T_1 = \frac{S_0 R}{S_1 - S_0}, \quad T_2 = \frac{S_1 R}{S_1 - S_0}. \quad (13)$$

If the cross-sectional areas of the two layers are known, the mean velocities of flow may be calculated. If V is the total volume of water contained in the estuary, the flushing time is given by

$$T = \frac{V}{T_1} = \frac{V(S_1 - S_0)}{S_0 R}. \quad (14)$$

The assumption made implicitly here is that all the water entering in the lower layer is mixed completely with the water inside the estuary before leaving it again. If the pollutant has a density less than that of the estuary water it may remain in the upper layer and be removed from the estuary more rapidly than the above calculation would suggest. An estimate of its rate of removal can be obtained from the velocity computed for the upper layer.

TIDAL PRISM AND SEGMENTATION METHODS

The two methods described above make use of observations of salinity and the river flow and do not consider tidal movements. If these are present, the methods may still be applied to average conditions over one or more tidal periods, allowing implicitly for the tidal effects in the exchange processes. An alternative approach, in estuaries where the tidal movements appear to be the main mixing process, is to attempt to calculate the rate of exchange from data on the tides and the physical dimensions only. In the "tidal prism" method it is assumed that all the water entering during the flood tide becomes completely mixed with the water in the estuary, and the ebb flow consists of this mixed water. If V is the total volume of the estuary at low water and P is the volume of water entering on the flood (the "intertidal volume"), then a fraction $P/(V+P)$ of the mean volume of water is removed each tide, so that the flushing time t in tidal periods is given by

$$t = \frac{V + P}{P}. \quad (15)$$

This method can give only a lower limit to the flushing time because the assumption of complete mixing in each tidal period may not be justified. In some estuaries the flushing time given by the method described earlier in this section is ten times that estimated by the tidal prism method.

A refinement of this method was introduced by Ketchum (1951) who divided the estuary into a series of segments, the length of each being equal to the tidal excursion. Complete mixing was assumed to take place within each segment, and an "exchange ratio" was defined for it. Thus if V_n = low tide volume of the n^{th} segment and P_n the corresponding intertidal volume, the exchange ratio r_n is given by

$$r_n = \frac{P_n}{P_n + V_n}. \quad (16)$$

It may be shown that the volume of river water accumulated in the segment is given by

$$Q = \frac{R}{r_n}, \quad (17)$$

where R is the river discharge per tidal period. The accumulated volume of fresh water, and hence the salinity, may thus be computed as a function of distance along the estuary. If observations of salinity show that mixing is confined to an upper layer, then the volume of this layer only, and not the complete volume of the segment, should be used in computing r_n .

Ketchum applied the method to the Raritan River, New Jersey; Alberni Inlet, British Columbia (for which only the upper layer down to 30 ft. was taken into account), and Grand Pond, Falmouth, Massachusetts (mixed layer taken as extending to half-depth), and good agreement was found with the observed distribution of salinity in each case. The method was applied by Ketchum and Keen (1953) to Passamaquoddy Bay and to the whole of the Bay of Fundy, where the authors found good agreement between the values of r_n computed from equation (16) and from $r_n = R/F$, where F was estimated from the observed distribution of salinity. This agreement confirms the validity of the assumption that complete mixing occurs within each segment during each tide.

The attraction of this method of estimating the flushing characteristics is that it requires only a knowledge of the mean range of tide, the river flow, and the topography of the estuary. A knowledge of the salinity distribution is not required.

MIXING LENGTH THEORY

The basic ideas of Ketchum's method were translated by Arons and Stommel (1951) into the "language of the physics of continua". They considered a model estuary of uniform width w , depth H , and length L . The OX axis was taken along the estuary, positive downstream, with $x = 0$ at the river end and $x = L$ at the sea end, the salinity there being S_0 . Considering average values over a cross section, the equation of continuity of salt takes the form

$$\frac{dS}{dt} + \bar{v} \frac{dS}{dx} - \delta \left(K_s \frac{dS}{dx} \right), \quad (18)$$

where \bar{v} is the mean velocity due to the river discharge and K_s the coefficient of horizontal eddy diffusion. The tides were regarded as a turbulent motion

superimposed on the river flow and K_s assumed to have the form

$$K_s = 2B\zeta_0 U_0, \quad (19)$$

where ζ_0 = amplitude of horizontal tidal displacement, U_0 = amplitude of the tidal current, and B is a constant. It may be shown that, in the simplified conditions assumed, K_s becomes

$$K_s = \frac{2B\zeta_0 \omega r^2}{H^3}, \quad (20)$$

where ζ_0 is the vertical amplitude of the tide and ω its angular frequency. The salinity distribution along the estuary is given by

$$S = S_0 e^{F(x-L)}, \quad (21)$$

where $\lambda = x/L$ and F is a "flushing number" given by

$$F = \frac{BH^3}{2B\zeta_0 \omega L}. \quad (22)$$

Comparing the theoretical curves with observed distribution, the authors found that the curve with $F = 0.08$ fitted the Raritan River, and $F = 0.3$ the Alberni Inlet. An attempt to calculate B , however, led to an order of magnitude difference between the two cases.

EFFECTIVE HORIZONTAL DIFFUSIVITY

Although the theories of Ketchum and of Arons and Stommel gave satisfactory results for certain estuaries, Stommel (1953b) found that they were quite inadequate in other cases and in particular when applied to the Severn River, England. Stommel suggested that, from a practical point of view, the best procedure is to use the distribution of river water as a means of determining the effective coefficient of horizontal diffusion at a series of cross sections and then to apply these coefficients to problems of pollution in the estuary. He stated that the method was intended to apply only to unstratified estuaries in which the mixing was due to the tides. From equation (18) it follows that, in the steady state, the effective value of K_s at a given section is

$$K_s = RS/A \frac{dS}{dx}, \quad (23)$$

where A is the cross-sectional area, since $\bar{v} = R/A$.

For a non-conservative pollutant of decay time τ (time for concentration to fall to $1/e^{\tau}$ of its initial value), the concentration c is given by

$$\frac{dc}{dx} \left[R - AK_s \frac{dc}{dx} \right] + \frac{A}{\tau} c = 0, \quad (24)$$

except at the outfall where the right-hand side = 0, the total rate of influx of pollutant.

Equation (23) may be expressed in finite difference form and applied to the salinity observations to compute K_s at a series of sections along the estuary. The distribution of a pollutant resulting from its release at a given section may then be computed from (24), also in finite difference form. Stommel illustrated the use of the method by applying it to the Severn.

OTHER METHODS

A method similar in principle to Stommel's, but entirely different in its formulation, was devised by Preddy (1954) in relation to the mixing processes in the Thames Estuary. He assumed that the water initially concentrated at a given section, at position x , would after one tidal period be dispersed over the distance from $x - L$ to $x + L$, where L is approximately equal to the amplitude of horizontal movement due to the tide. The dispersion may be represented by a dispersion curve which is usually asymmetrical, since, for example, dispersion may take place more readily downstream than upstream of the section. The distribution after a number of periods is the cumulative effect of the repeated application of the dispersion curve. Preddy showed that for this purpose the actual shape assumed for the dispersion curve is unimportant, and may be adequately approximated as shown in Figure 5.

Of the water initially at a given section, after one period a fraction P_1 is uniformly dispersed over a distance L to seaward, a fraction P_2 uniformly dispersed over a distance L upstream and the remainder, $1 - P_1 - P_2$, left in its original section. By applying the conditions of continuity of salt and of water to steady state conditions, Preddy derived equations for computing X and Y , where $X = A P_1$ and $Y = A P_2$ (A = cross-sectional area), from the river flow and distribution of salinity. Average values of river discharge and salinities at half-tide over a period of a year were used. X and Y were found to increase steadily towards the sea, although P_1 and P_2 varied irregularly where the cross section was irregular. The method was verified by using the values of X and Y so found to compute changes in salinity distribution resulting from given changes in river flow. The change in concentration C of any substance in one interval of time is given by

$$\Delta C = \frac{1}{A} \left[\int_{-L}^L C Y dx + \int_{-L}^L C X dx + C(A - X - Y) \right] \quad (25)$$

The method may then be used to compute the distribution of concentration of an effluent discharged at a given point. A further development of the method was described by Preddy and Webber (1963). It permits the distribution of various non-conservative quantities, such as dissolved oxygen, ammoniacal nitrogen, and oxidized nitrogen, to be computed. The equations were expressed in matrix form for solution by digital computer.

A somewhat similar mathematical model has been devised by Dorrestein (1960) for the longitudinal spreading of dissolved or suspended matter along an estuary in the steady state. The estuary is divided into a series of segments and exchange factors introduced to represent the turbulent and tidal mixing between segments. Another parameter allows for transport by the residual flow. If the volume of the n^{th} segment is V_n and the mean concentration in it of the substance considered is c_n , then the change in concentration occurring in a time interval Δt (preferably

one or one-half tidal cycle) is assumed to be given by the linear difference equation

$$V_n \Delta c_n = \Delta t \left[\sum R_{nn} (c_{n+1} + c_{n-1}) + D_{nn} (c_n - c_{n+1}) \right], \quad (26)$$

where the sum is taken over all segments n' (normally two) bordering on segment n ; c_n and $c_{n'}$ refer to the beginning of the interval; the coefficients $R_{nn'}$ represent net water fluxes towards n ; and $D_{nn'}$ are exchange factors. The values of $D_{nn'}$ can be determined from the mean distribution of salinity.

In carrying out the computation, Dorrestein considered first a number of basic initial distributions, so that the concentration c is zero in all sections except one, section m , where it is 1. The distribution resulting from this at time t is denoted by $y_{mn}(t)$. When the y_{mn} values have been found, the distribution at time t arising from any other initial distribution can be computed from the linear superposition

$$c_n(t) = \sum_m c_{mn}(0) y_{mn}(t). \quad (27)$$

The method has been applied to the Ems Estuary.

QUANTITATIVE TREATMENT OF CIRCULATION AND MIXING

Theoretical studies, laboratory experiments, and the analyses of full-scale observations have all been used for investigating the dynamics of estuarine circulation. Tidal currents play an important part in most types of estuarine circulation, but the dynamics of tidal movements will not be considered here. The currents, as they occur in a particular estuary, will be regarded as part of the physical environment.

SALT WEDGE ESTUARY

Several laboratory investigations and theoretical studies have been made of salt wedge estuaries. Keulegan (1949) described a series of model experiments in which the velocity in the upper layer was varied. At very low velocities the interface remained distinct and smooth. At slightly higher velocities internal waves formed at the interface and at a certain critical velocity U_c the crests of the waves broke, allowing elements of the denser liquid to be entrained in the upper layer flow. U_c could be expressed in terms of a parameter θ given by

$$\theta = \left(\frac{\rho_2 g \Delta \rho}{\rho_1} \right)^{1/4} \frac{1}{U_c} \quad (28)$$

where ρ_2 = viscosity of the liquid in the lower layer, $\Delta \rho$ is the difference in density between the layers, ρ_1 the density, and U the velocity of flow in the upper layer. For Reynolds numbers above 450, U_c corresponded to $\theta = 0.172$. At velocities above the critical value, the rate of entrainment corresponded to an upward velocity w across the interface, given by

$$w = 1.5 \times 10^{-4} (U - U_c) \quad (29)$$

The additional frictional drag due to the entrainment was found to be very small, corresponding to an increase in the drag coefficient of less than 0.0007.

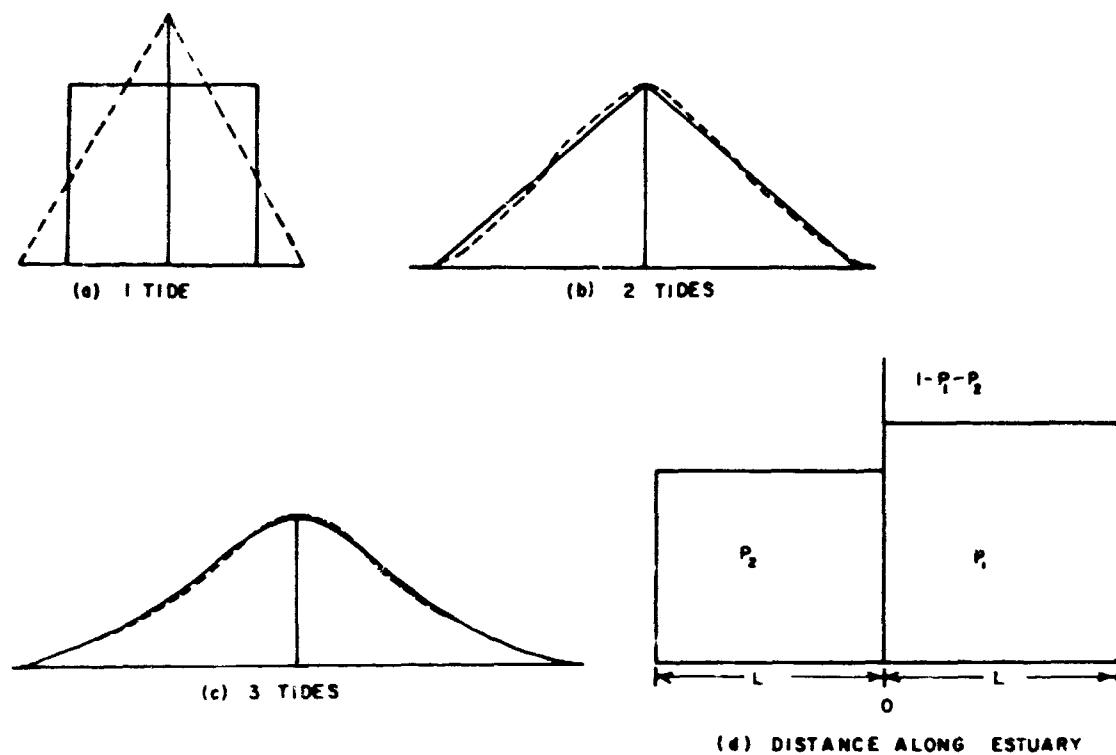


Fig. 5. Dispersion curve method of representing horizontal mixing (Preddy and Webber, 1963): (a) A rectangular distribution and a triangular distribution with equal first moments and equal second moments. (b) Distribution after two mixes. (c) Distribution after three mixes. (d) Chosen representation of the mixing in the Thames Estuary. The proportion P_1 is distributed uniformly over the distance L to seaward. The proportion P_2 is distributed uniformly over the distance L to landward. The remainder stays at 0.

Keulegan emphasized that caution would be needed in applying his results to large bodies of water, since the experiments really applied only to an "initial reach" in which steady flow conditions had probably not been attained. At the same time his work was very valuable in demonstrating the basic features in the development of this type of flow.

Another series of experiments in a laboratory flume was carried out by Farmer (1951, unpublished). He investigated the factors influencing the length and shape of the wedge and made measurements of the velocity profile both in the upper layer and within the wedge. Just below the interface the denser water moved forward with the overlying layer, but below this there was a slow drift in the opposite direction. An empirical equation was derived which represented well the profile of the salt wedge produced under varying conditions of upper-layer discharge and density difference in the model experiments. When applied to conditions in the Mississippi Estuary, however, this equation predicted lengths for the wedge which were much too small: 16.5 miles instead of 45 miles for the length above the Head of Passes, for instance. Farmer suggested that this prediction might be due to the shearing stresses being incorrectly scaled. Rather surprisingly, considerably better agreement was

found when the equation was used to compute the distance of saltwater intrusion into estuaries such as the Raritan River, New Jersey, where the turbulent mixing is quite large. In making this application it was assumed that the maximum intrusion of salt water was equal to the length of a stationary salt wedge, and that the salt content of a vertical column of water was the same whether the salt was confined to a wedge or mixed throughout the column.

A theoretical analysis of salt wedge flow was made by Farmer and Morgan (1953), based on the equations of motion and continuity for each layer. The existence of a sharp interface between the fresh water and the salt wedge was assumed, with no mixing between the layers. It was also assumed that the velocity within the wedge was small, that there was no friction at the surface or the bottom, but that there was a fractional stress at the interface, given by $\tau_2 = K \rho_2 U_2^2$ where U_2 is the mean velocity of the fresh water layer at the tip of the wedge and K is a drag coefficient which does not vary along the wedge. Equations were derived for the shape of the wedge and for its length as a function of the discharge in the upper layer and the relative density difference γ where $\gamma = (\rho_2 - \rho_1)/\rho_2$. The equation for the wedge profile gave results in agreement with the obser-

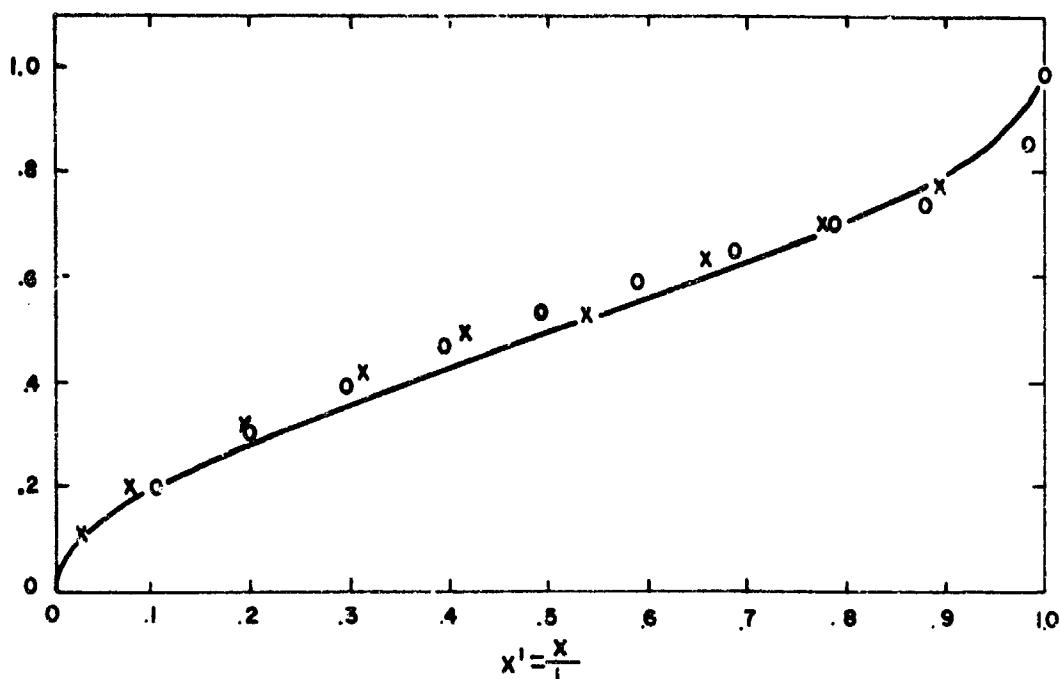


Fig. 6. Profile of a salt wedge: comparison of results from theory and observations (Farmer and Morgan, 1953). On left of graph: surface = 1.0, bottom = 0. The solid line is the form of the interface, derived from theory. X = O at the upstream tip of the wedge; L is the length of the wedge. O's refer to Mississippi River Southwest Pass and X's refer to a model experiment.

tions, both in the laboratory experiments and in the Mississippi (Fig. 6). The equation for the length of the wedge gave agreement with the Mississippi results if the friction coefficient K was taken as 0.001, whereas for the experimental data a value of 0.006 was required.

An important parameter in these studies is the interfacial Froude number, defined by

$$F_i = \frac{u^2}{\gamma g D}, \quad (30)$$

where u is the velocity in the upper layer and D its depth. In his experiments Farmer found that the flow adjusted itself so that at the transition from the flume to the saltwater reservoir $F_i = 1$ approximately. This was also found to hold at the section of the jetties in Southwest Pass on the Mississippi. For a given discharge and density difference, equation (30) enables computation of the depth of the upper layer at the transitional section (Stommel and Farmer, 1952).

TWO-LAYER FLOW WITH ENTRAINMENT

The qualitative features of flow with entrainment and the observations of Tully (1949) in Alberni Inlet, British Columbia, were mentioned earlier. A theoretical treatment of the flow in a two-layer model was given by Stommel (1951 unpublished, 1953a) and Stommel and Farmer (1952). The lighter water is assumed to be flowing seawards over a lower layer, which is very deep, has a uniform density ρ_2 , and in

which the velocity is very small. Entrainment is assumed to occur by the upward movement of deep water across the interface, but there is no downward movement of the lighter water. The density ρ_1 in the upper layer therefore increases seawards, approaching the value ρ_2 as $x \rightarrow \infty$. In the equation of motion for the upper layer, the field acceleration and pressure gradient terms are retained, but frictional stresses are neglected. From this equation and considerations of continuity of mass and conservation of salt, it is found that

$$\frac{d}{dx} [D\rho_1(u^2 + \frac{1}{2}\gamma g D)] = 0, \quad (31)$$

where u = velocity in the upper layer, D = depth of upper layer, and $\gamma = (\rho_2 - \rho_1)/\rho_2$. By introducing Q , the rate of mass transport, given by $Q = D\rho_1 u$, the above equation becomes

$$\frac{dD}{dQ} = \frac{D}{Q} \frac{(4F_i - 1)}{2(F_i - 1)}, \quad (32)$$

where F_i is the interfacial Froude number, as in equation (30).

Equation (32) shows that for $F_i < 0.25$, the thickness of the layer increases with increasing transport, but for $0.25 < F_i < 1$ the thickness decreases as the transport increases. This appears to correspond to conditions observed in Alberni Inlet and certain other fjord-type estuaries. When $F_i \rightarrow 1$, $dD/dQ \rightarrow -\infty$ in equation (32) and it may be concluded that the two-layer model breaks down. There is some evidence

that in actual estuaries the flow is such that $F_t \rightarrow 1$ at the mouth.

A different approach to the dynamics of a deep fjord estuary was made by Cameron (1951a) who assumed that the density, horizontal velocity, and vertical velocity were all continuous functions of depth. Lateral homogeneity was assumed and steady state conditions were considered. A frictional term, as well as the pressure gradient and field acceleration terms, was included in the equation of motion. Combining the equation for the horizontal and vertical components of flow, he obtained the relation

$$\frac{\partial}{\partial z} \left[\rho \left(u \frac{\partial u}{\partial x} + w \frac{\partial u}{\partial z} \right) \right] = -g \frac{\partial \rho}{\partial x} + \frac{\partial^2}{\partial x^2} \left(A_v \frac{\partial u}{\partial z} \right), \quad (33)$$

where A_v is the coefficient of vertical eddy viscosity. By introducing a stream function, a solution was found for the variation of velocity along the estuary and with depth. In this solution, the velocity has a maximum in the seaward direction at the surface, decreasing to zero at a depth which might be called the depth of no net horizontal motion. Below this depth the velocity is directed upstream and reaches a maximum value at about twice the depth of no motion. Below this it decreases asymptotically to zero in the deep water. The theory leads to a distribution of density, as expressed by γ , where $\gamma = (\rho_s - \rho)/\rho_s$, ρ_s being the density of undiluted sea water. Cameron's theory also leads to a critical velocity of surface flow at which the mechanism postulated in the model would break down.

The above theories have dealt with processes acting along the estuary and have not been concerned with the variation in conditions across it. The Coriolis force gives rise to a slope of the surfaces of equal density across the estuary and if all acceleration and frictional terms are negligible in comparison with the Coriolis term, observations of this slope may be used to compute the longitudinal velocity of flow. This in fact is the method widely used for ocean currents. From equation (2) in these conditions

$$fu = -\alpha \frac{\partial p}{\partial y}, \quad (34)$$

and $\partial p/\partial y$ can be determined from the density distribution if a level at which the pressure gradient is zero may be estimated. Cameron (1951b), from observations at the entrance to Portland Inlet, British Columbia, found that the depth-mean transport computed in this way agreed well with the freshwater transport derived from river gauge data. There was also satisfactory agreement with the net velocity which reached 0.68 knots measured at the surface. From the salinity structure the depth of no motion was taken to be at 90 ft. The agreement in the results indicated that, in this situation, the assumption was justified that the accelerations and frictional forces were negligible.

Tully (1958) suggested that similar conditions hold in a number of other fjord-type inlets, where the channel is comparatively straight and deep. From

equations (13) and (34) the transports T_1 and T_2 in the upper and lower layers respectively may be shown to be given by

$$\left. \begin{aligned} T_1 &= \frac{(\delta_2 - \delta_1)}{f\Delta y} \left(\frac{1}{A_1} + \frac{1-c}{A_2} \right) \\ T_2 &= -\frac{(\delta_2 - \delta_1)}{f\Delta y} \left(\frac{1}{A_1(1-c)} + \frac{1}{A_2} \right) \end{aligned} \right\} \quad (35)$$

where δ_1 and δ_2 are the anomalies of dynamic height at two stations in a cross-channel section, Δy is the distance between the stations, A_1 and A_2 are the cross-sectional areas of the upper and lower zones, and c is the fraction of fresh water in the upper layer. The anomalies δ_1 and δ_2 are computed from the surface to any level at or below the deepest value L of the inter-zone boundary in the section considered.

The depths limiting the upper and lower zones were derived from a curve of salinity S against $\log z$ (z = depth). Data from a number of regions, if plotted in this way, give a curve made up of three approximately straight lines, as in Figure 7, dividing the depth naturally into an upper zone, halocline, and lower zone. The lower limit of the halocline is regarded as the level through which transport takes place upwards only, whereas mixing as well as entrainment occurs within the halocline. The method was applied to Juan de Fuca Strait, the density and velocity structure of which are shown in Figure 8.

A method using heat-budget data to estimate the freshwater transport and provide information on the entrainment process was described by Pickard and Trites (1957). In the surface layer they considered the processes of seaward flow, upward entrainment of deeper water, and the passage of heat through the surface because of radiation, evaporation, and conduction. The equations of continuity were applied to the volume of water, heat content, and salt content. In this way it was found possible to determine: (1) the velocity at the head of the estuary, and hence the river inflow, given the heat-budget data and also the temperature and salinity of the entrained water; and (2) the depth of entrainment, given the temperature and salinity of the entrained water, the velocity of flow (from observation or previous calculation), and the heat budget data. The application of the first method to a number of inlets gave the freshwater discharge in fair agreement ($\pm 25\%$) with the data from precipitation and runoff. Application of the second indicated that the effective depth of entrainment was only slightly deeper than the depth of no motion, which ranged from 2 m to 9 m in the inlets studied. It was also possible to confirm that the downward penetration of water from the upper layer was small.

Stommel and Farmer (1952, 1953) considered the action of a restricted section in a channel on a two-layer flow. They derived a criterion based on the condition that interfacial waves formed there would

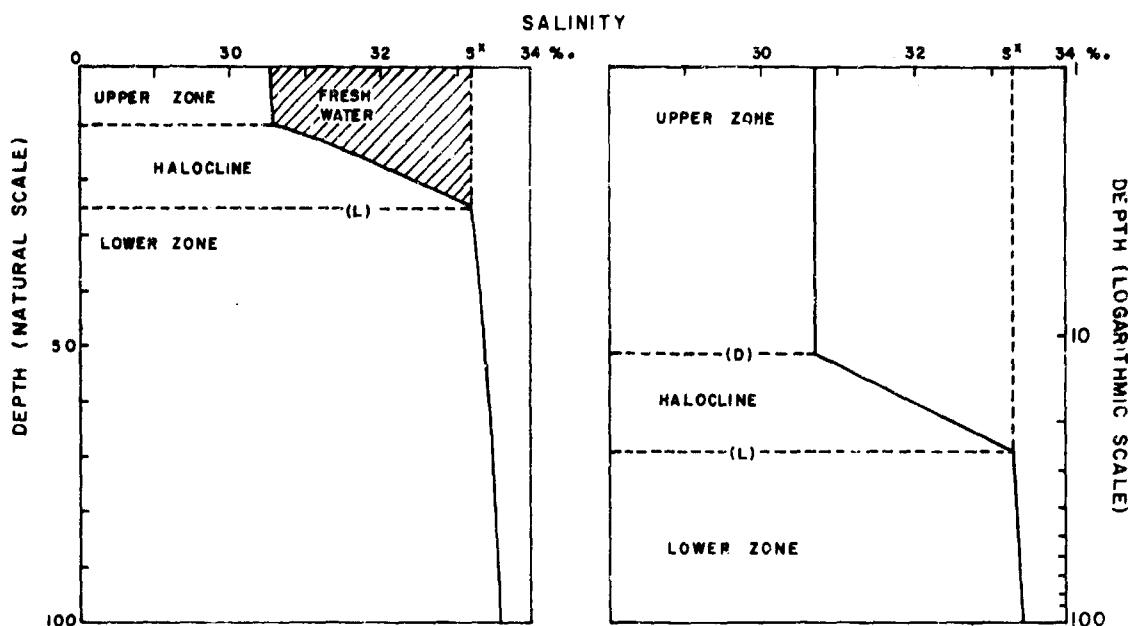


Fig. 7. Representation of salinity in a fjord-type estuary on a logarithmic depth scale (From Tully, 1958).

be stationary. In the case of a relatively shallow upper layer on a much deeper lower layer the criterion corresponds to $F_t = 1$ approximately. If the layers are of comparable depth, the critical value of F_t is a function of q_2/q_1 , the ratio of the discharges in the two layers, and n , the ratio of the depth of the upper layer to the total depth. It was found that the depth of the upper layer in the South Pass and Southwest Pass of the Mississippi River agreed with that given by $F_t = 1$. Stommel and Farmer (1953) extended the idea to show that there was a limit to the extent that vertical mixing within an estuary could influence the discharge or the salinity in the two layers at the mouth.

A theoretical and experimental study of turbulent entrainment was carried out by Ellison and Turner (1959). They defined the entrainment E by the equation

$$\frac{d}{dx}(UD) = EU \quad (36)$$

in the present notation, U being the mean velocity and D the depth of the layer into which entrainment is taking place. E was taken to be a function of R_t , the layer Richardson number defined by

$$R_t = \frac{\gamma g D}{U^2}, \quad (37)$$

where $\gamma = (\rho_2 - \rho_1)/\rho_2$ as before. R_t is thus the reciprocal of the interfacial Froude number used by Farmer and Stommel. Ellison and Turner found $E = 0.075$ for $R_t = 0$, that is, for no difference in density between the layers, decreasing to 0.01 for $R_t = 0.5$, and they deduced that E was probably negligible for $R_t > 0.8$. These results apply to $0 < R_t < 1$, when F_t

> 1 , and would therefore seem to be in a different range from those of Stommel and Farmer.

PARTIALLY MIXED ESTUARY

In an estuary in which the vertical mixing is greater or the depth is less than in the preceding cases, there is no deep layer of almost undiluted sea water which can be regarded primarily as a source of water for entrainment. The salinity and density decrease upstream from the mouth of the estuary at all depths. The qualitative features of this type of estuary have been described earlier. The development of a quantitative study of such estuaries is due mainly to a series of investigations by Pritchard and the following treatment is based on his work.

In order to take into account tidal currents as well as the turbulent character of the flow, each of the velocity components u , v , w and the salinity S are divided into three terms, which are uncorrelated with one another.

$$\begin{aligned} u &= \bar{u} + U + u', & v &= \bar{v} + V + v', \\ w &= \bar{w} + W + w', & s &= \bar{s} + S + s', \end{aligned} \quad \{ \quad (38)$$

where \bar{u} is the mean velocity averaged over one or more tidal periods, U is the tidal component and u' the turbulent component, the mean values of U and u' each being zero by definition.

Since the turbulent velocities have been taken into account explicitly, the stress terms on the right of equations (1) and (2) may be set equal to zero. Then on substituting from (38), above, in equations (1) and (2), taking mean values with respect to time, and setting terms such as $\langle uu' \rangle$, $\langle Uv' \rangle$ and $\langle UW \rangle$ equal to zero, the mean longitudinal equation of motion becomes

$$\begin{aligned} \frac{\partial \bar{u}}{\partial t} + \bar{u} \frac{\partial \bar{u}}{\partial x} + \bar{w} \frac{\partial \bar{u}}{\partial z} + \frac{\partial}{\partial x} (\bar{U} \bar{U}) + \frac{\partial}{\partial z} (\bar{U} \bar{W}) \\ = - \left\langle \alpha \frac{\partial p}{\partial x} \right\rangle - \frac{\partial}{\partial x} \langle u' u' \rangle - \frac{\partial}{\partial y} \langle v' u' \rangle - \frac{\partial}{\partial z} \langle w' u' \rangle, \quad (39) \end{aligned}$$

and the mean lateral equation

$$f \bar{u} = - \left\langle \alpha \frac{\partial p}{\partial y} \right\rangle - \frac{\partial}{\partial x} \langle u' v' \rangle - \frac{\partial}{\partial y} \langle v' v' \rangle - \frac{\partial}{\partial z} \langle w' v' \rangle, \quad (40)$$

where the brackets $\langle \rangle$ denote mean values with respect to time. As before, the molecular viscosity terms are omitted from the equation as, except very near the boundaries, they are several times smaller than the turbulent stresses.

It is assumed that the transverse velocity components \bar{v} and \bar{V} are small compared with \bar{u} and U and that the field acceleration terms involving them may be neglected. Stewart (1957) questioned this assumption, pointing out that if the flow has an appreciable curvature the term $\bar{u} (\partial \bar{v} / \partial x) + (\partial / \partial x) \langle \bar{U} \bar{V} \rangle$ should be added to the left-hand side of (40), and may be of the same order of magnitude on the turbulent stress terms. It seems likely that the corresponding terms in (39), as well as the Coriolis term $f \bar{v}$, may justifiably be neglected.

In the vertical direction, all the acceleration terms may be neglected, leaving the hydrostatic equation $0 = g - [\alpha (\partial p / \partial z)]$. Substituting for s from (38) in the equation for the continuity of salt, which may be written $Ds/Dt = 0$, and using the equation for continuity of water, gives

$$\begin{aligned} \frac{\partial \bar{s}}{\partial t} + \bar{u} \frac{\partial \bar{s}}{\partial x} + \bar{v} \frac{\partial \bar{s}}{\partial y} + \bar{w} \frac{\partial \bar{s}}{\partial z} \\ + \frac{\partial}{\partial x} \langle \bar{U} \bar{s} \rangle + \frac{\partial}{\partial y} \langle \bar{V} \bar{s} \rangle + \frac{\partial}{\partial z} \langle \bar{W} \bar{s} \rangle \\ = - \frac{\partial}{\partial x} \langle u' s' \rangle - \frac{\partial}{\partial y} \langle v' s' \rangle - \frac{\partial}{\partial z} \langle w' s' \rangle. \quad (41) \end{aligned}$$

If the tidal variation in salinity S is 90° out of phase with the velocity U , as is often approximately the case, terms such as $\langle \bar{U} \bar{s} \rangle$ vanish from (41).

In equations (39) and (40), the turbulent stress terms have been written $\langle u' u' \rangle$, etc. Although direct observations of turbulent fluctuations have been made on a few occasions (Bowden, 1962; Grant *et al.*, 1962), it is usually found necessary to relate these stresses to the mean velocity of gradients by coefficients of eddy viscosity, thus

$$\begin{aligned} \langle u' u' \rangle &= - \rho N_x \frac{\partial \bar{u}}{\partial x}, \quad \langle v' u' \rangle = - \rho N_y \frac{\partial \bar{u}}{\partial y}, \\ \langle w' u' \rangle &= - \rho N_z \frac{\partial \bar{u}}{\partial z}. \quad (42) \end{aligned}$$

Similarly the eddy fluxes of salt are related to the mean salinity gradients by coefficients of eddy diffusion, that is

$$\begin{aligned} \langle u' s' \rangle &= - \rho K_x \frac{\partial \bar{s}}{\partial x}, \quad \langle v' s' \rangle = - \rho K_y \frac{\partial \bar{s}}{\partial y}, \\ \langle w' s' \rangle &= - \rho K_z \frac{\partial \bar{s}}{\partial z}. \quad (43) \end{aligned}$$

Pritchard's development of the theory of flow in a partially mixed estuary was based largely on a detailed series of measurements of salinity and currents in the James River, flowing into Chesapeake Bay (Pritchard, 1952a). In a study of the salt balance, Pritchard (1954b) integrated equation (41) over an element of volume extending across the whole width of the estuary at depth z . The term $\partial \bar{s} / \partial t$ was shown to be negligibly small, from the actual rate of change of salinity with time, and the term $\partial \langle \bar{U} \bar{s} \rangle / \partial x$ was taken as zero on the grounds that S and U were 90° out of phase. The equation then becomes

$$\begin{aligned} \frac{\partial \bar{s}}{\partial t} + \bar{u} \frac{\partial \bar{s}}{\partial x} + \bar{w} \frac{\partial \bar{s}}{\partial z} \\ = - \frac{1}{b} \frac{\partial}{\partial x} \{ b \langle u' s' \rangle \} - \frac{1}{b} \frac{\partial}{\partial z} \{ b \langle w' s' \rangle \}, \quad (44) \end{aligned}$$

where b is the breadth of the element. Making use of the observations of currents and salinities, Pritchard was able to compute the values of all the terms in this equation.

This study showed that the most important terms in the salt balance were the mean horizontal advection $\bar{u} \partial \bar{s} / \partial x$, and the turbulent or non-adhesive, vertical flux term involving $\langle w' s' \rangle$. The mean vertical advection $\bar{w} \partial \bar{s} / \partial z$ was significant only very near the boundary between the upper and lower layer, and the horizontal turbulent flux term, involving $\langle u' s' \rangle$, was only of the order of 1 percent of the main terms.

By analogy with these results, Pritchard (1956) assumed that the horizontal components of the turbulent flux of momentum were negligible compared with the other terms in the equations of motion in the x and y directions. Equations (39) and (40) for the steady state then reduce to

$$\bar{u} \frac{\partial \bar{u}}{\partial x} + \bar{w} \frac{\partial \bar{u}}{\partial z} + U_0 \frac{\partial U_0}{\partial x} = - \left\langle \alpha \frac{\partial p}{\partial x} \right\rangle - \frac{\partial}{\partial z} \langle u' w' \rangle \quad (45)$$

$$f \bar{u} = - \left\langle \alpha \frac{\partial p}{\partial y} \right\rangle - \frac{\partial}{\partial z} \langle v' w' \rangle. \quad (46)$$

U_0 is the amplitude of the tidal current.

To evaluate the terms in these equations, the measurements of currents and densities as functions of depth were available. By assuming the shearing stress to be zero at the surface, and to be estimated at the bottom from the logarithmic velocity profile law, with a roughness length $z_0 = 0.02$ cm, all the terms could be computed except $\langle u' u' \rangle$ and $\langle w' w' \rangle$. The equations were thus solved for these two terms. It was concluded that, along the estuary, the pressure gradient was balanced mainly by the turbulent stress terms $\partial \langle u' u' \rangle / \partial z$, but the tidal acceleration term $U_0 \partial U_0 / \partial x$ may be important. The field acceleration terms related to the mean motion were relatively insignificant. Across the estuary, the Coriolis term, $f \bar{u}$, was balanced primarily by the lateral pressure gradient, but the turbulent stress term, $\partial \langle w' u' \rangle / \partial z$, was also significant. The depth of the level pressure surface and of the surface of no net motion were also determined; both were approximately at mid-depth.

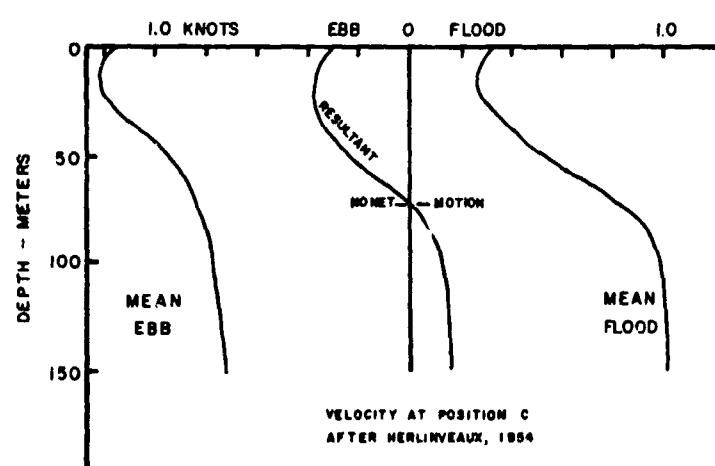
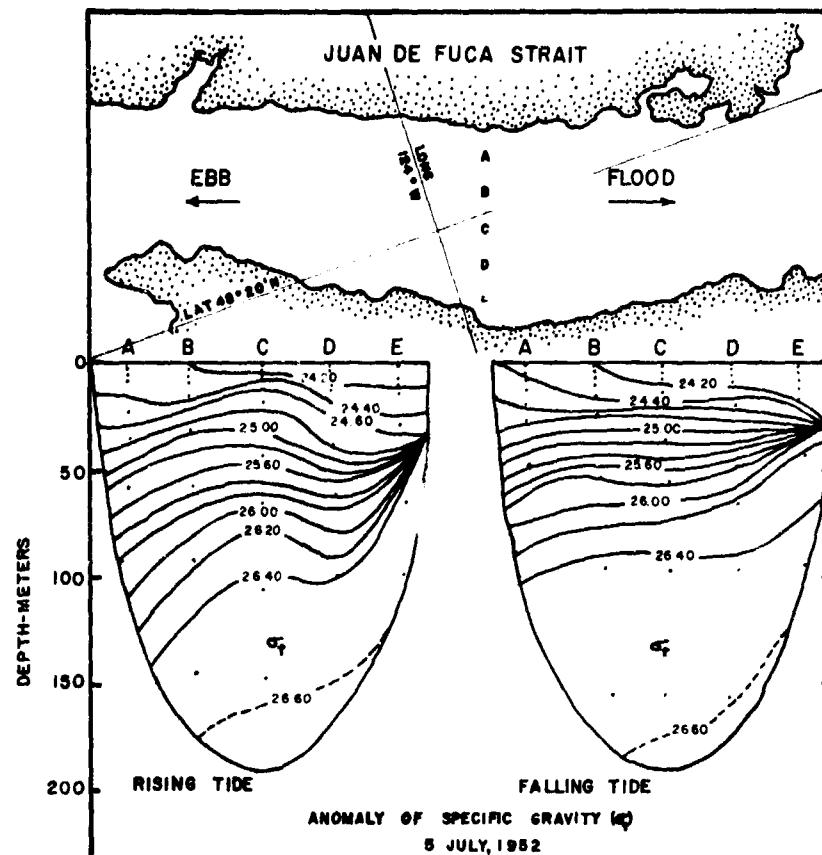


Fig. 8. Density and velocity structure in Juan de Fuca Strait, British Columbia (Tully, 1958).

It was found by Pritchard and Kent (1956) that the curves of the vertical and lateral shearing stresses as functions of depth were very similar, and they suggested that $\langle v'w' \rangle = \eta \langle u'w' \rangle$ where η is a constant, which from the observations was about 0.4.

Pritchard and Kent (1956) gave a procedure for calculating the mean velocity \bar{u} as a function of depth by using equations (45) and (46), with the first two terms in (45) set equal to zero. The internal parts of the horizontal pressure gradients were computed from temperature and salinity data and the $U_0 \partial U_0 / \partial x$ term from tidal current data. Then equation (45) enabled the constant in the pressure term and $\langle w'w' \rangle$ to be determined, with the aid of estimates of the surface and bottom stress. These conditions also allow $\langle w'v' \rangle$ to be found, and so finally \bar{u} can be determined

from equation (46). In the James River it appears that the $\partial \langle w'v' \rangle / \partial z$ term is approximately one-third of the $(\alpha \partial p / \partial y)$ term.

Observations have been made of the salinity distribution and circulation in a number of other estuaries of the partially mixed type. The Thames River was the subject of a full-scale and model investigation by Inglis and Allen (1957). The salinity difference between surface and bottom varies during the tidal period reaching values up to 2 %. Measurements of current showed the presence of an upstream flow near the bottom to approximately 12 miles below London Bridge, in conditions of normal river flow. This was within the reach of the estuary in which excessive deposition of silt occurred. Experiments on the model showed that an increased river discharge caused the

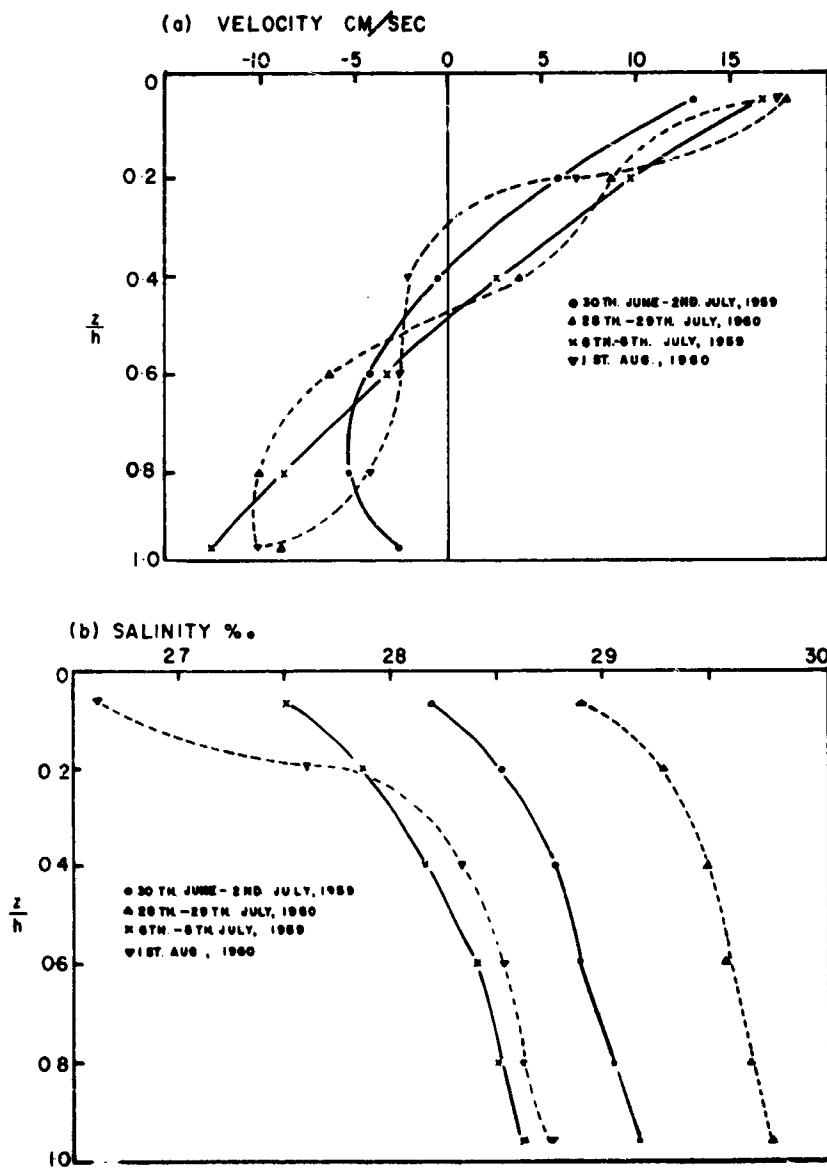


Fig. 9. Mean profiles of velocity and salinity in the Mersey Estuary (From Bowden, 1963).

Table 2. Mersey Estuary: effective values of stress τ , N_z , and K_z over a tidal period.

s/h	June 30-July 2, 1959			July 6-8, 1959		
	τ dyn/cm ²	N_z cm ³ /s	K_z cm ³ /s	τ dyn/cm ²	N_z cm ³ /s	K_z cm ³ /s
0.1	0.20	9	5	0.34	14	8
0.3	0.45	27	10	0.86	46	23
0.5	0.39	40	27	1.03	73	30
0.7	0.10	43	17	0.86	72	29
0.9	-0.42	(62)	(3)	0.34	25	13

limit of the upstream flow to move downriver by a distance of 12 miles when the discharge was increased ten times.

A similar investigation, involving both full-scale observations and model experiments, was carried out for the Mersey Estuary and Liverpool Bay by Price and Kendrick (1963). Other observations, made in the Narrows, a fairly straight channel about six miles long with a depth of approximately 20 m, connecting the upper estuary with Liverpool Bay, have been made the basis of a dynamic study (Hughes, 1958; Bowden, 1960, 1963). Figure 9 shows some profiles of velocity and salinity. The dynamics of the flow have been considered, making similar assumptions to those of Pritchard. Since the variation of tidal current in this stretch was small, the $U_0 \partial U_0 / \partial x$ term was neglected as well as the other terms on the left-hand side of equation (45). Expressing the pressure gradient in terms of the density, and applying suitable boundary conditions for the surface and bottom stress, equation (45) enables the shearing stress $\langle w'u' \rangle$ to be

Table 3. Horizontal eddy diffusivity, K_z , in some tidal estuaries.

Estuary & position	Vertical sal. diff. $\Delta S \%$	K_z from observations 10^6 cm ³ /sec	K_z calculated from Eq. (53) 10^6 cm ³ /sec
Severn (summer)			
Weston-super-Mare	—	5.4	0.53
Portishead	0.1	10.6	0.48
Aust	0.3	17.4	0.56
Sharpness	—	12.2	0.12
Severn (winter)			
Weston-super-Mare	—	12.4	—
Portishead	0.3	15.7	—
Aust	0.5	30.9	—
Sharpness	—	53.5	—
Thames (low river flow)			
10 miles below London Br.	1.0	5.3	0.17
25 miles below London Br.	1.0	8.4	0.24
Thames (high river flow)			
30 miles below London Br.	—	33.8	0.25
Mersey Narrows			
May, 1956	1.3	16.1	0.59
March, 1957	5.0	36.0	0.59

computed. Introducing the vertical eddy viscosity N_z , the stress may be written $\langle w'u' \rangle = -\rho N_z (\partial u / \partial z)$. Hence, from the observed profile of mean velocity, N_z was determined at various fractions of the total depth as shown in Table 2. N_z was small near the surface, but increased to values of 40 to 70 cm²/sec at mid-depth.

By making similar assumptions, the salinity equation (44) may be reduced to a form which enables the vertical turbulent salt flux $\langle w's' \rangle$ to be computed from the observations. Introducing K_z , the coefficient of eddy diffusion, $\langle w's' \rangle = -\rho K_z (\partial s / \partial z)$. The values of K_z , found in this way on two occasions, are also given in Table 2. The maximum values occur at mid-depths and the values of K_z are approximately half the corresponding values of N_z . In this case an attempt was made to apply the salinity equation, including the $\partial s / \partial t$ term, to hourly values of the data and so determine the variation of K_z within the tidal period. Consistent results were obtained with only one of the four sets of data to which the method was applied. These indicated that when the tidal velocity was large the values of K_z were three to five times as great as the effective values over a tidal period.

A theoretical treatment in which the circulation and mixing processes are regarded as parts of the same system has been given by Rattray and Hansen (1962). Considering a straight and narrow estuary of rectangular cross section, with uniform width but variable depth, and assuming it to be laterally homogeneous, they expressed the basic equations in the form

$$\left. \begin{aligned} \rho U_0 \frac{\partial U_0}{\partial x} &= -\frac{\partial p}{\partial x} + \frac{\partial}{\partial z} \left(A \frac{\partial u}{\partial z} \right) \\ 0 &= -\frac{\partial p}{\partial z} + \rho g \\ \frac{\partial u}{\partial x} + \frac{\partial w}{\partial z} &= 0 \\ u \frac{\partial z}{\partial x} &= \frac{\partial}{\partial z} \left(K_z \frac{\partial s}{\partial z} \right) \end{aligned} \right\} \quad (47)$$

The density was related to the salinity by $\rho = \rho_0 + k_3$ and a salinity defect σ introduced, defined by $\sigma = \rho_0 g (1 - s/s_b)$ where s_b is a base salinity taken to be that of the oceanic water. The boundary conditions taken were: (1) at the surface $w = 0$, and the shearing stress = wind stress, (2) at the bottom $u = w = 0$. The coefficients of eddy viscosity A and eddy diffusion K_z were assumed to be constant.

A stream function ψ was introduced, so that $u = -(\partial \psi / \partial z)$, $w = (\partial \psi / \partial x)$. Rattray and Hansen pointed out the resemblance of the resulting partial differential equation to those arising in thermal boundary layer problems and solved them by the method of similarity solutions which has been used in such cases. They obtained solutions for the velocity profile and the salinity profile both in the case of zero wind stress and for various values of wind stress. In the case of zero wind stress, the curves show a surface outflow and a deep inflow with the level of no motion at $z/h = 0.42$, h being the total depth. The magnitude of the velocity is directly proportional to the longitudinal

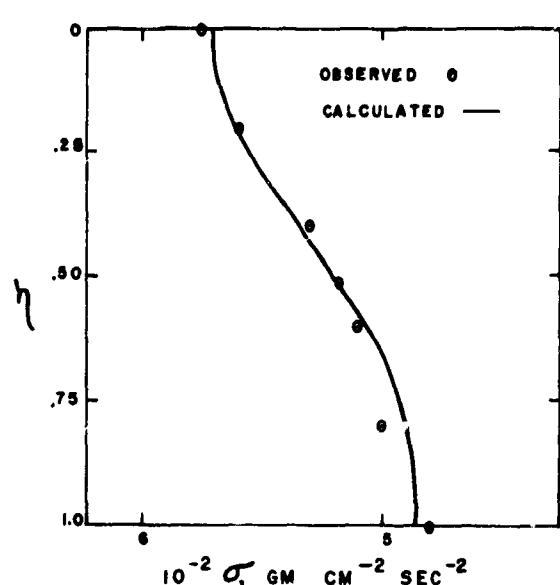


Fig. 10. (A) Comparison of theoretical and observed salinity profile in the James River Estuary (Rattray and Hansen, 1962).

density gradient and inversely proportional to the eddy viscosity. In comparing their results with Pritchard's data for the James River, Rattray and Hansen found fairly good agreement by taking $N_s = 4 \text{ cm}^2/\text{sec}$ and $K_z = 2 \text{ cm}^2/\text{sec}$. The comparison of the salinity and velocity profiles is shown in Figure 10.

An interesting series of laboratory experiments was carried out by Harleman and Ippen (1960), who varied the intensity of turbulence independently of the flow by using oscillating screens. They were concerned with the longitudinal concentration of dye or salt in a partially mixed or well mixed estuary, in which the vertical and transverse variations in concentration were small compared with those along the estuary. In the partially mixed case they defined an "adjusted" or "gross" eddy diffusion coefficient K_x' which included the advective effects arising from density differences. Using dye as a tracer, with no density difference they confirmed that K_x' was proportional to $G^{1/3}$, where G is the rate of dissipation of turbulent energy per unit mass, as given in Kolmogoroff's theory.

When fresh and salt water were used, Harleman and Ippen suggested that K_x' would be related to K_x by

$$\frac{K_x'}{K_x} = \varphi \left(\frac{G}{g' V_f} \right), \quad (48)$$

where $g' = g \Delta \rho / \rho$ and V_f is the velocity of the freshwater flow. An empirical equation for the function φ was determined from the experiments. They found that for given values of $\Delta \rho / \rho$ and V_f , K_x' decreases as G increases. The following pairs of values indicate the order of magnitude of the change in the ratio K_x'/K_x :

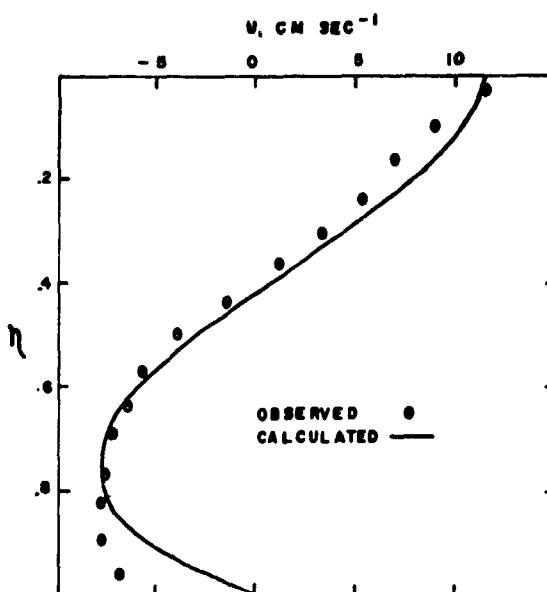


Fig. 10. (B) Comparison of theoretical and observed velocity profile in the James Estuary (Rattray and Hansen, 1962).

$$G/g' V_f = 60 \quad 10^3 > 10^4$$

$$K_x'/K_x = 50 \quad 6 \approx 1$$

From these results the "intrusion length", L_i , to a point where the salinity was reduced to 1 percent of its oceanic value, was deduced. It was found that, whereas in a partially mixed estuary L_i decreased with increasing turbulence, in a well mixed estuary ($K_x'/K_x = 1$) L_i increased.

The decrease in the effective value of the coefficient of horizontal diffusion as the vertical mixing becomes more effective has been noted in field observations. It is rather doubtful, however, whether the quantitative results from the laboratory experiments can be scaled up since the mode of generation of the turbulence is different. In a tidal current, the greatest rate of generation occurs near the bottom, and much of the turbulence at higher levels has probably diffused upwards, whereas in the laboratory experiments the turbulence was generated more or less uniformly throughout the depth.

VERTICALLY HOMOGENEOUS ESTUARY

The qualitative features and methods of treating the mixing of this type of estuary have been described earlier. It has also been mentioned that doubts have been expressed as to whether an estuary which is strictly vertically homogeneous really exists. A detailed study of the dynamics of this type of estuary seems not to have been made. However, a simple consideration of the nature of the terms in equations (45) and (44) would appear to show that a flow in which u and S are completely uniform with depth is not possible. If the density ρ can be regarded as con-

stant with depth in the hydrostatic equation, it follows from (7) that

$$\alpha \frac{\partial p}{\partial x} = \epsilon \frac{\partial r}{\partial x} - \alpha s \frac{\partial \rho}{\partial x}. \quad (49)$$

Thus the horizontal pressure gradient varies with s . In equation (45) only the term $\partial(w'u')/\partial x$ is available to balance this variation. Putting $\langle w'u' \rangle = -\rho N_s (\partial \theta / \partial s)$ shows that θ must vary with s (unless N_s is infinitely large).

In (44), $\partial \theta / \partial s$ will vary with depth if θ varies, and the only term capable of balancing this is that in $\langle w's' \rangle$. Introducing K_s shows that θ must vary with depth although this variation may be small if K_s is large enough.

It seems advisable to regard the so-called vertically homogeneous estuary not as a physically distinct type, but as a special case of the partially mixed estuary, in which the variations of velocity and salinity with depth are so small that it is impractical to measure them with sufficient accuracy; it becomes more convenient to include the advective effects of such variations in an effective longitudinal diffusion term. The experiments of Harleman and Ippen supporting this view have already been mentioned.

Taylor (1953) gave a theoretical treatment of the dispersion of matter in laminar flow through a pipe, showing that the dispersion was produced by diffusion across the pipe combined with a transverse variation in the velocity along it, arising from friction at the wall. He showed that the effective coefficient of diffusion along the pipe was inversely proportional to the molecular diffusivity. He later extended the theory to turbulent flow through the pipe (Taylor, 1954). In this case the transverse mixing is due to the eddy diffusivity in that direction. In the absence of a density gradient, assuming the coefficients of transverse eddy diffusivity and eddy viscosity to be equal, it was shown that the effective coefficient of longitudinal diffusion was given by

$$K_s = 10.1 a u_0. \quad (50)$$

where a is the radius of the pipe and u_0 is the friction velocity, given by $u_0 = (r_0 \rho)^{1/2}$, r_0 being the frictional stress at the wall. The same method was extended by Elder (1959) to flow in an open channel. Making similar assumptions, Elder found that for steady flow in neutrally stable conditions

$$K_s = 5.9 a h. \quad (51)$$

where h is the depth of water in the channel. If the bottom stress is related to the depth-mean velocity U by the equation $r_0 = k_p U^2$, and the friction coefficient k is taken as 0.0025, the above relation becomes

$$K_s = 0.295 U h. \quad (52)$$

In a tidal estuary the main source of turbulence is the tidal current and U is a periodic function of time. It may be shown, however, that the same process can still produce a net flux of a dissolved substance in the direction of the concentration gradient

(Bowden, 1963). If the current is simple harmonic with an amplitude U_0 then, with certain simplifying assumptions, the effective K_s is equal to half that in a steady flow of velocity U_0 . Thus, in the above case,

$$K_s = 0.15 U_0 h. \quad (53)$$

If the mixing is due primarily to the tidal currents and the water is vertically homogeneous so that the flow is neutrally stable, it should be possible to compute the values of K_s from this equation. This was done by Bowden (1963) for the Severn, Thames, and Mersey Estuaries, and the results compared with the values computed from the salinity observations by Stommel's method. The observed values of K_s were from 10 to 100 times greater than the computed values, as shown in Table 3.

This discrepancy is not surprising in the cases of the Thames and Mersey, where salinity differences of 1% or more between surface and bottom are known to occur at some states of the tide. It is more remarkable in the case of the Severn which has previously been regarded as a typical unstratified estuary.

The effect of the density gradient on the effective values of N_s and K_s on the Mersey can be seen in Table 2. On the basis of other observations, the maximum values of N_s are one-tenth of the values to be expected in a tidal current of the same amplitude in water of uniform density. There are two ways in which a density gradient can cause a large increase in K_s in an estuary. The reduced values of N_s and K_s would cause an increase in the tidal current effect, even if the velocity profile retained the same form. Secondly, the differential flow arising from the horizontal pressure gradient will be increased, and the advective effects of this will add to the effective value of K_s .

The reductions in N_s and K_s are sufficient to account for the large values of effective K_s in estuaries. It is interesting to note that Stommel and Farmer (1952), dealing with two-layer flow, pointed out that the horizontal transport of salt by this means was equivalent to longitudinal diffusion corresponding to a coefficient K_s , so that

$$K_s \propto \left(\frac{(u_1 - \bar{u})^2 h}{K_s} \right). \quad (54)$$

where u_1 is the velocity in the upper layer, \bar{u} the mean velocity, and h the depth of water.

When the density gradient is so great, however, that the two-layer structure, in salinity as well as in velocity, is clearly recognizable, the concept of an effective horizontal diffusivity loses its usefulness.

BOUNDARY LAYER THEORY

In a theoretical treatment by Abbott (1960a), the net drift of water near the bottom of an estuary was regarded as a mass transport effect associated with a progressive tidal wave. The flow was assumed to be irrotational, except in a boundary layer adjacent to the bottom, in which the eddy viscosity was constant. Using the method of successive approximations,

Abbott found that the second approximation gave a steady flow term which was non-zero, even beyond the boundary layer. He derived a criterion for the direction of the mean velocity at a point just above the bed, and applying it to data on the Thames Estuary (Inglis and Allen, 1957), he found satisfactory agreement in the position at which the net flow near the bottom was reversed. Some features of the theory were unsatisfactory, however. In particular, the constant value of N_s was estimated from the velocity profile to be $0.5 \text{ cm}^2/\text{sec}$, which corresponds to a maximum shear 30 times too small, while the energy dissipation is 40 times too small. Since these quantities are proportional to $N_s^{1/2}$, the value of N_s would have to be increased by a factor of 10^8 to meet these objections.

In a subsequent paper, Abbott (1960b) considered the longitudinal equation of motion when a density gradient along the channel is included. Assuming the density gradient effect to predominate over the advective acceleration terms, he obtained a criterion for the direction of the net drift near the bed in these conditions. Applied to the Thames, it showed that the density effect alone would not account for upstream flow anywhere in the estuary.

Abbott postulated that in the Thames the salinity gradient would not cause an upstream flow near the bed, whereas the mass transport effect because of the tidal current would. This appears to be in direct contradiction to the experimental results of Inglis and Allen. In their observations on a large model with the appropriate tidal conditions but no salinity difference in the water, they found that the upstream flow near the bed could not be produced. On introducing the salinity difference the upstream flow was correctly reproduced.

It seems doubtful if the concept of irrotational tidal flow above a boundary layer with a constant eddy viscosity is useful in this context. It is known that in practically all cases tidal flow is turbulent at all depths, as is shown in the current profile, while near the bottom the eddy viscosity increases approximately linearly with distance from the boundary.

DIFFUSION PROBLEMS

Estuarine salinity distributions caused by turbulent diffusion processes have been considered in the foregoing sections. Fresh water has been regarded as a tracer and the results obtained may be applied, directly or indirectly, to the spreading of any other substance dissolved or suspended in the water. The results of flushing-time computations may be applied to a contaminant introduced into the estuary in roughly the same way as the fresh water. From methods which derive mixing parameters for individual segments of the estuary, the diffusion of a contaminant introduced into any one of these segments may be calculated. This applies to the segmentation method of Ketchum, the horizontal diffusivity method of Stommel, the dispersion curve method of Preddy, or the exchange factor method of Dorrestein. In apply-

ing these methods it is possible to take into account the natural decay of non-conservative substances such as bacteria or radioactive wastes.

With the exception of Stommel's method, the procedures referred to above do not make explicit use of coefficients of eddy diffusion. In a second method, values of the eddy coefficients K_x , K_y , or K_z , derived from the salinity distribution, are used in applying the general diffusion equation to the contaminant. If c is the concentration per unit volume of the substance considered, the general equation is

$$\frac{\partial c}{\partial t} + u \frac{\partial c}{\partial x} + v \frac{\partial c}{\partial y} + w \frac{\partial c}{\partial z} = \frac{\partial}{\partial x} \left(K_x \frac{\partial c}{\partial x} \right) + \frac{\partial}{\partial y} \left(K_y \frac{\partial c}{\partial y} \right) + \frac{\partial}{\partial z} \left(K_z \frac{\partial c}{\partial z} \right) + Q, \quad (55)$$

where Q is the rate at which the substance is being added to an element of unit volume at the position x, y, z at time t .

A third method makes use of diffusion coefficients estimated in some other way than from the salinity distribution, either from theoretical considerations or special experiments.

The density of the contaminant is a factor to be considered, particularly in the case of a two-layer flow. If the substance is light enough to remain in the upper layer and be carried with it, it is clear that values of the velocity components and diffusion coefficients applicable to the upper layer must be used. In the case of a partially mixed or well mixed estuary, if a contaminant of density not significantly different from that of the water is introduced at a particular depth, it will at first diffuse vertically at a rate determined by the coefficient K_z . If after a certain time it is effectively uniformly mixed from surface to bottom, its subsequent spreading is two-dimensional only.

The value of K_z in homogeneous water increases with the velocity of flow and is a function of depth. If a density gradient is present, K_z is also a function of the Richardson number defined by

$$R_i = \frac{f}{\rho} \frac{\partial u}{\partial z} / \left(\frac{\partial u}{\partial z} \right)^2. \quad (56)$$

In general R_i is itself a function of depth and some examples of the computation have been given by Bowden (1963). In the Mersey, the effective values over a tidal period were found to be 0.1 near the bottom but were approximately 0.5 to 1 at mid-depth and near the surface. Various empirical formulas have been proposed to represent the variation of K_z , or the mixing length associated with it, with R_i . Kent and Pritchard (1959) compared several of these formulas with their James River data and derived an equation which allowed also for wave-generated turbulence in the surface layer. Apart from this latter term, the dependence of K_z on R_i is represented by

$$K_z = K_{z0} (1 + \beta R_i)^{-n}, \quad (57)$$

where K_{z0} is the value of K_z for $R_i = 0$ and β is a

constant which, from the James River data, has the value of 0.276. K_{e_0} , for a vertically homogeneous estuary in the absence of wind, was given by

$$K_{e_0} = 8.59 \times 10^{-8} \frac{Ug^4(h-s)^2}{h^3}. \quad (58)$$

The maximum value, occurring at mid-depth, was $5.37 \times 10^{-6} U/h$. Pritchard (1960) defined a Richardson number representative of the whole depth by

$$R_e = \frac{g}{\rho} \frac{\partial p}{\partial z} / \left(0.7 \frac{U}{h} \right)^2. \quad (59)$$

In the theory of locally isotropic turbulence, it was found originally by Kolmogoroff that the eddy viscosity and eddy diffusivity increase with the scale of the phenomena concerned. The application of this theory to horizontal motions in the sea was first considered by Stommel (1949). The basic idea is that a wide spectrum of turbulent motions, or eddies, exists with scales varying from less than a centimeter up to the dimensions of the body of water itself. In these conditions a patch of dye, for example, will be dispersed by eddies smaller than its own dimensions, while larger eddies will advect the patch as a whole. As the size of the patch increases, larger and larger eddies will take part in its dispersion. Thus the effective coefficient of eddy diffusion will increase with the size of the patch.

In the theory of locally isotropic turbulence, it is assumed that energy is supplied from external sources to the largest eddies, which pass on the energy through a cascade of eddies of decreasing size until, in the smallest eddies, it is dissipated by molecular viscosity. There exists an intermediate range of eddies which are in energy equilibrium, and which pass on the energy received without loss. It is shown that in this range

$$K \propto L^{4/3}, \quad (60)$$

where L is a linear dimension representative of the scale of diffusion being studied. A number of authors have suggested that this law should be applicable to horizontal diffusion in the sea. It is by no means clear, however, that the conditions of the theory are valid in the marine and estuarine environment. In particular, energy may be injected into the turbulence spectrum at almost any point, by wind squalls and gusts, for instance, or tidal ebbles and friction. In an estuary the application is complicated by the effect of density currents and the shear effect referred to above. It would seem unwise to assume that the $L^{4/3}$ law applies in a given estuarine situation unless an independent experiment there has indicated that it does so.

An alternative theory of diffusion was put forward by Joseph and Sendner (1958), whose basic postulate was that of a diffusion velocity P . This is equivalent to assuming an eddy diffusivity increasing linearly with the scale. Considering the case of radial spreading of a patch of contaminant in two dimensions, the diffusion equation may be written

$$\frac{\partial c}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left\{ K_r r \frac{\partial c}{\partial r} \right\}. \quad (61)$$

In the classical theory of diffusion by Fick's law, K_r is taken as constant, in Joseph and Sendner's theory $K_r = Pr$, in Kolmogoroff's theory $K_r = cr^{4/3}$ where c is a constant, and other powers of r have been suggested. The solutions obtained differ in the rate at which the concentration decreases at the center of the patch with time and in the rate at which the concentration falls off with distance from the center.

A method of treating turbulent diffusion in a sectionally homogeneous estuary was described by Kent (1958). Having determined K_{e_0} , the value of K_r for the diffusion of salt from the steady state conditions by Stommel's method, he found the value of K_r for the dispersion of a pollutant as K_p , where

$$K_p = \frac{L_p}{L_s} \quad (62)$$

and L_p and L_s represent the spatial extents of the distributions of pollutant and salt respectively. L_p is estimated from the distance at which the concentration falls to a certain level and thus increases with time as the dispersion proceeds. The method was found to give good agreement when tested in a model of Delaware Bay.

Various diffusion experiments have been carried out on full scale in estuaries using tracer methods, particularly the dyes fluorescein or rhodamine B. A series of experiments in Baltimore Harbor and other areas, using a rhodamine B technique, was described by Pritchard and Carpenter (1960). They compared their results, both from point sources and steady discharges, with the predictions from various theories. Other studies of horizontal diffusion, using tracers, have been carried out in the open sea and in lakes. A detailed review of theories of diffusion and their comparison with observed data has been given by Okubo (1962).

There is no general agreement on the way in which K_r or K_p vary with scale. Some workers, like Bowles et al. (1958) have found that in the English Channel the diffusion is adequately represented by a constant coefficient. A number of other workers have interpreted their results in terms of the $L^{4/3}$ law and have found satisfactory agreement. Joseph and Sendner were concerned with diffusion in the open ocean and found that their relation was valid over a wide range of scales, with $P = 1 \pm 0.5 \text{ cm sec}$. Attempts have been made to apply their method to estuaries and other partially enclosed bodies of water by restricting the area over which diffusion takes place.

WIND EFFECTS ON ESTUARINE CIRCULATION

The normal estuarine circulation may be taken to be that which is determined solely by the freshwater inflow and the mixing with sea water, as influenced by tidal currents. It is apparent that the wind can have an important influence on estuarine circulation and mix-

ing. Through the stress exerted on the surface it can produce a net transport of water, and the waves generated will increase the intensity of vertical mixing. In the surface layer the water transport will be mainly in the direction of the wind, so that the normal seaward flow will be increased if the wind is blowing down-estuary; it will be decreased, or even reversed in direction, if the wind is up-estuary. Compensating currents occur which influence the flow in the deeper layer also. The increased mixing because of wind currents and waves may have an important effect on the salinity structure, causing a breakdown in the normal pattern of stratification.

There are numerous observations of wind effects on estuarine circulation, one example being the work of Ketchum *et al.* (1951) in the New York Bight, in which they found that during storms there is an intense mixing effect, but that the normal circulation pattern becomes re-established about two days later. In a study of the currents in Knight Inlet, British Columbia, Pickard and Rodgers (1959) found that a wind of 20 knots blowing up the inlet caused the normal seaward current of 20 cm/sec to be reversed to a current of 50 cm/sec upstream in the first few meters. Below this there was an increased rate of outflow. The effect of wind on the velocity and salinity profiles was considered by Raistray and Hansen (1962). Their theory demonstrated the three-layer pattern which develops with an up-estuary wind of greater than a certain strength. There is an upstream flow in both the surface and the bottom layers, with downstream flow at intermediate depths. The salinity profiles indicate a reduction in the salinity gradient near the surface in these conditions and, in fact, the occurrence of unstable conditions when the wind stress exceeds a certain critical value. In practice this would result in a greatly increased value of K_z , increasing the vertical mixing.

VARYING CONDITIONS

Most of the methods which have been devised for analyzing the results of observations have treated the estuary as being in a steady state. The large changes which occur in river discharge and the changes in the estuary resulting from them have been recognized, but have been represented as a series of steady states, rather than a continuously changing state. This is largely because the observations have been the results of surveys carried out at somewhat infrequent intervals rather than of a continuous record of conditions.

In many estuaries there is a marked seasonal variation in the river flow, which is reflected in the salinity distribution. In some cases, the temperature changes due to the varying heat budget also have a significant effect. The heating of the surface layer in the summer months tends to increase the density stratification and hence reduce the vertical mixing.

Attempts have been made to compute the changes taking place due to varying river flow by using values of the horizontal eddy diffusivity K_x or of exchange coefficients derived from steady state conditions. This

may be only an approximation, however, because such coefficients themselves are variable parameters. An increased river flow, for example, will tend to produce greater vertical gradients of density, leading to less intense vertical mixing and a greater rate of horizontal circulation than would be expected from the horizontal salinity gradient alone. The resulting change in the volume of river water accumulated in the estuary will be the combined effect of these processes. One of the problems of estuarine circulation still outstanding is an adequate method of dealing with the variable state.

LITERATURE CITED

- ABBOTT, M. R., 1960a. Boundary layer effects in estuaries. *J. Marine Res.*, 18:83-100.
- ABBOTT, M. R., 1960b. Salinity effects in estuaries. *J. Marine Res.*, 18:101-111.
- ALEXANDER, W. B., B. A. SOUTHGATE, and R. BASSINDALE, 1931. Survey of the River Tees, I. *Gr. Brit., Dept. Sci. Ind. Res., Water Pollution Res. Tech. Rept. No. 2*.
- ALEXANDER, W. B., B. A. SOUTHGATE, and R. BASSINDALE, 1935. Survey of the River Tees, II. *Gr. Brit., Dept. Sci. Ind. Res., Water Pollution Res. Tech. Rept. No. 5*.
- ARONS, A. B., and H. STOMMEL, 1951. A mixing length theory of tidal flushing. *Trans. Am. Geophys. Un.*, 32:419-421.
- BASSINDALE, R., 1943a. Studies on the biology of the Bristol Channel, II. *J. Ecology*, 31:1-29.
- BASSINDALE, R., 1943b. A comparison of the varying salinity conditions of the Tees and Severn estuaries. *J. Animal Ecol.*, 12:1-10.
- BOWDEN, K. F., 1960. Circulation and mixing in the Mersey estuary. *I.A.S.H. Comm. of Surface Waters, Publ. 51*, pp. 352-360.
- BOWDEN, K. F., 1962. Measurements of turbulence near the sea bed in a tidal current. *J. Geophys. Res.*, 67:3181-3186.
- BOWDEN, K. F., 1963. The mixing processes in a tidal estuary. *Intern. J. Air Water Pollution*, 7:343-356.
- BOWLES, P., R. H. BURNS, F. HUDSWELL, and R. T. P. WHIPPLE, 1958. Sea disposal of low activity effluent. *Proc. Second Intern. Conf. Peaceful Uses of Atomic Energy*, vol. 18, pp. 376-389. United Nations, New York.
- CAMERON, W. M., 1951a. *On the dynamics of inlet circulation*. Doctoral dissertation, Scripps Institution of Oceanography, Univ. Calif., La Jolla, California.
- CAMERON, W. M., 1951b. On the transverse forces in a British Columbia Inlet. *Proc. and Trans. Roy. Soc. Canada*, 45(5):1-8.
- CAMERON, W. M., and D. W. PRITCHARD, 1963. Estuaries. In *The Seas*, edited by M. N. Hill, vol. 2, pp. 306-324. John Wiley and Sons, New York.
- CARPENTER, J. H., 1960. The Chesapeake Bay Institute study of the Baltimore Harbor. *Proc. 33rd Ann. Conf. Maryland-Delaware Water and Sewage Areas*, pp. 62-78.
- DORRESTEIN, R., 1960. A method of computing the spreading of matter in the water of an estuary. *Periodical of Radioactive Waste*, pp. 163-166. Intern. At. Energy Agency, Vienna.
- ELDER, J. W., 1959. The dispersion of marked fluid in turbulent shear flow. *J. Fluid Mech.*, 5:544-560.
- ELLISON, T. H., and J. S. TURNER, 1959. Turbulent entrainment in stratified flows. *J. Fluid Mech.*, 5:423-448.
- FARMER, H. G., and G. W. MORGAN, 1953. The Salt Wedge. *Proc. Third Conf. Coastal Eng.*, pp. 54-64.
- GRANT, H. L., R. W. STEWART, and A. MOIL,

- LIET, 1962. Turbulence spectra from a tidal channel. *J. Fluid Mech.*, 12:241-268.
- HACHEY, H. B., 1935. Tidal mixing in an estuary. *J. Biol. Board Can.*, 1:171-178.
- HARLEMAN, D. R. F., and A. T. IPPEN, 1960. The turbulent diffusion and convection of saline water in an idealized estuary. *I.A.S.H. Comm. of Surface Waters, Publ. 51*, pp. 362-378.
- HERLINVEAUX, R. H., and J. P. TULLY, 1961. Some oceanographic features of Juan de Fuca Strait. *J. Fisheries Res. Board Can.*, 18:1027-1071.
- HUGHES, P., 1958. Tidal mixing in the Narrows of the Mersey estuary. *Geophys. J., R. Astr. Soc.*, 1:271-283.
- INGLIS, SIR CLAUDE, and F. H. ALLEN, 1957. The regimen of the Thames Estuary. *Proc. Inst. Civil Engrs. (London)*, 7:827-868.
- JOSEPH, J., and H. SENDNFR, 1958. Über die horizontale Diffusion im Meer. *Deut. Hydrograph. Z.*, 11: 49-77.
- KENT, R. E., 1958. Turbulent diffusion in a sectionally homogeneous estuary. *Chesapeake Bay Inst. Tech. Rept. No. 16*.
- KENT, R. E., and D. W. PRITCHARD, 1959. A test of mixing length theories in a coastal plain estuary. *J. Marine Res.*, 18:62-72.
- KETCHUM, B. H., 1950. Hydrographic factors involved in dispersion of pollutants introduced into tidal streams. *J. Boston Soc. Civil Engrs.*, 37:296-314.
- KETCHUM, B. H., 1951. The exchange of fresh and salt waters in tidal estuaries. *J. Marine Res.*, 10:18-38.
- KETCHUM, B. H., 1953. Circulation in estuaries. *Proc. Third Conf. Coastal Eng.*, pp. 65-76.
- KETCHUM, B. H., and D. J. KEEN, 1953. The exchanges of fresh and salt waters in the Bay of Fundy and in Passamaquoddy Bay. *J. Fisheries Res. Board Can.*, 10:97-124.
- KETCHUM, B. H., A. C. REDFIELD, and J. C. AYERS, 1951. The Oceanography of the New York Bight. *Papers Phys. Oceanogr. Meteorol.*, 12(1):1-46.
- KEULEGAN, G. H., 1949. Interfacial instability and mixing in stratified flows. *J. Res. Natl. Bur. Std.*, 43: 487-500.
- OKUBO, A., 1962. A review of theoretical models for turbulent diffusion in the sea. *J. Oceanogr. Soc. Japan, 20th Anniv. Vol.*, pp. 286-320.
- PICKARD, G. L., 1955. British Columbia Inlets. *Trans. Am. Geophys. Un.*, 36:897-901.
- PICKARD, G. L., 1956. Surface and bottom currents in the Strait of Georgia. *J. Fisheries Res. Board Can.*, 13:581-590.
- PICKARD, G. L., and K. RODGERS, 1959. Current measurements in Knight Inlet, British Columbia. *J. Fisheries Res. Board Can.*, 16:635-684.
- PICKARD, G. L., and R. W. TRITES, 1957. Fresh water transport determinations from the heat budget with applications to British Columbia inlets. *J. Fisheries Res. Board Can.*, 14:605-616.
- PREDDY, W. S., 1954. The mixing and movement of water in the estuary of the Thames. *J. Marine Biol. Assoc. U. K.*, 33:645-662.
- PREDDY, W. S., and B. WEBBER, 1963. The calculation of pollution of the Thames estuary by a theory of quantized mixing. *Intern. J. Air Water Pollution*; Vol. 7:829-843.
- PRICE, W. A., and M. P. KENDRICK, 1963. Field and model investigation into the reasons for siltation in the Mersey estuary. *Proc. Inst. Civil Engrs.*, 24:473-518.
- PRITCHARD, D. W., 1952a. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11:106-123.
- PRITCHARD, D. W., 1952b. Estuarine Hydrography. *Advan. Geophys.*, 1:243-280.
- PRITCHARD, D. W., 1954a. A study of flushing in the Delaware model. *Chesapeake Bay Inst. Tech. Rept. No. 7*.
- PRITCHARD, D. W., 1954b. A study of the salt balance in a coastal plain estuary. *J. Marine Res.*, 13:133-144.
- PRITCHARD, D. W., 1955. Estuarine circulation patterns. *Am. Soc. Civil Eng., 31*. (Separate 717)
- PRITCHARD, D. W., 1956. The dynamic structure of a coastal plain estuary. *J. Marine Res.*, 15:33-42.
- PRITCHARD, D. W., 1960. The movement and mixing of contaminants in tidal estuaries. *Proc. First Conf. Waste Disposal in the Marine Environment (1959)*; pp. 512-525.
- PRITCHARD, D. W., and J. H. CARPENTER, 1960. Measurements of turbulent diffusion in estuarine and inshore waters. *Bull. Intern. Assoc. Sci. Hydrol.*, 20: 37-50.
- PRITCHARD, D. W., and R. E. KENT, 1956. A method for determining mean longitudinal velocities in a coastal plain estuary. *J. Marine Res.*, 15:81-91.
- RATTRAY, M., JR., and J. H. LINCOLN, 1955. Operating characteristics of an oceanographic model of Puget Sound. *Trans. Am. Geophys. Un.*, 36:251-261.
- RATTRAY, M., JR., and D. V. HANSEN, 1962. A similarity solution for circulation in an estuary. *J. Marine Res.*, 20:121-133.
- RILEY, G. A., 1952. Hydrography of the Long Island and Block Island Sounds. *Bull. Bing. Oceanogr. Coll.*, 13:5-39.
- SIMMONS, H. B., 1960. Application and limitations of estuary models in pollution analyses. *Proc. First Conf. Waste Disposal in the Marine Environment (1959)*; pp. 540-546.
- STEWART, R. W., 1957. A note on the dynamic balance in estuarine circulation (with comment by D. W. Pritchard). *J. Marine Res.*, 16:34-39.
- STOMMEL, H., 1949. Horizontal diffusion due to oceanic turbulence. *J. Marine Res.*, 8:199-225.
- STOMMEL, H., 1953a. The role of density currents in estuaries. *Proc. Minnesota Intern. Hydraulic Convention 1953*; pp. 305-312.
- STOMMEL, H., 1953b. Computation of pollution in a vertically mixed estuary. *Sewage and Ind. Wastes*, 25: 1065-1071.
- STOMMEL, H., and H. G. FARMER, 1952. On the nature of estuarine circulation, Parts I and III. *Woods Hole Oceanogr. Inst. Tech. Rept. Ref. 52-63 and 52-88*.
- STOMMEL, H., and H. G. FARMER, 1953. Control of salinity in an estuary by a transition. *J. Marine Res.*, 12:13-20.
- TAYLOR, SIR GEOFFREY, 1953. Dispersion of soluble matter in solvent flowing slowly through a tube. *Proc. Roy. Soc. A* 219:186-203.
- TAYLOR, SIR GEOFFREY, 1954. The dispersion of matter in turbulent flow through a pipe. *Proc. Roy. Soc. A*, 223:446-468.
- TRITES, R. W., and D. G. McGREGOR, 1962. Flow of water in the passages of Passamaquoddy Bay measured by the electromagnetic method. *J. Fisheries Res. Board Can.*, 19:895-919.
- TULLY, J. P., 1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. *Bull. Fisheries Res. Board Can.*, Vol. 83:1-169.
- TULLY, J. P., 1958. On structure, entrainment and transport in estuarine embayments. *J. Marine Res.*, 17:523-535.
- WESTBROOK, D. E., 1962. Tidal current survey—new field techniques. *Intern. Hydrogr. Rev.*, 39(2):77-90.
- WILLIAMS, J., 1960. A small portable unit for making in situ salinity and temperature measurements. *Proc. Instr. Soc. Am., Instrument-Automation Conf. and Exhibit*, New York, 1960. (Preprint 43)

Observations of Circulation in Coastal Plain Estuaries

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Coastal plain estuaries may be subdivided into four principal classes (Pritchard, 1955), differing one from the other in the character of the circulation pattern, in the intensity of vertical stratification, and in the extent of lateral homogeneity. These four classes actually represent distinct points in a continuous sequence of estuarine types.

First, I would like to describe, briefly, the estuarine sequence based on a synthesis of direct and indirect evidence about the character of estuarine circulation patterns. The description must be presented in a highly schematic manner, so that the real but vexing irregularities which tend to obscure the large-scale processes are ignored. During this quick tour along the estuarine sequence, I will offer no observational proof of the patterns to be described. After the schematic description, I will discuss in some detail certain results of direct and indirect observations of estuarine circulation.

THE HIGHLY STRATIFIED ESTUARY

THE FRICTIONLESS MODEL

Consider a schematic coastal plain estuary in the form of a long narrow coastal indentation with a river entering at its landward end and a free connection with the sea at its mouth.

Assume that there is no tidal motion and no significant mixing or friction. Undiluted sea water will extend up-estuary along the bottom to a point at which the river surface is approximately at sea level. The fresh river water will flow seaward on top of the salt water without any frictional drag at the interface between the fresh and salt water. Due to the Coriolis force, the fresh water in the estuary will tend to flow along the right shore, as seen by an observer in the northern hemisphere looking seaward. The interface between the fresh and salt water will be oriented horizontally in the longitudinal or flow direction, but will tilt down toward the right (again, looking seaward) when seen in a cross section perpendicular to the flow direction. The geostrophic flow of the fresh water determines the slope of the water surface.

In such a hypothetical case, under the simplified dynamic conditions specified, the estuarine circulation would simply consist of a seaward-moving freshwater flow equal in volume to the river discharge, superimposed upon a motionless lower saltwater layer, without any mixing.

In real estuaries, of course, mixing does take place,

and it is the differing degrees and causes of this mixing which create the various estuarine circulation patterns outlined below.

THE NON-TIDAL MODEL

The next hypothetical estuary has no tidal motion but is affected by frictional forces. Let us assume that the rate of river flow causes waves in the underlying salt water along the interface with the upper freshwater layer. These interfacial waves eventually become unstable and break, making some of the salt water transfer into the upper layer. This is essentially a one-way process, through which the salinity of the upper layer is increased progressively seaward. The volume transport seaward in the upper layer is increased by the amount of salt water which has been added. In order to maintain continuity of volume within the estuary, there must exist a slow compensating up-estuary flow in the lower seawater layer.

Entrainment of salt water into the upper, seaward-flowing, freshwater layer forces the upstream margin of the saltwater wedge to migrate seaward. This seaward shift is also partly a response to the altered distribution of force following transfer of parcels of salt water into the upper layer. In addition to the flux of volume into the freshwater layer, there is an upward flux of momentum which affects the upper layer as a force directed upstream. Under steady-state conditions this pressure force is exactly balanced by a downstream-directed counterforce set up by the redistribution of density near the interface. This is facilitated by a tilt of the interface and an increased seaward slope of the surface of the estuary. With increased river flow there is a greater frictional drag at the interface, which causes an increased tilt of the interface and the water surface, and a progressive seaward migration of the saltwater wedge. These phenomena have been empirically observed by Keulegan (1949) in experiments with stratified flows in flumes.

The up-estuary flow in the lower layer will be relatively slow, and we assume that the bottom friction will be negligible. Under these conditions there will exist only a very slight vertical gradient in the slopes of the pressure surfaces in the saltwater layer, and only a very slight density gradient vertically within the wedge.

In my original theoretical treatment of this type of estuarine system (Pritchard, 1955), I held that the horizontal and vertical advects of salt were the dominant processes in maintaining the salt balance.

In the present treatment I have emphasized the role of the flux of momentum and the resulting alterations in the density field. A steady state of both motion and salt requires a nice adjustment of momentum flux and salt flux.

The closest approach to the non-tidal model in nature is found where the influence of river flow is strongly dominant over tidal action. This occurs where the ratio of river flow to tidal flow is large. In such a situation the dominant salt flux is brought about by advection across the interface between the deeper salt water and the fresh surface layer. The mouth of the Mississippi River is an example of this simple salt wedge type of estuary.

THE MODERATELY STRATIFIED ESTUARY

Chesapeake Bay and its tributary estuaries in Maryland and Virginia represent moderately stratified estuaries; another example is the mouth of the Miramichi River, New Brunswick, Canada (Bousfield, 1955). Other estuaries which might be included are the estuarine portion of the Delaware River (but not the wider portion of Delaware Bay), the Savannah River Estuary in Georgia, and the harbor of Charleston, South Carolina.

In the moderately stratified estuary, the dominant mixing agent is turbulence caused by tidal action, rather than velocity shear at the interface between the salt water and overlying freshwater layer, as in the previous case.

The logical next step in the estuarine sequence, following the frictionless and the non-tidal models, is to introduce a tide of moderate amplitude, which will produce random water movements at all depths. Turbulent eddies transport fresh water downward and carry salt water upward, in contrast to the dominantly upward advection of salt across the interface which constitutes the vertical flux of salt in the non-tidal model. The result of this two-way mixing is that the salt content of both the upper and the lower layers increases toward the sea; at any given point the bottom layer is always higher in salt content than the top layer. The boundary between the seaward-flowing upper layer and the counter-flowing lower layer occurs with a mid-depth region of relatively rapid increase in salt content with depth, compared to the vertical gradient in either the upper or the lower layers. In this case, however, the sharp change in salinity which is characteristic of the salt wedge estuary is absent.

This type of mixing contributes a greater volume of salt water to the upper, seaward-flowing layer than in the salt wedge estuary. The rate of flow in the upper layer of the moderately stratified estuary is therefore much greater in volume than in the highly stratified estuary, necessitating a correspondingly larger compensating up-estuary flow in the lower layer.

The turbulent eddies produce a more extensive flux of momentum as well as salt. Eddy stresses are not

confined to the immediate vicinity of the interface between salt and fresh layers, but tend to extend from the surface to the bottom. If the estuary is to maintain a steady state over time, a more complicated distribution of pressure gradients must be postulated than was necessary for the salt wedge estuary. Specifically, pressure surfaces in the lower layer are no longer horizontal, but slope downward toward the head of the estuary in order to counterbalance the frictional effect of turbulence upon the compensating up-estuary flow in this layer. Conversely, in the upper layer, pressure surfaces will slope downward toward the mouth of the estuary. This configuration of pressure surfaces in the two layers is due to the mass distribution brought about by more vigorous mixing.

What is the ultimate physical mechanism which produces the typical circulation of a moderately stratified estuary? It has been attributed to the increased potential energy of the system which follows from increased exchange between the freshwater and saltwater layers. More accurately, tidal mixing produces horizontal density gradients of increased strength, which in turn produce horizontal pressure gradients of sufficient magnitude and extent to maintain the relatively higher velocities even in the face of increased eddy friction. Tidal mixing is responsible for both the increase in potential energy and the distribution of potential energy within the estuary.

Transient departures from the mean in response to ebb and flow of the tide are superimposed on the mean slopes of the pressure surfaces. Such variations have generally been assumed to be symmetrically distributed about the mean and to be suppressed in the averaging process. The time variation in inclination of the pressure surfaces has further been assumed to be independent of depth, reflecting only the variations in slope of the water surface. As a result of this assumption, workers have concentrated upon the vertical gradient of the pressure surfaces, as related to the dynamics of mean or net motion.

More critical attention needs to be directed toward the averaging process. The non-linear inertial terms in the equation of tidal motion involve products of velocities, and therefore do not average out over a tidal cycle. The effect of the non-linear term resulting from a variation in tidal excursion with distance along the estuary has been examined by the author (Pritchard, 1956). Stewart (1957) has pointed out that curvature in the tidal channel will produce a cross-channel inertial force which must be taken into account in the lateral equation of mean motion.

The role of the inertial forces may be considered as follows: If the effect of tidal oscillations upon the mean pressure distribution is not dependent on depth, it will be equally significant over the whole water column and detectable only by examination of the absolute slopes of the pressure surfaces. On the other hand, if there is considerable variation in the effect of tidal oscillation with depth, we may expect the mean effect of the non-linear terms to vary in a similar manner. It follows that the portion of the mean

pressure gradients required to balance the non-linear terms would also vary with depth. The salinity stratification within such an estuary would depend in part on the inertial forces associated with tidal motion, although the turbulent flux of momentum would probably always be the dominant agent because of the small absolute magnitude of the inertial effects.

Like the simpler salt wedge estuary, the partially mixed estuary shows the effect of Coriolis force operating laterally and normal to the direction of flow. A lateral asymmetry tends to develop, with the surface layer being thicker and fresher on the right side of the estuary as viewed by an observer looking toward the mouth. In at least two cases where this dynamic situation has been studied (Cameron, 1951; Pritchard, 1956) the Coriolis force was found to be balanced mainly by the lateral pressure force due to the lateral variations in mass.

The horizontal pressure gradients set up by the slope of the water surface and modified by the salinity distribution are balanced primarily by the frictional forces of tidally induced turbulence. It is desirable to obtain an estimate of the magnitude of the forces necessary to accelerate the seaward flow of surface water and decelerate the compensating headward flow of the deeper water. In the James River Estuary in Virginia (Pritchard, 1956), the field accelerations were found to be rather small in relation to friction. The field acceleration would be expected to increase as the salinity of the surface layer approaches that of sea water. In certain estuaries (Stommel and Farmer, 1953) the relation between inertia and the salinity stratification sets an upper limit on the amount of mixed water which flows seaward past a hydraulic control set up by appropriate variations of width and depth. St. John Harbor, New Brunswick, Canada, is an example of this estuarine situation, according to Stommel and Farmer.

In summary, the characteristic salinity distribution in moderately stratified estuaries may be said to be kinematically governed by both horizontal and lateral advection of salt, as well as by non-advection vertical flux.

THE VERTICALLY HOMOGENEOUS ESTUARY

When tidal mixing is sufficiently vigorous, the vertical salinity stratification breaks down, and the estuary approaches true vertical homogeneity. Under these conditions the dynamic and kinematic processes which govern circulation will be associated only with horizontal variations in salinity. The type of circulation which exists in a vertically homogeneous system depends upon the amount of lateral homogeneity. It should be borne in mind that the vertically homogeneous estuary may not exist except as a theoretical end member in the estuarine sequence. Present methods of observation may not be adequate in space and time to detect the very slight departure from true vertical homogeneity which may in fact be present in an apparently homogeneous system.

ESTUARIES SHOWING LATERAL VARIATION IN SALINITY

An estuary which is vertically homogeneous may show lateral as well as longitudinal variations in salinity. Owing to the Coriolis force, the water on the right of an observer looking seaward may be lower in salinity than the water to his left. A cyclonic circulation pattern is developed, with fresher, seaward-flowing water concentrated to the right of center and a compensating up-estuary flow of higher-salinity water to the left of center.

The processes which ultimately control salt distribution in such an estuary are imperfectly understood. In the absence of a vertical salinity gradient, we tend to think not of vertical mixing processes, but of lateral and longitudinal transfer of salt (by advection or non-advection processes) as the controlling factors. However, vertical mixing must be invoked to account for the vertical homogeneity. The difficulty may lie in an inadequate mathematical or conceptual representation of the process of non-advection flux. If we had some better means of observing and measuring short-term vertical variations in salinity, we could say much more about the processes of vertical mixing.

In contrast to the apparent lack of a vertical gradient in salinity, the vertically homogeneous estuary shows considerable variation in the gradient of the horizontal pressure field with depth. Vertical velocity shears are present, and there are significant vertical fluxes of momentum. The flux of momentum is balanced by an appropriate pressure-gradient field initiated and controlled by the slope of the water surface and the lateral salinity gradient. It is evident that the salinity distribution is closely linked to the eddy frictional forces set up by the vigorous tidal mixing.

THE LATERALLY HOMOGENEOUS ESTUARY

Certain vertically homogeneous estuaries, particularly those which are relatively deep and narrow, do not exhibit the cyclonic circulation pattern just described. The direction of water movement is symmetrical about the longitudinal axis. Fluctuations in velocity are related to the tides, and the net flow averaged over several tidal cycles is directed seaward at all depths. There is a tendency for salt to be driven out of the estuary by the action of this advective process. There must be a compensating non-advection longitudinal flux of salt directed toward the head of the estuary.

As with the laterally inhomogeneous estuary, this class of vertically and laterally homogeneous estuary exhibits significant variations in the horizontal pressure gradient with depth. The longitudinal salinity gradient produces a decrease in the seaward slope of the pressure surfaces with increasing depth. There must exist some counterforce which varies with depth in a like manner. In the present state of knowledge we are unable to identify this force, except to suggest that it may somehow be related to a vertical gradient in the asymmetry of tidal ebb and flow. More precise

and detailed measurements of tidal velocity, and further theoretical investigation of the non-linear terms in the tidal equation are necessary in order to improve our understanding of this feature of estuarine dynamics.

As mentioned at the beginning of this section, true vertically homogeneous estuaries may not exist in nature, and our task would be easier if they did not, for only a small, perhaps undetectable, vertical stratification would be necessary in order to remove certain of the anomalies which have been discussed.

FACTORS CONTROLLING POSITION IN THE ESTUARINE SEQUENCE

The physical parameters which appear to be most important in controlling the degree of vertical stratification, and hence the position of the estuary in the sequence of estuarine types, are the volume and rate of freshwater inflow, the strength of the tidal current, the width of the estuary, and the depth of the estuary. An estuary is moved along the sequence from the highly stratified salt wedge estuary, through the partially mixed estuary, to the vertically homogeneous estuary, with decreasing river flow and decreasing depth, and with increasing tidal current and increasing width.

The combination of parameters which has a dominant effect on the degree of stratification and on the character of the circulation pattern is the ratio of the volume of water flowing up the estuary through a given section during the flood tide to the volume of fresh water flowing into the estuary above the section during a complete tidal cycle. When this ratio is small (on the order of unity), the stratification and circulation approximate those of a salt wedge estuary. When the ratio becomes larger (on the order of from 10 to 100), the waterway has the characteristics described for a partially mixed estuary. Vertically homogeneous estuaries occur only when the ratio is of the order of 1,000.

OBSERVATIONS OF ESTUARINE CIRCULATION

As stated previously, evidence for these various classes of coastal plain estuaries comes from direct observations of the distribution of chemical and physical properties and from direct measurements and indirect inferences with respect to the circulation. In the case of the salt wedge estuary, observational evidence is quite conclusive. I have no doubt that the circulation pattern as described exists in such estuaries as the mouth of the Mississippi. Partially mixed estuaries are by far the most common, and here also direct observation of currents supports the circulation pattern described above. To my knowledge, no adequate set of long-term current measurements has directly established the existence of the non-tidal flow regime inferred for the vertically or sectionally homogeneous estuary.

I believe it is quite possible that no true vertically homogeneous or sectionally homogeneous estuaries exist. Only very small or even intermittent vertical

gradients need occur to provide for a significant vertical shear in the net non-tidal velocity field. This possibility is supported by measurements made in the Mersey Estuary by Bowden (1960). In the section of this waterway designated as the Narrows, previous investigators had considered the estuary as essentially vertically homogeneous. Bowden found that only a very small vertical salinity gradient existed at maximum flood, but that more significant gradients occurred at other times. The average difference in salinity over a tidal cycle between the surface and bottom in 20 m depth was about 1 %. Bowden made hourly current measurements for two separate 50-hour periods. In both cases he found that the net non-tidal velocity showed a down-estuary movement in the upper half of the water column and an up-estuary movement in the lower half of the water column. The vertical variation in net non-tidal velocity was remarkably similar to that observed in the James River (Pritchard, 1956), where the mean vertical variation in salinity was about 3 % in only 7.5 m.

Several other investigators have reported direct observations of the two-layered circulation pattern in partially mixed estuaries. Thus, Stewart (1958) computed the net non-tidal flow pattern through several sections in New York Harbor based on Coast and Geodetic Survey current observations. Simmons (1955) has summarized the findings of the U. S. Army Corps of Engineers for several estuaries, both from direct field measurements and from large-scale hydraulic model studies.

I believe about the most thoroughly analyzed set of observations from a partially mixed estuary are those made in the James River Estuary in the summer of 1950. Observations were made at three sections in the estuary, for three periods of time, each of which was from 4 to 11 days. The sections were located at approximately 20 km above the mouth of the estuary, where the mean salinity was about 17.0 %; at approximately 31 km above the mouth, where the mean salinity was about 12.5 %; and at approximately 44 km above the mouth, where the mean salinity was about 5.0 %. I will present results only for the middle section, and concentrate primarily on only one of the three periods of observation. The major features were similar, however, at all three sections for all three periods.

Figure 1 shows the general character of the salinity distribution at the surface in the area of the James studied. Note that in addition to the increase in salinity in a seaward direction, there is a lateral variation, with lower-salinity water on the right side of the estuary, looking downstream. The horizontal pattern remains similar at sub-surface depths, although, of course, the salinity increases with depth at any one point. The vertical variation at Station J-17 is shown in Figure 2 by the mean salinity profiles for the three periods of study. Note the surface layer of weak vertical gradient, an intermediate layer in which the rate of change of salinity with depth reaches a maximum,

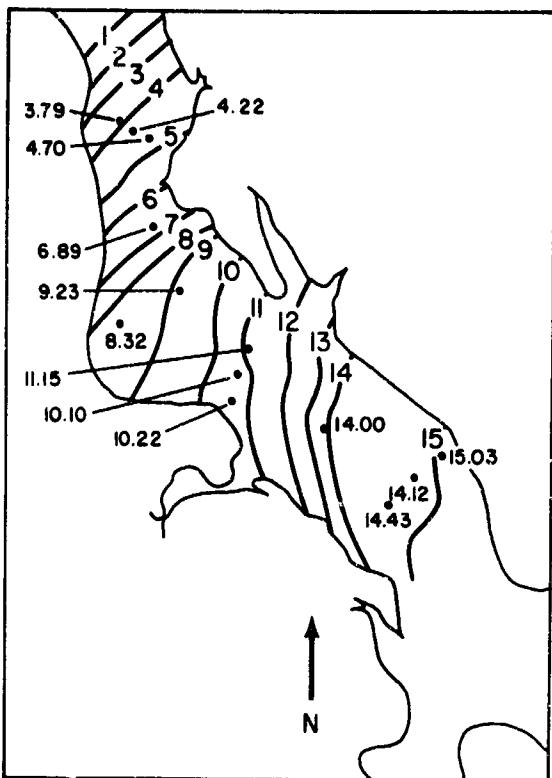


Fig. 1. Salinity distribution (in ‰) at the surface in a portion of the James River Estuary.

and a deeper layer having less rapid changes of salinity with depth.

Figure 3 gives the vertical profiles of the mean ebb currents and the mean flood currents for the three periods of study at Station J-17. The ebb flow is a maximum at the surface and decreases with depth. The current velocity during the flood period is a minimum at the surface, and increases with depth until near the bottom, where friction apparently has some influence.

The net non-tidal velocity is plotted as a function of depth in Figure 4. Positive values indicate down-estuary flow, and negative values, up-estuary flow. The vertical profiles of net non-tidal velocity obtained by Bowden in the Mersey are remarkably similar to those shown in Figure 4.

Note that the mean strength of the ebb and flood currents is about 0.35 m/sec. The vertical mean of the net non-tidal velocity directed down-estuary in the surface layer is 0.066 m/sec, or about 19 percent of the average tidal currents. The net up-estuary velocity in the lower half of the water column has a vertical mean value of 0.070 m/sec. This is about 20 percent of the average tidal velocity. The net non-tidal velocities are, in turn, much larger than the mean sectional velocity required to transport the volume inflow of river water seaward, which was computed to be 0.0073 m/sec, or 11 percent of the net non-tidal surface layer velocity.

The corresponding values observed by Bowden in the Mersey were: mean strength of ebb and flood currents, 0.71 m/sec; net non-tidal velocity in the surface layer, about 0.06 m/sec, or 8.5 percent of the average tidal current; and non-tidal current in the bottom layer, about 0.08 m/sec, or 11 percent of the average tidal current. The mean sectional velocity required to transport the volume inflow of the river seaward was about 0.002 m/sec for one period and only about 0.0009 m/sec for the other period of observation. These average only 2.5 percent of the surface layer non-tidal velocity.

Since current observations were made at three sections, it is possible, through a numerical, stepwise integration of the equation of continuity, to compute the average vertical velocity as a function of depth. A plot of the vertical velocity at Station J-17 is shown in Figure 5. In performing the integration, the kinematic boundary condition is applied at the surface (i.e., zero vertical velocity). If the bottom were perfectly horizontal, the vertical velocity should also be zero at the bottom. The slight departure of the computed value from zero at the bottom probably reflects the accumulated errors in the data, but it is interesting that the sign is correct considering the local bottom slope.

The vertical velocity is directed upward at all depths, except very close to the bottom as noted above, and has a maximum value of about 1×10^{-5} m/sec at mid-depth. While this is a very small number, it

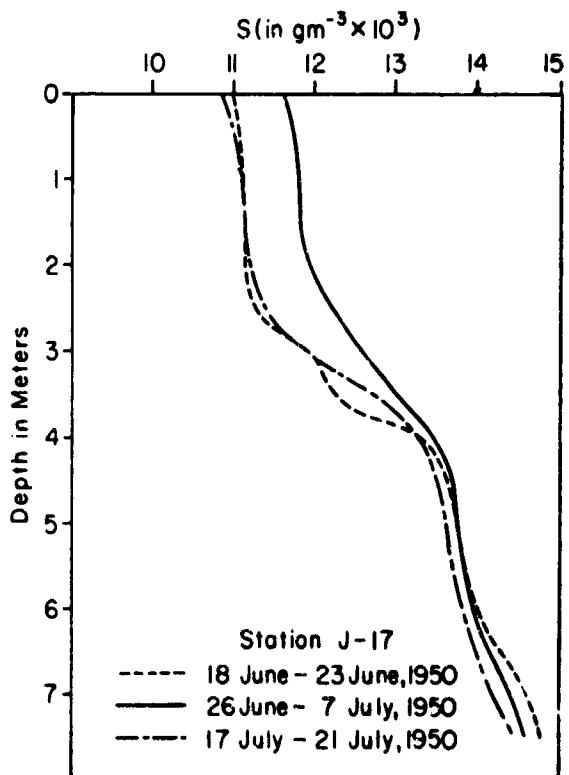


Fig. 2. Mean vertical salinity profile at Station J-17.

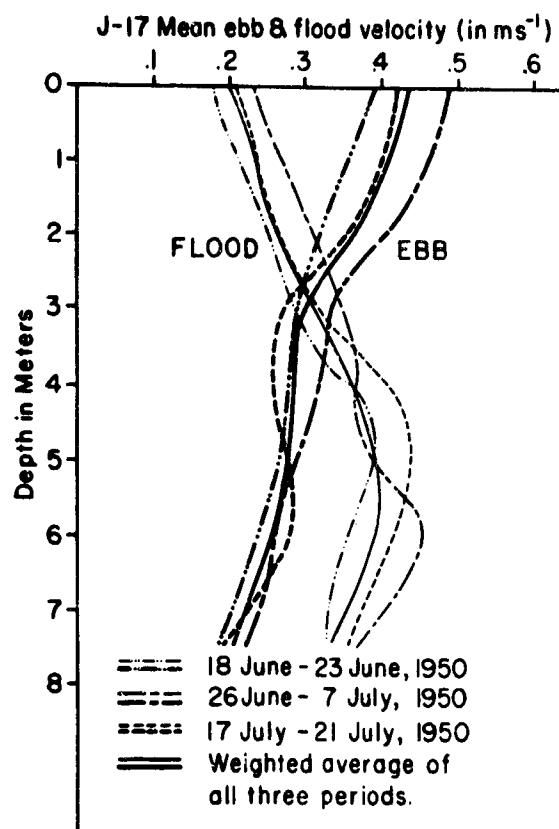


Fig. 3. Vertical profile of mean ebb and flood currents at Station J-17.

should be noted that this provides a volume rate of flow from the lower layers, which are moving up the estuary, into the upper layers, which are moving seaward, equal to the total inflow from the river in each 4 km of length of the estuary.

These data were also used to determine indirectly the longitudinal and vertical eddy flux terms from the salinity balance equation, and to estimate the magnitude of the various terms in the dynamic equations. Neglecting the lateral advective and non-advective terms, the salt balance equation can be written

$$\begin{aligned}\frac{\partial s}{\partial t} = & - [\partial(wu_1s)/\partial x_1] - [\partial(wu_3s)/\partial x_3] \\ & + [(1/w)(\partial/\partial x)] \{w \langle u_1's' \rangle\} \\ & + [(1/w)(\partial/\partial x_3)] \{w \langle u_3's' \rangle\},\end{aligned}$$

where:

- s = tidal mean salinity at x_1, x_3
- u_1 = longitudinal component of the tidal mean velocity
- u_3 = vertical component of the tidal mean velocity
- w = width of the estuary at the section x_1 , and depth x_3
- u_1', u_3' = turbulent velocity deviations
- s' = turbulent salinity deviation
- $\langle \rangle$ = time mean.

If this equation is integrated from the surface to

the bottom, the vertical terms drop out, and the vertical mean value of the horizontal eddy flux term, $\langle u_1's' \rangle$, can be computed from the observations of the mean salinity related to depth and the mean longitudinal velocity related to depth. Such a computation shows that the horizontal eddy diffusion is small compared to the advective flux of salt due to the net non-tidal horizontal flow.

Using the condition that there can be no flux of salt through the bottom, the salt balance equation can be numerically integrated stepwise, and thus values of the vertical eddy flux of salt can be computed as a function of depth. Figure 6 shows the results of such a determination for Station J-17, for the observational period 18-23 June. Computations for the other two sections, and for all three periods of observation, gave similar results.

These determinations showed that the salt balance is dominated by the horizontal advective term and the vertical eddy flux term, except near mid-depth where the vertical advective term becomes important.

Classically, the eddy flux terms have been assumed to be equal to the product of an eddy diffusivity times the mean salinity gradient. Thus

$$\langle u_3's' \rangle = - K_3 \frac{\partial s}{\partial x_3}.$$

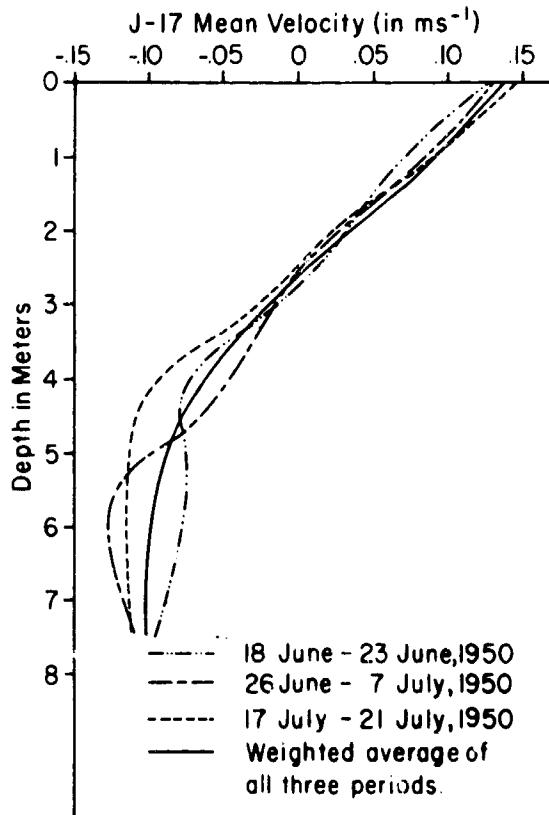


Fig. 4. Vertical profile of net non-tidal velocity at Station J-17. Net flow is seaward in the upper layer (positive values) and up-estuary in the lower layer (negative values).

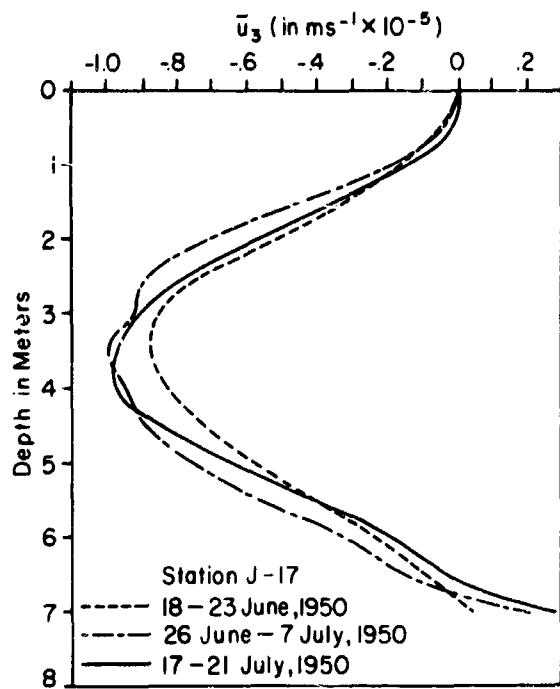


Fig. 5. Average vertical velocity (\bar{u}_3) as a function of depth at Station J-17.

Using this relationship, the vertical eddy diffusivity can be computed. Figure 7 gives K_3 related to depth. The minimum in this curve occurring at mid-depth is associated with the high vertical stability in the halocline.

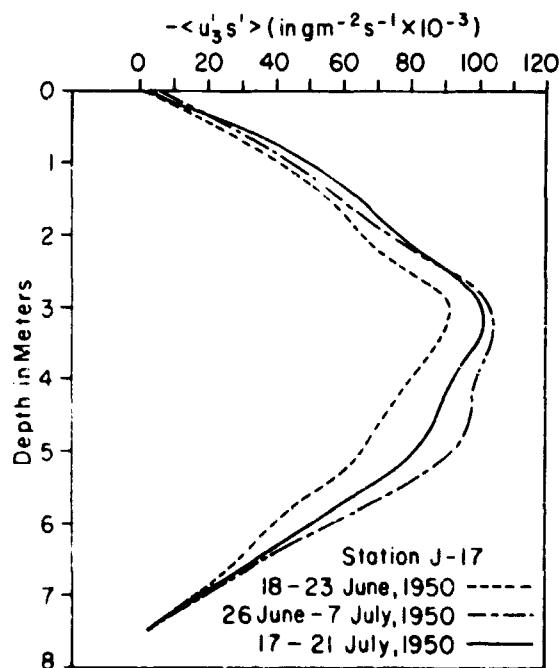


Fig. 6. Vertical eddy flux of salt ($w' s'$) as a function of depth at Station J-17.

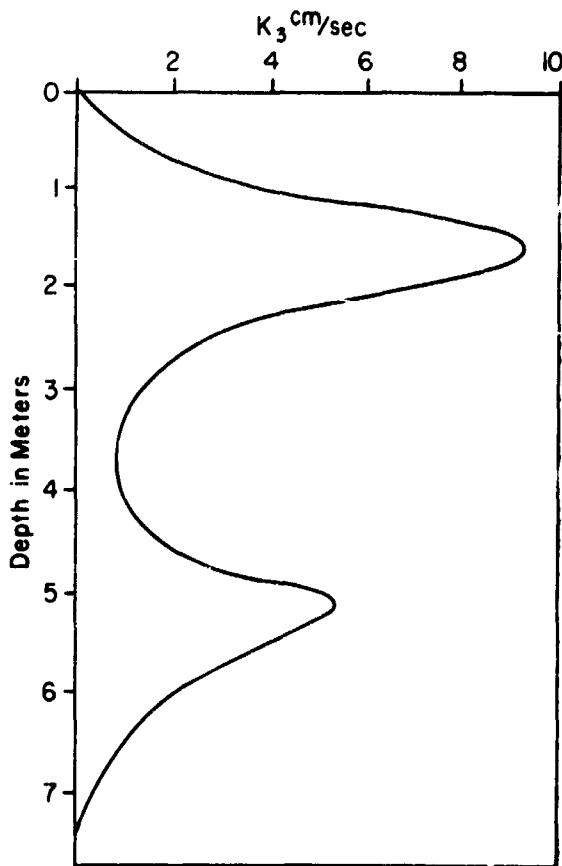


Fig. 7. Vertical eddy diffusivity (K_3) as a function of depth at Station J-17.

The appropriate time mean longitudinal equation of motion, for a point along the central axis of the estuary, can be written

$$\begin{aligned} \partial u_1 / \partial t + u_1 (\partial u_1 / \partial x_1) + u_3 (\partial u_1 / \partial x_3) \\ + (\partial / \partial x_1) \langle U_1 U_1 \rangle + (\partial / \partial x_3) \langle U_1 U_3 \rangle \\ = - \langle a (\partial p / \partial x_1) \rangle - (\partial / \partial x_3) \langle u'_1 u'_3 \rangle. \end{aligned}$$

and the corresponding lateral equation is

$$0 = - \langle a (\partial p / \partial x_3) \rangle - f u_1 - (\partial / \partial x_3) \langle u'_2 u'_3 \rangle.$$

where here the instantaneous velocity was assumed to be composed of a tidal mean term (u_1, u_3); a harmonic term of tidal period (U_1, U_3); and a turbulent deviation term (u'_1, u'_2, u'_3). The terms $\langle a (\partial p / \partial x_1) \rangle$ and $\langle a (\partial p / \partial x_3) \rangle$ represent the tidal mean pressure forces, and f is the Coriolis parameter.

Except for an undetermined constant representing the actual slope of the water surface, the terms $\langle a (\partial p / \partial x_1) \rangle$ and $\langle a (\partial p / \partial x_3) \rangle$ can be determined from observations of temperature and salinity, using the hydrostatic equation. Then, using the equation of continuity, together with reasonable values of the boundary stress, the vertically integrated equations allow the determination of the constant term representing the surface slope. Stepwise vertical integra-

tion then gives the values of the eddy flux of momentum, $\langle u_1' u_3' \rangle$ and $\langle u_2' u_3' \rangle$.

These computations show that, in the longitudinal equation, the important terms balancing the pressure force are the vertical eddy friction term and the term involving the longitudinal change in tidal current amplitude. In the lateral equation, the pressure term was very nearly balanced by the Coriolis term. That is, even in the estuary there is very nearly geostrophic balance if only the component of the pressure force perpendicular to the horizontal velocity is considered.

The vertical variation in the slope of the pressure surfaces is also determined by the procedure outlined above. The water surface slopes down toward the ocean and also from the right side of the estuary toward the left, looking down the estuary. Below the water surface the pressure surfaces decrease in slope, until at about mid-depth a level pressure surface occurs. The data were not adequate to determine whether the same pressure surface is level both longitudinally and laterally. Below mid-depth the pressure surfaces slope downward from the ocean toward the river and from the left side of the estuary to the right, looking seaward.

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LITERATURE CITED

- BOUSFIELD, E. L., 1955. Some physical features of the Miramichi estuary. *J. Fisheries Res. Board Can.*, 12:342-361.
BOWDEN, K. F., 1960. Circulation and mixing in the Mersey estuary. *Intern. Assoc. Sci. Hydrol. Publ.*, 51:352-360.
CAMERON, W. M., 1951. On the transverse forces in a British Columbia inlet. *Trans. Roy. Soc. Can.*, 45: 108, Ser. 3, Sect. 5.
KEULEGAN, G. H., 1949. Interfacial instability and mixing in stratified flows. *J. Res. Natl. Bur. Std.*, 43: 487-500.
PRITCHARD, D. W., 1955. Estuarine circulation patterns. *Proc. Am. Soc. Civil Engrs.*, 81:717/1-717/11.
PRITCHARD, D. W., 1956. The dynamic structure of a coastal plain estuary. *J. Marine Res.*, 15:33-42.
SIMMONS, H. B., 1955. Some effects of upland discharge on estuarine hydraulics. *Proc. Am. Soc. Civil Engrs.*, 81:792/1-792/20.
STEWART, H. B., JR., 1958. Upstream bottom currents in New York Harbor. *Science*, 127:1113-1115.
STEWART, R. W., 1957. A note on the dynamic balance for estuarine circulation. *J. Marine Res.*, 16:34-39.
STOMMEL, H., and H. G. FARMER, 1953. Control of salinity in an estuary by a transition. *J. Marine Res.*, 12:13-20.

Salt Balance and Circulation in Partially Mixed Estuaries

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An intrinsic feature of a coastal plain estuary is a supply of fresh water which exceeds loss by evaporation. Accordingly, the most basic contributions to the net circulation in these estuaries are the net seaward flow required for disposal of the fresh water, and the gravitational convection due to the density difference between fresh water and sea water. The first of these, which will be called the river discharge mode, is necessarily present in conventional estuaries. The gravitational convection mode, characterized by a landward flow near the bottom of the estuary, is a result of dynamic interactions between the salinity and current distributions and is particularly important in estuarine circulation studies.

There have been many qualitative discussions of the possible relations between the distributions of salinity and mean velocity, implying that gravitational convection is revealed by the vertical salinity gradient. The argument that a sectionally homogeneous salinity distribution implies a unidirectional mean velocity in an estuary has sometimes been offered in support of one-dimensional theories for calculation of dispersal of substances introduced into estuaries. On the other hand, it has not yet been unequivocally shown that sectionally homogeneous estuaries with significant freshwater discharge even exist.

This paper presents some results of theoretical studies undertaken to improve understanding of the relation between circulation and salinity distribution in estuaries with slight to moderate salinity stratification.

KINEMATIC RELATIONS

Consider a tidal river channel with freshwater discharge R_s and width b . Salinity is nearly constant in the ocean and approaches zero at some distance upstream. The extent of salinity intrusion is frequently controlled by dynamic rather than by purely geometric considerations and its determination is one of the goals of theoretical analysis. The Coriolis effect has been shown to lead to lateral variations of salinity and current, but this is a secondary effect of no great importance if the estuary is narrow.

Assuming that the estuary is laterally homogeneous, cross-estuary integral forms of the equations for mass and salt continuity may be derived as shown by Pritchard (1958). If conditions are stationary when

averaged over one or more tidal cycles, these equations are

$$\frac{\partial}{\partial x} (bw) + \frac{\partial}{\partial z} (bw) = 0, \quad (1)$$

and

$$b \left(u \frac{\partial S}{\partial x} + w \frac{\partial S}{\partial z} \right) = \frac{\partial}{\partial x} \left(b K_x \frac{\partial S}{\partial x} \right) + \frac{\partial}{\partial z} \left(b K_z \frac{\partial S}{\partial z} \right), \quad (2)$$

where S is the mean salinity, x and z are horizontal and vertical coordinates, positive seaward and vertically downward respectively, u and w are the components of the mean velocity, and K_x and K_z are the components of eddy diffusivity.

An important difference between moderately stratified estuaries and salt wedge or fjord estuaries is that, in the former, tidal currents are sufficient to cause turbulent mixing of fresh water and sea water over the full depth of the estuary and inhibit large variations in stability. It is assumed, therefore, that the eddy coefficients are determined primarily by tidal currents and river discharge but are independent of the details of the mean circulation and salinity distribution.

A frequent approach in estuarine work has been further simplification of equation (2) by assuming such vigorous tidal mixing that the estuary is vertically as well as laterally homogeneous. By integration over the section, one then obtains the one-dimensional relation

$$R_s \frac{dS}{dx} = \frac{d}{dx} \left(bh K_x \frac{dS}{dx} \right), \quad (3)$$

where h is the depth of the estuary.

A single integration of equation (3) gives, for R_s = a constant,

$$R_s S = bh K_x \frac{dS}{dx}, \quad (4)$$

which is the basis for the semi-empirical technique proposed by Stommel (1953) for determination of effective values of K_x from the observed distribution of salinity. When equation (4) is applied to estuaries which are not sectionally homogeneous, the meaning of K_x may be altered. In addition to upstream salt flux by fluctuations of salinity and current of tidal period or less, it must also include the flux due to vertical variation in mean velocity, which is advective rather than diffusive in character. This application of equation (4) has nonetheless found considerable practical application.

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A further integration of equation (4) yields

$$S = S_0 \exp \int_{x_0}^x \frac{R_0}{bK_s} dx, \quad (5)$$

where S_0 is the salinity at $x = x_0$. Expressions equivalent to equation (5) have been used by Arons and Stommel (1951), and by Ippen and Harleman (1961), in attempts to relate the diffusivity to tidal parameters. Hughes (1958) employed equation (4) to estimate the diffusivity from salinity data for the Narrows of the Mersey which has but slight salinity stratification. He found that the diffusivity was not determined uniquely by the tides, but varied markedly with the river discharge as well. This observation, among others, suggests that propositions based upon equation (5) are not likely to be very successful in moderately stratified estuaries. The one-dimensional theory, of course, cannot be applied in problems where vertical variations are important and it is of limited use in explaining phenomena related to these variations.

DYNAMIC RELATIONS

A more detailed treatment of the problem requires that the vertical distribution of velocity and salinity be taken into consideration. The velocity distribution is usually unknown and is determined in part by the salinity distribution. It must be obtained from appropriate dynamic equations.

Pritchard's (1956) study of the James River indicates that, except for nonlinear tidal accelerations which influence the surface slope but not the mean velocity, the dynamic balance in coastal plain estuaries is adequately expressed by

$$\frac{\partial p}{\partial x} = \frac{\partial r}{\partial x} = \frac{\partial}{\partial x} \left(\rho A \frac{\partial u}{\partial x} \right), \quad (6)$$

and

$$\frac{\partial p}{\partial z} = \rho g, \quad (7)$$

where p is the pressure, ρ the water density, and g the gravitational acceleration. The eddy stress, r , is represented in terms of an eddy viscosity, A , which, like the eddy diffusivity, is assumed independent of the details of the mean flow.

Eliminating the pressure between equations (6) and (7) and using the Boussinesq approximation, yield a vorticity equation for the mean flow,

$$\frac{\partial^2}{\partial z^2} \left(A \frac{\partial u}{\partial z} \right) = \frac{r}{\rho} \frac{\partial p}{\partial z}. \quad (8)$$

The relation between salinity and density of estuarine water may be taken simply as

$$\rho = \rho_0 (1 + \alpha S/S_1), \quad (9)$$

where ρ_0 is the density of fresh water and S_1 a convenient reference salinity.

Equation (1) permits definition of a transport stream function, ψ , so that

$$\frac{\partial \psi}{\partial z} = -Au, \quad \frac{\partial u}{\partial z} = -\frac{\partial \psi}{\partial x}.$$

In terms of ψ and $S/S_1 = \theta$, equations (2) and (8) become

$$\frac{\partial \psi}{\partial x} - \frac{\partial \theta}{\partial z} = \frac{\partial}{\partial x} \left(bK_s \frac{\partial \theta}{\partial x} \right) + \frac{\partial}{\partial z} \left(bK_s \frac{\partial \theta}{\partial z} \right) \quad (10)$$

and

$$\frac{\partial^2}{\partial z^2} \left[A \frac{\partial}{\partial z} \left(\frac{1}{b} \frac{\partial \psi}{\partial z} \right) \right] + \epsilon g \frac{\partial \theta}{\partial x} = 0 \quad (11)$$

Equations (10) and (11) are the governing equations for the circulation and salinity distribution in the estuary. They must be solved simultaneously, subject to appropriate boundary conditions. Solutions have been sought which satisfy, in addition to longitudinal conditions on the salinity distribution, conditions for conservation of salt and water at the boundaries, for no slip at the bottom, and for shearing stress to equal the wind stress at the surface, τ_w .

SOME SIMILARITY SOLUTIONS

Rattray and Hansen (1962) showed that similarity solutions were possible for a set of equations very similar to (10) and (11). Motivated by the results from Pritchard's (1954, 1956) studies of the James River Estuary, they included dynamic considerations equivalent to equation (11), but deleted vertical advection and horizontal diffusion from the salt flux equation. Whereas one-dimensional treatments suppress the gravitational convection mode of circulation, Rattray and Hansen had to suppress the freshwater discharge mode in order to complete their analysis. Their result applies to regions where the freshwater discharge mode is small in relation to the gravitational convection mode of circulation.

Similarity solutions have now been obtained which include both the freshwater discharge and gravitational convection modes of circulation. These solutions are possible when the horizontal variation of the eddy coefficients is appropriate in relation to that of the width, depth, and river discharge, any of which may vary as a power or an exponential function of the longitudinal coordinate. For concise presentation, only those examples will be considered in which the estuary is idealized and is assumed to have a rectangular cross section of constant width and depth b , and K_s , and eddy coefficients independent of depth.

SOLUTIONS WITH CONSTANT SALINITY GRADIENT

There are many estuaries in which both the horizontal salinity gradient and the top to bottom salinity difference are nearly constant over a considerable distance. Similarity solutions with this property are possible if A and K_s are constant and K_s has a seaward gradient equal to the river flow per unit cross section. A tendency for longitudinal mixing to be greater to seaward has been observed in flushing studies of the Thames by Preddy (1954), and of the Delaware River model by Kent (1958). This may be explained by longitudinal variation in either cross section or tidal current.

It is convenient to define dimensionless coordinates

for the vertical and horizontal directions by $\eta = (z/h_o)$, and $\bar{x} = (R_o/b_o) h_o K_{x0} x$, where K_{x0} is equivalent to the gross diffusion coefficient defined by equation (4) and can be inferred from the horizontal salinity gradient.

The solutions are

$$\theta = (\bar{x} - \bar{x}_0) + x(\eta), \quad (12)$$

and

$$\psi = R_o \phi(\eta), \quad (13)$$

where

$$x(\eta) = \frac{1}{M} \left(\eta - \frac{\eta^2}{2} - \int_0^\eta \phi d\eta \right). \quad (14)$$

and

$$\phi(\eta) = \frac{3}{4}(2 - 3\eta + \eta^2) - \frac{T}{4}(\eta - 2\eta^2 + \eta^3) - \frac{Ra}{48}(\eta - 3\eta^3 + 2\eta^4). \quad (15)$$

$M = [(K_{x0} K_z)/(R_o/b_o)^2]$ denotes the ratio of tidal mixing to river flow, and $T = (h_o^2 b_o \tau_w)/(\rho_o A R_o)$ is the normalized wind stress. $Ra = \epsilon g h_o^3 / A K_{x0}$ is an estuarine analog of the Rayleigh number of thermal convection theory.

Figures 1 and 2 show the horizontal and vertical aspects of the salinity distribution given by equations (12) and (14) with zero wind stress. Figure 3 shows the corresponding vertical variation of velocity which is independent of distance along the estuary. At zero Rayleigh number, the velocity has the parabolic profile characteristic of parallel flows with constant viscosity. Transition to two-layer flow occurs near a Rayleigh number of 30, and gravitational convection becomes well developed at large values of the Rayleigh number. For very large values of the Rayleigh number, these profiles are asymptotic to those obtained by Rattray and Hansen (1962).

Because the flow is normalized to the river discharge, the velocity profiles depend only upon the

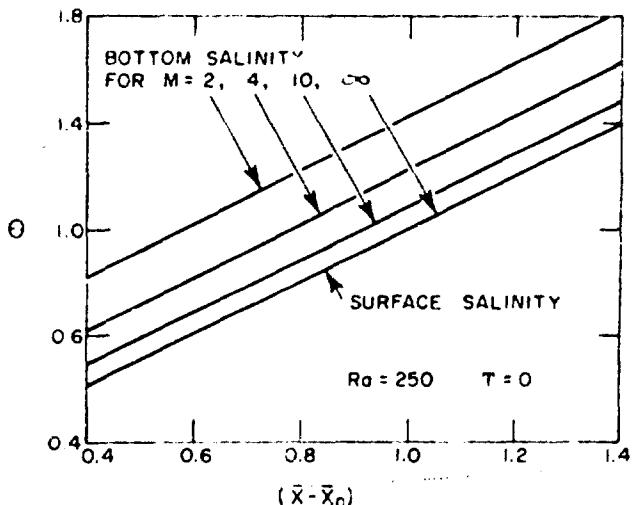


Fig. 1. Longitudinal distributions of salinity given by equation (12).

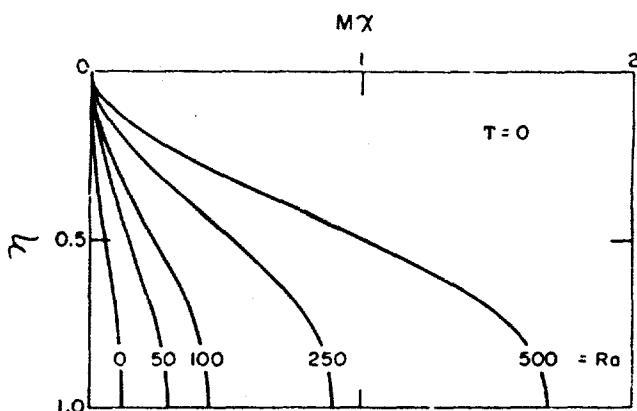


Fig. 2. Salinity profiles given by equation (14).

Rayleigh number. The vertical salinity gradient depends upon both the Rayleigh number and the tidal-mixing parameter. This indicates that sensibly homogeneous salinity over a section does not necessarily imply unidirectional mean flow except to the extent that $1/M$ correlates with Ra . Some correlation is to be expected, but depth is likely to have more influence upon Ra than upon M .

Figures 4 and 5 show the influence of surface wind stress on the vertical profiles of velocity and salinity. These variations are also very much like those shown by Rattray and Hansen (1962), including the possibility of three-layered flow for sufficiently great landward wind stress.

If the eddy coefficients could be estimated from river discharge and tidal parameters, equations (12) and (13) could be used to predict distributions of velocity and salinity. Since this is not yet possible, in order to compare theory and observations it is necessary to utilize data from regions where sufficiently detailed observations have been made to permit evaluation of the coefficients. The salinity distribution in the outer portion of the James River Estuary has the general aspect of Figure 1. Data from the Operation Oyster Spat, published by Pritchard and Kent (1953) and Pritchard (1956), are sufficient to permit estimation of all parameters required by the theory. Near station J-11, the values of Ra and M are estimated to be 850 and 15, respectively. Figures 6 and 7 show the vertical profiles of salinity and

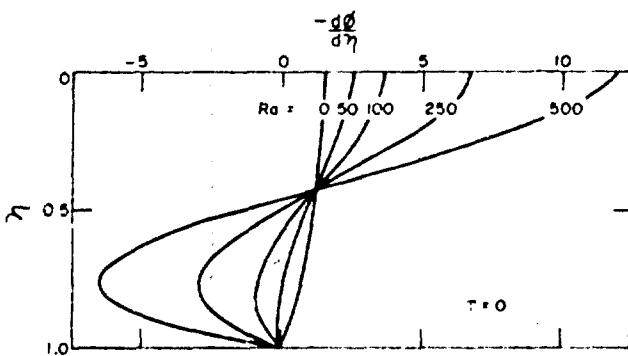


Fig. 3. Velocity profiles given by equation (13).

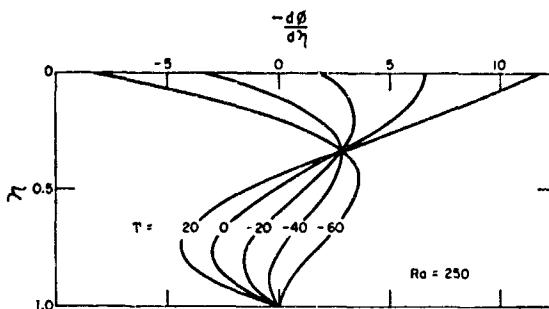


Fig. 4. Velocity profiles given by equation (13).

velocity calculated with these values, compared with those actually observed. The velocity profiles in particular do not agree well. Agreement can be improved somewhat by arbitrary adjustment of the Rayleigh number within the limits of its uncertainty, but an even greater improvement is effected by assumption of a small amount of surface stress. With surface stress equal to 0.1 dyne/cm², the agreement becomes reasonably good. A reliable estimate of the mean surface stress for the period of the current observations is not available. Winds of force 3 and 4, variable in direction, but with a slight preponderance from the west, were observed, so a small net stress is possible.

The observed velocities still lie almost uniformly to the left of the theoretical profile. Some discrepancy is no doubt due to the assumption of constant viscosity, but the considerable departure of the real channel shape from the rectangular cross section assumed in the model is probably of equal importance.

Assumption of surface stress as large as 0.1 dyne/cm² appears to impair agreement between the theoretical and the observed salinity profiles. However, the uncertainty in estimating the tidal-mixing parameter M is enough that the observed mean salinity is consistent with such a wind stress. The important point in wind stress is not so much what the actual stress may have been during observation, but rather recognition of the great influence of even fairly small wind stress on the distributions of mean velocity and salinity.

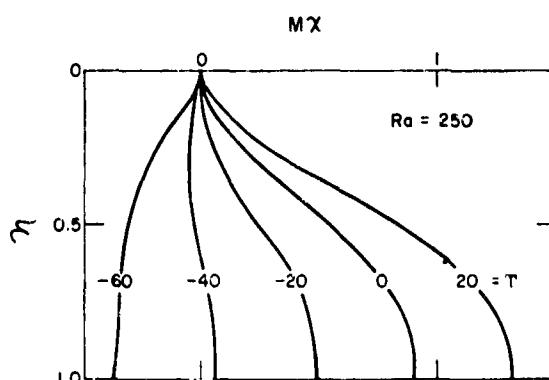


Fig. 5. Salinity profiles given by equation (14).

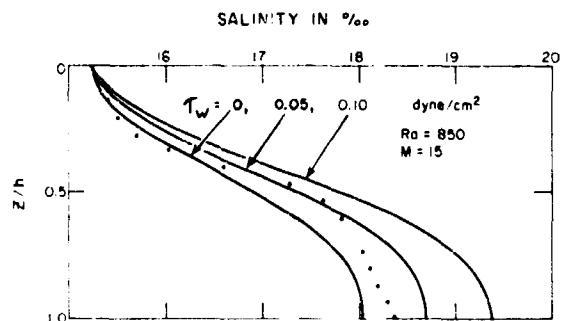


Fig. 6. Theoretical (—) and observed (•) mean salinity profiles at James River Station J-11.

The foregoing solutions are easily applied to obtain estimates of effective values of the eddy coefficients in estuarine regions which have a salinity distribution like that of the model. If surface stress is negligible, knowledge of the river flow and mean velocity at a depth other than near 40 percent of the total depth will suffice in principle to estimate the Rayleigh number. Observation of the horizontal and vertical salinity gradients will then permit estimation of M , and calculation of the eddy coefficients.

The salinity distribution in the Narrows of the Mersey Estuary also approximates that shown by Figure 1. Equations (12) and (13) have been used to determine effective values of A and K_z for the Narrows by using salinity and velocity data published by Bowden (1960). Figures 8 and 9 show the observed profiles of velocity and salinity and theoretical profiles calculated with $Ra = 2500$, and $M = 225$. These values of M and Ra imply values of A near 28 cm²/sec and K_z near 14 cm²/sec. With a more direct and detailed analysis of the observed data, Bowden (1960) obtained estimates of A and K_z at several depths. His estimates range from 9 to 62 cm²/sec for A and from 3 to 27 cm²/sec for K_z .

The horizontal diffusivity K_x may be estimated from the distribution of salinity and velocity by means of the condition for no net salt flux through any section,

$$\int_{-a}^{a} b \left(uS - K_x \frac{\partial S}{\partial x} \right) dz = 0. \quad (16)$$

Substitution of equations (12) and (13) into (16) yields, for zero wind stress,

$$\frac{K_x}{K_{xz}} = 1 + \frac{1}{1680M} \left\{ 66 + 64 \left(\frac{Ra}{48} \right) - \frac{152}{3} \left(\frac{Ra}{48} \right)^2 \right\}. \quad (17)$$

Applied to the Narrows of the Mersey, equation (17) indicates a value of K_x near 2×10^6 cm²/sec. Bowden (1960) found the value 3.5×10^6 cm²/sec for a comparable coefficient based on salt flux due to salinity-velocity fluctuations of tidal period. His results, however, indicated a net salt flux which he attributed to possible cross-channel variations or non-stationary conditions. When the Rayleigh number is large, equation (17) becomes very sensitive to errors in estimation of M and Ra , so that only very approximate values of K_x may be determined by it for estuaries.

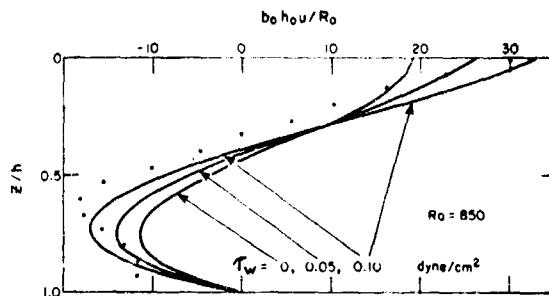


Fig. 7. Theoretical (—) and observed (•) mean velocity profiles at James River Station J-11.

aries with moderate salinity stratification and well-developed gravitational convection.

Equation (17) shows the influence of stratification upon the apparent horizontal diffusivity obtained by application of one-dimensional theory to estuaries which are not sectionally homogeneous. The ratio of the apparent diffusivity K_{x0} to the eddy diffusivity K_x tends to be large when Ra is large, because associated with the gravitational convection is a net upstream advection of salt which, in the one-dimensional theory, must be considered as diffusion. This effect will be more clearly shown in the next section.

These solutions also show the possibility of error in application of advection concepts when diffusion is important. If, for example, a regime described by equation (12) were to be interpreted in terms of a two-layered model at a section where the mean salinities are 27‰ and 30‰, application of advective budget concepts, like those given by Sverdrup *et al.* (1942, p. 148), for estimation of the inward transport V_i in the lower layer leads to the conclusion

$$V_i = \frac{S_o}{S_i - S_o} R_o = 9R_o.$$

The actual transport is given by equation (13) in terms of the Rayleigh number and wind stress and may be quite different. A Rayleigh number near 250 would yield $V_i = R_o$ with zero wind stress.

It is apparent that although the top-to-bottom salinity difference in the Narrows of the Mersey is only about one-third that in the James River Estuary, gravitational convection is nonetheless more developed

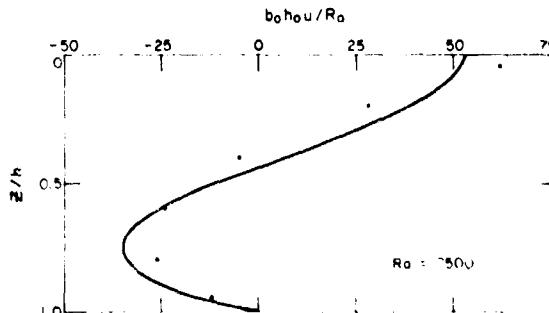


Fig. 8. Theoretical (—) and observed (•) mean velocity profiles for the Narrows of the Mersey.

in the Narrows. This reflects the influence of depth on the Rayleigh number, for the depth in the Narrows is about three times that in the James River.

SOLUTIONS WITH EXPONENTIAL SALINITY GRADIENT

In the inner part of many estuaries the vertical salinity difference is not constant but is more nearly proportional to the mean salinity over any section. Similarity solutions having this property are possible if K_x and K_z are constant and A varies as $A_0 e^{\lambda(\bar{x}-x_0)}$, where A_0 is a constant and \bar{x} is defined as before but in terms of the true horizontal diffusivity K_x rather than the gross diffusivity K_{x0} , and λ is the ratio K_x/K_{x0} . These solutions have the form

$$\theta = e^{\lambda(\bar{x}-x_0)}(1 + \chi(\eta)), \quad (18)$$

and

$$\psi = R_o \phi(\eta). \quad (19)$$

Assuming zero wind stress, the functions χ and ϕ are now given by

$$\chi(\eta) = \frac{\lambda}{M} \left(\eta - \lambda \frac{\eta^2}{2} - \int_0^\eta \phi d\eta \right), \quad (20)$$

and

$$\phi(\eta) = \frac{1}{2}(2 - 3\eta + \eta^2) - \lambda \frac{Ra}{48} (\eta - 3\eta^2 + 2\eta^3), \quad (21)$$

where M and Ra are now defined in terms of A_0 and K_x . The characteristic equation for λ is

$$1680M(\lambda - 1) = 234\lambda - (546 + Ra)\lambda^2 + \left\{ 280 - 28 \frac{Ra}{48} - \frac{152}{3} \left(\frac{Ra}{48} \right)^2 \right\} \lambda^3. \quad (22)$$

Figure 10 shows the nature of the horizontal salinity distribution defined by equation (18). The salinity distribution in the inner part of the James River Estuary is of this nature. Figure 11 shows a comparison of the observed horizontal salinity vari-

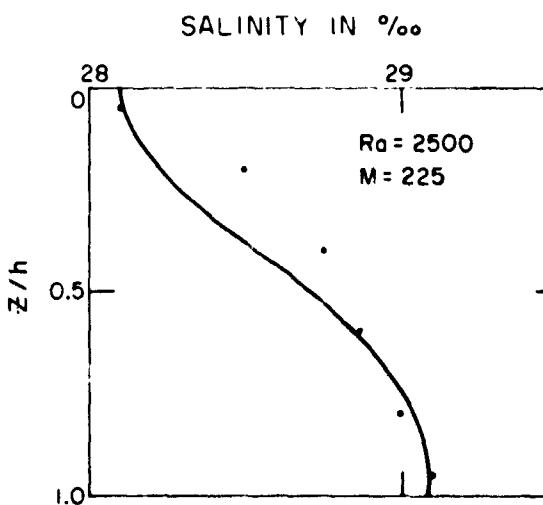


Fig. 9. Theoretical (—) and observed (•) mean salinity profiles for the Narrows of the Mersey.

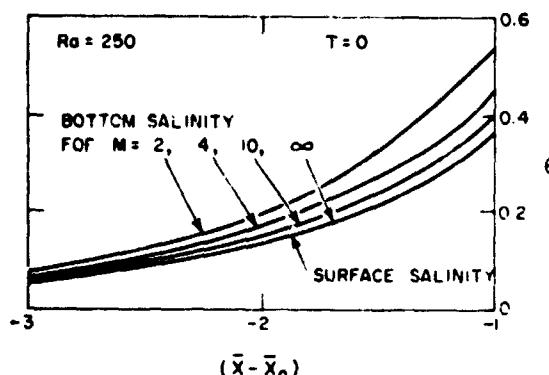


Fig. 10. Longitudinal distributions of salinity given by equation (18).

ation in this region in comparison with that calculated from equations (18), (20), (21), and (22) using parameters appropriate to Station J-24. Good agreement between theory and observations extends a surprising distance upstream from the reference station. Good agreement in the downstream direction is not to be expected because conditions in the outer part of the estuary are of the type described by equations (12) and (13).

The relative importance of upstream salt flux by horizontal diffusion and by gravitational convection may also be inferred from equation (22). For very large values of M at a fixed value of Ra , λ tends toward unity, while x tends to zero. The salinity distribution therefore approaches the one-dimensional result given by equation (5) with constant K_s , although gravitational convection may nonetheless occur. While a sectionally homogeneous salinity distribution does not necessarily imply unidirectional mean flow, it does imply that gravitational convection does not contribute to the longitudinal salt flux.

In the other limit, for very large Rayleigh numbers and a fixed value of M , λ becomes small. Under these conditions both the gravitational convection and the vertical salinity gradient are well developed. Upstream advection of salt by the gravitational convection mode may nearly balance the seaward advection by the freshwater discharge mode. Equation (22) gives a value near $1/3$ for λ in the inner part of the James River Estuary. This indicates that the horizontal salinity gradient is only $1/3$ that required to balance the seaward salt flux of the freshwater discharge mode by horizontal diffusion alone, and agrees with Pritchard's (1954) finding that the horizontal salt balance in this region is primarily advective.

A NON-SIMILARITY SOLUTION

Real estuaries generally will not rigorously satisfy the special conditions required for the existence of similarity solutions. This does not invalidate the results, but may limit the horizontal distance over which individual sets of solutions can be considered to apply.

Very similar results can be obtained without imposing the special conditions required for similarity.

To facilitate definition of dimensionless variables without losing sight of the principle involved, it can be assumed that A and K_s are constant, and K_s will be expressed as the product of a reference magnitude K_{s1} and an arbitrary variable $k(x)$. Then upon making the changes of variable,

$$\theta = \eta h_s, \quad x = \frac{h_s K_{s1}}{R_a} \xi, \quad \text{and} \quad \psi = R_a \phi(\xi, \eta), \quad (23)$$

equations (10) and (11) become

$$\partial_t \theta_0 - \phi_0 \partial_x = f k(\xi) \theta_0 + M \theta_m, \quad (23)$$

and

$$\phi_{mm} + Ra \phi_t = 0, \quad (24)$$

where subscripts indicate partial differentiation. M and Ra are defined as before but now in terms of K_{s1} rather than K_s .

M has been shown to be large in slightly stratified estuaries. Approximate solutions for this condition may therefore be generated by means of the series expansions.

$$\theta = \theta_0 + M^{-1} \theta_1 + \dots,$$

$$\phi = \phi_0 + M^{-1} \phi_1 + \dots,$$

Substituting the series into equations (23) and (24), collecting terms of equal degree in M , and integrating the resulting equations for θ_0 , θ_1 , and ϕ_0 by $d\eta$ two or four times yields (neglecting surface stress),

$$\theta = \theta_0(\xi) + \frac{1}{M} \frac{d\theta_0}{d\xi} \left(\eta - \frac{\eta^3}{2} - \int_0^\eta \phi_0 d\eta \right), \quad (25)$$

and

$$\phi_0 = \frac{1}{48} (2 - 3\eta + \eta^3) - \frac{Ra}{48} \frac{d\theta_0}{d\xi} (\eta - 3\eta^2 + 2\eta^4). \quad (26)$$

$\theta_0(\xi)$ is the solution of

$$\frac{d}{d\xi} \left(k(\xi) \frac{d\theta_0}{d\xi} \right) - \frac{d\theta_0}{d\xi} = 0, \quad (27)$$

a non-dimensional form of equation (3), which is easily solved when the variation of the eddy coefficient is specified.

At any section the vertical profiles of salinity and velocity given by equations (25) and (26) are like those given by the similarity solutions. Profiles obtained from similarity solutions can differ only by a factor at adjacent sections, but the x -dependence of equations (25) and (26) allows the possibility of a transition from one shape of profile to another between sections.

In the limit of very strong tidal mixing, equation (25), like (12) or (18), approaches the one-dimensional distribution of equation (5), but unlike (12) or (18) is not subject to the special conditions required for similarity.

The price paid for the greater generality of this result is that it is restricted in application to estuarine

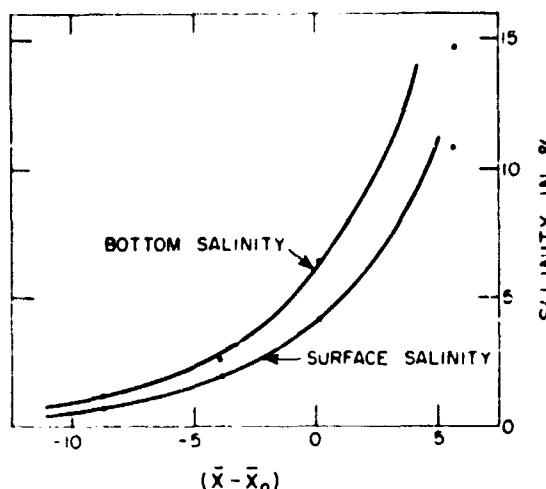


Fig. 11. Theoretical (—) and observed (•) salinity distributions near James River Station J-24.

regions with very slight salinity stratification or very poorly developed gravitational convection.

CONCLUSION

Theoretical results have been presented which show the relationship between the mean salinity distribution and the circulation in partially mixed estuaries and which define conditions under which different types of estuarine regime are likely to occur. These results concur in many respects with Pritchard's (1955) discussion of the relation between the nature of the salinity distribution and the external parameters: river discharge, tidal mixing, width, and depth.

It has been shown that the velocity structure in estuaries cannot be inferred with confidence from the salinity structure alone. Although gravitational convection tends to increase stratification, a sectionally homogeneous salinity distribution is not sufficient evidence for unidirectional mean flow. The nature of the velocity profile depends upon an estuarine counterpart of the Rayleigh number. Relatively deep estuaries, in particular, are likely to develop convection even in the presence of very strong tidal mixing. A sectionally homogeneous salinity distribution implies that the upstream salt flux is primarily caused by horizontal diffusion, but the same statement does not necessarily apply for concentrations of other materials, which, for a variety of reasons, may have vertical distributions different from that of salinity.

Observation of the mean wind stress and the mean

velocity at a single depth will suffice, at least in principle, to determine the Rayleigh number for an estuary if the river discharge is known. Observation of the salinity distribution will then permit calculation of estimates of local values of the eddy coefficients.

Finally, rather small values of mean wind stress appear to have greater significance for the circulation and salinity distribution than has perhaps been recognized.

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LITERATURE CITED

- ARONS, A. B., and H. STOMMEL, 1951. A mixing-length theory of tidal flushing. *Trans. Am. Geophys. Union*, 32:419-421.
- BOWDEN, K. F., 1960. Circulation and mixing in the Mersey Estuary. *I.A.S.H. Commission of Surface Waters, Publ. No. 51*:352-360.
- HUGHES, P., 1958. Tidal mixing in the Narrows of the Mersey Estuary. *Geophys. J., Roy. Astron. Soc.*, 1:271-283.
- IPPEN, A. T., and D. R. F. HARLEMAN, 1961. One-dimensional analysis of salinity intrusion in estuaries. *Committee on Tidal Hydraulics, U. S. Army Corps of Engineers, Tech. Bull. No. 5*.
- KENT, R. E., 1958. Turbulent diffusion in a sectionally homogeneous estuary. *Chesapeake Bay Institute, The Johns Hopkins Univ., Tech. Rept. XVI*, Ref. 58-1.
- PREDDY, W. S., 1954. The mixing and movement of water in the estuary of the Thames. *J. Marine Biol. Assoc. U. K.*, 33:645-662.
- PRITCHARD, D. W., 1954. A study of the salt balance in a coastal plain estuary. *J. Marine Res.*, 13:133-144.
- PRITCHARD, D. W., 1955. Estuarine circulation patterns. *Proc. Am. Soc. Civil Engrs.*, 81. (Separate No. 717).
- PRITCHARD, D. W., 1956. The dynamic structure of a coastal plain estuary. *J. Marine Res.*, 15:33-42.
- PRITCHARD, D. W., 1958. The equations of mass continuity and salt continuity in estuaries. *J. Marine Res.*, 17:412-423.
- PRITCHARD, D. W., and R. E. KENT, 1953. The reduction and analysis data from the James River Operation Oyster Spat. *Chesapeake Bay Institute, The Johns Hopkins Univ., Tech. Rept. VI*, Ref. 53-12.
- RATTRAY, M., Jr., and D. C. HANSEN, 1962. A similarity solution for circulation in an estuary. *J. Marine Res.*, 20:121-133.
- STOMMEL, H., 1953. Computation of pollution in a vertically mixed estuary. *Sewage and Ind. Wastes*, 25:1065-1071.
- SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING, 1942. *The Oceans—Their Physics, Chemistry, and General Biology*. Prentice-Hall, Englewood Cliffs, New Jersey.

Some Aspects of the Dynamics of Circulation in Fjords

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The term fjord is applied to an estuary or an inlet which has steep sides, a deep basin, and, in many cases, a sill at its mouth. The salinity distribution is typified by a rather shallow surface layer, appreciably diluted by freshwater runoff, below which the horizontal and vertical salinity gradients are small. The mean circulation under conditions of a large runoff and small tidal mixing is restricted to the surface layers but otherwise, significant velocities may exist at all depths.

Dynamically, the fjord is distinguished from the coastal plain estuary in that the primary circulation takes place in the upper layers alone. This situation can be called the "ideal" fjord circulation and occurs when the influence of the river runoff dominates that of tidal mixing; a condition commonly satisfied by fjord geomorphology. Under these conditions the frictional stresses and turbulent mixing depend on the mean circulation rather than on the tidal currents. The surface circulation consists of a strong outflow in a very shallow layer and an inflow immediately underneath.

Other circulations, which are dynamically more

similar to those occurring in coastal plain estuaries, can take place simultaneously with the surface circulation. A deep circulation is possible in which the forces are small and the turbulent mixing is generated by the tidal motion. With a shallow sill the tidal velocities may be sufficiently large to extend the circulation to the bottom over the sill.

Reviews which include a discussion of fjords have been given by Pritchard (1952) and Pritchard and Cameron (1963).

DYNAMIC BALANCE IN FJORD CIRCULATIONS

DIFFERENTIAL EQUATIONS

In order to describe the dynamics of fjord circulations a right-handed rectangular coordinate system is taken with the origin at mean sea level in mid-channel. The x -axis is taken positive seaward and the z -axis positive downward. The equations of the time-mean motion are

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} + v \frac{\partial u}{\partial y} + w \frac{\partial u}{\partial z} - fv = - \frac{1}{\rho} \frac{\partial p}{\partial x} + \frac{\partial \tau_{xz}}{\partial x} + \frac{\partial \tau_{zy}}{\partial y} + \frac{\partial \tau_{xz}}{\partial z}, \quad (1)$$

$$\frac{\partial v}{\partial t} + u \frac{\partial v}{\partial x} + v \frac{\partial v}{\partial y} + w \frac{\partial v}{\partial z} + fu = - \frac{1}{\rho} \frac{\partial p}{\partial y} + \frac{\partial \tau_{yz}}{\partial x} + \frac{\partial \tau_{yy}}{\partial y} + \frac{\partial \tau_{yz}}{\partial z}, \quad (2)$$

$$g = g - \frac{1}{\rho} \frac{\partial p}{\partial z}, \quad (3)$$

where u, v, w are the components of mean velocity, f is the Coriolis parameter, p is the pressure, ρ is the density, τ_{ij} are the components of stress due to the fluctuating components of velocity and g is the acceleration of gravity.

The t - and y -dependent terms in the x -component equation are usually negligible in comparison to the others. τ_{xz} depends on the rms tidal velocity, u_0 ; effects of tides are included by adding the term

$$- (\frac{1}{2}) [(\partial u_0^2)/(\partial x)] \quad (4)$$

to the right side of equation (1), and may be important in some cases.

The y -component equation usually represents a balance between the Coriolis term and the cross-channel

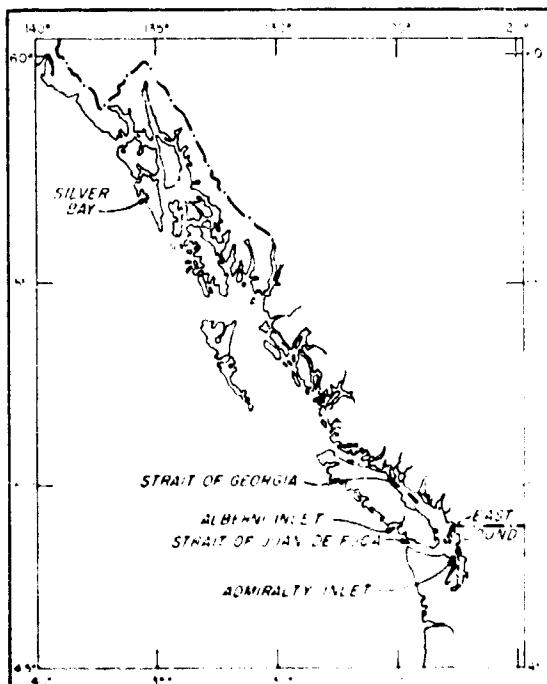


Fig. 1. Alaska and British Columbia fjord regions.

pressure gradient. With curved channels the term

$$\frac{\partial \tau_{yx}}{\partial x} = -\frac{u_s^2}{R} \quad (5)$$

with R equal to the radius of curvature, may also become important.

The salt balance equation is

$$\frac{\partial S}{\partial t} + u \frac{\partial S}{\partial x} + w \frac{\partial S}{\partial z} = -\frac{1}{b} \frac{\partial}{\partial x} (b \bar{u}' S') - \frac{1}{b} \frac{\partial}{\partial z} (b \bar{w}' S') \quad (6)$$

where S is the time mean salinity; u' , S' are the deviations of velocity and salinity from the mean; b is the width of the fjord and the bar represents a time average. Each term may be important in some aspect of fjord circulation.

CIRCULATION OVER SILLS

Because of larger tidal velocities and weaker stratification the circulation over a sill may be quite different from that occurring within the fjord, and may change from one identified as an "ideal" fjord-type circulation to one which corresponds to coastal plain estuaries. An example demonstrating this effect is encountered in the Strait of Juan de Fuca (Figs. 1 and 2). Redfield (1950) has described the circulation and mixing which occurs in this region by means of a composite temperature-salinity (T-S) diagram (Fig. 3); he shows a two-layer net circulation which extends to the bottom (Fig. 4). Further results reported by Herlinveaux and Tully (1961) confirm these features and make possible some quantitative deductions. The longitudinal pressure gradient and the frictional stress terms dominate in the equation of motion. The salt balance is maintained by horizontal advection, as well as vertical and horizontal diffusion. The circulation and salt balance are described by the theory developed for coastal plain estuaries and are presented by Hansen elsewhere in this volume.

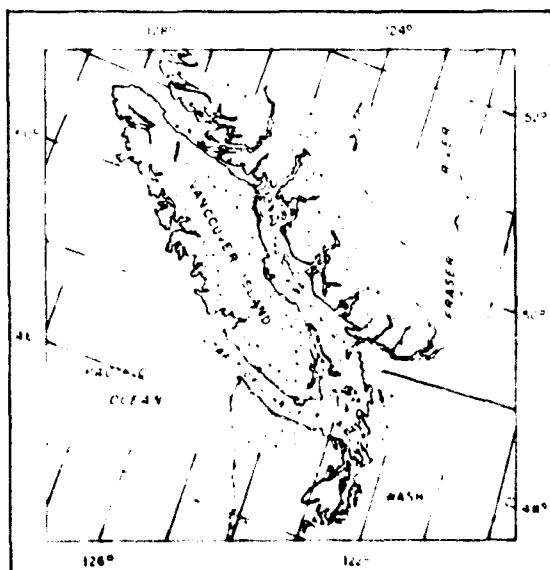


Fig. 2. Strait of Juan de Fuca-Strait of Georgia system.

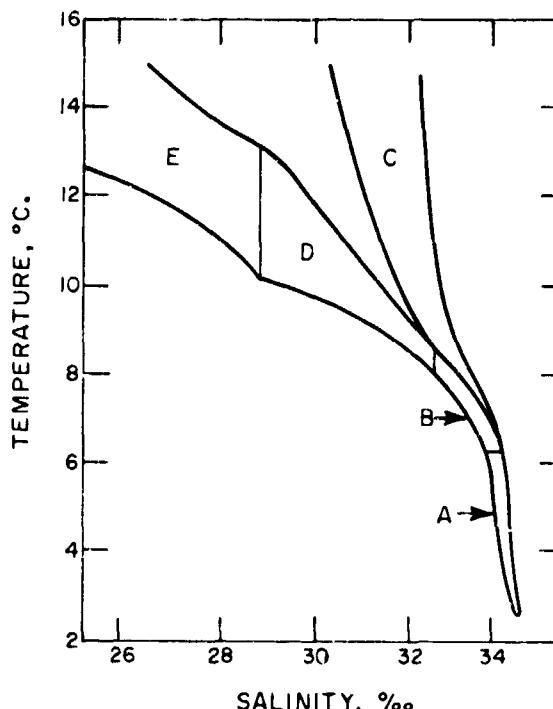


Fig. 3. Temperature-salinity diagrams for the Strait of Juan de Fuca-Strait of Georgia system. (Redfield, 1950).

DEEP CIRCULATION

Beneath the surface layers the circulation is governed by the pressure gradient and frictional stress terms, with acceleration terms possibly important due to local bathymetric features. The salt balance is maintained by means of local time change, vertical diffusion, and horizontal and vertical advection, depending upon the particular circumstances.

Because of small tidal velocities, the eddy diffusivity in the deep waters of most fjords is exceedingly small and a layered structure is often found showing successive advective intrusion of waters with differing

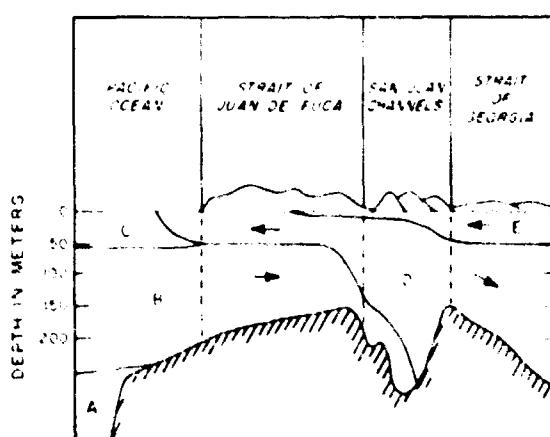


Fig. 4. Net circulation in the Strait of Juan de Fuca (Redfield, 1950).

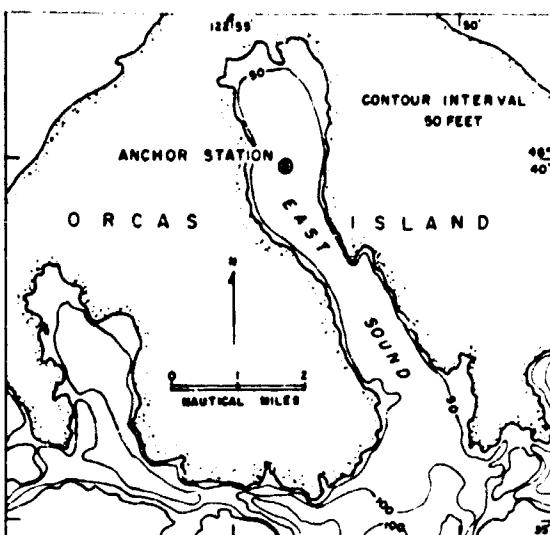


Fig. 5. East Sound.

properties. The rate of circulation in basins located behind sills depends upon the relative depth of the basin and the sill, the tidal mixing over the sill, the seasonal changes of the outside water density, and the amount of the freshwater runoff. As shown in Figure 4, the source water for the deep circulation is a mixture of a surface outflow from the fjord and the subsurface inflow of external waters. The density of this mixture depends upon the density of the two contributory sources and their relative rates of supply. Maximum rates of replenishment in these basins occur at times of maximum density of the source waters.

WIND-DRIVEN CIRCULATION, EAST SOUND

An example of the dynamic balance in a wind-driven fjord circulation is afforded by a study made in East Sound during a ten-hour period of steady 10 ms^{-1} wind blowing up the sound.

East Sound (Fig. 5) is 13 km long, 2 km wide and has a reasonably uniform mid-channel depth of 30 m. From 2300 hr July 30 to 0900 hr July 31, 1956, current observations and wind profile measurements were made at the anchor station. Average values of longitudinal velocity and wind stress were computed (the tidal velocity was negligible). The temperature distribution was determined in a longitudinal section before and after this period, and the density distribution determined from T-S curves obtained during the

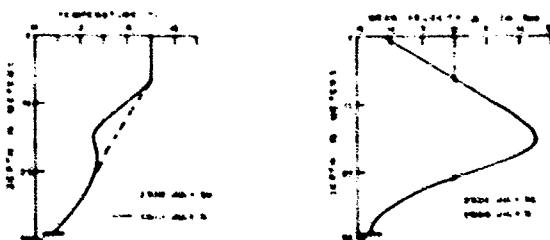


Fig. 6. Temperature and velocity profiles, East Sound—July, 1956.

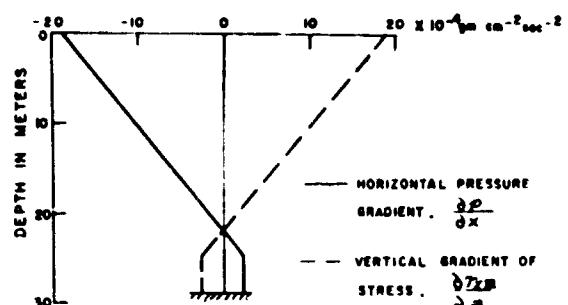


Fig. 7. Balance of forces, East Sound—July, 1956.

survey. The temperature and velocity profiles are shown in Figure 6. Initially there was an upper mixed layer below which the temperature decreased uniformly with depth. After ten hours the temperature at mid-depth fell to a minimum. The average longitudinal component of current shows a three-layer circulation with inflow at the surface and bottom, and outflow at intermediate depths.

Since the accelerations are small, the longitudinal equation of motion becomes simply a balance between the horizontal pressure gradient and the vertical gradient of stress. Setting the pressure gradient, determined to within a constant by the observed distribution of mass, equal to the stress gradient permits the stress distribution to be determined by integration downward from the surface. The sea-surface slope is obtained by setting the stress equal to zero at the depth of zero velocity gradient. A check on the assumptions is furnished by the stress going to zero again at the bottom. Figure 7 shows the balance of forces for this system. Figure 8 shows the relation between the stress and the velocity shear. The eddy coefficient of viscosity ranges from $90 \text{ cm}^2 \text{ s}^{-1}$ near the surface to $6 \text{ cm}^2 \text{ s}^{-1}$ near the bottom.

LOW-REYNOLDS CIRCULATION, SILVER BAY—March, 1957

Silver Bay (Fig. 9) is a fjord typical of many found along the coasts of British Columbia and Alaska. McAlister *et al.* (1959) determined the magnitudes of the terms in the equations of motion and salt balance for conditions of low and high runoff. During the period March 27–31, 1957, the runoff was $4.25 \text{ m}^3 \text{ s}^{-1}$. The corresponding temperature, salinity, and velocity profiles are shown in Figure 10. Outflow

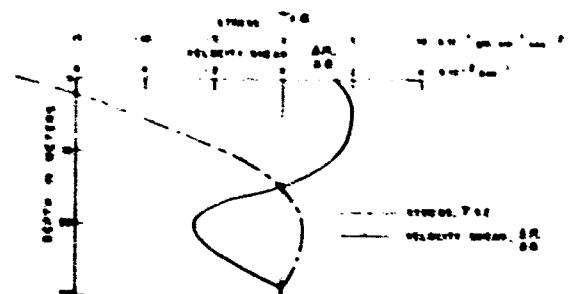


Fig. 8. Stress and velocity shear, East Sound—July, 1956.

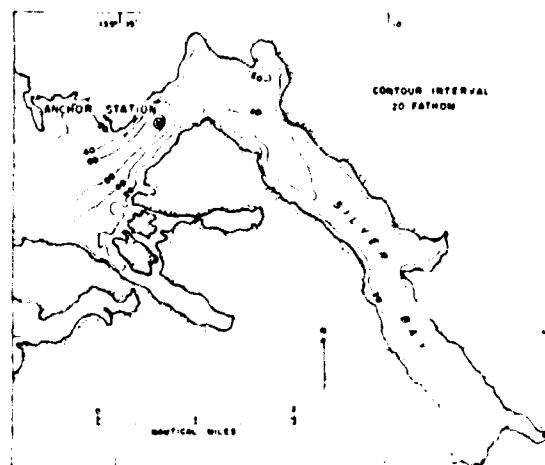


Fig. 9. Silver Bay.

occurs in an upper layer extending to almost one-third the total depth with inflow occurring below this depth. A large velocity shear is found in the upper few meters of the water column.

Figure 11 shows the vertical distribution of the dominant terms in the equation of motion. The horizontal pressure gradient, the vertical gradient of stress, and the horizontal field acceleration are all important. The field acceleration in the upper few meters balances the pressure gradient, but is small at depths greater than 10 m, except for the acceleration caused by the sill. The vertical distribution of stress and velocity shear is given in Figure 12. It can be noted that while the velocity shear is slightly negative between depths of 8 and 15 m, the stress has a minimum value but remains positive. Such conditions cannot be adequately described in terms of an eddy coefficient of viscosity. Values for an eddy coefficient of viscosity range from about $5 \text{ cm}^2 \text{s}^{-1}$ in the upper layer to about $120 \text{ cm}^2 \text{s}^{-1}$ in the lower.

HIGH-RESOLVING CIRCULATION, SILVER BAY— July, 1956

During the period July 4–11, 1956, the runoff into Silver Bay was $49 \text{ m}^3 \text{s}^{-1}$. The resulting salinity,

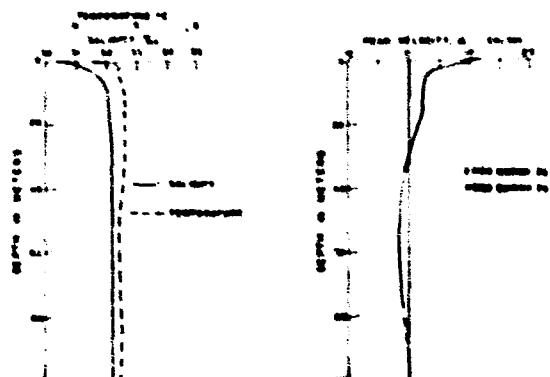


Fig. 10. Temperature, salinity, and velocity profiles, Silver Bay—March, 1957

temperature, and velocity profiles are shown in Figure 13. The surface outflow is restricted to the upper 6 m, a strong inflow occurs between depths of 6 m and 35 m, and the bottom layer has a small outward velocity. This is a typical fjord surface circulation where the effects of runoff predominate over those due to tidal mixing.

The balance of forces is given in Figure 14. The pressure, stress, and both field acceleration terms are important in the upper 20 m. Below 30 m the balance of forces is between the horizontal pressure gradient and the stress term. The stress and velocity shears are shown in Figure 15. Values of the eddy coefficient of viscosity range from $3 \text{ cm}^2 \text{s}^{-1}$ in the surface layers to $30 \text{ cm}^2 \text{s}^{-1}$ at mid-depth.

A SIMILARITY SOLUTION FOR FJORD CIRCULATION

EQUATIONS FOR CIRCULATION AND SALT BALANCE

Since the more interesting variations of properties occur in the longitudinal and vertical directions and the relative narrowness of fjords precludes, on the average, large lateral variations, it has been assumed

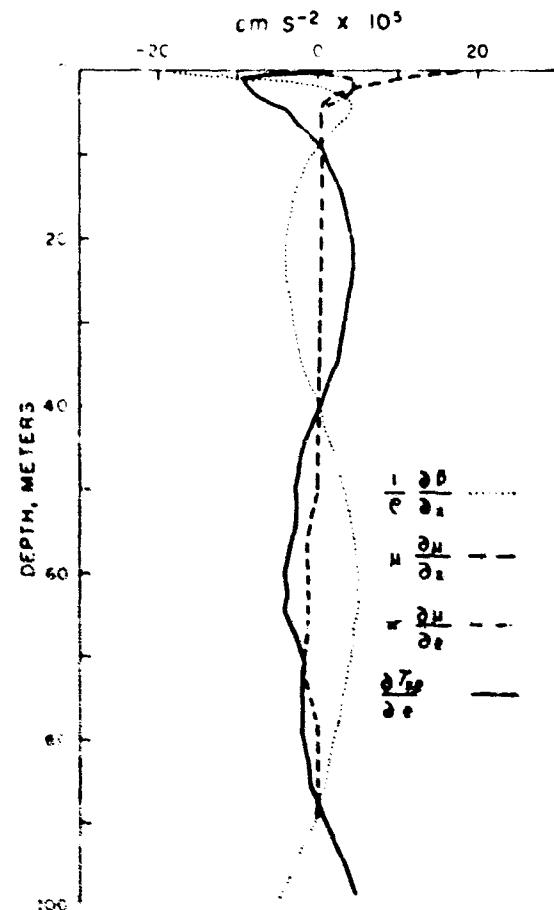


Fig. 11. Balance of forces, Silver Bay—March, 1957

in the following development that these variations are negligible. The Boussinesq approximation is used throughout. With these simplifications the equations which govern the steady-state circulation are

$$u \frac{\partial u}{\partial x} + w \frac{\partial u}{\partial z} = - \frac{1}{\rho} \frac{\partial}{\partial x} (p + \frac{1}{2} \rho u^2) + \frac{\partial}{\partial z} \left(A \frac{\partial u}{\partial z} \right), \quad (7)$$

$$0 = - \frac{\partial p}{\partial z} + \rho g, \quad (8)$$

$$\frac{\partial}{\partial x} (ub) + \frac{\partial}{\partial z} (wb) = 0, \quad (9)$$

$$u \frac{\partial S}{\partial x} + w \frac{\partial S}{\partial z} = \frac{\partial}{\partial z} \left(K \frac{\partial S}{\partial z} \right). \quad (10)$$

A and K are the vertical eddy coefficients of viscosity and diffusivity, respectively.

An approximate equation of state, suitable for fjords, is

$$\rho = \rho_0 + kS \quad (11)$$

where ρ_0 and k are constants.

It is convenient to introduce a salinity defect Σ , defined by

$$\Sigma = g \left(1 - \frac{S}{S_0} \right), \quad (12)$$

where S_0 is a reference salinity, taken to be that of the oceanic water at sill depth. A stream function, ψ , is introduced, such that the velocities are given by

$$\begin{aligned} ub &= - \frac{\partial \psi}{\partial z}, \\ wb &= \frac{\partial \psi}{\partial x}. \end{aligned} \quad (13)$$

Consideration will be restricted to those regions of fjords in which the total circulation is large compared to the freshwater runoff, and in which this circulation is confined to the upper layers. Under these conditions, an adequate approximation can be obtained by taking the depth to the bottom to be infinite and by considering the stream function to be zero at both the free surface and at great depth. Additional boundary conditions are: at the free surface, the stress is equal to the wind stress and the vertical salt flux is zero; at the bottom, the velocity is zero, the salt flux is zero and the salinity approaches its limiting value, S_0 . The condition of zero horizontal salt flux through each section gives a non-trivial integral constraint when the effect of freshwater runoff is included. These conditions are expressed by the following equations:

At the free surface, $z = 0$:

$$\psi(x, 0) = 0, \quad (14)$$

$$A[b^{-1}\psi_x(x, 0)]_s = \tau_w(x)/\rho_0, \quad (15)$$

where $\tau_w(x)$ is the wind stress on the surface.

At the bottom, $z = \infty$:

$$\psi(x, \infty) = \psi_x(x, \infty) = \Sigma(x, \infty) = K\Sigma_x(x, \infty) = 0. \quad (16)$$

The salt flux constraint:

$$\begin{aligned} 0 &= \int_0^\infty buS dz \\ &= S_0 \int_0^\infty bu dz + \frac{S_0}{g} \int_0^\infty \Sigma \frac{\partial \psi}{\partial z} dz \\ &= S_0 R(x) + \frac{S_0}{g} \int_0^\infty \Sigma \frac{\partial \psi}{\partial z} dz, \end{aligned} \quad (17)$$

where $R(x)$ is the river runoff into the fjord from its head to the section at x .

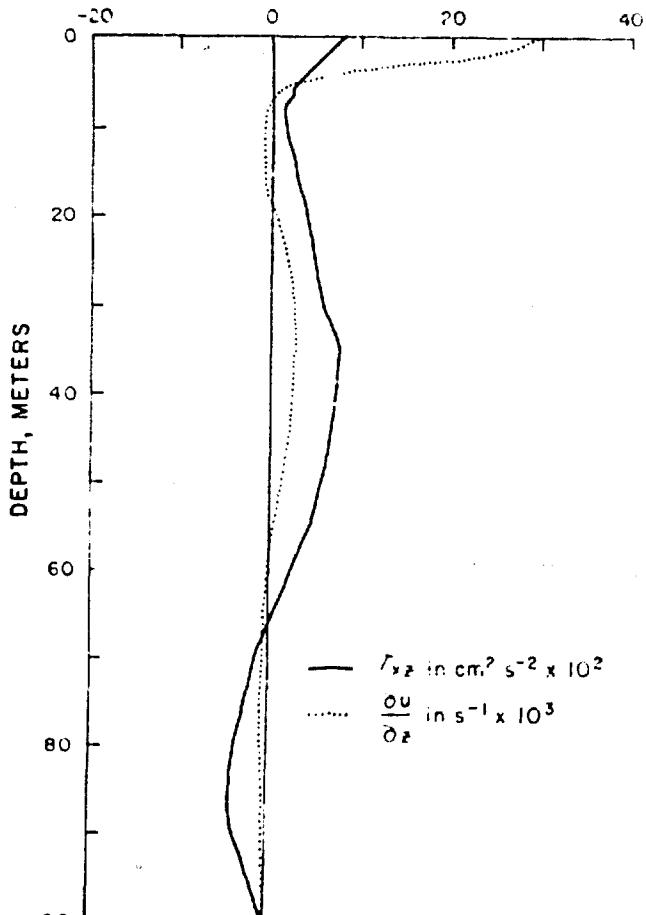


Fig. 12. Stress and velocity shear, Silver Bay—March, 1957.

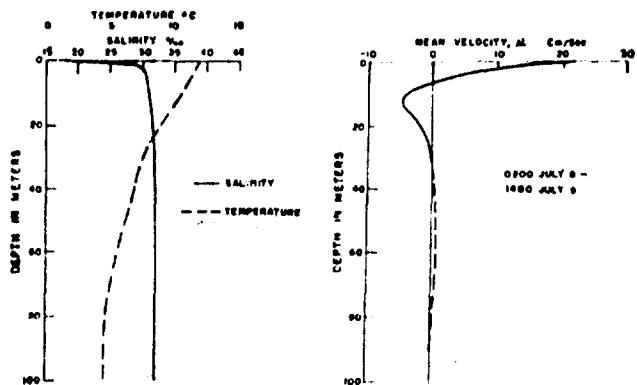


Fig. 13. Temperature, salinity and velocity profiles, Silver Bay—July, 1956.

THE SIMILARITY TRANSFORMATIONS

The procedure applied by Rattray and Hansen (1962) to coastal plain estuaries is followed in obtaining similarity solutions in the forms

$$\psi(x, z) = K_0 b_0 (x/l_0)^{\gamma} \phi(\eta), \quad (18)$$

$$\Sigma(x, z) = K_0^2 l_0^{-\lambda} (x/l_0)^{\lambda} \theta(\eta), \quad (19)$$

where

$$\eta = \frac{z}{l_0} (x/l_0)^{\sigma}, \quad (20)$$

and the parameters of the problem are given by

$$b(x) = b_0 (x/l_0)^{\mu}, \quad (21)$$

$$A(x, z) = \delta^{-1} K_0 (x/l_0)^{\rho} F(\eta), \quad (22)$$

$$K(x, z) = K_0 (x/l_0)^{\kappa} F(\eta), \quad (23)$$

$$R(x) = R_0 (x/l_0)^{\nu}, \quad (24)$$

$$\epsilon = k S_0 / \rho_0. \quad (25)$$

R_0 , K_0 , b_0 , l_0 are characteristic values for the appropriate quantities; k is a constant; ϵ is the differential density ratio, and δ is the ratio of eddy diffusivity to eddy viscosity (assumed constant). ϵ is small ($\sim 3 \times 10^{-2}$) while δ is less than or equal to unity (~ 1 to 10^{-2} , depending upon stratification).

Under the above transformations of variables, equa-

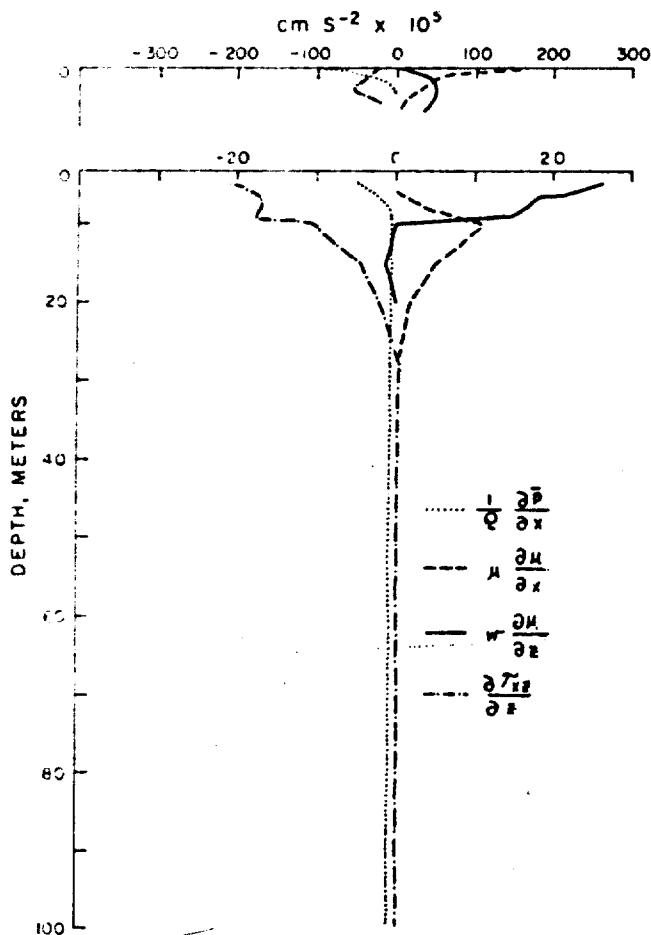


Fig. 14. Balance of forces, Silver Bay—July, 1956.

tions (7)–(13) reduce to

$$\gamma \phi \phi'' + \nu \phi \phi'' = \delta^{-1} (\gamma \phi'')'' + \epsilon (\lambda \theta + \alpha \eta \theta'), \quad (26)$$

$$\gamma \phi \theta' - \lambda \theta \phi' = (F \theta')', \quad (27)$$

where $\nu = 2\beta - 2\alpha - \gamma$, (28)

and the following conditions are imposed on the exponents:

$$\gamma = \alpha + \beta + \sigma + 1, \quad (29)$$

$$\lambda = 3\alpha + 2\gamma - 2\beta. \quad (30)$$

The salt flux condition, equation (17) becomes

$$\int_{-\infty}^{\infty} \theta \phi' d\eta = -1, \quad (31)$$

if l_0 is defined by

$$l_0^{\mu} = \frac{K_0 b_0}{g R_0}, \quad (32)$$

and the exponents satisfy the relation

$$\lambda + \gamma = \mu. \quad (33)$$

The boundary conditions, equations (14) and (16), are

$$\phi(0) = \phi(\infty) = \phi'(\infty) = 0, \quad (34)$$

$$\theta(\infty) = F(\infty) = \theta'(\infty) = 0. \quad (35)$$

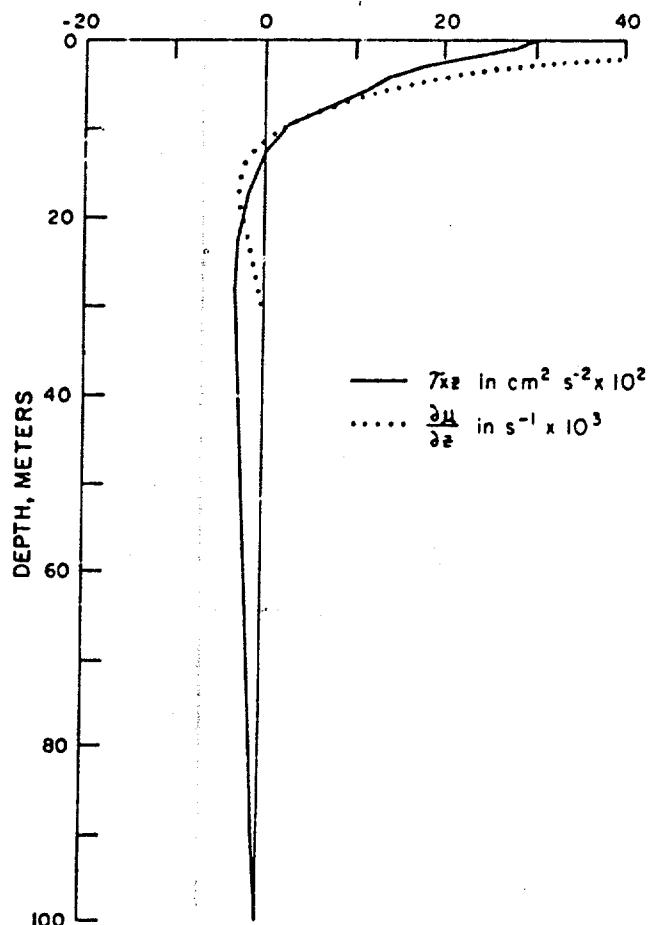


Fig. 15. Stress and velocity shear, Silver Bay—July, 1956.

The wind stress relation, equation (15), is

$$F(0) \cdot \phi''(0) = T_0, \quad (36)$$

where the wind stress $\tau_w(x)$ is given by

$$\tau_w(x) = T_0 \frac{\rho_a K_{\alpha}^2}{\delta f_i^2} (x/l_e)^{2\alpha+2\gamma-\theta}. \quad (37)$$

AN APPROXIMATE SOLUTION

An approximate solution to the problem is obtained by taking the function of η to be products of an exponential and a power series in η . The exponential term insures the correct asymptotic behavior as $\eta \rightarrow \infty$ and the power series expansion determines the shape of the profiles in the surface layers. The eddy coefficient of viscosity in the surface layer is taken to be of the form given by Ellison (1960), and at great depth, it is taken to decrease exponentially with the velocity. These conditions satisfy the boundary conditions, equations (34) and (35), and are expressed as follows:

$$\phi(\eta) = e^{-a\eta} \sum_{m=1}^{\infty} \Phi_m \cdot (a\eta)^m, \quad (38)$$

$$\theta(\eta) = e^{-2a\eta} \sum_{m=1}^{\infty} \Theta_m \cdot (a\eta)^m, \quad (39)$$

$$F(\eta) = e^{-a\eta} (a\eta), \quad (40)$$

where a is a measure of the depth of penetration of the circulation.

The eddy coefficient could readily be expressed in terms of a complete power series but this refinement is unwarranted with our present knowledge of its behavior. Ellison's coefficient is equal to zero at the free surface and also equal to zero for conditions of no surface stress. With density structure, these conditions no longer hold and the surface value for the eddy coefficient is taken to be

$$F(0) = a\eta_0 \quad (41)$$

where η_0 corresponds to some small but finite roughness length presumably related to the wind stress. η_0 is treated as a constant in the subsequent developments.

The solution is obtained by substituting equations (38)–(40) into equations (26), (27), (31), and (36); equating the coefficients of equal powers of $a\eta$ in equations (26) and (27); approximately satisfying equation (31) by including only those terms which are in equations (26) and (27); and by satisfying equation (36) exactly.

Defining new coefficients by

$$\phi_m = \Phi_m / \Theta_0^{\frac{1}{2}}, \quad (42)$$

$$\theta_m = \Theta_m / \Theta_0, \quad (43)$$

$$f_i = \Theta_0^{-\frac{1}{2}}, \quad (44)$$

the following relations are obtained for the lowest order of approximation:

$$2\pi a^4 (\phi_1 \phi_1 - \phi_1^2)$$

$$= \delta^{-1} a^4 f_i (10\phi_1 - 16\phi_2 + 12\phi_3) + \lambda \epsilon, \quad (45)$$

$$- \lambda \phi_1 = a f_i (\theta_1 - 2), \quad (46)$$

$$36\phi_1 + 24\phi_2 + 24\phi_3 + 15\phi_1 \theta_1 \\ + 18\phi_2 \theta_1 + 26\phi_3 \theta_1 = -27, \quad (47)$$

$$\phi_2 - \phi_1 = \frac{T_0}{2a^4 \Theta_0^{\frac{1}{2}} a \eta_0} = T. \quad (48)$$

To this order of approximation,

$$\phi(\eta) = \Theta_0 e^{-a\eta} \{ \phi_1(a\eta) + \phi_2(a\eta)^2 + \phi_3(a\eta)^3 \}, \quad (49)$$

and

$$\theta(\eta) = \Theta_0 e^{-2a\eta} \{ 1 + \theta_1(a\eta) \}. \quad (50)$$

Equations (45), (46), and (48) are solved for ϕ_2 , ϕ_3 , and θ_1 in terms of ϕ_1 and the external parameters. The resulting equations are

$$\phi_2 = \phi_1 + T, \quad (51)$$

$$\phi_3 = \frac{\phi_1}{2} + \frac{4}{3} T + \frac{\delta \nu}{6 f_i a} \phi_1 T - \frac{\delta \epsilon \lambda}{12 f_i a^4} \quad (52)$$

$$\theta_1 = 2 - \frac{\lambda}{f_i a} \phi_1. \quad (53)$$

Substitution into equations (49) and (50) yields

$$\phi(\eta) = \Theta_0 e^{-a\eta} \left\{ \phi_1 [a\eta + (a\eta)^2 + \frac{1}{2}(a\eta)^3] - \frac{\delta \epsilon \lambda}{12 f_i a^4} (a\eta)^3 \right. \\ \left. + T \left[(a\eta)^2 + \frac{4}{3} (a\eta)^3 + \frac{\delta \nu}{6 f_i a} \phi_1 (a\eta)^2 \right] \right\}, \quad (54)$$

$$\theta(\eta) = \Theta_0 e^{-2a\eta} \left\{ (1 + 2a\eta) - \frac{\lambda^2}{f_i a} a\eta \right\}. \quad (55)$$

Equation (47) with the aid of relations (51)–(53) gives the value of ϕ_1 . Θ_0 is determined by the magnitude of the horizontal salinity gradient and can be estimated from the length of the fjord and the salinity at its mouth. The value of a depends upon the relation of the eddy coefficients to the velocity shear and vertical density gradient.

The longitudinal distributions of properties are found from equations (29), (30), and (33); the unknown exponents α , γ , and λ are given by the relations

$$\alpha = -\frac{1}{2} - \frac{\beta}{6} + \frac{\mu}{6} - \frac{\sigma}{2}, \quad (56)$$

$$\gamma = \frac{1}{2} + \frac{5\beta}{6} + \frac{\mu}{6} + \frac{\sigma}{2}, \quad (57)$$

$$\lambda = -\frac{1}{2} - \frac{5\beta}{6} + \frac{5\mu}{6} - \frac{\sigma}{2}, \quad (58)$$

in terms of known exponents β , μ , and σ .

GENERAL DISCUSSION OF THE SOLUTION

Limiting forms of the salinity profile are given in Figure 16. The result given by equation (55) is a linear combination of these two profiles which depends on the quantity $\lambda \phi_1 / f_i a$. Because of the complicated dependence of this quantity on the external param-

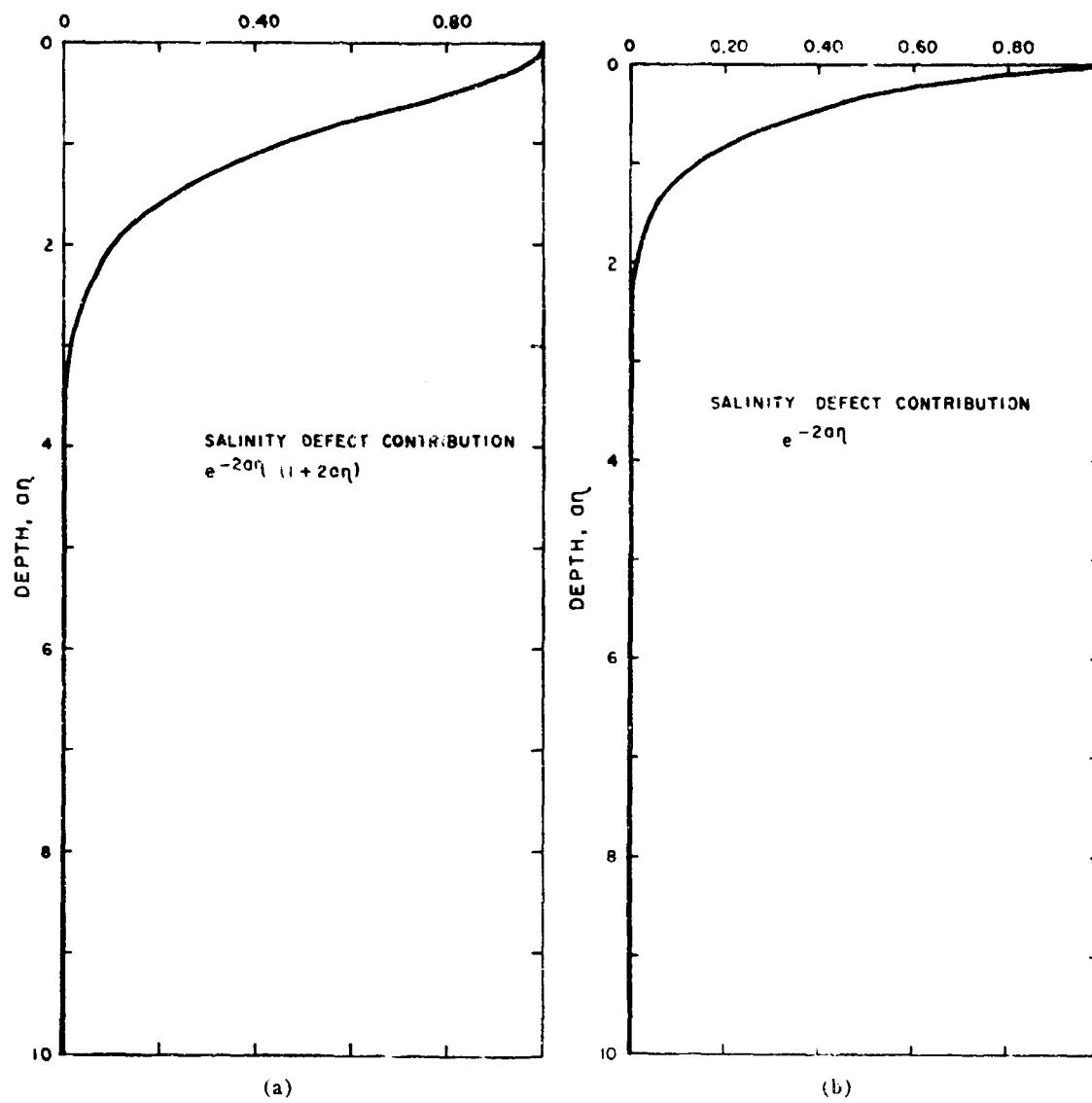


Fig. 16. Theoretical profiles of salinity defect contributions.

eters, it is not easy to see under which conditions the salinity profile will be similar to either curve. However, the dependence upon λ is rather straightforward. For small or positive values of λ the halocline will occur somewhat below the surface and a more homogeneous surface layer will exist as shown in Figure 16(a). For larger negative values of λ a maximum salinity gradient will occur at the surface as shown in Figure 16(b). The latter case is found when the relative local addition of fresh water is small, while the former is found when the local fresh water addition is large and the horizontal salinity gradients are small. Pickard (1961) has characterized the vertical profiles of salinity for fjords as Type 1 and Type 2 (Fig. 17). His Type 1 corresponds to the form given in Figure 16(a) and his Type 2 to that of Figure 16(b). Pickard's Type 1(a) cannot be reproduced unless higher terms in the expansion for θ are in-

cluded. Pickard finds Type 1 preferentially occurring near the head of highest runoff inlets while Type 2 occurs more commonly near the mouth and in low runoff inlets. This distribution corresponds to that deduced from the λ -dependence as given above.

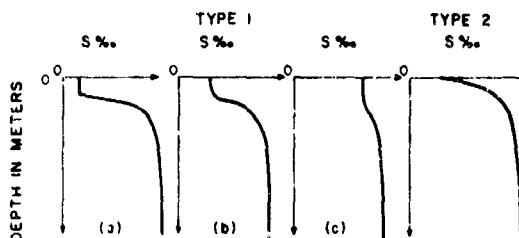
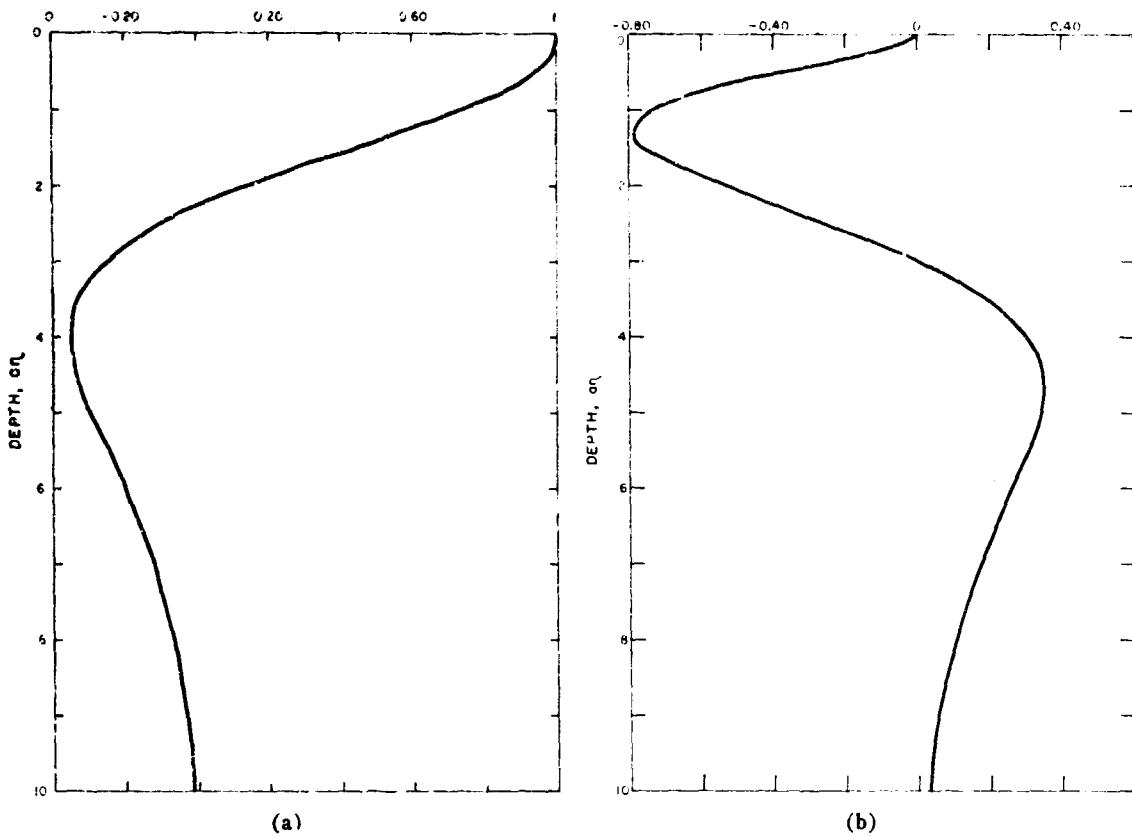


Fig. 17. Types of vertical profile of salinity in the shallow zone in British Columbia (Pickard, 1961).



Vertical profiles for the velocity terms derived from equation (54) are given in Figure 18. The term in Figure 18(a) gives the surface outflow; the term in Figure 18(b), whose magnitude is proportional to the quantity $\delta\epsilon\lambda/12f_1a^4$, represents the effect of the density distribution in modifying the basic velocity profile. The role of this term is to steepen the velocity shear in the upper layer, to decrease the depth of the inflowing water and thus confine the major portion of the circulation to a shallower layer. Figure 18(c) shows that the effect of positive wind stress (proportional to T) is similar to that of density distribution and, in addition, provides a velocity shear at the free surface. When the wind stress is directed up the fjord, it acts so as to counteract the effect of the density distribution. The wind stress term which includes the factor $\delta\nu\phi_1/6f_1a$ is not shown but will have a shape similar to that shown in Figure 18(b). It is noteworthy that appreciable currents extend well below the depth of appreciable dilution.

The longitudinal dependence of properties is given by equations (56)-(58). The expression for a in equation (56) shows that the depth of the circulation basically increases towards the mouth; that an increase of width or eddy coefficients augments this increase; and that local runoff will decrease the depth of the circulation. Equation (57) for y shows that the velocity increases towards the mouth and is increased further when the width, runoff, and eddy coefficients do likewise. The salinity defect, as shown

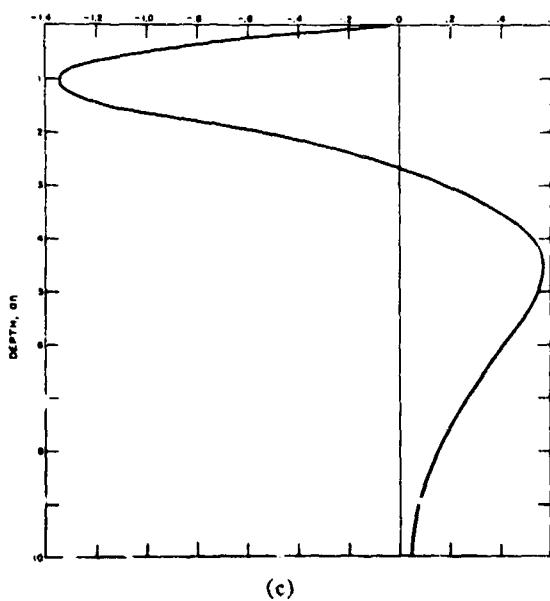


Fig. 18. Theoretical profiles of velocity contributions.

- (a) Velocity contribution is $e^{-\eta}(1 + a\eta + \frac{1}{2}a^2\eta^2 - \frac{1}{3}a^3\eta^3)$.
- (b) Velocity contribution is $-e^{-\eta}(3a^2\eta^2 - 3^4\eta^4)$.
- (c) Velocity contribution is $-e^{-\eta}(2a\eta + 3a^2\eta^2 - \frac{1}{2}a^3\eta^3)$.

by equation (58) for λ , decreases towards the mouth, is decreased further by an increase in width and eddy coefficients, but is increased by local runoff.

Previous theoretical investigations on the dynamics of fjord circulation have been carried out by Stommel and Farmer (1952) and Cameron (1951). Stommel and Farmer considered a very simplified two-layer model and were primarily concerned with the thickness of the upper layer and with the horizontal variations of properties. Cameron considered a more general model, but again imposed a particular velocity profile on his solutions. His assumed velocity profile is given by the first two terms in equation (54) and thus cannot reproduce all the features obtained above. The present theory is an extension of Cameron's which enables the velocity and salinity profiles, as well as the horizontal variations of these quantities, to be determined simultaneously from the basic equations. Cameron assumed a constant coefficient of eddy viscosity, while in the present development, the eddy viscosity has been assumed to depend upon the nature of the circulation. It is apparent that the reality of the theoretical results is limited by an incomplete knowledge of the dependence of the eddy coefficients of viscosity and diffusion upon velocity shear and stability. The expression for the eddy coefficients which is used to obtain the foregoing approximate solution can only be a rough approximation to the actual vertical dependence of these coefficients.

COMPARISON OF THEORY WITH OBSERVATIONS

LONGITUDINAL DISTRIBUTIONS OF PROPERTIES

A comprehensive set of data suitable for testing the theoretical longitudinal distributions of properties was obtained by Tully (1949) in Alberni Inlet (Fig. 19). For portrayal of those conditions, β was set equal to zero, indicating approximately constant width; σ was

set equal to zero although there is no *a priori* reason or knowledge of the distribution of the eddy coefficients along the channel; the value of μ was determined from drainage areas upstream of stations A, B, C, and D. The runoff data can be reasonably well fitted by taking μ equal to $\frac{1}{3}$; then α equals $-4/9$, γ equals $5/9$ and λ equals $-1/5$. Figure 20 shows curves corresponding to these values of the exponents and gives the observed values derived from the data reported by Tully. It can be seen that the observed values from stations A, B, and C conform rather well with the theoretical distributions. In three cases, the curves apply equally well to station D, but the corresponding value of the salinity defect shows the effects of the widening of the inlet.

VERTICAL DISTRIBUTION OF PROPERTIES

July conditions in Silver Bay are suitable for comparison with the theory, and although the simple form assumed for the vertical dependence of the eddy coefficient does not closely match that in Silver Bay, suitable values for the parameters can be found which yield results in reasonable agreement with the observed velocity and salinity profiles.

The values of the parameters chosen to match the given conditions are:

$$\begin{aligned} \epsilon &= 3 \times 10^{-2} & \lambda &= -0.5 & \alpha &= 0.24 \\ K_o &= 11 & \Theta_o &= 8.4 & \phi_1 &= -0.33 \\ l_o &= 0.14 \text{ cm} & \delta &= 0.29 & T &= 0 \end{aligned}$$

The resulting profiles are given in Figure 21. The observed values are shown for comparison. It can be seen that the theoretical velocity profile compares favorably with the observations while the fit for the salinity profile is not quite so good. The agreement can be improved by more adequately representing the actual vertical distribution of the eddy coefficients of viscosity and diffusion, and by including the effects of wind stress.

SUMMARY AND CONCLUSIONS

The circulation in fjords has been briefly reviewed in terms of the quantities responsible for the dynamic

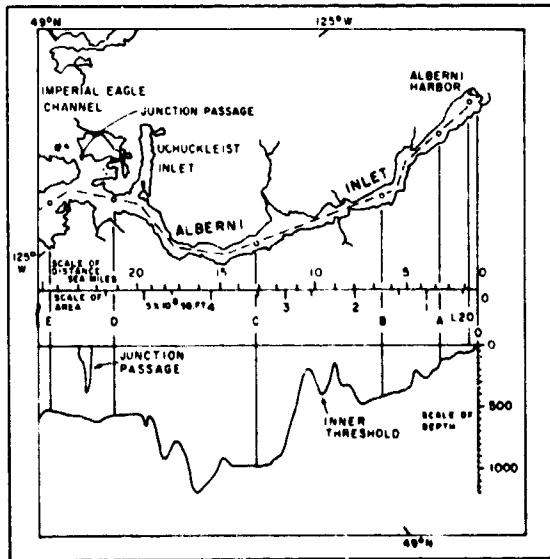


Fig. 19. Alberni Inlet (Tully, 1949).

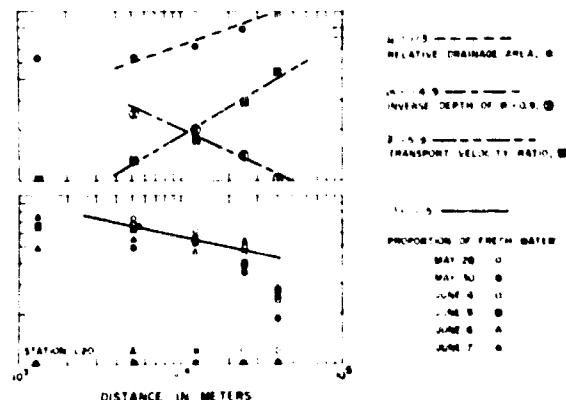


Fig. 20. Longitudinal distribution of properties in Alberni Inlet.

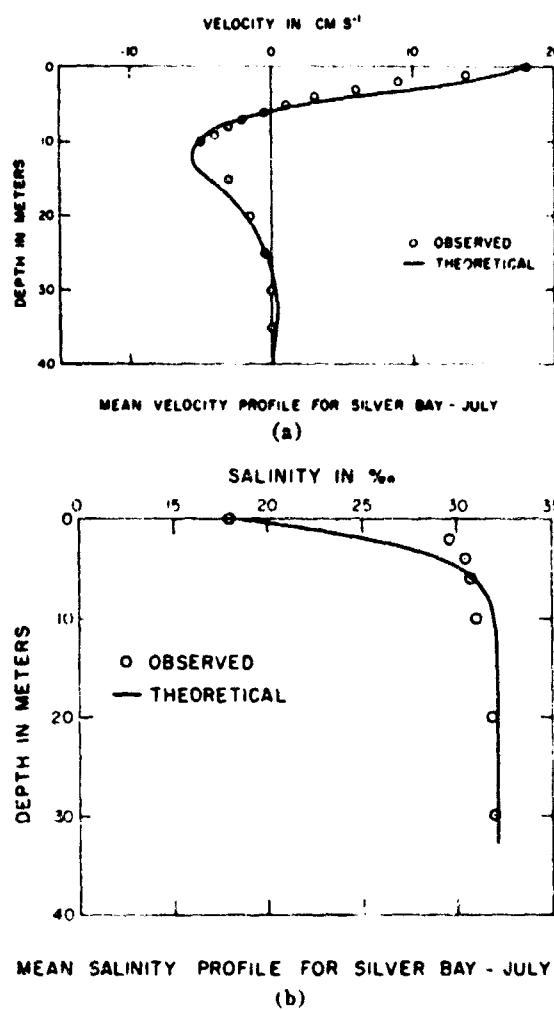


Fig. 21. Vertical distribution of properties in Silver Bay.
(a)

balance and the salt balance. In most cases, the balance of forces is given by the equality of the horizontal pressure gradient and the vertical gradient of turbulent stress. The exceptions occur when the horizontal acceleration terms become important in the upper circulation, or because of bathymetric effects. The upper circulation is the unique feature of fjords which separates them dynamically from other estuarine systems.

The salt-balance equation represents a balance between horizontal advection and vertical and horizontal diffusion over the sills; a balance between horizon-

tal advection and vertical diffusion and possible time changes in the deep circulation; and between horizontal and vertical advection and vertical diffusion in the near-surface circulation.

Examples have been given to illustrate the dynamic balance which exists for a wide range of fjord conditions.

An approximate similarity solution, given for the circulation in the upper layers of a fjord, gives a good representation of all the important features of this circulation. Refinement of the theory is hampered largely by incomplete knowledge of the appropriate vertical dependence for the eddy coefficients of diffusion and viscosity.

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LITERATURE CITED

- CAMERON, W. M., 1951. *On the dynamics of inlet circulations*. Doctoral dissertation, Univ. of California, Los Angeles, California.
- ELLISON, T. H., 1960. A note on the velocity profile and longitudinal mixing in a broad open channel. *J. Fluid Mech.*, 8(1):33-40.
- HERLINVEAUX, R. H., and J. P. TULLY, 1961. Some oceanographic features of Juan de Fuca Strait. *J. Fisheries Res. Board Can.*, 18(6):1027-1071.
- MCALISTER, W. B., M. RATTRAY, Jr., and C. A. BARNES, 1959. The dynamics of a fjord estuary: Silver Bay, Alaska. *Dept. of Oceanography Tech. Rept. No. 62*, Univ. of Washington, Seattle, Washington.
- PICKARD, G. L., 1961. Oceanographic features of inlets in the British Columbia mainland coast. *J. Fisheries Res. Board Can.*, 18(6):907-999.
- PRITCHARD, D. W., 1952. Estuarine hydrography. In *Advances in Geophysics*, edited by H. E. Landsberg; vol. 1, pp. 243-280. Academic Press, New York.
- PRITCHARD, D. W., and W. M. CAMERON, 1963. Estuaries. In *The Sea*, edited by M. N. Hill; vol. 2, pp. 306-324. John Wiley and Sons, New York.
- RATTRAY, M., Jr., and D. V. HANSEN, 1962. A similarity solution for circulation in an estuary. *J. Marine Res.*, 20(2):121-133.
- REDFIELD, A. C., 1950. Note on the circulation of a deep estuary - The Juan de Fuca-Georgia Straits. In *Proc. Colloquium Flushing of Estuaries*; pp. 175-177. Woods Hole Oceanog. Inst., Woods Hole, Massachusetts.
- STOMMEL, H. M., and H. G. FARMER, 1952. *On the nature of estuarine circulation*. Ref. Nos. 52-48, 52-51, 52-63. Woods Hole Oceanog. Inst., Woods Hole, Massachusetts.
- TULLY, J. P., 1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. *Fisheries Res. Board Can. Bull.* 83.

Some Features of the Hydrography of Norwegian Fjords

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It may seem restrictive to deal only with Norwegian fjords in this paper, but they are very similar to those in other parts of the world, for instance, those of British Columbia, which have been very thoroughly investigated by Canadian oceanographers (Pickard, 1961). The reason for this similarity is that they have a common origin as glacially cut structures, and that they are all situated in high latitudes and subjected to similar climatic influences.

I shall not try to formulate a new definition of a fjord, but will rely on the one given by Pritchard (1952): "A fjord is an elongated indenture of the coast line containing a relatively deep basin with a shallower sill at the mouth."

If you look at a map of Norway, you will find many bodies of water which are called "fjords". Most of them fit Pritchard's definition, but some of them are bays or sounds. The size of the fjords is highly variable, from small ones with a length of a few kilometers up to the 176 kms of the Sognefjord. The map (Fig. 1) shows the Norwegian fjords which are concentrated on the western and northern coast. Most of the large fjords are found there, with exception of the Oslo Fjord, a rather atypical one which will not be discussed in this paper. A group of large fjords in the northeasternmost part of the country have no sills and therefore do not fall within Pritchard's definition of a fjord.

HYDROGRAPHIC CONDITIONS

The sill depth is a factor of great importance to the hydrographic conditions in a fjord, particularly in respect to the conditions in the deeper layers. The sill and the sill depth are not always easy to define. In many cases, researchers will be most interested in the deepest connection between the fjord and the ocean outside, and define the sill accordingly. For the fjords of western Norway, the sill depth then might be determined by the coastal banks outside the skerries, and this could apply to many of the largest fjords. From a morphological point of view, however, such a definition may seem rather artificial. In other applications, the most appropriate definition might be the "real" sill, or the one which constitutes the natural termination of the fjord basin. The sill depths of Norwegian fjords, by either definition, vary from a few meters to 100-200 m, with corresponding differences in the hydrographic conditions in the deeper layers of the fjords. The depths of the fjord basins may be very great. The largest of the Norwegian fjords, the Sognefjord, is also the deepest; it has a maximum depth of nearly 1,300 m. Hardangerfjord is 900 m deep, but most other fjords do not exceed 600 m. The sides of the fjords are often very steep,

but the deeper basins are usually filled with sediments and may be flat and smooth.

If we consider the hydrographic conditions in the fjords, we may first make the broad statement that they represent a balance between two main water types: the water from outside (coastal and ocean water), and the fresh water supplied from land. Meteorological factors act as a modifying influence. Schematically, the fjord waters may be divided into an upper and a lower layer. In the upper layer, salinity and density are relatively low, but, like the temperature, they are highly variable with the season. In the lower layer, the seasonal variations are small. The distance between the two layers is variable in depth and sharpness. The layering is most pronounced during the summer when the supply of fresh water is greatest and heating is strongest. Furthermore, the layering pattern varies under different climatic conditions. This description is valid for the fjords in central western Norway (59-63°N). In this region, the convection in winter reaches a maximum depth of

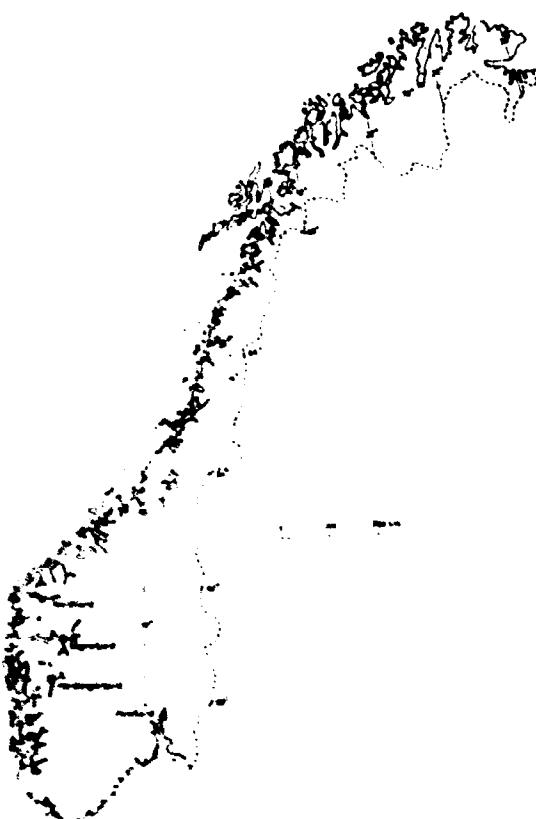


Fig. 1. Distribution of fjords along the Norwegian Coast.

ESTUARIES: PHYSICAL FACTORS

20-30 m. Under the more severe climatic conditions in the northern part of the country, the stratification may be completely broken up in winter, with convection reaching from top to bottom. Several examples of this have been found in the fjord system in Tromsø, about 70°N (Sælen, 1950).

In the fjords of central western Norway the layer of brackish upper water is thin. Below 20 m the salinity is above 30‰ all year. Figures 2 and 3 show the longitudinal salinity sections of the Hardangerfjord in August and February, 1956. The August section shows the strong stratification in summer and the thinness of the upper layer in comparison with the large deep water masses which have a salinity of

about 35‰. In the February section the stratification is not so pronounced; there still is an ample stability, but the salinity has not changed noticeably in the deeper layers. In the Sognefjord, the salinity is close to 35‰ in the deep water, whereas in the third of the large western fjords, the Nordfjord, it is between 34.8 and 34.9‰. This small difference between the deep water salinities of the three fjords is because the Nordfjord's effective sill is on the coastal banks, about 100 m outside, whereas the sills are 150 m outside Hardangerfjord and Sognefjord. Generally, the salinity of the deep fjord water is closely related to the depth of the sill. As the salinity of the surface layers of the coastal waters is more

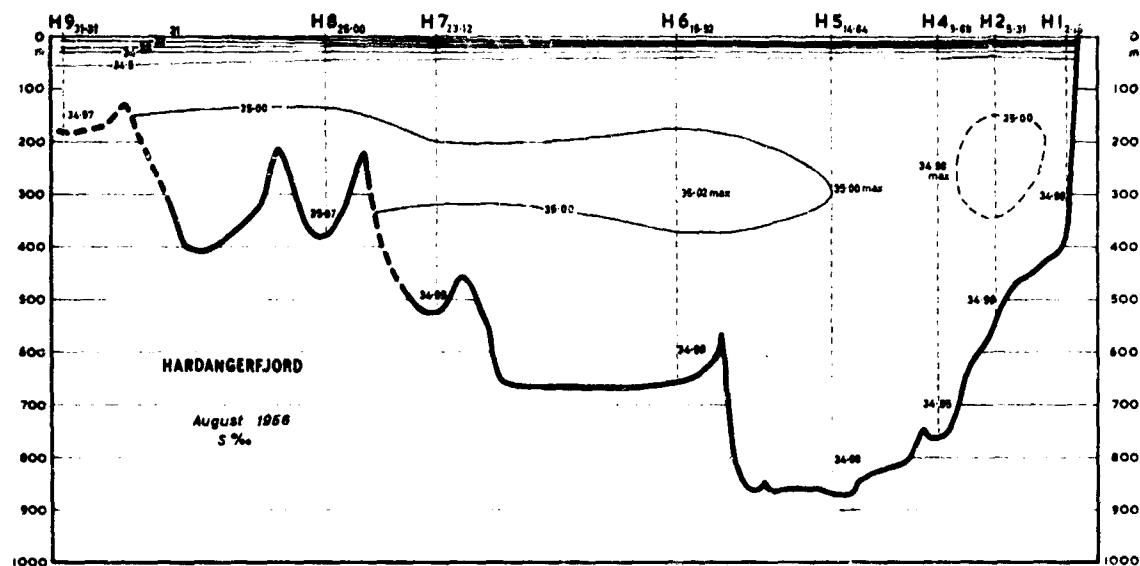


Fig. 2. Distribution of salinity in a longitudinal section of the Hardangerfjord, August, 1956.

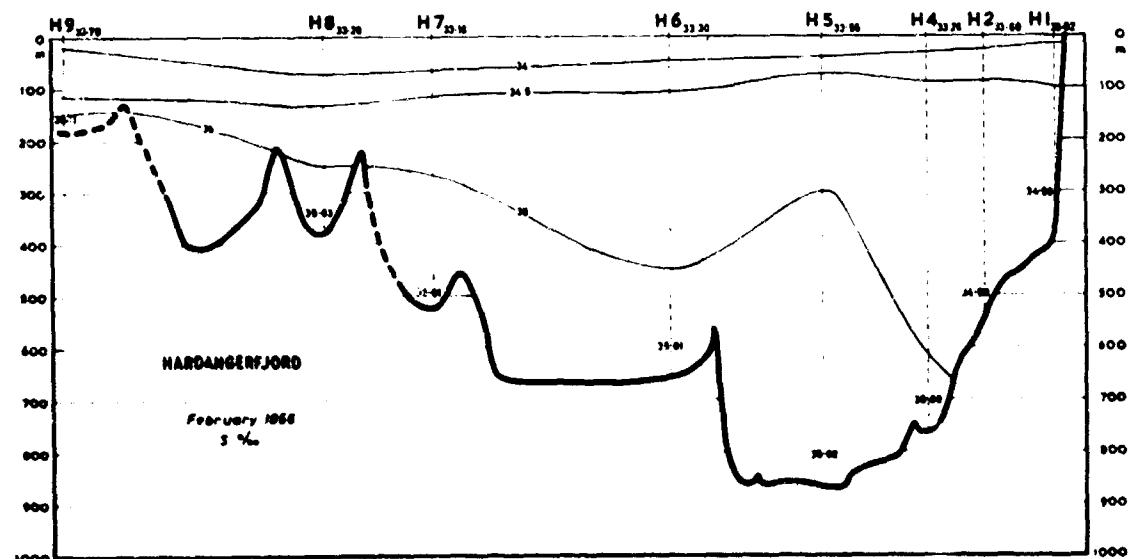


Fig. 3. Distribution of salinity in a longitudinal section of the Hardangerfjord, February, 1956.

than 33‰ in winter, however, it is possible for water to penetrate into the basins of fjords with shallow sills of just a few meters. Thus the Lysefjord near Stavaneer has a sill of 13 m and a salinity of 33.8‰ at 175 m deep.

FJORD CIRCULATION

There are two main features of fjord circulation, and they should be considered separately: first, the currents connected with the freshwater supply; and second, movements in the deeper parts of the fjord.

EFFECT OF FRESH WATER ON CIRCULATION

The freshwater supply and its immediate consequences are illustrated by the findings of station H4, in the inner Hardangerfjord, about 30 km from the head of the fjord (Fig. 1). Figure 4 shows the discharge from the biggest four rivers, and the surface salinity at the station is shown by the broken line. The inverse relationship between the surface salinity and the freshwater supply is obvious. The freshwater supply is very small during the winter, and the surface salinity is high, above 33‰. When the snow melts, large amounts of fresh water are discharged into the fjord and the surface salinity decreases to 9‰. Obviously, the circulation system conditioned by the freshwater supply develops primarily during the summer season. In winter, the fjord may be regarded as just another rather uninteresting bay. Figure 5 shows a period with a sufficient supply of fresh water and the conventional scheme of circulation. Through a cross section of the fjord an amount of water T_u , with salinity S_u and temperature θ_u , is carried out of the fjord as a surface current. Below this current an amount of water T_i , with salinity S_i and temperature θ_i , is flowing in while the freshwater supply during the period is denoted by R and its temperature by θ_r . Allowing for an increase M of the

salt content, we obtain, by considering the balance of water and salt:

$$T_u = \{[S_u/(S_t - S_u)] [R + (1000M/S_u)]\}$$

and (1)

$$T_u = \{[S_t/(S_t - S_u)] [R + (1000M/S_t)]\}.$$

Before the snow starts to melt in the spring, the salinity in the fjord will be high even in the surface layer. As the snow begins to melt, the upper layers will gradually be strongly diluted with fresh water. There will be a strong turbulent mixing both vertically and laterally, and the amount of salt contained in the fjord will decrease; that is, M will be negative. In such cases, the outflow T_u may not be much higher than the freshwater supply R , so that we find a weak circulation with a small value of the inflow T_i . In the Hardangerfjord, between April 26 and June 7, 1956, it was found that the inflow T_i could, at most, have been one-half of the freshwater supply during the same period. When the first rush of the snow melting is over, and a substantial surface layer of brackish water has been formed along the whole fjord, conditions gradually approach a stationary state, so that we can put $M = 0$ in equation (1). We may then use Knudsen's equations:

$$T_u = \{[S_u/(S_t - S_u)] R\}$$

and (2)

$$T_i = \{[S_t/(S_t - S_u)] R\}.$$

For the fjords in western Norway, the stationary state will be approximately realized during the period of June-August when the salt content of the fjord, with a large freshwater supply, will stay reasonably constant. In fact, in some cases one may find a slight increase in the mean salinity of the upper 30 m from one month to the next during this period. In equation (2), we always have $S_t > S_u$, so that the amount of outflowing water will be greater than the freshwater supply. The magnitude of the factor $S_t/(S_t - S_u)$ is difficult to determine without knowledge of the current profile. The outgoing current is probably concentrated to the uppermost few meters, so that an appropriate value of S_u can be found rather easily. It is more difficult to estimate the depth of the ingoing

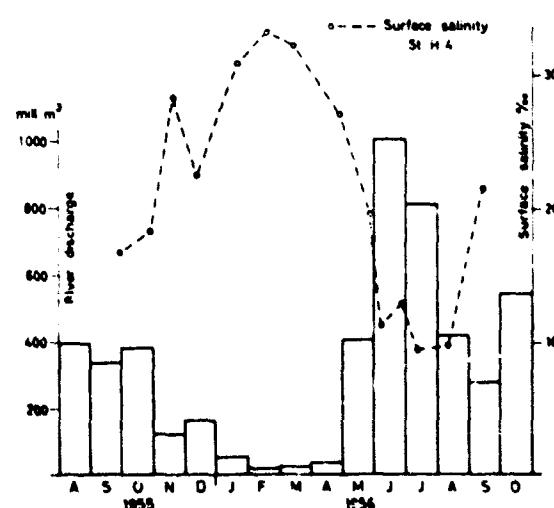


Fig. 4. Discharge of Eio, Kinsø, Opa, and Tyssø Rivers into the innermost areas of Hardangerfjord, and surface salinity at station H4.

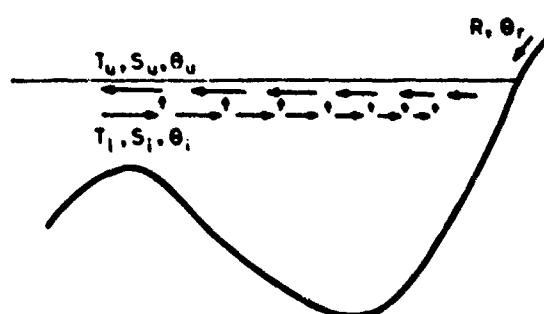


Fig. 5. Upper fjord circulation, schematically.

flow, even if there is evidence that it will be a relatively shallow flow rather close below the outgoing flow. The corresponding salinity S_i can thus be determined only within rather wide limits. For the larger Norwegian fjords, the factor $S_i/(S_i - S_u)$ will probably vary within an interval from 2 to 6, when the section is taken at the mouth of the fjord. That is, the surface outflow of low-salinity water will be between 2 and 6 times as large as the freshwater supply. These considerations apply to the fjord as a whole. The following qualitative sketch can be given for the circulation within the fjord, assuming the conditions are stationary and that there is an ample supply of fresh water.

The surface salinity will increase steadily from head to mouth, as will the amount of outflowing surface water. The low-salinity surface layer is thin, with a sharp vertical salinity gradient, so that we find more than 90% of the salinity of the bottom water at 20-30 m. At some depth below the outflowing surface water, more saline water is flowing inward in an amount which compensates for the difference between outflow and freshwater supply. In order to preserve continuity, the inflowing water must have an upward velocity component, so that along the fjord a total amount of water corresponding to the inflow is added to the outflowing upper water. In each cross section of the fjord, the horizontal convergence of the inflowing water equals the horizontal divergence of the outflowing water, with the vertical transport as the "connecting link". A rough estimate of the vertical velocity, taken as a mean for a certain period and for the whole area of the fjord, can be made from the equation:

$$\bar{w} \cdot I \cdot F = T_i = \{[S_u / (S_i - S_u)] R\}, \quad (3)$$

where I is the length of the period, \bar{w} is the mean vertical velocity, and F is the area of the fjord. For a numerical example, we have used the Hardangerfjord during a summer month. Then $F = 715 \times 10^4 \text{ m}^2$, $R = 3 \times 10^4 \text{ m}^3$, $I = 2.6 \times 10^4 \text{ sec}$, so that $\bar{w} = 1.6 \times 10^{-4} [S_u / (S_i - S_u)] \text{ cm sec}^{-1}$. With the factor $S_u / (S_i - S_u)$ between 1 and 5, \bar{w} will be between 2×10^{-4} and $8 \times 10^{-4} (\text{cm sec}^{-1})$, corresponding to a daily vertical ascent of the order of half a meter.

Perhaps more information could be obtained by relating the balance of heat to the balance of salt content. The increase of fjord temperature in sum-

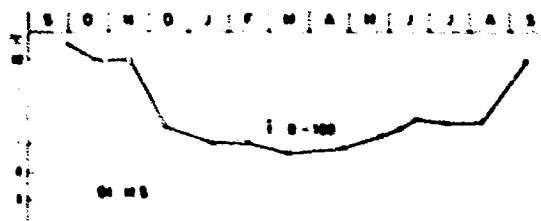


Fig. 6. Mean temperature 0-100 meters, station HS in central Hardangerfjord, 1955-1956.

mer is limited to a thin upper layer of warm surface water which is carried out of the fjord by the surface current, while the lower compensation current carries colder water. In spite of the heat supply from sun and atmosphere, there will be little or no increase in the heat content of the fjord as a whole. This is illustrated in Figure 6, which is based on data taken from a station in the center of Hardangerfjord. During the period of June-August, 1956, the variation of the mean temperature in the upper 100 m was so small that we might use the equation for a stationary heat budget: $T_i \theta_i = I \theta_i + R \theta_i + Q/cq$. In this equation q is density and c specific heat, and the net result of radiation, evaporation, and heat transfer processes is denoted by Q (integrated over the entire surface of the fjord). When we eliminate T_i and T_u by means of Knudsen's equations, we obtain a linear relationship between S_i and θ_i :

$$\theta_i - \theta_u = [1/S_u (\theta_u - \theta_i) - Q/cqR] (S_i - S_u). \quad (4)$$

If we can assign known values to all of the parameters in this equation except S_i and θ_i , then we can in a θ - S diagram draw a straight line on which the point (S_u, θ_u) must lie. This point must also be on the θ - S curve for the section which has been used as the outer limit of the fjord. If this curve has been observed, the values of θ_u and S_u may be found, in principle, by the intersection of the two curves (Fig. 7), and thus we might arrive at the approximate mean depth of the inflow. However, there are so many sources of error in this method that its practical use will probably be limited. The parameters in equation (4) are not precisely known; this applies to θ_u and even more so to Q . Moreover, the θ - S curve for the

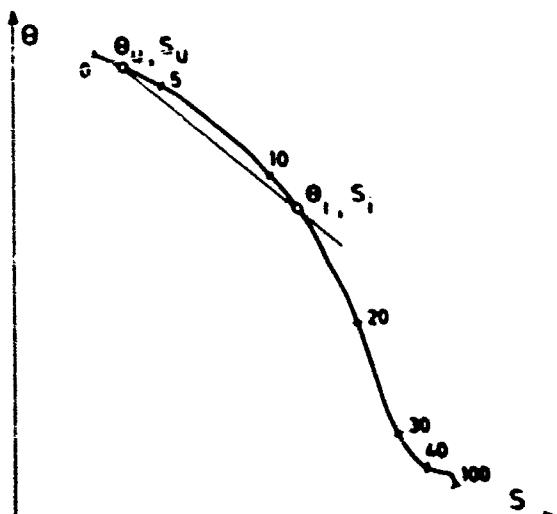


Fig. 7. Schematic determination of the depth of inflow by means of the heat balance. θ_u, S_u are temperature and salinity of the outflowing water and θ_i, S_i of the inflowing water. Depths in meters are indicated along the curve.

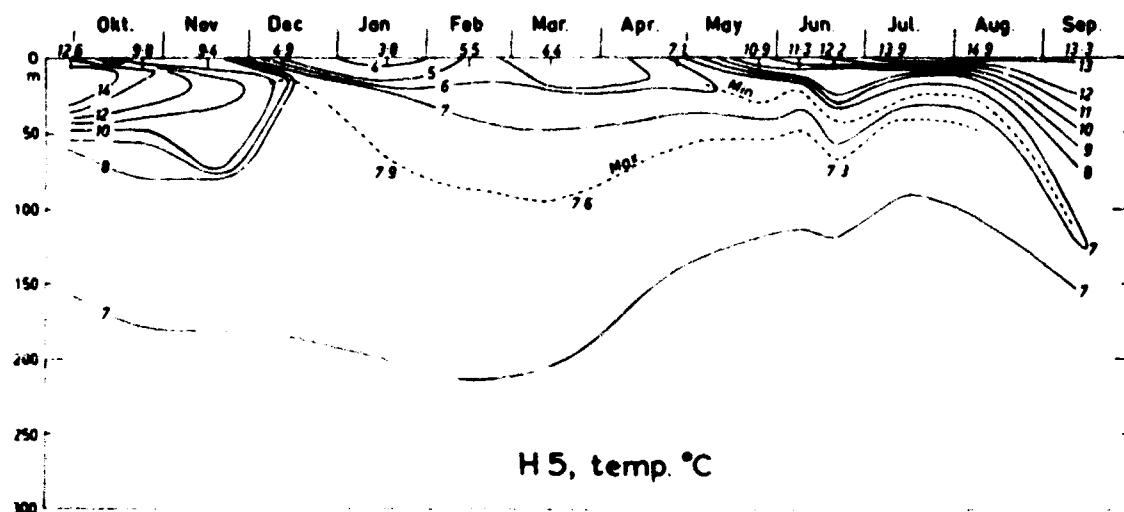


Fig. 8. Temperature isopleths for station H5 in central Hardangerfjord, 1955-1956.

limiting section should be taken as a mean for the period, whereas we usually have only a few hydrographic stations operating during that time.

From the test period of August to September, the mean temperature of the upper 100 m increases by 2°C. (Fig. 6). The sharp thermocline in the upper layer is broken down, and the warm water apparently has penetrated downward, as shown in the thermo-isopleth diagram for a station in central Hardangerfjord (Fig. 8). Evidently the heat supply from sun and atmosphere cannot, even with the most optimistic estimates, account for more than 1/3 of the increase of the heat content in the fjord. This phenomenon is not peculiar to the Hardangerfjord or to this specific testing year; it has been found to occur in other fjords and in other years. It seems difficult to escape the conclusion that the advective heat supply to the fjord must have been reversed; there must be an inflow of water at a subsurface level and a corresponding outflow of colder water at a still deeper level. The idea of such an inflow somewhere between 10 m and 100 m was strongly corroborated by a radical change

in the stock of phytoplankton that took place between August and September—a change that could only be explained by such an inflow. There are indications that the corresponding outflow has taken place at sill depth. I cannot yet offer any full explanation of this phenomenon, but it is probably connected with some general mechanism and is not just a local incident.

DEEP WATER AND CIRCULATION

The second main feature in fjord circulation is the movements in the deeper layers. They are closely connected with the depth of the sill, or with the possibilities of communication with the coastal and oceanic water masses. Even in fjords with shallow sills, the deep waters have a salinity of more than 32‰, so that there must at some time have been an inflow of deep water. In such fjords, however, it may be long between inflows, but the salt water may, under favorable circumstances, remain for a long time in the deep basins. This will sometimes result in stagnant conditions with an absence of oxygen and a development of hydrogen sulfide (H_2S). Relatively

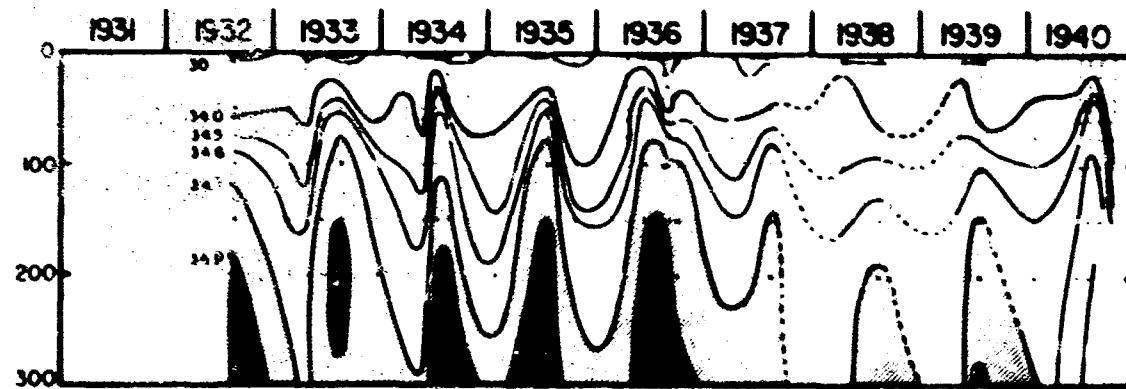


Fig. 9. Salinity isopleths for a station in the outer basin of the Nordfjord.

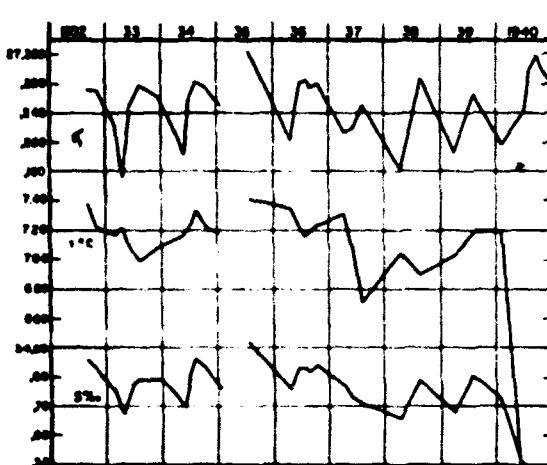


Fig. 10. Variation of temperature, salinity, and oxygen at 300 meters at a station in the outer basin of the Nordfjord.

few Norwegian fjords are of this type, and if we consider only fjords with a reasonable sill depth, such as the three large fjords of western Norway, it becomes obvious that their deeper layers are amply ventilated. The oxygen content is high, 5–6 ml/l or even more, corresponding to a percentage saturation of 80–90. This indicates frequent communication with outside water by inflow over the sill. The frequency and regularity of such inflows differ from one fjord to another. As an example we shall first use the Nordfjord, from which observations are available for a long series of years. This fjord is about 90 km long, and is divided into two basins by a secondary sill 125 m deep. Figure 9 gives an isopleth diagram for salinity during a period of eight years at a station in the outer basin. Obviously, saline water has flowed into the deeper layers of the outer basin every summer except in 1940. The variation of density at 300 m at the same station (Fig. 10) confirms this impression. There must be a regular annual mechanism; at some time during the summer, the water at sill depth outside the sill is heavier than that inside at the same depth, and it will therefore flow over the

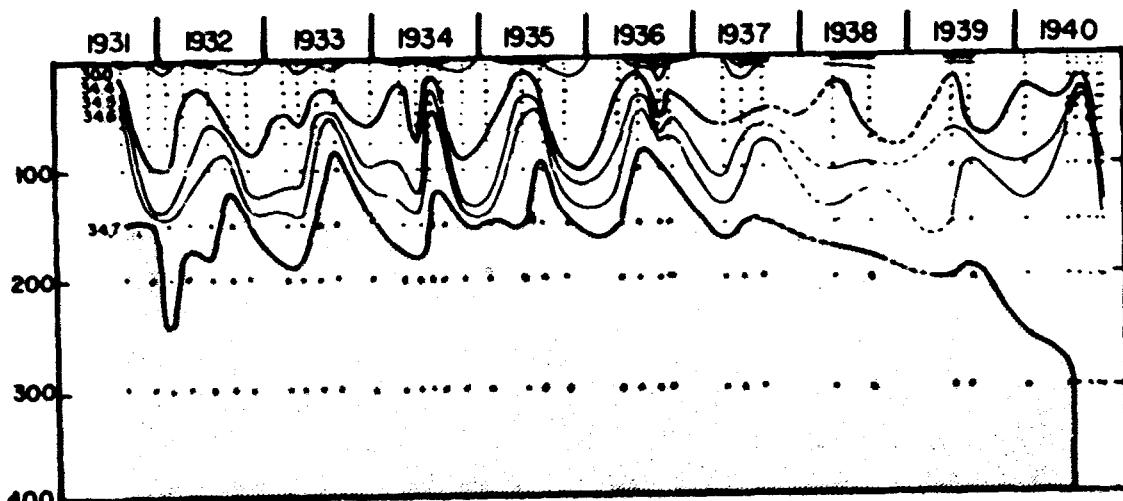


Fig. 11. Salinity isopleths for a station in the inner basin of the Nordfjord.

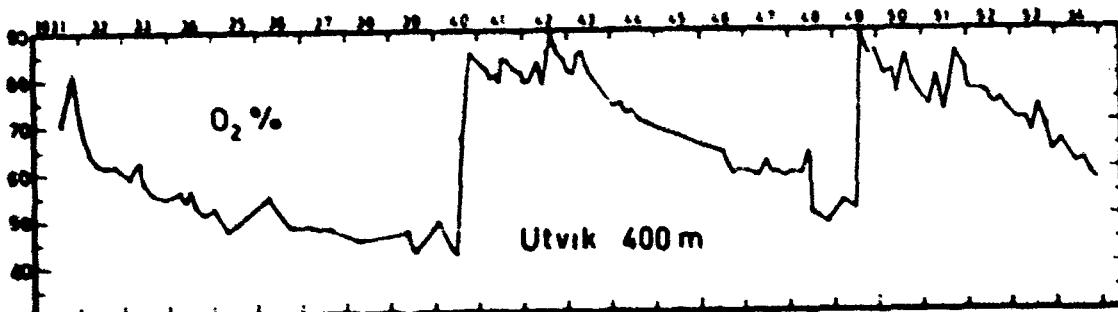


Fig. 12. Variation of oxygen at 400 meters at a station in the inner basin of the Nordfjord.

sill and mix with the deep basin water, or fill the deeper part of the basin. As in most other fjords on this coast, the inflowing water is the "Atlantic" type, with salinity close to 35‰. Under special circumstances, other water types may be flowing in, as shown in 1940 when the inflowing water had a salinity of only 34.5‰, and a very low temperature of 5.5°C. The inner basin of the Nordfjord forms an interesting contrast to the outer basin. In the inner basin, the deeper layers are obviously undisturbed for longer periods, as can be seen from the salinity isopleths for a station inside the secondary sill (Fig. 11). In the shaded area of that figure, the salinity is between 34.7 and 34.8‰. The variation of oxygen content at 400 m at the same station gives a striking illustration

of the conditions (Fig. 12). From 1932 to 1940 the oxygen percentage decreased steadily to a minimum of 43 percent, but in 1940 it suddenly increased to 90 percent and was accompanied by a temperature decrease of 1°C. After 1940 the oxygen percentage steadily decreased with only small changes in temperature and salinity until 1947, when it again rose suddenly to 90 percent—and this time it was accompanied by marked increases in temperature and salinity. In the following years, the oxygen content again steadily decreased. Evidently, the inflows that have occurred every year in the outer basin have not been strong enough to carry any appreciable quantity of water across the secondary sill. A change to high oxygen content takes place only in years with an exceptionally

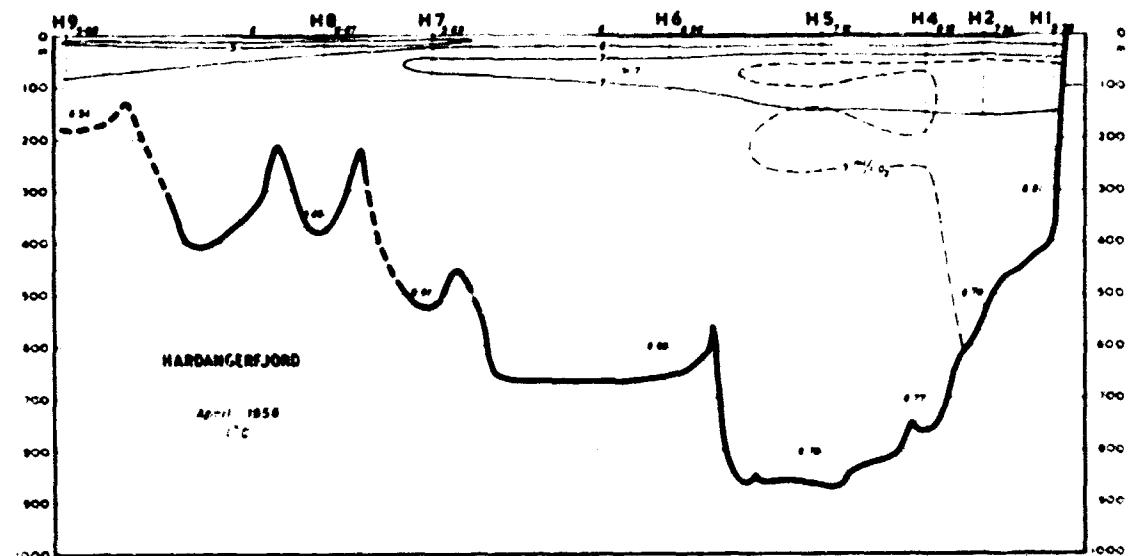


Fig. 13. Distribution of temperature in a longitudinal section of the Hardangerfjord, April 25, 1956.

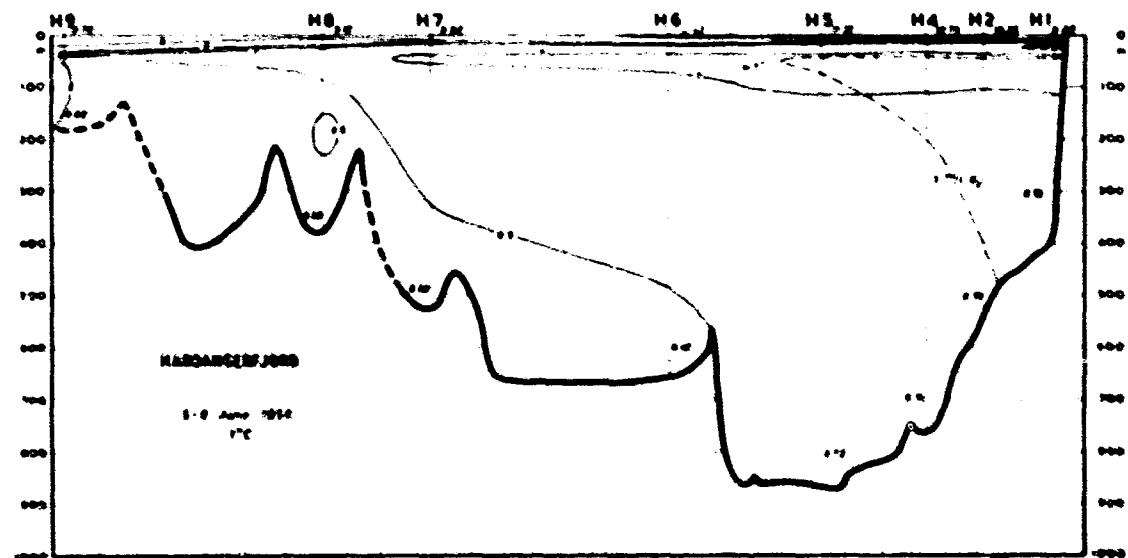


Fig. 14. Distribution of temperature in a longitudinal section of the Hardangerfjord, June 6, 1956.

strong inflow. Figures 13 and 14 show temperature sections from Hardangerfjord, which are excellent examples of inflow to the deeper fjord water. In the section for April 1956, the temperature of the bottom water was above 6.6°C., at the central stations 6.8°C., and these conditions remained for half a year. In the June section we get an excellent impression of the flow of colder water from outside along the bottom. We are not yet able to show whether such inflows are annually recurrent in Hardangerfjord, but in the Sognefjord the deep inflows do not seem to be so. The deep circulation in the fjords is probably independent of the upper-layer circulation. It is possible that deep circulation may influence the upper layer by taking the place of the compensatory flow in that system. We still know very little about the nature of the deep

inflows. Do they come as sudden gushes or as a smooth, gentle flow? In the near future, we shall try to place a recording current meter, some meters above the bottom, on the sill of the Hardangerfjord. If this experiment is successful, we may obtain more information on this interesting phenomenon.

LITERATURE CITED

- PRITCHARD, D. W., 1952. Estuarine hydrography. In *Advances in Geophysics*, edited by H. E. Landsberg; vol. 1. Academic Press, New York.
SAELEN, O. H., 1950. The hydrography of some fjords in northern Norway. *Tromsø Museums Årshefter, Nat. Hist. Avd. No. 38, Vol. 70* (1947).
PICKARD, G. L., 1961. Oceanographic features of inlets in the British Columbia mainland coast. *J. Fisheries Res. Board, Can.*, 18:6.

Salinity Measurements in Estuaries

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Of all the characteristics which typify estuaries, perhaps the most distinctive is salinity variation. The complete range of salinities from fresh water to sea water is always found, and only found, where freshwater runoff meets the sea. Here within a few miles, sometimes a few hundred yards, occasionally within a few feet vertically, the water changes its character from one natural extreme to the other. Superimpose upon this the ebb and flow of the tides and one has more salinity variations in a small area than deep-sea oceanographers encounter in a whole ocean.

Because salinity values are so local and transient in estuaries, there is rarely much to be gained in determining them with maximum precision. Chesapeake Bay, for example, is one of the larger estuaries. Presumably the salinity variations found there will be more gradual and more systematic, and hence more suitable for precise measurements, than in most smaller systems. And yet from the data of Pritchard (1952) one can readily estimate that the typical summer salinity gradients in the middle bay are such that a precision of $\pm 0.003\%$, which is now standard in deep-sea oceanography, would be wasted unless the position of the station were specified to within 40 feet, the time specified to within 90 seconds, and the depth specified to a quarter of an inch! (This latter specification, in particular, points up the amount of useless noise and random fluctuation which is invited by unnecessarily high sensitivity.)

Perhaps even $\pm 1\%$ would be wasted precision to a biologist slogging about in mud and *Spartina* along the edge of a tidal flat where the salinity of adjacent puddles can sometimes vary by several parts per thousand.

In most cases salinity measurements in estuaries call for greater convenience of measurement, not greater precision. It is not more decimal places which are needed, but simply more measurements in more places at more different times.

PURPOSES OF SALINITY MEASUREMENTS

Salinity measurements in estuaries can be used for four main purposes, to each of which a different level of precision is appropriate:

First, there are studies of transport, flushing, and mixing such as the Chesapeake Bay studies just mentioned. This volume includes contributions from Han-

sen, Pritchard, Saelen, and Rattray dealing with specific studies of this kind, as well as a general review by Bowden. Quantitative work of this nature, based on detailed salinity profiles, requires salinity data good to $\pm 0.1\%$, or even to $\pm 0.01\%$.

Second, salinity can be used in a more qualitative manner as a tracer to label different water masses in an estuary according to the amounts of sea water they contain. Following isohalines, one can trace out boundaries due to eddies, to stratified flow, and to "streakiness" of flow. Such a qualitative study of the dynamics of an estuary and of the changes in behavior during a tidal cycle should always precede any detailed quantitative measurements. Stations for repeated samplings or continuous observations should not be selected without some assurance that the location is reasonably representative of the condition one wishes to observe. For a qualitative survey of this sort, the important requirement is not precision, but a continuous, readily interpretable reading. A continuous *in situ* recording made from a small boat moving around an estuary is very enlightening if the record is interpreted on the spot and the boat is maneuvered accordingly.

Third, salinity, or the lack of it, is an ecological factor to the biologists. Salinity limits the distribution of various species, and some of them are economically important. Of course, no species which customarily makes its home in an estuary can afford to be too fussy about the exact limits of salinity which it will tolerate. Seasonal variations in freshwater runoff, variations in tidal height with lunar cycle and with storms and winds, random local fluctuations in currents are all going to subject an estuarine species, even a motile one, to an uncertain range of salinities. As Gunter (1961) pointed out, however, there is still plenty of reason to measure and report numerical values of salinity instead of falling back on ambiguous descriptions of estuarine waters as "fresh", "brackish", or "salt". In general, salinities measured to a relative precision of 5 percent should be quite adequate for ecological purposes. This would come to $\pm 1\%$ when the total salinity is about 20%, and $\pm 0.1\%$ when the salinity is only 2%, etc. Very shallow waters and waters along the shores of estuaries present special salinity problems which are interesting to biologists. The salinity of water amid a clump of

weeds may easily be several parts per thousand different from the salinity in a channel a few yards away. The salinity in the mud a few millimeters below the bottom can be almost constant while the salinity of the overlying water varies back and forth through a tidal range of perhaps 10 %. Groundwater seepage along the shore can affect local salinities. The biologist who wants to observe this kind of salinity variation needs a simple, rugged, easily portable salinometer. Again, precision is not called for.

Fourth, salinity concerns water users on the streams flowing into an estuary. Occasional salinity intrusions are a major factor in the quality of the water supply available to these people. For their purposes a reliable continuous monitor is required, such as the instrument described by Beamer (1962). A method which can detect small amounts of sea water in otherwise fresh water is particularly desirable. The problems of water quality control on tidal rivers, against the more general background of salinity variations in estuaries, have been thoroughly reviewed by Keighton in his report for the U. S. Geological Survey in 1954.

CONDUCTIVITY MEASUREMENTS

Despite this variety of purposes of salinity measurements and the markedly different levels of sensitivity required, almost all of these measurements can be well performed—in many cases best performed—by determinations of the electrical conductivity of the water. Sea salt is an electrolyte mixture which is completely dissociated in water into its component ions. Each ion carries an electric charge and is free to move. Every ion contributes to the electrical conductance of a seawater solution. The more sea salt, the greater the conductivity, almost (though not quite) in direct proportion.

There is, in principle, only one minor drawback to conductivity as a measure of salinity: The conductivity of salt water also depends on the temperature, and salinity and temperature frequently change together. The conductivity of water increases with temperature because the ions move faster as the water warms up, about 2½ percent faster per degree centigrade. Thus a temperature rise of 1°C. has the same effect on the conductivity of ordinary coastal sea water as adding 0.7 % to the salinity. Since the absolute error is proportional to the total salinity, this temperature error is less in brackish water, amounting to only 0.1 % when the total salinity is about 4.0 %.

A rough temperature correction is easy to make. In cases requiring greater accuracy, standard tables based on the data of Thomas *et al.* (1934) can be used. The corrected conductivity value is a direct measure of the total electrolyte content of the water. Marine scientists have been very slow in accepting conductivity measurements because these have had a reputation for inconvenience and unreliability in field use.

Many of the practical difficulties encountered in

conductivity measurements were discussed by Carritt (1952). The principal source of trouble has usually been the problem of connecting a seawater element into an electrical circuit.

All metallic electrical circuits are really electron circuits—the electric current is carried solely by electrons which pass freely from one metal to another. In sea water the current is carried by ions. If a current is to pass into water from an electrode, there must occur at that electrode one or more electrochemical reactions in which ions are converted to neutral atoms and molecules, or vice versa. If this conversion process gets jammed up in any way—a condition generically referred to as “polarization”—the apparent resistance of the cell is increased. One can minimize such effects by using platinum electrodes coated with finely divided platinum known as “platinum black”, but this coating wears off with time or gets poisoned. Moreover, all surfaces exposed to sea water tend to get fouled with a film of slime which can drastically affect electrode performance. Reliable salinity measurements can be assured only by carefully tending the electrode surfaces, or by making repeated calibrations.

Various conductivity devices using electrodes have been developed and used successfully for extended periods in spite of these electrode difficulties. Pioneers among these devices include the conductivity salinometer built for the International Ice Patrol by Wenner *et al.* (1930), the *in situ* salinity-temperature-depth recorder (STD) of Jacobson (1948), and the Woods Hole salinometer designed by Schleicher and Bradshaw (1956). These are all precision instruments designed especially for use with sea water. Many researchers have also made use of the various commercially available general-purpose conductivity devices, including some which are portable and designed for field use.

It is possible to reduce the electrode difficulties by using a four-terminal conductance cell in which there are two “active” or current-carrying electrodes and two “passive” or voltage-sensing electrodes. Such an arrangement is commonly used in resistance measurements when lead resistance is a problem, and may be used with any of the circuits devised for four-terminal resistors (Harris, 1952). With this arrangement moderate polarization at the active electrodes has only a negligible effect on the signal developed between the passive electrodes.

ELECTRODELESS INSTRUMENTS

A big breakthrough in conductance measurements of salinity was made when Esterson and Pritchard (1956) developed a satisfactory instrument without electrodes. They introduced the principle of inductive coupling to bring a seawater element into an electric circuit in the form of a single seawater loop threading a pair of toroidal iron-cored transformers, as shown in Figure 1.

In this system the sea water becomes an integral part of the electrical AC system. Indeed, without the

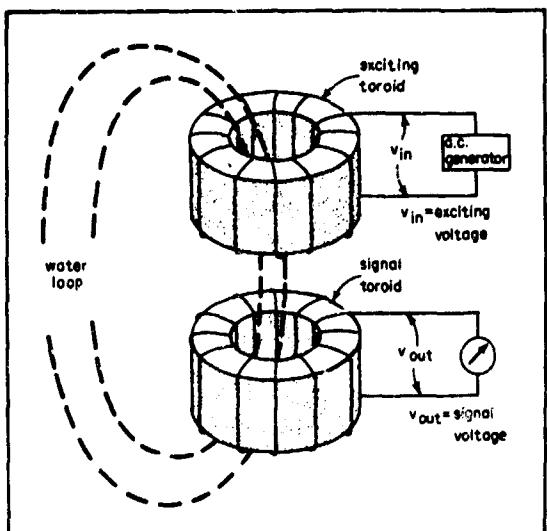


Fig. 1. Illustrating the principle of inductive coupling. The seawater loop threading the two toroids provides the only electrical connection between the two circuits. The output signal is directly proportional to the conductance of the water. (Reproduced by permission of Jerome Williams.)

seawater loop there would be no coupling to speak of between the two coils, and no output signal. Yet the ions move freely back and forth along the loop as the current alternates, so that no electrochemical reactions are required. A similar inductive arrangement for laboratory measurement of conductivity was devised independently by Gupta and Hills (1956) at about the same time.

Because of its practical value this principle of inductive coupling has been widely adopted in recent years. It is the basis of a number of *in situ* instruments now being developed, and is also employed in the precision salinometer designed by Brown and Hamon (1961) which is commercially available from a number of sources.

At the Chesapeake Bay Institute (CBI) where the induction method for salinity measurement was pioneered, the method has been used in two different instruments especially designed for estuarine work:

THE INDUCTION CONDUCTIVITY TEMPERATURE INDICATOR (ICTI)

This instrument has been described in detail by Schiemer and Pritchard (1961). It provides a direct automatic digital readout of both *in situ* conductivity and *in situ* temperature. The temperature readings are made with a thermistor bead and a servo-balanced bridge. With proper calibration these readings are considered to be good to $\pm 0.02^\circ\text{C}$. The conductivity readings can be accurate to ± 0.02 millimhos/cm if a calibration curve is used. From these data a salinity value can be computed to an accuracy of $\pm 0.03\%$. This accuracy is surely sufficient for all estuarine research and is probably more than can be used on smaller estuaries.

The instrument has been used routinely at CBI for standard hydrographic measurements for a number of years. Because of its size, weight, and requirement of 60 cycle, 115 volt power source, this system is suited only to use aboard ship or at permanent installations.

The ICTI can be read continuously and could presumably be modified to permit a continuous chart record.

THE CBI PORTABLE SALINOMETER

This little instrument, shown in Figure 2, was developed by Williams (1961) for general-purpose estuarine work and is well suited for almost all the kinds of estuarine salinity measurements considered earlier. It is a portable, battery-powered, miniaturized version of the ICTI which incorporates the added feature of direct digital readout of salinity. This extremely useful addition is achieved by an analogue computer circuit which sacrifices some of the input accuracy, but still yields salinity values good to 0.3 % at worst.

Readings of the Williams instrument are obtained by adjusting it to a null value and then taking the numbers from a readout built into the adjusting knob. To obtain a correct salinity readout it is necessary first to locate the conductivity null; but even so, the whole procedure is simpler than taking a pH reading with a conventional pH meter.

The instrument can be used anywhere the water is deep enough to cover the sensing head. For measurements near the bottom or near shore some care must be taken not to bury the sensor in the mud or otherwise obstruct the current loop through the toroid. This need for clearance is not very stringent, however, since six inches clearance on all sides is more than enough.



Fig. 2. The small portable salinometer developed by Williams at the Chesapeake Bay Institute. This instrument employs inductive coupling and was especially designed for estuarine work. The object on the right is the sensing head containing the two toroids and a pair of thermistors. (Reproduced by permission of Jerome Williams.)

A slightly modified version of this instrument is manufactured commercially, as is a similar but non-portable *in situ* instrument of about the same accuracy which can be set to read out conductivity, temperature, or depth.

PRECISION CONDUCTIVITY INSTRUMENTS

Several precision conductivity salinometers have been developed during the past decade, and they have been so successful that their use is now the standard method of oceanographic salinity determination at the major oceanographic laboratories. These machines are not generally recommended for estuarine work because they are usually expensive, and their typical accuracy of about $\pm 0.003 \%$ is far beyond what is needed for most estuarine purposes. Moreover, some of the machines are designed to cover only the narrow range of salinities encountered in the deep sea, and are not capable of measuring salinities of brackish waters. Nonetheless, if one happens to have one of the precision instruments available, it makes an excellent and convenient standard for checking calibrating solutions.

Of the various precision instruments, the one designed by Brown and Hamon (1961) is the most practical for estuarine laboratories, since it is portable, less expensive, and covers the entire salinity range from 0 to 40 %.

All of the precision instruments currently in use are briefly described and compared in a recent article by Cox (1963), and an earlier review of this field was made by Paquette (1959). A more general discussion of various precise methods of determining salinity and chlorinity may be found in a recent article by Carritt (1963).

In a slightly different category are the various instruments now being developed for deep-sea *in situ* measurements of temperature, salinity, and depth. Here again the precision required for oceanographic work is likely to be expensive and unnecessary for estuarine work. These instruments are usually too elaborate, or too limited, for estuarine work. This field was recently reviewed by Siedler (1963).

CHLORINITY TITRATIONS

Until the precision conductivity methods were developed, the most accurate salinities were inferred from chlorinity determinations. In the standard Mohr method (or "Knudsen method" as the seagoing version is known) the total chloride in a water sample is determined by titrating with silver ion, using potassium chromate indicator. Fluorescein indicator and indicator electrodes have also been used. The precision of the method is usually about 0.01 % in sea water, improving with dilution. In moderately soft fresh waters chlorinity can be determined to half a part per million. This method is suitable only for laboratory determinations on a finite number of discrete water samples. It can be adapted for field use, but not for continuous or *in situ* measurement.

The Mohr titration is still the standard measurement in many smaller laboratories, and it will surely continue to have a place in estuarine research. It does not require expensive equipment or facilities, and it can be used on any kind of water sample taken from any location. On the other hand, it lacks the immediacy and flexibility of the *in situ* methods, and its precision can be exceeded by the instrumental methods.

Regardless of advances in instrumentation, chlorinity titrations will always be useful for primary salinity calibrations of field instruments and also as especially sensitive indicators of minute seawater admixtures in nearly fresh waters.

SPECIFIC GRAVITY METHODS

Salinity measurements have been made by means of density or specific gravity determinations to various levels of precision. Hydrometers are available at all laboratory supply houses graduated in .001 specific gravity units. In seawater mixtures this would amount to about 1.4 salinity units per division, quite adequate to distinguish fresh water from brackish, and brackish from full sea water. Several firms advertise precision devices graduated in .0005, or even .0002 specific gravity units. With these, one could presumably estimate salinity to within $\pm 0.3 \%$, but only with careful precautions to eliminate surface tension errors.

The density of water changes with temperature, as well as salinity, so that hydrometer readings must be accompanied by simultaneous temperature readings which are accurate to a degree or better. (Some hydrometers have built-in thermometers for this purpose.) Because of the marked non-linearity of density with temperature, a set of density tables or, better still, a temperature-density-salinity grid chart is needed to determine a numerical salinity value. Care must be taken to minimize surface tension errors, and, if it is truly salinity rather than density which is wanted, time must be allowed for the settling out of the sediment load.

The great advantage of hydrometers is that they are very inexpensive (some can be bought for as little as three dollars), extremely portable, and can be used anywhere. For careful measurements they should be used in a water sample in a transparent cylinder, although rough and ready *in situ* measurements are possible if the water is calm and clear, and the operator can get his face close enough to take a reading.

Density measurements with pycnometers and with density balances can be made as precise as the laboratory weighings on which they depend, provided that the corresponding temperature control is achieved. Neither of these methods would seem practical for estuarine measurements.

REFRACTIVE INDEX

The refractive index has been used occasionally for salinity determinations, and it may eventually supplant conductivity as the ultimate precision measurement of

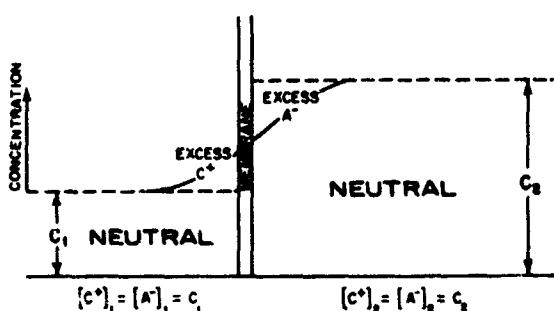


Fig. 3. Illustrating the generation of a membrane potential. The membrane in this case is taken to be a cation membrane passing only positively charged C^+ ions. The higher concentration of salt on the right causes a leakage of positive ions to the left through the membrane. The left-hand solution becomes positively charged with respect to the one on the right.

salinity. For one thing, the inherently greater precision of optical interference methods may be realized now that lasers are available to provide light which is more coherent and more monochromatic than was previously available from any practical light source. For another, the refractive index is more closely related to the density than is any other measure of salinity, so that it will be least biased by the small variations in the composition of sea water which render the conductivity/density correlation and the chlorinity/density correlation imperfect.

However, none of this potential precision is apt to have any value to estuarine research for the foreseeable future, unless—taking the broadest definition of an estuary—someone desires to trace the water from some particular river clear across the continental shelf. Meanwhile, a salinity measurement with a hydrometer can be just as easy and just as accurate as one made with a standard laboratory refractometer costing one hundred times as much. (There is now on the market an optical "total solids meter" designed for blood serum analysis, which has internal temperature compensation, is portable, and is relatively inexpensive as refractometers go. I am indebted to Dr. Earl W. Behrens for pointing out the possible usefulness of this instrument as an estuarine salinometer.)

SELECTIVE ELECTRODES

One method of salinity measurement which is especially well suited to estuarine work, and with which we have had some recent success at Woods Hole, is the use of electromotive force (EMF) measurements with selective electrodes. As the theory of these measurements is not widely understood, it might be well to preface the discussion with a brief explanation.

If two electrolyte solutions of similar ionic composition but at different concentrations are separated by a membrane, and if this membrane is permeable to only one of the various ionic species present, there will be a tendency for the ion to diffuse through the membrane from the side where there is more of it to

the side where there is less of it, as shown in Figure 3. But this process tends, in turn, to produce a net separation of charge. If the ion that moves is, for example, positive, the solution to which it moves gains a net positive charge, while the solution from which it came is left with a net negative charge. An electrostatic potential is set up across the membrane, and equilibrium is reached when the tendency of the ions to move one way because of the concentration gradient is balanced by their tendency to move the other way because of the local electric field. In this condition the electrical potential difference across the membrane—the voltage drop—just matches the difference in chemical potential due to the concentration difference. This condition may be expressed approximately as $\Delta V = [(2.303RT/ZF) \log_{10} (C_2/C_1)]$ where ΔV is the voltage drop across the membrane, C_2/C_1 is the concentration ratio across the membrane of the ion in question, T is the absolute temperature, Z is the charge on the ion, and the other things are constants. At 25°C. the factor $2.303RT/F$ is approximately 60 millivolts per \log_{10} unit, so that each factor of 10 in the concentration ratio adds 60 millivolts to the signal if the ion is monovalent.

When the membrane is permeable to more than one species of ion, the resultant voltage is a kind of average of the different voltages which the different species would produce. In this average, the weighting factor for each species is the fraction of the total current passing through the membrane which this species would carry if an external voltage were applied. This fraction is known as the "transference number" of the ion.

These principles still apply when the membrane is permeable to all ions, or, which is the same thing, if there is no membrane at all. Consequently, any concentration boundary tends to produce a junction potential unless the tendency of the positive ions to make the more dilute solution positive is exactly matched by the tendency of negative ions to make the more dilute solution negative. Concentrated potassium chloride solutions have just this property, presumably because the K^+ and Cl^- ions are identical except for nuclear charge. That is why concentrated KCl is often used for "salt bridges" in laboratory EMF measurements.

The measurement of pH with a glass electrode is the most familiar example of an EMF measurement involving a selective electrode. The glass acts as a membrane permeable only to H^+ ions. Many other examples are likely to be developed in the near future.

A thorough discussion of the subject of membrane electrodes may be found in the review by Hills (1961).

THE SODIUM ELECTRODE

The pH glass electrode has been known for years to be subject to an "alkaline error" in strongly basic solutions due to the slight permeability of the glass to sodium, potassium, and lithium ions. By varying the glass composition, Eisenman *et al.* (1957) found that they could increase this effect and produce a glass electrode that was especially selective for sodium ion.

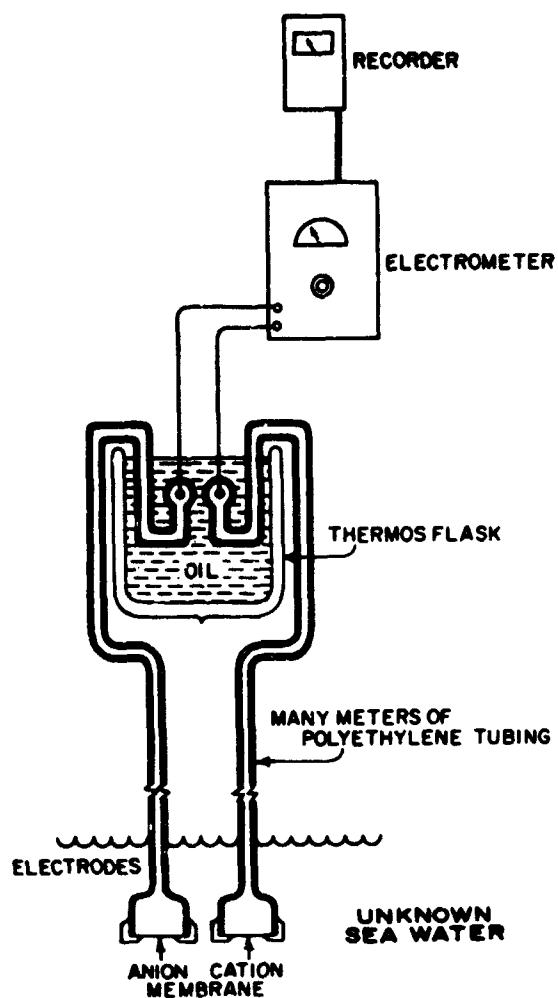


Fig. 4. A schematic diagram of the "salt-bridge salinometer" as developed by Ballard and used at Woods Hole. A key design feature is the thermal and chemical isolation of the metallic electrodes.

This development was followed up commercially by an instrument manufacturer, who now markets a sodium-selective glass electrode which can be used interchangeably with their pH electrodes in one of their pH meters.

With care, and using a reference standard, the sodium electrode can give salinity determinations good to 1 percent relative precision, even in the field. To get this precision, however, one has to measure to .004 pH units, or to about 0.3 millivolts, which requires either a pH meter with an expanded scale or an electrometer with a full-scale deflection of 30 millivolts or less.

The sodium electrode is not uniquely permeable to sodium ion. It is very permeable to hydrogen ion and to silver ion, and is slightly permeable to potassium and other alkali ions. However, none of these can be expected to cause any interference under normal estuarine conditions.

All glass electrodes have to be used in conjunction with a reference electrode. Because the thermal coefficients of the two electrodes are usually different, one may generally expect a small change in the total EMF with temperature at constant salinity. This has to be calibrated and corrected if the system is to be used in the field or *in situ*.

A major advantage of the sodium electrode is the small size of sample it requires. It can actually measure the salinity of anything wet. It can even be shoved into mud to measure the salinity of interstitial waters, as was done by Siever *et al.* (1961). (When this is done, the reference electrode should not enter the mud if it has a liquid junction.)

The properties and uses of the sodium electrode and other cation-selective glass electrodes have been extensively reviewed by Eisenman (1962).

ION-EXCHANGE MEMBRANE ELECTRODES

In recent years a number of firms have developed ion-exchange membranes for possible use in electrical desalination of sea water. These ion-exchange membranes are similar in their chemical properties to ordinary ion-exchange resins, but they come in thin sheets instead of granular form. Like the resins, the membranes come in two sorts: cation membranes which are essentially permeable only to positive ions, and anion membranes which are permeable only to negative ions.

At Woods Hole we have been experimenting with AMFion C-103C cation membranes and A-104B anion membranes. Both are manufactured by the same company, and both membranes have selectivities of about 98 percent.

Because the membranes we have been using are permeable to divalent ions as well as to monovalent ions the concentration EMF generated across a membrane by seawater solutions is less than the 60 millivolts per \log_{10} unit which one gets with monovalent ions. We use the membrane electrodes in pairs, one cation electrode and one anion electrode, so that their signals are additive. For such a combination the concentration EMF generated by sea salt amounts to about 97 millivolts per \log_{10} unit.

A schematic diagram of our measuring system is shown in Figure 4. It is essentially the same as a conventional pH system except for the battery-operated recorder and the unusually long solution path—sometimes as long as 200 meters—isolating the metallic circuit electrodes from the membranes. This isolation is more an accident of evolution than a necessity since the instrument without the membranes, and with probes widely separated, is the salt-bridge geomagnetic electrokinetograph (GEK) which I described in 1962. However, the internal zero-check and the low zero-drift which this arrangement made possible for the earlier use are also valuable here in measuring the membrane potentials. We find that much of the drift and most of the temperature sensitivity normally associated with membrane electrodes is eliminated by this arrangement. The design and

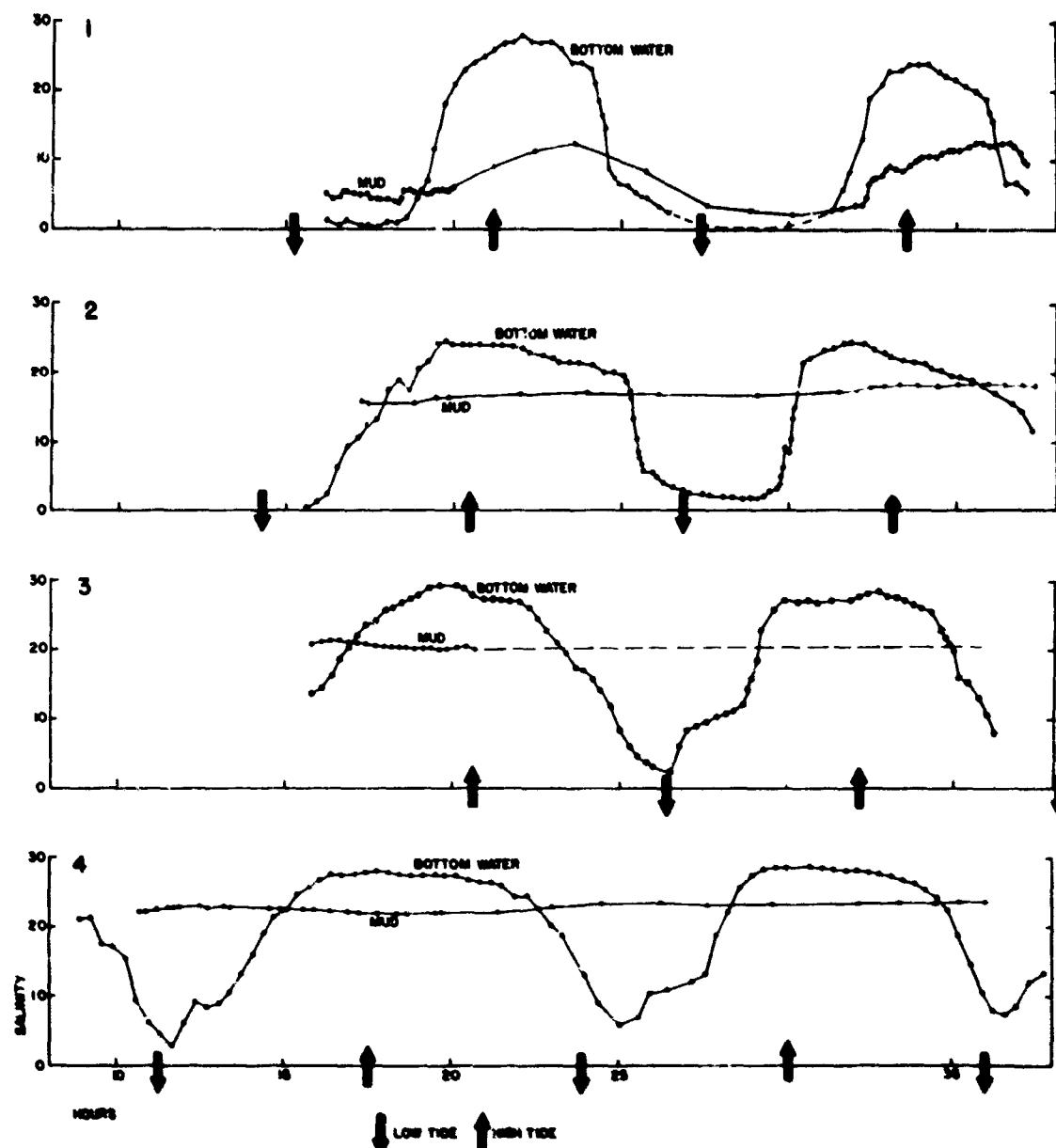


Fig. 5. Salinity measurements made in the Pocasset River Estuary by Howard Sanders and the author using the "salt-bridge salinometer". The salinity of bottom water and of interstitial water in the bottom sediment is compared over one or more tidal cycles by means of continuous simultaneous recordings of the *in situ* salinity.

techniques for using this "salt-bridge salinometer" were worked out by Philip Ballard in 1962.

Howard Sanders and I took this apparatus into the Pocasset River Estuary in a rowboat and made a number of qualitative and quantitative studies of the salinity for comparison with species distributions. At a number of stations we made continuous simultaneous records of the salinities of the bottom mud and the bottom water with results of the sort shown in Figure 5. We also analyzed several core samples.

We think that our usual accuracy is about the same

as one obtains with sodium electrodes, although the instrument is capable of a relative precision of 0.1 percent if pushed to the limit and if extensive precautions are taken, such as filling the two membrane cells with water of approximately the same salinity as the water to be measured.

"SALINITY" IN DILUTE WATERS

The definition of salinity is arbitrary; the concept of a single composition variable which it represents is only useful as long as the composition of the salt

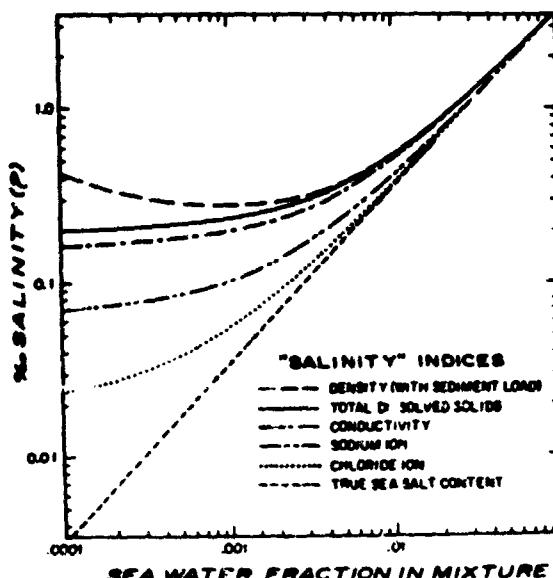


Fig. 6. The various possible indices of salinity diverge wildly as the river salt content approaches or exceeds the sea salt content. For the purposes of this comparison the various methods are represented as though calibrated with mixtures containing only sea salt.

mixture remains constant. As soon as sea water is substantially diluted with river water containing a salt mixture of a markedly different composition, all the various salinity indices which we have been discussing diverge wildly.

This is illustrated in Figure 6, which shows what would happen if we calibrated all the various methods of measuring salinity over the entire salinity range, using sea water diluted with various amounts of ion-free distilled water, and then applied these calibrations to sea water diluted with river water containing about 200 ppm dissolved solids. The curve for density in Figure 6 assumes an arbitrary sediment load diminishing as the salinity increases. The density without sediment would give a curve very close to the curve for "total dissolved solids" and so, presumably, would refractive index. The discrepancy between the various indices when applied to the river water, amounting almost to a factor of 10 between the dissolved-solids estimate and the chlorinity estimate, comes about primarily because the dominant role played by sodium ion and chloride ion in sea water is taken over by bicarbonate ion and calcium ion in river water.

Which of these indices is properly entitled to be called the true salinity? A purist would insist on the total dissolved solids as having the sanction of tradition, but of all the variables, this is the hardest to measure, has the least physical or chemical significance, and is least sensitive to the presence of small admixtures of sea water. One can make a better case for almost any one of the others. The fact of the matter is that there is really no such thing as salinity

in these circumstances, because salinity has only experimental meaning so long as all the salt components vary together. When they begin to vary independently, it becomes necessary to measure them independently and to report them independently.

In the hypothetical experimental situation described here, however, there is a single composition variable: the fraction of sea water in the mixture. This is a variable of practical and theoretical interest to people studying the dynamics of estuaries. It is evident that chlorinity gives the best indication of the actual proportion of sea water in the mixture over the widest range of compositions. This, and the directness of the experimental definition of chlorinity, makes a strong case for those who argue that we should use chlorinity rather than salinity as our basic composition index.

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LITERATURE CITED

- BEAMER, N. H., 1962. Continuous recording of salinity in an estuary. In *Proceedings of the First National Coastal and Shallow Water Conference, October 1961, Tallahassee, Fla.*, edited by D. S. Gorsline; pp. 266-268. Nat. Sci. Found.-Office Naval Res., Washington, D. C.
- BROWN, N. L., and B. V. HAMON, 1961. An inductive salinometer. *Deep-Sea Res.*, 8(1):65-75.
- CARRITT, D. E., 1952. Chemical measurements. In *Oceanographic Instrumentation*, edited by J. D. Isaacs and C. O. D. Iselin; publ. 309, pp. 166-193. Nat. Acad. Sci.-Nat. Res. Council, Washington, D. C.
- CARRITT, D. E., 1963. Chemical instrumentalities. In *The Sea*, edited by M. N. Hill; vol. 2, pp. 109-123. John Wiley and Sons (Interscience), New York.
- COX, R. A., 1963. The salinity problem. In *Progress in Oceanography*, vol. 1, pp. 241-261. Macmillan (Permagon Press), New York.
- EISENMAN, G., 1962. Cation selective glass electrodes and their modes of operation. *Biophys. J.*, 2:259-321.
- EISENMAN, G., D. O. RUDIN, and J. U. CASBY, 1957. Glass electrode for measuring sodium ion. *Science*, 126:831-834.
- ESTERSON, G. L., and D. W. PRITCHARD, 1956. C.I.T. salinity-temperature meters. *Proc. Conf. Coastal Engineering Instruments, Berkeley, Calif.*, 1955; pp. 260-271. Univ. of Calif. Council on Wave Research of the Engineering Foundation, Berkeley.
- GUNTER, G., 1961. Some relations of estuarine organisms to salinity. *Limnol. Oceanogr.*, 6:182-190.
- GUPTA, S. R., and G. J. HILLS, 1956. Precision electrode-less conductance cell for use at audiofrequencies. *J. Sci. Inst.*, 33:313-314.
- HARRIS, F. K., 1952. *Electrical Measurements*. John Wiley and Sons, New York.
- HILLS, G. J., 1961. Membrane electrodes. In *Reference Electrodes, Theory and Practice*, edited by Ives and Janech; ch. 9. Academic Press, New York.
- JACOBSON, A. W., 1948. An instrument for recording continuously the salinity, temperature, and depth of sea water. *Trans. Am. Inst. Elec. Engrs.*, 67:714-722.

- KEIGHTON, W. B., 1954. The investigation of the chemical quality of water in tidal rivers. *U. S. Geological Survey, Open File Report, August, 1954.* U. S. Geological Survey, Washington, D. C.
- MANGELSDORF, P. C., JR., 1962. The world's longest salt bridge. In *Marine Sciences Instrumentation*; vol. 1, pp. 173-185. Plenum Press, New York.
- PAQUETTE, R. G., 1959. *Salinometers. The Physical and Chemical Properties of Sea Water*; publ. no. 600, pp. 128-145. Nat. Acad. Sci.-Nat. Res. Council, Washington, D. C.
- PRITCHARD, D. W., 1952. The physical structure, circulation, and mixing in a coastal plain estuary. *Chesapeake Bay Inst. Tech. Rept. 3*.
- SCHIEMER, E. W., and D. W. PRITCHARD, 1961. An induction conductivity temperature indicator. *Chesapeake Bay Inst. Tech. Rept. 25*.
- SCHLEICHER, K. E., and A. J. BRADSHAW, 1956. A conductivity bridge for measurement of the salinity of sea water. *Conseil Perman. Intern. Exploration Mer., J. Conseil*, 22:9-20.
- SIEDLER, G., 1963. On the *in situ* measurement of temperature and electrical conductivity of sea water. *Deep-Sea Res.*, 10:269-277.
- SIEVER, R., R. M. GARRELS, J. KANWISHER, and R. A. BERNER, 1961. Interstitial waters of recent marine muds off Cape Cod. *Science*, 134:1071-1072.
- THOMAS, B. D., T. G. THOMPSON, and C. L. UTTERBACK, 1934. The electrical conductivity of sea water. *Conseil Perman. Intern. Exploration Mer., J. Conseil*, 9:28-35.
- WENNER, F., E. H. SMITH, and F. M. SOULE, 1930. Apparatus for the determination aboard ship of the salinity of sea water by the electrical conductivity method. *Natl. Bur. Std., J. of Res.*, 5:711-732. Res. Paper No. 223.
- WILLIAMS, J., 1961. A small portable salinometer. *Chesapeake Bay Inst. Tech. Rept. 23*.

Methods and Devices for Measuring Currents

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The development of flow theory has been motivated partly by curiosity and partly by medical and engineering needs. Flow measurement is centuries old, and much early work was done in connection with orifices, tubes, nozzles, and weirs during the 18th and 19th centuries. The art has developed most rapidly during the industrial age because of the need for controlled flow in manufacturing processes, the requirement for better bulk accounting methods, and the realization that strict control of flow is a simple and convenient method for control of other variables, such as temperature and pressure. A good summary on industrial flowmeters appears in the McGraw-Hill Encyclopedia (1960). In order to determine blood flow, the field of medical electronics has developed some of the most sophisticated flow-measuring devices.

Accurate measurements of currents in estuaries are necessary for navigation, for planning the disposal of industrial and domestic wastes, for forecasts of flooding and silting, for the design of piling and other substructures, to plan recreational uses of the water, to protect and develop fisheries, and to conduct other scientific studies. Currents affect navigation by direct action on ships, and they are also agents of bottom erosion and deposition, processes which change the orientation, size, and shape of navigable channels. Knowledge of current drag forces is required for the design and installation of piling, navigation and mooring buoys, and wharfs, as well as for understanding the forces on the floating vessels being used in such construction. In engineering design, as in navigation, the swifter currents are more critical. Strongest currents occur in upper narrow estuaries which become raging rivers when the maximum runoff is augmented by an ebbing tide, and in long inlets which resonate to the tide and have large tidal ranges and swift tidal currents. Examples of the latter are Cook Inlet, Alaska, and the Bay of Fundy. Current speeds of six to eight knots have been measured in Cook Inlet, and particle motion of the tidal bore, a sort of moving hydraulic jump, is calculated to reach 10 to 20 knots. The desirability of water for reclamation, a subject which is receiving ever-increasing attention, depends not only on the degree of concentration of wastes, but also on currents. Very swift currents, stirring up sediment and organic substances, cause water to be turbid; sluggish currents may permit it to stagnate to the point where hydrogen sulfide forms. Shoreline reshaping or other construction may be required to baffle swift and turbulent currents which are hazardous to bathers.

NATURE OF CURRENTS

Currents in estuaries and shallow coastal waters can be caused by: (1) differences in the distribution of density, (2) directly by the stress that the wind exerts on the water surface, (3) tides, (4) stream runoff, (5) transport induced by wind-generated surface waves, and (6) internal waves. Tidal currents and stream runoff are the strongest observed in estuaries, whereas the most feeble are the steady transports due to surface and internal waves. A general description of each type is given in the following paragraphs.

Currents related to variation in distribution of density are caused by gradients in water temperature, salinity, and sediment content. Because of the differences in density, the water surface slopes, and, as a result, a flow occurs in the direction of the down-slope pressure gradient. If the body of water is sufficiently large, the deflecting force of the earth's rotation may be significant, causing the flow to veer to the right (in the northern hemisphere).

Wind blowing over the water exerts a stress on the surface which causes the surface and the upper layer to move with the wind. In shallow-water coastal areas, the surface water flow has been found to attain between two and five percent of the value of the wind speed. Several hours of steady winds are required for the water at 50 to 100 feet below the surface to begin to respond to the wind.

Tidal forces due to the sun and the moon, combined with topographical features, give rise to three types of tidal currents: (a) the rotary type, experienced in shallow waters as well as in the deep ocean, (b) the rectilinear or reversing type, found in elongate bays and estuaries, and (c) the so-called hydraulic type, which is illustrated by the currents in straits connecting two independent tidal bodies, such as the Cape Cod Canal in Massachusetts. All three types are periodic and undergo a full cycle on the U. S. Atlantic and Gulf coasts in 24.8 hours; on the U. S. Pacific coasts, both a 24.8 and a 12.5 hour period are present, and they vary with time and their relative importance to each other.

River and stream runoff often achieve a swift flow which may protrude for great distances in bays and coastal waters because of the momentum and hydrostatic head. If the inflowing water is heavily laden with sediment, it may temporarily tend to overrun brackish waters regardless of temperature and salinity differences. If it is fairly clean, it will tend to overrun brackish estuary waters and will always overrun ocean water.

A fairly steady mass transport of water is caused by surface waves, but this is very small except in and near the surf zone. Because the waves break on shore, there is an outward transport along the bottom and an inward transport at the surface. It is well known that waves breaking at an angle to the shore produce a longshore current flowing parallel to the beach within and just outside of the surf zone. On open ocean coasts the longshore currents achieve one to two knots. Excesses of water piled up onshore by waves and moved parallel to shore by longshore currents turn seaward at intervals as rip currents, thus completing the horizontal cell-like circulation patterns. The rip feeder current and especially the rip current are swift, reaching three to four knots.

Some transport of water is associated with the particle velocity of internal waves. Internal waves occur in coastal waters along the thermocline (level of greatest temperature change with depth). They occur in estuarine waters along horizontal surfaces of density discontinuity caused by fresh and/or clean water overlying sea water or sediment-laden water. Internal wave currents have not been measured with much success; they are theoretically small, a few hundredths of a knot, except perhaps where the internal wave becomes unstable in traveling from deep to shallow water and tends to break.

METHODS

Methods used for measuring flow in estuaries and shallow coastal waters generally involve actually sensing the current directly. They contrast with a method widely employed for the deep ocean in which the current (geostrophic flow) is calculated from measurements of temperature and salinity. That particular calculation cannot be used in shallow coastal waters or estuaries because an essential assumption—that the water is deep enough for bottom waters to be motionless—is not met. Coastal and estuarine currents are measured by path (Lagrangian) or flow (Eulerian) methods. Discussions of some of the techniques used in both methods are given by Johnson and Wiegel (1959) and von Arx (1962).

PATH METHODS

In path applications, objects or substances placed in the stream are carried by the stream; their path-time history gives both flow speed and direction. Probably the best known path method is ship-set, which employs the ship itself as a tracer; the difference of its actual position from that predicted by dead reckoning is a measure of the integrated effects of surface current, wind, and waves. Another example is the drift bottle, or drift card (often ballasted to float mostly submerged), which is released from a known position at a recorded time and is later recovered on shore. This gives the current vector for the thin skin of surface water in which the object floats, but the magnitude is underestimated by an amount which depends on the delay in recovery after reaching shore. Sea anchors, called drogues, are re-

leased at known points, and their positions are determined at intervals along the drift paths; drogues may consist of a metal or wooden cross, fish net, aviator's parachute, or other device having a large drag at the level of measurement, and they are connected by fine wire or nylon filament to a small surface float that may support a pole with a flag, a radar reflector, or even a light for night observation. These are "free drifting" drogues. Another type, which may be called a "semi-captive" drogue, is allowed to drift away from an anchored boat by paying out a measured length of a line. The length of the line and drift time give speed, and the direction of the drogue drift gives current direction. These may be made like other small drogues or they may be current poles. Current poles are vertical shafts of wood or metal tubing suitably ballasted to drift with only a small portion of their length exposed to the wind. Nevertheless, all of the drogue measurements require some correction for direct effect of the surface current and wind on the surface float and other superstructure.

Neutrally buoyant floats constructed of alloy tubing to form a chamber which is less compressible than sea water will hover at a certain level in the sea, according to the amount of ballast added; they are tracked by acoustic ranging techniques. Usually estuaries are too shallow or the waters too well mixed to permit use of this oceanographic tool.

Patches of contaminants consisting of dye (such as fluorescein, Rhodamine, and Pontacyl), radioactive materials, and chemical wastes having sufficiently powerful responses to physical or chemical tests at extreme dilution, are sometimes released and their movement followed by a program of sampling or observing. Naturally occurring tracers, such as suspended matter, dissolved chemicals, and plankton, may be mapped at intervals in time and a general idea of current deduced from the change in pattern of iso-concentration lines. However, such non-conservative biological and chemical properties may change from non-physical causes; hence the determination of the physical motion of the water by using these properties is difficult.

To obtain a path-time history, which shows both speed and direction, all of the path methods require that the vessel's position and the time sequence plotting must be fairly accurately known. Positional surveying for path methods may be divided into visual, sonic, and electronic. The visual method is most commonly used within sight of land and consists of triangulation using transits or theodolites from shore or a sextant aboard ship. These methods are well known. The electronic and sonic methods are divided into two groups—the circular methods and the hyperbolic methods. The circular methods are the radio wave equivalent of surveying without a theodolite and chain, in that the position is determined by measuring distances or angles. Circular methods include radar, sonar, and the sonic method which utilizes a seismometer. The hyperbolic methods depend upon the fact that the lines of constant phase difference of radio

pulses or continuous waves of two different transmitting stations are hyperbolic. The intersection of hyperbolic lines from two signal-emitting stations determines the boat position. Examples of hyperbolic methods are loran, raydist, lorac, and decca. The desired accuracy of position for path method measurement is not great (compared with requirements of other surveying), and one of the less costly techniques can be used. In some areas advantage can be taken of an existing navigational system of good accuracy.

FLOW METHODS

In flow methods a device, restrained at a fixed point in intimate contact with the fluid, generates a signal. Often a secondary device is used to translate the signal into a motion or secondary signal for indicating, recording, or computing the volume of the flow. Flowmeters first transform the speed into differential pressure, differential temperature, electromagnetic induction, differential sound velocity, transit time, rotation, momentum, or displacement, and then measure these effects. Rotation is the most popular technique; some forty instruments used in streams or lakes and the ocean have used this principle.

The speed of water flowing past an instrument mounted above the bottom or suspended on a cable can be measured from (1) the number of rotations over an interval of time of a suitable freely turning propeller, wheel, or rotor, (2) the torque of an arrested propeller or rotor, (3) the ram pressure on a plate, membrane, sphere, or Pitot orifice, (4) the slope of a wire supporting a drag or the force on the drag, (5) the cooling effect of flow on a heated element, (6) the change of the velocity of sound between two points a known distance apart or sound Doppler effect, and (7) the motional e.m.f. of the flow through a known natural or artificial magnetic field.

In flowmeters, the flow direction is obtained by vane or foil alignment or by transit direction of a drifting substance. Usually only the angle in a horizontal plane is measured. Recording and telemetering have been performed by visual, audible, and photographic methods, by emulsion fixation, mechanical integration, chart recorder, paper punched tape, and magnetic tape. These instruments can be classified roughly into those which register or record internally, and those which transmit the speed or direction of flow to a remote observer or recording apparatus. Instruments in either category may be designed for intended measurements over a period of time.

Since many flow devices have been used and are available, the next section will list some basic types with comments on the characteristics of each.

FLOW DEVICES

DIFFERENTIAL PRESSURE CURRENT METERS

These devices register a difference in pressure between two points which must be measured and converted by equations or calibration to obtain flow. Methods of measuring differential pressure include the

simple, popular U-tube manometer as well as more refined readouts such as a float-operated mechanism or a weight-balanced ring-type meter to provide controlling, recording, and totalizing functions. Diaphragm and bellows-type differential pressure measuring devices were developed to eliminate manometer fluids or to provide faster response and easier installation. Examples of these include force balance and deflection. Both are well suited to either pneumatic or electrical transmission of the flow signal. Their output, of course, is proportional to the square of the velocity. The primary devices for the differential pressure measurements include an orifice, Venturi tube, flow nozzle, Pitot tube, and pipe elbow. The law of conservation of energy requires that the total energy at any given point in a stream be equal to the total energy at a second point in the stream, neglecting losses between the points. While it is possible to convert pressure (potential energy) to velocity (kinetic energy) and vice versa, the total amount of energy does not change. By use of a restriction or an angle in a pipe, a portion of the potential energy of the stream is temporarily converted to kinetic energy as the flow speeds up to pass through this primary device. Beyond the restriction the flow particles slow down until the velocity is once more the same as that in the conduit upstream of the restriction, except for the effect of turbulent and frictional losses associated with the acceleration and deceleration at the restriction. The magnitude of the loss depends upon the configuration of the primary device. All of these primary devices must be rotated or oriented into the stream by a vane or foil.

DIFFERENTIAL TEMPERATURE CURRENT METERS

Current meters based upon the principle of differential temperature consist of an electric current passing through a small resistance element (wire, film, or bead) causing its temperature to rise above the ambient temperature. Unless the resistance element is insulated from the surrounding fluid, there will be a flow of heat from the hot element into the cooler fluid. If the fluid is moving relative to the hot element, the rate of heat transfer will be considerably greater than if it is stationary. The rate of heat transfer depends on the difference in temperature between the element and surrounding fluid, the characteristics of the element, the free stream flow velocity, and the characteristics of the flow (laminar, transitional, turbulent). There are two basic types—the constant electric current type and the constant temperature type. Such a device must be calibrated against a primary flow standard. A reference element which is protected from the flowing stream is usually employed and the difference is measured between the element exposed to the flow and the protected one. As a rule, these systems require elaborate electronic circuits in order to insure constancy of the electric current or of the temperature. The systems have generally been inadequate for long-term, continuous measurements, but are very sensitive, being

capable of measuring quite small velocities and having the good response required for measuring turbulence.

ELECTROMAGNETIC INDUCTION CURRENT METERS

These may be divided into two types. The first relies upon the e.m.f. induced by water currents moving across the earth's magnetic field. The second type produces its own magnetic field and measures the resulting voltage gradient. Perhaps the major advantage of the geomagnetic type is that with proper calibration it can be used to measure the entire transport through the entrance to a bay or through an estuary. It cannot be used in the vicinity of the earth's magnetic equator. For the geomagnetic measurements, the electrodes may be either stationary or towed. Stationary electrodes are ideal for measuring total flow through a cross section of water, but because of the great variation in conductivity of the bottom and its effect on the measurement, they must be calibrated in place, using other techniques such as current meters or drogues to obtain the reference flow values. Towed electrodes have the advantage of permitting measurements in any part of the estuary, but because of the influence of bottom conductivity in shallow water, they are not recommended for use in estuaries unless they can be calibrated against other devices in all locations in which such measurements are to be taken.

With the electromagnetic meter, a magnetic field is applied to a localized area of the flowing liquid. By this method, it is possible to measure the voltage that is generated between two electrodes which are perpendicular to the magnetic flux and in contact with the liquid. Since this voltage is strictly proportional to the velocity, a linear flow record or indication results. Practical flow measurements can be made in any liquid that is at all conductive. The linear scale allows accurate flow measurements over a greater range than is possible in the differential pressure meters. Since there is no obstruction by the device to fluid flow, the method has particular advantages for measuring flow in pipes, which make it possible to measure thick slurries and gummy liquids. The electrodes have been mounted on a rod which protrudes from a ship's hull and is used for the ship's speed log. For estuarine and oceanographic use, the rod is mounted above the bottom on a stationary structure and measures the flow of water past it. The rod is about two inches in diameter and two feet long; if only two electrodes are used, the rod must be properly oriented to measure the flow. However, in two applications, a number of pairs of electrodes were placed on a cylindrical rod and the output obtained was used to determine the flow direction as well as the speed in horizontal plane. The electromagnetic meter is useful for measuring turbulence and a large range in velocities, but it is quite expensive. Both a geomagnetic-type measurement and an electromagnetic device used by Soviet oceanographers were described by Senezhinskii (1954).

DIFFERENTIAL SOUND VELOCITY AND DOPPLER CURRENT METERS

The velocity of sound in a fluid is different up and down stream, and this difference is indicative of the flow rate. In its simplest form this type of current-measuring device consists of a stationary acoustic wave transmitter, a stationary receiver, and a device to measure the transmission time. The practical system transmits the acoustic wave first in one direction and then in the opposite direction, and measures the difference between the transmission times. When used on moorings or suspended from a vessel, the transmitter and receiver are mounted in a fish or foil which aligns the two units along the axis of flow. Then it is necessary to measure the alignment of the fish by another technique to determine the flow direction. When mounted on the bottom or on a piling, however, an additional receiver and transmitter may be used to measure the two components of the horizontal flow at right angles to each other. The output from this three-transducer array may then be resolved to obtain the total velocity vector in a plane. The unit may be used for measuring turbulence that is relatively large scale compared with the spacing between the transmitters and receivers. The output is linear with flow velocity, and it may be used over a wide range of speed. This ultrasonic current meter is fairly expensive compared with other current meters. Electronic circuitry required to correct for ambient effects makes this type of flow measurement costly for multiple sensor installations.

Several acoustic current meters based on the Doppler shift principle have been designed and tested. One of the more recent is described by Koczy *et al.*, 1963. The instrument consists of a transmitting and receiving transducer operating on a five-megacycles per second acoustic signal. Measurement is made of the Doppler shift or frequency change that results when a transmitted wave is reflected from a moving object (in this case the particulate matter in the water). The Doppler current meter provides a sensitive and accurate sinusoidal output for measurements of a unidirectional, turbulence-free current containing particulate matter such as exists in a properly designed flow tube.

This meter, like the other devices described thus far, is non-inertial and responds to rapidly changing irregularities or turbulence in the medium, whereas most of the mechanical meters read the average or integrated gross water movement past them and smooth out these irregularities.

TRANSIT TIME

In simplest form, these instruments consist of a source probe and a pickup probe. Radioactive substances, dye, or other chemicals are introduced in spurts into the stream by the source probe, and the amount of time required for the water to transport the foreign matter downstream to the pickup probe is accurately measured. The tracer may be introduced

Table 1. Rotating element current meters (From Johnson and Wiegel, 1959).

Meter	Location of Recorder			Degree of Continuity in Record		Depth Limit (ft.)	Velocity Range (knots)	
	In Instrument	Remote Recording	Radio Transmission	Single Value	Several Values		Minimum	Maximum
Propeller Type Meters								
Ekman	x			x		None	0.1	1.5
Ekman Repeating	x				x	None	0.1	1.5
Ekman-Merz	x			x		None	0.04	5.8
Witting Magnetic		x			x	1500	?	?
Rauschelbach	x				x	200	?	?
Idrac Vertical		x			x	?	?	?
Sverdrup-Dahl (Bifilar)	x				x	150	0.1	0.9
Sverdrup-Dahl (Magnetic)	x				x	Large	0.1	0.9
Fjeldstad	x				x	None	?	?
Roberts Radio		x		x		x	300	7.0
von Arx-I		x			x	None	0.15	6.0
von Arx-II		x			x	1000	0.15	6.0
Iwamiya	x				x	650	?	?
Nan'niti		x			x	Large	?	?
Ono	x				x	160	0.1	6.0
BBT-Neyropic	x				x	800	?	9.0
Dunkerque	x				x	160	0.1	?
Chusey	x				x	320	0.1	?
Ott-V		x			x	150	0.06	10.0
Bohnecke	x			x		None	?	?
Komatsu		x			x	Large	?	5.0
Pegram	x				x	Large	?	?
Cup and Paddle Wheel Type Meters								
Price	x				x	100	0.07	5.3
Pettersson	x				x	150	?	?
Pettersson Bottom	x			x		?	?	?
Winters	x			x		150	?	?
Carruthers Drift Ind.	x			x		None	-	-
Carruthers Vertical Log	x			x		10	?	?
Idrac	x			x		300	?	?
Mosby	x				x	None	?	?
Hydrowerkstaten	x				x	160	?	?
Snodgrass	x				x	?	0.1	4.0

at regularly programmed intervals by electric pulses from the surface or by a lead weight messenger sliding down a wire from the surface. The source and pickup probes are mounted in a foil which aligns the two probes with the flow direction. Direction of the orientation of the foil must be measured in another manner in order to obtain current direction.

When it is possible to attach the device to a bottom mount or to a piling, then a number of pickup probes may be arranged in a circle with the source probe in the center, and by reading the output from all of the probes it is possible to obtain the direction as well as the speed. Several instruments of this sort have been built and tested, but no extensive use in estuarine or ocean waters is known to the writer.

The U. S. Geological Survey is developing an instrument for stream gaging which will give surface velocity only and will measure transit time by utilizing optics for pickup. In use, the instrument would be held a short distance above the water and aligned with the flow direction. A control is adjusted until two images (obtained from the fore and aft ends

of the instrument) of the suspended material pattern in the flowing stream are brought into superposition; a calibrated direct-reading meter shows the velocity.

ROTATION CURRENT METERS

Of the large number of current meters that have been developed over the years, those using propellers, cup systems, or other rotating devices have been the most popular. The flowing water rotates the element, the speed of rotation is determined, and the velocity of the stream is derived. The meter is calibrated by moving it through still water in a towing tank. Outside of industry, development of rotation current meters has been carried out principally by two groups: the oceanographers engaged in the study of ocean currents and the hydraulic engineers involved in stream gaging. The oceanographers have been greatly inconvenienced by the lack of a stable observing platform as well as the need to determine both speed and direction of the current throughout relatively great depths. Hydraulic engineers, on the other hand, usually have the convenience of a relatively stable plat-

form, such as a bridge or cableway, although gaging from a boat is necessary in some large rivers. Stream gagings are usually made upstream from the influence of tidal action; hence the flow is unidirectional and parallel to the stream banks so that current direction determinations are necessary only where cross flows exist. The estuary researcher may find himself using methods from either field, but it is a great convenience when he can utilize a fixed platform or anchor the vessel tautly.

The propeller and cup or paddle wheel are two types of meters which employ a rotating element. Those that have been proven to be fairly reliable after use for a period of time have been described in detail by Johnson and Wiegel (1959). A copy of a table from their report (Table 1) describes for these meters the location of the recorder, the degree of continuity in record, the depth limit in feet, and the velocity range in knots. Of the 32 meters listed, 17 record internally and the rest are set up for remote recording. Twenty-one of the 32 provide for continuous recording, whereas the others give only several readings or a single reading on a given lowering of the instrument. Of the internal recording devices, five record photographically; four drop shot into a compass box; one makes an impression of indicating dials on tinfoil; four have chronographs; one prints mechanically on a thin metal foil; and one prints mechanically on paper. Of the remote recording devices, two are direct reading; ten utilize a chart or chronograph; one provides electric pulses; and another acoustic pulses which may be either counted, recorded, or integrated. All are made for free suspension except the Carruthers vertical log, which is mounted over the side of light ships, and the Mosby meter, which was constructed for setting on the bottom and measuring velocity shear along the sea floor. Five of the meters do not measure direction; these include the Idrac vertical (direction not applicable) and the Mosby meter, in which direction was not of interest; the other three are the von Arx-I, Price, and Carruthers vertical log, whose orientations are intended to be observed visually from the surface. In addition to the rotation meters listed above, several kinds of propeller meters have been constructed in the past primarily for stream gaging, but very few of these are now in existence. Discussions appear in the literature on at least seven of them, including descriptions of the meters and their characteristics, but such information now is of only historical interest.

Six other rotation-type meters used in Russia have been described by Senezhinskii (1954). One of these is a cup-type rotor giving current speed only; five are the propeller type of which two measure current speed only, and three give both speed and direction. Two of the six current meters transmit signals to the surface for recording on board ship. The other four record internally; two of these four record photographically or on film, and one is a counter type. Several variations on the counter type include a metal foil record and an integrator.

Wave action and the roll of the ship cause many of the rotation-type meters to give erroneous results. In several of the instruments, some attempt has been made to overcome this by placing the rotating element in a ring or tube. Additional auxiliary equipment on some of the meters includes depth-measuring apparatus and temperature sensors.

Of the current meters listed, those which are in most popular use today for stream gaging are the Ott meter in Europe, Asia, and Africa and the Price meter (Fig. 1) which, together with the Pygmy meter (not described by Johnson and Wiegel) are used in the United States. In general, these are not used in sea water.

The primary instruments used by oceanographers in the United States are the Roberts meter (Fig. 2) and the Savonius rotor as modified by Snodgrass (Fig. 3). The modified Savonius rotor with direction vane is currently on the market with outputs suitable both for telemetering and for recording on ship or on other platforms as well as for self-contained recording photographically and on magnetic tape. The Roberts current meter has been modified for improved circuitry, larger fins, and a larger impeller for reaching lower thresholds; it may be suspended from shipboard or moored in shallow-water locations for telemetering to shore. The modified Savonius rotor meter is more practical than the modified Roberts meter for direct reading, but it is somewhat awkward to handle and has a maximum range of about five knots. With large end plates, the modified Savonius

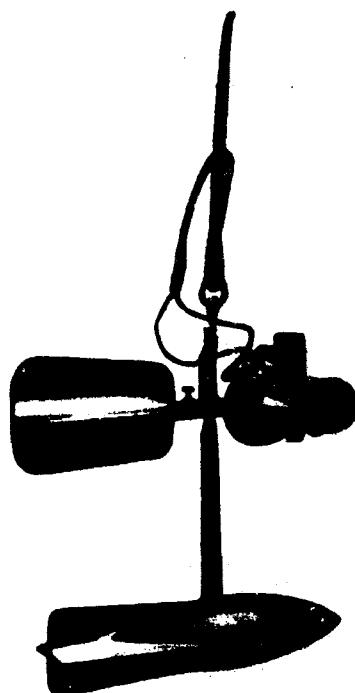


Fig. 1. The Price current meter (Courtesy of General Motors Defense Research Laboratories).



Fig. 2. The Modified Roberts current meter.

rotor response to vertical motion is minimal. In some configurations the modified Savonius rotor has lower threshold limits than the modified Roberts meter. The modified Roberts must record on a chart for analysis, because the direction reading is obtained from the ratio of the time interval between a direction and a velocity pulse relative to the time interval between two velocity pulses.

MOMENTUM OR DISPLACEMENT CURRENT METERS

These fall into several categories. One is the variable-area, constant-head meters which include the rotameter and piston slot. In the rotameter, the fluid flows upward through a tapered tube, lifting a shaped weight (possibly misnamed a float) to a position where the upper fluid force just balances its weight; elevation of the float is read against a vertical scale to give the current speed. In a piston-type current meter the buoyant force of the liquid carries the piston upward until sufficient area has been uncovered in a slot in the side of a vertical tube to allow the liquid to flow through the slot. The position of the piston indicates the flow rate, and by proper shaping of the slot, a meter may be made with a uniform flow scale. Mechanical, pneumatic, and electrical position-sensing mechanisms are available to make recorders, indicators, and totalizers of these devices.

Another type of meter depends upon measuring the force exerted upon a body by a fluid flow. The force being measured is that necessary to restrain the body in some equilibrium position. Force may be measured directly by spring balance, indirectly by strain gages, or the angle extended by a cable supporting the body. If these devices are large they are usually designed to measure a steady current. Reduced to small size, however, they will follow rapid fluctuations. An inexpensive device developed by Pritchard and Burt is known as a captive drag. It consists of a bi-plane cross which is suspended from an anchored ship by a small-diameter wire, and a gage is mounted on the wire to measure the deviation of the angle from the vertical. The magnitude of this angle depends upon the depth of the drag, the force exerted on the drag by the current, and the submerged weight of the drag. It is advantageous to use a plastic drag which elimi-

nates the need to make accurate measurements of its weight in the field, as are necessary when the drag is made of water-absorbing plywood. Theoretical relationships between the wire angle and velocity have been found adequate to a depth of at least 50 feet when a drag 2 X 3 feet has been used; a plastic drag of this size has been calibrated in a tow tank.

Several current meters have been designed to measure flow, using the principle of drag displacement of a small object; in these the measurement is done by wire angle gaging, or by measuring the horizontal displacement of the drag object, or by determining the force exerted by the fluid on a fixed object (example of the latter is the piezo-electric measurement). Methods of pickoff for these devices vary. In one case a pendulum and a compass are mounted within a case filled with gelatin. As the meter body cools, the gel viscosity increases considerably, which attenuates quasi-periodic motion. Finally, it freezes and the pendulum and compass are set in a mean position. For reuse, the unit is simply reheated in hot water to melt the gelatin. In one case, the recording principle is

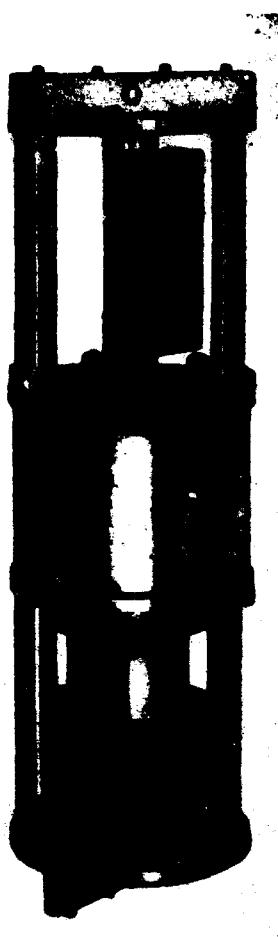


Fig. 3. The Snodgrass current meter (Courtesy of General Motors Defense Research Laboratories).

photographic. Nine such meters have been discussed in detail by Johnson and Wiegel.

MEDICAL ELECTRONICS COMPARISONS

It is interesting to examine what has been done on flow measurement in the field of medical electronics. The measurement of blood flow is one of the most fundamental of physiological measurements. Numerous methods for measuring various parameters of the circulation of the blood have been developed. Yet despite many years devoted to such studies, there is no generally accepted method for measuring the volume of flow. Many of the methods are adaptations of methods previously developed for use in industry. A few were developed originally for measuring the flow of blood and subsequently were adopted by engineers or physicists for other applications. Thirty papers were presented at a blood flowmeter symposium of The Institute of Radio Engineers (I.R.E.) in 1959; four were on the ultrasonic flowmeter (based on sound velocity differential); 12 dealt with electromagnetic flowmeters including gated sine-wave, chopper-operated, square-wave, and DC types; one concerned an orifice-plate producing a pressure differential; one utilized nuclear magnetic resonance; one was a miniature turbine; three dealt with measuring the transit time of various tracers, including air bubbles, dye, and radioactivity; two concerned measuring temperature transport or temperature differential; one involved measuring drag; and the remainder were theoretical or descriptive papers including one which compared the characteristics of a number of differential pressure meters used in blood flow measurements.

Most of the blood flowmeters have probe miniaturization, a feature which has not been generally required of flowmeters in other fields. Possibly some of these devices can be adapted in oceanography for cases in which miniaturization of the transducer is advantageous.

The nuclear magnetic resonance flowmeter (which is one of the newest of these blood flow devices) offers large dynamic range and theoretically good accuracy. The fundamental basis of the method is the absorption of r.f. energy by protons in a substance containing hydrogen, when subjected to a strong steady magnetic field of appropriate radio frequency. This absorption is due to induced transitions between energy levels of the spinning protons in the magnetic field, and depends principally on the magnitude of the magnetic and r.f. fields and on the number of susceptible nuclei present. If a substance is caused to flow through the combined magnetic fields, the amount of energy absorbed varies with the flow rate.

LIMITATIONS

Factors limiting measurements of estuarine flow are turbulence, organisms and suspended matter, motion of the platform or mooring, atmospherics (including ice), vandalism, and public accidents. Practical problems in the direct measurement of currents in the sea

have been described in detail by Paquette (1963) and only a summary will be given herein.

Previous discussion in this paper indicated that errors in currents measured by meters hung from a ship or buoy occur not only because of turbulence but also because of the motion of the platforms used for most meters. Errors which can occur without motion of the platform include distortion of the near-surface flow by the platform, deviations of a magnetic compass in the current meter by iron on the platform, elasticity and hence distorted response of a long suspending cable, dynamic errors of the current meter itself, and meter depth variations which are indeterminable when a long suspending cable without a depth element is used.

Dynamic errors associated with current meters have been classified by Paquette into five types: (1) those due to slow, more or less random movements of the platform, (2) those due to the elasticity of long suspensions and the elasticity and slack in moorings, (3) those due to dynamic insufficiencies in the meter itself which prevent accuracy when following rapid transients, (4) those due to pendulous or elastic cord types of oscillations of this suspension which are excited by the rolling and heaving of the platform or by turbulence, and (5) those due to vertical motions of the meter.

Slow movements of the platform occur with each change of current and with each gust of wind. Long suspensions buffer the current meter against short rapid movements of the platform but diminish the ability of the meter to detect transients in the velocity at depth. The mooring inevitably has elasticity (often by design) in order to absorb shock loadings. Taut moors are recommended wherever feasible to diminish this effect.

Rapid transient horizontal motions, real and artificial, are presented directly to the current meter by wave motion, or indirectly by wave-induced platform movement, or natural turbulence of the water. The effects are most serious when the real currents or their means are small compared to the real or artificial transients. Failure in directional response to these rapid changes by most propeller-type meters is apparent. In the presence of such transients, the modified Savonius rotor, which is equally sensitive to flow from all orientations, reads a fictitiously high value for the steady flow.

For a suspended current meter, errors occur because of pendulous elastic-cord and rotary oscillations. A calculation of resonant lengths shows that a suspension which is 300 feet in length will resonate to a 20-second period. Since most ships' rolls are in the region of 5 to 10 seconds, this corresponds to lengths of 20 to 80 feet, and one should anticipate a greater likelihood of resonance in this region. Of course, the small boats likely to be used in bays and estuaries have a shorter period of roll.

Errors due to vertical motions on current meters arise from four causes: (1) asymmetrical water flow about the rotor generated by the body of the current

meter, (2) direct sensitivity of unhoused rotors to vertical motion due either to front-to-back symmetry in the propeller blade or to a form of turbine action which occurs in horizontally oriented bucket wheels, (3) porpoising, and (4) fairly constant tilting of the meter due to current drag which exposes a projection of the face of the meter to vertical motion. To overcome the last effect, the original Snodgrass telemetering current meter was suspended in a gimbal and dynamically balanced for torque moment and therefore remained vertical from 0 to 5 knots.

In summary, with some suspended current meters and existing techniques, the problems of stray motion and limited dynamic response are serious when the current is feeble. Generally speaking, small short-period fluctuations are difficult to measure. The large, long-period transients may be measured with fair accuracy but may obscure mean currents in those areas where the transients far exceed the means. Of existing mooring systems, the stiff taut-wire moor with a small surface float serves fairly well in the depth below the submerged buoy.

Living organisms which infest current meters installed over a period of time provide a great deterrent to successful operation. The live foulants may be controlled rather well by applying the standard anti-corrosive, anti-fouling paint system such as that used by the U. S. Maritime Administration for ships' bottoms. Waterborne suspended matter, in estuaries which have very large tidal ranges or in swift streams, is abrasive to meters and it is especially wearing on non-purging bearings of the current meters with rotating elements.

If optical or visual sightings are used, the path method can suffer from adverse atmospheric. Vandalism is a sizable problem for unintended installations near shore or in heavily traveled water routes, including the high seas. Public accidents can occur and public curiosity has brought occasional delays or hindrance. The writer, conducting a path method study in San Diego Bay, released 12 near-surface drifting drogues. On the first positioning run three of the drogues were missing; one was found on the deck of a submarine moored in the middle of the Bay, and another was found sitting on a Broadway pier.

FUTURE DEVELOPMENT

Future solid state devices for measuring flow in estuaries and the ocean will continue to be expensive for some time since few such precise instruments are required. Examples of future development of solid state items may include a frequency-modulated acoustic flowmeter and a nuclear magnetic resonance flowmeter. The latter has been shown to be theoretically capable of more accuracy than the acoustic and electromagnetic meters for measuring blood flow (Symposium, I.R.E., 1959).

There is a great need for a current meter of rapid response in both direction and velocity which is insensitive to stray motion and will integrate accurately to zero all of the undesired cyclic motions (Paquette,

1963). A step in this direction could be a restrained drag or a rotor and a small vane with each having good and nearly equal response characteristics. The flow speed could be reduced into the net magnetic north and magnetic east components for the time interval sampled by using sine and cosine resolvers motivated by the vane; they could operate on the flow speed signal and provide the two component outputs to two integrators.

Lightweight, inexpensive current speed detectors with simple direct-reading meters will undoubtedly be required in larger quantities, and as the demand increases, they will become more economical to purchase and use. But their cost will be more than tripled when the requirement is added for direction, measured in relation to compass orientation.

RECOMMENDATIONS

Selection of a method and device for flow measurements depends upon available support facilities, type and training of personnel, planned use of data, budget, device availability, and data handling program. The importance of data handling cannot be overemphasized; it is now possible to record the data for ready input into machines and no manual handling is required. In this case an analog quick look or alternate method of scan to inspect the data for possible difficulties is desirable.

Plans for a current measuring program must consider time-space requirements for data, desired data accuracy, range of flow magnitude, data format, as well as some prior study of the flow regime to estimate its turbulent, oscillatory, slowly varying, or steady state. A combination of methods and devices for measurements is frequently used to provide cross calibration; a secondary method may be used to eliminate errors or interference from measurements taken by the prime device.

CONCLUSIONS

The swiftest currents in estuaries are due to tidal ebb and flood and to stream runoff. The current, averaged over a period of tens of minutes to several hours, may be measured by tracing and plotting the trajectory of drogues, patches of contaminants, etc.

Numerous flow-measuring devices have been developed. The cheapest and simplest of these is the captive drag, which is usable between the surface and depths of 50 or 100 feet. Current meters with rotating elements are in greater use than all other types. The popular ones include the Price meter (speed only) for stream gaging, the modified Roberts, and the modified Savonius rotor with vane; the last two register speed and compass direction and are used by oceanographers. Rotating meters are incapable of instantaneous response, but they are fairly suitable for averaging the current over periods of 10 to 20 seconds or longer. Rotating element meters are subject to errors due to wave action, ship roll, and relatively high frequency turbulence. Ideally, all of these devices should be suspended from an immobile plat-

form. In the absence of such a facility, it should be approximated by tautly anchoring the observing boat or by suspending the meter below a taut-wire anchored buoy.

Solid state flowmeters which are capable of measuring turbulence when rigidly fixed at a point in the flow have been developed, but these are relatively costly and somewhat complicated.

Recordings from current meters can be planned so that all data handling and processing is accomplished by a high-speed computer, but a visual scan by an experienced person is desirable.

In any current-measuring program, a cross-check on the method or device by an alternative method is recommended.

LITERATURE CITED

- JOHNSON, J. W., and R. L. WIEGEL, 1959. *Investigation of current measurement in estuarine and coastal waters*. Publ. No. 19, State Water Pollution Control Board, Sacramento, California.
- KOCZY, E. F., M. KRONENGOLD, and J. M. LOWENSTEIN, 1963. A doppler current meter. In *ISA Marine Sciences Instrumentation*; vol. 2, pp. 127-134. Plenum Press, New York.
- McGraw-Hill Encyclopedia of Science and Technology, 1960; vol. 5, pp. 315-321. McGraw-Hill Book Co., New York.
- PAQUETTE, R. G., 1963. Practical problems in the direct measurement of ocean currents. In *ISA Marine Sciences Instrumentation*; vol. 2, pp. 135-146. Plenum Press, New York.
- SNEZHINSKII, V. A., 1954. *Practical Oceanography*; pp. 318-435. Government Publishing House, Leningrad.
- SYMPOSIUM ON BLOOD FLOWMETERS, 1959. Reported in *I.R.E. Trans. Med. Electron.*; vol. ME-6, pp. 191-304. Institute of Radio Engineers, New York.
- VON ARX, W. S., 1962. Current measurements by direct methods. In *An Introduction to Physical Oceanography*; chapter 8, pp. 213-241. Addison-Wesley Publishing Co., Reading, Massachusetts.

III. GEOMORPHOLOGY

Origins of Estuaries

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This is an excellent time to discuss the origins of estuaries. Examples occur along practically all coasts. An even more appropriate time would have been about 3,000 years ago when the sea attained about its present level. A few ten thousands of years from now estuaries may be quite rare. In their place will be numerous valleys with alluvial flood plains widening seaward, and in some cases blending into deltaic or other coastal plains.

Estuaries have been uncommon features during most of the earth's history which started geologically when the oldest rock now exposed at the surface originated. Continents were low and relatively flat; climatic zoning was inconspicuous either between continental interiors and coasts or between equator and poles. During the more recent part of the earth's history, oceans stood somewhere above their present level. This "normal" condition has been interrupted now and then by crustal unrest, when earthquakes and volcanic activity increased in frequency and magnitude, when high mountains and plateaus became conspicuous topographic features, and when climatic continentality and zonation became striking, as is the case today (Brooks, 1926; Russell, 1941). During these "abnormal" times huge masses of continental ice now and then accumulated on land at the expense of oceanic volume, and seas retreated to lower levels. These interruptions in the customary tranquility of earth history are called Ice Ages. There have been several, the earliest of which was extremely ancient. There is no evidence in the geological record to indicate progressive refrigeration of the earth.

GLACIO-EUSTACY

The sea level was lowered during each glacial episode and was raised again when meltwaters were returned to the oceans. While almost nothing is known definitely about sea-level fluctuations of earlier geological time, we have an abundance of evidence concerning events during the Quaternary Ice Age, the one in which we are living. But earlier parts of the record are dim. It is evident that there have been five major fluctuations in ice volumes and stands of oceans. It is also highly probable that each lowering or raising of the sea level was now and then interrupted by minor stillstands or changes of trend (Eddy, 1961; Shepard, 1961). But our certain knowledge of events is limited to the relatively short interval between the culmination of the last main glaciation and the present

day—since the climax of the Würm, or Wisconsin, if we must apply a name.

We know that the precise level of modern strandlines depends on a delicate climatic balance. The first half of the twentieth century experienced warming trends in temperature, recession of ice masses on land, rising sea levels, and the disappearance of a large proportion of the small valley glaciers of our western states. A slight reversal of these trends may be in effect today. Within historical times there have been some fairly pronounced climatic fluctuations, but all were insignificant in comparison to what would happen if all the Antarctic and Greenland ice were to melt. If this should happen the sea level would probably rise more than 200 feet.

During the culmination of the last major glaciation, well over one-third—some 20 million square miles—of the land surface was covered by continental ice, presumably to an average depth of about a mile. Estimates vary as to the volume of ice and the effect of its subtraction from oceanic waters. Not long after Agassiz postulated the occurrence of an Ice Age, Charles Maclaren (1842) calculated that the sea level dropped about 800 feet, assuming that ice covered two-thirds of all land poleward from 35° and that it averaged a mile in thickness. Maclaren believed that enough meltwater had been returned during the last deglaciation to permit a recovery in sea stand of about 700 feet. Thirty years later, Alfred Tylor reduced the estimate of lowered sea level to 600 feet. Nansen (1922) and Ramsay (1930) regarded the drop as about 485 feet. All of these estimates were based on ice and water volumes. Our own evidence, which is based on depths of alluvial fill in valleys and hence is completely independent of volume estimates, indicates a sea stand of about 450 feet below present level (Russell, 1964a). Seas may have been slightly lower, but certainly were not higher, during the culmination of the last glacial stage.

It is doubtful that most of the last main rise of sea level occurred during the past 18,000 years. Radio-carbon dates on wood and peat samples from Mississippi Valley alluvium suggest this, but the estimate is based on minimal evidence. Samples presumed to be Recent from submarine deposits on the continental shelf of Louisiana appear to be twice that old, or even beyond the possibilities of C¹⁴ dating. Recent peat from the Swan River mouth near Perth, Australia, is more than 30,000 years old. The Quaternary geologist critical needs some means of reliable dat-

ing for the last 500,000 years. We incline toward a belief that the Recent rise may have started about 50,000 years ago (Russell, 1964b).

The drop in sea level during the waxing of the last major glaciation appears to have been rapid. We have little evidence from other parts of the world, but in the lower Mississippi Valley we know the thickness of Recent alluvium so accurately that we can establish precisely the positions and slopes of the pre-Recent trenches of the main river and its tributaries. From Cairo, Illinois, to the Gulf of Mexico, the Mississippi gradient leading to the lowest sea-level stand was essentially constant at 0.83 ft./mi. (Fisk, 1944). There is no suggestion of an exponential decrease such as is ordinarily exhibited by profiles along today's stream beds or longitudinal slopes of floodplain surfaces. The river eroded its relatively narrow trench in response to a dropping sea level, and it may be surmised that ice volumes on land increased at a rapid rate.

INITIATION OF ESTUARIES

The Recent rise of the sea level was initiated abruptly by a change from waxing to waning of ice volumes (Russell, 1957). There was little or no widening of valley walls during the lowest sea stand. The rise was undoubtedly variable in rate. Prior to 6,000 years ago, when the sea level stood about 20 feet lower than at present, the rate of rise decreased noticeably. It averaged about 0.5 feet per century until about 3,000 years ago, when an approximate stillstand was established (McIntire and Morgan, 1962). During the rise, coastal plains and deltas near the outer edge of today's continental shelves were the first to become submerged. Shorelines moved upward and across the shelves, and eventually into valley systems. At the lowest sea stand, estuaries were rare, but as the level rose they became numerous and later on grew more complex when their arms invaded tributaries of valley systems. The peak of estuarine development occurred when stillstand was established.

This general picture, of course, is fraught with overgeneralization and oversimplification. Natural settings varied from one estuary to another. Some rivers had cut narrow trenches between walls of solid rock. Marine invasion resulted in long, narrow estuaries like that of the Hudson for about 100 miles inland from New York City. In many cases complete valley systems were drowned and the resulting estuaries were characterized by many arms, each leading up a tributary valley as in the Chesapeake and Delaware Bays. Contrasts between individual estuaries usually were caused by differences in local topography, geological structure, rock composition and structure, processes of erosional sculpture, or a similar group of elements associated with depositional landforms.

EXAMPLES OF ESTUARIES

A taxonomic classification of estuaries would be even more complex than a catalog of shoreline types.

While many people find such exercises rewarding, I regard them as fruitless and unjustified because our knowledge of coastal features is so incomplete. It is necessary to recognize major types, but I feel that there will be little lasting value in detailed and specific classifications, particularly if the taxonomy is based on deductive approaches and if information gleaned from charts or aerial photographs is used as evidence.

Fjords rank high among the world's notable physical examples of estuaries, and certainly they are the most picturesque. Tongues of continental ice moved down and along pre-existing valleys, increasing their depths irregularly and accentuating the steepness of their walls. Above the level of marine invasion these valleys commonly exhibit glacial stairways in which the treads contain chains of lakes of highly variable depth, and the risers between them are likely to be abrupt and steep, facing downvalley. Continuation of the longitudinal profile under the estuary ordinarily reveals the presence of bedrock basins separated by sills that rise locally because the floor was particularly resistant to scour beneath the weight of moving ice. Oxygen-deficient water may remain quite stagnant in the lower parts of basins.

Dowthown blocks, or grabens, between fault zones account for similar estuaries and vary in size on up to the Gulf of California or the Red Sea. In some cases the seaward connection is fairly narrow, but in others it may be broad and open. It is improbable that the marine indentation of the False Bay graben, east of the Cape of Good Hope, would be regarded as an estuary by anyone. On the other hand, the narrow Gulf of Aqaba, a continuation of the Jordan Valley-Dead Sea graben, is typically estuarine, as is Tomales Bay, along the San Andreas fault zone, north of San Francisco.

San Francisco Bay occupies a complex basin of fault and erosional origin. The Golden Gate, which cuts across fault trends, is such a narrow outlet that the bay's estuarine status is probably unquestioned. Grabens and other fault-related estuaries in some cases were present during the pre-Recent low stand of oceans. But the depth of the Golden Gate is such that the sea level must have risen about 100 feet before the marine invasion started in San Francisco Bay. Another completely unrelated example of estuaries formed at a very recent date is the shallow lagoon within a coral atoll.

Most estuaries are drowned lower ends of river systems. They are as varied in appearance as the landscapes that surround them. There is great similarity, however, in landscapes that evolve on comparatively homogeneous, crystalline bedrock. Whether it be in the fells of northern Finland, the rugged High Sierra of California, parts of arid northwestern Australia, or the southern Appalachians, granite rock weathers into thin exfoliation layers that readily crumble into gritty debris consisting largely of fresh mineral crystals. As these layers are detached, the bedrock surface develops topographic forms dictated by rock structure. The landscape is commonly domi-

nated by domes and planes along joint surfaces. Stone Mountain, Georgia, the mountains above Yosemite Valley, or Sugar Loaf and similar features near Rio de Janeiro present greater landscape similarities than might be suggested by their varying climatic locations.

Estuarine Guanabara Bay in Brazil is particularly instructive. Its shores in many places are similar to those that would result if the Sierra Nevada were suddenly submerged to a depth where the Pacific Ocean lapped against Yosemite's Half Dome. Emphasis should be placed on "suddenly", because the granitic shores near Rio de Janeiro exhibit almost no evidence of attack by marine processes. Sea-level stillstand has not been sufficiently lengthy to permit notching or sea-cliff development. This is true on the Kola Peninsula, Scandinavia, the southern coast of Western Australia, and in all other places where I have had the opportunity to study granite coasts. Clear water is characteristic of these estuaries because arkose, the product of weathering, settles rapidly to the bottom and remains there as a clean mixture of quartz and comparatively fresh feldspar crystals.

Other "hard rock" coasts develop estuaries that in some ways resemble those in granitic rock. The calanques and other small coves along the southeastern coast of France, although developed in a variety of rocks, are as clear and picturesque as if they had been cut in granite. Durable rock, however, develops a wide variety of landscapes or estuaries. Bedding or other rock structures may dip at various angles; topographic grain may be fine or coarse, uniform or irregular; and folding or faulting may complicate matters. Such factors affect shorelines and the topographies above and below them.

The least scenic estuaries occur on low coasts where bedrock is poorly consolidated and flat-lying. These are most characteristic of coastal plains lying inland from broad continental shelves, particularly around the Atlantic Ocean. Erosional landscapes created during low stands of the sea are not particularly exciting, nor are there many scenic spots along shores standing some 450 feet above the pre-Recent low.

Coastal plain estuaries commonly originate or become modified by depositional landforms. Along much of the Gulf coast, for example, two distinct shorelines exist. The inner one is irregularly indented and bounds normal estuaries such as Galveston, Corpus Christi, San Antonio, and Galveston Bays. The outer shoreline is straight and continuous for a long distance. Behind it lies the linear estuary of Laguna Madre. The sounds between the Outer Banks of North Carolina and an irregularly indented coast are broad and complicated in pattern, but they are equivalent both to the bays and Laguna Madre of the Texas coast.

Barrier islands are but one of the depositional landforms associated with low-coast estuaries. Natural levees of rivers, beaches, rows of sand dunes, spits, and bars commonly form barriers that impound basins or restrict inlet widths to establish estuarine conditions in bays or other indentations that formerly were

more openly connected to the sea. The Pontchartrain Basin, Lake Borgne, and the western end of Mississippi Sound are denied free intercourse with the Gulf of Mexico by natural levee embankments along the lower Mississippi River and its Recent distributaries. Sabine and Calcasieu Lakes, to the west, have become increasingly estuarine because a succession of beaches and spits has restricted their outlets.

Tombolos are sand or gravel bars between a coast and its nearshore islands. In some cases they are compound and enclose triangular lakes. Beautiful examples occur on the northwest coast of Antigua and near the southwest corner of Puerto Rico. In these cases estuarine conditions prevail because the beaches have not become complete barriers. Tides rise and fall with ranges and timing that resemble, with some lag, changes of level in the adjacent Caribbean Sea.

Spits develop along practically all marine or lake coasts. As they advance into deep water, their ends commonly recurve at elbows and in some cases enclose sheltered bays, estuaries, lakes, or ponds. Toward the southeast end of the Baltic, the harbor of Puck is well sheltered by a long spit leading to Hel, in the Gulf of Danzig. Hafss, to the east, have become almost completely separated from the sea by spit growth. In other parts of the world, San Diego and many other bays are protected by lengthy spits.

Just as it is ordinarily futile to insist that precise definitions be applied to members of a continuous series, it is almost impossible to apply a strict scientific meaning to a word in popular local usage. Bayou is an example; estuary and lagoon are others. Laguna Madre on the coasts of Texas and Mexico, most of the lakes and bays eastward along the Gulf coast, and gulfs in various parts of the world are estuarine either as a whole or in part. River mouths, too, commonly pose difficult questions as to whether they should be regarded as estuaries.

The lower part of the St. Johns River, Florida, is essentially estuarine, but how should passes in the Lower Mississippi Delta be classified? Many abandoned passes and others with a limited freshwater flow gradually decrease in salinity upstream, with related changes in fauna. The more active Mississippi passes develop bars on a grand scale. In the vicinity of Head of Passes, channel depths reach 100 feet and more, but somewhat over 20 miles away rivermouth bars have natural depths that vary from about ten feet to almost nothing, depending on seasonal changes in river discharge. During most of the year there is active, upstream, saltwater underflow that ordinarily affects salinity upstream for some 100 miles, and occasionally for more than twice that distance. Some writers have regarded the lower part of the channel as estuarine, in spite of the fact that during high stages all of the salt water is returned to the Gulf (Rates, 1953). The estuarine condition has been accentuated artificially by dredging South and Southwest Pass channels to depths of 30 feet or more.

On small rivers, particularly those with long periods of little or no flow, bars may dam outlets for months

or years at a time. A full range of examples occurs along the coast of Western Australia. In some river mouths changes in salinity occur so often and are so pronounced that fauna are impoverished for long distances upstream. Others experience less sharp or sudden contrasts and maintain thriving fauna that grade upstream into typical freshwater assemblages. In northwestern Australia, where aridity is intense, hypersaline conditions are maintained as a result of high evaporation rates combined with seepage of marine water through bars. Far to the south on Rottnest Island, near Perth, detached remnants of former lagoons have become isolated lakes, with salinities running up to saturation as a result of evaporation of seawater seepage through several hundred yards of unconsolidated sand. But in the sediments around and under these lakes are fauna and flora that tell us of estuarine conditions some centuries ago.

MODIFICATION AND EXTINCTION

The continuing modifications that will make estuaries extinct are geologically more interesting than seasonal or ephemeral changes. Most estuaries have changed appreciably during the last 3,000 years. Fjords and estuaries bordered by durable rock are least affected, particularly where inflowing rivers are small or carry inconsequential sedimentary loads. Waves have done little to modify their shores. Deltas and bordering depositional flats have advanced but little, especially if bottom depths are considerable. Processes of mass movement may have done little more than plunge large blocks of rock into clear water or leave debris cones here and there along valley walls. Similar generalizations apply to many fault-related estuaries. Contemporaneous faulting usually results in lowering central blocks of grabens. In a rather anomalous case, however, the Colorado River succeeded in building its delta completely across the width of the Gulf of California, isolating nearly 200 miles of former estuary, which, in an extremely arid climate, now has become a below-sea-level desert with one large saline lake.

Estuaries in unconsolidated rock, like those along the coasts of our southern and southeastern states, have changed the most. Grassy marshes or swamps now occupy vast flat surfaces that have been built up to about the level of high tide. The Mobile Bay of three millennia ago, for example, is now practically filled, in spite of regional subsidence that has lowered some Indian mounds to depths of ten feet, a factor that favors estuary enlargement. The large rivers of Alabama converge into it and have deposited their loads. Maps indicate that about half of the original bay has been converted into swamp or marsh, but these are deceptive because they indicate that the other half is a residual water area, mostly of insignificant depth. The seaport of Mobile is served by a navigable channel that approximates a river course along the western side of the bay. Farther west, the extensive estuary of Pascagoula River is almost completely converted to marsh. Similar changes have occurred in Louisiana,

where most estuaries are now shallow and unimpressive.

DELTA GROWTH

Advancing deltas are the most formidable natural enemies of estuaries. Delta deposits include not only land surfaces but also subaqueous, prodelta accumulations that may have surprisingly large volumes. Excepting local situations where the generalization is untrue, current velocities in estuaries are likely to be so small that turbulence is insufficient to entrain or transport loads of sediment particles exceeding silt or clay size. Increase in the volume of prodelta deposits occurs far more rapidly in estuaries than along open coasts exposed to trains of steeper waves and various nearshore currents.

Deltaic extinction of a large estuary is well illustrated on the central Louisiana coast, where Lake Atchafalaya, a product of the Recent stillstand, has almost disappeared (Russell, 1938). This estuary was about 100 miles long and 40 miles wide (Fig. 1). Originally a large embayment extended inland, open to the Gulf of Mexico. Extremely old channels of the Mississippi led to its northern shore. About 4,000 years ago the Mississippi established a course it retained for more than a thousand years, close to its western valley wall. This Teche-Mississippi pushed its natural levees and delta eastward across the Atchafalaya Embayment, converting it into a huge estuary. Later the Mississippi diverted to its existing course along its eastern valley wall. Natural levee plus delta growth soon completed the barricade, isolating Lake

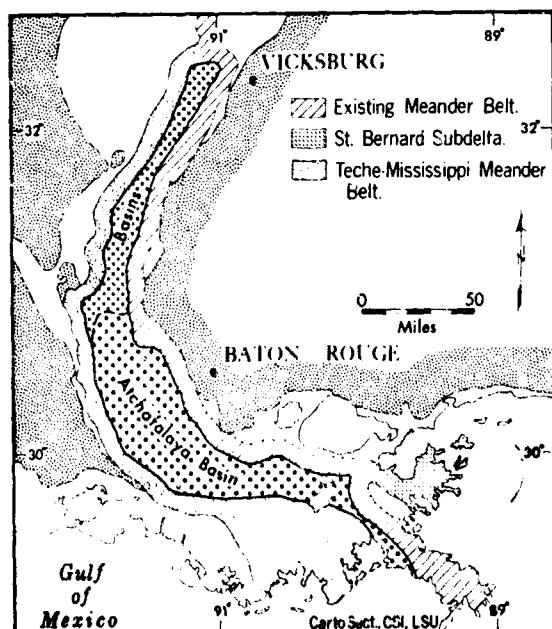


Fig. 1. The Atchafalaya Basin and other basins to its north are bounded on the west and south by higher natural levee deposits of an old course of the Mississippi River (Teche-Mississippi) and on the east and north by deposits of more recent Mississippi courses.

Atchafalaya from the Gulf. The lake had maximum areal extent at that time. Three outlets were established across the Teche barrier to the south and the intrusion of Gulf water accounted for brackish-water fauna that thrived in the seaward part of the lake. Sediments contributed by small rivers to the west, the Red and Atchafalaya Rivers to the north, and crevasses from the Mississippi to the east, accumulated so rapidly that by the time Europeans appeared on the scene, the original Lake Atchafalaya had been broken into many smaller lakes, some of considerable size. During the 30 years that I have been observing the basin, most of these lakes have been reduced to insignificant size and negligible depth. In some places sedimentary accumulations have raised the elevations of between-channel surfaces as much as 20 feet. An evolutionary history that started with an open body of water, and included the development and extinction of an estuary, has reached nearly the end of its final chapter: conversion into swamp with considerable areas of land high and dry enough for agricultural use. In 1947, sediment other than that of colloidal composition or finest-clay size began reaching the Gulf of Mexico (Morgan, Van Lopik, and Nichols, 1953). For more than 30 centuries it had been accumulating to fill lakes. Now that they are nearly filled, increasing amounts are reaching the coast and accumulating as a growing mudflat just outside beaches that have been active during the last 17 years and less. This mudflat, with widths up to two or three hundred yards and extending more than 125 miles westward, is now converting several small stream mouths into estuaries or lakes.

One of the world's most spectacular examples of estuary filling occurred along the Amazon for a distance of about 1,500 miles. The Amazon Valley, strictly speaking, is comparatively narrow. To the north it is bordered by plateaus of ancient rock and at many places to the south by uplands of Tertiary age. Little of the area between the confining walls is typical flood plain. The predominant alluvial surface is deltaic in origin and has advanced downstream to fill most of a magnificent estuary. The distinction between a flood plain and a delta surface is well worth making, not only here but generally, in cases where estuaries have been filled.

Stream channels exhibit comparatively simple patterns on flood plains. A winding major channel may be joined by tributaries, or an occasional branch in the downstream direction may divide a stream into distributaries. A delta surface, on the other hand, is characterized by intricate branching and rejoining of channels that are separated by lens-shaped islands (Fig. 2). The fundamental distinction, however, is a matter of genesis. Flood-plain topography originates subaerially, but channel and land patterns of deltaic surfaces are initiated as submerged features.

The water coming down a channel flares out in a plane-jet flow upon entering a lake, sea, gulf, or ocean (Bates, 1953). Natural levees along channel sides diverge and continue as submarine features. These

depositional ridges along the swiftest current boundaries become more widely separated, and their crests deepen with increasing distance from the shore. As sediments accumulate, crests grow upward and become proximal strips of land—extensions of the natural levees of the confined channel. Concurrent with the development of flanking depositional ridges is the growth of a shoal, more or less in mid-channel position. Here the flow is relatively uniform, and entrained sediment is deposited more effectively than toward the channel sides where threads of more active and complex flow parallel depositional ridges. The mid-channel shoal emerges as an exposed bar, or "middle ground" in Lower Mississippi Delta parlance, which eventually becomes the upstream end of a lenticular island (Welder, 1955). In an early stage of development the island exhibits an inverted V-pattern with its apex pointed upstream. The legs of the V are natural levees flanking the now-divided channel. As time goes on they lengthen and commonly converge downstream, enclosing an interior basin. The convergence is favored because the channels on either side have tendencies to flare and to create new mid-channel shoals. In time, the deltaic plain consists mainly of lenticular islands. Crevasses leading into their interior basins contribute sediment that eventually raises their levels. Downstream outlets from basins further complicate the deltaic pattern.

Excellent examples of rapid delta-surface advance are found along the Amazon and also in many other estuaries, including Mobile Bay and the Atchafalaya Basin. One of the most interesting is just east of South Pass in the Lower Mississippi Delta. Pass à Loutre crevassed in 1891 and soon filled most of Garden Island Bay with sediment (Russell, 1936). The upper half of the bay is a typical example of normal delta growth, but it is more interesting to observe the submarine patterns of channels and mid-channel shoals across the lower half of the practically extinct bay, where sediment accumulation has reduced depths to one-tenth or less of their pre-1891 values.

When the Recent stillstand of sea level was approached, the Amazon Estuary was a scenic, deep-water feature. As delta growth marched downriver it left the plain we see today. The advance was so rapid that tributary streams were dammed off and their lower courses became long, triangular lakes, with narrow bases along bars or natural levees at the sides of the master rivers. Depths in these lakes and in the nearby Amazon exceed 100 feet far more often than is indicated on charts.

Before visiting the Amazon, I had considered the islands between Belém and Macapá as being delta lands. In truth, they are remnants of Pleistocene terraces that remain residually between deep channels which were cut or accentuated during the pre-Recent low stand of the oceans. Their shores are retreating sea cliffs, some of considerable height, and their interiors contain extensive flats of dry land that stand high above local deltaic or flood-plain levels. In almost all aspects these islands contrast with the natural-

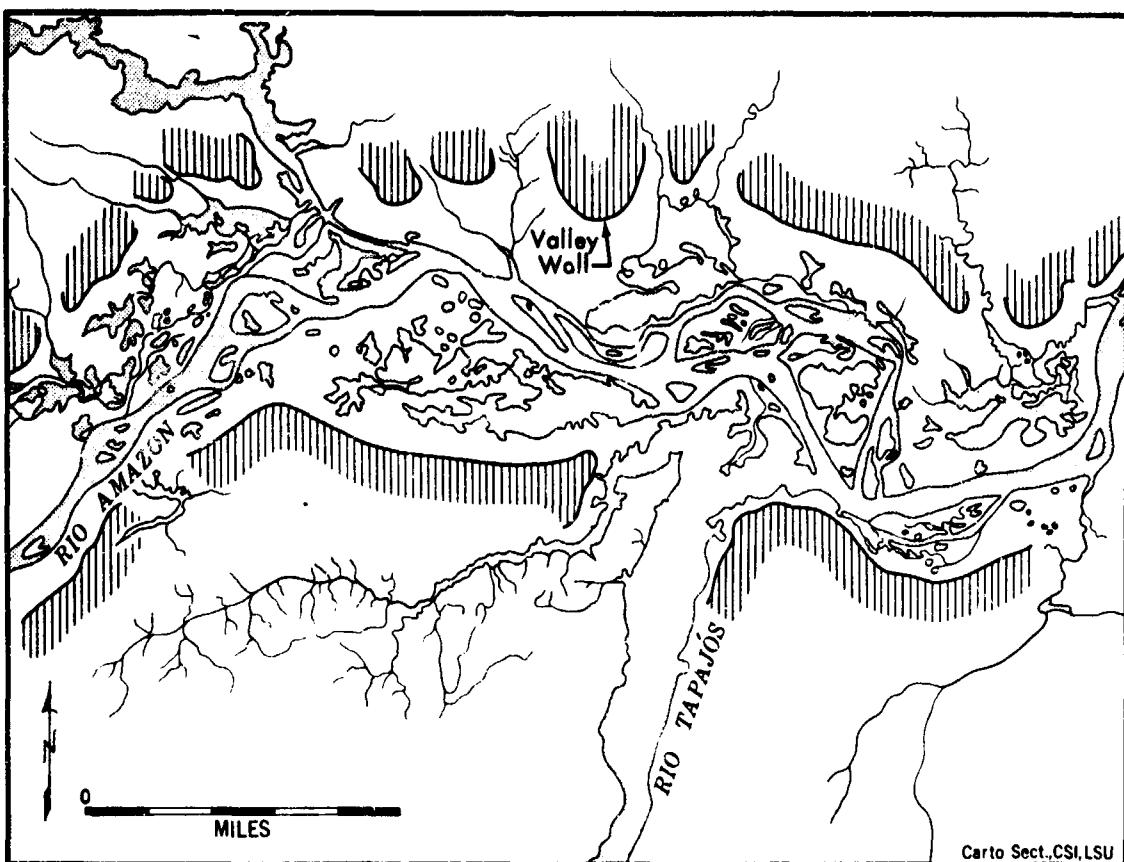


Fig. 2. The lower Amazon illustrates the development of a deltaic stream pattern. The valley is not typical of ordinary flood-plain deposition. Instead, the main channel is characterized by lenticular islands and shoals having patterns that originated in the deep estuary which crossed Brazil a few thousand years ago. Tributaries, such as Rio Tapajós, retain enormous depths behind alluvial barriers, deposited by the Amazon, that almost dam them off.

levee-flanked, lenticular islands upstream which have willow-covered stream banks and wet interior basins. The maze of outlets of the Amazon and Rio Pará are estuaries through which heavy loads of sediment are being transported to nourish an extensive submarine delta that is forming in the Atlantic.

An estuary of historical interest was the Latmian Gulf, in the vicinity of Miletus, Turkey, described by Herodotus. It no longer exists because the Maeander (Menderes) River has advanced its delta across it for a distance of ten miles during the last 25 centuries. The filling was so rapid that one arm of the estuary was dammed off and now is known as Lake Bafa, with a depth, according to local fishermen, of 60 fathoms (Russell, 1954). This happened so recently that the water is somewhat brackish.

EPHEMERAL STATUS

My purpose in describing Lake Atchafalaya, the Amazon deltaic plain, and the Maeander Delta, is to emphasize the ephemeral nature of most estuaries. Few can survive for more than a minute fraction of a geologic epoch. If any considerable volume of Ant-

arctic ice melted, it would rejuvenate many old estuaries and create new ones—but this is not in prospect. Our studies indicate a probability that no higher stand of Pleistocene sea level exceeded today's stand by more than 10 meters (Russell, 1964a). Fluctuations in ice volumes over Europe and North America apparently account for Quaternary sea-level oscillations, while Antarctic ice volume has remained fairly constant. Should the Recent sea level attain the highest stands of the Pleistocene, the effect on estuaries would be slight and in many cases insufficient to interrupt appreciably the effects of sedimentary filling. The prospect of the Antarctic ice melting completely within the next million years is negligible. It is more probable that the Recent will be followed by another glacial stage and the lowering sea level will be accompanied by the disappearance of practically all estuaries and the erosional entrenchment of rivers crossing their alluvial deposits.

In summary, neither the past nor the future of estuaries gives much promise. During most of the earth's history only a few examples have existed, and today's estuaries, in many cases, are headed for rapid extinction. Some of our studies will have important

historical value, just as has the faithful description of the Latmian Gulf by Herodotus, and in some cases this value will become significant within a few decades. In short, it is an excellent time to engage in estuarine research.

LITERATURE CITED

- BATES, C. C., 1953. Rational theory of delta formation. *Bull. Am. Assoc. Petrol. Geologists*, 37:2119-2162.
- BROOKS, C. E. P., 1926. *Climate through the ages: a study of climatic factors and their variations*. Yale Univ. Press, New Haven.
- EMERY, K. O. 1961. Submerged marine terraces and their sediments. In *Pacific Island Terraces: Eustatic? Supplbd. Z. Geomorphol.*, 3:17-29.
- FISK, H. N., 1944. *Geological investigation of the alluvial valley of the Lower Mississippi River*. Mississippi River Comm., Vicksburg, Miss.
- MACLAREN, C., 1842. The glacial theory of Professor Agassiz. *Am. J. Sci.*, 42:346-365.
- MCINTIRE, W. G., and J. P. MORGAN, 1962. Recent geomorphic history of Plum Island, Massachusetts, and adjacent coasts. *Coastal Studies Inst. Tech. Rept. 19-A, Coastal Studies Series No. 8*, 1963. Louisiana State Univ. Press.
- MORGAN, J. P., J. R. VANLOPIK, and L. G. NICHOLS, 1953. Occurrence and development of mud-flats along the western Louisiana coast. *Coastal Studies Inst. Tech. Rept. 2*, Louisiana State Univ. Press.
- NANSEN, F., 1922. The strandflat and isostasy. *Videnskps. Skriftr. I, Math-Naturv. Kl. II. (Kristiania) Oslo*.
- RAMSAY, W., 1930. Changes of sea level resulting from the increase and decrease in glaciations. *Fennia*, 52, No. 5.
- RUSSELL, R. J., 1936. Physiography of Lower Mississippi River delta. *Louisiana Dept. Conserv., Bull. Geol. Surv.*, 8:2-199.
- RUSSELL, R. J., 1938. Physiography of Iberville and Ascension parishes. *Louisiana Dept. Conserv., Bull. Geol. Surv.*, 13:3-86.
- RUSSELL, R. J., 1941. Climatic change through the ages. In *Climate and Man*; pp. 67-97. Dept. Agri. Yearbook, Washington, D. C.
- RUSSELL, R. J., 1954. Alluvial morphology of Anatolian rivers. *Ann. Assoc. Am. Geographers*, 44:363-391.
- RUSSELL, R. J., 1957. Instability of sea level. *Am. Scientist*, 45: 414-430.
- RUSSELL, R. J., 1964a. Techniques of eustasy studies. *Z. Geomorphol., Hans Mortensen festsch.*, 8(Sonderhft.): 25-42.
- RUSSELL, R. J., 1964b. Duration of the Quaternary and its subdivisions. *Proc. Nat. Acad. Sci.*, 52:790-796.
- SHEPARD, F. P., 1961. Sea level during the past 20,000 years. In *Pacific Island Terraces: Eustatic? Supplbd. Z. Geomorphol.*, 3:30-35.
- TYLOR, A., 1872. On the formation of deltas, and on the evidence and causes of great changes in sea level during the glacial period. *Geol. Mag.*, 9:392-399.
- WELDER, F. A., 1955. *Deltaic processes in Cubits Gap area, Plaquemines Parish, Louisiana*. Ph.D. Dissertation. Louisiana State Univ.

Geomorphology and Coastal Processes

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The Latin word *aestus* means tide, and "estuary" is a term applied to a land form in which the tide plays an important role. It is worthwhile to glance at one or two definitions. The Oxford Dictionary gives two meanings. The more modern is: "The tidal mouth of a great river, where the tide meets the current of fresh water." The second is rare in modern use: "A tidal opening, an inlet or creek through which the tide enters; an arm of the sea indenting the land." The second is the better because the first might apply to a delta. Webster's dictionary gives a more comprehensive meaning: "A passage, as the mouth of a river or lake, where the tide meets the river current; more commonly, a narrow arm of the sea at the lower end of a river, a firth."

Despite the difficulty of precise definition, most people probably agree that characteristically an estuary is trumpet-shaped and is usually the single mouth of a tidal river. There is no reason, however, why an original single mouth should not later be partially filled with sediments—nor, conversely, why a broad distributary of a delta should not be flooded and form an estuary. The Rio de la Plata, the wide opening between Uruguay and Argentina, conforms with all the usual ideas of an estuary; above Buenos Aires, however, there is a well-defined delta. Is the Amazon mouth a delta or an estuary? Any land form is in the process of evolution, and all estuaries have been changing in one way or another over considerable periods of time. Most people would agree that the Thames reaches the sea in a typical estuary. Nevertheless, there is a great deal of sedimentation in it and several true deltaic islands, of which Canvey and Foulness are the best known.

Our discussion will doubtless range over many accepted estuaries, as well as over other comparable coastal features: fjords, fiords, rias, the canale of the eastern side of the Adriatic, the firths of the eastern coast of Scotland, and other inlets. In one sense or another, all could be made to fit our definitions, even those in the Mediterranean and other seas where the tidal range is very small, but measurable. Mill (1897) remarked that the landward half of the Firth of Forth, on the east coast of Scotland, is an estuary, but that in the seaward half the fresh and salt waters are so thoroughly mixed that "the sea becomes slightly freshened through its whole depth for many miles from land". This implies that an estuary is definable in terms of its hydrology.

ORIGINS

A physiographer thinks of an estuary principally as a land form, and probably as one that has had a long history. The present land-sea boundary of most estuaries is the result of submergence. There is no need to discuss this in detail, but the Quaternary eustatic and isostatic changes of level are important, as are the movements of more ancient times, some of which may be connected with the origin of submarine canyons. The depression which preceded the Severn Estuary may date back to the Hercynian mountain building, when a low area existed between high ground over what is now South Wales to the north and Cornubia to the south. The Triassic and later rocks indicate a great deal of erosion in the area and suggest a river flowing to the east, which in early Triassic times formed a broad estuary. After a long period, the eastward-flowing river was reversed, possibly as a result of post-Cretaceous movements, and ran between east-west folds of Tertiary age. There may even have been an open connection between the Severn and the Thames. Since the estuary took on something of its present form, there have been many relatively small changes caused by erosion, accretion, and minor changes of level (Steers, 1948).

ESTUARIES IN ENGLAND AND WALES

THE WEST COAST

Let us now examine certain estuaries in England and Wales, in order to realize the wide interests of our subject. The Ribble, the Mersey, and the Dee are close together in Lancashire and Cheshire. In general form, the Ribble and Dee Estuaries are textbook examples, yet they are well on their way to becoming deltas. The Ribble Estuary has been frequently mapped, and Gresswell's work on the Lancashire coast has shown that it is easily traced in earlier times when the Hill House shoreline, correlated with the so-called 25-foot beach of Britain, was formed (Gresswell, 1953). The Ribble brings down a great deal of material, and the estuary is fast filling up. Marshes have been reclaimed from time to time; for example, in 1880 a bank was built around New Marsh, and enclosed about one mile of land which had been reclaimed in 50 years. The river is now controlled; previously the main channel reached Lytham and then bifurcated (Fig. 1). The shoals in the estuary are

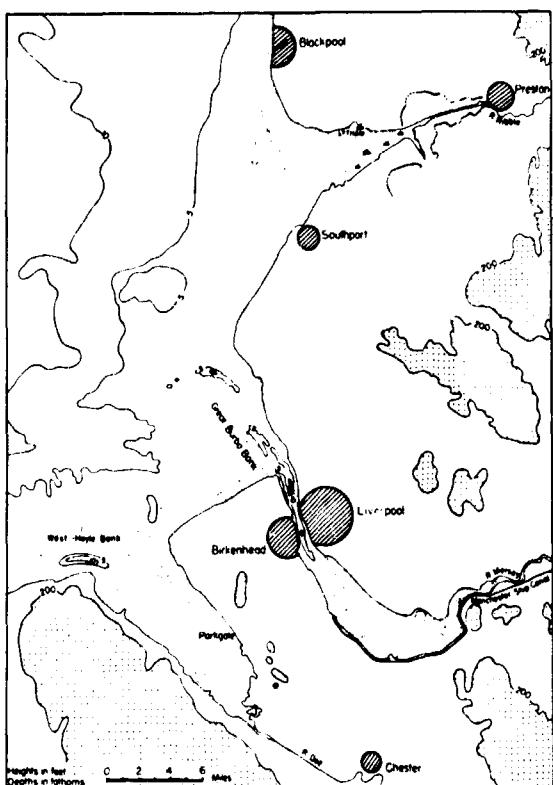


Fig. 1. The Ribble, Mersey, and Dee.

rising as a result of deposition of mud and fine material and continue to modify the appearance of the estuary.

About 20 miles farther south is the estuary of the Dee; in outline it resembles that of the Ribble. There are traces of a well-developed post-glacial cliff around it, and it is being rapidly filled with alluvium. The great thickness of the alluvium, much of which is presumably of marine origin, at the mouth of the estuary is not necessarily the result of depression; it has been suggested that a flooded river, opposed by strong winds, might well be able to cause deposition of mud at the present level of the flats. There is no doubt, however, that the Dee alluvium has been gathering since at least the post-glacial depression. It may reach 60 feet in thickness and consists mainly of loosely stratified, silty, quartzose, and fine-grained sand with occasional seams of gravel. Charts made in 1720 show that the lower estuary was open and ships could reach Parkgate (Fig. 1). Chester Haven, however, was ruined before the middle of the sixteenth century. Like the Ribble, the Dee Estuary is in a sense becoming a delta.

Between the Ribble and the Dee is another estuary, the Mersey, very unlike its neighbors. The Mersey has a narrow mouth and widens inward. Nature has thus provided the conditions to produce natural scouring which has kept it open. Man has made great use of this estuary; Liverpool and Birkenhead are the

main ports; there are others within, and the Manchester Ship Canal enters it at Eastham locks.

The volume of sediment fluctuates considerably in the Mersey, and in the nineteenth century variations of as much as 50 million cubic yards were noted. They oscillated about a mean value, and the changes took place in about five years. In 1906, however, there was a loss of about 90 million cubic yards. The Upper Mersey Navigation Commissioners have made a series of maps covering each month since 1867, showing the changes of the main channel. Up to 1891 these changes were fairly regular, but after that year the channel stayed on the Lancashire side. Experiments made in a model of the estuary demonstrated that the shifts in the channel in the upper estuary decreased when its capacity lessened, as a result of siltation. Experiments in the estuary itself have been made with radioactive tracers, which confirmed that density currents helped the upstream movements of materials in the layers near the bed, and proved that the principal source of the material was in the numerous sandbanks behind the West Crosby revetment outside the mouth of the estuary. It was also demonstrated that material dredged from the upper estuary and dumped behind the Great Burbo Bank was later taken back to its place of origin (Hydraulics Research Station, 1958).

Ptolemy's map of this part of Great Britain shows only two inlets, and many papers have tried to prove that in Ptolemy's time the Mersey did not exist (Fig. 2). The Romans had stations on the Ribble and the Dee, but their writings do not mention the Mersey. The estuary named Belisama is usually assumed to correspond to the Ribble, and Seteia to the Dee. It has been argued that slow post-Roman subsidence of a low marshy area, such as surrounded (before modern development) the lower Mersey, might have produced an estuary. But any attempt to equate inlets on Ptolemy's map with those on a modern one is not really worthwhile since his map is too highly generalized.

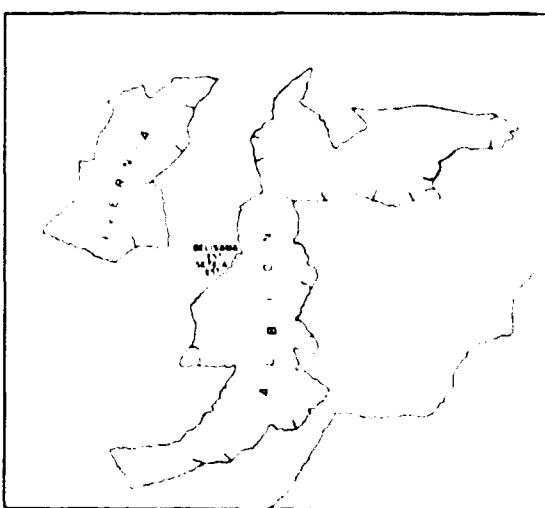


Fig. 2. Ptolemy's map of the British Isles.

THE EAST COAST

On the east coast of England there are several estuaries which vary greatly in appearance. It is appropriate to consider together the Humber and the Wash—in one sense the combined estuary of the Welland, Nene, and Great Ouse (Fig. 3). Both the Humber and the Wash breach the chalk, although formerly the chalk of Norfolk and Lincolnshire was continuous. Before complete breaches were made the rivers flowed through narrow valleys in the chalk to a North Sea somewhat more distant than that of today. In the Wash there is a belt of deep water, Lynn Deeps, which may mark the former combined channel of the three rivers. The Wash and Humber Estuaries were gradually widened by erosion and subsidence until the sea burst through the gaps and flooded the lowlands within. Today, landward of both estuaries, we have extensive fenlands which are now nearly all reclaimed.

We can trace the history of these areas in great detail as a result of the meticulous work of archaeologists, botanists, geographers, and historians. In the East Anglian Fenland there are two deposits of peat separated by the blue buttery clay—clear evidence of an inbreak in the sea. The seaward parts of the Fens are formed of marine silt; the peat fens are farther inland. The former gulf, or estuary, reached almost to Cambridge, Peterborough, and Lincoln. The present Wash may be regarded as the unfilled portion of

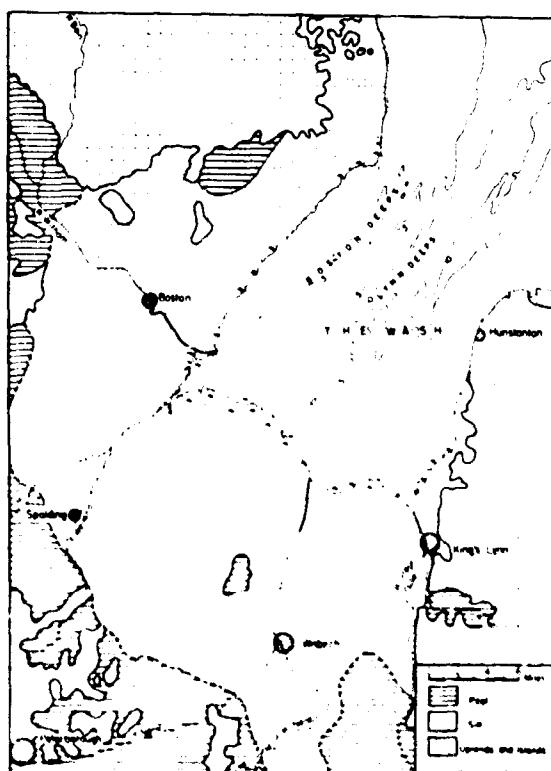


Fig. 3. The Wash and adjacent fens.

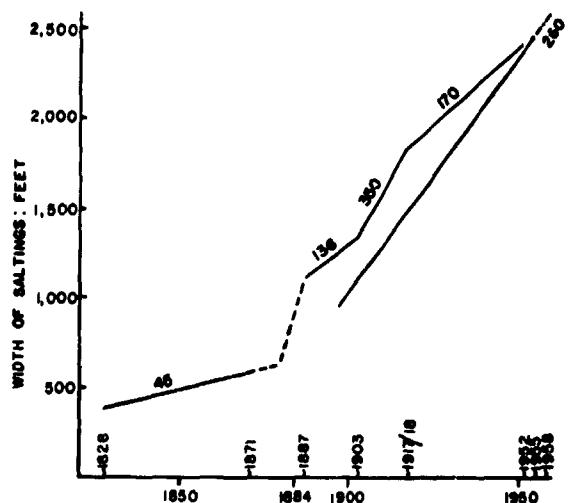


Fig. 4. Rate of advance of saltings at Butterwick (Based on Inglis and Kestner, 1958). Figures on the graph show the rate of advance in feet per 10 years. The straight line on the right shows the mean rate of advance of saltings as calculated from core sampling experiments. The dotted line in the graph indicates the Witham outfall cut, completed in 1884.

this great gulf. Some recent measurements (Inglis and Kestner, 1958) show how rapidly silting takes place (Fig. 4). The horizontal growth of 45 feet per ten years between 1828 and 1871 increased to 136 feet per ten years between 1887 and 1903; between 1903 and 1917–1918 it rose to 350 feet per decade, and later dropped to 170 feet per ten years between 1917–1918 and 1952. Similar changes have been measured near the Nene mouth and elsewhere. Careful estimates were also made of the rates of vertical accretion of silt; at Wingland a mean rate of rather more than three inches a year occurred; this was more than twice as fast as that at Butterwick. It was found that engineering works cause greater deposition, either because they reduce the volume of flow or dissipate energy as a result of altering the natural flow, although they were built in connection with outfall problems of the rivers and not to encourage accretion. In all cases the sediment is of marine origin.

The Humber is narrower than the Wash, and is perhaps the muddiest of our rivers (Fig. 5). Its fenlands are not quite so extensive as those of the Wash although they extend north and south along the valleys of the Ouse, Trent, and Ancholme. Recent work has shown that in the Ancholme Valley the general sequence of deposits is similar to, but not the same as, that in the East Anglian fens. Near the Humber, submergence began early in the Iron Age, and there has been some differential movement between the Humber and the Wash (Smith 1958). The main differences between the two areas are apparent in Figure 6. In the Humber itself there have been extensive reclamations at Broonfleet and Sunk Island, and the entrance is obstructed by the growth of the sand fore-

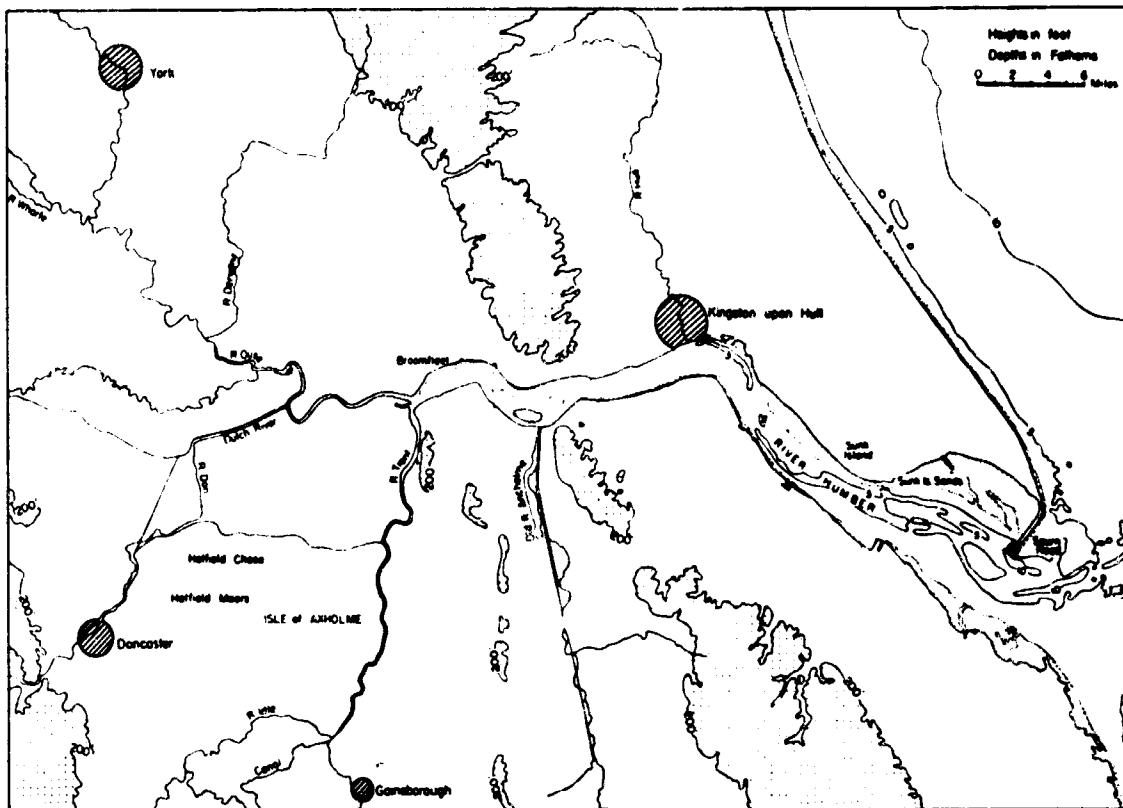


Fig. 5. The Humber and adjacent fenlands.

land of Spurn Head. In both the Humber and the Wash the mud and other deposits are gradually covered by salt marsh plants after the shoals have grown sufficiently high. The full study of these and other estuaries involves (1) their geological and archaeological past, (2) their present relations to both fluvial and marine agencies, (3) a study of their ecology, and (4) the effects of engineering works. There are buried channels in the Humber and other estuaries on the east of England which were created in the Ice Age, when boulder clay filled a wide estuary that debouched into the North Sea. Directly east of the present Humber gap, a trumpet-shaped mouth was formed through the chalk. This and other buried channels indicate changes of the relative levels of land and sea, and may be related to sea-bottom features farther out in the North Sea.

The estuaries of the east coast south of Yarmouth present many points of interest (Fig. 7a). In Roman-British times, and probably up to the early Medieval period, there was open tidal water up the Rivers Ant, Bure, Yare, and Waveney. Norwich stood on an arm of the sea. Few areas better illustrate the interrelation of physical, ecological, and human factors. The first major investigation of these rivers was made by Jennings (1952) shortly after World War II, and completed later by Jennings *et al.* (1960). Jennings established the sequence of deposits in the valleys by

means of bores and pollen analysis. These are shown in Figure 7b, and indicate a sequence not unlike that in the fens of the Humber and the Wash; but there are significant differences. The formerly open valleys, probably interglacial in age, have been filled by clays and peats, so that today the only open part of the original estuary is Breydon Water behind Great Yarmouth. The glacial sequence of this part of East Anglia is still uncertain, and the rivers may conceivably follow pre-glacial courses, even if they owe their present general outline to later events. Although we are concerned with the valleys as former estuaries, it may be noted that the Broads, small lakes which occur in the valleys although separated from the rivers by ronds (narrow banks of peat carrying an aquatic vegetation), are artificial in origin; they are Medieval peat-diggings.

The silting up of the valleys was partly the result of incursions of marine clay and partly because peat flourished during regressive phases. At the joint mouth of the rivers, coastal drift, which is here directed to the south, led first to the formation of a sandbank on which the earliest settlement of Great Yarmouth was made, and later to the junction of this bank with Flegg (i.e., the north side of the mouth of the estuary). The southern entrance, however, remained open. The changes in the length and form of the spit of sand which first obstructed and later de-

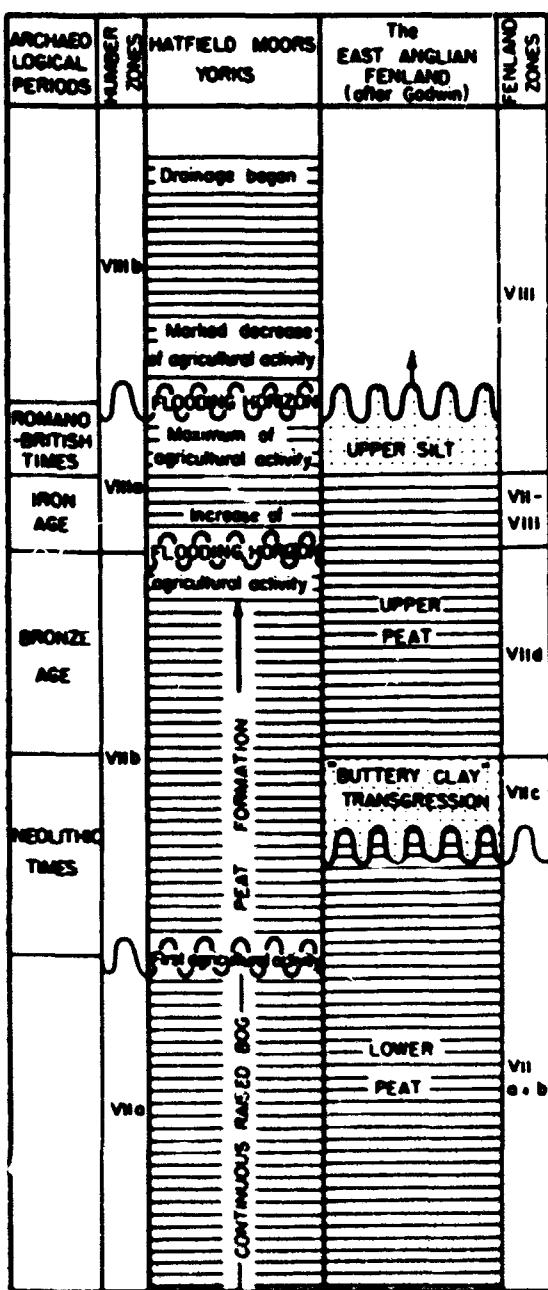


Fig. 6. Comparative chart of deposits in the Humber and East Anglian fenlands (based on A. G. Smith).

flected the river make a study in themselves. The present harbor entrance at Great Yarmouth was established in 1566. Some recent work on certain deposits found in this spit, when pylons for the new electricity grid were being built, make it probable that the later history of relative movements of land in post-Roman times has been more complicated than shown in Figure 7b (Green and Hutchinson, 1960).

Farther south there are some small but beautiful estuaries of which the more important are the Alde,

Deben, Orwell, Stour, and Blackwater. The northern ones are partly blocked by sand or shingle spits, and all are out of proportion to the rivers which drain into them. All owe much of their present general form to submergence, but their origins are not necessarily the same. The Alde, Deben, Orwell, Stour, and Colne are rivers in their own right, and were almost certainly modified by ice. The lower parts are in areas of sand and gravel and some clay, all of which are non-resistant to erosion, and the country is flat and seldom more than 100 feet above sea level. It is possible that at one time the estuaries marked the sites of sub-glacial valleys, and that they were deepened in part by sub-glacial waters under high pressure.

The Blackwater is out of proportion to the streams draining into it, and inland from it there is a belt of low ground running through Essex. To the north of this belt there is more or less continuous high ground, but to the south the country is more broken. It is generally believed that this belt represents a former line of the Thames. The Blackwater exit could not have remained open during the major glaciation of the area, and we may conclude that the position of the present mouth of the Thames, no less than that of

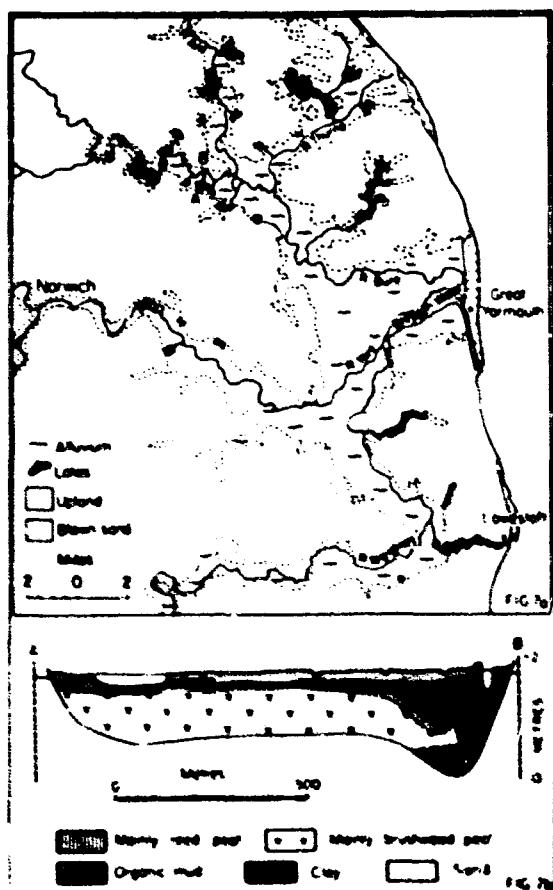


Fig. 7. The Broads and section through Ranworth Broad (After J. M. Lambert).

its present course through London, reflects the effects of glacial diversion (Woolridge and Linton, 1955). It is significant that during the accumulation of its "100-feet", "50-feet", and later alluvia, the Thames swung northward in the vicinity of the present coastline towards the region of its old mouth.

THE THAMES

The implication of this is that the present estuary of the Thames is comparatively recent. The general position of the lower Thames depression was determined by the earth movements which produced the London Basin, probably in pre-Eocene times. Earth movements during the mid-Tertiary modified its details, but not its major outline. The Miocene was a period of quiescence as far as tectonic movements were concerned. In Diestian times the basin was filled by the sea, and, since the beds of this age are not warped, it is assumed that there was no further tectonic movement during the Pleistocene. The basin is thus both a stratigraphic and a tectonic unit, and Woolridge (1926) summarized its history in three stages: (1) the syncline grew spasmodically from small beginnings and maintained throughout its growth the same major features of form and structure; (2) the successive phases of deepening coincided with, and are to be regarded as the cause of, the several temporary incursions of the sea; and (3) the syncline was drained throughout by a consequent longitudinal river system.

The Thames Estuary today offers several problems of great interest. It is in that part of Britain which is slowly sinking, relative to sea level. This is the combined effect of a downward isostatic movement and a very small eustatic rise of sea level as a result of the melting of the polar ice. The slow sinking has been continuous (not necessarily at the same rate) from early Pleistocene times. It is illustrated in the superimposition of Roman on Iron Age and Bronze Age remains in certain localities in the Lower Thames; by the occurrence of Roman remains now below mean sea level in central London; and by the gradual raising of the banks along the estuary from Medieval or earlier times. Today the measurements of sea level made by tidal records indicate that the movement continues. This may soon have a practical effect: a time may come when adjustments must be made to the level of dock sills, and a Thames barrage will be a necessity.

In the Thames and in the Yare at Great Yarmouth some interesting effects on the regime of estuaries were produced by alterations in bridges. The present bridge at Great Yarmouth allows greater access of the tide than did its predecessor, and this effect is felt throughout the Broads. A tidal lock has been suggested at Great Yarmouth, and if it were built the elimination of tidal rise and fall would have far-reaching physical and biological results. London Bridge, built in 1282, replaced an old bridge of 19 arches and a drawbridge, built in the reign of King John (1199-1215). The longest span was only 30 feet. This struc-

ture had a great effect on the tides, and after its removal the tidal range at and above London was increased up to 25 percent. "The increase in discharge caused by the removal of the bridge altered the regime of the whole estuary. Upstream of the old bridge, rapid deepening of the channel took place to such an extent that two or three other bridges were endangered. Downstream the effects tapered off, but must have been perceptible as far as Woolwich Reach and the Mud Reaches" (Inglis and Allen, 1957).

The Thames is one of the busiest rivers in the world and needs constant dredging. Experiments with a radioactive tracer (Scandium-46) were made in 1955. The tracer material was put down 26 miles below London Bridge in an area where accretion does not occur. Detectors found traces of activity as far as ten miles downstream the same day. It was later proved that this tracer material moved both up- and downstream and was detected upstream in reaches where there is a known net landward movement of water close to the bed (Hydraulics Research Station, 1956). Much of the material dredged from the Thames was dumped in the Black Deep, far down the estuary, where it was assumed it would be carried seaward; but a considerable amount was swept back up the estuary. The only way to get rid of it entirely is either to dump it on land or take it well out to sea. The problem is similar to that of the Mersey.

THE SOUTH COAST

On the south coast of England, in Sussex, there are several small streams which cut through the ridge of the South Downs and are obstructed by shingle bars which were built up by littoral drift (Fig. 8). The profiles of these rivers are unusual. Kirkaldy and Bull (1940) have shown that there are two distinct parts in each profile: a flat lower portion, and a steeper one upstream which is graded to a level below that of the present sea. Except for three cases which can be related to variations in the resistance of the rocks, the upper profiles show breaks which are assumed to be rejuvenation heads working upstream as a result of changes in sea level. The buried channels are probably graded to 80 or 100 feet below sea level. But the Arun and the Rother show that the present flood plain is enclosed in a shallow, distinct trough, about 100 yards wide, locally bordered by a low terrace. Trough and terrace are undoubtedly the result of a recent down-cutting in the old flood plain—but why has this happened in only two of the rivers? Kirkaldy and Bull considered various hypotheses and concluded that the increased erosion was the result of great runoff in the headwaters of the rivers following the clearing of the ancient forest of Anderida. All these small rivers were far more open in Medieval times; the great bridge at Bramber is out of all proportion to the present stream of the Adur. In short, they are all small open tidal inlets, and their present appearance results from oscillations of sea level, silting, littoral drift, and the peculiar circumstances which apply to the Arun and Rother. But should a river mouth of

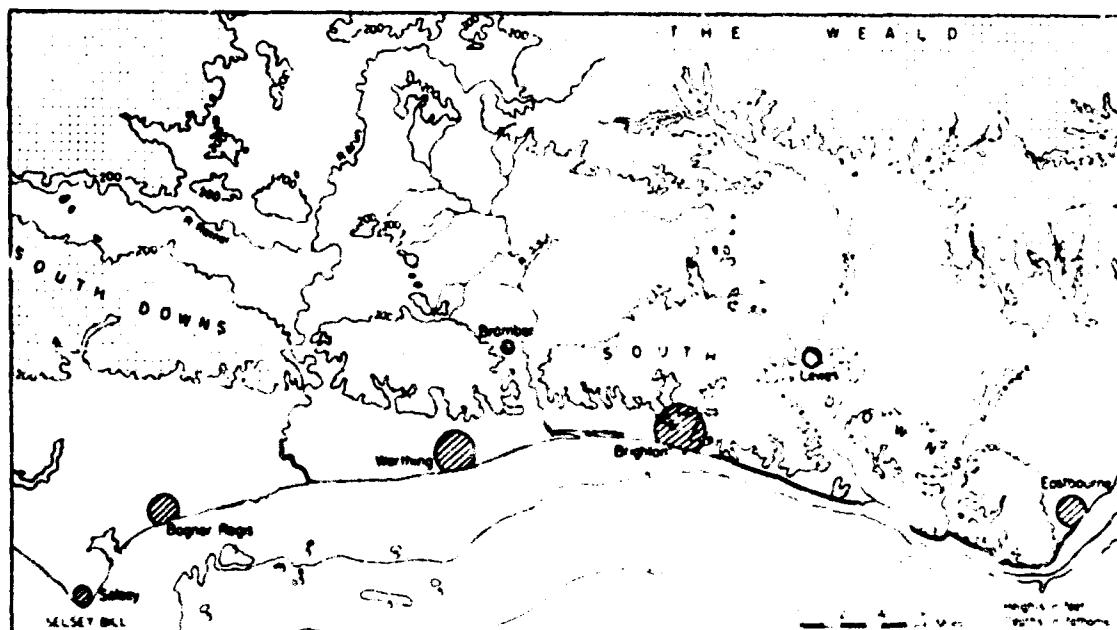


Fig. 8. The Sussex rivers and the gaps through the South Downs.

this type be called an estuary? When the sea level was higher, these mouths must have been close to the gaps cut through the South Downs. They are certainly not rias, and perhaps it is fortunate that the dictionaries already quoted do not specify any particular origin, because the definitions easily include the former and present outlets as estuaries.

WIND AND WAVE ACTION

An estuary is part of the coast, and the ordinary processes of erosion and accretion are at work. Since estuaries may be more sheltered than the open coast, accretion is usually more noticeable than erosion, but much depends on the relation of the estuary to wind and wave action. In the Lower Thames, for example, the Kent coast received severe damage in the great storm surge of 1953. In eastern England the winds were a little west of north, and consequently north Kent and the northeastern corner of the Wash suffered severely. The damage was extreme because the surge had caused a rise of about six feet in water level, and waves of greater size than normal were attacking cliffs, embankments, or masonry structures at an unusually high level (Streets, 1953). Since estuaries are usually narrow upstream, flooding, damage to banks, and ponding back rivers may all cause flooding in flat country well away from the sea.

In conditions of storm and surge the common processes at work on any coast are all speeded up. Beach material is often swept inland, and beaches themselves are combed down, exposing the underlying rock. The rise and fall of the water, as distinct from wave action, may have relatively small effects. The salt marshes along the east coast of England were inundated in 1953 to much greater depths than usual

but suffered no ill effects, but the dune ridges surrounding some of them suffered severely. Canvey Island, on the Essex shore of the Thames, was flooded, not because the main walls facing the Thames gave way, but because the water forced itself up a narrow creek behind Canvey and led to breaches in earth banks. These banks had been neglected because no one expected danger from that direction.

Because accretion of silt and mud often takes place readily in estuaries, they are excellent places in which to study the interactions of physiographical and ecological processes. The plants which are able to colonize mud and sand banks are adapted both to the nature of the substratum (mud, sand) and to the number of tidal inundations they undergo in a lunar cycle or longer period. The elaboration of this subject would occupy too much space in this paper, but it is a matter of the first importance in the investigation of an estuary, both from the purely natural point of view and from that of land reclamation or sea defense.

The transitional nature of estuaries cannot be over-emphasized. They are not only transitional as physiographical forms, but they also mark the change from purely fluvial to entirely marine action. They are also transitional in time: there are the very long-term changes that have characterized the Severn and Thames; the much shorter changes that can be measured in glacial, archaeological, and historical times; and, finally, the many local but significant changes that are taking place today—changes which are frequently brought about by the direct intervention of man. Our successors may soon have to take far more drastic action; the Delta plan in Holland is perhaps only a pointer to what may happen.

LITERATURE CITED

- GREEN, C., and J. N. HUTCHINSON, 1960. In *The Making of the Broads*: p. 129 et seq. Roy. Geogr. Soc., Res. Ser. No. 3.
- GRESSWELL, R. K., 1953. *Sandy Shores in South Lancashire*. Liverpool University Press, Liverpool.
- HYDRAULICS RESEARCH STATION, 1956. *Radioactive tracers in the Thames Estuary*. (D.S.I.R.) Rep. 1956.
- HYDRAULICS RESEARCH STATION, 1958. *Radioactive Tracers for the Study of Sand Movements: Report on an Experiment Carried Out in Liverpool Bay in 1958*. (D.S.I.R.) Rep. 1958.
- INGLIS, SIR CLAUDE, and F. G. ALLEN, 1957. The regimen of the Thames Estuary as affected by currents, salinities and river flow. *Mins. Proc. Inst. Civ. Engrs.* 7: 827.
- INGLIS, SIR CLAUDE, and J. J. T. KESTNER, 1958. Changes in the Wash as affected by training walls and reclamation works. *Mins. Proc. Inst. Civ. Engrs.* 11: 435.
- JENNINGS, J. N., 1952. *The Origin of the Broads*. Roy. Geogr. Soc., Res. Ser. No. 2.
- JENNINGS, J. N., J. M. LAMBERT, C. T. SMITH, C. GREEN, and J. N. HUTCHINSON, 1960. *The Making of the Broads*. Roy. Geogr. Soc. Res. Ser. No. 3.
- KIRKALDY, J. F., and A. J. BULL, 1940. Geomorphology of the rivers of the southern Weald. *Proc. Geol. Assoc.*, 51: 115.
- MILL, H. R., 1924 (1st Ed., 1897). *The Realm of Nature* (3rd Ed.); p. 186. John Murray, London.
- SMITH, A. G., 1958. Post-glacial deposits in south Yorkshire and north Lincolnshire. *New Phytol.*, 57: 19.
- STEERS, J. A., 1948. *The Coastline of England and Wales*; Ch. VI. Cambridge University Press.
- STEERS, J. A., 1953. The East Coast floods, January 31-February 1, 1953. *Geogr. Journ.*, 119.
- WOOLRIDGE, S. W., 1926. The structural evolution of the London Basin. *Proc. Geol. Assoc.*, 37: 162.
- WOOLRIDGE, S. W., and D. L. LINTON, 1955. *Structure Surface and Drainage in South-East England*. Chap. 10. George Philip, London.

The Ontogeny of a Salt Marsh Estuary

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"There is no other case in nature, say in the coral reefs, where the adjustment of organic relations to physical conditions is seen in such a beautiful way as the balance between the growing marshes and the tidal streams by which they are at once nourished and worn away." (Shaler, 1886).

The existing peat of tidal marshes preserves a record of the conditions which existed when the peat was deposited. This paper is an attempt to reconstruct the history of the development of a typical New England salt marsh and of the estuary which it occupies. The principal factors which interact to determine the development of the marsh appear to be the range of tide, the physiology of the plants which produce the peat in relation to tide levels, the process of sedimentation on open tidal flats and within the stands of plants, and the changing level of the sea relative to the land.

The basis for the interpretation of the conditions found in the peat was developed independently by Chapman (1960) and myself (Redfield, 1959), and grew out of an attempt to reconcile observations of Shaler, Mudge and others. Shaler (1886) concluded that a barren slope would become vegetated near the high-water level by a group of plants which can withstand limited submergence. In the New England marshes these include *Spartina patens*, a dwarf form of *S. alterniflora*, *Distichlis spicata*, and some others. The peat they produce will be referred to as high marsh peat. The intertidal slope would become covered with *S. alterniflora*, locally known as "thatch", which grows down from the high-water level through nearly two-thirds of the tidal range. The lower limit of *S. alterniflora* is quite definite and will be referred to as the thatch line. The accumulation of sediment within the stand of *S. alterniflora* builds up a layer of intertidal peat until the high-water level is reached, when high marsh vegetation succeeds it and a layer of high marsh peat is formed covering the intertidal peat. Mudge (1858) had pointed out that peat was found in the Lynn marshes at depths which greatly exceed those at which the salt marsh plants can grow, and considered this to be evidence of subsidence—that is, to a rise in sea level relative to the land. The effects of these processes on the structure of peat was discussed by Johnson (1925).

If sea level rises subsequent to the initiation of the marsh, the bordering upland will become submerged and covered with a layer of high marsh peat. If at

the same time sediment accumulates in the area beyond the thatch line at a rate as great as, or greater than, the rise in sea level, the intertidal marsh will grow out over the rising surface of the flat to such an extent that the thatch line retains its critical elevation relative to the rising high-water level. Meanwhile, high marsh will extend over the intertidal peat as far as the intertidal marsh has built up to the high-water level.

Accordingly, an ancient marsh should consist of high marsh peat increasing in depth from the upland to the site of the original high-water line and should be underlain by the surface of the submerged upland. Beyond this point the subsurface should consist of sedimentary deposits which slope upward away from the upland. These deposits should be covered by a layer of intertidal peat of a thickness equal to the critical depth of the thatch line. Over the intertidal peat, high marsh peat will occur as a wedge decreasing in thickness toward the outer margin of the marsh (Fig. 1). This, a highly idealized picture, may be expected to apply only if sedimentation occurs at a rate as great as, or greater than, the rise in sea level, and if development is not interrupted by episodes of erosion and redeposition. Johnson (1925) describes many cases in which the structure of salt marsh peat cannot be interpreted so simply.

This hypothesis has been applied to reconstructing the development of the salt marsh at Barnstable, Massachusetts. The estuary in which the marsh lies is bounded on the south by the upland of the Sandwich moraine. It is protected to the north from Cape Cod Bay by a sand spit, Sandy Neck, six miles in length, which appears to have grown eastward from an anchor point provided by an outlying moraine, Scorton Neck (Figs. 2 and 3F). About half the enclosed area is occupied by salt marsh, of which nine-tenths has developed to the high marsh condition. The open areas are occupied by sand flats drained by shallow channels at low tide (Ayers, 1959). Evidence of former exposure of the upland shore to the open sea is provided by a prominent sea-cut cliff at Calves Pasture Point (Woodworth and Wigglesworth, 1934) and by a similar cliff on the eastern end of Scorton Neck inside the base of Sandy Neck. The latter descends 18 feet below the marsh surface, reflecting the rise in sea level since it was originally cut. A series of sand hills submerged in the marsh along the western part of the sand pit also provides evidence of

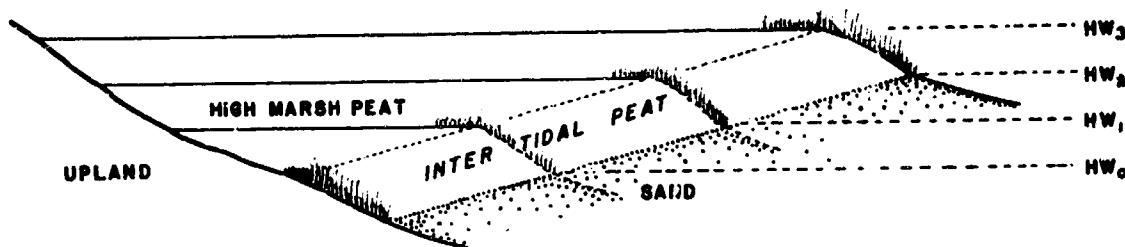


Fig. 1. Development of a typical New England salt marsh with rising sea level and continued sedimentation.

rising sea level (Figs. 3A and B), as do submerged deposits of freshwater peat and tree stumps in several places.

The entire marsh has been sounded with a rod in sufficient detail to establish the major topography of the substratum on which it rests. Supplementary information was obtained by coring. A contour map constructed from the soundings (Fig. 2) shows the following features:

1. Along the south side of Sandy Neck the depth of peat decreases progressively eastward, indicating the more recent development of the marsh as the sand spit grew. Five shallow tongues, which are attributed to terminal hooks that marked temporary interruptions of the growth of the spit, extend across the marsh along the eastern part.

2. Along the upland margin of the marsh, the depth contours suggest a relief similar to that of the adjacent upland. The depths increase to a series of basins of maximum depth not far from the margin. The soundings usually encountered soft peat at all depths to a subsurface containing gravel, stones, or a hard bottom. Deeper basins are also found along the western part of the marsh bordering Sandy Neck.

3. In the central part of the marsh the relief is relatively low. The depths of peat decrease toward the larger creeks which occupy broad areas with depths less than 12 feet. The peat usually becomes

more compact within five or six feet of the substratum, indicating intertidal peat of high mineral content. The substratum is usually sandy.

The block diagram (Fig. 4) shows the morphology more clearly. The deep trough along the margins and the thinning of the peat toward the major creeks and open water, and in the easterly direction, is seen in the vertical sections. Block A shows a vertical section at the head of the marsh, where the peat was formed by the flooding of an upland valley which had not been previously invaded by marine sediments.

These general features are in accordance with the expectations raised by the hypothesis. As a further test, a series of cores was collected across the marsh from the upland to one of the major creeks to examine the relation of high marsh peat, intertidal peat, and composition of the substratum. The water content provides an objective criterion of the character of the deposits, it being found that high marsh peat contains more than 60 percent water (usually more than 70 percent), intertidal peat between 60 and 30 percent, and the unvegetated substratum less than 30 percent. Figure 5 shows the water content of the series of cores. Its distribution confirms the expected structure.

The extent of the marsh as it existed in the past has been reconstructed from the contour map of depths of peat (Fig. 2) by applying the following rules:

- (1) The time at which mean high water reached any

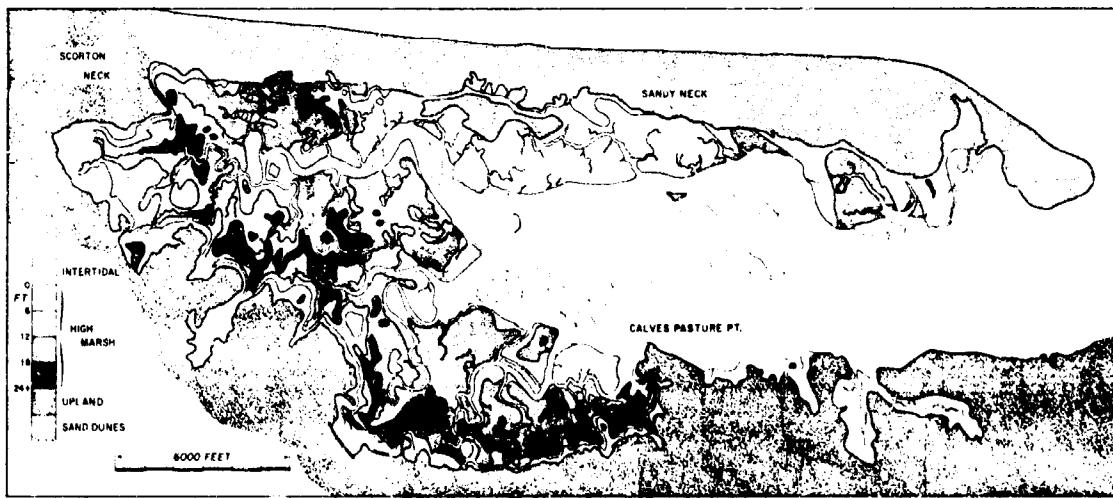


Fig. 2. The Barnstable Estuary, showing the distribution of depth of peat in the high marsh. Contour intervals, 6 feet.

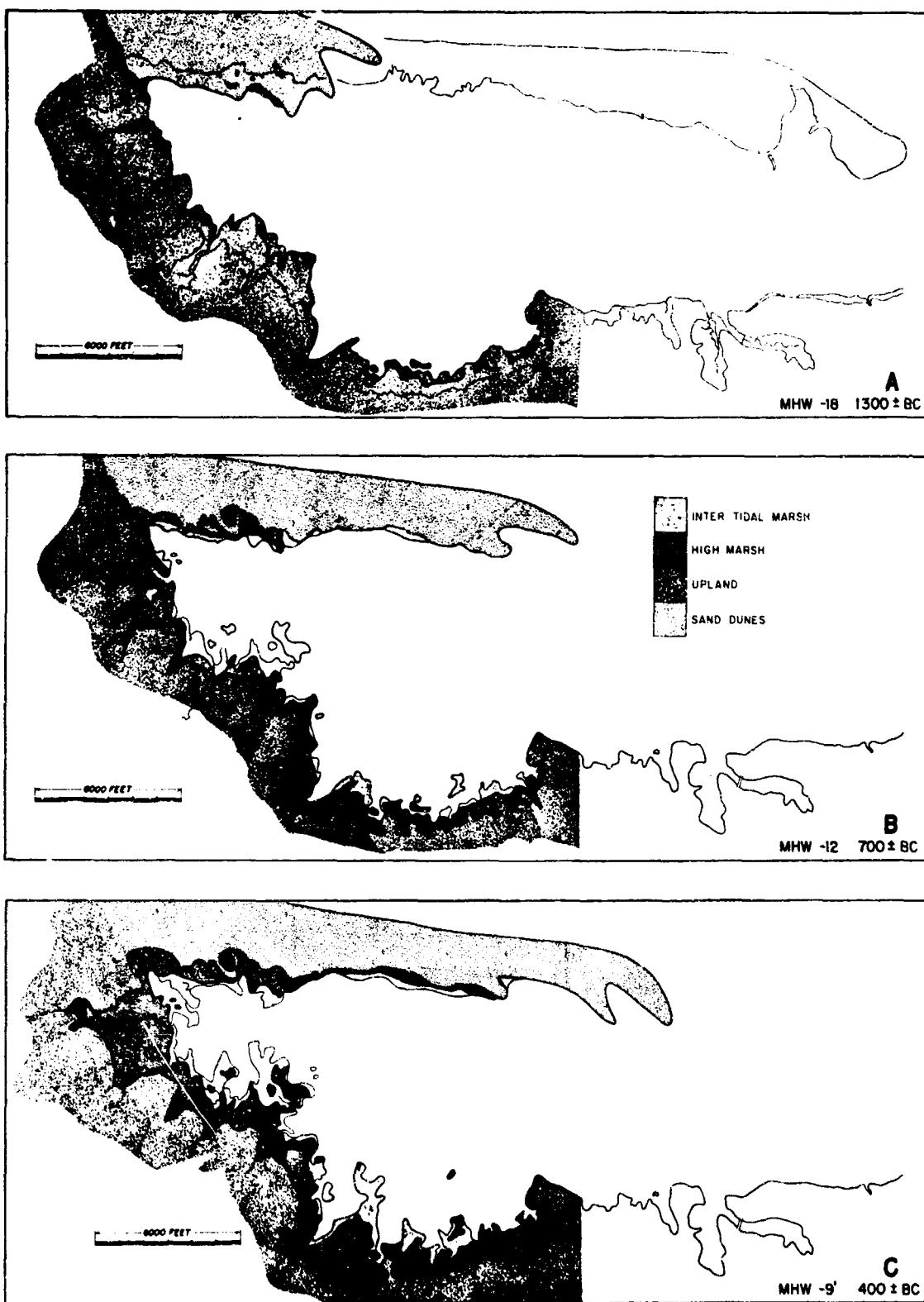


Fig. 3. Reconstruction of Barnstable Estuary and marsh.

- A. $1300 \pm$ b.c., mean high water, 18 feet below present level.
- B. $700 \pm$ b.c., mean high water, 12 feet below present level.
- C. $400 \pm$ b.c., mean high water, 9 feet below present level.

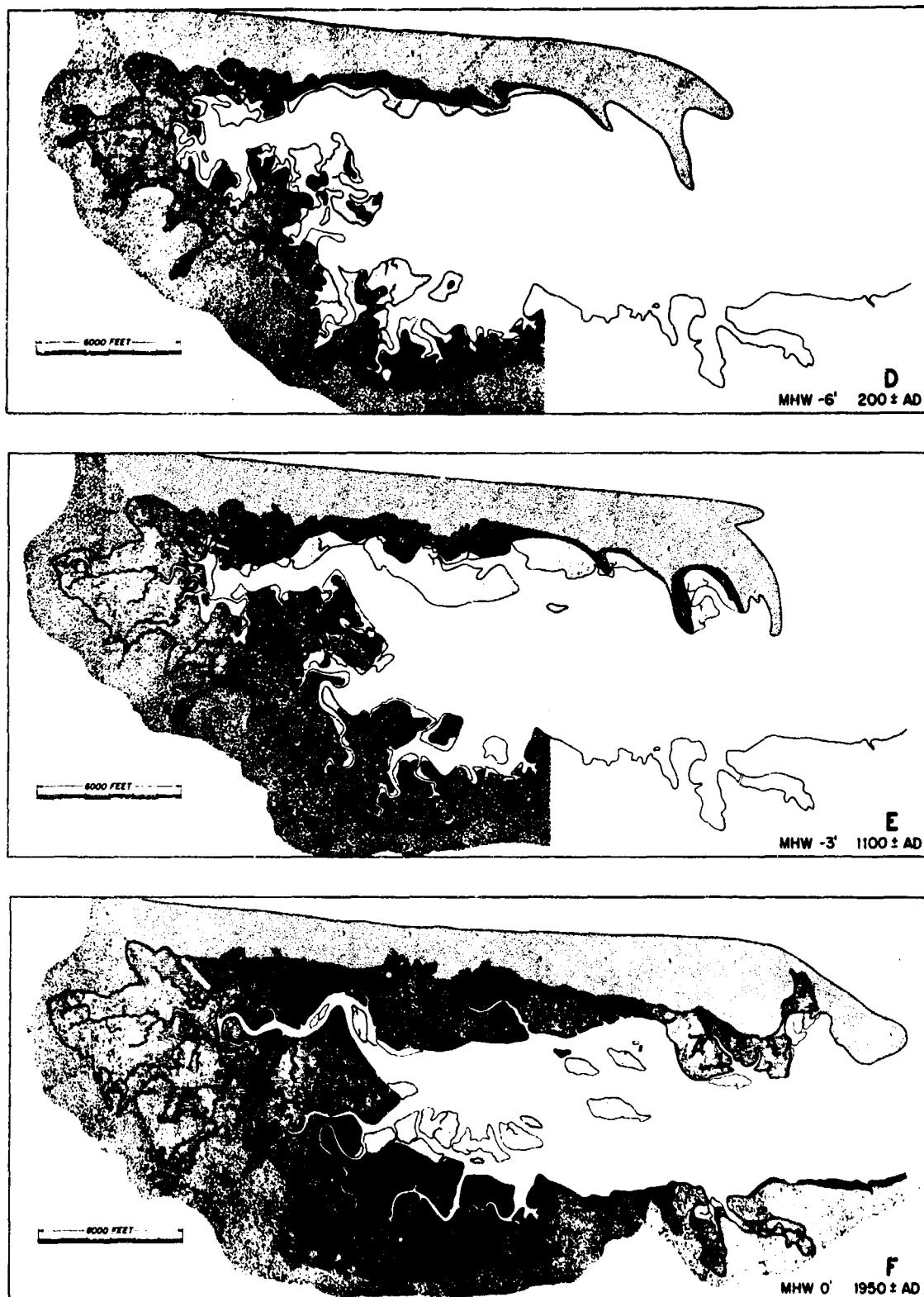


Fig.3. Reconstruction of Barnstable Estuary and marsh.
D. $200 \pm$ A.D., mean high water, 6 feet below present level.
E. $1100 \pm$ A.D., mean high water, 3 feet below present level.
F. $1950 \pm$ A.D., mean high water at present level.

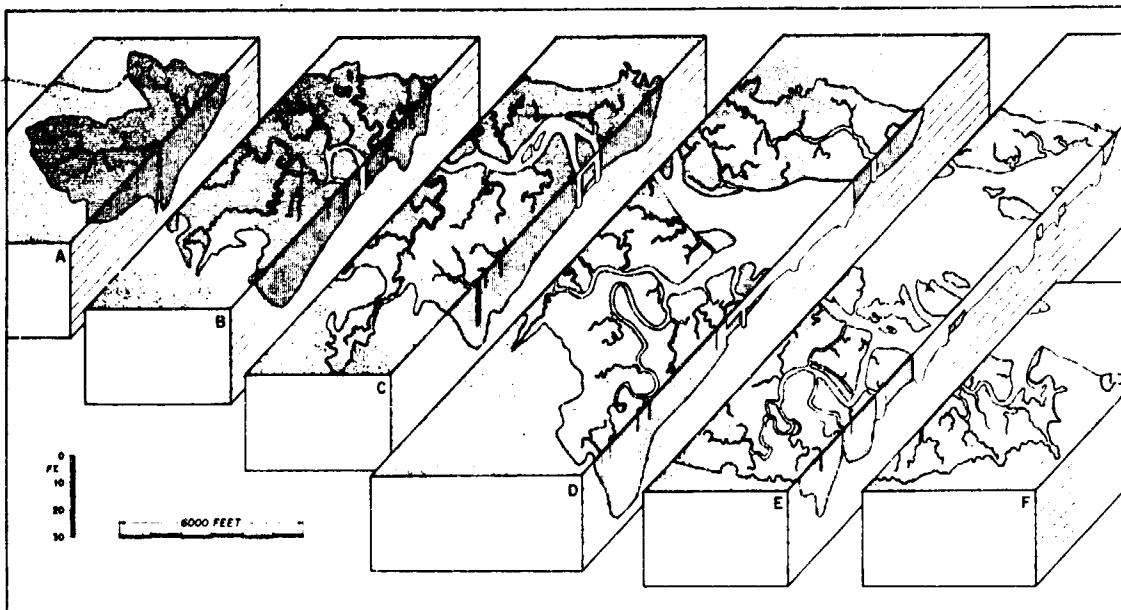


Fig. 4. Block diagram showing the depth of peat along sections across the marsh at Barnstable.

given elevation as sea level rose was established by Redfield and Rubin (1962) by carbon-14 dating of samples of peat collected at various depths at positions where the upland was covered by high marsh peat. They concluded that the mean high-water level has risen, relative to the land, at an average rate of 3.3×10^{-3} feet per year during the last 2,100 years. Prior to that time the average rate of rise was 10×10^{-3} feet per year extending back for at least 3,700 years. (2) The position of the inner margin of the marsh, where it met the upland or the sand spit, is given by the depth contour corresponding to the time in question. (3) The position of the outer margin of the marsh where it met bare flats is given by the depth contour which exceeded that of the inner margin by the critical depth of the thatch line. This depth was determined to be approximately six feet by measuring the elevation of a sand flat on which a vegetation of *S. alterniflora* became established while under

observation, controlled by tide gage measurements which fixed the local elevation of mean high water. (4) The position of the outer limit of high marsh is given by the depth contour nine feet below the level of the high marsh at the time in question. This somewhat arbitrary rule was based on the observation that the depth of high marsh along its present outer margin is usually not less than this.

The reconstructions shown in Figure 3 are thus based on objective interpretation of observed data. However, no criteria have been found for determining the extent of the sand spit beyond the positions where marsh occurred, other than the present condition. In this respect, the reconstructions of the extent of the spit are based on subjective judgment, as are also the diagrams in a few places where application of the rules was ambiguous.

The Sandwich moraine was deposited at the termination of the last advance of the Wisconsin glaciation

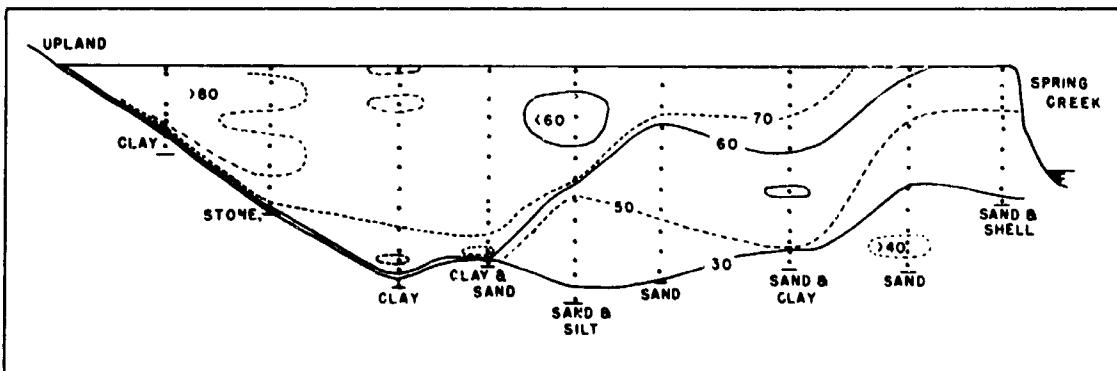


Fig. 5. Water content of peat in a section of marsh from upland to a tidal creek.

(Mather *et al.*, 1942). The earliest local organic remains which have been dated are freshwater deposits about 9,750 years old from a kettle hole at Falmouth, Massachusetts (Rubin and Alexander, 1960). The earliest undoubtedly saltwater peat recovered from the Barnstable marsh was at a depth of 23 feet below present mean high water and was about 3,660 years old. Many of the deeper basins along the margin of the upland were sounded to 25 or 30 feet, and it is not unlikely that they contained peat as old as 4,000 years or more. A sample collected near Scorton Neck at the base of Sandy Neck from 16 feet below the present marsh surface was 3,170 years old, indicating that the sand spit had developed prior to that time. The development of the features to be traced took place very recently—probably not more than 4,000 years ago.

The earliest state which has been reconstructed is that of 1300 B.C., when sea level was 18 feet below its present elevation (Fig. 3A). The sand spit was then little more than a mile in length. Its inner margin lay some 1,000 feet south of its present position. The intervening area has been flooded subsequently by the rising sea level, leaving the sand hills within it completely buried in marsh peat or as islands surrounded by marsh. The subsequent reconstructions show that the sand spit has grown progressively to the east, but at a rate that appears to have diminished since about 2,000 years ago. This is about the time that the rate of rise of sea level decreased greatly (Fig. 6). The terminal hooks, which are found buried in the peat at present, appear to have developed during this latter period of slowly rising sea level (Figs. 3D and E). The margin of the marsh along the western half of Sandy Neck is very irregular as a result of the flooding of sand hill topography by rising sea and marsh

level. Along the eastern half the margin is much smoother because the hooks have been covered by peat, and windblown sand has advanced over the marsh so rapidly that the marsh has not encroached on the sand hill topography.

The marsh itself at the earliest stage consisted of isolated pockets of peat occupying indentations in the upland. They resemble the discontinuous area of marsh found at present along the shore of the open harbor east of Calves Pasture Point (Fig. 2). Such areas appear to be eroding at the outer face and to be advancing over the upland as sea level rises. Presumably, similar pockets may have existed along the upland for an indefinite period prior to the earliest reconstruction. Figure 3B shows that, with the extension of the sand spit and the accumulation of sediment in the protected basin, the marginal marsh has become continuous and is extending as an intertidal marsh into the enclosure. At the same time it is invading the upland, particularly the more pronounced valleys and the areas of low relief to westward.

The subsequent reconstructions (Figs. 3C and E) show the marsh growing out into the basin as tongues whose beginnings are evident at the earlier stage. They occupy positions where, presumably, sand flats had built up. Growth appears to have resulted from the establishment on these flats of islands of intertidal marsh which subsequently became continuous, a process which can be seen to be taking place in the presently existing intertidal islands. The development of these tongues resulted in the separation of the open water into broad sounds which narrowed progressively to define the position of the present major creek systems.

A comparison of Figures 3C, D, and E suggests that these sounds narrowed by the spreading of intertidal marsh onto sand flats where a meandering channel system was already developed. The marsh peat may be expected to have stabilized the meander pattern, which has remained with little alteration as the peat has built up to the present high marsh level. Confirmation of this supposition is found in relatively young marshes at Provincetown and Wellfleet, Massachusetts, where the creeks at low tide meander between bare sand banks along a "thalweg" formed by relatively straight banks of peat.

High marsh has now extended to the banks of the present creeks, except in limited local areas. Goldthwait (1937) has commented on the stability of the meander patterns of tidal creeks. A quasi-equilibrium determined by hydraulic forces appears to have been reached between the processes of accretion and erosion. Leopold and Langbein (1963) and Langbein (1963) have shown that in a tidal estuary the width, depth, and velocity of flow vary with a power of the mean discharge, Q , so that

$$\begin{aligned} \text{width} &\propto Q^b \\ \text{mean depth} &\propto Q^f \\ \text{mean velocity} &\propto Q^m \end{aligned}$$

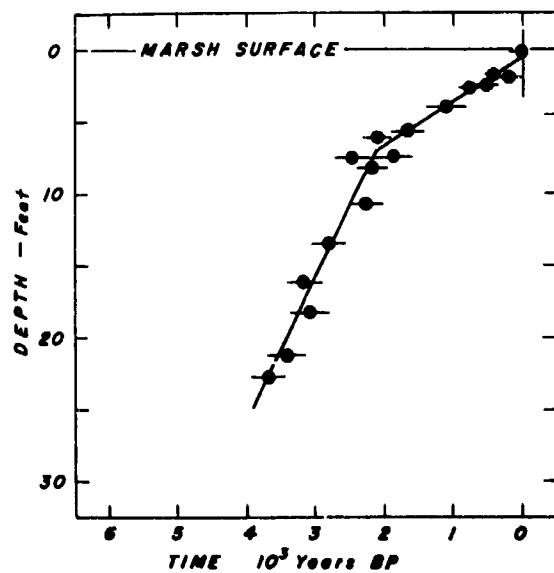


Fig. 6. Relation of age to depth of high marsh peat at Barnstable. (After Redfield and Rubin, 1962.)

From considerations which include continuity, theoretical relations between velocity, slope, and depth, and the conditions that at equilibrium the total work done in the system be minimal and that energy be dissipated uniformly along the channel, they have deduced theoretical relations between the exponents b , f , and m (Table 1). These values, which define the hydraulic geometry of a tidal stream, agree closely with those obtained by measurements in two tidal estuaries near Alexandria, Virginia. Measurement along Spring Creek, in the Barnstable marsh, yield values which agree well with theory.

The reconstructions provide a picture of the ontogeny of the Barnstable marsh which is orderly and plausible. They indicate that the sand spit has grown eastward during a period of about 4,000 years. The marsh, which consisted at first of isolated pockets in protected indentations of the upland, became continuous and began to spread into the enclosure from along the upland margin as sediment accumulated in its shallower parts and protection from the sea became more complete. The development of marsh along the margin of the sand spit proceeded more slowly, perhaps because the basin deepened with distance from the upland and more time was required for sedimentation to reduce its depth. The broad sounds between the advancing tongues of marshland became the site of the future creeks, and the meandering channels in the sand which formed their bottom defined the final pattern which these creeks assumed. High marsh has

Table 1. Exponents in the hydraulic geometry of tidal estuaries in Virginia and Massachusetts. (After Langbein, 1963.)

Exponent	Theoretical	Unnamed estuary, Virginia	Wrecked Recorder Creek, Virginia	Spring Creek, Barnstable, Mass.
Width, b	0.72	0.72	0.77	0.74
Depth, f	0.23	0.22	0.23	0.17
Velocity, m	0.05	0.06	0.00	0.09

now extended to the margin of these channels, and the creeks now are in quasi-equilibrium with the hydraulic forces which arise from the quantity of water which they must carry in response to the rhythm of the tide.

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LITERATURE CITED

- AYERS, J. C., 1959. The hydrography of Barnstable Harbor. *Limnol. Oceanogr.*, 4:448-462.
 CHAPMAN, V. J., 1960. *Salt marshes and salt deserts of the world*. Interscience, London and New York.
 GOLDFTHWAIT, J. W., 1937. Unchanging meanders in tidal creeks. *Proc. Geol. Soc. Am.*, 73:1937.
 JOHNSON, D., 1925. *The New England-Acadian Shoreline*. John Wiley and Sons, New York.
 LANGBEIN, W. B., 1963. The hydraulic geometry of a shallow estuary. *Bull. Intern. Assoc. Sci. Hydrol.*, 8:84-94.
 LEOPOLD, L. B., and W. B. LANGBEIN, 1963. Hydraulic geometry of a small tidal estuary. *U. S. Geol. Surv. Profess. Paper* 422B.
 MATHER, K. F., R. P. GOLDFTHWAIT, and L. R. THIESMEYER, 1942. Pleistocene geology of western Cape Cod, Massachusetts. *Bull. Geol. Soc. Am.*, 53: 1127-1174.
 MUDGE, B. F., 1858. The salt marsh formations of Lynn. *Proc. Essex Inst.*, 2:117-119.
 REDFIELD, A. C., 1959. The Barnstable marsh. In *Proc. of the Salt Marsh Conference, Marine Inst.*; pp. 37-39. University of Georgia, Athens, Georgia.
 REDFIELD, A. C., and M. RUBIN, 1962. The age of salt marsh peat and its relation to sea level at Barnstable, Massachusetts. *Proc. Nat. Acad. Sci.*, 48: 1728-1735.
 RUBIN, M., and C. ALEXANDER, 1960. U. S. Geol. Surv. radiocarbon dates. *V. Am. J. Sci. Radiocarbon Suppl.*, 2:129-185.
 SHALER, N. S., 1886. Preliminary report on seacoast swamps of the Eastern United States. *U. S. Geol. Surv. 6th Annual Report*; p. 364. U. S. Geological Survey, Washington, D. C.
 WOODWORTH, J. B., and E. WIGGLESWORTH, 1934. Geography and geology of the region including Cape Cod, the Elizabeth Islands, Nantucket, Martha's Vineyard, No Man's Land and Block Island. *Mem. Mus. Comp. Zool. Harvard*, 52.

Ephemeral Estuaries of the Deltaic Environment

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The usual definition of the term estuary is not sufficiently inclusive. Most textbook descriptions apply to coastal indentations like the Scandinavian fjords or drowned river mouths like the Chesapeake or Delaware Bays. In addition to these rather obvious illustrations, there are other transitional coastal conditions, including the deltaic environment described here, to which the term estuary is not usually applied. As the word is derived from the Latin *aestus* referring to "tides", an estuary will be considered here as any coastal embayment periodically affected by brackish oceanic waters. Because deltaic regions comprise the most dynamic of coastal areas, estuaries associated with this environment are short-lived and are characterized by rapid change.

QUATERNARY HISTORY OF RIVER MOUTHS

The physiography of a deltaic area is the product of fluvial deposition and coastal erosion as controlled by the underlying predeltaic topography, which was initiated during the last or Wisconsin glacial stage when continental ice sheets extracted sufficient water from the oceans to account for a worldwide sea-level lowering of some 450 feet (Fisk and McFarlan, 1955; Russell, 1957). Strand lines of the glacial stage were correspondingly farther seaward, near the continental shelf-slope break, and all river systems were elongated to adapt to this lowered base level. Although evidence is sparse, most streams seem to have scoured relatively straight valleys directly across the then-exposed continental shelf (LeBlanc and Hodgson, 1959). It can be deduced logically from the physiography of the entrenched Mississippi valley system (Fisk, 1944) that sea level dropped rapidly during the waxing glacial stage and did not remain long at its minimum stand before the ensuing rise began.

Evidence from radiocarbon dating of organic materials incorporated in deltaic deposits suggests that sea level rose to its present position in two phases, the first from its lowest stand (-450 feet) to about -250 feet prior to 35,000 years ago (McFarlan, 1961). The second rise began some 18,500 years ago and continued until about 3,000 years ago, when it reached approximately its present stand (Gould and McFarlan, 1959; McFarlan, 1961; Gould and Morgan, 1962). Through most of this interval, sea-level rise apparently exceeded sediment deposition by streams because glacially entrenched valleys became embayed and estuarine. Only after stillstand was achieved have

rivers been able to prograde actively. It need not be inferred that there has been no eustatic rise nor minor fluctuation in sea level during the stillstand interval, but such changes have been significantly less than during the preceding several thousand years.

Estuarine river valleys indenting the coasts of the United States, especially the Atlantic Coast, reflect the inability of most streams in the 3,000 or so years of stillstand to transport sufficient sediment to overcome ice-age erosional effects. Significantly, in the continental United States, deltaic progradation is not typical of Atlantic or Pacific Coast rivers. Instead it is associated with the streams which discharge into the relatively sheltered Gulf of Mexico. The comparatively small size of the Gulf with resulting low energy waves, a tidal regime of small magnitude, and only minor longshore currents favors deltaic accumulation of sediment. Several illustrations from the United States Gulf Coast serve to illustrate the varying degrees to which these depositional processes have modified glacial-age estuaries. The Nueces, Guadalupe, San Jacinto, and Trinity Rivers of Texas, and the Sabine and Calcasieu of Louisiana, have been unable as yet to completely fill their estuarine valleys. The same applies to the Pascagoula, Mobile, Escambia, and Choctawhatchee Rivers of the eastern Gulf. The Colorado-Brazos River complex of Texas and the Pearl River of Louisiana have barely filled their glacially scoured valleys, whereas the Rio Grande of Texas, because of greater sediment load, has been able to prograde somewhat during the last several hundred years.

The prime illustration of progradation occurs in the complex delta of the Mississippi River, which because of its enormous drainage basin and discharge transports an overwhelming load of sediment annually to the Gulf. Recent work by Coleman and Smith (1964) in the western part of the Mississippi deltaic plain reveals evidence of the oldest known Recent Mississippi River delta in the vicinity of Marsh Island, Louisiana (Fig. 1). Widespread blanket peats, representing a buried deltaic marsh surface, have been determined to be about 4,700 years old. The deltaic mass, surfaced by this marshy peat deposit, accumulated when the rising sea had attained a position perhaps ten feet below its present stand. Subsequent sites of Mississippi River deposition have coalesced to form the deltaic plain which extends some 200 miles east of the older Recent delta. This progradational plain represents deposition essentially contemporaneous with sea-level stillstand.

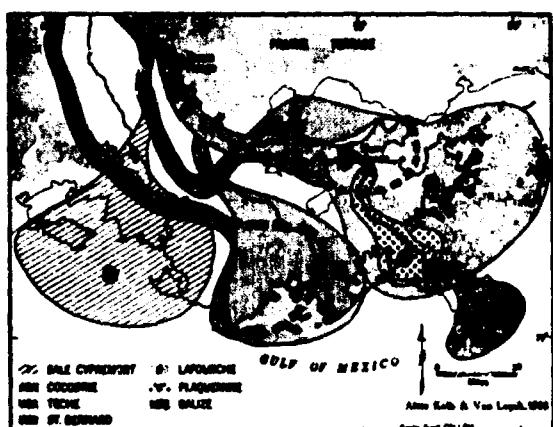


Fig. 1. Chronology of Mississippi River lobate deltas.

Many papers have described various aspects of the Mississippi River deltas, but the significant characteristics to emphasize here are the sedimentary properties and physical processes which serve to modify deltaic morphology during abandonment and deterioration. After a stream is able to fill its estuarine valley it progrades by normal processes of sediment deposition modified by coastal wave, tide, and current action. The deposit consists primarily of coarser material at the mouth of a distributary with finer material carried laterally and seaward onto the adjacent continental shelf. Distributaries extend themselves seaward as long radiating and branching fingers of coarser-grained sediments, overlapping previously deposited finer materials (Fisk, 1961). Progradation continues until deltaic distributary gradients become too flat to be efficient in transporting water and sediment to the Gulf. This sets the stage for an upstream diversion to a route with steeper gradient. During the last several thousand years there have been at least six such major diversions with corresponding lobate deltas, recently summarized by Kolb and Van Lopik (1958), and Saucier (1963) (Fig. 1). Major Mississippi River diversions are not a product of a single major flood as is the case in some rivers such as the Yellow of China or the Colorado River diversion of 1905. Instead they seem to follow a pattern of gradual abandonment of one course along with progressive enlargement of another involving perhaps a century or more (Fisk, 1952).

During abandonment, progressively less water and sediment is transported by the dying distributary. Finally, reduced sedimentation at its mouth cannot keep pace with normal coastal processes and, as the distributary ceases to prograde, erosion becomes the dominant process.

Subsidence is another significant process which leads to destruction of an abandoned deltaic complex. Regional geosynclinal downwarping is widely recognized as a subsidence process affecting deltaic regions, but another factor, the effect of overloading with resulting compaction and water loss by underlying sedi-

ments, is not so commonly considered. Although geosynclinal downwarping is a highly significant process when contemplating geologic spans of time, it is overshadowed by subsidence through compaction during shorter periods such as the interval of stillstand.

RATES AND CAUSES OF SUBSIDENCE

Coastal subsidence and shoreline retreat are well-documented phenomena. Tectonic downwarping of coastal regions, including geosynclinal processes, are widely recognized by geologists, as well as the alternate condition of structurally uplifted coastal segments. Only in the last few years, however, has it been possible, through radiocarbon dating of coastal marsh peats, to recognize and separate post-ice-age eustatic rise of sea level from coastal subsidence (Jelgersma, 1961; McIntire and Morgan, 1962). With recognition of the fact that eustatic rise has been insignificant for the last three millennia, it is now possible to discount that factor in evaluating subsidence rates affecting modern sediments. Because most Mississippi River deltaic progradation has occurred during this interval, the area furnishes many illustrations of deltaic estuaries which can be related directly to subsidence effects.

The modern, popularly named "birdfoot", delta of the Mississippi has been operative for some 500 to 600 years, and thus represents a region in which areas of marine inundation reflect sediment compaction and subsidence alone rather than being influenced appreciably by eustatic sea-level rise. Varying estimates of subsidence rates within the delta have been reported, many of which are summarized by Russell (1936). Figures cited range from a minimum of 0.02 feet/year to as much as 0.17 feet/year, based upon several types of evidence. Recent studies made by the writer, including data from some 140 detailed continuous shallow cores, reveal a recognizable time horizon from which subsidence rates can be calculated over some 100 square miles of the delta. Rates within this area vary from about 0.05 feet/year to 0.13 feet/year, not too dissimilar from previously published figures.

Such rapid subsidence rates are a product of the initial high water saturation of deltaic sediments. Contemporaneous with distributary elongation, coarser, massive bar and levee deposits compact underlying silts, silty clays, and fine-grained prodelta clays by elimination of interstitial water. Compaction initially is quite rapid but becomes progressively slower as moisture content is depleted. In addition, lateral displacement by plastic flow in underlying fine-grained sediments has been shown to be a significant process in a distributary mouth which results locally in abnormally high subsidence rates (Morgan *et al.*, 1963).

EFFECTS OF SUSPENSION

Following abandonment of a deltaic distributary system, sedimentation ceases, but subsidence continues and becomes the dominant modifying process. Effects are soon apparent, especially in the broad areas of near sea-level interdistributary marsh, which break up

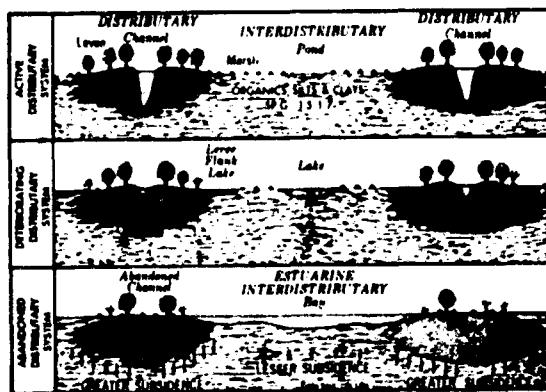


Fig. 2. Effects of deltaic subsidence during distributary system abandonment.

to form ponds and lakes. Distributary levees are more massive than adjacent marshes and consequently subside more rapidly. With subsidence, levees often drag down the adjacent marsh to form elongated open ponds paralleling the outer levee margins (Fig. 2). Such features have been named "levee flank depressions" by Russell (1936).

With continuing subsidence, aided by wave erosion of their banks, lakes, ponds, and levee flank depressions gradually enlarge and coalesce. In a comparatively few years marshy, interdistributary basins thus become open bays connected by devious routes with the adjacent Gulf. This process of reversion from land (i.e., marsh) to water parallels the diversion of fresh water to some other part of the delta. Therefore, the enlarging interdistributary bays progressively become more brackish in nature and are thus converted into estuaries.

DELTAIC ESTUARIES

An estuary of the type described is well illustrated within the area west of the Mississippi Delta known as West Bay. Maps and records of the late 1700's and early 1800's indicate that West Bay consisted of shallow (less than 6 feet deep), irregular, interconnecting bodies of water (Fig. 3). A small abandoned distributary, Grande Liard River or Bayou, had virtually closed itself off according to records of 1817. However, the same stream was known as Detour aux Plaquemines, some thirty years earlier, suggesting that it was somewhat more open and used for navigation at that time. In 1839 a crevasse called The Jump allowed Mississippi waters to flood West Bay. Sedimentation was rapid and by the late 19th century West Bay had been converted into a subdelta consisting of innumerable radiating, bifurcating, and reclosing distributaries with typical interdistributary marshy areas incorporating lakes and ponds. By the early 1900's a few major Jump distributaries had acquired most of the discharge and prograded to become 12 to 14 miles long, establishing too flat a gradient for efficient sediment transport (Fig. 4). During the past

half century sediment deposition and subdelta growth have virtually ceased except for local areas at major distributary mouths. Subsidence has now become dominant and many interdistributary lakes have interconnected to form brackish bays or estuaries (Fig. 5). Thus the West Bay area illustrates a complete cycle, including deterioration of the Grand Liard land mass, formation of a brackish West Bay, fill of the estuary by jump sedimentation, and, finally, present processes of subsidence and conversion to a second estuary. It is interesting to note that a study of sediments in the shallow subsurface also reveals evidence of a third land mass beneath that of the Liard complex. Surface evidence is obscured, but it is quite likely that this represents an even earlier subdelta which diverted from the Mississippi River slightly farther northwest.

Figure 6 illustrates three additional subdeltaic areas that reflect various stages in this process of cyclic sedimentation. The Cubits Gap and Baptiste Collette subdeltas have inundated what was formerly an open bay area (Bay Ronde) and converted it into a broad marshy complex (Welder, 1955). Both of these distributary systems have now passed their peak of sediment deposition and over the next 50 to 100 years will follow the pattern of subsidence and deterioration illustrated in the West Bay area. The crevasse into Garden Island Bay is the most recent of the several major subdeltas and is still actively transporting and depositing sediment. Its distributaries continue to prograde, and deposition in interdistributary basins exceeds subsidence rates.

It is apparent that estuarine East Bay is a potential crevasse site of the future. Early and somewhat unreliable charts of the 1700's suggest that East Bay, at that time, was partially filled with crevasse deposits. Since the advent of accurate mapping of the delta (1838) the area has become progressively more open with subsidence processes overshadowing those of sediment deposition. How long this will continue to be the case is questionable.

INTERDELTAIC ESTUARIES

Besides the comparatively small-scale interdistributary estuaries described, larger embayed areas exist between major deltaic lobes. One of these, the Atchafalaya Basin, is described elsewhere in this volume by Russell. A similar embayed area extends inland between the distributary system of the present Mississippi River levees and abandoned distributaries of the older Lafourche-Mississippi Delta (Fig. 7). A complex, interconnected bay-lake network extends inland from brackish Barataria Bay through less brackish Little Lake into freshwater Lakes Salvador and des Allemands. This entire lake and bay complex with interconnecting bayous traverses a low, generally marshy basin. Except for local rainfall, there is no freshwater influx, the Mississippi now being completely controlled by protective artificial levees. The Barataria-Salvador basin has been deprived of active sedimentation since the Lafourche-Mississippi system

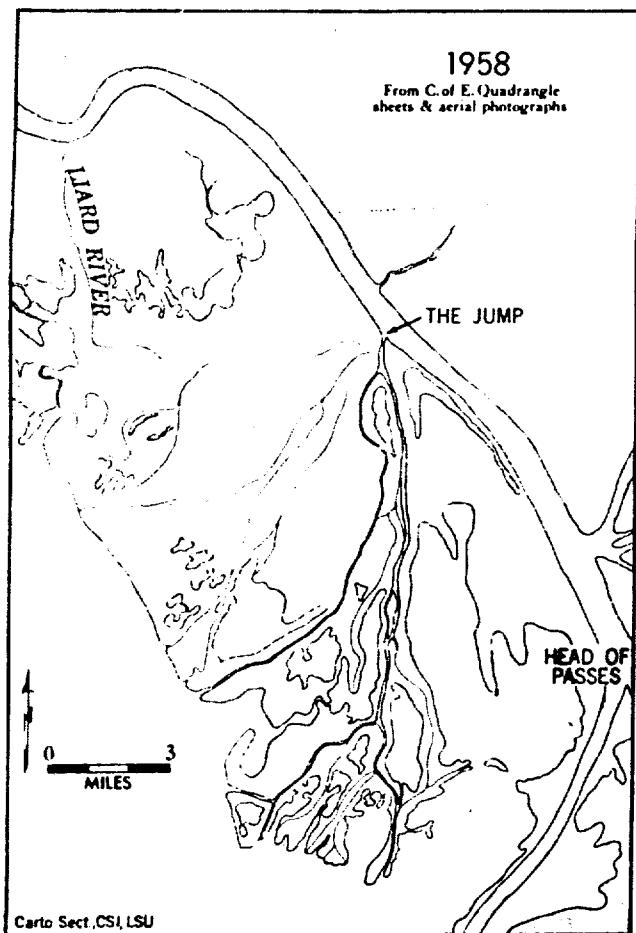


Fig. 5. The Jump (West Bay) subdelta showing subsidence effects during present process of abandonment.

ment compaction have caused levees and interdistributary basins to subside as in the Mississippi Delta, but tidally borne sediment has accumulated rapidly enough to counteract subsidence effects. Abandoned distributary levees slope seaward and pass gradually beneath an overlapping wedge of tidally deposited sediment. Levees have been traced several miles toward the Bay of Bengal by hand auger borings through as much as 12 to 14 feet of overlapping tidal plain deposits.

Highly efficient tidal ebb and flow have prevented channel fill during distributary abandonment. As a result, seaward portions of distributary channels not only remain open during river diversion, but in most instances broaden and deepen through tidal scour during and after abandonment. Fathometer profiles across a number of the principal tidal estuaries reveal depths of 80 to 100 feet (Fig. 8) which are equivalent to or greater than those attained by active distributaries.

Tidal estuaries are the most permanent of the types discussed. Despite deltaic subsidence they maintain channel cross sections adjusted to the prism of tidal water involved and continually build up the adjacent land surface to high-tide level. The sediment involved is apparently supplied by coastal erosion and retreat of the abandoned delta front. Comparisons of maps

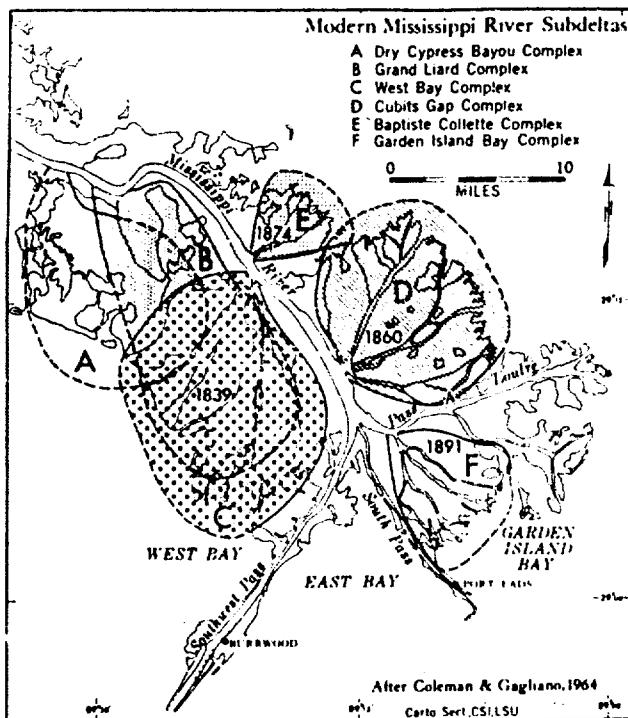


Fig. 6. The several subdeltas of the modern "Birdfoot" Mississippi deltaic system.

for a part of the region reveal retreat rates of about 50 feet a year for the last 40 or so years. Barring a change in tidal regime the drainage network, including principal estuarine channels, remains relatively stable. Termination of the estuarine tidal channel network could be brought about by coastal retreat, a very slow process considering the width of the tidal plain, or by a new influx of alluvial sedimentation from an upstream diversion of the principal rivers, a much more likely prospect, particularly in the Ganges-Brahmaputra area which is subject to considerable tectonic activity (Morgan and McIntire, 1959).

SUMMARY

Three distinct geomorphic estuarine types can be recognized in the environs of major river deltas. Illus-

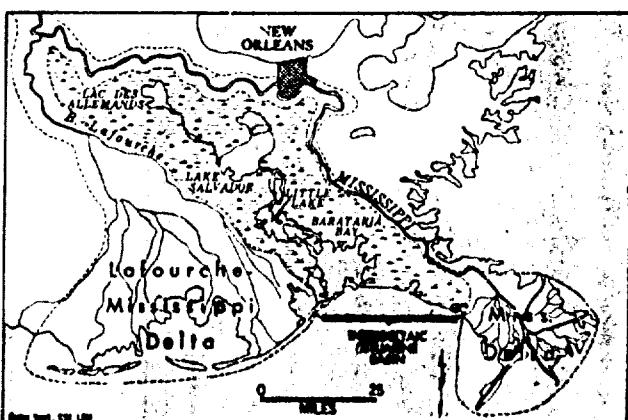


Fig. 7. Interdeltaic basin between two Mississippi River delta systems.

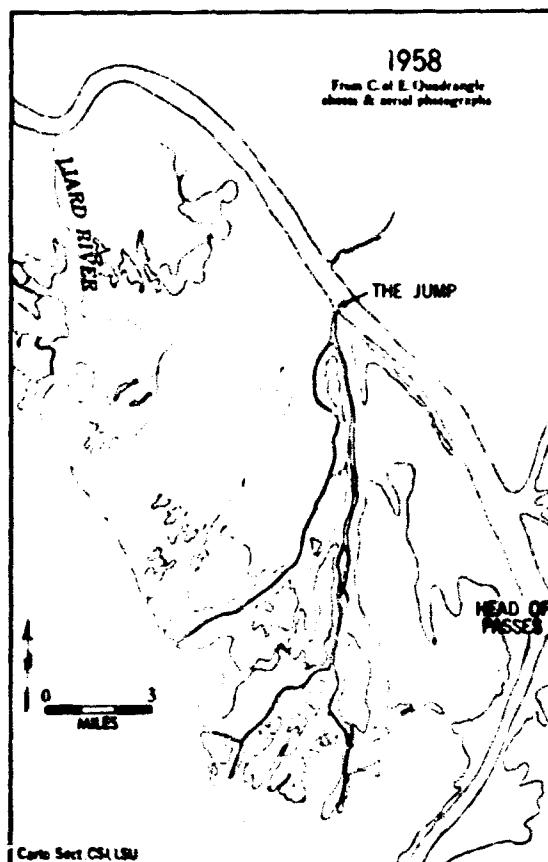


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Highly efficient tidal ebb and flow have prevented channel fill during distributary abandonment. As a result, seaward portions of distributary channels not only remain open during river diversion, but in most instances broaden and deepen through tidal scour during and after abandonment. Fathometer profiles across a number of the principal tidal estuaries reveal depths of 80 to 100 feet (Fig. 8) which are equivalent to or greater than those attained by active distributaries.

Tidal estuaries are the most permanent of the types discussed. Despite deltaic subsidence they maintain channel cross sections adjusted to the present of tidal water involved and continually build up the adjacent land surface to high tide level. The sediment involved is apparently supplied by coastal erosion and retreat of the abandoned delta front. Comparisons of maps

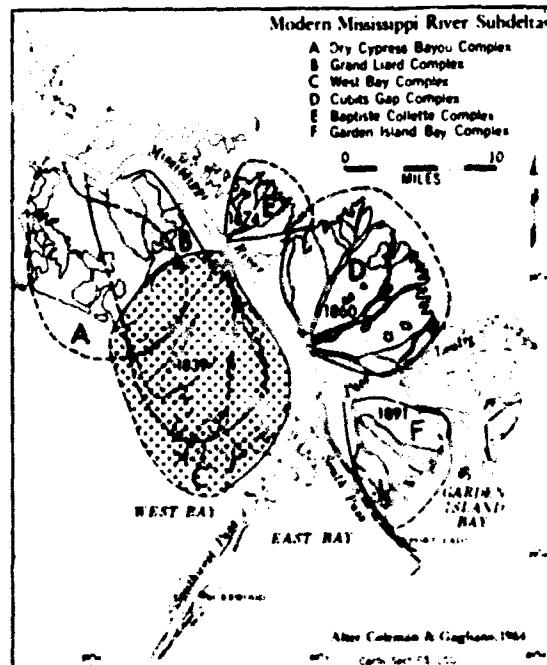


Fig. 6. The several subdeltas of the modern "Birdfoot" Mississippi deltaic system.

for a part of the region reveal retreat rates of about 50 feet a year for the last 40 or so years. Barring a change in tidal regime the drainage network, including principal estuarine channels, remains relatively stable. Termination of the estuarine tidal channel network could be brought about by coastal retreat, a very slow process considering the width of the tidal plain, or by a new influx of alluvial sedimentation from an upstream diversion of the principal rivers, a much more likely prospect, particularly in the Ganges-Brahmaputra area which is subject to considerable tectonic activity (Morgan and McIntire, 1959).

SUMMARY

Three distinct geomorphic estuarine types can be recognized in the environs of major river deltas. Illus.

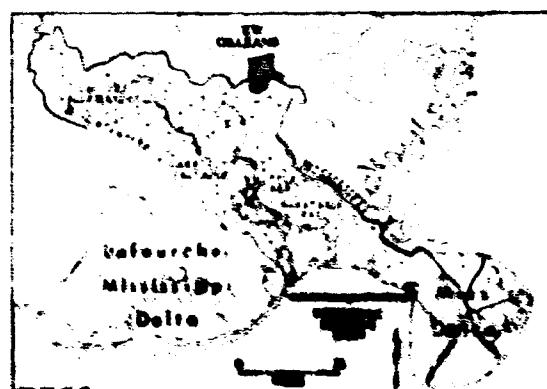


Fig. 7. Interdeltaic basin between two Mississippi River delta systems.

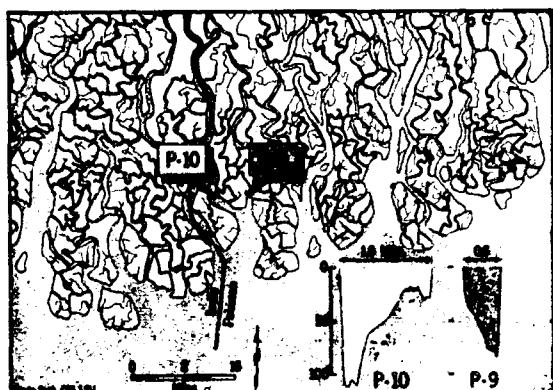


Fig. 8. Tidal patterns and abandoned distributary channel profiles of the Ganges-Brahmaputra system, India—East Pakistan.

trations have been chosen from the Mississippi Delta, a low-tide and low-energy environment, and the high-tide regime of the Ganges-Brahmaputra system. Other areas, subject to conditions between the extremes described, would display intermediate variations in effects of the processes considered.

All deltaic estuaries are a product of the delicate balance which exists between coastal progradation through sedimentation, coastal retreat under wave attack, and variations in sea level. The present happens to be a time of stability or near stability of sea level, consequently minor subsidence in deltaic land elevation through compaction or downwarping can lead to the formation of estuaries.

Currents resulting from a significant tidal range modify deltaic physiography by channel erosion and interdistributary deposition. Tidal processes serve to mask or obscure the estuarine types of the low tidal deltaic environment. In either case, estuarine morphology of the deltaic environment is subject to rapid modification, as are deltas themselves. From the standpoint of geologic time, deltaic estuaries are ephemeral in nature, but, when considering the relatively short span of time involved in recorded human history, these complex changing environments acquire great significance.

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LITERATURE CITED

- COLEMAN, J. M., and W. G. SMITH, 1964. Late Recent rise of sea level. *Bull. Geol. Soc. Am.*, 75:833-840.
- FISK, H. N., 1944. *Geological investigation of the alluvial valley of the lower Mississippi River*. Mississippi River Comm., Vicksburg, Mississippi.
- FISK, H. N., 1952. *Geological investigation of the Atchafalaya Basin and the problem of Mississippi River diversion*. Waterways Experiment Sta., Vicksburg, Mississippi.
- FISK, H. N., 1961. Bar-finger sands of Mississippi delta. In *Geometry of Sandstone Bodies*; pp 29-52. Am. Assoc. Petrol. Geologists, Tulsa, Oklahoma.
- FISK, H. N., and E. McFARLAN JR., 1955. Late Quaternary deltaic deposits of the Mississippi River. *Geol. Soc. Am., Spec. Paper*, 62:279-302.
- GOULD, H. R., and E. McFARLAN, JR., 1959. Geologic history of the chenier plain, southwestern Louisiana. *Gulf Coast Assoc. Geol. Socs. Trans.*, 9:261-270.
- GOULD, H. R., and J. P. MORGAN, 1962. Coastal Louisiana swamps and marshlands. In *Geol. Gulf Coast and Central Texas and Guidebook of Excursions*; pp. 286-341. Houston Geol. Soc., Houston, Texas.
- JELGERSMA, S., 1961. Holocene sea level changes in the Netherlands. *Mededel. Geol. Sticht., Ser. C-VI*, No. 7, p. 101.
- KOLB, C. R., and J. R. VAN LOPIK, 1958. Geology of the Mississippi River deltaic plain, southeastern Louisiana. *Waterways Experiment Sta., Tech. Rept. No. 3-483*, Vicksburg, Mississippi.
- LEBLANC, R. J., and W. D. HODGSON, 1959. *Origin and development of the Texas shoreline*; pp. 57-101. Second Coastal Geog. Conf., Baton Rouge, Louisiana.
- McFARLAN, E., JR., 1961. Radiocarbon dating of Late Quaternary deposits, South Louisiana. *Bull. Geol. Soc. Am.*, 72:129-158.
- MCINTIRE, W. G., and J. P. MORGAN, 1962. Recent geomorphic history of Plum Island, Massachusetts, and adjacent coasts. *Coastal Studies Inst., Coastal Studies Ser. No. 8*. Louisiana State Univ. Press, Baton Rouge, Louisiana.
- MORGAN, J. P., J. M. COLEMAN and S. M. GAGLIANO, 1963. Mudlumps at the mouth of South Pass, Mississippi River, sedimentology, paleontology, structure, origin and relation to deltaic processes. *Coastal Studies Inst., Coastal Studies Ser. No. 10*. Louisiana State Univ. Press, Baton Rouge, Louisiana.
- MORGAN, J. P., and W. G. MCINTIRE, 1959. Quaternary geology of the Bengal Basin, East Pakistan and India. *Bull. Geol. Soc. Am.*, 70:319-342.
- RUSSELL, R. J., 1936. Physiography of lower Mississippi River delta. *Louisiana Dept. Conserv. Bull. Geol. Surv.*, 8:2-199.
- RUSSELL, R. J., 1942. Flotant. *Geograph. Rev.*, 32:74-98.
- RUSSELL, R. J., 1957. Instability of sea level. *Am. Scientist*, 45:414-430.
- SAUCIER, R. T., 1963. Recent geomorphic history of the Pontchartrain basin, Louisiana. *Coastal Studies Inst., Coastal Studies Ser. No. 9*. Louisiana State Univ. Press, Baton Rouge, Louisiana.
- WELDER, F. A., 1955. *Deltaic processes in Cubit's Gap Area, Plaquemines Parish, Louisiana*. Ph.D. dissertation (Available from University Microfilms, Ann Arbor). Louisiana State Univ., Baton Rouge, Louisiana.

Regional Geomorphological Characteristics of Some Australian Estuaries

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Important contributions have been made to the study of estuarine hydrology in Australia (Rochford, 1951, 1959; Spencer, 1956; Thomson, 1959), but little detailed work has been done on the geomorphology of Australian estuaries. Study of the geomorphological characteristics of some representative Australian estuaries shows how their differences may be related to geological, climatic, hydrological, and biological factors which vary regionally around the margins of the continent. Many unsolved problems may not all be distinctive, but some are likely to be unfamiliar to those who have worked on estuaries elsewhere.

A complete definition of an estuary requires reference to its form, its tidal regime, and its salinity characteristics. Lake (1949) said of form, "The mouth is V-shaped and widens near the sea." Ketchum (1951) described an estuary as "a body of water in which the river mixes with and measurably dilutes sea water" as a result of tides. A geomorphologist is concerned primarily with the evolution of the configuration of an estuary and with changes in progress at the present time. He regards an estuary as an assemblage of land forms created by the submergence of a valley mouth, and retains an interest in its evolution when it has ceased to be an estuary: for example, when a coastal barrier has been built up across its mouth to enclose a lagoon, or when sedimentation has replaced it by a depositional plain which may protrude from the coastline in the form of a delta. Patterns of erosion and sedimentation within an estuary are influenced by waves, tides, and river currents. These patterns are also influenced by biological processes, notably in the development of halophytic and hydrophytic vegetation communities. The effects of these processes differ from estuary to estuary in Australia because of contrasts in the geological and geomorphological setting, and there are broad variations which can be related to regional differences in dynamic environmental factors.

DYNAMIC ENVIRONMENTAL FACTORS

Factor 1—Aridity is a prime factor in many aspects of Australian geography and estuaries are no exception. Except for Tasmania, parts of the southeastern mainland, and parts of the east Queensland coastal region, Australian rivers have low runoff coefficients and few have perennial flow (Fig. 1). Even these perennial rivers show marked seasonal variations, and spasmodic flooding is characteristic throughout Australia. These conditions affect the geomorphology

and the hydrology of estuaries; they weaken the ability of rivers to prevent barrier formation by marine action, and they limit the yield of fluvial sediment for delta and barrier construction. Certain coasts, notably along the Nullarbor Plain and also in the neighborhood of the Eighty Miles Beach in Western Australia, lack estuaries because they adjoin riverless areas.

Factor 2—More than half the coast of Australia (Fig. 2), from Shark Bay in Western Australia southwards to Cape Leewin, eastwards to Cape Howe, and northwards to Fraser Island in Queensland, is a coast of high wave energy subject to the effects of long-period (12–16 seconds) swell originating in the Southern Ocean (Davies, 1960). The same is true of much of the coast of Tasmania. On such coasts, extensive barriers have been built up by the action of ocean swell, and many of the river mouths are partly or wholly cut off from the sea; estuarine lagoons are therefore more common than simple estuaries. These estuarine lagoons are similar to the enclosed river mouths known as "blind estuaries" in South Africa (Day, 1951), where rivers with comparable regimes reach coasts confronted by strong ocean swell.

Few river mouths are completely and permanently enclosed by barriers. Usually there is a natural outlet,

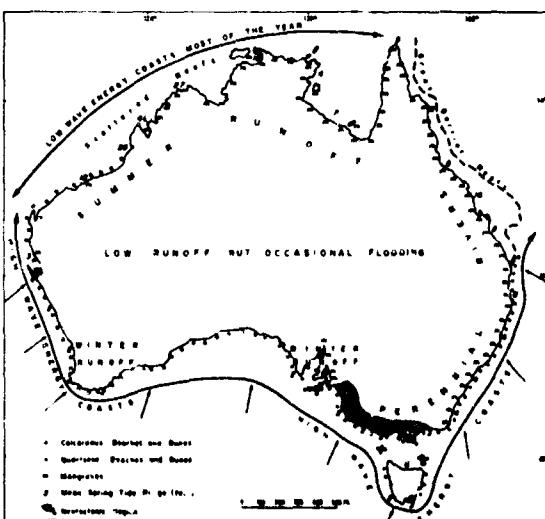


Fig. 1 Major dynamic factors affecting Australian estuaries.

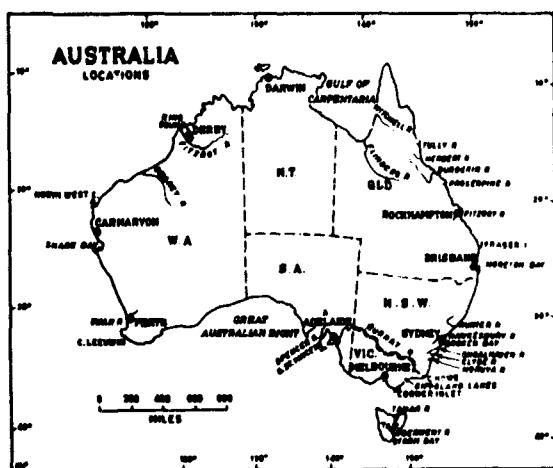


Fig. 2. Locations of places and features mentioned.

which may be sealed off by marine deposition when the river discharge is low, and reopened by augmented outflow after a heavy rainfall within the catchment region. The position of estuarine outlets is often related to patterns of refraction of ocean swell. The outlets occur where the swell is strongly refracted, and therefore weakened, in the vicinity of rocky headlands, or where there are islands or shoals immediately offshore (Bascom, 1954).

For various reasons, the tropical coasts of Australia are subject to less persistently energetic wave regimes. The barrier reefs off the east Queensland coast dissipate the South Pacific swell, so that this coast is subject only to the more variable wave action produced by winds blowing over coastal water. Waves generated by the southeasterly trade winds are dominant for much of the year, but northerly monsoons affect the coast north of Townsville during the summer months. Protection by coral reefs is more localized off the north coast of Australia (Fairbridge, 1950), but this coast is beyond the effective reach of ocean swell, and wave action here is related simply to wind conditions over the adjacent seas. The strongest wave action accompanies the summer monsoon. Regular ocean swell builds up barriers and smooths coastal outlines in plan, but the more variable wave action on the tropical coasts of Australia helps to maintain wide, open estuaries, and to create protruding deltas like those of the Burdekin and Herbert Rivers in Queensland and the De Grey in Western Australia. In addition to the importance of ocean swell in shaping coastal outlines, it is possible that these long ocean waves have swept sand across the continental shelf and delivered it to the coast during and since the postglacial marine transgression. Bird (1961a) has suggested that this may have contributed to the building of barriers on the southeastern coast of Australia; there is certainly less sand on the northern coast which is not exposed to ocean swell, and on the east Queensland coast where the reefs offshore are old enough to have prevented this landward drifting.

Factor 3—Tidal conditions generally show a com-

plementary pattern. The high wave energy coasts have low to moderate tidal ranges, but the tropical coasts are subject to tides of moderate or high range. As the morphological effects of waves and tides are often opposed, this complementary distribution has a strengthened significance: where the tidal range is large, strong transverse ebb and flow currents prevent the formation or completion of barriers and maintain good outlets through the existing barriers.

Factor 4—Sedimentation within estuaries is influenced by biotic factors where salt marsh, mangrove swamp, or reed swamp develop on their margins. Mangrove communities, which are important in many Australian estuaries, extend from the tropical coasts into the domain of high wave energy coasts. They occur as far south on the east coast as Corner Inlet in Victoria; they are found in estuaries and inlets around Spencer Gulf and Gulf St. Vincent in South Australia; on the west coast they reach southwards to the neighborhood of Carnarvon in Western Australia. Where the tidal range is large, mangroves form broad zones of swamp vegetation on intertidal land, but they are restricted or absent in estuarine lagoons where the tidal range is reduced. In the absence of mangroves, many Tasmanian estuaries are bordered by salt marshes similar to those found in northwestern Europe and eastern North America. The vigorous hybrid, *Spartina townsendii*, which has so strongly modified the geomorphological evolution of many estuaries in northwestern Europe (Bird and Ranwell, 1964) has recently been introduced to the Tamar Estuary in Tasmania, but is not yet common in Australian estuaries. Reed swamp encroachment is restricted to relatively fresh water and becomes more important where the enclosure of estuaries by barriers permits reduction of salinity by inflowing rivers.

Factor 5—A further differentiating factor affecting estuarine geomorphology derives from a marked regional contrast in the mineralogy of beach sands and the lithology of derived dune formations on the Australian coast. On the western and southern coasts, from Shark Bay down to northwestern Tasmania, beach sands are predominantly calcareous and older dune and barrier formations have become lithified as eolian calcarenite. On the eastern coast, from Fraser Island south to eastern Tasmania, quartzose beach sands predominate and dunes and barriers derived from them remain relatively unconsolidated. Depositional forms in calcarenite are more resistant to erosion by waves and currents and thus are more durable as land forms than similar features built of quartzose sand. In consequence, the geomorphological framework of estuaries and estuarine lagoons on the western and southern coasts is often better defined than those preserved in calcarenite on the eastern coasts with older barrier systems dating from Pleistocene times. On the tropical coasts the dunes are much more localized, and their virtual absence from the perennially humid sectors is consonant with what is known of other coasts in humid tropical regions (Jennings, 1964).

Factor 6—Neotectonic effects cannot be excluded from consideration of present-day estuaries, many of which certainly inherit morphological features from estuarine phases prior to the Recent (Holocene) marine transgression. Neotectonism is strongly suggested by the configuration of some estuarine lagoons and embayments on the coast between Cape Howe and the mouth of the Murray, in Victoria and South Australia, when taken in association with landform evidence of tectonic deformation and the proximity (in some cases) of fault lines still subject to earth movements. But proof must await detailed geomorphological and stratigraphic studies.

Each of the six dynamic factors we have listed works, of course, within the more static framework of the geological structure and geomorphological evolution of the coastal hinterland. This can best be illustrated by dealing with representative estuaries in greater detail.

REGIONAL EXAMPLES OF ESTUARIES

THE SWAN ESTUARY, WESTERN AUSTRALIA

The Swan Estuary (Fig. 3) falls within a Pleistocene coastal plain fronting a Precambrian shield, both thought to have been tectonically stable within the lifetime of the estuary. More precisely, the estuary transects two ancient dune systems, the inner of weak quartzose dunes, the outer of eolian calcarenite. The latter is quite resistant, in part, to erosion. Within the dune limestones there are successive belts, and the estuary cuts the outermost in a narrow, shallow, and winding channel which may have originated as a "constructional gorge" (Jennings, 1957).

The rivers entering the estuary have low discharge most of the year, though floods occur in the short winter rainy season. Astronomical tides have only a

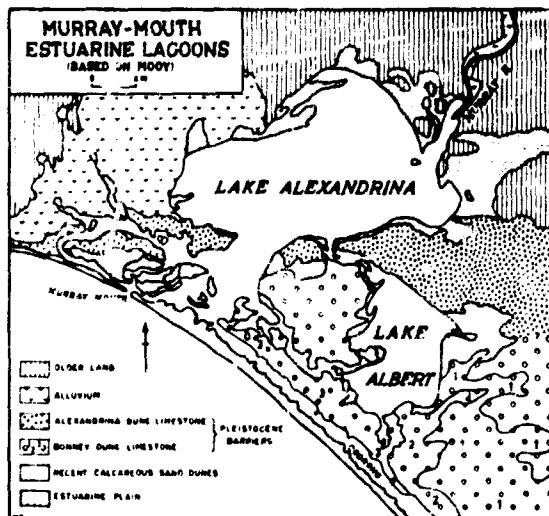


Fig. 4. The Murray River Estuary, South Australia.

two-foot range and are often exceeded by tides due to wind action. These dynamic factors, and the comparatively resistant rock of the coastal barrier, account for the meager outlet to this estuary which in many ways resembles an estuarine lagoon.

The constricted entrance, the river regime, and the small tides produce a distinctive hydrology with phases of prolonged and pronounced vertical stratification interspersed with spasms of cellular circulation. The stratification promotes an accumulation of black, richly organic silt on the floor of the estuary. The limited development of the salt marsh is also correlated with the smallness of the tide. Two partly emerged spits suggest a tendency towards segmentation—a process which takes place in estuarine lagoons where the tidal range is small (Price, 1947).

The age of the estuary is linked to that of the calcarenite, which McArthur and Bettenay (1960) infer belongs to the earlier Würm interstadials, so that in its present form the estuary may relate solely to the Holocene transgression (Churchill, 1959). This dating, however, depends ultimately on an altitudinal correlation with the European sequence of shorelines, and cannot command much confidence. The possibility remains that Pleistocene interglacial estuarine phases have contributed to the present morphology.

THE MURRAY ESTUARY, SOUTH AUSTRALIA

A long history is even more evident in the case of the Murray Estuary (Fig. 4), where successive calcarenous and calcareous sand ridges have produced an estuary-lagoon complex. The lithified dune ridges are regarded by Mooy (1959) and others as inherited from interglacial estuarine phases, whereas the outermost unconsolidated sand barrier is attributed to the Recent.

Though a big river, the Murray loses volume over much of its course through semi-arid country and has

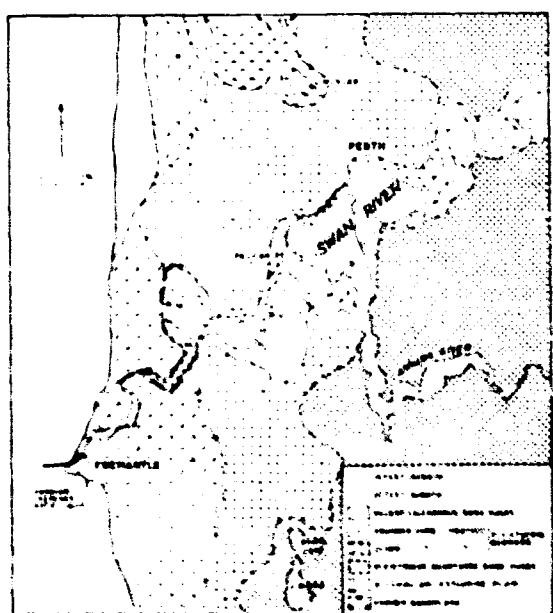


Fig. 3. The Swan Estuary, Western Australia.

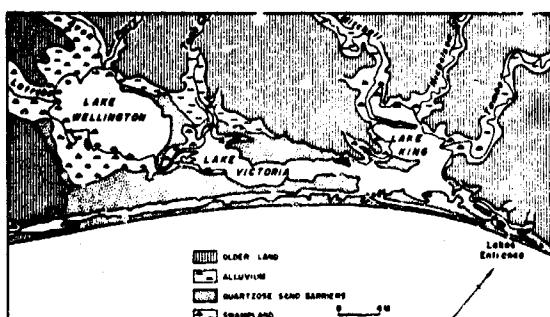


Fig. 5. The Gippsland Lakes, Victoria.

an exceptionally low ratio of mean annual discharge to basin area. Tides at the Murray's mouth are small (3 feet), and the same combination of factors as in the Swan Estuary account for narrow and shallow channels at the outlet. However, these lagoons are more extensive and their configuration may be due in part to a neotectonic factor of Quaternary warping.

Calcareous has provided a good foundation for the construction of barrages across the outlets, and since these were completed in 1940 the estuarine lagoons have become freshwater lakes, with consequent changes in littoral ecology and shoreline geomorphological processes. Reed swamp encroachment has become widespread and associated sedimentation is building up depositional land on sections of the shorelines of Lake Albert and Lake Alexandrina (Bird, 1962).

THE GIPPSLAND LAKES, VICTORIA

This is an estuary-lagoon complex (Fig. 5) replacing a former marine embayment. The strong swell from the Southern Ocean has built long coastal barriers, here of quartzose sand, which enclose Lakes King, Victoria, and Wellington. These lakes are fed by four rivers of more regular regime than those already discussed, but with seasonal variations in runoff. The natural outlet from these lakes used to be intermittent, blocked by sand in the summer and reopened by winter freshets. Tidal action is only moderate, permitting the segmentation of initially elongated lagoons into a chain of smaller, oval lagoons by the action of wind-generated waves in the manner described by Bird (1963). Rivers have built cuspate and digitate deltas within this sheltered and tidally inactive system of estuarine lagoons. Similar deltaic features are found elsewhere in other Australian coastal lagoons.

In recent years, much of the shoreline of the Gippsland Lakes has become subject to erosion, which is also consuming the deltas built by the Mitchell and Tambo Rivers. Bird (1961b) has shown that this is a consequence of replacement of the intermittent natural outlet through the barrier by an artificial cut made in 1889. The salinity of the Gippsland Lakes has evidently increased as a result. In the eastern part of the lakes a former reed swamp fringe (chiefly *Phragmites*) has died back, and erosion has ensued from the quite substantial waves generated within the lakes. These estuarine lagoons were formerly so well

enclosed from the sea that they were fresh enough for reed swamp to encroach from their shores in the manner of swamps bordering freshwater lakes. But reed swamp encroachment is now confined to sections of the lake shores remote from the artificial entrance, in waters where salinity remains relatively low. The geomorphological response to increasing salinity in the Gippsland Lakes may be contrasted with the geomorphological changes that have followed the freshening of the Murray lagoons. Neotectonic movements may be partly responsible for the shape of Lake Wellington; its shape seems to be related to a protrusion of the former marine embayment along the axis of the Latrobe syncline into an area that was probably subject to very recent tectonic subsidence.

Farther south, in Corner Inlet, the coastal barriers are less continuous and break up into a chain of barrier islands. Recent downwarping may be responsible for this, but other factors are the increased spring tidal range (8 feet, compared with 3 feet at the entrance to the Gippsland Lakes), and the more intricate wave refraction which results from waves encountering offshore islands and shoals within shallow coastal waters.

THE FITZROY ESTUARY, WESTERN AUSTRALIA

The Fitzroy (Fig. 6) is typical of many rivers along the Kimberley and Northern Territory coasts. It debouches into a funnel-shaped estuary at the head of King Sound, which is a ria *sensu lato*, as defined by Cotton (1956). The Fitzroy Estuary lacks the complications of a spit or barrier construction. The greater indentation of this coastal sector and greater depth of the margin of the continental shelf may point to regional epeirogenic subsidence accompanying the glacio-eustatic oscillations (Fairbridge, 1953). The mouth of King Sound is protected by bedrock islands and reef patches in the Buccaneer Archipelago so that wave action is attenuated even during the northwest monsoon. This and its large tidal range (30 feet) are probably responsible for the absence of wave-constructed features, although diminished yield of sand from a hinterland with tropical weathering may also be a factor. The funnel shape of this estuary is the optimum configuration for conserving tidal amplitude as the tide progresses headwards; in the absence of strong wave action the river load is fashioned into patterns of shoals and channels related to ebb and flood currents (Robinson, 1960). Some of the shoals have been colonized by mangroves.

The outstanding characteristic of this estuary is the great extent of intertidal land. This reflects the large range of astronomical tides and their augmentation during the wet season by the onshore monsoon and river floods to give "king tides". The mangrove fringe along the major channels is not very wide in the Fitzroy Estuary, but there are large areas of mud flats. The higher parts of these flats are subject to less frequent tides and they turn into glaring white salt crusts in the dry season. Higher still are salt meadows of grasses and sedges (dominated by species of *Sporobolus* and *Fimbristylis*) and shallow de-

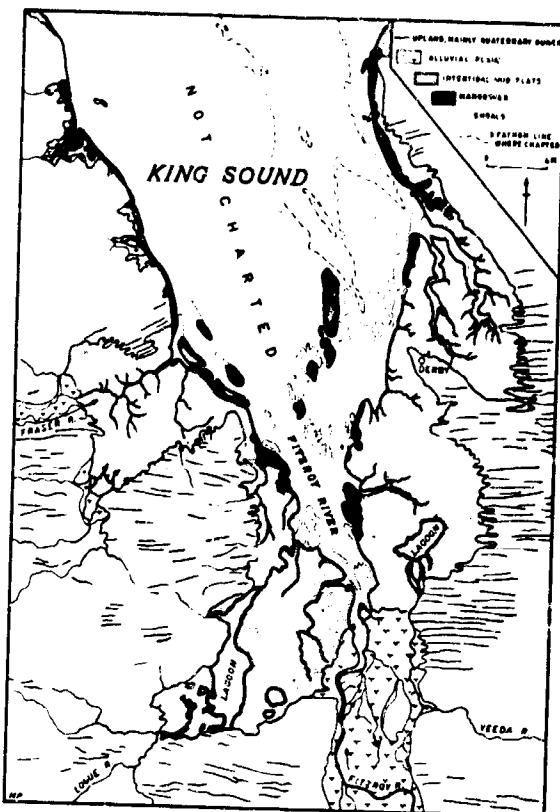


Fig. 6. The Fitzroy River Estuary, Western Australia.

pressions, occupied by salt marsh species, sometimes termed "salt pans" (Australia, C.S.I.R.O., 1953, 1960). Even the freshwater grassland swamp, dominated by *Oryza* and *Eleocharis* species, is liable to local and occasional inundation by brackish water. Lesser rivers feed lagoons in large, shallow, enclosed basins within these tidal flats. The relationships between plant communities and the micro-topography await investigation.

Parts of the inland margin of the King Sound tidal flats are serrated in plan because estuarine silts have been deposited in corridors within fields of fixed longitudinal desert dunes. The relationships with Quaternary arid-humid oscillations and changing Quaternary sea levels have still to be established.

INSIDE THE BARRIER REEF

Within the water protected by the Great Barrier Reef (Fig. 7), the local wind in relation to coastal aspect plays a greater part than it does on coasts subject to ocean swell, which can remain strong even after considerable refraction. As a result, estuaries in that area shew a greater variation in style, and no single type predominates. Many of these estuaries, however, are open-mouthed and funnel-shaped without the complications of wave-built features; they resemble broadly the Fitzroy Estuary of Western Australia, but in Queensland mangrove swamps are more extensive than salt flats. The geological strike and topographical trends inland intersect the coastline at

an angle so that many rivers open northward into gulfs protected from the dominant wind-waves from the southeast and east. Other estuaries, not facing north (for example, the Proserpine River Estuary, which faces southeast), are protected by groups of islands. But for the barrier reefs, these protected gulfs would be more subject to sand barrier construction, producing "cusp and node" shores like those on the New South Wales coast farther south, where rivers flow into estuarine lagoons behind depositional barriers. Instead, the estuaries are funnel-shaped and frequently exhibit well-developed shoal and channel patterns, as in the Fitzroy River Estuary at Rockhampton, far from the previously mentioned Fitzroy Estuary.

Estuaries exposed to the east and southeast are bordered by small sand barriers which are not surmounted by dunes—they resemble the cheniers of the Gulf Coast of the United States rather than the robust sand barriers of southern Australia. These cheniers are not backed by open estuarine lagoons but by areas of swamp grassland, salt meadow, and mangrove swamp. Wave action has not been strong enough to build barriers enclosing large bodies of water, and only modest features have been built along the margins of the estuarine alluvium. The estuaries are reduced to rather wide, simple river channels, like that of the Tully River.

A few of the larger Australian rivers have been able to build deltas beyond the general line of the

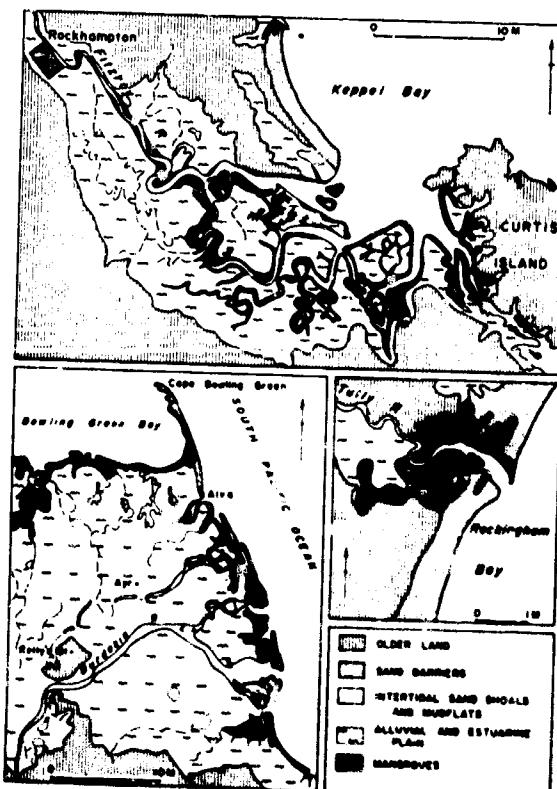


Fig. 7. Examples of estuaries from the Queensland coast inside the Great Barrier Reef.

coast into the protected waters behind the reefs. Of these, the Herbert River has a fairly well-distributed discharge, but the Burdekin River has markedly seasonal discharge. Some chenier development has taken place; in the Burdekin Delta they face northeast, like the free extension into Cape Bowling Green, a spit built by northward longshore drifting where the trend of the coast changes. This NW-SE alignment is not perpendicular to the direction-resultant of wind-work (Schou, 1952); it is a more complex resultant in which fetch and offshore water depths participate. The changing distributary patterns in the deltas can result in mangrove-fringed estuaries, which now receive decreased freshwater discharge, sometimes from previous tributaries of the river which built the delta (for instance, Seymour Creek in the Herbert Delta). The Burdekin Delta includes a number of estuarine creeks which were formerly distributary channels but which now receive river outflow only when there is general flooding in the delta. Kalamia and Plantation Creeks are ephemeral estuaries of this type.

NEW SOUTH WALES ESTUARIES: PROBLEMS OF INFILLING

We have endeavored to select estuaries representative of long coastal sectors, although for east Queensland it was impossible to select a dominant type. Consideration of some of the New South Wales estuaries may correct a misleading impression of simplicity. This coast possesses a basic uniformity: it is straight; it is subject to a powerful wave attack and to a small tidal range; and it also has the "geographical unity" (Andrews, 1910) of its hinterland of high plateaus with rather uniform geological structure and a steeped coastal slope. The prevailing characteristic of this coast is the existence of substantial quartz sand barriers and dunes along zeta-curve bays (Halligan, 1906; Jennings, 1955; Davies, 1959) fashioned by refracted southeasterly swell and breached most frequently at the southern side of the bays where the swell has been most weakened by refraction. Nevertheless, within this broad canvas there are innumerable contrasts and departures at all levels of magnitude, and each presents different research problems.

Excellent, although comparatively small, examples of the variation in degree of infilling of estuaries are evident (Fig. 8) in the Narrawallee Inlet and Burrill Lake on the South Coast (the coast south of Sydney). Two adjacent small catchments in broadly similar topography and lithology were drowned in their lower parts by the Recent marine transgression to produce rias which were roughly similar in plan. But whereas Narrawallee Inlet has been virtually reclaimed by infilling, Burrill Lake remains as an estuarine lagoon behind a barrier. There is a small delta at the head of Burrill Lake and deposition of a tidal delta in the vicinity of the entrance from the sea has lessened the depths of the seaward part of the lake to a few feet; deeper water lies inward. The most obvious difference between the surviving and the former estuary is the greater height and steepness of the bedrock slopes around Burrill Lake than those around the flats of

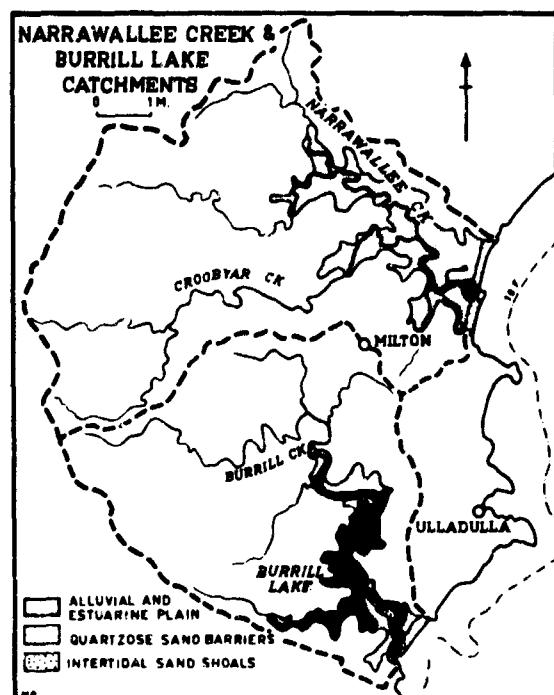


Fig. 8. The Narrawallee Inlet and Burrill Lake Estuaries, New South Wales.

Narrawallee Creek. A possible explanation is that the Narrawallee Inlet was much shallower at the height of Recent submergence and more quickly filled. Such an explanation, implying a coastal hanging valley, has its difficulties; for example, the offshore contours, which are subject to smoothing by marine action, do not indicate that the two valleys were cut to different depths prior to drowning.

Similar catchments of medium size along the South Coast present the same contrast (Fig. 9): the Clyde River has retained an open ria character with very little natural reclamation, but in contrast the Moruya Estuary has been much diminished. Both pass through bedrock upland "gates" of much the same width at about the same distance from the general line of the outer coast. Again, although they may be misleading, the offshore contours do not indicate that the Clyde was cut more deeply, or that more sediment was needed to fill Bateman's Bay than the bay of which the Moruya Estuary now occupies but a small part. It is true that the Moruya brings down large quantities of sand eroded from outcrops of deeply weathered granite during flash floods, as in 1925, but the proportion of coarse-grained rocks is similar in the two catchments; they are broadly alike topographically and the nature and amount of sediment yield should be much the same.

The contrast in rates of estuarine infilling is also posed in the largest coastal catchments in New South Wales (Fig. 10). Broken Bay is not a ria in the strictest sense, but it is a classic example of a dendritic drowned valley transverse to the coast. The mouth is

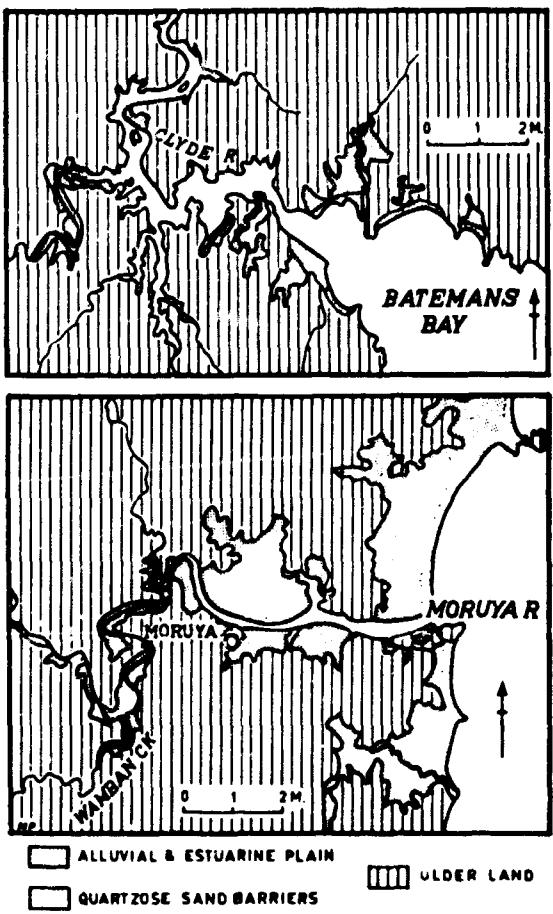


Fig. 9. The Clyde River and Moruya River Estuaries, New South Wales.

still wide open between rocky headlands, and there has been relatively little re-creation of land within the tidal reaches of Broken Bay and Hawkesbury River, which hydrologically have a free cellular circulation. To the south, with a smaller catchment, the Shoalhaven River has practically filled a broad embayment behind coastal sand barriers with deltaic sediment. To the north the Hunter River, with a catchment roughly equal to the Hawkesbury's, has advanced nearly as far in natural reclamation as the Shoalhaven.

A number of hypotheses present themselves:

1. On the Hawkesbury River system, the Cumberland Plain, an interior basin close to sea level, has acted in some degree as a sediment trap.
2. The effect may have been accentuated by tectonic sagging of the Cumberland Plain (Walker and Hawkins, 1957).
3. It is possible that sediment yield has been low from the highly permeable sandstone terrain around Broken Bay where surface runoff is relatively small.
4. After submergence, Broken Bay was left with a much narrower mouth than the estuaries of the Hunter and the Shoalhaven. This may have induced greater tidal scour, which prevented the

formation of spits and barriers at the entrance. A relatively sheltered lagoon environment like that of the Lower Shoalhaven, which promotes natural reclamation, was never established.

5. After submergence, Broken Bay may have been deeper than the Hunter and Shoalhaven Estuaries, so that its infilling was a larger task. There is no evidence of any deep channel crossing the continental shelf here. Moreover, it has long been known (Hedley, 1910) that the inner part of this shelf has been kept clear of Recent deposits, thus minimizing the possibility of obliteration of a channel by marine sedimentation. Surveys of the submarine topography off the New South Wales coast, now in progress, may throw some light on this matter.

But this geomorphological problem, in Australian estuaries remains virtually uninvestigated as yet.

EXCEPTIONS AND TRANSITIONS

There are estuaries on four sectors of the Australian coast which do not fit the broad categories of regional types. In South Australia, Spencer Gulf and Gulf St. Vincent are less affected by refracted ocean swell than the rest of the southern coast of the continent, and toward the heads of these gulfs the tidal ranges increase considerably. Wave action is related primarily to wind conditions and local fetch within these gulfs; as it is less strong and less regular the barrier construction is correspondingly poor. Some of the rivers flowing into these gulfs have deflected estuaries; for example, the Torrens Estuary is deflected northward by the building of the sand spit on which Port Adelaide stands. Others have mouths encumbered by sand deposition: the Wakefield River enters the head of Gulf St. Vincent where the shore is bordered by tidal salt marshes and mangrove swamps without sand spits or barriers. Such estuaries have more in common with those of the northern Australian gulfs than those of the southern coast.

Although the southern shores of the Gulf of Carpentaria are not protected by coral reefs or depositional

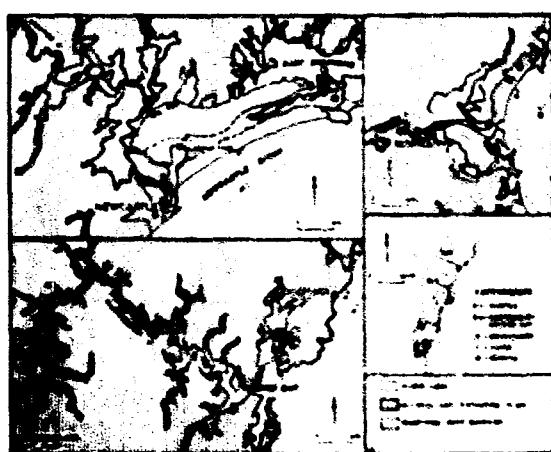


Fig. 10. The Hunter River, Hawkesbury River, and Shoalhaven River Estuaries, New South Wales.

barriers, wave action is weakened by attenuation in passing through broad tracts of shallow water. Little is known of the tides on this part of the coast, but they are thought to be relatively small compared with those of the gulfs farther west. In these circumstances, rivers such as the Mitchell and the Flinders have estuaries bordered by depositional plains, with corridors of swampland between wave-built chemiers of sand and shell. They resemble the estuary of the Tully River on the east Queensland coast, where low wave energy is a consequence of barrier reef protection, and are in marked contrast to the funnel-shaped estuaries of the gulfs farther west.

On the south coast of Queensland, beyond the protection of the Great Barrier Reef, large depositional features at Fraser Island, Stradbroke Island, and Moreton Island afford partial protection to river estuaries. The Brisbane River opens into the relatively sheltered waters of Moreton Bay by way of a deltaic tract, and off its mouth are complex shoal patterns, with ebb-and-flood channels. This estuary is transitional between the east Queensland type behind the barrier reefs and the enclosed type of the New South Wales coast to the south.

Finally, on the southeastern coast of Tasmania, around Storm Bay, is an extensive ria-type coast, possibly influenced by epeirogenic or local tectonic subsidence. In these terms it is comparable with the gulf coast of northern and northwestern Australia, but differs in that tidal range remains low (3 feet at Hobart), and that most of the shoreline is reached by the refracted southern ocean swell (Davies, 1959). Depositional shoreline features include curved beaches and barriers, spits, and tombolos, which deflect and locally seal off the mouths of the smaller rivers. The Derwent Estuary, however, is unenclosed and opens into the northwestern corner of Storm Bay.

With these exceptions and transitions, broad regional types of estuaries may be recognized. Consideration of the varied degree of infilling in the New South Wales estuaries has shown that static factors, such as geological structure and hinterland geomorphology, loom large on the local scale. These factors are particularly important when comparisons are made between neighboring systems. When widely separated estuarine systems are compared, full account must be taken of the dynamic factors that vary regionally on the coasts of the Australian continent.

LITERATURE CITED

- ANDREWS, E. C. 1910. The geographical unity of Eastern Australia in Late and Post-Tertiary Time. *J. Proc. Roy. Soc. N. S. Wales*, 44: 420-480.
- AUSTRALIA, CSIRO. 1953. General report on survey of Katherine-Darwin Region, 1946. Australia, Commonwealth Sci. Ind. Res. Organ., Land Res. Ser. No. 1.
- AUSTRALIA, CSIRO. 1960. The lands and pastoral resources of the North Kimberley Area, W. A. Australia, Commonwealth Sci. Ind. Res. Organ., Land Res. Ser. No. 6.
- BASCOM, W. H. 1954. The control of stream outlets by wave refraction. *J. Geol.*, 62: 600-605.
- BIRD, E. C. F. 1961a. Reed growth in the Gippsland Lakes. *Victorian Naturalist*, 77: 262-268.
- BIRD, E. C. F. 1961b. The coastal barriers of East Gippsland, Australia. *Geograph. J.*, 127: 460-468.
- BIRD, E. C. F. 1962. The utilization of some Australian coastal lakes. *Australian Geographer*, 8: 199-206.
- BIRD, E. C. F. 1963. The physiography of the Gippsland Lakes, Australia. *Z. Geomorphologie*, 7: 232-245.
- BIRD, E. C. F., and D. S. RANWELL. 1964. The physiography of Poole Harbour, Dorset. *J. Ecol.*, 52: 355-366.
- CHURCHILL, D. M. 1959. Late Quaternary eustatic changes in the Swan River district. *J. Roy. Soc. W. Australia*, 42: 53-55.
- COTTON, C. A. 1956. Rias *sensu stricto* and *sensu lato*. *Geograph. J.*, 122: 360-364.
- DAVIES, J. L. 1959. Wave refraction and the evolution of shoreline curves. *Geograph. Studies*, 5: 1-14.
- DAVIES, J. L. 1960. Beach alignment in southern Australia. *Australian Geographer*, 8: 42-43.
- DAY, J. H. 1951. The ecology of South African estuaries, I: A review of estuarine conditions in general. *Trans. Roy. Soc. S. Africa*, 33: 53-91.
- FAIRBRIDGE, R. W. 1950. Recent and Pleistocene coral reefs of Australia. *J. Geol.*, 58: 330-401.
- FAIRBRIDGE, R. W. 1953. The Sahul Shelf, Northern Australia: its structure and geological relationships. *J. Roy. Soc. W. Australia*, 37: 1-34.
- HALLIGAN, G. H. 1906. Sand movement on the New South Wales coast. *Proc. Linnean Soc. N. S. Wales*, 31: 619-640.
- HEDLEY, C. 1910. The submarine slope of New South Wales. *Proc. Linnean Soc. N. S. Wales*, 35: 9-21.
- JENNINGS, J. N. 1955. The influence of wave action on coastal outline in plan. *Australian Geographer*, 6: 36-44.
- JENNINGS, J. N. 1957. Coastal dune lakes as exemplified from King Island, Tasmania. *Geograph. J.*, 123: 60-70.
- JENNINGS, J. N. 1964. The question of coastal dunes in tropical humid climates. *Z. Geomorphologie*, 8: 150-154.
- KETCHUM, B. H. 1951. The exchange of fresh and salt water in tidal estuaries. *J. Marine Res.*, 19: 18-38.
- LAKE, P. 1949. *Physical Geography*, 2nd Edition. Cambridge Univ. Press, Cambridge, England.
- MCARTHER, W. M., and E. BETTENAY. 1960. Development and distribution of soils on the Swan coastal plain, W. A. Australia. *Commonwealth Sci. Ind. Res. Organ., 2d Publ. 16*.
- MOODY, C. J. de. 1959. Notes on the geomorphic history of the area surrounding Lakes Alexandrina and Albert, S. A. *Trans. Roy. Soc. S. Australia*, 82: 99-118.
- PRICE, W. A. 1947. Equilibrium of form and forces in tidal basins on the coast of Texas and Louisiana. *Bull. Am. Assoc. Petrol. Geologists*, 31: 1619-1663.
- ROBINSON, A. H. W. 1960. Ebb-flood channel systems in sandy bays and estuaries. *Geography*, 45: 183-199.
- ROCHFORD, D. J. 1951. Studies in Australian estuarine hydrology, I: Introduction and comparative features. *Australian J. Marine Freshwater Res.*, 2: 1-116.
- ROCHFORD, D. J. 1959. Classification of Australian estuarine systems. *Arch. Oceanogr. Limnol.*, 11: 171-177.
- SCHOU, A. 1952. Direction-determining influence of the wind on shoreline simplification and coastal dunes. *Proc. 15th Intern. Geograph. Congr. (Washington)*, pp. 370-373.
- SPENCER, R. S. 1956. Studies in Australian estuarine hydrology, II: The Swan River. *Australian J. Marine Freshwater Res.*, 7: 193-231.
- THOMSON, J. M. 1959. Summary review of a scientific survey of Lake Macquarie. *Australia, Commonwealth Sci. Ind. Res. Organ., Div. Fisheries Oceanogr. Bull.* 26.
- WALKER, P. H., and C. A. HAWKINS. 1957. A study of river口 rates and sand development on the Nepean River, N.S.W. *J. Roy. Soc. N. S. Wales*, 91: 67-84.

Estuarine Research in the Danish Moraine Archipelago

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Denmark is an archipelago in the strictest sense. It includes the peninsula of Jutland (30,000 km²), and it has a coastline of over 7,400 km. In comparison, 742 km would enclose the area if Denmark's land was not so dissected by water.

TIDAL ENVIRONMENT IN DENMARK

In the estuarine environment of this archipelago, the tides and tidal currents play a dominant role in shoreline development and in the formation of offshore relief features by erosion and sedimentation. The tidal range (Fig. 1) of the North Sea near the Danish-German border is 2 m. In Eshjerg, the difference between the tidal levels is only 1.5 m, and along the western coast of Jutland, farther north, the range diminishes. At the Skaw spit, near the entrance to the inner Danish seas, the tidal range is insignificant because of the interference of the North Sea amphidromic system. In the Kattegat, as well as in the Baltic, only very small waves are generated. The small tidal amplitudes are normally entirely masked by non-periodic changes of level which are caused by wind pressure. Thus, estuarine conditions occur only on the southwest shoreline of the Jutland Peninsula.

GLACIO-GEOMORPHOLOGICAL CHARACTERISTICS

The types of coasts and the development of the shorelines are caused by an interplay between two distinctly different phenomena: (1) the geological structures of the land and (2) the marine activities of the surrounding seas. Denmark is an area of glacial accumulation formed by deposition in the marginal zones of the Pleistocene icecap. The terrestrial nuclei which form the skeleton of the Danish landscape pattern consist of the enormous quantities of boulders, gravel, sand, and clay that form a pattern of moraine landscapes and glaciofluvial plains.

During the Riss-Saale glaciation, Denmark was completely covered by an icecap. In the last glacial period, the Wurm-Weichsel glaciation, the extreme limits of the icecap did not cover the southeastern part of the peninsula of Jutland, which explains the great difference in the types of coast and relief that exist between western and eastern Denmark.

The main stationary line of the last ice sheet through Jutland (Fig. 1) is a geomorphological borderline of distinct significance. Southwest of this line, old moraine landscapes of the Riss-Saale glaciation lie between the vast outwash plains of the last glacial

period; this region is characterized by its flat topography.

Beneath the glacial deposits in the southwestern part of Denmark, Tertiary sediments of sand and clay have been found. Cretaceous limestones, which form a mosaic of dislocated layers under the whole Denmark area, do not crop out in this area as in the northern and eastern part of Jutland and on the Danish islands (Fig. 1). The shoreline development in the Danish tidal area has not been determined by resistant rocks, but by glacial deposits and other non-resistant loose sediments. From a geological point of view, alterations are rapid when new environmental factors are introduced. This area has a special value as a research field, because of this adjustment of the relief complexes to establish equilibrium forms in response to new influences. Short-time observations can give results which under less favorable conditions can be obtained only by means of less accurate historico-cartographic methods.

The construction of the dam which connects Jutland with the island of Rømø has served as a gigantic experiment. Observations concerning sedimentation, tidal creek development, ebb channels, and flood channels have increased our knowledge of coastal geomorphology.

MARINE ACTIVITY

There are pronounced differences in marine activity between the North Sea and the inner Danish seas such as the Kattegat, the Danish Straits, and the Baltic. In the North Sea, the maximum height of waves is 5 m, but in the Danish part of the Baltic, only 3 m. As a result, the west coast of Jutland is exposed to strong wave activity. The fetch in the northwesterly direction ranges between 1,500 and 500 km, and water depths of 10 m may occur very near the coast.

The west coast of Jutland, with its north-south orientation, is almost a straight line. Marine activity driven by westerly winds has simplified the shoreline. The orientation of the shoreline was not determined by the initial relief, but by the forces of the sea. These forces, in turn, are governed by the direction-resultant of the wind (DRW). The terminant direction of the shoreline has developed at right angles to DRW (Schou, 1952; Gudber, 1954, 1958). The sea has eroded elevated lands and has built bars at the mouths of the intermediate bays. A zone of dune landscapes has developed along the west coast, from the Skaw to Blavandshuk, west of Eshjerg, and

continues southward on the west coast of Jutland between the islands of Fanø, Mandø, and Rømø. The area between these islands and the coast of Jutland, extending from the German border northward to the Bay of Ho Bugt, forms Vadehavet, the Danish tidal region (Fig. 2).

TIDAL FLATS AND TIDAL CHANNELS

Wide tidal flats extend seaward from reclaimed marshes on the Jutland coast and are dissected by systems of tidal creeks and tidal channels. The largest

tidal flats are Gradaub, between the peninsula of Skallingen and the island of Fanø; Knudedyb, between the islands of Fanø and Mandø; Juvre Dyb, between Mandø and Rømø; and Listerdyb, south of Rømø and north of the German island of Sylt.

The Danish tidal and tidal marsh areas cover approximately 200 km². These wide shallow stretches are called "waddens", which are areas under water at flood tide and dry at ebb—the existence of the waddens is conditioned by the vast expanse of the out-

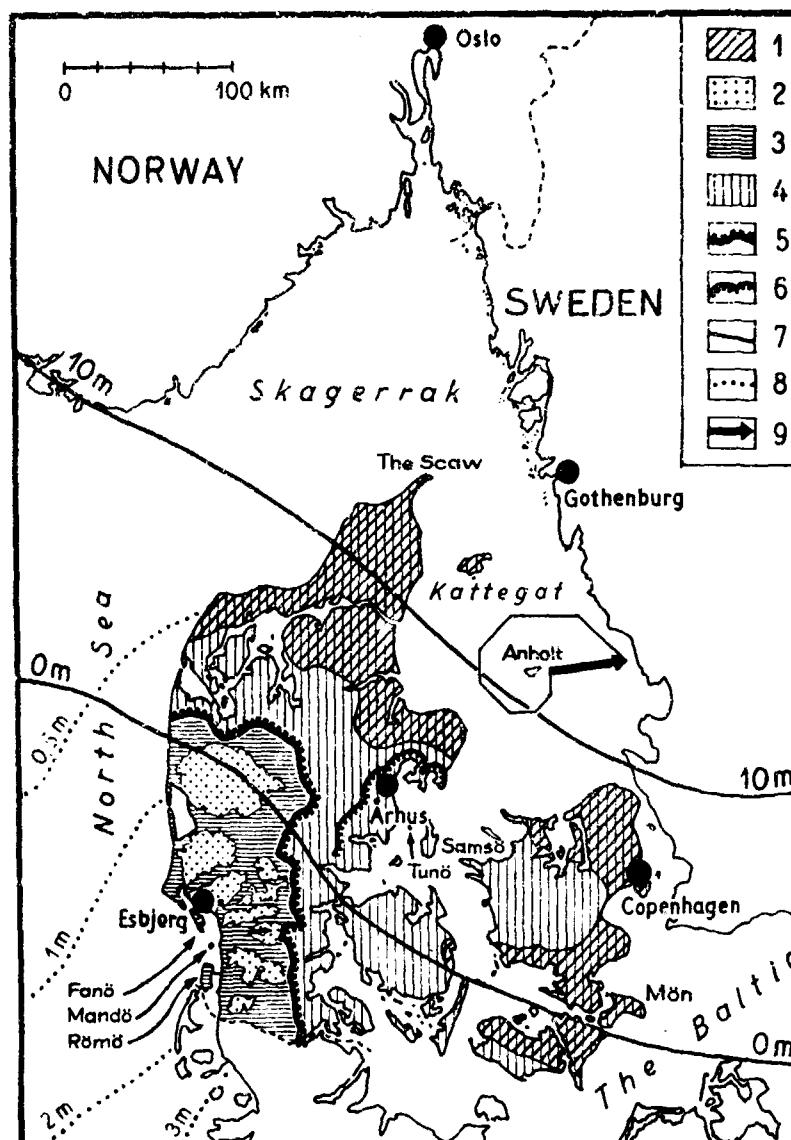


Fig. 1. The physico-geographical environment of the Danish moraine archipelago (Schou, 1960).

1. Area where limestone rocks form the substratum under the Quaternary deposits.
2. Old moraine landscapes, Riss-Saale glaciation.
3. Outwash plains of the Würm-Weichsel glaciation.
4. Predominant young moraine landscapes, Würm-Weichsel glaciation.
5. Main stationary line of the last glaciation.
6. Terminal moraine in the Djursland Peninsula.
7. Lines of equal elevation since the Stone Age (Littorina-Tapes epoch).
8. Lines of equal tidal amplitude.
9. Direction resultant of wind work.

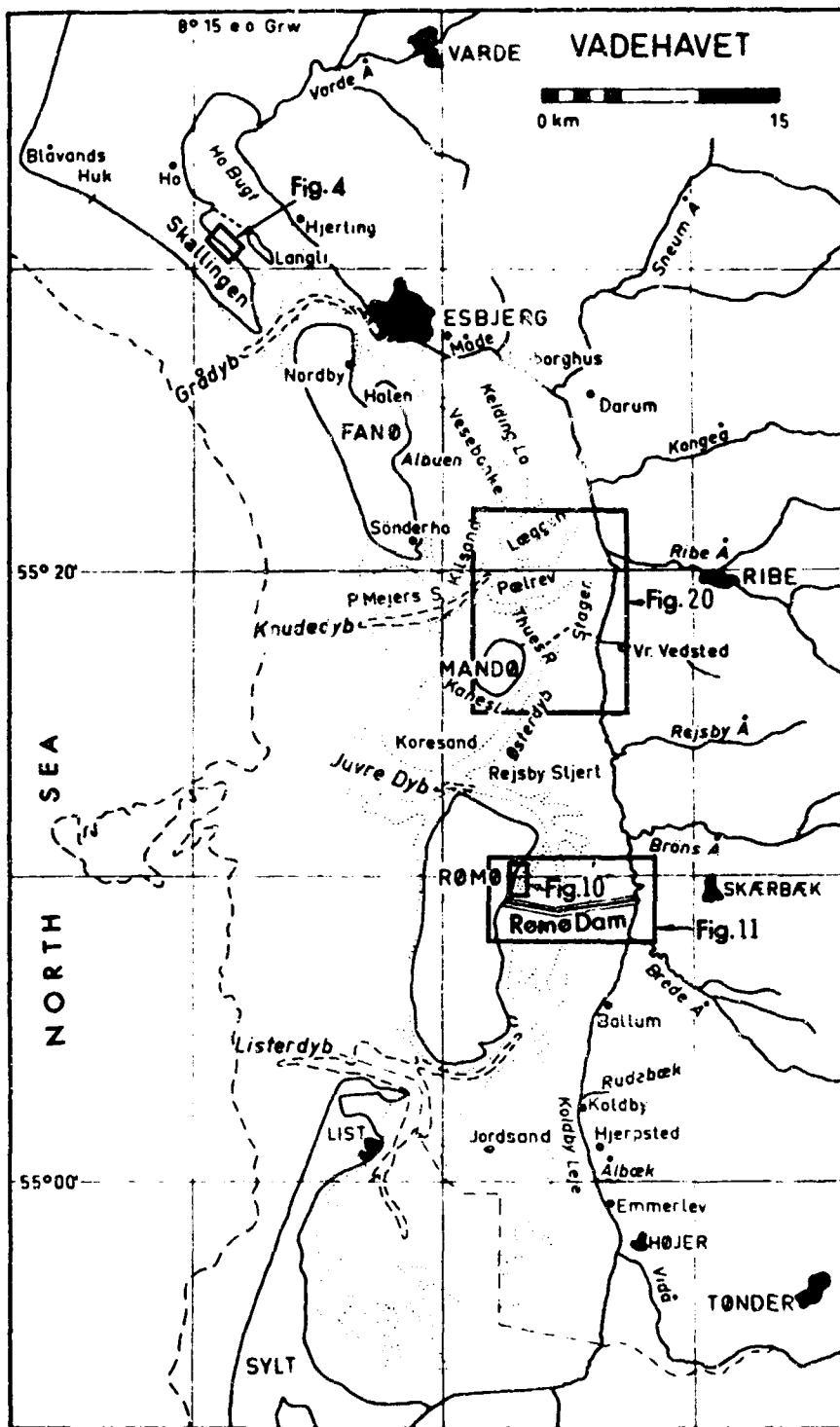


Fig. 2. Vadehavet, the Danish tidal area. The map shows the tidal flats, tidal creeks, and tidal channels: Grædyb, Knudedyb, Juvre Dyb, and Listerdyb. Frames indicate areas with the corresponding figures elsewhere in this article (From Møller, 1964).

wash plains in western Jutland (Figs. 1 and 3). The flat bottom and shallow water of this region can be attributed to the absence of relief in these outwash plains. The surface slopes very slightly and large areas alternate between a marine and terrestrial existence. The distance between high and low spring water marks may be as much as 10 km.

DEVELOPMENT OF RESEARCH IN THE DANISH TIDAL REGION

DEVELOPMENT OF RESEARCH WORK.

Research on the geomorphology and dynamics of Danish tidal flats started in 1930 when Niels Nielsen founded "Skalling Laboratoriet" as a field station for

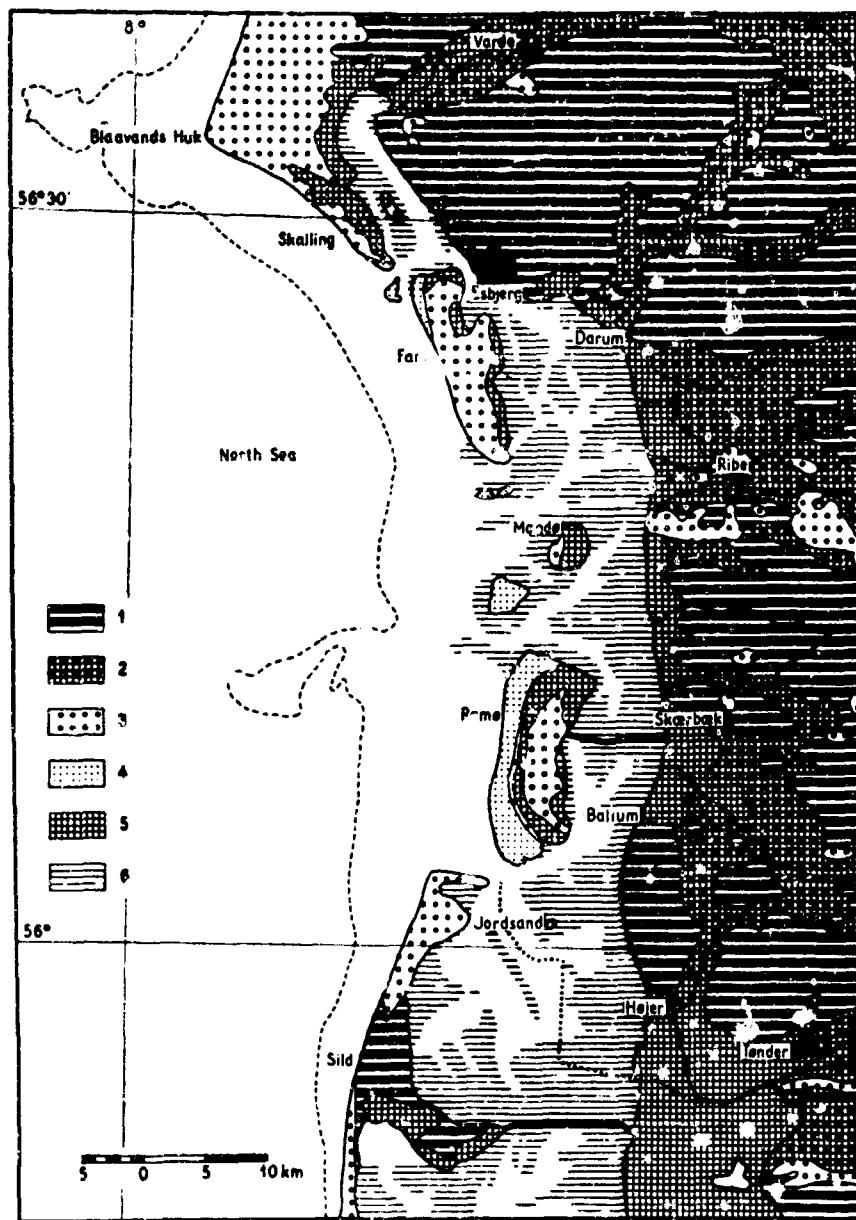


Fig. 3. Geomorphological map of southwestern Jutland. (From Jakobsen, 1954. Map base partly from Schou. Atlas of Denmark. I. The Landscapes.)

- 1. Moraine landscapes from the Riss glacial period.
- 2. Outwash plains.
- 3. Dune landscapes.
- 4. Foreshore plains and "high sands".
- 5. Salt marshes.
- 6. Tidal flats (wadden).

the study of tidal flats, salt marshes, and dunes on the peninsula of Skallingen.

In 1938 a branch of Skalling-Laboratoriet was established in Esbjerg, where the port authorities and others provided a building and equipment for sedimentological and hydrographic analyses and biological experiments.

Since 1930, Skalling-Laboratoriet has conducted a great number of research investigations, which included: (1) the natural formation of salt marshes; (2) the biological conditions in dunes, salt marshes, and tidal flats; (3) sand drift and sand deposition; (4) tidal processes; (5) transport of materials; (6) soil conditions; (7) habitation; (8) general coastal evolution; and (9) the formation of channels. The results of these studies have been published in "Meddelelser fra Skalling-Laboratoriet", volumes I-XVII. Annual grants from the Carlsberg Foundation, encouragement of the Esbjerg authorities, and aid from other institutions have made it possible to carry on this research and to maintain the two laboratories.

Comprehensive hydrographic studies of the tidal area between Esbjerg and the German frontier were conducted between 1938-1941. A systematic, quantitative analysis of sediment drift was also initiated which emphasized the study of sedimentation in areas close to the coast, particularly the beach meadows. The work was performed with the cooperation of the Danish Ministry of Public Works, the Danish Ministry of Agriculture, and the Department of Hydraulic Engineering.

In the years following World War II it was recognized that a need existed for studies of land reclamation as related to economic life and conditions of habitation. Competent authorities realized that, to arrive at methods which would serve this purpose, it would be necessary to combine fundamental research with an experimental approach. This preliminary work was directed by Niels Nielsen.

ORGANIZATION AND SCOPE

The work was organized to promote cooperation between the Skalling-Laboratoriet and "De Danske Vade- og Marskundersøgelser". The former undertook the solution of questions in the northern part of the wadden area, and the latter conducted investigations in the region extending from the isle of Mandø to the German frontier. Centers were established in Skaerbaek and in Tønder, and were combined with the laboratories in Esbjerg and those on Skallingen.

At Skaerbaek, the majority of work was concentrated on studying the tidal flats, while at Tønder the study of the diked-in salt marsh areas (polders; Danish: kog) was pursued. The analysis of data has been carried out, for the greater part, in the Geographical Institute at the University of Copenhagen. The results have been represented in reports to the Danish Ministry of Agriculture and in publications of the Royal Danish Geographical Society.

Since 1958, research work at the four stations has

continued. Further, an experimental field for reclamation of land and a department for surveying have been established close to the village of Rejsby. In 1964, Skalling-Laboratoriet was taken over by the University of Copenhagen as a field laboratory for the Department of Geography.

PROGRAM OF ESTUARINE RESEARCH WORK

Nielsen began to study salt marsh development in 1931 (Nielsen, 1935a, b, c), and soon thereafter hydrographic research facilities were established to measure the velocity of tidal currents and the volume of tidal water exchange, in order to estimate the transport caused by flood and ebb currents (Gry, 1942).

When basic studies regarding reclamation planning were incorporated as part of the research, surveying was organized. The bottom of the wadden area is seemingly flat. However, the very small variations in topography are so important that it was necessary to design maps in such a way that the relief features could be clearly demonstrated. The surveying methods have made it possible to produce maps in the scale 1:10,000 with a 10 cm contour interval. Descriptions of the mapping project and details of the surveying technique are described by Jakobsen (1963) and Møller (1960, 1961). The mapped area covers a zone from the German border to the island of Mandø; its width extends 2-3 km outside the mean high tide (MHT) shoreline. The tidal area of the Juvre Dyb, between the islands of Rømø and Mandø, has been mapped in the scale 1:25,000.

The program also includes investigations of vegetation (Jakobsen, 1963; Jakobsen and Jensen, 1956; Møller, 1964), analysis of soil and the wadden sediments (Hansen, 1951), and tide gauge measurements and research concerning suspended sediments (Jakobsen, 1961). The geomorphology and dynamics as well as the developmental stages of the tidal creeks have been studied in detail (Jakobsen, 1962). The man-influenced alterations in sedimentation caused by the construction of the Rømø Dam have been investigated (Olsen, 1959) and the same phenomenon under natural conditions also has been studied (Møller, 1961). In the Tønder area paleogeographical investigations were conducted to widen the knowledge concerning the morphogenetic development of the Danish salt marsh region (Jacobsen, 1959).

The soil types and their local variation during post-glacial periods have been studied in the old polders of the Tønder region through an extensive boring project (Jacobsen, 1960a, 1964), and land use maps have been prepared to establish a base for regional planning (Jacobsen, 1960b). Population problems and the distribution of habitations have been studied (Jespersen, 1959, 1961) to obtain information concerning human-geographical patterns of a former estuarine environment reclaimed as an agricultural area and cultivated for centuries.

RESULTS OF RESEARCH WORK

EROSION FORMS: TIDAL CREEKS AND TIDAL CHANNELS

Waters carried in, over, and out from the marsh meadows every day are the cause of peculiar erosion phenomena, apart from their role in sedimentation. When the water at flood tide is high over the whole meadow surface there is little movement. But when ebb begins, water movement gradually increases and locally becomes actively erosive. Channels with vertical walls are formed, because of the fine grain and cohesion of the loam. These channels are also subjected to erosion by the inflowing water until the level is sufficiently high to allow the water to spread over their banks.

The channels form river-like arms; the small ones converge in the tidal area to form larger ones which continue into the channels and end in the deeps. The latter are the largest erosion channels in this curious tidal region. In Graadyb, between Skallingen and Fanø, the depth is great (16 m) and there are similar depths in Knudedyb between Fanø and Mandø. The depth ranges up to 35 m in Listerdyb. The deeps end 5 km west of the islands. With sand brought from adjacent sea areas, the material which is carried out forms bars which have only a few meters of water over them.

The initial developmental stages of these tidal channels have been studied by Jakobsen (1953), who pointed out that the invasion of vegetation is intimately related to the formation of tidal creeks, which, by headward erosion, spread back into the sand flat (Figs. 4 and 5). The foundation on which the marsh has formed is sand flat of a higher elevation than the normal tidal flats; hence, it is not covered by all high tides. The salt marsh on the eastern part of the peninsula of Skallingen has developed since the beginning of this century, when several gaps in the dunes were closed by dams. There seems to be some correlation between the formation of that protective

bar against the inroads of the North Sea and the spreading of the vegetation on the sand flat. The first marsh developed from small islands along the coast of the wadden, and probably at the same time the poorly drained inner part of the flat was covered with *Salicornia* and algae; in the lower parts of the flat, numerous salt pans developed. The spreading of the vegetation depended on the drainage of these salt pans, which was facilitated by the development of a tidal creek pattern.

The mature stages of the tidal channels have been described by Jakobsen from points of view initially introduced in coastal geomorphology by Van Veen (1950). According to Van Veen's hypothesis, all tidal channels are cut into ebb channels and flood channels. This is caused by the transport of sand in opposite directions during the ebb and flood, and the different way in which the two types of currents meander (Fig. 6). The results of detailed surveys and systematic observations of current velocity, variations of water level, and the amount of tidal exchange have been reported by Jakobsen (1962) and are summarized here: An ebb channel is generally open to the ebb current and has a bar at its mouth, while a flood channel is generally open to the flood current and has a bar at the upper end. The morphology of the tidal areas is caused primarily by the tidal currents, and most sections are dominated by either the ebb current or the flood current (Figs. 7, 8, 9, and 10). Hydrographic measurements and soundings in the tidal channel Juvre Priel at Rømø (Fig. 10) indicate that ebb channels and flood channels are formed by ebb and flood currents, respectively, and not by a combination of the two. Since both currents occur in the same tidal channel, they will, however, influence and transform ebb and flood channels.

The tidal channels in the marsh and in the Danish wadden are generally formed by the ebb current. In the mouth area, the ebb channel is often narrow and deeply cut with a bar formation in the very mouth. Often mouths of the tidal channels are unfavorably situated, and the flood current may flow across the waddens at the mouth area into the tidal channel.

During the initial portion of the flood tide, while the water level is still low, the flood current will follow the meandering main channel; as the water level rises and the strength of the current increases, the flood current may cease to adapt to the meanders of the ebb channel. The flood current may diverge from the channel and overflow the waddens, locally forming flat, tongue-formed flood channels, and may penetrate and shorten the meanders of the ebb channel. In this way short, relatively deep, rectilinear flood channels are made, surrounded by horseshoe bars at the upper end (Figs. 7, 8, 9, and 10). The formation of the flood bars may cause the ebb channel to meander still more. The Juvre Priel, a tidal channel north and east of the island of Rømø, has been the site of a magnificent experiment executed under natural conditions. During the years 1939–1948, the island was

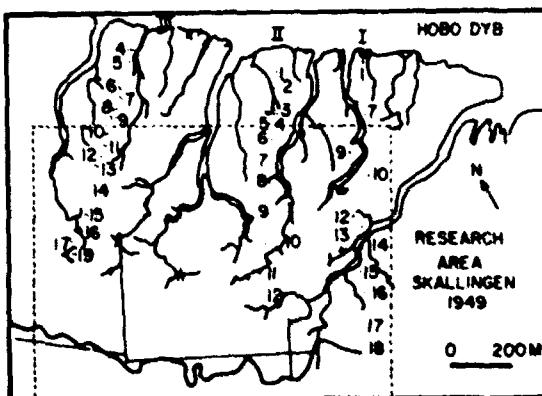


Fig. 4. Research area on the east shore of the peninsula of Skallingen, west of Esbjerg. Dots and figures indicate sample localities. The dotted line encloses the maps in Fig. 5 (From Jakobsen, 1953).

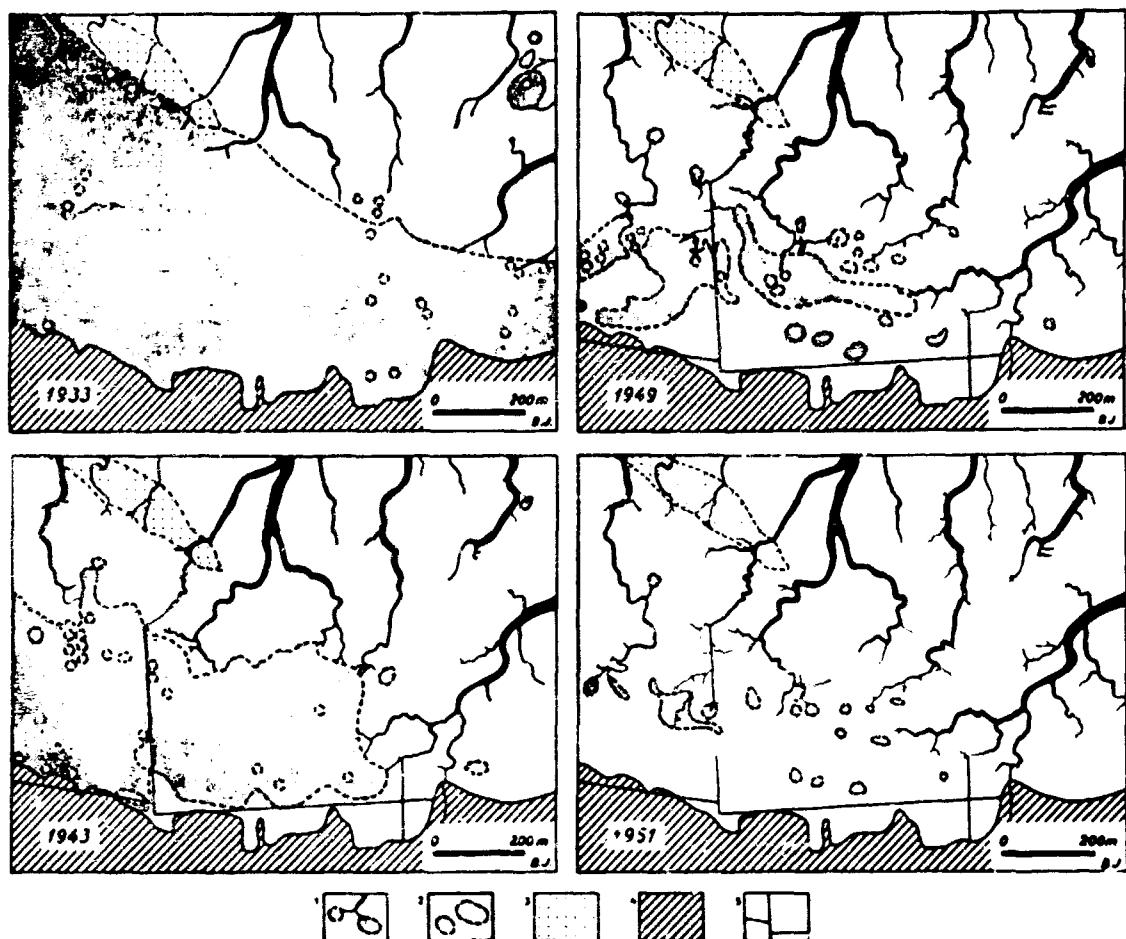


Fig. 5. Spreading of the vegetation on a tidal flat. Peninsula of Skallingen. The vegetational development is governed by the drainage of salt pans in the inner part of the flat caused by headward erosion of tidal creeks (From Jakobsen, 1953).

1. Draining of salt pans.
- 2 Isolated *Puccinellia* areas in the *Salicornia*-algae flat.
3. Ridge of windblown sand.

4. Windblown sand area behind the dunes.
5. Ditches.

connected with Jutland by the Rømø Dam, which has a length of 9 km (Figs. 2 and 11). The conditions existing in the region of the dam, based on Olsen's investigations (1959), can be described as follows: The tides of the region are derived partly through Listerdyb to the south and partly through Juvre Dyb to the north of the isle of Rømø. The tide decreases from south to north, and high water occurs later in Juvre Dyb than in Listerdyb. Because of this, an equalization of the water levels at high tide took place between the two tidal regions before the construction of the dam. This produced, from east to west, a northward current creating the three channels: Pajdyb, Rømø Leje, and Rømø Dyb. Observations of the water levels in 1955 in Rømø Dyb to the south and north of the dam proved that the high water level was 2-4 cm higher to the south of the dam than to the north on quiet days. This difference of water level

was further increased since the tide arrived at Juvre Dyb later than at Listerdyb to the south. Because the low tide arrives earlier at Listerdyb than at Juvre Dyb, one might expect a southward current to be produced; however, the height of the watershed and the prevailing (WSW) winds prevented the creation of such a flow, and the resulting current became a one-way, northward stream.

The Juvre Priel began to develop rapidly as a result of the new conditions brought about by the construction of the Rømø Dam. As there was a danger of encroachment by this channel on the eastern dikes of Rømø, the channel was kept under observation and periodically surveyed. Even though the Juvre Priel is a phenomenon influenced by man, it is evident that the dynamics of erosion in this particular case are typical for tidal channels. The development of significant erosional features in the tidal flat pattern have

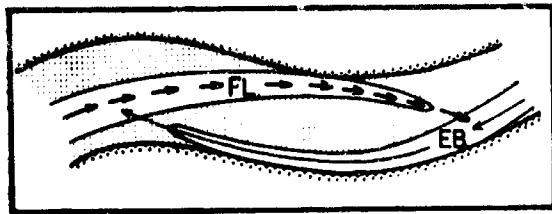


Fig. 6. A tidal channel divided into ebb and flood channels by the different meander action of the ebb and flood currents, according to Van Veen (From Jakobsen, 1962).



Fig. 9. The intrusion of a flood current in a wadden gully falling into a greater channel. The gully mouth is an ebb channel unfavorably situated for the flood. The greater part of the flood flows into the gully across the waddens and tends to narrow the mouth. Farther up, the channel is as favorable for ebb as for flood currents, i.e., a neutral channel. F—The prevalent direction of the flood current. E—The prevalent direction of the ebb current. b—A bar at the gully mouth formed by both flood and ebb (From Jakobsen, 1962).

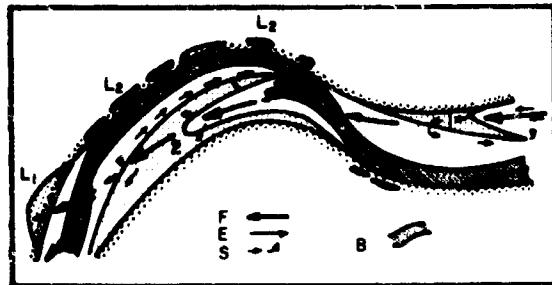


Fig. 7. Wadden gully divided into ebb and flood channels. The flood current cuts into the main channel's meanderings and forms bars 1 and 2, which will force the ebb channel to meander still more. The levees result from the deposition of the flood current on the outer side of the bend. Large levees are formed where the bend is very sharp. F—The prevalent direction of the flood current. E—The prevalent direction of the ebb current. B—The main channel—mostly ebb channels. S—Circulating sand currents around a flood bar at L₁ and L₂ levees (From Jakobsen, 1962).



Fig. 8. Ebb and flood channels in the salt marsh. As a consequence of the high level of the salt marsh (higher than MHT) the flood current is relatively stronger in these creeks than in the wadden gullies. The flood bars 1 and 2 are correspondingly more dominating and form flood deltas in the main channel b, which will be cut into separated ebb channels. For explanation of the symbols, see Fig. 7 (From Jakobsen, 1962).

been studied and mapped, stage by stage (Jakobsen, 1962). Similar features have been described from other parts of the wadden (Møller, 1964).

The tidal area and the tidal currents of Juvre Dyb have been studied carefully by Møller (1956). The tidal area is a rectangular basin with Juvre Dyb as the only opening of any importance directed towards

the North Sea. The basin is dominated by two large channels, Rømø Leje and Øster Dyb, which extend from Juvre Dyb to the farthest corners of the basin. The flat Rejsby Stjert is situated between the two main channels and forms, together with the deeps, an equilibrant caused by the shape of the area and the forces active there (Fig. 2).

Juvre Dyb is provided with sediment from the south by a tidewater current. The northward drift is checked by the powerful currents in Juvre Dyb; at outgoing tide the material is carried westward where it contributes to the building up of the Rømø Flat. At incoming tide the sediment is transported in an easterly direction along the north coast of Rømø, where the mouths of the existing tidewater creeks are shifted easterly in the course of time. The latter shift of sediment is strongly intensified by the prevailing western winds. In the wadden sections next to the coast, the shape of the tidal creeks seems to indicate that the rising tide normally follows the coast and shapes the inner parts of the tidewater creeks (which run almost parallel to the coast), whereas the falling tide tends outwards towards the deeps at right angles to the coast line, thereby shaping the outer part of the tidal creeks.

Abølling Lo, an example of such an ebb creek, is at a right angle to the coast. It is supplied with water, from the Rejsby and the Bryns Rivers, having erosive power sufficient to maintain this watercourse as a relatively deep and pronounced channel. Abølling Lo continues westward from the Rejsby Dike for a distance of almost 2 km and debouches into a large, shallow basin which extends to Rømø Leje. Here it is separated by a very broad levee, which is not penetrated during ebb tide.

In addition to the channels, there are depressions in the marsh meadows which have vertical walls and irregular contours. They are the result of erosion a-

places where the vegetation does not provide sufficient protection during inundations and gales, for example, in salt pans, which are depressions where sea water stagnates and evaporates to high salinity.

RATE OF SEDIMENTATION

The rate of sedimentation and the manner in which salt marsh plains are formed has been studied by Nielsen since 1931. At that time, Nielsen placed thin layers of red sand on several areas in the salt marsh to provide an accurate basis for measuring the rate

of accretion. Later, other series of red sand layers were made. His technique of coloring sand with a solution of Sudan Red III in benzol (Nielsen, 1935d) has proved to be very useful. After 30 years, it was still possible to recognize the layer of colored sand in samples taken from the research locality on the eastern shore of the peninsula of Skallingen (Fig. 4).

The salt marshes are formed in areas encompassed by the average high tide level; however, on the Skalling Peninsula, sedimentation will continue over an area about 60 cm above that level. The rate of sedimentation as stated by Nielsen averages 3.6 mm per

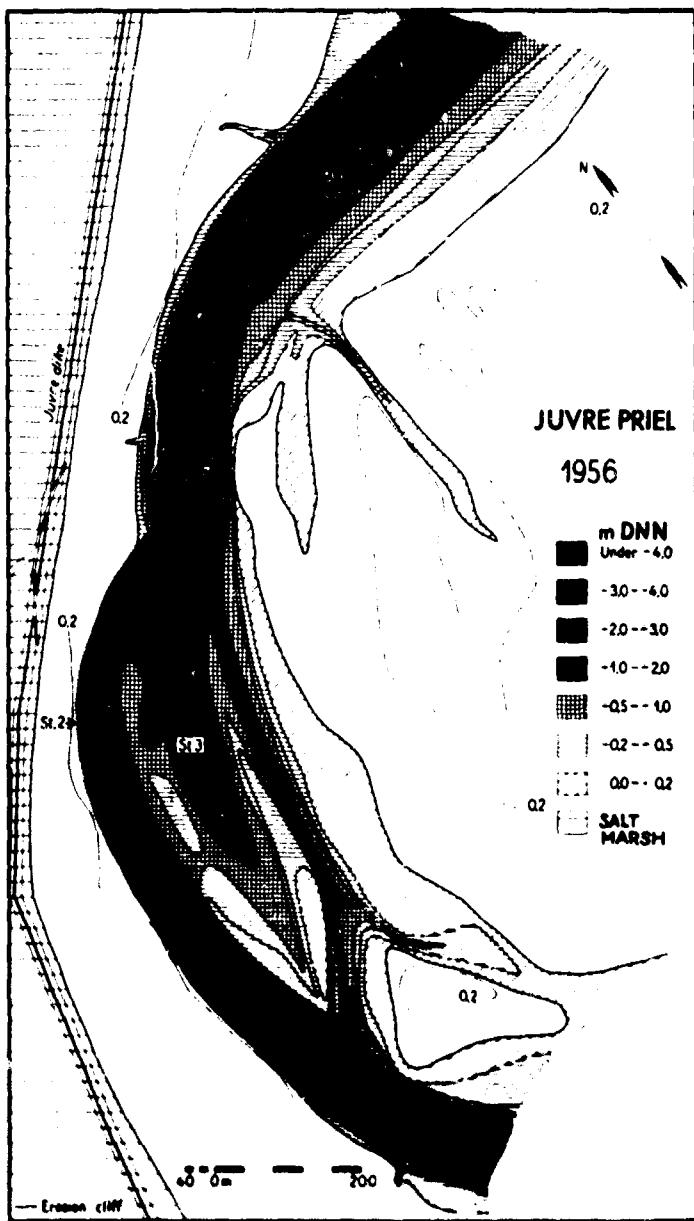


Fig. 10. The Juvre tidal channel east of the island of Rømø, north of the Rømø Dam. The flood bar at St. 3 forces the ebb channel (St. 2) to move constantly towards west and northwest (From Jakobsen, 1962).

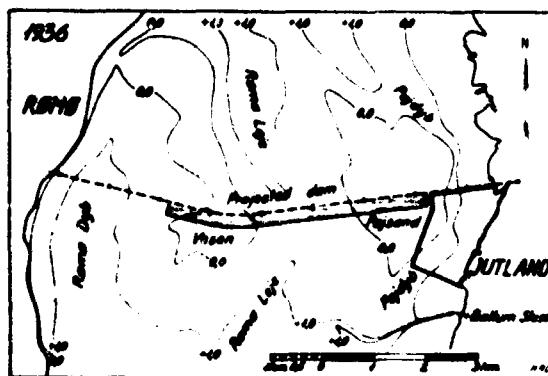


Fig. 11. Part of the wadden area between Jutland and the island of Rømø, 1936, with the projected dam. Only the contours 0.0 m and 1.0 m DNN (Danish Zero Level) are shown. The two framed regions to the south of the dam indicate the areas in which the development of the sedimentation has been examined. Compare with Figs. 13, 14, and 15 (From Olsen, 1959).

year, but settling in the young deposits limited the real accretion to about 2 mm per year.

The increase in elevation at which sedimentation occurs causes alterations in the biological environment which, in turn, results in a succession of vegetational zones. *Salicornia herbacea* is the first plant that invades a tidal flat having suitable elevation. On most of the outer part of the marsh, the successions following the *Salicornia* are *Puccinellia maritima* followed by *Aster tripolium*. Later, *Plantago maritima* is abundant and is followed by *Statice limonium* and, at higher levels, *Artemisia maritima*. At present, a *Plantago-Statice-Puccinellia* vegetation is common. Since about 1945, *Obione portulacoides* has increased very fast and is now dominating large areas. On the ridges and other high areas *Festuca rubra* is the dominant plant. In the inner part, which is drained by the creeks, a *Puccinellia maritima* - *Snadep maritima* vegetation develops and is followed by *Statice* and *Obione*.

The study of salt marsh formation has been continued by members of the team Nielsen organized. Jakobsen (1953) showed that the spreading of vegetation on the poorly drained parts of the flats is closely associated with the formation of tidal creeks which, by headward erosion, spread back into the sand flat (Fig. 5).

Based on quantitative measurements, Jakobsen (1961) gave a description of the sediment budget of the wadden area that is summarized here. In some parts it is possible, by means of surveys and comprehensive cartography, to determine the extent of the deposit accumulation over long periods. Quantitative computations make it seem improbable that the finer components of the marsh originate in any large volume from coastal erosion or from leaching of the tidal flats.

Between 1941 and 1961, in the tidal area of Listerdyb, at least 3 million cubic meters of marsh sediment

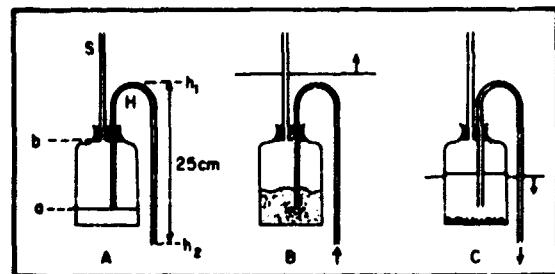


Fig. 12. Siphon sampler used to determine the quantity of suspended material in flood tides over long periods. A shows the design in the siphon sampler. As the tide rises the bottle is filled by the siphon, B, and it is emptied again at ebb tide, C. As it takes 20 to 30 minutes to empty, the sediment which has settled in the bottle cannot return to a state of suspension. The siphon sampler can thus collect material in several tidal periods. The variation of the quantity of suspended material ranges from 10 mg/l in quiet periods to 1,000 mg/l, and sometimes several thousand mg/l in stormy periods. The average content of suspended material from several stations is between 90 and 175 mg/l over long periods (From Jakobsen, 1961).

were deposited in the Danish part alone; of this quantity, a million are clay. This clay cannot have been due to coastal erosion, which is very slight there. Since the tidal flats contain only a small percentage of clay (5 percent maximum on an average), the transfer of a million cubic meters of clay sediment would involve at least the leaching of 20 million cubic meters of tidal flat sediments. This can scarcely have been the case, because sediment analyses in 1941 and in the period 1955-1961 reveal no alteration in the grain-size composition of the flats. At the same time, deposition increased as a result of reclamation work.

Hydrographic research in Graadyb in 1938 made it evident that there was a loss of sediment from that part of the wadden. Based on the calculated loss the entire tidal area of Graadyb—130 km²—would have had to lose a layer 25 cm thick between 1900 and 1960, which it did not. The error must be due to two causes: the hydrographic stations are established in the ebb channels (fairways), and the measurements were not taken in periods of rough weather when sediment transport is at its height.

A new sediment sampler has been tested in the wadden area to study the quantity of suspended material in flood tides over long periods. Figure 12 describes the siphon sampler. Investigations so far have been few in number, but based on preliminary measurements it may be estimated that under the best possible conditions for sedimentation—in dense salt marsh vegetation—not more than half the material suspended in the water is deposited. The sampler may also be used in localities with no natural salt marsh formation to ascertain if they receive adequate suspended material to permit reclamation.

Extensive systematic measurements of the rate of sedimentation were conducted during the years 1939-

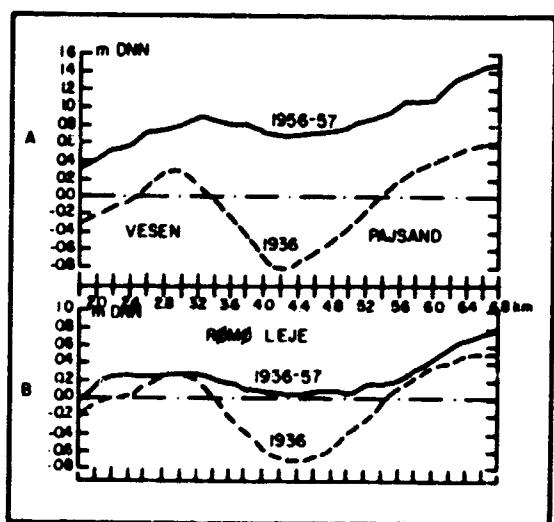


Fig. 13. Profiles showing the levels of the tidal flat before and after the construction of the Rømø Dam. Profile A is through the tidal flat along a line at the southern base of the dam. Profile B is 200 m to the south of the Rømø Dam. Compare with Fig. 11. The profiles are cut along the northern and southern limits of the hatched area (From Olsen, 1959).

1948 after the construction of the Rømø Dam (Olsen, 1959). The dam represented an artificial interference in the natural conditions of the wadden; as a result, the tidal flats and channels immediately began to change in response to the new conditions. This situation offered a favorable occasion for studying the destructive and constructive effects of the extant forces. These effects, which may normally be difficult to trace, now appear in overdimensioned form until a new state of equilibrium has been established.

In Figure 11 an area marked by horizontal hatching, having a width of 200 m and a length of 5 km, is shown along the southern side of the dam at distances of 1.8 km to 6.8 km from its point of origin on the mainland. An examination of the variation in the sedimentation in this area makes it possible to point out several geographic effects caused by the presence of the dam, in combination with the topography of the tidal flats. Comparison of maps compiled in 1936 with those of 1956-1957 permitted construction of the profiles in Figure 13. Profile A is through the tidal flat at the base of the dam. Profile B passes through the tidal flat at a distance of 200 m south of and parallel to the dam. The contour elevations during 1936 and 1956-1957 are marked by a dotted line and a solid line, respectively.

When comparing profiles A and B, greater sedimentation in A will be noticed. This must be caused by the dam (i.e., the effect of forces—beach effect—becoming active in this case when the newly formed artificial shoreline tends to establish a normal beach). It appears from profile A that on Paj sand, between the points 5.6 km and 5.8 km, sedimentation of about 0.5 m has taken place since 1936, while in profile B

only little sedimentation has taken place and on Vesen between the points 2.8 km and 3.0 km no sedimentation at all has been observed. This suggests that the beach effect does not extend to a distance of 200 m from the dam, and that sedimentation which has occurred in profile B must be due to other influences. It is possible to separate further two geographically conditioned factors: the barring effect and the bay effect. The barring effect is clearly evident in profile A as well as profile B (Fig. 13) in the barred channel bed of Rømø Leje. In profile B, the sedimentation must be attributed to the bay effect which reaches as far as the dam.

The development of sedimentation in the wadden region during the period 1936-1959 has been examined (Fig. 11), and the geographic conditions for sedimentation correspond to those existing in Rømø Leje. However, the bay effect is more pronounced because the bay between the foreland and the high-lying tidal flat, Paj sand, is fjord-shaped. The beach effect, the bay effect, and the barring effect, are clearly recognizable in a comparison of Figures 3 and 4.

Figures 14 and 15 show an extremely strong sedimentation between 1936 and 1955; it is greatest at the base of the dam and least at the southern frontier of the area. The extent of this area is 200 hectares, and the quantity of material deposited amounts to 1 million cubic meters. The original surface consisted of ordinary, well-sorted, tidal flat sand with a mean grain size of 90 μ and a clay content of less than 10 percent (Hansen, 1951). The material which has been deposited since the construction of the dam is poorly sorted silt with a mean grain size of 6.17 μ and a clay content of up to 36 percent (Hansen, 1956).

Investigations have been conducted to determine how the rate of sedimentation has varied over the area. Contourings of the whole area were made in 1936 and in August, 1955. Other contourings of a zone 320 m wide along the base of the dam were also used. These were made in August, 1941, March, 1943, June, 1944, October, 1945, October, 1947, and February, 1959. On the basis of these eight contourings, six profiles have been drawn through the tidal flat parallel to the dam. In each profile are four vertical profiles at horizontal intervals of about 400 m. In each vertical section the sedimentation (in cm) within the respective time intervals has been measured, and the amount of sedimentation in cm/month calculated (Fig. 16). This is considered to be the intensity of sedimentation in the mean level (i.e., the mean datum between two leveling planes in the vertical section). The six profiles extend southward from the base of the dam and at distances of 70 m, 170 m, 370 m, 1,200 m, and 2,100 m (Fig. 17).

The results all show the same tendency (Fig. 18). Sedimentation is greatest at a low level, decreases at rising elevations to + 0.8 to + 0.9 m Danish Zero Level (DZN)—a little below the mean high-water level—and then increases again. Sedimentation is less at the high-water level than at any higher or lower

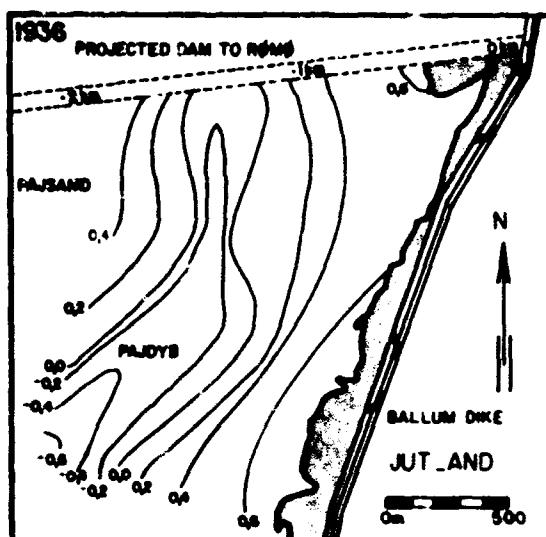


Fig. 14. Area of research concerning sedimentation caused by the Rømø Dam. Map dating from 1936, showing the area between the Rømø Dam and Jutland. The contours (0.2 m) show the levels in Pajdyb and those of the tidal flats before the construction of the Rømø Dam (From Olsen, 1959).

level when no consideration is given to the variation of the water cover. In other words, at high-water level sedimentation is less in proportion to the water cover than at any other level. This phenomenon occurs everywhere in the wadden area; it is evident when an analysis is made of an area of rapid sedimentation like the one in question, but it may be difficult to observe otherwise.

Erosion at the high-water level is probably the primary factor which prevents the vegetation from starting easily on a high-lying tidal flat, though the height necessary for immigration of vegetation should be optimal. It has also been observed that even a rather dense growth of *Salsola* on a high-lying tidal flat is often destroyed by erosion. Contrary to this, once a growth of *Glyceria* vegetation has immigrated, it is difficult to destroy, as it catches and retains the sediment which has been whirled up, thereby consolidating its own position (Fig. 19). On the sides exposed to the wind, however, this vegetation will erode the border, which can be counteracted only by fascines or other artificial means.

For a period of 20 years the investigation of sedimentation south of the Rømø Dam has provided evidence that the geographically conditioned beach, barring, and bay effects are of great importance and must be considered in land reclamation projects. Investigations concerning accumulation and abrasion between the western coast of Jutland, southwest of Ribe, and the island of Mandø (Figs. 20 and 21) have been carried out by Møller (1964).

A demand for further knowledge as a basis for regional planning is also an important stimulus. A dam from Møn to Jutland was proposed to improve

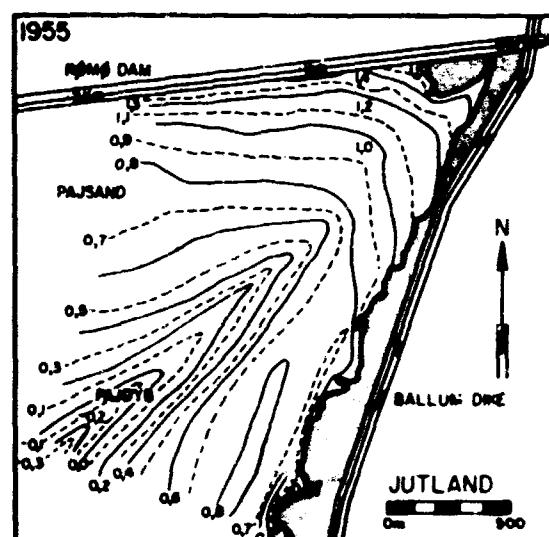


Fig. 15. Area of research concerning sedimentation caused by the Rømø Dam. Map dating from 1955 of the same area as in Fig. 14, showing the levels 15 years after the construction of the Rømø Dam. A comparison shows that the contours in the vicinity of the dam have completely changed. The effect of the coast, the bay effect, and the cutting-off effect are clearly recognized (From Olsen, 1959).

communications and transport of agricultural produce, and investigations have been directed towards its optimum location and its effects on the tidal area. These studies could be considered as applied geographical research.

ACCUMULATION FORMS: TIDAL FLATS AND SALT MARSHES

The morphological features of the tidal area in the southwestern part of Denmark have been described by Jakobsen (1961) as a terrace of deposits laid over earlier glacial areas. Two main elements exist: the wadden (tidal flat) and the salt marsh. The salt marshes of this area are higher than the tidal flats and terminate in a low erosion cliff which has a height of up to 1 m. The salt marsh plains are similar to the marine forelands which are found on many other Danish coasts. These forelands have level plains with difficult drainage conditions and are exposed to temporary inundation. Most of the marine forelands in the northern and northeastern parts of Denmark are true raised sea floors caused by the post-Littorina emergence. The salt marshes do not originate from a normal elevation of the sea floor, but are formed by deposition in a salt marsh vegetation or in a reed swamp. In the course of time, the sediment raises the level of the salt marsh to such a height that there is practically no inundation; consequently, at that point, little sedimentation takes place. For this reason, salt marshes form at places where a downward vertical displacement of the land occurs, provided that deposition takes place faster than the lowering of the surface



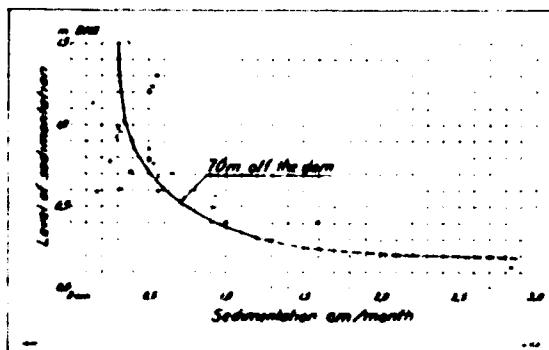


Fig. 16. Example of curve construction concerning mean sedimentation for measuring profile. Rømø Dam research area. The individual points represent the sedimentation (cm month) and the mean level (m DNN). The black points to the right of the curve indicate that the sedimentation in these cases has taken place in a *Glycera* vegetation (From Olsen, 1959).

of the land. The large salt marshes along the southern part of the North Sea, stretching from Denmark to France, have been formed in areas which have been periodically exposed to lowerings of the land surface. Under such circumstances, the salt marsh sediments may become very thick since the progressive subsidence of the land surface permits the deposition to continue. This explains why one can find areas in the salt marsh with fairly ancient deposits which have a thickness of several meters. The profile (Fig. 22) shows a cut through a coastal area in the wadden which exposes the various types of landscapes and their position in relation to DNN and the tidal range.

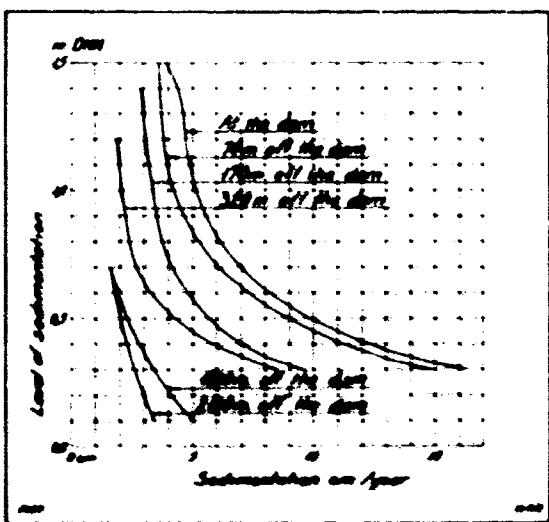


Fig. 17. Rømø Dam research area. The mean sedimentation per year in proportion to the level and the distance from the dam. The curves have been drawn as in Figure 16 and show the sedimentation at the base of the dam and at a distance from this of 70 m, 120 m, 170 m, 220 m, 1,200 m, and 2,100 m (From Olsen, 1959).

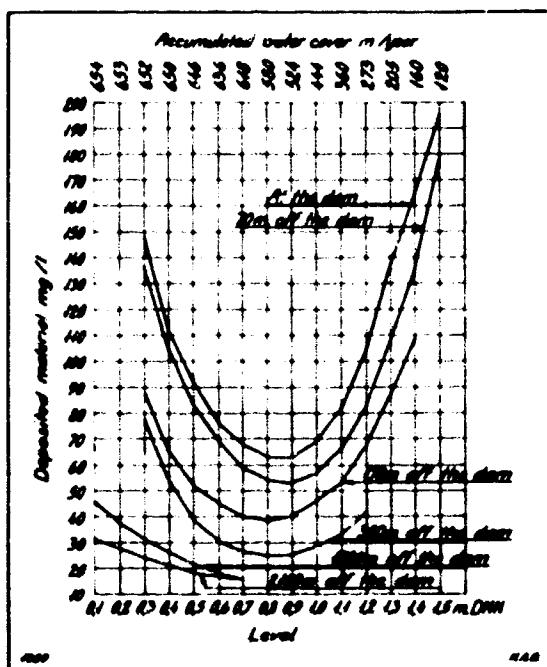


Fig. 18. Rømø Dam research area. The quantities of deposited material per year (mg/l) in proportion to the level at the base of the dam and at the distances from the dam of 70 m, 120 m, 170 m, 220 m, and 2,100 m. Each curve represents the quantity of deposited material per liter of the accumulated water cover per year at the different levels. The mean sedimentation has been compared with the accumulated water cover per year. The specific gravity of the dry wadden sediment (0.6) has been introduced in order to express the amount of sediment in units of weight (From Olsen, 1959).

The wadden is exposed at low tide and inundated again at high tide. The mean high tide level (MHT), which nearly corresponds to the morphological shoreline, in the northern part of the Danish wadden area is about 0.55-0.75 m, and in the region at the Rømø Dam is about 0.80-0.90 m above DNN.

In the eastern part of the wadden area, close to the coast, some tidal flats are high (Fig. 21). As a rule, the highest elevation can be found at a distance of a few hundred meters from the coast, whereas the area next to the border of the foreland is at a somewhat lower level. This part, the "landpriel" (offshore channel), usually conveys water, even at low water, because of the poor drainage conditions and the constant flow of water from the tidal flats. Furthermore, in some places the landpriel serves as an outlet for the watercourses which flow into the wadden.

The tidal flats situated at a high elevation off the coast are not continuous, but are separated into irregular bars. Between these bars, the water from the landpriels searches its way to the depths through shallow inlets or through marked tidal channels. The tidal flats outside the landpriels are generally hard and sandy. At places, the most elevated areas may be

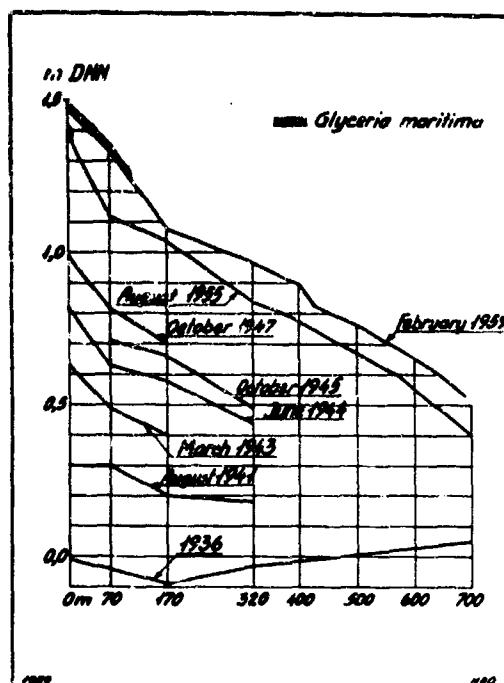


Fig. 19. Rømø Dam research area. Profile through the tidal flat to the south of point 1.2 km of the Rømø Dam. All the measurements executed in the years 1936-1959 are indicated. The extent of the *Glyceria* vegetation in this period is shown (From Olsen, 1959).

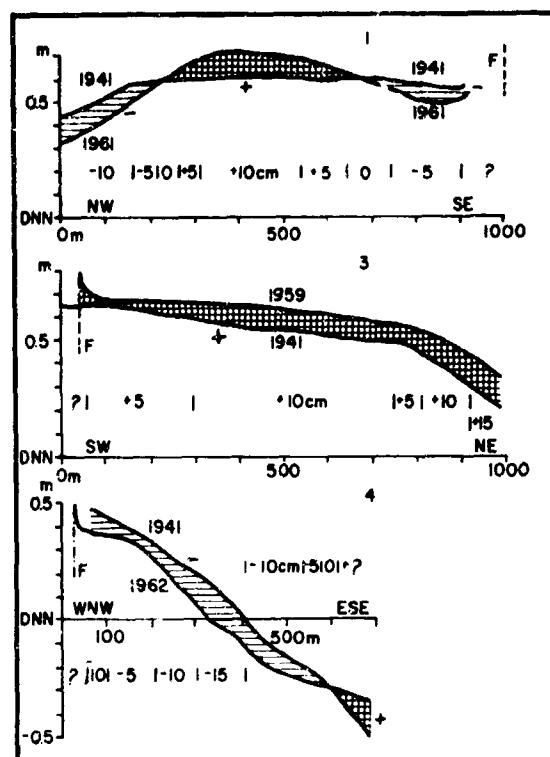


Fig. 21. Accumulation and abrasion in a tidal area. Examples of double profiles. The numbers refer to the position of the profiles in Figure 20. Profile 1 shows the accumulation flat as related to the eastern offshore tidal channel to the south. Profile 3 is from the accumulation area, and profile 4, from the abrasion area. The size in centimeters of the changes appears from the slanting figures between the vertical lines. ? means doubtful parts of the profiles. F is the situation of the vegetation border of the salt marsh foreland (From Møller, 1963).

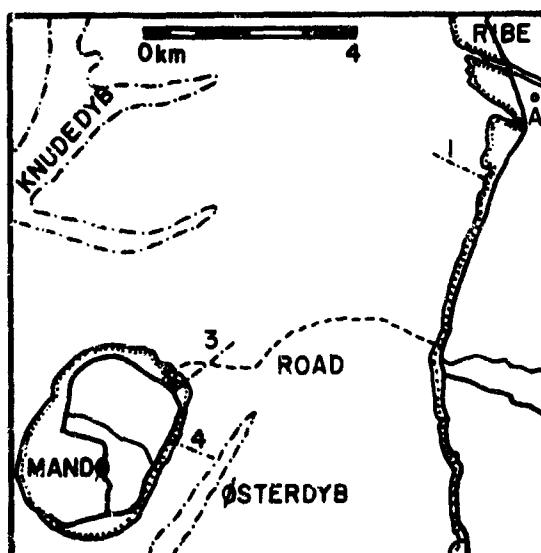


Fig. 20. The wadden area between the western coast of Jutland south of the outlet of Ribe Aa and Mandø. The depth contours indicate the -4 m DNN. The indentation in the coast south of the present outlet of Ribe Aa is the old outlet. The present route of the ebb road to Mandø is indicated by the dotted line. The sea dikes are marked by full-drawn lines. The numbered lines indicate the situation of the profiles 1, 3, 4 (Fig. 21). Aa is the river. Østerdyb is the eastern tidal channel (From Møller, 1963).

situated at a level which almost corresponds to the MHT, so that ordinarily they are covered with water for only a short time; when there is an easterly wind, or at neap tide, they may occasionally be dry during a high-water period.

The largest growths of *Salicornia herbacea* are found on such tidal flats. The quantity and occurrence of *Salicornia* changes considerably from one place to another and from year to year, but even the presence of dense growths of this plant during several succeeding years does not make extensive changes in the level of the tidal area or the composition of its soil. In certain cases, the true salt marsh plants (principally *Glyceria maritima* or *Puccinellia maritima*) may suddenly appear on the highest parts of the tidal flat outside the landpriels. This rarely happens and seems to require a combination of favorable factors.

The material transported by the water can easily be deposited in the *Glyceria* vegetation, where it is sheltered against waves and currents. The surface of a wadden, which is usually at a rather stationary level, begins to change after the immigration of

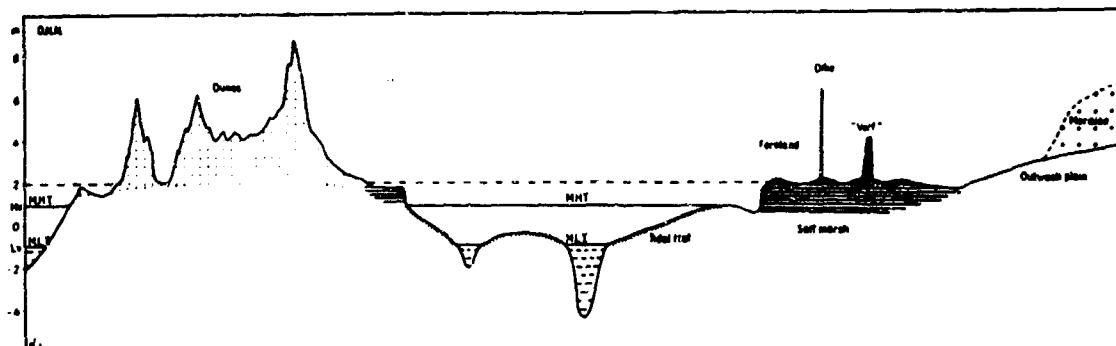


Fig. 22. Landscape types and levels in the Danish tidal area. Idealized cut through a tidal area in the southwestern part of Jutland. The various types of landscapes are shown (right to left) from a level point of view in relation to Danish Zero Level (DZN) and the tidewater. The height is much exaggerated in comparison with the length. MHT and MLT: Mean high tide level and mean low tide level. Dashed line above MHT indicates the level which the high tide reaches about ten times a year (From Jakobsen, 1963).

Glyceria. At first, the material accumulates in the sparse tufts of *Glyceria*, which spread rapidly by means of numerous offshoots. Later, as deposition proceeds, small hummocks are formed, which eventually rise above the surface of the tidal flat.

In the outer part of the newly formed marsh, the hummocks are pronounced (Fig. 23A), and rapidly rise to a level several decimeters above the tidal flat, owing to the deposition of sand by wave action. Farther inland the hummocks are flatter and the material deposited is principally silt or fine-grained sand. Eventually the hummocks grow together (Fig. 23B), and in the course of a few years the tidal flat may thus be transformed into a dense *Glyceria* meadow.

Simultaneously with the creation of the new marsh, the sea commences to erode its outer parts, and in the course of time a distinctly marked cliff is formed facing the tidal flat. In the original landpriel, where the sheltering effect increases, an additional quantity of "slik" (ooze) is deposited and *Salicornia herbacea*, followed by *Glyceria maritima*, spreads in the direction of the old foreland. Gradually, as deposition causes the level to rise, the number of tidal submersions decreases appreciably; the highest parts, in particular, may be dry for long periods during the summer season (Fig. 23C). The above-described process continues through cycles of deposition and erosion in such a manner that the outer parts remain the highest. The level decreases in the direction of the landpriel, where deposition of silt becomes more and more prominent.

Seaward from the new marsh a new coastal profile with a pronounced landpriel is apt to form, and on the tidal flat off this landpriel a new marsh may be created. Sometimes, even before the formation has been accomplished, one or more new marshes are developed outside the first area. The individual "isles" can be traced for a long distance in the surface profile and in the distribution of the layers of sand and clayey sediments. In some cases, erosion is so rapid that a new marsh area will be obliterated, totally or in part, before its formation is complete.

The hypothesis of discontinuous salt marsh formation, through the welding of marsh islets, is the result of Jakobsen's investigations (1954), based on Nielsen's initial research. A marsh plain may also form in a reed swamp as, for example, at Varde Aa. The annual sediment increment varies between 3 and 10 mm, which in a century gives an average thickness of 50 cm. Unless a change of land surface level occurs, marsh formation in the locality will eventually cease of its own accord within a geologically brief span of time. The thickness of the loam layers will be limited and will be proportionate to the local tidal difference. The old theories of marsh plain formation in the tidal areas, brought about by certain animal forms (sandworms, for example) as ooze binders, or by plants, especially *Salicornia*, as the collector of deposit particles, must now be abandoned. In other words, there is no general transformation of tidal areas to marsh plains.

ESTUARINE RESEARCH AS A BASIS FOR LAND RECLAMATION

In the early 1930's Nielsen's original concepts of tidal area research and investigations concerning salt marsh development were to expand scientific knowledge and, in this way, procure data which could be used as basic information for the execution of reclamation projects. The scope of the work has been summarized by Jakobsen and Jensen (1956). In 1963 a proposal was presented to the Danish authorities concerning regional reclamation planning, based on organized field work during 1953-1962 and 20 years of previous studies sponsored by the Skalling Laboratory (Jakobsen *et al.*, 1963).

PALEOGRAPHY OF THE DANISH ESTUARY REGION

The salt marsh area at Tønder has been carefully examined on the basis of soil studies (Jakobsen, 1956), geographical surveying (Jakobsen, 1964), and a dense network of borings. The program, started in 1952, consists of a network of borings to a depth of

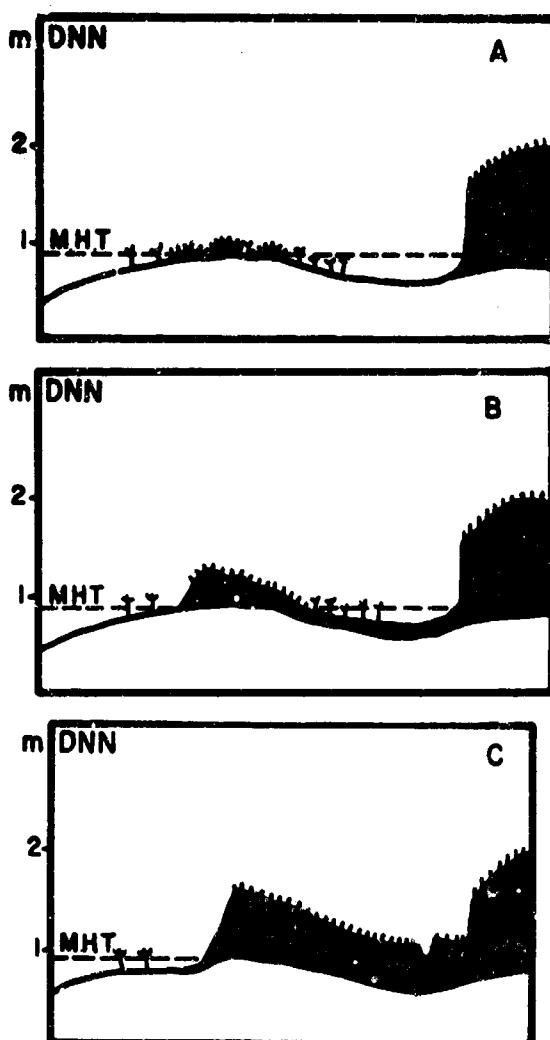


Fig. 23. Developmental stages in salt marsh formation.
 A—Beginning salt marsh formation on a high-lying tidal flat outside an old salt marsh area. (In a *Salicornia* vegetation, *Glyceria* recently immigrated has begun to form hummocks.)
 B—In the course of time a new marsh island is formed.
 C—The landpriel between the island and the old erosion cliff is filled and transformed into a salt marsh. MHT: Mean high tide level. The height is much exaggerated in comparison with the length (From Jakobsen, 1963).

1.25 m at horizontal intervals of 50 m and a system of transects, with borings to the old surface of the outwash plains of the Würm glaciation, or to the old morainic isles of the Riss glaciation—the "geest" surface.

The following description has been compiled from Jakobsen (1960a): The Tønder salt marsh is situated just south of the Fennoscandian rising block, the outer limit of which extends from the Esbjerg region through Aarsø and the Fehmarn Belt. Epeirogenetic subsidence in the southern part of the North Sea has

been estimated to be about 2-3 cm per century; this small amount of subsidence excludes epeirogenetic forces from important consideration in this relation. What remain to be considered are the eustatic movements which, on the whole, must be regarded as the principal cause of the relative subsidence of about 17 m since the beginning of Atlanticum (i.e., for the last 7,500 years). Of course, this relative rise of sea level has been subjected to fluctuations caused by climatic changes and changes in the local meteorological and hydrographic conditions.

The Tønder salt marsh and the wadden area immediately to the west are considered as a delta region for the Vidaa River (Fig. 2) and its tributaries, which have been drowned by the rise of the sea level. However, the rise has taken place slowly enough to be balanced by sedimentation, through the formation of the island arc, the adjoining wadden area, and the fringe of marine foreland along the mainland. Because of this, belts of salt marshes are found mainly in the estuaries of the rivers, and are separated by remnants of older moraines with steep erosion cliffs which face the wadden. Højer is situated on a small, isolated remnant, and immediately to the north the older moraine, Hjerpsted, displays an erosion cliff 11 km long which faces the west.

The topography of the late-glacial subsurface (geest surface) in the salt marsh has been surveyed, and a hypsometric map with 1 m contours has been published (Schou, 1960). A more detailed map in the scale 1:10,000 and with 50 cm contours is in print. The geest surface is comprised of three morphological types. The western half forms part of the outwash plain, gently sloping towards the west; it was formerly intersected in the middle by a channel (the former Vidaa) which now is filled with marine sand. In this area the gradient of the outwash plain is .75 m per km, and the mean levels range from about -5 m DNN to -8 m DNN. To the east of the area described above, a higher lying terrace is found which is characterized by dune topography. The mean level of this undulating surface is -1 m DNN. It stands with a cliff facing the outwash plain to the west and has a large blowout to the east in the direction of the older moraine of Møgeltønder. The Møgeltønder moraine where the salt marsh area ends in an escarpment represents the third type.

Longitudinal sections through the post-glacial deposits of the Tønder salt marsh have been constructed on the results of borings. These sections demonstrate the differentiation in sediment cover and facies types (marine sand, clay of foreland type, clay of basin type, silt, "gytje", peat, etc.) in relation to the relative rise of the sea level.

The slowly progressing subsidence caused by the glacial-eustatic rise of sea level has, in general, been compensated for by sedimentation. In the old salt marsh areas this has resulted in the formation of a series of facies influenced by sedimentation factors which vary with the physiographic elements: tidal flats, foreland with vegetation cover, deeps, channels,

gullies, etc. The variation in facies has also been conditioned by the effect of varying salinity, caused partly by the influence of fresh water from the rivers, and partly by the formation of sand bars of different age and location. These sand bars have created basins either essentially closed or in more or less open connection with the sea. It further appears that two systems have been active: (1) quiet periods, in a state of equilibrium, during which the individual facies were formed and gradually integrated; and (2) powerful, short interventions by extraordinarily high storm floods which created new conditions, to which the whole system rapidly adapted.

Jacobsen's detailed work has resulted in a geographic monograph (1964) treating the topography of the geest surface and the description of the genesis of a salt marsh landscape in a drowned delta region. It also includes an analysis of human influence: mound building as a base for habitation, dike construction, establishment of polders, and land-use patterns of various kinds.

The Danish estuarine research started with Nielsen's method for quantitatively measuring the sedimentation in a salt marsh and, after 35 years under his leadership, has developed as interdisciplinary investigations treating hydrology, geomorphology, geology, soil science, botany, zoology, and archaeology—all kept in focus by the geographer's point of view.

LITERATURE CITED

- GRY, H., 1942. Das Wattenmeer bei Skallingen I. Quantitative Untersuchungen über den Sanktstofftransport durch Gezeitenströmungen. *Folia Geograph. Danica*, Tom. II, No. 1.
- GUILCHER, A., 1954. *Morphologie Littorale et Sous-Marine*. Orbis. Presses Universitaires de France, Paris.
- GUILCHER, A., 1958. *Coastal and submarine morphology*. Methuen and Co., London.
- HANSEN, K., 1951. Preliminary report on the sediments of the Danish Wadden Sea. *Medd. Dansk Geol. Foren.*, Vol. 12, Bd. 1.
- HANSEN, K., 1956. The sedimentation along the Rømø-dam. *Medd. Geol. Foren.*
- JACOBSEN, N. K., 1956. Soil investigations in the salt-marsh area at Tønder; method and interpretation. *Geograf. Tidsskr.*, Vol. 55.
- JACOBSEN, N. K., 1959. Topography of the Late-Glacial surface in the salt-marsh at Tønder. *Geograf. Tidsskr.*, Vol. 58.
- JACOBSEN, N. K., 1960a. Types of sedimentation in a drowned delta region. *Geograf. Tidsskr.*, Vol. 59.
- JACOBSEN, N. K., 1960b. Agricultural geography and regional planning in a marine foreland. *Geograf. Tidsskr.*, Vol. 59.
- JACOBSEN, N. K., 1964. Geographical observations in the salt-marsh at Tønder with special reference to the morphogenesis. *Folia Geograph. Danica* Tom. VII, No. 1.
- JAKOBSEN, B., 1953. The development of the salt-marsh at the Skalling Peninsula. *Geograf. Tidsskr.*, Vol. 52.
- JAKOBSEN, B., 1954. The tidal area in Southwestern Jutland and the process of the salt-marsh formation. *Geograf. Tidsskr.*, Vol. 53.
- JAKOBSEN, B., 1961. The suspension of sediment in the Wadden Sea investigated through quantitative measurements. An experiment with a new type of instrument—A Siphon Sampler. *Geograf. Tidsskr.*, Vol. 60.
- JAKOBSEN, B., 1962. The formation of ebb and flood channels in tidal channels described on basis of morphological and hydrological observations. *Geograf. Tidsskr.*, Vol. 61.
- JAKOBSEN, B., 1963. The morphology of the Wadden Sea. A geographical analysis of the configuration of the tidal flats, especially regarding the tidal area of Juvre Dyb. *Folia Geograph. Danica*.
- JAKOBSEN, B., and K. M. JENSEN, 1956. Investigations of land reclamation methods in the Danish Wadden Sea. *Geograf. Tidsskr.*, Vol. 55.
- JAKOBSEN, B., M. JESPERSEN, and H. A. OLSEN, 1963. The regional planning of the land reclamation in the Wadden Sea at the Southwestern coast of Jutland between the Danish German Border and the marsh at Ribe. *Folia Geograph. Danica*, Tom. VIII, No. 1.
- JESPERSEN, M., 1959. Map of habitation in the County Tønder and in North Friesland. *De Danske Vade-og Marskundersøgelser*, Rept. No. 3.
- JESPERSEN, M., 1961. Eiderstedt. A stagnant salt-marsh area. *Geograf. Tidsskr.*, Vol. 60.
- MEDDELELSER FRA SKALLING-LABORATORIET, Vol. I-XVII. Geographical Institute, University of Copenhagen, Copenhagen, Denmark.
- MØLLER, J. T., 1956. Map of the tidal area of Juvre Dyb in relation to some topographical and hydrographical problems. *Geograf. Tidsskr.*, Vol. 55.
- MØLLER, J. T., 1960. The Mandø Ebb-Road. *Folia Geograph. Danica*, Tom. VIII, No. 2.
- MØLLER, J. T., 1961. A description of the survey of the tidal flats along the west coast of Jutland between Emmerlev and Ballum near the towns Ribe and Tønder. *Folia Geograph. Danica*, Tom. VIII, No. 3.
- MØLLER, J. T., 1963. Accumulation and abrasion in a tidal area. Cartographical methods and results. *Geograf. Tidsskr.*, vol. 62.
- MØLLER, J. T., 1964. Flatcoast and river morphology in tidal areas and the special vegetation and hydrology of these regions. (Private printing, Department of Geography, University of Copenhagen, Copenhagen, Denmark).
- NIELSEN, N., 1935a. Das Skalling-Laboratorium, 1930–1935. *Medd. Skalling-Laboratoriet*, Vol. 1.
- NIELSEN, N., 1935b. The Scientific Investigation of the Peninsula of Skallingen. *Medd. Skalling-Laboratoriet*, Vol. 1.
- NIELSEN, N., 1935c. The communal ownership of land at Skallingen. *Medd. Skalling-Laboratoriet*, Vol. 1.
- NIELSEN, N., 1935d. Eine Methode zur exakten Sedimentationsmessung. *Kgl. Danske Videnskab. Selskab. Biol. Medd.* XII, No. 4.
- OLSEN, H. A., 1959. The influence of the Rømø Dam on the sedimentation in the adjacent part of the Danish Wadden Sea. *Geograf. Tidsskr.*, Vol. 58.
- SCHOU, A., 1952. Direction determining influence of the wind on shoreline simplification and coastal dunes. *Proc. 17th Congr. Intern. Geograph. Union, Washington*, 1952.
- SCHOU, A., 1960. The coastline of Djursland. A study in East-Danish shoreline development. *Geograf. Tidsskr.*, Vol. 59.
- VAN VEEN, J., 1950. Eb- en Vloedschaar systemen in de Nederlandse getijwateren. *Tijdschr. Koninkl. Ned. Aardrijksk. Gen. Amsterdam. Waddensymposium*, Groningen, Netherlands.

IV. SEDIMENTS AND SEDIMENTATION

Origin of Sediments in Estuaries

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The origin of sediments in estuaries has been widely discussed in Europe and America during the past 25 years. These discussions have led to differing conclusions, which may be ascribed either to the contrasts between areas and estuaries, or to differences in methods of investigation and schools of research. Conflicting findings can exist because the same estuary has been studied by two qualified teams of geologists using different methods and different basic principles.

Since rivers carry suspended materials in their upper and middle courses, one theory supported by a number of geologists is that the sediments found in the estuaries have come from inland. Others believe that estuarine sediments come from the sea. In some areas, the conclusion is that they derive from Pleistocene deposits outcropping on the slopes or in the beds of the estuaries themselves. Another premise is that the source is to be found at the mouth of the estuary. All these opinions will be reviewed here.

SEDIMENTS COMING FROM THE SEA

DUTCH ESTUARIES

The Dutch school in sedimentary petrology has arrived at such conclusions from numerous studies in the Wadden Zee, Friesland, Holland, and Zeeland (Baak, 1936; Crommelin, 1940; Favere, 1951). The Wadden Zee is not an estuary, but a tidal flat area; however, the sediments in the mouths of the rivers Scheldt, Rhine, Ems, Weser, and Elbe are also said to be carried from the North Sea, but there are some reservations. For example, Van Straaten (1961) writes, after Zonneveld's investigations (1960), that, "in the innermost parts of some of the estuaries, e.g. the Biesbos area on the Rhine, a significant fluvial deposition takes place." In referring again to the Rhine, Van Straaten (1963) says, "according to Van Veen (1936), the transport of (relatively coarse) bed load material decreases strongly beyond Krimpen, on the Lek, and beyond Moerdijk, on the Hollands Diep (these two places are located at 30 and 48 kilometers from the North Sea). In the most seaward parts of the rivers, downstream of Schiedaw on the Nieuwe Maas, and of Willemstad on the Hollands Diep (22 and 37 kilometers from the North Sea), great displacements of sand take place again, but the sand is, at least for a great part, of marine origin. It is brought by the wedges of salt water flowing inward along the river bottom." In another paper, Van Straaten and Kuenen (1957) accept the idea that "a

part of the mud in the Wadden Zee has been supplied via the former Zuider Zee by the river IJssel, a distributary of the Rhine . . . [but] the contributions of the IJssel were only of subordinate importance." These conclusions are based on mineralogical and petrographical analyses. As to the Scheldt Estuary, on the Netherlands-Belgium boundary, Crommelin (1949) concludes: "on granulometrical basis one is forced to accept a very small direct influence of the fine Scheldt material on the sedimentation along the estuary. Most of the fine silt seems to originate from the southern North Sea."

The evidence for the Ems Estuary, at the German-Dutch boundary, is based on the exposition of Van Straaten (1960), who considers successively the different fractions of the sediment. For the coarse fraction above 2 mm, accurate data are available only for the organic constituents, which are mollusc shells, and are mostly of local estuarine origin. For inorganic constituents, "it can hardly be doubted that they are of the same character as in the Wadden Zee and west of the estuary," that is, outside of the latter.

Between 2 mm and 50 μ , the organic elements (shells of molluscs, ostracods, foraminifers, etc.), "have been washed in by the flood currents from the North Sea for a considerable part"; some of them only live in the open North Sea environments and in the inlets between the Frisian Islands. In the inorganic material, the composition of the heavy mineral residues between 50 and 200 μ shows that this material represents a transition between two petrological provinces which were previously defined in the North Sea by Baak (1936) and Crommelin (1940): the A province, in Friesland and on the sea floor off the Frisian Islands, includes garnet, epidote, amphibole, but only little saussurite; the H province, to the west of Holland, is relatively rich in saussurite. Apparently it originates in the North Sea, in which the A material is of northern, mainly glacial origin, and the H material was probably supplied in large part by the Rhine, during the Pleistocene.

The 25-30 μ fraction was also investigated by Crommelin, who concluded that it fits well with the North Sea material of the same size and differs from the sediments of the Ems River upstream.

For the finest particles, less than 25 μ , DeSmet and Wiggers concluded that 5 percent, at most, have been supplied by the Ems, the remaining part (Wadden Zee and North Sea) are of marine origin. Van Straaten assumed that 5 percent can actually come

from the river, 10 percent is of local origin, and 85 percent is supplied from the sea.

It must be pointed out that the average water discharge of the Ems is very small, $60 \text{ m}^3/\text{sec}$, and the yearly discharge of sediment by this river is estimated at 56,000 tons. Even if the second figure is considerably underestimated, the contribution of the river to the sedimentation in the estuary appears to have only minor importance. The average water discharge of the Rhine is as high as $2,200 \text{ m}^3/\text{sec}$ ($1 \text{ m}^3 = 35 \text{ ft}^3$). Also, if the estuarine sedimentation in the Netherlands now comes mostly from the sea, these sediments were supplied to the sea floor from the land during the Pleistocene, except for the organic (skeletal) fraction, before the North Sea was formed.

THE SEINE ESTUARY

The sedimentation in the Seine Estuary, which opens into the English Channel, has been studied by Rajcevic (1957), who concluded that "three-quarters of the sediments forming the mud (in the Seine Estuary) are of marine origin." His conclusion is unconvincing because it is supported mostly by the calcium carbonate content of the sediments, which, in my opinion, could have been supplied by the river as well as the sea. I think that the properties of the sediments in this estuary (grain size, chemical composition, heavy minerals, roundness, etc.) do not give definite evidence of a marine origin for the larger part of the materials.

More recently, however, an accurate discussion of data gathered by Rouen harbor engineers has led Vigarie (1965) to the same idea as Rajcevic. Between 1834 and 1956, a large part of the Seine Estuary was filled with sediment at the rate of about $5,600,000 \text{ m}^3$ a year. Between 1874 and 1913 a cutting was observed reaching about $2,400,000 \text{ m}^3$ a year at the entrance of the estuary (the Baie de la Seine). It may be that the difference between the two figures is caused by an extension of the erosion of the sea bottom to adjoining areas, other than those which were investigated. Between 1834 and 1913, hydrographic surveys in the Baie de la Seine showed a mean increase in depth of 0.68 m. On the other hand, the supply of sediments by this river seems to be small, probably much less than $1,000,000 \text{ m}^3$ a year. This amount does not seem to account for the filling which was observed. From September 30, 1959, to November 30, 1960, more than $9,500,000 \text{ m}^3$ were deposited in the estuary, although the river discharge during this period was exceptionally small. None of these observations provides indisputable evidence, but a high probability appears to indicate an origin of sediment which is marine in nature.

What is called "the Seine Estuary" includes only the outermost course of the river, about 40 km long, which widens greatly downstream from Tancarville. This is the only part of the estuary in which salt water penetrates to any significant degree, although the tide extends much farther up the river. Nothing can be said at present concerning the sedimentation in

the tidal area where the water is predominantly fresh. On the other hand, even during exceptional floods the average discharge of the Seine is small, so that we cannot extend these conclusions without qualification to other rivers; and the conclusions are valid only for modern times. At the end of the Pleistocene, when the Rhine was overloaded, it built a braided channel system near Nijmegen (Scheur, in Guilcher and Cailleux, 1950). But this section of the Rhine was not an estuary.

SEDIMENTS COMING FROM THE LOWER SLOPES BORDERING THE ESTUARIES

SMALL BRETON ESTUARIES

The numerous small rivers running to the sea around Brittany become comparatively long estuaries in which extensive mud flats (slikkes) and tidal marshes (schorres) are generally found. The slopes of these valleys were partly drowned during the post-glacial transgression, but are still covered by periglacial deposits known as "head" in northwestern Europe, which are sometimes several meters thick. They were laid down by solifluction under cold conditions during the last glaciation. Head is also present in many places under the estuarine mud in which frost-shattered angular stones are commonly present. In northern Brittany, for example, in the Rance Estuary, these deposits are finer as a whole than in the west and in the south and may be referred to as "loam". Investigations concerning the origin of the mud were carried out in these estuaries by Berthois and Berthois (1954, 1955), and by Guilcher and Berthois (1957). They used three methods: grain-size, thermal differential, and X-ray analyses.

In the Rance Estuary, samples were taken in the different areas from the tidal flats, the tidal marshes, and the loam. At La Vallée Creek (Fig. 1), the loam was taken from under the tidal marsh. The grain-size analysis shows three curves which are almost identical; the small discrepancies do not exceed the possible error in determination of percentages. At Minihic (Fig. 2), the three curves (loam on slope, mud flat, tidal marsh) display the same general trend: there is only a small amount of coarser particles in the loam, and they were not included in the more recent sediment when the former was reworked. The same results were found in two other places investigated in the same estuary.

Other grain-size analyses were made on sediments from Tariec, northwestern Brittany, and from Le Faou, Keroualle, and Rade de Brest, in western Brittany. Since very coarse particles and angular stones are present in the head, the particles which were finer than 60μ were selected in the samples to be compared with those from tidal flats and marshes. At Tariec (Fig. 3), the differences between two mud-flat samples (SC 4 and 3) are greater than those between one of the finer parts of the periglacial deposits (SC 2) and one of the mud-flat samples (SC 4). At Keroualle (Fig. 4), the curves of high marsh

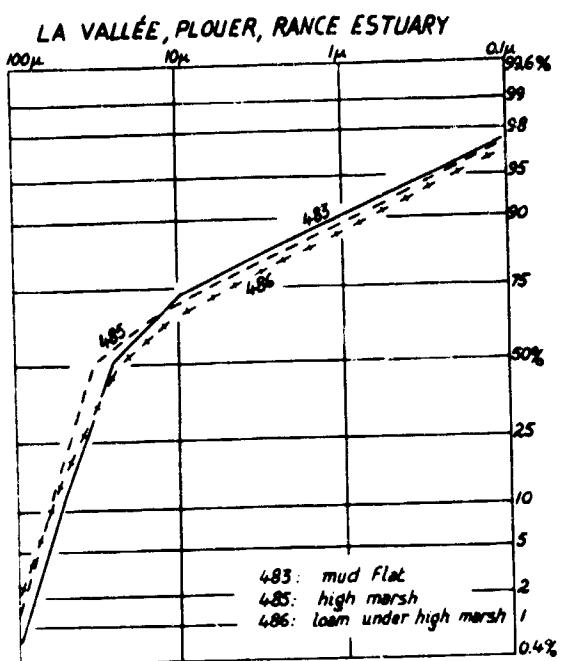


Fig. 1. Grain-size analyses of samples from La Vallée, Rance Estuary, northeastern Brittany. (After Berthois and Berthois, 1954, 1955.)

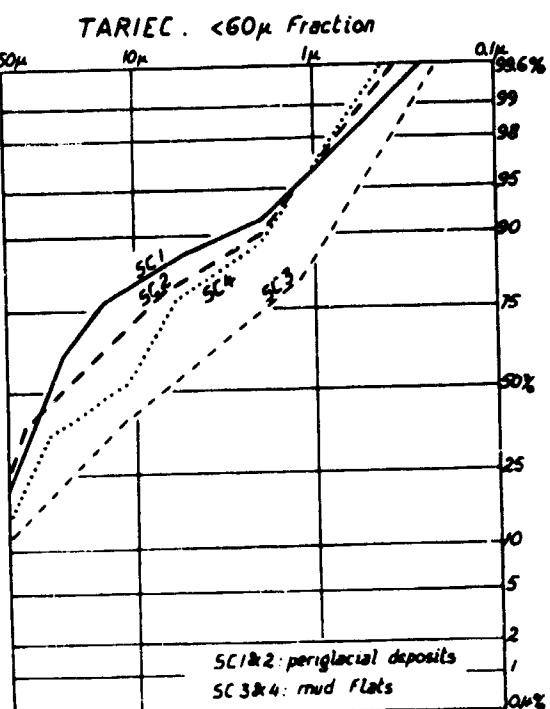


Fig. 3. Grain-size analyses of samples from Tariec, northwestern Brittany. (After Guilcher and Berthois, 1957.)

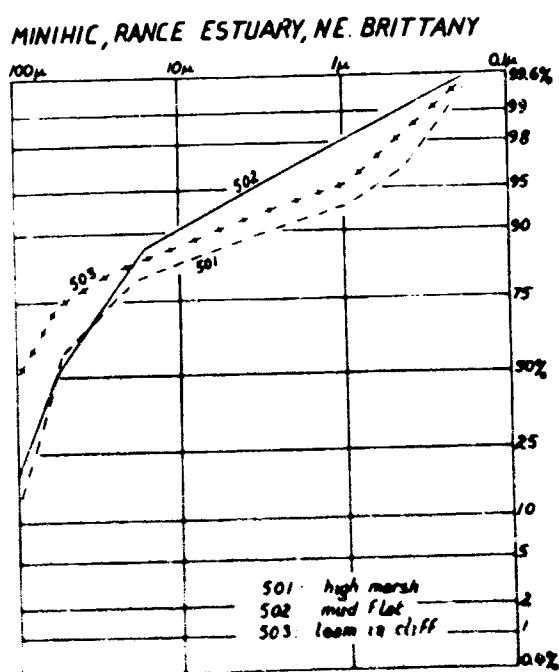


Fig. 2. Grain-size analyses of samples from Minihic, Rance Estuary. (After Berthois and Berthois, 1954, 1955.)

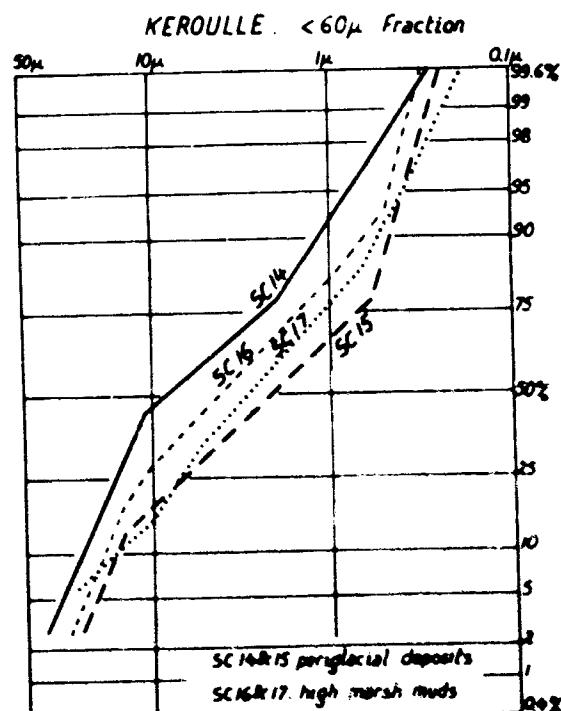


Fig. 4. Grain-size analyses of samples from Keroulle, western Brittany. (After Guilcher and Berthois, 1957.)

muds (SC 16 and 17) are included inside of two curves of periglacial deposits (SC 14 and 15). At Le Faou (Fig. 5), the curves for periglacial deposits, tidal marshes, and mud flats resemble each other very much; the differences between SC 9 (head) and SC 11 and 12 (marshes) are not larger than those between two head samples SC 9 and 10. It may thus be said that the periglacial deposits include all sizes of particles which are found in the mud and only the coarser particles were eliminated.

The clay fraction was investigated by means of differential thermal analyses, which were carried out after the organic matter and the carbonates were destroyed (Figs. 6 and 7). The figures show sediments from four estuaries in northwestern and western Brittany. Between 0° C. and 250° C., the curves are distinctly different from each other. These discrepancies are due to colloidal matter, the amount of which is variable from sample to sample. At about 300° C. some curves show a small endothermic inflection, coming from traces of goethite (SC 5, 6, 8, 9, 10, and 11). This inflection is found in estuarine muds as well as in periglacial deposits from the same estuary. Above 480° C., all the curves have a large endothermic inflection, which results from a mixing of kaolinite and illite, as shown by the reference curves at the bottom of Figure 7. The small inflections between 700° C. and 1,000° C. are imputed to be small quantities of chlorite or even smaller quantities of calcite which were not completely destroyed. The result is that the composition of the periglacial deposits is the same as

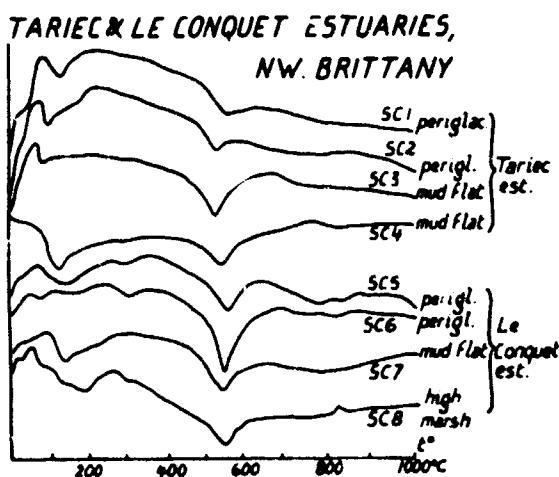


Fig. 6. Thermal differential analyses of samples from Tariec and Le Conquet, northwestern Brittany. (After Guilcher and Berthois, 1957.)

the composition of the mud flats and the high marshes. X-ray analyses lead to the same conclusions for sediments from the Rance Estuary. The calcium carbonate fraction, which comes from shells living *in situ*, is generally poor in Breton estuaries, except for the outer parts of those lying in northeastern Brittany, where a calcareous sediment is found, the so-called "tangue", which includes many fine broken shells of local origin.

The process of formation of estuarine muds from periglacial deposits in these small estuaries is easy

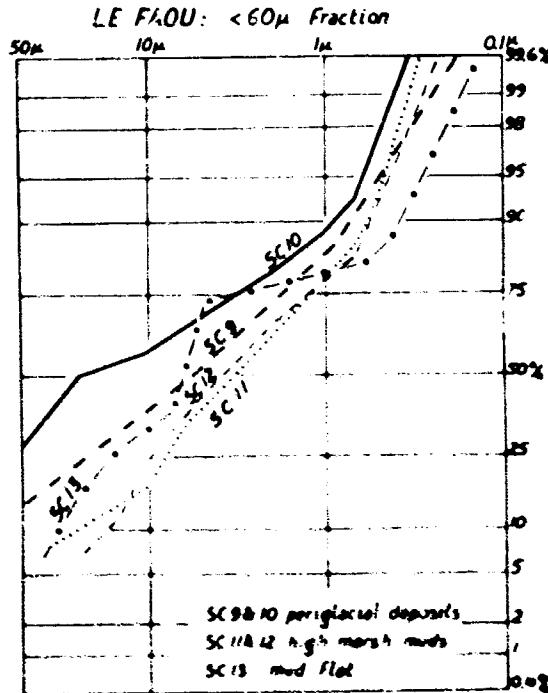


Fig. 5. Grain-size analyses of samples from Le Faou, western Brittany. (After Guilcher and Berthois, 1957.)

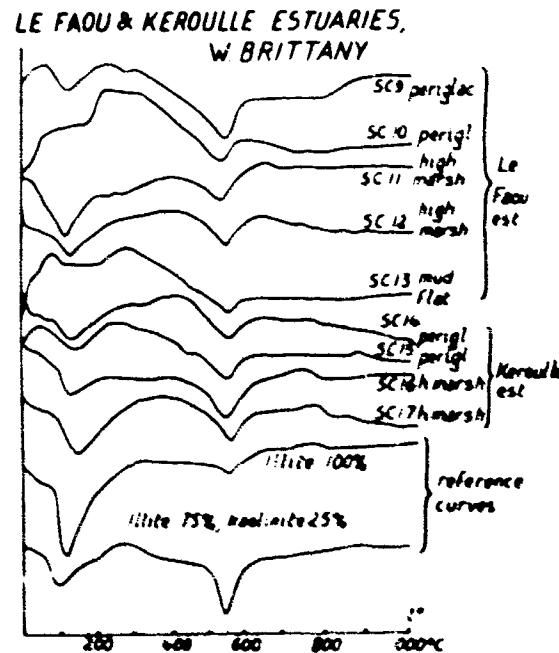


Fig. 7. Thermal differential analyses of samples from Le Faou and Keroualle, western Brittany. (After Guilcher and Berthois, 1957.)

DERRYMORE MARSH, CO. KERRY, IRELAND

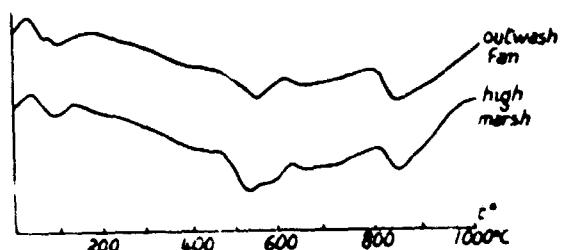


Fig. 8. Thermal differential analyses of samples from Derrymore, Co. Kerry, Ireland. (After Berthois in Guilcher and King, 1961.)

to observe in the field. The Pleistocene head is cliffed in the lower parts of the slopes, because, at high spring tides, the tidal marshes are under water and the fetches are large enough to allow the formation of waves of moderate or middle size when the wind is strong. The coarser fraction of the head settles at the foot of these cliffs where sand and stones form narrow, thin, discontinuous beaches, and the finer particles are brought into suspension in water and continue to feed the mud flats and marshes. In the Rance Estuary, calcareous concretions coming from the loam, the "poupees", are found in some places on the upper beach and sometimes on the mud flats. In the inner reaches of Rade de Brest, frost-shattered stones washed from the cliffs are strewn on the shore. The periglacial head, which was cut during the retreat of the cliffs, is often seen on the strand "under a thin cover of loose deposits.

OTHER SMALL ESTUARIES

In County Kerry, Ireland, investigations were made in a tidal marsh lying behind Derrymore Spit, at the mouth of Tralee Estuary (Guilcher and King, 1961). Thermal differential analyses made by Berthois on samples from the Derrymore high marsh, and from an alluvial outwash fan which ends close to the marsh, show exactly the same composition (Fig. 8); dominant illite and chlorite, doubtful traces of chrysotile, and rare vermiculite. This evidence is supported by the examination of the samples. The outwash fan consists of reworked Old Red Sandstone (Devonian), and, in the estuarine mud, many Old Red Sandstone particles appear under the microscope at all sizes as far down as 60μ . The remaining fraction consists of quartz. Moreover, the mud has a characteristic pink color, as does the Old Red Sandstone.

In the marshlands of Newport Bay, California, the mud is fed by surrounding cliffs, according to Stevenson and Emery (1958), who wrote: "Great blocks of loosely consolidated shales and siltstones, which are readily eroded, frequently slump down during heavy rains and are worn away by the waters or rest upon the marsh borders for extended periods . . . During infrequent rainy periods, much material may be added to the water . . . tidal currents carry most of the

material to the sea . . . little eroded material is added to the surface of the marshes . . . most of it is deposited along sheltered edges of the marshes, in small embayments, and in the shallows."

It thus appears that marshes and mud flats are commonly fed by fine material coming from cliffs along small estuaries, where the supply of suspended material from upstream is insignificant because the river is small.

SEDIMENTS COMING FROM THE MOUTHS OF THE ESTUARIES

An example of this is given by the estuary of the small Kapatchez River, in the northwest of the Republic of Guinea, West Africa (Guilcher, 1956a). Between 1930 and 1954 the Kapatchez Estuary was quickly filled up by a tremendously muddy sedimentation at a time when other estuaries in the same region were approximately in a state of equilibrium. A study was undertaken in order to determine the origin of this sudden deposition, which rendered the rice cultivation in the lowlands almost impossible because it completely modified the circulation of fresh and salt water in the creeks. The filling up of the Kapatchez Estuary could not be explained by material carried from upstream by the river, because the catchment area is extremely small and the sedimentary load almost nil above the tidal area. Sediments coming from upstream are more abundant in the larger rivers of this region; however, the Company, Nunez, Pongo, and Konkoure Rivers do not show any important deposition on mud flats. In fact, the mass of mud which settled in the Kapatchez came from old mud flats in front of the open sea immediately west of the mouth of the estuary. These mud flats were retreating rapidly in 1954, perhaps as a consequence of recent changes in tidal currents, so that mud was put in suspension, went into the estuary with the incoming tide, and settled there at slack tide.

Thus, in this case, the mud comes from the outer coast and is carried upstream. However, it may be noticed that this mud was first deposited on the outer coast after the postglacial transgression. It is possible or even probable that it came originally from the larger rivers of this area, such as the Nunez or the Konkoure. If this is true, the transportation of mud into the small Kapatchez River would be only the last stage in a longer history.

SEDIMENTS COMING FROM UPSTREAM BY RIVERS

Everybody thinks that sediments forming deltas come exclusively or mostly from inland by the river. Thus, in the Rhône Delta in southern France, heavy-mineral analyses have shown that "at least four-fifths of the sediments have been derived from the Alps; a comparatively small contribution is made by the Massif Central" (Van Andel, 1955). This fits well with the water discharge from either area of the river catchment. However, Dubouloz-Razavet (1936) found that a minor fraction comes to the Rhône from the west

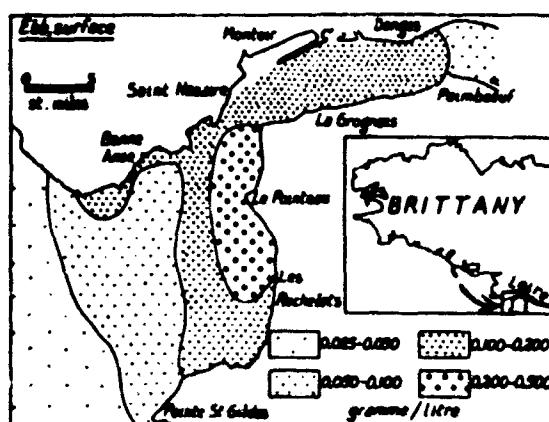


Fig. 9. Loire Estuary. Suspended-matter content during floods, Jan.-Feb., 1955. Ebb, surface. (After Berthois, 1956a.)

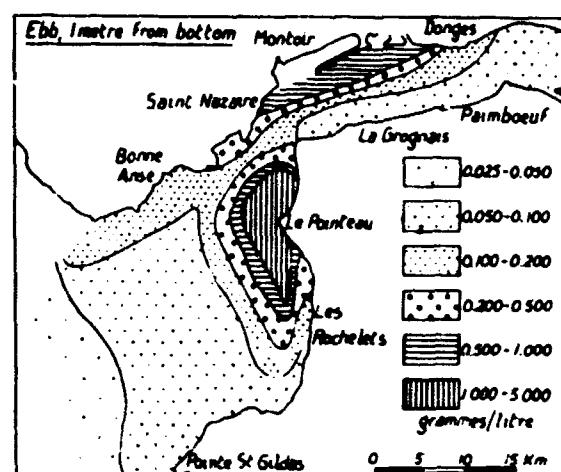


Fig. 11. Loire Estuary, ebb; 1 meter from bottom.

by alongshore drift, although this contribution is exceedingly small. Similarly, the Orinoco River, in Venezuela, has formed a delta at its mouth and furnishes sediments to the adjoining Gulf of Paria (Van Andel and Postma, 1954).

The most intensive research which points to a fluvial origin of sediments in estuaries, deltas excluded, has been carried on for more than ten years in the Loire Estuary, southern Brittany, by Berthois, with much help from the civil engineering services of Nantes Harbor. A wealth of simultaneous observations were made of currents, temperature, salinity, and suspended-matter content at many stations in the inner, middle, and outer estuary at different depths. These observations were made during various conditions, such as river floods and low stages, spring tides and neap tides, summer and winter.

Berthois (1956b) found that, in a wide range of situations, the suspended-matter content in the Loire Estuary is almost always higher at all depths during the ebb than during the flood; his findings indicate

that the origin of sediments is fluvial rather than marine. However, a situation which deserves attention was noticed during river floods in January and February, 1955, when the water discharge was as high as 4,770 m³ sec (Berthois, 1956a).

At the surface, the suspended-matter content was distinctly higher during the ebb than during the incoming tide (Figs. 9 and 10); but at 1 m above the bottom the content was higher during the flood than during the ebb between Dangis, Saint Nazaire, and Le Pointeau (Figs. 11 and 12). Berthois explains that the river floods had suppressed the tidal currents upstream of Dangis, so that an incoming current related to the flood tide existed only downstream beyond this point, while upstream the water ran continuously to the sea. During the flood tide, the sea water entering the estuary in the Saint Nazaire-Le Pointeau area slackened and stopped the freshwater flow from upstream for some time, so that the suspended-sediment content increased near the bottom in

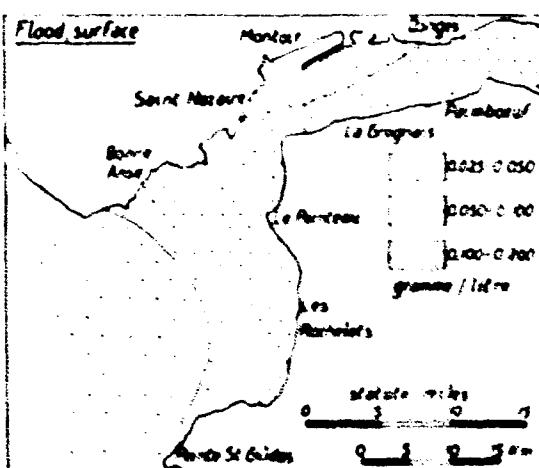


Fig. 10. Loire Estuary, flood, surface.

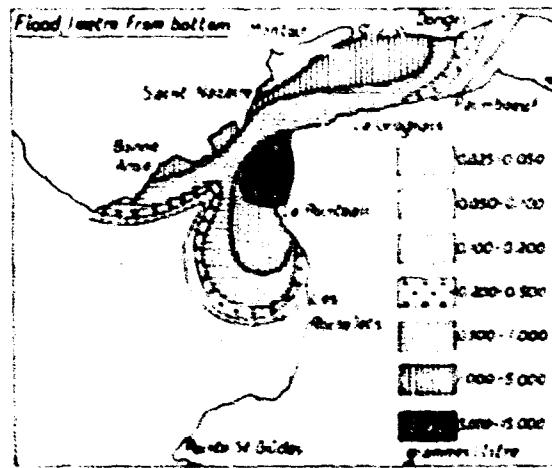


Fig. 12. Loire Estuary, flood, 1 meter from bottom.

the motionless water. In other words, the high turbidity near the bottom at Le Pointeau during flood tide does not prove that sediments have a marine origin.

The supply from upstream was carefully studied in the Loire Estuary for several years. The measurements of turbidity are much easier than the determinations of the bed load in transport on the bottom, and it was found that in 1955 the river carried 1,100,000 tons of sediments in suspension (Berthois, 1956a). For all sediments, the solid discharge was 825,000 tons in 1957, 1,548,000 tons in 1958, and 642,000 tons in 1959 (Berthois and Morize, 1960). The solid discharge is highly variable, according to the stage of the river and the importance of floods in each particular year. In 1955, 86 percent was transported from upstream during the floods from January to April. Moreover, during the floods the river is able to carry not only silt and clay in suspension but sand as well, and the sand settles between Donges and Saint Nazaire (Berthois, 1955c). But all the finer particles do not settle in the estuary alone. A part of them can be transported out of the estuary in two kinds of situations: (1) during spring tides, at the end of the ebb—this occurred in September, 1953, during a very large spring tide (Berthois, 1955a) and again during the river floods in January and February, 1955 (Berthois, 1956a); (2) the second possibility is shown in Figures 9 and 11 (suspended-matter content still noticeable between Bonne Anse and Pointe Saint Gildas). Thus, the Loire River can intermittently feed the tidal flats along the outer coast, especially those lying to the south of Pointe Saint Gildas in Baie de Bourgneuf. The sedimentation is more active in summer than winter, because viscosity is lower in warm water (Berthois, 1955b) and turbidity decreases gradually. When the winter floods arrive, they again supply large quantities of material which will be carried to and fro in the estuary before they settle to the bottom, because the water is cold.

Also in the Vigo River, Galicia, Spain, data from Nonn (1966) seem to point to a largely continental origin of sediments. This estuary consists of an outer part which is open to the Atlantic Ocean, and an inner part, the Ensenada de San Simon, about 10 km long, connected with the former by a strait less than 1 km wide. The crystalline and metamorphic rocks surrounding Ensenada de San Simon are weathered into two kinds of alterites: fine clays of kaoline nature, which are Tertiary in age; and a more recent weathering product including illite and a mixture of vermiculite-chlorite. In the Ensenada de San Simon there are extensive mud flats in which the clay fraction, analyzed in six samples by the X-ray method, was found to have the following composition: 10-20 percent kaolinite, 70-80 percent illite, and 10-15 percent vermiculite-clayite. This shows that the estuarine muds come from the washing of the continental weathering products. Moreover, the calcium carbonate content is very low, 1.6 percent on the average

(from 0.8 to 7.4 percent). In other words, the contribution of marine shells to the sedimentation is extremely low. Another evidence is that the sand fraction in the mud is angular, and, according to Sainz Amor (unpublished), includes the same heavy mineral assemblage as the surrounding formulations on dry land.

Yet, in the outer part of the Vigo River, the skeletal content is higher (Margalef and del Riego, unpublished) with many remains of foraminifers, echinoderms, sponges, etc. Since the clay fraction of the muds in this part of the river has not been analyzed, however, one may wonder whether these marine elements do not represent merely a further stage in the evolution of the mud, including more and more calcium carbonate as it proceeds from the land to the sea.

Large quantities of kaolinitic clay have also been found in the Pontevedra River, another Galician estuary near Vigo, where the mud was fed in the same way.

The problem of the origin of sediments has been discussed for Chesapeake Bay, eastern United States. A marine origin could have been expected here, since the net transport along the bottom of the bay goes upstream, whereas it is directed to the sea in the surface layer (Pritchard, 1952). However, Burt (1955) assumes that the suspended particles come mostly from the rivers ending in the bay. The suspended-matter content was measured near the surface and at depth with a spectrophotometer, which showed that the maximum turbidity occurs in spring and the minimum in fall. The turbidity depends on the suspended minerals, the production of organic matter, and the tidal currents and storms which can return sediments previously deposited on the bottom into suspension. An annual cycle in turbidity cannot be caused by tidal currents, because wind is rather strong in all seasons except the fall and the production of organic matter is large in spring and summer. Finally, the minimum turbidity in the fall is related to the fading of all causes of turbidity except tide; the maximum in spring is chiefly due to the distributaries, since the peak in river discharge occurs at that time. It may be supposed that the bottom current carries along particles of continental fluvial origin, which first traveled downstream in the surface current.

In the northeastern Gulf of Mexico, the Apalachicola and Mobile Rivers supply clay to the continental platform and not the reverse (Griffin, 1962). Their behavior is similar to that of the Mississippi River, which has a delta, and transports mostly montmorillonitic sediments to the sea, since montmorillonite is prevalent in its basin. The Apalachicola River carries essentially a kaolinitic suite, and the Mobile River a suite intermediate between the two other ones. Consequently, the sediments passing through their estuaries include the same mineral suites as those prevailing inland.

In tropical regions, a continental origin seems certain in a number of cases. In Madagascar, the Betsiboka River (LaFond, 1957) carries to the sea a huge

mass of red lateritic clays, supplied by the erosion in the catchment area of the river as a consequence of deforestation. The origin of the red sediments in suspension in the estuary (even during the dry season) has been established, so a marine source is quite impossible. These sediments have completely filled up the dock area which was dredged at Majunga immediately before World War II. Successive surveys of the estuary and its opening on Mozambique Channel have shown that they have become shallower and shallower since the first soundings in the 19th century. The Loza River, on the northwestern coast of Madagascar, also carries fine mud to the sea, and the deposit is visible in front of the estuary on coral reefs. The corals must take the shape of micro-atolls to struggle against the sedimentation (Guilcher, 1956b). Since soil erosion is severe on this large island, many other examples will probably be found as research goes on.

The same is true along the coast of the Bight of Benin. It is instructive to fly over this coast in October, during the second rainy season of the year, and see the turbid waters flowing from the rivers into the coastal lagoons and spreading as "clouds" into the sea through the outlets. The sandy fraction of the sediments is transported from west to east by the longshore drift, and it may be said that the sea plays a large part in its deposition on the outer coast and even in the lagoons, but it initially comes as a fine fraction from inland, and is derived from the late Tertiary deposits outcropping on the coastal plateau (Guilcher, 1959).

CONCLUSIONS

One possible cause of estuarine differences may be the quantitative contrasts in discharge of solid materials by rivers. It is evident that a river carrying a great amount of suspended particles is better able to fill its estuary with fluvial sediments than a river with a small sedimentary load. The differences in opinions about the Loire River on one hand, and the Seine and Ems Rivers on the other, are perhaps caused by this. When fine material is available on the slopes of the estuaries, as in Brittany, this source can take the place of sediments coming from upstream when the river discharge is insignificant.

But the water motion within the estuary must also be taken into account. We have said in this paper that the penetration of marine sediments into estuaries can be due to the wedge of salt water flowing upstream along the bottom, as in the Rhine; in Chesapeake Bay the salt wedge probably acts in the same way to carry sediments inward which were first carried down by rivers. Another hydrological structure in estuaries also deserves attention. Berthois (1958, 1960a, 1960b) found that in a number of estuaries (for example, the Loire, small Breton rivers, several French Guiana rivers, and the Konkoure River in Guinea) a motionless lens of water persists near the bottom during a large part of the tidal period. The position and duration of this motionless water body

varies with estuaries, and in the same estuary, with the river discharge and tidal range. The lens acts as a weir in which the coarse particles flowing along the bottom are trapped, whereas the finer elements flowing in suspension in the upper water layer pass over it. If the lens is located out of the mouth of the river, a delta can be built; but if it is located far upstream, the fluvial sediments settle before they reach the middle and lower parts of the estuary. It would be interesting to determine if such an estuarine structure exists which has not been studied by Berthois—one in which, however, sedimentation data are already available. Simultaneous measurements on currents in different parts of the same estuary unfortunately require much material, several boats, and many research workers. But it is frequently possible to receive help from civil engineering services since knowledge of the origin of sediments may be important in dredging harbor accesses.

LITERATURE CITED

- BAAK, J. A., 1936. *Regional petrology of the southern North Sea*. Thesis. Leiden, Wageningen, Netherlands.
- BERTHOIS, L., 1955a. La sédimentation en Loire en grande marée de vive eau. *Compt. Rend. Acad. Sci.*, 240:106-108.
- BERTHOIS, L., 1955b. Sédimentation dans l'estuaire de la Loire en période hivernale. *Compt. Rend. Acad. Sci.*, 240:1691-1693.
- BERTHOIS, L., 1955c. Evaluation du tonnage des sables apportés en suspension pendant les crues de la Loire en 1955. *Compt. Rend. Acad. Sci.*, 241:1605-1607.
- BERTHOIS, L., 1956a. Comportement du "bouchon vaseaux" dans l'estuaire de la Loire. *Soc. Hydrochim. Fr., 4es J. de l'Hydraulique*; pp. 564-568. La Houille Blanche, Grenoble, France.
- BERTHOIS, L., 1956b. Turbidité des eaux à l'entrée de l'estuaire de la Loire. *Compt. Rend. Acad. Sci.*, 243: 2113-2115.
- BERTHOIS, L., 1958. La formation des estuaires et des deltas. *Compt. Rend. Acad. Sci.*, 247:947-950.
- BERTHOIS, L., 1960a. La répartition des sédiments actuels sur les plates-formes continentales. *Compt. Rend. Acad. Sci.*, 250:2239-2240.
- BERTHOIS, L., 1960b. Etude dynamique de la sédimentation dans la Loire. *Cah. Océanogr.*, 12:631-657.
- BERTHOIS, L., and C. BERTHOIS, 1954, 1955. Etude de la sédimentation dans l'estuaire de la Rance. *Bull. Lab. Dinard*, 40:15 and 41:18.
- BERTHOIS, L., and J. MORIZE, 1960. Première évaluation du débit solide total de la Loire. *Compt. Rend. Acad. Sci.*, 251:1543-1545.
- BURT, W. V., 1955. Interpretation of spectrophotometer readings on Chesapeake Bay waters—Distribution of suspended materials in Chesapeake Bay. *J. Marine Res.*, 14:33-62.
- CROMMELIN, R. D., 1940. De herkomst van het zand van de Waddenzee. *Tijdschr. Kon. Ned. Aardr. Gen.*, (2)57:347-361.
- CROMMELIN, R. D., 1949. Quelques aspects granulométriques et minéralogiques de la sédimentation le long de l'estuaire de l'Escaut. *Sédimentation et Quaternaire, La Rochelle*; pp. 63-71. Led Sam, Bordeaux.
- DUBOUL-RAZAVET, C., 1956. Contribution à l'étude géologique et sédimentologique de delta du Rhône. *These Paris, Me. Soc. Geol. France*, 76:234.
- FAVEJEE, J. C. L., 1951. The origin of the Wadden Mud. *Med. Landbouwhogeschool Wageningen*, 51(5): 113-141.

- GRIFFIN, G. M., 1962. Regional clay-mineral facies: products of weathering intensity and current distribution in the northeastern Gulf of Mexico. *Geol. Soc. Am. Bull.*, 73:737-768.
- GUILCHER, A., 1956a. L'envasement du Rio Kapatchez (Guinée française) et ses causes. XVIIIe Congr. Inter. Géog., Rio de Janeiro; Vol. 2, Sect. 2:241-247.
- GUILCHER, A., 1956b. Etude géomorphologique des récifs coralliens du Nord-Ouest de Madagascar. *Ann. Inst. Océanogr.*, 33(2):65-36.
- GUILCHER, A., 1959. Coastal sand ridges and marshes and their continental environment near Grand Popo and Ouidah, Dahomey. In *Second Coastal Geog. Conf.*, edited by R. J. Russell; pp. 189-212. Louisiana State Univ.
- GUILCHER, A., and L. BERTHOIS, 1957. Cinq années d'observations sédimentologiques dans quatre estuaires témoins de l'Ouest de la Bretagne. *Rev. Géomorph. Dyn.*, 8:67-86.
- GUILCHER, A., and A. CAILLEAUX, 1950. Reliefs et formations quaternaires du centre-est des Pays-Bas. *Rev. Géomorph. Dyn.*, 1:128-143.
- GUILCHER, A., and C. A. M. KING, 1961. Spits, tonnholes and tidal marshes in Connemara and West Kerry, Ireland. *Proc. Roy. Irish Acad.*, 61(B):283-338.
- LA FOND, E. C., 1957. Aperçu sur la sédimentologie de l'estuaire de la Betsiboka (Madagascar). *Rev. Inst. Français Pétrole*, 12:425-431.
- NONN, H., 1966. *Les régions côtières de la Galice (Espagne), étude géomorphologique*; p. 304. Thesis, Univ. of Paris.
- PRITCHARD, D. W., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11:106-123.
- RAJCEVIC, B. M., 1957. Etude des conditions de sédimentation dans l'estuaire de la Seine. *Ann. Inst. Tech. Bâtiment et Trav. Publ.*, 10(117):743-775.
- STEVENSON, R. E., and K. O. EMERY, 1958. *Marshlands at Newport Bay, California*. Allan Hancock Publ., 20:110. Univ. of Southern Calif. Press, Los Angeles.
- VAN ANDEL, T. J. H., 1955. Sediments of the Rhône Delta. II. Sources and deposition of heavy minerals. *Verhandel. Koninkl. Ned. Geol. Mijnbouwk. Genoot. Geol. Ser.*, 15(3):515-543.
- VAN ANDEL, T. J. H., and H. POSTMA, 1954. Recent sediments of the Gulf of Paria. *Verhandel. Koninkl. Ned. Akad. Wetenschap., 1e Reeks*, 20(5):1-245.
- VAN STRAATEN, L. M. J. U., 1960. Transport and composition of sediments. In: *Symposium Ems-Estuarius, Nordsee*. *Verhandel. Koninkl. Ned. Geol. Mijnbouwk. Genoot. Geol. Ser.*, 19:279-292.
- VAN STRAATEN, L. M. J. U., 1961. Sedimentation in tidal flat areas. *J. Alberta Soc. Petrol. Geol.*, 9:203-236.
- VAN STRAATEN, L. M. J. U., 1963. Aspects of the Holocene sedimentation in the Netherlands. *Verhandel. Koninkl. Ned. Geol. Mijnbouwk. Genoot.*, 21(1):149-172.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1957. Accumulation of fine grained sediments in the Dutch Wadden Sea. *Geol. en Mijnbouw, new ser.*, 19: 329-354.
- VAN VEEN, J., 1936. *Onderzoeken in de Hoofden*. Den Haag, Netherlands.
- VIGARIE, A., 1965. Les modalités du remblaiement alluvial dans l'estuaire de la Seine. *Cah. Oceanogr.*, 17: 301-330.
- ZONNEVELD, I. S., 1960. *De Brabantse Biesbosch. Een Studie van bodem en vegetatie van een soetwatergetijdendelta*. Mededel. Sticht. Bodemkartering, Bodemk. Studies, 4, A. Engl. Summ. and B. Nederlandse Tekst.

Sediment Transport and Sedimentation in the Estuarine Environment

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The processes involved in the movement of water and its relationship to sedimentary patterns have interested geologists, geographers, biologists, and coastal engineers for a long time. Tides, freshwater outflow, and waves cause complicated water movement which transport, fractionate, and modify the properties of particulate matter in shore regions. An attractive field of study lies in estuaries, tidal deltas, tidal flats, coastal lagoons, and shallow coastal areas. These areas differ geomorphologically, but have the common feature that suspended matter is carried back and forth, deposited, and eroded many times before it finally settles, either permanently or for a long period. Although the problem of the source of the sediments is often very complex, the processes of sorting and grain-size selection usually establish an equilibrium between the bottom, the suspended sediment, and the water.

The existence of essentially closed circulation systems for suspended matter is due to the character of water movements in estuaries and in tidal areas, and these features tend to cause entrapment of particles. Water passes freely through these areas, but particulate matter is caught or its escape to open water is retarded. One example is the movement of suspended sand in front of beaches under the influence of wave and surf action. This process, however, is restricted to a rather narrow strip of water. Two other mechanisms cover greater areas. One is the entrapment of suspended matter in river mouths and the consequent formation of areas of great turbidity (turbidity maxima), and the other is the accumulation of fine-grained matter by tidal action. These two processes will be discussed in detail.

During transport and after deposition, sediments may undergo many changes as a result of chemical and biological processes, salinity variations, the presence or absence of vegetation, burrowing animals, etc. Most of these subjects will only be touched upon; however, the process of flocculation and deflocculation under the influence of changes in salinity will be treated in more detail, because it is a primary characteristic of the meeting place of fresh and salt water and because it exerts a great influence on the settling velocity of suspended particles.

In many cases the distribution of sediments over a certain area is more closely related to its geological history than to present movements of water. The discussion of this distribution will be restricted to examples where a relation between forces of transportation and sedimentary patterns seems evident.

EROSION, TRANSPORTATION, AND DEPOSITION

CRITICAL CURRENT VELOCITIES

The dynamics of sediment transport in moving water have been studied in much more detail in rivers than in tidal areas. In spite of the special characteristics of tidal flow and density differences, the results obtained in rivers may be used in coastal areas.

Relations between erosion, transportation, and deposition velocities and the grain size of sediments have been developed by Hjulstrom and reexamined by Sundborg (1956). The "critical erosion velocity" is the minimum current velocity at which sediment of a particular size begins to move. The movement stops at a flow velocity called the "lowest transportation velocity" or the "deposition velocity". Figure 1 shows curves of critical velocities for different particle sizes. Critical values depend on current velocity only indirectly; the important factors are the tractive forces acting on the bottom, the roughness of the bottom, turbulence, etc. However, since this paper does not aim at exact hydrodynamic calculations, it is sufficient to use flow velocity. An example of velocities at 15 cm above bottom is shown in Figure 1. From a size of 0.2 or 0.3 mm upward, the critical erosion velocity increases with increasing grain size. The deposition velocity is slightly smaller, and is usually about two-thirds of the erosion velocity. The difference in the

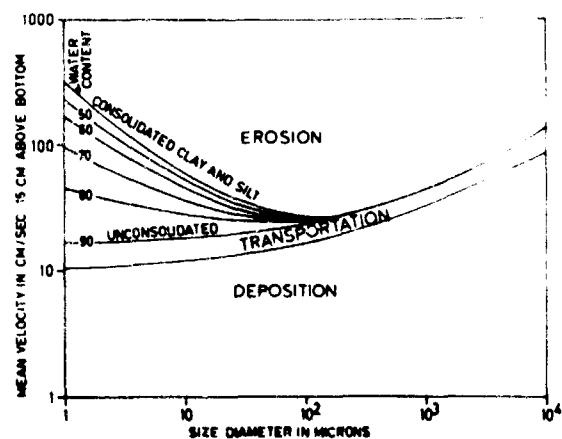


Fig. 1. Erosion, transportation, and deposition velocities for different grain sizes. The diagram indicates possible values for various stages of consolidation. (Data from various authors in Sundborg (1956) and observations of the author.)

velocity between erosion and deposition is of great importance for the behavior of suspended matter in tidal streams. The material above 0.3 mm is supposed to be quartz sand with a specific weight of 2.65. For grains with a lower density the curves move downward; if the density is higher the curves are located above those shown in the graph.

For diameters smaller than 0.2 mm and especially below about 0.05 mm, one set of curves is insufficient to describe the relationships, as the cohesiveness and duration of consolidation are important (left portion of Fig. 1). No great numerical value should be attached to this part of the graph because the course of the lines will depend on the type of fine-grained matter under consideration. It is clear, however, that the difference between erosion and transportation velocities is much larger for consolidated than for unconsolidated clays or for sands.

COHESIVENESS AND CONSOLIDATION

Recently deposited, very loose, and unconsolidated fine-grained matter may easily be carried away by quite a small change in current velocity. When the material has been deposited for a longer time, it gradually loses water and becomes increasingly difficult to erode.

The process of consolidation is essentially the result of the expulsion of water from the interstices between soil grains under load. The water escapes through microscopic channels interconnecting the interstices. During the process the soil particles are displaced relative to one another and form a more closely packed sediment of greater density and lower water content. In sands and most clays these movements are irreversible. Consolidation proceeds very rapidly in sand, but very slowly in silts and clays; the rate depends on the type of clay mineral and the degree of flocculation.

In the course of time the water content decreases as the critical erosion velocity increases (Fig. 2, right). To measure this increase a ring-shaped perspex tank (Fig. 2, left) was used; it had an outer diameter of 74 cm, an inner diameter of 44 cm, and a height of 33 cm (Creutzberg, 1961; Demerara Coastal Investigation, 1962). The water in the tank was set in circular motion by means of four paddles fixed to a central axis. A special gear enabled a continuous increase of the current velocity from zero to about 100 cm/sec, measured along the outer circumference of the ring. The lower end of the paddles was about 15 cm above the surface of a mud layer, a few centimeters deep, that had settled from the suspension. The velocity at

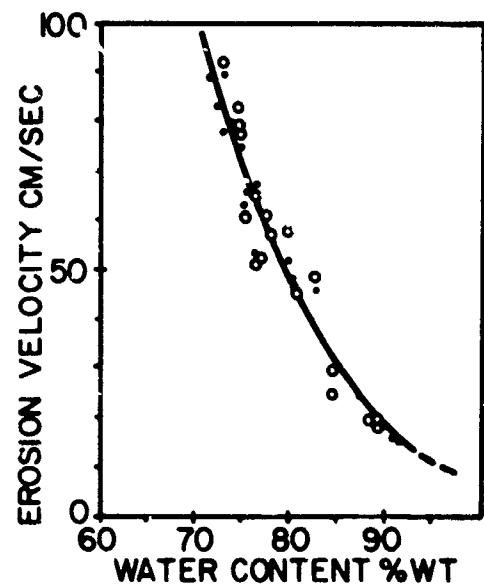
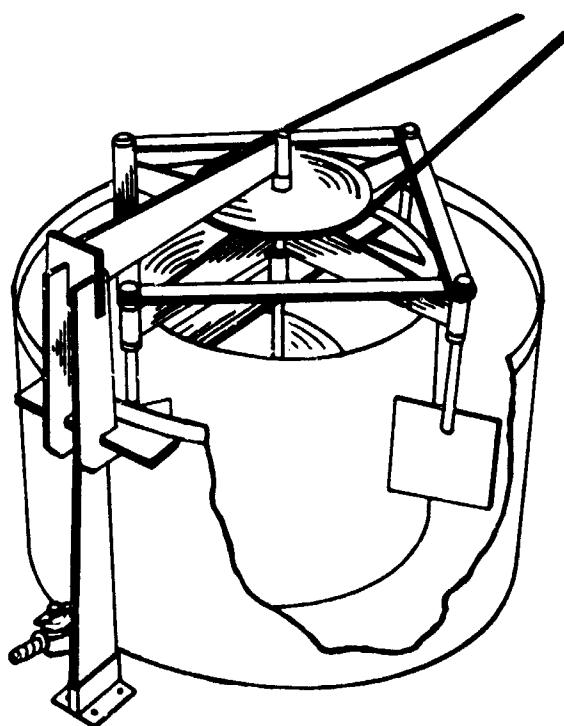


Fig. 2. Left: Circular tank ("carousel") used for the determination of critical velocities. Results of an experiment in this tank are shown at right (Demerara Coastal Investigation, 1962; Creutzberg, 1961).

Right: Erosion velocity and water content (in weight percentages) of a Demerara clay. Mineral composition: 25% quartz, 15% chlorite, 5% feldspar, 25% exp. illite, 15% kaolinite (Demerara Coastal Investigation, 1962). Circles: measurements in salt water (17‰ Cl). Points: measurements in fresh water (0.2‰ Cl). A water content of 91% corresponds with a consolidation time of 3 hours; 73% with about one month. The values presented were obtained in laboratory experiments.

which the material was set in motion was measured after different periods of consolidation. Except when the consolidation times were short, this velocity could be determined very sharply. The movement started at a few discrete spots of the mud surface, first by forming a shallow scour, and, after some time, a deeper scour. This scour was gradually widened and deepened by strong local turbulence, but eventually, by keeping the current velocity constant, all the material was swept away.

The increase of erosion velocity with decreasing water content must be caused by the increase of cohesive forces generated by the bonds of thin layers of oriented water molecules around the particles, and by electrostatic attraction. As these forces are largely dependent on the physical and mineralogical properties of the clays, the values shown in Figure 2 are valid for only one specific clay assemblage.

It should be noted that the critical erosion velocities found in the experiments are not necessarily equal to those found in nature because of a different velocity-turbulence relationship. Moreover, settling and consolidation takes place in completely motionless water; at sea, currents and wave action influence the speed of consolidation and prevent the formation of a level surface.

The highest erosion velocity measured was about 90 cm/sec at a water content of 73 percent. For the sediments used in the experiment, the lowest water contents observed in the field were about 40 percent. The erosion velocity for this material may considerably exceed 100 cm/sec and may be approximately the same as that for pebbles.

Experiments were also conducted to determine the lowest transportation velocities for fine-grained matter. The values obtained for the clay (Fig. 2) appeared to be about 10 cm/sec, but they were measured in rather dense suspensions (10 g/l and more). Values in nature may be lower than those found in the experiments.

In tidal areas, where the same matter is picked up after every slack tide, the material has little time to consolidate. The curve for unconsolidated matter will apply to this deposit, and the ratio between erosion and transportation velocity will not vary much with grain size. In areas where part of the material is mobilized between longer time intervals, the ratio may increase considerably with decreasing particle size.

FLOCCULATION AND DEFLOCCULATION

PHYSICO-CHEMICAL PROCESSES

Elementary particles of colloidal or semi-colloidal dimensions may contain an electric charge which influences their behavior in suspension; of these particles, clay minerals are of primary importance. It has been found that they usually have a negative charge, which may be explained by: (1) preferential adsorption of anions, especially hydroxyl ions; (2) cationic substitutions within the crystal lattice; and (3) resid-

ual valences (broken bonds) at particle edges. The negative charge is balanced by a double layer of hydrated cations which tend to move away from the surface of the clay mineral, although electrostatic attraction prevents a complete escape. There is a correlation between the stability of the suspension and the electrolytic potential. The thickness of the double layer depends on the valence of the sorbed ions, the total ion concentration in the surrounding water, temperature, and pH.

If the electrolytic potential (the thickness of the double layer) decreases below a critical value, coagulation occurs. That is, the elementary particles conglomerate to larger units and tend to settle (Berthois, 1961; Committee on Tidal Hydraulics, 1960; Whitehouse and Jeffrey, 1955). In this process, while the double layer is present two clay particles approaching each other by Brownian movement are repelled, because their charges are equal. Other forces, however, tend to cause the particles to approach each other. In water with a small electrolytic content a thick double layer may be formed and the suspensions are stable. If more electrolyte is added, the thickness and electrolytic potential of the double layer decreases, and the possibility for two particles to unite increases. Cations in the solution, moreover, are exchanged for cations in the double layer. If ions with a higher valence than one are present, the same amount of cations has a greater effect. As a result, clay minerals flocculate in sea water, especially under the influence of magnesium and calcium ions.

Flocculation in very pure river water has never been observed with certainty, but it has been noted that sediments deposited in some water reservoirs containing very pure water are partly flocculated (Committee on Tidal Hydraulics, 1960). Most rivers carry mainly unflocculated matter to the sea. However, the increase of pollution in many rivers causes the process of flocculation to be completed far upstream of the salt boundaries, perhaps because of the presence of polyvalent cations in industrial wastes and excessive amounts of particulate organic sewage which acts as a binding substance for fine-grained particles. Dissolved organic matter such as humic substances may prevent flocculation to a certain degree; this is especially evident in kaolinitic clays.

The electrolytic coagulation process is, in most instances, reversible, and marine flocs carried upstream into fresh water may be deflocculated (Demerara Coastal Investigation, 1962).

The diameter of a flocule may be very much larger than the "diameter" of its individual components. As a result, clays settle more rapidly in flocculated than in peptized form. It should be noted, however, that much water is included in the flocs so that the increase in settling velocity may be rather small. For example, a unit particle with a diameter of 5 μ and a specific weight of 2.7 has a settling velocity in sea water of 0.002 cm/sec. A particle of 500 μ and the same density sinks at about 20 cm/sec, but a flocule of clay particles of the same size, containing 95 per-

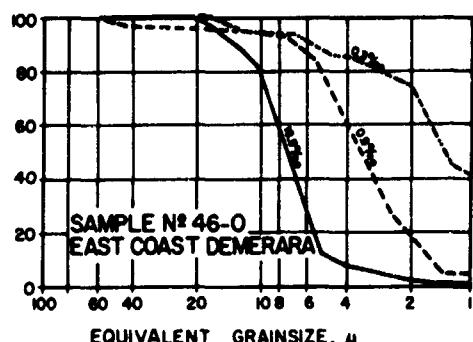
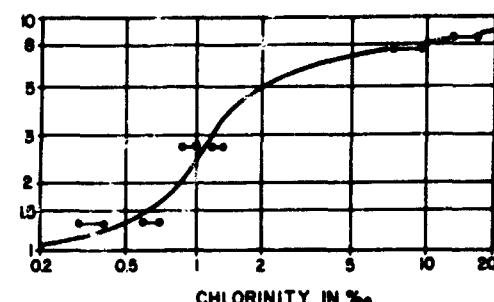


Fig. 3. Left: equivalent particle-size distributions measured at different chlorinities by the pipette method; scale at left indicates the weight percents of silt, finer than indicated size. Right: relation between median equivalent particle size and chlorinity; scale at left indicates median equivalent particle size μ ; silt concentrations: 1,000 mg/l (Demerara Coastal Investigation, 1962).



cent water, settles with a velocity of only 0.4 cm/sec, or as slowly as a quartz sphere of about 20 μ .

It is customary to characterize flocs by their "apparent" or "equivalent" grain sizes; that is, it is assumed that all particles are spherical and have the specific weight of quartz. Figure 3 presents the equivalent sizes of suspensions at different chlorinities (Demerara Coastal Investigation, 1962). The median equivalent diameter in the flocculated form is about 7 μ , as compared to 1.5 μ in the deflocculated state. The true median diameter of the flocs, however, may be many hundreds of microns.

DIFFERENTIAL FLOCCULATION

Experiments and observations on differential flocculation are restricted to clay minerals (Welder, 1959; Whitehouse and Jeffrey, 1955; Whitehouse and McCarter, 1958; Whitehouse *et al.*, 1960). Because of structural differences, every type of clay mineral may flocculate in a different manner. The most common clay types are kaolinite, illite, and montmorillonite. Less common clay types are vermiculite and chlorite; the latter mineral is frequently found in marine sediments. It must be stressed that the minerals found in nature are often not well defined because of chemical variations, poor crystallinity, and random interstratification of clay sheets (Grim, 1953).

Illite particles are usually smaller than kaolinite, but are considerably larger than montmorillonite. This might in itself lead to differential settling, but the

physico-chemical differences are more important. Experiments have shown that flocculation of kaolinites and illites is mainly completed at very low chlorinity, whereas the flocculation of montmorillonite increases gradually with increasing chlorinity (Whitehouse *et al.*, 1960). This difference between the minerals is because of the very stable double layer of montmorillonite. Table 1 shows the relationship between chlorinity and settling velocity; Table 2 shows the relationship between chlorinity and light transmission. Both settling velocity and light transmission are influenced by the particle size.

In rapidly moving water the various clay minerals may be transported without differentiation, but at low current velocities illites and kaolinites may be deposited, whereas montmorillonites remain in suspension. The difference may be greater in fresh and

Table 1. Representative settling velocities (cm/min $\times 10^{-4}$) of clay mineral types in artificial sea water. Pipette method, 26° C., pH = 8.2 (Whitehouse *et al.*, 1960).

Clay mineral	Chlorinity, %					
	0.5	1.0	2.0	6.0	10.0	18.0
Illite	89.1	90.1	105.0	110.0	110.0	110.0
Kaolinite	80.1	80.5	81.1	81.2	81.2	81.2
Montmorillonite	0.23	0.36	0.78	4.06	7.55	8.77

Table 2. Light transmission of clay minerals as a function of chlorinity (wave length 400 m μ ; 26–27° C.; 0.2 g clay mineral); transmission values in %. (Whitehouse *et al.*, 1960).

Clay mineral	Chlorinity, %								
	0.2	0.4	0.8	1.0	2.0	4.0	8.0	12.0	18.0
Illite	11.0	13.4	29.8	38.8	43.3	45.0	45.0	45.0	45.0
Kaolinite	12.1	15.7	23.3	26.0	27.2	27.2	28.0	28.0	28.0
Montmorillonite	3.7	5.4	7.4	9.0	20.0	26.0	38.5	43.0	45.0
Chlorite	9.6	21.4	27.9	31.2	31.5	31.5	31.5	31.5	31.5

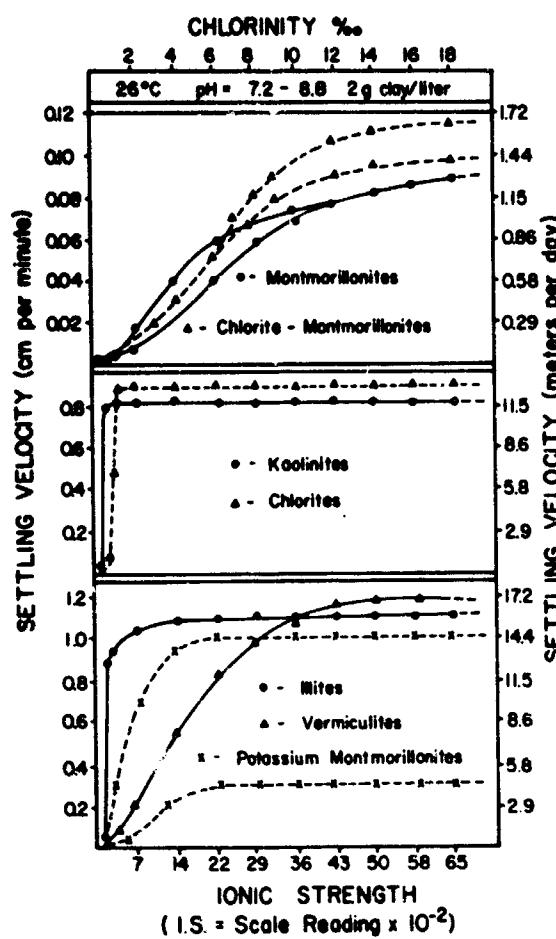


Fig. 4. Settling velocities of clay minerals in sea water at different chlorinities (Whitehouse *et al.*, 1960).

brackish water than in salt water. A summary of relative settling rates is given in Figure 4.

TRANSPORT OF SUSPENDED MATTER BY TIDAL CURRENTS

WATER MOVEMENTS IN TIDAL AREAS

In shallow water the vertical tide is accompanied by ebb and flood currents which often reach considerable strength. Maximum current velocities of 300 cm/sec and more have been registered in narrow tidal inlets. In its most simple form the horizontal tide has a sinusoidal, symmetrical shape, and the amount of water carried through a certain point over the ebb equals the amount carried over the flood. In very shallow water, slack water coincides with high and low tide; this is the case, for example, in small tidal gullies such as those occurring in tidal flats. In deeper water, the turn of the tide falls behind high and low tide; the time lag may vary from 20 minutes in water five meters deep, for example, to three hours in 30 meters.

The ideal situation of a symmetrical tide is not often realized. In coastal seas a residual component is often present which causes the amount of water car-

ried over the flood to exceed that of the ebb. In that case a water particle after one full tidal period has not returned to the same place. Also, the tides often rotate. The current ellipses mostly have their long axes parallel to the coastline, whereas the short axes are perpendicular to the coast (See Fig. 13).

The tidal regimes in tidal flat areas (including wadden areas) have characteristics which deserve special consideration. In the tidal inlets and larger channels the tidal currents may reach very high values. The strength of the currents decreases rapidly towards the tidal flats bordering these channels and near the coast. The decrease is less rapid along the axis of a channel. Even in small tidal gullies, high current velocities may be reached during part of the tidal phase. This peculiar condition is because tidal flats emerge around low tide when a relatively small part of the tidal area is covered with water (Van Straaten and Kuenen, 1958). The "wet cross section" of a gully is therefore considerably smaller around low tide than around high tide. As a result, the water leaving a tidal flat area at the end of the ebb has only a small cross section available to pass through; the same applies to the water entering in the first part of the flood. Therefore, in small tidal gullies maximum ebb current velocities occur shortly before low tide, and maximum flood currents shortly after low tide (Postma, 1961). Ebb and flood velocity curves thus may deviate considerably from a symmetrical shape (See Fig. 7).

The high current velocities occurring in tidal streams are accompanied by strong turbulence, and eddy diffusivity values up to 500 cm²/sec have been found (Gry, 1942). Thorough mixing of water layers obliterates vertical density differences. Within the system of estuarine classification the tidal areas belong to the well-mixed estuaries.

TIDAL VARIATIONS IN SUSPENDED MATTER

Tidal currents are usually sufficiently strong and turbulent to set in motion considerable amounts of suspended matter. The quantities and grain sizes of the material at a fixed point fluctuate with current velocity (Gry, 1942; Lüneburg, 1958; Postma, 1954). Examples are shown in Figures 5-7. The turbulent motion of the water may carry even coarse sand into the surface layers, especially when tides are at a maximum. During such periods certain parts of the sea surface may look patchy with "clouds" or "mushrooms" of suspended sand separated by less turbid areas. Changes in sediment concentration, as measured by point samples, are therefore sometimes irregular. Nevertheless, tidal variations in suspended matter concentration are seldom wholly obscured.

In a detailed study of the variations of suspended matter over a tidal period, it is advantageous to consider separately the behavior of "sand" and fine-grained suspended matter or "silt" (Postma, 1954). In shallow tidal waters the boundary between the two fractions may often be placed at about 50 μ , but the division is not so much a matter of principle as one of

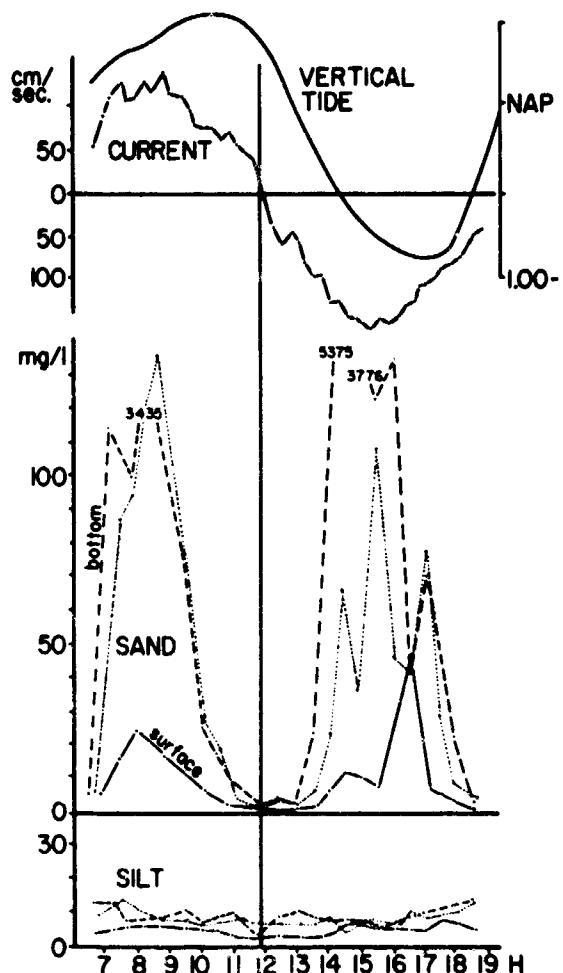


Fig. 5. Vertical and horizontal tide and suspended matter. Sand and silt are separated at about 50 μ . Texel area, Wadden Zee (Postma, 1954).

convenience. The argument for a division in two fractions is that the material called sand reacts differently on the tidal currents from silt (Fig. 5). Of course, silt, defined in this vague manner, may contain a significant amount of fine-grained sand besides clay minerals, particulate organic matter, etc. It must be observed, as pointed out earlier, that all grain sizes refer to "equivalent sizes" measured in a settling tube without pre-treatment of the material.

ACCUMULATION OF FINE-GRAINED SUSPENDED MATTER BY LAG EFFECTS

The fine-grained suspended matter reacts with a certain inertia to changes of current velocity. Usually there is a time lag between the turn of the tide, when current velocity is zero, and the moment at which the lowest figures for suspended silt are found. This lag can be explained by the fact that in a period of decreasing current velocity, some time is needed for the material to settle (Luttmann, 1950; Postma, 1954).

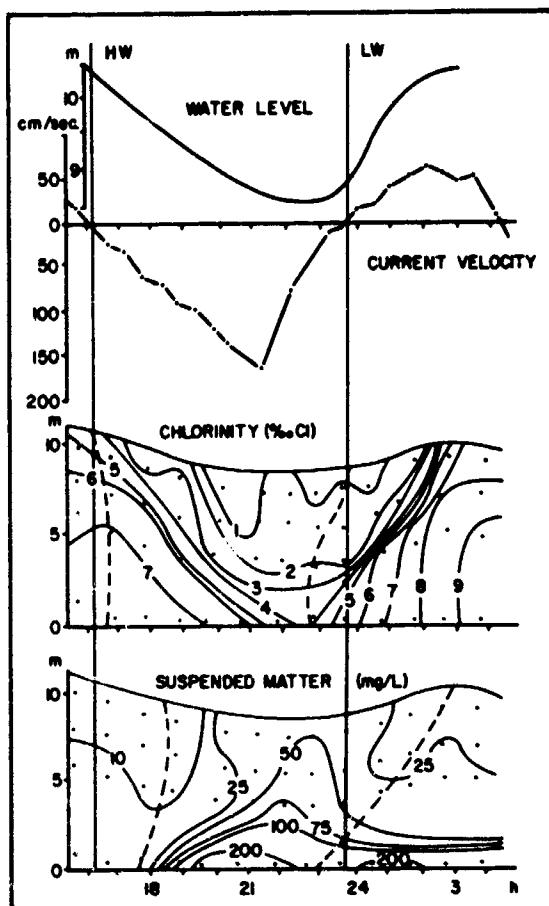


Fig. 6. Tidal variations of water level (m above bottom), current velocity (cm/sec.), salinity (% Cl), and suspended matter (mg/l) in the Boca Vagre of the Orinoco Delta (Van Andel and Postma, 1954).

When the current increases, it takes time before the material is resuspended.

The lag effect has been used to explain why in many tidal flat areas the amounts of fine-grained suspended matter are often considerably higher than in the adjoining open sea. Further (see Figs. 14 and 15), it has been used to explain why, proceeding landward in a tidal flat area, the grains in the bottom sediment gradually become smaller.

The decrease of grain size on the bottom is, primarily, a result of the reduced average and maximum current velocities from the open sea towards the coast. In a tidal area connected with the sea by tidal inlets between barrier islands, it is evident that in and near the inlets the bottom will consist of coarse sand, because fine sand and silt are winnowed out by the strong currents. Near the coast and on tidal flats where currents are weaker, fine-grained matter prevails—the coarse sand cannot reach these places and the fine materials can.

In a steady state, one might expect a decrease of fine-grained matter in suspension towards the coast,

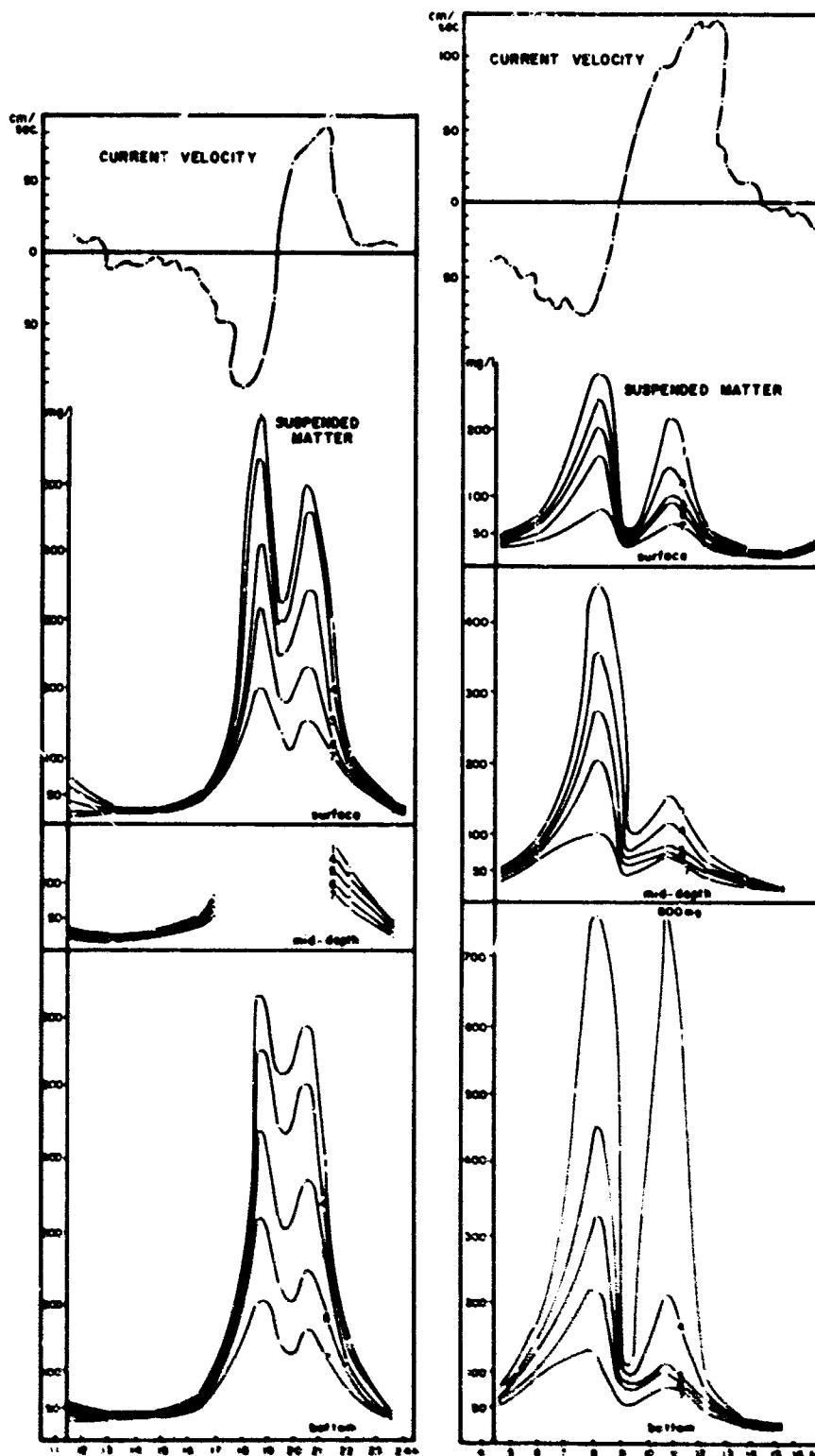


Fig. 7. Current velocities at mid-depth and contents of suspended matter at three depths. Observations at two fixed points in the Wadden Zee (Ameland area). Flood currents above and ebb currents below the horizontal line. The curves for suspended matter refer to the following grain-size fractions: 1, total suspended matter; 4, fraction below 64 μ ; 5, below 32 μ ; 6, below 16 μ ; and 7, below 8 μ . Depth at high water in Station A, 4.5 m; in Station B, 7.3 m (Postma, 1961).

or no concentration differences at all. That the concentration of suspensions increases towards the coast has been demonstrated extensively for various parts of the tidal flat areas (wadden) along the North Sea coasts of Denmark, Germany, and the Netherlands. The increase is found during calm weather as well as during storms.

The phenomenon has been explained on the basis of the lag effect mentioned above. Instead of considering the behavior of suspended matter at a fixed point, it is advantageous to follow a water mass over a tidal cycle (Postma, 1954; Van Straaten and Kuenen, 1957, 1958). When water is carried landward through a tidal channel with the flood, it is traveling in a large channel, its flow is much faster than farther landward, and it contains the amount of silt appropriate to the turbulence caused by this rate of flow. As the current velocity gradually decreases, part of the silt content, being too high in relation to the slower rate of flow, will sink to the bottom. Because silt sinks slowly, it will be transported farther into the flood direction than if sinking took place more quickly.

After the turn of the tide the water mass will move in an opposite direction. However, the slow reaction of silt on the decrease of current velocity causes the silt to settle in places where the current is too weak to carry it away. Therefore, if ebb and flood are symmetrical, a certain fraction of silt is left on the bottom. The process repeats itself every tide. As a result, the bottom in the inner parts of the area becomes very silty and there is a high concentration of suspended matter in the water. In the steady state the inward residual movement of silt is balanced by the loss of silt seaward due to the silt gradient in the water.

Settling Lag and Scour Lag (Distance-Velocity Asymmetry)

Considering lag effects in more detail, it will be assumed that: (1) the current velocity is equal at all points in a cross channel section; (2) the tidal curve is a symmetrical sinus curve at all points; (3) the high and low tide occur at the same moment throughout the area; (4) the average tidal current velocity shows a linear decrease from the open sea to the coast or a watershed; and (5) the vertical tidal range is constant.

Under these assumptions the shapes of the curves representing the relation between velocity and position of water masses at various distances from the shore are shown in Figure 8. Velocity is plotted on the vertical axis and distance on the horizontal axis. Although the tide at fixed points is symmetrical, the distance-velocity curves are asymmetrical (Van Straaten and Kuenen, 1957, 1958). A water mass moves in and out along one such curve. The tangent (p) at these curves represents the maximum current velocity in each point; consequently, this tangent meets each curve at a point attained by the water mass at half tide. The higher velocity and the greater distance covered lie on the seaward side of this point.

With the aid of the curves, the movement of a sediment particle during a tidal period can be described in more detail. Two lag phenomena must be taken into account. First, particles settling in a slackening current are not deposited vertically below the place where they start to drop out; they require time to reach the bottom and are carried along some distance before they come to rest (settling lag). The other phenomenon, based on the difference between transport velocity and erosion velocity, is called scour lag.

The effect of settling lag will be considered first, and the scour lag will be assumed to be zero. Suppose that a particle requires a velocity, V_1 , to be held in suspension and that it is lying on the bottom at point 1. As soon as the passing flood current has attained the velocity V_1 , the particle starts to travel landward. On reaching point 3, the current has slackened to the velocity at which the particle begins to settle while the surrounding water is still carrying it landward. The distance covered depends on the settling velocity of the particle, the current velocities in the period of sinking, and the depth of the water. We will assume that the particle reaches the bottom at point 5.

The water which surrounded the particle continues to travel landward until point A', and then returns with the ebb. When it reaches point 5 again on the ebb, it is still moving too slowly to pick the particle up. It remains on the bottom until water of sufficient velocity starts to pass. This water belongs to a curve BB' located farther landward than the curve AA'. At point 7 the particle starts sinking again, and, because of the settling lag, it is deposited at point 9.

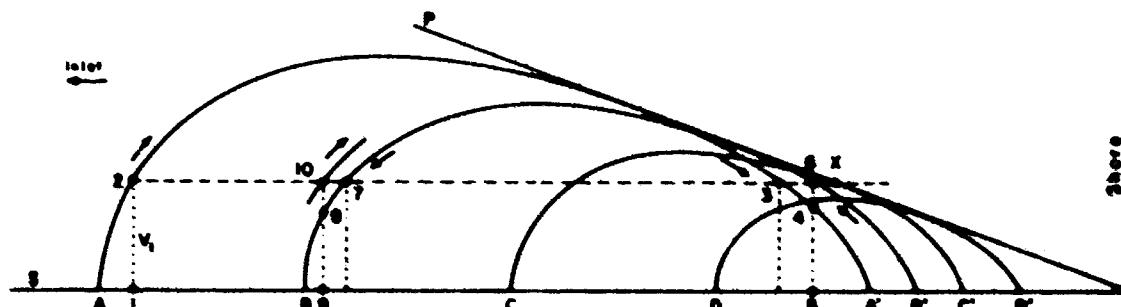


Fig. 8. Diagram showing the velocities with which different water masses move with the tides at each point along a section through a tidal area from the inlet to the shore. The curves apply only to idealized, average conditions. This illustrates the effects of settling lag and scour lag (Van Straaten and Kuenen, 1958).

Hence, in the course of one tidal period it has traveled landward from point 1 to point 9. The particle will move closer to the shore with each tidal cycle, until the flood current deposits it permanently at a spot so far landward (to the right of point X) that the ebb current is unable to lift it.

We will now suppose that the settling lag is zero, but the critical erosion velocity is greater than the lowest transportation velocity. This effect can also be demonstrated by Figure 8. It will again be assumed that the particle is lying on the bottom at point 1. When the critical erosion velocity is attained the particle is set in motion. Assuming that the current has slackened to the lowest transportation velocity in point 4, the particle will be dropped at point 5. During the ebb, the critical erosion velocity is shown by curve BB'. The water mass corresponding to this curve will carry the particle away and deposit it at point 9. Clearly, if settling lag and scour lag act simultaneously, each tide will bring the particle landward faster than each lag acting separately.

A convincing explanation has been given of the mechanism of accumulation of fine-grained material in tidal flat areas from the inlets towards the shore, or in shallow seas where the horizontal tide decreases towards the coast. But it should be kept in mind that a number of simplifying conditions have been assumed which may not be present in natural circumstances. The movement of individual particles is treated with the assumption that the quantity of per unit volume particles does not play a role. In other words, the importance of competency (the size of the grains a water mass at a given velocity can carry) has been emphasized and the capacity (the amount that can be transported) has been considered to be of no importance. The reason for this assumption is that in most tidal flat areas the amounts of suspended sediment are far below the capacity of the strong current velocities. The only suspendable fine-grained matter that is supposedly available to the currents when these begin to run after slack water is that which lies at or close to the surface of the bottom sediments between larger grains. Even in the period of maximum current velocity, only a minute fraction of the enormous masses of sand in the tidal area is set in motion, and only a very small amount of clayey matter is set free. All mud particles are therefore supposed to be taken into suspension as soon as the current attains the necessary velocity to move them. It follows that from the moment the particles of a certain size fraction are set in motion, the concentration of this fraction should undergo no further change until it settles again at the end of the tidal phase.

Observations indicate (Fig. 7) that concentrations of a certain size fraction actually fluctuate more with current velocity than would be expected. Mud particles seem to become available in greater amounts with increasing current velocity. Increasing current velocities may cause gradually deepening bottom scour, so that fine sediments are set in motion which at lower current velocities were protected against

transportation by sand grains. When the current slackens, part of the finely divided suspended material may already be deposited in sheltered places before the main current has dropped below the critical value. Hence, even if capacity in the strict sense does not play a role, something very much like it probably does.

Time-Velocity Asymmetry

Another effect is the influence of tidal asymmetry. It has been shown above that the theoretically symmetrical tide is lost if a specific water mass is followed. Similarly, the time-velocity curve is asymmetrical (Postma, 1961). This means that, in an area where tidal currents decrease from the open sea to the coast, the period of low current velocities is longer around high tide than around low tide (Fig. 9).

It has further been shown that the tidal velocity curve at a fixed point in a small tidal channel is in fact asymmetrical, having its maximum nearer to low tide than to high tide; this holds for the ebb as well as for the flood phase (Figs. 7 and 10) and results in a much longer period of low current velocities around high tide than around low tide.

Further, in a tidal flat area the water is alternately spread horizontally over a large area at high tide and confined in the tidal channels at low tide. Consequently, the average depth of the water is greater at low tide than at high tide, and more suspended matter will reach the bottom at high tide. This condition may contribute to an accumulation of fine-grained matter in tidal flat and coastal areas. Most of the sediments carried landward with the flood are deposited on the bottom near high tide. Owing to settling lag or scour lag, or both effects together, the material is not picked up by the body of water which carried it landward, but by water located farther landward. Thus, around high tide the particles undergo a shift toward shore. At low tide more of the particles remain in suspension and do not undergo a seaward shift. The net result is, therefore, a landward shift in each tidal cycle. This mechanism needs less specific assumptions than the one discussed earlier.

Difference Between Spring and Neap Tides

The strong currents prevailing during spring tides will generally bring more material into suspension than the neap tide currents (Fig. 11). Hence, in the neap tide period, part of the material participating in the tidal circulation will remain on the bottom for as long as a week or ten days. The material will have time to consolidate, and erosion is at first difficult in the next spring tide. Once the material is set in motion it will be resuspended by every tide until maximum tidal current velocities again decrease.

Considering a whole semilunar cycle, a tidal period before the spring tide maximum must carry less material than the corresponding period after the spring tide maximum. In the course of this cycle there must be a time lag between mean tidal current velocities and mean silt concentrations. This effect is demon-

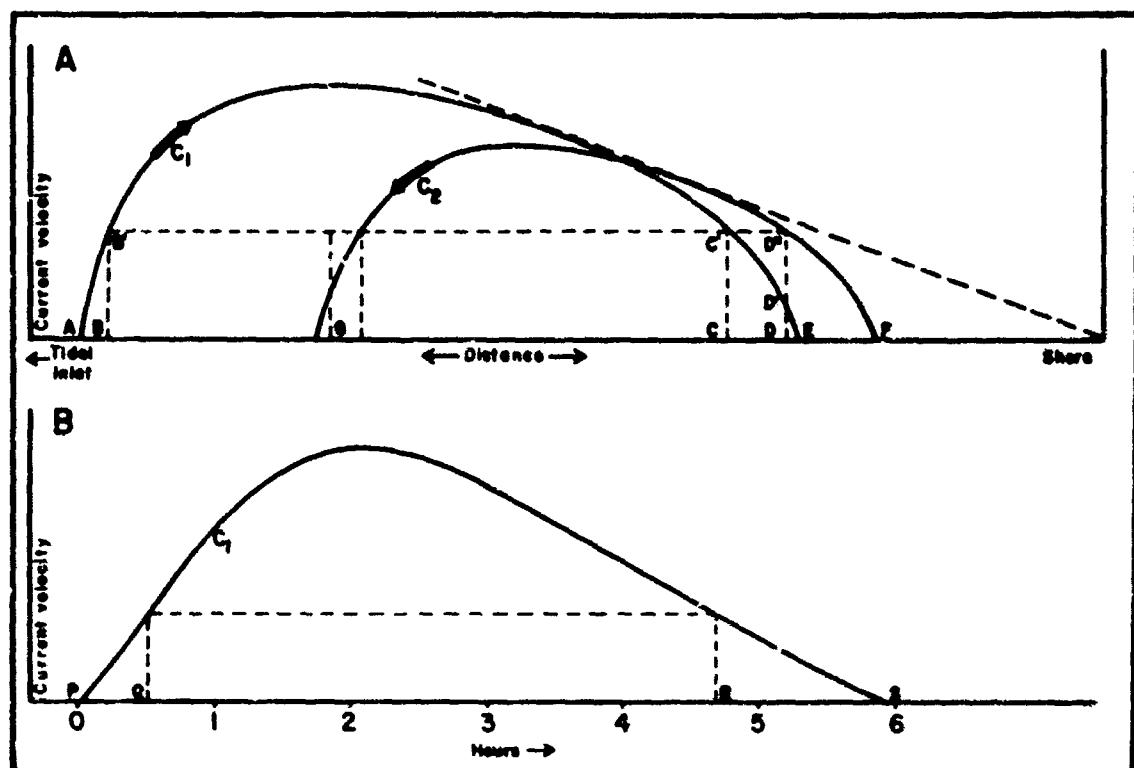


Fig. 9. Distance-velocity (A) and time-velocity (B) curves for water masses moving in a tidal area (compare Fig. 8) showing that these curves are asymmetrical, although the corresponding tides (water movements at fixed points) are symmetrical. The asymmetry is due to the decrease of horizontal tidal amplitude towards the shore (Postma, 1961).

strated in Figure 12 for stations off the coast of British Guiana (Demerara Coastal Investigation, 1962). The suspended matter has the same properties as that shown in Figure 2. The time lag between the velocity maximum and the silt maximum is about four days (April 13-17, 1961).

Rotating Tides

In many shallow coastal seas the horizontal tide does not simply carry the water back and forth, but rotates. A typical stream rosette, with a residual current to the right, is shown in Figure 13. The tide is supposed to rotate clockwise. If it is further assumed that a particle is picked up at a velocity V_1 and deposited at lower velocity V_2 , it will only be transported by the currents in the shaded part of the rosette. The sum of the current vectors in this part can be resolved in a component parallel to the coast and another component perpendicular to and directed towards the coast. In this manner suspended matter may be carried towards the coast, and loss to the open sea may be prevented.

Grain-Size Selection

The efficiency of the accumulation processes described above depends on differences between erosion velocities and minimum transportation velocities, and on the settling velocities. Accumulation may therefore

be quantitatively different for particles of different sizes (Postma, 1961). Scour lag and settling lag both increase with decreasing diameter of particles; however, the relative amount reaching the bottom at slack water decreases with decreasing particle size. Consequently, with increasing size the efficiency of accumulation should first increase and then decrease.

An example of the distribution of suspended matter from a tidal inlet to the coast is illustrated in Figure 14; the distribution of different size fractions over a tidal flat area in the Wadden Zee is shown in Figure 15. The concentration appears to increase towards the shore for sizes below 128μ . A distinct optimum size cannot be indicated. Even material smaller than 8μ (equivalent diameter) shows considerable accumulation. This material settles with a velocity of about 20 cm/hr or less. Assuming a transportation velocity of 10 cm sec, the time over which the particles will settle at about high water amounts to approximately five hours (Fig. 16). The water depth in the inner part of the area at high water will not be more than one meter. Hence, all 8μ material will just be able to reach the bottom in that period, so that this may be approximately the optimum size for accumulation.

The suspended matter piled up against the coast of the Guianas (See Fig. 11) also has an equivalent size of about 8μ (Demerara Coastal Invest., 1962). Although these examples form an insufficient basis for

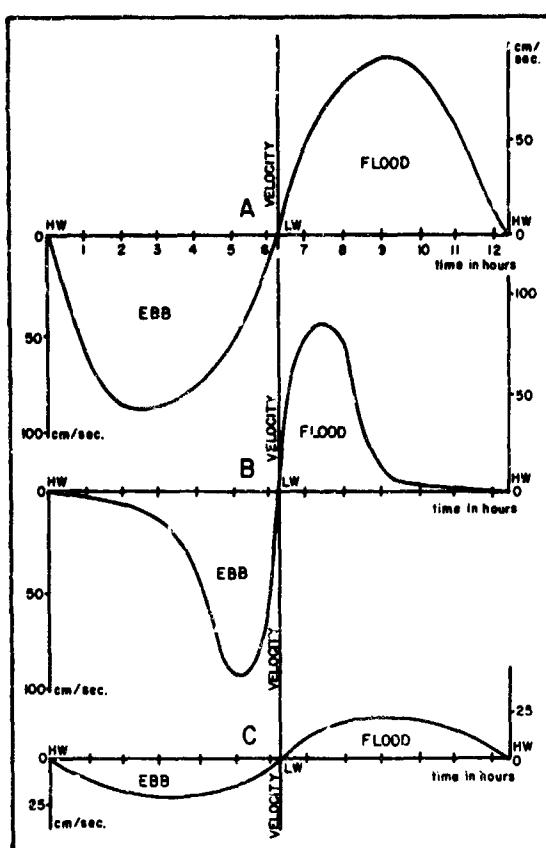


Fig. 10. Tidal asymmetry. Curves show the variations of current velocity with time for water masses in a tidal flat area; A for a water mass moving in a channel, B for a water mass moving half of the time in a channel and half of the time over a tidal flat, and C for a water mass traveling over a tidal flat and reaching the low-water line at low tide (Postma, 1961).

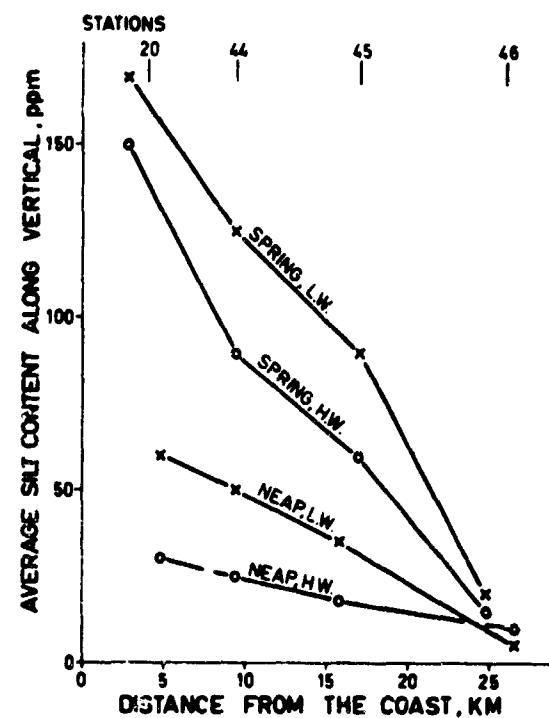


Fig. 11. Decrease of suspended matter with increasing distance from the coast of British Guiana during spring and neap tides (Demerara Coastal Investigation, 1962).

general conclusions, it may be tentatively assumed that the accumulation mechanisms described act with good efficiency from about 100μ to at least 8μ .

TRANSPORT OF COARSE-GRAINED MATTER

Information concerning the transport of sand in tidal streams is rather scarce. Coarse-grained material is transported with greater difficulty than uncon-

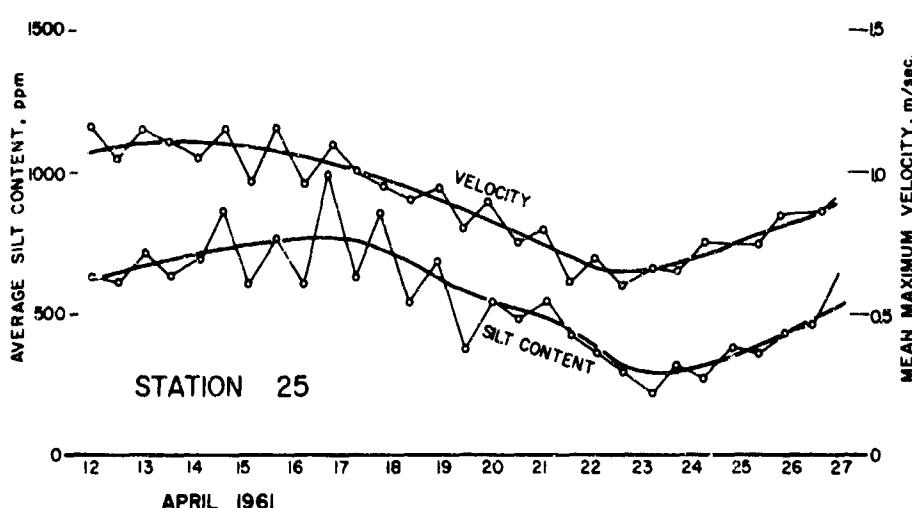


Fig. 12. Average daily silt content and mean maximum ebb and flood velocity, showing lag of silt maximum after the spring tide maximum. Station near the coast of British Guiana (Demerara Coastal Investigation, 1962).

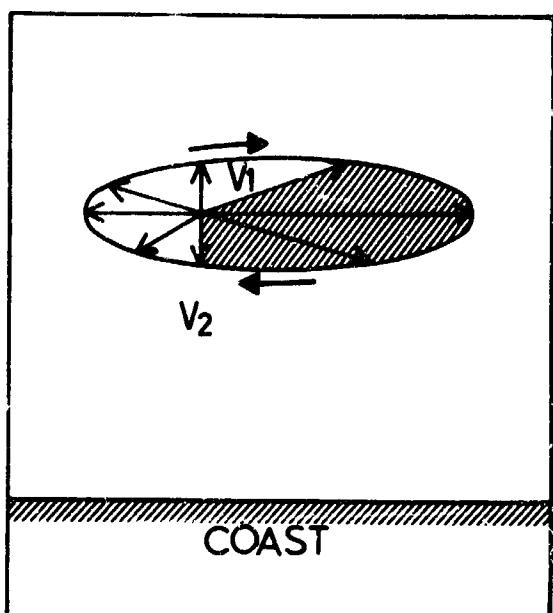


Fig. 13. Lag effects in a rotating tide.

solidated fine-grained matter and is at the same time transported closer to the bottom, partly as bed load (Niebuhr, 1955). Besides strong currents, wave action is often needed to set material into motion (Postma, 1957). As a result, important sand transport may be restricted to periods of strong winds. It is difficult to obtain satisfactory observations during such periods.

The information discussed above, obtained in tidal flat areas and tidal lagoons, indicates that lag effects are of no importance for sand grains larger than about 100μ . Evidently, such particles sink too fast (about one meter in two minutes) to show an important settling lag. There must be some scour lag, but this effect seems insufficient to generate a significant concentration gradient towards the coast. Moreover, at a relatively great distance from the coast the strength of the tidal currents is apparently inadequate to keep sand in suspension. This fact contributes to the formation of tidal flat areas. An imaginary tidal area may be visualized in which no depth differences have yet developed (Van Bendegom, 1950). In principle, the current velocities in parallel stream trajectories are the same, but actually slight differences will occasionally occur. The slightly stronger current will erode more sand, thus forming a channel; the eroded sand will be passed laterally to the weaker current and be deposited. In this way, differences in depth will be created; the currents in the channels will increase in strength and those on the shallows will diminish. More sand will be transported from the former to the latter until differences in depth and current velocity have become so large that nearly all sand transport is confined to the channels. In more precise terms, the process will come to an end when

all concentration differences in a horizontal plane have disappeared. Because of the great depth differences on tidal flats and near the coast, only small amounts of sand are in suspension.

Continuing this line of reasoning, it seems evident that even small amounts of sand should eventually increase the height of the tidal flats to the high tide level. Many tidal flats indeed attain this stage of development and are finally covered with fine-grained matter. But a number of them never develop to this level either because of wave action caused by wind or sand shortage combined with the rise of sea level. The development depends on the amounts of sand available or the climate and the exposure to the wind of the region. In a moderately exposed area like the Wadden Zee, the waves may prevent the growth of tidal flats to the final stage (Postma, 1961). Current velocities determine deposition in tidal channels, but sedimentation on the tidal flats is often regulated by wave action.

A typical phenomenon in tidal flat areas is the formation of ebb and flood channels (Van Straaten, 1960a, b; Van Veen, 1950). A tidal channel cross section should often be subdivided into two parts. In one part the ebb current predominates; in the other, the flood current. The phenomenon is caused by the inertia of flowing water, which tends to follow a straight line. If the tidal flats were constantly emergent, this inertia would result in a normal meandering system. In the period of submergence, however, the water is able to follow a path over the banks instead of the meanders, which results in a secondary channel, becoming gradually shallower with increasing distance from the main channel. In this manner, the main channel may be divided into two branches; in one, the flood predominates, in the other, the ebb. In most cases the original meandering course is followed by the ebb and the shortcuts, by the flood. The development of shortcuts by the ebb may be prevented

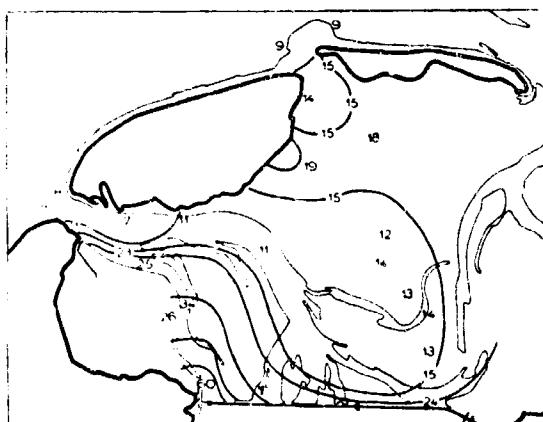


Fig. 14. Distribution of suspended matter $<50\mu$ in the Texel area (Wadden Zee), showing the increase of concentrations from the tidal inlet to the coast. The values (in mg/l) are the averages of measurements over a full tide at different depths (Postma, 1954).

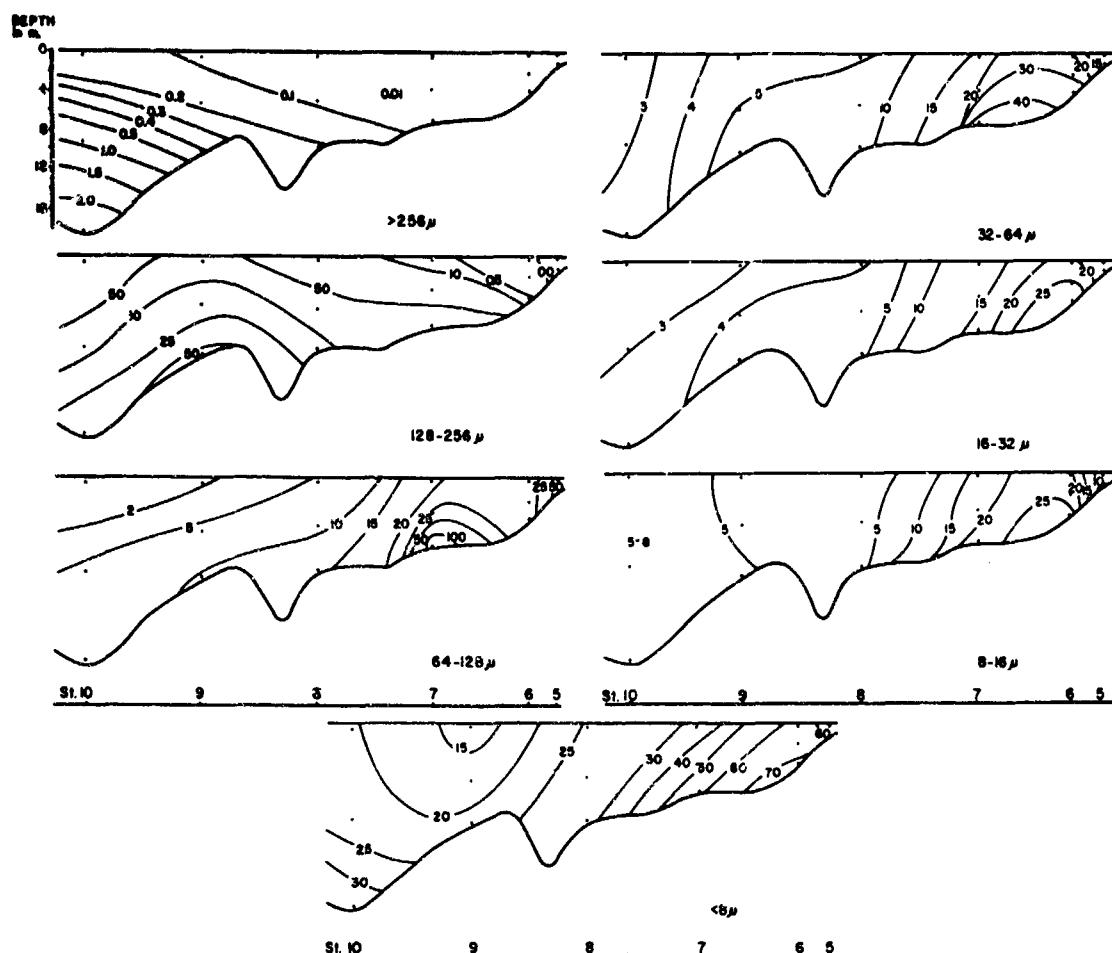


Fig. 15. Distribution of suspended matter in a vertical profile of the Wadden Zee (Ameland area) from a tidal inlet to the shore. The values are average concentrations, in mg/l, of different grain-size fractions through a tidal period. The concentrations appear to increase towards the shore for five fractions (<8 , $8-16$, $16-32$, $32-64$, and $64-128\mu$). The coarser fractions do not show this increase (Postma, 1961).

by the return of water from the tidal flats to the channel, thus confining the current to its original course. During the flood, water flowing from the channel to the tidal flats may assist in attacking the sides of the channel.

TRANSPORT OF SUSPENDED MATTER IN ESTUARINE CIRCULATION SYSTEMS

ESTUARINE WATER MOVEMENT

The term "estuarine circulation" is applied to water movement in which density differences caused by the supply of river water are second in importance only to tidal influence. In the lower part of the river the influence of the tide is first observed as a slight periodical rise and fall of the water level, which hardly influences the seaward flow of fresh water (upper boundary of the vertical tide). Gradually the tide becomes more important, and the runoff is periodically retarded until, at a certain point, a weak flood tide

becomes perceptible. The point where the one-way movement of water changes to a back-and-forth movement will be called the upper boundary of the horizontal tide. Below this boundary the water may still remain fresh over a large distance. The horizontal tide, however, becomes gradually more pronounced, and at a certain point at the river bottom the first traces of salt water can be detected. Soon the salt influence becomes perceptible at the surface. The salt boundary can be described as a plane sloping landward and moving up and down with the tide.

Below the salt boundary the salinity gradually increases to open sea values. Close to the boundary the horizontal tide is usually relatively weak and salinity differences along the vertical are large. Farther seaward the tidal influence increases and gradually causes a better mixing of bottom and surface water. If the tide is sufficiently strong, a point will be reached where vertical salinity differences have practically disappeared. This point is the lower limit of the

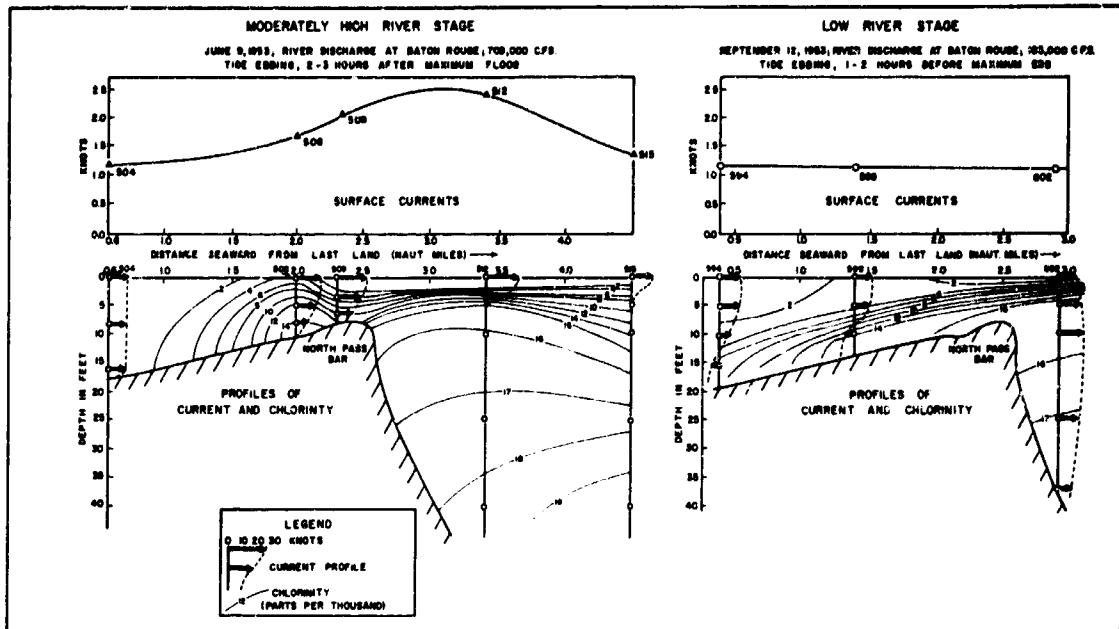


Fig. 16. Profile showing current velocity and chlorinity at the mouth of North Pass, Mississippi River Delta. Upper diagrams show surface speeds along channel axis. Diagrams on the left show the outward flow during moderately high river stage extending to the bottom at the bar. Salt water included during the preceding high tide is rapidly flushed out during the ebb. Profiles at right show the lower river stage: the current is not affected by the bar, the water rides over the salt wedge, and the speed decreases smoothly in the channel and over the bar (From Scruton, 1960; Shepard, 1960).

"stratified estuary" and the upper boundary of the "mixed estuary". The mixed parts of the estuary closely resemble the tidal areas discussed.

The estuarine circulation takes place in the stratified area. Due to density differences, mainly caused by salinity differences, saltwater movement in the lower water layer has a net transport upstream. It mixes in a vertical direction and carries part of the salt water upward into the upper water layers, where it is carried seaward with the fresh water (Figs. 16 and 17).

One consequence of this manner of transport is that in the estuarine region the river loses its contact with the river bed. This does not mean that no river water reaches the bottom, for part of it is mixed downward. As a result of the mixing processes, the underlying saltwater body, the salt wedge (Van Veen, 1952), becomes gradually less salt upstream, and the overlying water increases in salinity downstream.

Averaged over a whole tidal cycle there is a plane of no motion between the upper seaward-moving water and the lower landward-moving water (Fig. 16). River water supply, mixing intensities, and tidal currents change from one moment to the other. During the flood maximum, for example, the whole estuarine water body may move landward, and turbulence may be so strong that vertical salinity differences practically vanish; such a state of complete mixing rarely occurs during the ebb tide.

In estuaries with a weaker tidal influence, stratifi-

cation is maintained over the whole tidal cycle, and the salt wedge is a permanent feature. Water movement inside this wedge may be very slow. In such cases the wedge may be filled up with sediments, so that a bar is formed.

TURBIDITY MAXIMA

In the lower reaches of many rivers where an estuarine circulation is developed, the concentrations of

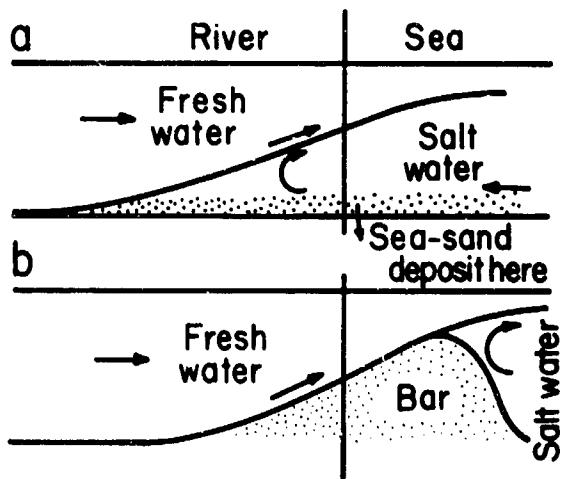


Fig. 17. Formation of a bar in a salt wedge (Van Veen, 1950).

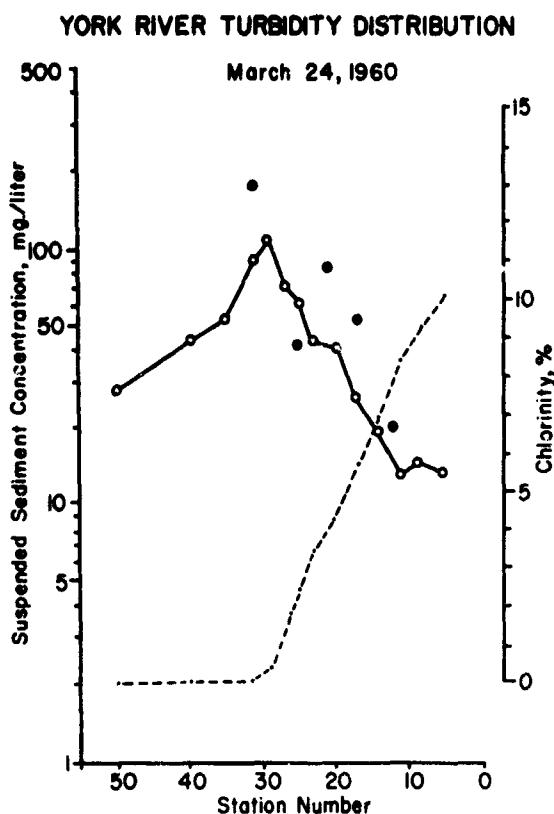


Fig. 18. Turbidity maximum and salinity in the York River (Nelson, 1960).

suspended matter often attain values considerably higher than those in the river water and in the sea (Alexander *et al.*, 1935; Glangeaud, 1938; Lüneburg, 1939; Mann, 1958; Postma and Kalle, 1955). The existence of these turbidity maxima has been proved in many river mouths (Figs. 18-20). Since the peak of the turbidity maximum is often located near the salt boundary, it has sometimes been assumed to be caused by flocculation processes (Lüneburg, 1939). Usually its existence is due to hydrodynamic conditions (Postma and Kalle, 1955).

A sediment particle carried downstream with the river water may sink into the lower water layer. Since residual water movement in this layer is directed upstream, the particle will now move in the opposite direction. Vertical mixing may eventually bring the particle back into the upper water layer, so that it is again carried seaward. The process may be repeated, or the particle may be carried to the sea. Theoretically, a particle may be carried back and forth a number of times before it finally escapes.

Similarly, suspended matter of marine origin is carried upstream in the salt wedge. The stratified region therefore acts as a sediment trap in which sedimentary material of either freshwater or marine origin may be circulated many times. Thus, high concentrations of suspended matter may be accumulated.

The magnitude of a turbidity maximum depends on

a number of factors, and the amount of suspended matter in the river or the sea is most important. The strength of the estuarine circulation is a second important factor. The settling velocity (equivalent grain size) of the available material also exerts a strong influence. Turbidity maxima exist not only in stratified flow conditions, but also in well-mixed estuaries.

Greater river flow pushes the turbidity maximum towards the sea and at the same time depresses its magnitude. The depression may be explained as follows: assuming that the tidal forces remain the same, an increase of river discharge will cause better stratification and less vertical mixing. This will decrease

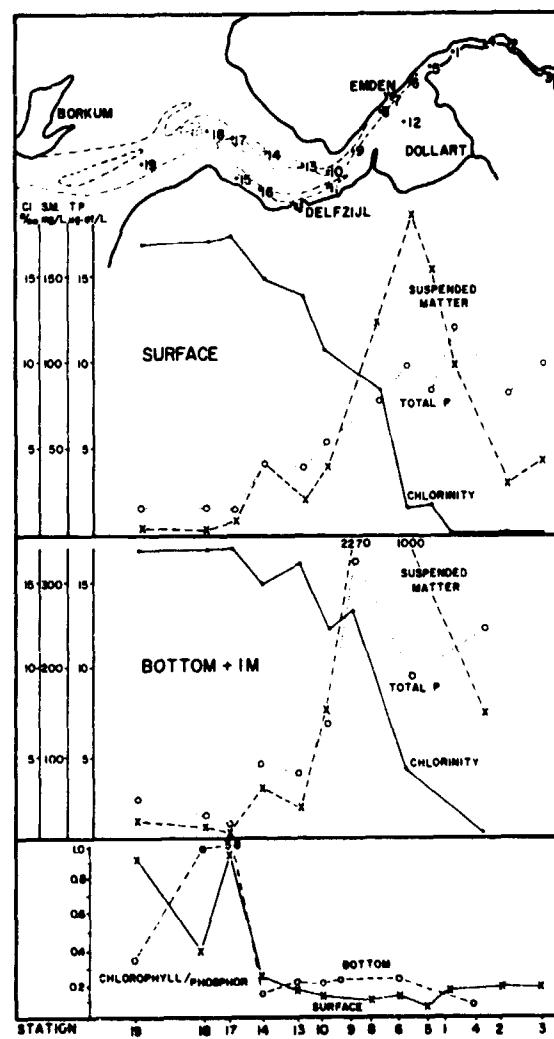


Fig. 19. Turbidity maximum in the Ems Estuary. Suspended matter in mg/l; chlorinity in ‰; total phosphorous in µg-at/l. Observations at the surface and near the bottom (bottom + 1 m). The phosphorus distribution shows that mainly inorganic matter is accumulated in the turbidity maximum; the chlorophyll-phosphorus relation indicates the boundary between organic marine matter (high values) and organic matter of the fresh water (low values) (Postma, 1960).

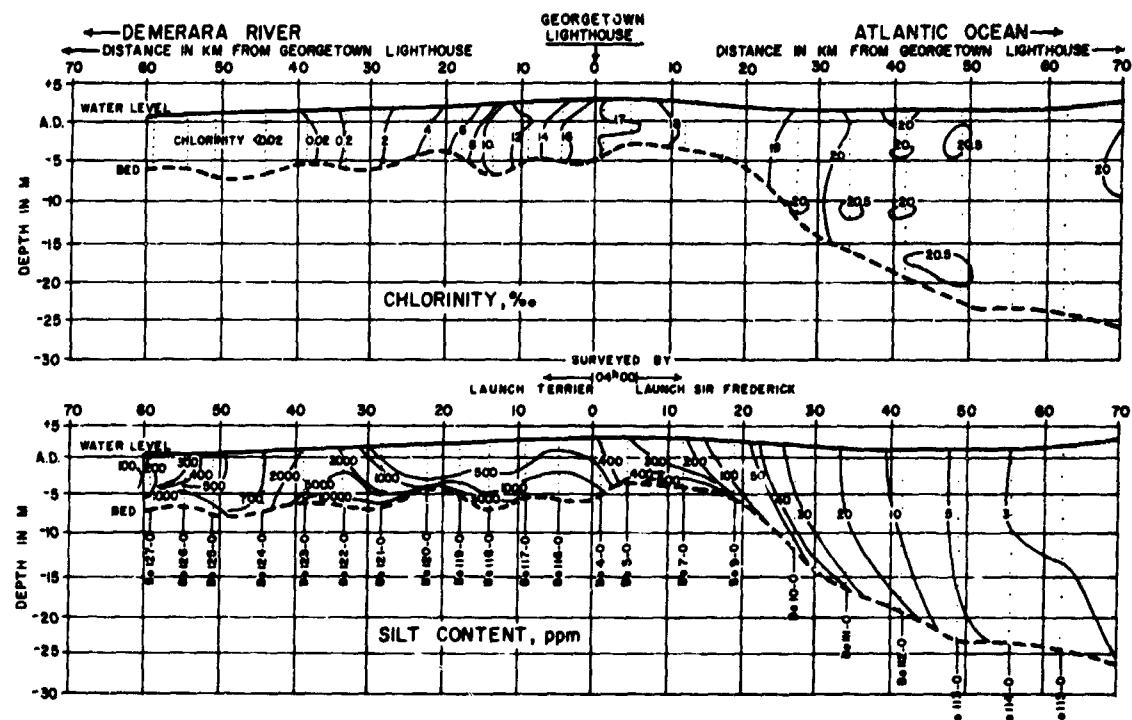


Fig. 20. Chlorinity and suspended matter in the Demerara River, showing the turbidity maximum and "diffusion" of suspended silt from salt into fresh water (Demerara Coastal Investigation, 1962).

upstream water transport in the salt wedge. The flow of river water to the sea will be accelerated. As a result, the opportunity for entrapment of particles is reduced, and concentrations of suspended matter must decrease.

It should be added that very low river discharges must also be detrimental to the development of a turbidity maximum, since the estuarine circulation may practically disappear. Hence, in a constant tidal regime, a certain volume of river discharge will be optimal for the formation of the turbid zone.

Only a few observations are available concerning the grain size of the suspended matter caught in a turbidity maximum (Postma, 1960). It seems reasonable to assume that under a given set of conditions only a restricted size range can be present. If particles sink slowly they will escape to the open sea, as there will not be sufficient time to settle into the bottom layer (Fig. 21). The concentration of such particles in the turbidity maximum should, therefore, hardly exceed the concentrations in the river and the sea. If, on the other hand, particles sink rapidly, vertical mixing will not be able to carry them back into the surface layer. Hence, only suspended matter of a specific size will be repeatedly recirculated and participate in the formation of the turbidity maximum.

Size fractionation may be important when the grain size of suspended matter of the river differs from that of the sea. If, for example, the river material is considerably finer than the marine matter, the turbidity maximum may be formed chiefly of the latter. The

reverse may also occur, but the predominance of marine sediments in many estuaries suggests that the first example is of greater importance.

PENETRATION OF SUSPENDED MATTER FROM SALT INTO FRESH WATER

Upstream from the peak of the turbidity maximum the silt content of the water gradually decreases. This decrease does not end where the water is completely fresh, as would be expected, but is often continued in the pure river water (Figs. 18-20). Evidently, suspended silt can "diffuse" from the turbidity maximum against the residual flow into the fresh water (Demerara Coastal Investigation, 1962). This upstream diffusion is influenced by the tide. One might suppose that suspended matter carried upstream by the flood temporarily settles during the ebb and is subsequently carried farther upstream by the following flood. Obviously this process works only as long as the tide is strong enough to cause a reversal of the current.

The important conclusion of this observation is that deposition of marine mud can take place in the lower parts of a river where salt water never penetrates. Remains of marine diatoms have been observed in freshwater deposits (Brockmann, 1908, 1929).

It has been shown that particulate matter is flocculated by sea water. Since this process is often reversible, material carried from the sea into the fresh water may be deflocculated. Eventually, it will again move downstream into the salt water and flocculate

CONCENTRATION OF SUSPENDED MATERIAL

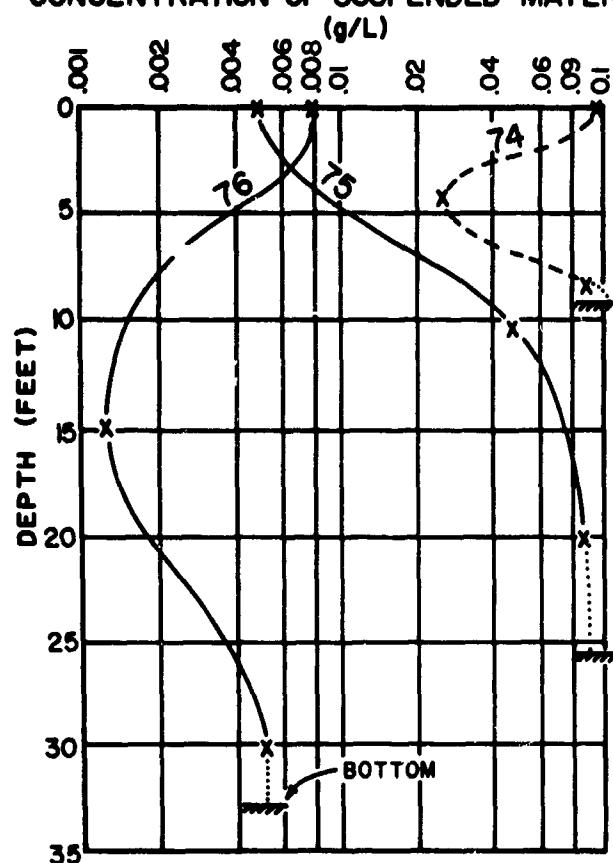


Fig. 21. Vertical distribution of suspended matter off the Mississippi Delta, indicating slow settling velocity of particles in the upper layers (surface maxima at Stations 74 and 76) (Scruton, 1956).

again. In principle, this may be repeated many times. The process described here illustrates that, in order to obtain reliable measurements on the silt supply of rivers, it is necessary to carry out observations upstream from the upper boundary of the horizontal tide.

BOTTOM SEDIMENTS

TIDAL FLAT DEPOSITS

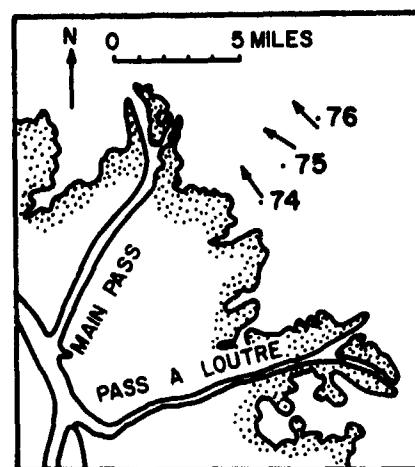
The deposits in tidal flat areas such as the wadden along the North Sea coast vary from coarse sand to very fine-grained mud (Guilcher, 1963; Häntzschel, 1939; Lüneburg, 1957; Postma, 1954; Van Straaten and Kuenen, 1957, 1958). The average grain sizes tend to decrease from the tidal inlets towards the coast and the tidal flats. The clay content generally increases in the same direction (Figs. 22 and 24).

This configuration can be explained partly by the landward decrease of tidal current velocities, the decrease of wave action in that direction, or the supply of fine-grained matter from the land. The accumulation processes described earlier will, however, give strong support to the formation of fine-grained muds. It may even be asked whether in many areas such a formation is not a result of these processes. Often

the concentration of suspended matter in the sea adjoining the tidal flat area is very low. If no other sources of silt are available, it is difficult to understand how large amounts of mud could be deposited without the action of accumulation mechanisms, particularly in areas where storms seem capable of removing all fine material.

These are not simple questions—several organic factors also come into play. Dense shell populations may filter clay from the water and return it in the shape of pseudo-faeces and fecal pellets which are difficult to erode. In some instances, the bottom animals are able to filter the whole water mass of a tidal area within a few weeks or even a few days (Verwey, 1952). On tidal marshes, mud may be caught by various plants, and mud flats formed along coasts where suspended clay in the ocean water is almost absent (Phleger and Ewing, 1962). Bottom diatoms may produce thick cohesive layers of organic matter which prevent the escape of clay.

Since the material in a tidal flat area is moved back and forth many times by tidal action before being deposited for a longer period, a correlation of sedimentary properties and environmental conditions can be attained (Krumbein and Aberdeen, 1937; Krumbein,



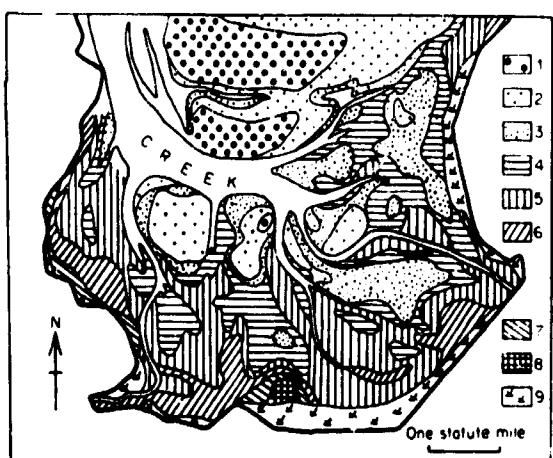


Fig. 22. Percentages of fine-grained matter ($<2\mu$) in the Lauwers Zee, showing increase towards the coast. Wadden Zee. 1 = 0-1.5%; 2 = 1.5-3.0%; 3 = 3-5%; 4 = 5-8%; 5 = 8-12%; 6 = 12-17%; 7 = 17-25%; 8 = >25%; 9 = marshes (Van Straaten and Kuenen, 1957).

1939). Not only the grain-size distribution, but that of other components such as organic matter, iron oxide, calcium carbonate, etc. indicate that the distribution patterns are determined by slight differences in current velocities or wave action (Lüneburg, 1957).

It has been shown that on tidal flats, wave action often predominates over currents. The distribution of wave activity over a tidal flat is determined by the force of incoming waves and the generation of waves on the flats themselves (Postma, 1957). Waves may arrive from a neighboring deep channel and gradually lose strength when travelling in shallow water. This effect in itself results in a decrease of grain size away from the channel. Waves formed in the flats cause more turbulence where the water is shallow, and grain size increases with decreasing depth. Quite frequently the second effect is of greater importance than the first. An example is given in Figure 23. To understand the grain-size distributions, one should know that the wind and the larger waves travel from west to east. The distance travelled by the waves over the tidal flat is clearly the most important factor, because the median grain size decreases from west to east. In other instances the isolines may partly follow the depth contours, except near the coast, where fine-grained muds are deposited.

Figure 23 further illustrates the fact that in the Wadden Zee current influence prevails in the channels, whereas wave influence dominates on the tidal flats. A grain-size minimum is found on the slope between channel and flat. This minimum indicates that the channel edge is too deep to be influenced by the waves, but at the same time is too far away from the axis of the channel to be exposed to strong currents.

The distributional patterns of sediments in tidal flat areas reflect rather faithfully the hydrodynamic pat-

terns. The recurrent selective operation of tidal currents and waves results in a very good degree of sorting of the sand deposits comparable to that on beaches and in dunes.

As the distribution of sediments is primarily determined by oscillating water movements, it provides no clue to the origin of the deposits. Reliable information concerning the source of tidal flat sediments is therefore rather scarce. The major problem is to decide whether the material is of marine or fluviatile origin, taking the location of the sediments after the last glacial stage as a starting point. The two principal possibilities are that sediment moved landward with the rise of sea level, or that sediments were carried down by the rivers. Extensive investigations in the Wadden Zee have led to the conclusion that all grain-size fractions present in this area originate from the North Sea (Crommelin, 1940, 1948; Favejee, 1951; Postma, 1954; Van Straaten, 1954, 1960; Wiggers, 1960). In the lagoons along the Gulf of Mexico the rivers apparently are the principal source of sediments (Shepard, 1953; Shepard and Moore, 1954). It should be realized, however, that these conclusions are reached by indirect evidence. A definite answer to the question is impossible, because the division into marine and terrigenous sediments is rather artificial.

NEARSHORE DEPOSITS

The distribution of sediments on a nearshore slope which gradually descends into deeper water is essentially characterized by zones of different deposits with boundaries parallel to the depth contours or to the coastline. The characteristics of the sediments are largely determined by water movements. In the Rockport area of the Gulf of Mexico, for example, the deposits near the coast consist of coarse sand. Seaward, the sand content decreases rapidly, and the outer shelf

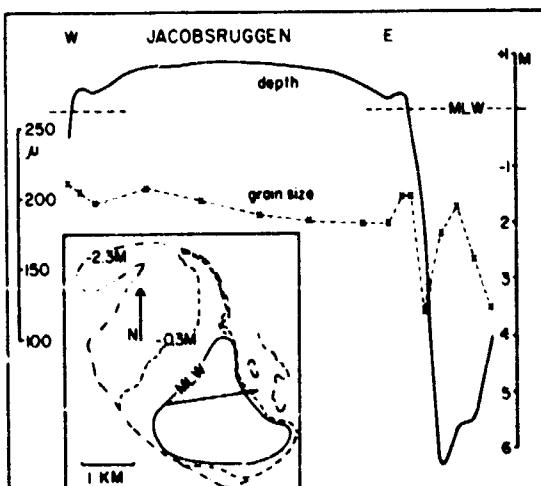


Fig. 23. Variations of median grain sizes in a traverse over a tidal flat and a channel in the Wadden Zee (Terschelling area). Note the grain-size minimum on the slope (Postma, 1957).

sediments consist of clay and silt. The presence of coarse sands near the coast is due to wave action which, in the case of the Texas coast during hurricanes, can reach to a depth of at least 10 meters. The waves stir up the fine sediment, part of which may be deposited in the lagoons; the remainder is deposited on the shelf in deeper water. Tides and currents are of small importance in this area. Similar conditions occur in the Mediterranean (Van Straaten, 1960a, b).

A decrease of grain size away from the coast is by no means a general phenomenon. In areas where tidal streams or currents are strong, no silt at all may be deposited and sandy deposits may prevail to the edge of the shelf (Guilcher, 1963). In many cases grain sizes even increase in this direction.

Sandy deposits may also be an inheritance from Pleistocene conditions. Such deposits often are not in equilibrium with present hydrodynamic conditions which would allow the deposition of smaller grains. In many areas deposits have not been covered by fine-grained matter because water movements are still too rough to allow deposition of silt, or because no silt or fine sand is carried over these parts of the shelf. Examples are the deposits on the shelf off the Mississippi Delta.

In areas with a very large supply of mud, as the coast of the Guianas, the sediment may become progressively finer towards the coast, notwithstanding considerable activity of waves and currents up to the coastline (Demerara Coastal Investigation, 1962). Any of the accumulation processes already discussed may be responsible for the mud against the shore. As a result of these processes the mud cannot escape to the outer shelf, and concentrations of suspended matter reach very high values on the inner shelf. These high concentrations in turn give rise to mud deposition, although strong wave and tidal action occur. The situation is comparable to conditions under which fine-grained matter is deposited in tidal flat areas. Also, the outer part of a shelf can be kept free of mud even if very large amounts are present in the adjoining coastal zone.

The action of distributive forces is also reflected in secondary properties of nearshore sediments, such as the percentages of organic carbon and nitrogen, the distribution of organic remains, the concentration of calcium carbonate and iron, the roundness of sand grains, etc.

As an example, Figure 24 shows the relative abundance of three clay mineral types in the environmental succession. Montmorillonite is relatively most abundant in fine-grained deposits of bays and outer shelf areas; chlorite and illite show approximately the same distribution. It has been supposed that this distribution is caused by the transition of one clay mineral into another. The supposition is based on the observation that montmorillonite in sea water may be slowly transformed into illite, and it explains why the rate of montmorillonite to illite at one point decreases with the depth of burial or the time of deposition. It

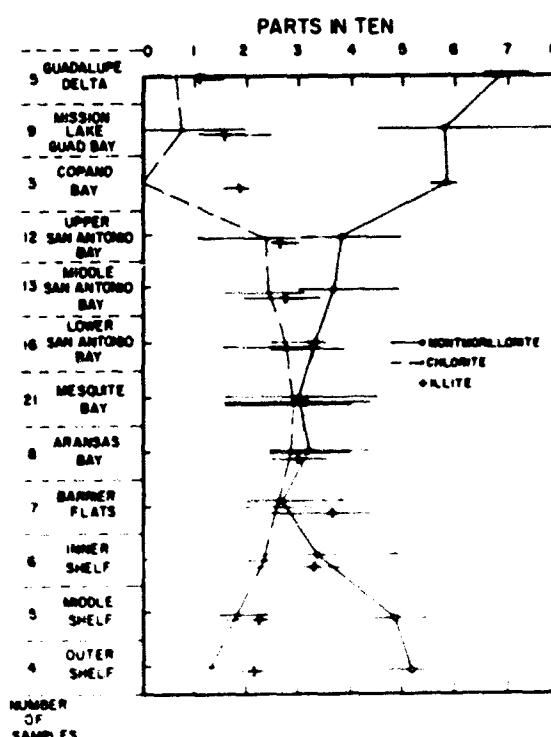


Fig. 24. Relative abundance of three clay minerals in the Rockport area in a series of deposits from a delta to the open sea (From Shepard and Moore, 1954).

is not evident, however, why sediments in the middle part of the section shown in the diagram should be older than the sediments on the two ends. It seems more convincing to ascribe the difference in relative abundance to differential sedimentation, because montmorillonite settles less rapidly than the other minerals. Differential sedimentation in the same sense has also been observed off the coast of Venezuela at the mouth of the Orinoco River (Van Andel and Postma, 1954).

Along many shores, oblique waves and residual currents generate sediment transport parallel to the coastline. This phenomenon has been studied extensively for sands in the surf zone, but it also applies to fine-grained materials which may be transported much more rapidly than sands. Losses to deeper water may be prevented or diminished by accumulation processes. It seems probable, for example, that the suspended matter of the Amazon River is carried to the west along the coast of the Guianas over many hundreds of miles (Demerara Coastal Investigation, 1962; Revne, 1961). During this transport, mud from the Amazon apparently travels upstream in many river mouths. Mud found at a certain part of a coastline may have its origin at a quite different part of the coast, and mud found in an estuary may not all originate from the river of that specific estuary but from another estuarine region.

ESTUARINE DEPOSITS

From a sedimentological point of view, it seems

appropriate to restrict the use of the word "estuary" to those portions of a river's mouth where river water is subject to tidal action and where river water mixes with and is measurably diluted with sea water. This definition includes the upstream section of the river above the upper salt boundary as far as tidal action is perceptible. It excludes the nearshore section, the open sea, the tidal flat, or the lagoon areas, where salinity differences are of secondary importance.

Like tidal flat areas, estuaries may contain coarse-grained sediments as well as fine-grained deposits. Which of the two is more important depends on the shape of the estuary, the strength of tidal currents and river flow, and the amounts of fine-grained suspended matter available.

Areas like the Rhine-Meuse Delta are mainly composed of sandy deposits (Terwindt *et al.*, 1963) and form a transition between tidal flat areas and estuaries of the river mouth type. This is partly because the fine-grained bodies of sediments are separated from the coarse-grained ones by dikes.

One of the most important characteristics of a sandy estuary is the existence of separate ebb and flood channels. The flood predominates in channels which gradually shoal landward, whereas ebb channels follow a meandering course. In contrast to tidal flats, the grain size of the sandy deposits on the shoals is mainly regulated by current velocities and not by waves (Terwindt *et al.*, 1963). The mineralogical properties of estuarine sands are mostly determined by the geology of the catchment area of the river. In the Rhine-Meuse Estuary, for example, marine sands predominate; the rivers do not supply any sand to this estuary and the boundary between marine and fluviatile sands approximately coincides with the salt boundary.

The typical deposits of most estuaries are not the sands, but the fine-grained muds which form the shoals and tidal flats that emerge at low tide (Bourcart and Francis-Boeuff, 1942; Francis-Boeuff, 1947; Guilcher, 1958; Milon, 1935; Müller, 1964; Nelson, 1960; Scruton, 1958). The presence of these clayey deposits is partly due to the absence of wave action. In brackish water, moreover, mud deposition is supported by flocculation. Another effect which promotes deposition is the rise and fall of the water level. Particles may adhere to the mud surface in a manner comparable to the adhesion of lather against the side of a bathtub (Francis-Boeuff, 1947). This process is essentially the same as the scour lag effect. After deposition, high current velocities are necessary to resuspend the mud. Deposition of mud is further promoted by the accumulation of suspended matter in turbidity maxima, as the material has an opportunity to settle at slack tide.

The physico-chemical characteristics of mud deposits are determined by the estuarine circulation and salinity differences. It has been shown that this circulation may distribute marine as well as fluviatile material over the whole length of the estuary. This mechanism tends to smooth differences in sedimentary

properties along the stream axis. However, gradual downstream changes in mineral composition are by no means an exception. An example from the Rappahannock Estuary is given in Table 3.

There is a distinct change in mineral composition downstream in the estuary. It seems feasible to explain this change as the result of diagenetic modifications (transformation of one clay mineral into another) by the transition from fresh to salt water. It is also possible that the changes are due to differential settling, perhaps assisted by differential flocculation and supply of mineral types by the river and the sea. Rivers in the area considered are relatively rich in kaolinite and contain variable amounts of illite, very little montmorillonite, and no chlorite.

Very little is known about the influence of estuarine circulation on sorting of deposits. Consider the theoretical case of an estuary where the salt wedge has a fixed position: material will be carried upstream to the tip of the wedge and be deposited; sand-size particles rolling downstream along the river bed will be deposited in front of the wedge. Under these conditions, the tip of the wedge might be the boundary between two distinct types of deposits. However, the wedge in most instances moves up and down the estuary with the tides, and its position may shift over very great distances as a result of changes in river discharge. Therefore, it seems unlikely that sharp sedimentary boundaries will be developed sufficiently to be preserved in the geological column.

Beyond changes caused by differential settling and different supply of marine fluviatile materials, variations in properties of fine-grained deposits in an estuary can be ascribed to differences in salinity in the overlying water (Müller, 1964). If principally calcium ions are available in fresh water, adsorption of these ions will predominate in fresh and slightly brackish sediments. In brackish sediments magnesium becomes more important than calcium; but in sea water, although monovalent ions have only a small bonding energy, sodium takes over because its concentration is much higher than that of magnesium or calcium.

Table 3. Changes in mineral composition in the Rappahannock Estuary according to Nelson (1960). Presence of a mineral is indicated by a cross.

	Upper river	Lower river	Upper estu- ary	Mid- dle estu- ary	Lower estu- ary
Kaolinite	X	X	X	X	X
Ung. Illite	X	X	X	X	X
Vermiculite	X	X	X	X	X
12.4 Å					
Montmorillonite		X	X	X	X
14.2 Å				X	X
Montmorillonite				X	X
Illite			X	X	X
Chlorite					X
Feldspar					X

The packing of the sediments, as measured by the percolation time for water of corresponding salt content, is also a function of salinity. Brackish-water muds show the closest packing. This may be related to the fact that wholly flocculated particles form a very loose deposit, since much water is trapped in the floccules. Wholly dispersed particles have a water layer and therefore settle with large pore spaces. Partly flocculated suspended matter has lost this water layer, but has not yet attained the structure to entrap water. These relationships should depend to a large degree upon the type of clay mineral, and the packing curve should be quite different from montmorillonite and illite clay. At present, such differences have not been observed in nature.

A considerable number of observations are available concerning grain-size variations in fine-grained deposits in estuaries, including examples of progressive sorting along transportation paths. Almost all measurements, however, have been carried out after removal of organic matter from the samples, and by using peptizers. In this procedure the original state of flocculation is dissolved, so that the settling velocities obtained will, in most cases, be completely different from those under natural circumstances, impeding determination of the true relations between transport forces and sorting. It would be better to determine settling velocities and equivalent grain sizes *in situ*. However, it is very difficult to evaluate the actual settling velocity of floccules in nature, because their size is regulated not only by salinity differences and type of mineral assemblage, but also by sediment concentration and flow conditions. Moderate turbulence appears to be favorable for the formation of large flocculates, but these may be disintegrated again if water movement becomes too rough. Settling velocities may therefore change immediately after a sample has been collected.

SUMMARY

A review of sediment movement in nearshore waters, tidal flat areas, and estuaries shows that various transport mechanisms may be active which tend to hold the material within these regions. Loss to offshore and deep waters seems to be less than one should expect from the rates of coastal water removal and the concentration gradients of suspended sediments from the shores to the sea. Among the accumulation mechanisms holding suspended matter near the coast are settling and scour lag effects, which, in combination with tidal movements, can lead to residual transport towards the coast. Density differences, especially those occurring in and near rivers owing to freshwater runoff, may result in the concentration of suspended materials in turbidity maxima.

The sizes of the particles which are efficiently retained depend on local conditions and on the type of accumulation process, but the retention is usually most effective for fine grained matter. A grain size of about 100μ may tentatively be considered as the upper limit; the lower limit may be as low as $5-10 \mu$. These

values refer to equivalent grain sizes. Retention and sedimentation of fine-grained matter are promoted by flocculation. Scour lag effects are increased if the material is given time to consolidate.

The confinement of suspended matter within a certain region, combined with movement by tidal and density currents, has an important selective effect on the grain-size distribution of the deposits. In many areas the distributional patterns are closely related to water movements, including that of waves. However, the grain size and the concentrations of the suspended matter present are also important. Deeper waters offshore are often sufficiently quiet for mud deposition, but the deposits are coarse since no fine-grained suspended matter is available. Conversely, muddy deposits may be formed in rough water if sufficient fine-grained materials are supplied.

LITERATURE CITED

- ALEXANDER, W. B., B. A. SOUTHGATE, and R. BASSINDALE, 1935. Survey of the River Tees. Part II. The estuary, chemical and biological. *Tech. Paper No. 5, Water Pollution Res., Dept. Sci. Industr. Res.*, London.
- BERTHOIS, L., 1961. Observation directe des particules sédimentaires fines dans l'eau, *Revue Geogr. Phys. Geol. Dyn.*, 4: 39-42.
- BOURCART, J., and C. FRANCIS-BOEUFF, 1942. *La vase*, Hermann, Paris.
- BROCKMANN, C., 1908. Über das Verhalten der Planktoniatomeen des Meeres bei herabsetzung der Konzentration des Meerwassers und über das Vorkommen von Nordseediatoen im Brackwasser der Wesermündung. *Wiss. Meeresunters. Helgoland*, 8: 1-18.
- BROCKMANN, C., 1929. Das Brackwasser der Flussmündungen als Heimat und Vernichter des Lebens. *Senckenberg am Meer*, 29. *Natur und Museum*, 59: 401-414.
- COMMITTEE ON TIDAL HYDRAULICS, CORPS OF ENGINEERS, U. S. ARMY, 1960. Soil as a factor in shoaling processes, a literature review. *Tech. Bull. No. 4, U. S. Army Corps of Engineers*, Washington, D. C.
- CREUTZBERG, F., 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. *Neth. J. Sea Res.*, 1: 257-338.
- CROMMELIN, R. D., 1940. De herkomst van het zand in de Waddenzee. *Tijdschr. Naukd. Ned. Aardrk. Geol. Leiden*, Ser. 2, 57: 347-361.
- CROMMELIN, R. D., 1948. Een onderzoek naar de aard en herkomst van het silt in de Westerschelde en enige aanverwante gebieden. *Nupt. Landbouwhogeschol.*, Wageningen, Netherlands.
- DEMERRA COASTAL INVESTIGATION, 1962. *Report on salinity of Demerara Bar Channel and coastal erosion in British Guiana*. Delti Hydraulics Laboratory, Delft, Netherlands.
- FAVEJEE, J. C. L., 1951. On the origin of the "Wadden" mud. *Mededel. Landbouwhogeschol.*, 31, 5: 113-141.
- FRANCIS-BOEUFF, C., 1947. Recherches sur le milieu fluvial et les dépôts d'estuaire. *Ann. Inst. Océanogr.*, fasc. 23.
- GLANGEAUD, L., 1938. Transport et sédimentation dans l'estuaire et à l'embouchure de la Garonne. Caractères pétrographiques des formations fluviales, sanguines, littorales, et néréites. *Bull. Soc. Géol. France*, 1: 599-630.
- GRIM, R. E., 1951. *Clay Mineralogy*. McGraw-Hill, New York.

- GRY, H., 1942. Das Wattenmeer bei Skallingen, No. 1. Quantitative Untersuchungen über den Sanktstofftransport durch Gezeitenstromungen. *Folia Geogr. Danica*, 11:1-138.
- GUILCHER, A., 1958. *Coastal and submarine morphology*. Transl. by B. W. Sparks and R. H. W. Kneese, Methuen, London.
- GUILCHER, A., 1963. Estuaries, deltas, shelf, slope. In *The Sea*, edited by M. N. Hill; pp. 620-668. John Wiley and Sons, New York.
- HÄNTZSCHEL, W., 1939. Tidal flat deposits (Wattenschlick). In *Recent Marine Sediments*, edited by P. D. Trask; pp. 195-207. Am. Assoc. Petrol. Geologists, Tulsa, Oklahoma.
- KRUMBEIN, W. C., 1939. Tidal lagoon sediments on the Mississippi delta. In *Recent Marine Sediments*, edited by P. D. Trask; pp. 178-195. Am. Assoc. Petrol. Geologists, Tulsa, Oklahoma.
- KRUMBEIN, W. C., and E. ABERDEEN, 1937. The sediments of Barataria Bay. *J. Sediment. Petrol.*, 7: 3-17.
- LUNEBURG, H., 1939. Hydrochemische Untersuchungen in der Elbmündung mittels Elektrokolorimeter. *Arch. Deut. Seewarte*, 59(5):1-27.
- LUNEBURG, H., 1957. Die Oberflächenbeschaffenheit bestimmter Watt-typen der Wesermündung. *Veröff. Inst. für Meeresf. Bremerhaven*, 5:63-103.
- LUNEBURG, H., 1958. Untersuchungen über der quantitativen Wassertransport im Fedderwardes Priel (Wesermündung). *Veröff. Inst. für Meeresf. Bremerhaven*, 5:257-298.
- LUTTMER, J. H., 1950. Zur Schlickbildung im Mündungsgebiet der Ems. *Kolloid-Z.*, 118:1-78.
- MANN, H., 1958. Abwasserprobleme in Tideflüssen. *Ber. Abwasser-techn.* Vertrau., 9:1-12.
- MILON, Y., 1935. Observations sur l'origine et la formation des tangues et vases littorales. *Bull. Soc. Geol. Bretagne*.
- MÜLLER, W., 1964. Unterschiede in den chemischen und physikalischen Eigenschaften vom fluviatilen, brackischen und marinem Sedimenten. *Proc. Sedimentological Congr.*, Amsterdam.
- NELSON, B. W., 1960. Clay mineralogy of the bottom sediments, Rappahannock River, Virginia. *Proc. 7th Natl. Conf. Clays, Clay Minerals*; pp. 135-147.
- NIEBUHR, W., 1955. Beobachtungen über den Sandtransport in der unteren Ems. *Die Küste*, 4:67-93.
- PHLEGER, F. B., and G. C. EWING, 1962. Sedimentology and oceanography of coastal lagoons in Baja California, Mexico. *Bull. Geol. Soc. Am.*, 73:145-182.
- POSTMA, H., 1954. Hydrography of the Dutch Wadden Sea. *Arch. Néerl. Zool.*, 10:405-511.
- POSTMA, H., 1957. Size and frequency distribution of sands in the Dutch Wadden Sea. *Arch. Néerl. Zool.*, 12:319-349.
- POSTMA, H., 1960. Einige Bemerkungen über den Sanktstofftransport im Ems-Dollart Gebiet. *Verhandel. Koninkl. Ned. Geol. Mijnbouwk. Genoot. Geol. Ser.*, 19: 103-110.
- POSTMA, H., 1961. Suspended matter and secchi disc visibility in coastal waters. *Neth. J. Sea Res.*, 1:390-390.
- POSTMA, H., and K. KALLE, 1955. Die Entstehung von Trübungszonen im Unterlauf der Flüsse, speziell im Hinblick auf die Verhältnisse in der Unterelbe. *Deut. Hydrograph. Z.*, 3:137-144.
- REYNE, A., 1961. On the contribution of the Amazon River to accretion of the coast of the Guianas. *Geol. Mijnbouwk.*, 40:219-224.
- SCRUTON, P. C., 1956. Oceanography of Mississippi Delta sedimentary environments. *Bull. Am. Assoc. Petrol. Geologists*, 40(12): 2064-2082.
- SCRUTON, P. C., 1958. Sediments in the eastern Mississippi delta. *Contre Scripta Inst. Geograph. N.S.*, 79.
- SCRUTON, P. C., 1960. Delta building and deltaic sequences. In *Recent Sediments, N.W. Gulf of Mexico, 1951-1958*; pp. 82-102. Am. Assoc. Petrol. Geologists, Tulsa, Oklahoma.
- SHEPARD, F. P., 1953. Sedimentation rates in Texas estuaries and lagoons. *Bull. Am. Assoc. Petrol. Geologists*, 37:1919-1934.
- SHEPARD, F. P., 1960. Mississippi Delta: Marginal environments, sediments and growth. In *Recent Sediments, N.W. Gulf of Mexico, 1951-1958*; pp. 56-81. Am. Assoc. Petrol. Geologists, Tulsa, Oklahoma.
- SHEPARD, F. P., and D. G. MOORE, 1954. Central Texas coast sedimentation: characteristics of sedimentary environment, recent history, and diagenesis. *Bull. Am. Assoc. Petrol. Geologists*, 39:1463-1593.
- SUNDBORG, F. A., 1956. The river Klarälven, a study on fluvial processes. *Geogr. Ann. Arg.*, 37:125-316.
- TERWINDT, J. H. J., J. D. DE JONG, and E. VAN DER WILK, 1963. Sediment movement and sediment properties in the tidal area of the lower Rhine (Rotterdam Waterway). *Verhandel. Ned. Geol.-Mijnbouwk. Genoot. Geol. Ser.*, 21.
- VAN ANDEL, T. H., and H. POSTMA, 1954. Recent sediments of the Gulf of Friesland. *Verh. Kon. Ned. Akad. Wetensch. Ier reeks*, 20:1-245.
- VAN BENDEGOM, L., 1950. Enkele beschouwingen over de vorming en vervorming van Wadden. *Waddensymposium*; *Tijdschr. Koninkl. Ned. Aardrijksk. Genoot.*; pp. 66-74.
- VAN STRAATEN, L. M. J. U., 1954. Composition and structure of recent marine sediments in the Netherlands. *Leidsche Geol. Mededel.*, 9:1-110.
- VAN STRAATEN, L. M. J. U., 1960a. Some recent advances in the study of deltaic sedimentation. *Liverpool and Manchester Geol. J.*, 2:3, 411-442.
- VAN STRAATEN, L. M. J. U., 1960b. Transport and composition of sediments. *Verh. Kon. Ned. Geol.-Mijnbouwk. Genoot. Geol. Ser.*, 19:279-292.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1957. Accumulation of fine-grained sediments in the Dutch Wadden Sea. *Geol. Mijnbouwk.*, 19:329-354.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1958. Tidal action as a cause for clay accumulation. *J. Sediment. Petrol.*, 28:406-413.
- VAN VEEN, J., 1950. Eb- en vloedschaarsystemen in de Nederlandse getijwateren. "Waddensymposium". *Tijdschr. Kon. Ned. Aardrijksk. Genoot.*, pp. 43-65.
- VAN VEEN, J., 1952. Development of marine plains (penetration of sea water in Dutch tidal rivers and inland waters). *Publ. 38, Assoc. Intern. Hydrol.*; pp. 101-111.
- VERWEY, J., 1952. On the ecology of distribution of cockle and mussel in the Dutch Wadden Sea, their role in sedimentation and the source of their food supply. *Arch. Néerl. Zool.*, 10:171-230.
- WELDER, F. A., 1959. Processes of deltaic sedimentation in the Lower Mississippi River. *Tech. Rept. 12, Coastal Studies Inst.*, Baton Rouge, Louisiana.
- WHITEHOUSE, U. G., and L. M. JEFFREY, 1955. Peptization resistance of selected samples of kaolinitic, montmorillonitic, and illitic clay minerals. *Proc. 2nd Natl. Conf. Clays, Clay Minerals*; pp. 260-281.
- WHITEHOUSE, U. G., and R. S. McCARTER, 1958. Diagenetic modification of clay mineral types in artificial sea water. *Proc. 3rd Natl. Conf. Clays, Clay Minerals*, pp. 81-119.
- WHITEHOUSE, U. G., L. M. JEFFREY, and J. D. DEBRECHT, 1960. Differential settling tendencies of clay minerals in saline waters. *Proc. 5th Natl. Conf. Clays, Clay Minerals*, pp. 1-79.
- WIJGERS, A. J., 1960. Die Kongrowenverteilung der holozänen sedimente im Dollart-Ems-Estuarium. *Arch. Néerl. Geol. Mijnbouwk. Genoot. Geol. Ser.*, 19: 111-129.

Rates of Sediment Accumulation in Modern Estuaries

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If one approaches the problem of estuarine sedimentation from a philosophical vantage point, it is clear that the depositional mechanism follows the classic format of energy gradients. The sediment flux proceeds from the area of higher energy to the area of lower energy; the suspended or tractive sediment concentration is directly proportional to the transportation energy, but only when the sediment source is not a limiting factor. High sediment concentrations may come into an estuary either from entering rivers or from the sea by tidal inflow. If we accept the normal flow sense from stream gradient concepts as *positive* towards the sea (i.e., downslope), then the flow sense directed from the sea may be considered *inverse*. Although Pritchard (elsewhere in this volume) has modified his earlier views somewhat, his original terminology for describing the dynamic balance of estuaries followed this logic. Pritchard (1952) described the temporal balance attained by the dynamic mixing of fresh and salt water in an estuary, when operating under the modulating climatic influence of rainfall and evaporation, as two of the *positive* and *inverse* end-members of precipitation versus evaporation. Thus, the hydrological and sedimentological concepts are directly comparable.

Estuaries fronting streams with high sediment discharge rates may fill very rapidly by deposition of tractive and suspended loads at their heads, prograding the delta front (as in the case of Grand Lake, Louisiana), or they may fill relatively more slowly in their basin centers where vertical accretion of suspended sediment occurs. Basins filled entirely by river-transported sediment inflow may be considered as the *positive-filled* end-member of basic estuarine types. Estuaries with entering streams of low sediment discharge may be filled solely or to the largest extent by sediments entering the estuary from the sea with every flood tide (as is the case in the Dutch tidal flats). This second type can be considered as an *inverse-filled* estuary and thus the opposite end-member.

Through the Late Pleistocene epoch, sedimentation rates in the marine and marginal marine environment containing the estuaries have varied from times of relatively intense deposition to periods of extremely slow deposition or wholesale erosion and deep weathering. The rate of sediment supply in the Pleistocene

was controlled largely by sea-level oscillations, while geographic position and the topography of the area receiving the sediment influenced the amount of material accumulated.

Interglacial periods provided conditions for vast sediment accumulation in the marginal marine environment of bays, lagoons, and the continental shelf. The subsequent onset of a glacial period brought about the release of these previously deposited unconsolidated sediments to the continental slopes and to the deep sea; this release was caused by the erosive action of the receding seas and by stream degradation. Post-glacial sediments are now blanketing the deeply incised stream channels which formed during the glacial eustatic fall of the sea. During earlier high stands of the sea, however, marginal marine deposits of bays and lagoons were formed at elevations higher than now. The bays, lagoons, and estuaries with which studies of Recent sediments have been concerned are multiple scars testifying to the action of many glacial-eustatic changes in sea level.

The present discussion applies specifically to those events which have accompanied the Late Pleistocene and Recent epochs. A few tentative conclusions new can be drawn from the many investigations which have applied radiocarbon dating to these depositional products, when the resulting rates of sediment accumulation are considered in the light of established curves of eustatic sea-level rise (Siepman, 1964).

PROCESSES AND PRODUCTS

Marine sedimentation is commonly related to four broad environmental categories: (1) the marginal marine environment containing estuaries such as bays and lagoons; (2) the continental shelf; (3) the continental slope; and (4) the deep sea. Accumulative processes and products vary sharply between these areas and locally within any one environment. For the purpose of the present discussion, we can disregard the continental slopes and the deep sea as specific sources for estuarine sediments, but the continental shelf areas are an important consideration. Figure 1 illustrates schematically the various generalized environments to show their interrelationships. The area of concern here is mainly the small square perched at the landward edge of the continental shelf that has been enlarged to show the marginal marine environment.

The continental shelf is a transitional sedimentation area where accretion or erosion is dependent upon the

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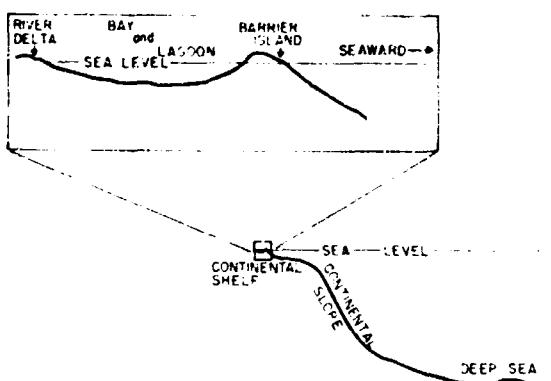


Fig. 1. Schematic representation of the four broad environmental areas of marine sedimentation. The small area representing the marginal marine environment has been enlarged to show the details of the setting.

relative behavior of waves and sea-level oscillations. Sediment accumulation on the continental shelves, as well as in adjacent open bays and lagoons, occurs during periods of low wave activity, whereas high wave activity tends to sort sediments and, in part, remove them to deeper water (Inman and Rusnak, 1956; Curray, 1960). With falling sea level the sediments on the shelf are rigorously reworked by the regressing breaker zone which transports finer material seaward and leaves coarser sands lagging behind as regressive sheet sands (Curray, 1960; Rusnak, 1960). With rising sea level, the breaker zone of the transgressive sea establishes new profiles of equilibrium by throwing unconsolidated coarser sediments up before the advancing shore and washing finer material out to deeper water. Barrier islands and transgressive sheet sands are formed by this dynamic process (Curray, 1960; Rusnak, 1960; Shepard, 1960).

Within the marginal marine environment transported sediments are generally fixed in locally migrating beach dunes and barrier islands, or they are trapped within protected segments of adjacent estuary basins. A covering mantle of successive sediment accumulations fixes each underlying layer unless a change in sea level exposes them to weathering and erosion. As sea level falls, a portion of the marginal basin deposits can become deeply incised by stream cutting, but most of the strata will remain within the original basin configuration unless subjected to very extensive weathering. Many remnants of previous bays, which formed at higher elevations, are present along stable coasts such as segments of the Atlantic coastal plain. In contrast to falling sea level, rising seas may completely obliterate barrier islands, bays, and lagoons: deposits during the processes of establishing a new wave equilibrium profile with each advancing wave front. The development of wave equilibrium profiles on unconsolidated sediments is a very rapid process, occurring even within very short periods of high storm-wave activity or with sudden sea-level fluctuations (Price, 1954; Inman and Rusnak, 1956; Rusnak, 1960; Shepard, 1960). Sediments of a gradu-

ally sloping coastal plain may be removed by wave-equilibrium profile development in an advancing sea to a probable maximum depth of ten meters, judging from studies of maximum shoreface slope development and erosion in alluvial regions of moderate wave activity (Price, 1954; Inman and Rusnak, 1956).

Figure 2 represents a schematic view of estuarine dynamics showing river flow as moving obliquely towards the viewer carrying sediment into the basin, lateral distributive processes acting to spread sediments, and tidal inlet flow carrying sediment into the basin during flood tide. Also, in addition to local biological activity, particulate matter may be derived from within the basin itself by wave erosion of the estuary boundary during normal periods of wind-generated wave activity. The material from the basin margins is "self-digested" and merely redistributed over the basin floor, as an internal source of supply. The external sources of supply are from the river and the tidal influx. Sediment derived from the adjacent continental shelf area, through "wave breaker" erosion and alongshore drift, can supply basin fill and create the commonly observed tidal deltas formed at inlets (Fig. 3).

It is clear that only external sources of supply can

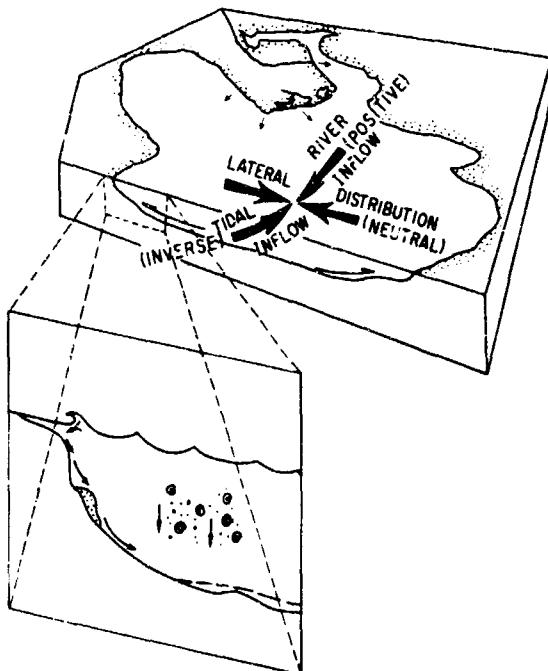


Fig. 2. Schematic representation of estuarine dynamics showing river flow moving obliquely towards the viewer, tidal inlet flow moving obliquely away from the viewer during flood tide, and lateral distribution processes acting to disperse sediment throughout the basin. The enlarged section illustrates vertical accretion of suspended material and lateral distribution of previous deposits by shoreline erosion and redistribution. Basin sediments accumulate by positive-filling from rivers, inverse-filling from the sea by flood tides, and neutral-filling by self-digested materials eroded from the basin margin.

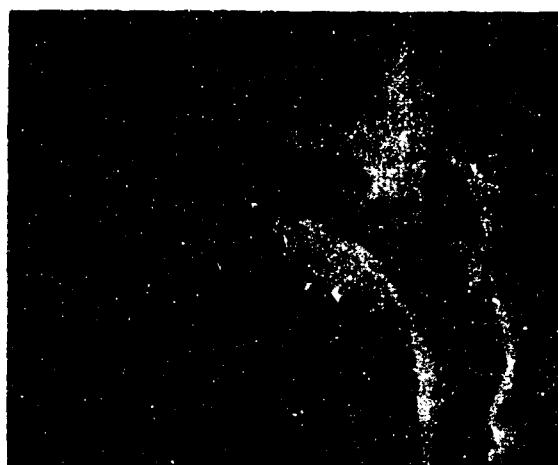


Fig. 3. Aerial photograph of tidal delta formed at the inlet of an estuary.

fill a basin, whether these sources be wind, river, biological, or tidal. Self-digestion of basin boundaries can only redistribute sediment already present without decreasing the basin's volume.

Because these several forms of basin filling tend to overlap somewhat and because there may be some confusion between concept and process, estuarine filling is here defined categorically. Basins which are filled by lateral distribution of suspended river and biological materials can be considered as *positive-filled basins*. Redistribution of basin sediment from local shoreline margins within the basin can be thought of as *neutral-filled (non-filling) basins*. This type may smooth over the basin floor by removing "highs" and filling "lows", but it does so without a change in basin volume. The last type considered is the *inverse-filled basin* whose source of sediment supply is from the sea by eroding locally available deposits and carrying them into the basin through inlets.

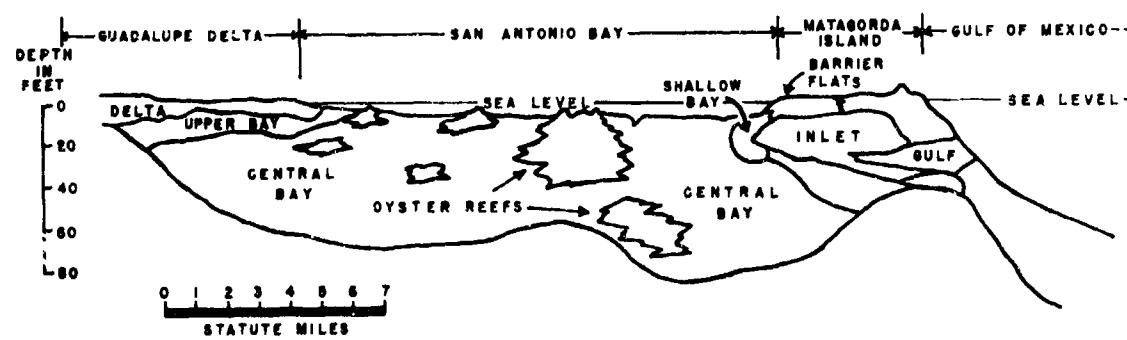
CLIMATE AND RATES OF ACCUMULATION

The rate at which sediment will accumulate in a

basin is dependent, however, not only upon its source of supply and geographic position, but also on its local climate. In humid regions with major river sources, the rate of accumulation can be very high, as in the deltas of the Mississippi or the Orinoco Rivers. In arid regions the rate of accumulation may be very low because sediment can be supplied only by winds and the sea. The rate at which terrigenous materials are transported and supplied by streams and winds is thus largely a matter of local climate. Moreover, climate controls the degree of biological productivity within the basins by influencing the supply of required nutrients, and other factors. Biological productivity and rates of accumulation, such as oyster reefs, however, are mentioned only in passing, as the emphasis is placed on rates of changing supply and deposition of terrigenous material.

Most temperate estuaries with moderate runoff fall into the first category as positive-filled basins. If runoff is deficient for some reason, a temperate estuary may be inverse-filled, as described by Van Straaten and Kuenen (1957, 1958), Van Straaten (1961), and Postma (1957, and elsewhere in this volume) of the Dutch estuaries and tidal flats. Inverse-filled estuaries are undoubtedly most commonly found in semi-arid situations such as the Laguna Madre of Texas (Fisk, 1959; Rusnak, 1960). Neutral filling does not appear to be a pure form in nature, but it may exist. The closest relative of a neutral basin would seem to be the smooth oval lakes on the Mississippi Delta (Shepard, 1960), the remarkable Carolina Bays, or the modified forms described from along the Texas Gulf Coast by Price (1947).

Many modern temperate estuaries (Fig. 4) are to some extent a combination of each end-member. The bay head is generally filled by a prograding delta front advancing toward the positive-filled basin floor which extends outward from the foot of the delta to the typical central depression. The bay center contains both river sediments and organic products such as oyster reefs. Bay margins may be greatly extended laterally by shoreline erosion, forming more circular



SUBSURFACE LITHOFACIES

Fig. 4. Diagrammatic cross-section of a positive-filled modern estuary (San Antonio Bay) from the central Texas coast showing the numerous environmental facies.

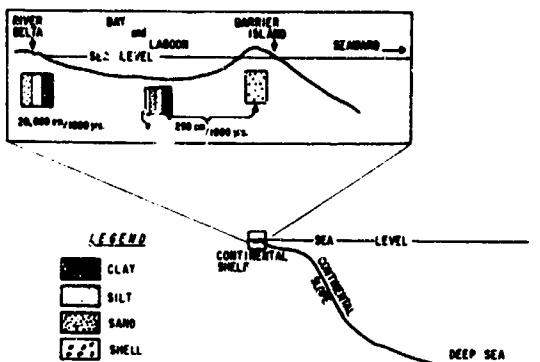


Fig. 5. Schematic representation of textural types and long-term average rates of sediment accumulation in a marginal marine environment.

basin boundaries, and supplying eroded sediment to the deep central area. Lastly, the inlet mouth of the estuary is constantly under the influence of the tidal delta, as well as the adjacent sand source, supplied by winds, from the fronting barrier island which characteristically encloses the bays.

Proceeding from our present knowledge of sea-level rise, it seems evident that we may consider the rate of sediment accumulation between two extremes: first, the estuary which has no sediment entering it is obviously one of zero accumulation rate; and second, the estuary which fills at the same rate at which its water level rises is one having the highest rate of sediment accumulation possible, by definition of estuarine sedimentation. The first extreme is certainly unlikely and the second extreme would border on becoming a marshland. Now, it is clear from many recent studies (Shepard *et al.*, 1960; Van Straaten, 1964) that many modern estuaries formed semi-enclosed basins with a fronting barrier bar or barrier island some time after sea level had drowned the previously exposed depressions. Thus, the estuaries did not become effective entrapping basins until some of the large-scale flushing activity of the tides could be diminished. Under the new conditions, the estuary could become a more effective settling basin, and sedimentation could continue until a balance was attained between wave, current, and tidal energy dissipation. Once a balance is established between these factors, no marked change in basin geometry will follow (Phleger and Ewing, 1962).

We may conclude, therefore, that if a balance of sediment accumulation with energy dissipation occurs, the rate of sediment accumulation must be equal to the sea-level rise. The best estimates of sea-level rise over the period of 15,000 to 6,000 years ago, when most of our modern estuaries came into existence, appear to be those estimates which have been published by Shepard (1964) and Stuiver and Daddario (1963). These writers indicate that sea level has gradually slowed in its rate of rise from 2.8 feet (0.85 m) per hundred years between about 15,000 and 6,000 years ago, to a rate of 1 foot (0.3 m) per hundred

years between 6,000 and 2,600 years ago, and then to about 0.5 feet (0.15 m) per hundred years between 2,600 years ago and the present. As most of the modern estuaries do not appear to have become semi-enclosed embayments until about 6,000 years ago (in areas along the Atlantic and Gulf Coast where data are available) we need only consider the past 6,000 years in this analysis.

Thus, if a balance exists between basin filling and sea-level rise, maximum sediment accumulation of 1 foot (0.3 m) per hundred years may be considered for the period 6,000 to 2,600 years B.P. A lower rate of 0.5 feet (0.15 m) per hundred years should be required after about 2,600 years ago.

If we can now draw upon a few well-documented examples from the area of the Gulf of Mexico, we have at our disposal several estimates of accumulation rates for various environments. For humid regions, the estimated accumulation rates vary from a high of about 300 m per thousand years for the prograding Mississippi Delta deposits (Shepard, 1960; Scruton, 1960) to a low of about 2 to 4 m per thousand years for bays and estuaries (Shepard, 1953; Shepard and Moore, 1960). For semi-arid lagoons the rate is only 1 m per thousand years (Rusnak, 1960). The rate of accumulation given is averaged over the greater part of these basins although local topographic highs, or areas of little supply, may have little or no sediment accumulation, while depressions may fill at a slightly higher rate. Inlets, which may cut and fill at an extremely rapid rate, are excluded.

Neglecting the extremely high rate of accumulation represented by the deltas, we can estimate the rate of accumulation for the marginal marine environment with a probable error of no greater than a factor of two. These estimates (Fig. 5) are 2 m per thousand years for humid bays and estuaries, and 1 m per thousand years for arid and semi-arid lagoons. These rates apply only to the accumulation which has occurred since the last post-glacial rise of sea level, or to no more than about 10,000 to 15,000 years B.P. Prior to this time, of course, sedimentation was not taking place in these specific areas because of lowered sea level. Instead, erosion by wind deflation and stream incision was taking place to add to the supply being contributed to the continental slopes and deep sea by the abundant supply of glacial debris. If sedimentation rates equaled the rate of sea-level rise for any given area, the marginal marine environments could be typified by extensive marshlands and tidal flats. Because many of our estuaries are unfilled remnants of previously incised stream beds, this must mean that sediment accumulation rates within them were lower than sea-level rise. An upper limit of sediment accumulation based on the overall, time-average, glacial-eustatic rise in sea level would have to be no greater than 6 m per thousand years over the span of the last 15,000 years. A higher rate of accumulation would cause the building of a prograding delta front extending into the sea. It is obvious that most estuaries have had a lower rate of accumu-

lation because they are still embayments in the coastline.

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LITERATURE CITED

- CURRAY, J. R., 1960. Sediments and history of Holocene transgression, continental shelf, northwest Gulf of Mexico. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and Tj. H. van Andel; pp. 221-266. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.
- FISK, I., 1959. *Padre Island and the Laguna Madre Flats, Coastal South Texas: Second Coastal Geog. Conf. Coastal Studies Inst.*; pp. 103-152. Louisiana State Univ., Baton Rouge, Louisiana.
- INMAN, D. L., and G. A. RUSNAK, 1956. Changes in sand level on the beach and shelf at La Jolla, California. *U. S. Army Corps of Engineers, Beach Erosion Bd., Tech. Memo. 82.*
- PHLEGER, F. B., and EWING, G. C., 1962. Sedimentology and oceanography of coastal lagoons in Baja California, Mexico. *Geol. Soc. Am. Bull.*, 73:145-182.
- POSTMA, H., 1957. Size frequency distribution of sands in the Dutch Wadden Sea. *Arch. Neerl. Zool.*, 12:319-349.
- PRICE, W. A., 1947. Equilibrium of form and forces in tidal basins of coast of Texas and Louisiana. *Am. Assoc. Petrol. Geol. Bull.*, 31:1619-1663.
- PRICE, W. A., 1954. Dynamic environments; reconnaissance mapping, geologic and geomorphic, of continental shelf of Gulf of Mexico. *Trans. Gulf. Coast Assoc. Geol. Soc.*, 4:75-107.
- PRITCHARD, D. W., 1952. A review of estuarine hydrography. In *Advances in Geophysics*; pp. 243-280. Academic Press, New York.
- RUSNAK, G. A., 1960. Sediments of Laguna Madre, Texas. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and Tj. H. Van Andel; pp. 153-196. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.
- SCRUTON, P. C., 1960. Delta building and deltaic sequence. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and Tj. H. Van Andel; pp. 82-102. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.
- SHEPARD, F. P., 1953. *Sedimentation rates in Texas estuaries and lagoons*; vol. 37, no. 8, pp. 1919-1934. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.
- SHEPARD, F. P., 1960. Gulf Coast barriers. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and Tj. H. Van Andel; pp. 197-220. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.
- SHEPARD, F. P., 1964. Sea level changes in the past 6,000 years; possible archeological significance. *Science*, 143:574-576.
- SHEPARD, F. P., and D. G. MOORE, 1960. Bays of central Texas coast. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and Tj. H. Van Andel; pp. 117-152. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.
- SHEPARD, F. P., F. B. PHLEGER, and T. H. VAN ANDEL, 1960. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and Tj. H. Van Andel; p. 394. Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.
- STUIVER, M., and J. J. DADDARIO, 1963. Submergence of the New Jersey coast. *Science*, 142:951.
- VAN STRAATEN, L. M. J. U., 1961. Sedimentation in tidal flat areas. *J. Alberta Soc. Petrol. Geologists*, 9(7):203-226.
- VAN STRAATEN, L. M. J. U., 1964. *Deltaic and shallow marine deposits. Development in Sedimentology*. Elsevier Publishing Co., Amsterdam.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1957. Accumulation of fine-grained sediments in the Dutch Wadden Sea. *Geol. Mijnbouw. (NW Ser.)*, 19:329-354.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1958. Tidal action as a cause of clay accumulation. *J. Sediment. Petrol.*, 28:405-409.

Quantitative Research on Littoral Drift and Tidal Inlets

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A number of factors play a role in the regime of inlets, and many are interdependent. Moreover, most of them vary continuously in intensity with the result that conditions are never steady. It is not surprising, therefore, that our knowledge of the processes taking place in inlet environments shows many deficiencies. It is necessary to fill the gaps in our knowledge, in view of the economic interests in shipping and coastal stability. Such knowledge must be of a quantitative nature to permit a more rational approach to the solution of inlet problems.

This paper gives an account of quantitative research on the problems of littoral drift and tidal inlets in progress or in preparation at the Coastal Engineering Laboratory of the University of Florida. We will confine attention to tidal inlets on sandy coasts with littoral drift, and will focus on the sand drift alongshore, the sand transport through the inlet, the interplay of both in the inlet regime, and the resulting stability of the inlet.

LITTORAL DRIFT

The complex situation at seashores with regard to sediment movement has prohibited an analytical approach to the solution of the littoral drift problem. Attempts have been made to determine the rate of littoral drift as a function of the pertinent variables in laboratory and in field experiments; both have drawbacks. In the field, the conditions cannot be controlled, whereas the laboratory data are not directly comparable to the prototype because of scale effects. About all we can say now is that the rate of littoral drift is probably proportional to the wave power expended on the coast and to some function of the angle of wave incidence with a maximum for a deep water angle near 50° and a zero value for a zero angle of incidence. It is true that some knowledge has been gained in the last decade on some special problems, for example, laminar and turbulent boundary layers under waves, ripple formation, and the onset of motion of sand grains on a sloping bed by waves, but our present knowledge is insufficient for a complete analysis of the problem.

There are two research programs in progress at the Coastal Engineering Laboratory dealing with the problem of littoral drift. Together they constitute a combined field and laboratory approach, whereby the conditions in the laboratory tests are as close to prototype conditions as possible to minimize scale effects.

FIELD TESTS

In the field tests fluorescent tracers are used for the detection of the pattern and the rate of movement of beach sand under various conditions of waves and longshore currents (Bruun and Battjes, 1963). The procedure is to coat sand grains with colored fluorescent substances. Care is taken that the tracer grains have the same mechanical properties as the grains of the test beach. A certain amount of this tracer material is added in water-soluble bags on the updrift side of a 1,000-foot-long pier extending in the ocean to about a 20-foot depth below mean sea level. Suspended load samplers and bed load samplers are operated from the pier at various distances from shore. Simultaneously, environmental factors such as waves, longshore currents, tide, wind, and bottom topography are measured. The sand sampling continues until no tracer material appears in the samples. Because visual analysis of the samples is too tedious and time consuming, an electronic scanner was constructed for this phase of the work.

The fluorescent tracer method allows a determination of the rate of movement of individual sand grains as well as of the total rate of transport. However, it does not give details of the longshore variation in the rate of littoral sand transport in connection with sand waves migrating alongshore. Such migrating waves are significant in littoral processes, and it is important to know more about them. The best way to trace them would seem to be frequent, detailed, accurate, hydrographic surveys of several wave lengths of the migrating sand waves, in the longshore direction. Aerial photography has tremendous advantages for this purpose as compared to conventional survey methods (Sonu, 1964). It gives simultaneous quantitative data over an extended area and shows patterns and details.

The objection might be raised that the fluorescent tracer technique does not explain a number of details of the phenomenon. With the present state of knowledge and instrumentation, however, it is impossible to accomplish complex and detailed studies under field conditions. Nevertheless, the results can be of scientific and practical value inasmuch as they give the integrated effect of the many factors involved with a degree of accuracy and detail which is not possible using conventional field techniques. Data on the rates of littoral drift obtained from measurements of rates of accretion on the updrift side of littoral barriers do

not give any clue as to the distribution of the rate of littoral drift normal to shore, nor do they relate the rate of littoral drift to particular wave conditions because of the rather long time interval between successive surveys; they give the net drift only. The tracer measurements have a duration of but a few hours so that the wave conditions may be unchanged, in terms of spectra, during the measurements. Knowledge concerning the distribution normal to shore of the rate of longshore drift is obtained in the tracer experiments by simultaneous employment of tracers of various colors placed at certain distances from shore but at equal distances from the pier.

LABORATORY TESTS

The laboratory experiments are aimed at a more detailed observation and analysis of sand transport by the combined action of waves and currents. Two main problem areas are being investigated: (1) waves and currents running perpendicular or nearly perpendicular to each other (littoral drift problem). (2) waves and currents running with or against each other (inlet channel problem).

The experiments are carried out in a 150-foot-long, 6-foot-wide wave tank with a diffraction basin at the downwave end. Currents are run through the wave tank or transversely through the diffraction basin.

The conditions in this laboratory study are close to prototype conditions. The water depths are up to 3 feet, wave periods are from one-half second up, wave heights are up to $1\frac{1}{2}$ feet, current velocities are up to 2 feet/second, and sand is used as bed material. The overall result is that scale effects are minimized.

In both series of experiments the development of bed roughness and the rate of sand transport are measured for various relative strengths of waves and currents ranging from predominant wave action to predominant current action. The bed roughness is interpreted in terms of friction coefficients. The fluorescent tracer technique will be employed in the laboratory tests and should be of particular value in cases where the sand transport is not unidirectional because of the wave action. By using these techniques, the following may be accomplished:

1. Determining the rates of sand transport caused by waves and currents in various combinations of direction and relative strength. These data are important for evaluating littoral drift as well as solid transport in tidal inlets and estuaries where the direction of wave propagation and the direction of the current may nearly coincide.
2. Determining the bed roughness in terms of friction coefficient for the experimental conditions. Such data are pertinent to tidal hydraulics computations as well as to computing longshore currents. Lack of knowledge of friction coefficients has prohibited reliable predictions of longshore currents.

SAND TRANSPORT THROUGH INLETS

Even though the current activity is mainly respon-

sible for the sand transport through tidal inlets, the conditions differ appreciably from those in rivers, because of the greater unsteadiness of the flow and the effect of wave action. The considerable knowledge in the field of sediment transport in rivers is, therefore, not directly applicable to inlet conditions. It has long been known that wave action would increase the material transport, particularly when the current is weak and incapable of setting the grains in motion, but a quantitative understanding of the processes has not yet been obtained. Recent experiments by Inman and Bowen (1963) gave new information on the subject, but their experiments were representative of conditions on a beach between rip currents where the velocities, which are due to mass transport in the waves, are very low compared to the velocities occurring in tidal channels. The maximum current velocity used by Inman and Bowen was only 6 cm/sec. The Coastal Engineering Laboratory is presently conducting laboratory tests on this aspect of the sand transport problem.

SAND TRANSFER AND INLET STABILITY

An analysis of the interplay of littoral drift and sand transport at unimproved inlets should provide information on how the littoral drift is transferred across the inlet to the downdrift side, how the inlet is affected, and what the resulting stability characteristics will be.

Three kinds of inlet stability were distinguished by Bruun and Gerritsen (1960):

Bypassing stability—the ability of the inlet to bypass littoral drift from the updrift shore to the downdrift shore.

Location stability—associated with the rate of migration of the inlet as a whole or of individual channels in the shoals.

Cross-sectional stability—the ability of the inlet to maintain a certain cross section or at least a certain cross-sectional area.

The stability of inlets, like the stability of anything which is in a state of dynamic equilibrium, is brought about by a balance between antagonistic agencies. In the case of the stability of a tidal inlet, these agencies are the sand transport through the inlet and the littoral drift. Bruun and Gerritsen (1960) mention the back-and-forth movement of sediments through the inlet as a "rolling carpet". Part of this carpet is continuously deposited at both ends, that is, in the bay and in the ocean. Therefore, without a supply of littoral drift this carpet would "wear out" completely and a nonscouring channel would develop. The characteristics of such an inlet are very different from those of tidal inlets on littoral drift shores and will not be considered.

The fact that the relative strength of littoral drift and flow through the inlet is of great importance to inlet stability has been known for a long time, but Bruun and Gerritsen (1960, 1961) were the first to express this in quantitative terms. They analyzed a great number of tidal inlets and found that

$\Omega/M > 300$	indicates a higher degree of stability
$\Omega/M < 100$	indicates a lower degree of stability
$M/Q_M > 200-300$	indicates predominant bar bypassing
$M/Q_M < 10-20$	indicates predominant tidal flow bypassing

where

Ω = tidal prism

M = mean annual net amount of littoral drift

Q_M = maximum discharge through the inlet during an average spring tide.

M is expressed in cubic units per year.

Ω is expressed in cubic units per half tidal cycle.

Q_M is expressed in cubic units per second.

Three factors should be considered when applying these criteria:

1. Both Ω and Q_M are used to indicate the flushing power of the inlet. This does not seem to be necessary inasmuch as they are proportional to one another. For a simple harmonic tide $\Omega = Q_M T/\pi$ (T is the tidal period) and from this relationship deviations are minor compared to the uncertainties and approximations involved in the criteria.

2. The parameter to be used to indicate the flushing power of the inlet should not be the tidal flow as such but an expression for the actual material movement, say the maximum rate of sand transport through the inlet in absence of littoral drift, V_o . That still Ω or Q_M could be used is due to the fact that for natural conditions V_o is roughly proportional to Ω or Q_M .

3. The parameter describing the littoral drift should be the rate of movement of material along adjacent shores, regardless of direction. We will use M' , the mean total rate of transport from both sides, instead of M , the mean net rate of transport.

With reference to Items 1, 2, and 3 above, we will use M'/V_o instead of Ω/M and M/Q_M as a dimensionless parameter indicative of the overall stability of the inlet as well as of the mode of bypassing littoral drift.

BYPASSING STABILITY

In the study of natural bypassing of the littoral drift, Bruun and Gerritsen (1961) noted that at most inlets a combination of bar bypassing and tidal flow bypassing occurs. The relative importance of both is determined by the ratio M'/V_o . Denoting by " p " the fraction of M' bypassed by tidal flow action (so that $(1-p)$ is the fraction of M' bypassed over the outer bar), we write

$$p = f_1(M'/V_o) \quad (1)$$

Function f_1 is not known exactly, but we do know that

$$p \rightarrow 1 \quad \text{for small } M'/V_o$$

$$p \rightarrow 0 \quad \text{for large } M'/V_o$$

and that f_1 must be continuous, monotonic, and differentiable. (There is no rigorous proof presented for the latter statements but they should hold true for physical reasons.)

Based on this information we tentatively draw f_1 as in Figure 1. Actual measurements, in the field or in the laboratory, should enable us to determine f_1 quantitatively.

Knowledge of p gives information as to the distribution of the littoral drift bypassing the inlet: pM' by tidal flow, $(1-p)M'$ over the outer bar. Still, there is no indication of the effect of littoral drift on the inlet stability. For this we have to consider these rates of transport in relation to the material transport through the inlet in absence of littoral drift:

$$pM'/V_o = f_2(M'/V_o) \quad \text{— relative drift load in tidal channels} \quad (2)$$

and

$$(1-p)M'/V_o = f_3(M'/V_o) \quad \text{— relative drift over the outer bar.} \quad (3)$$

The functions f_2 and f_3 are plotted in Figure 2,

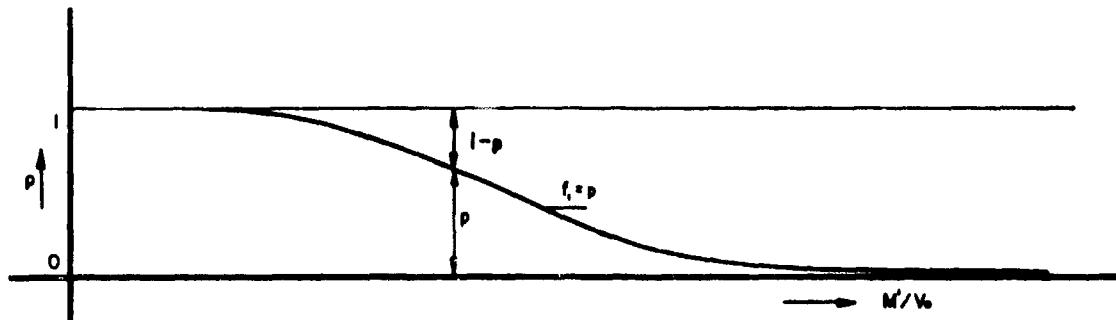


Fig. 1. p vs. M'/V_o . V_o = Maximum rate of sand transport through inlet in absence of littoral drift. M' = Total (not the net) rate of littoral drift. pM' = Total rate of drift bypassed by tidal flow through the gorge. $(1-p)M'$ = Total rate of drift bypassed by wave action over the outer bar.

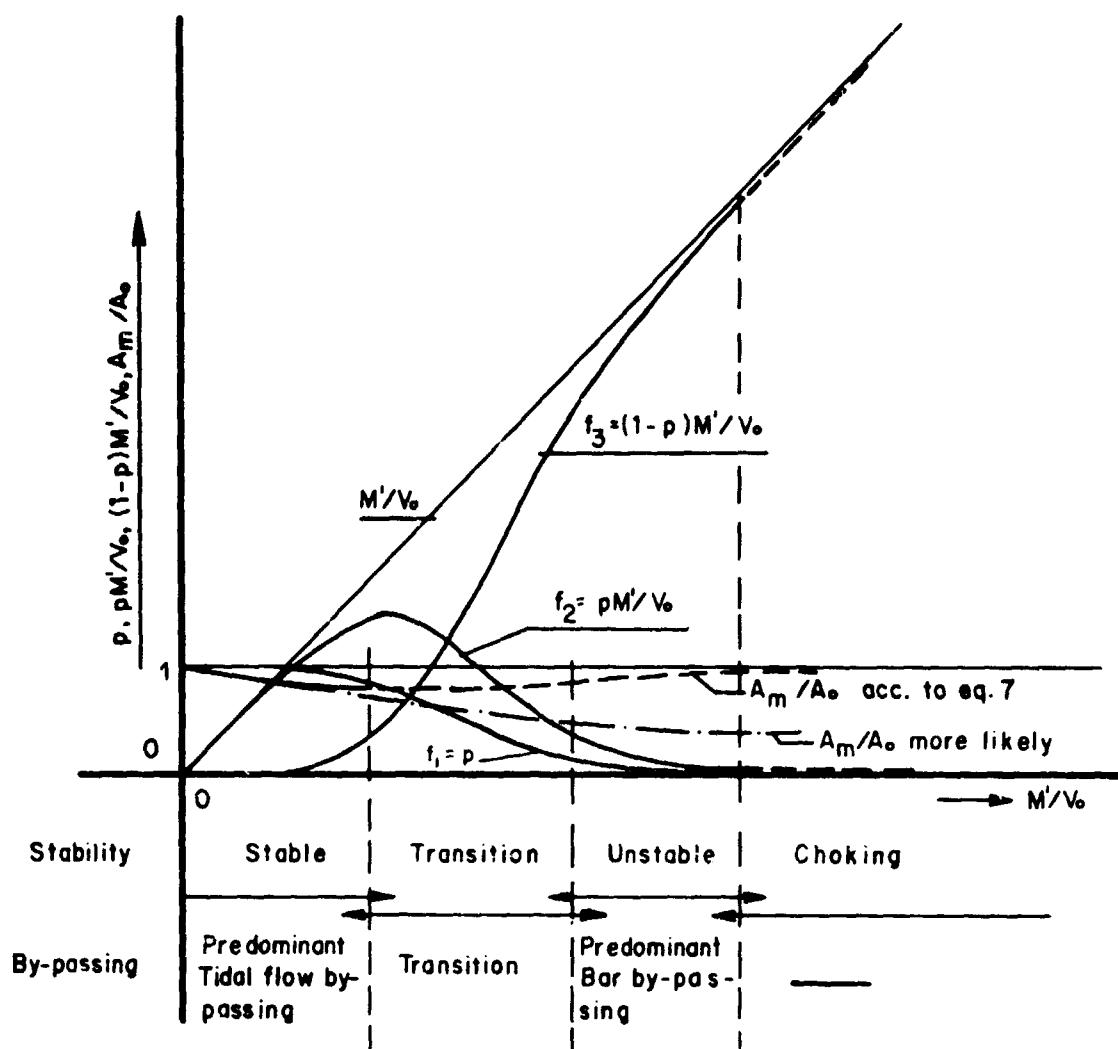


Fig. 2. Various functions of M'/V_0 . A_m = Cross-section of gorge in presence of littoral drift M' . A_0 = Cross-section of gorge in absence of littoral drift.

using the tentatively assumed function f_1 . The function f_1 is replotted for reasons of clarity.

One of the striking results evident in Figure 2 is that the relative drift load (f_2) in the tidal channels, including the gorge, shows a maximum for a certain value of M'/V_0 . The physical explanation is that for very low values of M'/V_0 practically all the littoral drift is bypassed by tidal flow and the relative drift load in the tidal channels increases in proportion to M'/V_0 . However, the bar gradually takes over more and more of the bypassing of the littoral drift with the result that the rate of increase of f_2 tapers off. At a certain critical value of M'/V_0 the rate of decrease of f_2 ; it is here that the relative drift load in the tidal channels (f_2) obtains its maximum. For values of M'/V_0 exceeding the critical value, f_2 gradually decreases to zero. In practice the lower limit of zero

will not be reached, however, because the inlet is choked at a certain high value of M'/V_0 .

Considering the relative drift over the outer bar (f_3), we can briefly explain why it continuously increases with increasing M'/V_0 : The fraction $(1-p)$ of the littoral drift bypassing over the outer bar increases with increasing M'/V_0 , while at the same time (by identity) the relative drift itself increases, so that their product must continuously follow the same trend.

The fact that the bar transfer partly takes place in discrete bulk quantities which are intermittently delivered to the downdrift shore is not important with respect to the above: we are dealing with the mean rate of transport in the bar zone.

Usually not all of the littoral drift bypasses the inlet; part of it may be deposited in the bay, part of it may be jetted out to deep water. In such cases the downdrift shore may be subject to erosion.

Table 1. Values of τ_s as a function of littoral drift load.

Littoral drift and Sediment load	τ_s kgf/m ²
Heavy	0.50
Medium	0.45
Light	0.35

LOCATION STABILITY

Location stability of the inlet is associated with the rate of migration of the inlet and of the channels in the outer bar. The general trend is that low values of M'/V_o indicate good stability and high values of M'/V_o indicate poor stability. Tentatively, four zones of stability are indicated in Figure 2: stable, transition, unstable, and choking. It should be made clear that these can only be approximate because of the gradual transitions, the variability of the determining factors, and the present lack of quantitative knowledge.

CROSS-SECTIONAL STABILITY

Bruun and Gerritsen (1960), when considering cross-sectional stability, used the following pertinent relationship between the cross-sectional area of the gorge A and mean maximum rate of discharge during spring tides Q_M :

$$A = \frac{Q_M}{C\sqrt{\tau_s/\rho g}} \quad (4)$$

where C is the Chezy coefficient of the gorge channel, ρg is the specific weight of water and τ_s is the stability shear stress which is the average shear stress along the bed of the stable gorge for maximum rate of flow during an average spring tide. The value of τ_s depends upon the bed material, the load of littoral drift and upland sediments and its concentration, the intensity of the wave action, the freshwater flow, and the shape of the cross section. We will examine the influence of the littoral drift load on τ_s . Bruun and Gerritsen recognized that it was the most important single factor determining τ_s , after the properties of the bed material, which varied little from one inlet to the other.

The variation of τ_s due to littoral drift can be approximated by comparing the transport rates through a stable gorge when the inlet is not subject to littoral drift and when it is, V_o and V_M respectively:

$$\frac{V_M}{V_o} = \frac{V_o + \rho M'}{V_o} = 1 + \frac{\rho M'}{V_o} \quad (5)$$

The rate of sand transport may be shown to be approximately proportional to the 2.5 power of τ_s so that

$$\frac{V_M}{V_o} \propto 1 + \frac{\rho M'}{V_o} \propto \left(\frac{\tau_M}{\tau_o} \right)^{2.5}$$

or

$$\frac{\tau_M}{\tau_o} = \sqrt[2.5]{1 + \frac{\rho M'}{V_o}} \quad (6)$$

as long as the change in other determining factors is small compared to the change in τ_s , which will be the case for small values of M'/V_o .

Based on analysis of existing inlets according to equation (4) Bruun and Gerritsen (1960) found the values of τ_s as a function of the littoral drift load listed in Table 1.

The great effect of the littoral drift on τ_s is very apparent. The terms heavy, medium, and light are used, of course, in a relative sense, meaning high, medium, and low values of M'/V_o , respectively. Lack of quantitative data makes it impossible, at the present time, to assign specific values of M'/V_o to the limits of these intervals.

In view of equation (4) a change in τ_s must be accompanied by a change in A . From equations (4) and (6), it follows that

$$\frac{A_M}{A_o} = \frac{1}{\sqrt[2.5]{1 + \rho M'/V_o}} \quad (7)$$

provided that the changes in C and Q_M are small compared to the changes in A and τ_s . This is the case for the values of M'/V_o that are not too high. In equation (7), A_M and A_o represent the cross-sectional area of the gorge in presence and in absence of littoral drift.

Equation (7) is plotted vs. M'/V_o in Figure 2. According to equation (7), A_M/A_o would have a minimum value where $\rho M'/V_o$ shows a maximum. For larger values of M'/V_o , A_M/A_o would increase again according to equation (7). This is not expected to occur, however. In considering larger values of M'/V_o the assumption that the change in Q_M is small compared to the change in A is not justified; at that stage the outer bar grows to such size that Q_M decreases considerably with the result that A probably does not increase beyond its minimum value. At still larger values of M'/V_o the outer bar chokes the inlet which still has an open gorge. The probable trend of A_M/A_o vs. M'/V_o is indicated in Figure 2 by the dot-dash line.

There is still one deduction of physical significance to be made from Figure 2.

Thus far we have considered the general stability of the inlet explicitly as a function of M'/V_o ; we will now consider how the stability varies as a function of the relative drift load in the gorge (f_2) and over the outer bar (f_3).

Because f_2 has a maximum for a certain value of M'/V_o , the stability is not uniquely determined by f_2 . But f_3 is monotonic throughout the interval of M'/V_o from no drift to choking; therefore f_3 , that is, the relative bar drift, does determine the stability uniquely. The physical interpretation is that it is the relative drift over the outer bar which is important to the inlet stability, rather than the relative drift load through the gorge. This is exemplified by the fact that the location stability is mainly associated with the migratory behavior of the outer bar and its channels which are much more mobile than the inner bar or the inlet as a whole, and that the point of choking of the inlet



Fig. 3. Aerial photograph of closed inlet at Hutchinson Island, Florida.

is determined by the outer bar, not by the gorge. Refer to the section above on cross-sectional stability and to Figure 3 which shows a closed inlet at Hutchinson Island, on the east coast of Florida. It can be seen clearly that the gorge stayed open although the inlet deteriorated completely.

It should be remembered that Figure 2 depicts the possible stages of development of one single inlet and also compares various inlets to one another.

The ideas outlined above are believed to constitute a useful working hypothesis for research programs aimed at enhancing our knowledge of tidal inlets. They should be useful in the design of tidal inlets when experiments have proved their usefulness and

provided the necessary quantitative data. One research program which is intended to provide that information is outlined below.

PLANNED LABORATORY RESEARCH

The Coastal Engineering Laboratory expects to conduct a basic study of tidal inlets by experiments with movable bed models (Bruun and Battjes, 1963). The factor $M' U_0$ will be varied while other influencing factors, such as the direction of propagation of tidal wave, initial bay and inlet geometry, and intensity of wave action will be kept constant. By measuring the rates of transport alongshore and through the inlet, the theory outlined above can be checked and quantitative information obtained. The pattern followed by the transported material will be checked by use of tracers. For each value of $M' U_0$ the tests will be repeated while slightly modifying $M' U_0$; an indication of the sensitivity (the reproducibility) of the model can thus be obtained. The effect of factors other than $M' U_0$ can be checked by running several tests with different values of the factor considered, the others—including $M' U_0$ —being constant.

LITERATURE CITED

- BRUUN, P., and J. A. BATTJES, 1963. Tidal inlets and littoral drift. *I.A.H.R. Congress, London, Paper 1.17*, pp. 123-130.
- BRUUN, P., and F. GERRITSEN, 1960. *Stability of Coastal Inlets*. North Holland Publishing Co., Amsterdam.
- BRUUN, P., and F. GERRITSEN, 1961. Natural bypassing of sand at coastal inlets. *Transactions A.S.C.E.*, vol. 126, part IV: 823-854.
- INMAN, D. L., and A. J. BOWEN, 1963. Flume experiments on sand transport by waves and currents. *Proc. 8th Conf. Coastal Eng., Council on Wave Res., Berkeley*, pp. 137-150.
- SONN, C. J., 1964. Study of shore processes with aid of aerial photogrammetry. *Photogrammetric Engineering*, XXX(6): 932-941.

Layered Sediments of Tidal Flats, Beaches, and Shelf Bottoms of the North Sea

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Sedimentary deposits of the past are frequently described on the basis of layers, banks, burrows, and other features of their structure; by grain size, mineral composition, and other characteristics indicative of the nature of the sediment; and by fossil content. These qualities are interpreted in relation to the environment of the deposition. The structures of sedimentary deposits often receive limited treatment by marine geologists because of technical difficulties. On the other hand, marine geologists are able to make observations which are helpful in interpreting the nature of fossil deposits. This paper approaches the study of sedimentary structures through use of a special apparatus, the grabsampler ("Kastengreifer") (Reineck, 1963a), and other new methods of preparing the probes, or corers.

METHODS

Undisturbed probes of tidal flat and beach sediments, as well as samples from muddy and sandy sea bottoms with the most minute sedimentary structure intact, were taken to the laboratory in their original corers ("Stechkasten") (Hantschel, 1936; Goemann, 1937; Baudoin, 1951; Reineck, 1957a). The sand probes were impregnated with ARALDIT Giessharz F and fixed with Hardener 902 (Reineck, 1962a). When prepared in this manner, even seemingly structureless sands showed the finest lamellae. Muddy probes were prehardened in Arigal C while they were still wet and, after drying, fixed in ARALDIT Giessharz F and Hardener 905. Thin sections were then prepared for slides from these samples; they showed the sedimentary structure in the finest detail (Reineck, 1963b).

LOCATION OF THE STUDY AREA

The research was carried out to a depth of 40 m in the German Bay, in the southeastern part of the North Sea. The tidal range was 2.4 m on the open sea and on the beach, and 3.6 m in Jade Bay. Current velocity in the open sea was <80 cm/sec. During certain phases of the Pleistocene, the basin presently occupied by the North Sea lay dry and was covered by morainic material from Scandinavia. These morainal deposits are the main source of the sediments which are now being transported and redeposited.

PHYSIOGRAPHIC DIVISIONS

According to Moore and Scruton (1957), the deposits of a particular environment are influenced by

the type of available sediment, the physical processes and their intensity, and the rate of sedimentation. An additional environmental influence is that of biogenetic factors, for example, shell, coral, and other hard parts, and biogenetic reworking.

A number of interrelationships exist between these various factors. In shallow water there is a distinct relationship between water depth and water movement. Seaward from a depth of 20 m, we find that waves have a diminishing effect on the sea bottom. The zone of greatest turbulence lies in the breaker area, that is, where currents are dependent on breakers and rip currents are created.

Waves and currents sort the materials present. Where relatively intense wave action and currents exist, coarser sediments, sand, and pebbles are found, in contrast to places of weaker turbulence and current. Therefore, sandy sediments are predominantly deposited at depths of 20 m, and muddy sediments at greater depths (Fig. 1). Finer sediments are transported to deep areas faster than coarser constituents are transported to shallow zones. Therefore, because of rapid transgression, we often find sandy sediments in deep water. At places with cyclic water movement, where currents alternate with periods of no water movement, deposition of correspondingly coarse and fine sediments will occur.

The sediment distribution scheme of tidal flats is also developed by currents and waves. Near the level of low tide, current and wave forces are greater than in the high tide area, and so muds are found near the high tide level and sand at the low tide line (Fig. 2).

This distribution pattern of sediment type in relation to current and wave action is upset where a considerable amount of new sediment is brought in, as at the mouth of a river; in places with great dust or volcanic ash accumulation, or where there is sediment from glacial drift, or the erosion of a steeply inclined coast, or the erosion of channels in the basement strata. The pattern also may be interrupted where "foreign" sediments come into another physiographic province through transgressing seas, as in most extant shelf areas.

Sedimentary structure also develops as a result of water movement. Horizontal silty-clay lamellae originate in areas with little water movement. Cross-bedded sands result from greater movement. Flaser bedding and lenticular bedding are caused by a changing water action, while horizontally laminated sand is developed in strong turbulence.

BIOTURBATE STRUCTURES

The relationship between water movement (oxygenation) and the existence of bottom life led Schmidt (1935) and Schäfer (1962) to propose their biofacies division. Schmidt emphasized the role of water movement in determining the degree of O₂ saturation, while Schäfer studied the effect of water movement on the sediment.

The forms living on the bottom of the shelf area are not only the chief source of shells and other animal hard parts (Schäfer, 1952), but they are also the originators of bioturbate structure (sediments in which the primary structure is reworked by the activity of organisms). The extent of bioturbation depends on the number and agility of the infauna, and on the abundance of benthic life, including benthic fish. Organisms are abundant in the oxygen-rich shelf area, except where strong physical reworking takes place, as in the breaker zone and in erosion channels, where burrows are few. Even when the population is as dense as in another area, where physical reworking is strong the primary structure predominates over the bioturbate structure (Richter, 1931).

The rate of sedimentation also influences the number of burrows. If the burrowing activity of the organisms cannot keep up with the deposition of sedi-

ment, they are few, even in an area that was thickly populated before the onset of rapid sedimentation (Richter, 1931). The choice of a place of settlement by the larval form of organisms often depends on the nutrient content, rate of sedimentation, and extent of reworking of the bottom.

Moore and Scruton (1957) have pointed out some of the relationships between water movement and burrowing organisms, and the resulting sedimentary structures. Through new sampling techniques we can contribute to and correct this scheme and extend the shelf profile to include beach sands. Waves and currents always permit primary structures to appear again. The primary structures are typical for a given environment, whether they are actually primary or repeatedly destroyed and formed anew. Burrowing organisms produce very different secondary or bioturbate structures, and we do not add the activity of organisms to the effect of currents and waves to get a total, because water movement and burrowing work against each other. The stronger the physical reworking, the fewer the indications of burrowing activity.

SURF ZONE TO SHALLOW SEA BOTTOM

A profile section from the surf zone to shallow sea bottom is presented in Figure 1. On approaching shal-

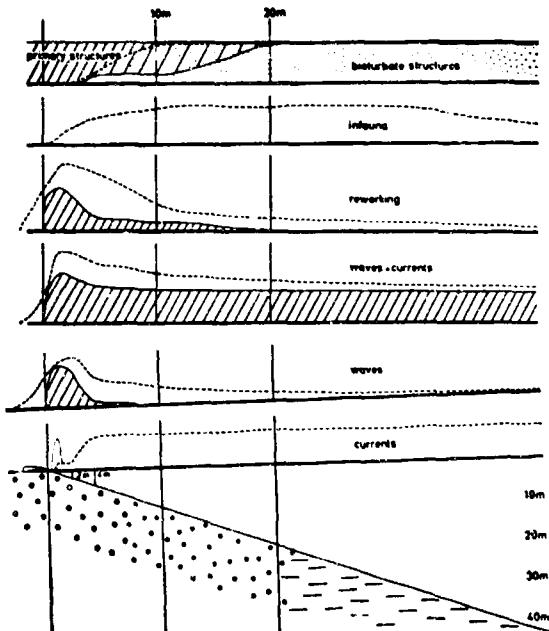


Fig. 1. A schematic section showing the beach to the open sea, and the relations between waves, tidal currents, and water depth. A comparison may be made of the colonization by infauna and sediment type and minor structures.

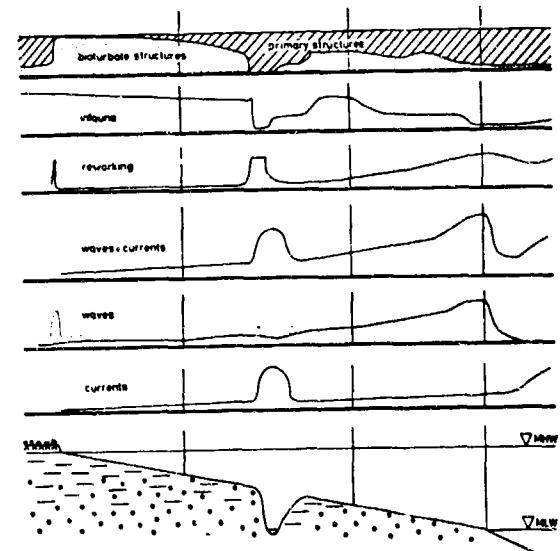


Fig. 2. Schematic section of a tidal flat showing the relationships between waves, currents, and infauna, and the sediment distribution and minor structures. The latter are divided into primary and biogenetic (bioturbate).

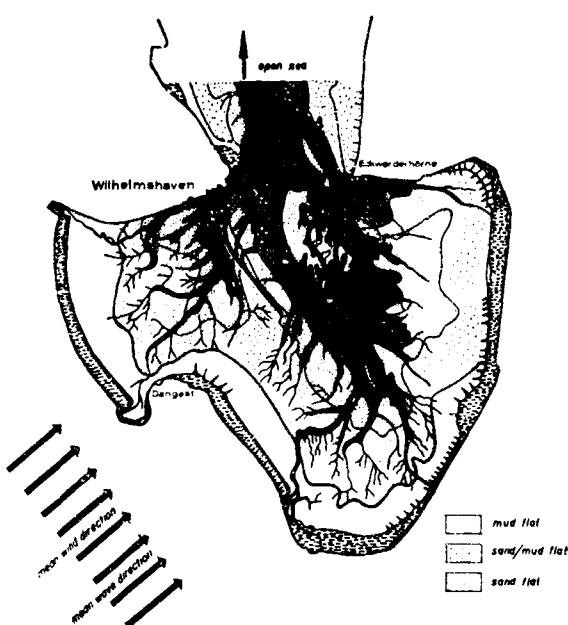


Fig. 3. Sediment distribution on the tidal flats of Jade Bay, North Sea. The mud lies on the lee side of the mainland, protected from wind and waves.

lower water and the surf zone, the effect of the waves becomes stronger (hatched area) and, during rough seas, reaches greater depths (dashed line). The tidal current weakens as it approaches the beach and the surf current develops. Both current and waves affect all points of the area, but their total activity is greatest as the shallower surf zone is approached.

The sediments are coarser on the beach than in deeper water. Reworking is strongest on the beach, but with a rough sea deeper areas are also affected. The boundary between sand and mud lies at about 20 m, although there are numerous exceptions.

Infaunal colonization decreases as the littoral zone is approached from deeper water, and the resulting bioturbate structures become less frequent because of greater physical reworking. A primary structure is usual in this zone. Going seaward, the next zone has a bioturbate structure destroyed during storms and replaced by a primary structure. Farther seaward the bioturbate structure becomes more frequent, and, in many places, completely replaces the primary structure.

TIDAL FLAT SURFACE

On the tidal flat surface, in contrast to the sediment distribution in the shallow sea, finer sediments lie on the shore near the high-water line, and the coarser, sandy sediments lie at the low-water level (Van Straaten and Kuenen, 1957, 1958; Postma, 1954, 1961; Stevenson and Emery, 1958). Thus, the distribution of tidal flat sediment can be divided into mud, mud-sand (Misch), and sand flats (Fig. 3).

The current is greater on the lower part of the

tidal flat than at the upper regions; and greater current velocity is found in the tidal channels than on the open tidal flat itself. Current velocities of 1 m/sec may be recorded in channels, although not more than 30 cm/sec is reached on the surface of the tidal flat.

Waves are strongest near the low-water line and become weaker as they continue landwards, because of the friction on the inclining tidal flat surface. Stronger wave effects are possible at the sides of the tidal channels. During unusually high water (storm floods), the waves may reach the salt marsh and erode its fore-edge to form a cliff.

Both waves and current are stronger at the lower part of the tidal flat; therefore, the coarse sediments are distributed near the lower part of its surface and the finer sediments above. This observation complements and adds to the concepts of "settling lag" and "scour lag" of Postma (1954, 1961), and Van Straaten and Kuenen (1957, 1958). Reworking is dependent on the effect of waves and currents and decreases on approaching the high-water line; but tidal flat sediments at and above the high-water mark are reworked and sand is deposited during a storm. Under normal weather conditions greater reworking takes place in the tidal channels. The infaunal population is noticeably larger in the mud flat than in the sand flat, and is very small in the tidal channels. Most burrows lie in the mud flat, and the amount of bioturbation is less in the Misch and the sand flats.

THE SEDIMENTARY STRUCTURES

Sedimentary structures are partly dependent on the type of sediment they are composed of; ripple structures, for instance, are formed in sand but not in mud. Other structures are strongly influenced by the areas in which they occur, for example, salt marsh deposits. The characteristics of some of the more common sedimentary structures are discussed and illustrated below.

LAMINATED SAND

Single lamellae are a few millimeters thick (Fig. 4); the constituent sand grains may be distinguished by their medium grain size (Emery and Stevenson, 1950). Laminated sand originates when sand settles from clouds of sand in suspension. This type of sedimentation is very common in beach sediments and in zones exposed to strong surf action.

RIPPLE BEDDING

Ripples are made up of (spoon-shaped) lamellae, inclined in an oblique, sideward, and downward position; only infrequently are the lamellae straight (Fig. 5). These structures are developed from current and asymmetrical oscillation ripples by deposition on the foreset flank of the ripple (Nehoff, 1958; Wurster, 1958; Einsele, 1960; Reineck, 1961).

When the course of the ripple crest oscillates back and forth the foreset laminae will weave back and forth (Fig. 6a). If the formation of the ripples con-

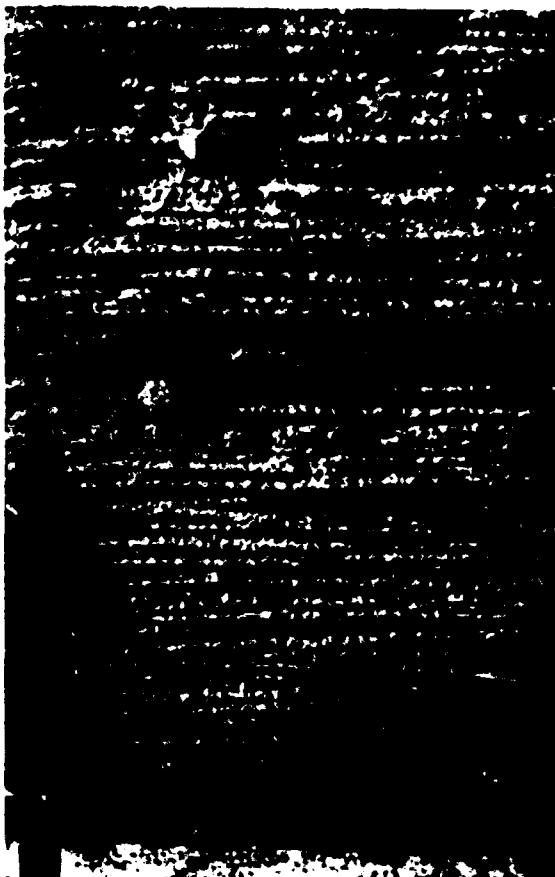


Fig. 4. Laminated sand of a breaker zone. Each lamina corresponds to a wave from which the suspended sand has settled. Not every wave produces such a lamina; per tide only 5-16 laminae are deposited. North Beach, Norderney, North Sea. (Scale in centimeters)

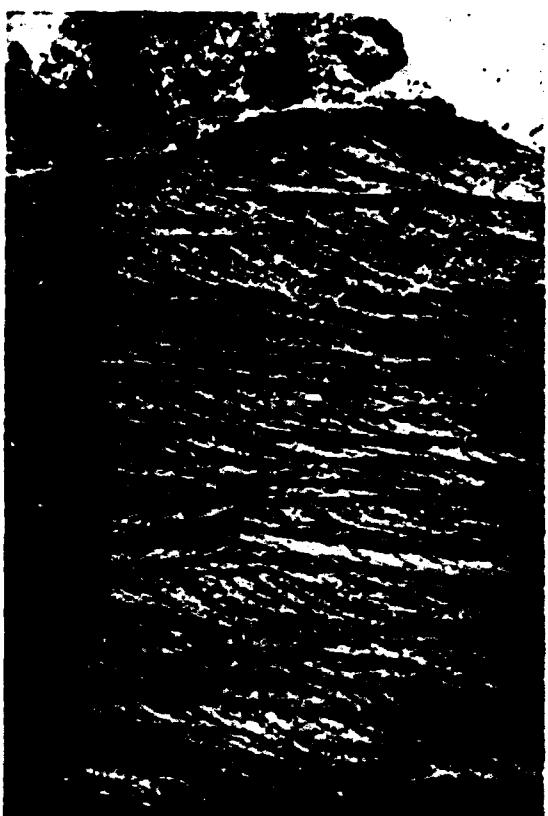


Fig. 5. Ripple bedding in a sand flat; current-produced ripples. The illustration shows on the top a ripple with natural form showing the inner structure of the laminae developed on its lee side. The vertical section has been prepared as a relief cast. Jade Bay, North Sea.

tunes, the foresets will be eroded by the resulting rolling current. The advancing laminae are not very thick; the forelayers which are inclined backwards reach much deeper and, therefore, occasionally remain intact. As seen from the front (Fig. 6b), festoon bedding originates in this manner. On the remaining horizontal section we find a series of arcs whose apexes are directed against the current (Figs. 6d and 7).

Two size-classes of ripple bedding can be distinguished (Reineck, 1963a): (1) ripple bedding that is developed from current ripples of short wavelength; the thickness of the individual sets of cross-strata is not greater than 4 cm, and the radius of the arcs of festoon bedding is generally less than 20 cm; and (2) ripple bedding that develops from current-produced megaripples; the thickness of the individual groups of cross-strata is, in general, more than 4 cm, and the arc radii of the festoon bedding are always greater than 20 cm.

There is another ripple bedding that originates from symmetrical and asymmetrical oscillation ripples, but these apparently play only a minor role in



Fig. 6. Origin of ripple bedding from current ripples.
Plane a: Surface section of ripples with crests having opposite apical directions. This section cuts into the foremost ripple and the cut is shifted forward about half the ripple length to show the structure which exists beneath the ripple.

Plane b: Front view of the structure yields festoon bedding.

Plane c: Side view shows cross bedding.

Plane d: Horizontal view of the remaining structure. The forepointing parts of the crests disappear (compare Figure a), eroded from the bottom of the ripple troughs, leaving only the structure of the backpointing part of the lee laminae intact.



Fig. 7. Breaker zone. Surface of a longshore bar in the foreshore area showing the structure of a megaripple uncovered by wind action; migration toward the right. Side of the compass = 10 cm. North Beach, Norderney, North Sea.



Fig. 9. Petrological section of flaser bedding in a misch flat, showing oblique bedding in a sandy layer. Jade Bay, North Sea (Vertical high = 4 cm).

the tidal flat, beach, and open sea provinces. To the contrary, single oscillation ripples are frequently noted in lenticular bedding.

Megaripple bedding originates where high velocity currents (greater than 80 cm/sec) predominate, and it is frequently associated with coarse sand.

FLASER BEDDING

This structure (Figs. 8 and 9) implies sand and mud, as well as current activity and pauses in this activity (Hantzschel, 1936; Reineck, 1960a, b). During times of current activity, the sand will be transported and deposited in ripple structures while the mud is held in suspension. When the current pauses, the mud in suspension is deposited and either completely covers the ripples or covers only the ripple troughs. At the start of the next current cycle, new sand is transported over the deposited mud layer (Fig. 10), or the mud is eroded from the crests of the buried ripples and remains only in the troughs.



Fig. 8. Flaser bedding in a marsh flat, developed from degeneration of mud in the troughs of current ripples. Jade Bay, North Sea.

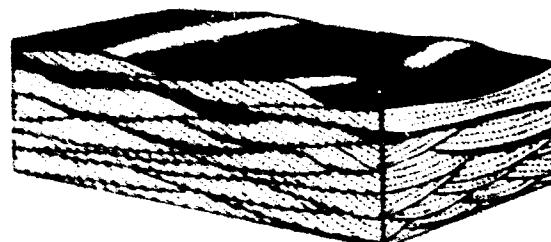


Fig. 10. The evolution of flaser bedding from mud-covered ripples.



Fig. 11. Misch flat bedding. Middle—flaser bedding developed from oscillation ripples. Below—lenticular bedding caused by mud deposited over incomplete ripples. Vertical section. Jade Bay, North Sea.

The mud-flasers are geopetal indicators, as the thickest part of the flaser lies in the deepest part of the trough.

LENTICULAR BEDDING

Lenticular bedding shows sand lenses in a muddy groundmass (Fig. 11). The sand lenses represent oscillation or current ripples which have wandered onto a muddy basal layer and in whose troughs "windows" of this basal layer remain open; Schrock (1948) described them as incomplete ripples. When a new mud layer is deposited in contact with the old basal mud layer in the troughs of the sand ripples, the sand ripples appear as lenses which float in a muddy matrix. When a vertical cross section is made parallel to the ripple axis, this deposit appears as alternating sand and mud bedding.

FINE RHYTHMICALLY LAMINATED BEDDING

This bedding (Fig. 12) consists of vertical alternation of thin sand and mud layers (Richter, 1929;

Lüders, 1930). According to the latest unpublished research of Wunderlich (personal communication), sometimes the thin mud layers are the bottom-set laminations of ripples. The sand layers are remnants of very flat-crested ripples that possess nearly straight crests. This bedding type originates in moderately fast-flowing water having a very high suspension content. With every tide, many single laminae can be deposited; but a fine rhythmically laminated bedding is also due to tides.

COARSE RHYTHMICALLY LAMINATED BEDDING

This type of bedding is formed of sand and mud layers which are many mm to several cm thick (Fig. 13). Ripple structure is recognizable in the sand layers.

Previous authors have called the fine rhythmically laminated bedding "tidal bedding", holding that one sand lamella was deposited during flood tide, and one mud lamella during ebb tide. Wunderlich, however, has shown (unpublished) that in some cases many sand and mud sheets originate with every tide. It is known, of course, that bedding types do exist which can originate during the tidal cycle. They are (Reineck, 1960a, b) flaser, lenticular, and the coarse rhythmic bedding types. On the basis of previous research, we believe the sand layers originate during current activity while the mud is laid down in periods of slack water. Rhythmic bedding of a seasonal nature, such as that illustrated by varves or as described from recent sediments of the Adriatic Sea (Seibold,



Fig. 12. Finely laminated mud-sand alternation in a misch flat. Vertical petrological section. Jade Bay, North Sea (Vertical high = 4 cm).



Fig. 13. Misch flat bedding. Coarsely alternating mud-sand bedding; lenticular bedding can be seen above the sand. Vertical section (Scale in centimeters).

1955), has not as yet been identified from the North Sea.

MUD DEPOSITS

These deposits, having a thickness which lies in the range of several cm, are mostly non-homogeneous. The petrological sections show that there are weak or strong inclusions of individual sand grains (Fig. 14). Frequently, thick mud deposits are thoroughly burrowed by a dense infaunal population.

SALT MARSH OR FLOOD DEPOSITS

These sedimentary structures consist of very irregular alternating beds of sand and mud (Figs. 15 and 16). The individual layers are undulating, as they were laid down over the uneven, plant-covered, salt marsh surface (Van Straaten, 1954). Many shell deposits are found inserted in the strata of the salt marsh (Hantzschel, 1936; Schäfer, 1963). An essential characteristic of these deposits is the pres-

ence of many root canals with iron hydroxide on their surfaces.

BIOTURBATE STRUCTURES

The primary sedimentary structure may be slightly changed or completely altered by the formation of bioturbate or secondary structures. Schäfer (1956) distinguished the *fossilextructura deformativa* from the *fossilextructura figurativa*. The former are formless activity traces such as flecks (Figs. 17 and 18); the latter, *fossilextructura figurativa*, have form and they burrow (Fig. 19). The formless structures originate mainly from the activity of benthic fish and from crabs or starfish (Schäfer, 1962). Within our study area we have noted very characteristic *figurativa* traces.

Nereis diversicolor builds multi-walled burrows in the tidal flat (Reineck, 1957b, 1958a; Seilacher, 1957). Sediment introduced into the burrow is coated with mucus and pressed into the burrow walls. At the same time, the animal restores its burrow to its original diameter by the lateral expansion of its body. A similar, double-walled scheme is found in the siphonal burrow of *Mya arenaria* (Reineck, 1958a).

Burrows which are U-shaped are made by *Polidora*, *Irenicola marina*, and *Corophium edentatum*. *Corophium* lives predominantly in muddy areas of the tidal flat (Seilacher, 1957); the animal initially makes a flat U-tube, which it progressively deepens.



Fig. 14. Mud flat bedding. Fine sand grains are found in particular layers in the muddy ground mass. Vertical petrological section through a mud bank, Jade Bay, North Sea (Vertical high = 4 cm).



Fig. 15. Salt marsh cliff. The weakly undulating beds contain plant roots and inserted shell layers. The basal beds are strongly knotted because the salt marsh surface was irregularly shaped by the individual plant groups which grew there. Jade Bay, North Sea.

Arenicola marina lives in the sand flats. A shell deposit is often formed beneath an *Arenicola* community and consists of shell fragments and *Hydrobia* shells that have silted down (Van Straaten, 1952).

Infaunal bivalves must be able to move toward the surface as sediment is quickly deposited over them (Fig. 20), and we often find escape paths beneath these pelecypods (Reineck, 1958a).

Especially common on the shallow shelf are the large branching passages of the crabs *Callianassa* and *Upogebia*, which often reach depths of 50 cm and more, and have cave-like expansions in which the animal may turn itself around (Schafer, 1962).

An exceedingly widespread structure is that produced by the activity of the heart urchin, *Echinocardium cordatum*. This species builds a long passage in which the sand layers appear as a series of hemispheres packed one upon the other as the animal proceeds away from the concave end (Schafer, 1962). As shown in Figure 21, in the middle of this sand-filled passage we sometimes find mucus-coated fecal pellets (Reineck, 1963c). *Echinocardium cordatum* leaves no open passages.

REGIONAL DISTRIBUTION OF SEDIMENTARY STRUCTURES

When one speaks of a regional distribution of sedimentary structure, a quantitative division is implied. However, a true quantitative approach is applicable only to the salt marsh where accurate observations can be made.

SALT MARSH

This area is covered by a thick halophyte growth. During a storm flood it is built up with new sediment which, in Jade Bay, can occur to a height of 1.5 m above the high tide line. A lower salt marsh develops a knotted surface due to the overgrowth of plants. This strongly undulating surface, often having differences in elevation of more than 20 cm, gradually becomes more level as further growth continues. However, traces of this original salt marsh surface are seen in the basal part of the present profile (Reineck, 1962b). In the salt marsh strata we find deposits of shell which were thrown onto the marsh by surf action in the area of the high water line (Figs. 15 and 16).

TIDAL FLAT

The boundary of the tidal flat extends not only from the low-water to the high-water line, but higher, as can be inferred from the growth of the salt marsh. In the German Bay there is a drop in elevation of 2.6 to 3.6 m within a distance of 4.7 km.

Essentially, two morphologically distinguishable tidal flat types are found in the bay flats (Fig. 3) and the flats landwards of the East Frisian Islands (Fig. 22), in the German Bay. Both have the same sediment type, but the bay flats' boundaries extend to the middle of the bay. Mud is deposited near the high-water line (mud flat) and mostly sand near the low-water line (sand flat). In between lies an area of both mud and sand.



Fig. 16. Salt marsh bedding. Irregular sandy or silty areas with embedded plant parts and root canals. Vertical petrological section. Jade Bay, North Sea (Vertical high = 4 cm).



Fig. 18. Petrological section showing mottled structure; 47 m, North Sea (Vertical high = 4 cm).



Fig. 17. Mottled structure. The silty sand shows no structure because of bioturbation. Vertical section of the contents of a Kastengreifer probe, 35.5 m, North Sea.



Fig. 19. Misch (sand mud) flat. Multi-walled, filled-in burrow of *Nereis diversicolor*. The encountered sedimentary layers are slightly bent downward by the widening of the burrow. Vertical petrological section. Jade Bay, North Sea.



Fig. 20. *Mru arenaria* in its living position, showing the path of escape made necessary by the rapid deposition of sediment at the surface. Jade Bay, North Sea.

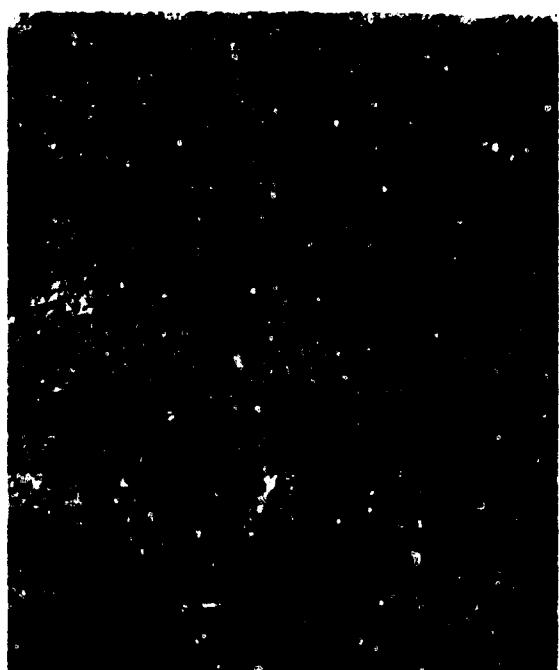


Fig. 21. Sand in the vicinity of the coast. The layers of a megaripple can be seen. Below, right—a bioturbate structure produced by *Eumicocardium cordatum*, in the middle of which sand and fecal pellets are compressed into a bowl-in-bowl structure. Kastenreiter probe, 8 m, North Sea.

Mud predominates on the mud flat, but enough sand is present to build different bedding types (Table 1). Because of the thick infaunal population and the low rate of physical reworking, many bioturbate structures originate here and remain intact. About 40 percent of the deposit is completely burrowed through, chiefly by *Corophium rotundatum*, *Heteromastus filiformis*, *Nereis diversicolor* (Fig. 19), and *Scrobicularia plana*.

Disturbance of the primary structure can also be



Fig. 22. Tidal flats between the East Frisian Islands and the mainland: (1) open sea and channels; (2) tidal flat surfaces; and (3) islands and mainland.



Fig. 23. Schematic section of a tidal channel with receding and prograding banks. The longitudinal oblique bedding is found at the prograding bank, as the base a shell bed is formed. Tension faults, resulting from the gravitational sagging of mud layers, develop in the prograding bank.

Table 1. Abundance of structure types: mud, mud-sand (Misch), and sand flat.

Structure type	Mud flat (%)	Mud-sand (Misch) (%)	Sand flat (%)
<i>Mud bank</i>			
Without recognizable lamination	14	2	+
With fine sandy laminations	17	3	+
Bank of sandy mud	11	7	+
<i>Rhythmically laminated bedding</i>			
Fine	10	18	3
Coarse	3	23	2
<i>Lenticular and flaser bedding</i>			
Lenticular and flaser lenticular bedding	1	9	1
Flaser bedding	5	13	13
<i>Ripple bedding</i>			
Short-wave	—	2	54
Mega	—	—	5
<i>Laminated sand</i>			
—	—	1	10
<i>Bioturbate structure</i>			
—	39	21	12

caused by plants. However, there are few plants on the tidal flats; among these are *Salicornia herbacea* and *Spartina townsendii*.

The widest spectrum of bedding types is found in the Misch Flat. About 20 percent of the bedding is bioturbated, chiefly through the activity of *Nereis diversicolor*, *Heteromastus filiformis*, *Mya arenaria*, and *Cardium edule*. Possible plant originators of a bioturbate secondary structure are *Zostera marina* and *Z. nana*.

The effects of the meandering tidal channels are especially important on the Misch flat. Lateral sedimentation is evident, with erosion of the regrading bank and a lateral deposition on the point bar. On the channel floor, beds of shell and mud pebbles are found (Van Straaten, 1954).

Reineck (1958a) termed these laterally deposited layers "longitudinal oblique beds" because the strike of these is parallel to the direction of the flow of water (Fig. 23). Conversely, the strike of ripples runs perpendicular to the direction of flow. The longitudinal oblique bedding contains predominantly less bioturbate structures than the nearly horizontal bedding of the tidal flat surface because the sedimentation rate is very high in the tidal channels.

This longitudinal oblique bedding is also found on the Misch flat (Fig. 24) and the sand flat. The angle of dip of these beds in the latter area is very much smaller than in the former. It can be found in the sand flat because its ripples have a smaller angle of dip than those that form in megaripples; ripple structure is developed mainly in the individual banks and indicates a current direction parallel to the strike of the entire bank. In the Misch flat, the muddy component (flaser, lenticular, and rhythmic bedding) is great in contrast to its occurrence in transverse

oblique bedding. Frequent tension faults are developed in the banks (compare Figs. 23, 24, and 25). The shell layer of the tidal channel remains intact at the base of these oblique beds (Jarke, 1949).

SAND FLAT

Ripple bedding (Fig. 4) is almost always present on the sand flat (Table 1), and here the bioturbation (about ten percent) is the rarest of all the tidal flat types, except in *Arenicola* communities where bioturbate structures become very numerous. The main bioturbators are *Arenicola marina*, *Cardium edule*, *Scoloplos armiger* (Fig. 26), and *Lanice conchilega*.

A summary of the percentage of the various bedding types represented in the tidal flats is given in Table 2. A summary of the distribution is given in Figure 27.

SHORE AREA

The morphology of the foreshore and inshore is very well divided by the sublittoral channel, the beach



Fig. 24. Longitudinal oblique bedding, from a misch flat, shewing a tension shear. Vertical section. Jade Bay, North Sea.



Fig. 25. Longitudinal oblique bedding, from the prograding bank of a tidal channel, showing some complete and some newly developed tension shears. Jade Bay, North Sea.



Fig. 26. *Scoloplos armiger* burrows in a sand flat. The primary structures are almost entirely replaced by the bioturbation of this form. Vertical section prepared as relief cast. German Bay, North Sea.

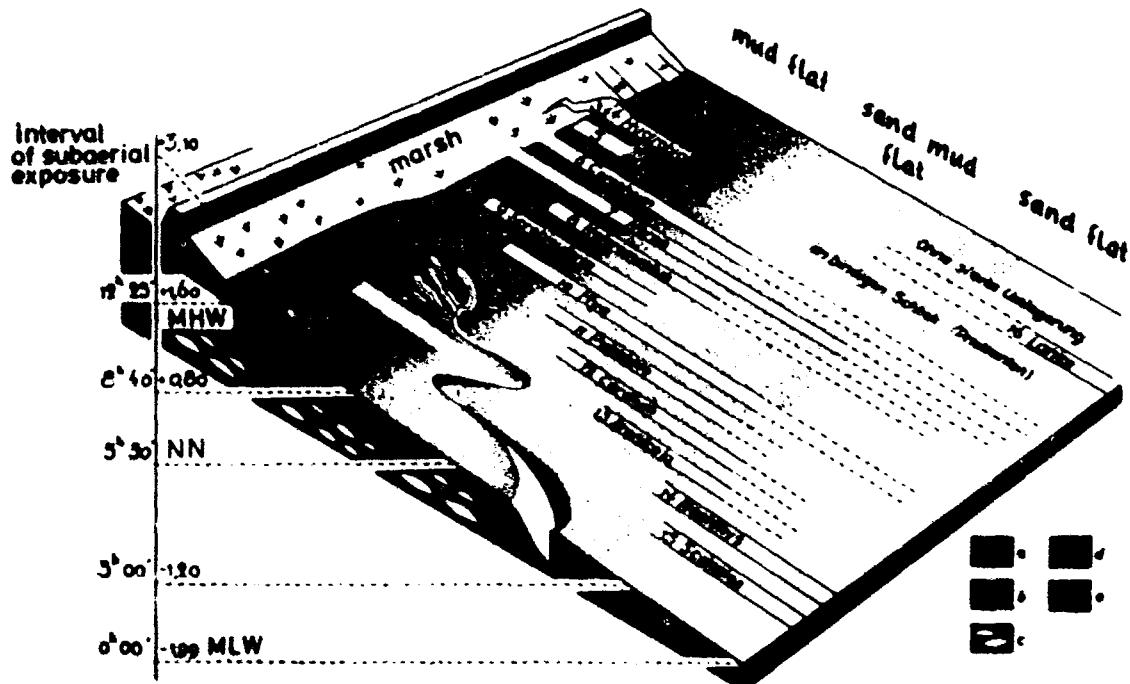


Fig. 27. Schematic section of a tidal flat surface showing the distribution of the dominant infaunal species: (a) salt marsh deposits; (b) alternating mud-sand layers; (c) linear bedding; (d) ripple bedding; and (e) shell fragments.

Table 2. Abundance of tidal flat structure types.

Structure type	Total profiles (%)
<i>Mud bank</i>	
Without recognizable lamination	3
With fine sandy laminations	3
Bank of sandy mud	5
<i>Rhythmically laminated bedding</i>	
Fine	11
Coarse	14
<i>Lenticular and flaser bedding</i>	
Lenticular and flaser/lenticular bedding	5
Flaser bedding	12
<i>Ripple bedding</i>	
Short-wave	21
Mega	1
<i>Laminated sand</i>	
Bioturbate structure	20



Fig. 28. Transport directions of sand in a foreshore area. The sand crosses the longshore bar, frequently in the form of megaripples. The sand is transported farther seaward through the beach channels. Open sea above.

wall, and the longshore bar. The beach wall is composed primarily of laminated sand, dipping weakly toward the sea. The foreset bedding dips in a landward direction.

The beach channels contain current ripples, commonly built as megaripples (Häntzschel, 1938), with crests perpendicular to the beach front. The megaripple orientation is changed to parallel to the sea

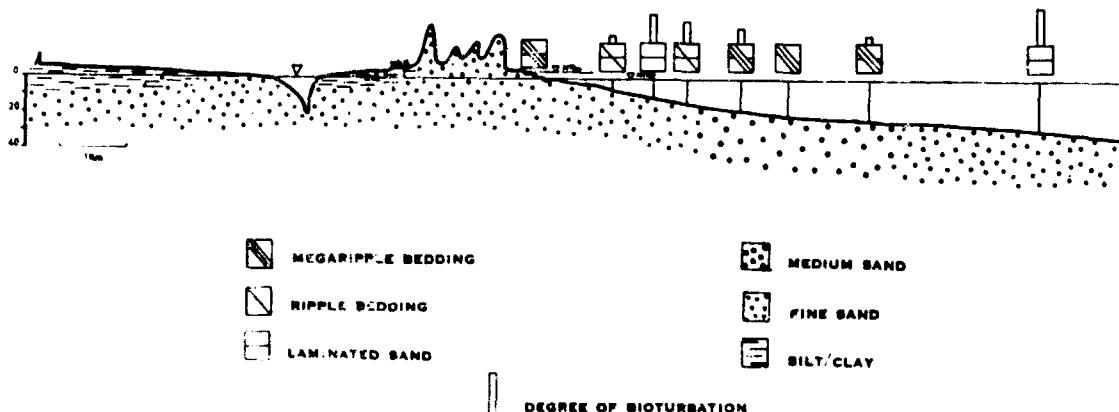


Fig. 29. Beach profile showing dominant sedimentary structure. A cut through a dune-island with dominant sedimentary structure in the area of the foreshore, inshore, and offshore.

Foreshore: Megaripple bedding, laminated sand and short-wave ripple bedding. Few burrows.

Inshore and offshore: Burrows increase. Megaripple structures exist only where coarser sand is found; the burrows are less frequent here (See Fig. 30).

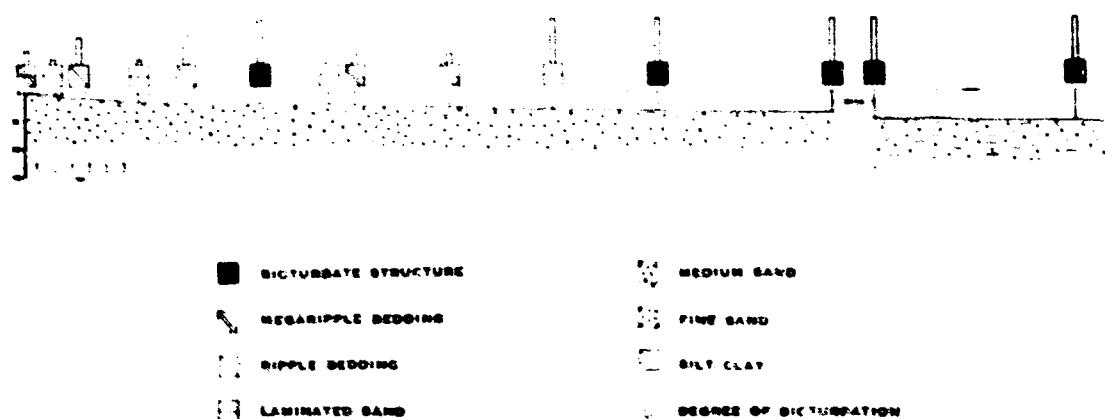


Fig. 30. Foreshore profile of the East Frisian Island, Norderney, proceeding northward to the open sea. The sediment becomes finer as the depth of the water increases, at the same time the frequency of bioturbate structure increases until the primary structure is completely destroyed.

Table 3. Abundance of primary and bioturbate structure types in relation to water depth.

	Bioturbate structure (%)	Mega-ripples (%)	Short-wave ripples (%)	Laminated sand (%)	Laminated mud sand (%)	Flaser bedding (%)
<i>Inshore to -10 m.</i>						
Medium sand; fine sand	28	12	16	41	—	3
<i>Deeper than -10 m.</i>						
Fine sand	52	5	11	29	3	—
Medium sand	25	50	15	7	2	1

where the longshore bar is broken through by rip currents flowing seaward (Fig. 28).

The longshore bar consists of layers of laminated sand, ripple bedding, and sometimes of megaripple bedding (Figs. 4 and 7).

Bioturbate structures are rarely observed on the foreshore. Hoyt and Weimer (1963) have shown that these structures first appear in the inshore area.

INSHORE TO SHELF AREA

A diagrammatic profile of the inshore to shelf area is presented in Figures 29 and 30. With increasing

depth, the effect produced by wave action on the bottom sediments grows weaker, whereas the effects of the tidal current become important. The combined effect of waves and current is so strong that usually only clean sand is found from the tidal flats to a depth of about 20 m. These sands are laminated and ripple bedded, but where coarser sand originating mainly from morainic material is present, megaripples formed by the tidal current can be observed.

At a depth of about 2 m, burrowing (in order of decreasing importance) by *Echinocardium*, the bivalve, *Angulus*, and in places by the worm, *Lanice conchilega*, begins to appear (Reineck, 1963c). In comparing the proportion of burrows in the inshore regions to those in sands deeper than 10 m (Table 3), we note that burrows increase as the depth increases; this is expected because of weaker physical reworking. The megaripples become less frequent, except in coarser sand, where they are formed at depths greater than 20 m (Fig. 7). As the depth increases the occurrence of laminated sands decreases.

At depths greater than 20 m, the mud component

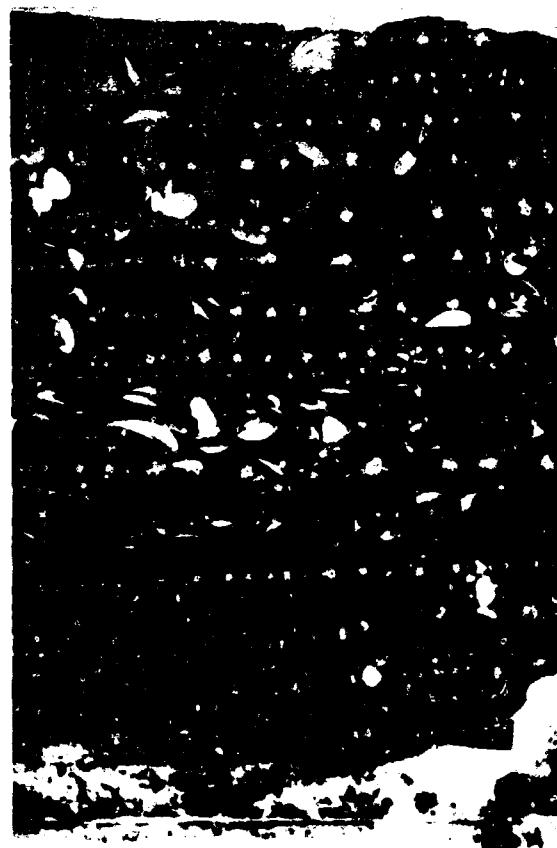


Fig. 31. Bioturbate structures. Upper right: burrow of *Echinocardium*. Many mollusc valves are displaced through the burrowing of the infauna, and many are broken by fish. Vertical section of a Kastengreifer probe, prepared as relief cast. 21 m, North Sea.



Fig. 32. Burrows with numerous fecal pellets. Vertical section. 30 m, North Sea (Black rectangle = 1 cm).

of the sand increases, and, after a short transition, sandy mud is found. Primary structures seldom remain intact, because of the bioturbation by *Echinocardium* (Fig. 21), *Callianassa stebbingi*, *Upogebia litoralis*, *Amphiura filiformis*, and also starfish and flatfish. According to Moore and Scruton (1957), the resulting structure can be termed mottled (Figs. 16 and 17).

Mud from the Elbe and Weser Rivers is deposited in water at depths of 20–40 m southeast of Helgoland (Pratje, 1931; Reineck, 1963c). These muds began being deposited after the post-Pleistocene transgression and now attain a thickness of over 4 m. They contain bioturbate structures to a moderate degree and have numerous sand layers.

The high content of shell fragments is also obtained at depths greater than 20 m. Krause (1950) and Schäfer (1962) attribute these fragments to the predatory action of fish (Fig. 31). Fecal pellets are present in the petrological sections of both tidal flat and shallow shelf sediments (Fig. 32), whereas they are completely absent in beach samples.

SUMMARY

The methods and observations presented here offer promise of new insight into the realm of present and past marine sedimentation. Our deductions concerning geological and paleontological phenomena can be only partly understood or interpreted as long as we have insufficient knowledge of the variability of present sedimentary environments.

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LITERATURE CITED

- BAUDOIN, R., 1951. Nouvelles observations sur les Sables Alvéolaires. *Bull. Soc. Géol. France*, 1:213–220.
- INNSELE, G., 1960. Schrägschichtung im Raumbild und einfache Bestimmung der Schüttungsrichtung. *Neues Jahrb. Geol. Palaeontol. Monatsh.*, 12:546–559.
- EMERY, K. O., and R. E. STEVENSON, 1950. Laminated beach sand. *J. Sediment. Petrol.*, 20:220–223.
- GOEMANN, H. B., 1937. Ein sediment-härtungsverfahren mit Dioxan und Paraffin. *Senckenbergiana*, 19: 77–80.
- HÄNTZSCHEL, W., 1936. Die Schichtungsformen rezenten Flachmeer-Ablagerungen im Jade-Gebiet. *Senckenbergiana*, 18:316–356.
- HÄNTZSCHEL, W., 1938. Bau und Bildung von Gross Rippeln im Wattmeer. *Senckenbergiana*, 20:1–42.
- HOYT, J. H., and R. J. WEIMER, 1963. Comparison of modern and ancient beaches, central Georgia coast. *Bull. Am. Assoc. Petro. Geologists*, 47:529–531.
- JARKE, J., 1949. Die Unterschiede in der Sedimentation vor der Ost-und West-Küste Schleswig-Holsteins. *Diss. Kiel*, ungedruckt; pp. 1–125. (Cit. Gripp, 1956).
- KRAUSE, H. R., 1950. Quantitative Schilluntersuchungen im See-und Wattengebiet von Norderney und Juist und ihre Verwendung zur Klärung hydrographischer Fragen. *Arch. Molluskenk.*, Senckenberg. *Naturforsch. Ges.*, 79:91–116.
- LÜDERS, K., 1930. Entstehung der Gezeitenschichtung auf den Watten im Jadebusen. *Senckenbergiana*, 12: 229–254.
- MOORE, D. G., and P. C. SCRUTON, 1957. Minor internal structures of some recent unconsolidated sediments. *Bull. Am. Assoc. Petro. Geologists*, 41:2723–2751.
- NIEHOFF, W., 1958. Die primär gerichteten Sedimentstrukturen, insbesondere die Schrägschichtung, im Koblenzquarzit am Mittelrhein. *Geol. Rundschau*, 47:252–321.
- POSTMA, H., 1954. Hydrography of the Dutch Wadden Sea. A study of the relations between water movements, the transport of suspended materials and the production of organic matter. *Arch. Nederl. Zool.*, 10: 1–106.
- POSTMA, H., 1961. Transport and accumulation of suspended matter in the Dutch Wadden Sea. *Neth. J. Sea Res.*, 1:148–190.
- PRATJE, O., 1931. Die Sedimente der Leutschen Bucht. *Wiss. Meeresuntersuch. NF* 18:1–126.
- REINECK, H. E., 1957a. Stechkasten und Deckweiss, Hilfsmittel des Meeresgeologen. *Natur Volk.*, 87:132–134.
- REINECK, H. E., 1957b. Über Wühlgarde im Watt und deren Abänderung durch ihre Bewohner. *Palaont. Z.*, 11:32–34.
- REINECK, H. E., 1958a. Wühlbau-Gefüge in Abhängigkeit von Sediment-Umlagerungen. *Senckenbergiana Lethaea*, 39:1–56.
- REINECK, H. E., 1958b. Longitudinale Schrägschicht im Watt. *Geol. Rundschau*, 47:73–82.
- REINECK, H. E., 1960a. Über die Entstehung von Linsen- und Flaserschichten. *Abhandl. Deut. Akad. Wiss.*, 1:370–374.
- REINECK, H. E., 1960b. Über Zeitlücken in rezenten Flachsee-Sedimenten. *Geol. Rundschau*, 49:149–161.
- REINECK, H. E., 1961. Sedimentbewegungen an Kleinstrippeln im Watt. *Senckenbergiana Lethaea*, 42:51–67.
- REINECK, H. E., 1962a. Reliefgüsse ungestörter Sandproben. *Zeit. Pflanzenernaehr., Dueng., Bodenk.*, 99: 151–153.
- REINECK, H. E., 1962b. Die Orkanflut vom 16. Februar 1962. *Natur Museum*, 92:151–206.
- REINECK, H. E., 1963a. Der Kastengreifer. *Natur Museum*, 93:65–68.
- REINECK, H. E., 1963b. Nasshärtung von ungestörten Bodenproben im Format 5 × 5 cm für projizierbare Dickschliffe. *Senckenbergiana Lethaea*, 44:357–362.
- REINECK, H. E., 1963c. Sedimentgefüge im Bereich der südlichen Nordsee. *Abhandl. Senckenberg. Naturforsch. Ges.*, 505:1–136.
- RICHTER, R., 1929. Grundsätzliches zur Erweiterung der Forschungsanstalt für Meeresgeologie und Meerespaläontologie "Senckenberg" in Wilhelmshaven. *Natur Museum*, 59:250–253.
- RICHTER, R., 1931. Tierwelt und Umwelt im Hunsrückschiefer; zur Entstehung eines schwarzen Schlammsteins. *Senckenbergiana*, 13:299–342.
- SCHÄFER, W., 1952. Biogene Sedimentation im Gefolge von Bioturbation. *Senckenbergiana*, 33:1–12.
- SCHÄFER, W., 1956. Wirkungen der Benthos-Organismen auf den jungen Schichtverband. *Senckenbergiana Lethaea*, 37:183–263.

- SCHAFER, W., 1962. Aktuo-Paläontologie nach Studien in der Nordsee. 666 S., 277 Abb., 36 Taf. Kramer. Frankfurt/Main, Germany.
- SCHÄFER, W., 1963. Aktuopaläontologische Beobachtungen. I. Sturmflut-Marken. *Natur Museum*, 93:496-500.
- SCHMIDT, H., 1935. Die bionomische Einteilung der fossilen Meeresböden. *Fortschr. Geol. Palaeont.*, 38: 1-154.
- SEIBOLD, E., 1955. Rezente Jahresschichtung in der Adria. *Neues Jahrb. Geol. Palaeont.*, 1955:11-13.
- SEILACHER, A., 1957. An-aktualistisches Wattenmeer? *Paläont. Z.*, 31:198-206.
- SHROCK, R. R., 1948. *Sequence in layered rocks*. McGraw-Hill, New York.
- STEVENSON, R. E., and K. O. EMERY, 1958. Marsh-lands at Newport Bay, California. *Allan Hancock Foundation Pubs.*, 20:1-109.
- VAN STRAATEN, L. M. J. U., 1952. Biogene textures and the formation of shell beds in the Dutch Wadden Sea. *Koninkl. Ned. Akad. Wetenschap. Proc. Ser. B.*, 55:500-516.
- VAN STRAATEN, L. M. J. U., 1954. Composition and structure of recent marine sediments in the Netherlands. *Leidse Geol. Mededel.*, 19:1-110.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1957. Accumulation of fine-grained sediments in the Dutch Wadden Sea. *Geol. Mijnbouwk.*, 19:329-354.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1958. Tidal action as a cause of clay accumulation. *J. Sediment Petrol.*, 28:406-413.
- WURSTER, P., 1958. Geometrie und Geologie von Kreuzschichtungskörpern. *Geol. Rundschau*, 47:322-359.

Comparison of Recent and Ancient Tidal Flat and Estuarine Sediments

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The delineation of mixed sedimentary environments is one of the more difficult problems faced by geologists. The problem is not only interesting as an aid in interpreting the history of the earth, but also has economic interest. Mixed environments are represented in most of the recoverable stratigraphic record. Extensive energy fuels are stored in rocks deposited in these environments. Therefore, delineation of mixed environments has become a critical function of sedimentary geology.

Tidal flat and estuarine environments have received considerable study in the past decade. The tidal flats of the Wadden Zee of the Netherlands were studied in great detail by Van Straaten (1961) and have served since then as a reference model for comparison of other modern and ancient tidal flats. Estuarine sediments were studied very early by geologists who recognized many ancient counterparts (Sollas, 1883; Twenhofel, 1932). Detailed work on other mixed environments has shown, however, that many of the rocks believed to be estuarine represent other shallow marine environments.

Because of the recent surge in sedimentological research, it is appropriate to compare the studies of recent data with studies of ancient rocks. The purpose of this paper is to determine what features of modern tidal flats and estuarine sediments are preserved in their ancient counterparts. After these features are identified and distinguishing criteria become established, it should be possible to improve our genetic interpretation of ancient sedimentary rocks.

RECENT TIDAL FLAT SEDIMENTS

Many variables characterize the sedimentation of intertidal zones. The most common feature of this environment is that water periodically rises and falls so that the sediment is alternately submerged by salt water and exposed to the atmosphere. Some of the environmental variables include the type of sediment present, bottom slope, tidal range, fetch distance available to winds at high tide, coastal morphology, climate, organisms, and the long-term position of the sea in relation to the land.

Studies by Van Straaten (1961) and Klein (1963a) show that tidal flat sedimentation occurs in two distinct settings which are controlled by the nature of the flanking coast. Tidal flats are known to occur along soft-sediment coasts of low relief, typified by the Wadden Zee tidal flats of the Netherlands, the Wash of England, and the Gulf Coast of the southern

United States. Tidal flats also flank rocky coasts like the coast of the Bay of Fundy or the coast of Maine. These types of tidal flats will be referred to as "Wadden-type" for the former and "Fundy-type" for the latter.

WADDEN-TYPE TIDAL FLATS

The Wadden Zee is a large lagoon separating the Frisian Islands from the mainland of the Netherlands. During low tide, the water of this lagoon drains off and exposes extensive tidal flats. Because of its shallow depth and a tidal amplitude ranging from 1.5 to 2.75 meters, most of the Wadden Zee floor is exposed at low tide.

Sedimentary Processes

The sediments of the Wadden Zee tidal flats consist of fine sand, silt, clay, and shell debris. These components are sorted into different primary structures depending upon the influence of the various inorganic and organic processes which operate singly or in combination in various tidal environments. The distinctive features of the tidal flat sediments are direct results of the intensity of reworking mechanisms which constantly attack the sediments.

Inorganic Processes—Inorganic processes operating on the Wadden Zee tidal flats include tidal currents, waves, lateral and downcurrent shifting of streams, and changes of level between land and sea.

Tidal currents transport mud from the North Sea floor into the Wadden Zee area. The mechanism of landward clay transportation has been described by Van Straaten and Kuenen (1958) and confirmed by deGroot (1963). Tidal currents also produce current ripple marks in the channel floor sediments and on the broader parts of the tidal flat (Van Straaten, 1949, 1950a, 1953). Wave action generates ripples in fine sand on all exposed flats.

Lateral and downcurrent shifting of streams, particularly the meandering creeks of lower tidal flats, is the most effective method of sediment reworking. The features existing in the sediment on the creek oxbanks, such as burrow structures and shells in growth position, are completely destroyed when the material slumps or falls by undercutting into the creek bank. The water in the creeks washes away the finest sediment and concentrates shells on the creek bottom as a lag pavement. Muddy or sandy sediment barren of shells accumulates on the point bars, and, during lateral shifting, this sediment builds over the

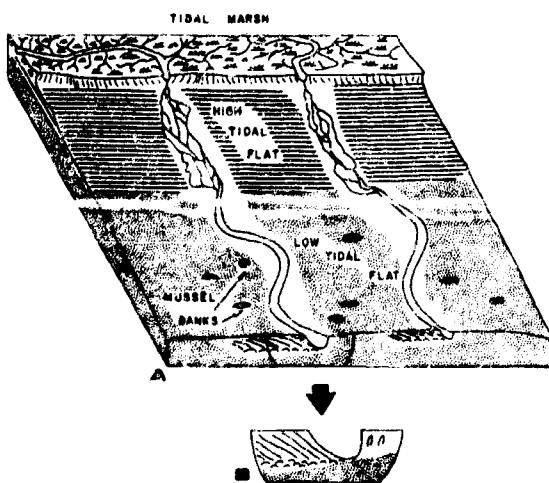


Fig. 1. (A) Block diagram showing relations of sedimentary environments in tidal flats in Dutch Wadden Zee (After Van Straaten, 1954b, 1961).

(B) Enlarged cross-section through the laterally migrating tidal channel, point bar, and tidal flats (After Van Straaten, 1952).

shell pavement of the creek floor. Point-bar sediments may consist of interstratified mud and sand laminae; it is possible that the mud is dropped at the turn of high tide and covered by sand before it is washed away by the ebb flow. Van Straaten refers to this complex process as lateral sedimentation (Van Straaten, 1951, 1954a, b). It generates a vertical sequence of sediments representing, from base to top, the channel floor, the point bar, and the tidal flat environments.

Changes of level between the land and the sea influence the vertical dimension and determine the position of tidal flat deposition. If a slow relative subsidence increases in subsidence rate, the upper sediment layers become buried by newly deposited material. Such changes have been called "vertical sedimentation" by Van Straaten (1951, 1954a, b). The extent to which this vertical factor has entered into tidal flat sedimentation is difficult to determine; more reliable findings may be obtained by studying the stratigraphic thicknesses of salt marsh peat.

Organic Processes—Organic sedimentary processes which influence tidal flat sedimentation include secretion of shells, disruption of structures by burrowing and detritus-feeding organisms, entrapment of sediment by grasses, and bacterial reduction of iron.

Shells secreted by marine invertebrates are incorporated with and are created on the tidal flat sediments. Shells and shell fragments accumulate in the sediment where the animal lived, or are shifted by waves and currents to form shell concentrates not related to the living position of the organism. *Mytilus* and several gastropods are the most common forms living on the tidal flats. Most other invertebrates are burrowing clams, worms, and gastropods. Shells of burrowing clams line the shell pavement of the channel floor.

Burrowing and detritus-feeding organisms destroy primary structures and create new structures. Burrowers destroy lamination. The worm *Arenicola marina* forms stratification at its feeding depth by rejecting particles which are too large for digestion. Because the coarse residue contains numerous shells of the small gastropod *Hydrobia*, the residue layer has been named the *Hydrobia bed* (Van Straaten, 1950b, 1952).

Van Straaten (1952) estimated the potential reworking of sediment by *Arenicola*, which reworks completely the entire sandy sediment above its feeding level every 20 months (Klein and Sanders, 1964).

Sedimentary Environments

The sedimentary environments of the Wadden Zee have been studied in great detail by Van Straaten (1949, 1950a, b, 1959, 1961). He recognizes four principal environments which, proceeding seaward from land, are (1) salt marshes, (2) high tidal flats, (3) low tidal flats, and (4) tidal channels. The geographic interrelationships of these environments are summarized in Figure 1. Similarly dispersed environments occur in many coastal settings, but their relative size may vary, or additional types of environments can occur, for example, those reported by Evans (1958) from the Wash of eastern England. Distinct subenvironments also occur within these four environments.

The type of sediment occurring on any part of the tidal flats of the Wadden Zee is determined by the interplay of the inorganic and organic sedimentary processes described previously. The processes which operate, and where they operate, are controlled by the various environments. Because sediment supply to these tidal flats is of a restricted grain size, textural variations are determined more by local conditions and processes than by external supply.

Salt Marshes—Salt marshes are characterized by abundant grass and few marine invertebrates. The grassy areas are traversed by a network of incised watercourses or creeks (Fig. 1). These marsh creeks meander and are sometimes bordered by low natural levees. In some areas, the streams show a striking flow pattern which consists of a network of small creeks that flow landward and a few major creeks which flow directly seaward (Van Straaten, 1951, 1954b).

Salt marsh sediments are influenced mostly by their marsh grasses, as evidenced by wavy lenticular laminae of fine sand and clay. The grass of the salt marshes and higher tidal flats traps sediment by obstructing and baffling the flow of water. Grass tufts form an irregular depositional surface, so the sediment laminae overlying these tufts are wavy and uneven in thickness. Furthermore, sediment deposition in depressions between elevated plant stems causes a small-scale lenticular stratification in cross section. Such laminae are absent in the meandering creek sediments where current ripples occur.

High Tidal Flats—Seaward from the salt marshes

is a more variable zone called the high tidal flats. Although the higher tidal flats are underlain by sand, they are normally devoid of incised watercourses. Where salt marsh creeks debouch into higher tidal flats, the meandering habit changes to a series of small braided, shallow, ephemeral channels (Fig. 1). Narrow and muddy higher tidal flats are drained by incised watercourses which do not change in channel habit at the boundary of the salt marsh and the high tidal flat. The chief organic content of these flats is a marine invertebrate fauna consisting of crustaceans, worms, gastropods, and pelecypods.

High tidal flat sediments vary with areal morphology. If the high flats are wide, they consist of sand reworked by waves, currents, and burrowing organisms (notably *Arenicola marina*). The surface of the sandy higher flats is abundantly rippled and the sediment shows ripple lamination or structures formed by burrowing organisms. The *Hydrobia* bed is almost ubiquitous at depths of 20 to 30 cm below the surface. The surficial layers of sediments contain animals preserved in life position, but, where such forms occur, lamination has been destroyed. Narrow or muddy high tidal flats differ from wide ones in that there are no sand-dwelling burrowers and, where there are incised watercourses, they may contain deposits of rippled sands.

Lower Tidal Flats—The lower tidal flats consist of grassless tracts of mud into which meandering creeks have been incised. These streams resemble marsh creeks, but unlike marsh creeks they shift position rapidly in both the lateral and downcutting directions. A lateral displacement of 10 m in 118 days was measured in one creek. A maximum value of 14.6 cm per day occurred during one 12-day interval (Van Straaten, 1951). Clusters of *Mytilus edulis* cover wide areas of the lower tidal flat environment and form large banks. Burrowing organisms are also present.

Most of the sediment is mud and muddy sand. In addition to meandering creeks reworking this sand, wave action and tidal currents rework the sediment, which forms megaripples. The surficial layers of sediment are densely inhabited by burrowing pelecypods and capped by mussel banks. Sediments near a mussel bank are influenced by both organic and inorganic processes. The profile of a mussel bank is often asymmetrical, being steep on the lee side and gentle on the windward side. Waves tend to erode the exposed side and wash out sediment from between individual shells, and sediment is trapped between shells on the protected side. Consequently, certain mussel banks shift laterally, analogous to a megaripple. Lateral displacement of 6 m in 46 days was measured on one mussel bank (Van Straaten, 1951). Though both shells and fecal pellets are contributed to the sediments from the mussel banks, mussel shells are not common in the sediment underlying the banks because wave erosion is concentrated on the exposed parts of the bank. Fecal pellets are abundant in the surface layers of the sediment underlying the mussel banks, but these are lost at depth. Lamination under the mussel banks may

or may not be disturbed, although burrow-filings which have been deformed by compaction have been observed.

Marine invertebrates are abundant on and immediately below the surface, but shells are rare in the underlying sediment. Where shells occur, they are concentrated into distinct layers. This distribution fosters the curious paradox of the concentration of shells in tidal flat sediments not necessarily proving that the organisms lived in profusion at that place, and the absence of shells not proving that organisms did not live at that place or were not abundant. This paradox is explained by the upward migration of burrowing organisms through the sediments, and by a rapid reworking of the sediment by shifting meandering creeks (Van Straaten, 1950b).

Tidal Channel—The tidal creeks carry the bulk of the water in and out of the Wadden Zee. Channel floors are always submerged even at low tide, and the channel courses are greatly curved, rather than completely meandered. The highest current velocities in the channels develop immediately before and immediately after high water (Van Straaten, 1949, 1954b).

Sediment from channel floors consists of shells which are oriented convex upward, imbricated upcurrent, and with long axes aligned parallel to current direction. Coarse sand and clay pebbles may also be present in the channel floors. Channel floor sediment is usually overlain by point-bar sediments which consist of interlayered and finely laminated clay and sand, in which the clay may consist wholly of fecal pellets. Abandoned creeks may be filled with mud that has been washed in by waves and tidal currents.

Ripple-marked sand with different patterns of ripples predominates in tidal channels. Cores from the channels show ripple-laminated sand and occasional sand and clay alternations. Shell beds are present also in tidal channel deposits and form the creek floor. Burrowing structures are rare except in the upper layers of mud-filled abandoned channels.

The channel sediments tend to show a definite vertical succession of textures and primary structures. From the base upward, they are (1) shell lag concentrate, (2) cross-stratified, point-bar sands, (3) ripple-laminated sand, silt, and clay from tidal flats. These are well exposed in construction sites (Van Straaten, 1957; Sixth International Sedimentological Congress, 1963).

Other Examples of Wadden-Type Tidal Flats

Noteworthy examples of Wadden-type tidal flats are those described by Evans (1958) from the Wash of eastern England and the tidal flats of northwest Germany (Hantschel, 1939). The Wash tidal flats can be subdivided into environments almost identical to those of the Wadden Zee, but Evans made more detailed biological subdivisions.

FUNDY-TYPE TIDAL FLATS

The Bay of Fundy intertidal zone (Fig. 2) includes more diverse sedimentary environments than the

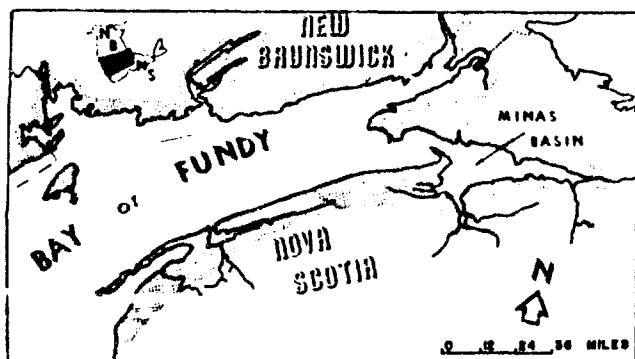


Fig. 2. Index map of the Bay of Fundy showing the limit of low tide (dotted line flanking shoreline).

Wadden Zee because of the variations in bedrock, topographic relief in coastal areas, tidal amplitude, and the extent of wave action. Klein (1963a) has distinguished the following four major sedimentary environments: (1) wave-cut benches, (2) estuarine clay flats, (3) tidal flats in the lee of barrier islands, and (4) tidal marshes.

Wave-cut Benches—Thin (0 to 2 feet) sediment veneers on wave-cut benches occur in 75 percent of the tidal areas in the Bay of Fundy. The physical features of these veneers are determined by waves, tidal action, and the physical properties of underlying bedrock. The composition, texture, and color of these sediments is controlled directly by underlying bedrock. Triassic red-bed wave-cut benches generate a veneer sediment which possesses the same color, texture, and composition. Mississippian bedrock (black siltstone, black claystone, brown sandstone) generates black, brown, and gray veneer sediment. A similar relationship between bedrock properties and sediment veneer properties occurs along most of the Bay of Fundy coast.

Wave action winnows the fine sediment and concentrates coarser sediment. Clay is removed from the uppermost cm of the sediment veneer. Braided streams crossing the sediment veneers also erode fine-grained sediment while the tide recedes. Clay deposition occurs at the high water line by a process similar to that described by Van Straaten and Kuennen (1958). Marine invertebrates are almost completely absent on wave-cut benches.

The combination of braided drainage and wave action produces the following combinations of primary structures: lenticular cross-stratification, flutes, grooves, current lineation, scoured and flat-topped current and oscillation ripple marks, scoured and flat-topped rhombic interference ripple marks, megaripples, and imbricated boulders and cobbles.

Estuarine Clay Flats—Estuarine clay flats are the large areas of clay and accessory silt accumulation in the protected mouths of rivers where vigorous wave action does not take place. Meandering creeks cross the clay flats, but shell pavements do not develop because there are no shells. The estuarine clay flats contain a large molluscan and worm fauna, compared

to the wave-cut bench sediments. The only stratification observed in these sediments is color changes from brown to gray and black, 5 cm below the top of the flats.

Tidal Flats in the Lee of Bedrock Islands—The Five Islands, in Colchester County, Nova Scotia, consist of Triassic bedrock. In the lee of these islands stands a protected intertidal area in which sediments somewhat analogous to those from the Wadden Zee are accumulating. High and low tidal flats are recognized, although they have different sedimentary features. The high tidal flats consist of narrow fringes of gravel, sand, and silt. These areas are drained by braided streams at low tide. The low tidal flats are wider and consist of silt, clay, and accessory sand and gravel. These low tidal flats are drained by meandering creeks whose channel floors consist of a lag concentrate of coarse sand, gravel, and clam shells which lie with the convex side up. The channel floor lag deposit is buried by finer-grained sediments of an accreting point bar. Cores show the coarse lag concentrate underlying fine sediment at the channel depth (Klein, 1963a).

The presence of coarse sediment is the only distinctive common feature of the Five Islands tidal flats and the Wadden Zee. The coarser sediment is brought in by streams which erode and drain the bedrock in the surrounding highlands, and finally becomes lag concentrate on the channel floor.

Salt Marshes—The tidal salt marshes of the Bay of Fundy have been described adequately by Johnson (1925) and Goldthwait (1924), so only the briefest summary is needed here. The marshes, drained by meandering creeks, are closely associated with estuarine clay flats and consist of a surficial plant veneer on these clayey sediments.

Other Examples of Fundy-type Tidal Flats

Other examples of Fundy-type tidal flats are rare. Bradley (1957) has described the tidal flats along the coast of Maine and indicated many similarities to the tidal flats of the Bay of Fundy. Trefethen and Dow (1960) have shown that the ripple marks along the Maine tidal flats are similar to the variety of ripple marks one can observe on the Bay of Fundy.

ANCIENT TIDAL FLAT DEPOSITS

SILICA CLASTIC COUNTERPARTS

Ancient counterparts of both the Wadden-type and Fundy-type tidal flats are not common. There have been only a few examples of ancient tidal flat deposits recorded in geological literature, and they all resemble the Wadden-type tidal flats.

A classic example of such an ancient counterpart is the Psammites du Condroz of the Upper Devonian (Fammenian) age of Belgium. The Psammites du Condroz consist of interbedded fine sandstones and shales. Within these beds, one can observe thin laminae, current and oscillation ripple marks, cross-stratification, and megaripples. Macar (1963) and Van

Straaten (1954a) described washout phenomena and the preservation of circular erosion remnants. During Field Trip E (in the Psammites du Condroz) of the Sixth International Sedimentological Congress (1963), the writer observed that oscillation ripple marks were refracted around the muddy areas, confirming that they are erosional remnants, and also were exposed during later deposition of sandier beds.

Potter and Glass (1958), in their study of the Pennsylvanian System of Williamson County, Illinois, also recognized tidal flat phases within the spectrum of marginal marine sedimentary rocks. Their analysis is based on direct comparison of primary structures in the Dutch Wadden Zee and the Psammites du Condroz.

Allen and Tarlo (1963) report an ancient counterpart of Wadden-type tidal flats from the Lower Devonian of the Welsh Borderland of England. Their interpretation of such an origin for these rocks came from comparing vertical sequences of lithologies, textures, and primary structures. By assuming a regression of higher tidal flats over lower tidal flats and tidal channels, they reconstructed a vertical column which would consist of basal channel deposits grading upward into well-sorted sands and capped by muddy sands with silt lenticles and burrows (Evans, 1958). The upper flat sediments were predominantly ripple marked, whereas the lower flat sediments were cross-stratified sands in the channel fills and ripple-marked and flat-bedded sands in the interchannel flats. Similar vertical sequences have been illustrated by Van Straaten (1957) and more recently by the Sixth International Sedimentological Congress (1963). The use of such profiles makes a direct comparison possible, assuming, of course, that there is lateral and regressive sedimentation.

No counterparts of Fundy-type tidal flats are known. However, it is possible that some transgressive marine sequences, unconformably overlying older beds, may have been formed on some wave-cut bench tidal flats.

CARBONATE COUNTERPARTS

Most tidal flats and ancient counterparts have been described from environments where the source of clastic sediment was outside the depositional basin. Graham Evans, in a personal communication, reported to this writer in 1963 that recent work along the Trucial Coast of the Persian Gulf has shown that broad tidal flats are common in areas of carbonate sedimentation. Textural changes in these carbonate flats are similar to those in areas of siliciclastic deposits. The tidal marsh zone appears to be replaced instead by broad Sebkhas and supratidal areas in which penecontemporaneous dolomite is presently being formed (Deshayes *et al.*, 1965; Illing *et al.*, 1965; Shinn *et al.*, 1965). The writer (Klein, 1963b), describing some channelized limestones in the Middle Jurassic Great Oolite Series of southern England, indicated that they may represent intertidal zone channel deposits. A more detailed explanation of the channelized limestone follows.

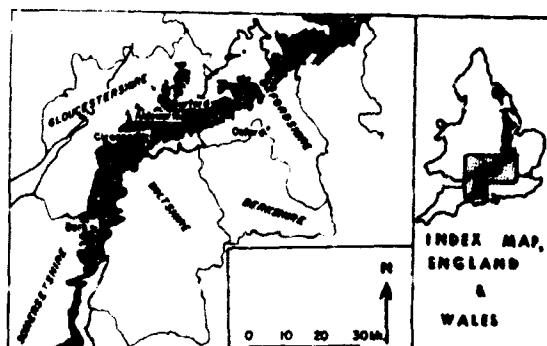


Fig. 3. Map of south-central England showing outcrop distribution of Great Oolite Series (Middle Jurassic). (Reproduced by permission of the Society of Economic Paleontologists and Mineralogists.)

The Middle Jurassic Great Oolite Series has been the object of extensive paleontological and stratigraphic study (Arkell, 1933; Arkell and Donovan, 1952). It occurs in a linear outcrop belt which passes through north and central Oxfordshire, north and central Gloucestershire, northwestern Wiltshire, and northern Somersetshire (Fig. 3). The Great Oolite ranges in thickness from 140 to 200 feet.

Rapid lateral facies changes characterize the Great Oolite. Broadly, these facies can be resolved into five lithological types. They are (1) coarse- to medium-grained, thick- to medium-bedded, channeled, oolitic, and shelly limestones ("channel limestones"); (2) fine-grained, even-bedded, oolitic, fossiliferous limestone ("flat-bedded limestone"); (3) fine-grained, even-bedded, thin-bedded recrystallized limestone; (4) black and olive claystone and siltstone; and (5) quartzose sandstone. Stratigraphically, the "channel limestones" include the Wychwood Beds, Kemble Beds, Acton Turville Beds, Bath Oolite and Lower Rags, Hens Cliff Oolite, Taynton Stone, Chipping Norton Limestone, and Farmington Oolite Member of the Stonesfield Slate.

The "channel limestones" are characterized by channel sets which average about 3 feet in thickness, al-

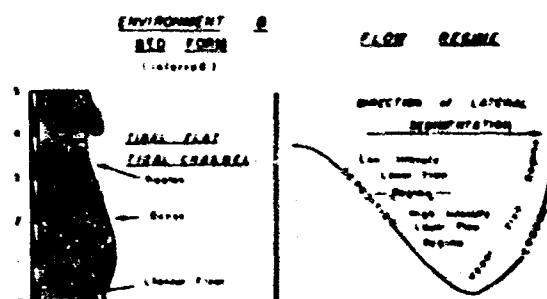


Fig. 4. Vertical profile of channelized limestone, Great Oolite Series (Middle Jurassic) showing inferred bed forms, depositional environments, and flow regime. (Reproduced by permission of the Society of Economic Paleontologists and Mineralogists.)

though they range from 1 foot to 12 feet. The depth of channeling ranges from 3 inches to 12 feet.

Within each channel set, as Figure 4 shows, is a definite vertical sequence of lithologies, primary structures, and textures. At the base of each channel set is a concentration of imbricated, disarticulated shells of brachiopods, clams, oysters, oriented echinoid spines, algal chips, and clay chips. These shelly limestones are found at the base, and were observed to overlie the undulating surface which defined the base of each channel set. This shelly limestone zone is overlain by thick (1 to 11 feet), shelly, oolitic limestones. The limestones are planar and lenticularly cross-stratified into 2-foot and 3-foot sets. The surfaces of some of these cross-strata show current lineation if the limestone contains 15 to 25 percent detrital quartz.

The individual cross-strata are thin-graded beds (1 to 1½ inches thick), and consist of a basal shelly zone overlain by oolitic limestone. The ooids are as large as 1½ mm at the base of the stratum and become progressively finer in particle size (¼ mm) at the top of the stratum. The oolitic zone is overlain by another graded layer.

Outcrop study has shown that the particle size of the layer of shells becomes coarse and thickens towards the base of the cross-stratified set. In the up-dip direction of a cross-stratum face, the shelly base of the graded layer tapers to a knife edge and disappears. Furthermore, the graded oolitic layers are found to channel into the underlying shell chips. The shell-chip layer, however, does not always channel into the oolite layer; it is sometimes mixed with fine-grained oolite. Thus, what on first observation appears to be a reduction in particle size from coarse shelly material to fine-grained oolite is in fact an alternating couplet of graded oolite and shell chips. This alternation of oolites and shell chips is deposited by a combination of current flow and foreset avalanching (Klein, 1965).

The thick-bedded, cross-stratified zone is overlain by finer-grained oolitic limestone which is either wavy-bedded or ripple-marked. Excavation of these beds in quarries shows that the wavy-bedded limestone represents nothing more than limestone with surfaces covered by interference ripples. This limestone grades upward into fine-grained limestone or olive claystone. Usually, the entire sequence is channeled by a second, down-cutting set of channelized limestone.

In an earlier paper, the writer (Klein, 1963b) concluded that the channelized limestones were tidal in origin; this conclusion was based on a comparison of textural and vertical-upward changes in primary structures within similar channelized sequences in classic rocks deposited in fluvial, estuarine, and tidal environments. A comparison of lag concentrates eliminated fluvial sediments from consideration, because fluvial beds contain clay chips and plant stem lag concentrates. The assumption of marine origin is logical because the shells lining the base of the channel sets

are marine fossils. An estuarine origin cannot be considered because of the great variety of fossils in the channel sets and the limited number of marine faunal species in estuaries (Emery and Stevenson, 1957). Because marine channels are known only from tidal channel deposits, the conclusion is inescapable that these limestones are tidal channel sediments.

What, then, is the significance of the vertical sequence of primary structures in the limestones? Recent hydraulic studies in alluvial channels by Simons and Richardson (1961) have shown that the channel bed form is controlled by the Froude number and velocity of the stream. In a channel regime which is laterally sedimented, flow intensities tend to be highly variable and vertically zoned. Ripples tend to form in a lower-intensity lower-flow regime, whereas dunes (or megaripples) tend to form in a high-intensity lower-flow regime. Standing waves occur when the Froude number exceeds 0.8, and characterize upper-flow regime.

Allen (1963) has applied this distribution of vertical velocity and flow regime to infer that flow regimes and bed forms in older sandstones are ancient. In Figure 4, a similar interpretation of environment, bed form, and flow regime is presented for the channelized limestones. The cross-bedded zone represents a high-intensity lower-flow regime formed by point-bar deposits similar to those which accrue over the basal channel lag concentrates in the tidal channels of the Wadden Zee (Van Straaten, 1952). The ripples represent the low-intensity lower-flow regime which one finds in the upper parts of a point bar in a tidal channel or in the flats of the low tidal flat environment. Obviously, when so much rippled and cross-stratified material is present, the entire depositional regime has to be at a lower-flow level. Lower-flow regimes imply low velocities, according to Simons and Richardson (1961). From this, it seems that the rate of discharge (a velocity function) is also relatively low. The tidal channel environment is characterized by a relatively low discharge at low tide, and, for that reason, these channels tend to be narrow and shallow. Consequently, the extent of downcutting, which is controlled by discharge, is also small. (See discharge formula of Leopold and Maddock, 1953.) Therefore, these tidal channels do not cut extensively into the underlying sediment and are probably expending most of their erosive energy in lateral cutting. It is probably only at the low-water level that tidal channels represent such zones of sedimentation. This interpretation is confirmed by the fact that the thickest channels in the Great Oolite cut into the finer-grained limestones which contain thick shell lenses resembling shell banks at the subtidal and lowest tidal flat margin (Klein, 1963).

RECENT ESTUARINE SEDIMENTS

In contrast to the tidal flat environment, the estuarine environment has not received detailed sedimentological analysis. Many studies of estuaries were made and summarized by Emery and Stevenson (1957);

and Twenhofel (1932). Although some preliminary studies have been made, details for comparing modern and ancient sequences are lacking.

Part of the problem centers around the geological definition of an estuary. An estuary represents that zone where salt water and fresh water become mixed, and usually the mixing takes place at a river mouth, although some authors (Emery and Stevenson 1957) extend their definitions to include arms of the sea where such mixing occurs. The physical circulation system of an estuary generally forms a salt wedge circulation pattern (Pritchard, 1952). This salt wedge pattern occurs not only in river mouths, but also in lagoons, deltas, tidal channels, and salt marsh channels. For that reason Emery and Stevenson (1957) pointed out that these environments may not necessarily be mutually exclusive. Thus, geologically, the estuarine environment represents the superimposition of a specific circulation plan on several geologically distinct environments. The problem of discrimination of estuarine environments becomes merged with the problem of determining the other environments on which an estuarine circulation pattern is superimposed.

The discrimination of estuarine environments in deltas has been achieved by Fisk (1961), Fisk *et al.* (1954), Guilcher (1963), Shepard (1960), and Scruton (1960); the sedimentological features of lagoons are also understood (Rusnak, 1960; Phleger and Ewing, 1962). Therefore, this paper emphasizes the sedimentology of estuarine river mouths.

There are few sedimentological studies of river estuaries. Sollas (1883) presented the first study of modern sediments after his investigation of the Severn River Estuary of western England. He showed that the muds came mostly from an oceanic source and were brought upstream by currents at flood tide. A seaward source was confirmed by the presence of marine organisms in the muds. He also showed that scouring of the bottom of the Severn River was negligible; the scoured material was moved upstream and downstream by tidal currents. At low tide, however, the scouring at the bottom of the channel was greater.

In his study of cores from the Severn, Sollas described a vertical sequence of sediments; the gravels of the channel floor were overlain by mixed sand and mud. This sequence is overlain by two peat horizons interbedded with clay. The hydraulic significance of this profile will be discussed below in a review of the Rhine and Meuse Estuary.

BAY OF FUNDY ESTUARINE SEDIMENTS

Estuaries are common in the mouths of the rivers which drain into the Bay of Fundy, particularly the mouths of the Annapolis, Cornwallis, Avon, Salmon, Petitcodiac, Gaspereau, and St. John Rivers. The Avon Estuary has been studied by Kindle (1917), who emphasized the upstream transport and migration of sand from the Bay of Fundy.

In conjunction with studies of tidal flats, the author

also examined the estuarine sediments of the Cornwallis, Gaspereau, and Avon Rivers of Nova Scotia. These rivers are characterized by banks consisting almost entirely of silt and clay. In this respect, they are similar to the estuaries in France and Madagascar described by Guilcher (1963). During low water stages, these three rivers transport silt and clay from surrounding highlands into the Bay of Fundy. It is only as the tide turns and floods that the silt and clay are partly retransported upstream. At high water, silt and clay settle out, primarily because the velocity of the incoming salt wedge is reduced to almost nothing. The upstream momentum of the flow and the time lag in particle settling through a column of water 15 feet deep delays mud deposition. As the tide ebbs, mud is deposited temporarily, but with increasing ebb velocities any mud remaining in suspension is transported back into the Bay of Fundy. This process is similar to what Van Straaten and Kuenen (1958) found in tidal flats, and Guilcher (1963) in Brittany and Madagascar estuaries.

The channel floors of the estuaries are covered by sand. This sand is similar in mineral composition, texture, and color to the sands found on tidal flats in the Minas Basin. This physical similarity suggests that tidal currents erode these tidal flats and transport the sand to estuary mouths where the incoming flood currents carry it back upstream. In the lower Avon Estuary, the orientation of steep faces of current ripples and megaripples is upstream, and they can be seen migrating in that direction during rising tide. This orientation and migration confirms Kindle's (1917) earlier conclusion that the sand on the floor of the Avon Estuary was derived from tidal flats flanking estuarine mouths.

It is noteworthy that the coarsest debris (sand) is confined to the channel bottoms. Lateral migration of the estuaries should generate a vertical sequence of sediments consisting of channel floor sands which are rippled, cross-stratified and overlain by silt and clay. Excavations at the dock site in Walton, Hants County, Nova Scotia, show that such a profile was developed and preserved in the prograding banks of these estuaries.

RHINE AND MEUSE ESTUARY

The most detailed modern study of a fluvial estuary is the description by Oomkens and Terwindt (1960) of the inshore sediments of the Haringvliet, one of the estuarine arms of the Rhine and Meuse Rivers in the Netherlands (Terwindt, 1963). The Haringvliet is the construction site of a major seawall which will separate what were once inshore areas from tidal flats. During excavation of the site, several vertical cuts were opened into the bottom sediments of this estuary.

The sediments of the Haringvliet are predominantly sand, with subordinate quantities of clay pebbles and clay laminae. These sediments are cross-stratified, rippled, and graded from gravel size at the base of an estuarine succession to silt and clay at the top.

Sand found in the intervening zone shows a vertical decrease in particle size from coarse sand at the base to fine sand at the top.

These sediments and primary structures are arranged in a definite vertical sequence. From the base upward, the succession consists of a coarse, clay-pebble mixture within which are shells of marine bryozoa, foraminifera, mussels, echinoid spines, and peat lumps (Terwindt, 1963). These are overlain by cross-stratified sands. The orientation of the cross-stratification is upstream, suggesting that maximum erosion and sand deposition take place during flood tide (Oomkens and Terwindt, 1960). This deduction is confirmed by current velocity data, which show that at flood tide, velocities of 70 to 80 cm/sec are observed, whereas at ebb tide, velocities do not exceed 44 cm/sec (Oomkens and Terwindt, 1960).

The cross-stratified coarse sands are overlain by thin-bedded, even-bedded, rippled, finer-grained sands. In the upper part of these rippled sands, one finds interbedded clay laminae, which Oomkens and Terwindt (1960) attributed to deposition at slack water during rising and falling tides; the clay was deposited in the same way as in the Wadden Zee tidal flats (Van Straaten and Kuenen, 1958).

The significance of this vertical sequence of textures and structures was related to "rapid" lateral migration of the Haringvliet by Oomkens and Terwindt (1960). This lateral migration characterizes not only estuarine areas such as the Haringvliet, but also tidal channels and meandering rivers (Klein, 1963b). Each of these generates a similar vertical profile of primary structures and textures (Allen, 1963). Simons and Richardson (1961) showed that primary structures such as flat bedding, ripples, and cross-stratification reflect the nature of the bed form of the depositional surface. This, in turn, is controlled by the Froude number, a ratio of fluid velocity to depth, and the constant of gravitational acceleration. At low velocities, the bed form tends to be flat and correspondingly, one would expect thin laminae to result. As velocities increase, the bed form tends to become rippled and the internal lamination becomes ripple stratification. As velocities increase, the bed form becomes large-scale ripples or megaripples (called dunes by Simons and Richardson, 1961) and cross-stratification is developed internally. As the velocities increase and the Froude number exceeds 0.8, the entire bed form is changed to flat beds and standing waves. With increased velocities, antidunes are formed. Two flow regimes characterize this series, a lower-flow regime where the Froude number is less than 0.8, in which ripples and dunes are the predominant bed form, and an upper-flow regime, where the Froude number exceeds 0.8 and standing waves and antidunes develop.

Oomkens and Terwindt's (1960) vertical sequence can now be interpreted hydraulically. The channel lag concentrate of clay pebbles, marine shells, and peat chips represents an upper-flow regime which eroded one of the banks of the Haringvliet. The

cross-stratified sands must represent preserved remnants of a dune bed form, suggesting a lower-flow regime with higher velocity. The flat-bedded and rippled zone must represent a lower-flow regime with lower velocity. Such a sequence (Fig. 4) characterizes all rivers, estuaries, and tidal channels. The high-velocity lower-flow regime represents the fore-slope of a migrating point bar which buries the channel lag concentrate, and the low-velocity lower-flow regime characterizes estuarine conditions during slack periods. This hydraulic framework is also applicable to the vertical profile of the Severn and the estuaries of the Bay of Fundy (Sollas, 1883).

If these vertical sequences of primary structures and texture characterize migrating estuarine, fluvial, and tidal channel sedimentation, how can one recognize them? The writer (Klein, 1963b) suggested that in clastic sequences, the only way to distinguish between them is by a comparison of channel lag concentrates. Tidal channel deposits are floored almost exclusively by shell lag concentrates. Estuarine channels appear to be floored by a mixture of both, or by clay chips (Oomkens and Terwindt, 1960). Fluvial channels are floored by gravel, clay pebbles, and logs. A comparison of such vertical sequences should make it possible to identify the estuarine sediments of the geological past.

ANCIENT ESTUARINE SEDIMENTARY ROCKS

Recognition of ancient estuarine sediments has been limited to a few stratigraphic sequences. Most of these, such as the Middle Jurassic of Great Britain (Arkell, 1933), were recognized as estuarine because of their limited fauna and their dark clay content.

Although proven estuarine deposits of the past are few in number, several stratigraphic sequences contain estuarine elements. Recent studies by Williams (1960) and Degens *et al.* (1957, 1958) suggested that estuarine beds occur in the Lower Pennsylvanian Coal Measures (Pottsville and Allegheny Groups) of the Allegheny Plateau. By analyzing the types of fossils occurring in shales overlying coal seams, Williams (1960) recognized that their geographic faunal distribution was environmentally controlled. Along the Allegheny Front, restricted marine and nearshore fossils (phosphatic brachiopods and pectinids) occur in shales overlying the Lower Clarion, Upper Clarion, Lower Kittanning, and Middle Kittanning Coals. Some of the beds represent estuarine conditions, although more detailed paleoecological discrimination was not possible.

Working with a related suite of samples from the same Coal Measures, Degens *et al.* (1957, 1958) tried to determine marine, marginal marine, and non-marine shales by analyzing the distributions of trace elements within clay minerals. They defined these three broad environments paleontologically and then showed that marine clays were high in boron, whereas freshwater clay minerals were high in gallium and tin (Degens *et al.*, 1957). Their transitional "zone of no decision",



Fig. 5. Repeated vertical sequences of channel lag concentrates, cross-stratified sandstones, and ripple-stratified sandstones. Berea Sandstone, North Wall, Buckeye Quarry, South Amherst, Lorain County, Ohio. Each bed represents such a vertical sequence.

passing through the rhubidium pole of their gallium-boron-rhubidium diagram, might indicate the presence of estuarine and brackish sedimentary rocks.

A second sedimentary rock sequence that may contain estuarine sediments is the Mississippian Berea Sandstone of northern and central Ohio. In a detailed study, Pepper *et al.* (1954) showed that the Berea Sandstone was deposited in a channel regime. In



Fig. 6. Close-up of layer in Berea Sandstone showing repeated cross-stratified sandstone and ripple-stratified sandstone. South Wall, Buckeye Quarry, South Amherst, Lorain County, Ohio.



Fig. 7. Vertical profiles of channel floor lag concentrate, thick-bedded, cross-stratified sandstone, and thinly-laminated, ripple-stratified sandstone. Berea Sandstone, Nichol Quarry, Kipton, Lorain County, Ohio.

part of this sequence the channel sands indicate deltaic distributaries in northern Ohio.

A close examination of vertical faces in quarries and road cuts (Pepper *et al.*, 1954) shows a great similarity between them and the vertical sequences of the Haringvliet described by Oomkens and Terwindt (1960). In fact, Pepper *et al.* (1954) pointed out repeatedly that the Berea Sandstone is characterized by a vertical sequence of basal clay pebble conglomerates, overlain by cross-stratified sand and capped with a flat-bedded zone of rippled sandstone (Figs. 5, 6, 7). An examination of the paleogeographic maps of Pepper *et al.* (1954) also shows that the Berea Sandstone of central and northern Ohio was part of a deltaic distributary system close to the mouth of an inferred delta. Thus, the Berea Sandstone of that area probably represents estuarine distributaries subjected to salt wedge influxes.

Another example of an estuarine sedimentary rock is the Holdgate Sandstone of Lower Devonian age, found in the Welsh Borderland of England (Allen and Tarlo, 1963). Tidal influx into a river system was postulated from siltstone intercalations, animal burrows, and calcareous concretions.

The Middle Jurassic Great Estuarine Series of western Scotland was considered estuarine by many workers (Arkell, 1933). Equivalents occur in central England and comprise the Upper Estuarine Series of Lincolnshire, Northamptonshire, and Rutlandshire (Arkell, 1933). Recent work by Hudson (1962, 1963a, b) has shown that the fauna of the Great Estuarine Series had great affinities with the modern

molluscan fauna of the lagoons along the Texas coast. From these paleontological comparisons, Hudson concluded that these rocks are lagoonal, not fluvial-estuarine, in origin. However, Rusanek (1960) and Emery and Stevenson (1957) have demonstrated that an estuarine circulation system can characterize lagoons, and that, therefore, these environments are not mutually exclusive. Furthermore, many lagoons and bays may have a seasonal estuarine circulation system (Van Andel and Postma, 1954). Thus, the Great Estuarine and Upper Estuarine Series of Great Britain may represent a lagoonal environment on which estuarine circulation could have been superimposed.

ESTUARINE SEDIMENTOLOGY AND EVAPORITE DEPOSITION

Evaporite deposition is controlled by estuarine circulation. In the previous discussion the data cited from Recent estuarine sediments were confined to areas subjected to humid climates. Under these conditions, upstream and downstream shifts of salt water can be observed.

Chemical analysis of evaporite precipitation (Ussiglio, 1849a, b; Van't Hoff and Weigert, 1901) has shown that to deposit gypsum, four-fifths of the original volume of sea water must be evaporated and that to deposit halite, nine-tenths of the original volume of sea water must be evaporated. Considering the large volume of gypsum and salt deposits throughout the world, the assumption is that a considerable volume of ocean water has been evaporated. All these salt deposits are interbedded and interfingered with shallow marine sediments, so, obviously, gypsum and salt precipitation took place in coastal environments in the geological past.

Scruton (1953) argued that the only way thick shallow-water evaporites can form is by imposing an estuarine circulation system on an area flanked by broad lagoons and tidal flats. Such an area must occur in an arid climate because tidal influxes of oceanic salt water renew the supply of water from which salt can be precipitated. Morris and Dickey (1957) have described such an estuary from the Bocana de Virrila of northwestern Peru. The tidal influx of salt water renews the supply of potentially precipitable salts. As this water surges upstream, part of it is evaporated, its density increases, gypsum and, farther inland, halite precipitate. A corresponding increase in ppm of potassium, sodium, and magnesium is observed. The calcium concentration increases up to the central part of this estuary and then decreases upstream because gypsum has precipitated (Morris and Dickey, 1957).

Salt deposits are extensive in the Silurian rocks of Michigan, Ohio, and New York, the Permian of West Texas and Russia, and the Middle Jurassic of Wyoming. Briggs (1958) observed lateral variations in the types of salt that occur in the Silurian of the Michigan Basin and established a depositional model combining Scruton's (1953) circulation system and the

order of precipitation of salt minerals (Ussiglio, 1849a, b). Using these data, he concluded that the Michigan Basin was subjected to estuarine influxes of salt water from southern Ohio and south central Ontario during late Silurian time. No other salt sequences have been studied using this combined approach.

CONCLUSIONS

Tidal flat sedimentation can occur along soft-sediment coasts and along bedrock coasts. Each of these areas generates its own sequence of sediments and environments. These two types of tidal flat are designated by the author as Wadden-type and Fundy-type, respectively.

Ancient tidal flat deposits have been described from the Upper Devonian of Belgium, the Lower Devonian of England, and the Pennsylvanian of Illinois. Carbonate tidal flat sediments occur in the Middle Jurassic rocks of England.

Estuarine sedimentation is dominated by a circulation plan involving the influx of a salt wedge during high tide and the retreat of such a salt wedge during low tide. This pattern is superimposed on tidal channel, tidal marsh, lagoon, river, and deltaic environments. River estuaries are characterized by sedimentary vertical sequences consisting of a basal lag concentrate of clay pebbles, marine shells, and peat fragments, overlain by cross-stratified sands and capped by flat-bedded, rippled sands, and clay laminae. They record the predominance of upper-flow regime during bank erosion and lower-flow regime during sediment deposition.

Ancient counterparts to estuaries are believed to have existed, because of the studies of the Coal Measures of Pennsylvania and the Berea Sandstone of Ohio. The Middle Jurassic Great Estuarine Series of Scotland and England represent lagoonal environments on which an estuarine circulation system may have been imposed. Deposition of evaporites in the geological past took place in mixed shallow marine environments and required an estuarine circulation system in an arid climate to supply continuously the large volume of water from which salt was precipitated.

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LITERATURE CITED

- ALLEN, J. R. L., 1963. Henry Clifton Sorby and the sedimentary structures of sands and sandstone in relation to flow conditions. *Geol. Mijnbouw*, 42:223-228.
- ALLEN, J. R. L., and L. B. TARLO, 1963. The Downtonian and Dittonian facies of the Welsh Borderland. *Geol. Mag.*, 100:129-155.
- ARKELL, W. J., 1933. *Jurassic geology of Great Britain*. Clarendon Press, Oxford, England.
- ARKELL, W. J., and D. T. DONOVAN, 1952. The fuller's earth of the Cotswolds and its relation to the Great Oolite. *Geol. Soc. London Quart. J.*, 107:227-253.
- BRADLEY, W. H., 1957. Physical and ecologic features of the Sagadahoc Bay tidal flat. *Geol. Soc. Am. Mem.*, 67:641-682.
- BRIGGS, L. I., 1958. Evaporite facies. *J. Sediment. Petrol.*, 28:46-56.
- DEFFEYES, K. S., F. J. LUCIA, and P. K. WEYL, 1965. Dolomitization of Recent and Plio-Pleistocene sediments by marine evaporite waters on Bonaire, Netherlands Antilles. In *Dolomite and Limestone Diagenesis—A Symposium*, edited by L. C. Pray and R. C. Murray; pp. 71-88. Soc. Econ. Paleontologists and Mineralogists, Tulsa, Oklahoma.
- DEGENS, E. T., E. G. WILLIAMS, and M. L. KIETH, 1957. Environmental studies of carboniferous sediments, Part I: Geochemical criteria for differentiating marine and fresh-water shales. *Bull. Am. Assoc. Petro. Geologists*, 41:2427-2455.
- DEGENS, E. T., E. G. WILLIAMS, and M. L. KIETH, 1958. Environmental studies of carboniferous sediments, Part II: Applications of geochemical criteria. *Bull. Am. Assoc. Petro. Geologists*, 42: 981-997.
- EMERY, K. O., and R. E. STEVENSON, 1957. Estuaries and lagoons. In *Treatise on Marine Ecology*, edited by J. W. Hedgpeth; vol. 1. *Geol. Soc. Am. Mem.*, 67:673-750.
- EVANS, G., 1958. Some aspects of recent sedimentation in the Wash. *Ectogae Geol. Helv.*, 51:508-515.
- FISK, H. N., 1961. Bar-finger sands of Mississippi Delta. In *Geometry of Sandstone Bodies*, edited by J. A. Peterson and J. C. Osmond; pp. 29-52. Am. Assoc. Petro. Geologists, Tulsa, Oklahoma.
- FISK, H. N., E. McFAKLAND, C. R. KLOB and L. J. WILBERT, 1954. Sedimentary framework of the modern Mississippi Delta. *J. Sediment. Petrol.*, 24: 76-99.
- GOLDTHWAIT, J. W., 1924. Physiography of Nova Scotia. *Geol. Surv. Canada Mem.*, 140: 1-179.
- GROOT, A. J. DE, 1963. Mangaantoe stand van Nederlandse en Duitse Holocene sedimenten in verband met slibransport en bodengenese. *Wageningen, Verslag Landbouwk. Onderzoek. N.R.*, 69:7.
- GUILCHER, A., 1963. Estuaries, deltas, shelf, slope. In *The Sea*, edited by M. N. Hill; vol. 3, pp. 620-659. Interscience, New York.
- HANTZSCHEL, W., 1957. Tidal flat deposits. In *Recent Marine Sediments*, edited by P. D. Trask; pp. 195-209. Soc. Econ. Paleontologists and Mineralogists, Tulsa, Oklahoma.
- HUDSON, J. D., 1962. The stratigraphy of the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. *Edinburgh Geol. Soc. Trans.*, 19:139-165.
- HUDSON, J. D., 1963a. The recognition of salinity-controlled mollusc assemblages in the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. *Paleontology*, 6:318-326.
- HUDSON, J. D., 1963b. The ecology and stratigraphical distribution of the invertebrate fauna of the Great Estuarine Series. *Paleontology*, 6:327-348.
- ILLING, L. V., A. J. WELLIS, and J. C. M. TAYLOR, 1965. Peneccontemporary dolomite in the Persian Gulf. In *Dolomite and Limestone Diagenesis—A Symposium*, edited by L. C. Pray and R. C. Murray; pp. 89-111. Soc. Econ. Paleontologists and Mineralogists, Tulsa, Oklahoma.
- JOHNSON, D. W., 1925. *The New England-Acadian Shoreline*. John Wiley and Sons, New York.
- KINDEL, E. M., 1917. Recent and fossil ripple marks. *Geol. Surv. Can. Museum Bull.*, 25:1-56.
- KLEIN, G. DEV., 1963a. Bay of Fundy intertidal zone sediments. *J. Sediment. Petrol.*, 33:844-858.
- KLEIN, G. DEV., 1963b. Intertidal zone channel deposits in Middle Jurassic Great Oolite Series, southern England. *Nature*, 197:1060-1062.
- KLEIN, G. DEV., 1965. Dynamic significance of primary structures in the Middle Jurassic Great Oolite Series, southern England. In *Primary Sedimentary Structures and Their Hydrodynamic Interpretation—A Symposium*, edited by G. V. Middleton; pp. 173-191. Soc. Econ. Paleontologists and Mineralogists, Tulsa, Oklahoma.
- KLEIN, G. DEV., and J. E. SANDERS, 1964. Comparison of sediments from Bay of Fundy and Dutch Wadden Sea tidal flats. *J. Sediment. Petrol.*, 34:19-24.
- LEOPOLD, L. B., and T. MADDOCK, JR., 1953. The hydraulic geometry of stream channels and some physiographic implications. *U. S. Geol. Surv. Profess. Papers*, 252.
- MACAR, P., 1963. Etude de structures sedimentaires et de pseudo-nodules du Devonien de L'Ardenne. *Guide-book for Excursions E/F, Sixth Intern. Sediment. Congr.*, Brussels, Belgium.
- MORRIS, R. C., and P. A. DICKEY, 1957. Modern evaporite deposition in Peru. *Bull. Am. Assoc. Petro. Geologists*, 41:2467-2474.
- OOMKENS, E., and J. H. J. TERWINDT, 1960. In-shore estuarine sediments in the Haringvliet (Netherlands). *Geol. Mijnbouw*, 39:701-710.
- PEPPER, J. F., W. DEWITT and D. F. DEMAREST, 1954. Geology of the Bedford Shale and Berea Sandstone in the Appalachian Basin. *U. S. Geol. Surv. Profess. Papers*, 259.
- PHLEGER, F. B., and G. C. EWING, 1962. Sedimentology and oceanography of coastal lagoons in Baja California, Mexico. *Geol. Soc. Am. Bull.*, 73:145-182.
- POTTER, P. E., and H. D. GLASS, 1958. Petrology and sedimentation in southern Illinois: A vertical profile. *Illinois Geol. Surv. Rept. Invest.*, 204:1-60.
- PRITCHARD, D. W., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11:106-123.
- RUSNAK, G. A., 1960. Sediments of Laguna Madre, Texas. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and T. H. Van Andel; pp. 153-169. Am. Assoc. Petro. Geologists, Tulsa, Oklahoma.
- SCRUTON, P. C., 1953. Deposition of evaporites. *Bull. Am. Assoc. Petro. Geologists*, 37:2498-2512.
- SCRUTON, P. C., 1960. Delta building and the deltaic sequence. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger and T. H. Van Andel; pp. 82-102. Am. Assoc. Petro. Geologists, Tulsa, Oklahoma.
- SHEPARD, F. P., 1958. Mississippi Delta: marginal environments, sediments and growth. In *Recent Sediments, Northwest Gulf of Mexico*, edited by F. P. Shepard, F. B. Phleger, and T. H. Van Andel; pp. 56-81. Am. Assoc. Petro. Geologists, Tulsa, Oklahoma.
- SHINN, E. A. R. N. GINSBURG, and R. M. LLOYD, 1965. Recent supratidal dolomite from Andros Island, Bahamas. In *Dolomite and Limestone Diagenesis—A Symposium*, edited by L. C. Pray and R. C. Murray; pp. 112-123. Soc. Econ. Paleontologists and Mineralogists, Tulsa, Oklahoma.
- SIMONS, D. B., and E. V. RICHARDSON, 1961. Forms of bed roughness in alluvial channels. *Am. Soc. Civil Engrs. Proc.*, 87:87-106.
- SIXTH INTERNATIONAL SEDIMENTOLOGICAL CONGRESS, 1963. *Guide to Fieldtrips A and B*; p. 52. Antwerp, Belgium.
- SOLLAS, W. J., 1883. The estuaries of the Severn and

- its tributaries. *Geol. Soc. London Quart. J.*, 39:611-626.
- TERWINDT, J. H. J., 1963. Excursion Rhine-Meuse Estuary (Haringvliet). *Sixth Intern. Sediment. Congr. Guidebook*, Amsterdam.
- TREFETHEN, J. M., and R. L. DOW, 1960. Some features of modern beach sediments. *J. Sediment. Petrol.*, 30:589-602.
- TWENHOFEL, T. H., 1932. *Treatise on Sedimentation* (2nd Ed., 1961). Dover Publications, New York.
- USSIGLIO, J., 1849a. Analyse de l'eau de la Méditerranée sur côtes de France. *Ann. Chim. Phys.*, 27:92-107.
- USSIGLIO, J., 1849b. Etudes sur la composition de l'eau de la Méditerranée sur l'exploitation des sels qu'elle contient. *Ann. Chim. Phys.*, 27:172-191.
- VAN ANDEL, T. H., H. POSTMA, 1954. Recent sediments of the Gulf of Paria. In Reports of the Orinoco Shelf Expedition, Vol. I. *Koninkl. Ned. Akad. Wetenschap. Afdel. Nat.*, vol. 20, No. 5:1-245.
- VAN STRAATEN, L. M. J. U., 1949. Quelques particularités du relief sousmarine de la Mar des Wadden (Hollande). *Congr. Sediment. Quat. France, CR*; pp. 139-145.
- VAN STRAATEN, L. M. J. U., 1950a. Giant ripples in tidal channels. *Koninkl. Ned. Aadr. Gen. Tijdschr.*, 67:336-341.
- VAN STRAATEN, L. M. J. U., 1950b. Environment of formation and facies of the Wadden Sea sediments. *Koninkl. Ned. Aadr. Gen. Tijdschr.*, 67:354-368.
- VAN STRAATEN, L. M. J. U., 1951. Texture and genesis of Wadden Sea sediments. *Third Intern. Congr. Sediment. Proc., Netherlands*, pp. 225-244.
- VAN STRAATEN, L. M. J. U., 1952. Biogene textures and the formation of shell beds in the Dutch Wadden Sea. *Koninkl. Ned. Akad. Wetenschap., Proc. Ser. B.*, 55:500-516.
- VAN STRAATEN, L. M. J. U., 1953. Megaripples in the Dutch Wadden Sea and the Basin of Arachon (France). *Geol. Mijnbouw*, 16:25-47.
- VAN STRAATEN, L. M. J. U., 1954a. Sedimentology of Recent tidal flat sediments and the Psammites du Condroz (Devonian). *Geol. Mijnbouw*, 16:25-47.
- VAN STRAATEN, L. M. J. U., 1954b. Composition and structure of Recent marine sediments in the Netherlands. *Leidse Geol. Mededel.*, 19:1-110.
- VAN STRAATEN, L. M. J. U., 1957. The Holocene deposits. In *The Excavation at Velsen*, edited by L. M. J. U. Van Straaten and J. M. de Jong; vol. 17, pp. 158-173. Koninkl. Ned. Geol. Mijnbouw. Genoot., Verhandel. Geol. Ser.
- VAN STRAATEN, L. M. J. U., 1959. Minor structures of some Recent littoral and neritic sediments. *Geol. Mijnbouw*, 21:197-216.
- VAN STRAATEN, L. M. J. U., 1961. Sedimentation in tidal flat areas. *Alberta Soc. Petrol. Geologists J.*, 9:203-226.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1958. Tidal action as a cause of clay accumulation. *J. Sediment. Petrol.*, 28:406-413.
- VAN'T HOFF, J. H., and F. WIEGERT, 1901. Untersuchungen über die bildungs-verhältnisse der oceanischen salzablagerungen, insbesondere des Stassfurter Salzlagers. *Koninkl. Preuss. Akad. Wiss. Sitzb.*, 23: 1140-1148.
- WILLIAMS, E. G., 1960. Marine and fresh water fossiliferous beds in the Pottsville and Allegheny group of western Pennsylvania. *J. Paleontol.*, 34:905-922.

Contrasts in Coastal Bay Sediments on the Gulf and Pacific Coasts

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The terms "bay", "lagoon", and "estuary" have unfortunately been used in so many different ways that it is difficult to establish precise meanings. As an example, Mobile Bay is a classic estuary; Florida Bay is a lagoon behind a fringing reef; and Apalachicola Bay is composed of a true estuary, barrier island lagoons, and open coastal embayments. The term estuary implies the effect of tides and is derived from the Latin word for tide (American Geological Institute, 1957). Thus, an estuary is an indentation in a coast in which tidal circulations meet land runoff and generally prevail over the land contributions. Morphologically, estuaries are generally triangular in shape with the apex inland and the long axis oriented normal to the trend of the shore and parallel to the regional slope of the land. They are typically the broad mouths of river valleys which have been drowned by the latest advance of the sea upon the land. The estuary is a relatively transient feature geologically and will ultimately be filled by marsh, tidal flat, and deltaic deposits. The relative length of any one estuary's life will be determined primarily by the rate at which sediment is introduced into it, either from terrestrial or marine sources. Where large volumes of sediment are introduced by streams, estuaries will be short-lived or may never develop; and the typical coastal feature will be a delta.

General coastal configuration is a factor, since rugged coasts typically exhibit narrow shelves, sea cliffs, fjords, or rias. Coastal plains are fringed by barrier islands, broad estuaries, by deltas and their associated forms, and typically by broad shelves. The two main types of coasts are exemplified in the United States by the coastal plains of the Gulf and Atlantic Coasts and the relatively bluffed coasts of the Pacific. The Florida Peninsula is a carbonate plateau and thus differs in detail from both of the other major types.

PREVIOUS RESEARCH

During the past ten years, the writer and various associates have observed shore and coastal features at many localities on all of the major coasts. These have been reported in several papers (Emery *et al.*, 1957; Goodell and Gorsline, 1961; Gorsline, 1957, 1963a, b; Gorsline and Stewart, 1962; Kofoed and Gorsline, 1963; Stewart and Gorsline, 1962) which have been primarily concerned with the character of the sedimentary materials in the bays and estuaries and with

the morphology of the bays. Water characteristics and circulation have been examined in some detail in Florida Bay (Gorsline, 1963a, b) and Apalachicola Bay (Gorsline, 1963a) in Florida, and in San Quintin Bay in Baja California (Grady, 1965). Numerous studies by other workers have influenced the writer's thoughts, including the pioneering work of Price (1954) on the Gulf Coast; Shepard (1953, 1960) and Shepard and Moore (1954) in the Texas bays, Phleger and Ewing (1962) in Mexican coastal areas; Emery (1960), Stevenson and Emery (1958), and Shepard (1963a, b) on the Southern California coasts; Byrne (1963) in Oregon; Creager (1963) in Washington and Alaska; and such foreign workers as Reineck (1956a, b) and Evans (1959). A number of excellent recent studies on sea-level changes include the discussions of Curray (1961), Macfarlan (1961), Shepard (1963a, b), Kaye and Barghoorn (1964), Bloom (1963), and Russell (1963). More theoretical considerations of interest include Tanner's discussions of shoal formation (1960, 1961) and general coastal classification (1960). Erosion-deposition studies by Jordan (1963) and his map of areas of net cut and fill in parts of Chesapeake Bay are examples of types of work that should be carried out in all areas.

GENERAL CONCEPTS

A discussion of coastal features must inevitably begin with a consideration of the recent history of the coasts. This leads to the question of changes of sea level over the past few thousands of years. Although some writers postulate a recent higher stand of the sea (Fairbridge, 1961), the prevailing opinion now seems to be in favor of a relatively rapid rise from about 100 meters below the present level commencing around 17,000 years B.P. and reaching a level three to five meters below present datum about 6,000 years B.P., after which the sea rose slowly to its present level about 2,000 years ago and may still be slowly rising. This last portion of the cycle is a point of conjecture and much has been written concerning the problems of deciphering the record (Kaye and Barghoorn, 1964; Bloom, 1963). It seems unlikely at present that levels have ever been above the present datum during the present cycle or since something more than 30,000 years B.P. (Curray, 1961; Macfarlan, 1961; Shepard, 1960, 1963a, b). Work on shore and coastal features in areas adjacent to the Mississippi Delta (Gould and Macfarlan, 1959; Byrne

et al., 1959) and in the southern Gulf Coast of Florida (Scholl, 1963), as well as field evidence from central Baja California bays (Gorsline and Stewart, 1962), support this contention and moreover argue that the present aspect of these shores is the product of the last cycle of rising sea level. Pilkey and Gorsline (1961), in a study of sedimentary structures in the Apalachicola Bay area, found evidence which suggests that much of that area is of quite recent development. Stewart and Gorsline (1962) have noted that the pattern of earlier Apalachicola sedimentation may have been to the west into the present St. Joseph Bay, rather than to the south as at present.

Phleger and Ewing (1962) present convincing evidence for a recent age for the coastal features along the southern shore of Sebastian Viscaino Bay in Baja California. Byrne (1963) has examined the Oregon coastal features and notes that changes can be very rapid along these bluff clifffed shores. Similar conclusions can be drawn from the other papers on this subject in this volume.

The writer, therefore, would suggest that a first general concept is that all present major coastal features are no older than Recent and more specifically have been molded predominantly by processes operating over the past 6,000 years. In many areas, this period may be less than 3,000 years. It is accepted that many individual features and structures are undoubtedly older and the materials and surfaces being reworked are also much older, but the general present configuration must certainly be the product of very recent time.

Turning to the question of the origin of the embayments on the various coasts, an examination of small-scale maps of individual bays and estuaries from many parts of the North American coastline impresses one that the large reentrants in the shores of the coastal plains are invariably oriented with their major axes roughly perpendicular to the shore and generally parallel to the regional slope of the coastal plain surfaces. In other words, the inner portions of the larger embayments have the roughly triangular outline associated with the classic estuarine form. The shore faces of all these are often much modified by parallel belts of barrier islands and lagoons, which in turn front older series of filled lagoons, marshes, and parallel lines of older beach ridges. Thus, the typical large embayments have two quite different parts: a coastal lagoon and barrier island zone, and an inner estuary receiving the waters of none to several streams depending on climate and stream shifting. In the western Gulf of Mexico and parts of Southern and Baja California, the climate has apparently changed sufficiently in relatively recent time that the streams entering the heads of the estuaries are now much smaller during much of the year than the valleys they occupy. In some instances in the Baja California area, the streams no longer flow except in years of exceptionally high rainfall.

Most estuaries can be described as features pro-

duced by submergence in which tidal currents predominate over stream flow. This has been postulated by many workers including Johnson (1919), although the development of the submerged forms is probably quite different from his original evolutionary sequence. It is obvious that in those instances where stream action is dominant, the fluvial sediments will fill the submerged reentrant and then prograde the shore by deltaic sedimentation. The fact that many large estuaries are fronted by barrier islands and lagoons is also evidence of the dominance of the marine agents. Apalachicola Bay on the Florida Panhandle Coast is an example of an area that was probably essentially deltaic in a previous cycle and is now predominantly estuarine and has many coastal lagoons, thus indicating that the capacity of its river has changed markedly either because of change in grade or change in the drainage area.

This leads us to a second general concept that the existence of the estuarine environment and its attendant coastal lagoons and barriers is a product of relatively small supply of local stream-borne materials and the dominance of marine agents of transport of sediment from coastal or nearshore sources.

Circulation in most of these embayments is typically of the classic estuarine form with freshwater and saltwater wedges interacting to form the great contrasts in salinity typical of estuaries, and with tidal currents acting as the principal agent of transport. In a very shallow estuary on the Florida Coast, the intrusion of the tidal wedge is a lateral phenomenon rather than an underflow, and it is likely that a similar system may be present in other equally shallow embayments (less than 3 meters deep). Pritchard and others have ably described these mechanisms of exchange in other parts of this volume; Phleger and Ewing (1962) have also noted that the lag in time of the tidal stages in different parts of estuarine systems, as a result of topographic effects and bottom friction, produces a mechanism which can govern the number and location of inlets into the system and will probably also determine the positions of loci of erosion or deposition. The writer (Gorsline, 1963b) has employed this principle in explaining the present configuration of deposition in Florida Bay, with the added factor of inlets which are fixed in position by the limestone masses of the raised reefs which form that bay's seaward boundary. This modification produces a static bay floor topography, while the shifting inlets of detrital bays allow for a constantly shifting bay floor topography. That embayments are sensitive to changes in the volume of water enclosed by the bay is evident in the few studies of change in bay bathymetry which have been compiled (Jordan, 1963). An unpublished study of the effect of cutting an artificial inlet in the barrier enclosing St. Andrews Bay, Florida, by T. L. Hopkins and R. A. Waller of Florida State University, revealed that the bay floor topography underwent marked changes as the bay reacted to the new inlet. The

older natural inlet filled up rapidly and the positions of shoals changed in the central bay.

Gorsline and Stewart (1962) have noted that the sediment volume deposited in San Quintin Bay, Baja California, is as much as the amount that has probably been eroded by wave attack on the open shore adjacent to the bay during the rise in sea level over the past few thousand years. A comparison of old and recent charts for that bay also demonstrated the shifting that takes place in the channels and distributaries of a bay. It would appear that the shallow sand flats, typical of most bays and estuaries, accumulate quite rapidly until they approach the low tide level and then they remain relatively static until the next shift in channels takes place.

Studies of the clay mineral suites in estuarine and bay sediments may provide clues as to the sources of these materials. In the eastern Gulf of Mexico, as will be described later, these suites show striking regional associations with the large drainage systems and are apparently accumulated in adjacent bays by tidal mechanisms of the type described by Van Straaten and Kuennen (1958), thus producing fine-grained deposits in the heads and central basins of bays. Some estuaries possess small deltaic deposits in the arms fed by streams, but many stream mouths have no obvious deltaic deposition and appear to be inactive sediment sources.

One may state a third general concept, which is that estuarine sediments are often transported and distributed primarily by marine mechanisms and, in many instances, may be moved into the embayment from the sea or from the shoals in the bay system rather than from fluvial sedimentation. Fine-grained sediment may travel from large rivers into adjacent coastal embayments downstream from the large river mouths and deltas.

Most students of estuarine sediments have been struck by the association of particular sediment characteristics with bay floor topography and circulation (Ingram, 1962; McMaster, 1962). Shoals form in zones of low current velocity in areas where the tidal flow from adjacent inlets meets or where the shelter provided by headlands, depth, or barriers creates eddies of quiet water. Marsh plants damp the velocity of currents and assist the settling of fine materials. Some fines are caught by benthic organisms and sedimented. The tendency for currents to hug one shore preferentially on the ebb and another on the flood creates central zones of slow circulation, which also effect the settling of sediment. In the shallow waters of bays and estuaries, the deposited sediments may be made resistant to resuspension by the development of algal films and mats and by the spread of marine grasses. Where water conditions are suitable, oyster reefs grow and may initiate deposition of sediment. The effect on shoal location of changes in the inlet positions has been mentioned earlier. The tidal deltas common to all inlets are a product of rapidly changing velocity as the tidal currents move from the re-

stricted inlet into the bay or out to the open sea and are modified by open shore waves and longshore drift or by waves and currents inside the bay.

Estuaries, like lakes, have relatively short lives, geologically speaking, and rapidly fill. This has been noted by all students of estuaries. Areas of quiet water become sites of deposition which in turn become the substrate for marine plants as the water shoals. Ultimately, marsh plants and continued sedimentation reclaim the area for the land. Estuarine sedimentary accumulations are probably a relatively small part of the geological record and have been estimated to form less than one percent of the total continental area at present. Estuarine sedimentary deposits probably could be recognized best by their geometry and the presence of organic sediments such as peats and coals. They would probably be roughly triangular in plan and relatively thin, possibly a few meters to tens of meters. Tidal flat features, including raindrop impressions, tracks and trails, ripples, burrows, and their associated fossil communities would aid diagnosis. They could be expected to grade into marine littoral deposits and linear sand bodies on their seaward sides and into fluviatile deposits on their landward sides.

CONTRASTS BETWEEN LOW- AND HIGH-ENERGY COASTS

THE GULF COAST

The regional trends in the eastern Gulf of Mexico provide an interesting example of the operation of the concepts noted earlier. As one moves east from the Mississippi Delta and the major source of fine sediment, the coast changes abruptly from the deltaic form to a series of large estuaries whose outer portions are typically shallow lagoons oriented parallel to the coast and formed by the development of a line of barrier islands. Washovers generated by hurricanes have laid down great lobes of sand on the lagoon side of these barriers which have formed into large areas of sand flats behind the barriers. The coastal shores of the lagoons typically contain belts of older beach ridges, which are also parallel or subparallel to the coastal trend. The inner portions of the embayments preserve the classic estuarine form and have their long axes oriented roughly normal to the general coastal trend. Each of these embayments differs in detail, but all are similar in that the contribution of the local streams is small, as evidenced by the limited areas of or absence of deltaic deposits in their mouths and the marked influence of the tides upstream. The waters of these tributary streams are often sluggish and heavily stained by organic compounds derived from plants, but are relatively free of suspended sediment. Marshes line the shores of these bays, and the estuarine sections contain large areas of tidal flats and marshes. In Mobile Bay, these flats are silts and clays, but the flats become sandy in all bays farther east. The deeper central basins of Mobile, Pensacola, Choctawatchee, and St. Andrews Bays are covered by fine silts and

clays. Sands cover the floors of the coastal lagoons, and coarse sands, shells, and exposed bedrock are typical of the inlet floors. Currents are strong in these inlets and reach velocities of three meters per second and more. Within the bays, the currents are slow and variable and generally are a few tens of centimeters per second or less. Water characteristics are uniform from surface to bottom in water of less than two to three meters depth, but masses of different salinity shift laterally with the tide and thus produce variations in the observed salinity at a single station over the course of a tidal period. The range of salinity is from oceanic to fresh. In water deeper than five meters, a salinity stratification appears and probably marks the limits of wave mixing in the protected bay waters. Sediments in these deeper zones are usually fine-grained, high in organic content, and in a reduced state. Temperatures are uniform throughout the water masses, except near rivers where the water is generally cooler. Temperature inversions are not uncommon in deeper parts of the bays where warmer saline Gulf water moves below the fresher surface waters. Slicks, foam lines, and debris lines are common; they separate tidal water masses of slightly different composition which move in variable directions within the bays and apparently preserve their identity for some time. On those occasions when strong local winds mix the bays, these individual masses lose their character in the homogenizing process.

Wolf Bay, Pensacola Bay, and Choctawatchee Bay all contain broad flat-floored basins covered by fine sediment which lie deeper than the sills of the inlets to the open Gulf. These floors have the appearance of flat pans, with relatively abrupt slopes separating these floors from the surrounding sand flats. Depths of the floors are typically 10 to 20 meters. The outlines of the inner portions of these large bays are arcuate and these sections are cliffted shores cut into old higher terrace surfaces of the coastal plains. These may possibly have been cut by broadly meandering streams moving in broad flat-floored valleys cut during lower stands of the sea. Local wind waves may have contributed to this cutting, but some of the cliffted shores are in the lee of the bays.

Clay mineralogy of the bay floor sediments indicates that the montmorillonitic suites, typical of the Mississippi sediments, prevail in the area immediately adjacent to the Mississippi Delta (Griffin, 1962), but rapidly yield to the kaolinitic suite of the Apalachicola River sediment. Pensacola and Choctawatchee Bay sediments are in an intermediate category. They may reflect equal contributions from both sources, or the effect of transport on a predominantly kaolinitic Apalachicola type in which transport has augmented the montmorillonite because of differences in settling characteristics (Whitehouse and Jeffrey, 1955). More detailed studies in progress may clarify this picture. Scattered samples collected from the adjacent shelf would indicate that Mississippi sediments move into the deeper water at about the DeSoto reentrant in the

shelf and that sands are typical of the shelf off Pensacola. Field evidence supports the tentative conclusion that little local fine sediment is contributed to these bays except in the central arms of Pensacola Bay, where some small deltaic features are present. St. Andrews Bay has been part of the Apalachicola system, and some of the fine sediments may be relict.

The sands in all of these northern Gulf Coast bays are virtually identical clean quartz sands with negligible heavy mineral content and generally uniform texture. These are in part reworked from the terrace deposits exposed in some of the bay shores, but much also comes from the coastal beach and nearshore belt of quartz sand and is transported into the bays by the strong tidal currents and by storm wave washovers. Wind probably contributes some sediment, but the back beach dunes tend to be fixed rapidly by lush plant growth. Profiles of the bottom topography of the bays extended seaward past the barrier islands suggest that little sediment is present in the deeper flat floors and that the principal movement and deposition of sediment takes place in the channels and sand shoals of the coastal lagoons and inlets.

Apalachicola and St. Joseph Bays are similar, except that their fine sediment is probably all of Apalachicola origin. Much of the St. Joseph fines are probably relict from an earlier period of river deposition at a somewhat lower sea level. Tidally moved sands are now burying these finer sediments in the central basin.

The shelf off the big bend coast of Florida is covered by biogenic sediments and quartz sands nearshore, with relatively little fine sediment. This relative absence of silts and clays is strikingly evident in the Tampa Bay sediment, where only a small pocket of silt is present in the head of one arm of the bay. Griffin (1962) defines the clays as Mississippian in composition. This same end product could be the result of long transport of Apalachicola sediments.

In any event, the clay content decreases rapidly away from the major sources in the northern Gulf Coast. Tidal flats and marsh sediments in the eastern Gulf estuaries and bays are thus sands with low fine sediment content, principally because of lack of supply.

Limited data from wells and test drill holes for construction indicate that the lens of sediments in the Florida Gulf bays is about 5 to 20 meters thick. Below the unconsolidated sands, shell, silt, and occasional peats are semi-consolidated Late Tertiary detritals or limestones. The deepest inlets in all of these bays sever down to this bedrock surface at depths of about 15 to 30 meters. Data are not available for Mobile Bay, but a similar pattern probably exists, judging from the general geology of the land surface surrounding the estuary. All of these deposits have probably accumulated during the last rise in sea level, since a few radiocarbon dates on peats in basal parts of these sections are all less than 15,000 years old. Dates from some of the beach ridges and older dunes range from 1,200 to 3,000 years before the present. These dates

are similar to dates from the chenier plains of western Louisiana, and the deposits dated are in harmony with present sea level, or nearly so. Thus, the entire barrier island-coastal lagoon portions of these bays are no older than 3,000 years and net sedimentation rates are similar to those described by Rusnak in this volume.

THE PACIFIC COAST

Studies in several bays of the Southern California and Baja California coasts show some similarity to the Gulf of Mexico embayments in that they are also controlled by tides and waves. The sedimentary materials are quite different in composition, as would be expected considering the very different sources. Fine-grained material is more common in the northern parts of the area, and preliminary studies in progress suggest that there may be different clay suites present. In San Francisco Bay, the clay suites show a marked difference between the outer Bay and the estuary of the San Joaquin River in Suisun Bay. Whether this reflects differences in source or the effects of sorting in transport is not yet known.

Clays and silts are relatively minor in the Baja California estuaries and coastal lagoons, and sands predominate. The aspect of the barriers and coastal portions of these embayments are quite different in appearance from their counterparts on the Gulf Coast. Rapid growth of vegetation in the humid Gulf area fixes the back beach dune sands into beach ridges. On the Pacific Coast, the climate is arid or semi-arid and the wind-blown sands march across the barriers and coastal plains in fields of barchan dunes and are an active mode of transport of sand into the lagoons. Washovers are not typical of the Pacific barriers as they are in the Gulf. The stream courses leading into the Baja California estuaries and lagoons are dry for years at a time and are dominated by the tidal incursions of open ocean water. Mangroves are important in marshes south of Sebastian Viscaino, and the more typical temperate marsh grasses hold sway in the north. Marsh sediments are increasingly more sandy to the south. Beach sands which have drifted along-shore are moved across the barriers and coastal margins of the big estuaries and fill the margins of the bays. In the San Francisco area, the rivers of the Central Valley of California are the principal contributors to the system.

Stronger wave action on the Pacific Coast tends to obscure the effects of storms. This contrasts with the low-energy Gulf Coast shores, where hurricanes may move beach and shore sediments in sheets over the inner bays and lagoons. Beaches fronting the Pacific coastal areas are also broader and of greater volume than along the lower-energy coasts of the east.

The thickness of sediments is probably similar in both areas, as evidenced in detailed sections compiled for the Southern California shore from water-well data. The bays of the West Coast are generally deeper than on the Gulf Coast, probably because of

the much narrower and deeper shelves along the Pacific border. Barrier islands are rare or absent and the embayments are either open to the sea or have inlets that are narrow channels in the bluff coastal foothills and mountains. The Southern California rivers are seasonal streams and in their natural state are sealed off at their mouths by beach deposits during the dry seasons. A few Southern California estuaries (Mugu Lagoon, Newport Bay) are abandoned mouths of the major streams which have been closed off by longshore drift and then opened to the sea by artificial channels. Many of the coastal estuaries are separated from the sea by spits and tombolos (San Diego Bay, Mission Bay, Morro Bay). All of these characteristics are products of the strong surf of the exposed Pacific shore.

SUMMARY

The above discussion and previously published studies can be summarized in terms of the following conclusions:

1. Estuaries, bays, and lagoons are probably all the products of processes active over recent time and probably for no more than the past 3,000 years.
2. Sedimentary patterns in these bodies of water reflect the combined effect of bottom topography and circulation, and sands are the major size grade present.
3. Estuaries are primarily products of coastal submergence, although secondary processes and climate may create somewhat different local forms of estuaries.
4. On bluff, high-energy coasts with narrow shelves, estuaries are separated from the open sea by spits or beach deposits, and barrier islands and their associated lagoons are rare or absent.
5. On low- and medium-energy coasts with broad shelves, estuaries commonly are fronted by barrier islands and coastal lagoons; often at least two sequences of these are present.
6. Circulation in estuaries is predominantly by tidal currents.
7. The positions of inlets in the barriers or spits are probably determined and maintained by the tidal pattern in each bay, and these in turn determine the location of areas of deposition and erosion in the bays.
8. Much of the sediment in estuaries is derived from seaward or coastal sources. When stream-borne sedimentation is dominant, the estuary soon yields to the delta.
9. Composition of estuarine and bay sediments reflects local sources and climates, but the textures are generally quite similar because of the similarity of agents acting within the environment.
10. Estuarine and bay sediments tend to be relatively thin because of the geometry of the form and the fact that they are simply drowned

segments of the coast. Thus, the thickness of accumulation is a result of the rate of sea-level rise and the slope of the adjacent shelf. Broad shelves produce shallow estuaries, while narrow steep shelves produce deep embayments. The glacially produced fjord is a separate and special category which is not considered here.

11. The aspect of an estuary changes with time as sedimentation progresses, or as climate and source and volume of sediment supply change. Thus, virtually all coastal embayments have passed through some part of the estuarine sequence. The fact that estuaries are primarily features of submergence means that they occupy the low parts of coastal topography. These lows are also the focal points of drainage and thus all embayments inevitably must have been or will be estuarine.

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LITERATURE CITED

- AMERICAN GEOLOGICAL INSTITUTE, 1957. *Glossary of geology and related sciences*. Nat. Acad. Sci.-Nat. Res. Council Publ. No. 501, Washington, D. C.
- BLOOM, A. L., 1961. Late Pleistocene fluctuations of sea level and post-glacial crustal rebound in coastal Maine. *Am. J. Sci.*, 261: 862-879.
- BYRNE, J. V., 1963. Coastal erosion, Northern Oregon. In *Essays in Marine Geology in Honor of K. O. Emery*; pp. 11-30. Univ. of Southern California, Los Angeles.
- BYRNE, J. V., D. O. LEROY, and C. M. RILEY, 1959. The chenier plains and their stratigraphy, southwestern Louisiana. *Gulf Coast Assoc. Geol. Soc. Proc.*, 9: 257-260.
- CREAGER, J. S., 1963. Sedimentation in a high energy, embayed, continental shelf environment. *J. Sediment. Petrol.*, 33: 813-820.
- CURRAY, J. R., 1961. Late Quaternary sea level: a discussion. *Geol. Soc. Am. Bull.*, 72: 1707-1712.
- EMERY, K. O., 1960. *The Sea off Southern California*. John Wiley and Sons, New York.
- EMERY, K. O., D. S. GORSLINE, E. UCHUPI, and R. D. TERRY, 1957. Sediments of three bays of Baja California: Sebastian Vizcaino, San Cristobal, and Todos Santos. *J. Sediment. Petrol.*, 27: 95-115.
- EVANS, G., 1959. The development of the coastline of the Wash, England. In *Proc. of the 2nd Coastal Geography Conference*; pp. 265-284. Louisiana State University, Baton Rouge, Louisiana.
- FAIRBRIDGE, R. W., 1961. Eustatic changes in sea level. In *Physics and Chemistry of the Earth*; pp. 99-185. Permagon Press, London.
- GOODELL, H. G., and D. S. GORSLINE, 1961. A sedimentologic study of Tampa Bay, Florida. *Proc. Intern. Geol. Congr.*, 21st Session, Copenhagen, 23: 75-88.
- GORSLINE, D. S., 1957. The relationship between water motion and bottom sediment type: Sebastian Vizcaino Bay, Baja California, Mexico. *Rev. Geog. Phys. Geol. Dyn.*, 1: 83-94.
- GORSLINE, D. S., 1963a. Oceanography of Apalachicola Bay, Florida. In *Essays in Marine Geology in Honor of K. O. Emery*; pp. 69-96. University of Southern California, Los Angeles.
- GORSLINE, D. S., 1963b. *Environments of carbonate deposition, Florida Bay and the Florida Straits*. Four Corners Geological Society Symposium Volume; pp. 130-143. Farmington, New Mexico.
- GORSLINE, D. S., and P. A. STEWART, 1962. Benthic marine exploration of Bahia de San Quintin, Baja California, Marine and Quaternary Geology. *Pacific Naturalist*, 3: 282-319.
- GOULD, H. R., and E. MACFARLANE, JR., 1959. Geologic history of the chenier plain, southwestern Louisiana. *Trans., Gulf Coast Assoc. Geol. Soc.*, 9: 237-260.
- GRADY, J. R., 1963. Oceanography of Bahia de San Quintin, Baja California, 1960-1961. *Pacific Naturalist*, 6: 1-35.
- GRIFFIN, G. M., 1962. Regional clay-mineral facies—products of weathering intensity and current distribution in the northeastern Gulf of Mexico. *Bull. Geol. Soc. Am.*, 73: 737-768.
- INGRAM, R. L., 1962. Modern sediment patterns in the Morehead City area, North Carolina. *Geol. Soc. Am. Spec. Papers*, 73: 301. (Abstract)
- JOHNSON, D. W., 1919. *Shore Processes and Shoreline Development*. John Wiley and Sons, New York.
- JORDAN, G. F., 1963. *Erosion and sedimentation—eastern Chesapeake Bay at the Choptank River*. U. S. Coast and Geodetic Surv. Publ., Washington, D. C.
- KAYE, C. A., and E. BARGHOORN, 1964. Late Quaternary sea level change and crustal rise at Boston, Mass., with notes on the autocompaction of peat. *Bull. Geol. Soc. Am.*, 75: 63-80.
- KOFOED, J. W., and D. S. GORSLINE, 1963. Sedimentary environment in Apalachicola Bay and vicinity, Florida. *J. Sediment. Petrol.*, 33: 205-223.
- MACFARLANE, E., JR., 1961. Radiocarbon dating of later Quaternary deposits, southern Louisiana. *Bull. Geol. Soc. Am.*, 72: 129-158.
- MCMASTER, R. L., 1962. Petrography and genesis of recent sediments in Narragansett Bay and Rhode Island Sound, Rhode Island. *J. Sediment. Petrol.*, 32: 484-501.
- PHLEGER, F. B., and G. C. EWING, 1962. Sedimentology and oceanography of coastal lagoons in Baja California, Mexico. *Bull. Geol. Soc. Am.*, 73: 145-162.
- PILKEY, O. H., and D. S. GORSLINE, 1961. Recent root casts in sediments of the Apalachicola Delta, Florida. *Southeastern Geol.*, 3: 37-47.
- PRICE, W. A., 1954. Shorelines and coasts of the Gulf of Mexico. U. S. Fish and Wildlife Serv. Fisheries Bull. No. 59: 39-65.
- REINECK, H.-E., 1956a. Der wattenbedeckte und das leben im wattenbedeckten Natur und Fisch, 8: 204-204.
- REINECK, H.-E., 1956b. Die oberflächen Spannung als geologischer faktor in sedimenten. *Sedimentologische Zeitschrift*, 8: 265-267.
- RUSSELL, R. J., 1962. Retreat of cliffy coasts. *Nature*, 199: 5-14.
- SCHOELL, D. W., 1963. Sedimentation in eastern coastal swamps, northeast Florida. *Bull. Am. Assoc. Petrol. Geologists*, 47: 1591-1603.
- SHEPARD, F. P., 1953. Study of marshes Recent sediments and their environments in the northern Gulf of Mexico. *API Project 51, Rept. No. 1*.

- SHEPARD, F. P., 1960. Gulf coast barriers. In *Recent Sediments, Northwest Gulf of Mexico*; pp. 197-220. Am. Assoc. Petrol. Geologists Publ., Tulsa, Oklahoma.
- SHEPARD, F. P., 1963a. Thirty-five thousand years of sea level. In *Essays in Marine Geology in Honor of K. O. Emery*; pp. 1-10. Univ. of Southern California, Los Angeles.
- SHEPARD, F. P., 1963b. *Submarine Geology*; (2nd Ed.) Harpers, New York.
- SHEPARD, F. P., and D. G. MOORE, 1954. Sedimentary environments: coarse fraction studies. *Bull. Am. Assoc. Petrol. Geologists*, 38:1792-1802.
- STEVENSON, R. E., and K. O. EMERY, 1958. *Marshlands at Newport Bay, California*. Allan Hancock Foundation Publ., Occ. Paper 20.
- STEWART, R. A., and D. S. GORSLINE, 1962. Recent sedimentary history of St. Joseph Bay, Florida. *Sedimentology*, 1:251-286.
- TANNER, W. F., 1960. Expanding shoals in areas of wave refraction. *Science*, 132:1012-1013.
- TANNER, W. F., 1961. Offshore shoals in areas of energy deficit. *J. Sediment. Petrol.*, 31:87-95.
- VAN STRAATEN, L. M. J. U., and PH. H. KUENEN, 1958. Tidal action as a cause of clay accumulation. *J. Sediment. Petrol.*, 28:406-413.
- WHITEHOUSE, U. G., and A. M. JEFFREY, 1955. Peptization resistance of selected samples of kaolinite, montmorillonite and illite clay minerals. In *Clays and Clay Minerals*; pp. 260-281. Nat. Acad. Sci.-Nat. Res. Council Publ. No. 395, Washington, D. C.

Sediments of Yaquina Bay, Oregon

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Diverse hydrographic properties and accessibility make estuaries excellent places in which to study the relationship of sedimentation to the various aspects of oceanography. The hydrographic system within the estuary affects both the distribution of the sediments and their composition.

Numerous estuaries indent the relatively straight coastline of Oregon. Yaquina Bay, one of these estuaries, is situated on the central Oregon coast (Fig. 1). This bay, which is bordered by the coastal hills of the Oregon Coast Range, has an area of approximately four and one-half square miles, and extends inland 23 miles. It experiences mixed semi-diurnal tides, characteristic of the North Pacific, with an average tidal range of 5.5 feet.

This paper presents the results of a study of the nature and origin of the Recent sediments of Yaquina Bay and of the associated coastal beaches and dunes. The only study of Recent sediments in this area prior to the present investigation was that of Twenhofel (1946), which was limited to the coastal dunes south of the bay entrance and to a restricted portion of adjacent ocean beach. An attempt is made here to show the relationship of the sediment to the hydrography of the estuary and to the nearshore oceanographic processes.

PHYSIOGRAPHY AND REGIONAL GEOLOGY

COAST RANGE

Yaquina Bay and its drainage are situated on the western flank of the central Oregon Coast Range, a north-south trending geanticline consisting of more than 20,000 feet of Middle Eocene to Middle Miocene sandstones, siltstones, and mudstones. The sequence of sedimentary rocks overlies a Lower Eocene volcanic complex of flows, tuffs, and breccias. Both the sedimentary and volcanic rocks are intruded by numerous basic and syenitic dikes and sills considered to be of Oligocene age (Baldwin, 1959).

Erosion during the Late Cenozoic uplift stripped younger sediments from the region and superimposed the present drainage system on the older sedimentary rocks. The Yaquina River excavated its present valley as the Coast Range was slowly uplifted. The rugged topography of the relatively small (240 square miles) and maturely dissected drainage basin of the Yaquina River leads to rapid erosion during periods of high rainfall.

YAQUINA BAY

Although the Yaquina Estuary reaches to a point 23 miles inland measured along the sinuous Yaquina River, its freshwater head in the vicinity of Elk City (see Fig. 5) is only about ten miles east of the shoreline. Included in the lower estuary are the two large tidal flats, Sally's Bend Tidal Flat and Southbeach Tidal Flat, both marginal to the main channel. The estuary reaches a maximum width of two miles in a northeast-southwest direction across these flats, and decreases abruptly in width upstream of the flats. Above the tidal flats the channel narrows gradually to the head of the estuary. Although the tidal flats are extensive, the river channel and sloughs from the bay mouth to the vicinity of Elk City comprise the major portion of the estuary.

The depth of Yaquina Bay (Fig. 1) has been altered repeatedly since 1888 by man's efforts to industrialize the area. Starting with the initial installation of the twin jetties in 1888, and through periodic additions to the retaining walls and dredging in the main channel, notable changes of depth have occurred. These changes have been accompanied by changes in the sedimentary processes both within the bay and along the shoreline. In particular, the shoreline immediately south of the bay entrance has prograded seaward progressively with each new addition to the jetties, while the north shore has remained relatively unchanged.

The present channel is dredged to a depth of 26 feet from the jetties to the turning basin adjacent to McLean Point. The deepest depressions are found in the turning basin and along the north side of the dredged channel beneath the highway bridge at Newport. A navigational channel 12 feet deep is now maintained from the turning basin upstream to Toledo (see Fig. 5).

North of the bay entrance the coastline consists of a narrow sand beach backed by moderately high sea cliffs cut in Tertiary sedimentary rocks and capped by a thin accumulation of Quaternary terrace deposits. Erosion by landsliding and slumping is prevalent in this area. Three and one-half miles north of the bay the relative straightness of the coastline is interrupted by Yaquina Head, a terraced volcanic headland, which projects seaward about one mile and serves as an obstacle to southward littoral drift. A series of disrupted nearshore reefs of exposed basalt sills, parallel the beach from Yaquina Head to the vicinity of the bay entrance.

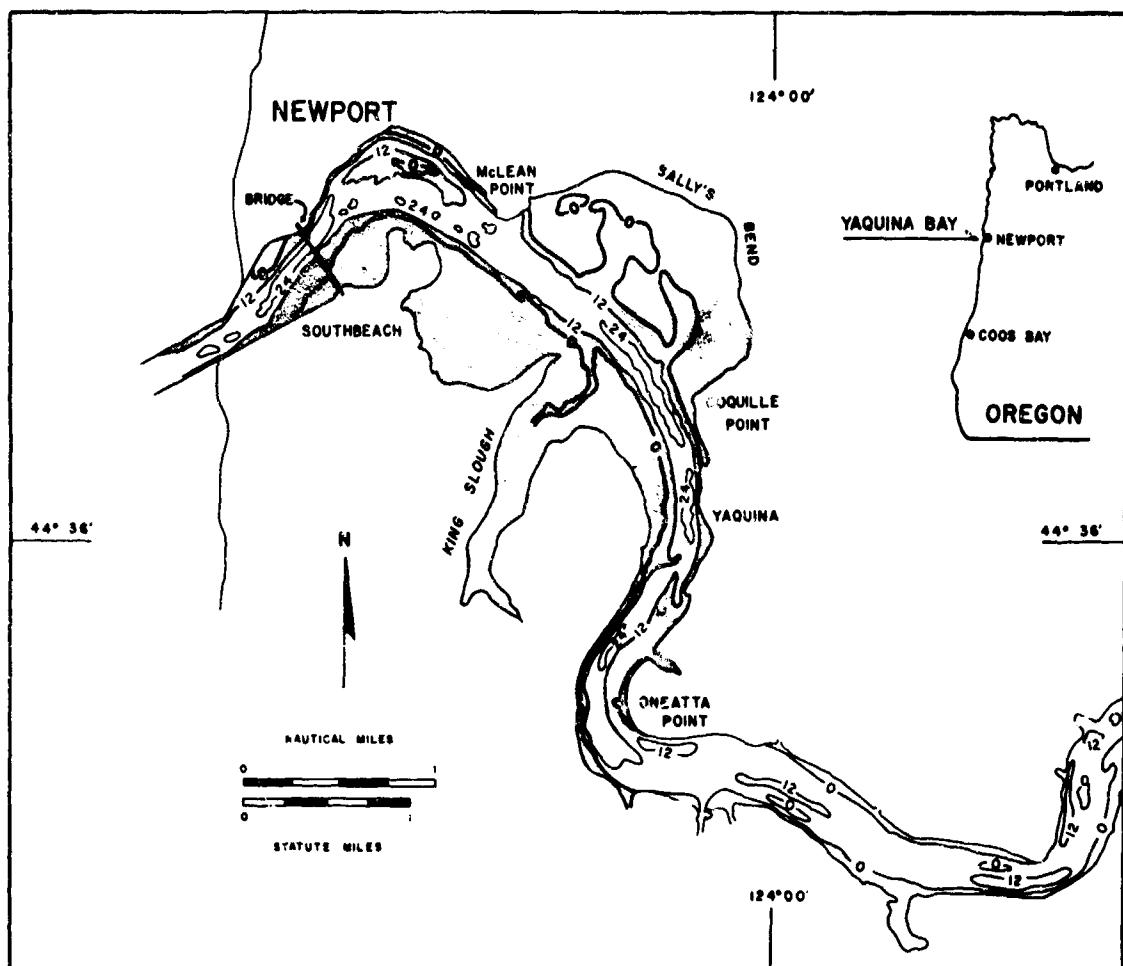


Fig. 1. Bathymetry of Yaquina Bay, Oregon. Contours compiled from 1953 U.S. Coast and Geodetic Survey smooth sheets. Contour interval 12 feet. Datum line indicates the mean lower low water.

South of the bay the coastline is relatively straight for about 20 miles without interruption by headlands. The beach immediately south of the bay entrance is backed by an undulating surface of recently migrating coastal dunes, which at present cover portions of the Pleistocene marine terraces and low hills to the east of the shoreline. The dune sands apparently were derived from the neighboring beaches, terraces, and estuarine deposits. The migrating coastal dunes are now encroaching inland into the forested low-lying hills and northeastward onto the south shore of Yaquina Bay.

HYDROGRAPHY AND CLIMATE

ESTUARINE CLASSIFICATION

Burt and McAlister (1959) have classified Oregon estuaries on the basis of circulation patterns and salinity distribution according to the system of Pritchard (1955). Their survey of Yaquina Bay is limited to seven months of the year and shows that the estuary is probably partly mixed in the winter and spring, and

is well mixed in the summer and fall. The average flow values of the Yaquina River were found to be 600 cubic feet per second (cfs) during February, 1955, but only 33.5 cfs during August, 1956.

More complete data on seasonal and annual variations in the distribution of salinity from top to bottom of the channel were obtained by the present writers for the following years: 1940-1941, 1960-1961, and 1961-1962. During 1940-1941, daily salinity measurements were taken in the vicinity of the town of Yaquina in conjunction with a native oyster study by the Oregon Fish Commission. The more recent data were reported in unpublished weekly salinity measurements taken at Buoy 15 (near Coquille Point) by the Department of Oceanography, Oregon State University. The salinity data for these years were treated in a manner similar to that used by Burt and McAlister. Inequalities due to tidal variations in the daily and weekly observations were minimized by using monthly averages.

The average difference in salinity between surface and bottom waters is plotted for each month of the

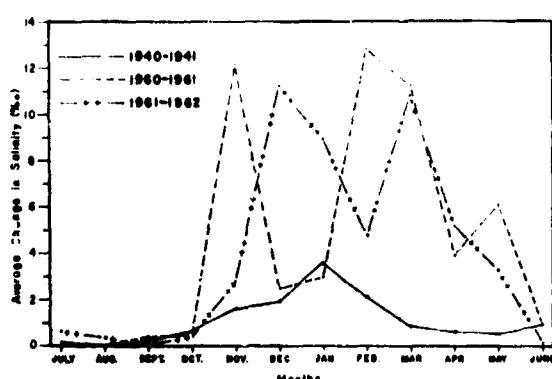


Fig. 2. Average monthly change in salinity between surface and bottom waters in Yaquina Bay. Oregon estuaries are classified on the basis of salinity change from top to bottom: 20 % or more, two-layered; between 4 and 19 %, partly mixed; and 3 % or less, well mixed (Burt and McAlister, 1959).

year (Fig. 2). When compared with the results of Burt and McAlister (1959), the same seasonal trends in estuarine types were noted. However, estuarine types during a particular season vary somewhat annually. In general, from June to October the estuarine system is well mixed. The estuary may alternate between a well mixed to partly mixed system from November to May.

CLIMATIC CONTROL

If tidal and basin characteristics are constant, river discharge is the principal factor which effects changes in the type of hydrographic system present during the year. River discharge is, in turn, related to the seasonal precipitation.

The amount of precipitation is recorded daily by the U.S. Weather Bureau at Newport, the focal center of the drainage system. The total monthly rainfall for 1940-1941, 1960-1961, and 1961-1962 is shown in Figure 3. The similarities between the precipitation curves and the curves for salinity difference between surface and bottom water is striking. Such a parallelism between the curves reflects strong local climatic control of the estuarine system and suggests that the various types of estuarine mixing patterns in Yaquina Bay can be related to precipitation.

The annual precipitation varies greatly from year to year. The mean annual precipitation at Newport over a 24-year period is 67.40 inches. In the year 1940-41, there were only 43.40 inches of rainfall; whereas in 1960-61 about twice this amount, 83.35 inches, was recorded, and in 1961-1962, 58.41 inches. It is interesting to note the marked annual cycle in precipitation as well as the monthly variations in the data presented. These cyclic variations in precipitation represent long-term changes when compared with frequent diurnal fluctuations of more than one inch. Extreme diurnal maxima in rainfall of up to 2.9 inches were recorded during November and February in 1960-1961.

The change in salinity lags behind the increase of precipitation during the first few months of fall, following the dry summer season. The marked increase in precipitation during October generally is not reflected by an increase in the average change in salinity until a month or so later. Apparently the soil in the drainage basin becomes undersaturated during the extended dry periods of the summer and initially absorbs large quantities of water without excessive runoff at the beginning of the subsequent rainy season.

ESTUARINE CURRENTS

Few current measurements are available for Yaquina Bay. According to Burt and McAlister (1959), the general current patterns may be inferred from the type of mixing patterns that develop in the estuary. When the estuary is partly mixed, the strongest flood currents occur near the bottom. A well-mixed system, in certain Oregon estuaries, may be expected to have a slow net drift of water outward at all depths regardless of the superimposed tidal exchanges. A very slow net non-tidal flow was measured in Yaquina Estuary when the system was well mixed (Burt and McAlister, 1959). If the above generalizations are true, it becomes apparent that the current patterns may vary seasonally as a result of changes in the mixing patterns which are dependent on seasonal variations of precipitation.

LITTORAL DRIFT

Although the littoral drift along the Oregon coast is thought to be seasonal, no direct measurements of the magnitude or direction of drift have been made for any given time of the year. Measurements of the magnitude of drift are difficult to make, but an approximation of the drift direction can be determined if the directions of wave travel due to sea and swell are known.

Reliable wave hindcast data have been computed by National Marine Consultants (U.S. Army Engineers, 1961) for three deepwater stations off the Oregon-Washington coast. The data from one of these stations located off Newport, Oregon have been used to analyze littoral drift.

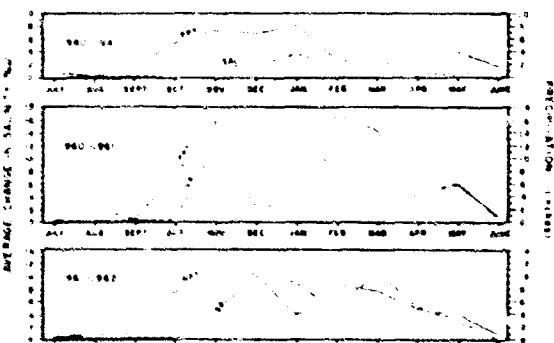


Fig. 3. Correlation between the monthly precipitation at Newport and the average monthly change in salinity between surface and bottom waters in Yaquina Bay.

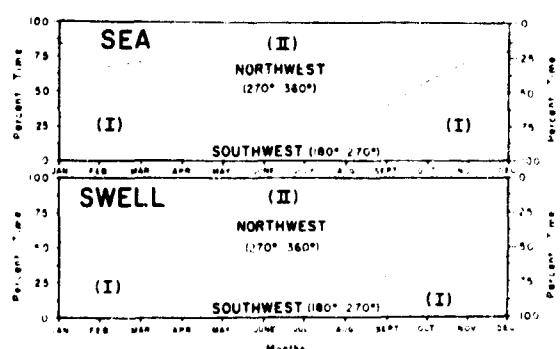


Fig. 4. Prevailing directions of onshore wave travel due to sea and swell. Left-hand scale designates the percent of time wave directions approach the shore from the southwest (quadrant I); right-hand from the northwest (quadrant II).

The results of the wave hindcast analysis are summarized in terms of the average monthly wave height, wave period, and wave direction frequency distributions for the years 1956, 1957, and 1958. These data were derived from U. S. Weather Bureau synoptic weather charts and are considered to be representative of nearly average conditions.

From the wave direction frequency data, it is possible to compute the littoral drift direction. If the direction of wave travel is not normal to the shore, the accompanying discharge of water will result in a longshore component. Since the coast of Oregon trends in a north-south direction, the longshore drift, which parallels the shore, will be either in a southerly or northerly direction, depending upon the prevailing direction of onshore wave travel due to sea and swell. For example, waves with a prevailing north-northwesterly component would give rise to a southerly longshore drift; conversely, a south-southwesterly component would result in a northerly drift.

The prevailing direction of wave travel due to sea and swell was determined by dividing the data into two categories. Directions from 180° to 270° (south to west) were designated as quadrant I; directions from 270° to 360° (west to north) as quadrant II. The percentage of observations falling into each of these quadrants was obtained for both sea and swell for each month.

From Figure 4 it can be seen that only during January and February does the prevailing swell come from the southwest (the mean direction of quadrant I). This indicates that longshore drift due to swell is southward most of the year.

Sea conditions, because of the local wind regime, present a somewhat different picture. The seasonal wind regime has been summarized by Cooper (1958) for Newport, Oregon. During the month of July, onshore winds predominate and originate from the north to northwest. This is assumed to represent summer conditions. During the month of January there is a preponderance of low velocity offshore winds, indicative of winter conditions. Also high velocity,

but less frequent, onshore winds occur from the south parallel to the coast or slightly seaward of the coastal trend. Fall and spring winds are transitional. Fall winds alternate between winter and summer types. In the spring, the north to northwest winds reappear and alternate with the frequent low velocity offshore breezes and high velocity, less frequent south to southwest winter winds.

From October to March, the prevailing wave directions due to sea are from the southwest, which would result in a northerly longshore drift; however, from April to September prevailing wave directions occur from the northwest (mean direction of quadrant II), indicating a southerly drift.

On the basis of both sea and swell data it appears that from November or December to March longshore drift is northward along the coast of Oregon, and from April to October or November it is southward. Therefore, the longshore drift is seasonal. However, southerly drift appears to be prevalent during the spring, summer, and early fall, whereas northerly drift probably occurs only in the late fall and winter. As a whole, the dominant drift along the coast in the vicinity of Newport is southward.

SEDIMENTS

SAMPLING

Two major sampling trips were made during August and September, 1960, to collect 133 sediment samples (Fig. 5) from the Yaquina Estuary, adjacent ocean beaches, and nearby coastal dunes. Bottom samples of estuarine and river sediments where the water was too deep to hand-sample were collected from a small skiff. A messenger-operated Ekman dredge and a Dietz-LaFond grab sampler were used in the channel and on the tidal flats at high tide. Where sediment type permitted penetration and subsequent retention of a core, a Phleger corer with plastic liners and a homemade piston corer (Byrne and Kulm, 1962) were employed.

TECHNIQUES

The grain-size analyses of all sediments were carried out using particle-settling velocity techniques. All sediments of sand-size were analyzed with the settling tube (Emery, 1938), whereas the fine fractions containing appreciable percentages of silt and clay were analyzed with a soils hydrometer. The median diameter, mean, and Inman's (1952) sorting, skewness, and kurtosis coefficients were calculated from the cumulative frequency curves.

The measure of roundness was obtained by a visual comparison with Powers' (1953) roundness chart. All determinations of roundness were made on particles of clear quartz of approximately the same size.

Bromoform was used to separate the sand-sized grains into light and heavy mineral fractions. Heavy mineral fractions (unsized) were split with a micro-splitter and mounted on glass slides with Lakeside cement. Identification of mineral species was done

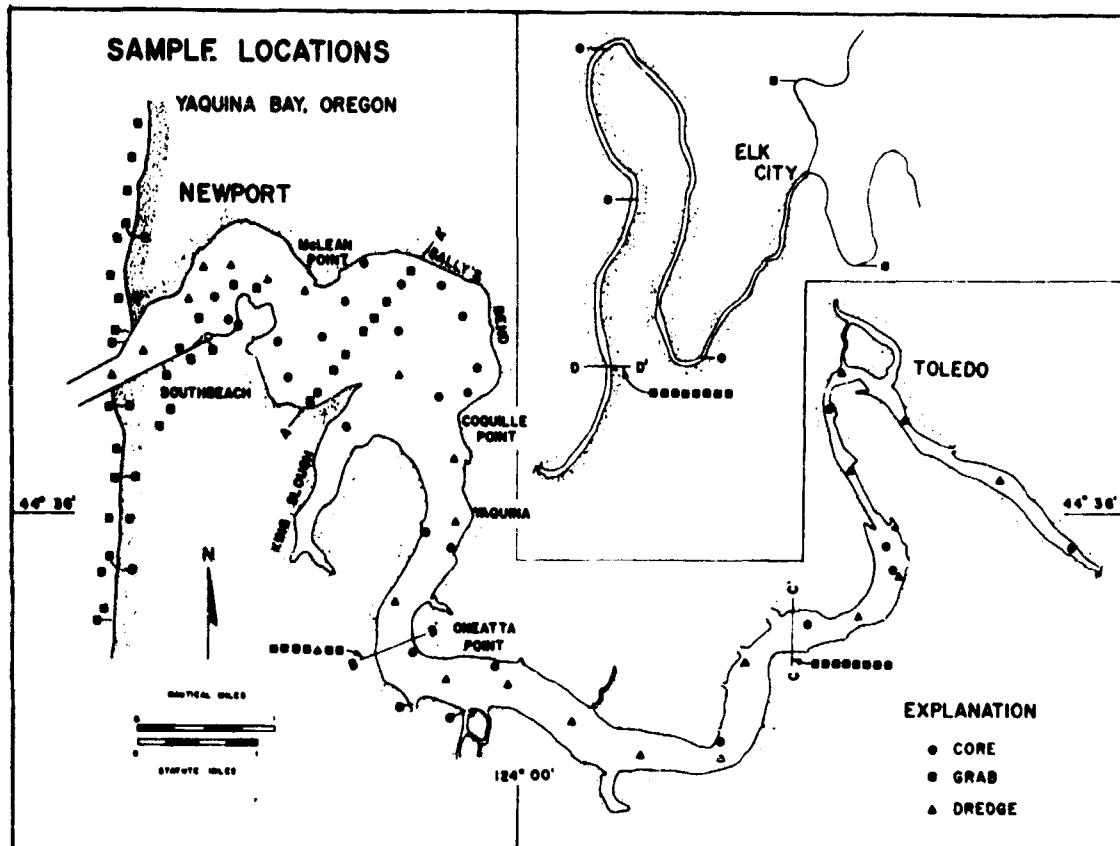


Fig. 5. Yaquina Bay, adjacent ocean beaches, and nearby coastal dunes, showing sample locations.

with the aid of a petrographic microscope. Percentages of mineral species were determined from 200 to 400 grains per slide. Light mineral fractions were etched with hydrofluoric acid and treated with barium chloride, sodium cobaltinitrite, and potassium rhodizonate according to the procedure employed by Bailey

and Stevens (1960). This method of staining plagioclase was combined with the staining of potash feldspar with cobaltinitrite originally developed by Gabriel and Cox (1929).

REALMS OF DEPOSITION

Three realms of deposition based on sediment texture and mineralogy are recognized within Yaquina Bay. These realms, marine, fluviatile, and marine-fluviatile, include a number of distinct depositional environments (Fig. 6). The marine realm, which includes the beaches and dunes adjacent to the bay, extends 1.5 miles into the entrance of the estuary, and is typified by water of normal marine salinity and by vigorous tidal action. Estuarine sediments of this realm are similar to the sediments of the adjacent beaches and coastal dunes. They consist of well-sorted, subangular to subrounded, fine to medium sand. The immature arkosic sands in this realm are distinguished by the marine suite of heavy minerals, including abundant pyroxenes, primarily hypersthene and diopside, and such metamorphic minerals as kyanite, sillimanite, and staurolite. Especially diagnostic of the marine realm are the "yellow grains" of Twenhofel (1946), which invariably constitute about ten percent of the light mineral fraction.

The fluviatile realm occurs between the freshwater

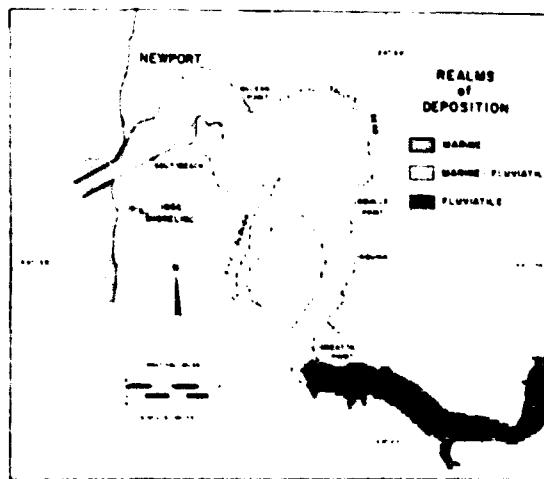


Fig. 6. Realms of deposition in Yaquina Bay.

head of the estuary near Elk City and Oneatta Point, six miles from the entrance. Brackish water conditions prevail in this area. The poorly sorted, angular to subangular sediments of this realm range in grain size from silt to coarse sand. They are somewhat more arkosic than the sands of the marine realm and are represented by the fluviatile suite of heavy minerals. This suite includes such diagnostic minerals as biotite, muscovite, hematite, and limonite. Diopside is absent and minor amounts of hypersthene occur in only a few samples. There is a marked decrease in the abundance of garnet and the number of metamorphic species, compared with the marine realm.

The marine-fluviatile realm, which consists of the river channel and the two marginal tidal flats, lies between the fluviatile and marine realms. Normal marine to brackish-water conditions are characteristic of this zone. A wide range of sediment texture and mineralogy occur in the marine-fluviatile realm. The well- to poorly sorted, angular to subrounded particles vary in grain size from silt to medium sand. Wide variations in mineralogy result because of admixtures of sediments from the adjoining marine and fluviatile realms. The diminishing marine influence upstream from the bay entrance to Oneatta Point is demonstrated by the progressive landward decrease in the percentage of "yellow grains", and of certain heavy minerals such as hypersthene, diopside, kyanite, sillimanite, and staurolite. In the vicinity of Oneatta Point, most of these minerals terminate, marking the maximum landward intrusion of marine sedimentation.

The two tidal flats are quite dissimilar in sediment texture and mineralogy. Sediments on Southbeach Tidal Flat are weighted as much towards the marine sands as those of Sally's Bend Tidal Flat are towards the fluviatile sediments.

ENVIRONMENTS OF DEPOSITION

Beach

The ocean beaches north and south of the bay entrance (a total distance of 4.5 miles) can be considered together since their texture and mineralogical characteristics are similar. The beach is divided into two zones, the lower foreshore or the zone of permanent saturation affected by waves and tides, and the upper foreshore, beyond the zone of permanent saturation.

The lower foreshore of both beaches is composed of fine to medium sand (median diameter average, 217μ) with a range in particle diameter from 185 to 254μ . The finest sands appear to be localized in the vicinity of the twin jetties. The coarsest sands are generally found 2 miles north of the jetties. These well-sorted sands (σ_d average, 0.27) have a narrow range in sorting (σ_d , 0.20 to 0.48) and are characterized generally by a coarse skewness (a_s) of -0.08.

Sediments of the lower foreshore have a wide range of roundness (angular to rounded) but are mainly subangular to subrounded. This range in roundness suggests several different sources of sediment, and the

angularity of the sands indicates that the majority of the sediments have not undergone prolonged transport and abrasion.

On the upper foreshore, recently migrating dune sands are derived from the often wet sands of the lower foreshore through eolian transport by high velocity onshore winds. On the northern beach this zone is narrow and restricted because of the clifftop coastline, but it extends as a wide plain over the length of the southern beach.

The average grain size of the recently migrating upper foreshore dune sands is 198μ while that of the lower foreshore sands, from which they were derived, is 217μ . The decrease in particle size probably results from the selective sorting during eolian transport. Likewise, the average skewness (a_s) changes from a coarse skewness of -0.08 to a fine skewness of 0.02, while the sorting remains nearly the same.

No appreciable difference in roundness because of the transportation of sediment from one environment to another could be determined.

Mineralogically, the beach sands are very immature. In the light mineral fraction, quartz and feldspar generally occur in a 1:1 ratio with some local variation, but the potash-plagioclase ratio is about 1:5. These arkosic sands contain intermediate to calcic plagioclase feldspar (andesine to labradorite), and orthoclase generally predominates over microcline in the potash feldspars.

Although the bulk of the light mineral fraction is quartz and feldspar, it invariably contains about ten percent "yellow grains" (primarily weathered feldspars, chert, and volcanic rock fragments) and five percent assorted rock fragments (chiefly basalt, andesite, felsite, metaquartzite, schist, and chert). These components occur in a constant 2:1 ratio over the length of beach sampled and in a coastal terrace deposit along the northern beach. Because the yellow colored grains are such a diagnostic and easily recognizable characteristic of the beach sands, they serve as an excellent tracer for the movement of marine sands into and within other environments.

Concentrations of heavy minerals in all beach sands from the lower foreshore range from less than one percent in the vicinity of the jetties to 12 percent two miles north on the northern beach. However, the average concentration on both beaches is 3.5 percent. The higher concentration of "heavies" in the beach sands north of the jetties on the northern beach may be due to the higher percentage of heavy minerals in the adjacent terrace sands. The heavy minerals in the terrace sands are further concentrated by small streams and creeks that empty onto the beach.

The marine suite of heavy minerals, which is characteristic of the sands in the beach environment, is shown in a frequency diagram (Fig. 7). Four beach stations, two north and two south of the bay entrance, were selected for comparison of heavy mineral assemblages. Although the heavy mineral species of both beaches are the same, the frequency of occurrence of several species varies significantly over the stretch

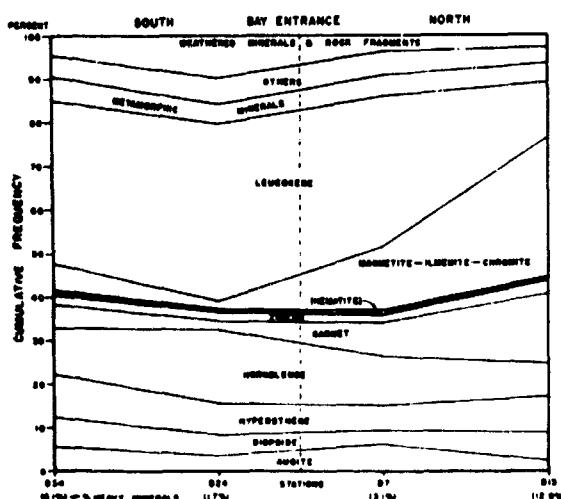


Fig. 7. Heavy mineral profile of the ocean beaches flanking Yaquina Bay. The bay entrance is marked by the vertical broken line.

of beach sampled. Magnetite-ilmenite-chromite is six times more abundant in the sands of the northern beach than in the southern, but leucoxene is only one-half as abundant. Even though the relative frequency of each opaque species varies along the beach, the total percentage of opaque minerals remains constant. The relative frequency of non-opaque minerals is the same over most of the beaches with the exception of garnet, which is three times more abundant two miles north of the jetties on the northern beach than at any other location. The relative percentages of garnet and opaque minerals in the sands of the north beach coincide with those of the terrace deposit sampled in that area.

Although the mineralogy of the light and heavy mineral fractions of the upper foreshore dune sands is identical to that of the lower foreshore sands, there is a significant increase in the total heavy mineral content. The heavy mineral concentration of the upper foreshore dunes reaches a maximum of 40 percent of the total sediment and averages 21 percent for the four samples collected. However, the two upper foreshore dune samples on either side of the twin jetties average only about six percent in heavy minerals, which is probably due to the low percentage of "heavies" on the lower foreshore in these areas.

Coastal Dunes

The dune environment is comprised of a series of disrupted transitory and semi-stable coastal dunes that lie landward of the southern ocean beach and along the southwestern border of the estuary adjacent to Southbeach. This undulating surface of separated dune ridges is progressively being shifted to the east into an adjacent forested area and onto Southbeach.

Like the upper foreshore beach dunes, the transitory coastal dunes are composed of fine sands. Their average median diameter is 195μ . They are excep-

lently sorted ($\sigma\phi$ average, 0.23) and are skewed to the coarse fraction ($\alpha\phi$ average, -0.19). The semi-stable dune masses are finer grained (median diameter average, 181μ) and somewhat better sorted than the transitory dunes.

There is a significant difference in particle roundness between the sands of the coastal dunes and of the upper foreshore dunes. Coastal dune sands exhibit the full spectrum of rounding but for the most part are subrounded, whereas the beach dune particles are subangular to subrounded or slightly more angular. The higher degree of roundness of the coastal dune sands may be attributed to the vigorous abrasive action of the wind over a long time or to the selective winnowing of rounded particles or both. Typical surface textures, such as pitting and frosting that accompany dune sands, are readily discernible and prominent in these sands.

As was noted in the sands of the beach dunes, the coastal dunes are also exceptionally high in heavy mineral content. These sands have "heavy" concentrations that range between 22 and 62 percent of the total sand fraction. The distribution of volume of "heavies" is irregular in the area sampled.

Both the light and heavy mineral assemblages of the coastal dune sands are similar to those found in the lower foreshore sands of the beaches adjacent to the bay and in the terrace deposit north of the bay entrance. The mineralogical similarity suggests that the recently migrating coastal dunes were probably derived from the Pleistocene terrace sands and nearby beach sands in the Yaquina Bay area.

Estuary Channel

Yaquina Estuary is divided into two physiographic areas, the river channel and marginal tidal flats. Included with the two large tidal flats are numerous sloughs that empty into the main channel. The river channel is by far the larger of the two areas. Its depth is variable but decreases gradually with distance upstream as does its width.

Sediments in the channel (Fig. 8), from the entrance to Oneatta Point, are composed of fine to medium sand and have the same average median diameter (217μ) as the fine to medium sand of the lower foreshore of the beaches. However, the range in grain size is greater (150 – 291μ compared with 185 – 254μ respectively). These sands are not as well sorted ($\sigma\phi$ average, 0.39) as the beach sands and generally are more coarsely skewed ($\alpha\phi$ average, -0.11). The channel sediments grade laterally into poorly sorted, very fine sand between Coquille Point and Oneatta Point.

In the vicinity of Oneatta Point there is a marked local gradation in the channel from the fine sand seaward of the point to medium sand between Oneatta Point and a position 1.6 miles upstream from the point. Sediments upstream from Oneatta Point are characterized by alternating longitudinal zones of fine and medium sand, except for an occasional coarse sand lens between Toledo and Elk City. In contrast

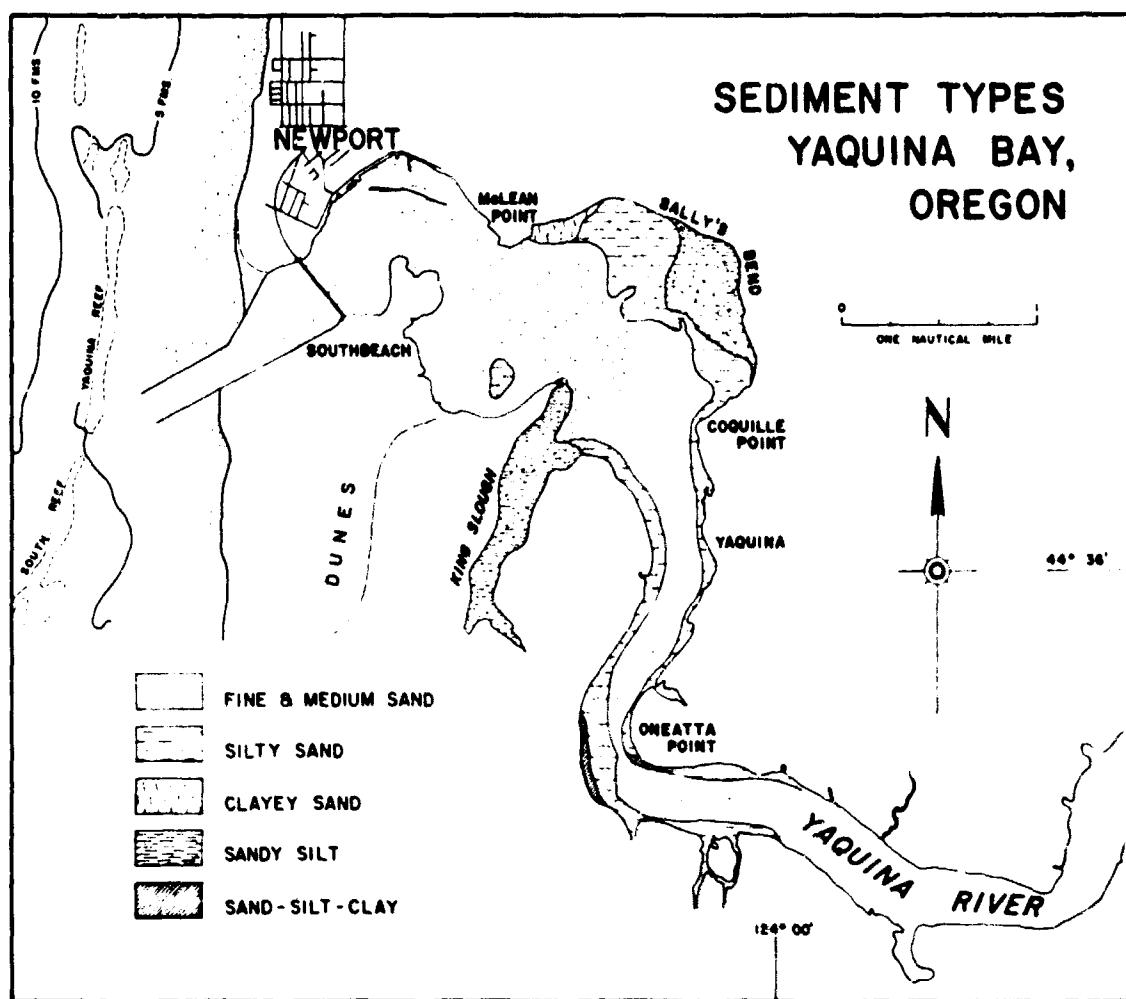


Fig. 8. Distribution of sediment types in Yaquina Bay, according to the nomenclature diagram proposed by Shepard (1954).

to the estuary below Oneatta Point, the sediments between Oneatta Point and Toledo have a larger average median diameter (279μ), are more poorly sorted ($\sigma\phi$ average, 0.49), and are generally skewed to the fine size fraction (α_0 average, 0.09).

Channel sediments between the estuary entrance and Oneatta Point are generally subangular to subrounded, but between Oneatta Point and McLean Point there is a progressive increase in particle roundness with distance downstream. Seaward of McLean Point no gross changes in roundness could be determined, but discrete components of well-rounded grains were observed. Since the adjacent transitory coastal dunes are the only sediments in the bay having these grain properties, and the wind direction and velocity are favorable for the transport of dune sands into this portion of the estuary, these sediments undoubtedly contain varying admixtures of dune sands.

Landward of Oneatta Point the channel sediments are usually angular to subangular, and are therefore significantly more angular than those seaward of the

point. They are definitely the most angular sediments in the Yaquina Bay area.

The progressive increase in particle roundness seaward of Oneatta Point is largely the result of increasing amounts of the more rounded beach and dune sands with decreasing percentages of angular fluviatile sediments, rather than the customary rounding due to abrasion during transport with distance downstream.

The ratio of quartz to feldspar for channel sediments can be divided into two groups: those greater than one, seaward of Oneatta Point; and those less than one, landward of the point. As a rule, the difference in the ratios of these two components is not great, but a general trend does exist. The low ratios upstream of Oneatta Point reflect the arkosic composition of the central Oregon Coast Range rocks. The higher percentages of quartz in the sediments seaward of Oneatta Point are probably because of the addition of beach and dune sands, which contain more quartz than feldspar, rather than because of the de-

struction of feldspars in transit with distance downstream. As is generally the case for all sediments in the Yaquina Bay area, the potash-plagioclase feldspar ratios are low (average 0.15) but consistent.

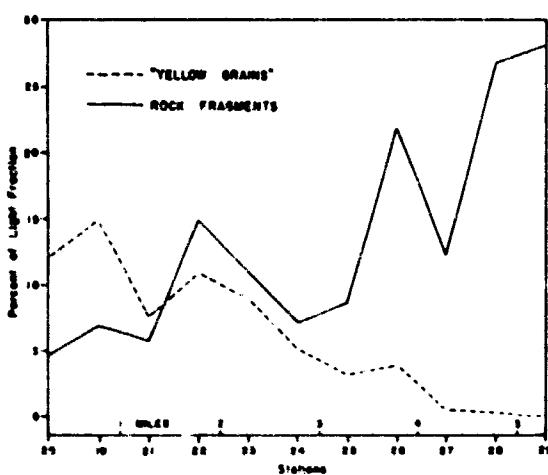


Fig. 9. Relationship between "yellow grains" and rock fragments from the bay entrance to Oneatta Point. Station 20 is located at the bay entrance and station 29 near Oneatta Point.

The "yellow grain" and rock fragment relationship characteristic of the beach and dune sands was also observed in the channel sediments from the bay entrance to Oneatta Point (Fig. 9). For about 1.3 miles upstream from the bay mouth, these two components occur in nearly the same ratio (2:1) as those in the beach sands. However, an inversion in the abundance of these two components occurs 1.5 miles from the entrance, indicating the beginning of the influence of fluvial sedimentation. From the turning basin adjacent to McLean Point to Oneatta Point, "yellow grains" decrease gradually in abundance and finally terminate at the upstream extremity of marine sedimentation.

Heavy mineral concentrations of more than 15 percent occur in the fine sands of the channel banks or sand flats near Southbeach, and on the margin of the prominent sand spit that projects northeastward into the estuary. This increase in heavy mineral content is attributed to the eolian transport of heavy minerals from the dunes to the channel banks when the wind direction is from south to southwest, usually in the winter.

Three distinctive suites of heavy minerals, marine, marine-fluviatile, and fluviatile, are recognized from the entrance of the estuary to its head near Elk City.

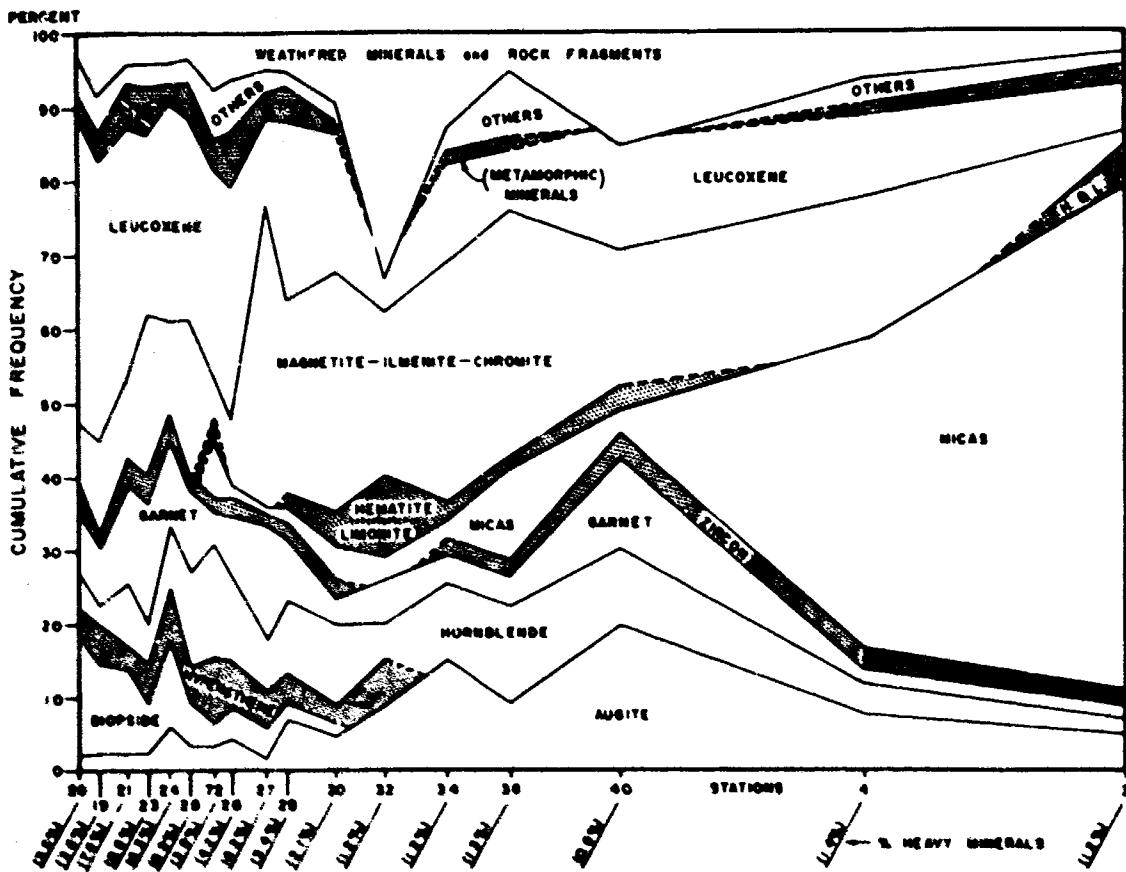


Fig. 10. Heavy mineral variations along a 24-mile longitudinal profile extending from the entrance of Yaquina Bay to one mile above the head of the estuary.

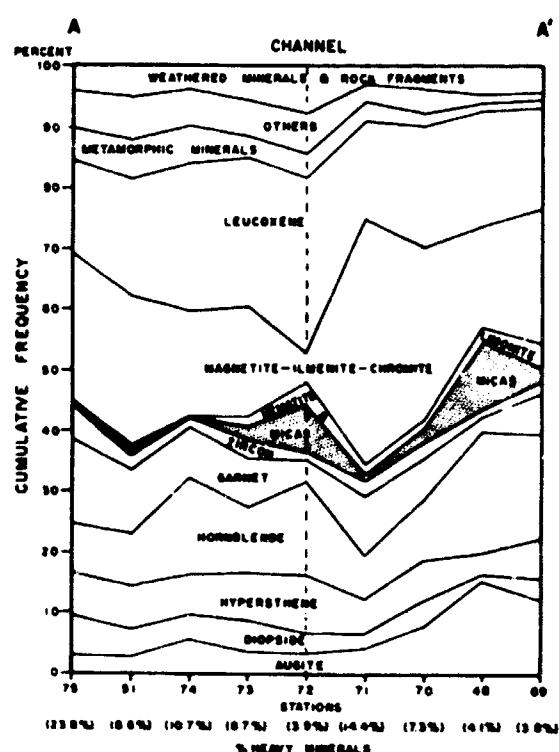


Fig. 11. Transverse heavy mineral profile (A-A') across Southbeach Tidal Flat and Sally's Bend Tidal Flat in Yaquina Bay. The broken line indicates the intervening river channel.

The greatest variation in the heavy mineral assemblage in the bay area can be seen in the longitudinal profile of the 24 miles of estuary and river drainage sampled (Fig. 10).

The marine assemblage is prominent between the estuary entrance and McLean Point, and terminates where the first appearance of the micas marks the beginning of fluvial influence. When the heavy mineral species in this portion of the channel are compared with those of the beaches, it can be seen that the gross mineralogy is the same. The ratio of leucocite to magnetite-ilmenite-chromite, for example, is similar to that found on the southern shore.

The marine-fluvial suite occurs between the marine inland boundary and Oneatta Point. In this segment of the channel the marine-fluvial assemblage of heavy minerals is characterized by the presence of the micas, muscovite and biotite, and a reduction in the number of species and the abundance of such metamorphic minerals as kyanite, staurolite, and sillimanite. The inland boundary of the marine-fluvial sediments is marked by the abrupt termination of the metamorphic minerals and of two pyroxenes, hypersthene and diopside.

The fluvial suite extends upstream from the marine-fluvial inland boundary in the vicinity of Oneatta Point and reaches to the head of the estuary above Elk City. This assemblage is characterized by

a marked increase in abundance of micas upstream and a decrease of the opaque minerals. Hematite and limonite are prominent in the sediments of this portion of the estuary.

Tidal Flats

A comparison of the two major tidal flats on the basis of grain size shows that Sally's Bend Tidal Flat is substantially finer grained than Southbeach Tidal Flat (Fig. 8). The channel banks bordering both flats are composed of fine, moderately sorted sand. The similarity of the two flats ends here.

Southbeach Tidal Flat is composed of fine sand, with the exception of one isolated area of very fine sand. The sediments of this flat are moderately to poorly sorted (σ_d average, 1.00) and are skewed to the fine fraction. In contrast, the sediments of Sally's Bend Tidal Flat grade laterally away from the channel from fine sand to silt. There is also a progressive decrease in sorting away from the channel, which results from increasing admixtures of finer sediments toward the north shore of the flat.

When the tidal flats are compared on the basis of particle roundness, the sediments of Sally's Bend Tidal Flat appear to be more related to the sediments of fluvial origin and those of Southbeach Tidal Flat to those of marine origin. However, the variation in grain size may account for this difference in roundness.

The "yellow grains" occur only on the southern shore of Southbeach Tidal Flat and usually in small percentages. Here they are derived from the adjacent terrace sands that make up the foundation of a road that borders the shore.

A comparison of the percentage of heavy minerals in the sand fraction of the sediments of the two tidal flats shows that on Southbeach Tidal Flat the concentration of "heavies" (15 percent) is more than twice that on Sally's Bend Tidal Flat (7 percent). Areas of highest heavy mineral content on Sally's Bend Tidal Flat occur in the fine sands of the channel banks, while the fine sands of the south shore of Southbeach Tidal Flat contain the highest percentage of "heavies" (20 percent).

The profile A-A' (Fig. 11) shows the heavy mineral distribution and frequency across approximately two miles of tidal flat and the intervening river channel. Although the heavy mineral assemblage of both tidal flats is characteristic of the marine-fluvial suite, there are major differences that distinguish the two flats. For example, Sally's Bend Tidal Flat has a significantly higher concentration of micas (muscovite predominating over biotite in a 2:1 ratio) than does Southbeach Tidal Flat. In the Yaquina River drainage muscovite also is more abundant than biotite. Also more common to Sally's Bend Tidal Flat are the opaque minerals, hematite and limonite, and augite and hornblende. There is a marked decrease and often an absence of such metamorphic minerals as staurolite, kyanite, sillimanite, and tourmaline and a noticeable decline in the abundance of garnet, diopside, and

hypersthene on Sally's Bend Tidal Flat as compared with Southbeach Tidal Flat.

Sediment Sources

The sources of Recent sediments in the Yaquina Bay area are diverse and widespread. The chief sources of sediment carried by the Yaquina River drainage to Yaquina Bay are the Tertiary sandstones, siltstones, mudstones, and basic intrusive rocks of the central Oregon Coast Range. Near the bay mouth, Pleistocene marine terrace sands and estuarine deposits have been reworked by the wind and by tidal currents. These sediments have been incorporated into the Recent beach, dune, and estuarine deposits. Since the beach sands are transported along the coast by seasonal littoral drift, other distant sources of sediment may include the Klamath-Siskyou Mountain complex in southern Oregon and northern California, and the numerous geological provinces of the Columbia River drainage basin.

Processes of Transportation and Deposition

Sites and Rates of Deposition

In Yaquina Bay, known areas of shoaling occur on the bar, in the main channel, and in the turning basin adjacent to McLean Point. The shoaled areas have maintained a fairly constant position with only minor changes in the depositional pattern from 1950 to 1961. On the basis of material removed by dredging, the average rate of sedimentation in the channel between the entrance of the twin jetties and the upstream end of the turning basin is estimated to be nine inches per year. Marine sand is the principal shoaling material in these areas.

Extensive deposition has occurred on the southern ocean beach behind the south jetty since its construction in 1888. This barrier to the northward longshore drift has caused the shoreline to prograde seaward with each new addition of the seawall. An estimated 275 cubic yards of material have accumulated annually from 1888 to 1961. On the other hand, very little sediment has accumulated behind the north jetty on the northern ocean beach. Such physiographic barriers as Yaquina Head and several shallow offshore reefs apparently divert or disrupt the southward drift of beach sands between Yaquina Head and the entrance of Yaquina Bay, thus inhibiting the supply of sediment to the northern ocean beach.

Seasonal Fluctuations

Four factors influence the rate, magnitude, and extent of sedimentation in Yaquina Bay. They are the type of estuarine system, river runoff, direction of littoral drift, and wind direction. All four factors are related to meteorological conditions and, consequently, change with seasonal climatic fluctuations.

Sedimentation in Yaquina Bay appears to be largely seasonal (Fig. 12). Maximum deposition occurs in the bay during the winter and early spring. At this time river runoff is highest, the longshore drift is

from south to north, and the highest velocity winds originate from the southwest. During periods of high runoff, the tidal circulation pattern of the partly mixed estuarine system is especially effective in transporting drifting beach sands into the entrance of the estuary. This is also the period of maximum contribution of suspended sediment to the estuary by the river. Strong southwest winter winds also enhance the movement of coastal dune sands into the tidal entrance and onto the southwestern shore of Southbeach Tidal Flat.

During the summer and early fall deposition is at a minimum because precipitation is negligible, littoral drift is from north to south, and the relatively low velocity winds are predominantly from the northwest. In summer the well-mixed estuarine system inhibits the transport of marine sands into the estuary, since there is a net non-tidal flow outward at all depths. The physiography of the coast north of the bay entrance, especially Yaquina Head, and nearshore reefs impede the supply of sediment from the north; thus, little marine sand is available for deposition onshore or in the estuary. The predominant northwest winds also divert the coastal dune sands away from the southwest shore of the bay entrance.

CONCLUSIONS

Three realms of deposition, marine, fluviatile, and marine-fluviatile, can be defined in Yaquina Bay on the basis of sediment texture and mineralogy.

Sedimentation in Yaquina Bay appears to be largely seasonal. Maximum deposition occurs in the bay during the winter, whereas very little deposition occurs in the summer.

The chief sources of Recent sediments in the Yaquina Bay area are the Tertiary rocks of the central Oregon Coast Range, the Pleistocene marine terrace sands and estuarine deposits near the bay mouth, and the Recent transitory beach and dune sands that flank the bay entrance.

Marine sand from the adjacent ocean beaches is transported by strong tidal currents to Oneatta Point, six miles inside the entrance to the estuary. Nearby coastal dune sands are blown into the tidal channel near the mouth of the estuary and onto the southwestern shore of Southbeach Tidal Flat by strong onshore winds. Suspended sediments are contributed by the Yaquina River during periods of high runoff.

The type of estuarine system present at any given time in Yaquina Bay is dependent upon seasonal and annual climatic conditions. In general, from June to October all existing data indicate the estuarine system is well mixed, but it may alternate between a well-mixed to partly mixed system from November to May. The precipitation recorded at Newport reflects the type of estuarine system present during each month of the year for any given year.

In Yaquina Bay, known areas of shoaling occur on the bar, in the main channel, and in the turning basin. The shoaled areas have maintained a fairly constant position from 1950 to 1961. Estimated average rate of deposition in the dredged channel is nine

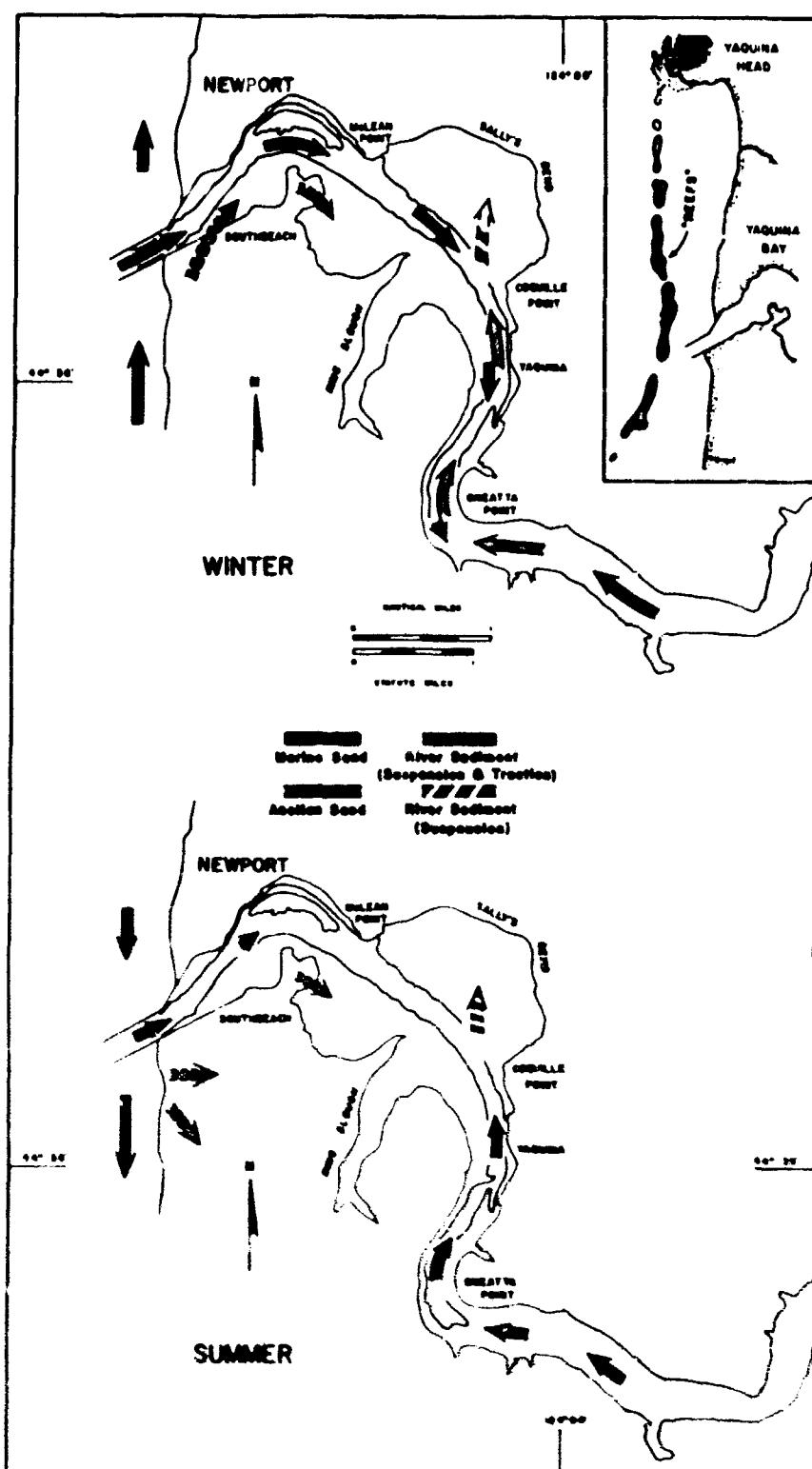


Fig. 12. Inferred seasonal depositional patterns in Yaquina Bay. The lengths of the arrows indicate the relative magnitude of sediment deposition by the various sedimentary processes.

inches per year. Marine sand is the principal shoaling material in these areas.

As a result of jetty construction in 1888, and through subsequent additions, extensive deposition has occurred on the southern ocean beach behind the south jetty. An estimated 275 cubic yards of material has accumulated annually from 1888 to 1961.

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LITERATURE CITED

BAILEY, E. H., and R. E. STEVENS, 1960. Selective

- staining of K-feldspar and plagioclase on rock slabs and thin sections. *Am. Mineralogist*, 45:1020-1025.
- BALDWIN, E. M., 1959. *Geology of Oregon*. Edwards Brothers, Ann Arbor, Michigan.
- BURT, W. V., and W. B. McALISTER, 1959. Recent studies in the hydrography of Oregon estuaries. *Res. Briefs, Fish Comm. of Oregon*, 7:14-27.
- BYRNE, J. V., and L. D. KULM, 1962. An inexpensive lightweight piston corer. *Limnol. Oceanogr.*, 7:106-108.
- COOPER, W. S., 1958. Coastal sand dunes of Oregon and Washington. *Geol. Soc. Am., Mem.* 72.
- EMERY, K. O., 1938. Rapid method of mechanical analysis of sands. *J. Sediment. Petrol.*, 8:105-111.
- GABRIEL, A., and E. P. COX, 1929. A staining method for the quantitative determination of certain rock minerals. *Am. Mineralogist*, 14:290-292.
- INMAN, D. L., 1952. Measures for describing the size distribution of sediments. *J. Sediment. Petrol.*, 22:125-145.
- POWERS, M. C., 1953. Roundness of sedimentary particles. *J. Sediment. Petrol.*, 23:117-119.
- PRITCHARD, D. W., 1955. Estuarine circulation patterns. *Proc. Am. Soc. Civil Engrs.*, 81:1-11.
- SHEPARD, F. P., 1954. Nomenclature based on sand-silt-clay ratios. *J. Sediment. Petrol.*, 24:151-158.
- TWENHOFEL, W. H., 1946. *Mineral and physical composition of Oregon Coast—Coos Bay to mouth of Columbia River*. Oregon Dept. Geol. Mineral Ind. Bull. 30, Salem, Oregon.
- U. S. ARMY CORPS OF ENGINEERS, 1961. *Wave statistics for three deep-water stations along the Oregon-Washington coast*. Report prepared for Dept. of the Army, U. S. Army Corps of Engineers District, Seattle, Washington, Portland, Oregon, by National Marine Consultants, Santa Barbara, California.

The Sediments of Chesapeake Bay

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Most recent investigators of sediments have been concerned with the physical and chemical properties of sediments in areas where the environments of deposition have a relatively stable oxygen concentration in the water column. Some characteristics of typical sediments from several of these modern basins are presented in Table 1.

Light-colored, rather homogenous, oxidized sediments are found in the Norwegian Sea, Wakasa Bay in Japan, along the shelves of Iceland, and the Atlantic and Gulf Coasts of the United States, to mention a few. In these environments, the water column is oxygenated throughout, and benthic organisms are abundant.

In parts of the Black and the Baltic Seas, in some of the offshore California basins, and in Lake Maracaibo, the lower part of the water column is permanently low in oxygen. The sediments are dark colored and generally chemically reducing, and benthic organisms are absent or rare.

The shallow waters of Chesapeake Bay are always oxygenated, but deeper waters are periodically oxygen-deficient (Pritchard, 1952). In an areal survey of the physical parameters of Bay sediments, Ryan (1953) found that most of the sediments were dark colored, evolved hydrogen sulfide, and were occasionally laminated or banded.

The investigation reported in this article was undertaken to determine the processes of sedimentation and

early diagenesis in Chesapeake Bay sediments, in view of the unstable hydrography of the area.

To this end, 120 coring stations were located in a mid-Bay area adjacent to Solomons, Maryland (Fig. 1). This study area has a deep trough extending its length, a marked depletion of oxygen in the trough during the summer months, and thick black sediments in the deeper areas (Ryan, 1953).

CHEMICAL PROPERTIES OF THE BAY WATERS

The water salinities in all parts of Chesapeake Bay vary seasonally and daily, and in many places, tidally. The distribution of mean annual salinity in the Bay is presented by Whaley and Hopkins (1952). The circulation of the Bay is such that dense oceanic water flows beneath light river-derived water in a two-layer system (Fig. 2). At all seasons there is considerable vertical mixing of these layers, but during the summer and fall the surface waters are warmer and less saline, and the boundary between the layers is most distinct.

Data from Cruises 1-7 of the Chesapeake Bay Institute indicate that in the late fall, winter, and spring, the waters at all depths in the Bay are nearly saturated with oxygen. Oceanic waters enter the Bay over the sill, they then flow into the deeper basins, and gradually migrate toward the head of the Bay. Biological and chemical processes remove oxygen

Table 1. Some characteristics of modern marine basins.

Area		Sediment color	Sedimentary structures	Hydrography
Lake Maracaibo	(1)	black and gray-green	banding	low oxygen
Black Sea	(2)	black and gray	banding and laminations	low oxygen
Baltic Sea	(3)	black and gray-green	banding	low oxygen
California basins	(4)	dark gray-green	banding	low oxygen
Norwegian Sea	(5)	light brown	homogeneous	well aerated
Iceland Shelf	(6)	light brown	homogeneous	well aerated
Wakasa Bay, Japan	(7)	light brown	homogeneous	well aerated
East Coast, U. S.	(8)	light brown	homogeneous	well aerated
Dutch Wadden Zee	(9)	light brown at surface	banding and laminations	well aerated

(1) Redfield, 1958; (2) Smirnow, 1958; (3) Manheim, 1961; (4) Emery and Rittenberg, 1952; (5) Gorshkov, 1960; (6) Hartsock, 1960; (7) Nino, 1950; (8) Moore and Gorsline, 1960; (9) Van Straaten, 1954.

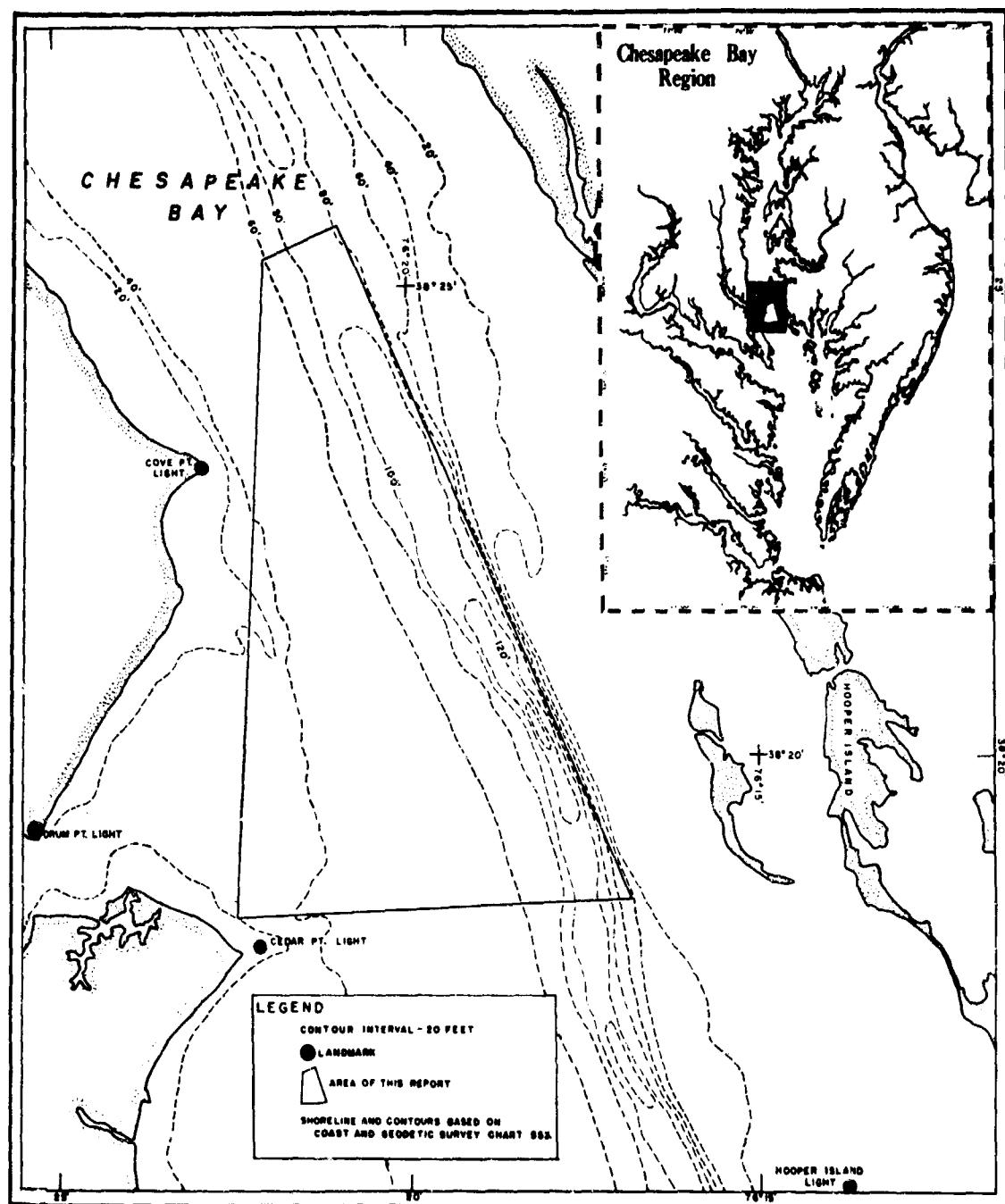


Fig. 1. Location and bathymetry of study area.

from these waters as they move northward during the summer months, and oxygen depletion results.

Typical summer oxygen profiles reveal the characteristic loss of oxygen as these deeper, more saline waters move northward. Below 40 ft., oxygen depletion is severe and limits the growth of higher organisms.

HYDROGRAPHIC CONDITIONS IN THE BAY EAST OF SOLOMONS, MARYLAND

The bathymetry of the study area east of Solomons (Fig. 1) is similar to that of the rest of the Bay. Maximum depth of 154 ft. in the study area occurs on its eastern margin. From May through October,

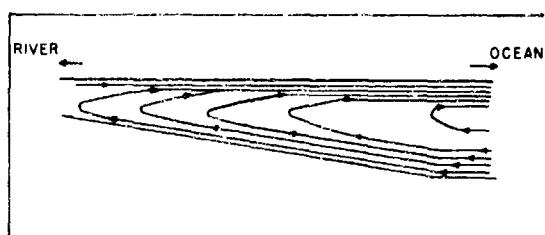


Fig. 2. North-south schematic circulation pattern in Chesapeake Bay estuarine system (Pritchard, 1952).

vertical mixing is at a minimum and water stratification at a maximum (Fig. 3).

Oxygen content, as determined by the Winkler method, decreases to zero to 0.5 ml/l in some of the deepest areas during this period. For the remainder of the year a salinity-temperature stratification remains, although it is not sharp nor characterized by the depletion of oxygen in the deeper water.

SEDIMENTS OF THE STUDY AREA

Data from long-term hydrographic stations maintained by the Chesapeake Biological Laboratory in the

Bay east of Solomons (Fig. 3) reveal that the zone of marked transition in temperature, salinity, and oxygen content occurs at a depth between 40 and 50 ft., thus defining the minimum depth of oxygen-deficient conditions during the summer months. A preliminary survey of the bottom sediments indicated that deep-water silts and clays grade into shallow-water sands at a depth of about 30 ft. The eastern and western boundaries of the study area were defined as the shallowest zone in which silt- and clay-sized particles predominate in the sediments. In the particular region of the Bay east of Solomons Island, this definition of the boundary facilitates study of fine-grained sediments in three rather distinct hydrologic zones: (1) the bottom sediments at depths less than 40 ft., where the water column is continuously oxygenated; (2) those sediments lying between the 40-ft. and 50-ft. contours, where the hydrologic conditions are transitional and fluctuating; and (3) those sediments found below the 50-ft. contour, where extreme oxygen deficiency prevails during the summer months.

SAMPLING AND STORAGE

After definition of the borders of the study area, a

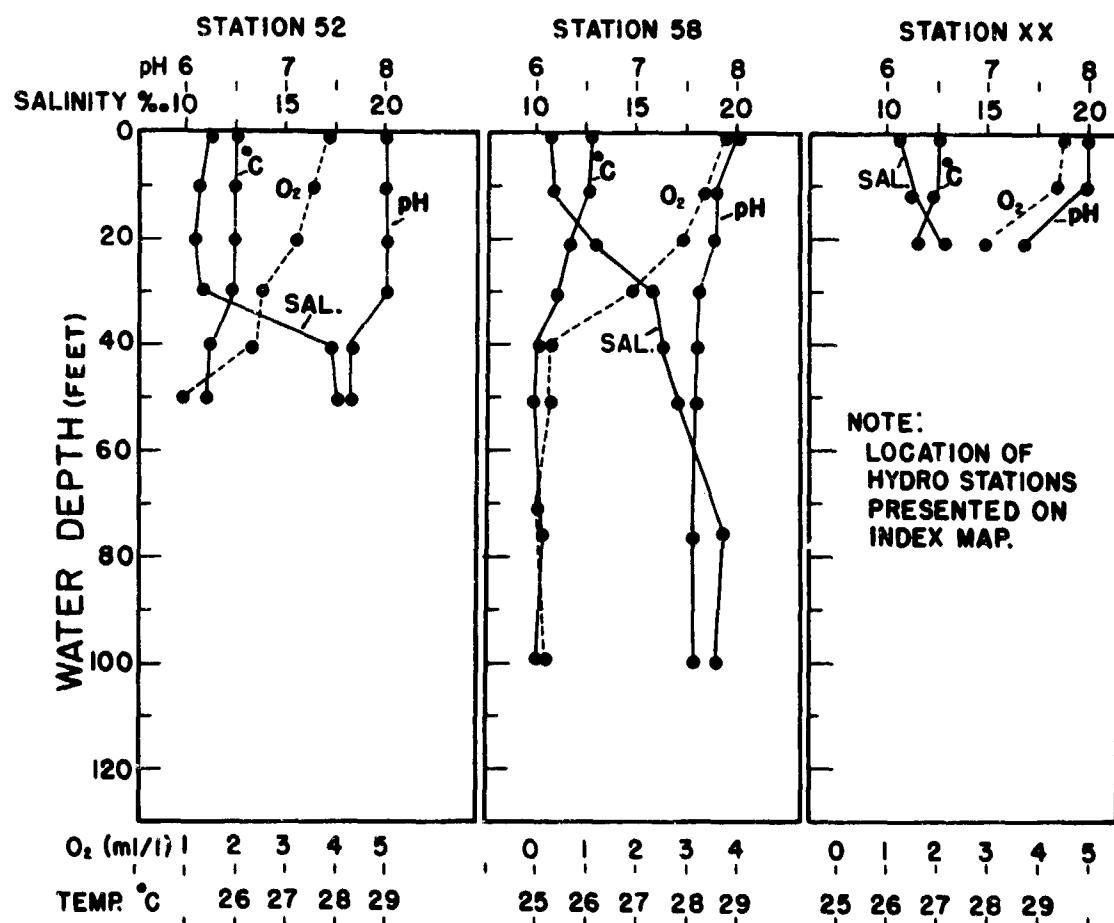


Fig. 3. Variation of salinity, temperature, oxygen concentration, and pH in the water column, east of Solomons, Md., on August 16, 1960; location of stations presented in Fig. 4.

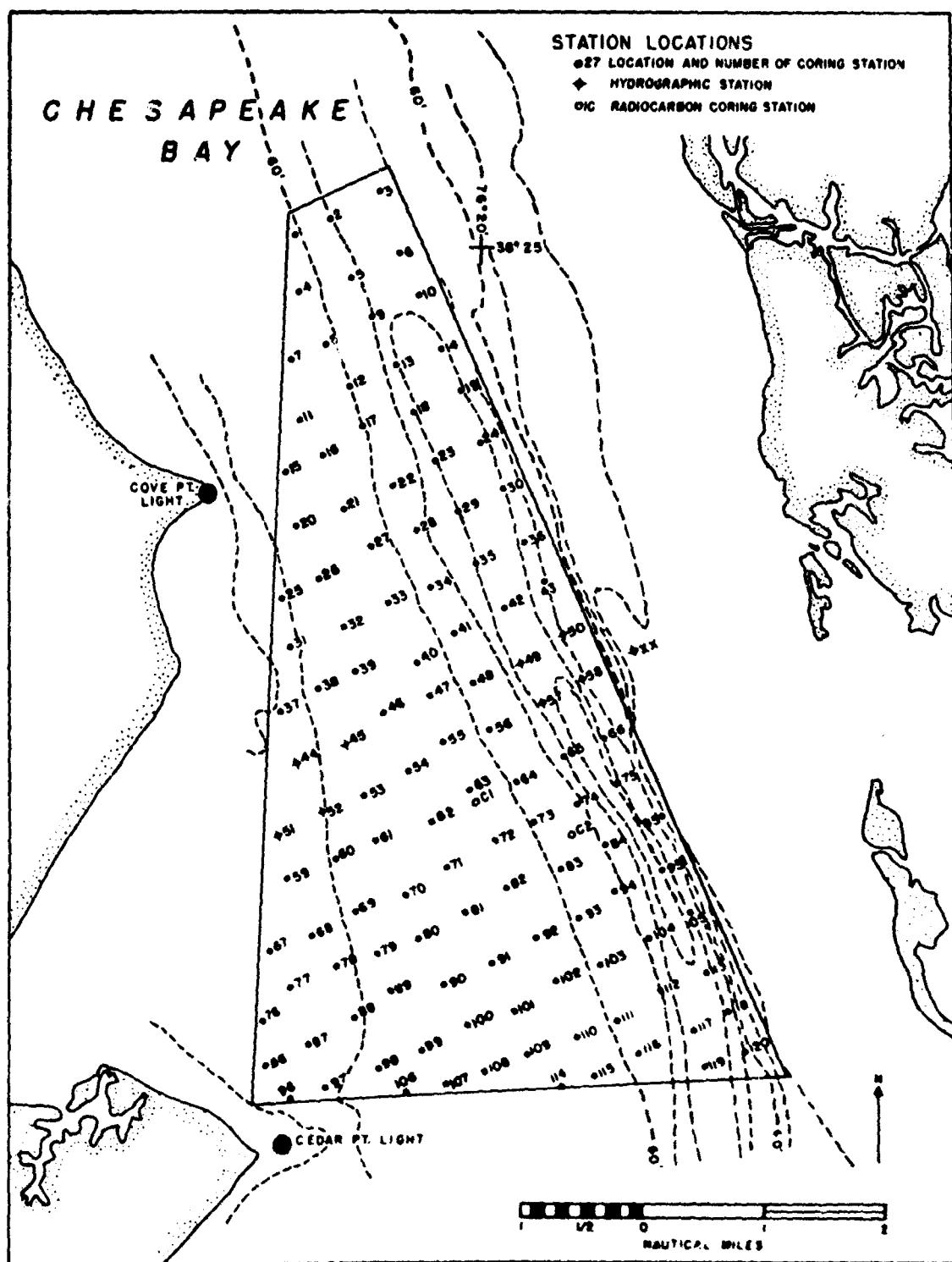


Fig. 4. Location of core and hydrographic stations for this study.

grid system of 120 squares, each 800 yd. on a side, was used as a sampling guide. Samples were taken with a 3-ft. gravity corer at all stations where the water depth was less than 60 ft., and with a 6-ft. Kullenberg corer for deeper stations. Precise location entailed the use of a sextant with landmarks as triangulation points. One station was occupied randomly within each square. Location of the stations is shown in Figure 4. All cores were taken in plastic core liners, removed from the corer, and sealed with plastic caps. Cores were returned to the laboratory after each cruise and were refrigerated within ten hours of sampling.

Sediment samples were taken at both the top and bottom of each core, and two samples each from other depths in the core where recognizable lithologic or color changes occurred. One sample from each of the horizons was quick-frozen for future organic analysis, and the second sample was used immediately for analyses of parameters which may change during storage. The odor of H_2S was evident from all depths of all cores except those from the shallow southwestern portion of the area.

The refrigerated cores were extruded from their core liners, split longitudinally with a scalpel, and examined for gross physical characteristics. Each core was then photographed and the depth to recognizable lithologic and color changes measured. No estimate of compaction due to coring is available.

Physical Parameters of the Sediments

Color—All the sediments in the study area are either black or gray-green. Cores from the shallow areas are gray-green for their entire length, while the samples from deeper water are characterized by the appearance of overlying black sediment whose thickness generally increases with increasing water depth. Exception to this observation occurs in the central portion of the area where gray-green sediment is exposed at the surface at moderate water depths. The contact between the black and gray sediment is usually sharp and striking on a freshly cut surface. Figure 5 illustrates the thickness of the black sediment, which varies from less than 5 in. in the north central and western area, to 15 in. in the south central portion, and to 40 in. in the deep eastern channel.

Upon splitting the cores, it was noted that black sediments faded to gray-green without drying in less than one hour of exposure to the air. This suggests extreme instability, under normal laboratory conditions, of the material imparting the black color to the sediments.

Sedimentary Structures—Structures found in the sediments include color banding, laminations, shell layers, and sand layers (Fig. 6).

Banding—The color banding consists of alternating black and gray-green layers ranging in thickness from 1 to 4 in. each. These alternating bands are found on the western side of the area only at depths from 40 to 60 ft. in the transitional hydrographic zone between the permanently oxygenated and periodically oxygen-

starved environments. This banding does not appear to be continuous from station to station. The black portion of banded cores exhibits the same rapid fading as does the black sediment of the tops of the unbanded deep-water cores.

Laminations—Thin color laminations were found in the upper 4 in. of four cores, all in the northern portion of the study area, and all at depths of less than 60 ft. These consist of alternating 1 mm thick black and gray-green sediments in which the black color rapidly fades on short exposure to air. The laminations, where observed, occur in zones from 1 to 3 in. thick. There is no apparent textured difference between the different color bands and laminations.

Shell Layers—Layers composed entirely of shells of the pelecypod *Mulinia lateralis* occur in 26 of the cores. The layers are usually $\frac{1}{2}$ to 1 in. thick and are composed of specimens from 5 to 9 mm long, most of which are still articulated. Parker (1956), working in the Mississippi Delta region, found representatives living in silty sand, sandy silt, and clayey silt substrates. Living *Mulinia* have a wide distribution in Chesapeake Bay at the present time, according to a personal communication from H. Pfizenmeyer. Thus, a natural habitat of *Mulinia* may be fine-grained sediments. The fact that the *Mulinia* layers have a wide distribution over the study area, occur in discrete zones, and are composed of articulated specimens suggests that the shells are in their location of growth. Thus, perhaps even in the deepest parts of the area, benthic environmental conditions were at one time or another conducive to growth of higher organisms. Lack of systematic variation in sediment depth where *Mulinia* layers were found precludes their use as a time horizon.

Sand Layers—One- to three-in. layers of sand-sized material occur sporadically in the deep eastern portion of the study area. The sands cannot be traced laterally from one station to the next either parallel or perpendicular to the axis of the Bay. They are characteristically composed of quartz, minor glauconite, feldspar, and heavy minerals, and rarely show graded bedding. Upper and lower contacts with the mud are sharp. The sandy sediments of the deeper areas may be produced by slumping of the prominent underwater escarpment which borders the eastern edge of the area.

Grain Size—The percentage, by weight, of material coarser and finer than 62μ was determined for 382 sediments by wet-sieving samples through a 230-mesh standard sieve. The distribution of grain size in the surface sediments is illustrated in Figure 7. Emery (1960), and others, found that sediments deposited in the shallowest water contain the largest percentages of sand-size material, probably because of the nearby source of the sand and the relatively higher energy of the shallow water environment. The Miocene-Pleistocene sediments exposed along the western shore of the Bay provide a source of sand-sized sediment and are being actively eroded. The shallow water deposits of the study area are influenced by strong tidal currents

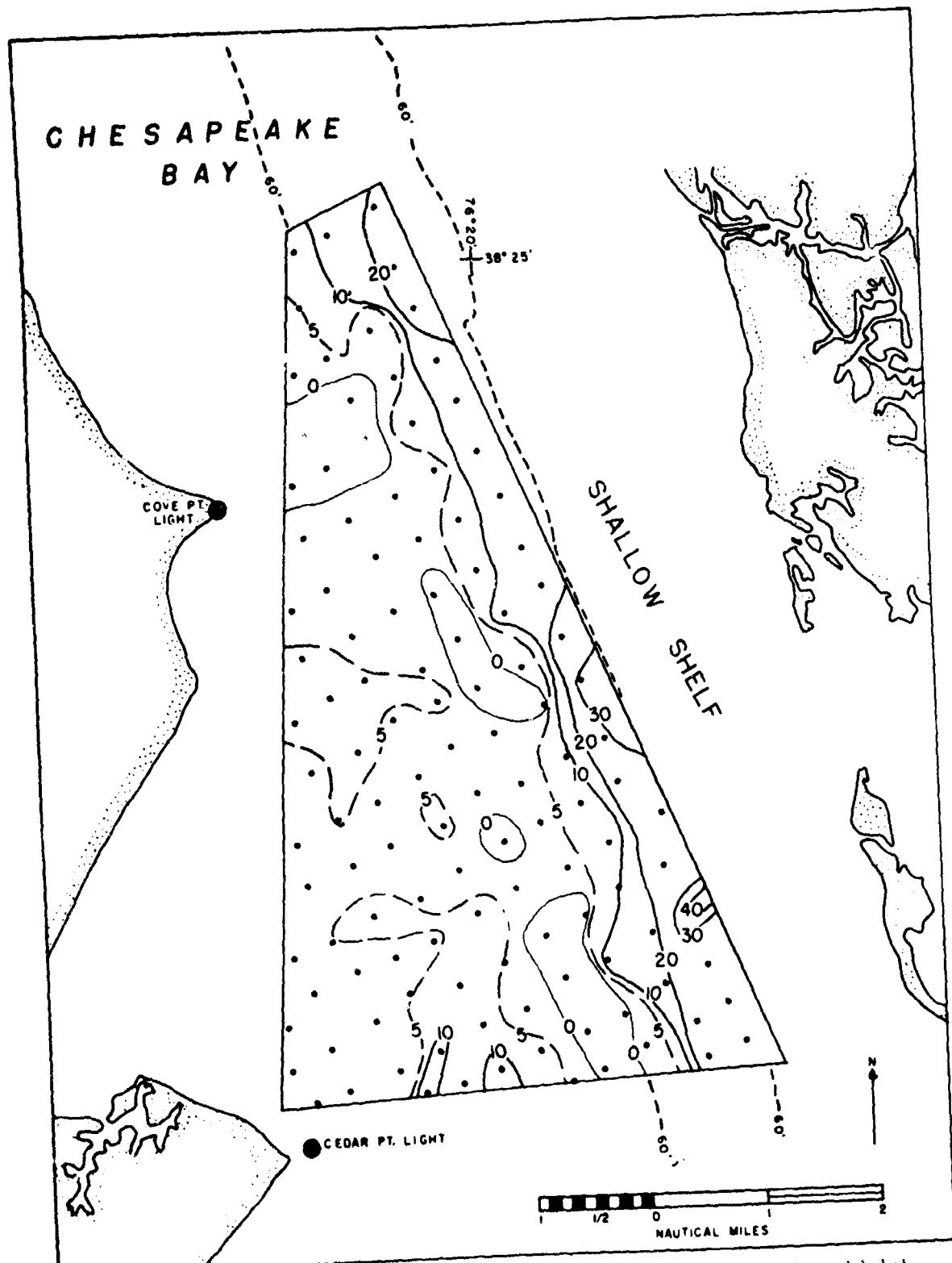


Fig. 5. Thickness of black sediment over study area. Contour interval ten inches; five-inch interval dashed.

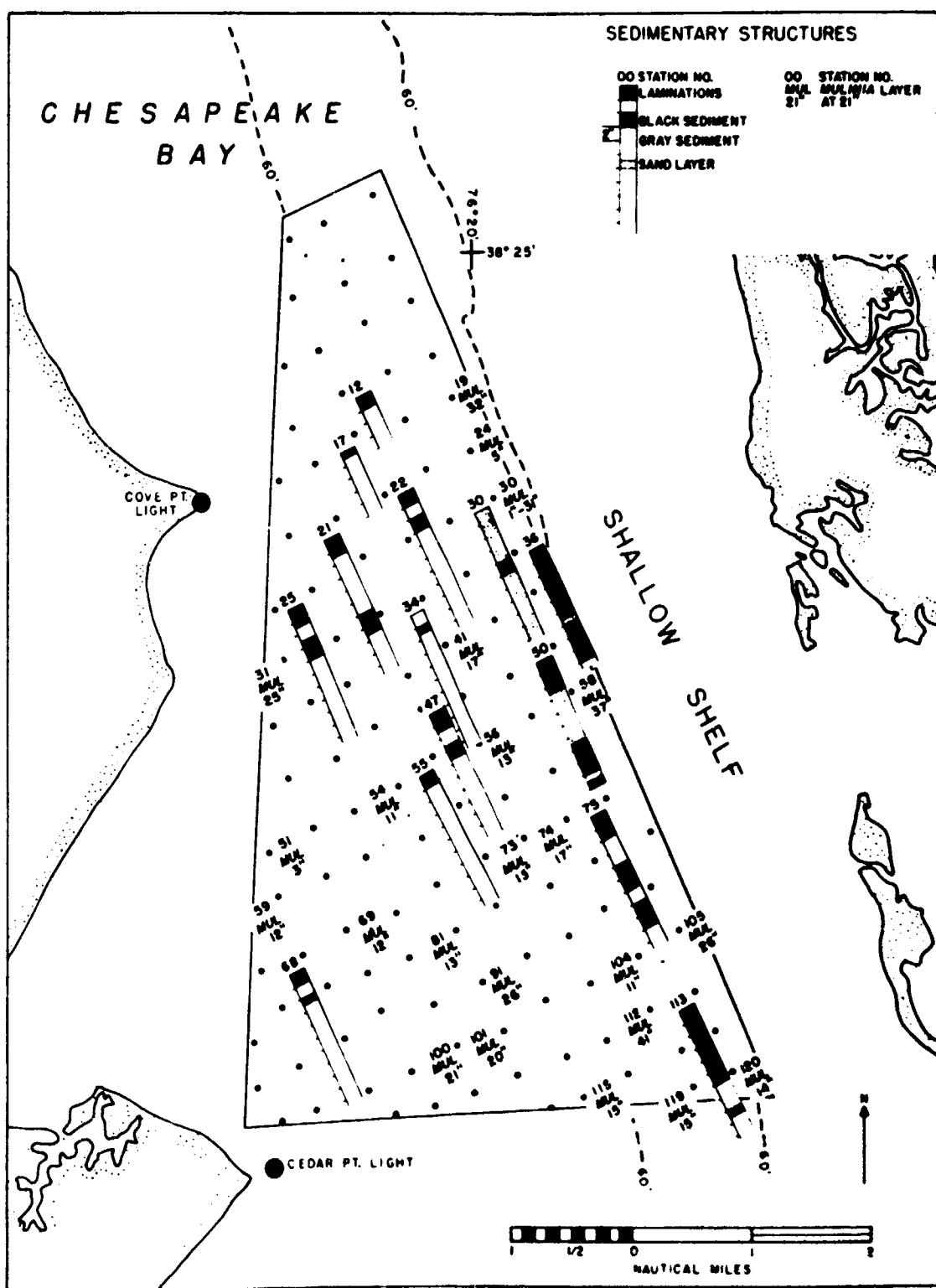


Fig. 6. Sedimentary structures. Distribution of color banding, laminations, shell and sand layers in the study area.

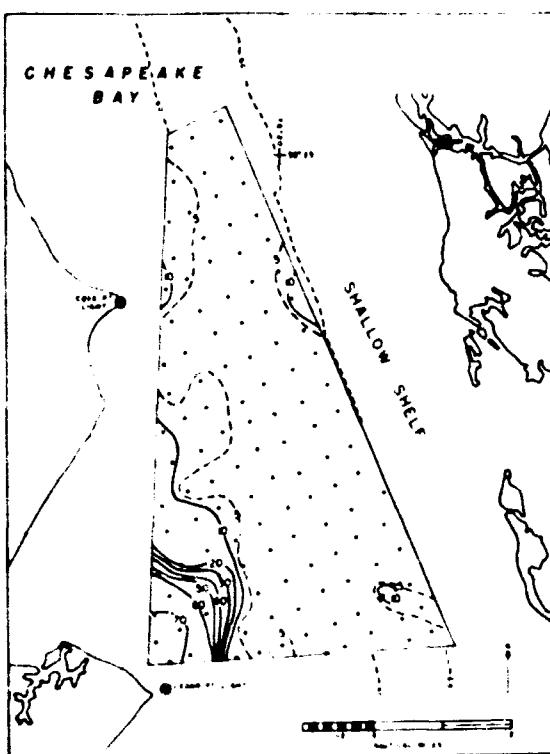


Fig. 7. Grain size in surface sediments. Distribution of the dry weight percentage of material greater than 62 μ in the surface sediment. Contour interval—10 wt %, 5% contour dashed.

and are subject to the winnowing action of storm waves.

Pipette analyses (Krumbein and Pettijohn, 1938) of several samples of the <62 μ fraction from the deeper areas of the Bay indicate that it is composed of approximately equal parts of silt- and clay-size material, probably a result of the lower physical energy in the deep water. The bulk sediment may be characterized as a sandy silt in the shallow areas, grading into clayey silt or silty clay (Trefethen, 1950) in the deepest portions (Table 2).

A histogram of the percentage of sediment greater than 62 μ for all samples indicates that there is no distinction between sediment color and grain size among the finer-grained sediments (Fig. 8).

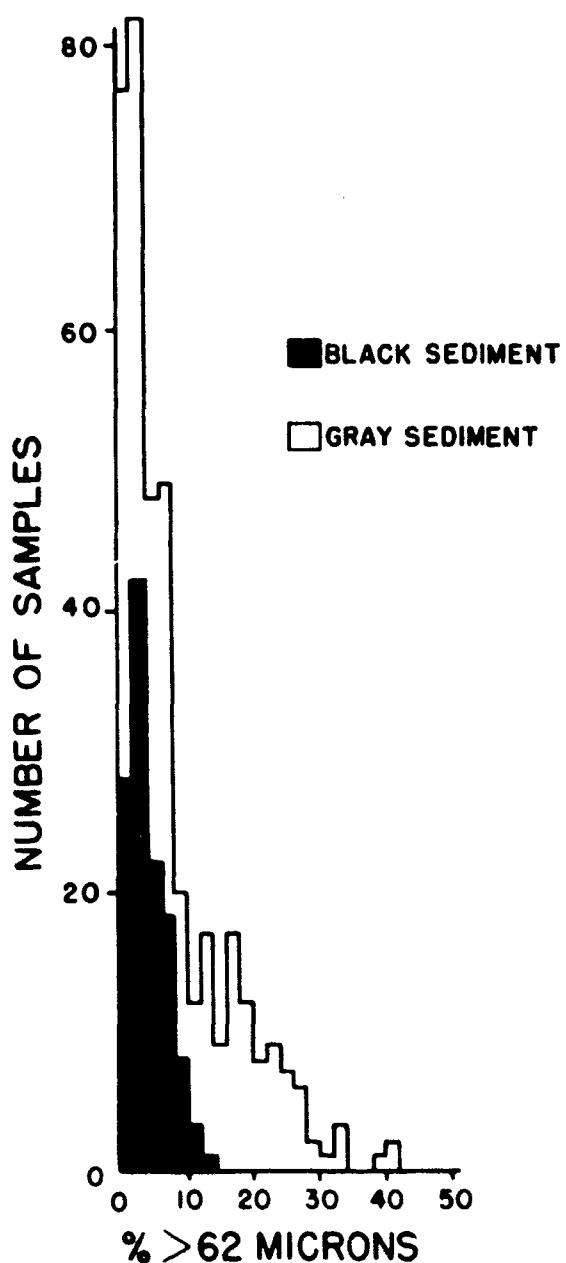


Fig. 8. Relationship between s. e. fraction greater than 62 μ and sediment color.

Table 2. Size analyses of seven surface samples.

Station No.	% Sand	% .062 mm-.031 mm	% .031 mm-.016 mm	% .016 mm-.004 mm	% .008 mm-.004 mm	% <.004 mm
44	13	15	26	21	8	14
45	6	17	21	28	11	17
46	7	14	23	25	14	17
47	2	13	26	18	16	25
48	7	11	21	23	20	25
49	2	8	18	20	19	33
50	3	6	13	19	28	31

Table 3. Clay mineral composition of sediments sampled at the station locations presented in Fig. 4.

Sam- ple	Depth of water (in feet)	Sedi- ment color	Depth in sediment	Chlo- rite	Illite	Kaoli- nite
16-2	52	gray	4"- 5"	31.9*	41.7*	26.4*
16-4	52	gray	12"-13"	29.8	42.1	28.1
17-2	60	gray	5"- 6"	38.1	36.5	25.4
17-4	60	gray	18"-19"	32.2	41.9	25.8
19-2	110	black	4"- 5"	30.0	39.5	29.6
19-4	110	gray	14"-15"	30.1	38.3	29.6
31-1	38	black	0"- 1"	23.8	50.4	25.7
31-4	38	gray	17"-18"	25.9	47.2	26.7
33-1	48	black	0"- 1"	31.4	40.9	27.1
33-4	48	gray	11"-12"	28.7	44.2	27.7
35-1	109	black	0"- 1"	33.2	45.0	21.8
35-3	109	gray	14"-15"	30.7	42.6	26.7
36-1	102	black	0"- 1"	29.7	40.0	30.3
36-3	102	gray	39"-40"	24.1	37.7	38.2
36-5	102	gray	53"-54"	30.2	42.2	27.6
68-1	31	black	0"- 1"	32.1*	42.0*	25.0*
68-3	31	gray	8"- 9"	33.0	43.8	22.8
80-1	45	black	0"- 1"	32.4	45.9	21.6
80-3	45	gray	7"- 8"	29.0	45.0	25.8
85-1	150	black	0"- 1"	33.7	40.1	26.2
85-3	150	gray	17"-18"	30.2	39.6	30.2
107-1	45	black	0"- 1"	31.9	38.3	29.7
107-3	45	gray	9"-10"	27.6	39.4	32.9
107-4	45	gray	19"-20"	31.7	34.9	33.3
115-2	55	gray	9"-10"	28.8	42.3	28.8
115-4	55	gray	20"-21"	31.2	41.7	27.1
118-1	118	black	0"- 1"	28.3	38.8	32.8
118-3	118	gray	19"-20"	36.7	38.3	25.0
118-6	118	gray	24"-25"	28.5	38.1	33.3

* Relative peak intensities to the base 100.

Gross Mineralogy of the Sediment

The minerals in the sediment were identified by optical, X-ray, and electron microscope techniques.

Coarse Fractions—The coarse fraction of the sediment (that portion retained on a 230-mesh U. S. Standard sieve) was mounted in Canada balsam and studied microscopically. In all cases quartz comprises more than 90 percent of the sample. The grains are subangular to subrounded and contain minute inclusions. Some grains show undulatory extinction. Feldspar, glauconite, and heavy minerals comprise the remainder of the sample. The feldspar is rounded to subrounded and clouded by alteration. Glauconite, composed of well-rounded grains, occurs most commonly in the shallow sandy samples and is probably derived from nearby glauconitic Cretaceous and Eocene formation. Heavy minerals consist of grains of hornblende, diopside, epidote, biotite, garnet, and opaques (magnetite, hematite, and ilmenite).

Fine Fractions—The fine fraction (all material finer than 62 μ) comprises the bulk of the sediment in the study area. The fine fraction of 13 samples was divided into ($>4 \mu$) and clay ($<4 \mu$) fractions. Oriented samples of both fractions were sedimented onto glass slides, X-rayed with Ni-filtered Cu K₂ radiation, glycolated, and X-rayed again. Separate

samples were heated in 100°C. intervals, from 200°C. to 700°C., and diffraction patterns were obtained for each interval. In addition, five samples of the $<2 \mu$ fraction were prepared for electron microscopy.

Because of the subjectivity involved in the interpretation of X-ray diffraction patterns of clay minerals, a brief summary of the criteria used for identification in this study is necessary. The methods employed for identification are essentially those of Nelson (1960).

Kaolinite was identified by strong diffraction maxima at 7.2A and 3.58A which were not affected by glycolation or mild thermal treatment. Heating to 400°C. produced diminution of intensities, and at 500°C. the peaks were completely gone.

Material with a maximum at 10.0A which is not affected by glycolation and is intensified by heating is here termed "illite".

Chlorite was identified by a prominent diffraction maximum at 14.2A which was not affected by glycolation and was intensified by heating to 500°C.

Vermiculite was detected in small quantities by heat treatment. The basal vermiculite peak at 14.2A is masked by the chlorite maximum and in the untreated or glycolated sample is not resolvable. However, upon heating to 200°C. a peak at 12.99A was produced. After heat treatment to 400°C. the peak shifted to 12.27A, and disappeared at higher temperatures.

Optical studies reveal that opaline diatom tests constitute 10 to 20 percent of the silt-size fraction. Subangular quartz grains are numerous. X-ray diffraction studies confirm the presence of quartz and indicate the presence of small amounts of illite and chlorite. Weak peaks at 3.21A and 3.27A were occasionally observed. These were probably due to the presence of one or more feldspars.

The clay mineral composition of sediment samples was determined at various depths for 13 stations representing three cross sections of the area. Semiquantitative diffractometer peak height measurements of the basal clay mineral reflections indicate a fairly constant relationship among chlorite, illite, and kaolinite (Table 3). Relative amounts of vermiculite were not determined because of the diffuse character of the peak. Quartz was present in all clay-size samples. Electron microscopy revealed hexagonal flakes, irregular flakes, and skeletal (diatom) fragments. The hexagonal flakes are probably kaolinite, while the irregular material may represent illite, chlorite, or organic matter.

Nelson (1960) studied the clay mineralogy of the bottom sediments of the Rappahannock River and Powers (1954), the Patuxent. Both investigators found illite, chlorite, and kaolinite, while Nelson, in addition, found two montmorillonites and vermiculite. Both found that the relative amounts of chlorite increased downstream. Powers attributed this increase in chlorite to diagenetic alteration of illitic material by addition of Mg. According to Nelson, relative amounts of kaolinite and vermiculite remained constant for all samples, while both montmorillonites disappeared rapidly down the salinity gradient. Hurley

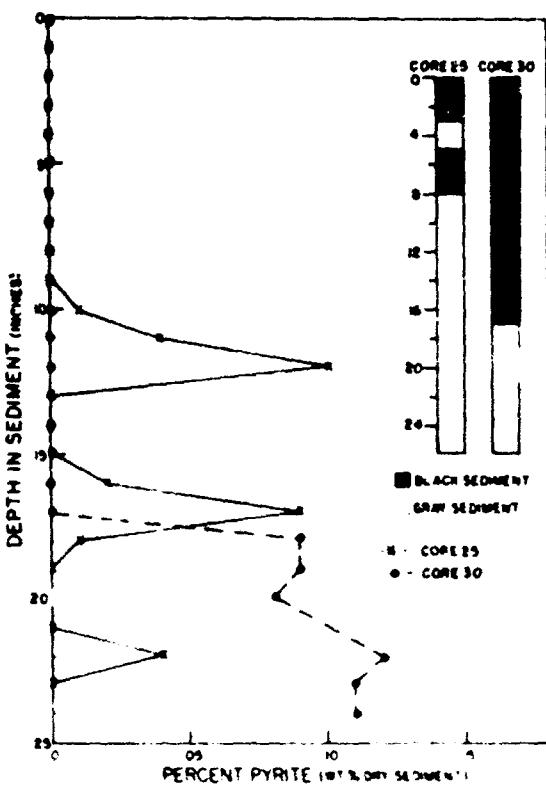


Fig. 9. Vertical distribution of pyrite in the sediments. Station locations presented in Fig. 4.

et al. (1961) determined the K^{40} - Ar^{40} ages of the K-bearing clay material from the mouth of the Rappahannock River, and obtained values of 497 million years and 680 million years for two samples. Hurley concluded that the illite fraction was detrital.

In the Chesapeake Bay area, three rather distinct environments are represented during the summer months: the oxidizing environment of the shelf, characterized by high pH (8.0-8.3), high dissolved oxygen content, and relatively low salinity (10‰-15‰); the reducing environment of the channel, characterized by low pH (7.2-7.6), low dissolved oxygen content, and relatively high salinity (17‰-22‰); and the buried or diagenetic environment, characterized by high and variable pH (7.8-8.6), and relatively high salinity (19‰-21‰). Regardless of where samples were taken, whether at the surface or at depth in the sediment, in the black or gray sediment, or in shallow or deep water, the clay minerals are similar. Thus, none of the above-mentioned parameters appear to affect the gross composition of the clay minerals of this area.

Quartz and feldspar observed in the clay fraction represent detrital material, while siliceous skeletal remains are the principal biological contribution to the sediment.

DETAILED MINERALOGY

Color distributions similar to those described for

Chesapeake Bay have been observed in Recent sediments by Smirnow (1958) in the Black Sea; Emery and Rittenberg (1952) in San Pedro Harbor; Van Straaten (1954) in the Dutch Wadden Zee; Manheim (1961) in the Baltic; Oppenheimer (1960) in Redfish Bay, Texas; and Priddy *et al.* (1955) in Mississippi Sound. In all the above-mentioned localities, the investigators have, at least partially, attributed the color of black sediment to hydrotroilite ($FeS\cdot nH_2O$), an amorphous ferrous sulfide.

A test for hydrotroilite (Emery and Rittenberg, 1952), involving treatment of sediment samples with dilute hydrochloric acid, with the evolution of H_2S if soluble sulfides are present, was completed on all sediment samples. Black sediment evolved H_2S , while gray samples yielded none, indicating the possible presence of hydrotroilite in black sediment.

Van Straaten (1954) found that with time the monosulfide (hydrotroilite) altered to the bisulfide (pyrite). Gray samples digested in 50 percent HCl and 50 percent HF followed by boiling $AlCl_3$ (Neuburg, 1961) yielded a black residue which gave an X-ray pattern of pyrite. This pyrite comprises about 0.15 percent of the bulk sediment sample and 0.3 percent of the clay-size fraction. Exceptions to this observation occurred in banded cores where gray bands gave no pyrite pattern after digestion. Figure 9 illustrates the pyrite distributions in two cores. The shallow-water core contains black and gray banding, and the deepwater core is uniformly black followed at depth by gray color. Black sediment in the color-banded core (core 25) contains no detectable pyrite, nor does the enclosed gray band. In underlying gray sediment, however, pyrite occurs in the same sequence where black color would be expected if the banding were continuous with depth. This observation strongly suggests that black sediment containing hydrotroilite alters to gray sediment containing pyrite, while originally deposited gray sediment contains neither pyrite nor hydrotroilite. Gray sediment from deep water contains relatively constant quantities of pyrite, suggesting that it has been altered to its present state from originally hydrotroilite-containing black material. Pyrite was not detected in black sediment.

The presence of small amounts of pyrite in the sediments is not unusual. Emery and Rittenberg (1952) describe a somewhat similar situation in the sediments of the offshore California basins, where pyrite occurs as spherical masses and irregular grains which increase in abundance with depth in the sediment. They feel two mechanisms may be involved in the production of authigenic pyrite: alteration in the sequence hydrotroilite \rightarrow melanokovite \rightarrow pyrite in areas of rapid deposition such as rivers, harbors, and bays, and pyrite formed directly in areas of slow detrital sedimentation, such as offshore basins.

In the Chesapeake area, the presence of hydrotroilite in the black sediments has already been indicated. The occurrence of pyrite in the gray sediments but not in the black supports the hypothesis that the

pyrite is an authigenic mineral formed at the expense of hydrotroilite.

CHEMICAL PARAMETERS

In this region of Chesapeake Bay the writer has measured sulfate and chloride from the water column and from interstitial water, and organic carbon, Eh, pH, ferric and ferrous iron, and sulfur in the sediments. Changes in these parameters across the basin and with depth in the sediment have been noted, and an attempt has been made to relate the interplay of the chemical properties with the physical and biological environment.

Sulfate, Chlorinity, and the Sulfate-Chlorinity Ratio

Sulfate to chlorinity weight ratios in interstitial waters were determined for the purpose of approximating the redox state of this environment. The ratio of sulfate to chlorinity in normal marine waters is about 0.14. The tendency in reducing environments is for this ratio to be lower than 0.14 because of the breakdown of the sulfate molecule by bacterial and inorganic processes.

Sulfate was determined gravimetrically on interstitial water centrifuged from sediment samples (Bather and Riley, 1954). Triplicate results are precise to ± 0.1 percent. Accuracy is approximately ± 0.05 percent of the amount present in synthetic samples. Chlorinity was determined volumetrically by the standard Mohr method on the same samples. Accuracy of this method approaches ± 0.05 percent. Examples of the vertical distribution of the sulfate-chlorinity ratio in the water column and the sediments are presented in Figure 10.

The wide variation of the sulfate-chlorinity ratio in the water column samples is difficult to explain. Cor-

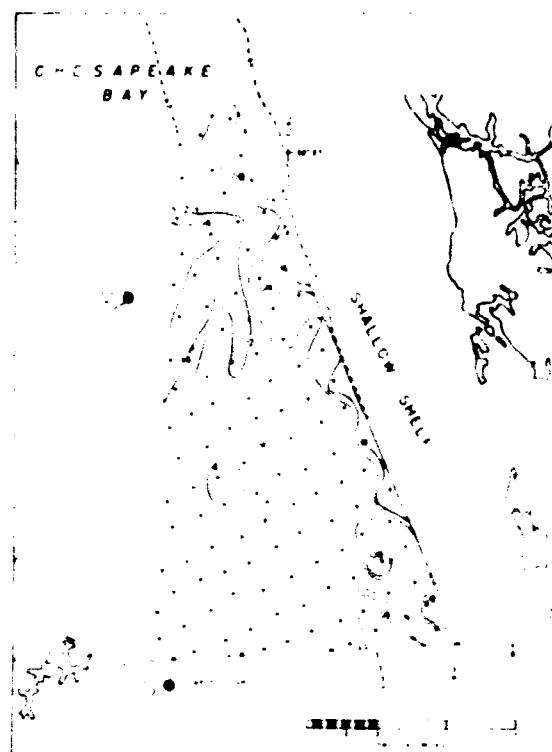


Fig. 11. Distribution of the sulfate-chlorinity ratio in surface sediments during the sampling periods. Contour interval 0.02.

relation of higher chlorinity and slightly higher sulfate concentrations in surface samples over deep areas and relatively lower chlorinity and higher sulfate values over shallow areas suggests local runoff of high sulfate affecting the quality of the shallow water in this area of the Bay. Sverdrup *et al.* (1942) report sulfate to be twice as abundant as chloride in fresh waters. The two shallow stations are characterized by average or higher than average ratios throughout the depth sampled, while the two deep stations show erratic but increasing sulfate-chloride ratios with depth.

Table 4. Sulfate-chlorinity relationship in the water column at Station 58.

	Cl X found gm/l	Cl X 0.14 = SO ₄ calc gm/l	SO ₄ found gm/l	SO ₄ excess gm/l	% excess SO ₄ over cal value
0'	6.58	9.21	8.60	-0.71*	-7.7
10'	5.98	8.23	7.94	-+0.71	+8.6
20'	7.77	10.08	9.22	-+1.66	+15.2
30'	9.14	12.8	11.17	-+1.10	+8.5
40'	8.66	12.1	12.8	-+0.70	+5.8
50'	9.14	12.8	14.0	-+1.13	+10.2
75'	9.16	12.8	14.7	-+1.19	+14.9
100'	9.37	13.1	14.6	-+1.15	+11.4

* = SO₄ deficiency.

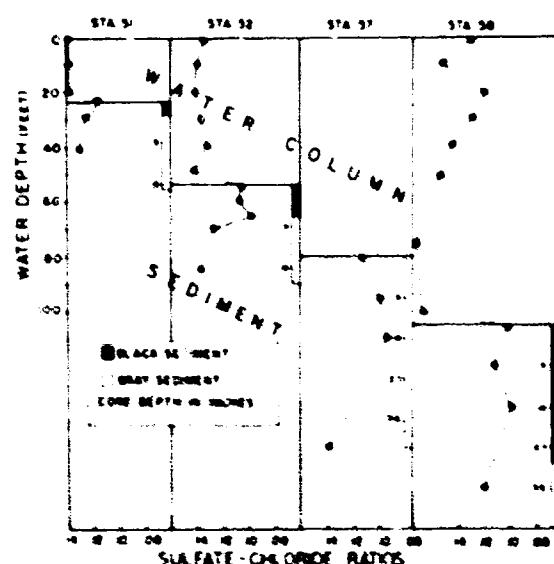


Fig. 10. Sulfate-chlorinity ratios versus water and sediment depth for four stations during the summer months. Station locations presented in Fig. 4.

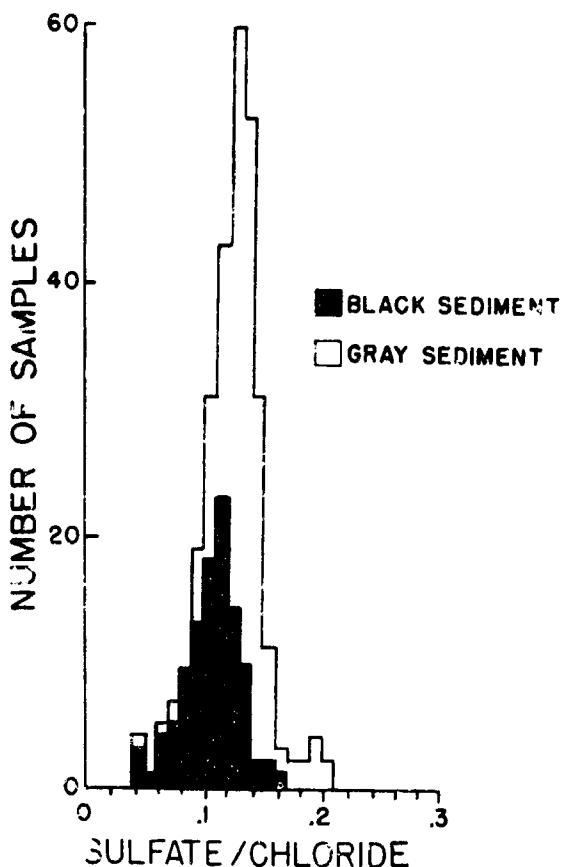


Fig. 12. Variation of SO_4/Cl with sediment color.

Ratios of sulfate-chlorinity for surface sediments indicate reduction of the SO_4 component in the samples from deeper water (Fig. 11). Generally the ratio is erratically lower, reaching a minimum and then rising with increasing sediment depth to values similar to those found in surface sediments. Sulfate is never completely absent from the interstitial water at any depth.

Sulfate-Chlorinity Ratios: Discussion

The distribution of the sulfate-chlorinity ratio in the water and sediment pore-water has already been discussed. Data presented in Table 4 indicate that an increase in the ratio with increasing water depth is due to the high sulfate concentration, probably resulting from H_2S production in the sediment; its migration upward into the water column; and its oxidation to sulfate. Although a freshwater sulfate correction was not taken into account in the calculations, the upper river-derived waters appear deficient in sulfate, while the deeper, marine derived waters contain a marked concentration of sulfate over the theoretical value. With the approximate enrichment of 10 percent sulfate in the deep water, it should be expected that sulfate concentrations in the sediment pore-water would be deficient by an amount equal to the 10 per-

cent enrichment in the water column plus any sulfide remaining in combination in the sediment. The observed 10 percent enrichment of sulfate in the water column falls within the deficiency range of the sulfate-chlorinity ratio found in the sediment pore-water. However, variation of the sulfate-chloride ratio in the interstitial water is greater than that of the overlying water column, because of the intensity of the processes used in removing sulfate from any given sediment.

No marked variation exists between the sulfate-chlorinity ratio of the interstitial water of black or gray sediments (Fig. 12). Slightly higher ratios in the deeper gray sediment (Fig. 10) may indicate a decrease of bacterial reduction of sulfate and the adjustment to inorganic equilibrium conditions.

Organic Carbon and Organic Matter

Three hundred and fifty dry-combustion organic carbon determinations (Nierdahl and Nierdahl, 1942) were completed on nitrogen-dried, HCl-digested sediment samples. The combustion apparatus was standardized using spectrographic graphite as a carbon source, and recoveries of 99.9 percent were obtained. Triplicate sediment analyses indicate the results are precise to ± 0.19 percent. Horizontal and vertical sample variations over the area of interest are presented in Figures 13 and 14.

Values obtained in surface sediment samples range

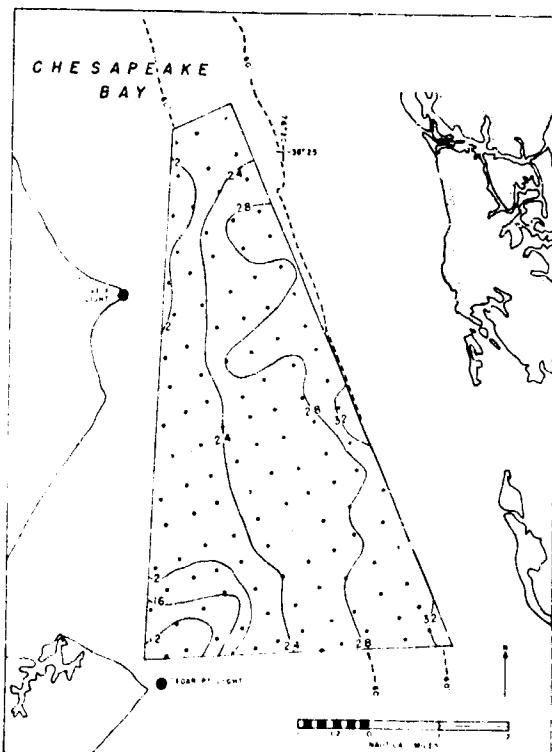


Fig. 13. Variation of organic carbon in surface sediments. Contour interval—0.4% C.

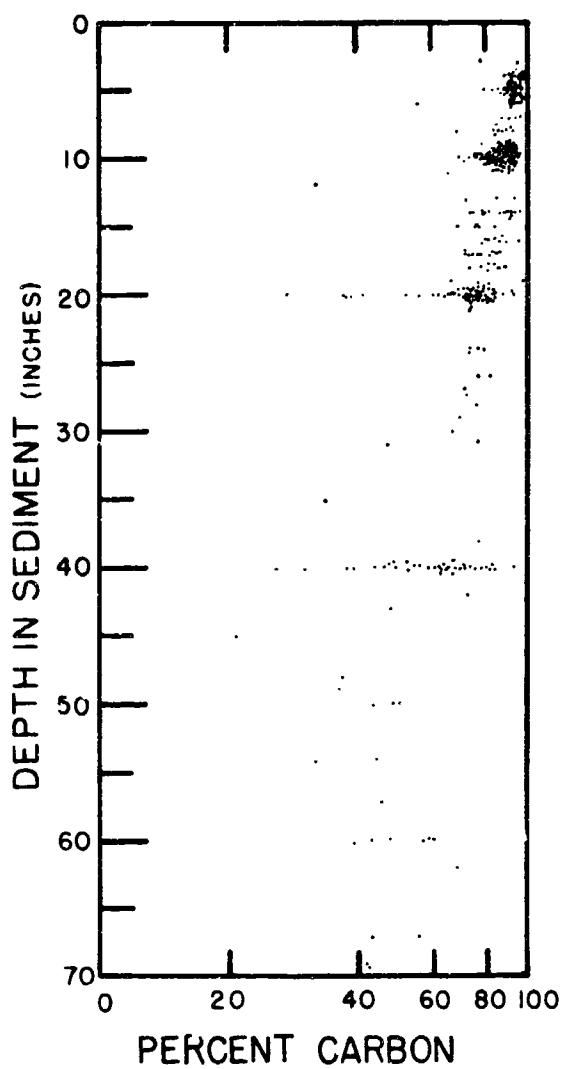


Fig. 14. Percentage of organic carbon remaining with depth in sediment.

from 0.95 percent carbon in the shallow silty sands to 3.4 percent carbon in the silty clays and clayey silts of the deepest regions.

Figure 14 illustrates the distribution of organic carbon with depth in sediment for all buried samples. The percentage of carbon remaining with depth was calculated assuming that the carbon found in the upper inch of the core represents 100 percent of the carbon deposited with the sediments.

A gross loss of approximately one percent of the organic carbon per inch of burial is evident from the graph. With increasing depth the percentage of organic carbon remaining in the samples becomes more variable. At a depth of 5 in. the range of carbon remaining is from 80 to 98 percent, at 10 in. the range is from 69 to 96 percent, and at 40 in. the range is from 26 to 92 percent.

In addition to the organic carbon analyses, four

Table 5. Organic extraction of Chesapeake Bay sediments.

Core 103	1	2	3	4
Inches below surface	0-1	9-10	13-14	25-26
Sediment color	black	black	gray	gray
Weight percent organic carbon	2.97	2.81	2.72	2.41
Weight percent organic carbon extracted with ethanol	0.151	0.128	9.116	0.062
Weight percent organic carbon extracted with benzene	0.023	0.014	0.024	0.047
Weight percent organic carbon extracted	0.174	0.142	0.140	0.109
Extractable % of total organic carbon	5.8%	5.0%	5.1%	4.5%

nitrogen-dried samples from core 103 were subjected to Soxhlet extraction for 24 hours. Sediment samples were extracted with ethanol, then benzene, to obtain soluble organic material. Pertinent data appear in Table 5.

It appears that the quantity of soluble organic material decreases slightly relative to the depths sampled in this area of Chesapeake Bay. The decrease is comparable to the overall decrease in total carbon.

Organic Carbon: Discussion

The distribution of organic carbon content in relation to the sediment color is illustrated in Figure 15.

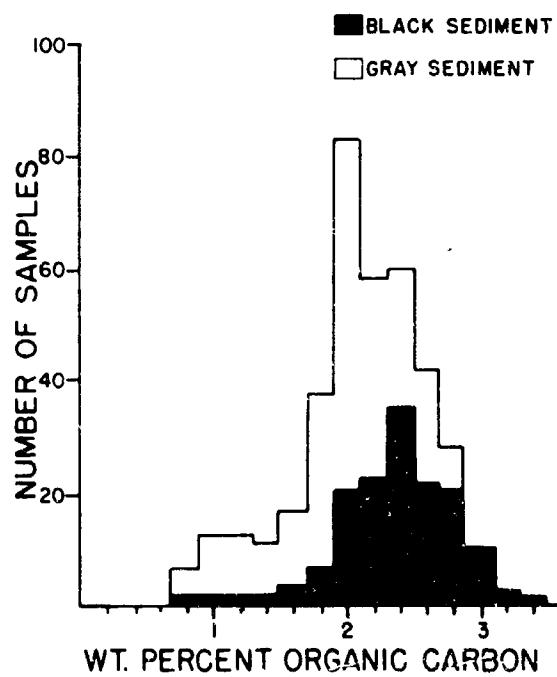


Fig. 15. Relationship between the percentage of organic carbon and sediment color.

No distinct correlation of sediment color with the percentage of organic carbon is obvious from the histogram. The tendency for most black sediments to have relatively higher organic carbon values is considered to be a result of the distribution of the samples. Many workers have found a general decrease in the content of organic matter with increasing depth of burial in modern sediments (Barghoorn, 1952; Mohamed, 1949; Smith, 1954; Waksman, 1933). The loss of organic carbon from these sediments, assuming constant supply throughout the depositional interval, has been attributed to bacterial activity and inorganic destructive processes. The association of black color with surface or near-surface sediments correlates well with the higher organic content found in them. The amount of overlap between the black and gray sediments, however, with respect to the organic carbon content, precludes a basic cause-and-effect relationship between quantity of organic matter and sediment color. The observed increase of organic carbon in surface sediments with increasing water depth may be attributed to: (1) a higher rate of sedimentation in shallow water, causing dilution of the organic matter by a detrital component; (2) a relatively higher rate of inorganic oxidation of organic matter in shallow areas, owing to the higher oxygen content of the overlying waters and larger sediment grain size, thereby permitting circulation of these waters through the sediment; (3) the scavenging activity of organisms in shallow areas; and (4) the higher physical energy of the environment, causing non-deposition or resuspension of fine sediments including fine organic detritus.

The factors which are predominant in causing the observed carbon distribution appear to be the energy of the environment and the inorganic oxidation of organic matter because of dissolved oxygen in the shallow areas. Scavenging organisms are present during the cold seasons, when they appear to be inactive and thus may not consume much organic matter. The shifting of submarine bars indicates strongly that bottom material in shallow regions is reworked, shifted,

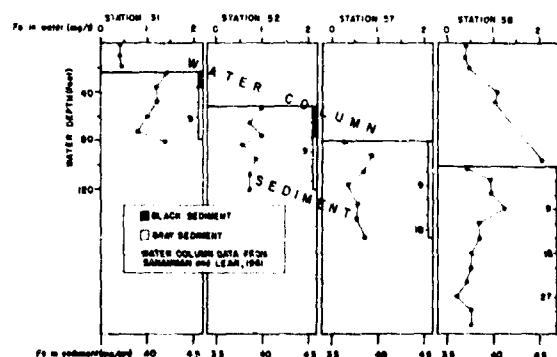


Fig. 16. Distribution of iron in the water and sediment of four stations from the study area. Data in the water column represent summer distribution only. Station locations presented in Fig. 4.

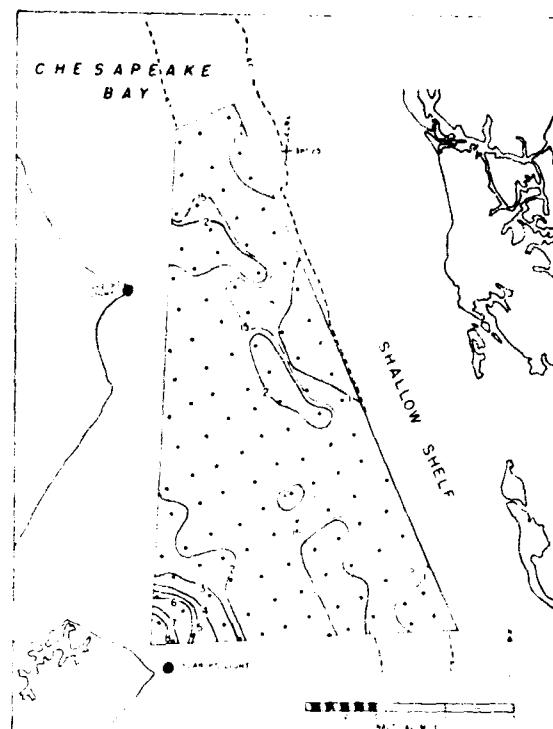


Fig. 17. Variation of $\text{Fe}^{3+}/\text{Fe}^{2+}$ ratio in surface sediments during the sampling period. Contour interval—0.1.

and resuspended by currents and waves, causing included organic material to be oxidized and/or redeposited in areas of lower environmental energy.

Iron—Ferric and ferrous iron were determined on 409 samples of sediment at various water depths and depths within the sediment. Frozen sediment samples were dried to constant weight at 95°C. in a nitrogen atmosphere. The material was then digested for 45 minutes in 1.2N HCl on a steam bath.

Ferric and ferrous iron were determined colorimetrically on the filtered HCl solution by a modification of the method of Lewis and Goldberg (1954), using 2,2'-bipyridyl as complexing agent. The complexing agent and a buffer were added with the HCl at the initiation of digestion, thus preventing oxidation of ferrous iron by atmospheric oxygen as described by Shapiro (1960). The complexed solution was then divided and diluted into two 25-ml samples. The optical density of the first was measured on a spectrophotometer at 522 m μ , the quantity of ferrous iron read from a previously determined calibration curve, and this quantity of iron was termed ferrous iron. A reducing agent, hydroxylamine hydrochloride, was added to the second sample, the optical density determined, the quantity of ferrous iron read from a second graph, and the result reported as total iron. Ferric iron is calculated from the difference between total iron and ferrous iron. As the true value of ferrous iron is unknown, a measure of accuracy is not obtainable. Precision, except for an occasional large

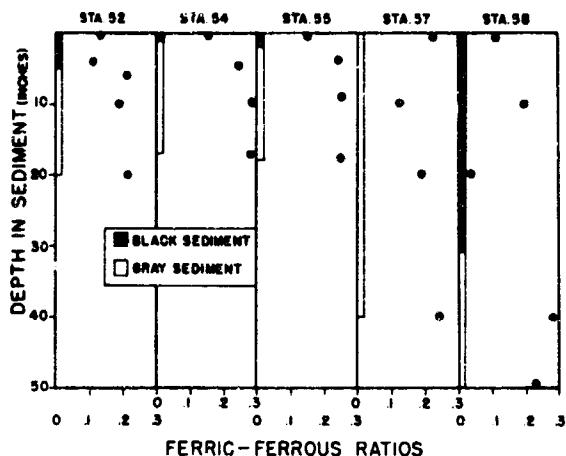


Fig. 18. Variation of $\text{Fe}^{\text{3+}}/\text{Fe}^{\text{2+}}$ ratio with sediment depth. Station locations presented in Fig. 4.

deviation (due to an inhomogeneous sample), was within ± 2 percent in the concentration range 25 γ -140 γ Fe.

The HCl digestion was used in order to study "environmental" iron, that is, iron present in clay minerals as acid-soluble sulfides, and in organic matter. X-ray analyses of digested material indicate that the clay minerals, with the exception of small quantities of kaolinite, were destroyed by HCl treatment, while organic carbon determinations reveal a 10 to 20 percent loss of organic matter.

Iron in the waters of Chesapeake Bay has been investigated by Garland (1952), Martin (1956), and Sananman and Lear (1961). Martin, studying the iron content of tributaries to Chesapeake Bay, found 0.01 to 0.10 mg Fe/l. Garland found a maximum of 140 mg Fe/l in polluted Baltimore Harbor, but concluded that the high iron content of harbor water had no significant effect on water quality outside the harbor. Sananman and Lear studied the Fe content of waters in the Bay east of Solomons, within the boundary of the study area, and found from 0.04 mg Fe/l at the surface to 0.205 mg Fe/l at 100 ft. depths.

Total HCl-soluble iron in the sediments varies closely about the mean value of 3.9 percent Fe (range 3.2 to 4.7 percent). Cross sections illustrating the distribution of total iron in the water and HCl-extractable iron in the sediments are presented in Figure 16. Figure 17 illustrates the lateral distribu-

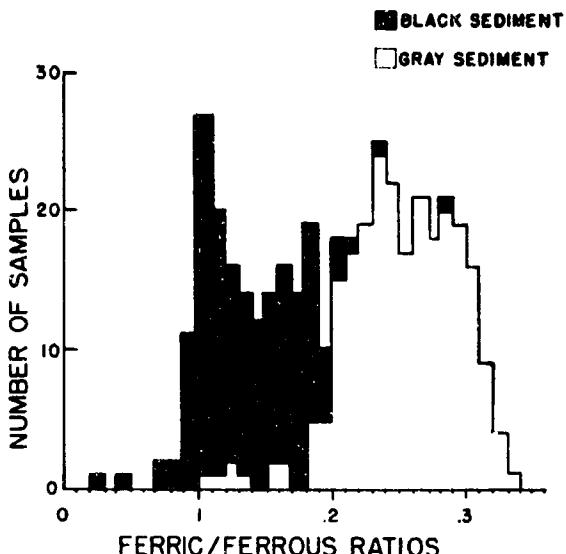


Fig. 19. Relationship between $\text{Fe}^{\text{3+}}/\text{Fe}^{\text{2+}}$ and sediment color.

tion of the ferric-ferrous ratio in the sediments of the Bay. Contours of the ratio in surface sediments indicate that ferrous iron predominates in all samples, even those from shallow depths in contact with oxygenated water. In the southwest portion of the area, the ferric-ferrous ratio is highest, and gradually decreases with increasing water depth.

The vertical distribution of the ferric-ferrous ratio is illustrated in Figure 18. In general, the ratio is higher in the gray sediment than in overlying or nearby black material. Since the ferric-ferrous ratio is an indication of the oxidation-reduction potential, it appears that the gray sediment is less reduced than the black. This is in good agreement with the less pronounced difference exhibited by the $\text{SO}_4^{2-}/\text{Cl}^-$ ratio of the interstitial water.

Total sample variation of the Fe ratio with respect to sediment color is presented in Figure 19. A marked correlation exists between the color of the sediment and the ferric-ferrous ratio. The black sediments of the area contain relatively more acid-soluble ferrous iron than the gray material, while the total iron content remains essentially constant. The ferric portion may represent iron which remains unreactive in the depositional environment.

The correlation between sediment color and ferric-

Table 6. Iron concentrations in organic fractions.

Sample No.	Color	Depth in sediment	% Fe ₂₊	% C	% of Iron removed by:		
					Water	Ethanol	Benzene
61-1	black	0"- 1"	4.2	2.37	0	9.0	1.1
61-2	black	3"- 4"	4.0	2.21	0	11.0	1.9
61-3	gray	4"- 5"	3.6	2.07	0	7.2	1.4
61-4	gray	15"-16"	3.6	1.98	0	5.1	1.3

Table 7. Sulfide determinations and relationships in Chesapeake Bay sediments.

Sample #	61-1	61-2	61-3	61-4
Depth in Sediment	0"-1"	3"-4"	4"-5"	15"-16"
Color	black	black	gray	gray
(a) Weight percent HCl soluble Fe in sediment	4.2	4.0	3.6	3.6
(b) Weight percent HCl soluble sulfide sulfur in sediment	0.51	0.40	T	T
(c) Weight percent hydrotroilite in sediment (1)	1.3	1.0	T	T
(d) Weight percent pyrite in sediment (2)	T	T	0.8	0.7

(1) calculated, assuming all sulfide sulfur is FeS; (2) insoluble residue from HCl + HF leach.

ferrous iron is consistent with the distribution of hydrotroilite in the sediments. The higher ferrous iron of the black sediment may be attributable to the presence of hydrotroilite, while the lower ferrous iron content of the gray material may be explained by the alteration of hydrotroilite to acid-insoluble pyrite.

Further investigation was attempted into the partition of iron in the various organic and inorganic phases present. The quantity of iron partitioned in the organic matter of the sediments was determined by successive extractions of sediment samples with distilled water, ethanol, and benzene. The quantity of iron found in the various solvents after filtration is presented in Table 6.

HCl-soluble sulfide sulfur was determined volumetrically by the method of Kitchener *et al.* (1951). All sulfur determined was then calculated into FeS and the maximum percentage of hydrotroilite in the sediment was estimated. The results are shown in Table 7.

There is an apparent difference of 0.5 wt. percent of acid-soluble iron between the black and gray sediment. If this difference were due to the conversion of hydrotroilite to acid-insoluble pyrite, then the calculated value of the pyrite formed, based on the loss of acid-soluble iron, would be ~1 wt. percent. The amount of pyrite which could be formed in the gray sediment, calculated from the amount of hydrotroilite found in the black sediment, would be ~1.3 wt. percent. Both of these calculated values, for the amount of pyrite which could be formed, agree closely with the quantity of pyrite found by acid insoluble leaching. The fact that the observed value of pyrite is lower than either of the calculated values may indicate that sulfur is the limiting factor in the genesis of pyrite in Chesapeake Bay.

Data presented indicate that the quantity of FeS calculated for the black sediment and the amount of pyrite found in the gray material (assuming the transition $\text{FeS}-\text{FeS}_2$) are in good agreement. It would be

expected and is sometimes true that total HCl-extractable iron (Fig. 16) should be lower in the gray sediment than in the black, due to removal from analysis of some iron during the conversion hydrotroilite \rightarrow pyrite. However, binding of 20 percent of the extractable iron as pyrite represents less than 1 percent of the sediment, and variations greater than 1 percent (Fig. 17) of total iron have been noted in similar black sediments. Therefore, total HCl-extractable iron may be fortuitously lower in deeper sediments from a single core, but the quantity found in any given sample is a result of supply to and fixation in the sediment, and may vary independently from the hydrotroilite-pyrite reaction.

Thus, metallo-organics and iron sulfides account for 25 to 35 percent of the total acid-soluble iron in the sediments. The remainder may be distributed among the ethanol- and benzene-insoluble organic fraction, as surface or exchangeable iron associated with clay minerals (Carroll, 1958), and as free iron oxides. Small quantities of hematite in the sediment have already been noted.

Water Content—The quantity of interstitial water in the sediments was determined by drying weighed bulk samples to constant weight at 95°C. in a nitrogen atmosphere. When higher drying temperatures were employed, there was liberation of CO_2 , evidence of breakdown of sedimentary materials. Water content is reported as percentage of wet weight of the samples.

Figure 20 illustrates the vertical variation of the water content of sediment samples from the study area. A pronounced difference in water content between the black and gray sediment samples is evident. In several cores black- and gray-banded sediments occur where the black sediment has a higher water content than either the over- or underlying gray material. Gray sediment exposed at the sediment-water interface has a characteristically lower water content than nearby exposed black sediment.

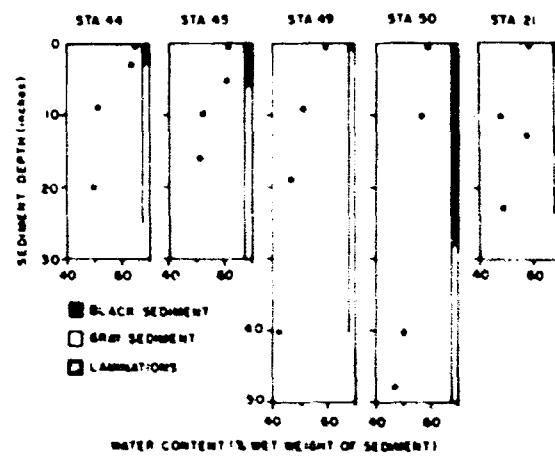


Fig. 20. Vertical variation of water content in Chesapeake Bay sediments. Water content expressed as percent wet weight of the sediment. Station locations presented in Fig. 4.

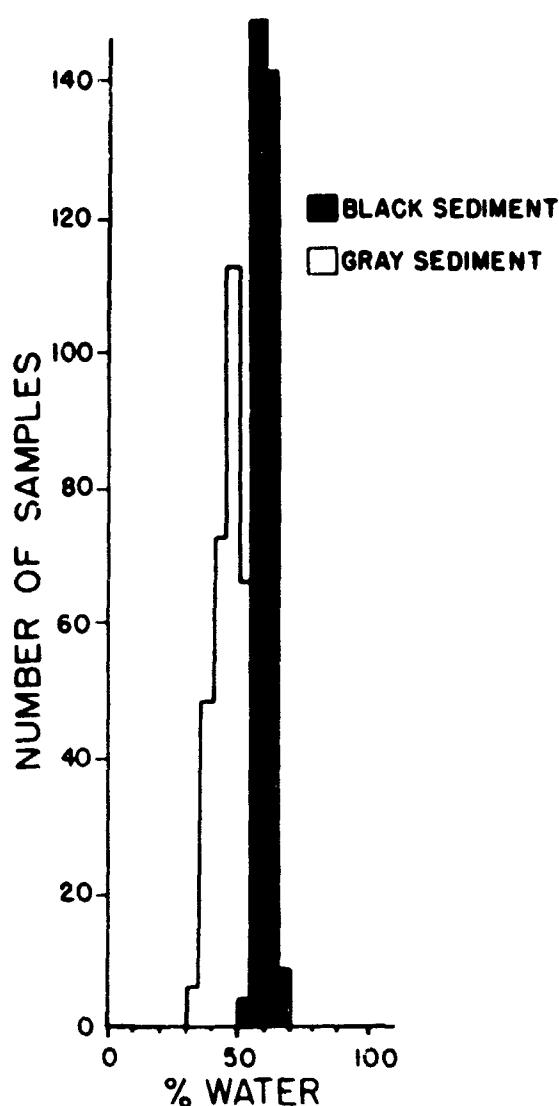


Fig. 21. Relationship between water content (percent wet weight of sediment) and sediment color.

The high degree of correlation between interstitial water content and sediment color is illustrated in Figure 21.

Normal sedimentary compaction and the expulsion of interstitial water will not explain the distribution of water in the banded cores (Fig. 20). Laboratory experiments were carried out to determine the relationship between water content and the hydrotroilite-induced color of the black sediments.

Quantities of artificial sediment (50 percent kaolinite-50 percent illite) were suspended in distilled water containing various concentrations of NaCl, FeCl₃, and H₂S. A portion of the flocculated sediment was withdrawn 48 hours after suspension, and the percentage of water determined by drying at 95°C. to constant weight. Results of the analyses are presented in graphic form in Figure 22.

Chloride, iron, and H₂S concentrations, when introduced independently, had little effect on the water content of the flocculate, which had been allowed to settle 48 hours after introduction of the sample. When H₂S was bubbled through a solution containing dissolved iron, however, a black iron sulfide, perhaps hydrotroilite, precipitated, and the presence of this precipitate in the sediment markedly increased the water content of the sediment samples. It appears that FeS may contribute to the high water content of Bay sediments the same way it does in the artificial ones. This finding, if true, is in contradiction to the view of Van Straaten (1954), who attributed the variation of water content in similar sediments to a period of non-deposition.

pH and Redox Potential—The pH and Eh (redox potential) of soils and sediments have been measured by many investigators (for summary of literature see Garrels, 1960; ZoBell, 1946), and have been used to describe changes in composition, chemical reactivity, biological populations, diagenesis, color, and other properties of recent sediments. Most authors agree that pH and Eh of sediments are primarily a result of the balance between types of bacteria, organic matter, buffering and poising capacity of the sediments and interstitial waters, and the rate of oxygen diffusion in the pore-water.

By measuring the pH and Eh of Chesapeake Bay bottom muds, relationships between these properties and chemical and mineralogical analyses were obtained. Hydrogen ion concentration of the sediments was measured using a shipboard portable pH meter with glass and calomel electrodes. Electrodes were inserted into the sediment through pre-drilled holes in the core liner. All measurements were taken within five minutes of sampling, and were reproducible to ± 0.05 units.

The horizontal distributions of pH in the surface sediment are illustrated in Figure 23. Examples of the vertical distribution are presented in Figure 24. All samples measured have pH greater than 7. In the black portion of cores the pH is lowest at the inter-

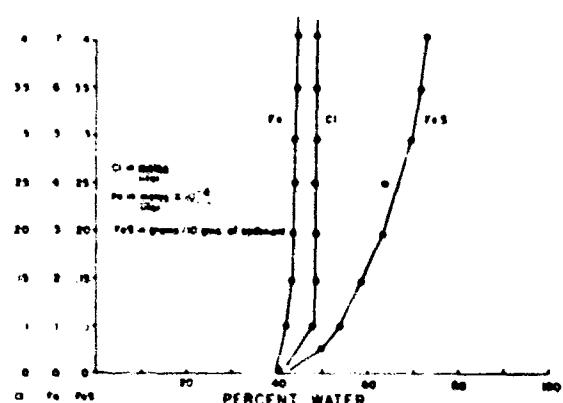


Fig. 22. Variation in water content of artificial sediment with concentration of Cl, Fe, and weight of FeS precipitate.

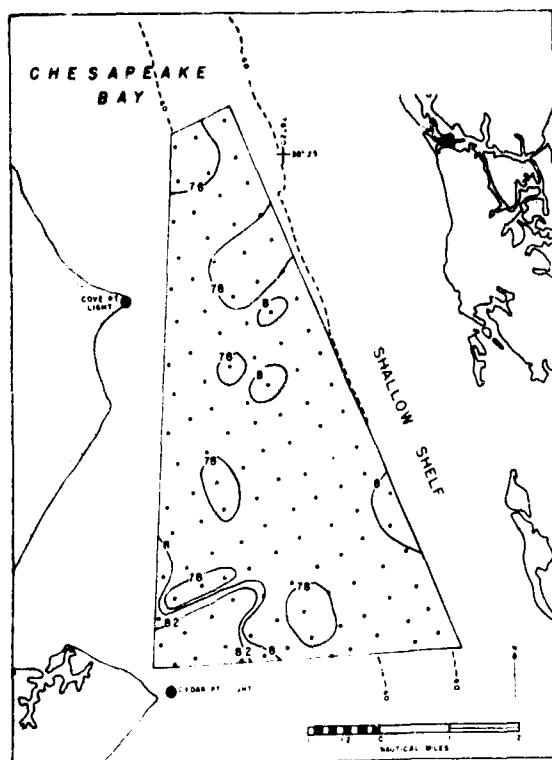


Fig. 23. Variation of pH in surface sediments during the sampling interval. Contour interval—0.2 pH units.

face, increases rapidly reaching a maximum a few inches below the surface, and increases slowly throughout the remaining depth of the core. The gray portion of cores is characterized by a gradual rise of pH with decreasing rate of increase with sediment depth.

The Eh of samples from the sediment and water column was measured using calomel and platinum electrodes attached to a portable shipboard pH meter. The Eh of Bay water was measured on samples taken

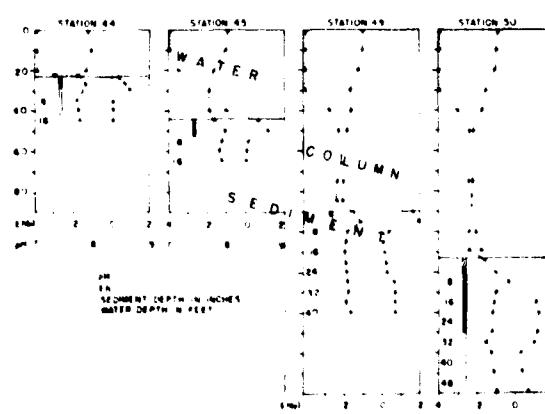


Fig. 24. Distribution of pH and Eh with sediment depth for four stations. For sediment color see Fig. 10. Station locations presented in Fig. 4.

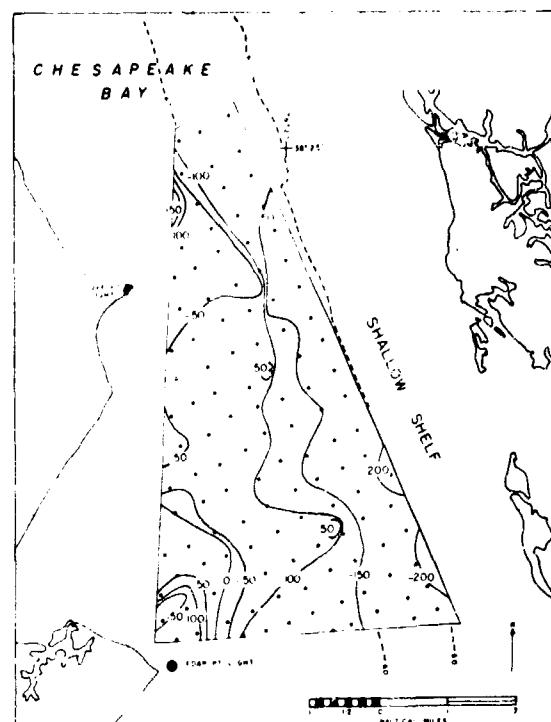


Fig. 25. Variation of Eh in surface sediments during sampling period. Contour interval—50 mv.

with a Kemmerer sampler. Electrodes were inserted directly into sediments through pre-drilled holes in the core liner for determination of sediment Eh. All measurements were taken within five minutes of sampling. All measurements are reported at the pH of the sample. The lateral and vertical distribution of Eh values is presented in Figures 24 and 25. Surface water values are highly positive, water from the mixed zone is intermediate, and deep water is lower with Eh values around +100 to +200 mv. A sharp difference in Eh is observed between exposed black sediment and the overlying water. Eh values for the top inch of black sediment are commonly lower than -150 mv. Below the surface Eh varies inversely to the pH; that is, a minimum Eh is usually found associated with the maximum pH, and as pH gradually increases with sediment depth, Eh decreases slowly. Gray sediments have less negative Eh values than overlying or nearby black material.

pH: Discussion

It appears that CO_2 production by bacterial oxidation, although it may well explain the relatively low pH of the bottom water, will not suffice to explain the observed pH variation in the sediment. The types of organic matter attacked at a given depth, however, as well as the products of the reactions, may significantly contribute to the pH. No data are available to interpret the effect of either of these parameters of the sediments. The action of sulfate-reducing bacteria

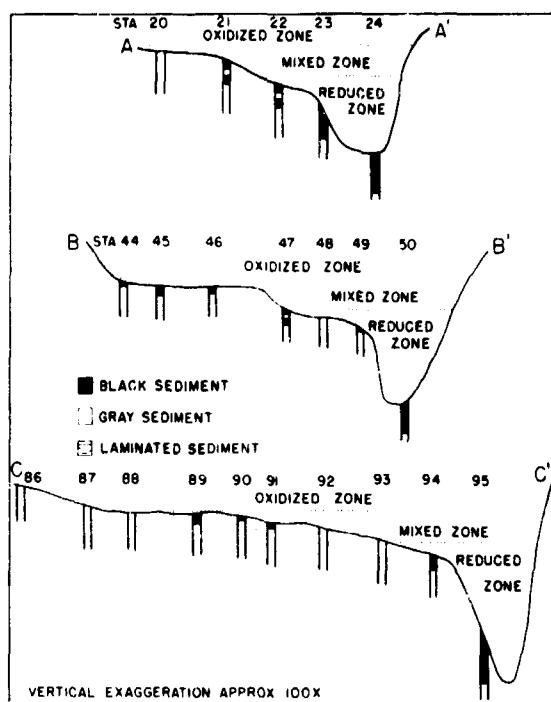


Fig. 26. Distribution of sediment color perpendicular to axis of Bay. Hydrographic zones represent averages for summer months. Station locations presented in Fig. 4.

may result in an increase in the pH of the pore-water. The product of sulfate destruction at the pH observed in the sediments would be HS^- or H_2S , resulting in the balance of a weak acid with a strong base. Maximum loss of sulfate, reflected in the sulfate-chlorinity ratio, occurs in the black sediment where the pH is highest and bacterial activity is probably greatest. On the other hand, in deep waters overlying the sediments, the sulfate-chlorinity ratio is highest and the pH is low. It appears that production of H_2S or HS^- may be related to the increase of pH in the sediment, while the oxidation of these components in the overlying water aids in decreasing the pH. Although the organic matter- CO_2 transformations probably control the pH of the sediments, it is quite possible that the described sulfate-sulfide system is a major contributor to pH variation.

Eh: Discussion

Eh in sediments is a direct result of oxygen content, bacterial activity, and organic matter (Allgeier *et al.*, 1941; Burrows and Cordon, 1936; Willis, 1943). Other parameters which have been found to affect the Eh of a system include iron, hydrogen sulfide, and nitrogen compounds (Pearsall and Mortimer, 1939). In Chesapeake Bay sediments, it seems that the presence of quantities of organic matter, bacterial activity, and the absence of oxygen are major contributors to the low Eh observed. When superimposed on the effect of bacteria on organic matter, sulfate reduction

may play a significant role in the variation of the observed Eh. Lowest Eh values occur in the region of maximum sulfate reduction and minimum ferric-ferrous ratios, both of which may lower the Eh of the sediments.

MODEL OF SEDIMENTATION IN CHESAPEAKE BAY

The inferred relationship and development between the black and gray sediments is illustrated in Figure 26. The proposed model involves fluctuations of the surface of the reducing zone in the water column because of storm, tide, wind, and runoff. These agencies may influence the depth to the reducing surface by changing the thickness of the mixed layer. Thus, during a hot dry summer, vertical mixing would be reduced and the surface of the oxygen-deficient layer would migrate upward.

In cross section A-A' (Fig. 26), Stations 23 and 24 at depths of 80 and 115 ft., respectively, are always below the surface of the reducing zone and have thick black deposits; Stations 21 and 22 at depths of 50 ft. and 65 ft. are alternately oxidized and reduced by fluctuations of the reducing surface and are laminated and banded accordingly; and Station 20, at a depth of 45 ft., is in an oxidizing hydrographic environment and is composed entirely of gray sediment. Thus, relatively long-term fluctuations in the depth to the oxygen-deficient zone may produce banding in sediments whose depth is near that of the seasonally oxygen-deficient zone, while minor oscillations in the surface of the reducing zone would produce laminations in the sediments lying at depths where the reducing zone "feathers out" against the bottom. Sections B-B' and C-C' show incomplete sedimentary structures, assuming the proposed model. In section B-B' a banded core (Station 47) occurs at a depth of 60 ft. (compare with banded core 22 at a depth of 65 ft. in A-A'), but no trace of laminations is evident in shallower sediments. Section C-C' contains neither banding nor laminations.

The incomplete nature of the structures in B-B' and C-C' may be attributable to sampling, bottom configuration, non-deposition or erosion, or destruction. Sampling error cannot be evaluated but always exists as a possibility. In section B-B' and C-C' a break in slope occurs at a depth of 40 to 50 ft. with pronounced flattening of the bottom at shallower depths. A small decrease in the depth to the oxygen-deficient zone would flood large areas in the southern portion with low-oxygen waters. There, influxes of the reduced water into shallow regions would produce black sediments which are represented as a thin surface layer. Samples 48 in B-B' and 92 and 93 in C-C' exhibit the anomalous characteristic of being entirely gray while lying at depths sufficient to produce black sediment. Explanations for this phenomenon include the possibilities that the central portion of the Bay is one of non-deposition, and that the occurrence of the gray sediment at or near the break in slope along the western edge of the channel suggests slumping of the

relatively weak black sediment. This area of gray sediment with little or no black overlying it extends the length of the study area and from depths of 50 to 80 ft. (Fig. 5).

Organisms may play a significant role in the destruction of sedimentary structures by burrowing activities which homogenize the sediments. Quantitative data are not available on the distribution or significance of burrowing organisms in this area of the Bay.

GEOLOGICAL SIGNIFICANCE

Three points of geological significance may be inferred as a result of this study. Chesapeake Bay may serve as a model for the deposition of disseminated and bedded sedimentary pyrite; for sufficient conditions for the deposition of dark, highly organic shales; and for a possible explanation concerning the nature and significance of the color of modern and ancient "euxinic" sediments.

Love (1962) and Love and Zimmerman (1961) have studied pyrite-bearing Permian and Precambrian shales. They have shown that the pyrite is intimately associated with microfloral remains, and argue for early diagenetic formation of the pyrite. The presence of authigenic pyrite in buried Chesapeake Bay muds provides an environmental model suggesting the time of formation and the conditions under which such deposits may have originated.

Bates and Strahl (1957), and Campbell (1946), in studies of the Chattanooga and New Albany shales, found pyrite occurring in three "genetic" types: (1) massive crystals up to one-half inch square; (2) fine (15μ) pyrite disseminated throughout thick stratigraphic sequences; and (3) finely crystalline-bedded pyrite occurring as stringers or lenses. Small pyrite crystals occur disseminated throughout the deeper water sediments of Chesapeake Bay and discrete zones of disseminated pyrite occur in the shallower water

Table 8. Measured parameters and inferred causes in Chesapeake Bay sediment and water.

WATER COLUMN		Dominating Influence
<i>Observation</i>		
Shallow	pH 8 High O ₂ Average SO ₄ Eh++	Normal estuarine conditions
Intermediate	pH 7.8 Intermediate O ₂ Fluctuating SO ₄ Eh +	Mixing of surface and deep waters
Deep	pH 7.6 O ₂ = O High SO ₄ Eh = O	Oxidation of organic matter H ₂ S → SO ₄ + H ⁺ Biological activity, inorganic reduction Oxidation of H ₂ S to SO ₄ O ₂ = O
SEDIMENT		
<i>Interface</i>		<i>Interface</i>
Black		
Black color		Presence of hydrotroilite
pH increasing then decreasing		Bacterial reduction of SO ₄ , Inorganic oxidation of SO ₄ , CO ₂ from organic matter
O ₂ = O		Inherited from overlying water
Decreasing SG _r		Microbiological reduction of SO ₄
Eh = -		State of organic matter, iron, and sulfur species
High water content		Presence of hydrotroilite
Gray		
Gray color		Natural sediment color
O ₂ = O, pH 8		Diminution or cessation of biological activity, approach to inorganic equilibrium
SO ₄ constant Eh ≈ O, slightly Low water content		Absence of hydrotroilite

sediments. No massive pyrite crystals occur in modern Chesapeake Bay sediments. The model presented for deposition of Chesapeake Bay sediments may be useful in determining the origin and relationship between bedded and disseminated pyrite in ancient sediments.

Geologists have long believed highly organic, non-fossiliferous, pyritiferous shales to be the product of extended stagnant hydrographic conditions. In Chesapeake Bay, however, stagnant conditions exist in the water column only for short periods, yet are sufficient to produce what may be characterized as an euxinic sediment. Thus, in the interpretation of the environment of deposition of similar ancient sediments, short-term stagnancy is a condition sufficient to produce the effect of permanent stagnancy. This observation has paleo-ecological implications in that the so-called "dwarfed" fauna of highly organic shales may in fact merely be juvenile in some cases. Cloud (1948) suggested accumulation of immature specimens as a possibility for producing assemblages of small brachiopods.

Investigators of Recent euxinic sediments generally attribute black color to metastable hydrotroilite (Emery, 1960; Emery and Rittenberg, 1952; Manheim, 1961; Oppenheimer, 1960; Priddy, 1954; Smirnow, 1958; Van Straaten, 1954). Black color in shales is usually attributed to carbonaceous matter, black rock or mineral fragments, or amorphous ferrous sulfide (Twenhofel, 1926). There is only one reported instance of amorphous ferrous sulfide (hydrotroilite) in ancient sediments (Priddy, 1954). On the other hand, data from this report (Emery and Rittenberg, 1952; Van Straaten, 1954) suggest that hydrotroilite in Recent sediments alters to pyrite within a relatively short interval, and the sediments lose their black color. Two possibilities are suggested as explaining the scarcity of permanently black sapropelic modern sediments: they are not being deposited in modern environments thus far sampled, or black color in shales is not necessarily a "primary" feature.

SUMMARY

As a result of data accrued from this and previous geological and oceanographic investigations of Chesapeake Bay, correlations between observations and dominating influences seem justified. A "typical" sequence of measured parameters is presented in Table 8, together with assigned major influences on these parameters, both in the water column and the sediment.

It appears that the difference between pH in the water column and in surface water is due to the CO_2 produced by oxidation of organic matter in sediments, as well as H_2S oxidation upon escape from the sediments. Low O_2 concentrations in deep water are primarily a result of biological and inorganic depletion. The high SO_4^{2-} concentration in deep water is a result of H_2S oxidation there, while Eh in the water column appears to be a function of O_2 concentration.

Black color in the sediments is due to the presence of hydrotroilite, while gray-green appears to be the

"natural" color reflected in those sediments where hydrotroilite has been converted to pyrite or has never been deposited (as in banded cores). Oxygen is not detectable in the sediment pore-water, this being either an inherited characteristic from the overlying water or a result of organic or inorganic processes. Sulfate in the black sediments varies with microbiological reduction, and becomes stabilized in deeper gray sediment. Eh varies with the state of organic matter, iron, and sulfur. It is low in black sediments where sulfate and the $\text{Fe}^{+++}/\text{Fe}^{++}$ are lowest and organic matter is highest, and is higher in the gray sediment where SO_4^{2-} and $\text{Fe}^{+++}/\text{Fe}^{++}$ are highest and organic matter lowest. The pH of the sediments basically reflects organic oxidation on which is superimposed the degree of sulfate reduction. Water content is high where hydrotroilite is present, and characteristically lower in non-hydrotroilite-bearing gray sediments.

The widespread occurrence of black sediment underlain by gray material containing pyrite is the result of sedimentation in areas where the overlying water contains no oxygen and $\text{FeS H}_2\text{O}$ or hydrotroilite is precipitated. With time the hydrotroilite is converted to pyrite and the sediment loses its black color. Restricted occurrences of banded black and gray sediments result from deposition in alternating oxygen-starved and oxygenated waters.

Some gray sediments from the shallow western portion of the study area contain no pyrite, indicating that hydrotroilite was never precipitated.

It seems quite probable that, in the geological record, deep-water Chesapeake Bay sediments would be characterized as homogeneous gray-green organic shales containing pyrite and scattered shell and sand layers. The present banded sediments may result in gray-green organic shales and sandy shales with alternating pyrite- and non-pyrite-bearing beds.

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LITERATURE CITED

- ALLGEIER, R. J., B. C. HAFFORD, and C. JUDAY, 1941. Oxidation-reduction potentials and pH of lake waters and of lake sediments. *Eidronis Stifromy Drv. Fnd.*, 44:115-133.
- BARGHOORN, E. S., 1952. Degradation of plant tissue in organic sediments. *J. Sediment. Petrol.*, 22:61-69.
- BATES, F. T., and E. O. STRAHL, 1957. Mineralogy, petrography and radioactivity of representative samples of Chattanooga shale. *Bull. Geol. Soc. Am.*, 68:1305-1314.
- BATHER, J. M., and J. D. RILEY, 1954. The chemistry of the Irish Sea. (1) sulfate-chlorinity ratio. *J. Consil. Pern. Intern. Exploration Mer.*, 20:145-152.
- BURROWS, W., and T. C. CORDON, 1936. The influence of the decomposition of organic matter on the

- oxidation-reduction potential of soils. *Soil Sci.*, 42: 1-10.
- CAMPBELL, G., 1946. New Albany shale. *Bull. Geol. Soc. Am.*, 57: 829-908.
- CARROLL, D., 1958. Role of clay minerals in the transportation of iron. *Geochim. Cosmochim. Acta*, 14: 1-28.
- CLOUD, P. E., 1948. Assemblages of diminutive brachiopods and their paleoecological significance. *J. Sediment. Petrol.*, 18: 56-60.
- EMERY, K. O., 1960. *The Sea of Southern California*. John Wiley and Sons, New York.
- EMERY, K. O., and S. C. RITTENBERG, 1952. Early diagenesis of California basin sediments with special reference to the origin of oil. *Bull. Am. Assoc. Petro. Geologists*, 36: 735-806.
- GARLAND, C. F., 1952. A study of water quality in Baltimore Harbor. *Maryland Dept. Res. Ed., Chesapeake Biol. Lab. Publ.*, 96: 1-132.
- GARRELS, R. M., 1960. *Mineral Equilibria*. Harper and Bros., New York.
- GORSHKOVA, T. L., 1960. Sediments of the Norwegian Sea. *Intern. Geol. Congr. Proc., Part 10, Submarine Geol.*; pp. 16-22.
- HARTSOCK, J. K., 1960. Submarine topography and bottom deposits off the southeastern coast of Iceland. *Intern. Geol. Congr. Proc., Part 10, Submarine Geol.*; pp. 7-15.
- HURLEY, P. M., D. G. BROOKING, W. H. PINSON, and H. W. FAIRBAIRN, 1961. K-Ar age studies of Mississippi and other river sediments. *Bull. Geol. Soc. Am.*, 72: 1807-1816.
- KITCHENER, J. A., A. LIVERMAN, and D. A. SPRATT, 1951. An improved volumetric method for the determination of H_2S and soluble sulfides. *The Analyst*, 76: 509-516.
- KRUMBEIN, W. C., and F. J. PETT!JOHN, 1938. *Manual of Sedimentary Petrography*. Appleton-Century-Crofts, New York.
- LEWIS, G. J., JR., and D. O. GOLDBERG, 1954. Iron in marine waters. *J. Marine Res.*, 13: 183-197.
- LOVE, L. G., 1962. Biogenic primary sulfide of the Permian Kupferschiefer and Marl slate. *Econ. Geol.*, 57: 350-366.
- LOVE, L. G., and D. O. ZIMMERMAN, 1961. Bedded pyrite and microorganisms from the Mount Isa shale. *Econ. Geol.*, 56: 878-896.
- MANHEIM, F., 1961. Geochemical cross-section in the Baltic Sea. *Geochim. Cosmochim. Acta*, 25: 52-70.
- MARTIN, R. O. R., 1956. The water resources of Baltimore and Harford Counties. *Maryland Board Nat. Resources, Dept. Geol., Mines, Water Resources, Bull. No. 17*.
- MOHAMED, A. F., 1949. The distribution of organic matter in sediments from the Northern Red Sea. *Am. J. Sci.*, 247: 116-127.
- MOORE, J. F., and D. S. GORSLINE, 1960. Physical and chemical data for bottom sediments, South Atlantic coast of the United States. *U. S. Fish and Wildlife Serv., Spec. Sci. Rept., Fisheries*, No. 366.
- NELSON, B. W., 1960. Clay mineralogy of the bottom sediments, Rappahannock River, Virginia. *Proc. 7th Nall. Conf. Clays, Clay Minerals*, 5: 135-147.
- NEUERBURG, G. J., 1961. A method of mineral separation using hydrofluoric acid. *Am. Mineralogist*, 46: 1498-1501.
- NIERDAHL, J. B., and V. NIERSDAHL, 1942. *Micro-methods of quantitative organic analysis*. John Wiley and Sons, New York.
- NINO, H., 1950. Bottom deposits at the mouth of Wakasa Bay, Japan, and on the adjacent continental shelf. *J. Sediment. Petrol.*, 20: 37-54.
- OPPENHEIMER, C. H., 1960. Bacterial activity in sediments of shallow marine bays. *Geochim. Cosmochim. Acta*, 19(4): 1614-1623.
- PARKER, R. H., 1956. Macro-invertebrate assemblages as indicators of sedimentary environments in the east Mississippi Delta region. *Bull. Am. Assoc. Petro. Geologists*, 40: 295-376.
- PEARSALL, W. H., and C. H. MORTIMER, 1939. Oxidation-reduction potentials in waterlogged soils, natural waters, and muds. *J. Ecol.*, 27: 483-501.
- POWERS, M. C., 1954. Clay diagenesis in the Chesapeake Bay area. *Second Clays and Clay Minerals Nall. Conf., Nall. Acad. Sci.-Nall. Res. Council Publ.*, 327: 68-80.
- PRIDDY, R. R., 1954. Recent Mississippi Sound sediments compared with some upper cretaceous sediments. *Trans. Gulf Coast Assoc. Geol. Soc.*, 4: 159-168.
- PRIDDY, R. R., J. M. CRISLER, M. D. JOHNSON, and W. C. SMYTH, 1955. Sediments of Mississippi and inshore waters. *Mississippi State Geol. Surv. Bull.*, 82.
- PRITCHARD, D. W., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11: 106-123.
- REDFIELD, A. C., 1958. Preludes to the extraptation of organic matter in the sediments of Lake Maracaibo. In *Habitat of Oil*, edited by Lewis G. Weeks; pp. 968-981. Am. Assoc. Petro. Geologists, Tulsa, Oklahoma.
- RYAN, J. D., 1953. The sediments of Chesapeake Bay. *Maryland Board Nat. Resources, Dept. Geol., Mines Water Resources, Bull. No. 12*.
- SANANMAN, M., and D. W. LEAR, 1961. Iron in Chesapeake Bay waters. *Chesapeake Sci.*, 2: 207-209.
- SHAPIRO, L., 1960. A spectrophotometric method for the determination of FeO in rocks. *U. S. Geol. Surv. Prof. Paper 400B*; pp. 496-497.
- SMIRNOW, L. P., 1958. Black Sea Basin. In *Habitat of Oil*, edited by Lewis G. Weeks; pp. 922-994. Am. Assoc. Petro. Geologists, Tulsa, Oklahoma.
- SMITH, P. V., 1954. The origin of petroleum; occurrence of hydrocarbons in recent sediments. *Bull. Am. Assoc. Petro. Geologists*, 38: 377-404.
- SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING, 1942. *The Oceans—Their Physics, Chemistry, and General Biology*. Prentice-Hall, New York.
- TREFETHEN, J. M., 1950. Classification of sediments. *Am. J. Sci.*, 248: 55-62.
- TWENHOFFEL, T. H., 1926. *Treatise on Sedimentation*. The Williams and Wilkins Co., Baltimore, Maryland.
- VAN STRAATEN, L. M. J. U., 1954. Composition and structure of recent marine sediments in the Netherlands. *Leyden Geol. Mededel.*
- WAKSMAN, S. A., 1933. Distribution of organic matter in the sea bottom and the chemical nature and origin of marine humus. *Soil Sci.*, 36: 125-147.
- WHALEY, H. H., and T. C. HOPKINS, 1952. Atlas of salinity and temperature distribution of Chesapeake Bay, 1949-1951. *Chesapeake Bay Inst. Graphical Sum. Rep. No. 1*.
- WILLIS, L. G., 1943. Oxidation-reduction potentials and the hydrogen ion concentration of a soil. *J. Agric. Res.*, 63: 571-575.
- ZOBELL, C. E., 1946. Studies on redox potentials of marine sediments. *Bull. Am. Assoc. Petro. Geologists*, 30: 477-513.

Compactness Variability of Estuarine Sediments: An *In Situ* Study

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In a recent study compactness variability of marine sediments was investigated under laboratory conditions. Several types of marine sediments were maintained in a continuous unfiltered saltwater flow for one observational year (McMaster, 1962). In water temperatures that ranged from 18°C. to 5°C. sands were found to show a significantly greater dilatancy in summer than in winter whereas the compactness values for the clayey silts indicated no significant seasonal variation.

The purpose of this paper is to report further investigations into compactness of marine sediments *in situ*.

In this study, as in the previous one, variations in degrees of compactness for natural sediments include both volume expansions and contractions.

FIELD INVESTIGATION

INSTRUMENTATION

The instrument used to study compactness of marine sediments *in situ* was the "Narragansett Penetrometer" which has been described previously (Miller and Nixon, 1953). Briefly, the basic part of this device is an electric motor that drives a threaded rod. This rod engages a special nut that has been welded to a long stainless steel tube with a cylindrical probe (area—521.2 cm²) secured to its end. The direction in which the motor turns causes the threaded rod to move the tube and its probe either up or down. This assembly is mounted on a heavy frame by means of a

thrust plate and this plate is subject to bending stresses as the probe moves against a resisting surface. The penetrometer unit is supported by a 1.5 m diameter steel plate ring on which lead weights may be placed. For this investigation the total weight, in salt water, was maintained at 232 kg.

Strain gauges are attached to the thrust plate and the responses of these gauges under stress are fed into a time axis recorder with a 25 cm diameter chart. These load responses are calibrated in pressure units by means of special springs.

In the field, the penetrometer was used to apply an increasing load at a specific rate upon the surface layers of certain sediment types, and record the behavior of these sediments to this compressional force in units of grams per square centimeter and seconds. During this study the probe moved at a rate of 3 mm/sec whereas the clock-driven chart made a revolution every six minutes.

TEST SITES AND TESTING PROCEDURES

The Narragansett Bay system is an extensive series of deep but connected embayments which lies within Rhode Island and southeastern Massachusetts. A small area in West Passage of this system was selected for compactness studies (Fig. 1). In this area a variety of sediment types occur on the bottom: salinities vary between 31–32‰; water temperatures along the bottom range from 0°C. to 21°C. during the seasons (Fig. 2); tidal currents, flowing north-south, attain velocities of 0.5 to approximately 1 knot at the surface.

Within this area four test stations, based primarily on sediment type, were established and with the aid of scuba divers and bottom photographs, a description

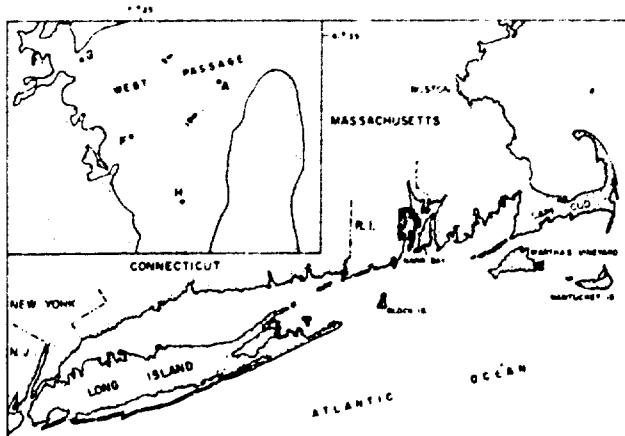


Fig. 1. Index map of the study area with the locations of the testing stations.

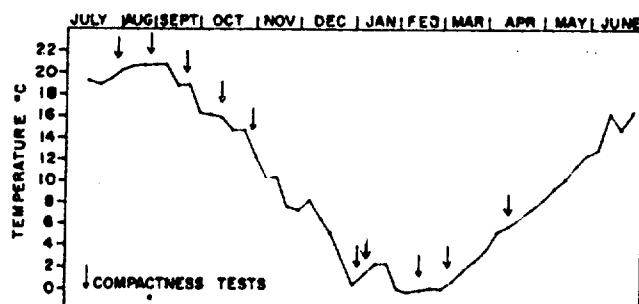


Fig. 2. Bottom water temperatures within the study area for 1962–63 (From D. M. Pratt, personal communication).

Table 1. Texture of sediments at test stations.

Station	Components by percent				Quartile measures		
	Gravel ¹	Sand	Silt	Clay	Md. (mm)	So ²	Sk ³
S	2 ⁴	76	18	4	0.11	1.8	1.09
F	6 ⁵	37	45	12	0.05	3.2	1.08
A	1 ⁶	16	63	20	0.02	2.8	0.70
H	4 ⁷	80	11	5	0.21	1.7	1.09

¹ Plus 2 mm particles.² Sorting coefficient (Trask, 1932).³ Skewness (Trask, 1932).⁴ Mostly shells.⁵ All shell.

of the bottom at each of these stations can be summarized. Station H, depth 7.3 m, is a sand bottom which is almost completely covered with *Crepidula* shells (1-2.5 cm in height) and shell fragments. Worm tubes are also common. Station A, depth 8.2 m, is a clayey silt with pronounced biological activity. Some mounds, pits, and shells are found in the bottom. Station F, depth 5.5 m, is sandy silt with numerous shells and shell fragments. Station S, depth 3 m, has a sand bottom with a few shells, but abundant worm tubes.

Although it was planned to visit each of these stations at monthly intervals during the observational year, weather and instrument failures modified this effort. When tests were made, however, the vessel was anchored on station and the penetrometer placed on the bottom. After each measurement the instrument was raised and the anchor line was adjusted so that the ship moved some 3 m from the previous spot. In this manner approximately ten random tests were made over a small area around the station.

At the same time water temperatures were measured some 2.5 cm above the bottom interface by means of a telethermometer. An attempt was made to record temperatures in the softer silts, but as the results were essentially the same as the bottom water measurements the effort was not continued.

Bottom grab samples were also collected several times during the investigation at random spots near each station. These samples were analyzed by sieving and hydrometer according to standard procedures, and representative results for each station are shown in Table 1. Previous mineralogical studies in the same area show that the sand fraction is composed essentially of quartz; the silt fraction of quartz and illite-chlorite mixture; and the clay fraction of illite and some chlorite and montmorillonite.

RESULTS

Several underwater observations were made by scuba divers in an attempt to learn something of the relationship between the action of the probe and reaction of the sediment. On sand bottoms the probe apparently pushed down about 1 cm below the interface during the testing period. No obvious displacement of sediment around the outside of the probe was

observed, nor was there any noticeable recovery of the sediment following the extraction of the probe. At Station H jets of fine sediment and organic matter were visible as the probe made initial contact with the bottom; also some *Crepidula* shells were found beneath the probe after it was raised. At Station S imprints of the probe from previous tests were observed in the bottom. These imprints, measuring about 1 cm in depth, had well-defined edges. These features were not seen at Station H, however.

In clayey silt, observations indicated that after contact there was some flowage of fine sediment from beneath the penetrating probe in which the material actually surged during its upward and outward movement. The probe moved only some 5 cm below the undisturbed interface but flowage built up a rim of sediment about 2.5 cm in height.

Representative compression curves for various sediment types during two periods of the year are presented in Figure 3. These curves, composed of several segments, begin with downward or negative slopes which level off in distinctive terraces. These terraces are followed by abrupt changes in slope as the pressure builds up. This latter segment is characterized by several minor changes in inclination and other irregularities. Hooks mark the points at which the probe was stopped arbitrarily, but apparently reflect some readjustment of the sediment to the applied load. The sand curves are smooth and descend more sharply

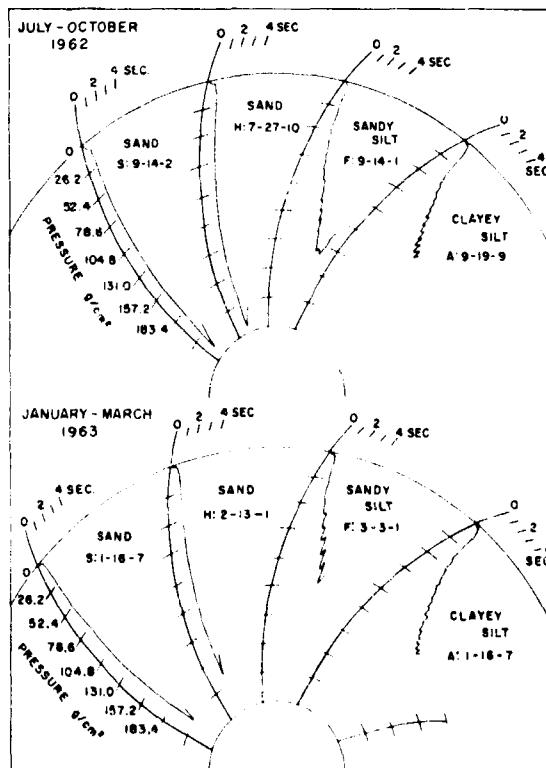


Fig. 3. Representative compression curves for sediment types during the testing period (1962-63).

Table 2. Analysis of variance for compression values—Station S.

	Sum of squares	d.f.	Mean square	F ratio
Category means	601.76	1	601.76	347.84 ¹ (S)
Within	154.05	89	1.73	
Total	755.81	90		

¹ F₉₅ (1, 89) = 3.96.

than those of sandy silt and clayey silt. The lower parts of the sandy silt and clayey silt curves show a distinct pulsating effect which gives these curves a very irregular appearance.

Apparently the variation in the degree of compactness for each sediment type is related to the changing position of the terrace in the initial part of its compression curve. Close scrutiny of the curves in Figure 3 reveals that the location of these terraces varies with sediment types and time of the year.

STATISTICAL ANALYSES

An analysis of variance was used to compare the positions of the terraces for each sediment type during the two periods of the year (Dixon and Massey, 1957). First, mean values and variances were determined for the compression readings (g/cm^2) of the terraces for the test populations of July–October and January–March. As the variances were approximately the same during these periods for the same sediment type, an analysis of single classification variance was used to test the hypothesis that the mean pressure values of the July–October period were equal to the mean pressure readings for the January–March period. The results are presented in Table 2. At the 5 percent confidence level, means for each sediment type during the July–October period are significantly different from those of the winter months.

Confidence limits for the means were calculated at the 95 percent level and these results are presented in Figures 4 and 5 (Dixon and Massey, 1957).

DISCUSSION

Is variation in the degree of compactness for the sediment type represented by the changing position of the terrace in the initial parts of the compression curves? Laboratory studies strongly suggest that the answer is affirmative.

Table 3. Analysis of variance for compression values—Station F.

	Sum of squares	d.f.	Mean square	F ratio
Category means	190.72	1	190.72	108.98 ¹ (S)
Within	143.80	82	1.75	
Total	334.52	83		

¹ F₉₅ (1, 82) = 3.97.

Table 4. Analysis of variance for compression values—Station A.

	Sum of squares	d.f.	Mean square	F ratio
Category means	20.9	1	20.9	22.96 ¹ (S)
Within	70.4	77	0.91	
Total	91.3	78		

¹ F₉₅ (1, 77) = 3.98.

Simulated laboratory tests were made in a large pan (diameter 34.3 cm, depth 15 cm) which was filled with beach sand to a height of 10 cm. The sand was packed and then 4 cm of water were added above the saturated sand surface. The load probe was run against the sand and its resistance recorded in the same manner as in the field. Next the top 1 cm of sand was raked and the probe was lowered again. These tests were repeated several times with the results which are summarized in Table 6. In packed sand the terrace of the curves developed at a pressure of 2.6 g/cm² whereas in loose surface sand the terrace did not form until the compression reached 6.5 g/cm² when the load was applied at the same rate.

As Abbott (1960) states, "All processes of consolidation in semi-pervious compressible soils can be explained in terms of a transfer of load from an incompressible pore-water to a compressible soil structure. The consolidating load is generally initiated by changes of pressure at the soil boundaries, these changes setting up pressure gradients in the soil with a consequent flow of water to the boundaries. The loss of soil-water resulting from this flow allows the transfer of load to the soil structure and hence consolidation."

Sugden (1950) has presented and discussed a mechanism of sedimentary compaction. For normal sediments he recognized a pressure system that is composed of hydrodynamic and intergranular pressures. The hydrodynamic pressure is defined as the fluid pressure in excess of normal hydrostatic pressure within the sediment which results from external compression. On the other hand, intergranular pressure is defined as the pressure excluding ionic or atomic structural forces, active between the points of contact of the grains of a sediment or between the points of contact of the adsorbed water films surrounding the grains.

Table 5. Analysis of variance for compression values—Station H.

	Sum of squares	d.f.	Mean square	F ratio
Category means	10.15	1	10.15	8.19 ¹ (S)
Within	93.91	75	1.24	
Total	103.06	76		

¹ F₉₅ (1, 75) = 3.98.

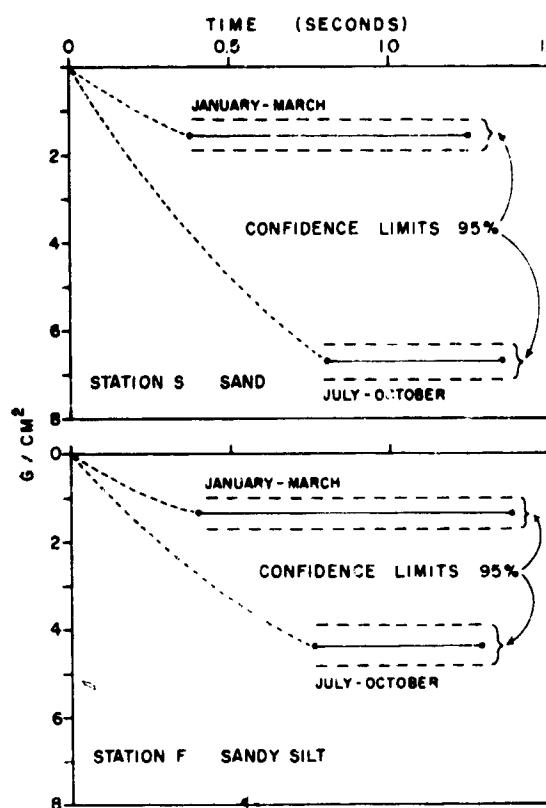


Fig. 4. Comparison of mean terraces of compression curves during July–October and January–March at Stations S and F.

At the time of deposition Sugden (1950) hypothesizes the following conditions. For a coarse sediment with greater permeability but lower porosity than its finer-grained equivalents, the volume of adsorbed film water will be very small as compared with the total volume of particles or pore space so that the grains may be considered as virtually touching one another. The fine sediment, composed in part of clay-sized grains, normally consists of a number of flocculated or partly flocculated particles, the majority of which may not be in full contact with most of their neighbors because of the presence of adsorbed water films.

When a sedimentary load is applied to fine-grained sediments Sugden finds that the increasing pressure will reduce the equilibrium volume at which adsorbed water films of smaller thickness surround the grains and the permeability will be reduced by the closer approach of the particles and their quasi-rigid ad-

sorbed water films. The rate at which the water is driven out will depend, in part, on the permeability of the sediment and the viscosity of the water. Eventually the intergranular pressure will virtually eliminate the water films at the points of contact of the grains. If compression is applied rapidly enough to a very porous sediment the impermeable internal structural framework may be partly destroyed and the sediment may become more or less fluid.

With this background, we can now focus attention on the behavior of various sediments under the influence of the penetrometer probe. Any given small area of bottom is not necessarily level or smooth. When the impervious probe strikes the sediment surface, contact is made first with the irregularities caused by differing grain sizes or structures in the form of shells or animal effects. This contact is reflected by the initial downward slope of the compression curve. As the probe moves down the resulting resistance is transmitted within the surface layers as an increase in hydrodynamic and intergranular pressures. The equilibrium-adsorbed water films are disturbed and finally reduced in thickness as the pore water begins to move away from the center of increasing pressure. At the same time some readjustment of grains is taking place, especially along the sediment interface. A critical pressure is soon reached,

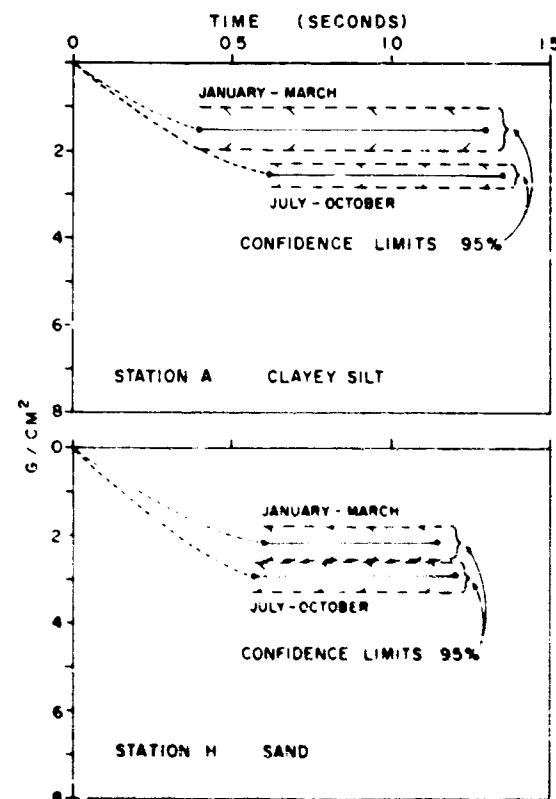


Fig. 5. Comparison of mean terraces of compression curves during July–October and January–March at Stations A and H.

Table 6. Laboratory tests of compactness in sand.

Condition of sand	Time terrace appears (sec.)	Pressure (g/cm ²)	Time terrace terminates (sec.)
Loose	0.8	6.5	1.3
Packed	0.5	2.6	1.3

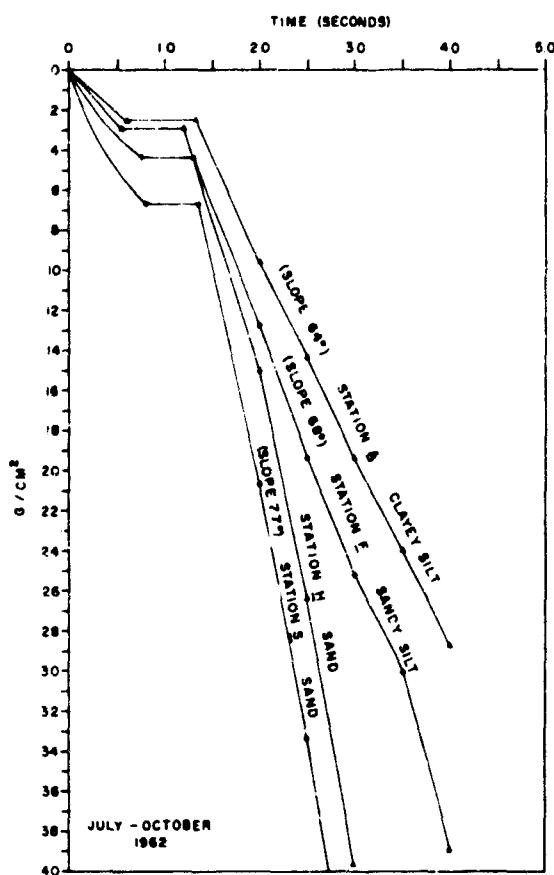


Fig. 6. Mean compression curves for the various sediment types during the July-October period. Pulsating part of the curves is not included.

ment, a greater pressure over a slightly longer time is needed to bring these laminae to the point of general particle readjustment and water expulsion (i.e., the terrace effect).

It is believed that the pulsating effect noted on the lower part of the sandy silt and clayey silt compression curves (Fig. 3) is the result of oozing of the sediment from beneath the descending probe. This effect begins when the probe reaches some 1-1.2 cm below the original sediment interface and corresponds to the action hypothesized by Sagden and observed by the scuba divers. Apparently a critical pressure, which is sufficient to cause a breakdown of the internal structure of this high-porosity sediment, is reached and the material flows. This interval is marked by a terracing or upward slope on the curves and occurs systematically as the sediments surge in response to each increasing buildup of pressure.

For each sediment type, regardless of the season, it is apparent that the terraces terminate at roughly the same time (Figs. 4 and 5). This means that the probe moves approximately the same depth into the sediment and therefore produces the same equilibrium volume under differing conditions, but requires sig-

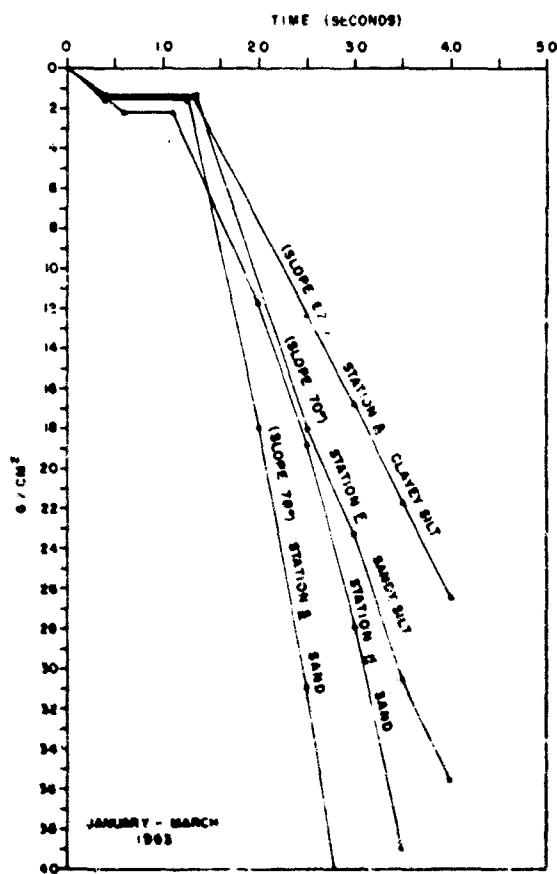


Fig. 7. Mean compression curves for the various sediment types during the January-March period. Pulsating part of the curves is not included.

Table 7. Comparative compression values for several observation periods.

	Pressure (g/cm^2)		
	Jan.-Mar.	April	July-Oct.
St. S. (sand)	1.6	3.5	6.7
St. F (sandy silt)	1.4	2.8	4.4
St. A (clayey silt)	1.5	1.4	2.6
St. H (sand)	2.2	3.9	2.9

nificantly different compression values to create the same volumetric effects.

If mean curves are prepared by averaging pressure-time points for each sediment type during each period (Figs. 6 and 7) comparisons may be made of the orientation of the mean terraces and post-terrace curves for the various sediment types. During warm-water conditions (Fig. 6), with the exception of the Station H sand, one finds a relationship between grain size and position of the terraces. As the particle size decreases there is a regular decrease in the pressure of the corresponding terrace so that higher compression values are associated with sand and the lowest pressure level with clayey silt. When a load is applied to sand it takes a greater force to initiate a general readjustment of the surface grains than that necessary for the more porous sandy and clayey silts. Consequently, over the initial segment of the curve there is a systematic increase in the rate at which the pressure rises as the proportion of sand becomes larger.

The curves for January-March do not show the pattern exhibited by those of the July-October period (Fig. 7). The terraces for sand occur at the highest pressures but the terraces for clayey silt are above those of sandy silt. Initial rates of increase in pressure follow the same order. In interpreting this apparent pattern one must recognize the difficulties in reading values for the 0-0.5 second time interval on the scale of these curves. A slower probe velocity coupled with a faster chart speed might have made this pattern more consistent with that of the July-October period. However, none of these initial slopes for the January-March period is as great as that of clayey silt during July-October. This finding may be related to the magnitude of loosely packed grains at or near the interface.

Within each observation period the length of time that each terrace is maintained shows no consistent trend (Figs. 6 and 7). However, in the January-March period the duration of terraces for all sediment types is consistently longer than that for the July-October period.

It is disturbing that the behavior of the sand at Station H is anomalous. Apparently the widespread occurrence of *Crepidula* shells along the bottom surface is a factor in modifying the normal behavior of the inorganic particles under the probe. Because of the heavy concentration of these shells, it is almost impossible to run the probe into the bottom without making contact with at least one of these shells.

A study of the mean curves (Figs. 6 and 7) indicates that there are greater rates of pressure buildup after the terraces than over the initial part of the curves before the terraces. Moreover, these curves show that beyond the terrace break there is a progressive decrease in rate at which the pressure is very similar for each sediment type regardless of season, again with the exception of the sand of Station H.

Although data are meager, some consideration must be given to transitional periods. It seems apparent that the tightest packing conditions must be associated with the periods in which the water temperatures are almost at their minimal readings. Characteristic open packing conditions were recorded on the last day of October when the bottom waters were at 12°C. In early April, as the temperature reached 6°C., the results suggested that the tight packing of winter had ended and conditions were transitory, at least at Stations S and F (Table 7). Apparently the clayey silt of Station A was still under winter conditions but the sand of Station H continued to show an anomalous behavior. Unfortunately, a mechanical failure in the penetrometer prevented additional tests after this date.

CONCLUSIONS

Compression studies of various sediments reveal that, regardless of season, each sediment type has a characteristic curve determined by the textural and compositional properties of the particular sediment. In plotting pressure against time these curves show a decreasing average slope with decreasing sand content.

It is possible that changes in the viscosity of the water could account for the differences in sediment compactness during the two periods of study. However, as the initial slopes of the compression curves are less steep in the colder January-March period than during July-October, viscosity can not be a major factor in this phenomenon.

Although water temperature was used constantly to define bottom conditions in reference to compactness variability during the observation period, there is no justification for assuming a simple cause and effect relationship. A previous investigation (McMaster, 1962) suggested that during periods of high temperatures biological, chemical, and biochemical activities may be stimulated, whereas during cold periods the rate of these activities may be retarded.

This supposition is based on the fact that the metabolic activity of cold-blooded animals and bacteria is governed by the temperature deceleration of reaction rates (the Van't Hoff-Arrhenius law) in which there is a twofold or threefold decrease in the rate of energy-yielding reactions for each decrement of 10°C. from a maximum temperature of about 40°C. (Prosser and Brown, 1961). Thus, metabolic processes become sluggish as the temperature approaches 0°C.

Several recent findings corroborate this supposition. Rhoads (1963) reports that water temperature influences the rate at which sediment is reworked by a deposit-feeding pelecypod, *Yoldia limatula*. When

temperatures are less than 8°C. no feeding was noted for this animal, but there was an increase in average rate of sediment displacement over the 8°–10°C., 15°–17°C., and 20°–21°C. temperature ranges. Studies of the polychaete, *Pectinaria gouldii*, also indicate that temperature affects the rate of sediment reworking (D. C. Gordon, 1963, personal communication). Oppenheimer (1960) finds that the warm temperature of the surface sediments exerts a great influence on the activities of living microorganisms and also that bacteria are able to produce and destroy surface-active agents, thus affecting compaction of hydrated and thixotropic sediments. Experiments on the cultivation of bacteria at the ambient water temperature of Narragansett Bay (−1.5°–23.5°C.) indicate, too, that temperatures below 12.5°C. inhibit bacterial development. In addition, the cold-water population which can form at these low temperatures shows a rate of growth only one-half as great as that at the higher temperatures (Sieburth, 1962; Sieburth and Lear, 1962). Wheatland (1954) found that the rate of sulfide formation in deposits of mud is approximately twofold greater for each 10°C. rise in temperature. Furthermore, H. L. Sanders (1964, personal communication) has observed from processing bottom samples of Buzzards Bay, Massachusetts, at monthly intervals that the infauna are much less active during the winter than the summer. Also, Sanders finds that most of the subtidal and intertidal benthic animal species cease growing during the winter months.

Finally, it is postulated that compactness variability of Narragansett Bay sediment follows a cycle which begins with relatively open packing for the grains of the surface sediment layers during those periods when the bottom waters are warmer than 8°–10°C. and biological and chemical processes are more active. As temperatures fall below 5°–3°C. these same biological and chemical activities are retarded and the particles assume a more closely packed condition. The short periods between these extremes are apparently transitional when the temperature ranges from 3°–10°C. It seems possible that the periods of transition may not be in harmony. When water temperatures are falling in response to winter weather the first transition may

cover the 8°–3°C. temperature range whereas in spring it may be confined to the 5°–10°C. range.

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LITERATURE CITED

- ABBOTT, M. B., 1960. One-dimensional consolidation of multi-layered soils. *Geotechnique*, 10:151–165.
DIXON, W. J., and F. J. MASSEY, 1957. *Introduction to Statistical Analysis*. McGraw-Hill, New York.
MCMASTER, R. L., 1962. Seasonal variability of compactness in marine sediments: a laboratory study. *Bull. Geol. Soc. Am.*, 73:643–646.
MILLER, C. E., and J. D. NIXON, 1953. The Narragansett Penetrometer: An instrument for measuring compaction of marine sediments *in situ*. *Narragansett Marine Lab. Rep. No. 53-25*.
OPPENHEIMER, C. H., 1960. Bacterial activity in sediments of shallow marine bays. *Geochim. Cosmochim. Acta*, 19:244–260.
PROSSER, C. L., and F. A. BROWN, 1961. *Comparative Animal Physiology*. W. B. Saunders Company, Philadelphia, Pa.
RHOADS, D. C., 1963. Rates of sediment reworking by *Yoidia limatula* in Buzzards Bay, Massachusetts, and Long Island Sound. *J. Sediment. Petrol.*, 33:723–727.
SIEBURTH, J. McN., 1962. Growth-temperature spectra of marine bacteria—an index of seasonal variation and activity. *Bacteriol. Proc. (Abst. 62 Ann. Meeting—Am. Soc. Microbiol.)*, p. 21.
SIEBURTH, J. McN., and D. W. LEAR, 1962. The significance of psychrotropic bacteria in boreal and temperate marine waters. *Proc. First Nat. Coastal and Shallow Water Res. Conf. of 1962*.
SUGDEN, W., 1950. The influence of water films adsorbed by mineral grains upon the compaction of natural sediments and notes on allied phenomena. *Geol. Mag.*, 87:26–40.
TRASK, P. D., 1932. *Origin and Environment of Source Sediments of Petroleum*. Gulf Publ. Co., Houston, Texas.
WHEATLAND, A. B., 1954. Factors affecting the formation and oxidation of sulphides in a polluted estuary. *J. Hyg. Cambridge*, 52:194–210.

Diagenesis of Iron Sulfide in Recent Marine Sediments

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The term hydrotroilite has been used frequently to refer to the black, fine-grained, iron sulfide which imparts a grey or black color to many Recent sediments. Several different chemical formulas have been used for this substance. Some examples are:

1. $\text{FeS} \cdot \text{H}_2\text{O}$ - Sidorenko (1907)
2. $\text{FeS}_n \text{H}_2\text{O}$ - Doelter (1926)
3. $\text{Fe}(\text{HS})_2$ - Baas-Becking (1956)
4. $\text{FeS} \cdot \text{H}_2\text{S}$ - Volkov (1959)

The first two formulas are speculative. The latter two are based on chemical analyses of impure natural materials. In none of the studies was X-ray diffraction used.

X-ray and chemical study of natural hydrotroilite is very difficult because of its fine-grained nature, generally low concentration in sediments, and extreme susceptibility to air oxidation. Natural sediments contain other forms of iron and sulfide from which hydrotroilite generally cannot be separated with complete assurance of purity for chemical analysis. The poorly diffracting character of the iron sulfide, whose pattern is easily masked by small amounts of other minerals such as quartz and clay minerals, makes essentially complete separation necessary for X-ray study. Because of these difficulties, an attempt was made to simulate natural conditions in the laboratory by synthesizing iron sulfides free of all contaminating phases. This enabled X-ray and chemical characterization.

In the laboratory study (Berner, 1964b) metallic iron, dissolved ferrous iron, and synthetic and natural goethite of varying degrees of crystallinity were used. The iron sources were reacted with buffered solutions of H_2S or Na_2S over a pH range of from 3 to 10. Aging took place at atmospheric pressure and low temperatures ($20^\circ\text{C.} - 90^\circ\text{C.}$), over periods ranging from 15 minutes to 200 days. Lowered pH and increased temperature, along with the use of metallic iron, promoted the formation of well-crystallized standards which could be used to identify poorly crystallized substances formed under conditions most closely approximating natural marine sediments.

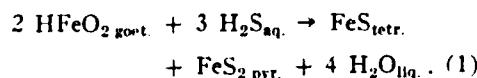
As a result of this study the following phases were synthesized and identified: tetragonal FeS (Berner, 1962), cubic Fe_3S_4 (Yamaguchi and Katsurai, 1960), X-ray amorphous FeS, hexagonal FeS (stoichiometric pyrrhotite), pyrite, marcasite, and elemental sulfur.

Tetragonal FeS and cubic Fe_3S_4 have been recently given the mineral names mackinawite and greigite by several members of the U. S. Geological Survey.

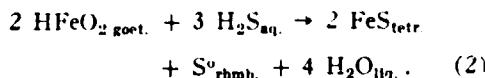
(Evans *et al.*, 1962; Skinner *et al.*, 1964) for two newly discovered natural occurrences (a high temperature ore deposit and a Tertiary saline lake sediment, respectively).

The only crystalline iron sulfide which was synthesized from all iron sources and at all pH's and temperatures was tetragonal FeS. Non-crystalline FeS (identified by chemical analysis) was the initial precipitate resulting from the reaction between dissolved sulfide and ferrous ion. The most important chemical reaction studied was that of H_2S with goethite which was adduced from X-ray identification of the products. It is:

At pH 4:



At pH 6-9:



Note the effect of pH at pH 6-9 characteristic of marine sediments; the iron sulfide first formed was amorphous to X-rays and crystallized very slowly. Barely recognizable patterns of tetragonal FeS were obtained only by aging at room temperature for several weeks or at elevated temperature for shorter periods. At pH 7-9 no pyrite was formed from FeS + S° even over the maximum aging period of 200 days at 40°C. At pH 4, on the other hand, well-crystallized pyrite and tetragonal FeS were formed in a matter of hours at room temperature.

Limonite, a general term for poorly crystallized hydrous ferric oxide, is a common product of rock weathering and can be considered as an important source of iron for many marine sediments where hydrotroilite is formed. For example, observations of tidal flat sediments of Cape Cod have shown that the iron that reacts with H_2S to form iron sulfide is supplied mainly as limonitic coatings of sand grains and other detrital particles. The H_2S is produced by sulfate-reducing bacteria which live upon decomposing organic matter in the anaerobic sediments. If weakly diffracting synthetic goethite can be taken to represent natural limonite, then the reaction of limonite with H_2S under marine conditions can be represented by reaction (2). Therefore, it is suggested that

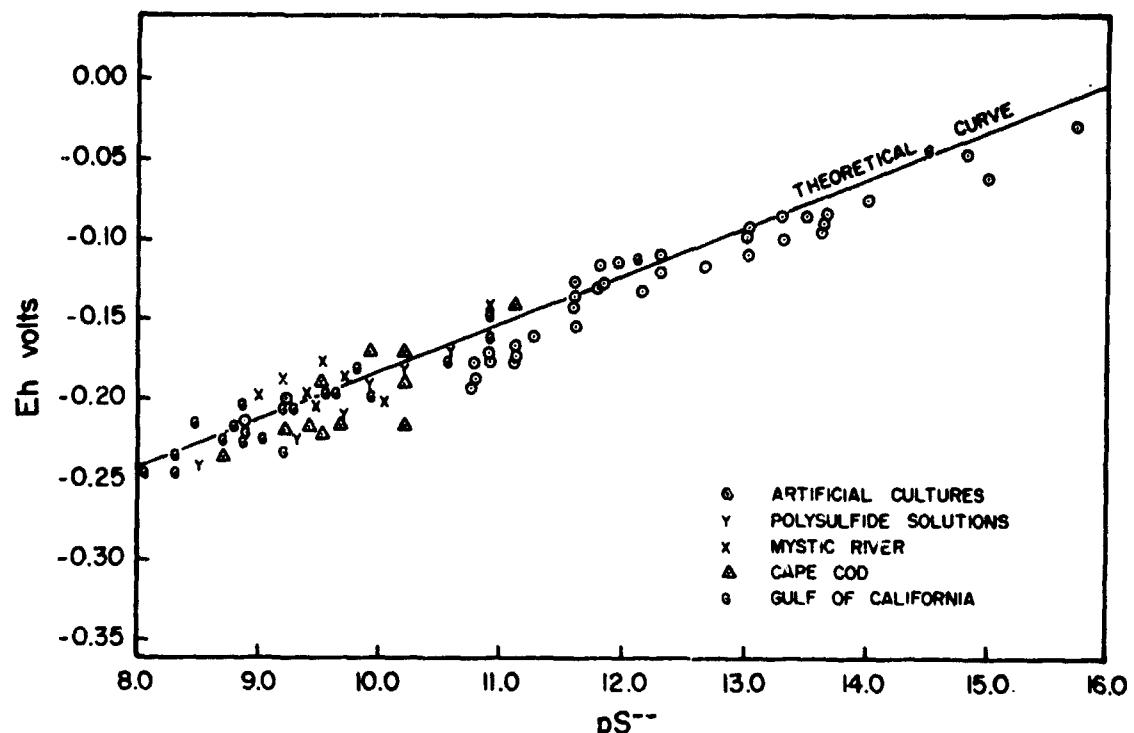


Fig. 1. Measured values of Eh and pS^{--} for natural H_2S -containing sediments and artificial sulfide systems. The line marked "theoretical curve" represents the half-cell equation for the reaction: $S^{2-}_{eq} \rightleftharpoons S^0_{reduc.} + 2e$.

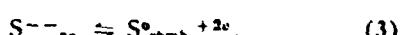
in many occurrences the iron sulfide commonly referred to as hydrotroilite consists, at least in part, of poorly crystallized tetragonal FeS. The fine-grained nature of the material accounts for the high water content due to adsorption, and the formula suggested by Doelter (1920), $FeS \cdot H_2O$, is most nearly correct.

The occurrence of tetragonal FeS in natural sediments can be seen from the data of Volkov (1961) who has described an almost pure iron sulfide concretion found at depth in the sediments of the Black Sea. Chemical analysis and an unidentified X-ray pattern published by Volkov show that the concretion consists of a mixture of tetragonal FeS and cubic Fe_3S_4 . The cubic phase was called melnikovite by Volkov because of its strong magnetism. It is possible that other occurrences of black magnetic iron sulfide commonly referred to as melnikovite, including the original type occurrence described by Doss (1912), may actually consist of cubic Fe_3S_4 or other known magnetic iron sulfides such as pyrrhotite and snythite (rhombohedral Fe_3S_4).

THE EH OF SEDIMENTS CONTAINING H_2S

Through the use of the silver-silver sulfide electrode (Berner, 1963) it has been possible to deduce the Eh controlling mechanism in many sediments containing H_2S . Figure 1 shows values of the negative logarithm of the activity of sulfide ion, pS^{--} (as measured with the silver-silver sulfide electrode), plotted against Eh for laboratory sulfate reduction experiments and sedi-

ments from the Gulf of California, Cape Cod, and Boston, Massachusetts. The points fall along a line with a slope of 29.5 mv per unit of pS^{--} , which corresponds to a thermodynamically reversible half-cell involving the transfer of two electrons. The equation of this curve is best explained by the following mechanism:



which is better expressed at pH 7-9 as:



The thermodynamic reversibility of this overall half-cell has been demonstrated by the exchange of radioactive sulfur (Voge, 1939) and by electrode determination of intermediate steps involving polysulfide ions (Peschanski and Valensi, 1949). The mechanism is also geologically reasonable in that elemental sulfur is a common, though minor, constituent of sediments containing H_2S . Very little elemental sulfur (~ 4 ppm) is needed to bring about the formation of a saturated polysulfide solution whose Eh is controlled by the sulfide-sulfur mechanism. Therefore, more sediments should be found exhibiting this Eh- pS^{--} relationship.

THE TRANSFORMATION OF FeS TO PYRITE

Because the pH of anaerobic marine sediments is quite uniform compared to pS^{--} , in such sediments

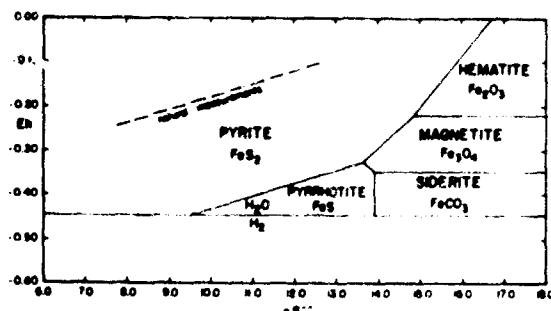


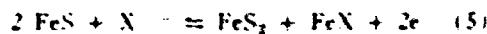
Fig. 2. Stability fields, calculated from thermodynamic data, of selected iron minerals for an "average" anaerobic marine sediment, pH = 7.5, $\text{P}_{\text{CO}_2} = 10^{-2.5}$.

the stability of iron minerals is best expressed in the form of Eh-pS⁻ diagrams calculated from thermodynamic data (Berner, 1964c). Figure 2 depicts the case of a typical anaerobic marine sediment of pH = 7.5 and $\text{P}_{\text{CO}_2} = 10^{-2.5}$. Note that the natural measurements (i.e., the sulfide-sulfur half-cell) all fall in the stability field of pyrite and not FeS. This conclusion is corroborated by the observation that in all the sediments studied either FeS was transformed to pyrite with depth (i.e., time), or no FeS and only pyrite was found.

Actual transformation of FeS to pyrite was found in tidal flat sediments of Cape Cod. Figure 3 shows typical curves of HCl-soluble iron and sulfide sulfur with depth. The sulfide data do not include dissolved H₂S which is removed prior to analysis by washing the sediment. The decrease of iron and sulfide with depth is attributed to the formation of pyrite which is insoluble in HCl and which occurs in the sediment as minute ($\sim 10\mu$) frambooidal microspheres. The constant excess of iron over sulfide with depth is ascribed to the extraction, by HCl, of iron from other ferruginous phases (such as iron silicates) which have not reacted with H₂S to form FeS. If conditions of steady state deposition are assumed, the other iron-bearing phases represent a constant source of excess Fe with depth. The parallelism of the iron and sulfide curves can, therefore, be used to delineate the type of chemical mechanism by which FeS is transformed to pyrite.

The transformation of FeS to pyrite, which is an oxidation, either involves the subtraction of iron or the addition of sulfur as follows:

Subtraction of iron:



$X^- \approx \text{CO}_3^{2-}, \text{OOH}^{1/2}$, etc.

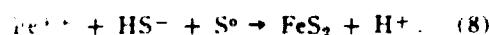
Addition of sulfur:



If the subtraction of iron, reaction (5), were the case, then another iron-bearing mineral other than pyrite would be formed with depth such as siderite, goethite,

etc. These minerals, of course, could only be formed under conditions of high pS⁻ or low concentration of H₂S. Even under such conditions the formation of siderite, goethite, etc., with depth still would not result in a parallelism of the curves for sulfide and iron because HCl would also remove iron from these compounds. This mechanism would result in a divergence of the curves for iron and sulfide with depth. Therefore, in sediments containing excess H₂S, the latter type of mechanism involving the addition of sulfur is more reasonable.

A possible generalized mechanism for the transformation of FeS to FeS₂ is:



Overall reaction:



Written in terms of H₂S instead of HS⁻, reaction (8) can easily be demonstrated at room temperature in the laboratory, but only at low pH (< 5). At higher pH values characteristic of marine sediments, reaction (8) is retarded in the laboratory and possibly in nature by the low concentration of ferrous ion in equilibrium with FeS. At a typical sedimentary value of pS⁻ of 10, the equilibrium activity of ferrous ion is less than 10⁻⁷.

The entire transformation (9) may also be limited by the availability of elemental sulfur. This explanation has been suggested by Volkov (1961) to explain the lack of complete transformation of FeS to pyrite in the sediments of the Black Sea and the finding of such phases as well-crystallized tetragonal FeS and cubic Fe₃S₄ at depth. The mechanism suggested by Volkov is:

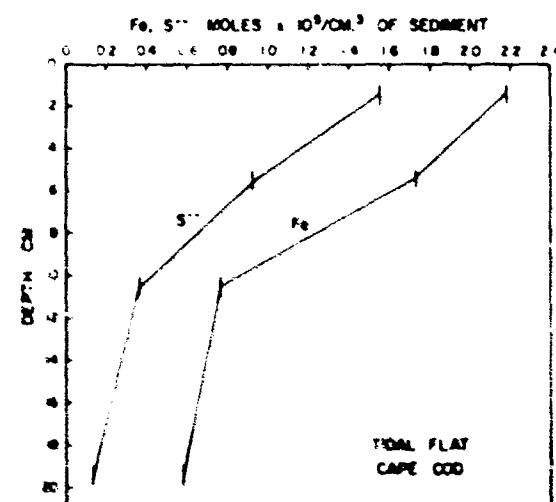
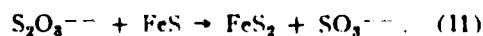
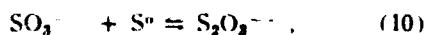
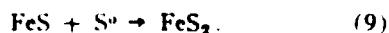


Fig. 3. Typical curve of HCl-soluble iron and sulfide as a function of depth, for tidal flat sediments of Cape Cod.



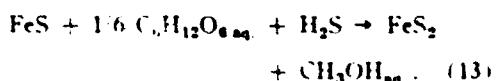
Overall reaction:



i. e., thiosulfate acts as a catalyst. This writer has not been able to verify this catalytic role of thiosulfate in the laboratory at the pH of marine sediments. Note that Volkov's mechanism results in the same overall reaction that has already been suggested.

Several sources of the necessary elemental sulfur in sediments can be mentioned. Air oxidation of H_2S or FeS at an interface between overlying oxygen-containing sea water and the reduced sediment is one such source. Tidal fluctuations and burrowing activities of organisms resulting in constant reoxidation of the sediment would promote this process on tidal flats. Aerobic or photosynthetic sulfur-oxidizing bacteria may play a role. The isotopic data of Kaplan *et al.* (1963) suggest that elemental sulfur can also be formed with depth within the reduced sediment.

Other possible mechanisms for the transformation of FeS to FeS_2 are:



The former mechanism would necessarily imply a considerably lower Eh than that found in most sediments because of the production of appreciable molecular hydrogen. Also, this reaction could not be demonstrated in the laboratory by the writer (Berner, 1964b). Pyrite formed only in runs where there was elemental sulfur present which in turn was formed by the oxidation of H_2S by air oxygen or ferric ion in goethite.

The latter type of mechanism (which is, of course, generalized) cannot be refuted and may be a better explanation than using elemental sulfur. The hydrogenation of organic matter, however, may simply produce elemental sulfur, which in turn reacts with FeS to form FeS_2 . Such a mechanism as this, if true, would probably be biological, and falls more properly into the general field of microbiology. It is offered here only as another possible mechanism.

Many sediments in which pyrite is found do not contain hydrotroilite. Good examples of this are the fine-grained diatomaceous muds of the Santa Barbara basin off Southern California (Emery and Rittenberg, 1952) and similar sediments of the western slope of the Gulf of California (Berner, 1964a). Figure 4 illustrates results of sulfur determinations for a core of typical pyrite content from the Gulf of California. Note the logarithmic scale. If the only source of sulfur for pyrite formation is sulfate in sea water buried in the sediment, the total concentration of sulfur would fall roughly along the sulfate curve shown in Figure 4.

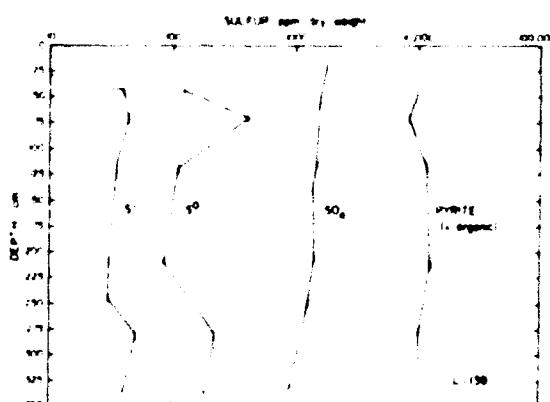


Fig. 4. Distribution of various forms of sulfur in a sediment core taken from the western slope of the Gulf of California.

The concentration of pyrite, however, is considerably greater than this, which implies that extra sulfate must have diffused into the sediment from the overlying sea water. This sulfate, along with the original sulfate, was then reduced to sulfide by bacteria and combined with iron to form pyrite. Formation of pyrite near the sediment-water interface would aid in this process because in this case the diffusion path length would be minimized. Kaplan *et al.* (1963) have shown by means of sulfur isotopes that most of the pyrite in the Santa Barbara basin sediments also must have formed near the sediment surface in contact with an infinite reservoir of sulfate ion, the overlying sea water.

The absence of black hydrotroilite in the upper 25 cm of these sediments can be explained by the formation of the pyrite near the sediment-water interface. Complete transformation of any initially formed FeS to FeS_2 at the sediment surface would prevent the development of a black FeS transition zone as found in tidal flat and estuarine sediments. This transformation could be accomplished either by a slower rate of deposition or accelerated chemical reaction in the Gulf of California sediments. Because, at present, there is no reason to suspect an unusual chemistry in these sediments and, in general, short-time rates of deposition near shore often exceed those in deeper water, it is probable that the absence of hydrotroilite in these sediments is due to a slower rate of deposition. The finding of black FeS in more rapidly deposited deltaic sediments in the eastern part of the Gulf of California would tend to substantiate this conclusion.

LITERATURE CITED

- BAAS-BECKING, L. G. M. 1956. Biological processes in the estuarine environment. VI. State of the iron in the estuarine mud iron sulfides. *Koninkl. Ned. Akad. Wetenschap. Proc. Ser. B*, 59: 181-189.
- BERNER, R. A. 1962. Tetragonal iron sulfide. *Science*, 137: 669.
- BERNER, R. A. 1963. Electrode studies of hydrogen sulfide in marine sediments. *Graham-Carrick Ann. Sci.*, 27: 563-575.

- BERNER, R. A., 1964a. Distribution and diagenesis of sulfur in some sediments from the Gulf of California. *Marine Geology*, 1:117-140.
- BERNER, R. A., 1964b. Iron sulfides formed from aqueous solution at low temperatures and atmospheric pressure. *J. Geol.*, 72:293-306.
- BERNER, R. A., 1964c. Stability fields of iron minerals in anaerobic marine sediments. *J. Geol.*, 72:826-834.
- DOELTER, C., 1926. Hydrotroilit. *Hanbuch der Mineral-Chemie*, 4:526.
- DOSS, B., 1912. Über die Natur und Zusammensetzung des in Miocanen Tonen der Gouvernements Samara auftreten Schwefeleisens. *Neuer Jahrb. Min., Geol., Paleont., Beil. Bd. Abt. A*, 33:662-713.
- EMERY, K. O., and S. C. RITTENBERG, 1952. Early diagenesis of California basin sediments in relation to the origin of oil. *Am. Assoc. Petrol. Geol. Bull.*, 36: 735-806.
- EVANS, H. T., R. A. BERNER, and C. MILTON, 1962. Valerite and mackinawite. *Geol. Soc. America, Program of 1962 Annual Meeting*, p. 47a.
- KAPLAN, I. R., K. O. EMERY, and S. C. RITTENBERG, 1963. The distribution and isotopic abundance of sulphur in recent marine sediments off southern California. *Geochim. Cosmochim. Acta*, 27:297-332.
- PESCHANSKI, D., and G. VALENSI, 1949. Contribution à l'électrochimie des solutions aquées de polysulfures. *J. Chim. Phys.*, 46:602-619.
- SIDORENKO, M., 1907. Hydrotroilit. *Mem. Soc. Nat. Nouvelle Russie, Odessa*.
- SKINNER, B. J., R. C. ERD, and F. S. GRIMALDI, 1964. Greigite, the thio-spinel of iron, a new mineral. *Am. Mineralogist*, 49:543-555.
- VOGE, H. H., 1939. Exchange reactions with radiosulfur. *J. Am. Chem. Soc.*, 61:1032-1035.
- VOLKOV, I. I., 1959. Free hydrogen sulfide and iron sulfide in mud sediments of the Black Sea. *Dokl. Akad. Nauk. S. S. S. R., Earth Sci. Sect.*, (English translation-Am. Geol. Inst.), 126:396-398.
- VOLKOV, I. I., 1961. Iron sulfides, their interdependence and transformation in the Black Sea bottom sediments. *Trudy Inst. Okeanol. Akad. Nauk. S. S. S. R.*, 50: 68-92.
- YAMAGUCHI, S., and T. KATSURAI, 1960. Zur bildung des ferromagnetischen Fe₃S₄. *Kolloid Zeit.*, 170: 147-148.

Concentrations of Minor Elements in Diatomaceous Sediments of a Stagnant Fjord

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The marine sediments of Saanich Inlet, British Columbia, were chosen for an initial survey of the effects of biological, chemical, and sedimentary processes on the concentrations of minor elements in sediments deposited in a sulfide environment. The Saanich Inlet sediments are the result of deposition in a sedimentary environment formed by an isolated part of an estuarine system, the Strait of Georgia. The isolation of the inlet permits an evaluation of the processes which affect the sediments deposited in it. Analytical techniques were chosen which would provide the best coverage of the most elements, even at the sacrifice of some precision, in order to determine the major effects of the environment and to determine which elements warrant future, more detailed investigations.

PREVIOUS INVESTIGATIONS

Previous investigations of the inlet (Herlinveaux, 1962) and its sediments (Gross *et al.*, 1963; Gucluer, 1962; Gucluer and Gross, 1964) provide some information about the inlet as a sedimentary environment and about the textural and chemical properties of the sediments accumulating in it.

Data are available on the concentrations of some minor elements in nearshore marine sediments from the eastern side of the Strait of Georgia (White and Northcote, 1962), in Cowichan River sediments (Warren and Delavault, 1960), and in volcanic rocks near Saanich Inlet (Warren and Delavault, 1961). These investigations were limited in the number of elements covered and did not include Saanich Inlet sediments.

The review by Kaplan and Rittenberg (1963) of the literature on sedimentation in marine basins illustrates the scarcity of data on the concentrations of minor elements in sediments from sulfide environments. Strøm (1948) showed the enrichment of U in sediments from stagnant Norwegian fjords. Manheim (1961) studied the sediments of the Baltic Sea, including those deposited in sulfide environments.

Krauskopf (1955) reviewed the voluminous literature on concentrations of minor elements of sedimentary rocks, showing that black shales and sediments deposited in stagnant environments are frequently enriched in Ag, As, Mo, and Ni. Krauskopf (1956) also studied the concentrations of Zn, Cu, Pb, Bi, Cd,

Ni, Co, Hg, Cr, Mo, W, and V in aerated sea water and concluded that it is undersaturated with respect to the most insoluble compounds of these metals. He suggested that biological processes and adsorption on particulate matter furnish at least a qualitative explanation for the observed abundance of these metals in sea water and their distribution in marine sedimentary rocks.

Almost no data are available on the concentrations of minor elements in diatom frustules, a major component of the Saanich Inlet sediments. The data on the concentrations of minor elements of the sedimentary accumulations of diatom frustules and radiolarian tests were summarized by Cressman (1962) who agreed with Krauskopf (1955) that such deposits are not conspicuously enriched in "rare metals". Revelle (1944) detected B and Ba in diatom oozes from the northwest Pacific Ocean off Japan.

LOCATION AND GENERAL FEATURES OF SAANICH INLET

Saanich Inlet, the only fjord on southeastern Vancouver Island, British Columbia (Fig. 1), is approximately 26 km long, with a maximum width of 7.6 km. The inlet is connected with the Strait of Georgia by Satellite Channel, but the interchange of water with Satellite Channel is restricted by a sill (Fig. 2) which comes to within 70 m of the surface. The inlet occupies a glaciated valley cut in metamorphosed volcanic and sedimentary rocks of Jurassic and Cretaceous ages (Clapp, 1917).

The inlet's small drainage basin lies in a "rain shadow" (Fig. 1), so it receives less precipitation than adjacent areas (Tully and Dodimead, 1957). The inlet receives little runoff from streams discharging into it (Herlinveaux, 1962). The surface circulation of the Strait of Georgia brings into the inlet low-salinity water derived from the discharge of the Cowichan River (6 km north of the inlet) between December and April, and from the discharge of the Fraser River (50 km northeast of the inlet) in June and July (Herlinveaux, 1962).

Because of the small amount of fresh water in the surface waters of the inlet, only a very weak estuarine and tidal circulation takes place in the waters above sill depth (Pickard, 1961; Herlinveaux, 1962). Herlinveaux suggested that dense, oxygenated waters from Haro Strait may occasionally flow into Satellite

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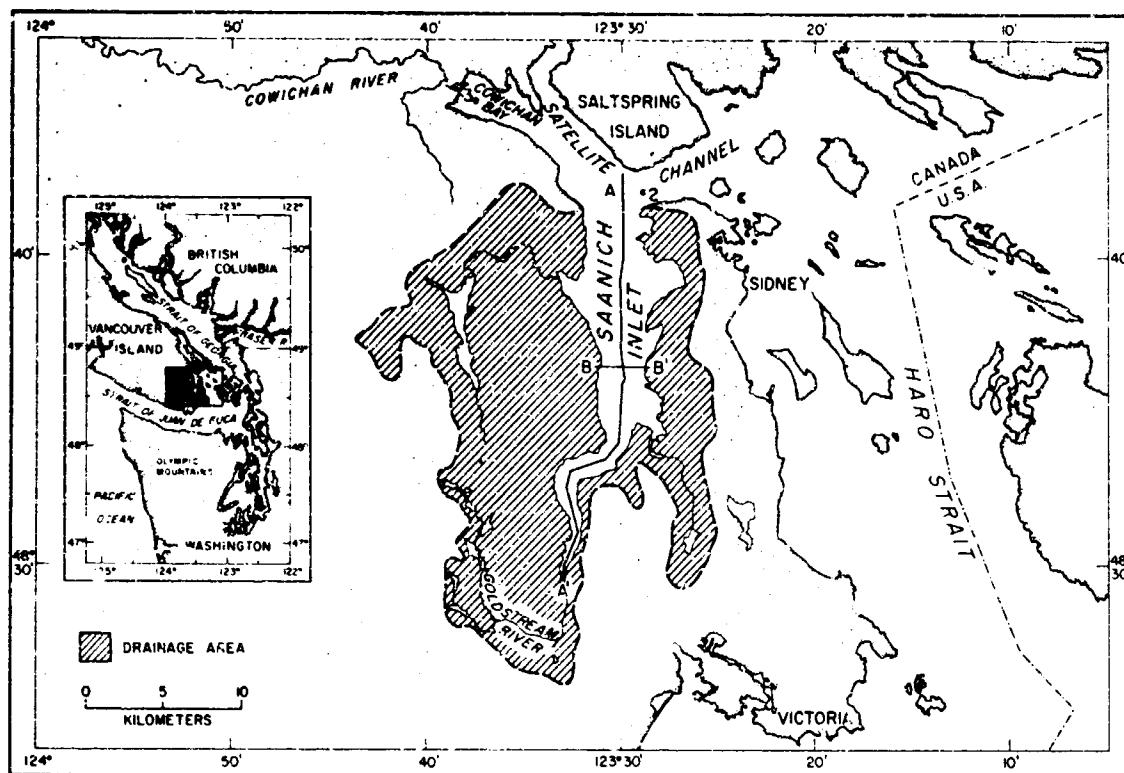


Fig. 1. Saanich Inlet and environs. Longitudinal and cross-sectional profiles are shown in Figure 2.

Channel and spill over the sill into the inlet to replace completely the deep waters of the inlet, or, at least, to bring oxygenated water into the deep part of the basin.

Although no data are available on the production of phytoplankton in the inlet, it is probably large since there are large populations of fish in the inlet and high concentrations of dissolved oxygen in the sur-

face waters during the summer. Apparently the largest phytoplankton populations are present from April through July when the surface waters are most turbid (Herlinveaux, 1962). The oxidation of the large amounts of organic matter depletes the dissolved oxygen in the partially isolated bottom waters. Hydrogen sulfide is formed by the activity of sulfate-reducing bacteria in the oxygen-deficient waters of the deepest parts of the basin (Kaplan *et al.*, 1963; Redfield *et al.*, 1963).

MARINE SEDIMENTS

In the sulfide environment of the central portion of the inlet (Fig. 3), black clayey silts are deposited containing hydrogen sulfide in the interstitial water. Core No. 4 recovered approximately 20 m of laminated sediments, consisting of alternating olive-gray and black laminae, each one between 2 and 5 mm thick. These laminae form varves indicating an average rate of deposition for the central part of the basin of 4 to 6 mm per year of wet sediment, corresponding to an annual deposition of approximately 10^5 metric tons of sediment (Gross *et al.*, 1965). The thickness and continuity of the varved sediments indicate that the sedimentary environment has not changed significantly in the past 4,000 to 5,000 years.

The sill sediments are similar in mineral composition to the central basin sediments; both are mixtures of silt and clay-sized particles (Table 1). Chemically, the sediments in the two localities are distinctly dif-

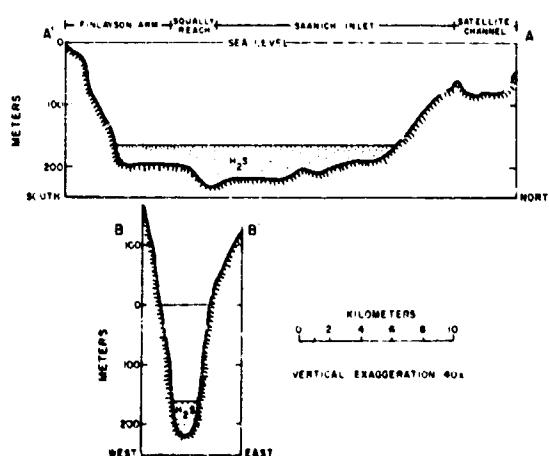


Fig. 2. Longitudinal and cross-sectional profiles of Saanich Inlet, showing a generalized distribution of H₂S in November, 1961 (F. A. Richards, personal communication).

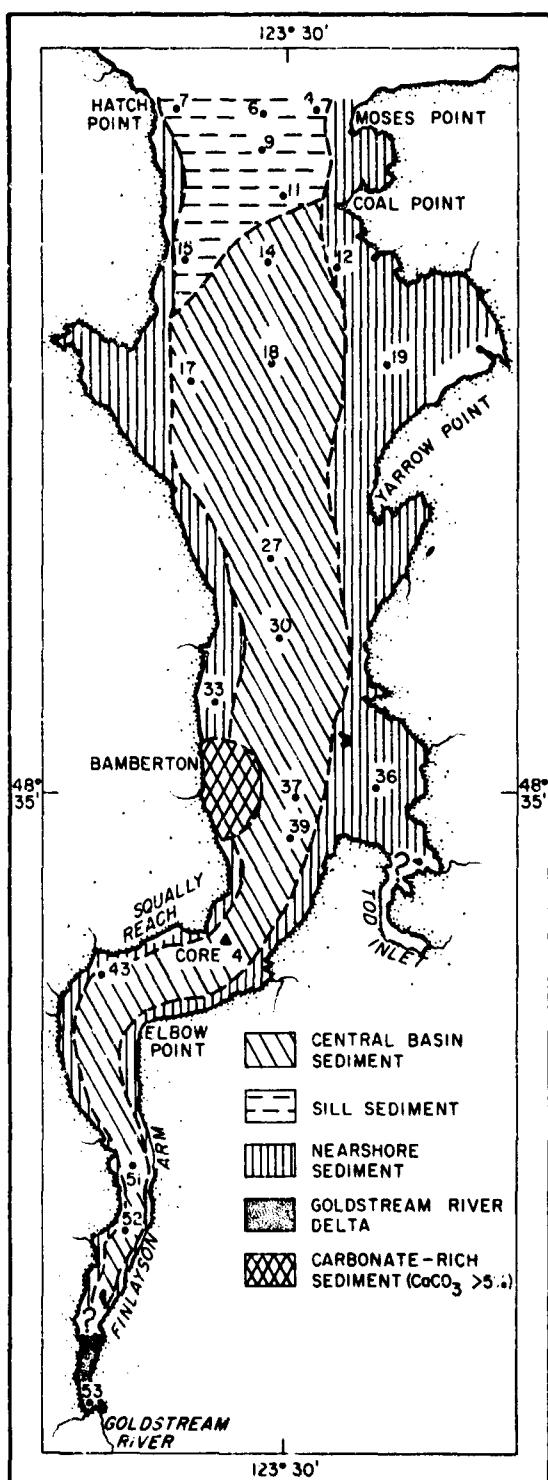


Fig. 3. Distribution of the surface samples and the major sediment types in Saanich Inlet (After Gucluer and Gross, 1964).

ferent (Fig. 4). The fine sands of the nearshore areas are different, texturally and chemically, from the clayey silts of the inlet.

The phosphorus content is essentially the same in all the sediments; organic carbon, nitrogen, and opal are most abundant in the clayey silts of the central basin area and least abundant in the nearshore sands. Carbonaceous compounds and biogenous components such as opal constitute up to 45 percent of the clayey silts of the central basin area but make up less than 5 percent of the nearshore sands.

The major sources of the sediment deposited in the inlet appear to be the sediment-laden, low-salinity waters derived from the Fraser and Cowichan Rivers, and the phytoplankton growing in the surface waters of the inlet. Less important sources of sediment include discharge of local streams, erosion of the shoreline, and debris from the limestone quarry and cement plant at Bamberton (Fig. 3). There are no other industrial operations in the inlet or its drainage basin which might contaminate the waters or the sediments.

Sediments apparently accumulate in the deeper parts of the basin I, the continuous particle-by-particle deposition of silt and clay-sized particles mixed with the frustules and resting spores of diatoms. Because of their small size (approximately 6μ or less), lithogenous particles may require up to several years to settle through 200 m of water to reach the bottom. Consequently, the particles are mixed and distributed throughout the basin, so that no major variations have been detected in mineral composition of sediments in various parts of the inlet or in individual laminae from cores.

Superimposed on this continual deposition of lithogenous and biogenous particles are seasonal pulses of the frustules of marine planktonic diatoms which form the light-colored laminae; some of these laminae apparently consist almost entirely of diatom frustules. The light-colored laminae contain the biogenous opal probably formed during the time of peak phytoplankton production in the inlet, April through July.

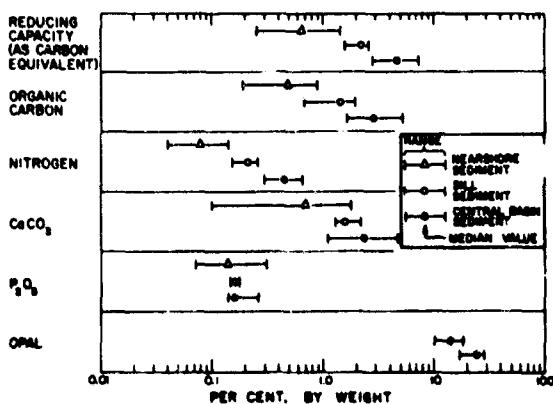


Fig. 4. Variation of certain chemical properties among the major sediment types (After Gucluer and Gross, 1964).

Table 1. Textural, physical, and chemical properties of the sediment.

Sediment type	Description	Median diameter (mm)	Average textural composition (%)				Density (g/cc)	H ₂ S odor	Average pH (range)
			Clay-sized	Silt	Sand	Gravel			
Central basin sediment	Clayey silt, olive-black to black, very poorly sorted, diatomaceous	0.006	43.8	44.4	11.2 (wood chips and diatom frustules)	0.6 (wood fragments)	2.40	Present in all samples	7.0 (6.6-7.6)
Sill sediment	Clayey silt, light olive-gray, very poorly sorted	0.025	23.3	66.2	10.5 (some diatom frustules)		2.67	None	7.1 (6.9-7.3)
Nearshore sediments	Fine sand, yellow-green to olive-green, poorly sorted	0.27	2.9	7.7	79.3	10.1	2.82	None	7.1 (6.7-7.3)

Settling velocities of diatoms are controlled by their physiological state (Harvey, 1957); diatoms below the euphotic zone may settle with velocities of 5 to 40 m/day (Margalef, 1961). Thus the bulk of the diatom frustules added to the sediments may be deposited within a few days or a few months after they sink below the euphotic zone.

The opal and nitrogen contents and the reducing capacity are different in the light- and dark-colored laminae of the central basin sediment (Fig. 5). Other properties, including mineral composition, show little or no variation between laminae, or with depth in the core. The differences between laminae may be explained by the greater abundance of diatom frustules in the light-colored laminae.

ANALYTICAL TECHNIQUES

Concentrations of minor elements, except Zn, were determined by E. Bingham, California Institute of Technology, using optical-emission spectroscopy (Engel and Engel, 1958). The values reported (Tables 2 and 3) are the averaged results of two to five separate analyses of each sample. Engel and Engel (1958) estimated that the results obtained using these techniques are reproducible to within 25 percent of the value reported. The experimentally determined values for rock samples G-1 and W-1 are within 30 percent of the preferred values (Fleischer and Stevens, 1962) for all elements except for Ti which is approximately 40 percent too low. For Sc, Y, Zr, Cu, and Pb the values agreed to within 10 percent. No attempt was made to correct the Ti values because the apparent discrepancy does not affect the results of comparisons among the various sediment types.

Zinc concentrations in the surface sediments were determined by an X-ray fluorescence method using standards prepared by mixing Saanich Inlet sediments with known amounts of Zn.

The estimates of opal abundance were obtained by heating the sediment to 900° C., forming cristobalite which was detected by X-ray diffraction techniques (Goldberg, 1958). The results were reproducible to within 10 percent of the amount reported but they may be systematically low.

DISCUSSION

The median concentrations of minor elements (Fig. 6) in the sill and nearshore sediments (both deposited in oxygenated environments) are very similar, except for B and Zn which are slightly higher in the sill sediments. For all the other elements (Sc, Y, Ti, Zr, Cr, Mn, Fe, Co, Ni, Cu, Ga, and Pb) the median concentrations of the sill sediments are nearly equal to or less than the concentrations of the nearshore sediments. The ranges of concentrations of minor elements are greater in the nearshore sands than in the sill sediments, most probably a reflection of the local origin of the nearshore sediments.

The local origin and resulting heterogeneity of the nearshore sediments greatly restricts their usefulness



Table 2. Concentrations of minor elements in surface sediments. Values in percent by weight (Analyst: E. Birmingham).

Specimens from here were found: Ag., Aa., Au., Bi., Cd., Sb., W.
None different.

Table 3. Concentrations of minor elements in individual laminae from various depths in core No. 4. Values in percent by weight. Lead was detected in dark-colored laminae at 1,180 cm (0.016), 1,400 cm (0.034), and 1,500 cm (0.003) (Analyst: E. Bingham).

Elements in laminae	400 cm	500 cm	600 cm	700 cm	800 cm	900 cm	1,050 cm	1,100 cm	1,180 cm	1,300 cm	1,400 cm	1,500 cm	1,600 cm	1,700 cm	1,780 cm	
Sc	L 0.001	D 0.0013	0.0014	0.0016	0.0014	0.0008	0.0012	0.001	0.0012	0.0012	0.0012	0.0012	0.0014	0.001	0.0015	
Y	L 0.002	D 0.0021	0.0022	0.002	0.0022	0.0023	<0.002	<0.002	<0.002	0.0022	0.0022	0.0023	0.0021	<0.002	0.0016	0.0014
Ti	L 0.18	D 0.21	0.17	0.27	0.27	0.15	0.25	0.12	0.23	0.25	0.23	0.25	0.19	0.19	0.16	0.3
Zr	L 0.0058	D 0.0067	0.0065	0.0062	0.0068	0.0077	0.0053	0.0068	0.0043	0.0066	0.0073	0.0066	0.0068	0.0058	0.0079	
V	L 0.0063	D 0.0067	0.0059	0.0058	0.0068	0.0058	0.0058	0.0058	0.0052	0.0046	0.0046	0.0069	0.0065	0.0059	0.0083	0.0076
Cr	L 0.0055	D 0.0054	0.0056	0.004	0.0043	0.0044	0.0064	0.0043	0.0034	0.0057	0.0049	0.0053	0.0048	0.006	0.006	
Mo	L 0.0064	D 0.0054	0.006	0.0066	0.0079	0.0062	0.0052	0.0057	0.0062	0.0085	0.0063	0.0079	0.0058	0.0056	0.0051	
Mn	L 0.0031	D 0.0036	0.0042	0.004	0.0031	0.0032	0.0027	0.0034	0.0034	0.004	0.0038	0.004	0.0045	0.0056	0.0031	
Fe	L 0.0037	D 0.0034	0.0039	0.0036	0.0048	0.0036	0.0031	0.0033	0.0024	0.0056	0.0056	0.0063	0.0053	0.0033	0.0037	0.0028
Co	L 0.026	D 0.027	0.019	0.027	0.027	0.026	0.032	0.019	0.03	0.036	0.045	0.027	0.03	0.041		
Ni	L 0.017	D 0.025	0.041	0.028	0.039	0.036	0.034	0.037	0.033	0.04	0.067	0.05	0.049	0.043		
Cu	L 1.5	D 1.7	1.5	1.2	1.6	1.5	1.5	1.6	1.0	1.9	2.0	2.3	1.3	1.8	2.0	
B	L 0.0022	D 0.0024	0.0022	0.0017	0.0025	0.0021	0.0018	0.0021	0.0015	0.0024	0.0024	0.0025	0.0018	0.0023	0.0025	
Ge	L 0.001	D 0.0008	0.0006	0.0008	0.0007	0.0007	0.0005	0.0005	0.0003	0.0006	0.0006	0.0006	0.0004	0.0005	0.0006	

L = Light-colored laminae.

D = Dark-colored laminae.

T = Trace.

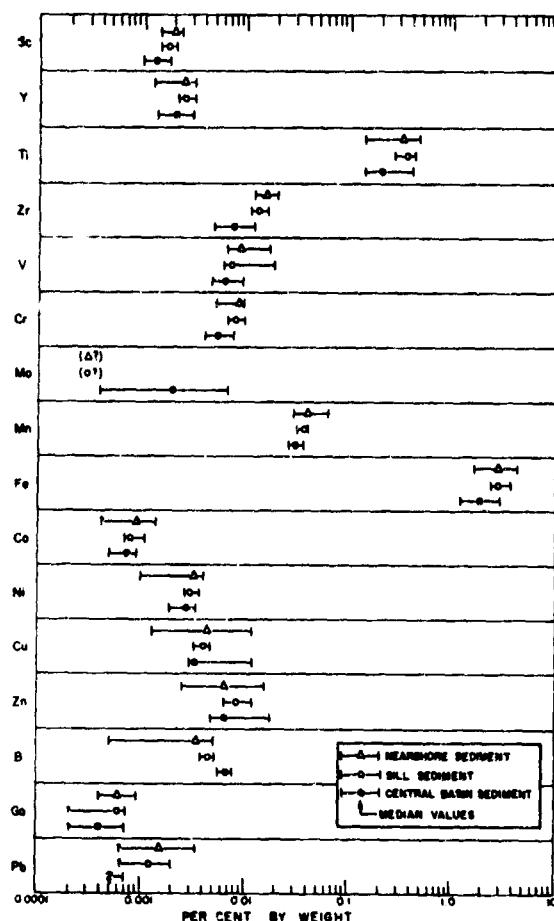


Fig. 6. Ranges and median values of the concentrations of minor elements in the surface sediments.

in studying the effects of the sedimentary environment. The data do indicate, however, the absence of major local sources for any of the elements studied.

Except for B and Mo, which will be discussed later, all the elements studied (Fig. 6, Table 2) are least abundant in the central basin sediments where the lithogenous constituents are most diluted by the addition of biogenous constituents. From this we can deduce that Sc, Y, Ti, Zr, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, Ga, and Pb are primarily associated with the lithogenous rather than the biogenous constituents. This agrees with the data for the Gulf of Paria (Hirst, 1962), where Ga, Cr, V, Cu, Pb, Ti, and, to a lesser extent, Co, Ni, and B were found to be associated with clay minerals.

No data are available on the concentration of minor elements in the biogenous constituents of the Saanich Inlet sediments, but it is possible to determine which elements are least abundant in the biogenous matter, relative to their concentrations in the lithogenous matter, by comparing concentrations of each element in sediments from the sill with those from the central basin areas.

Relative to the median value for each element in the sill sediments, the median values in the central basin sediments are reduced by the following amounts: Sc - 28%, Y - 20%, Ti - 43%, Zr - 53%, V - 5%, Cr - 35%, Mn - 17%, Fe - 38%, Co - 13%, Ni - 7%, Cu - 8%, Zn - 21%, and Ga - 17%. The data for Pb cannot be used because the concentrations in most central basin sediments are below the detection limits.

The differences in concentration are greatest for Zr and Ti, indicating that these elements are least abundant in the biogenous constituents, compared with their abundance in the lithogenous constituents. Similarly, the small differences for V, Ni, Cu, and Co may indicate that the concentrations of these elements in the biogenous and lithogenous constituents are not radically different. This is consistent with the concentrations of these elements in ashed marine zooplankton (Nicholls *et al.*, 1959); no data are available for phytoplankton. The apparent differences for Sc, Y, Cr, Mn, Fe, Zn, and Ga may thus indicate that their concentrations in the biogenous matter, compared with the lithogenous matter, fall between these two extremes.

There is no compelling evidence to indicate any enrichment of Sc, Y, Ti, Zr, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, Ga, and Pb in the sediments deposited in the sulfide environment of the inlet. If local precipitation

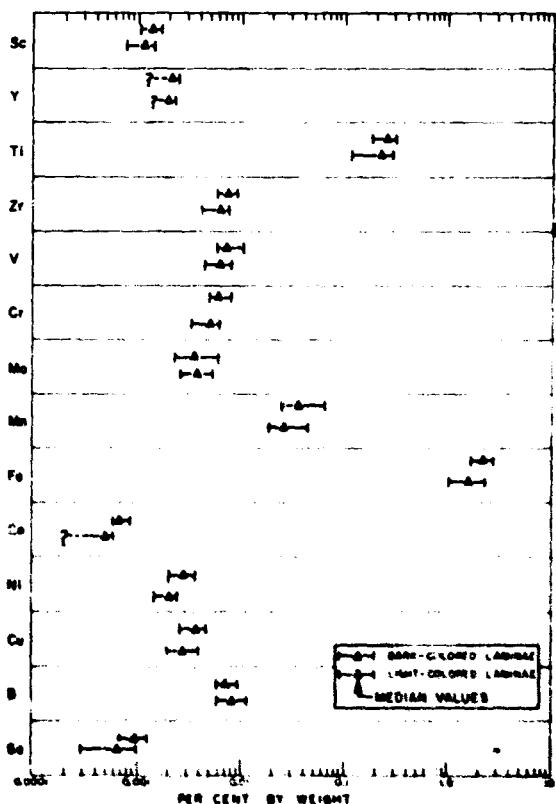


Fig. 7. Ranges and median values of concentrations of minor elements of individual laminae from core No. 4.

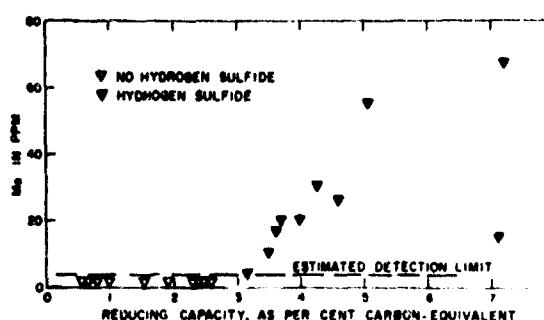


Fig. 8. Variation of Mo concentrations of surface sediments as a function of reducing capacity, expressed as the amount of carbon necessary to produce the same reducing capacity.

of the sulfides of Zn, Cd, Bi, or Pb occurs, as Krauskopf (1956) suggested, the effects were not detected in the Saanich Inlet sediments.

Except for B and Mo, the median concentrations of the minor elements in the light-colored laminae are distinctly less than in the dark-colored laminae (Fig. 7, Table 3). This general distribution is apparently caused by the greater abundance of diatom frustules in the light-colored laminae. The differences in the median concentrations indicate that the light-colored laminae should contain 20 to 25 percent more opal than the dark-colored laminae. This agrees reasonably well with the estimates (Fig. 5) of opal abundance in light-colored laminae (average 28 percent opal) and dark-colored laminae (average 21 percent opal).

There is no systematic variation in the concentrations of minor elements with depth (Tables 2 and 3), indicating that the concentrations in the surface sediments in the central basin area are not controlled by contamination of the environment. This is consistent with other data (Gucluer and Gross, 1964) which indicate that the sedimentary environment in the inlet has persisted essentially unchanged for the past 4,000 to 5,000 years.

MOLYBDENUM

Marine sediments from oxygenated environments in the inlet and in adjacent areas contain so little Mo that it was not detected; the detection limit for Mo is estimated to be approximately 0.0003 percent. Warren and Delavault (1961) report Mo concentrations of less than 0.0005 percent in volcanic rocks near the inlet. There is no evidence to suggest that large amounts of Mo are contributed to the sediments by lithogenous constituents. In the central basin sediment, however, Mo is present in concentrations of up to 0.0067 percent, approximately twenty times the Mo content of normal oceanic sediments (Goldschmidt, 1954; Kuroda and Saito, 1954; Yamamoto, 1961; Sugawara et al., 1961).

The concentration of Mo in the surface sediments from this sulfide environment is clearly related to their reducing capacity (Fig. 8), but shows no corre-

lation with the concentrations in the sediments of organic carbon, nitrogen, opal, total sulfur, or iron. Also, there is no difference in the ranges or median values of Mo concentrations in individual laminae in core No. 4 (Fig. 7). Thus the enrichment of Mo in the Saanich Inlet sediments is predominantly the result of a process related to the reducing environment in which the surface sediments are deposited. Molybdenum is not preferentially associated with either the biogenous or lithogenous constituents.

A possible small contribution of Mo to the sediments by marine organisms cannot be eliminated. Nicholls *et al.* (1959) reported Mo concentrations up to 0.0036 percent in ashed marine zooplankton. Molybdenum is known to be a component of certain enzyme systems in the nitrogen cycle (Weissner, 1962), and C. H. Oppenheimer (personal communication) finds Mo enriched in cultures of sulfate-reducing bacteria.

Korolev (1957) showed that Mo was concentrated in the sulfide fraction in certain coal deposits and that its accumulation depended on the "intensity" of the recycling process. Korolev (1958) showed, experimentally, that Mo was co-precipitated by iron sulfides. This was confirmed by Sugawara *et al.* (1961), who found that Mo was removed from sea water by precipitation of ferrous sulfide and was re-dissolved when the system was oxygenated.

Regardless of the process by which Mo is incorporated into the sediments, whether by sulfide precipitation or by biological processes, the bulk of the Mo must come from the sea water. The amount of Mo deposited with the sediment each year amounts to less than 5 percent of the Mo contained in the sea water (Goldberg, 1963) below 100 m in the inlet. Thus, even a relatively inefficient process of extracting Mo from a large volume of sea water would account for the annual addition of Mo to the sediments. On the other hand, one may also account for the Mo in the sediments by assuming that all the Mo is removed from a layer of sea water within 5 m of the water-sediment interface. If there were some exchange of the water near the interface, the thickness of the layer involved could be less than 5 m.

Removal of the Mo from the sea water near the water-sediment interface seems the more probable of the two alternatives. Korolev (1958) found that soluble thiomolybdates form at pH 7.2 or more and concluded that the pH of "normal" sea water (pH 8.1) does not favor the removal of Mo. Korolev showed that at pH 7.2 or less, Mo formed a colloidal sulfide sol or was co-precipitated with iron sulfides.

No data are available on the chemical properties of the water near the water-sediment interface in Saanich Inlet, but Emery and Rittenberg (1952) found that in certain California basins the pH of the "bottom waters" near the water-sediment interface was lower than the sea water or the uppermost layer of sediment. If the water-sediment interface in Saanich Inlet were actually a transitional zone where the pH of the water approached the values observed in the

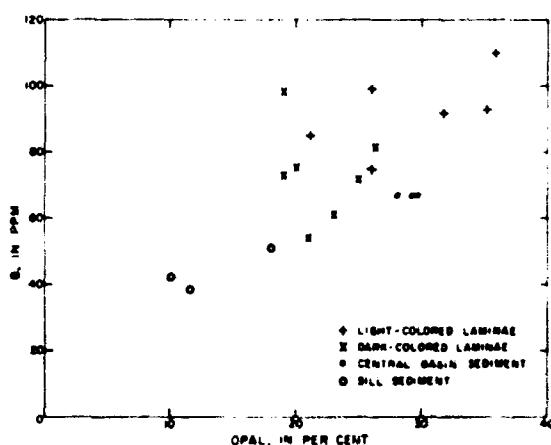


Fig. 9. Variation of B concentrations as a function of the opal content of surface sediments and individual laminae from core No. 4.

interstitial waters of the central basin sediments (average pH 7.0), it would favor the removal of Mo from the water.

An ill-defined water-sediment interface (or transitional zone) may exist in Saanich Inlet, where there are no strong bottom currents and no filter-feeding organisms, which remove suspended sediment from the water, to cause a sharply defined interface. The chemical properties of the water associated with the interface would be affected by the high bacterial activity commonly observed near the interface, and by the flow of interstitial water expelled from the sediments by compaction taking place below the interface. On the basis of Korolev's data, such a system seems especially favorable for the formation of Mo sulfide phases. In addition to the possible co-precipitation of Mo by iron sulfides, the large surface area of the suspended sediments would also afford a mechanism for the removal from the water of colloidal sulfide phases which would then be readily incorporated in the sediments.

BORON

The boron concentrations in the sediments are directly related to the abundance of opal in the clayey silts of the central basin area (Fig. 6); within these sediments, B is most abundant in the opal-rich, light-colored laminae (Fig. 7). The relationship of B to diatom frustules is further substantiated by a comparison of the B concentrations with the opal contents of the sediments and the individual laminae (Fig. 9).

Boron is required for the growth and metabolism of higher plants (Skok, 1958) and for the growth of certain diatoms (Wessner, 1962); the function of B and its location in plants has not been established. Skok and Wessner suggest that it is involved in the formation of cell walls and may be localised in the cell walls, a hypothesis which is consistent with the

apparent concentrations in the Saanich Inlet sediments.

The correlation between the B concentrations and the abundance of clay minerals in the sediments may be evaluated (Fig. 10) by comparing the B content of the total sediment and the abundance of clay-sized ($< 2 \mu$) particles (Gucluer, 1962). This comparison is far from satisfactory because the clay-sized fractions of the sediments include various silicate minerals (predominantly quartz and feldspar) in addition to clay minerals. Also it is impossible to eliminate the effects of the varying opal contents in these sediments. No tourmaline was detected by X-ray diffraction analysis of the sediments but the extreme variation in the B concentrations of the nearshore sands suggests the presence of some lithogenous component containing B.

The B in the sediments not contained in the lithogenous components must be derived from the sea water in the inlet. It is difficult to evaluate this contribution; but even assuming that all the B now in the sediments is derived from sea water, it can be shown that the amount removed each year is insignificant compared to the amount of B contained in the sea water (Goldberg, 1963) in the inlet.

SUMMARY

Three of the factors determining the concentration of a minor element in the sediments of Saanich Inlet are: (1) its concentration in the lithogenous constituents, (2) its concentration in the biogenous constituents, and (3) its concentration in any sulfide phase formed in the sulfide-bearing waters of the inlet. In the Saanich sediments Sc, Y, Ti, Zr, V, Cr, Mn, Fe, Co, Ni, Cu, Zn, Ga, and Pb are primarily associated with the lithogenous constituents. For the most part, these elements are not abundant in the biogenous constituents, so that addition of biogenous matter to the sediments reduces their concentrations.

Of the minor elements studied, only Mo is added in sufficient quantities to change the concentrations in the sediments. The mechanism by which Mo is removed from sea water and incorporated in the sediments is not known, but may involve a co-precipitation by iron sulfides removing Mo from sea water near the water-sediment interface.

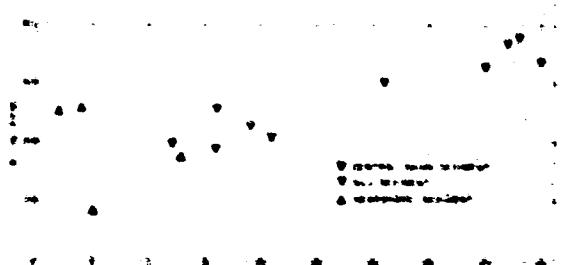


Fig. 10. Variation of B concentrations as a function of the abundance of clay-sized particles in the surface sediments.

Apparently the frustules of planktonic marine diatoms incorporated in the sediments are a major source of B. Clay minerals appear to be less important.

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LITERATURE CITED

- CLAPP, C. H., 1917. Sooke and Duncan map-areas, Vancouver Island. *Can. Dept. Mines Tech. Surv., Geol. Surv. Can., Mem. 36.*
- CRESSMAN, E. R., 1962. Nondetrital siliceous sediments. *U. S. Geol. Surv. Profess. Papers 440-T.*
- EMERY, K. O., and S. C. RITTENBERG, 1952. Early diagenesis of California basin sediments in relation to origin of oil. *Bull., Am. Assoc. Petro. Geologists, 36:* 735-806.
- ENGEL, A. E. J., and C. G. ENGEL, 1958. Progressive metamorphism and granitization of the major paragneiss, northwest Adirondack Mountains, New York. Part 1: Total Rock. *Bull. Geol. Soc. Am., 69:* 1369-1414.
- FLEISCHER, M., and R. E. STEVENS, 1962. Summary of new data on rock samples G-1 and W-1. *Geochim. Cosmochim. Acta, 26:* 525-544.
- GOLDBERG, E. D., 1958. The determination of opal in marine sediments. *J. Marine Res., 17:* 178-182.
- GOLDBERG, E. D., 1963. The oceans as a chemical system. In *The Sea*, edited by M. N. Hill; vol. 2, pp. 3-25. Interscience, New York.
- GOLDSCHMIDT, V. M., 1954. *Geochemistry*. Oxford University Press, Oxford, England.
- GROSS, M. G., S. M. GUCLUER, J. S. CREAGER, and W. A. DAWSON, 1963. Varved marine sediments in a stagnant fjord. *Science, 141:* 918-919.
- GUCLUER, S. M., 1962. *Recent sediment in Saanich Inlet, British Columbia*. (Unpublished M.S. thesis) Univ. of Washington, Seattle, Washington.
- GUCLUER, S. M., and M. G. GROSS, 1964. Recent marine sediments in Saanich Inlet, a stagnant marine basin. *Limnol. Oceanogr., 9:* 359-376.
- HARVEY, H. W., 1957. *The chemistry and fertility of sea waters*. Cambridge University Press, Cambridge, England.
- HERLIVEAUX, R. H., 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. *J. Fisheries Res. Board Can., 19:* 1-37.
- HIRST, D. M., 1962. The geochemistry of modern sediments from the Gulf of Paria—II. The location and distribution of trace elements. *Geochim. Cosmochim. Acta, 26:* 1147-1167.
- KAPLAN, I. R., K. O. EMERY, and S. C. RITTENBERG, 1963. The distribution and isotopic abundance of sulphur in recent marine sediments off southern California. *Geochim. Cosmochim. Acta, 27:* 297-331.
- KAPLAN, I. R., and S. C. RITTENBERG, 1963. Basin sedimentation and diagenesis. In *The Sea*, edited by M. N. Hill; vol. 3, pp. 583-614. Interscience, New York.
- KOROLEV, D. F., 1957. Some peculiarities of molybdenum distribution in rocks of the Bylymsk coal deposits. *Geochemistry (U.S.S.R.) (English Transl.), 1957:* 493-499.
- KOROLEV, D. F., 1958. The role of iron sulfides in the accumulation of molybdenum in sedimentary rocks of the reduced zone. *Geochemistry (U.S.S.R.) (English Transl.), 1958:* 452-463.
- KRAUSKOPF, K. B., 1955. Sedimentary deposits of rare metals. *Econ. Geol., 50th Ann. Vol.*; pp. 411-463. Society of Economic Geologists, Lancaster, Pennsylvania.
- KRAUSKOPF, K. B., 1956. Factors controlling the concentrations of thirteen rare metals in sea-water. *Geochim. Cosmochim. Acta, 9:* 1-32d.
- KUNODA, P. K., and E. B. SANDELL, 1954. Geochemistry of molybdenum. *Geochim. Cosmochim. Acta, 6:* 35-63.
- MANHEIM, F. T., 1961. A geochemical profile in the Baltic Sea. *Geochim. Cosmochim. Acta, 25:* 52-70.
- MARGALEF, R., 1961. Velocidad de sedimentación de organismos pasivos de Fitoplankton. *Invest. Pesquera, 18:* 3-8.
- NICHOLLS, G. D., H. CURL, Jr., and V. T. BOWEN, 1959. Spectrographic analyses of marine plankton. *Limnol. Oceanogr., 4:* 472-478.
- PICKARD, G. L., 1961. Oceanographic features of inlets in the British Columbia mainland coast. *J. Fisheries Res. Board Can., 18:* 908-999.
- REDFIELD, A. C., B. H. KETCHUM, and F. A. RICHARDS, 1963. The influence of organisms on the composition of sea-water. In *The Sea*, edited by M. N. Hill; vol. 2, pp. 26-77. Interscience, New York.
- REVELLE, R. R., 1944. Marine bottom samples collected in the Pacific Ocean by the Carnegie on its seventh cruise. *Carnegie Inst. Publ. 556*, Washington, D. C.
- SKOK, J., 1958. The role of boron in the plant cell. In *Trace Elements*, edited by C. A. Lamb, O. G. Bently, and J. M. Beattie; pp. 227-243. Academic Press, New York.
- STRÖM, K. M., 1948. A concentration of uranium in black muds. *Nature, 162:* 922.
- SUGAWARA, K., S. OKOBE, and M. TANAKA, 1961. Geochemistry of molybdenum in natural waters. II. *J. Earth Sci., Nagoya Univ., 3:* 114-128.
- TULLY, J. P., and A. J. DODIMEAD, 1957. Properties of the water in the Strait of Georgia, British Columbia, and influencing factors. *J. Fisheries Res. Board Can., 14:* 241-319.
- WARREN, H. V., and R. E. DELAVault, 1960. Trace element variations in related rocks. *Intern. Geol. Congr., 21st Session, Novosibirsk, 1960, Part II:* 57-64.
- WARREN, H. V., and R. E. DELAVault, 1961. Aqua regia extractable lead and molybdenum in eruptive rocks. *Trans. Roy. Soc. Can., Ser. 3, 55:* 67-73.
- WEISSNER, W., 1962. Inorganic macronutrients. In *Physiology and Biochemistry of Algae*, edited by R. A. Lewin; pp. 267-288. Academic Press, New York.
- WHITE, W. H., and K. E. NORTHCOTE, 1962. Distribution of metals in a modern marine environment. *Econ. Geol., 57:* 405-409.
- YAMAMOTO, Y., 1961. Chemical studies on the Ocean - 47. Molybdenum content of the shallow-water deposits (2). *J. Oceanogr. Soc. Japan, 17:* 15-20.

Sedimentary Patterns of Microfauna in a Coastal Plain Estuary

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Terrigenous sediments are alternately transported, mixed, and redistributed in the complex environment of an estuary. Inasmuch as fluctuating currents and environmental factors influence the distribution of sediments and of benthic microfaunal elements, a study of microfaunal distributions may strengthen our understanding of estuarine sedimentation. This study is an attempt to show the relation of the microfauna to their environment of deposition and to certain processes of sedimentation. Systematics and detailed aspects of the ecology will be reported elsewhere.

This study is based on 225 quantitative core samples of surface sediment which were collected from 148 stations in the estuary and marshes of the Rappahannock Estuary in northeastern Virginia (Fig. 1). From these samples of relatively undisturbed sediment, 20 sq cm in area and 1 cm thick, specimens of Foraminifera, Ostracoda, and Thecamoebina larger than 0.062 mm were concentrated. Standard methods of preparation and analysis were used (Phleger, 1960); living specimens were identified by use of rose Bengal stain.

The Rappahannock Estuary, an elongate tributary of Chesapeake Bay, is a drowned river valley cut in coastal plain sediments. A narrow channel, 20 to 25 feet deep, meanders seaward down the center of the estuary and, in lower reaches, deepens into an elongate basin, 60 to 70 feet deep with a shallow 30-foot sill at the mouth. Water in the estuary and in the basin is freely exchanged with water of the Chesapeake Bay. The mean tidal range increases upstream from about 1.1 feet at the mouth to 2.6 feet near the head. Tidal currents, the primary cause of turbulence, also increase toward the head; maximum velocities reach 1.5 knots in the lower estuary and 2.1 knots 35 miles above the mouth. The Rappahannock River supplies most of the inflow, but about 20 percent is contributed by tributary creeks. Salinity ranges from almost zero at the head to 9 to 21‰ at the mouth; horizontal gradients are most pronounced in the upper estuary. The seaward increase of salinity in the estuary is part of a progressive change extending to the mouth of the Chesapeake Bay system. Extensive marshes fringe the upper estuary and tributary creeks, whereas in the lower estuary marshes are restricted largely to low-lying recesses in the shoreline between bordering cliffs.

Sediments in the channel range from silty clay in the upper estuary to clayey silt on the basin floor. Marginal shoals in the upper estuary are chiefly silty clay, whereas shoals in the lower estuary are chiefly sand. Nelson (1959, 1961) has shown that suspended river-borne sediment is flushed through the upper estuary and appears to deposit in the lower estuary or farther seaward; bed load tends to accumulate in the middle estuary.

BIOFACIES

Foraminiferal standing crops in the estuary are slightly smaller than those in other marginal marine environments (Table 1). Living populations exceed 20,000 per sq m in several scattered marshes, in two tributary creeks, and on shoals of the middle estuary. Although nearly 30 species of Foraminifera live in the Rappahannock Estuary and marshes, the populations are dominated by four species. The distribution of five specimens and empty tests, primarily of these four species, is used to define two major biofacies and several subfacies. The "estuary" facies is divided into "basin", "shoal", and "river" subfacies (Fig. 2). The "marsh" facies is divided into "inner marsh" and "outer marsh" subfacies. The basin subfacies of the estuary is characterized by calcareous Foraminifera, largely *Elphidium incertum*. In this subfacies, the standing crop is small, generally consisting of fewer than 2,500 per sq m. The boundary separating this subfacies from the overlying shoal subfacies is relatively sharp and trends horizontally along the estuary at about the 25-foot depth. Total populations of Ostracoda, like Foraminifera, are relatively small in the basin.

On shoals of the lower estuary, and across the middle and upper reaches of the estuary, the foraminiferal populations of the shoal subfacies are dominated by arenaceous species, chiefly specimens of *Ammobaculites crassus*. Standing crops reach 50,000 specimens per sq m and, in addition to *A. crassus*, specimens of *Millammina fusa* and *Ammobaculites solida* are present. Total populations of ostracods are relatively large on the shoals between low tide and the 18-foot depth. They are characterized by carapaces of several species, including *Cytheridella seminuda* and species of *Cythere*.

In the river subfacies, thecamoebiids are abundant

in the sediment to the complete exclusion of Foraminifera. The boundary between the river and shoal subspecies of the estuary is relatively sharp. A few Ostracoda, chiefly *Darwinula stevensoni*, penetrate the fresh upper reaches of the estuary and tributary creeks from the lower estuary. The two marsh subspecies are dominated by a typical arenaceous marsh fauna, similar to those found in many other parts of the world.

ENVIRONMENTAL RELATIONSHIPS

It is difficult, and perhaps fallacious, to relate the distribution of microfauna to specific physico-chemical factors of the environment. Ecological requirements of particular species have not been fully evaluated by experimental work. Further, environmental factors, which typically range widely with time and from place to place, are only partly known. However, distributions of salinity, drawn from numerous hydrographic observations of the Chesapeake Bay Institute (1952, 1954, 1955) and from various biological surveys including data collected for the present study, are sufficient to delineate the general physical structure

and different types of water. The discussion that follows is an attempt to relate the distribution of microfauna to principal types of water which appear to have a collective influence on the dominant faunal elements.

WATER CHARACTERISTICS

The estuary is a typical two-layered system with moderate haline stratification. In the lower estuary, under normal conditions of inflow, a vertical salinity gradient at a depth of about 16 to 20 feet beneath the surface separates an upper layer of freshened water from a lower layer of saltier water (Fig. 3). The lower layer is characterized by relatively high salinity and diminished oxygen content. Turbulence is generally less than in the upper layer and the net flow is up the estuary. In contrast, the outflowing water of the upper layer has lower salinity, greater turbulence, and higher oxygen content. In the middle estuary, salinity of the upper layer decreases rapidly with distance upstream in a section called the "gradient" zone (Rochford, 1951). In this zone the water is relatively well mixed as a result of tidal action. When strong winds blow seaward down the estuary, mixing may be

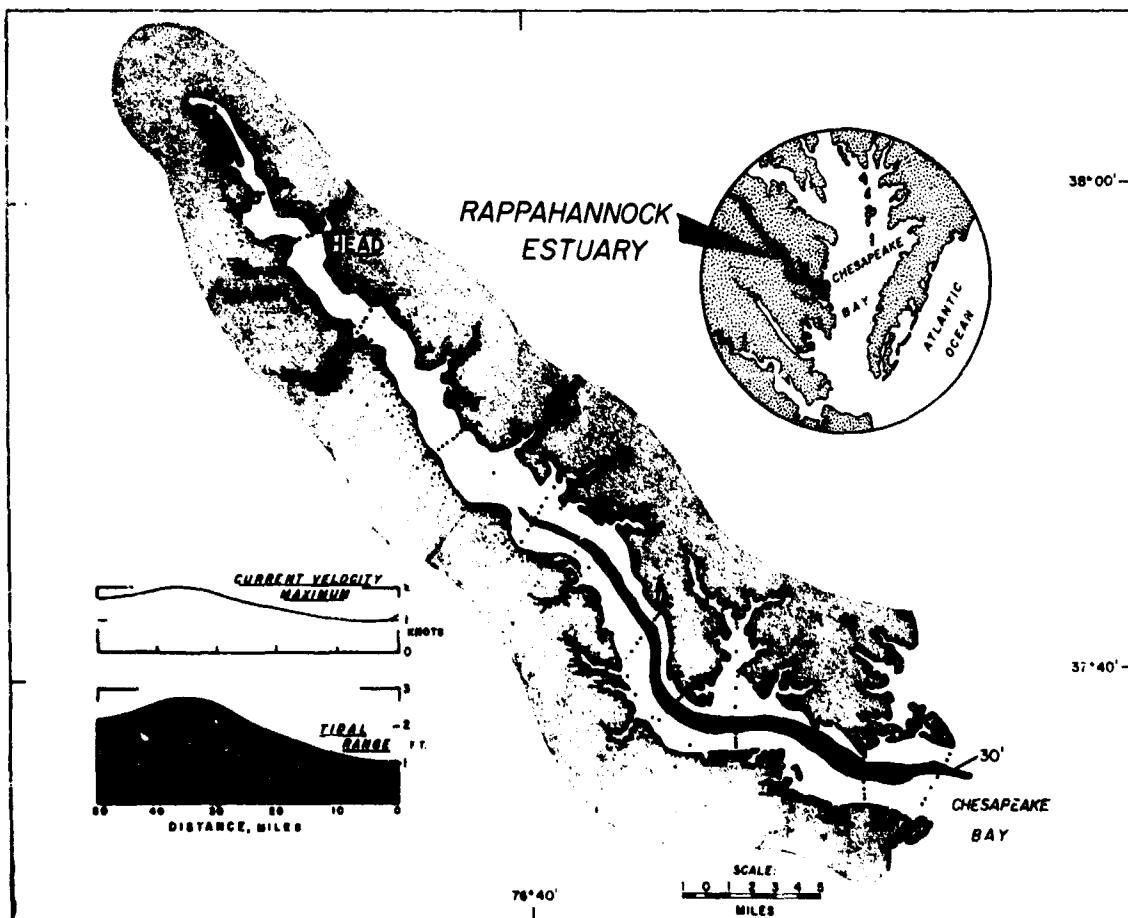


Fig. 1. Location of the Rappahannock Estuary, Virginia, principal environmental features, and general plan of sampling stations (dots).

Table 1. Standing crops of Foraminifera expressed as number of living species per square meter.

	Average	Maximum
Rappahannock River		
Estuary	8,900	142,000
Creeks	20,900	167,000
Marshes	5,500	41,500
Texas Bays	50,000-200,000	2,600,000
Mobile Bay	130,000	277,000
Mississippi Sound	42,000	451,000
Mississippi Delta	90,000	8,000,000

augmented by a convective rise of water flowing upstream from the lower layer of the basin. Headward, above the gradient zone, influence of the river and tributary creeks predominates. Water is turbulent, turbid, and fresh.

MICROFAUNAL RELATIONSHIPS

The three microfaunal biofacies in the estuary approximately correspond to the three water types or biotopes. The river subfacies with *Thecamoebina* is confined to the freshened part of the estuary above the gradient zone; the shoal subfacies of the estuary, containing abundant arenaceous Foraminifera, lies within the upper layer in and downstream from the gradient zone; and the basin subfacies of calcareous Foraminifera inhabits the lower, deeper water of the estuary. The basin subfacies is associated with fine-grained sediment, largely clayey silt, whereas the shoal subfacies occupies both sand and mud from the mouth to the head of the estuary.

Under conditions of extremely low inflow in the summer of 1963, salt water penetrated upstream beyond its normal limit exhibited in the summer of 1962 and haline gradients were relatively weak throughout

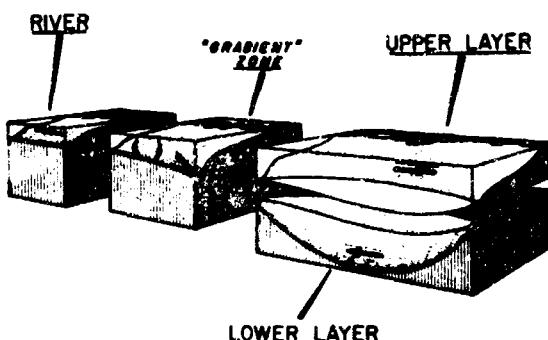


Fig. 3. Principal types of estuarine water and general pattern of circulation, schematic.

the estuary. In response to these conditions the microfauna boundary between the river and shoal subfacies shifted upstream from its position in the previous year; and, in a similar manner, the upstream limit of the basin subfacies progressed headward about eight miles and integrated laterally to a slight degree with the shoal subfacies.

The relationship of microfaunal patterns to estuarine water types is supported by similar distributions in the James Estuary, a nearby tributary of Chesapeake Bay. Salinity gradients are more pronounced than in the Rappahannock Estuary and turbulence is generally greater. A traverse across the mud-floored middle estuary exhibits the two principal facies elements: an arenaceous Foraminifera fauna on shoals bathed by the upper layer and a calcareous Foraminifera fauna in the shallow channel. The lower calcareous fauna predominates on the right side of the channel (looking upstream) which appears to respond to the crowding and slight rise of the upstream-flowing lower layer (Pritchard, 1952).

SEDIMENTATION

MIXING AND REDISTRIBUTION

The distribution of empty foraminiferal tests parallels the patterns of the standing crop. Both empty tests and living specimens of *Elphidium incertum* are relatively abundant in the samples from the basin, whereas empty tests as well as living specimens of *Ammobaculites crassus*, and to a lesser extent *Miliammina fusca*, abound in samples from the shallow reaches and from the upper estuary. A facies map could, therefore, be drawn equally well from the distribution of living specimens or from the distribution of empty tests. However, certain relationships between the distribution of empty tests and the distribution of living specimens may provide insights into processes of estuarine sedimentation.

Inasmuch as currents reach velocities competent to transport tests, as well as sediments, microfaunas are subject to reworking and redistribution. In the upper estuary, where shorelines are extensively bordered by marshes, and where current-washed tributary creeks are well flushed, tests of certain species presumed to

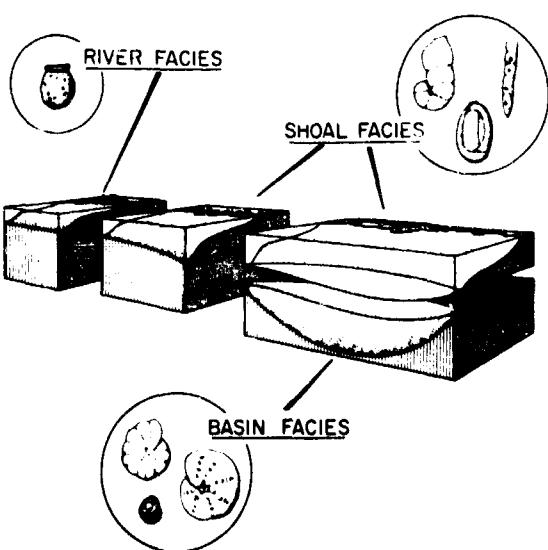


Fig. 2. Distribution of estuarine microfaunal facies, Rappahannock Estuary.

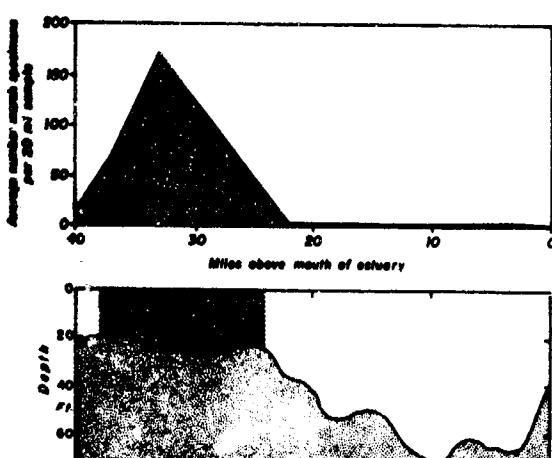


Fig. 4. Average number of marsh Foraminifera in the estuary with distance above the mouth (upper). Profile of channel and basin floor; gradient zone, shaded (lower).

be indigenous to the marsh are present in the estuary. Marsh specimens are most numerous at the mouths of tributary creeks in the upper estuary, and they are dispersed downstream in diminishing numbers approximately to the limit of bed-load transport in the gradient zone (Fig. 4). Marsh-derived organic detritus may supply nutrient material important to estuarine productivity. Specimens of marsh Foraminifera are scarce in the lower reaches of the estuary. Marshes are less extensive than in the upper reaches and exchange of water between marsh-fringed tributary creeks and the estuary is reduced. Wave action on marginal shoals of the lower estuary removes many tests. Displaced tests tend to be spread laterally and downward but few reach the basin floor.

RATES OF DEPOSITION

Relative rates of sedimentation have been estimated by numerous workers in other areas, using ratios of living specimens of Foraminifera to total tests, a high L/T ratio indicating more rapid sedimentation than a low L/T ratio (Phleger, 1960). Briefly the rationale is that if the birth and death rates are more or less uniform in time and space, the rate of addition of tests to the sediment is fixed and, therefore, the rate of dilution by sediment can be approximated. For a given number of living specimens, a specified volume of sediment in an area of rapid sedimentation should contain fewer foraminiferal tests than an equal volume of sediment in an area of slow deposition.

The distribution of average total Foraminifera populations with distance up the estuary shows an irregular increase with values reaching 7,500 tests per 20 ml near the head (Fig. 5). Corresponding living populations vary within relatively narrow limits ranging from 0 to 41 tests per 20 ml. Average live-total ratios indicate relatively high sedimentation in the middle estuary where values reach .053. Comparison of live/total ratios for 1962 and for 1963 shows that

the middle estuary continued to be an area of rapid sedimentation from year to year. In 1963, three samples were collected at each of four stations 22 miles above the mouth; live/total ratios for three species are in good agreement between samples at a station, and relative rates of sedimentation as indicated for each station by these ratios are in agreement between species (Table 2).

DISCUSSION

The patterns of microfauna in the Rappahannock Estuary appear to be related to different types of estuarine water. Although the facies, as established by standing crops of microfauna, correspond with biotopes of the overlying water, certain aspects of the distributions suggest that transportation by currents and varying rates of sedimentation are also operating.

The rate of sedimentation certainly may be an important factor influencing the relationship between the distribution of living Foraminifera and the distribution of total tests. However, relative rates of sedimentation, as determined by using live/total ratios, and those determined from successive changes of depth on hydrographic charts during the periods 1855-1909-1955 show little relationship. Nevertheless, the middle estuary, just downstream from the gradient zone, appears to be one of relatively rapid sedimentation. The rapid accumulation on shoals represents the river-borne bed-load deposition delineated by Nelson (personal communication), whereas the high accumulation in the basin is associated with deposition of a fraction of the river-borne suspended load.

Standing crops of Foraminifera may change in size

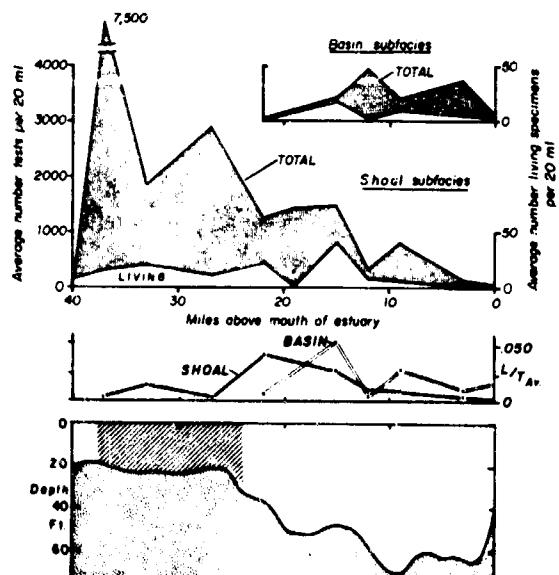


Fig. 5. Average total and living populations of Foraminifera with distance upstream in the basin subfacies and the shoal subfacies (upper). Corresponding living-total ratios with distance above the mouth (middle). Profile of channel and basin floor; gradient zone, shaded (lower).

Table 2. Comparison of live/total ratios for four stations in the middle estuary in July 1963.

Station	Sample No.	<i>Elphidium</i> vars. D-E	<i>Ammonia beccarii</i> var. <i>tepidia</i>	<i>Ammono- baculites</i> <i>crassus</i>
55	1	.00	.11	.00
	2	.00	.76	.00
	3	.00	.23	.00
	Average	.00	.37	.00
55a	1	.80	.64	.40
	2	.72	.71	.44
	3	.89	.95	.47
	Average	.80	.76	.44
56	1	.75	.88	.58
	2	.71	.83	.58
	3	.79	.82	.52
	Average	.75	.84	.56
57	1	.04	.47	.00
	2	.00	.29	.04
	3	.03	.00	.02
	Average	.03	.26	.02

and position from year to year. However, an abundance of empty tests at a specific station apparently is not related to a large standing crop at the station in the previous year. A chi-square test showed no significant association between living specimens in 1962 and total tests in 1963, as compared at each of thirty-three stations.

Redistribution of empty tests in a coastal plain estuary may be significant. Foraminiferal tests introduced partly from marshes appear to be washed down the estuary on the shoals to a greater extent than on the channel floor. Further, near the basin head, empty tests of *Elphidium incertum* are distributed upstream more than 5 miles beyond the limit of living specimens. In the Mississippi Delta area, Miller has shown that foraminiferal numbers are related only to the strength of the bottom current (Miller and Kahn, 1962). This suggests that the accumulation of tests is the product of redistribution by the current. Similarly, Rottgardt (1952) states that the foraminiferal distributions in Kiel Bay reflect, at least partly, the prevailing current conditions. In the Rappahannock, patterns of facies, characterized by relatively abrupt boundaries, are maintained because redistribution occurs in accordance with the relatively sharp contrasts in estuarine circulation.

COMPARISON WITH OTHER AREAS

In order to distinguish different types of estuaries in ancient rocks, it is useful to contrast the microfaunal patterns in the Rappahannock Estuary with those of a sound and of a coastal lagoon. Phleger (1960) summarizes the chief features of distributions and related oceanographic conditions in San Antonio Bay, Texas, a restricted lagoon in which the influence of river inflow is relatively low and variable, and in Mississippi Sound, with discontinuous barriers in which runoff is abundant and continuous. The micro-

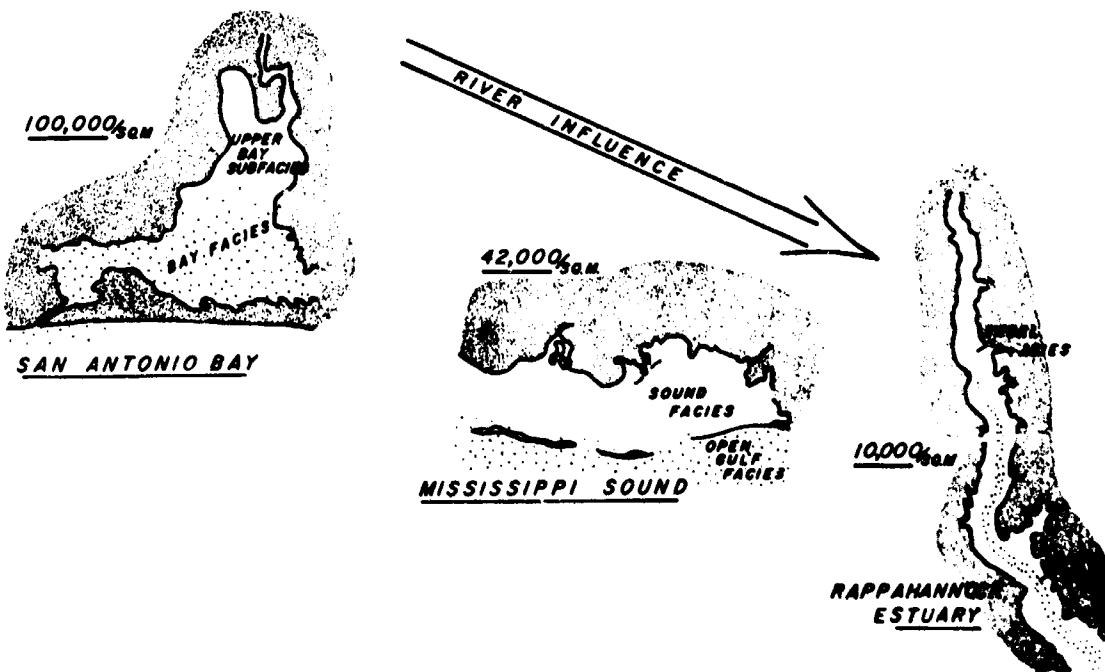


Fig. 6. Diagrammatic contrasts of facies patterns in a sequence of estuaries with different degrees of river influence: San Antonio Bay, Texas (left), Mississippi Sound (middle), and Rappahannock Estuary (right). Numerical values represent average living populations in each area.

fauna in these areas is constituted of elements similar to those found in the Rappahannock, with an arenaceous foraminaliferous facies in inner freshened areas, and a calcareous facies in seaward parts (Fig. 6). In San Antonio Bay the calcareous facies is relatively widespread over a broad area of the lower lagoon. Phleger believes this distribution is related to invasion of open-ocean water during long periods of low inflow. In Mississippi Sound the calcareous facies largely extends inward to the barrier islands and inlet passes where it forms a relatively sharp boundary with the arenaceous fauna of the sound. In the Rappahannock Estuary the influence of river inflow is relatively great and favors development of a two-layered estuarine system. The calcareous facies penetrates inward in the lower layer to the gradient zone of the middle estuary and persists within relatively narrow limits. Marsh species spread into the estuary are largely restricted to the upper reaches and marginal shoals of the Rappahannock, whereas in Mississippi Sound marsh specimens are mixed with the sound fauna over a wide area along the open shoreline. The average number of living specimens in the Rappahannock is much smaller than in the other areas.

Conditions of sedimentation may be inferred from the distribution of microfauna. However, before these organisms can be used with complete confidence for such purposes, techniques of study need refinement and much needs to be learned about living habits and the structure of populations.

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LITERATURE CITED

- CHESAPEAKE BAY INSTITUTE, 1952. Operation RAP, March 15, 1951-March 24, 1951. *Data Rept. 8* (Ref. 54-3). Chesapeake Bay Inst., The Johns Hopkins University, Baltimore, Maryland.
- CHESAPEAKE BAY INSTITUTE, 1954. Cruise XII, July 15-August 6, 1952. *Data Rept. 18* (Ref. 54-5). Chesapeake Bay Inst., The Johns Hopkins University, Baltimore, Maryland.
- CHESAPEAKE BAY INSTITUTE, 1955. Cruise XIII, February 17-March 18, 1953. *Data Rept. 26, revised* (Ref. 55-5). Chesapeake Bay Inst., The Johns Hopkins University, Baltimore, Maryland.
- MILLER, R. L., and J. S. KAHN, 1962. *Statistical analysis in the geological sciences*. John Wiley and Sons, New York.
- NELSON, B. W., 1959. Transportation of colloidal sediment in the freshwater marine transition zone. *Intern. Oceanogr. Congr. (preprints)*, p. 640.
- NELSON, B. W., 1961. Dispersal of clay sediment in the Rappahannock River. *Am. Assoc. Petrol. Geologists, preprints*. (Abstract)
- PHLEGER, F. B., 1960. *Ecology and distribution of Recent Foraminifera*. Johns Hopkins Press, Baltimore, Maryland.
- PRITCHARD, D. W., 1952. Distribution of oyster larvae in relation to hydrographic conditions. *Gulf and Caribbean Fish. Inst. Proc.*, 5:123-132.
- ROCHFORD, D. J., 1951. Studies in Australian estuarine hydrology. I. Introduction and comparative features. *Australian J. Marine Freshwater Res.*, 2(1): 1-116.
- ROTTGARDT, D., 1952. Mikropalaontologisch wichtige Bestandteile recenter brachischer Sedimente an den Küsten Schleswig-Holsteins. *Meyniana*, 1(1):169-228.

V. MICROBIOTA

The Microbiota of Estuaries and Their Roles

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In discussing the roles of microorganisms in estuarine situations, the implication is that an estuary is a special kind of place. Essentially, a marine estuary is a place where fresh and salt water mix. It is a place where freshwater organisms encounter salt water, and oceanic organisms enter water that is less salt. Obviously, unless these plants and animals can adapt to a wide range of chemical and physical changes, they perish. Undoubtedly, many microscopic creatures do perish in the changing environment. However, qualitative and quantitative analyses of the biota reveal a large population in both categories—many species, and, for some species, many individuals. There are indications that certain species may be found only in estuaries.

BACTERIA

Marine bacteria and their place in estuarine ecology have been well considered by ZoBell (1946), with the exception of those bacteria which accumulate sulfur within their cells. ZoBell and Upham (1944) also listed the sulfur bacteria of marine situations, 17 genera of which are included herewith, but also including eight species not in our list. This listing includes 25 genera and 64 species belonging to several orders. Except in sulfur springs and certain types of sewage treatment plants, the filamentous Beggiatoales are rather uncommon in fresh water, whereas Thiorhodaceae and *Achromatium* Schewiakoff are common, at least in stagnant waters. Beggiatoales are common in salt water, as are the others, and *Beggiatoa gigantea* Klas, *B. mirabilis* Cohn em Klas, and *Thiodendron mucosum* Lackey and Lackey have been reported only from brackish or salt water (Lackey, 1960; Lackey and Lackey, 1961). Sulfur is the fourth most abundant element in sea water—884 ppm—and is both oxidized and reduced by sulfur bacteria. The reactions yield energy, 460 and 29 kcal, and the quantity of available sulfur, as well as the energy relationships involved, is an obvious answer to the abundance of these organisms in salt water.

An important function of these bacteria is the removal of H₂S in sea water. H₂S is directly toxic to living organisms, although different species vary in their reactions to various concentrations. Thus, samples brought in from sulfur springs where there are 2-3 ppm must not be tightly stoppered because even in a few hours, and with lowered temperatures,

the accumulation of H₂S is toxic and the biota in the sample is markedly changed. Use of H₂S by organisms such as the Beggiatoales, resulting in its change from a sulfide in the water to non-toxic elemental sulfur within the organism (or precipitated outside the cell) eliminates it as a deterrent to a rapid mineralization of organic matter.

Sulfur bacteria may become most abundant in common situations, as in the large sulfur springs of Florida with their white coatings of sulfur bacteria. A most striking example is Warm Mineral Springs (Lackey and Lackey, 1961), which is half sea water, and which has huge populations of virtually all the sulfur bacteria, including *Beggiatoa gigantea*, which can be picked up there by the handful. In this case the immediate sulfur source is H₂S. But in many Air Force camps of the southwestern United States investigated during World War II by Lackey and Dixon (1943) for the white and purple bacteria on transite plates in Hays process sewage treatment plants, the principal sulfur source was probably the high SO₄ content of the ground water. Several Beggiatoales are also common in the mud-water interface in ocean waters. The most abundant yet seen were *Beggiatoa gigantea* in the polluted mud of the Los Angeles harbor region, where Reish (1957) investigated the annelid population.

There are obviously limits to the concentration of H₂S which can be biologically mineralized. The Oslo Fjord and the Black Sea are examples. It is interesting that Kriss (1963), who studied the bacteria of the Black Sea at length, had no statement about sulfur-accumulating bacteria as suspended forms, and that by implication he strongly supports the idea of the limitations imposed by dissolved H₂S.

ALGAE

For this discussion, the algae can be treated as plankton forms, generally containing chlorophyll with or without other pigments; and as benthic forms, usually non-pigmented, although in the photic zone there are large numbers of photosynthetic forms. Blue-green algae attain importance in biomass as epiphytes on estuarine mud flats and in very shallow water.

It is widely accepted that the amounts of available PO₄ and NO₃ generally govern the abundance of green plants. A favorable N/P ratio is somewhere between 10:1 and 30:1 as far as abundance is concerned, but deviations from these ratios are common

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and effective, and there are various other limiting factors as well. The amounts of available NO_3 and PO_4 are small in oceanic waters, except in regions of upwelling, as along the Pacific Coast. In estuarine situations the amounts may be much larger, depending on the amount of drainage (1) from urban areas, (2) from agricultural land, and (3) from areas underlain by calcareous rocks. In areas underlain by granitic rocks there is a smaller amount of solution, and drainage from forested land and sandy areas is generally poor in nitrates and phosphates. It seems almost certain that green Volvocales and some Euglenophyceae utilize organic compounds, and that Chrysophyceae and dinoflagellates not only utilize soluble organic compounds, but often ingest solid food. Therefore, aside from important roles in re-aeration and as food organisms, they must have an important but imperfectly understood role in the degradation of organic matter.

Published papers do not contain many qualitative and quantitative listings of the microbiota of estuaries. Personal experience has included the inshore waters around Woods Hole; Plymouth, England (Lackey and Lackey, 1963), where the harbor waters are fed by the Rivers Plym and Tamar; San Diego Bay (Lackey and Clendinning, 1960), whose huge harbor receives very little fresh water other than the sewage of a city of 500,000 (at the time of study); Mission Bay, with almost no inflow except during a short rainfall season of 5 to 10 inches; the Chesapeake Bay around Solomons Island; Great South Bay, Long Island, New York (Lackey, 1963), with substantial ground water leached from its urban population and numerous small streams; Waccasassa Bay, whose streams are from forested sandy areas; and limited experience with the Fenholloway Estuary, whose waters are heavily polluted by paper mill wastes. The Waccasassa and Fenholloway are small rivers entering the Gulf of Mexico west and northwest of Gainesville, Florida. For most of these, lists of the plankton algae and protozoa are available. In addition, there are many papers on the Oslo Fjord by Braarud and his co-workers, and papers on the estuaries of other European rivers.

VOLVOCALES

The Volvocales are relatively common to inshore waters. In Great South Bay (Lackey, 1963), 19 genera or species were listed, of which six are distinctly freshwater forms. *Carteria* Diesing, *Chlamydomonas* Ehrenberg, and *Dunaliella* Teodoresco were probably represented by several species. In the Waccasassa Estuary there were 20 genera and species of which five are regarded as freshwater. There are at least five genera which occur so frequently that they may be regarded as characteristic of estuarine water—the most abundant and most frequently occurring being *Pyramimonas grossi* Parke. In fresh water, Volvocales tend to occur in abundance in polluted situations, so that large numbers are certainly indicative of a high organic content. This illustrates an-

other role of microorganisms—the connotation of their presence. Few species might properly be classed as indicators of a specific characteristic of a body of water, but certain groups and high occurrences certainly are indicators. Rock pools at Woods Hole, Plymouth, and the University of Rhode Island Narragansett Marine Laboratory, contaminated with gull droppings, often contain huge numbers of *Dunaliella* and *Chlamydomonas*. These small pools vary greatly in salinity because of rainfall, tides, and evaporation; salinity is not necessarily a factor. The nitrogenous excreta of birds is uric acid, not as easily broken down as urea, but the bird egesta probably contains abundant nitrogenous matter. Certainly such pools are often heavily polluted, and their populations are preponderantly Volvocales.

CHLOROCOCCALES AND OTHER CHLOROPHYCEAE

Plankton Chlorophyceae tend to be sparse in oceanic and estuarine waters. Those which enter from freshwater situations, *Scenedesmus* Meyen, for example, do not survive very long. The only abundant ones in Great South Bay in 1961 were two species of *Chlorella* Beijernick, and *Nannochloris* Naumann. This latter genus was incriminated there in the disappearance of the oyster industry in the 1940's. Its actual role was never determined, but studies (Glancy, 1944; Bidwell, 1949) indicated that its behavior as a persistent dominant may have prevented growth of a mixed food population for oysters, that it may not itself have been a proper food, or that it produced metabolites which were unfavorable to oyster growth.

Its growth in Great South Bay indicated that whereas it was a very minute organism, 2-3 μ in length, its numbers were sufficient to produce a considerable biomass. Often a Secchi disk would become invisible at 12 inches where this plankter was in bloom. Table 1 is a listing of species and numbers of organisms in Great South Bay on three dates, and illustrates the dominance of *Nannochloris*. Given the proper environment, this organism and *Chlorella* have the ability to attain great numbers in estuarine waters, but they are the only plankton Chlorophyceae for which we have such a record.

EUGLENOPHYCEAE

Green flagellates of this group are confined to two genera, as far as abundant occurrence is concerned. These are *Eutreptia* Perty and *Eutreptiella* Da Cunha which differ, according to Butcher (1959), largely in a very marked difference of the two flagella in the latter, whereas in *Eutreptia* the flagella are both long, but subequal. There are some species of *Euglena* Ehrenberg which occur in brackish water, notably *E. vermiformis* Carter, but we have never found them in quantity. *E. limosa* Gard. is supposedly common on the mud banks of at least one estuary in England (Fraser, 1930). Table 2 shows the numbers of green Euglenophyceae in four estuaries studied intensively. It is apparent that only two genera occur in abundance. It has not been feasible to separate

Table 1. Organisms in one milliliter of water in the polluted area of Great South Bay on four dates in 1952.

Sample Location	Pouquogue Bridge	Shinnecock Bay	Forge River Dock	Forge River Dock
Date	5-13-52	5-13-52	6-16-52	7-21-52
Temperature	56°F.	56°F.	77°F.	82°F.
Secchi disc visibility	17"	12"	11"	
<i>Actinastrum hantzschii</i> Lagerheim				792
<i>Actinopychus undulatus</i> (Corda) Ralfs	4	1		
<i>Actinopychus</i> Ehrenberg	1			
<i>Ankistrodesmus falcatus</i> Ehrenberg			1	256
<i>Coscinodiscus</i> Ehrenberg, large				
<i>Coscinodiscus</i> Ehrenberg, small	7	3		
<i>Clasteriopsis longissimum</i> Lemmermann				96
<i>Cryptomonas</i> Ehrenberg				128
Ciliata unid.		6	4	6
Dinothagellata unid.			48	
<i>Gymnodinium splendens</i> Lebour			6	
Green cells, unid.				
<i>Hastatella radians</i> Erlanger				768
<i>Melosira sulcata</i> (Ehrenberg) Kutzin		4		4
<i>Microctenium pusillum</i> Fresenius			48	112
<i>Microgromia</i> Hertwig	12	1		
<i>Monodinium balbiani</i> Fabre-Domergue			2	
<i>Narcicula</i> sp. Bory	1			
<i>Oocystis</i> Nageli				2
<i>Oscillatoria</i> Vaucher				3
<i>Paramecium trichium</i> (Stokes) Wenrich				1
<i>Pleurosigma fasciata</i> (Ehrenberg)	1	1		
<i>Polyedriopsis spinulosa</i> Schmidle				26
<i>Prorocentrum triangulatum</i> Martin	8	2		
<i>Scenedesmus quadricauda</i> Chodat				48
<i>Syracospheara carterae</i> Braarud and Fager			1	
<i>Tintinnopsis minuta</i> Wailes	1	1		
<i>Urotricha farcta</i> Claparede and Lachmann			48	
<i>Vorticella</i> (Linne) Ehrenberg		5		
Total	35	24	158	2,242
<i>Nonnochloris bacillaris</i> Naumann	3,240	8,000	1,430,784	776,352
Species	9	11	9	15

Entrepia and *Entrepelta* in counting, although this can be done by examining the population by phase microscopy. This table shows that certain freshwater species enter waters of various degrees of salinity and survive there for a time. It also shows that *Entrepia* and *Entrepelta* are responsive to recent organic contamination, because all the blooms except those in the Waccasassa have occurred in such areas. In Great South Bay (Lackey, 1963), the most dense aggregate of these organisms was below the sewer outfall of Riverhead, in Peconic Bay.

The colorless Euglenophyceae are far more common (in number of genera and species) and often more abundant in estuarine waters than the green ones. They rarely occur in blooms, however, for one reason. Most of them are creeping forms, and they live in the sediment-water interface, that thin layer which is the recipient of all the organic debris rained down from the overlying waters. A few ingest solid food; most of them are saprotic.

At Plymouth, 23 of the 29 species of Euglenophyceae were found in the sand and mud flats or the

sediment-water interface (Lackey and Lackey, 1963). Three of the remaining four were green swimming forms; and two of the five green species were found only in the sediment. Table 3 is a list of the colorless Euglenophyceae from several estuarine situations. It includes a large number of species, but not numbers. No satisfactory sampling procedure has yet been developed which permits a count per ml of the thin, two to five mm sediment-water interface. Core samples are the best so far, but a good core is not often obtained.

When a good core is obtained in a glass or plastic tube, the flocculent interface is usually brown. This is true even for a sand core. Within a few millimeters below the surface, the sediment is blackened, due to sulfide. While many colorless Euglenophyceae are facultative anaerobes, few, if any, are obligate. Consequently, they do not inhabit the black layer, where there is no oxygen, and H_2S probably exists in toxic amounts. A large part of the interface population consists of these euglenids, ciliates, and bacteria. It seems part of an acceptable theory that the

Table 2. Green Euglenophyceae from estuarine waters showing organisms and number of occurrences.

Location	Great South Bay	San Diego Bay	Plymouth	Waccasassa
No. Samples	132	89	ca. 96	221
<i>Cymbomonas</i> Schüller	3			1
<i>Euglena acus</i> Ehrenberg				
<i>Euglena frustula</i> Elenkenin			1	
<i>Euglena fusa</i> (Klebs) Lemmermann	1			
<i>Euglena gracilis</i> Klebs	2			
<i>Euglena graciliformis</i> Klebs	1			10
<i>Euglena rostellata</i> Klebs	1			
<i>Euglena vermiformis</i> Carter			1	
<i>Euglena viridis</i> Ehrenberg	2			1
<i>Euglena</i> Ehrenberg				1
<i>Eutreptia laevis</i> Steyermark			6	13
<i>Eutreptia viridis</i> Perty			1	44
<i>Eutreptia</i> Perlt			1	
<i>Eutreptiella</i> Da Cunha	98	1		16
<i>Lepocinclis</i> strobli (Ehrenberg) Carter				2
<i>Phacus hispidulus</i> (Eichh.) Lemm.	1			
<i>Phacus plurorectus</i> (O. F. Müller) Dujardin				1
<i>Phacus pyrum</i> (Ehrenberg) Stein	1			3
<i>Phacus triquetus</i> (Ehrenberg) Dujardin	1			
<i>Trachelomonas rachlorus</i> (Ehrenberg) Lemmermann sec Conrad				2
<i>Trachelomonas obvoluta</i> Stokes em Deflandre	2			
<i>Trachelomonas rotundata</i> Ehrenberg	2			10
<i>Trachelomonas</i> Ehrenberg em Deflandre				3
Species	12	1	5	13

euglenids share with bacteria the digestion of rained-down organic debris. Perhaps their digestion is at an intermediate level rather than at the initial breakdown of proteins, fats, and carbohydrates. Virtually none of them have been grown in quantity in axenic culture on chemically defined media, but at least eight species grow abundantly in organic media if bacteria are present.

The marine genera and species are not well defined. Many marine samples, for example, yield large numbers of unflagellate forms which are apparently *Petalomomas*, but which intergrade and do not fit any of the many described species. There also seems to be much dependence on microclimatic factors. Thus, we have found *Calkiniam aurans* Lackey only in the Eel Pond at Woods Hole, although a similar organism, except without a spine, has been found in the surf at the Scripps Institution bathing beach. It is still imperfectly known. *Petalomomas spinifera* Lackey has been found at the Narragansett Marine Laboratory of the University of Rhode Island; at Drake's Island, Plymouth, England, and in the surf at Scripps. It is always in the sand between tide elevations. No amount of hunting in similar locations in Florida has provided a single one. These are interesting species, because if we knew the microclimatic reasons for their existence in a particular location we could better assess their environmental roles.

Many of the salt water Euglenophyceae are also found in fresh water, and seem to thrive in brackish water. This is important in accounting for their

Table 3. Colorless Euglenophyceae in four estuaries.

	Plymouth	Great South Bay	San Diego Bay	Waccasassa Bay
<i>Anzunema</i> sp. A Duj. em. Stein	X			
<i>Anzunema</i> sp. B Duj. em. Stein	X			X
<i>Anzunema</i> sp. C Duj. em. Stein			X	X
<i>Anzunema emarginata</i> Stokes	X			
<i>Anzunema grande</i> in ms.				
<i>Anzunema lucens</i> in ms.				X
<i>Anzunema murorum</i> Skuja				X
<i>Anzunema ovale</i> Klebs	X			
<i>Anzunema pusilla</i> Stokes	X			
<i>Anzunema transitoria</i> Stein			X	X
<i>Anzunema</i> sp. Duj. em. Stein	X		X	X
<i>Atiana</i> klebsii Lemn.				
<i>Atiana longa</i> Pringsheim			X	X
<i>Cultivaria aurans</i> Lackey			X	X
<i>Cultivaria</i> sp. Lackey			X	
<i>Cultivaria mobilis</i> Massart				X
<i>Duncina granulata</i> Perty	X		X	X
<i>Duncina laterale</i> Skuja	X		X	
<i>Dunignea</i> sp.				
Ehbg. em. Prings.				
<i>Eulonchus</i> sp. Klebs			X	
<i>Eutreptiella</i> sp. Klebs			X	
<i>Eutreptiella caliginosa</i> Klebs				
<i>Eutreptiella caliginosa</i> (Duj.) Stein			X	X
<i>Eutreptiella</i> sp. Stein	X			
<i>Heterozema</i> sp. (Ehbg.) Stein	X			
<i>Heterozema</i> sp. Duj. em. Stein			X	
<i>Melanoma</i> varabile Klebs	X		X	X
<i>Melanoma</i> sp. Klebs				
<i>Nekemias</i> aff. <i>variegata</i> Stokes	X	X	X	X
<i>Nekemias</i> subalata Stokes			X	

Table 3 (Continued)

	Plymouth	Great South Bay	San Diego Bay	Waccasassa Bay
<i>Notosolenus</i>				
sp. Stokes em. Skuja				
<i>Pentamonas spinifer</i> Lackey	X	X		
<i>Pentamonas</i> sp. Lackey			X	
<i>Peranema asperum</i> Playfair			X	
<i>Peranema cuneatum</i> Playfair	X			
<i>Peranema granuliforme</i> Penard			X	
<i>Peranema inflexum</i> Skuja		X		
<i>Peranema trichophorum</i> (Ehbg.) Stein	X	X	X	X
<i>Peranemopsis striata</i> Lackey			X	
<i>Petalomonas obscissa</i> (Duj.) Stein			X	
<i>Petalomonas angusta</i> (Klebs) Lemm.			X	
<i>Petalomonas carinata</i> France		X	X	
<i>Petalomonas disomata</i> (Stokes) Lemm.			X	
<i>Petalomonas excavata</i> Skuja	X			
<i>Petalomonas mediocostellata</i> Stein	X			
<i>Petalomonas mira</i> v. <i>bicarinata</i> Skuja			X	
<i>Petalomonas pusilla</i> Skuja	X	X		X
<i>Petalomonas steini</i> Klebs				X
<i>Petalomonas striata</i> in ms.			X	
<i>Petalomonas tricarinata</i> Skuja			X	
<i>Pleotrichia</i> Duj.			X	
<i>Plectio</i> sp. Duj.			X	
<i>Protaspis glans</i> Skuja				X
<i>Scytonomas pusilla</i> Stein	X	X	X	
<i>Sextomonas</i> sp. Stein	X		X	
<i>Sphenomonas elongata</i> Lackey		X	X	
<i>Sphenomonas quadrangularis</i> Stein		X	X	
<i>Sphenomonas teres</i> (Stein) Klebs			X	
<i>Triangulomonas rigida</i> Lackey		X	X	
<i>Tropidosecyphus octocostata</i> Stein	X			
<i>Urecoctus cyclostomus</i> Stokes	X	X	X	
<i>Urecoctus pascheri</i> Korschikov	X			
<i>Urecoctus subulatus</i> Stokes	X	X	X	X
	25	6	31	32

numbers in estuaries. It is noted that the number of species in Great South Bay is small by comparison. All these samples were from the surface and there was little vertical mixing. Unless bottom material is included in a sample, very few of the colorless species will be found.

CHLOROPHYCEAE

The scarcity of Chlorophyceae in salt water is partially compensated for by the abundance of Chrysophyceae. This is not so much a matter of numerous genera (Table 4) and species, as frequency of occurrence. However, the very small size and rapid movement of many of these plankters make identification extremely difficult. Another deterrent to recognition is their early cytolysis after being centrifuged

and placed on a slide. Species of *Chrysochromalina* Lackey as described by Parke et al. (1955, 1956), and *Isochrysis* Pascher, *Monochrysis* Skuja, and *Pedinella* Wyssotz are abundant, but they need a high magnification, and to be relatively still, to be identified. Most of them cytolize soon after becoming quiet. The blotch of color they leave is usually enough to indicate that the remains are those of a chrysophycean, although *Rhodomonas* Karsten and *Chroomonas* Hansgirg, both cryptomonads, and *Masseria-Ketodinium* Fott *rotundata* (Lohmann) Schiller em Loeblich, a dinoflagellate, behave similarly. *Olisthodiscus luteus* Carter, a common larger chrysophycean, is different from its published description and figure (Carter, 1938). It was brought into unialgal culture before it was identified in the United States. Once identified, many of these small species exhibit a characteristic movement, or gross morphology, which enables recognition.

In the Waccasassa Estuary studies some 18 or 20 species of Chrysophyceae were found. None of them occurred as 500 or more per ml (bloom), and scarcity, coupled with a small biomass, indicated relative unimportance for the group. In San Diego Bay in 1959 there were nine blooms of five species. Fourteen species were identified. In Great South Bay in 1961, eleven species occurred. *Olisthodiscus* was found in 35 of 93 samplings, four times in bloom numbers. The highest was 46,400 ml, obviously enough to affect the environment. The remaining species of Chrysophyceae were noted in 56 of 94 samples. This included six blooms; the occurrences and numbers were ample evidence for both frequency and occurrence.

The Chrysophyceae already discussed are those containing pigment. A dense unialgal culture of *Olisthodiscus* is almost brown; its chromatophores are not deeply colored as are the green ones of a desmid or a *Englena*. Other Chrysophyceae have even less color—*Dinobryon* Ehrenberg, for example, is very pale. This poses an interesting question as to the efficiency of chrysophycean re-aeration; i.e., O₂ production by Chrysophyceae, as compared with, say, *Enteromorpha*.

In the colored Chrysophyceae, volutin granules are usually conspicuous in the cell, but starch is not produced. These reserve substances have had too little attention from biochemists for us to know their role

Table 4. Genera of Chrysomonads noted in the estuaries studied.

1. <i>Berkholzia</i> Runnen	11. <i>Mallomonas</i> Perty
2. <i>Chromalina</i> Cienkowski	12. <i>Monas</i> (Cienk.) Senu
3. <i>Chrysomonads</i> Klebs	13. <i>Monochrysis</i> Skuja
4. <i>Chrysophyllum</i> Pascher	14. <i>Ochromonas</i> V. sotakii
5. <i>Chrysodictis</i> Schiller	15. <i>Ochromonas</i> (Ehbg.) Kent
6. <i>Chrysotrichomonas</i> Lackey	16. <i>Pedinella</i> Wyssotz
7. <i>Chrysosarcus</i> Klebs	17. <i>Potriochromonas</i> Scherffel
8. <i>Chrysopelta</i> Pascher	18. <i>Paradipediella</i> Carter
9. <i>Dinobryon</i> Ehbg.	19. <i>Sternomonas</i> Stokes
10. <i>Kephrium</i> Pascher	20. <i>Stereomonas</i> Pascher

Table 5. Numbers per ml of pigmented Cryptophyceae found once each week during an eight-week study of Great South Bay, Long Island, New York. The thirteen stations were scattered the length and breadth of the bay. The blanks indicate no samples were taken.

Station	Weeks							
	1	2	3	4	5	6	7	8
1	280	35	25	416	751	51	810	
2	936	0	468	1300	336	224	313	206
3a	88	8	1672	1312	350	64	248	144
4				160	164	224	280	140
5	586	540	280	236	600	192	472	246
6	64	1900	2708	125	10476	7830	3040	28
7	222	2333	816	240	600	16	204	500
8	242	28		488	248		69	
9	260	16	144	244	96	160	248	170
10	88	46	32	52	13	8	50	
11	100	120	112	32	48	24	48	
12	84	198	352	64	396	50	94	
13	80	300	380	780	388	176	80	480

in estuarine ecology. Presumably, when a *Chrysocromulina* is eaten by a *Euploites* Ehrenberg, its volutin is digested; but there is little evidence, possibly because so few Chrysophyceae have been grown in mass culture.

Chrysophyceae without pigment are often regarded as an uncertain taxonomic group. Hollande (1952), considering 129 possible genera of Chrysophyceae, recorded 17 colorless genera. Three of these, *Oicomonas* (Ehrenberg) Kent, *Monas* (Cienkowski) Sern, and *Paraphysomonas vestita* Stokes, have been common to estuarine situations. Since all three are prime consumers of bacteria, and because they sometimes attain large numbers, they might have an important role in estuarine ecology. The Fenholloway Estuary on February 10, 1964, contained 2,656 *Monas* sp. per ml, 48 *Bodo* Stern sp. per ml, 200 unidentified flagellates per ml, and 32 *Paraphysomonas vestita* per ml. This was in an area strongly polluted with paper mill waste and with a dense bacterial population, on which these colorless flagellates were actively feeding.

CRYPTOPHYCEAE

Cryptophyceae seem to be the most ubiquitous of all the plankters. The number of genera and species is small—Pascher (1913) lists seven genera and 18 species in fresh water. Occurrence in waters we have examined is widespread, and the organisms abundant. Table 5 shows the numbers of pigmented Cryptophyceae at 13 Great South Bay stations, sampled once weekly during July and August, 1961. Nineteen times they were in excess of 500/ml (bloom), and were missing in only one of 94 samples. Stations 10, 11, and 12 showed the fewest, and these stations were the greatest distance from human habitation. These three stations were consistently lowest in coliform bacteria, which are regarded as indicators of fecal contamination. Evidently the numbers of Cryptophyceae were a response either to man's contribution of

NO_3 and PO_4 , or to some other animal contribution, possibly an organic one. Nitrates varied from 0.0 ppm, at Stations 11 and 12 in the first week, to 0.08 ppm, and phosphates from 0.040 to 0.110 ppm. This is a high content for each of these, but is far from an N/P ratio of 10:1.

Chilomonas paramecium Ehrenberg occurs sparingly, if at all, in salt water, but *C. marina* Braarud is common to the open ocean and to estuaries. During the same period, and at the same Great South Bay stations referred to in Table 5, it occurred in all but ten samplings, and twice in numbers exceeding 500/ml. This colorless member is saprozoic. The inference is that it uses soluble organic substances. Cryptophyceae do not elaborate starch, and again either liberate volutin and other non-starch carbohydrates to the environment, or to predators who digest them.

The common genera of Cryptophyceae are *Chromonas*, *Cryptomonas* Ehrenberg, *Rhodomonas*, *Chilomonas* Ehrenberg, and *Cyathomonas* Frontel. The last is normally a bottom dweller, and often not seen in plankton samples, or only sparingly. All five genera were found at Plymouth and in San Diego Bay. In the Waccasassa Estuary, 11 species, including all these genera, were very common in 1963. Nevertheless, they were few in numbers per ml there, and it was concluded that they were relatively unimportant in the ecology of the estuary. It must be noted that the wide distribution of this group is an assurance of great numbers of them when conditions become favorable.

DINOFLAGELLATA

There are pronounced differences between estuarine dinoflagellates and those of the open sea. The latter are more disposed to unusual morphology which makes them easy to identify, to a larger size, and to multiplicity of species. Estuarine species tend to small sizes, to a generally ovoid shape, and to frequent localized blooms. Nevertheless, a concentration of nutrients is necessary for large populations. The only one to bloom in a year's study of the Waccasassa Estuary was the very small *Massartia rotundata*, and this estuary is regarded as low in nutrients. Table 6 is a listing of the identified species from five estuarine waters. Most of them have photosynthetic pigments, but about one-fourth are holozoic or saprozoic. It is noteworthy that the blooms which appear from time to time are almost invariably pigmented forms. Several species which have given rise to blooms elsewhere are listed in Table 6: *Prorocentrum triangulatum* Martin, a cause of dense blooms in Great South Bay and Chesapeake Bay; *Gymnodinium splendens* Lebour, likewise in Great South Bay; and *Ceratium furca* Ehrenberg (Claparde and Lachmann), in several places. The only dinoflagellate blooms in San Diego Bay or Mission Bay during this study were of *Gymnodinium farreri* Kofoid and Swezy; (Lackey and Clendenning, 1963) and *Protodinium simplicius* Braarud.

Table 6. Occurrence of Dinoflagellates in five estuarine situations.

Organisms	San Diego Bay	Mission Bay	Waccasasa Bay	Plymouth	Great South Bay
<i>Amphidinium bipes</i> C. E. Herdmann			X		
<i>Amphidinium crassum</i> Lohmann	X	X			
<i>Amphidinium cucurbita</i> Kofoid & Swezy	X	X	X		
<i>Amphidinium klebsii</i> K. & S.					
<i>Amphidinium operculatum</i> Clapared & Lachmann	X	X		X	
<i>Amphidinium ovum</i> C.E.H.				X	X
<i>Amphidinium parva</i> in ms.					X
<i>Amphidinium rhyncoclephalum</i> Anissimowa	X		X		
<i>Amphidinium scissoides</i> Lebour	X				
<i>Amphidinium scissum</i> K. & S.	X				
<i>Amphidinium stigmatum</i> Schiller	X				
<i>Amphidinium sulcatum</i> Kofoid			X		
<i>Amphidinium testudo</i> C.E.H.		X			
<i>Amphidinium vigorensis</i> Wołoszynski			X		
<i>Amphidinium vitreum</i> (C.E.H.)			X		
<i>Amphidinium</i> sp. Clap. & Lach.	X	X	X	X	X
<i>Ceratium fulciforme</i> Jorgensen					
<i>Ceratium furca</i> (Ehlg.) Clap. & Lach.	X	X	X	X	
<i>Ceratium fusus</i> Ehbg.					X
<i>Ceratium longipes</i> (Bailey) Gran			X		
<i>Ceratium minutum</i> Jorg.	X	X		X	
<i>Ceratium tripos</i> O. F. Müller	X	X		X	
<i>Ceratium</i> spp. Schrank	X	X			
<i>Cochlidinium catenatum</i> Okamura	X			X	
<i>Cochlidinium pulchellum</i> Lebour	X	X			
<i>Dinophysis fortis</i> Pavillard	X	X		X	
<i>Dinophysis norvegica</i> Clap. & Lach.					
<i>Dinophysis ovum</i> Schutt					
<i>Dinophysis tripos</i> Gourret	X	X	X	X	
<i>Diplopeltis minor</i> Lebour					
<i>Ditlopsalis lenticula</i> Bergh					
<i>Ditlopsalis orbicularis</i> (Paulsen)					
<i>Entomospira peridioides</i> Schiller					
<i>Erythrops</i> sp. Hertwig					
<i>Exuviaella dactylus</i> (Stein) Schutt	X				
<i>Exuviaella marixa</i> Cienk.					
<i>Exuviaella vaginula</i> (Stein) Schutt		X		X	
<i>Exuviaella</i> sp. Cienk.			X		
<i>Fragilidium heterolobum</i> Balech					
<i>Glenodinium gymnodinium</i> Penard					
<i>Glenodinium lenticula</i> (Bergh) Schiller	X	X			
<i>Glenodinium oculatum</i> Stein	X	X	X		
<i>Goniadoma</i> sp. Stein	X				
<i>Gonyaulax catenata</i> (Levander) Kofoid					
<i>Gonyaulax diegensis</i> Kofoid					
<i>Gonyaulax digitalis</i> (Pouchet) Kofoid					
<i>Gonyaulax polyedra</i> Stein					
<i>Gonyaulax polygramma</i> Stein					
<i>Gonyaulax scripta</i> Kofoid					
<i>Gonyaulax tamarensis</i> Lebour					
<i>Gonyaulax tricornata</i> Jorg.					
<i>Gonyaulax</i> sp. Diesing					
<i>Gymnodinium acruginosum</i> Stein					
<i>Gymnodinium alba</i> in ms.	X	X	X	X	
<i>Gymnodinium album</i> Lindemann	X	X	X	X	
<i>Gymnodinium aureum</i> K. & S.	X	X	X		
<i>Gymnodinium biconicum</i> Schiller	X	X			
<i>Gymnodinium flavum</i> K. & S.					
<i>Gymnodinium fuscum</i> (Ehbg.) Stein			X		
<i>Gymnodinium grammaticum</i> (Pouchet) K. & S.		X			
<i>Gymnodinium helicoides</i> K. & S.	X				
<i>Gymnodinium heterostriatum</i> K. & S.	X				
<i>Gymnodinium lebouri</i> Pav.					
<i>Gymnodinium lunula</i> Schutt			X	X	
<i>Gymnodinium minor</i> Lebour			X	X	
<i>Gymnodinium minutum</i> Lebour			X		
<i>Gymnodinium paradoxum</i> Schilling			X	X	
<i>Gymnodinium puniceum</i> K. & S.			X		
<i>Gymnodinium ravenescens</i> K. & S.	X				
<i>Gymnodinium simplex</i> (Lohm.) K. & S.	X		X		
<i>Gymnodinium splendens</i> Lebour		X	X	X	
<i>Gymnodinium uberrimum</i> (Allman) K. & S.		X	X		
<i>Gymnodinium variable</i> C.E.H.	X	X	X	X	X
<i>Gymnodinium</i> sp. Stein	X	X	X	X	X
<i>Gyrodinium achronaticum</i> (Lebour) K. & S.	X				
<i>Gyrodinium aureum</i> Conrad (Schiller)	X	X			
<i>Gyrodinium contortum</i> (Schill.) K. & S.	X				

Table 6 (Continued)

Organisms	San Diego Bay	Mission Bay	Waccasasa Bay	Plymouth	Great South Bay
<i>Gyrodinium corallinum</i> K. & S.	X				
<i>Gyrodinium falcatum</i> K. & S.	X		X		
<i>Gyrodinium lacryma</i> (Meunier) K. & S.			X	X	X
<i>Gyrodinium pingue</i> (Schütt) K. & S.		X	X	X	X
<i>Gyrodinium</i> sp. K. & S.		X			
<i>Hemidinium nasutum</i> Stein			X		
<i>Heterodinium</i> sp. Kofoid			X		
<i>Massartia glandula</i> (C.E.H.) Schiller	X		X	X	X
<i>Massartia glauca</i> (Lebour) Schiller			X	X	X
<i>Massartia rotundata</i> (Lohm.) Schiller			X	X	
<i>Massartia</i> sp. Conrad		X			
<i>Miniscula bipes</i> Lebour	X	X		X	X
<i>Oxyrrhis marina</i> Senn	X	X	X		
<i>Oxytorma belgicae</i> Meunier					
<i>Oxytorma cribrosum</i> Stein		X			
<i>Oxytorma depressum</i> Schiller			X		
<i>Oxytorma gracile</i> Schiller			X		
<i>Oxytorma milneri</i> Murray & Whitting	X	X			
<i>Oxytorma</i> sp. Stein	X				
<i>Peridiniopsis rotunda</i> Lebour					
<i>Peridinium cerasus</i> Paulsen		X	X	X	X
<i>Peridinium claudicans</i> Paulsen					
<i>Peridinium depressum</i> Bailey			X		
<i>Peridinium diabolus</i> Cleve					
<i>Peridinium divergens</i> Ehbg.	X	X	X		X
<i>Peridinium macrosporum</i> Mangin					
<i>Peridinium monosporum</i> Paulsen			X	X	
<i>Peridinium minusculum</i> Pav.			X		
<i>Peridinium</i> sp. (Gauss F. mire) (Pavillard)	X				
<i>Peridinium pellucidum</i> (Bergh) Schütt					
<i>Peridinium pentagonum</i> Gran					
<i>Peridinium quadratum</i> Stein				X	X
<i>Peridinium subinerme</i> Paulsen			X	X	X
<i>Peridinium rochaeum</i> (Stein) Lemm	X		X	X	X
<i>Peridinium triquetrum</i> (Ehbg.) Lebour					
<i>Peridinium wisconsinensis</i> Eddy				X	
<i>Peridinium</i> sp. Ehbg.					
<i>Phalacroma acutum</i> (Schütt) Pav.	X	X	X		X
<i>Phalacroma mitra</i> Schütt					
<i>Phalacroma ovum</i> Schütt					X
<i>Phalacroma rotundatum</i> (Clap. & Lach.) Kofoid & Michener					
<i>Podoiampas palmipes</i> Stein				X	
<i>Polykrikos labours</i> C.E.H.		X	X		
<i>Polykrikos schwartzii</i> Butschli		X			
<i>Pouchetia maxima</i> K. & S.					
<i>Pouchetia polyphemus</i> Pouchet					
<i>Pronociliula pelagica</i> Fabre-Domergue				X	
<i>Protorcentrum gracile</i> Schütt		X	X		X
<i>Protorcentrum micans</i> Ehbg.		X	X		X
<i>Protorcentrum triangulatum</i> Martin		X	X	X	X
<i>Protodinium balteatum</i> Brarud		X	X	X	X
<i>Protodinium simplicis</i> Schiller		X			
<i>Protodinium</i> sp. Lohmann em Schütt					
<i>Pyrodinum bahamense</i> Plate				X	X
<i>Spirodinum</i> sp. Paulsen				X	X
<i>Thecadinium kofoidi</i> Lebour				X	X
<i>Torodinium robustum</i> K. & S.				X	X
<i>Warmowia polyphemus</i> (Pouchet) Schütt					
Totals	135	57	49	40	42

In the 1959 San Diego Bay studies, 99 genera and species were found. Only 54 of these occurred in the bay proper. The following year, 24 additional ones were found in Mission Bay. Similar additional lists and a portion of previous lists could be made up for most new localities, if sampled extensively. The large number of species (135) in Table 6 is not evidence that dinoflagellates dominate estuarine situations, but merely that they are the second largest group in number of species. Actually, we have found offshore dinoflagellate blooms more common than those inshore or in estuaries we have studied. Nevertheless, their roles are disturbing. The killing of any and all

animals by *Gymnodinium breve* Davis (Gunter *et al.*, 1948) in the waters around Trinidad, along the Mexican Coast near Vera Cruz, and along the Florida Gulf Coast is a major effect. *Gonyaulax catenella* (Levander) Kofoid is a food for California mussels (probably), but it leaves behind in the mussel tissues a toxin lethal to man (Sommer *et al.*, 1937); and *Gymnodinium flavum* is now reported as a probable fish killer (Lackey and Clendenning, 1963). There is no control at present for these organisms, and, since there are other dinoflagellates which might have similar effects, they pose real problems. Fortunately, they are amenable to laboratory culture (Barker, 1935; Delany, 1946; Sommer *et al.*, 1937), so their problems can be studied.

In large numbers, they may completely deplete the surrounding waters of PO₄. Lemon Bay, Florida, is an estuarine situation in that it receives the runoff of several small creeks. On June 18 and 19, 1964, samples of a bloom in the bay were counted; the water was centrifuged free of suspended organisms and particles; and soluble PO₄ and NO₃ were analyzed. Following are the results for four samplings:

Date	Sample	No./liter	PO ₄ (ppm)	NO ₃ (ppm)
6-18	1011	4,814,000	0.0	0.507
6-18	1013	3,230,000	0.0	0.541
6-18	1015	212,000	0.011	0.188
6-19	1031	580,000	0.011	0.217

The PO₄ loss is understandable, but the high nitrogen values are not, unless they represent a nitrogenous metabolite excreted by the dinoflagellate. *Gymnodinium breve* does not kill plants or other microorganisms, but its high numbers are coincident with a reduction of other microscopic species. On January 6, 1954, in the presence of 240,000/l *Gymnodinium breve*, there were present 4 species of other dinoflagellates, 18 diatoms, 1 blue-green alga, 2 chrysomonads, and 2 ciliates. These outnumbered *Gymnodinium breve* by 32,750/l, but this is a much smaller number of species and individuals than is usually found in a liter of such waters. How long the PO₄ remains depleted from *Gymnodinium breve* water is not known and is dependent on many factors, but it is serious for photosynthetic forms as long as it lasts.

BACILLARIEAE

Diatoms are considered elsewhere in this volume and will therefore receive scant attention here. Suffice it to say that in the estuarine situations studied, benthic diatoms far outnumbered plankton forms, and that, in most cases, they constituted a large percentage of the organisms present. This is not a generalization, however, because *Detonula* (Cleve) Gran was at times abundant in Great South Bay, and *Cyclotella* Brebisson attains high numbers at inshore situations, especially the mouths of rivers. Diatoms are impor-

tant in O₂ production, in the food chain, and in some other respects.

CHLOROMONADIDA

There is little available information relative to estuarine chloromonads. *Gonyostomum* Diesing and *Merotrichia* Mereschowsky do not survive long in brackish water. *Trentonia* Stokes is rarely seen, but is abundant in Warm Mineral Springs and in brackish water along the Inland Waterway of Florida. The organism is typical and easily recognized, and is not *Vacuolaria* Cienkowski, as suggested by Hollande (1952). *Thaumatomastix* Lauterborn and *Reckertia* Conrad, both doubtful as to taxonomic location, occur in estuaries, and there are several somewhat similar unidentified organisms which eventually may be placed here. The whole group needs very careful investigation, but their numbers in estuaries have not, thus far, been great.

PROTOZOA

MINOR GROUPS

If we follow Grasse, there are three groups of animals, primarily marine, some with chromatophores, and relatively few genera, which have not been thus far considered. These are the Ebridens, Silicoflagellides, and Coccolithophorides. The first, with two genera, *Ebria* Borgert and *Hermesinum* Zacharias, is encountered only occasionally in the estuaries we have studied; and the second, with the genus *Dicyosphaera* Ehrenberg, is even less common. Coccolithophora are more frequent, *Syracosphaera carterae* Braarud and Fager being the principal brackish-water species in these studies. No blooms appeared in the situations studied, but a very dense bloom appeared in a large outdoor laboratory tank. Huge populations of Coccolithophora like those known in the Oslo Fjord may not be typical estuarine phenomena.

ZOOFLAGELLATA

Three Orders of free-living zooflagellates are Choanoflagellata, with 23 genera; Bicoecidea, with five genera plus a sixth doubtful one; and Bodonidea, with 17 genera. Choanoflagellata are principally planktonic, Bicoecidea are epiphytic or sessile, and Bodonidea are creeping. About half the genera from each Order have been found in brackish water.

Many of them are abundant, and they are voracious eaters of bacteria. They also, like *Monas* (Ehrenberg) Stein and *Oicomonas* S. Kent, are active at lowered oxygen levels. This makes them important in recently polluted waters. However, no bloom of any single species has been recorded in the estuaries studied. It is the cumulative effect of some 25 genera living at approximately the same physiological level which becomes important. Earlier, for example, a summary of 2,936 small colorless flagellates per ml in water from the Fenholloway Estuary was presented. The unidentified group of 200 were almost certainly predominantly *Pteridomonas pulex* Penard, difficult to classify if in preserved material or while

Table 7. Ciliata recorded from five estuarine situations. X indicates presence, numbers indicate how many times recorded. P is a plankton sample, S a sediment, PS is no separation.

Location						
	Plymouth		Waccasassa Bay		San Diego	
	P	S	PS	PS	P	PS
<i>Aegyria reesi</i> (Rees) Kahl				1		
<i>Amphisiella multiseta</i> Sterki				2		
<i>Amphisiella</i> sp. Sterki	X					
<i>Amphorellopsis acuta</i> (Schmidt)					5	
<i>Amphorellopsis</i> sp. Kofoid & Campbell					1	
<i>Amphorellopsis tetragona</i> (Jorgensen)				1		
<i>Arachnella globosa</i> Kent		4				
<i>Askenasia faurei</i> Kahl				1		
<i>Askenasia volvorum</i> Clap. and Lach.		4				
<i>Aspidisca costata</i> (Duj.) Clap. & Lach.	X	8	4	1		
<i>Aspidisca heterix</i> Quennerstedt	X	5	3		1	
<i>Aspidisca leptaspis</i> Fresenius	X	1				
<i>Aspidisca lyncetus</i> Ehbg.	X	5	3			
<i>Aspidisca polystyla</i> Stein			2		2	
<i>Aspidisca pulcherrima</i> Kahl	X					
<i>Aspidisca turrita</i> Ehbg.	X	1				
<i>Aspidisca</i> sp. Ehbg.		1				
<i>Bursaria truncatella</i> O.F.M.				11		
<i>Chaeneca minor</i> Kahl	X	6		2		
<i>Chilodonella uncinata</i> Ehbg.						
<i>Chilodonella</i> sp. Strand	X					
<i>Chilodontopsis caudata</i> Blochmann	X					
<i>Chlamydodan triquetrus</i> (O.F.M.)	X					
<i>Cinetochilum marginatum</i> Perty		23	1			
<i>Cinetochilum marinum</i> Kahl		4				
<i>Codonella cratera</i> (Leidy) Vorce	X	33	39	2		
<i>Codonella</i> sp. Haeckel						
(E. M. Brandt, em. Jorg.)		4				
<i>Coleps hirtus</i> Nitzsch		4				
<i>Coleps pulcher</i> Spiegel						
<i>Coleps remanei</i> Kahl	X					
<i>Coleps</i> sp. Nitzsch	X					
<i>Culpoda inflata</i> (Stokes)			2			
<i>Condylostoma patens</i> (O.F.M.) Duj.	X	1	1			
<i>Cothurnia plectostyla</i> Stokes	X	2				
<i>Cothurnia</i> sp. Ehbg.		2	1			
<i>Coscillio quadruplicata</i>				1		
(Daday) Brandt						
<i>Cristigera media</i> Kahl		X				
<i>Cristigera minor</i> Penard	X	X				
<i>Cristigera phoenix</i> Penard			2			
<i>Cryptolophosia mucicola</i> Stokes						
<i>Cyclidium candens</i> Kahl						
<i>Cyclidium glaucoma</i> O.F.M.	X	X	27	18	33	4
<i>Cyclidium saltans</i> in ms.			2			
<i>Cyclidium</i> sp. O.F.M.	X					
<i>Cyclotrichium meunieri</i> Calkins		1	1			
<i>Cyclotrichium gigas</i> Faure-Fremiet				8		
<i>Didinium nasutum</i> O.F.M.		1		4		
<i>Diaphrys appendicularia</i> (Ehbg.) Duj.		1				
<i>Diaphrys scutum</i> Duj.	X	1				
<i>Diaphrys</i> sp. Duj.	X	1				
<i>Drepanomonas revoluta</i> Penard						
<i>Dysteria aculeata</i> Clap. & Lach.	X			3		
<i>Dysteria</i> sp. Huxley					1	
<i>Enchelyodon farctus</i> Clap. & Lach.	X					
<i>Enchelyodon laevis</i> Stokes		1				
<i>Epiplatys ambiguus</i> (Muller) Bartschi	X					
<i>Euploites karpa</i> Stein		X	1			
<i>Euploites rannus</i> (O.F.M.) Griffin	X	X	1			
<i>Euploites</i> sp. Ehbg.	X					
<i>Favella confessa</i> Kofoid & Campbell				1		
<i>Favella franciscanus</i> K. & E.	X					
<i>Favella markusovii</i> (Daday) Jorg.						
<i>Favella panamensis</i> K. & C.		3	1			
<i>Fronstonia leucostoma</i> Ehbg.		1				
<i>Fronstonia marina</i> Fabre-Domergue	X					
<i>Glebia fossata</i> Kahl	X					
<i>Glaucoma scintillans</i> Ehbg.		3				
<i>Gruberia unisulcata</i> Kahl	X					
<i>Halteria grandinella</i> O.F.M.		11	1			
<i>Helicostomella edentata</i>				1		
Faure-Frem. em K. & C.						

Table 7 (Continued)

Location						
	Plymouth		Waccasassa Bay		San Diego	
	P	S	PS	PS	P	PS
<i>Helicostomella kiliensis</i> (Lauckman) Jorg.						5
<i>Hemicyclidium</i> sp.						2
<i>Nannophrya truncata</i> Kahl						4
<i>Holophrya marina</i> Mansfield						
<i>Holophrya</i> sp. Ehbg.						
<i>Holosticha discocephala</i> Kahl	X				1	
<i>Holosticha multistriata</i> Kahl						
<i>Holosticha</i> sp. Kahl						
<i>Kentrophorus fasciolata</i> Sauerbrey	X					
<i>Keroplosis flavicans</i> Kahl						
<i>Laboea</i> sp. Lohmann						
<i>Lacrymaria olor</i> O.F.M.						
<i>Lacrymaria pupula</i> O.F.M.						
<i>Lagynopsis pumila</i> Mansfield						61
<i>Lembadion bullinum</i> Perty						
<i>Lembus infusorium</i> Calkins						
<i>Lembus pusillus</i> Quennerstedt	X	X			2	
<i>Lionotus cygnus</i> O.F.M.						
<i>Lionotus fasciolata</i> Ehbg.-Wrzesinski	X				6	
<i>Lionotus</i> sp. Stokes					1	
<i>Loxophyllum undulatum</i> Sauerbrey					3	
<i>Loxophyllum uninucleatum</i> Kahl	X				1	
<i>Mesodinium acarus</i> Stein					1	10
<i>Mesodinium cinctum</i> Calkins					3	
<i>Mesodinium pulex</i> Clap. & Lach.					26	2
<i>Mesodinium rubrum</i> Loam.	X	X			14	65
<i>Metacystis truncata</i> Cohn					1	4
<i>Metopus es</i> O.F.M.						1
<i>Microthorax pusillus</i> Engelmann						1
<i>Microthorax sulcata</i> Engelmann						1
<i>Monodinium balbiani</i> Fab.-Dom.						
<i>Nassula aurea</i> Ehbg.						
<i>Ophrydium</i> sp. Kent						1
<i>Opisthoceta henneguyi</i> Faure-Frem.						
<i>Oxytricha fallax</i> St. in						1
<i>Oxytricha petionella</i> Calkins						17
<i>Oxytricha</i> sp. Wrzes.						3
<i>Paramecium</i> sp. Hill						1
<i>Peritromus californicus</i> Kirby						
<i>Peritromus emarginatus</i> Stein						
<i>Placus incus</i> Kahl						
<i>Placus striatus</i> Cohn						
<i>Pleuronema crassum</i> Duj.						2
<i>Pleuronema marinum</i> Duj.						2
<i>Prorodon morganii</i> Kahl						
<i>Prorodon</i> sp. Ehbg.						
<i>Protoceratium pigerrima</i> (Cohn) Da Cunha						
<i>Remanella brunnescens</i> Kahl						2
<i>Remanella margaritifera</i> Kahl						
<i>Remanella rugosa</i> Kahl						
<i>Spatinidium procerum</i> Kahl						
<i>Stenozemella nivalis</i> (Meunier) em. K. & C.						
<i>Stephanopogon colpoda</i> Entz.						
<i>Stephanopogon mesnilii</i> Wolff						
<i>Strobilidium marinum</i> Faure-Frem.						5
<i>Strobilidium</i> sp. Schewiakoff						79
<i>Strobilidium cinctum</i> Kahl						9
<i>Strombidium cornicopium</i> (Wailes)						
<i>Strombidium legumen</i> Faure-Frem.						
<i>Strombidium pulchrum</i> Leegard						
<i>Strombidium sulcata</i> Clap. & Lach.	X	X				
<i>Strombidium</i> sp. Clap. & Lach.						
<i>Strongylium</i> sp. Sterki						
<i>Tachysoma petionella</i> (Muller-Stein) Stokes						
<i>Telostoma ferreri</i> R. & L. Granadori						
<i>Tetrahymina</i> sp. Furgason						
<i>Tiarina fuscata</i> Clap. & Lach.						
<i>Tintinnidium floridense</i> (Stein) Kent						
<i>Tintinnidium primatum</i> Busch						
<i>Tintinnidium semiciliatum</i> (Sterki) Kent						
<i>Tintinnopora berolinensis</i> Stein						
<i>Tintinnopora bermudensis</i> Brandt						
<i>Tintinnopora butchellii</i> Daday						

Table 7 (Continued)

Location	Plymouth		Waccasass Bay	San Diego	Great Bay	South Mision
	No. Samples	96	221	96	132	24
	P	S	PS	PS	P	PS
<i>Tintinnopsis compressa</i> Daday						1
<i>Tintinnopsis exserta</i> K. & C.						3
<i>Tintinnopsis ambristis</i> Meunier	X		7			2
<i>Tintinnopsis lindeni</i> Daday			1			
<i>Tintinnopsis minuta</i> Wailes	X	88	25	81	5	
<i>Tintinnopsis planaria</i> Cunha & Fonseca			1	6		
<i>Tintinnopsis provocans</i> Fariz & Cunha					1	
<i>Tintinnopsis schatti</i> Brandt					1	
<i>Tintinnopsis subacuta</i> Jorg.				1		
<i>Tintinnopsis tubulosa</i> Levander			1			
<i>Tintinnopsis urmiger</i> (Entz, Sr.) Daday	X					
<i>Tintinnopsis urnula</i> Meunier				1		
<i>Tintinnopsis</i> spp. (Stein em. Brandt) em. Jorg.	X	1				1
<i>Tintinnus pectinatus</i> K. & C.		14		36		
<i>Tintinnus tenuis</i> K. & C.				2		
<i>Tintinnus</i> sp. Schrank em Jorg	X	1		1		
<i>Trachelocerca entzii</i> Kahl	X				5	
<i>Trachelocerca coluber</i> Kahl						
<i>Trachelocerca phoenicopterus</i> Cohn	X		7			
<i>Trachelocerca</i> sp. Ehbg.	X					
<i>Trachelostyla candaia</i> Kahl				5		
<i>Trachelostyla pediculiformis</i> (Cohn)	X					
<i>Trichopelma sphagnorum</i> (Levander)			1			
<i>Trichopelma torpens</i> Kahl	X	1				
<i>Trochilia flavifilis</i> Smith	X					
<i>Trochilia salina</i> Entz	X					
<i>Uroleptus piscis</i> (Muller) Stein		1				
<i>Uroleptus</i> sp. Stein		2	7			
<i>Uronema filicium</i> Kahl						
<i>Uronema marinum</i> Duj.	X	X	4			
<i>Uronychia setigera</i> Calkins			5			
<i>Uronychia transfuga</i> (O.F.M.)						
<i>Urostromylium candanatum</i> Kahl	X					
<i>Urotricha farcta</i> Clap. & Lach.			4			
<i>Urotricha marina</i> Mansfield				2		
<i>Urotricha</i> sp. Clap. & Lach.			4	5		
<i>Vorticella microstoma</i> Ehbg.			1			
<i>Vorticella</i> sp. (Linn.) Ehbg.	X	4	9	2		
<i>Zoothamnium</i> (Ilogy) Ehbg.-Stein						
	181	13	80	82	41	42
					23	

swimming. Some workers regard this species as a stage of a heliozoan; others, as a zooflagellate. There are at least three widely separated colorless flagellates in this group, but direct microscopic observation shows all of them to be active ingestors of bacteria, thus, closely akin physiologically.

Edmondson (1959) loosely grouped 90 genera under "zooflagellates". Thirty-five of these have been found in the estuaries studied, and closer taxonomic attention would increase the number. For example, there are two undescribed organisms tentatively assigned to the genus *Pleuromonas*; various other new ones have simply been termed unidentified zooflagellates. Some, such as *Diphanoeca* Ellis and *Stephanoea* Ellis, we have found only in estuaries. The colorless flagellates, regardless of taxonomic status, are important in estuaries, primarily as holozoites.

CILIATA

More ciliates were identified in the estuarine studies than any other group. Table 7 lists 181, and a

number which could not be placed are, therefore, either given provisional names or listed simply as "sp". Distinctly planktonic occurrences, as shown in columns 1 and 5 of Table 7, are not numerous, and are principally tintinnids which live in a shell, and strombidia which typically do not. The two blooms in San Diego Bay were of *Glaucoma scintillans* Ehrenberg and *Mesodinium rubrum*. There are other reports of *Mesodinium rubrum* being a cause of "red water", but we have seen no records of other ciliates as bloom causes. Personal records include blooms of vorticellids in sewage treatment plant effluents, and in the Damariscotta River of Maine. This last (for which the original count is lost) was material sent on August 20, 1953. Evidently ciliate blooms are rare.

Ciliates are large and easy to identify, which accounts for the large number in Table 7. Their size makes them important in the ecology of an estuary. They are primarily bacterial consumers, and are found in the sediment-water interface where bacteria are abundant. *Euploites* demonstrably consumes sulfur bacteria, and observation of many other ciliates is equally convincing as to their food. In consuming bacteria, ciliates tend to keep bacteria in the growth phase. In turn, ciliates become a ready food for larger animals; a population of *Halteria* O. F. Muller is quickly decimated by copepods under laboratory experimentation.

Some ciliates eat other ciliates—*Didinium* O. F. Muller and *Condylostoma* (O.F.M.) Dujardin, for example. Whether food is absorbed is a moot point, but it can be done by some species. Size, abundance, and mode of living lend a large importance to ciliates in estuaries.

DISCUSSION

In considering estuaries as places where physical and chemical changes cover a wide range, it is apparent that food is brought in by the land-fed streams, and that the death of plants and animals on meeting adverse conditions adds further organic matter. One result is a large population of bacteria both in the water and in the sediments. This population, aside from its function of mineralization, may become direct food for large animals, as shown by ZoBell and Feltham (1938). Certainly it is effective in mineralization. But there are increasing evidences that soluble organic food is utilized by both chlorophyll-containing organisms (Volvocales, Euglenophyceae, and Chrysophyceae) and colorless saprozoites, such as the large populations of colorless euglenids in the sediment-water interface. It is with these four groups that critical culture work is badly needed. In this connection, more evidence might be accumulated as to the extracellular metabolites liberated by large populations of a single species, such as *Nannochloris bacillaris* Naumann and *Gymnodinium breve* which apparently liberate their metabolites into the surrounding water, and *Gonyaulax catenella* which frees toxin into the tissues of mussels.

The limiting effects of salinity are also seen in these surveys. By studying several estuaries and correlating organisms living and reproducing there with salinities, we can determine how sharp are the limits. The organisms discussed here certainly tolerate a wide range of salinity. Gunter (1961) has reviewed this matter, but not for the microscopic algae and protozoa. From the number of species listed here, it appears that a very large number of these microorganisms are widely tolerant. We are, however, basing this on morphology of field organisms and not on laboratory testing.

It is not presumed that any of these organisms are specific indicators of estuarine conditions. To begin with, estuaries are too diverse. Nevertheless, a number of organisms have not been found elsewhere. It is fascinating to find an organism repeatedly in the same set of environmental conditions, but these are too difficult to define. Thus, *Thiodendron mucosum* has occurred only where salinities were about 17 %. Other conditions, however, varied widely, and it would be naive to assume that a single salinity value is the determining factor. *Culkinsia aureus* has probably been found only in the Eel Pond at Woods Hole because not enough other possible habitats have been sampled.

Jeffries (1962) decided eight copepod species indicated certain water masses in Raritan Bay. It seems more probable that for the microscopic algae and protozoa, abundance and repeated occurrence in an estuary, compared with small numbers and limited occurrence elsewhere, might mark a species as an indicator organism. *Gymnodinium flatum* occurred in numbers and widely along the coast near San Diego while it was also abundant in Mission Bay. It could not be regarded as an indicator for the bay. But *Protodinium ostianum* might be, since it is restricted in occurrence to estuaries, in our experience. The same is true of *Massartia rotundata*.

SUMMARY

In summary, we may say that in estuaries the microbiota present depends upon the chemical composition of the water, with such factors as light, temperature, toxins, etc., exerting modifying influences. This is nowhere better illustrated than in the estuary of the Fen holloway. The normal biota of the stream and its tributaries virtually disappears at the entrance of paper mill waste. But with some dilution Eubacteriales, yeasts, filamentous bacteria, and fungi appear in enormous numbers. They are concerned with normal processes of decay, as in any situation. But the substrate here is specialized and rich in sulfur compounds, so that in the huge population, Chlamydomonadales and sulfur bacteria appear in quantity.

Eubacteriales and yeasts are food for large numbers of colorless *Monas* and *Pteromonas*. The former is ubiquitous but the latter is rarely seen. Thus, specialized substrates call forth specialized biotas.

All of the green, olive-green, blue-green, yellow-

brown, and red organisms offer as a primary role mineralization of organic compounds, whether they start with simpler ones elaborated by bacterial action, or with complex soluble compounds, or by ingestion of living creatures. Additionally, they add O₂ and CO₂ to the water, so that saturation, hardness, and pH are affected. Some microorganisms produce antimetabolites, and some, in decay of great populations, become nuisances because of the O₂ demand and because of odors. Finally, a normally numerically unimportant organism may assume great importance in a special environment.

Perhaps too little is known of the species and numbers of chrysomonads, colorless euglenids, and ciliates, the first in the marine environment generally, and the last two in the sediment-water interface, to assess their roles properly. It is postulated that the colorless euglenids share with bacteria and fungi the decomposition of organic matter, and that the ciliates keep the sediment-water interface bacteria in the endogenous growth phase.

Few rhizopods seem to attain significant numbers in estuaries, but certain species apparently are characteristic of brackish waters and may have some value as indicators. The three orders of colorless zooflagellates, despite a small number of genera and species, often attain large populations in estuaries, where their principal functions are the consumption of bacteria and becoming a part of the food chain. Estuarine waters have been the principal situations in which some of the rarer and unique species have been found.

Among the ciliates, the planktonic tintinnids are principally consumers, both of bacteria and other microbiota. The more numerous benthic ciliates share the same role.

The mixing of fresh and salt waters in estuaries has marked effects. Just as water hyacinths die on drifting downstream into salt water, so do many microbiotic species. There is too short a time for adaptation. And just as mangroves push upstream into brackish water, so do many oceanic species. There is some evidence that a real estuarine microbiota exists, and that its members attain greatest numbers there.

There are many indications that estuaries are specialized environments and that we need to know much more about the composition of their biotas before we can properly assess roles in productivity and mineralization.

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LITERATURE CITED

- BARKER, H. A., 1935. The culture and physiology of the marine dinoflagellates. *Arch. Mikrobiol.*, 6:157-181.
BIDWELL, H., 1949. *A Critical Review of Long Island's Pollution Problems as they Affect Shellfish*.

- Paper presented at N. Y. State Sewage Wks. Assoc., Long Island Section, West Hempstead, Long Island, pp. 1-5.
- BUTCHER, R. W., 1959. An introductory account of the smaller algae of British Coastal waters. Part VII. Euglenophyceae, Eugleninae. *Fisheries Invest. Ser.*, 4:1-17. H. M. Stationery Office, London.
- CARTER, N., 1938. New or interesting algae from brackish water. *Arch. Protistenk.*, 90:1-68.
- DELANY, M. J., 1946. The mass culture of a presumably autotrophic dinoflagellate. *Am. Midland Naturalist*, 56(1):126-132.
- EDMONDSON, W. T., 1959. *Fresh Water Biology*, second ed. John Wiley and Sons, New York.
- FRASER, J. H., 1939. Observations on the fauna and constituents of an estuarine mud in a polluted area. *J. Marine Biol. Assoc. U. K.*, 18(1):69-85.
- GLANCY, J. B., 1944. Observations on the fattening of oysters in Great South Bay, New York. *Proc. Nat. Shellfisheries Assoc.* pp. 1-6. Atlantic City, New Jersey. (mimeographed)
- GUNTER, G., 1961. Some relations of estuarine organisms to salinity. *Limnol. Oceanogr.*, 6(2):182-190.
- GUNTER, G., R. H. WILLIAMS, C. C. DAVIS, and F. G. W. SMITH, 1948. Catastrophic mass mortality of marine animals, and coincident phytoplankton bloom on the west coast of Florida, November 1946 to August 1947. *Ecol. Monographs*, 18:309-324.
- HOLLANDE, A., 1952. Classe des Chrysomonadines. In *Traité de Zoologie, Tome 1, Premier Fascicule*, edited by Pierre P. Grasse; pp. 471-570. Masson et Cie, Paris.
- JEFFRIES, H. P., 1962. Copepods as indicator species in estuaries. *Ecology*, 43(4):730-733.
- KRISS, A. E., 1963. *Marine Microbiology (deep sea)*. (Transl. from Russian) John Wiley and Sons, New York.
- LACKEY, J. B., 1960. Factors determining habitats of certain sulfur bacteria. *Quart. J. Florida Acad. Sci.*, 23(3):215-221.
- LACKEY, J. B., 1963. The microbiology of a Long Island Bay in the summer of 1961. *Intern. Rev. ges Hydrobiol.*, 48(4):577-601.
- LACKEY, J. B., and K. A. CLENDENNING, 1963. A possible fish-killing yellow tide in California waters. *Quart. J. Florida Acad. Sci.*, 26(3):263-268.
- LACKEY, J. B., and K. A. CLENDENNING, 1965. Ecology of the Microbiota of San Diego Bay, California. *Trans. San Diego Soc. Nat. Hist.*, 14(2):9-40.
- LACKEY, J. B., and R. M. DIXON, 1943. Some biological aspects of the Hays process of sewage treatment. *Sewage Ind. Wastes*, 15(6):1139-1152.
- LACKEY, J. B., and E. W. LACKEY, 1961. The habitat and description of a new genus of sulphur bacterium. *J. Gen. Microbiol.*, 26:28-29.
- LACKEY, J. B., and E. W. LACKEY, 1963. Microscopic algae and protozoa in the waters near Plymouth in August 1962. *J. Marine Biol. Assoc. U. K.*, 43(3):797-805.
- PARKE, M., I. MANTON, and B. CLARKE, 1955. Studies on marine flagellates, II: Three new species of *Chrysochromulina*. *J. Marine Biol. Assoc. U. K.*, 34:559-609.
- PARKE, M., I. MANTON and B. CLARKE, 1956. Studies on marine flagellates, III. Three further species of *Chrysochromulina*. *J. Marine Biol. Assoc. U. K.*, 35:387-414.
- PASCHER, A., 1913. Crytomonadinae. In *Die Süßwasserflora Deutschlands, Österreich und der Schweiz. Heft 2, Flagellatae 2*, edited by A. Pascher and E. Lemmermann; pp. 96-111. Gustav Fischer, Jena, Germany.
- REISH, D. J., 1957. Effect of pollution on marine life. *Ind. Wastes*, 1957:114-118.
- SOMMER, H., H. F. WHEDON, C. A. KOFOID, and R. STOHLER, 1937. Relation of paralytic shellfish poison to certain plankton organisms of the genus *Gonyaulax*. *Arch. Pathol.*, 24(5):537-559.
- STRICKLAND, J. C., 1946. A culture method for certain marine algae. *Science*, 103(2665):112-113.
- ZOBELL, C. E., 1946. *Marine microbiology*. Chronica Botanica Coll. Waltham, Massachusetts.
- ZOBELL, C. E., and C. B. FELTHAM, 1938. Bacteria as food for certain marine invertebrates. *J. Marine Res.*, 1:312-329.
- ZOBELL, C. E., and H. C. UPHAM, 1944. A list of marine bacteria including descriptions of sixty new species. *Bull. Scripps Inst. Oceanogr.*, 5(2):239-292.

The Estuarine Mycoflora

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Representatives of all commonly recognized classes of fungi have been collected from estuarine waters and sediments. For the most part, studies of this mycoflora have been taxonomic, but with some emphasis on ecology and distribution. Physiological investigations have been limited, and generally confined to experiments in saline tolerance. This paper is a brief review of the scope of the estuarine mycoflora and the investigations of elements of it.

COMPOSITION OF THE MYCOFLORA

All major groups of fungi are known to be represented in estuaries. Chytridiomycetes are found in various filamentous and planktonic algae. Oomycetes occur in some algae, but can also be collected in sediments, as can members of the Zygomycetes. A few plasmodiophoraceous fungi have been found in maritime vascular plants. Even the small class Hypochytridiomycetes is represented in estuarine waters. Ascomycetes and Fungi Imperfecti seemingly predominate in frequency in estuarine waters and sediments. Two Basidiomycetes have been reported from saline waters, but whether these are truly representative of a marine flora remains to be confirmed. Trichomycetes, of course, are well represented in estuarine and marine habitats on various crustaceans and arthropods.

The general constituency of the marine mycoflora is not at all different from that in a terrestrial or freshwater habitat. Indeed, many fungi recognized as common inhabitants of soil are to be found in estuarine sediments and as viable spores or conidia in estuarine waters. Water molds, commonly thought to be adapted only to fresh water, occur in the low-salinity reaches of estuaries. Other fungi, collected or isolated originally from marine habitats, occur widely throughout estuaries, although a few seem limited to the high saline portions. Parasitic and pathogenic forms associated with various substrates and hosts are also found in estuaries. One of the most important of these fungi is *Allescheria boydii*, the causal agent of madura foot in humans. This fungus is quite common on wood submerged in waters approaching the salinity of sea water.

ECOLOGY

Several investigators have attempted ecologically oriented studies of estuarine fungi (Johnson and Sparrow, 1961). Only those of a synecological nature are summarized here.

NON-LIGNICOLOUS SPECIES

Fungi in this category were first studied ecologically in the 1950's; the work of Höhnk (Johnson and Sparrow, 1961) is extensive. He showed that in coastal waters and sediments there was a general increase in the "phycomycetous" flora as the salinity became less, and conversely, a decrease in the density of Ascomycetes and Fungi Imperfecti. Considering the Chytridiomycetes (uniflagellates) as opposed to the Oomycetes (biflagellates), Höhnk found fewer of the former in increasingly saline conditions than in decreasing salinity, while the non-filamentous biflagellate species increased as salinity rose.

In a seven-year ecological distribution study of one estuary, Johnson (unpublished) found very few Chytridiomycetes and Oomycetes. Two, a *Rhisophydium* and an *Olpidium*, occurred throughout the estuary up to salinities of 32‰. Two Oomycetes, species of *Pythium*, had a similar wide tolerance for salinity. There was no evidence of any distributional patterns in relation to dissolved oxygen, nitrates or phosphates, nor to pH.

Much of the pertinent ecological information on fungi in dunes and marshes has come from Pugh's studies (1962, 1963), although others have also contributed (Johnson and Sparrow, 1961). It has been shown, for example, that fungi are more numerous in alkaline than in acidic sand dunes. Others have reported seasonal variations in occurrence of fungi in salt marshes and tidal flats, and there is good evidence that there is a greater percentage of frequency of fungi in high humus sediments than in sediments low in organic material. Pugh (1962) was able to categorize fungi in a developing salt marsh. Certain species increased in frequency upshore; these were considered salt marsh inhabitants. Salt marsh transients, on the other hand, increased downshore. Quantitatively but not qualitatively there are fewer fungi in salt marsh muds than in sand dune soils (Pugh, 1963). The low oxygen tension in the mud may be one reason for this difference.

LIGNICOLOUS SPECIES

Some attempts have been made at plotting geographical distribution of wood-inhabiting marine fungi (Ascomycetes and Fungi Imperfecti), but few if any patterns exist. These fungi seem widely distributed in both temperate and tropical waters. Only

one species, an ascomycete, seems limited to submerged bark; the remaining known species occur on wood.

Independently, Gold and Ritchie (Johnson and Sparrow, 1961) found that certain lignicolous species were influenced in estuarine distribution and growth in culture by both temperature and salinity. This dual influence, the "Phoma pattern", is exhibited by the occurrence of some species in higher saline waters only at high water temperatures. Similarly, *Phoma* species have an increasing tolerance to salinity as the incubation temperature is increased. Hughes (unpublished) observed a *Phoma* distribution with one ascomycete from an estuary, and an inverse *Phoma* pattern with another.

Johnson (unpublished) conducted a seven-year study of the distribution of lignicolous fungi in a North Carolina estuary. Seventy-three percent of the fungi collected were representative of genera known to contain terrestrial species, or were identifiable as soil-inhabiting species. Of these, 81 percent occurred on wood submerged in waters of less than 18% salinity, 7 percent occurred only in the freshwater portion of the estuary, and 12 percent were found throughout the entire estuary, from 0-32%. Five marine species, two Ascomycetes and three Fungi Imperfecti, developed on wood submerged at stations embracing a salinity range of 0-34%; the greatest density of marine species occurred in salinities of 18-30%.

The *Phoma* pattern was detectable for three Ascomycetes, but only if the fructification stage was considered. If the panels were incubated (Johnson and Sparrow, 1961) at room temperature after being removed from the water, and the populations tallied, no *Phoma* pattern was evident. A fungus showing the *Phoma* pattern in the estuary, for example, was not in evidence on panels in waters of 18-22% at 15°C., but was found in water at 10-12% at the same temperature. On incubation, however, panels from the higher salinity waters developed that same species. Thus, the *Phoma* pattern is exhibited by differential fruiting on panels from one salinity-temperature range, but the fungus may be present on panels from another range, although without producing ascocarps.

Three investigators have reported that a succession of fungi can occur on submerged wood. This problem has been studied incidentally to the aforementioned ecological distribution study. It is true that an apparent succession of fungi appears on submerged wood left in the water for varying periods of time. However, if panels are submerged for short periods and then incubated, all species within a successional scheme develop, indicating that all were present on the panel at harvest. Thus, succession is an expression of differential fruiting time, rather than replacement of one species by another.

PHYSIOLOGY

Physiological aspects of estuarine fungi have scarcely been investigated, although there are the beginnings of biochemical studies on marine fungi. For

the most part, even these attempts at biochemical analysis deal largely with nutrition. Early work on the physiology of estuarine and marine fungi (Johnson and Sparrow, 1961) was exclusively aimed at growth in culture containing various nutrients.

Borut and Johnson (1962) tested 21 isolates from estuarine sediments. While growth in none of these was inhibited by salinity stress when adequate nutrients were available, spore germination was markedly influenced by salinity. Goldstein (1963a) reported an NaCl requirement for two species of *Thraustochytrium*. The NaCl was not replaceable by KCl, and omission of the latter resulted in reduced growth. Neither species could utilize nitrogen in KNO_3 or $(\text{NH}_4)_2 \text{SO}_4$. Another species of the same genus utilizes nitrogen in the form of $(\text{NH}_4)_2 \text{SO}_4$, and although it requires NaCl for maximal growth, omission of KCl does not affect yields (Goldstein, 1963b).

In a study of the salt-tolerant imperfect *Zalerion cistula* (synonymous with *Z. maritima*, according to Anastasiou, 1963), Ritchie and Jacobsohn (1963) reported that the higher tolerance of the fungus to increasing salinity with rising temperature was a matter of osmotic pressure of the medium rather than a response to nutrients. They concluded that nutrient level was not a factor in dual temperature-salinity effects on fungal growth. Another approach to the physiology of fungi from saline waters was taken by Sgurros and Simms (1963). They have shown the lignicolous ascomycete *Halosphaeria mediosetigera* to have a thiamin requirement, and at least a partial requirement for biotin.

The foregoing studies serve to illustrate the status of knowledge of the physiology of estuarine and marine fungi. Clearly, emphasis has been on nutritional requirements and salinity tolerance. An extensive study of the biochemistry of numerous species is needed.

MORPHOLOGY

Initial taxonomic studies on marine Ascomycetes stressed spore appendages as generic characteristics. Since 1960, however, emphasis has shifted to utilization of the internal structure of the fructification as the most important criterion for generic delimitation. The arrangement of asci, presence or absence of interascicular filaments, and the general nature of the ascocarp wall have been employed to make taxonomic rearrangements. There is little agreement on the suitability of such characteristics, and as Johnson (1963a, b, c, d) has shown, the origin and development of ascospore appendages in species of certain genera offer little hope for establishing precise and unvarying taxonomic criteria.

CONCLUSIONS

Knowledge of fungi in estuaries is still fragmentary. Experimental work aimed at discovering ecological and physiological information is beginning, however, and could well lead, if combined with precise biochemical work, to explanation of the adaptability of fungi

to changing stresses in the saline environment. A few of the numerous unsolved problems are the inception of infection in the case of parasitic species, the role of fungi in estuarine productivity, and the interrelations of fungi to other segments of the estuarine biota.

LITERATURE CITED

- ANASTASIOU, C. J., 1963. The genus *Zalerion* Moore and Meyers. *Can. J. Botany*, 41:1135-1139.
- BORUT, S. Y., and T. W. JOHNSON, JR., 1962. Some biological observations on fungi in estuarine sediments. *Mycologia*, 54:181-193.
- GOLDSTEIN, S., 1963a. Development and nutrition of new species of *Thraustochytrium*. *Am. J. Botany*, 50: 271-279.
- GOLDSTEIN, S., 1963b. Morphological variation and nutrition of a new monocentric marine fungus. *Arch. Mikrobiol.*, 45:101-110.
- JOHNSON, T. W., JR., 1963a. Some aspects of morphology in marine Ascomycetes: *Halosphaeria* Linder. *Nova Hedwigia*, 6:67-79.
- JOHNSON, T. W., JR., 1963b. Some aspects of morphology in marine Ascomycetes: *Corollospora* Werdermann. *Nova Hedwigia*, 6:83-93.
- JOHNSON, T. W., JR., 1963c. Some aspects of morphology in marine Ascomycetes: *Amylocarpus* Currey, *Herpotrichiella* Petrak, and *Torpedospora* Meyers. *Nova Hedwigia*, 6:157-168.
- JOHNSON, T. W., JR., 1963d. Some aspects of morphology in marine Ascomycetes: *Ceriosporopsis* Linder. *Nova Hedwigia*, 6:169-178.
- JOHNSON, T. W., JR., and F. K. SPARROW, JR., 1961. *Fungi in oceans and estuaries*. J. Cramer. Weinheim, Germany.
- PUGH, G. J. F., 1962. Studies on fungi in coastal soils. II. Fungal ecology in a developing salt marsh. *Trans. Brit. Mycol. Soc.*, 45:560-566.
- PUGH, G. J. F., 1963. Ecology of fungi in developing coastal soils. In *Soil Organisms*, edited by Doeksen and Van der Drift; pp. 439-445. North Holland Publ. Co., Amsterdam, Netherlands.
- RITCHIE, D., and M. K. JACOBSON, 1963. The effects of osmotic and nutritional variation on growth of a salt-tolerant fungus, *Zalerion cistula*. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 286-299. Thomas, Springfield, Illinois.
- SGUROS, P. I., and J. SIMMS, 1963. Role of marine fungi in the biochemistry of the oceans. III. Growth factor requirements of the Ascomycete *Halosphaeria mediosetigera*. *Can. J. Microbiol.*, 9:585-591.

Occurrence and Origin of Yeasts in Estuaries

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It has long been known that yeasts occur in natural bodies of water (Fischer and Brebeck, 1894). Only recently, however, have specific studies been made of the ecology of these yeasts. A detailed account of developments up to 1960 was given in the monograph of Johnson and Sparrow (1961).

A number of reports on the quantitative distribution of yeasts in natural water bodies is now available (Table 1). In the open sea, average population densities of between 34 and 57 viable yeasts per liter have been found (Kriss and Novozhilova, 1954; Kriss, 1962; Van Uden and ZoBell, 1962). In littoral zones off Florida and California the population densities were higher, ranging from about 100 to 130 cells per liter (Roth *et al.*, 1962; Van Uden and Castelo Branco, 1963). In Douglas Lake, Michigan, the average count was as high as 273 cells per liter (Van Uden and Ahearn, 1963). No data are available on the population densities of yeasts in rivers. In the estuaries of the Tagus, Sado, and Guadiana Rivers, in Portugal, population counts ranged from 118 to 1,228 cells per liter (Taysi and Van Uden, 1964).

These data, though scarce and incomplete, indicate the quantitative distribution of yeasts occurring in marine, freshwater, and estuarine environments, and suggest that yeast populations attain their highest densities in inland waters and have their lowest densities in the open sea. In littoral zones, yeast population densities apparently are somewhat higher than in the open sea, but lower than in inland waters. Estuaries probably take an intermediate position with yeast populations fluctuating between the high levels of inland waters and the moderate levels of littoral zones. Differences between the various types of natural bodies of water are manifest not only in the magnitudes of population densities, but also in species composition.

There is evidence that estuarine waters contain not only more yeast cells per volume but also more yeast species than the adjacent sea. In the Tagus Estuary, for example, an average of 1,228 viable yeasts per liter was counted, while a total of 14 species was isolated (Taysi and Van Uden, 1964). With increasing distance from the estuary, the average yeast counts decreased to 95 per liter and the number of species isolated to five. A similar situation (Table 2) was found in the Sado Estuary and its adjacent littoral zone (Taysi and Van Uden, 1964).

As shown in Table 3, the species composition of

four estuaries has been studied: Biscayne Bay, Florida (Fell *et al.*, 1960; Fell and Van Uden, 1963; Roth *et al.*, 1962), and the estuaries of the Tagus, Sado, and Guadiana Rivers (Taysi and Van Uden, 1964).

Comparable data are available on the occurrence of yeast species in other bodies of water, for example: the Northwest Pacific, the Sea of Okhotsk, and the Black Sea (Kriss and Novozhilova, 1954; Kriss, 1962); the Atlantic near the Bahamas (Fell *et al.*, 1960); the Northeast Pacific (Van Uden and Castelo Branco, 1963); the Indian Ocean (Bhat and Kachwala, 1955); the Miami River (Capriotti, 1962); and Douglas Lake, Michigan (Van Uden and Ahearn, 1963).

When we consider the five yeast species most frequently isolated in each of the four estuaries and list their occurrence in the six marine waters and the two inland waters, two groups of species can be distinguished (Table 4). One group contains the species that occurred in most water bodies studied. This group includes species of the genus *Debaryomyces* with its imperfect forms *Torulopsis famata* and *T.*

Table 1. Average population densities of yeasts in natural bodies of water.

Water body	Average number of yeasts per 100 ml	References
Open Sea		
Pacific Ocean and Okhotsk Sea	3.4	Kriss and Novozhilova, 1954
Black Sea	5.4	Kriss and Novozhilova, 1954
Torres Strait	5.7	Van Uden and ZoBell, 1962
Littoral Zones		
Off S.E. Florida	<10	Roth <i>et al.</i> , 1962
Off S. California	13	Van Uden and Castelo Branco, 1963
Estuaries		
Guadiana, Portugal	11.8	Kawakita and Van Uden, unpublished
Sado, Portugal	24.5	Taysi and Van Uden, 1964
Tagus, Portugal	122.8	Taysi and Van Uden, 1964
Inland Waters		
Douglas Lake, Michigan	27.3	Van Uden and Ahearn, 1963

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Table 2. Yeast population densities and number of species at two estuarine stations and adjacent littoral zones (adapted from Taysi and Van Uden, 1964).

Distance from estuary (km)	Average number of yeasts per liter	Number of species
Tagus Estuary		
0.0	1,228	14
5.5	375	6
23.0	140	5
30.0	95	5
Sado Estuary		
0.0	245	9
7.0	148	5
17.0	123	6

candida, species of the genera *Rhodotorula* and *Cryptococcus*, *Candida guilliermondii*, *C. pulcherrima*, and *Kloeckera apiculata*. Though all these species are well known in their terrestrial habitats, apparently they are also well adapted to marine and aquatic environments. A few yeast species which have been isolated from marine habitats only (Van Uden and ZoBell, 1962) have not yet been encountered in estuaries.

A second group contains those yeast species that were found predominantly in estuaries but have been isolated only rarely from the open sea. This group includes forms like *Candida tropicalis*, *C. krusei*, and *C. parapsilosis* which are known to occur in the digestive tract of man and warm-blooded animals (Van Uden, 1958, 1960, 1963); and other species like *C. intermedia*, *C. catenulata*, *C. mycoderma*, and *C. zeylanoides* which occur on vegetable and inanimate terrestrial substrates.

Table 3. Yeast species most frequent in four estuaries.

Estuary and reference	Yeast species	Frequency percent
Biscayne Bay, Florida Buck and Van Uden, cited by Fell and Van Uden, 1963.	<i>Candida krusei</i> ¹	14
	<i>C. tropicalis</i>	13
	<i>Rhodotorula rubra</i>	13
	<i>R. glutinis</i>	11
	<i>C. guilliermondii</i>	10
Tagus, Portugal Taysi and Van Uden, 1964	<i>C. intermedia</i>	23
	<i>R. rubra</i>	17
	<i>Torulopsis candida</i>	15
	<i>R. glutinis</i>	15
	<i>Kloeckera apiculata</i>	10
Sado, Portugal Taysi and Van Uden, 1964	<i>Debaryomyces</i> sp.	52
	<i>R. glutinis</i>	10
	<i>C. catenulata</i>	8
	<i>C. mycoderma</i>	5
	<i>Cryptococcus albidus</i>	5
Guadiana, Portugal Kawakita and Van Uden, unpublished	<i>T. candida</i>	25
	<i>C. guilliermondii</i>	23
	<i>K. apiculata</i>	7
	<i>Candida pulcherrima</i>	6
	<i>Candida zeylanoides</i>	6

¹ *C. parapsilosis* was found as a dominant form instead of *C. krusei* in another survey of the same area (Roth et al., 1962).

The apparently dominated occurrence of some yeast species in estuaries and their apparent absence from or rarity in the open sea may be the result of a variety of causes, including the scarcity of available data. One obvious possibility which we explored in some detail was that of critical differences in salinity tolerance (Van Uden and Quinta, unpublished).

The maximum sodium chloride concentration (w/v)

Table 4. The occurrence of dominant estuarine yeast species in other bodies of water.

Species	Estuaries				Inland waters			Oceans and seas					
	Biscayne Bay	Tagus	Sado	Guadiana	Miami River	Lake Michigan	N. W. Pacific	(Baltic Sea)	Black Sea	Atlantic (Bahamas)	N. E. Pacific	Indian Ocean	
<i>Torulopsis famata</i> (<i>Debaryomyces</i>)	+	+	0	+	+	+	+	+	+	+	+	+	+
<i>Rhodotorula glutinis</i>	0	0	0	+	+	+	+	+	+	+	+	+	+
<i>K. rubra</i> (<i>Debaryomyces</i>)	0	0	0	+	+	+	+	+	+	+	+	+	+
<i>T. candida</i>	0	0	0	0	+	+	+	+	+	+	+	+	+
<i>Cryptococcus albidus</i>	+	0	0	0	+	+	+	+	+	+	+	+	+
<i>C. guilliermondii</i>	0	0	+	0	+	+	+	+	+	+	+	+	+
<i>C. pulcherrima</i>	0	0	0	0	+	+	+	+	+	+	+	+	+
<i>Kloeckera apiculata</i>	0	0	0	0	+	+	+	+	+	+	+	+	+
<i>C. parapsilosis</i>	0	0	+	0	+	+	+	+	+	+	+	+	+
<i>C. tropicalis</i>	0	0	0	0	+	+	+	+	+	+	+	+	+
<i>C. intermedia</i>	+	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. krusei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. catenulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. mycoderma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>C. zeylanoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0

0 Occurred as one of five most frequent species.

* Uncertain (dominant or not) reported.

Table 5. Salt tolerance of estuarine and marine occurring yeasts.

Species and occurrence	Number of isolates tested	Maximum NaCl tolerance (percent W/V)
Estuaries		
<i>Candida intermedia</i>	7	9 - 11
<i>C. krusei</i>	19	7 - 10
<i>C. catenulata</i>	5	10 - 11
<i>C. mycoderma</i>	8	5 - 9
<i>C. zeylanoides</i>	7	11 - 12
Estuaries and sea		
<i>C. guilliermondii</i>	8	10 - 15
<i>C. pulcherrima</i>	16	9 - 13
<i>Torulopsis famata</i>	11	17 - 24
<i>T. candida</i>	7	13 - 19
Sea		
<i>Metschnikowia sobellii</i>	12	12 - 18
<i>M. kriegeri</i>	4	11 - 14
<i>T. haemulonii</i>	2	24 - 25
<i>T. torresii</i>	1	16 - 17
<i>T. muris</i>	1	10 - 11
<i>C. marina</i>	1	12 - 13

which still permits growth in broth was determined for 119 yeast isolates (Table 5); 46 isolates belonged to five species that occurred as dominant forms in estuaries but have not been isolated from the open sea; 52 isolates were of four species that occur frequently in estuaries as well as the open sea; 21 isolates belonged to six species that have been isolated only from the open sea. The results indicated a tolerance of relatively high salt concentrations for all isolates tested. Phaff *et al.* (1952) made similar observations of yeasts isolated from shrimp in the Gulf of Mexico, and Bhat *et al.* (1955), of yeasts from the Indian Ocean. However, high salt tolerance is not restricted to yeast species that occur in natural bodies of water; it is rather common with yeasts as a group. For example, among about 100 species of the genera *Candida* and *Torulopsis* we found only three species of which some or all strains tested had a sodium chloride tolerance below 3.5 percent (Van Uden and Quinta, unpublished). Most known yeast species have sufficient salt tolerance to grow in estuaries and the seas. It was found by Ross and Morris (1962), however, that even in yeast species with a high maximum salt tolerance, growth phenomena like the lag and the yield, but not the rate, may be affected by sodium chloride concentrations well below the salinity of the sea. Sodium chloride, thus, does affect the adaptability of different species of yeast to marine and estuarine environments.

An obvious possible source of yeasts in estuaries is sewage pollution, and an extensive yeast speciation study of polluted streams and sewage treatment plants was executed by Bridge *et al.* (1960). When the species most frequently isolated by them are listed and the reported occurrence of these same species in estuaries is noted (Table 6), it is seen that most species from sewage and polluted streams are also dominant forms in one or more estuaries. In fact, we find the

same two ecological groups outlined before: (1) yeasts like *Rhodotorula glutinis* which are widespread in estuaries, the open sea, and inland waters; and (2) intestinal yeasts like *Candida tropicalis*, as well as yeasts from terrestrial substrates like *C. intermedia* which were found as dominant forms in estuaries but are rare in the open sea.

Besides sewage, gulls and terns were found to constitute sources of yeasts that occur in estuaries and other bodies of water. High numbers of viable yeasts were found in the intestinal contents of the Western Gull (*Larus occidentalis*) by Van Uden and Castelo Branco (1963). Recently we took samples from 69 gulls and terns caught in the Tagus Estuary. The average number of yeasts was 23,900 cells per gram of intestinal contents. Birds that harbored yeasts were found in all seven genera sampled, suggesting that gulls and terns are, as a group, suitable hosts for intestinal yeasts and, consequently, possible sources of marine and estuarine-occurring yeasts throughout the world (Table 7). However, when the species most frequently isolated from gulls and terns are listed and the reported occurrence of these same species in estuaries is noted, it is seen that of the four estuaries studied, only Biscayne Bay harbored, as dominant forms, yeast species that also occurred in the feces of gulls and terns (Table 8). Thus, it seems that some yeast species which thrive in one estuary may not develop detectably in other estuaries even though they are regularly introduced into the water. Intestinal yeasts like the species that occurred in the digestive tract of gulls and terns and in the water of Biscayne Bay have also been reported from other subtropical and tropical waters such as the Miami River (Capriotti, 1962), the Gulf of Mexico (Phaff *et al.*, 1952), and the Indian Ocean (Bhat *et al.*, 1955), but not from waters in colder zones.

Preliminary results of work under way in our laboratory (Van Uden and Ruivo, unpublished) indicate

Table 6. Yeasts in sewage and estuaries.

Species most frequent in polluted streams and sewage treatment plants (After Bridge <i>et al.</i> , 1960)	Percent frequency	Occurrence of same species in estuaries			
		Biscayne Bay	Tagus	Sado	Guadiana
<i>Rhodotorula glutinis</i>	13	O	O	O	+
<i>Trichosporon cutaneum</i>	13	+			
<i>R. rubra</i> (<i>mucilaginosa</i>)	10	O	O		+
<i>Candida parapsilosis</i>	7	O			
<i>C. krusei</i>	6	O			
<i>C. tropicalis</i>	6	O			
<i>C. guilliermondii</i>	5	O		+	O
<i>C. humicola</i>	4	+			
<i>C. intermedia</i>	4	+	O		
<i>Torulopsis famata</i>	4	+	O	O	+
<i>T. candida</i>	4	O	O	O	O

O Occurrence as one of five most frequent species.

† Occurrence (dominant or not) reported.

Table 7. Occurrence and population densities of yeasts in intestinal contents of gulls and terns.

Species	Number tested	Number with yeasts	Average of yeasts per gram of feces	
			Positive birds	All birds
Lesser Black-Backed Gull (<i>Larus fuscus</i>)	26	12	11,280	(5,210)
Slender-Billed Gull (<i>Larus genei</i>)	4	3	29,600	(22,200)
Herring Gull (<i>Larus argentatus</i>)	4	1	22,500	(5,600)
Black-Headed Gull (<i>Larus ridibundus</i>)	11	5	7,000	(3,180)
Sandwich Tern (<i>Sterna sandvicensis</i>)	3	2	70	(50)
Common Tern (<i>Sterna hirundo</i>)	6	5	253,100	(211,000)
Hooded Tern (<i>Sterna minuta</i>)	15	9	11,500	(9,200)
TOTAL	69	37	44,600	(23,900)

that the intestinal yeast *C. tropicalis* grows faster than *T. candida* in enriched sea water at 30° C.; at 20° C., however, *T. candida* has the higher maximum growth rate. *Candida tropicalis* is dominant in warm Biscayne Bay (mean June temperature near 30° C.) whereas *T. candida* predominates in the much colder water of Portuguese estuaries (mean June temperature near 20° C.). This suggests that the temperature of the water into which intestinal yeasts find their way may determine whether a population will build up. This example illustrates the almost total lack of knowledge regarding the factors that govern yeast ecology in bodies of water. What has been learned, during the last ten years or so, is that yeasts are a regular component of life in natural bodies of water, and we do have some knowledge now of the densities of yeast populations and of the species of yeasts that occur in these environments. Even this inventory knowledge is still very fragmentary, and the under-

taking of surveys designed to detect densities and specific compositions of yeast populations in oceans, seas, estuaries, rivers, and lakes should be encouraged.

Our present knowledge of the occurrence of certain well-defined yeast species in different natural water bodies, however, should now permit the selection of suitable strains for experimental ecology in the laboratory. Since yeasts are much easier to grow and handle than algae and many bacteria, but behave, unlike most other fungi, as unicellular organisms, the use of yeasts for the experimental elucidation of problems of microbial ecology, in general, in bodies of water may sometimes be of advantage.

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LITERATURE CITED

- BHAT, J. V., and N. KACHWALLA, 1955. Marine yeasts off the Indian Coast. *Proc. Indian Acad. Sci.*, **B41**:9-15.
- BHAT, J. V., N. KACHWALLA, and B. N. MODY, 1955. Some aspects of the nutrition of marine yeasts and their growth. *J. Sci. Ind. Res.*, **14C**:24.
- BRIDGE, C. W., H. J. PHAFF, M. W. MILLER, M. SHIFRINE, and E. KNAPP, 1960. Yeasts in polluted water and sewage. *Mycologia*, **52**:210-230.
- CAPRIOTTI, A., 1962. Yeasts of the Miami, Florida, area. II. From the Miami River. *Arch. Mikrobiol.*, **41**:147-153.
- FELL, J. W., and N. VAN UDEN, 1963. Yeasts in marine environments. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 229-340. C. C. Thomas, Springfield, Illinois.
- FELL, J. W., D. G. AHEARN, S. P. MEYERS, and F. J. ROTH, Jr., 1960. Isolation of yeasts from Biscayne Bay, Florida, and adjacent benthic areas. *Limnol. Oceanogr.*, **5**:366-371.
- FISCHER, B., and C. BREBECK, 1894. *Zur Morphologie, Biologie und Systematik der Kohlpilze, der Monilia candida Hansen und des Soorerregers*. J. Cramer, Weinheim, Germany.
- JOHNSON, T. W., Jr., and F. K. SPARROW, Jr., 1961. *Fungi in oceans and estuaries*. J. Cramer, Weinheim, Germany.
- KAWAKITA, S., and N. VAN UDEN, 1965. Occurrence and population densities of yeast species in the digestive tracts of gulls and terns. *J. Gen. Microbiol.*, **39**:125-129.

O Occurrence as dominant form.

+ Occurrence but not dominant.

¹ Fell and Van Uden, 1963.

Species most frequent in feces of gulls and terns (After Kawakita and Van Uden, 1964)	Percent frequency	Occurrence of same species in estuaries			
		Biscayne Bay	Tagus	Sado	Guadiana
<i>Saccharomyces cerevisiae</i>	20				
<i>Torulopsis glabrata</i>	12				
<i>S. oleaginosus</i>	10				
<i>Candida tropicalis</i>	9	O			
<i>C. albicans</i>	9	O ¹			
<i>T. pintoipesii</i>	7				
<i>C. krusei</i>	4	O			
<i>C. norvegensis</i>	4				
<i>C. tenuis</i>	4				
<i>C. parapsilosis</i>	2	O		+	

- KRISS, A. E., 1962. *Marine Microbiology*. Translated from Russian by J. M. Shewan and Z. Kabata. Oliver Boyd, Edinburgh and London.
- KRISS, A. E., and M. I. NOVOZHILOVA, 1954. Are yeasts inhabitants of seas and oceans? *Mikrobiologiya*, 23:669-683.
- PHAFF, J. J., E. M. MARK, and O. B. WILLIAMS, 1952. Yeasts isolated from shrimp. *Mycologia*, 44:431-451.
- ROSS, S. S., and E. O. MORRIS, 1962. Effect of sodium chloride on the growth of certain yeasts of marine origin. *J. Sci. Food Agr.*, 13:467-475.
- ROTH, F. J., JR., D. G. AHEARN, J. W. FELL, S. P. MEYERS, and S. A. MEYER, 1962. Ecology and taxonomy of yeasts isolated from various marine substrates. *Limnol. Oceanogr.*, 7:178-185.
- TAYSI, I., and N. VAN UDEN, 1964. Occurrence and population densities of yeast species in an estuarine-marine area. *Limnol. Oceanogr.*, 9:42-45.
- VAN UDEN, N., 1958. Intestinal yeasts of man and domestic animals. *Proc. 6th Intern. Congr. Trop. Med. Mal.*, 4:612-616.
- VAN UDEN, N., 1960. The occurrence of *Candida* and other yeasts in the intestinal tracts of animals. *Ann. N. Y. Acad. Sci.*, 89:59-68.
- VAN UDEN, N., 1963. Factors of host-yeast relationship. In *Recent Progress in Microbiology*; vol. 8, pp. 635-643. Univ. of Toronto Press, Toronto, Canada.
- VAN UDEN, N., and D. C. AHEARN, 1963. Occurrence and population densities of yeast species in a freshwater lake. Antonie van Leeuwenhoek. *J. Microbiol. Serol.*, 29:308-312.
- VAN UDEN, N., and R. CASTELO BRANCO, 1963. Distribution and population densities of yeast species in Pacific water, air, animals, and kelp off Southern California. *Limnol. Oceanogr.*, 8:323-329.
- VAN UDEN, N., and C. E. ZOBELL, 1962. *Candida marina* nov. spec., *Torulopsis torresii* nov. spec., and *T. maris* nov. spec., three yeasts from the Torres Strait. Antonie van Leeuwenhoek. *J. Microbiol. Serol.*, 28:275-283.

Diatom Communities in Estuaries

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The types of diatoms which compose estuary communities are usually benthic and neritic species, although some truly oceanic plankton species may be brought in by tidal action or wind. Benthic species are those which live close to or on the substrate, or they may be attached to plants or various kinds of debris. The neritic species are those which have resting cells which remain on the bed of the estuary during unfavorable conditions but spend most of their vegetative stage afloat. The oceanic or plankton species are those which spend their vegetative and resting stages afloat.

The diatom community is therefore composed of both the bottom-living species and the floating species which are usually referred to as plankton. The floating species are neritic and also benthic species which have been brought up from the bed of the estuary by turbulence. Many of the neritic species have various types of structures which increase their ability to float. Gran (1912) classifies them as follows: the "bladder type", that is, *Coscinodiscus*, in which the center of the large cell is filled with a thin fluid having a specific gravity a little lighter than water; the ribbon or filamentous type, exemplified by *Fragilaria*; the hair type, the shape of which is greatly prolonged in one direction, as in *Rhizosolenia*; and the branching type, which has a surface enlarged by various types of hair-shaped outgrowths, as in *Chaetoceros*.

ECOLOGICAL FACTORS AFFECTING THE OCCURRENCE OF DIATOMS

The abundance of diatoms is determined by the interaction of many factors in the environment, any one of which may be limiting. Often the numbers of diatoms present increase suddenly; this increase is called a diatom bloom. These blooms may occur once or several times during the year, as pointed out by Patten *et al.* (1963) in the Chesapeake Bay. Usually the spring bloom is in April-May and the fall bloom, in September-October. However, Riley (1959) found a winter flowering in Long Island Sound between January and March and an autumn flowering between August and October. In coastal areas where there is a continuous runoff from the land or where upwelling occurs, such cyclic variation in the abundance of diatoms may not occur if other factors, such as light, are not limiting.

Light and temperature seem to be important environmental factors which influence diatom abundance. It is difficult under natural conditions to dis-

sociate these two factors. Atkins (1928) observed at Plymouth that the spring bloom occurred when the length of the day was 10-12 hours and about three hours of sunlight was present. The variation in the time of outbreak seemed to be brought about by variation in the amount of sunlight. Riley (1942) concluded that a balance between the effects of vertical turbulence and the increase of vernal radiation determines the beginning of spring flowering. The duration of the autumn bloom often seems to be controlled by the amount of light available (Harvey *et al.*, 1935). Davidson and Huntsman (1926) state that the reason for the negligible amount of diatom growth in winter is the small amount of light and low temperature. Often, however, it does not seem to be the amount of incident light that is limiting, but rather the turbidity of the water caused by turbulence producing the limiting light effect. Riley (1941) found that at Georges Bank in the Gulf of Maine vertical turbulence and solar radiation were the chief limiting factors on plankton growth throughout the late autumn, winter, and early spring. Gran and Braarud (1935) attributed the small diatom growth in the Bay of Fundy and along the New Brunswick coast to lack of sufficient light due to turbulence. They state that in order to survive a diatom must be exposed to light at least one-fifth of the time.

Riley (1959) found that the variations in the times of the winter outbursts of diatoms which he observed in Long Island Sound were caused by variations in radiation and temperature. Radiation controls the photosynthetic rate, and temperature affects the rate of growth by its effect on respiration. According to Riley's estimate, radiation of approximately 100 cal/day is necessary to maintain a steady state in winter, whereas 500 cal/day is required in the autumn.

The kinds and the abundance of diatoms in estuaries seem to be influenced by temperature. Yentsch and Ryther (1959) found that the proportion of nanoplankton (small diatoms) in the total population increased sevenfold between March and July when the temperature rose from 2-21°C. However, they concluded that temperature was probably not the only factor producing the change. Balech (1960) has found that collections from the same region off the California coast at the same season of the year had very different species present in a warm year than in a cold year.

Sato (1958), studying the diatoms in Shiogama Harbor, found that the neritic species became more

abundant when the attached species disappeared. The attached species were rather abundant between April and July, very abundant between October and December, almost absent from January to March, and very few in August to September.

Castenholtz (1963) has found that in the intertidal zone the vertical species pattern and the species present depended principally on the time the diatoms were exposed to direct sunlight during emergence and, therefore, were influenced by the sky conditions and the position of the sun during low water. Furthermore, it was shown that it is probably the desiccation, high temperature, and high light intensity that limits the growth of diatoms in these intertidal zones. Various species seem to grow best under different light intensities and different amounts of insolation exposure.

Temperature also influences the time of optimum development of many species in estuaries. For example, Allen (1928) noted that *Skeletonema costatum* prefers cool water for its best development and *Chetoceros curvisetum* requires a temperature of 18–20°C. for optimum growth. It is believed by many that the length of the day and the temperature are among the more important factors causing the succession of dominant or common species in an estuarine diatom community.

Since much of the diatom community in an estuary is in the form of plankton, turbulence is an important factor, as it greatly affects the ability of a diatom to float. The lessening of turbulence of the water as spring approaches contributes to the production of the spring bloom. Turbulence also affects the distribution of water masses, brings about mixing, and produces turbidity which affects light penetration.

The nutrient level of the water has a great deal to do with the number of diatoms an estuary will support. Compared with the open sea, estuaries are usually fairly high in nutrients. Gran (1912) pointed out that in northern Europe the plankton development may be one of three types. When the nutrients are continually augmented by a supply from land or from vertical currents, a well-developed diatom flora may continue throughout the year, unless light is a limiting factor in winter. If the nutrient supply is intermittent, the diatom maximum and minimum will alternate. In some cases little or no supply of nutrients is derived from land, and vertical circulation is possible only early in the spring. Such conditions produce only one diatom bloom, and that early in the spring. On the western coast of Africa, Hentschel (1928) found that the regions of diatoms and phosphorus abundance were similar. Likewise, on the western coast of South America, Gunther (1936) found that the diatoms are particularly well developed in waters rich in phosphorus.

Lack of phosphorus may also limit diatom growth. Marshall and Orr (1928) noted that when the PO₄ was used up, the diatom maximum disappeared. Nitrogen in the Bay of Fundy and the Gulf of Maine may be responsible for diatom succession (Gran and

Braarud, 1935). Lillick (1937), from her study of diatoms in the Woods Hole region, concluded that NO₃ is more critical for phytoplankton production than PO₄. One of the causes for a succession of different species in a flora seems to be the varying requirements for these mineral substances. Gran and Braarud (1935) found that when the water in the Gulf of Maine was rich in nutrients, *Thalassiosira* was dominant. As the NO₃ and PO₄ were used up, species such as *Rhizosolenia alata*, which can live on a smaller amount of nutrients, became more common. Thus, depending on the nutrient supply, the species of a flora may vary. Braarud and Hope (1952) found that the entrance of sewage into an estuary greatly increased the phosphorus and nitrogen content of the water and was responsible, in part, for the rich growth of diatoms.

Besides nitrogen and phosphorus, iron and silicates have been found to be important in determining the abundance of diatoms. Certain species of diatoms (Guillard and Cassie, 1963) such as *Skeletonema costatum* require vitamin B₁₂. The number of molecules per cubic microgram varied from 5–18.4, which is similar to the requirement of other organisms. Guillard and Cassie point out that the time at which B₁₂ is present during the development of a bloom may be more important than the total amount present. Likewise, Hulbert and Rodman (1963) have found that neritic species were favored by the availability of B₁₂, iron, and silicates. Patten *et al.* (1963) found that in Chesapeake Bay *Skeletonema costatum* is more common in upper inland areas where one might expect the greatest amount of vitamin B₁₂.

Salinity is an important environmental factor which affects the number of species and, more particularly, the kinds of species present. Uyeno (1957) found in Osaka Bay that in summer the quantity of diatoms could be expressed as a function of salinity and temperature. In Chesapeake Bay, Patten *et al.* (1963) found the lowest diversity of species on the eastern side where the salinity was highest.

STRUCTURE OF DIATOM COMMUNITIES

There are many kinds of species in estuaries because the water characteristics are so variable. This is particularly true in the mouths of rivers. At seasons of high flow the water may have fresh characteristics and the predominant flora may be one which is found in the lower part of freshwater rivers, whereas during periods of low flow and high salinity the flora may be primarily brackish-water types with a few marine species. The cause of this complete change in kinds of species of collectable flora is the rapid reproductive rate which diatoms may have under favorable conditions. There are relatively few species which are characteristic of the wide range of salinity and other water characteristics associated with estuaries. They are referred to as euryhaline species.

Under natural conditions in estuaries—conditions which have not been adversely affected by pollution—

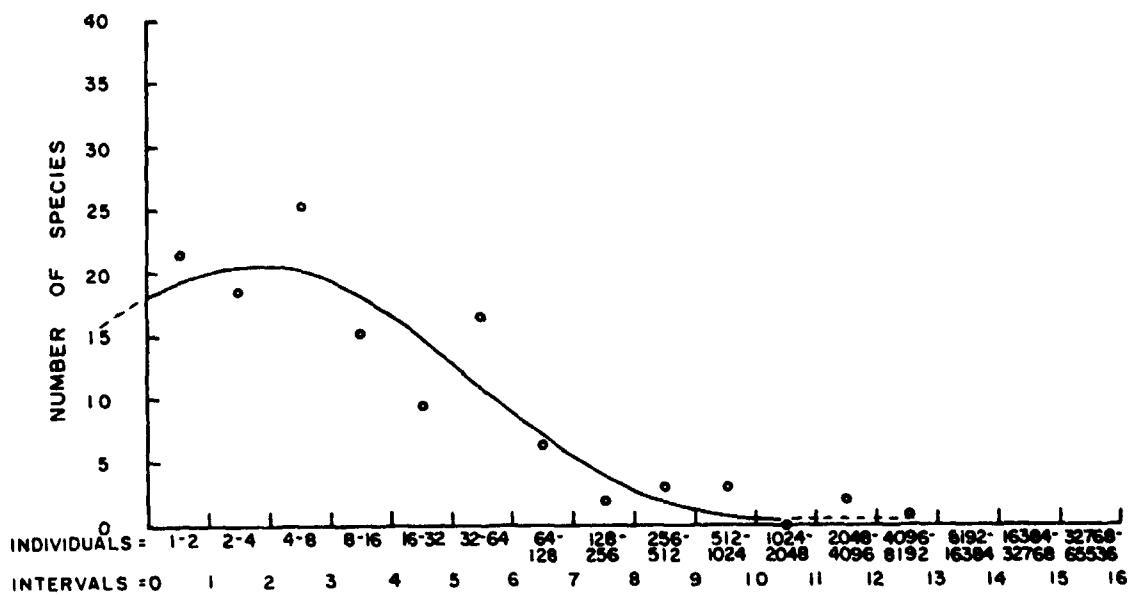


Fig. 1. Structure of a natural diatom community (Chocolate Bay, Texas).

the diversity of species is high and the populations of most of the species are fairly small. This structure of the diatom community can be expressed by the formula for a truncated normal curve. The graph of the curve in Figure 1 shows that the height of the mode is 21 species and the curve extends over 13 intervals. Other studies show the height of the mode to vary from 17-24 species. The shape of the curve is similar to that for natural rivers, in which the height of the mode is usually 22-28 species and the curve covers 10-12 intervals (Patrick *et al.*, 1954). Thus, the height of the mode in estuaries is not quite so great as in rivers, and the sizes of the populations are more variable. The shape of these curves (the diversity pattern) is quite stable unless pollution occurs. So, although the kinds of species may change, the numbers and the relative sizes of populations of species composing the community do not change greatly. It is true that during some seasons of the year a few species may be represented by large populations, but this does not alter the basic structure of the community. Patten (1961) has found that the number of species forming a phytoplankton community has a high stability coefficient, and that it is much higher than the stability coefficient of the environmental factors. Subrahmanyam and Viswanatha (1960) found that the diatom flora on the west coast of India was characterized by a large number of species, but only a few of them (about 12 percent) formed large populations. Hulbert (1963) found, in the coastal waters of Venezuela, that the phytoplankton was characterized by many species of very small populations, and only a few were characterized by large populations.

If, however, the environmental conditions are extremely unfavorable for diatoms, and as a result only a few species can live in these conditions, the sizes of diatom populations are more variable; some are

very small as represented by species that can barely exist, and the very few that can thrive under such conditions have large populations, providing the nutrient level is high enough to support such populations. This is the condition we find in many polluted waters (Fig. 2).

In order to evaluate correctly an algal community, one must take into consideration the number of cells or individuals present. This is largely determined by the chemical constituents in the water (for example, nitrates, phosphates, and the other chemicals necessary to build protoplasm) and by the various physical characteristics of the environment which promote photosynthesis. The quantities of these environmental characteristics determine the number of cells which can be supported. The number of taxa into which these cells are distributed determines the diversity of the community. A well-diversified community is probably capable of using the variable environment to its fullest capacity. A community of a few species might use the environment as effectively as one of many species at any given point in time, but the evidence suggests that this is not so over time.

The algae are one of the most important groups at the base of the food chain or web, and so the more diversified the community of algae is, the more useful it will be to a greater variety of organisms which prey upon it. The distribution of the biomass of algae into a few species jeopardizes its usefulness as food. For example, if the algae community is composed of only a few species of blue-green algae, which often happens in a polluted estuary, the biomass may be as great as in a naturally eutrophic estuary, but its usefulness as a source of food is greatly decreased.

Not only the biomass, but the diversity pattern and the kinds of species must be considered to understand a community or to relate it to the flow of energy in

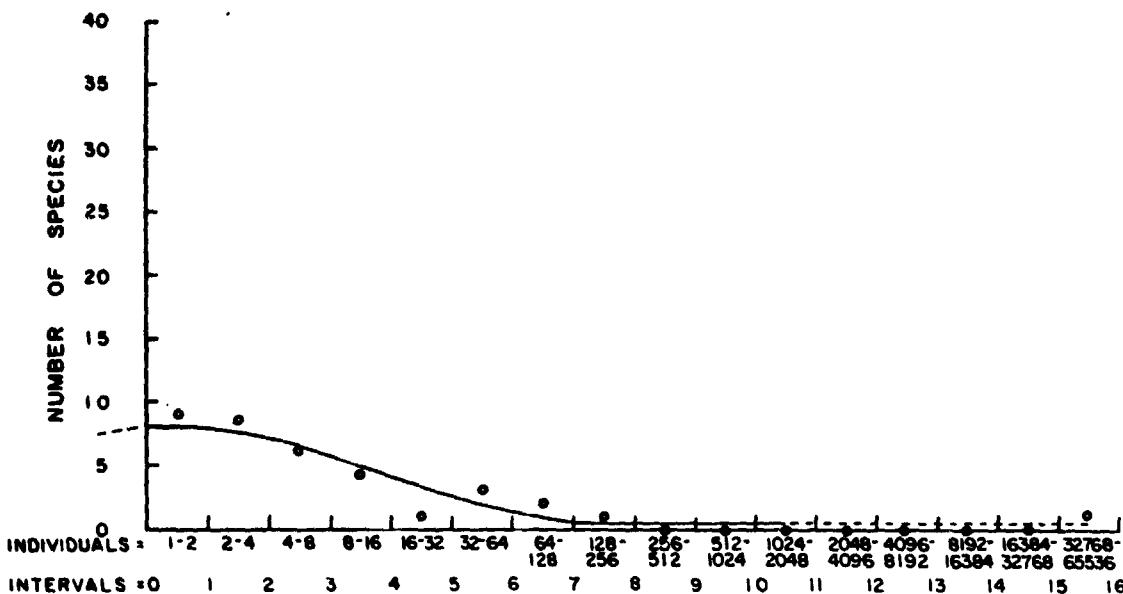


Fig. 2. Structure of a diatom community in a polluted area, showing the relatively small number of species and the unequal sizes of populations of various species (Houston Ship Channel, Texas).

the food chain. Examples of various types of diatom community structures are shown in Figure 3. The first diagram illustrates a diatom community composed of many species with very small populations (indicated by narrow lines). These types of communities are typical of low nutrient-level water, and the biomass is very small. The second and third diagrams represent diatom communities with the same biomass. The difference is that in the second diagram the nutrients are in proportions suitable for many species, and as a result each of these has a relatively small population. In the third diagram there is an imbal-

ance of nutrients and as a result only a few species can utilize them and the sizes of the populations of the species are very different. It is conceivable that a much smaller biomass of species which provides desirable sources of food might be more valuable to the food chain than a larger biomass fixed in undesirable food species. The total biomass may be correlated with nutrient level of the water, but its importance in the food chain is greatly influenced by the kinds of species which compose it.

SUMMARY

From this discussion it is evident that estuaries include a highly variable group of environmental characteristics, and that under most conditions there is a very large group of diatom species that can live in them. The particular species that occur and the size of their populations depend upon specific combinations of environmental conditions. However, there is a high consistency in the diversity which any particular area will support so long as the environmental characteristics of that particular area do not change radically. Such radical changes may be brought about naturally, and often occur as a result of pollution.

LITERATURE CITED

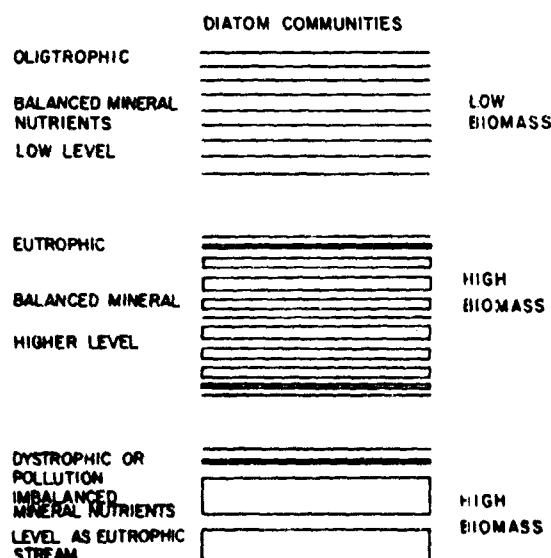


Fig. 3. Relationships of the amount of biomass and species diversity to various nutrient conditions in water.

- ALLEN, W. E., 1928. Review of five years of study on phytoplankton at southern California piers, 1920-1924 inclusive. *Bull. Scripps Inst. Oceanog. Tech. Ser.*, 1: 357-401.
- ATKINS, W. R. G., 1928. Seasonal variations in phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *J. Marine Biol. Assoc. U. K.*, 15: 191-205.
- BALECH, E., 1960. The changes in the phytoplankton population off the California coast. *Scripps Inst. Oceanogr. Contr.*, 1960: 499-504.

- BRAARUD, T., and B. HOPE, 1952. The annual phytoplankton cycle of a landlocked fjord near Bergen. *Rept. Norweg. Fisheries and Marine Invest.*, 9(16):1-26.
- CASTENHOLTZ, R. W., 1963. An experimental study of the vertical distribution of littoral marine diatoms. *Limnol. Oceanogr.*, 8(4):450-463.
- DAVIDSON, V. M., and A. G. HUNTSMAN, 1926. The causation of diatom maxima. *Trans. Roy. Soc. Can., Sect. V*, 20:119-125.
- GRAN, H. H., 1912. Pelagic plant life. In *Depths of the Ocean*, edited by J. Murray and T. Hjort; pp. 307-386. Macmillan and Co., Ltd., London.
- GRAN, H. H., and T. BRAARUD, 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. *J. Biol. Board Can.*, 1:279-467.
- GUILLARD, R. R. L., and V. CASSIE, 1963. Minimum cyanocobalamin requirements of some marine centric diatoms. *Limnol. Oceanogr.*, 8(2):161-165.
- GUNTHER, E. R., 1936. A report on oceanographical investigations in the Peru coastal current. *Discovery Rept.*, 13:107-276.
- HARVEY, H. W., L. H. N. COOPER, M. V. LABOUR, and F. S. RUSSELL, 1935. Plankton production and its control. *J. Marine Biol. Assoc. U. K.*, 20:407-441.
- HENTSCHEL, E., 1928. Die Grundzüge der Planktonverteilung im Südatlantischen Ozean. *Intern. Rev. Ges. Hydrobiol. u. Hydrol.*, 21:1-16.
- HULBURT, E. M., 1963. Distribution of phytoplankton in coastal waters of Venezuela. *Ecology*, 44(1):169-171.
- HULBURT, E. M., and J. RODMAN, 1963. Distribution of phytoplankton species with respect to salinity between the coast of southern New England and Bermuda. *Limnol. Oceanogr.*, 8(2):263-269.
- LILLICK, L. C., 1937. Seasonal studies of the phytoplankton of Woods Hole, Mass. *Biol. Bull.*, 73:488-503.
- MARSHALL, S. M., and A. P. ORR, 1928. The photosynthesis of diatom cultures in the sea. *J. Marine Biol. Assoc. U. K.*, 15:321-360.
- PATRICK, R., M. H. HOHN, and J. H. WALLACE, 1954. A new method for determining the pattern of the diatom flora. *Notulae Naturae Acad. Nat. Sci. Phila.*, 259:1-12.
- PATTEN, B. C., 1961. Preliminary method for estimating stability in phytoplankton. *Science*, 134:1010-1011.
- PATTEN, B. C., R. A. MULFORD, and J. E. WARINER, 1963. An annual phytoplankton cycle in the lower Chesapeake Bay. *Chesapeake Sci.*, 4(1):1-20.
- RILEY, G. A., 1941. Plankton studies. IV. Georges Bank. *Woods Hole Oceanogr. Inst. Coll. Papers*, 287.
- RILEY, G. A., 1942. The relationship of vertical turbulence and spring diatom flowering. *J. Marine Res.*, 5:67-87.
- RILEY, G. A., 1959. Environmental control of autumn and winter diatom flowerings in Long Island Sound. *Intern. Oceanogr. Congr.*, 1959; *Preprints*, 850-851.
- SATO, S., 1958. Ecological studies on attaching diatoms, with special reference to the relations to planktonic and benthic diatoms. I. General aspects of the seasonal variation of the attaching diatoms at the Shiogama Harbour. *Bull. Tohoku Regional Fisheries Res. Lab.*, 11:94-111.
- SUBRAHMANYAN, R., and A. H. VISWANATHA SARMA, 1960. Studies on the phytoplankton of the west coast of India. III. Seasonal variation of the phytoplankters and environmental factors. *Indian J. Fisheries*, 7(2):307-336.
- UYENO, F., 1957. The variation of diatom communities and the schematic explanation of their increase in Osaka Bay in summer. III. Schematic explanation of increase of diatoms in relation to the distribution of chlorinity. *J. Oceanogr. Soc. Japan*, 13(3):107-110.
- YENTSCH, C. S., and J. H. RYTHER, 1959. Relative significance of the net phytoplankton and the nanoplankton in the waters of Vineyard Sound. *Conseil Perm. Intern. Exploration Mer*, 24(2):231-238.

The Plankton of Estuaries

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The estuarine environment, commonly denoted as a river mouth, an embayment, or a narrow sound, has many variants. Biologically speaking, it has the common denominator that the semi-enclosed nature of this environment permits the maintenance of a population that is at least native, if not strictly endemic.

The salinity is usually altered from that of sea water, and in a typical estuary the salinity is reduced. Some investigators recognize the term "negative estuary", denoting an embayment with little freshwater drainage and with sufficient evaporation to increase the salinity significantly. In its biological generalities this kind of estuary is somewhat similar to the freshened one, although the details of species composition will be very different.

The real division is between the shallow, well-mixed estuary and the fjord. The latter is usually well stratified and may have severely reduced oxygen in the lower waters. As an environment for plankton, it ranges from virtually oceanic to conditions which are quite specialized, but nearly the opposite of those found in shallow estuaries.

It should be apparent at this point that the plankton of estuaries cannot be discussed in generalized terms. It seems desirable to limit this discussion to some particular types, and those which are chosen here are the shallow estuaries of reduced salinity, which are the most common ones.

On the east coast of the United States is a series of large bays and sounds of this general type, including Narragansett Bay, Long Island Sound, the Delaware and Chesapeake Bays, and the Albemarle and Pamlico Sounds, together with many smaller bays and estuaries. These have been studied with varying degrees of intensity and with differences in focus, but enough information is available to describe their characteristics with some degree of generality.

THE ESTUARINE ENVIRONMENT

Some of the general features of shallow estuarine environments and their biological significance include morphometric features, temperature and salinity, circulation, and the cycling rate of elements.

MORPHOMETRIC FEATURES

The degree of enclosure and shape of the basin are significant items. The degree of enclosure is sufficient to maintain an environment that is distinctly different

from that of offshore waters and to protect its population from catastrophic loss by water exchange. The population, of course, will be continually diluted by exchange with offshore waters and will be seeded by offshore populations, a system which fosters selection by biological competition of those species which are able to maintain the most effective growth rate under the prevailing conditions.

The shallow nature of the basin, frequently accentuated in its effects by rapid tidal mixing, provides conditions that are optimal for rapid cycling of the biological and chemical resources of the environment. Nutrients produced on the bottom by bacterial regeneration and animal excretion are rapidly returned to the phytoplankton. Organic metabolites produced on the bottom, such as cobalamin, probably have a very significant influence on the composition of phytoplankton species. Looking at the matter from a different point of view, a depth of water within or not greatly exceeding the potential depth of the euphotic zone provides benthic filter feeders and superficial detritus feeders with an abundant food supply. This results in an abundant bottom fauna, probably somewhat at the expense of zooplankton, as compared with deeper water; offshore where zooplankton is able to eat almost all of the phytoplankton that is produced. But, in general, this leads to rapid cycling, a relatively high level of primary productivity, and a smoothing of the seasonal cycle of phytoplankton.

TEMPERATURE AND SALINITY

Shallow water and proximity to land promote heat exchange and lead to an extreme range in the temperature. There is no escape from winter rigors and generally no summer refuge for cold-water stenotherms in the bottom waters. A surprising number of the common species, both phytoplankton and zooplankton, can thrive through most or all of a seasonal temperature range that may be as much as 25° C. or more, and eurythermy is certainly a salient feature of the estuarine population.

The reduced salinity of estuaries probably limits the population. This is almost certainly true in cases of extreme freshening, and even in less marked cases there is some indication of this. But the argument for direct effects of salinity usually becomes tenuous upon close examination. Organisms can commonly tolerate a lower salinity in laboratory experiments than in their normal habitat, and the normal salinity range for a particular species may vary considerably even

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from one estuary to another. The biologist tends to conclude, in such cases, that salinity operates in an indirect way, affecting the delicate balance of inter-specific competition at ranges that are well within the limits of absolute tolerance, but critical information on this kind of problem is difficult to acquire.

CIRCULATION

The amount of inflow of fresh water and the rate of exchange with coastal waters regulate the salinity of an estuary, which presumably is important, although, as just indicated, its importance is not easily documented. The fresh water usually enriches the estuary. This may include an organic as well as an inorganic input of nutrients, and the organic substances may have a qualitative influence on species composition as well as a generally enriching effect. Vishniac and Riley (1961) found a distribution of thiamine in Long Island Sound which indicated that it was largely derived from drainage, as contrasted with cobalamin which was distributed more uniformly and seemed to be a product of benthic metabolism.

Estuaries with a considerable depth of water and with vertical density gradients at their mouths commonly have a two-layered transport system in which a freshened surface layer moving seaward is replaced by an inflow of more saline water at the bottom. If the water is sufficiently deep to develop a negative gradient in nutrients so that a nutrient-poor surface layer drains off and is replaced by inflowing bottom water that is comparatively rich, the exchange pattern will enrich the estuary. Harris (1959) analyzed the exchange pattern in Long Island Sound with reference to nitrogenous nutrients, which were the most important limiting factors in that area, and concluded that enrichment from the two-layered transport system was approximately equal to that supplied by freshwater drainage.

In this particular system, an as yet unpublished analysis of salinity balance indicates that excessive freshwater drainage results in a rapid outflow of a thin, freshened, and highly stable surface layer, with an actual reduction of mass interchange between the main body of Sound water and the outlying coastal region. In more thoroughly mixed estuaries, increased drainage increases the flushing rate (Ketchum, 1951). The dynamics of the estuarine exchange system have been discussed by Cameron and Pritchard (1963) at some length. For present purposes it is important only to point out that considerable differences exist in the types of exchange and that these differences are important biologically, affecting both nutrient balance and exchange of populations.

Another common factor associated with freshwater drainage and estuarine circulation is the delivery of a load of river-borne silt. This can have the immediate effect of reducing transparency and tending to offset the effects of nutrient enrichment upon the level of primary productivity. There will be sorption processes that conceivably can affect mineral nutrition of phytoplankton. Deposition of silt in an enclosed

basin can alter bottom sediments to a point that drastically affects higher elements of the trophic system. The extensive mud bottoms found in many estuaries are more favorable for microfauna and microbial flora than for the support of potential fish food. Some of these estuaries, despite their high level of primary productivity, are disappointing in terms of practical returns to mankind, and serve as a brake to optimistic notions of dramatically increasing food yields by artificial fertilization.

CYCLING RATE OF ELEMENTS

In deep ocean waters, with residence times of some hundreds of years, biological transformations tend toward completion, and additions of nonconservative concentrations are approximately in proportion to their concentrations in organisms. Then, when deep water is transferred into the surface layer by vertical diffusion or advection, it is well supplied with a balanced array of the elements required for phytoplankton growth.

The fertility of coastal and estuarine waters is generally high, but the balance of essential elements is not so simply regulated. During much of the year elements are used as fast as they are returned to the water, and the rate of cycling, rather than the total potential stock of the element, becomes crucial in determining what factor will be most important in limiting production. Commonly N:P ratios are low as compared with open ocean waters, and nitrogen is likely to be an important limiting factor. It is commonly supposed, with some support from experimental work on rates of bacterial degradation of plankton material, that this is due to a relatively slow rate of regeneration of nitrogenous materials. This situation is typical of coastal waters in general, although it is particularly marked in estuaries.

This discussion merely touches on the important issues. Certainly some of the fertility of coastal waters depends upon the fact that deep, nutrient-rich water which is originally a balanced medium is cast upon the continental shelf. But it is transported shoreward with much recycling along the way, and the rate of recycling is important in determining the proportions of the elements that finally reach the shore zone and the estuaries. But these effects can be altered in various ways by the kind and quantity of freshwater enrichment. The effect of freshwater drainage probably has been overemphasized in textbooks, but cannot be discounted. Both kinds of processes tend to enrich estuarine waters, but many aspects of nutrient cycles are only vaguely understood and need further study.

PHYTOPLANKTON

QUANTITATIVE ASPECTS OF THE SEASONAL CYCLE

Having characterized the estuarine environment in broad terms, we turn now to a consideration of phytoplankton populations, drawing particularly upon studies of Narragansett Bay by Smayda (1957), of Long

Island Sound by S. Conover (1956) and Riley and S. Conover (1956), and of Chesapeake Bay by Cowles (1930). Useful comparisons can be made with inshore coastal populations in the Gulf of Maine (Burkholder, 1933; Bigelow *et al.*, 1940), Woods Hole Harbor (Fish, 1925), and southern New England coastal waters (Lillick, 1937; Riley, 1952). Unpublished data by Conover and the present writer will be drawn upon extensively. There is, in addition, a large body of literature on inshore and estuarine waters of Britain, Scandinavia, and Japan, which will not be quoted extensively, but is essentially in agreement with the results reported here.

We shall deal first with some gross quantitative aspects of the seasonal cycle. There is a period of relative poverty from midautumn to midwinter in most estuaries, when growth is minimal because of reduced light intensity and winter turbulence. During this period regeneration of nutrients exceeds utilization, and nutrient concentrations rise to a high level. The stage is being set for the so-called spring diatom flowering, which is really likely to be a mid- to late-winter flowering in most estuaries, rather than a spring flowering.

The flowering is triggered by the vernal increase in light intensity. Many years ago Atkins (1928) demonstrated that year-to-year fluctuations in the time of the flowering in the English Channel depended on the amount of radiation during the preceding month. Similar observations have been obtained in other areas, and there is now little doubt of the validity of that kind of analysis, although admittedly there are complexities which prevent comparison of different areas on such an unsophisticated basis. For the moment it seems desirable to consider the simplest aspects of the initiation of the flowering. The complexities and the qualifications will be taken up later.

During six years of observations in Long Island Sound, the peak of the flowering varied between late January and early March. Examination of environmental data indicated that the radiation level during the period from mid-December to the onset of the flowering was the most important factor involved. There was also an indication of an inverse temperature effect. The rationale here is that an increase in phytoplankton, which seems to be largely controlled by radiation, depends on an excess of photosynthesis over respiration which has a strong temperature effect. An equation representing this relationship is postulated as

$$dC/dt = C(f(I_0) - 0.0175e^{-0.007T}), \quad (1)$$

where C is μg of chlorophyll a per liter in the total phytoplankton population, I_0 is incident radiation in $\text{g cal cm}^{-2} \text{ day}^{-1}$, and T is temperature in centigrade. The temperature function is expressed in a form implying that respiration has a Q_{10} of 2, and with a constant that is essentially in agreement with experimental data on phytoplankton respiration.

Figure 1 shows radiation and temperature data used in this problem and also in a later analysis of

autumn flowerings. Vertical stability is also included; it has no significance here but will be used later.

The combination of observed radiation and temperature and observed changes in chlorophyll in the Sound can now be used for statistical derivation of the radiation function in equation (1). The best statistical fit is

$$dC/dt = C(0.00031I_0 - 0.0175e^{-0.007T} + 0.007). \quad (2)$$

This is obtained by first computing coefficients of mean daily increase in chlorophyll between successive observation dates and then subtracting the postulated respiratory function; the difference is then correlated with radiation. The small constant of 0.007 in the equation is merely the statistically computed constant in the regression equation. It has no biological meaning, but is small enough to be of no real concern.

Application of equation (2) to observed values of radiation and temperature provides an estimate of relative changes in chlorophyll during the period in question. These changes were converted to absolute concentrations by adjusting the relative concentra-

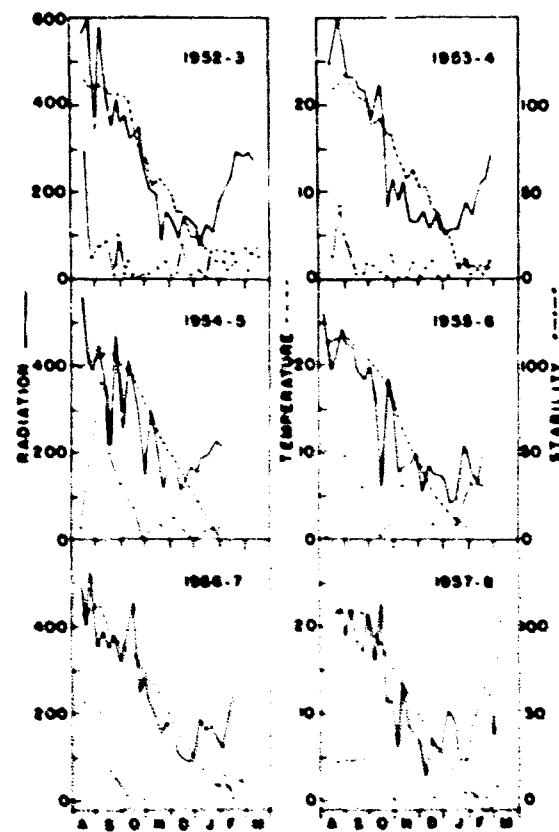


Fig. 1. Seasonal variation in environmental factors used in analysis of autumn and winter diatom flowerings in Long Island Sound. Temperature in centigrade, stability is given as $10^6 E$, radiation in $\text{g cal cm}^{-2} \text{ day}^{-1}$. The first two variables are obtained from station data, radiation is an average for a week or more, depending on the time interval between oceanographic sampling.

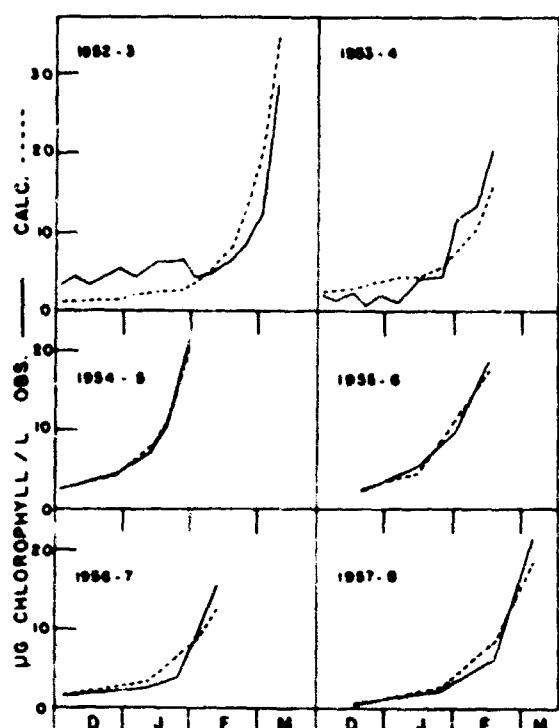


Fig. 2. Comparison of observed chlorophyll in winter flowerings with values computed from equation (2).

tions so that their mean value during the whole period was equal to the observed mean. The computed values are compared in Figure 2 with observed chlorophyll, and the degree of agreement leaves little doubt that the main factors have been identified.

As indicated earlier, this treatment is oversimplified. A complex of factors, including incident radiation, transparency of the water, turbulence, and depth, determine whether the average amount of light in the vertical column will be sufficient to support an increase in the population as a whole. These complexities may be ignored in studying a particular area, at least in a shallow and well-mixed body of water, because most of the factors other than radiation are more or less constant from year to year. However, comparison of different areas requires a more detailed treatment. No one has as yet devised a fully satisfactory means of comparison, but Riley (1957) suggested a rule of thumb which deserves brief mention.

Assume first a thorough mixing of a column of water between the surface and a depth z , which may be the total depth of water in a shallow area, or may represent a discontinuity layer which puts an effective limit on further downward mixing. Within the framework of this assumption, the mean amount of light received by each phytoplankton cell will equal the mean light \bar{I} in the water column above depth z , which is given by

$$\bar{I} = I_0 k z (1 - e^{-kz}). \quad (3)$$

where k is the extinction coefficient, and other quantities are as previously defined. We may suppose that a certain critical value of \bar{I} must be exceeded before effective increase can occur. Comparison of a number of areas suggests that the critical level is about 40 g cal/day. The formula suggests that in some very shallow waters growth may never be seriously limited by winter reduction in radiation. This may be true of Narragansett Bay, where Smayda (1957) found a winter flowering beginning to develop in December, although the peak was not reached until January. In most estuarine and coastal waters of 20–50 m depth the flowering is likely to start between mid-January and mid-March. In deeper waters the flowering commonly does not begin until the onset of thermal stability in midspring (Bigelow *et al.*, 1940; Riley, 1957), when the depth of effective vertical mixing becomes limited and the mean radiation in the surface layer immediately rises well above the critical level.

Once underway, the flowering progresses to a peak which is large in estuaries, but not markedly larger than in open coastal or bank waters. Termination of the flowering may be caused by one or more factors, including grazing by zooplankton, depletion of essential nutrients, and self-inhibition caused by an increase in the turbidity of the water and reduction in effective light intensity for the population as a whole.

Over thirty years ago Harvey *et al.* (1935) documented the importance of grazing in terminating the flowering in the English Channel, and Marshall *et al.* (1934) showed that the first spring brood of *Calanus finmarchicus* in Loch Striven develops during, and presumably as a result of, the flowering. More recent work by Cushing (1961) and others continues to stress the importance of the grazing phenomenon.

In many of our local estuaries, however, the main vernal increase in zooplankton comes well after the flowering. Toward the end of the flowering, we have observed large concentrations of diatoms in the bottom waters and in the superficial layer of bottom sediments, indicating sinking of unconsumed diatoms. Termination of the flowering appears to be most obviously a result of depletion of one or more nutrients, commonly nitrate, and while an ecologist must be very brave to claim complete ecological control of any situation by just one factor, certainly nutrient depletion seems to be the most significant one in the present case.

Nutrients continue to be limiting, moreover, through much of the rest of the year. Of course the keynote of the estuarine situation during spring and summer is the rapid turnover of essential nutrients. Feeding by animals and recycling of metabolic products are rapid, and vertical stability is seldom strong enough to lock up the store of materials regenerated by benthic fauna and flora. There may be a quasi-steady state or a series of small flowerings. There may even be occasional large flowerings of the type commonly designated as red tides, particularly in small harbors and estuaries subject to considerable freshwater drainage and some pollution.

Experiments indicate that the level of primary productivity may be almost as high in summer as it is during the winter flowering (S. Conover, 1956; Riley, 1941, 1956), despite the fact that the standing crop of phytoplankton is much lower and the concentration of limiting nutrients may be almost immeasurably small. The effect of high productivity is chiefly noticeable in the maintenance of an abundant stock of animals.

In temperate oceanic waters, by contrast, the period of summer stability is one of relative poverty in the surface layer. With gradual deepening of the thermocline in late summer or early autumn, nutrients that have been locked up in the thermocline are released to the surface layer, commonly resulting in an autumn diatom flowering.

Autumn flowerings in some estuaries rival or exceed the winter diatom maximum. In others they are reduced, absent, or only occasionally present. When they do occur, they can hardly be regarded as analogous to those in oceanic waters. There is no great stock of nutrients to be had simply by destruction of summer stability, for tidal mixing prevents the accumulation of such a stock. There is commonly a small increase in nutrient supply in late August or September, but this finds no ready explanation except in terms of a slight shift in biological balance—a decrease in phytoplankton production with declining radiation, or increased regeneration at the time of the seasonal temperature peak, or both.

In Long Island Sound two requirements for an autumn flowering are a preliminary slight increase in nitrate and a slight degree of stability in the water column. The latter may be due either to a lingering remnant of the seasonal thermocline or a salinity gradient that has usually been present as a result of excessive freshwater drainage following a hurricane. When both of these requirements are met, an autumn flowering develops in the upper 5-10 m.

The stability requirement and its occurrence only in the surface layer suggest that light limitation is critical in early autumn. This may seem paradoxical, for the radiation level is higher than in the late winter when the other flowering develops, although stability is negligible at that time. However, the phytoplankton respiratory requirement is also greater because of high temperature, and there is more zooplankton grazing at that season.

A statistical analysis was developed, comparable to the one for winter flowerings, but with a more complicated algebraic and statistical manipulation of terms in order to state the variables in as meaningful a way as possible. The result is

$$dC/dt = C [(0.00031 + 2.18E)I_0 - 0.152], \quad (4)$$

where the stability E ($10^{-3}\Delta\sigma_t/m$) is an average figure for the whole vertical column. The results are statistically significant ($P < .001$), although the calculated curves in Figure 3 show a poorer measure of agreement with observed chlorophyll data than in the earlier analysis.

It will be noted in equation (4) that as stability

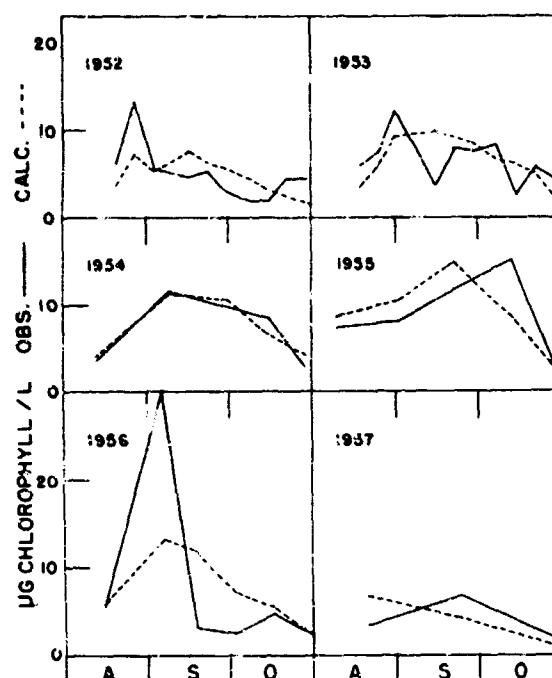


Fig. 3. Comparison of observed chlorophyll in autumn flowerings with values computed from equation (4).

approaches zero, the radiation function approaches the value previously determined in equation (2). These essentially identical functions have of course both been derived statistically—a matter of some interest, since they show no evidence of any seasonal change in the relation between radiation and photosynthesis. As far as species composition is concerned, two species are major constituents in both autumn and winter flowerings, while certain others are important in one flowering or the other, but not both.

The final term in equation (4) is a statistically derived constant which is assumed to represent the combined effects of grazing and phytoplankton respiration and is, in fact, a reasonable figure for this time of the year. The average temperature in September and October is about $18^\circ C$, and the respiratory coefficient according to equation (2) should be about 0.061. The September-October zooplankton crop has averaged about $0.73 \text{ ml}/\text{m}^3$ displacement volume. *Acartia tonsa* is the dominant species. According to grazing experiments by Conover (1956), this species is able, at the prevailing temperature, to graze at a rate of 120 l of water swept clear of phytoplankton per ml displacement volume in a day. Applying this figure to the total zooplankton crop, the daily filtration would be $88 \text{ l}/\text{m}^3$ or 0.088 of the phytoplankton crop. The sum of estimated respiratory and grazing coefficients is 0.149, essentially in agreement with the constant in equation (4).

SPECIES COMPOSITION

The phytoplankton of estuaries tends to be abundant in total quantity, but limited as to the number of

important species. Indeed, a single species of diatom, *Skeletonema costatum*, is almost overwhelmingly dominant in our east coast estuaries and inshore coastal waters, as well as in similar habitats in other parts of the world. Smayda (1957) reported that *Skeletonema* constituted an average of 81 percent of the total cell count in Narragansett Bay. Similar results are common elsewhere.

There is also a considerable degree of agreement as to general species lists obtained in the various estuaries, although the relative importance of particular species may vary considerably. Smayda listed ten species and three groups of uncertain specific identification which were the most important forms in lower Narragansett Bay and together constituted 94 percent of the total population. Of these, only three would warrant similarly high rank in Long Island Sound, but all ten were occasionally important in the latter area and certainly would be included among the first 30 species. Reasons for these minor differences are generally speculative, although the types of environment give some clues as to species requirements. For example, there is a considerable array of winter and spring species in the southern New England waters which have more extensive seasonal occurrence north of Cape Cod and presumably may be regarded as cold stenotherms. Relations between seasonal occurrence in different areas and the depth of water sometimes provide clues as to tolerance to temperature or to low light intensity. There are many apparent examples of salinity effects, but for reasons expressed earlier, these are regarded with some suspicion. One of the most clearcut examples is the diatom *Corethron hystrix*, a common and abundant form in coastal waters which occasionally achieves considerable dominance in Long Island Sound, but only when the salinity is greater than 27‰.

Although the reasons for species distribution are more in the nature of clues than definitive information, some generalizations about estuarine communities can be derived readily. S. Conover (1956) described a two-year series of weekly phytoplankton collections in Long Island Sound. Later six more years of sampling were carried out at a somewhat reduced level of intensity, and the results have been examined and are in preparation for publication. This study constitutes the most extensive set of observations available in east coast estuarine waters and will be used as a basis for generalization.

A total of 150 species has been found. This list excludes a number of small, fragile forms which occur in considerable quantities, but are not readily preserved. Of those which could be examined in preserved samples, 34 species can be designated as major constituents by a not very stringent criterion, namely, that the species constituted at least five percent of the average cell count in samples taken on at least one sampling date during the eight-year period.

Most of the species removed by this paring of the list are probably derived from outside coastal waters or inshore microhabitats; certainly they cannot be re-

garded as successful "native" species in the main body of Sound waters. However, some of the remaining 34 species also are immigrants in the sense that they have a more successful existence in offshore waters and only occasionally become important in the Sound. Six species of this sort have, at one time or another, comprised more than 50 percent of the population, but they have failed to appear consistently year after year, and normally have only a marginal existence in Sound waters. These include *Asterionella japonica*, *Cerataulina pelagicus*, *Chaetoceros compressus*, *Corethron hystrix*, *Leptocylindrus danicus*, and *Nitzschia seriata*.

The list can be further pared by creating a criterion that includes both a measure of dominance and a degree of consistency in the time when the species becomes a major constituent. Any criterion of dominance that is chosen will, of course, be somewhat arbitrary; the present one merely indicates that the species in question are well enough suited to the environment to be significant in normal patterns of seasonal succession, rather than strays which achieve some degree of success on rare occasions. If we define such a species as one which has constituted five percent of the population during any particular month for at least four of the eight years of sampling, the list will be reduced to 13 species, which are shown in Figure 4.

In this figure, the presence or absence of a base line indicates whether the species was observed, at least in minimal amounts in routine plankton counts, during the month in question. The small vertical lines below the base line indicate the number of years that the relative concentration exceeded five percent during any given month. In the latter years of the survey there were occasional months when no sample was taken; for practical purposes a score of either seven or eight means that the species was a major constituent every year.

The curve above the base line is the average concentration (percentage of total population) during the period when it was a major constituent. The scale

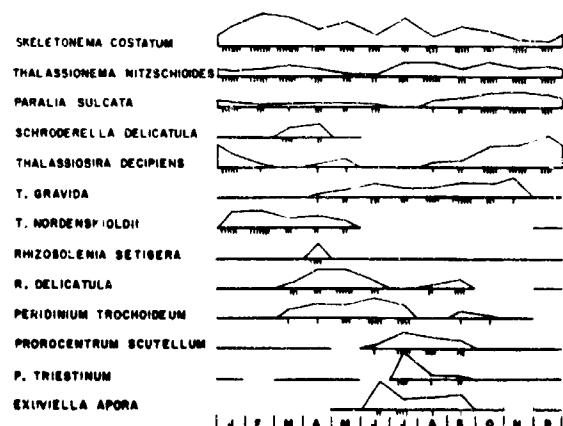


Fig. 4. Seasonal occurrence, degree of dominance, and frequency of year-to-year occurrence as properties of thirteen of the most important species of phytoplankton in Long Island Sound.

shows the distance from one base line to the next one above to be equivalent to 50 percent.

Two generalizations immediately emerge from this analysis. First, although a modest criterion has been set for rating the most important species, only a small number can qualify; and second, most of these are present 10-12 months of the year in sufficient abundance to be found in ordinary plankton counts, and, hence, must be regarded as species with broad tolerance to all or most of the rather extreme range of environmental conditions found in such waters. This is true even of three of the dinoflagellates, which commonly are regarded as being seasonally limited. The basic and most consistent seasonal succession, then, consists of seasonal pulses of growth of a population that is present in recognizable amounts virtually all the time.

Even among species that are more properly regarded as coastal water forms, which only occasionally become major constituents in the Sound, a similar degree of tolerance is not uncommon. In all, 21 species have been found in the Sound at least ten months of the year.

Notes on individual species are in order. *Skeletonema costatum* is preeminently successful at temperatures of 2-20° C. In unusually cold winters it yields dominance to *Thalassiosira nordenskiöldii*, and in the warmest summers several other species are more successful. Nor is this species abundant in late autumn and early winter, and limitation of light is suspected. But it is a generally successful dominant in winter and early autumn flowerings and a major constituent (at the five percent level, at least) during much of the rest of the year.

Skeletonema requires cobalamin, and it has not been resolved why this species is found only in shallow, inshore waters. The writer tends to subscribe to the view of vitamin limitation, although the problem needs further study.

The original argument advanced by Droop (1957) was based on studies of *Monochrysis lutheri* grown in batch culture with varying amounts of added cobalamin. He assumed that *Skeletonema costatum* required a similar amount (about 3 molecules of B_{12}/μ^3 of cell tissue), and, if this were so, the known quantity of cobalamin in offshore waters would be sufficient to support a sizable flowering. Later studies by Guillard and Cassie (1963) showed that *Skeletonema* had a somewhat higher requirement of about 10 molecules/ μ^3 , but this was not a serious discrepancy. However, E. A. Wood (unpublished dissertation, Yale University) has demonstrated that the requirements for chemostatic production of *Skeletonema* are a whole order of magnitude higher than the figures obtained in batch cultures, and Vishniac and Riley (1961) found that the observed decrease of cobalamin in Long Island Sound during the winter flowering was in agreement with a similarly high rate of utilization in nature.

The matter resolves itself into a question of whether the sea behaves like a batch culture or a chemostat.

If continued log phase growth is necessary for maintenance of a species in the sea, then probably the concentration of cobalamin in offshore waters is low enough to exclude species that need as much of it as *Skeletonema* does. Further work is needed to evaluate this matter. This problem, however, seems to parallel the more extensive work that has been done on inorganic nutrients such as nitrogen and phosphorus. Ketchum and Redfield (1949) and others have demonstrated that senescent batch cultures can become extremely deficient in these elements. Similar deficiencies are seldom seen in nature (Harris and Riley, 1956), implying that active growth and a "normal" content of essential substances are necessary for survival in the sea.

With regard to some of the other species listed in Figure 4, *Thalassionema nitzschiooides* and *Pocalia (Melosira) sulcata* seem to have even broader tolerance to changing physical conditions than *Skeletonema*, but at an inherently slower growth rate. They tended to fill the gaps when *Skeletonema* was relatively unsuccessful. *P. sulcata* and *Thalassiosira decipiens* achieved their greatest dominance in autumn, but their cell concentrations did not increase markedly, and the percentages rose because other species declined.

The three *Thalassiosira* spp. exhibited a seasonal succession of a more nearly classic nature than most other species in the list. Both *T. decipiens* and *T. nordenskiöldii* occur in summer in the Gulf of Maine, where the water is colder, but are largely replaced during that season by *T. gravida* in local waters. *T. nordenskiöldii* and the remainder of the diatoms on the list are more successful in offshore waters than in the Sound, but are able to invade estuarine waters consistently enough to meet the predetermined and arbitrary qualifications.

The last four species in Figure 4 are dinoflagellates, which achieve brief dominance over diatoms during the summer. This is in the classic tradition. Some texts say (for example, Sverdrup *et al.*, 1942) that the dinoflagellates are warmth-loving creatures which have a fairly low nitrogen requirement; both of these characteristics favor the summer change from diatom to dinoflagellate dominance. However, the facts of the case do not fully support these generalizations. Three of the four major species have wide temperature tolerances, and *Peridinium trochoideum* sometimes becomes a major constituent when the temperature is little higher than the late winter minimum. Their peak months are June and July, and they decline in August as the temperature rises still higher. If temperature is important, there is clearly a closely defined optimum rather than a general tendency toward warm stenothermy.

The postulated nitrogen effect is even more ambiguous. Following a severe post-flowering depletion of nitrogen, there appears to be a series of small resurgences of ammonia in late spring and early summer, each of which leads to phytoplankton growth. Harris (1959) described one of these spring periods.

In May, *Skeletonema costatum* was dominant; in June, *Peridinium trochoideum*. The amount of ammonia available was essentially the same.

Complete nitrogen data are not available for other years, but the same pattern of succession has often been observed. Diatoms are dominant until the middle or the end of May, and then dinoflagellates. The only obvious environmental changes during this period are slight increases in temperature and radiation, and a considerable increase in vertical stability.

The question of the possible significance of vertical stability is raised by some observations obtained during an early June flowering of *P. trochoideum*. An *in situ* turbidity meter revealed a tremendous increase in turbidity in a 1 m stratum centered around a depth of 3 m. Detailed sampling showed that 90 percent of the total population of *P. trochoideum* was in this narrow stratum. This result is disturbing in one sense, because it shows that an ordinary sampling program at a series of standard depths may be quite inadequate in describing the population when it occurs as a massive and closely defined concentration. But aside from this, it is apparent, first, that these dinoflagellates tend to congregate at a narrowly defined depth, and second, that near-surface stability facilitating such congregation is found in the Sound only during a limited period which coincides with the period of dinoflagellate dominance. The question remains open as to whether the observed depth range represents a preference for a particular temperature or light intensity, and how effective these may be in promoting the growth of the organism. Possibly the chief advantage is simply the maintenance of a reasonably adequate depth at a time when stability increases the problems of diatom flotation. Species succession may well hinge upon subtle interrelations of this type.

Thus, the discussion of phytoplankton ends on an uncertain note. Observations have provided some understanding of quantitative aspects of seasonal cycles in estuaries and clues as to the requirements of particular species with respect to light, temperature, and some other factors. But we are still very far from a solid understanding of the dynamics of seasonal succession.

ZOOPLANKTON

The zooplankton of estuaries can be characterized in much the same terms as phytoplankton; it is volumetrically abundant, but limited as to species composition. The form of the seasonal cycle is extremely variable, sometimes changing drastically from one year to the next, as indicated in a study of the zooplankton of Delaware Bay by Deevey (1960a). Possibly the most common and significant difference between estuaries and the open ocean is the relatively large summer estuarine population. This is a result of a high level of primary production. It also reflects the addition of numerous larvae of benthic invertebrates to the plankton population during the summers.

Cronin *et al.* (1962) described a distinct and persistent change in species composition along the length

of the Delaware River Estuary, which could be related to salinity distribution. *Gammarus fasciatus* was particularly important in the upper reaches where the salinity was less than 5‰. In the middle reach, with salinities of 5–18‰, a numerically abundant and typically estuarine population developed, with the copepod *Acartia tonsa* as the dominant species and with *Eurytemora hirundooides*, *E. affinis*, and *Pseudodiaptomus coronatus* as important elements. These together constituted 84 percent of the number of animals in all catches. The lower estuary, with a salinity range of 18–30‰, contained small quantities of species characterized by these investigators as oceanic intruders.

According to Deevey (1960a), *A. tonsa* is a eurythermal and euryhaline species found from the Gulf of St. Lawrence to the Gulf of Mexico, and is a dominant species in many semi-enclosed waters. In Long Island Sound (Deevey, 1956), it is dominant from midsummer to early winter, at which time dominance shifts to *Acartia clausi*, a more northerly species which is found north of Cape Hatteras and is also a common species in European estuarine waters. In general, *A. clausi* is more successful in Long Island Sound than *A. tonsa*, but is a relatively minor form in Delaware Bay.

The *Eurytemora* spp. mentioned above appear to be truly brackish-water forms. They are virtually absent from Long Island Sound, where the salinity is about 24–29‰. *Pseudodiaptomus coronatus* also is relatively uncommon.

Temora longicornis, listed by Cronin *et al.* (1962) as occurring primarily at the mouth of Delaware Bay, was regarded by Deevey (1960a) as a euryhaline neritic copepod. It was not excluded from Long Island Sound; in fact, Deevey (1956) found it to be the third-ranking species (after the *Acartia* spp.), and it was more abundant there than in open coastal waters. Several other species found only in the more saline waters of Delaware Bay had a widespread distribution in Long Island Sound, but a limited degree of abundance as compared with offshore waters. These included the copepods, *Centropages hamatus*, *Pseudocalanus minutus*, and *Labidocera aestiva*; and the cladocerans, *Evdadne nordmanni* and *Penilia avirostris*. But *Centropages typicus* and *Calanus finmarchicus*, both important coastal copepods, were relatively unsuccessful in either of the estuarine habitats under consideration.

The authors quoted here have dealt in some detail with problems of temperature and salinity tolerance. Cronin *et al.* (1962) has demonstrated the partitioning effect along a salinity gradient, and Deevey (1960a) has given detailed consideration to temperature cycles in the examination of both the north-south geographical range and seasonal occurrence in particular locations. But the situation is not entirely clearcut. As so often happens in nature, there is little evidence of utter exclusion at some definite point in the range, but rather of a gradual reduction in number and a gradual yielding of dominance to other species. The impression is that suboptimal temperature and

salinity reduce metabolic efficiency, and that biological competition at these suboptimal levels is more important than direct effects of salinity or temperature upon survival. This point of view is somewhat bolstered by an argument of a negative sort. R. Conover (1956) found that the *Acartia* are inefficient feeders in comparison with open ocean forms. Their success in competition in the estuarine environment with coastal water forms of known ability to survive finds no ready explanation except in terms of sublethal effects of the kind postulated.

Conover also examined the problems of competition between the two *Acartia* species in Long Island Sound. *A. clausi* was dominant from midwinter to about July; *A. tonsa*, from July to early winter. Thus, each species, at its own time, was successful through most, but not quite all, of the observed temperature range in these waters. At the lowest temperature range *A. tonsa* appeared to be sluggish and was found mainly near the bottom in early winter. *A. clausi* had a superior feeding rate. *A. tonsa* increased somewhat during the late winter flowering, but largely disappeared during the period of post-flowering poverty—a situation which Conover regarded as indicative of biological competition for the limited food available.

A. tonsa appeared again in early summer and gradually won dominance over the waning *A. clausi* population as the summer progressed. At this time the latter still seemed to be more effective than *A. tonsa* in feeding on phytoplankton, but *A. tonsa* seemed to be able to supplement its diet by selective feeding on small animals and the largest members of the phytoplankton population. Thus, the laboratory feeding experiments provided no critical evidence that the shift in dominance during this season was due to competition for food. Field observations showed a slow decline in the young stages of *A. clausi* as the summer progressed, perhaps because of a direct effect of temperature upon reproduction or, more likely, an indirect effect on some aspect of competition among the immature stages. Conover's results show that these competition problems are subtle and are not easily resolved even under intensive study. Thus, while estuarine distribution is statistically related to temperature and salinity, it would be naive to suppose that this is more than a small part of the story.

One is also reminded here of an earlier study of temperature zonation by Hutchins (1947), which was primarily concerned with benthic animals, but led to generalizations that are theoretically applicable to zooplankton. His chief point was that both northern and southern limits of distribution may be demonstrated in different ways—by affecting either the survival of adult populations or their ability to reproduce—and that comparison of observed distribution with the radically different kinds of temperature zonation found on the various coastlines can provide clues to the type of limitation. Application of these principles to benthic organisms is far easier than to movable and somewhat ephemeral plankton populations, but data of some interest in this connection have been

compiled by Deevey (1960a). She was able to show that the breeding range of certain copepods might be coextensive with, or more limited than, the extreme range of occurrence at one temperature extreme or the other, suggesting that different kinds of factors might have been operating. Her analysis dealt mainly with distribution on the east coast of North America, but results indicated that more extensive zoogeographical analyses of ubiquitous species might be instructive.

The maintenance of a "native" population in an estuary and, conversely, the rate of invasion by coastal water forms will depend in part on the flushing rate and circulation pattern. From a dynamic standpoint, obviously, the rate of increase of the population must balance the rate of loss by flushing, predation, and all other natural causes in order for the population to maintain itself. In general, this problem is most severe for long-lived and slow-growing organisms, and it is more of a problem for zooplankton than for phytoplankton. Ketchum (1954) analyzed the dynamic aspects of this problem, and Barlow (1955) reported a detailed study of factors involved in the maintenance of zooplankton in a small estuary on Cape Cod. It was apparent that native copepods could maintain themselves readily in summer, but low growth rates and insufficient food in winter created a critical situation. Barlow postulated that resting eggs on the bottom helped to alleviate the problem of maintenance.

The pelagic larvae of barnacles (Bousfield, 1955) and winter flounders (Pearcy, 1962) apparently spend much of their time in bottom waters. These authors show that the natural pattern of vertical distribution increases the chances of these animals living in any estuary that has a net inward flow along the bottom. Thus, while loss by physical dispersion is a very real danger to any pelagic estuarine species, there are biological adaptations which can lessen this danger. But probably the most important requirement is simply the ability to maintain rapid growth under a wide range of environmental conditions.

The zooplankton population of estuaries, measured in terms of displacement volume, is usually about 1 ml/m³. This is generally somewhat larger than the concentration in adjacent coastal waters. However, in these shallow waters the total quantity in the water column underlying a square meter of sea surface often is less than in offshore areas. As a herbivore population, the estuarine zooplankton is relatively inefficient in its utilization of the available plant food. In Long Island Sound the best estimates now available indicate that the zooplankton consumes, at most, some 50–60 percent of the net phytoplankton production, the remainder going mainly to benthic fauna and flora. A number of factors contribute to this situation. They are easily listed, although their relative significance cannot be evaluated easily:

1. Some of the common dominants are inefficient feeders, as indicated earlier. Their dominance presumably depends upon wide tolerance to variations in

temperature and salinity and to various other factors. But the offshore species appear to be able to catch and utilize the available phytoplankton more efficiently in their own environment than does the estuarine population.

2. In some estuaries the seasonal cycles are not closely geared. In Long Island Sound there is a mid-winter minimum in zooplankton which does not respond sufficiently during flowering to make effective use of the abundant food that becomes available at that time. The flowering is then terminated by nutrient deficiency and rapidly sinks, enriching the bottom rather than benefiting the zooplankton. However, this situation does not apply to all estuaries. Deevey (1960a) found, on some occasions, large midwinter zooplankton populations in Delaware Bay.

3. In shallow estuaries the bottom fauna compete directly with zooplankton for food to a degree that is impossible in deeper waters. Water samples taken near the bottom often have fairly large phytoplankton counts. The surface of sediment cores may be greenish with sedimented phytoplankton or, more frequently, may be a flocculent slurry in which many intact cells can be seen. Thus, bottom filter feeders and detritus feeders have a ready source of living material.

4. Deevey (1960b) examined the size of certain species of copepods in a variety of habitats in relation to temperature and food supply. Significant correlations between size and quantity of phytoplankton were demonstrated in some areas, but not in highly productive waters such as Long Island Sound. There is the implication here that food is not a significant limiting factor in determining the size of individuals.

5. Predation upon zooplankton has not been investigated as thoroughly as might be, but this factor may be significant in controlling population density. Estuaries often are nursery grounds for a variety of fishes which, in the larval and juvenile stages, are voracious plankton feeders. Swarms of etenophores are known to have catastrophic effects on zooplankton which may also, when in the immediate vicinity of the bottom, be eaten by amphipods and other filter feeders. There is also the problematical question of whether selective feeding upon large copepods significantly affects the competition between species. The dominant estuarine species are small. As indicated earlier, it is not entirely clear why the larger coastal forms have only a limited degree of success in such waters. Predation is an obvious possibility, but there is little evidence.

LITERATURE CITED

- ATKINS, W. R. G., 1928. Seasonal variation in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *J. Marine Biol. Assoc. U. K.*, 15:191-205.
- BARLOW, J. P., 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biol. Bull.*, 109:211-225.
- BIGELOW, H. B., L. C. LILLICK, and M. SEARS, 1940. Phytoplankton and planktonic protozoa of the offshore waters of the Gulf of Maine. I. Numerical distribution. *Trans. Am. Phil. Soc.*, 31:149-191.
- BOUSFIELD, E. L., 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. *Bull. Nat. Muscum Can.*, 137:1-69.
- BURKHOLDER, P. R., 1933. A study of the phytoplankton of Frenchman's Bay and Penobscot Bay, Maine. *Intern. Rev. ges. Hydrobiol. Hydrogr.*, 28:262-284.
- CAMERON, W. M., and D. W. PRITCHARD, 1963. Estuaries. In *The Sea*, 2; ch. 15, pp. 306-324. Interscience, London.
- CONOVER, R. J., 1956. Oceanography of Long Island Sound, 1952-1954. VI. Biology of *Acartia clausi* and *A. tonsa*. *Bull. Bingham Oceanog. Coll.*, 15:156-233.
- CONOVER, S. M., 1956. Oceanography of Long Island Sound, 1952-1954. IV. Phytoplankton. *Bull. Bingham Oceanog. Coll.*, 15:62-112.
- COWLES, R. P., 1930. A biological study of the offshore waters of Chesapeake Bay. *Bull. U. S. Bur. Fisheries*, 46:277-381.
- CRONIN, L. E., J. C. DAIBER, and E. M. HULBERT, 1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. *Chesapeake Sci.*, 3:63-93.
- CUSHING, D. H., 1961. On the failure of the Plymouth herring fishery. *J. Marine Biol. Assoc. U. K.*, 41(3):799-816.
- DEEVEY, G. B., 1956. Oceanography of Long Island Sound, 1952-1954. V. Zooplankton. *Bull. Bingham Oceanog. Coll.*, 15:113-155.
- DEEVEY, G. B., 1960a. The zooplankton of the surface waters of the Delaware Bay region. *Bull. Bingham Oceanog. Coll.*, 17(2):5-53.
- DEEVEY, G. B., 1960b. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bull. Bingham Oceanog. Coll.*, 17(2):54-86.
- DROOP, M. R., 1957. Vitamin B₁₂ in marine ecology. *Nature*, 180:1041-1042.
- FISH, C. J., 1925. Seasonal distribution of the plankton of the Woods Hole region. *Bull. U. S. Bur. Fisheries*, 41:91-179.
- GUILLARD, R. L., and V. CASSIE, 1963. Minimum cyanocobalamin requirements of some marine centric diatoms. *Limnol. Oceanogr.*, 8:161-165.
- HARRIS, E., 1959. The nitrogen cycle in Long Island Sound. *Bull. Bingham Oceanog. Coll.*, 17(1):31-65.
- HARRIS, E., and G. A. RILEY, 1956. Oceanography of Long Island Sound, 1952-1954. VIII. Chemical composition of the plankton. *Bull. Bingham Oceanog. Coll.*, 15:315-323.
- HARVEY, H. W., L. H. N. COOPER, M. V. LABOUR, and F. S. RUSSELL, 1935. Plankton production and its control. *J. Marine Biol. Assoc. U. K.*, 20:407-441.
- HUTCHINS, L. W., 1947. The bases for temperature zonation in geographical distribution. *Ecol. Monographs*, 17:325-335.
- KETCHUM, B. H., 1951. The flushing of tidal estuaries. *Sewage Ind. Wastes*, 23:198-208.
- KETCHUM, B. H., 1954. Relation between circulation and planktonic populations in estuaries. *Ecology*, 35:191-200.
- KETCHUM, B. H., and A. C. REDFIELD, 1949. Some physical and chemical characteristics of algae growth in mass culture. *J. Cellular Comp. Physiol.*, 33:281-299.
- LILLICK, L. C., 1937. Seasonal studies of the phytoplankton off Woods Hole, Massachusetts. *Biol. Bull.*, 73:488-503.
- MARSHALL, S. M., A. G. NICHOLLS, and A. P. ORR, 1934. On the biology of *Calanus finmarchicus*. V. Seasonal distribution, size, weight and chemical composition in Loch Striven in 1933, and their relation to the phytoplankton. *J. Marine Biol. Assoc. U. K.*, 19:793-827.
- PEARCY, W. G., 1962. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). II. Distribution and dynamics of larvae. *Bull. Bingham Oceanog. Coll.*, 18(1):16-38.

- RILEY, G. A., 1941. Plankton studies. III. Long Island Sound. *Bull. Bingham Oceanog. Coll.*, 7(3):1-93.
- RILEY, G. A., 1952. Phytoplankton of Block Island Sound, 1949. *Bull. Bingham Oceanog. Coll.*, 13(3): 40-64.
- RILEY, G. A., 1956. Oceanography of Long Island Sound, 1952-1954. IX. Production and utilization of organic matter. *Bull. Bingham Oceanog. Coll.*, 15:324-344.
- RILEY, G. A., 1957. Phytoplankton of the north central Sargasso Sea, 1950-1952. *Limnol. Oceanog.*, 2:252-270.
- RILEY, G. A., and S. M. CONOVER, 1956. Oceanography of Long Island Sound, 1952-1954. III. Chemical oceanography. *Bull. Bingham Oceanog. Coll.*, 15: 47-61.
- SMAYDA, T. J., 1957. Phytoplankton studies in lower Narragansett Bay. *Limnol. Oceanog.*, 2:342-359.
- SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING, 1942. *The Oceans*. Prentice-Hall, New York.
- VISHNIAC, H. S., and G. A. RILEY, 1961. Cobalamin and thiamine in Long Island Sound: patterns of distribution and ecological significance. *Limnol. Oceanog.*, 6:36-41.

VI. NUTRIENTS AND BIOLOGICAL PRODUCTION

Phytoplankton Nutrients in Estuaries

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Estuaries are frequently areas of high fertility and large phytoplankton populations. The high primary production is reflected in the dense stands of attached sedentary organisms and may be an advantage to the many marine species which breed in the estuaries, since their larvae have a plentiful supply of food at a critical period. The influence of estuaries on the biota of surrounding coastal water is, therefore, commonly greater than the surface area would suggest.

Estuaries may be fertilized in three main ways: (1) river waters leach plant nutrients from the soil and carry a constant supply through the estuary; (2) pollution, either locally within the estuary or indirectly through the river, may enrich the waters and increase productivity; and (3) the subsurface counter current, which is a unique characteristic of many estuarine circulations, may enrich the estuary when the sea water is drawn from below the euphotic zone where nutrient concentrations are higher than at the surface. In each estuary these three enrichment processes proceed simultaneously, but an understanding of the fertility of an estuary requires an evaluation of their relative importance. This objective has not been fully achieved in any estuary, though the problem has been studied piecemeal in many. This paper will review briefly, by example, how effective these various sources of enrichment may be, suggest how it may be possible to identify different sources of water, and evaluate the contribution of each source to the fertility of the estuary.

ENRICHMENT BY THE RIVER

The nutrient carried to the sea by rivers has sometimes been invoked as the principal mechanism for maintaining the fertility of the oceans. In a local area this is no doubt frequently true; Riley (1927), for example, has traced the effluent of the Mississippi River many miles to sea in the Gulf of Mexico and the effluent of the Amazon River appears to affect the surface sea water for several hundred miles from its mouth. Within estuaries the continuous flow of nutrients in the river water must frequently be important in controlling their fertility, especially since rivers today carry a pollution load in addition to elements leached from the land.

On an ocean-wide basis, however, the annual contribution of nutrients by all of the rivers of the world appears to provide for only a small part of the total marine productivity. Emery *et al.* (1955) estimated (Table 1) that the annual rate of use of nitrogen and

phosphorus by phytoplankton is only about one percent of the reserve in the oceans, but, even so, the use is about 100 times greater than the amounts contributed by rivers and rain annually. The contributed amounts of phosphorus and of silica were not greatly different from the estimated additions to the sediments on the ocean floor. Thus, the oceans appear to be nearly in steady state with regard to the contributions of these elements by the rivers. Nitrogen was contributed, mostly in rain, in excess of the amount sedimented, and it was postulated that denitrification in the oceans maintained the nitrogen balance. Great as the local enrichment of estuaries by the river may be, however, it appears that the oceanographer need not invoke this supply to maintain productivity of the oceans.

ENRICHMENT BY POLLUTION

The effects of local pollution within the estuary are diverse and each case requires separate and individual study. Pollution effects have received much attention and commonly the relationships to the oxygen supply are considered, but rarely has pollution been related to the productivity of the phytoplankton within the estuary.

One example where this relationship has been explored is in Great South Bay and Moriches Bay on Long Island, New York. In addition to the usual domestic pollution and river contributions of nutrients, this area supports a population of millions of domestic ducks. Their waste matter, a very rich fertilizer, is added directly to the waters of small creeks and greatly enriches the estuary. This fertilization has produced dense populations of small chlorophycean algae, sometimes reaching several million cells per milliliter.

Table 1. Nutrient budget of the oceans (After Emery *et al.*, 1955).

	Millions of metric tons		
	Nitro-	Phos-	Sili-
	gen	phorus	con
Reserve in ocean	920,000	120,000	4,000,000
Annual use by phytoplankton	9,600	1,300	—
Annual contribution by rivers			
(dissolved)	19	2	150
(suspended)	0	12	4,150
by rain	59	0	0
Annual loss to sediments	9	13	3,800

Ryther (1954) found that the green algae isolated from the bays were able to grow, in media characteristic of the waters of the bays, much more rapidly than *Nitzschia closterium* (*Phaeodactylum tricornutum*), a common estuarine diatom. These waters had an unusually low nitrogen to phosphorus ratio and nitrogen appeared to be the element ultimately limiting the size of the population. Ryther conducted enrichment studies (unpublished) in which the growth of the algae in waters collected at various locations within the bays was compared with growth in the same waters enriched with phosphate or ammonia. Enrichment with phosphate actually decreased the rate of growth to 44 percent of that in the controls. The addition of ammonia produced populations in various waters which averaged 19 times greater than those observed in the controls. Obviously available nitrogen was limiting the population size and the high concentrations of phosphorus in the water reflected the excess of this element above the requirements of the phytoplankton.

Phosphorus can thus be used as an index of excess pollution of these waters. Figure 1 shows the concentrations of inorganic phosphorus and phytoplankton in water samples taken along a section in the central region of the bays. The concentration of inorganic phosphorus is several times greater than the usual content of sea water in this area (see below) and the phytoplankton counts reflect a true bloom, far exceeding the populations to be found in normal unpolluted estuarine waters.

This is a clear example of the deleterious effects of excess pollution. Not only is the water discolored by the algal bloom with Secchi disk transparencies which are limited to a foot or so, but the entire ecological cycle is drastically changed. The "weed" species, which grow so prolifically in this estuary, are not themselves good food for many of the normal populations, such as the oyster, but their growth excludes the normal estuarine phytoplankton species. While fertilization may increase the production of species of

value to mankind, uncontrolled pollution, even though it may increase the total productivity of phytoplankton, may destroy the natural resources of an estuary.

ENRICHMENT FROM THE SEA

Circulation in estuaries is frequently characterized by a two-layered flow with the surface layers, diluted by river water, escaping seaward and the salt water entering near the bottom. The estuary may be fertilized by this seawater countercurrent, since, in many cases, the sea water is drawn from depths below the euphotic zone in the ocean where the concentration of nutrients has not been depleted by the growth of phytoplankton. This effect may be further augmented by a process which Redfield (1955) has termed the biochemical circulation. Organisms grown in the surface layers of the estuary may sink to countercurrent depths where decomposition releases the nutrients, which will then be returned again for reuse within the estuary. Nutrients can thus become trapped within the estuary and build up unusually high concentrations. The most dramatic examples of nutrient traps are those fjords with a shallow outer sill which produces relative quiescence in the deep water within the fjord. The particulate organic matter which falls through the sea water in the countercurrent can accumulate in the slow moving or stagnant deep water, where its decomposition produces large concentrations of nutrients, anoxic conditions, and hydrogen sulfide.

To evaluate this process it is necessary to identify the proportions of fresh and salt water in various parts of the estuary. If the estuary is a simple one with only two main sources of water, the river and the sea, the proportion of each water in any sample can be derived from the salinity, since:

$$F = (1 - S \sigma)$$

in which F is the fraction of fresh water, S is the salinity of the mixture and σ the salinity of the source sea water. The distribution of salinity in estuaries has been used in various ways to evaluate the circulation of water, determine the rate of flushing, and predict the fate and distribution of pollutants added to the estuary. Examples will be found in Ketchum (1951), Preddy (1954), Pritchard (1952), Stommel (1953), and Tully (1949).

Where more than two sources of water are involved in the circulation, salinity cannot be used alone to determine the proportions of the various types of water. In the open sea, except for the surface layers, temperature is a conservative property, i.e., one which is not modified by external processes, but only by mixing. Oceanographers have long used the temperature-salinity correlation diagram to characterize water masses. Although many estuaries are so shallow that the temperature is modified greatly by solar radiation and other exchanges of heat with the atmosphere, the T-S (temperature-salinity) diagram may be useful in relatively deep estuaries.

Redfield (1950, unpublished) used temperature and salinity to define different waters in the Straits of

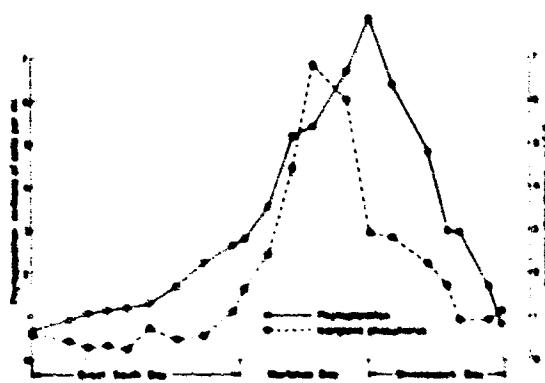


Fig. 1. The distribution of inorganic phosphate and of phytoplankton in a section along the central regions of Great South Bay, Montauk Bay, and Shinnecock Bay, Long Island, New York, in August 1952 (Ryther, unpublished).

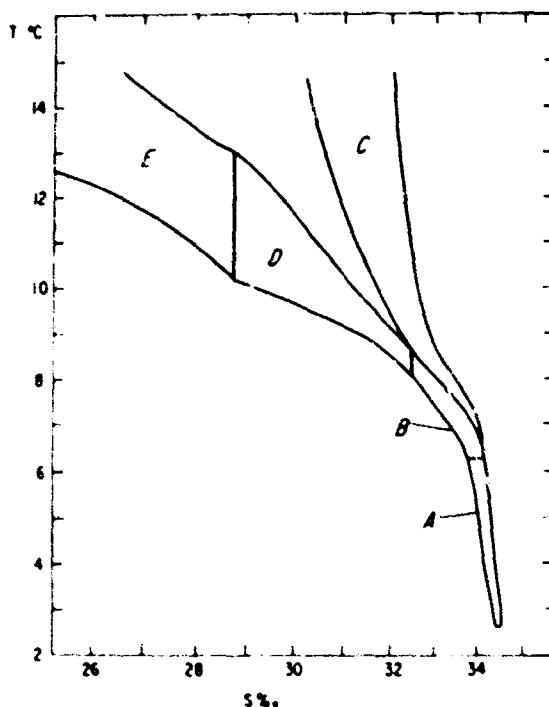


Fig. 2. The temperature-salinity correlation diagram for the waters of the Straits of Juan de Fuca and of Georgia (After Redfield, 1950-unpublished).

Juan de Fuca and of Georgia in the Pacific Northwest. The temperature-salinity correlation diagram in Figure 2 served to identify five different sources of water. The distribution of these different types of water in the estuary is shown in Figure 3. The deeper Pacific Ocean water (Type A) is excluded from the estuary by the bottom contour and the Pacific surface water (Type C) is excluded by the net seaward drift of the surface water of the strait. The deeper parts of the Strait of Juan de Fuca are occupied by water of Type B, similar to that found in the Pacific at comparable depths. This water is the source sea water which mixes with the fresher surface water of the Strait of Georgia (Type E) to form Type D water which is at the surface in the Strait of Juan de Fuca, at intermediate depths in the San Juan channels, and forms the deep water of Georgia Strait. The mixing appears to take place primarily in the San Juan channels where irregular topography and strong tidal currents produce considerable turbulence. While Redfield did not specifically relate the distribution of nutrients to this pattern, the Straits of Juan de Fuca are known to be rich in plankton and nutrients (Thompson and Gorham, 1930) and sea water drawn from the depths which supply Type B water would certainly enrich the estuary with these elements (Igeland et al., 1950). Another clue to the rich production in this area is the exceptionally fine benthic collecting grounds available to the Friday Harbor Laboratory of the University of Washington.

SOURCES OF ENRICHMENT OF THE NEW YORK BIGHT

In shallow areas, where temperature cannot be considered a conservative property, another characteristic must be selected. In the New York Bight we have used total phosphorus and salinity to identify three different sources of water. Inorganic phosphate concentrations may be greatly modified by the growth of phytoplankton populations, but the total phosphorus is much more constant. Its distribution may be affected by the sinking of particulate matter, but, since the phosphorus in particulate matter rarely exceeds 10 percent of the total at any one time, its removal by sinking is probably slow compared to the mixing processes being evaluated.

The waters of the New York Bight are measurably diluted by the Hudson and Raritan River waters so that it may be treated as an estuary, even though the area considered lies outside the geographical boundaries which define what most people would consider the estuary. The distribution of salinity in the Bight at various times of year is shown in Figure 4 which is modified from Ketchum et al. (1951). The dilution by the river water is apparent at all times of year though the distribution varies widely. At some times, the diluted water escapes in a narrow band close to the New Jersey coast; at others, it spreads more widely. The three sources of water to be identified are the brackish water showing the pronounced effect of river water dilution, the surface coastal water entering the area from the eastward and the deep ocean water brought in by the countercurrent in the estuarine-type circulation.

In September, 1958, observations of the salinity, total phosphorus, and chlorophyll *a* were made at stations shown in Figure 5. The vertical distributions are shown in Figures 6 and 7. As mentioned above, total phosphorus and salinity are considered to be conservative properties used to evaluate the sources of water. Chlorophyll, on the other hand, is a variable which reflects the response of the phytoplankton

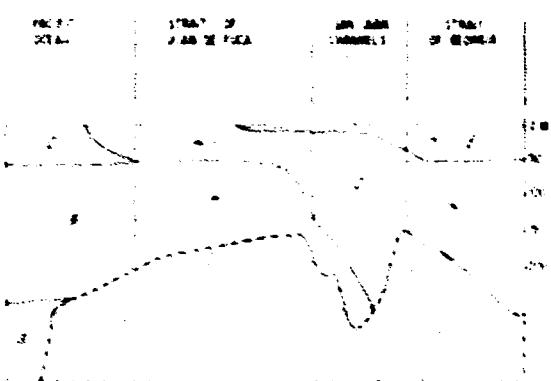


Fig. 3. The distribution of the water types defined in Fig. 2 in the Pacific Ocean, the Strait of Juan de Fuca, the San Juan Channels, and the Strait of Georgia (After Redfield, 1950).

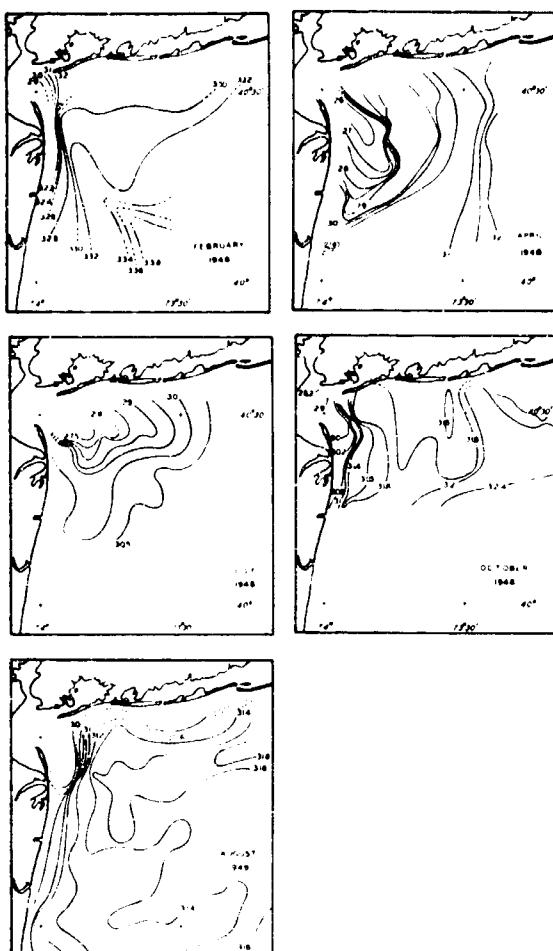


Fig. 4. The distribution of salinity (\textperthousand) in the surface waters of the New York Bight (Modified after Ketchum *et al.*, 1951).

to the water conditions, and especially to the enrichment. In the section extending seaward from Scotland Lightship, near the entrance to the Hudson River, the freshening effect of the river water is obvious at Station 17 where the lowest surface salinity ($30.06\text{\textperthousand}$) was found. In this same water the total phosphorus and chlorophyll concentrations were high. Near the New Jersey coast (Station 11 in Fig. 7) the surface salinity was greater than $31\text{\textperthousand}$, indicating admixture of higher salinity sea water, but total phosphorus concentrations in excess of $2\mu\text{gA/l}$ demonstrate enrichment by the brackish river water. The chlorophyll content at this location was the highest found within the area (21.0 mg/m^3). Both sections show the intrusion of more saline water ($>32\text{\textperthousand}$) within and inshore of the indentation in the bottom, which is the upper end of the Hudson canyon. The offshore coastal waters in both sections had surface salinities of about $31\text{\textperthousand}$ and low concentrations of total phosphorus and chlorophyll. Station 14 was near the location where industrial wastes are discharged at

sea and the high concentration of total phosphorus in the deep water at this station may reflect this pollution.

Qualitatively, these distributions suggest enrichment of the surface waters by the river and by the advection of the high-salinity, nutrient-rich, deep water. The proportions of these sources of water in any sample can be derived from the relationship between total phosphorus and salinity. The correlation diagram for these is given in Figure 8 where the triangle is drawn to include all of the observations. Three types (sources) of water may be characterized from these data as follows:

- A. Brackish river water :
salinity $30\text{\textperthousand}$. Phosphorus $2.9\mu\text{gA/l}$
- B. Surface coastal water :
salinity $30.95\text{\textperthousand}$. Phosphorus $0.50\mu\text{gA/l}$
- C. Deep ocean water :
salinity $34\text{\textperthousand}$. Phosphorus $1.25\mu\text{gA/l}$

Type C water was not found within the area and its properties were established by extrapolation of two sides of the triangle. Numerous other studies of the coastal water of the continental shelf in this area indicate that these characteristics are reasonable, and that this type of water exists within a few miles of our stations at depths of less than 100 meters.

Any point within the triangle of Figure 8 describes a water sample which may consist of unique proportions of the three types of water defined above. The equations necessary to determine the fraction of each type of water in a sample x are:

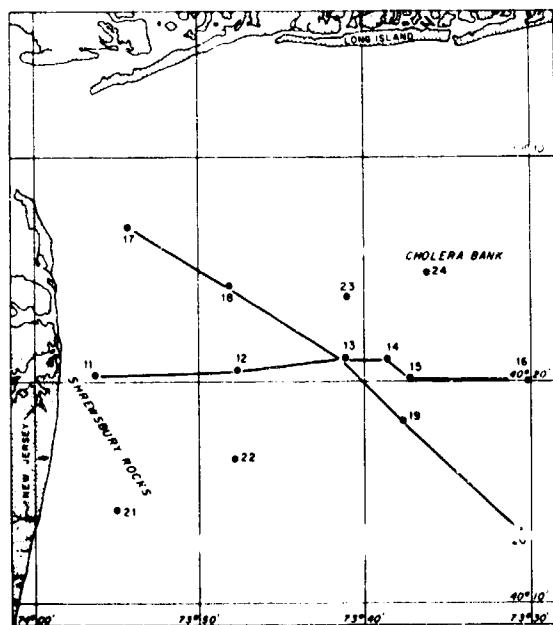


Fig. 5. Location of stations in the New York Bight. The lines mark the sections for which properties are illustrated in Figs. 6 and 7.

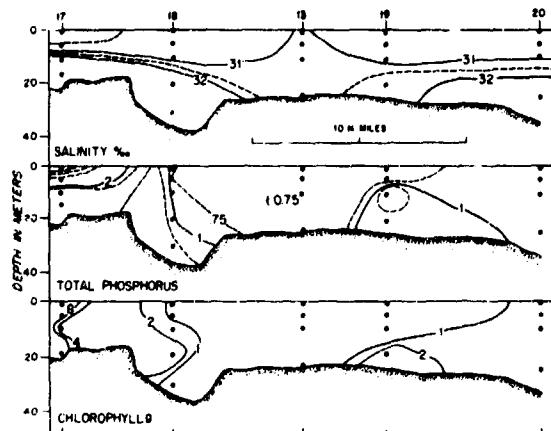


Fig. 6. The distribution of salinity (%), total phosphorus ($\mu\text{gA/l}$), and chlorophyll a ($\mu\text{g/m}^3$) in the section extending from Scotland Lightship (Station 17) to sea.

$$S_x = A S_a + B S_b + C S_c;$$

$$P_x = A P_a + B P_b + C P_c; \text{ and,}$$

$$A + B + C = 1$$

where A , B , and C are the volume fractions of the three types of water and S and P are the salinity and phosphorus content of the water indicated by the subscript.

The results are presented in the proportional triangular graphs in Figures 9 and 10, which show the relationship between total phosphorus and chlorophyll and the sources of water. Each point represents a sample containing the indicated proportions of the three types of water. In both these figures, the blank area at the top of the triangle indicates that our samples did not include any mixture which contained

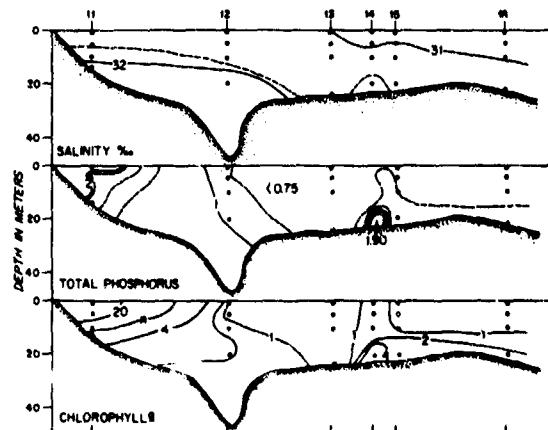


Fig. 7. The distribution of salinity (%), total phosphorus ($\mu\text{gA/l}$) and chlorophyll a in the section extending from Shrewsbury Rocks (Station 11) to sea. The high concentration of phosphorus in the deep water at Station 14 may reflect the industrial wastes which are discharged in this area.

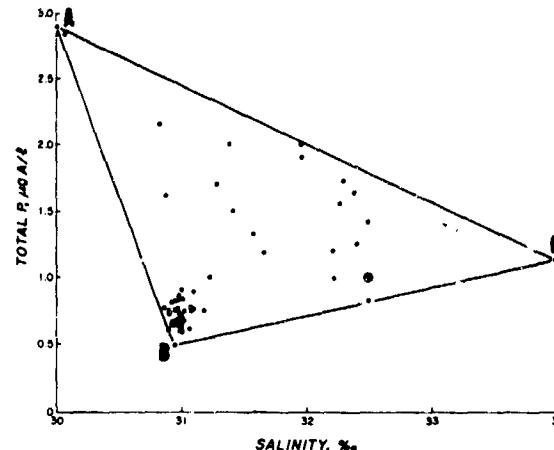


Fig. 8. The phosphorus-salinity correlation diagram for waters of the New York Bight at Stations shown in Fig. 5.

more than 60 percent deep water as defined by the above extrapolation.

The concentrations of total phosphorus have been contoured in Figure 9. This shows a consistency which was completely obscured by the plot of the phosphorus-salinity relationship of Figure 8. The impoverished surface coastal water (B) is represented by points in the lower right-hand corner. Admixture of either deep water (C) or brackish water (A) increased the total phosphorus content of the sample. Since the brackish water contained the greatest amount of phosphorus of any of the sources, it has the greatest effect on the phosphorus content of the mixtures.

The chlorophyll content is contoured in Figure 10. Those samples containing high proportions of surface

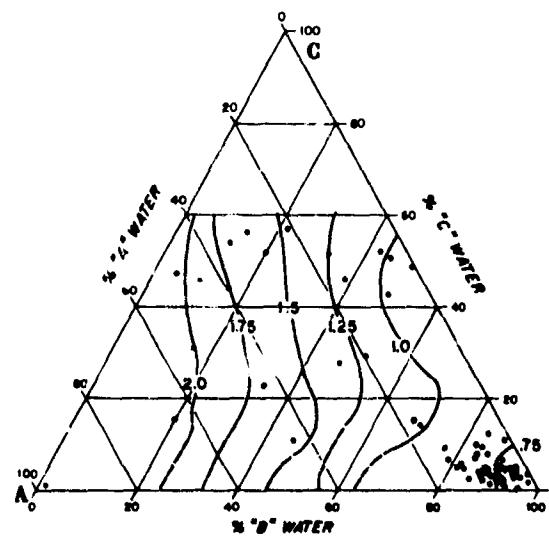


Fig. 9. The relationship between total phosphorus ($\mu\text{gA/l}$) and the proportion of three source waters in the sample.

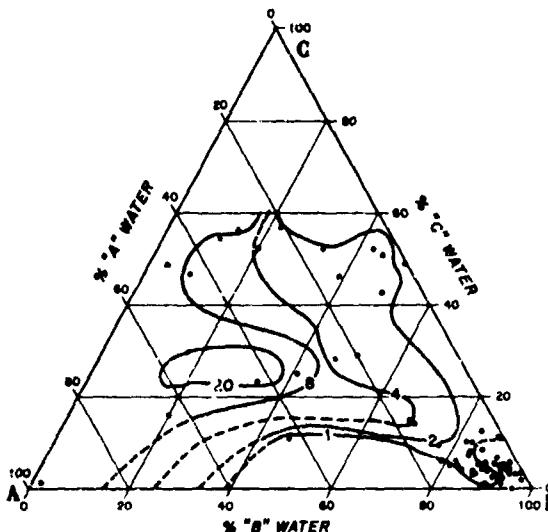


Fig. 10. The relationship between chlorophyll *a* ($\mu\text{g}/\text{m}^3$) and the proportion of three source waters in the sample.

coastal waters (B) are consistently low in chlorophyll. The largest concentrations of chlorophyll ($>20\mu\text{g}/\text{m}^3$) were found in mixtures containing 40–60 percent of the brackish water and 20–30 percent of the deep water.

The highest chlorophyll was not found in the sample showing the greatest enrichment as indicated by the phosphorus content, and we may speculate concerning the reasons for this difference. One possibility is that as the river water enriches the sea it also increases the turbidity, and would thus limit photosynthesis and growth of phytoplankton near the surface. Only after the water clarifies are the plants able to take full advantage of the added nutrients. Another possibility is that the populations are changing, with a decrease of fresh- and brackish-water forms and the growth of marine forms. In either case, the maximum chlorophyll would take some time to develop, and it would be expected, therefore, at some distance from the source of enrichment. Previous studies by Ketchum *et al.* (1951) suggest that it would take a few days for the brackish water at Scotland Lightship (Station 17) to reach the area of Shrewsbury Rocks (Station 11) where the maximum chlorophyll was found. This would be a reasonable lapse of time for the development of maximum phytoplankton populations.

Obviously the proportion of water from different sources in any given sample is not, in itself, adequate to explain the phytoplankton cycle of an estuary. The population of phytoplankton will still depend, as in any aquatic environment, on many factors such as grazing, the stability of the water column, the presence of vitamins or inhibitors in the water, and the transparency of the water and its effect on light intensity at various depths. However, since estuaries may be fertilized in various ways, the source of the enrichment must be evaluated as an essential step in understanding the

system as a whole. Our results on the New York Bight are presented as an example of one way in which this can be done.

DISCUSSION

The natural resources of estuaries are continuously threatened by the expanding populations along their shores. This inevitably raises problems because of conflicts of interest among the diverse groups who want to use the waters primarily for fisheries, for recreational purposes, for transportation, or for the disposal of the waste products of our civilization. Only within narrow limits can all these uses of an estuary develop without severe conflicts and interference. In a highly prosperous and industrialized society, we cannot hope to return our estuaries to their unspoiled natural state, but we can hope, as our knowledge increases, to control the effects of man's activities so that the interests of all are respected and protected.

Our lack of understanding of estuaries can be blamed for much of the existing confusion. We are unable to define accurately the factors which control the circulation in estuaries, for example, and are consequently unable to predict the effects of proposed dredging of channels or of diversion or modification of river flows by the construction of reservoirs. The biologist fears all changes of the environment since he knows that each will modify in some way the normal balance of populations. Although he is unable to predict what the changes will be, history provides ample evidence that there will be a loss of some biological resources. However, natural populations do change even if there is no man-induced change in the environment, and the biologist still cannot predict these changes nor explain them when they occur. Sometimes man's activity is the scapegoat, blamed for all changes the scientist cannot explain.

In the past, some communities and industries have been very callous about the effects of their operations on the natural resources of an estuary. In early days it appeared that man's puny efforts could not drastically affect natural resources, but in many cases the insidious and gradual increase of pollution destroyed the resource before the problem was recognized. When suddenly faced with a major program to reverse the deterioration of the estuary as a natural resource, the expense seemed intolerable. Today, at last, many communities and industries recognize that adequate pollution control is a necessary part of their continued existence, but there is a long way to go to reverse the trends of past generations.

The engineer is in the middle of this conflict. His employers, the community or industry, demand an adequate system at the least cost. The conservationist demands complete protection regardless of cost. The engineer must search for a glimmer of understanding of what effect his operations will have upon the environment. Unfortunately, he can always find dogmatic and conflicting opinions among the scientists

who should be able to provide the definitive answers so desperately needed.

What, then, should society expect and demand of the scientist interested in these problems? Since man's activities will inevitably affect, in some way or other, the ecological cycle in any environment, the scientist's ultimate goal should be to develop the understanding which will allow him to predict the effects of changes, whether they are man-made or natural. When we reach this goal, we will be able to define the limits of acceptable conditions and to answer the difficult questions we are now avoiding. This is a real challenge to the scientist interested in estuaries and the goal will not be reached easily or soon. Until we can define these limits, however, it is unrealistic to oppose all changes because of fears that deleterious effects will result.

In an oversimplified way, this paper has attempted to define the ways by which an estuary may be fertilized. Mankind has made great progress in increasing the fertility and productivity of the land, but only in isolated ponds has aquatic fertility been similarly controlled. The estuaries, naturally highly productive and readily available to man, could logically become more important sources of natural resources. Controlled fertilization could increase their productivity many-fold, but uncontrolled fertilization by pollution leads only to excessive production of undesirable forms, to the elimination of valuable species, and to hydrogen sulfide-laden, anoxic waters. Greater scientific understanding of the natural processes in estuaries is an essential first step in our efforts to reverse the progressive deterioration and to preserve our estuaries in the most useful possible way for the future.

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The equations for phosphorus-salinity correlation (Fig. 8) were solved on a GE 225 computer with the kind assistance of Miss Jean English.

LITERATURE CITED

- EMERY, K. O., W. L. ORR, and S. C. RITTENBERG, 1955. Nutrient budgets in the ocean. In *Essays in the Natural Sciences in Honor of Captain Allan Hancock*; pp. 299-309. Univ. of Calif. Press, Los Angeles, California.
- IGELSRUD, I., R. J. ROBINSON, and T. G. THOMPSON, 1936. The distribution of phosphates in the sea water of the northeast Pacific. *Univ. of Washington Publ. in Oceanography*, 1-34.
- KETCHUM, B. H., 1951. The exchanges of fresh and salt waters in tidal estuaries. *J. Marine Res.*, 10:18-38.
- KETCHUM, B. H., A. C. REDFIELD, and J. C. AYERS, 1951. The oceanography of the New York Bight. *Papers Phys. Oceanog. and Meteorol.*, 10(1).
- PREDDY, W. S., 1954. The mixing and movement of water in the estuary of the Thames. *J. Marine Biol. Assoc. U. K.*, 33:645-662.
- PRITCHARD, D. W., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11:106-123.
- REDFIELD, A. C., 1955. The hydrography of the Gulf of Venezuela. *Papers Marine Biol. Oceanog., Deep-Sea Res., Suppl to 3*:115-133.
- RILEY, G. A., 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. *J. Marine Res.*, 1:60-74.
- RYTHER, J. H., 1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. *Biol. Bull.*, 106:198-209.
- STOMMEL, H., 1953. Computation of pollution in a vertically mixed estuary. *Sewage Ind. Wastes*, 25: 1065-1071.
- THOMPSON, T. G., and H. H. GRAN, 1930. The diatoms and the physical and chemical conditions of the sea water of the San Juan Archipelago. *Publ. Puget Sound Biol. Sta.*, 7:169-204.
- TULLY, J. P., 1949. Oceanography and prediction of pulp mill pollution in Alberni Inlet. *Bull. 82, Fisheries Res. Board Can.*

Biological Production and Distribution of pCO₂ in Woods Hole Waters

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Carbon is not ordinarily considered one of the nutrients worthy of investigation in estuarine waters. It is normally abundant even as free CO₂ (Watt and Paasche, 1963) and therefore not important in limiting the growth of estuarine plants. Carbon is undeniably necessary for photosynthesis, however, and we can learn a good deal about the course of photosynthesis in natural waters by following the changes in their carbon content. Since the infrared analyzer has been available it has been possible to follow changes of pCO₂ in waters continuously and thus to have a record of the balance between photosynthesis and respiration that has taken place in those waters.

REACTIONS BETWEEN CO₂ AND WATER

When CO₂ dissolves in water, it forms an acid and dissociates according to well-known reactions. In sea water there is a further complication, in that carbonate complexes with sodium and magnesium (Garrels *et al.*, 1961). The solubility of CO₂ is about 1 ml/ml. Since the average partial pressure of CO₂ in the air is about 0.03 percent, there should be about 0.3 ml/l dissolved in the water. Actually, there are about 45 ml/l of total CO₂ which can be removed from sea water by acidification and vacuum extraction. Since very little undissociated carbonic acid is present, 99 percent of the CO₂ is present in ionic form. At the other extreme, in distilled water about 97 percent of the total CO₂ is in dissolved form. In intermediate waters, the state in which the CO₂ exists will be determined by the alkalinity.

Since the reactions are complicated by complexing, I preferred to measure the equilibria rather than try to calculate them. Water for this purpose was freed from most of its contained CO₂ by bubbling with CO₂-free air for 4 to 12 hours. Two liters were then continuously equilibrated with about 200 ml air which was circulated through an infrared analyzer by a drying tube. CO₂ gas was injected with a syringe at intervals and the resulting changes in pH and pCO₂ recorded.

In distilled water the addition of 1 ml CO₂ results in a pCO₂ change 15 times that occurring in water buffered by 29 % salt (Fig. 1). In the latter case, an increase in 1 ml/l total CO₂ results in a pCO₂ change of 60 ppm. Under poor working conditions, using an open boat with a portable electric generator, I have been able to measure pCO₂ in the water to better than 10 ppm. In 29 % water, this would correspond to 0.09 mg C/l.

The equilibrium curves also give information as to how persistent changes in pCO₂ in the water will be compared with changes in pO₂. Gas exchange between the air and the sea is limited by molecular diffusion through a surface film (Kanwisher, 1963). The flux per unit area through this film is given by $f = (D \times S \times d \text{ } \mu G)/t$ where f is the flux in cm³/cm²/sec; D is the diffusivity which will be taken as equal to 2×10^{-5} cm²/sec for both oxygen and carbon dioxide; S is the solubility of the gas in water for which I will use 1 cm³/cm³ atm for CO₂ and $1/_{35}$ cm³/cm³ atm for O₂; $d \text{ } \mu G$ is difference in the partial pressure of the gas between the atmosphere and the water in atm; and t is the thickness of the surface film in cm. Under normally windy conditions, CO₂ reacts too slowly with water for the alkalinity (salinity) to have any effect on the flux. In distilled water, where there is no buffering, a change of concentration in one of the gases will produce a partial pressure change inversely proportional to the solubility. Therefore, with equal changes in concentration, CO₂ and O₂ will approach equilibrium with the atmosphere at the same rate. By contrast, in 29 % salinity estuarine water, there is only $1/_{15}$ as much change in pCO₂ as the change in total CO₂, and changes in pCO₂ would persist 15 times as long as changes in O₂. Notice that even in distilled water where pCO₂ as a measure of biological activity has no advantage over pO₂ as far as persistence of changes is concerned, pCO₂ has the advantage that t varies in magnitude much more than pO₂. For example, a 0.5 ml decrease in O₂ will produce a pO₂ change of about 8 percent from the equilibrium value, while the corresponding pCO₂ change will be more than 160 percent.

The denominator of the flux equation is the thickness of the surface film, which, in turn, depends upon wind velocity. Kanwisher's (1963) determinations of film thickness were done in a tank and extended to velocities of only 12 m/sec (24 knots). Higher winds are quite common during winter at Woods Hole. By good fortune, we had measured a pCO₂ of 240 ppm in Buzzards Bay just before the gale winds which blew directly up the bay on November 30, 1963, unaccompanied by rain. Measurement after the gale showed that the pCO₂ had increased to 285 ppm. The value for air is about 320 ppm. This flux spread over 24 hours would give an equivalent surface film thickness of 2.4 μ . (Since a surface film concept has no physical reality under gale conditions,

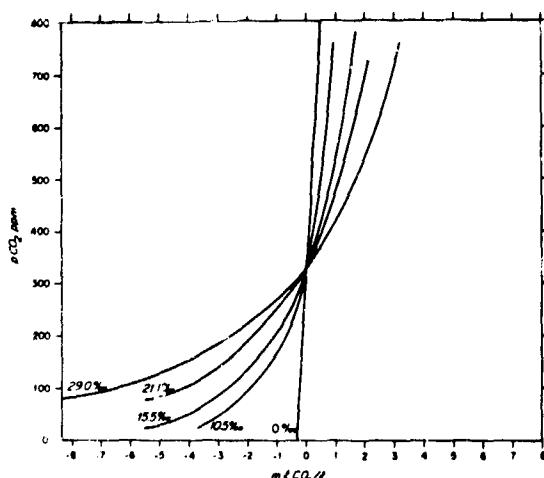


Fig. 1. Variation of pCO_2 with variations in total CO_2 for waters of different salinities, found by titrating natural waters with CO_2 gas.

it may be easier to think of this as an exit coefficient (E) of $300 \text{ cm}^3/\text{cm}^2/\text{hr}$ defined from: flux = $E \times$ partial pressure difference). By plotting Kanwisher's data with wind velocity squared as the abscissa, a straight line is obtained which intersects the calculated thickness for the gale observations at a wind velocity of 52 knots. The root mean square velocity was about 43 knots as measured with an anemometer about one mile from the bay. Presumably, over the open water the velocity would have been greater, although this might not have been true close to the surface where the waves would have offered wind resistance. The agreement with the extrapolation of Kanwisher's data is good enough to allow applying them with some confidence to natural situations and high winds. The fact that the data from the bay seem to require a slightly higher average wind than actually existed indicates the importance of processes other than thinning of the film at higher wind velocities. With breaking waves, the film is continuously torn and reformed.

The best way to summarize these results may be to give an example. Suppose photosynthesis has removed 0.5 ml/l of CO_2 and added 0.5 ml/l O_2 to water of 29% which is well mixed for a depth of two meters. Assume a reasonably constant breeze of 4 m/sec. The pO_2 will have increased by 0.02 from 21 to 23 percent, which will require 6 days to disappear. The pCO_2 will have decreased from 320 to 290 ppm, which will take 3 months to disappear.

THE DISTRIBUTION OF pCO_2

Field measurements of pCO_2 were made by pumping water continuously into an equilibration chamber, out of which it drained through a constant level trap. Air and water in the chamber were violently mixed and the air circulated through the analyzer after drying. The pCO_2 in the equilibrated air was continuously compared with outside air pumped through the

other path in the analyzer. Bottled gases of known concentration were used for periodic calibrations of the analyzer. By varying the pumping rate and volumes of gas and water, the resolution can be adjusted to the speed of the boat so that the desired detail is evident.

The persistence of variations in pCO_2 makes it very suitable for showing some of the discontinuities that occur in waters. During periods of intense activity in the spring, the phytoplankton patchiness is apparent from the patchiness in pCO_2 (Fig. 2). A record taken from the center of the Gulf of Maine in March 1962, shows patches of water 20 to 30 miles across which have values of pCO_2 in their centers as much as 60 ppm below that at the edges, which are only slightly below equilibrium with the air. We mapped some of these patches and showed that they were roughly circular in outline and scattered over the surface. The patches had faded considerably by May, and were no longer distinguishable by June.

Smaller-scale patchiness is shown by the record made in late January, 1964, in Vineyard Sound, from a small boat moving slowly through the water. Here the variation is about 10 ppm on top of the 120 ppm deficit existing in the water at that time. The patches are from 10 to 100 m across.

Although pCO_2 variations are an indication of net production that has already occurred, it is still possible roughly to correlate low pCO_2 with high chlorophyll for the Gulf of Maine data. I did not attempt chlorophyll measurements in connection with the small-scale patches.

With a small boat it is possible quickly to map the distribution of pCO_2 in the surface water of a small estuary and to follow it through the day (Fig. 2). Eel Pond, Woods Hole, is about 275 m across. It receives a small freshwater inflow on the eastern side

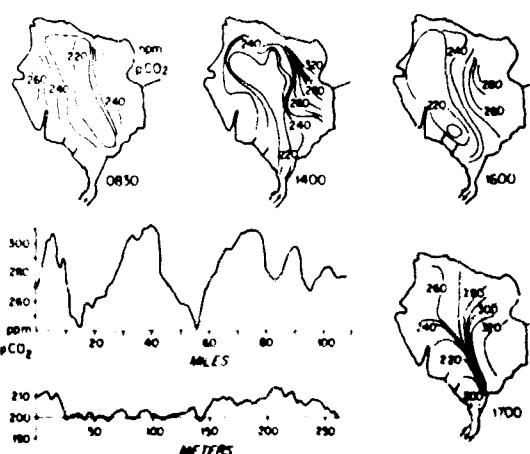


Fig. 2. Variations of pCO_2 in natural waters. Chart is Eel Pond, Woods Hole, Massachusetts, with pCO_2 plotted for January 23, 1964. Top graph shows large-scale pCO_2 variations in central Gulf of Maine in March, 1962. Lower graph is small-scale variation in Vineyard Sound, Massachusetts, January, 1964.

and sewage seepage all around the edges. On January 23, 1964, the pCO_2 distribution was mapped four times. At 8:30 A.M. the tide had been ebbing for five hours, but it was apparent that very little flow was taking place. The tide in Eel Pond is less than 0.5 m, and a relatively light wind can change the tides considerably. By 2:00 P.M. the tide had been flooding for two hours, and the inflow, marked by a lower pCO_2 , was clearly apparent, crowding the seepage with its high pCO_2 over to the side. By 4:00 P.M. the ebb had again begun, and the low pCO_2 water had formed a bubble which was moving out. One hour later the water low in pCO_2 was leaving the pond in a manner that produced a very high gradient across the middle.

I have also looked at the pCO_2 in the water flooding and draining from a salt marsh on Buzzards Bay in early December, 1963. The water in the bay from which the marsh tides came had a pCO_2 of 280 ppm. As the water flooded into the shallow marsh creeks during the day, photosynthesis reduced the pCO_2 until the water farthest up the creeks, which had been there the longest, had a pCO_2 of only 210 ppm, equivalent to the removal of 0.8 mg C/l in about 4 hours of sunshine. When the tide turned and the water began to flow off the marsh, the pCO_2 rose steadily. Water flowing from the smaller creeks was

distinguishable for some distance after it entered larger ones by its higher pCO_2 , and water flowing from the surface of the marsh into the creeks just before the marsh surface was uncovered had a pCO_2 of 400 ppm. Near low tide the last water draining the marsh had reached 480 ppm.

I was unable to follow the water as it flooded the marsh grass areas, so I could not make any calculations of the rate of CO_2 production by the mud surface. It was apparent that production was limited to the phytoplankton and fixed algae in the creeks and that there was no appreciable production on the surface of the mud. The CO_2 moving from the mud surface into the shallow water flooding the marsh surface completely swamped any production by phytoplankton that may have been carried along in the water. The small creeks were marked during the ebb by the fact that they carry proportionately more of the water draining the surface of the marsh and less of the water that has remained in the creeks where most of the production took place.

It is apparent that, while the persistence of pCO_2 changes are of great value in marking water and indicating the biological activity that has occurred in that water, it is necessary because of that persistence to know something of the history of the water being studied and to be certain that the mass can be followed throughout the study. One cannot assume equilibrium as a starting condition, as one can often do with oxygen.

PRODUCTION IN WOODS HOLE WATERS pCO_2 MEASUREMENTS

Measurements of pCO_2 were made at irregular intervals on the water flowing through Woods Hole from October, 1961, up to March, 1964. A small boat was taken into the current through the Hole, or measurements were made at the dock at times when there was a strong flow past it from the Hole. Temperatures were measured at the same times. Wind velocities were taken from U. S. Weather Bureau records for Nantucket Island. The root mean square from the daily weather maps as used in winter, the average from the weather summaries in summer, when there is less variation.

The pCO_2 is high during the summer (Fig. 3) while the production from the spring and summer is being respired by the bacteria and other consumers in the water column. Values reach nearly twice saturation. Biological activity drops off in fall, and the concurrent temperature drop and autumnal storms reduce the pCO_2 toward equilibrium with the air. Further temperature drop and the beginning of the spring bloom, better called the winter bloom, reduce the pCO_2 to as little as 150 ppm. Warming in spring and decomposition of the winter bloom again raise the pCO_2 to summer levels.

Values for net production are calculated from the pCO_2 in Table 1. Flux through the surface film is calculated with the formula above and is negative

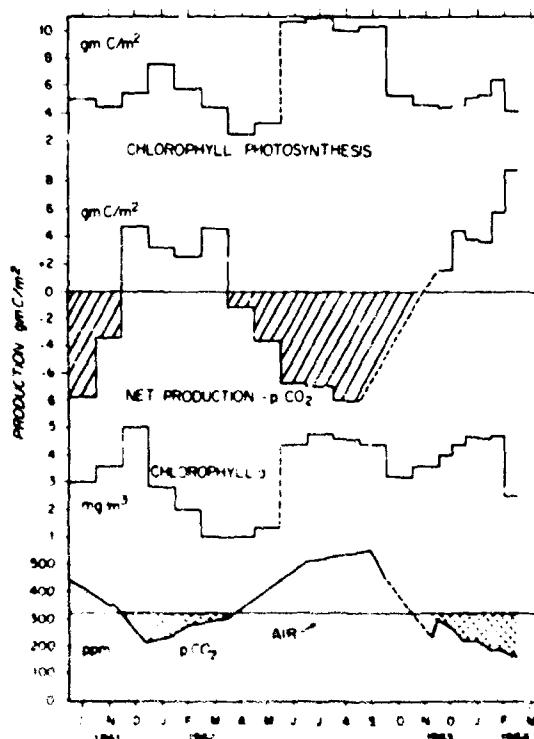


Fig. 3. Measured values for pCO_2 and chlorophyll *a* for Woods Hole waters, with net production and photosynthesis values calculated from them. CO_2 values change from 1962 to 1963 at October; chlorophyll values change between May and June.

Table 1. Production calculated from pCO₂ data for Woods Hole waters. Monthly intervals for 1961 and 1962, two-week intervals for 1963-1964.

Date	Av. pCO ₂ ppm	Sur- face film μ	Flux ml/ cm ²	Δ pCO ₂ ppm	pCO ₂ due to temp.	Δ pCO ₂ ppm	Prod. gm C/m ²
Oct. 61	425	38	-1.43	-95	-95	-7.7	
Nov.	360	38	-0.55	-70	-75	-3.0	
Dec.	275	40	0.58	-100	-64	4.7	
Jan. 62	225	38	1.30	30	-41	3.2	
Feb.	260	39	0.80	45	0	2.5	
Mar.	290	29	0.54	15	68	4.8	
Apr.	335	37	-0.21	70	70	-1.1	
May	410	62	-0.75	70	90	-3.6	
June	480	61	-1.36	70	105	-6.7	
July	520	70	-1.48	15	60	-6.8	
Aug.	535	70	-1.59	15	65	-7.9	
Sept.	525						
Nov. 63	270						
Dec.	290	56	0.14	25	0	1.6	
	240	26	0.40	55	0	4.4	
Jan. 64	220	36	0.72	0	0	3.8	
	205	56	0.30	30	0	3.6	
Feb.	190	31	1.09	0	0	5.8	
	170	31	1.26	30	0	8.9	

when CO₂ is lost from the water, CO₂ tension increases by 4½ percent °C, with rising temperature. Production is calculated by:

$$P \text{ in ml/cm}^2 = f - \left[10^{-3} D \frac{d\Delta\text{CO}_2}{d \text{ pCO}_2} (\Delta - \Delta_t) \right]$$

where f is the flux through the surface film in cm³/cm²; D is the depth of the mixed layer in cm taken to be 400 for Woods Hole; $d\Delta\text{CO}_2/d \text{ pCO}_2$ is the reciprocal of the slope taken from the line of appropriate salinity in Figure 1, expressed in ml/l atm; Δ is the change in pCO₂ in atm; and Δ_t , the change in pCO₂ due to temperature change. The production value was converted to units of gm C/m² by multiplying by 12/224.

Net production was positive from December or late November through March in both winters. It was highest toward the end of winter when the light was greatest, and somewhat lower during the height of winter when cloudy weather was most common. There was a rapid change to negative values in early spring and high negative net production throughout the summer. The positive net production between October, 1961, and August, 1962, amounts to a little more than 15 gm C/m², while the negative production is nearly 37 gm C/m².

CHLOROPHYLL MEASUREMENTS

Chlorophyll determinations were made by Yentsch on water collected at the dock in Woods Hole (Table 2 and Fig. 3). Radiation values were taken from U. S. Weather Bureau records for Newport, Rhode Island, for 1961-1962, and the later values were esti-

mated by comparing records of radiation and weather for previous years with current ones. The extinction coefficient was taken to be 0.5/m during winter and 1/m during the rest of the year. Production was calculated by the method of Ryther and Yentsch (1957). These data change from 1962 to 1963 at the beginning of June, while the pCO₂ data change at the end of September.

Chlorophyll is high during the winter bloom and in the summer, slightly low in the autumn, and very low during the spring. Calculated photosynthesis is highest in summer, with a smaller peak in midwinter.

Respiration was calculated by subtracting the net production from photosynthesis (Table 2). Respiration ranged from 2.5 to 0.04 of photosynthesis. If algal respiration ranged between 1/10 and 1/20 of photosynthesis, which might be expected, then most of the time respiration of the consumers is considerably greater than that of the producers.

In two intervals the calculation yields a negative value for respiration. This results from the arbitrary choice of sampling times and lack of coordination between the two sets of data.

The total calculated photosynthesis was 70 gm C/m² for the October to August interval; total respiration in the same interval was 92 gm C/m². The imbalance in net production, therefore, amounts to about 1/3 of the photosynthesis. The difference can be attributed to inflow of organic matter from Nantucket Sound to the east. Nantucket Sound, with its broad areas of shallow, well-mixed water over the shoals, is more productive according to our pCO₂ measurements than the Vineyard Sound-Woods Hole-Buzzards Bay water which we are discussing here. The net non-tidal drift southwest along the coast would bring some of this

Table 2. Photosynthesis calculated from light and chlorophyll *a*, and calculation of respiration.

Date	Chl mg m ³	Light		Net prod gm C/m ²	Resp. gm C/m ²	Resp. photo
		cal cm ² day	Photo- syn gm C/m ²			
Oct. 61	3.0	240	5.0	-7.7	127	2.5
Nov.	3.6	165	4.5	-3.0	70	1.6
Dec.	5.0	139	5.6	4.7	0.9	0.16
Jan. 62	2.8	174	7.6	3.2	4.4	0.58
Feb.	2.0	203	5.8	2.5	3.3	0.57
Mar.	1.0	377	4.4	4.8	0.4	
Apr.	1.0	431	2.3	1.1	3.4	1.5
May 62	1.3	491	3.2	3.6	6.8	2.1
June 63	4.4	477	10.7	6.7	17.4	1.6
July	4.8	421	11.0	6.8	17.8	1.6
Aug.	4.6	376	10.0	7.9	17.9	1.8
Sept.	4.4	317	10.4			
Oct.	3.2	235	5.3			
Nov.	3.6	153	4.6			
Dec.	4.0	135	4.4	1.6	2.8	0.64
	4.4	120	4.6	4.4	0.2	0.04
Jan.	4.7	130	5.1	3.8	1.3	0.25
	4.6	140	5.3	3.6	1.7	0.32
Feb.	4.7	180	6.5	5.8	0.7	0.11
	2.5	250	4.2	8.9	-4.7	

water with its organic matter into our study region where it would be consumed.

The measurement of carbon dioxide tension in waters is a quick and efficient way of measuring what biological activity has actually occurred in the water. It avoids the problems encountered by enclosing water in bottles or assuming a constant relationship between pigment, light, and photosynthesis; and it often yields the added dividend of information on the circulation and distribution of organisms in the water being studied.

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LITERATURE CITED

- GARRELS, R. M., M. E. THOMPSON, and R. SIEVER, 1961. Control of carbonate solubility by carbonate complexes. *Am. J. Sci.*, **259**:24-45.
- KANWISHER, J., 1963. On the exchange of gases between the atmosphere and the sea. *Deep-Sea Res.*, **10**: 195-207.
- RYTHER, J. H., and C. S. YENTSCH, 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. *Limnol. Oceanog.*, **2**:281-286.
- WATT, W. D., and E. PAASCHE, 1963. An investigation of the conditions for distinguishing between CO₂ and bicarbonate utilization by algae according to the methods of Hood and Park. *Physiol. Plantarum*, **16**: 674-681.

Microbiological Assays of Sea Water Using Radioisotopes— An Assay for Vitamin B₁₂ Measured by C¹⁴ Assimilation

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Our knowledge of the distribution and amounts of organic constituents of sea water is sparse. It is widely believed, however, that these substances play an important role in regulating species distribution, succession, and blooms of phytoplankton. Since the compounds involved exert their influence at extremely low concentrations, often submicrogram amounts, biologists have had to rely upon microbiological determinations for their detection. Such assays have been made available for most of the compounds which stimulate the growth of laboratory cultures.

In marine bioassay technology, the greatest emphasis has been placed upon methods of detecting vitamin B₁₂. It has not yet been shown whether or not the vitamin is a limiting factor in estuaries, where B₁₂ concentration is usually high as a result of its terrigenous origin or of bacterial activity. However, the fact that it is an absolute requirement of so many phytoplanktons in culture has resulted in considerable speculation about its role in triggering blooms. As a result there are almost a dozen organisms which can now be used for assaying the vitamin in sea water. Belser (1963) listed six freshwater and marine species. The lowest limits of sensitivity were between 0.1 and 1.0 $\mu\text{g}/\text{ml}$. Assays employing photosynthetic organisms usually take from 4 to 21 days for completion, whereas heterotrophic assays are considerably faster (20–36 hr). Ryther and Guillard (1962) reported an assay using the rapidly growing sensitive marine diatom *Cyclotella nana*, and demonstrated that it responded linearly to B₁₂ from 0 to 2 $\mu\text{g}/\text{ml}$ in four days.

The responses to varying concentrations of B₁₂ are measured directly in one of several ways. The most usual is to compare cell density or optical density after incubation. Less frequently extracted pigments are used as the criterion of response to B₁₂.

Standards are prepared with known amounts of B₁₂ added to a B₁₂-free medium (external standard), or with B₁₂ added to sea water which is being assayed (internal standard). Growth in seawater samples, suitably diluted or full strength, is then compared with the standards.

MICROBIOLOGICAL ASSAYS USING RADIOISOTOPES

Microbiological assays using radioisotopes are a new concept in microdeterminations of seawater constituents. It is hopefully believed that a number of isotopes will be useful for such analyses. This paper, however, will be confined to a bioassay using carbon-14.

Microbiological determinations using radioisotopes have been reported in allied fields. Levin *et al.* (1957) used a basal medium with C¹⁴-labeled substrates in an analysis of water for coliform organisms. Heim *et al.* (1960) determined antibacterial activity of four antibiotics to four species of bacteria by a radioisotope method. Some other unusual applications of these methods are in the detection of extraterrestrial microbial activity, in petroleum geology (Levin, 1963) and in the detection of biological activity in jet fuel filters (Becker and Calvelli, 1964).

The criterion of response in seawater assays is the incorporation of a radioisotope through a metabolic process as a measure of the stimulatory effects of a growth factor. The process need not be the incorporation of the labeled growth factor itself, but this possibility is not ruled out (e.g., isotope dilution). In the assay presented here, C¹⁴ incorporation through photosynthesis by a sensitive marine diatom is the criterion of response to B₁₂. This indirect approach is useful for a number of reasons. Since the common physiological denominator is the rate of photosynthesis, the physiological condition of every cell in the population is considered. Live and moribund cells are immediately differentiated, and size variation among cells becomes less important. This factor may be of considerable importance under extreme conditions of depletion and enrichment, and no attempt has been made in the past to account for it. Optical density measurements, and to some extent pigment analyses, partially overcome these difficulties.

We know that considerable amounts of extracellular materials may be produced by photosynthetic protists (McLaughlin *et al.*, 1960). When they are labeled with C¹⁴, these exudates can help to increase the sensitivity and speed of microbiological assays. Insoluble C¹⁴-labeled organic compounds are easily collected

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by filtration along with labeled cells. It is not yet known to what extent soluble compounds add to the sensitivity of assays, and under what conditions they appear in the supernatants of culture media.

Rapid assays offer additional advantages: (1) Cultures have less time to accumulate auto-inhibitory products. These depend on the species, of course, but organisms which may have been unsatisfactory for assays because of self-poisoning may now be useful. (2) Nutrients, other than the experimental growth-factor, will not become limiting before the end of the assay. This possibility always exists when nutrients for a week or more must be present at the beginning of an assay. A careful balance must exist between what is required during the growth period, and concentrations which inhibit growth at the outset. This limitation is unlikely in short-term assays. (3) A final advantage is that a small number of cells is required and only one or two divisions occur. Shading of cells within the tubes or flasks is therefore minimized.

Ryther and Guillard (1959) found that when Sargasso Sea water was enriched with a trace element mixture, one or more of its components stimulated C^{14} assimilation. Menzel and Ryther (1961) determined by the enrichment- C^{14} method that the active member of the mixture was iron. Their experiments represented a considerable saving of time over the usual methods which relied on changes in cell density. Goldman (1960, 1961) used similar enrichment methods in fresh water. He found that production was limited by molybdenum in a California lake, and by magnesium in a lake in Alaska. He also found that when *Scenedesmus quadricauda* was depleted in nitrogen and subsequently enriched with nitrate, C^{14} assimilation increased within minutes. Assimilation in the unenriched control remained at a low and constant level.

It was not unreasonable to believe, therefore, that if a depleted culture responded to an enrichment by a several-fold increase in C^{14} assimilation, it might respond proportionately to varying amounts of the nutrient. Furthermore, it should be possible to measure threshold levels of the enrichment. The lowest concentration to elicit a response would be the "limiting concentration" for that population. The threshold responses would be a function of the number and physiological condition of the cells, and the degree of their depletion of the growth substance.

Experiments were performed to test these hypotheses. It was not possible to predict whether the increased C^{14} assimilation would result from a new and larger stationary population, or from populations with metabolic rates which varied due to differing concentrations of enrichment.

In the initial experiments *Skeletonema costatum* was grown in an iron-deficient, enriched-seawater medium. Aliquots of depleted culture responded to additions of iron within a 24-hr period. The ratio between C^{14} assimilated (heavily enriched) and C^{14} (unen-

riched) was 9:1, and there were intermediate responses for concentrations of iron.

Intensive experimentation with *Glenodinium halli* followed (Gold, 1964a). It was depleted in B_{12} by serial transfers in B_{12} -free medium. Aliquots were enriched with varying amounts of B_{12} and incubated for 24 hr. Rates of photosynthesis were measured by C^{14} assimilation (C^{14} as $C^{14}O_2$). Linear dose-response curves were obtained at low B_{12} concentrations. A comparison with cell counts after 48 hr showed that the number of cells had tripled at the highest B_{12} concentration, whereas the C^{14} assimilation was approximately ten times greater than in the unenriched control. The increased sensitivity was more striking in cultures where it was impossible to detect cell differences between B_{12} concentrations, but there were differences in C^{14} assimilation.

The results with *Nitzschia closterium* gave essentially the same picture for responses to phosphorus using C^{14} . The number of cells doubled where phosphorus was high. However, C^{14} assimilation with high phosphate was eight times greater than in the unenriched control.

ASSAYING SEA WATER BY RADIOCARBON

A complete procedure and a discussion of the physiological implications of this assay have been reported elsewhere (Gold, 1964b).

This assay requires a sensitive test organism which is well depleted in the growth factor, B_{12} . *Cyclo-*

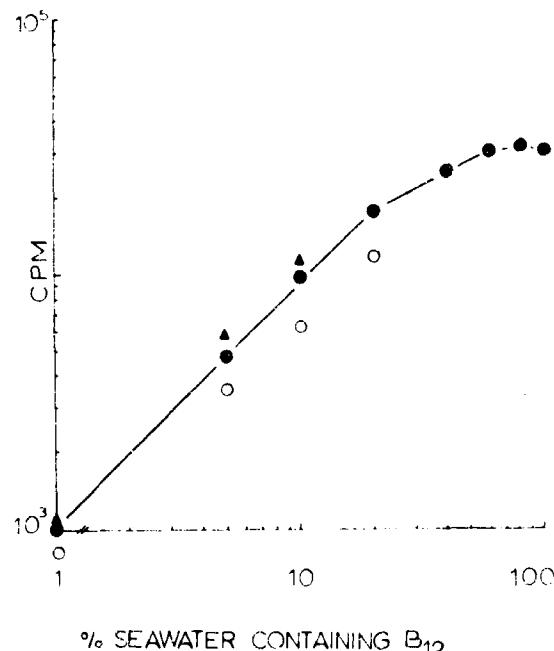


Fig. 1. A typical B_{12} assay showing external standard (closed circles), internal standard (triangles), and assayed sea water (open circles). The external standard contained $30\mu\text{g } B_{12}/\text{ml}$ at 100 percent (Gold, 1964b).

Cyclotella nana was used, which was generously supplied by Drs. J. H. Ryther and R. R. L. Guillard of the Woods Hole Oceanographic Institution. It was depicted by two successive transfers in B_{12} -free medium. When the second transfer was 3-7 days old, the cells were viable, but growth was limited by the absence of B_{12} . One-ml aliquots of inoculum were added to 9-ml portions of assay medium, which resulted in extremely low initial cell densities and little, if any, B_{12} carried over.

The assay solutions were prepared in a new way:

External Standard—Usually the contents of each tube is added separately; that is, by combining aliquots of solutions containing varying amounts of B_{12} , an aliquot of nutrient solution, and an aliquot of sea water or artificial medium without B_{12} . Instead, B_{12} -free (activated charcoal-treated) sea water was enriched and divided into two aliquots. One aliquot was further enriched with a known amount of B_{12} (10, 20, 30 $\mu\text{g}/\text{ml}$) and was dispensed into tubes in varying amounts of 0, 0.1, 0.2, ..., 9 ml. The volume was then brought to 9 ml, wherever possible, with the B_{12} -free aliquot. When one ml of B_{12} -free inoculum was added to each tube, the dilutions represented 1-90 percent of the initial B_{12} concentration.

Assay—Enriched sea water which was not charcoal treated was diluted with charcoal-treated (enriched) sea water in the same proportions as the external standard.

Internal Standard—This solution was the same as Assay, above, with the exception that prior to dispensing the sea water a known amount of B_{12} (usually 15 $\mu\text{g}/\text{ml}$) was added. By comparing the three curves, it was possible to calculate the amount of B_{12} in the sea water and determine whether any other growth stimulants or inhibitors were present.

Incubation—The tubes were placed in a temperature-controlled room ($21^\circ\text{C}.$) at 600 ft-c light intensity. The cultures were incubated overnight. Approximately 20 hr after inoculation each culture received an aliquot of a C^{14} -containing solution (C^{14} as $\text{Na}_2\text{C}^{14}\text{O}_3$). Incubation was then continued for another 2- to 4-hr period during which the radioactive carbon was fixed.

Harvesting the Cells and Plotting the Data—In all, approximately 24 hr elapsed between the time of inoculation of the assay and the end of the C^{14} incorporation period. Then the cells were filtered off under vacuum onto membrane filters. The filters were dried and the radioactivity which had been incorporated into cellular material was measured in an automatic gas-flow counter. The data were plotted on logarithmic graph paper. The lowest limits of sensitivity vary somewhat among the different figures as a result of the degree of B_{12} depletion of the inoculum.

The results of representative assays are illustrated graphically in Figures 1-5. The lowest limits of response in the external standards were not always determined. It appeared from the data in Figure 1 that there was still a greater useful range of linearity below 0.3 $\mu\text{g}/\text{ml}$, since, by comparison, the B_{12} -free

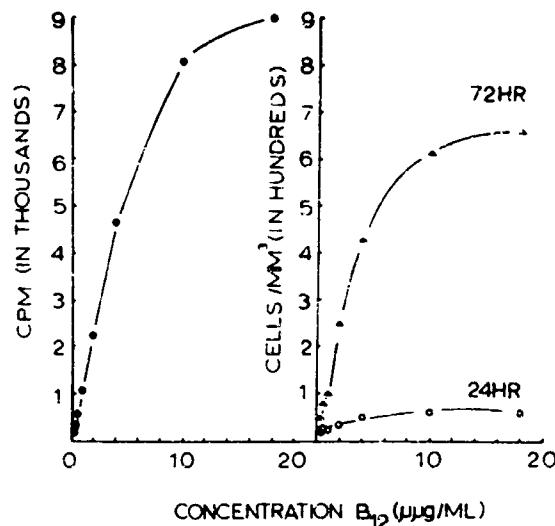


Fig. 2. A comparison between a 24-hr C^{14} -assimilation curve (left) and curves based on cell density after 24 and 72 hr (right) (Gold, 1964b).

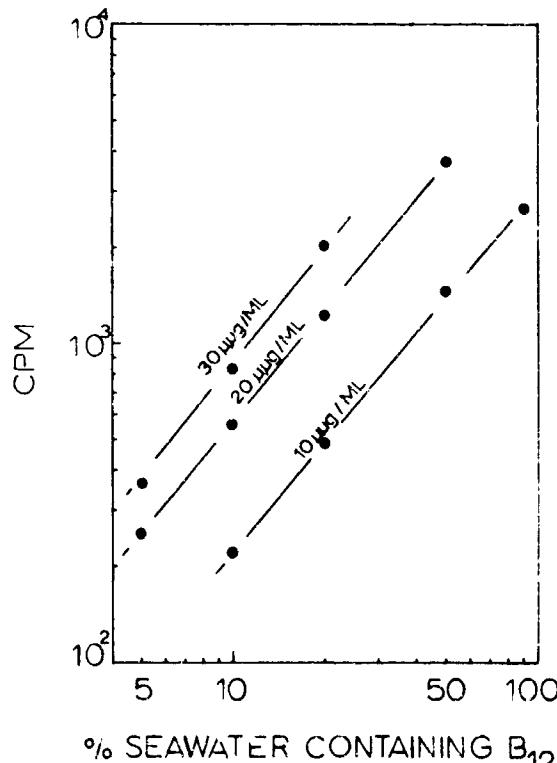


Fig. 3. Responses of *Cyclotella nana* to different concentrations of B_{12} added to enriched B_{12} -free sea water. The amount of B_{12} ($\mu\text{g}/\text{ml}$) added to each sample before dilution appears along each C^{14} response curve.

control showed very low activity. Sensitive responses have been obtained from 0.1 $\mu\text{g}/\text{ml}$, and since the threshold level of response is a function of the degree of depletion, it is believed that the lowest limits can be extended still further without sacrificing speed of the assay.

In the same sample there were differences in B_{12} concentration which depended upon the seawater dilution chosen for comparison with the standards. The differences were not appreciable and are probably attributable to the use of a seawater diluent which was made B_{12} -free by activated charcoal treatment. The sea water was slightly improved as a result of this treatment, based on 24-hr C^{14} tests. The cells adapted to the differences, however, since the total cell yield after six days' growth was the same in treated and untreated water.

It was stated earlier that it was impossible to predict at the outset whether the increased rates of photosynthesis were the results of denser cultures in a new stationary phase of growth, or of varying metabolic rates. It is clear now that both factors influence the C^{14} fixation, and the relative importance of each must now be determined.

The experiment in Figures 3 and 4 was to determine whether parallel responses would be obtained when the initial concentration of B_{12} varied in the range 5-30 μg at 100 percent. The results at 5

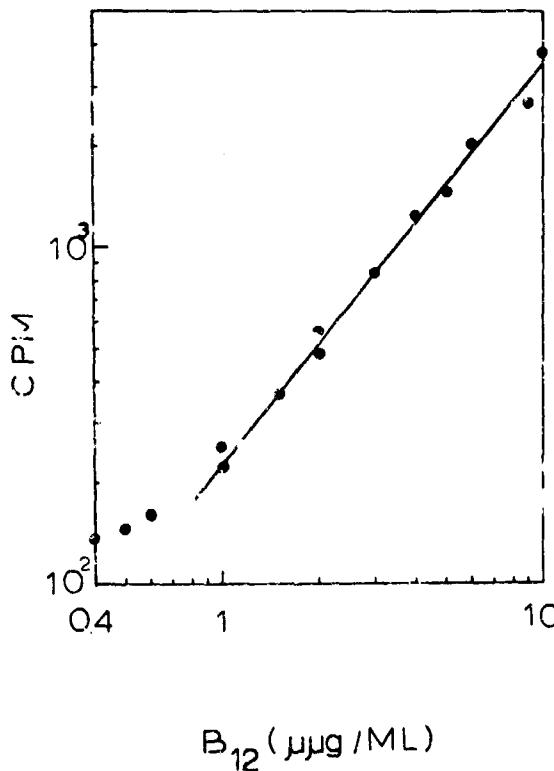


Fig. 4. The C^{14} -assimilation data from Figure 3 along with additional values from the same experiment were plotted with respect to B_{12} concentration.

$\mu\text{g}/\text{ml}$ have been included in Figure 4, but were not included in Figure 3 because they were somewhat erratic. Five $\mu\text{g}/\text{ml}$ is not recommended, therefore, as an initial concentration. These figures also demonstrate that total depletion is not essential for linear responses, but sensitivity is sacrificed when depletion is inadequate.

Figure 5 represents the first assay of an unknown field sample using this new technique. The arrows indicate the range of B_{12} concentrations of diluted (1:10) samples of Long Island Sound water. There is agreement between B_{12} measured this way and the value obtained by Visbniac and Riley (1959). In September, 1958, they detected 8.8 $\mu\text{g}/\text{ml}$. The range corresponding to the arrows in Figure 5 is 8.4-9.4 $\mu\text{g}/\text{ml}$ (September, 1963).

Author's Note: The Long Island Sound samples were collected aboard the Shang Wheeler, U. S. Bureau of

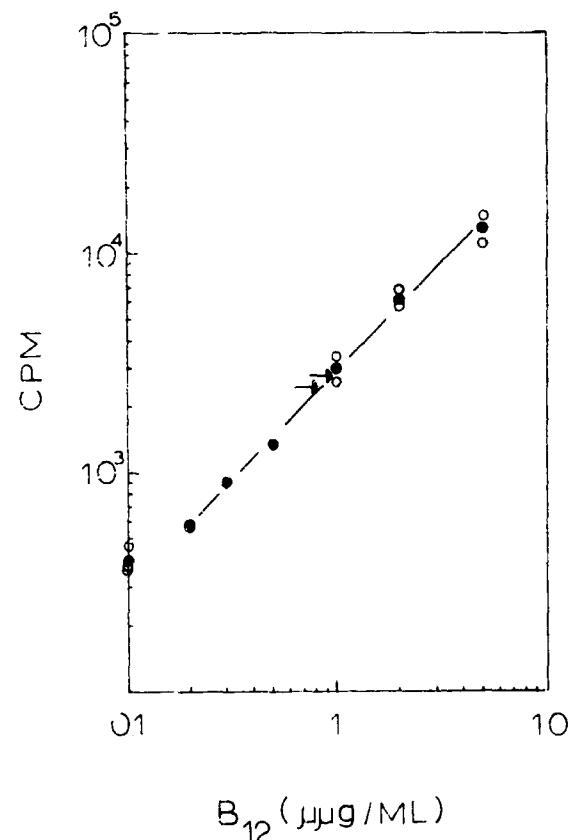


Fig. 5. A 24-hr assay for B_{12} in sea water using *Cyclotella nana* and the new C^{14} -assimilation method. The closed circles represent the mean of three separate tubes. The open circles represent the individual tubes. The arrows indicate the range of B_{12} which was found in four samples of Long Island Sound water which had been diluted to 10 percent of its original value with B_{12} -free medium. (The samples were obtained September, 1963.) The concentration of B_{12} in the original sample was, therefore, 8.4-9.4 $\mu\text{g}/\text{ml}$.

Commercial Fisheries, Milford, Conn. I am grateful to the director of the laboratory and the captain for the opportunity to collect them.

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JITERATURE CITED

- BECKER, D. J., and E. A. CALVELLI, 1964. Radioisotopic detection of microbial contamination present in jet fuel. *BioScience* 14(1):23-25.
- BELSER, W. L., 1963. Bioassay of trace substances. In *The Sea*, edited by M. N. Hill; vol. 2, pp. 220-231. Interscience, New York.
- GOLD, K., 1964a. Aspects of marine dinoflagellate nutrition measured by C^{14} assimilation. *J. Protosool.*, 11(4): 85-89.
- GOLD, K., 1964b. A microbiological assay for vitamin B_{12} in seawater, using radiocarbon. *Limnol. Oceanog.*, 9:343-347.
- GOLDMAN, C. R., 1960. Molybdenum as a factor limiting primary productivity in Castle Lake, California. *Science*, 132:1016-1017.
- GOLDMAN, C. R., 1961. Primary productivity and limiting factors in Brooks Lake, Alaska. *Verhandl. Intern. Ver. Limnol.*, 14:120-124.
- HEIM, A. H., J. A. CURTIN, and G. V. LEVIN, 1960. Determination of antimicrobial activity by a radioisotope method. *Antimicrobial Agents Ann.*; pp. 123-128. Plenum Press, New York.
- LEVIN, G. V., 1963. Microbiological determinations using radioisotopes. *Advan. Appl. Microbiol.*, 5:95-133.
- LEVIN, G. V., V. R. HARRISON, and W. C. HESS, 1957. Use of radioactive culture media. *J. Am. Water Works Assoc.*, 49(8):1069-1076.
- MC LAUGHLIN, J. J. A., P. A. ZAHL, A. NOWAK, J. MARCHISOTTO, and J. PRAGER, 1960. Mass cultivation of some marine phytoplankton. *Ann. N. Y. Acad. Sci.*, 90(3):856-865.
- MENZEL, D. W., and J. H. RYTHER, 1961. Nutrients limiting the production of phytoplankton in the Sargasso Sea, with special reference to iron. *Deep-Sea Res.*, 7(4):276-281.
- RYTHER, J. H., and R. R. L. GUILLARD, 1959. Enrichment experiments as a means of studying nutrients limiting to phytoplankton production. *Deep-Sea Res.*, 6(1):65-69.
- RYTHER, J. H., and R. R. L. GUILLARD, 1962. Studies of marine planktonic diatoms II. Use of *Cyclotella nana* Hustedt for assays of vitamin B_{12} in seawater. *Can. J. Microbiol.*, 8(4):437-445.
- VISHNIAC, H. S., and G. RILEY, 1959. B_{12} and thiamine in Long Island Sound: Patterns of distribution and ecological significance. *Intern. Oceanog. Congr. Preprints*; pp. 942-943. American Association for the Advancement of Science, Washington, D. C.

Integration of Field and Laboratory Experiments in Productivity Studies

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Aquatic environments, both marine and freshwater, provide unusual opportunities for combining field and laboratory experiments. Optimum results can be achieved only through the careful integration of *in situ* and *in vitro* studies. There are certain advantages to conducting experiments *in situ*, where organisms are maintained in their physico-chemical environment under the most natural conditions possible. If field conditions of light and temperature alone are desired in an experiment, we are painfully aware of the difficulty or impossibility of reproducing them precisely in the laboratory. The intensity, spectrum, angle, and polarization of incident light change during the day, with small concomitant changes in temperatures. Further, the organisms may show varying responses in accordance with their light history. The difficulty with light simulation has been clearly shown when attempting to convert shipboard incubation of primary productivity samples to *in situ* measurements. One of the most successful of these was that of Sorkin (1960), who made several comparisons of shipboard and *in situ* measurements in the Sea of Japan. The problem has been further investigated in two lakes by Saunders *et al.* (1962).

FIELD AND LABORATORY EXPERIMENTATION

Although pure cultures of organisms may be useful, it is often more meaningful to use the naturally occurring organisms at their normal concentration. This helps the investigator to determine how the whole community of organisms reacts to the experimental variables. These advantages are balanced, in part, by certain inherent disadvantages in almost any field experimentation that make execution and interpretation more difficult. The environmental variables are so numerous that field experiments are often difficult to control adequately, and experimental error is apt to be higher than would be the case if similar experiments were conducted *in vitro*. The choice of an experimental site is certainly important, because *in situ* experiments are usually conducted more easily in small lakes and estuaries than they are in large lakes or at sea.

With good design, interesting field observations may be better understood by running complementary experiments in the laboratory. The general availability of isotope-labeled compounds makes it possible to conduct a variety of experiments in the field which might otherwise be confined to the laboratory. Even

under Antarctic field conditions, numerous experiments involving interactions of light and temperature were accomplished with natural phytoplankton populations. Some examples of the experimental work done in both the Antarctic and California illustrate this point. In these studies, the isotope C¹⁴ bioassay method developed in 1957 for investigations of lakes on the Alaska Peninsula was used (Goldman, 1960). The methods generally employed in fresh waters are reviewed by Goldman (1963a), and results are reported here in counts per second (cps) where counting geometry and sample thickness are the same throughout an experiment. Where carbon fixation rates are given, isotope counting is based on the absolute disintegrations as determined by gas phase counting.

LIGHT AND TEMPERATURE IN PHOTOSYNTHESIS

Work on light and temperature was done in some freshwater lakes of Antarctica. Phytoplankton physiologists have traditionally devoted most of their efforts to algal populations in the laboratory, and considerable progress has been made in understanding the relationship of temperature to light (Steemann-Nielsen, 1962). Our work has been mainly with natural populations in the field with light intensities which frequently inhibit photosynthesis (Goldman *et al.*, 1963). Most of a series of complementary experiments involving recovery from light injury were carried out in the laboratory with the same natural phytoplankton populations.

Diel studies of photosynthesis in shallow lakes along the Antarctic coast showed that maximum rates of photosynthesis occurred during the evening when light intensity was at its lowest (Fig. 1). By using plastic screening of different thicknesses, we were able to get neutral density light filtration for *in situ* incubation of samples at different depths and in water baths at various temperatures along the shore. The photo-inhibition curves of these natural phytoplankton populations could then be investigated under natural and altered environmental light and temperature conditions. Ryther (1956), working primarily with pure cultures of marine phytoplankton, found an almost linear relationship between light intensity and photosynthesis in the inhibitory range; however, caution should be exercised to avoid oversimplification in interpreting any aspect of the environmental control of photosynthesis (Strickland, 1960). We have previ-

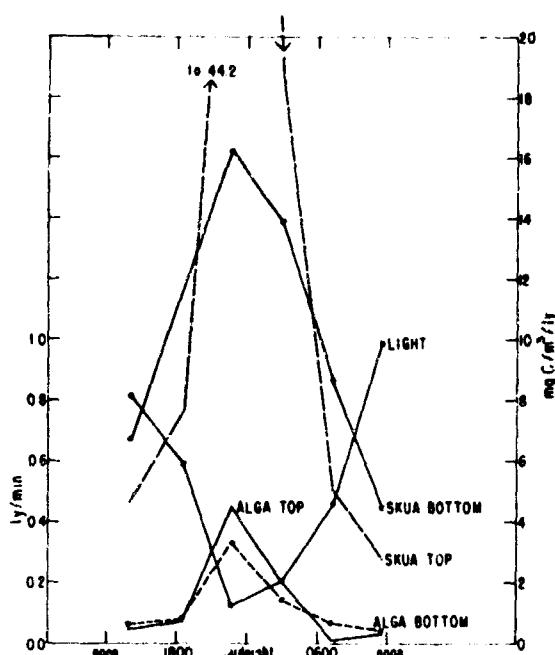


Fig. 1. Light inhibition of photosynthesis in Skua and Alga Lakes during periods of high light intensity. Carbon fixation on January 15-16, 1962, expressed as mg carbon fixed per langley of incident photosynthetic light during the incubation time (4 hr each), is plotted against time. The diel course of total incident light is also shown (Goldman *et al.*, 1963).

ously presented evidence (Goldman *et al.*, 1963) of the two-fold nature of the effects of high light intensities on natural photosynthesis, applying the terms "inhibition" to an immediately reversible depression effect and "injury" to a long-lasting effect apparently involving a significant alteration of cellular machinery. Recovery time for the phytoplankton and periphyton which have been light "injured" was measured by removing the population to lower light and constant temperature. This could be achieved in the field, but is accomplished best under the more constant conditions of a laboratory incubator.

An experiment on plankton from Alga Lake, a clear, sheltered, relatively plankton-poor pond on Cape Evans, indicated that the quantitative relation of high light intensities to photosynthesis may involve two stages. In Figure 2 we see that as the light rose beyond the optimum, the photosynthesis fell at a rate which would bring it to almost zero at ambient sunlight intensities (1 ly (langley)/min). However, at about 0.5 ly/min, the effect of increased sunlight was reduced, and inhibition became less marked. In full sunlight (1 ly), the natural population photosynthesized at about 45 percent of its maximum rate. Above 0.5 ly/min photosynthesis dropped linearly at a rate of 32 percent of maximum per langley per minute, which would bring it to zero net photosynthesis at slightly over 2.3 ly-min.

The simplest explanation for these results would involve an increase of photosynthesis to some optimum light intensity, followed by exponential inhibition. The initial phase of photosynthetic depression corresponds to the "inhibition" phases measured by other means. At this point the plankton apparently is not protected against the harmful effects of the full sunlight, and the depression of photosynthesis is immediate and short-lived. As light increases, a sparing mechanism reduces the harmful effect of the high light in a phase which may correspond to "injury". Presumably such plankton are physiologically altered to compensate for the bright light, and this change requires some time for recovery.

The apparent linearity of these two phases of the inhibition curve is also noteworthy. The deleterious effects of radiation are usually considered to be logarithmically related to the dosage. Here, however, we are apparently dealing not only with a two-fold depressive system, but also with the effect upon photosynthesis of the increase in usable energy.

By altering the temperatures of cultures in water baths on the lakeshore, the effect of varied tempera-

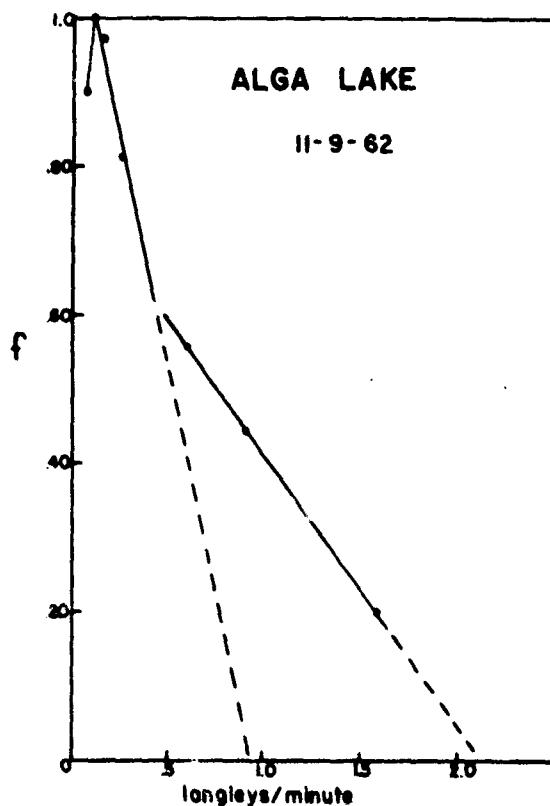


Fig. 2. Photosynthetic inhibition of Alga Lake phytoplankton exposed to direct sunlight under neutral density filters. Light intensities over 1.0 langley/minute were achieved by adding reflectors. Values of *f* are equal to photosynthetic carbon assimilation at a given light intensity divided by the maximum photosynthesis that was achieved by the phytoplankton in the experiment.

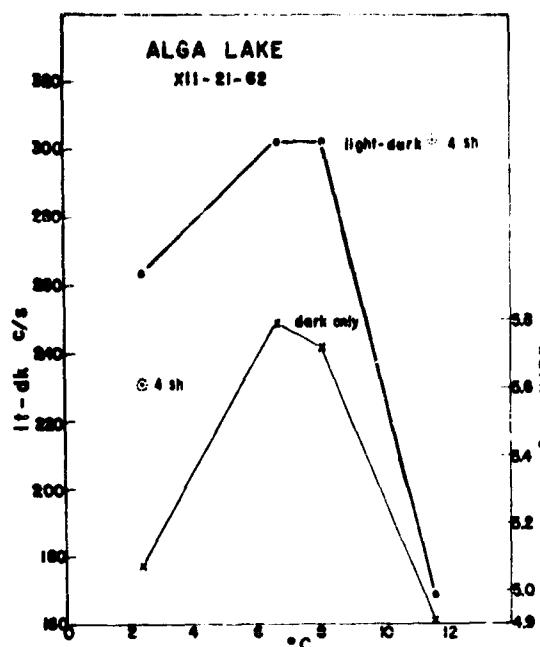


Fig. 3. Alga Lake phytoplankton cultured in the light and dark at various temperatures. Light bottles were exposed to inhibiting incident light. The depressing effect of high light was removed by shielding a culture with four neutral density filters, as indicated in the figure by 4 sh. Response was measured in counts/second of assimilated C^{14} . Geometry and sample thickness were the same for all samples counted.

tures on carbon assimilation by the phytoplankton of Alga Lake was investigated under the prevailing inhibitory light conditions. Dark controls were maintained in these experiments as a measure of non-photosynthetic carbon uptake and adsorption. The Alga Lake phytoplankton at this time consisted largely of *Rhodomonas* sp., a cryptophycean unicell. Members of this division contain phycobilin pigments simi-

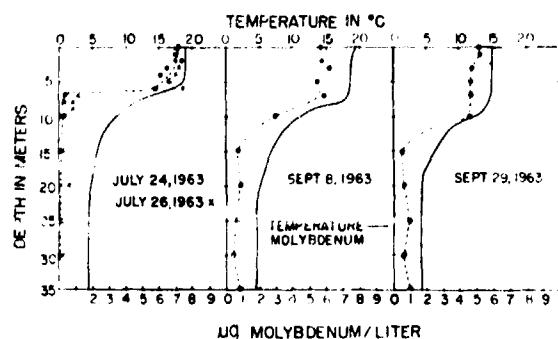


Fig. 5. Distribution of molybdenum and temperature in Castle Lake, California, after an experimental addition of sodium molybdate on July 23, 1963.

lar to blue-green and red algae (O'hEocha, 1962), and some species have been shown to excrete an extracellular carbohydrate (Guillard and Wangersky, 1958). It would be interesting to learn through *in vitro* studies how the pigment composition affects sensitivity to light inhibition and injury, and if the production of extracellular products of photosynthesis is related in any way to the sparing mechanism suggested above. The Antarctic experiments revealed that at a light level of one ly/min a metabolic optimum was found at about 7°C with minima at both higher and lower temperatures (Fig. 3). By shielding two cultures to give 14 percent of incident light, it was possible to remove the depressing effect of high temperature at the inhibiting light level. The depression of carbon assimilation at high temperatures in the dark as well as in the light in these psychrophilic algae is of interest. High temperatures are thought to increase dark uptake of C^{14} (Saunders *et al.*, 1962), but these workers dealt with organisms adapted to thermal regimes of temperate regions rather than of very cold ones.

These conclusions were confirmed by later experiments in Alga Lake (Fig. 4), which indicated that

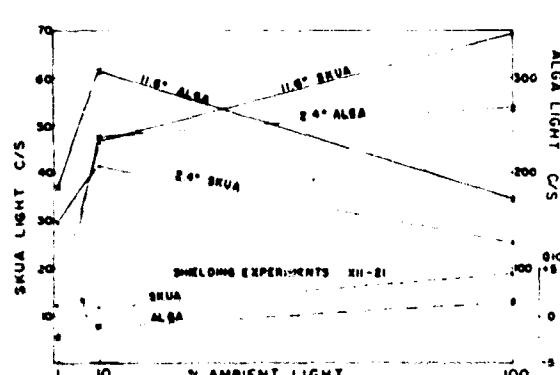


Fig. 4. Variation in photosynthesis (solid lines) and Q_m (dashed lines) as measured by C^{14} assimilation by phytoplankton in Alga and Skua Lakes at 2.4 and 11.6°C. Reduced light was obtained with neutral density filters.

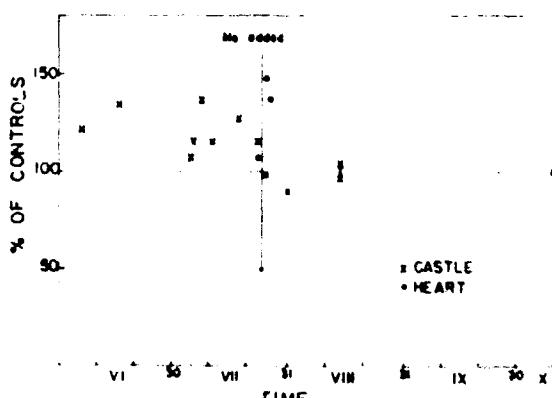


Fig. 6. Response by cultures of natural phytoplankton populations in Castle and Heart Lakes to molybdenum additions before and after a molybdenum addition to Castle Lake on July 23, 1963.

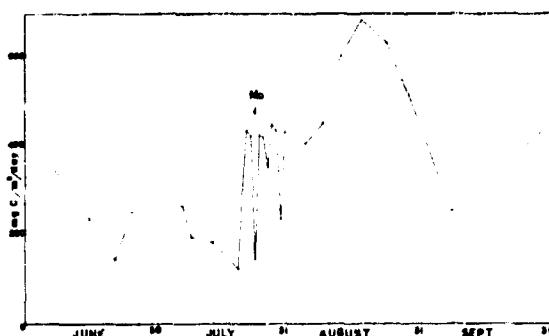


Fig. 7. Primary productivity as measured by the C^{14} method in Castle Lake, California, during the summer of 1963. A molybdenum addition of 7.5 parts per billion was made on July 23, 1963, to the lake's epilimnion.

low temperature has a sparing effect on photosynthesis in inhibiting light. This was not found to be the case in the more turbid and somewhat warmer Skua Lake, which may indicate that the species present in Skua Lake were not so adapted to cold as those found in Alga Lake.

NUTRIENT LIMITING FACTORS AND INTERACTION

Since the discovery that molybdenum, potassium, and sulfur are nutrient factors limiting productivity in Castle Lake, California (Goldman, 1960), the lake has been under continuous study. The addition of K_2SO_4 was more stimulating than the addition of either potassium or sulfate separately. After developing a method sufficiently sensitive to detect molybdenum to 0.5 g/l (Bachmann and Goldman, 1964), an addition calculated to give 7.5 g/l in the epilimnion was made to the surface waters of the entire lake. An analysis, made immediately after the addition of molybdenum, indicated that the wind had thoroughly mixed the molybdenum into the water to the depth of the thermal discontinuity. The extreme stability of the thermocline and the conservative behavior of the element is shown in Figure 5.

The culture experiments which paralleled the addition of molybdenum to the lake showed continued stimulation with the addition of molybdenum to control cultures from Heart Lake, but there was an immediate end of response in Castle Lake after fertilization (Fig. 6). The use of a control lake enabled us to be certain that the end of the molybdenum response in the lake was not caused by some population change within the lake. Figure 7 indicates the annual primary productivity before and after the Mo addition. The initial inhibition that immediately follows the molybdenum addition is characteristic of response to trace element addition. The fertilizing effect is less apparent because the molybdenum was confined to the epilimnion and productivity of the whole water column is shown in the Figure. The initiation of greater *in situ* culture response to potassium and sulfur additions was interesting, as well as the first evidence of

nitrogen and phosphorus deficiency in the lake after the molybdenum deficiency was alleviated (Fig. 8).

When dealing with nutrient factors, it is obvious that one must be alert to the intricate interrelationships of the nutrient requirements of phytoplankton. Not only does the level of one factor affect the availability of others (Goldman, 1960), but also the seasonally changing phytoplankton populations have different nutrient requirements. An effective treatment of this problem strains to the limit the integration of field and laboratory experimentation. The best solution is an experimental design which will allow a multiple analysis of interrelated variables which can be handled under field conditions, and this approach now appears to be feasible. The use of response surfaces is described by Box (1954) as a means of attaining optimum conditions in industrial experiments. Although developed for purely chemical experiments, the general approach has been used in other research areas, and appears promising for determining optimum nutrient concentrations in both field and laboratory experiments. Box stressed the point that the experimenter must decide what space is to be explored; the statistician can only indicate the best way it can be explored.

The first of a series of these four-dimensional *in situ* experiments on limiting factors was conducted during March, 1964, at Castle Lake, California. In the study at Castle Lake, productivity, as measured by C^{14} assimilation, is a function of the three nutrient variables—the molybdenum, potassium, and sulfur concentrations. A graph of this function would show each point on the surface with four coordinates—three for the three elements, and one for the change in the productivity value (Fig. 9). The productivity value is derived from the slope $\times 10^{-3}$ of each response curve as measured by C^{14} assimilation. If a mathematical expression for the function were known, the location of the relative maximum or minimum point or points on the surface could easily be found, be-

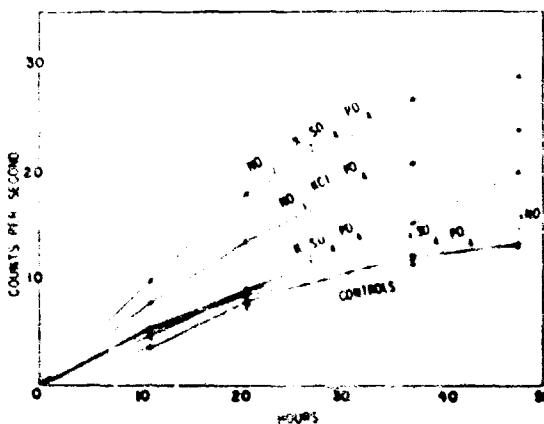


Fig. 8. Culture response of phytoplankton in Castle Lake, California, after the molybdenum addition of July 23, 1963, to the lake. Nitrate and phosphate were added as sodium salts. Bioassays were made with C^{14} .

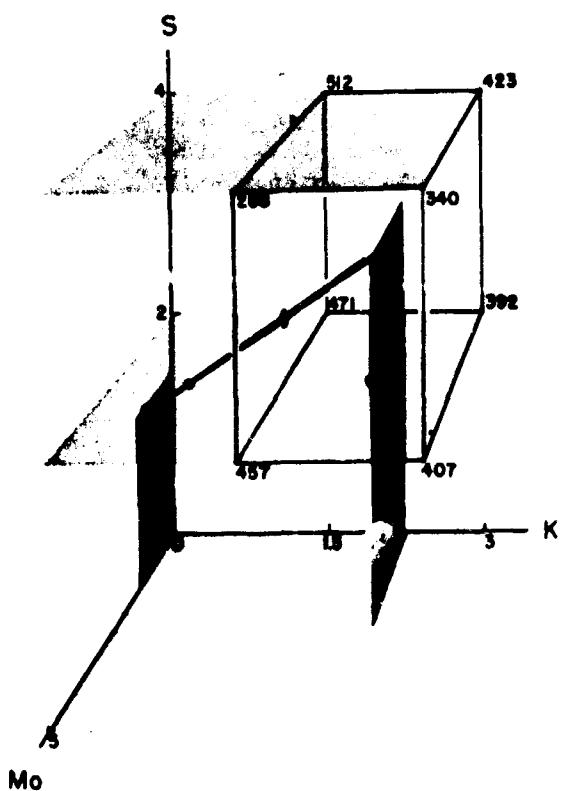


Fig. 9. The 3-dimensional factor space of a March, 1964, culture experiment at Castle Lake, California. The response, which is measured by rate of C^{14} uptake, is indicated beside each experimental point. The arrow indicates the calculated direction of maximum increase in response.

cause they would be the points where all partial derivatives of the function would equal zero. Although a mathematical expression for the function is not known, it can be approximated in the region of several experimentally determined points by fitting a polynomial expression by the method of least squares. An easy way to find the approximate location of the maximum is to determine a few experimental points,

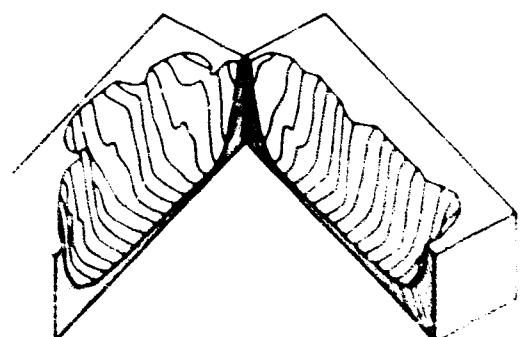


Fig. 10. The morphometry of Lake Tahoe, California-Nevada, drawn with a 225:1 vertical exaggeration. The basin is exposed along a line of maximum length.

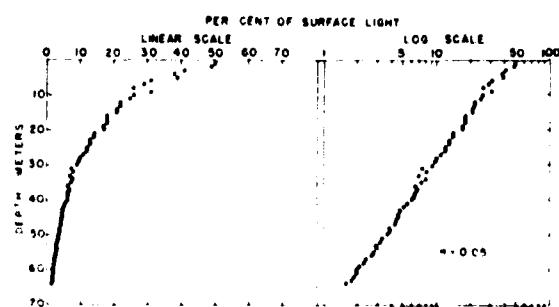


Fig. 11. Extinction of incident light in Lake Tahoe, California-Nevada, on August 27, 1960. Measurements were made with a submarine photometer (Weston 856 RR Photocell) without filters.

fit a first degree polynomial, and then make further investigations in the direction of maximum increase of this polynomial. Despite some five years of practice with Mo, K, and S additions, it is obvious that the area of the maximum was missed in this first experiment. Once the maximum has been approximately located, however, it can be surrounded by several experimental points in order to fit a polynomial of high enough degree to be a good approximation of the actual function. The more variable the response surface the higher the degree required. By setting the partial derivatives of this high degree polynomial equal to zero, the maximum can be located with precision. The arrow is therefore a vector, pointing in the direction of highest response with the numbers defining its direction.

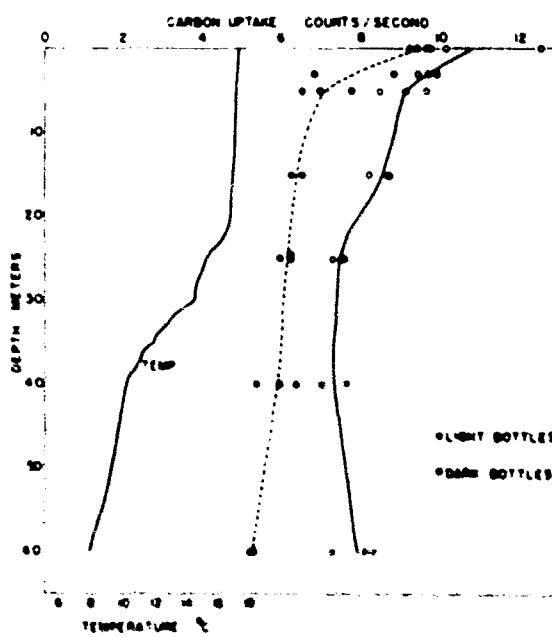


Fig. 12. Light and dark uptake of C^{14} in replicated samples and temperature distribution in Lake Tahoe, California-Nevada, at the control station (see Fig. 13) on August 30, 1962.

STUDIES OF LAKE TAHOE

As a last example of field and laboratory experiments, consider Lake Tahoe, California-Nevada which has received considerable attention since the threat of cultural eutrophication aroused great public concern. This remarkable lake, with a maximum depth of 501 m and a surface area of 499 km², has been the subject of productivity studies since 1959 (Goldman, 1963b; Goldman and Carter, 1965). Lake Tahoe was formed in a block-faulted basin, and contains 156 km³ of water with a mean depth of 313 m. It is characterized by steep sides and a flat bottom (Fig. 10). The great transparency of the water, with an extinction coefficient for unfiltered light of only 0.05 m⁻¹, is one of the major esthetic attractions of this extremely oligotrophic lake (Fig. 11). The photosynthetic zone in the lake extends to approximately 100 m in the summertime, and Secchi depths of 36 m have been recorded by the author. *In situ* productivity

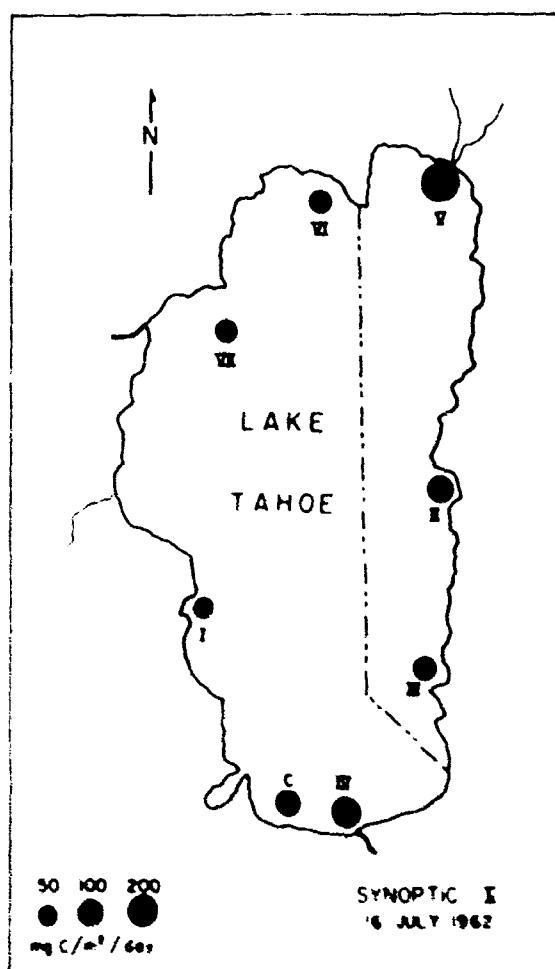


Fig. 13. Variation in carbon fixation in Lake Tahoe as measured by C^{14} assimilation during the synoptic cruise of July 16, 1962. Total solar radiation equaled 2570 langley's day (Goldman and Carter, 1965).

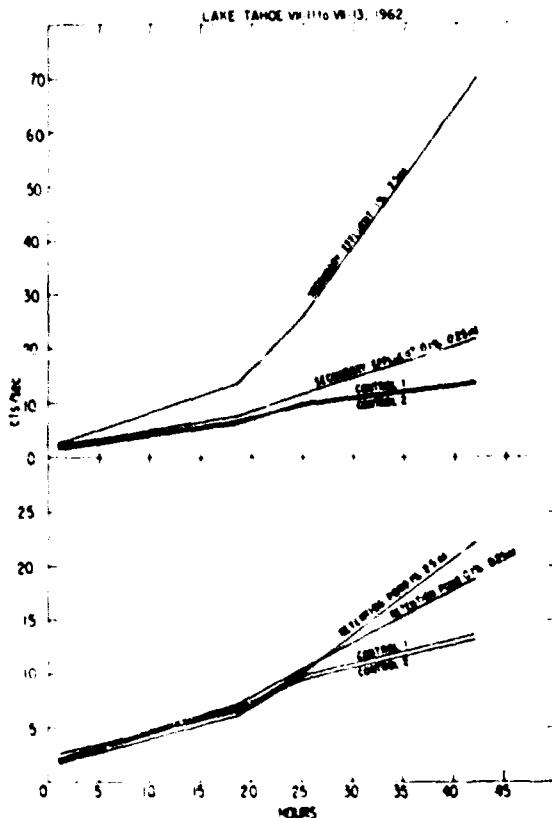


Fig. 14. Stimulation of photosynthesis in cultures of Lake Tahoe surface water by the addition of secondary treatment plant effluent at 0.1 and 1 percent by volume (upper graph). Similar additions of the same plant effluent after retention in a shallow pond are shown in the lower graph. Assay was by relative photosynthetic uptake of C^{14} (Goldman and Carter, 1965).

measurements with C^{14} from 1959 through 1962 give an average production of 99.2 mg C m² day. On the basis of a 60 m profile, this amounts to only 1.65 mg C m³ day. The degree of reproducibility is indicated in Figure 12, where the results of replicated light and dark bottle sample incubations are given. The standard deviation of the integral carbon fixation amounts to ± 15.7 percent of the cps when single light and dark bottles are used at each of the depths sampled. *In situ* bioassays have indicated micronutrient deficiencies in the natural phytoplankton population of iron, manganese, and zinc (Goldman, 1965).

The variation in productivity within a large lake is well documented (Sorokin, 1959; Goldman, 1960). To determine the degree of variability in Lake Tahoe, two synoptic cruises were made during the summer of 1962. One small and two large boats were utilized simultaneously on the lake to sample four stations each. The *in situ* measurements at each station were converted to a day's photosynthesis by comparison with the continuous diel study at an index station. The diel study was necessary to correct for any diurnal periodicity in photosynthesis as well as the

changes in light that occurred during the time the two large boats were putting out and retrieving their four stations. The rather high degree of variation at the different stations on July 16, 1962, is indicated in Figure 13. In view of the land use around the shoreline and the distribution of tributaries contributing nutrients to an unusually oligotrophic lake, these differences, although they are cause for concern, are not too surprising. To complete the study, in vitro bioassays were made in the laboratory with tributary waters, and with sewage effluent after both secondary treatment and a month's retention in a holding pond (Fig. 14). The high stimulation to photosynthesis from the addition of treated sewage to Lake Tahoe water is clearly indicated, and provides strong evidence for its dangerous eutrophinating potential.

CONCLUSION

In conclusion, it should be noted that estuaries, like lakes, provide environments well suited to a combination of field and laboratory experimentation. They have the advantages of shallowness, accessibility, and the opportunity of using natural gradients of temperature, salinity, and other environmental variables. Further, tidal flushing provides a unique opportunity for short-term fertilization experiments. There are good reasons for conducting field experiments, where natural conditions of light, temperature, and biota persist, to determine what further experiments should be conducted in the laboratory.

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LITERATURE CITED

- BACHMANN, R. W., and C. R. GOLDMAN. 1964. The determination of microgram quantities of molybdenum in natural waters. *Limn. & Oceanogr.*, 9:143-146.
- BOX, G. E. P. 1954. The exploration and exploitation of response surfaces: some general considerations and examples. *Biometrika*, 41:16-60.
- GOLDMAN, C. R. 1960. Primary productivity and limiting factors in three lakes of the Alaska peninsula. *Ecol. Monographs*, 30:207-230.
- GOLDMAN, C. R. 1963a. The measurement of primary productivity and limiting factors in fresh water with carbon-14. In *Proceedings of the Conference on Primary Productivity Measurement, Marine and Fresh Water*, edited by M. S. Doty; pp. 103-113. TID-7633. U. S. Atomic Energy Commission, Washington, D. C.
- GOLDMAN, C. R. 1963b. Primary productivity measurements in Lake Tahoe. In *Comprehensive Study on Protection of Lake Tahoe Basin*, Appendix I, pp. 154-163. Engineering-Sciences, Inc.
- GOLDMAN, C. R. 1964. Primary productivity and micro-nutrient limiting factors in some North American and New Zealand lakes. *Verhandl. Intern. Ver. Limnol.*, 15:365-374.
- GOLDMAN, C. R., and R. C. CARTER. 1965. An investigation by rapid carbon-14 bioassay of factors affecting the cultural eutrophication of Lake Tahoe, California - Nevada. *J. Wat. Poll. Contr. Fed.*, 37:1044-1059.
- GOLDMAN, C. R., D. T. MASON, and B. J. B. WOOD. 1963. Light injury and inhibition in Antarctic freshwater phytoplankton. *Limnol. Oceanogr.*, 8:313-322.
- GUILARD, R. R. L., and P. J. WANGERSKY. 1958. The production of extracellular carbohydrates by some marine flagellates. *Limnol. Oceanogr.*, 3:449-454.
- O'NEOCHA, C. 1962. Phycobilins. In *Physiology and Biochemistry of Algae*, edited by R. A. Lewin; pp. 421-443. Academic Press, New York.
- RYTHER, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. *Limnol. Oceanogr.*, 1:61-70.
- SAUNDERS, G. W., F. B. TRAMA, and R. W. BACHMANN. 1962. Evaluation of a modified C¹⁴ technique for shipboard estimation of photosynthesis in large lakes. *Great Lakes Res. Div. Inst. Sci. and Techn. Univ. Mich. Publ. No. 8:1-61.*
- SOROKIN, Y. I. 1959. Determination of the photosynthetic productivity of phytoplankton in water using C¹⁴. *Foto. Rast.*, 6:125-133.
- SOROKIN, Y. I. 1960. On the method of determining primary production of the sea by means of C¹⁴. *Tr. Upr. Radiobiol. Okeanichesk. Akad. Nauk SSSR*, 10:235-254.
- STEEMAN-NIELSEN, E. 1962. Inactivation of the photochemical mechanism in photosynthesis as a means to protect the cells against too high light intensities. *Phycol. Plantarum*, 15:161-171.
- STRICKLAND, J. D. H. 1960. Measuring the production of marine phytoplankton. *Bull. Fisheries Res. Board Can.*, No. 122:172.

Fatty Acids in Certain Plankton Organisms

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The presence of extracellular organic materials in natural sea water is now generally recognized. The precise roles that these compounds may play in the biodynamics of the sea will be the subject of investigation for years to come. We know that they may be in both dissolved and suspended states and that they may possess biological activity (Collier *et al.*, 1950). More recently it has been shown that these materials may form platelike aggregates which may be important as particulate food for small organisms (Baylor and Sutcliffe, 1963; Riley, 1963). A precise differentiation between the truly dissolved materials and colloidal dispersions has not yet been made, although 1μ has been used as an arbitrary lower limit (Parsons, 1963).

Investigations of the biological roles of these materials have been largely devoted to the nutrition of the unicellular marine biota (Trovasoli, 1963). Some comparatively recent work has been done on the assimilation of dissolved substance by metazoa (Secondat and Quillier, 1959). Collier (1959) has made some studies on the relationship of dissolved materials to the respiration of the oyster.

The investigation of the chemical nature of these compounds has been handicapped by difficulties inherent in isolating them from the relatively large masses of sea water involved. Although progress in this area has not been as rapid as would be desired, there has been sufficient progress to stimulate interest. The work of Collier *et al.* (1953) demonstrated the presence of variable quantities of dissolved carbohydrate-like materials and their biological activity. Wangersky (1952) isolated and identified ascorbic acid and rhinomides. Slowey *et al.* (1962) concentrated and identified fatty acids from deep sea samples taken in the Gulf of Mexico. Further work on lipids in ocean waters was done by Jeffrey *et al.* (1962).

Another approach to an understanding of the problem is the production of metabolites by specific organisms grown under controlled conditions. Collier (1958) reported the production of appreciable quantities of carbohydrate materials by the armored dinoflagellate *Protocentrum*, and Wangersky and Guillard (1960) studied a low molecular weight organic base produced in cultures of the dinoflagellate *Ampidinium carolinense*.

Parsons *et al.* (1961) presented data on the chemical composition of certain phytoplankton forms. Korn (1963) identified 51 fatty acids isolated from *Euglena gracilis*. The study of acids produced under laboratory

conditions and the trophic relationship in the natural environment were investigated and discussed by Ackman *et al.* (1964). The organic compounds present as dissolved or suspended materials in sea water originate as metabolites of living organisms or residues of disintegrating organisms. Where large blooms of unicellular algae occur, it is impossible to differentiate the origins of the extracellular compounds. A first step in this direction is the analysis of the whole cell. Following this, a separation of the cells from the aqueous medium with separate analyses of both is helpful. It is the purpose of this paper to present the results of investigations concerning the production of fatty acids in laboratory cultures.

METHODS

The mass cultures of the dinoflagellates and diatoms were produced in 10- and 16-liter Pyrex bottles fitted with polyethylene caps molded in the laboratory. These were filled with 10 liters of a defined medium developed by W. B. Wilson as a general-purpose medium for the growth of dinoflagellates. The medium was inoculated with 10 ml seed cultures derived from established stocks of isolated organisms.

The very small diatoms were isolated by a combination of millipore filtration and serial dilution. The latter takes advantage of the high rate of cell division of these diatoms. The formula of the culture medium used for these organisms was as follows:

Component	Amount per 1,000 ml of distilled water
NaCl	24.0 g
KCl	0.6 g
MgCl ₂ ·6H ₂ O	4.5 g
MgSO ₄ ·7H ₂ O	6.0 g
CaCl ₂	0.7 g
NH ₄ Cl	10 mg
K ₂ HPO ₄	100 mg
Na ₂ S ²⁻ H ₂ O	10 mg
KNO ₃	100 mg
Disodium ethylenediamine tetraacetate	100 mg
Tris (hydroxymethyl) -aminoethane (pH 8.2)	0.4 g
Vitamin B ₁₂	10 µg
Thiamine HCl	100 µg
Biotin	0.5 µg

Component	Amount per 1,000 ml of distilled water
Fe	0.25 mg
B	0.25 mg
Cr	0.001 mg
Mn	0.05 mg
Si	0.1 mg
Er	0.025 mg
Ti	0.25 mg
V	0.01 mg

This medium is sterilized by autoclaving at 15 psi for 1 minute and then dispensed in amounts of 10 ml into pre-treated culture tubes.

For comparative studies other organisms were investigated. These were collected from the waters of the Gulf of Mexico and were used whole without any type of preservation in the field.

The extraction procedures were adapted for the specific materials being studied, and included filtration, centrifugation, homogenization, and solvent extraction with appropriate solvent systems, lyophilization, and flash evaporation. Materials in their final stages were stored at 10°F. No attempt was made to assay the actual quantity of fatty acids per unit of raw material. All concentrations are given as relative percentages of total acids.

Preparation of materials for submission to gas-liquid chromatography was by methylation with the boron trifluoride-methanol reagent (Metcalfe and Schmitz, 1961).

The columns used in the Research Associate's gas-liquid chromatograph were composed of 20 percent diethylene glycol succinate on Chromosorb W and 20 percent Apiezon M on Chromosorb W, 6080 mesh. Control runs of known mixtures of fatty-acid esters were made, with each of the columns packed to insure proper interpretation of retention times and peaks for the unknown samples. Helium was the carrier gas, and the flow rate was 35 to 55 ml/min, depending upon the column used. Column temperatures were likewise from 188° to 225° C., and current on the detector was 300 ma.

The submission of a sample to the gas-liquid column resulted in the separation of many minor components which were indicated on the recording as small peaks between those produced by the known and major components. Without an expenditure of time and funds beyond the scope of this project, it would have been impossible to identify all of these minor components.

In Tables 6, 7, and 8, these components are indicated in quantity in their proper position according to their relative retention time, but without designation of identity.

In some of the first experiments it was not possible to resolve arachidic from linoleic acids, and behenic from arachidonic acids. Where these ambiguities occur in the tables they are shown.

RESULTS

FATTY ACIDS IN DINOFLAGELLATES

The dinoflagellates studied were *Gymnodinium breve*, *Gymnodinium splendens*, *Glenodinium* sp., and *Prorocentrum* sp. All of these are associated with the estuarine environment, with the possible exception of *G. breve*, which more characteristically inhabits the littoral area of the Gulf of Mexico.

As compared with the other dinoflagellates, the fatty acid spectrum of *Glenodinium* was by far the highest in saturated acids, the total being 73.6 percent. Next was *G. splendens* with a total of 61.5 percent. *G. breve* and *Prorocentrum* were considerably lower, 43.6 percent and 42.1 percent, respectively. The individual acids are shown in Table 1. When this table is examined we see that *Glenodinium* and *G. splendens* were also characterized by high relative concentrations of palmitic acid, 42.6 percent and 44.6 percent, respectively. *Prorocentrum* and *G. breve* yielded less than half of these amounts, 12.7 percent and 15.4 percent, respectively. There are other points of difference between these species within the saturated group, which, though of relatively minor quantities, are definitely characteristic. These differences, upon exami-

Table 1. Fatty acids in dinoflagellates, percent methyl esters. Unidentified materials are not included. See text concerning identification of organisms. T = trace.

Acid type	<i>Proro-</i> <i>centrum</i> sp.	<i>G.</i> <i>splendens</i>	<i>G.</i> <i>breve</i>	<i>Glenodinium</i> sp.
Saturated				
C ₈	0.3	0.7	1.4	0
C ₁₀	0.4	0.1	1.2	0.3
C ₁₂	15.0	5.2	11.0	0.8
C ₁₄	2.5	5.2	4.9	11.4
C ₁₆	12.7	44.6	15.4	42.6
C ₁₈	11.2	4.3	7.7	7.8
C ₂₀	0	1.4	2.0	10.7
	42.1	61.5	43.6	73.6
Unsaturated (1=)				
C ₁₁	2.7	1.0	0.6	T
C ₁₅	5.7	11.0	6.6	8.9
C ₁₇	8.0	13.9	22.6	3.2
C ₂₀	0	0.6	0	0
C ₂₂	0	0	0	0.1
	16.4	26.5	29.8	12.2
Unsaturated (2=)				
C ₁₄	0.1	1.6	1.4	1.6
C ₁₈	1.4	0.6	1.6	3.5
C ₂₀	0	0.2	0.1	0.4
C ₂₂	0	0	0	0.2
C ₂₄	0	0	0	1.0
	1.5	2.4	3.1	6.7
Unsaturated (3=)				
C ₁₄	0	0.5	0.9	3.8
C ₂₀	0	0	0	2.4
	0	0.5	0.9	6.2

nation of Table 1, will be found to involve lauric (C_{12}), myristic (C_{14}), and stearic (C_{18}) acids.

When the distribution of unsaturated acids is considered, it is seen (Table 1) that *G. breve* is characterized by 22.6 percent oleic acid. In fact, this characteristic in combination with the 11 percent lauric acid in the saturated group differentiates *G. breve* not only from the other dinoflagellates but also from all other organisms used in this study. In the more highly unsaturated groups, *Glenodinium* is the only dinoflagellate with appreciable amounts, and these are 3.5 percent for linoleic and 3.8 percent for linolenic acids.

As a group it would appear that the dinoflagellates used in this study tend to have fatty acid spectra characterized by low values for the more highly unsaturated acids.

FATTY ACIDS IN DIATOMS

The two diatoms for which data are presented here are in a group of very small organisms which we have designated as ultradiatoms. One of these, *Chaetoceros galvestonensis*, has been described only recently (Collier and Murphy, 1962), and the other has not been described. The latter is designated provisionally as "Holothermia" because of its tolerance of a broad range of temperatures in the laboratory.

Two cultures of *C. galvestonensis* were used. An inspection of Table 2 will reveal substantial differences between the fatty acid spectra for these two cultures of the same organisms. These differences may be due to different growth stages of the cultures at time of harvest. Except for myristic acid, the differences in the saturated group are not great; the major deviations are in the unsaturated groups. The mean total saturated acids for the two cultures was 39 percent, and for the unsaturated acids the mean total was 36 percent. This leaves a remainder of 26 percent for the unidentified acids (actually peaks on the chromatograms). This amount is spread over a large range of retention times on the columns used in the chromatograph. Various odd-numbered chains and isomers are probably represented in this group of compounds.

"Holothermia" is distinguished from *C. galvestonensis* by its large relative amounts of palmitic acid (26 percent) and palmitoleic acid (17 percent). It is not possible to make valid interpretations of those acids which are involved in the ambiguities mentioned in the description of the analytical methods. Because of this, a comparison of the total saturated and the total unsaturated compounds is not possible. It is reasonable to assume, however, that the amounts indicated by the footnotes are divided between the members of the ambiguous pairs. In this case "Holothermia" would show a greater fraction of saturated acids than *C. galvestonensis* and a correspondingly lesser amount of unsaturated acids. Beyond this *C. galvestonensis* does yield a significantly greater proportion of the higher unsaturated acids, especially those with five double bonds, than does "Holothermia".

FATTY ACIDS IN BLUE-GREEN ALGAE

At the same time as the ultradiatoms were being isolated and obtained in pure culture, some blue-green algae were obtained. Two morphologically distinct types were used in these studies, and are referred to as Alga 2 and Alga 4. The spectra for two different cultures are given for Alga 2. In all three of these cases only 9 percent, or less, of the components of the spectra are unidentified. The ambiguities involving arachidic and behenic acids are still present in the spectrum for Alga 4, but not in that for Alga 2.

Table 2. Fatty acids in diatoms, percent methyl esters. Unidentified materials are omitted from the tabulation. See text concerning identification of organisms. T = trace.

Acid type	<i>Chaetoceros galvestonensis</i>		"Holothermia"
	Culture 1	Culture 2	Culture 1
Saturated			
C_6	0	0	0
C_8	0	0	0.5
C_{10}	0	0	0
C_{12}	0	0	0.1
C_{14}	2.1	T	0.5
C_{16}	1.2	0.7	1.6
C_{18}	5.6	14.6	11.7
C_{20}	2.5	2.5	2.7
C_{22}	7.3	9.1	26.0
C_{24}	4.2	4.1	3.3
C_{26}	1.5	0.9	5.9
C_{28}	10.7 ^a	—	0
C_{30}	12.7 ^b	5.9	1.9
	47.1	37.8	54.8
Unsaturated (1=)			
C_{16}	2.5	11.3	17.1
C_{18}	7.5	5.0	2.8
C_{20}	0	0	0.6
	10.0	16.3	20.5
Unsaturated (2=)			
C_{18}	8.7	3.5	2.7
C_{20}	9.7	0	3.8
C_{22}	—	—	1.4
	18.4	3.5	7.9
Unsaturated (3=)			
C_{18}	1	0	4.6
C_{20}	0	0	0.4
C_{22}	3.6	0	0
	3.6	0	5.0
Unsaturated (4=)			
C_{20}	12.7 ^b	5.9 ^b	3.9
Unsaturated (5=)			
C_{18}	6.2	10.5	0
C_{20}	0	3.9	0
	6.2	14.4	0
Total			
Unsaturated ^c	38.2	34.2	37.1

^a Unresolved arachidic or linoleic acids.

^b Unresolved behenic or arachidonic acids.

^c Total does not include 1 and 5.

In the group of saturated acids, Alga 2 is quickly differentiated from Alga 4 (Table 3) by the amount of myristic acid. Further, its spectrum is completely dominated by five acids: myristic, palmitic, palmitoleic, oleic, and elenodonic, whereas the spectrum for Alga 4 is scattered over a large number of acids and the inclusion of a C₂₂ form with six double bonds (docosahexaenoic acid). Assuming that the ambiguous items (¹ and ² in the tables) are arachidic and behenic acids and belong in the corresponding unsaturated listing, it can be said that this group of organisms produces dominantly an unsaturated spectrum. The presence of timnodonic acid (C_{20:5}) (eicosapentaenoic) in the blue-greens, as well as in the diatoms, is pointed out.

Sargassum weed is common in the Gulf of Mexico and is often driven onto the beaches in extensive windrows. The samples used in these analyses (Table 4) were from rafts of living plants and are mixtures of *S. natans* and *S. fluitans*.

Table 3. Fatty acid distribution in blue-green algae, percent methyl esters. T = trace.

Acid type	Alga 2		Alga 4
	Culture 1	Culture 2	
Saturated			
C ₈	0	0	T
C ₁₀	1.0	0	0.3
C ₁₁	1.1	0	2.0
C ₁₂	T	T	0
C ₁₄	9.5	14.9	1.3
C ₁₅	0	0	3.5
C ₁₆	18.8	23.5	14.3
C ₁₇	0	0	3.9
C ₁₈	1.9	2.8	6.0
C ₂₀	0	0	5.1 ¹
C ₂₂	0	0	5.4 ²
	32.3	41.2	41.8
Unsaturated (1=)			
C ₁₀	22.2	26.2	0.1
C ₁₁	12.4	6.9	14.3
C ₂₂	0	0	0.4
	34.6	33.1	14.8
Unsaturated (2=)			
C ₁₅	0	0	7.3
C ₂₀	0	0	6.5
	—	—	13.8
Unsaturated (3=)			
C ₁₆	0	0	5.1 ¹
C ₂₂	0	0	15.7
	—	—	20.8
Unsaturated (4=)			
C ₂₀	0	0	5.4 ²
Unsaturated (5=)			
C ₁₀	3.4	3.2	6.5
C ₂₂	21.3	14.7	0
	24.7	17.9	6.5
Unsaturated (6=)			
C ₂₂	0	0	6.8

¹ Unresolved arachidic or linoleic acids.

² Unresolved behenic or arachidonic acids.

Table 4. Fatty acids in *Sargassum natans* and *Sargassum fluitans* (mixed), percent methyl esters. All acids showing on the chromatographic trace are included.

Acid type	Sample 1	Sample 2
Saturated		
C ₈	0.26	0.16
C ₉	0.07	0.06
C ₁₀	0.29	0.39
C ₁₁	0.02	0.02
C ₁₂	0.30	0.21
C ₁₄	2.66	2.53
C ₁₅	0.45	0.51
C ₁₆	26.73	33.18
C ₁₈	1.90	1.74
C ₂₀	1.18	0.99
C ₂₂	0.73	0
	34.59	39.79
Unsaturated (1=)		
C ₁₆	8.15	6.20
C ₁₈	12.93	11.44
	21.08	17.64
Unsaturated (2=)		
C ₁₆	0.74	1.05
C ₁₈	6.95	6.01
	7.69	7.06
Unsaturated (3=)		
C ₁₈	7.70	6.83
Unsaturated (4=)		
C ₁₆	6.84	6.42
C ₂₀	13.34	13.22
	20.18	19.64
Unsaturated (5=)		
C ₂₂	7.41	6.83

The unidentified materials in this spectrum amounted to approximately 1 percent and the two independent analyses are in good agreement.

The most outstanding characteristic of these spectra is the dominance of unsaturated acids. Palmitic acid is the only saturated component present in significant amounts. In contrast to the other algae, myristic acid is not very abundant.

The unsaturated acids which stand out are oleic and arachidonic. When this spectrum is compared to that of the other organisms it is interesting to note that timnodonic (C_{20:5}) is present. It should also be mentioned that in addition to the acids shown in the table there were some odd-numbered chains in the spectra for Sargassum. All were present at relative concentrations of less than 1 percent.

CTENOPHORES

Two genera of ctenophores as representatives of the zooplankton were included in this investigation (Table 5). The two genera, *Mnemiopsis* and *Beroë*, yielded somewhat different fatty acid spectra, the principal difference being in the relative percentage of oleic and arachidonic acids. Although the odd-numbered acids are not present in high concentrations in the case of the ctenophores, they are certainly

Table 5. Fatty acids in ctenophores, percent methyl esters. Unidentified components are omitted from the tabulation.

Acid type	<i>Mnemiopsis</i> sp.	<i>Beröe</i> sp.
Saturated		
C ₁₀	0	0.84
C ₁₁	4.28	0.97
C ₁₂	0.92	0.09
C ₁₃	3.35	1.87
C ₁₄	2.49	0.59
C ₁₅	16.53	12.84
C ₁₆	3.99	2.32
C ₁₇	13.47	11.80
C ₁₈	0.93	4.56
C ₁₉	1.99	0.49
	47.95	36.37
Unsaturated (1=)		
C ₁₈	6.49	3.27
C ₁₉	6.56	12.26
C ₂₀	0.21	0
	13.26	15.53
Unsaturated (2=)		
C ₁₈	2.49	0.90
C ₂₄	1.2	3.30
	3.69	4.20
Unsaturated (3=)		
C ₁₈	2.83	4.49
C ₂₀	6.27	3.50
	9.10	7.99
Unsaturated (4=)		
C ₂₀	7.34	10.32

present in noticeable amounts, and provide some interesting points for differentiating the spectra for *Mnemiopsis* and *Beröe*. For instance, *Mnemiopsis* gave 4.28 percent of undecanoic (C₁₁) acid as compared to 0.97 percent for *Beröe*. In the case of pentadecanoic (C₁₅) the concentrations were 2.49 percent for *Mnemiopsis* and 0.59 percent for *Beröe*. Heptadecanoic acid (C₁₇), or margaric acid, was present in concentration of 3.99 percent for *Mnemiopsis* and 2.32 percent for *Beröe*.

The principal contrast between the ctenophore spectra and all the others is the presence of stearic acid; the only exception in this respect is that for the armored dinoflagellate *Prorocentrum*.

Finally, a C_{24:2} acid (tetracosadienoic) was found in both of these organisms and it did not appear in any of the other spectra.

DISTRIBUTION OF FATTY ACIDS IN CULTURE MEDIA

The foregoing pages have described and compared the spectra of fatty acids contained in a group of planktonic organisms. The presence of chemical compounds in organisms neither precludes nor assures their presence in the fluids in which the organisms are suspended. It is desirable to know something of the kinds of organic materials which may escape into the media and their behavior after escape. The experimental materials available for this study pre-

sented an opportunity to investigate this aspect of the problem.

The experimental method was as follows: (1) the surface materials were collected from a 10-liter culture (16-liter Pyrex wide-mouth bottle) by means of a special collecting device; (2) the whole culture was processed with a continuous-flow centrifuge; and (3) samples drawn from the centrifugate were collected and analyzed. Tables 6, 7, and 8 summarize the results from 8 independent cultures involving 2 blue-green algae and 1 diatom. Unfortunately, in these preliminary experiments, it was not possible to analyze organism, film, and supernatant from each culture. Complete comparative data are available for only one culture—culture 4 of *Chaetoceros galvestonensis*.

An examination of the tables reveals that: (1) the relative quantities of the fatty acids in the films show no apparent relationship to those present in the cells; (2) the spectrum displayed by the aqueous phase in all cases is dominated by the 20:4/22:0 grouping. It is quite likely that the variations within each of the organisms and film groups, as well as between organism and film, are subject to the age of the culture. The characteristic distribution of acids in the aqueous phase seems to hold in all three organisms.

Evidently there is a partitioning effect which may be of considerable interest in its ecological implications. These observations should be confirmed and

Table 6. Fatty acid composition of the cells, surface film, and supernatant of *Chaetoceros galvestonensis* from a unicellular culture. Culture numbers in parentheses. T = trace.

Carbons double bonds	Cells		Film	Aqueous phase
	(4) per- cent	(7) per- cent	(4) per- cent	(4) per- cent
10:0			0.7	9.8
11:0	2.1	T	0.6	31.0
	0.9	T	5.1	T
12:0	1.2	0.7	2.0	
		T	1.9	
		1.4	0.5	0.6
14:0	5.6	14.6	15.6	2.9
15:0	2.5	2.5	5.3	2.4
16:0	7.3	9.1	27.4	8.9
16:1	2.5	11.3	17.0	2.3
				0.9
17:0	4.2	4.1	T	1.9
18:0	1.5	0.9	4.5	5.6
18:1	7.5	5.0	26.5	2.1
	0.4	1.6		
18:2	8.7	3.5		2.1
18:3 or 20:0	10.0			T
		1.7		82.7
20:2	9.7			2.7
			19.2	
20:4 or 22:0	12.7	5.9		1.6
20:5	6.2	10.5		3.7
		10.4	6.8	20.5
22:3		3.6		
22:5			3.9	
Total	100.1	100.1	100.1	99.9
				100.0

extended to other organisms and a variety of experimental conditions.

DISCUSSION

The data presented in this paper may be of interest to those concerned with inter-taxa relationships. Interpretations about these relationships are necessarily limited by the conditions under which the data were collected. The values for the fatty acids of the diatoms, dinoflagellates, and blue-green algae came from laboratory cultures, while those for the ctenophores, *Sargassum*, and fish came from samples collected in the field. It has already been mentioned that variations in the relative concentrations of the individual acids can be expected when there are variations in culture conditions, especially the age of the culture at time of harvest. This point has been illustrated by Ackman *et al.* (1964).

However, when the variation between samples for materials brought directly from the field is considered, that shown by laboratory-grown materials cannot be

Table 7. Fatty acid composition of the cells, surface film, and supernatant of Alga 2. Culture numbers in parentheses. T = trace.

Carbons double bonds	Cells		Film		Aqueous phase
	(5) percent	(8) percent	(2) percent	(8) percent	(5) percent
9:0			0.4		
			0.8		
10:0	1.0		2.2	T	
			2.8		
11:0		1.3		3.8	T
		1.1		1.8	T
			3.7		
12:0		T	T	3.0	0.2
				2.7	T
		0.8	0.7	0.8	1.0
		T	T	4.3	1.1
14:0	9.5	14.9		3.3	4.1
15:0				5.8	6.4
	1.1	1.9	4.7		
	T	T	1.5		
16:0	18.8	23.5	5.7	15.6	2.6
16:1	22.2	26.2	T	1.8	
17:0			7.8	10.8	
			3.3	T	
18:0	1.9	2.8	7.2	14.0	5.8
			3.9	6.1	
18:1	12.4	6.9			4.6
18:2		1.4	7.2	12.4	
18:3 or 20:0				0.7	75.3
20:1			3.3	T	
		0.8			
		1.2			
20:2			6.7	9.4	2.7
20:4 or 22:0			3.8	4.5	
20:5	3.4	3.2			
	2.5				
22:5	21.3	14.7			
Total	100.0	100.0	94.3	99.1	100.0

Table 8. Fatty acid composition of the cells, surface films, and supernatant of Alga 4. Culture numbers in parentheses. T = trace.

Carbons double bonds	Cells (6) percent	Film (3) percent	Aqueous phase percent
8:0		0.2	
9:0	T	T	
		0.4	
10:0		0.3	0.3
		2.7	4.6
11:0		2.0	1.1
			1.7
	1.4		0.8
12:0		2.1	
	0.9	T	
	0.9	1.6	0.6
14:0	1.3	2.3	0.7
			2.1
15:0	3.5	3.4	0.6
	T	0.9	
16:0	4.3	7.8	5.0
	0.1		
16:1	0.1	3.6	
17:0	3.9	5.5	
18:0	6.0	12.9	3.1
18:1	14.3	2.2	
18:2	7.3	9.2	
18:3 or 20:0	5.1	6.0	82.5
			3.5
20:2	6.5	22.4	2.0
20:4 or 22:0	5.4	11.1	
22:1	0.4		
20:5	6.5		
	6.1		
22:3	15.7		
22:6	6.8		
Totals	101.5	100.1	100.1

considered as unexpected. For instance, the analyses for the two samples of freshly collected *Sargassum* show good qualitative agreement, but with a significant difference in the amounts of C_{16} (Table 9). The picture in this case is somewhat analogous to the results from two independent cultures of Alga 2. Reiser *et al.* (1963) in tabulating the spectra for whole carcasses of mullet (direct from nature) indicated a similar situation except for greater differences in some cases; for example, 24.0 percent and 13.3 percent of C_{16} acid found in two independent samples.

It seems that some acids might be subject to greater variation than others, and until more is known about the metabolic situations controlling the variation, inter-taxon interpretations will be very difficult to make.

In looking at Table 9 we can draw a few generalizations which may be of general interest. The dinoflagellates and the blue-green groups seem to be low in long-chain polyunsaturates, while for all groups C_{16} and $C_{18:1}$ acids are dominant. The very small diatoms show comparatively large concentrations of polyunsaturates, suggesting that as primary producers these organisms may play a significant role in supplying the marine food chain with such fatty acids.

Table 9. Comparative data for major acids for all groups used in this study. Concentrations of 10 percent and over are in parentheses; those of 5 percent and over are italicized.

Diatoms	<i>C₁₂</i>	<i>C₁₄</i>	<i>C₁₆</i>	<i>C₁₈</i>	<i>C₂₀</i>	<i>C₂₂</i>	<i>C₂₄</i>	<i>C₁₀(1=)</i>	<i>C₁₀(2=)</i>	<i>C₁₀(3=)</i>	<i>C₁₀(4=)</i>	<i>C₁₀(5=)</i>	<i>C₁₀(6=)</i>
<i>Chlorococcales</i>													
<i>Chlorostichus</i> 1	1.2	5.6	7.3	1.5	(10.0*)	2.5	7.5	8.7	(10.0*)	9.7	0	(12.7*)	6.2
<i>Chlorostichus</i> 2	0.7	(14.6) (11.2*)	9.1 (25.96)	0.9	0	5.9* (17.05)	5.0 2.71	3.5 4.64	0	0	0	5.9* (10.5)	0
" <i>Hedothermia</i> "	1.57					1.85				0.4	3.9		0
Dinoflagellates													
<i>Peridinium</i>	(15.0)	2.5	(12.7)	(11.2)	0	0	5.7	8.0	1.4	0	0	0	0
<i>Gymnodinium</i>													
<i>splendens</i>	5.2	5.2	(44.6)	4.3	1.4	0	(11.0)	(13.9)	0.6	0.5	0.2	0	0
<i>Gymnodinium</i>													
<i>brevic</i>	(11.0)	4.9	(15.4) (42.6)	7.7 7.8	2.0 (10.7)	0	6.6 8.9	(22.6) 3.2	1.6 3.5	0.9 0.4	0	0	0
<i>Gymnodinium</i> sp.	0.8												
Blue-greens													
Alga 2, No. 1*	T	9.5	(18.8)	1.9	0	0	(22.2)	(12.4)	0	0	0	0	3.4
Alga 2, No. 2*	T	(14.9) 1.3	(23.5) (4.3)	2.8 6.0	0 5.1*	0 5.4*	(26.2) 0.1	(6.9) (14.3)	0	0	0	0	3.2
Alga 4	0												6.5
Sargassum													
Sample No. 1	0.30	2.66	(26.73)	1.90	1.18	0.73	8.15	(12.93)	6.95	7.70	0	0	(13.3)
Sample No. 2	0.21	2.53	(33.18)	1.74	0.99	0	6.20	(11.44)	6.01	6.83	0	0	(13.2)
Ctenophores													
<i>Mesaphysis</i>	0.92	3.35	(16.53)	(13.47)	0.93	1.90	6.49	6.56	2.49	2.83	0	6.27	7.34
<i>Beroe</i>	0.09	1.87	(12.84)	(11.80)	4.56	0.49	3.27	(12.26)	0.90	4.49	0	3.50	(10.32)
<i>Fundulus</i> g.	0.1	1.6	19.1	6.4	0.3	0	7.7	24.7	7.7	1.7	2.4	0	5.2
													0.6
													9.8

* Unresolved stearic and linoleic acids.

† Unresolved behenic and arachidic acids.

* Alga 2, No. 1 = Alga 2, culture No. 1; Alga 2, No. 2 = Alga 2, culture No. 2.

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LITERATURE CITED

- ACKMAN, R. G., P. M. JANGAARD, R. J. HOYLE, and H. BROCKERHOFF, 1964. Origin of marine fatty acids. I. Analyses of the fatty acids produced by the diatom *Skeletonema costatum*. *J. Fisheries Res. Board Can.*, 21:747-756.
- BAYLOR, E. R., and W. H. SUTCLIFFE, Jr., 1963. Dissolved organic matter in sea water as a source of particulate food. *Limnol. Oceanogr.*, 8:369-371.
- COLLIER, A., 1958. Some biochemical aspects of red tides and related oceanographic problems. *Limnol. Oceanogr.*, 3:33-39.
- COLLIER, A., 1959. Some observations on the respiration of the American oyster *Crassostrea virginica* (Gmelin). *Publ. Inst. Marine Sci., Univ. Texas*, 6: 92-108.
- COLLIER, A., and A. MURPHY, 1962. Very small diatoms: Preliminary notes and description of *Chaetoceros galvestonensis*. *Science*, 136(3518):782.
- COLLIER, A., S. M. RAY, and A. W. MAGNITZKY, 1950. A preliminary note on naturally occurring organic substances in sea water affecting the feeding of oysters. *Science*, 111:151-152.
- COLLIER, A., S. M. RAY, A. W. MAGNITZKY, and J. O. BELL, 1953. Effect of dissolved organic substances on oysters. *U. S. Fish and Wildlife Serv., Fishery Bull.*, 54:167-185.
- JEFFREY, L. M., B. F. PASBY, B. STEVENSON, and D. W. HOOD, 1962. *Lipids of ocean water*. Paper presented at the International Meeting on Organic Processes in Geochemistry. Milano, Italy, September 10-12, 1962. In *Advances in Organic Geochemistry*, edited by U. Columbo and G. D. Hobson; pp. 175-197. Macmillan (1964), New York.
- KORN, E. D., 1963. The fatty acids of *Euglena gracilis*. *J. Lipid Res.*, 5:352-362.
- METCALFE, L. D., and A. A. SCHMITZ, 1961. The rapid preparation of fatty acid esters for gas chromatographic analysis. *Anal. Chem.*, 33:363-364.
- PARSONS, T. R., 1963. Suspended organic matter in sea water. In *Progress in Oceanography*, edited by M. Sears; vol. 1, pp. 205-293. Macmillan Co., New York.
- PARSONS, T. R., K. STEPHANS, and J. D. H. STRICKLAND, 1961. On the chemical composition of eleven species of marine phytoplankton. *J. Fisheries Res. Board Can.*, 18:1001-1016.
- PROVASOLI, L., 1963. Organic regulation of phytoplankton fertility. In *The Sea*, edited by M. N. Hill, E. D. Goldberg, C. O'D. Iselin, and W. H. Munk; vol. 2, pp. 165-219. Interscience, London.
- REISER, R. B., STEVENSON, M. KAYAMA, R. B. R. CHOUDURY, and D. W. HOOD, 1963. The influence of dietary fatty acids and environmental temperature on the fatty acid composition of teleost fish. *J. Am. Oil Chemists Soc.*, 41:81-85.
- RILEY, G. A., 1963. Organic aggregates in sea water and the dynamics of their formation and utilization. *Limnol. Oceanogr.*, 8:372-381.
- SECONDAT, M., and R. QUILLIER, 1959. Utilization des solutions de saccharose et modifications de la glycémie chez la carpe *Cyprinus carpio* L. *C. r. Seanc. Acad. Sci. Paris*, 250:2274-2276.
- SLOWEY, J. F., L. M. JEFFREY, and D. W. HOOD, 1962. The fatty acid content of ocean water. *Geochim. Cosmochim. Acta*, 26:607-616.
- WANGERSKY, P. J., 1952. Isolation of ascorbic acid and rhamnosides from sea water. *Science*, 115:685.
- WANGERSKY, P. J., and R. R. L. GUILLARD, 1960. Low molecular weight organic base from the dinoflagellate *Amphidinium carteri*. *Nature*, 185:689-690.

Excretion of Organic Compounds by Cultured and Natural Populations of Marine Phytoplankton

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Scientists concerned with the measurement of primary production and with algal physiology have recently become increasingly aware of the importance of gaining more knowledge about the quantity and quality of algal excretion products. Antia *et al.* (1963) showed indirectly that phytoplankton growing in a large plastic sphere excreted as much as 35-40 percent of the photoassimilated carbon. Other indirect estimates of excretion, however, have varied from negligible amounts to as much as 80 percent of the assimilated carbon (Gaarder and Gran, 1927; Gillibrich, 1952; Marshall and Orr, 1930). Some of these estimates were rather crude, and did not give any information about the composition of the excreted substances. A few studies on specific kinds of materials excreted by marine phytoplankton in culture have recently been published; for instance, carbohydrates by several marine flagellates (Guillard and Wangersky, 1958), an organic base by a marine dinoflagellate (Wangersky and Guillard, 1960), and amino acids and peptides by blue-green algae (Stewart, 1963).

This paper concerns the quantity and composition of substances excreted by cultured and natural phytoplankton populations. The details of these studies have been published elsewhere (Hellebust, 1965). The cultured bacteria-free algae were kindly supplied by Dr. R. R. L. Guillard of the Woods Hole Oceanographic Institution. The natural marine phytoplankton samples were from Vineyard Sound, Massachusetts, and from the Gulf of Maine (Atlantis II, Cruise II, April 8-18, 1963). Practically all the work with cultures of single species was done when the algae were in log-phase growth, in order to make the results strictly comparable.

The excreted organic carbon was measured by taking portions of membrane-filtered media from algal cultures which had been allowed to photoassimilate $C^{14}O_2$ for a given period of time. The remaining inorganic $C^{14}O_2$ was removed from the filtered portions, which were then plated, dried, and counted for C^{14} activities. All the counts were corrected for self-absorption, which was due almost entirely to the salt, for background, and for variation in counting efficiency. Since only 0.1 ml portions of the cultures were filtered in order to determine the assimilation of

C^{14} by the algae, no self-absorption correction was made for counts obtained in this way. The specific activity of the bicarbonate in the algal media, which was kept in tightly glass-stoppered bottles, was the same throughout any one experiment. The radioactivity counts of the filtered phytoplankton is, therefore, strictly proportional to the absolute amount of bicarbonate assimilated. The composition of the excreted material was studied by direct chromatography of the filtered medium with known substances; by solvent extraction and coprecipitation with albumin; and by removing the salts by electrodialysis followed by cochromatography with known substances or by removing them by acid hydrolysis followed by cochromatography and autoradiography. Details of the experimental procedure have been published elsewhere (Hellebust, 1965).

The amount of organic material excreted by the algae was expressed as a percentage of the photoassimilated carbon. The latter quantity was considered to be equal to the C^{14} taken up by the algae plus the organic C^{14} excreted. The photoassimilated carbon respired during the experiment was neglected. (This will be discussed later.)

RESULTS AND DISCUSSION

The effect of light intensity on excretion by representatives of the five major classes of marine phytoplankton was studied by growing the algae under 300 and 1,000 ft-c. It is evident that while many of the species show only small differences in the relative amounts of photoassimilated carbon excreted at the two light intensities, some of the algae (e.g., *Coccolithus huxleyi*, *Gymnodinium nelsoni*, *Chaetoceros pelagicus*, and *Skeletonema costatum*) excreted considerably more at the lower than at the higher light intensity (Table 1). In a separate experiment in which the phytoplankton were exposed to full sunlight (10,000-12,000 ft-c), very high excretion rates resulted (8.5-52 percent of the photoassimilated carbon), probably due to photo-oxidative damage to the cells (Hellebust, 1965).

There were considerable variations in the relative magnitudes of organic carbon excreted even among species belonging to the same class of algae (Table 1). It should be noted that two diatoms, *Chaetoceros pelagicus* and *Chaetoceros simplex*, consistently excreted very large fractions (17-25 percent) of their

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Table 1. Excretion of photoassimilated carbon by algae at high and low light intensities during two days of alternate 12-hour light and dark periods.

	1000 ft-c			300 ft-c		
	Carbon excreted of total assimilate (%)	Excreted carbon as glycolic acid (%)	Carbon excreted of total assimilate (%)	Glycolic acid (%)	Protein (%)	Lipid (%)
CHYSOPHYCEAE						
<i>Coccolithus huxleyi</i> (BT-6)	1.3	2.7	4.4	2.4	1.0	4.5
<i>Monochrysis lutheri</i> (Mono)	4.5	1.7	3.6	3.6	1.6	4.6
<i>Olisthodiscus</i> sp. (Olisth.)	9.8	4.0	10.0	9.3	5.0	5.3
DINOPHYCEAE						
<i>Euxinella</i> sp. (Exuv.)	3.3	<1.0	2.5	<1.0	2.2	5.8
<i>Amphidinium carteri</i> (Amphi)	9.3	3.3	10.0	3.7	0.8	3.2
<i>Gymnodinium nelsonii</i> (?) (GSBL)	5.7	2.3	7.8	2.0	2.8	3.8
BACILLARIOPHYCEAE						
<i>Chaetoceros pelagicus</i> (Ch 4)	17.0	16.0	25.0	15.0	0.5	7.4
<i>Cyclotella nana</i> (13-1)	4.0	5.6	4.6	1.3	1.1	6.0
<i>Cyclotella nana</i> (3H)	4.2	3.1	6.7	1.9	1.3	4.0
<i>Skeletonema costatum</i> (Skel.)	4.6	38.5	9.0	35.0	0.4	4.3
<i>T. nordenstkioldii</i> (T-Nord)	4.1	1.5	—	—	—	—
CHLOROPHYCEAE						
<i>Chlorella</i> sp. (580)	1.6	0.8	2.4	1.0	0.8	4.5
<i>Dunaliella tertiolecta</i> (Dun.)	4.4	3.1	3.9	2.2	0.2	5.0
<i>Pyramimonas</i> sp. (Pyr 1)	5.1	1.0	9.1	4.2	0.7	4.2
CYANOPHYCEAE						
<i>Coccochloris</i> sp. (Syn)	5.4	2.0	2.7	3.0	0.9	10.3

photoassimilated carbon during log-phase growth (Hellebust, 1965). It is possible that under ideal growth conditions, nutritional and otherwise, these algae would excrete a smaller proportion of their photoassimilated carbon.

It was mentioned earlier that the amount of excreted carbon was calculated as a percentage of C¹⁴ taken up by the cells (net photosynthesis) plus the C¹⁴ excreted, not taking into account the respiratory loss of photoassimilated carbon during the experimental period. It is possible that the organic carbon excreted by healthy cells represents a relatively fixed proportion of the total photoassimilated carbon rather than the net photoassimilated carbon for each individual species. This would explain, at least in part, why higher excretion values may be obtained at low light intensities than at intensities approaching light saturation (Fogg, 1958, 1963a).

Following the discovery of glycolic acid excretion by *Chlorella pyrenoidosa* (Tolbert and Zill, 1957), a great deal of attention has been paid to the possible excretion of this substance by other algae. Nalewajko et al. (1963) demonstrated that a planktonic freshwater isolate of *Chlorella pyrenoidosa* excreted considerable amounts of glycolic acid. Fogg (1963b) proposed that this acid may be excreted by both freshwater and marine phytoplankton during photosynthesis, and may represent a reservoir which can be used for heterotrophic growth by algae and other microorganisms.

Table 1 shows the results of chromatographic sepa-

ration and quantitative determination of glycolic acid in marine algal culture filtrates. Although small amounts or traces of glycolic acid were detected in all the algal media, only a few algae excreted this organic acid in considerable quantities. *Skeletonema costatum* excreted the largest fraction, about 35 percent of the total excretion, while *Chaetoceros pelagicus* and *Olisthodiscus* sp. excreted 9-15 percent. A marine *Chlorococcum* sp., not included in this table, produced about 12 percent of its excreted material as glycolic acid.

The effect of light intensity on glycolic acid excretion was investigated, using cultures of *Skeletonema costatum* adapted to high and low intensities (Fig. 1). The relative amounts excreted increased strikingly with decreasing light intensity below about 1,500 ft-c. Only 0.2-0.3 percent of the photoassimilated carbon was excreted as glycolic acid at 6,500 ft-c, but at 180 ft-c the excreted glycolic acid accounted for about 6 percent of the photoassimilated carbon. Very little glycolic acid (less than one percent in a medium containing 3 mg glycolic acid per liter) was taken up during 12 hours in the dark by a relatively dense culture of *Skeletonema*. This finding does not agree with the suggestion that glycolic acid is rapidly excreted and re-absorbed by the algal cells (Fogg, 1963b).

Negligible quantities of protein were excreted by the algae listed in Table 1, except for *Olisthodiscus* sp., in which about 5 percent of the total excreted material was protein. It may, therefore, be general-

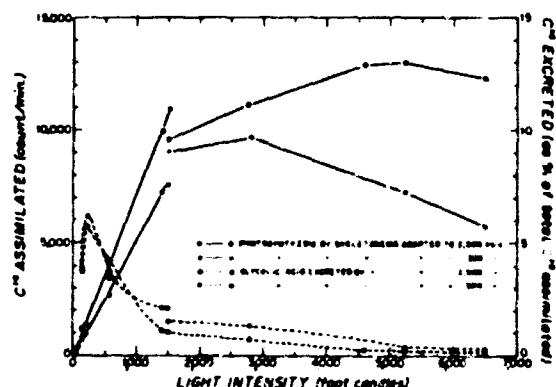


Fig. 1. Photosynthesis and excretion of glycolic acid by *Skeletonema costatum* at various light intensities.

ized that healthy, rapidly growing marine phytoplankton excrete little or no protein. In the case of stationary-phase cultures of *Skeletonema costatum* and *Olisthodiscus* sp., however, when some of the cells were obviously in poor condition, relatively large amounts of protein (almost 10 percent of the photo-assimilated carbon) appeared in the medium. Chloroform-soluble compounds (lipid column in Table 1) constituted 4.2–10.3 percent of the excreted material. These compounds probably consist partly of various glycerol derivatives, because this compound appeared in the hydrolyzed neutral fraction of the excreted material of many of the algae.

More detailed information about some of the constituents of the neutral fractions of the excreted material appears in Table 2. The most frequently occur-

ring substances were amino acids, sugar alcohols, and peptides (detected as amino acids appearing after hydrolysis of the neutral fraction). Some of the algae excreted mainly a single substance. *Cricosphaera* (*Syracospaera*) *carterae*, *Isochrysis galbana*, and *Monochrysis lutheri* (Table 2, and Hellebust, 1965) excreted mainly the unknown U₁. It may be noted that this particular unknown substance was excreted only by the Chrysophyceae and the Dinophyceae, and not by the other classes of algae. *Olisthodiscus* sp. excreted almost exclusively mannitol, and *Dunaliella tertiolecta* mainly glycerol. The marine *Chlorella* sp. excreted mainly proline. The two clones of *Cyclotella nana*, which were isolated from very different environments (13-1 from the Sargasso Sea, and 3H from an estuary), showed distinct differences in the kinds of compounds they excreted. These findings agree well with other physiological differences observed by Guillard and Ryther (1962).

Free sugars were found in the media of only a few algae (Table 2). Furthermore, following acid hydrolysis of the excreted material, identifiable sugars appeared in small amounts only in the case of three of the algae investigated, indicating that few or no polysaccharides were excreted by these algae during logarithmic growth. Since relatively drastic conditions were used for the hydrolysis of the excreted substances (4N HCl at 100° C. for 6 hr), however, pentoses and ketoses would probably be largely destroyed. Therefore, polysaccharides consisting mainly of such sugar residues would not be detected in the hydrolysate. On the other hand, Guillard and Wangersky (1958) found little polysaccharide excretion by marine flagellates as long as the cells remained in log-

Table 2. Organic compounds excreted by algae during log-phase growth.

	Compounds observed prior to hydrolysis	Compounds observed after hydrolysis
CHRYSPHYCEAE		
<i>Coccolithus kuroshio</i> (BT-6)	mannitol, U ₁ , aspartic acid, arabinose	U ₁ , glucose
<i>Monochrysis lutheri</i> (Mono)	>50% U ₁ , mannitol	very small amounts of unknowns
<i>Olisthodiscus</i> sp. (Olisth.)	>90% mannitol, U ₁	very small amounts of unknowns
DINOPHYCEAE		
<i>Erythrops</i> sp. (Eryx)	50% U ₁ , 40% U ₂ , glutamic acid	very small amounts of unknowns
<i>Amphidinium carterae</i> (Amphi)	>50% U ₂ , arabinose	U ₂ , other unknowns
<i>Gymnodinium nelsoni</i> (?) (GSBL)	>50% U ₂ , U ₁ , glutamic acid	arginine, valine, leucine
BACILLARIOPHYCEAE		
<i>Chaetoceros pelagicus</i> (Ch-4)	90% U ₁ , glycerol, glucose, arabinose	aspartic, glutamic, lysine, glycerol
<i>Cyclotella nana</i> (13-1)	>50% U ₁ , U ₂ , glycerol, mannitol	U ₂ , glutamic, aspartic, alanine
<i>Cyclotella nana</i> (3H)	>90% proline, mannitol, arginine, glycerol	U ₂ , glutamic, aspartic, alanine, valine
<i>Skeletonema costatum</i> (Skel.)	>50% glycerol, U ₁	U ₂ , glycerol, glucose, 10 α-amino acids
<i>T. thuretii</i> (Actin.)	U ₁ , U ₂ , mannitol, glutamic acid	U ₂ , glucose, aspartic, glutamic, glycerol
CHLOROPHYCEAE		
<i>Chlorella</i> sp. (SB)	>80% proline, glycerol	U ₂ , 12 amino acids, glycerol
<i>Dunaliella tertiolecta</i> (Dun)	>90% glycerol	U ₂ , 10 amino acids, glycerol
<i>Paraclosteromonas</i> sp. (Pyr-1)	>70% mannitol, glycerol, U ₁	U ₂ , glycerol, aspartic, glutamic
CYANOPHYCEAE		
<i>Cyanothece</i> sp. (Sm)	50% U ₁ , U ₂ , glycerol	U ₂ , glycerol, aspartic, glutamic, a trace

Table 3. Excretion by phytoplankton samples taken from the surface water of Vineyard Sound during the late winter and spring of 1963.

Sampling time	Water temp °C	Sample composition	Incubation conditions	Carbon excreted of total assimilated %
Feb. 17	-12	Mainly <i>Thalassiosira</i> and <i>Chaetoceros</i> spp.	48 hr at 5°C., 500 ft-c	6.7
Apr. 29	8.2	Mainly <i>Leptocylindrus danicus</i>	3 hr <i>in situ</i> , 8,000-11,000 ft-c	8.1
May 6	10	Mainly <i>Leptocylindrus danicus</i> , many empty frustules present ditto	6 hr <i>in situ</i> (7 AM-1 PM), 10,000 ft-c at noon ditto (1 PM-7 PM)	22 38
May 15	12	Mainly small flagellates and dinoflagellates	9 hr <i>in situ</i> , (6 AM-3 PM), 5,000 ft-c at noon	12

phase growth. This agrees with the present data which show little or no polysaccharide production by lag-phase cultures of marine phytoplankton.

The identification of excreted substances was based on cochromatography with compounds that commonly occur in plant cells, such as sugars, sugar derivatives, organic acids, and amino acids. Compounds excreted by marine algae would presumably be identical with commonly occurring metabolites in these organisms. However, so little is known about the nature of metabolites in marine algae that the number of excreted metabolites that could be identified by the above procedure was quite limited. In order to obtain more information about the identity of algal metabolites of low molecular weight, alcohol-soluble compounds were extracted from several species, and some of the extracted substances were tentatively identified by paper chromatography and by using various specific spray reagents (Helebust, 1965). Relatively large amounts of glycerol and mannitol were found in several chrysophyte and diatom species, and large quantities of proline were detected in a marine *Chlorella* sp. Only small amounts of free sugars were detected (Budwell et al., 1952). Many of the most radioactive, alcohol soluble substances ap-

pearing in several diatoms, chrysophytes, and dinoflagellates after photosynthesis in C^{14}O_2 were not identified, but were found by cochromatography to be identical to excreted compounds of the same algae.

Quantitative estimates of the excretion of organic compounds by natural phytoplankton populations were made on samples of water from Vineyard Sound and the Gulf of Maine during the late winter and spring of 1963. Three of the samples studied from Vineyard Sound (Table 3, Feb. 17, Apr. 29, and May 15) consisted of healthy, rapidly photosynthesizing algae. These phytoplankton samples excreted small amounts of organic substances (6.7 and 8.1 percent of the photoassimilated carbon for the two diatom populations and 12 percent for the population consisting mainly of flagellates). However, the sample of *Leptocylindrus danicus* investigated on May 5 at the end of a bloom and containing about 20 percent of empty frustules excreted 22-38 percent of its photoassimilated carbon.

The phytoplankton populations studied in the Gulf of Maine all consisted of apparently healthy and rapidly growing algae with densities approaching two million cells per liter, indicating bloom conditions. From 4.5 to 16 percent of the photoassimilated car-

Table 4. Excretion by phytoplankton samples from the Gulf of Maine during a phytoplankton bloom in April, 1963.

Sampling time	Water temp °C	Sample composition and depth of sampling	Incubation conditions	Carbon excreted of total assimilated (%)
Apr. 19	14	Mainly <i>Thalassiosira</i> and <i>Chaetoceros</i> spp., surface water	7 hr (11 AM-6 PM), 5°C a) 2,500 ft-c b) 800 ft-c	16 8.2
Apr. 19	17	Mainly <i>Thalassiosira</i> and <i>Chaetoceros</i> spp., 50 m	7 hr (11 AM-6 PM), 5°C a) 2,500 ft-c b) 800 ft-c	8.5 4.5
Apr. 19	18	Mainly <i>Chaetoceros</i> and <i>Thalassiosira</i> spp., 10 m	3 hr (2 PM-6 PM), 5°C 2,500 ft-c 12 hr (6 AM-6 PM), 5°C 2,500 ft-c	6.9 12.5
Apr. 19	30	Mainly <i>Chaetoceros</i> and <i>Thalassiosira</i> spp., some empty frustules present, surface water	24 hr (12 noon Apr. 18-12 noon Apr. 19), 5°C 2,500 ft-c	13

Table 5. Loss of radioactivity from C¹⁴-labeled *Thalassiosira fluitans* after transfer to non-radioactive medium.

Time days	Cell num- ber $\times 10^4$ / ml	C ¹⁴ in cells/ $\times 10^4$	Organic- C ¹⁴ in medium/ min. $\times 10^4$	Organic- C ¹⁴ excreted/ min. $\times 10^4$	Total C ¹⁴ lost (%)	Total C ¹⁴ lost (%)
0	1.2	56.0 ± 0.8	—	—	—	—
2	6.1	53.1 ± 0.8	1.0 ± 0.2	1.9 ± 0.4	5.4 ± 1.4	—
3	6.6	51.2 ± 0.8	1.4 ± 0.2	2.7 ± 0.4	8.6 ± 1.4	—

bon was excreted by these phytoplankton populations (Table 4). It appears from these studies that about 10 percent of the photoassimilated carbon of natural populations of healthy, growing phytoplankton from Vineyard Sound and the Gulf of Maine is generally excreted. Considerably higher levels of excretion may be expected at the end of a phytoplankton bloom, if the algae remain in a stationary growth phase, or disintegrate by autolysis and bacterial degradation instead of being removed through grazing by zooplankton.

Only one attempt was made to identify the compounds excreted by the natural phytoplankton, because they occurred in such low concentrations as to make isolation extremely difficult. Direct chromatography of excreted compounds by a very dense population consisting mainly of *Leptocylindrus danicus* (Table 3) revealed the presence of small amounts of glycolic acid.

The cultured and natural phytoplankton populations were allowed to photoassimilate C¹⁴O₂ for varying lengths of time before excretion estimates were made. Therefore, it was important to establish if the excreted material consisted mainly of newly assimilated carbon, or if relatively older cellular constituents also contributed to the excreted material. If only recently assimilated carbon is excreted, duration of the experiment should not influence the magnitude of excretion expressed as a percentage of the photoassimilated carbon. In order to determine whether relatively old cellular constituents are excreted to a significant extent, uniformly labeled *Thalassiosira fluitans* (an estuarine diatom species) was transferred to a medium containing no C¹⁴O₂. The C¹⁴ activity of the cells and medium were determined after two and three days in the light (800 ft-c). It can be seen from Table 5 that only 1.9 percent of the activity in the cells appeared in the medium as organic carbon after two days in the light, during which time the algal population had increased almost five times. Since the excretion of this species is known to be about 3 percent under similar conditions (Hellebust, 1965), it is evident that only a very small amount of the organic carbon present in the cells before the transfer could have contributed to the total amount of organic compounds excreted during this period. This agrees well with Ryther's observation that C¹⁴-labeled *Dunaliella eichhorniae* lost almost no activity during 24

hours in light after transfer to a non-radioactive medium (Ryther, 1956).

Significant amounts of organic matter may be excreted by non-growing natural phytoplankton populations (Table 3), or by cultures in the stationary phase (Guillard and Wangersky, 1958). The studies described in this report have dealt only with logarithmically growing algal cultures. To supplement these observations, the excretion of organically bound carbon by *Thalassiosira fluitans* was followed through the log phase of culture into the stationary phase brought about by nutrient deficiency. Cells were transferred at time zero (Fig. 2) from a log-phase culture with excess nutrients to a medium containing no phosphorus and nitrogen. The amount of excretion as a percentage of the photoassimilated carbon remained at about 5 percent while the cells were still dividing, then rapidly increased to over 20 percent as the culture went into stationary phase growth. However, the absolute amount excreted per unit time (the slope of the curve marked "C¹⁴ in medium" in Fig. 2) did not increase significantly, because of the sharp fall in rate of photosynthesis. It may therefore be concluded that, although a stationary population of phytoplankton will excrete a large proportion of its photoassimilated carbon, the absolute rate of excretion by such a population may not be any higher than that of a rapidly growing population with a smaller relative excretion rate.

An estimate of the annual contribution of dissolved carbon by the excretion of healthy phytoplankton may be made by making certain assumptions: (1) the depth of the uniformly mixed surface layer is 100 m, (2) the annual primary productivity is 100 g carbon m⁻², and (3) the excretion of organic carbon is 10 percent of the primary productivity value. Then the annual contribution of excreted substances to the reservoir of dissolved organic compounds of this water mass would be 0.1 mg carbon l, which is approximately one-tenth of the dissolved carbon in the open ocean (Duursma, 1963; Menzel, 1964). If the depth of the mixed surface layer is less and the excretion rate higher than that assumed above, the annual contribution will, of course, be correspondingly higher. Since the concentration of dissolved organic carbon does not change on a yearly basis (Duursma, 1963), the same amount of dissolved organic carbon will have to be converted to the mor-

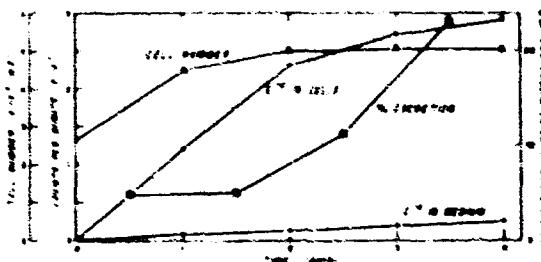


Fig. 2. Photosynthesis, cell division, and excretion by nutrient-deficient *Thalassiosira fluitans*.

ganic phase (per year) by chemical or bacterial processes, and possibly also by algal respiration within the upper mixed layer in which the substances are produced (Menzel, 1964).

Another source of dissolved organic substances in the sea is the loss of soluble substances from algae when they are being grazed by zooplankton. An experiment with *Calanus hyperboreus*, feeding on C¹⁴-labeled *Thalassiosira fluvialis*, showed that about 15 percent of the carbon of the grazed algae appeared in the medium as dissolved substances after 24 hr. If most of the marine phytoplankton is grazed by zooplankton rather than dying a natural death (Harvey *et al.*, 1935; Clarke, 1939; Menzel and Ryther, 1961), the total amount of dissolved organic substances resulting (1) from excretion by healthy phytoplankton (about 10 percent of the primary productivity), and (2) from grazing by zooplankton (about 15 percent of the primary productivity), will equal about 25 percent of the primary production of organic carbon. If these estimates are correct, the peak of dissolved carbon resulting from excretion and from grazing of a phytoplankton bloom ought to occur later than that of the standing stock of phytoplankton. This was found by Duursma (1961) to be the case in the North Sea. Duursma, however, contended that the time lag indicated that most of the dissolved carbon resulted from the decay of algae after the peak of the phytoplankton bloom. His explanation would be correct only if (1) little primary productivity took place between the peak of the phytoplankton bloom and the peak of the dissolved organic carbon, and (2) the phytoplankton bloom was not chiefly controlled by grazing. This cannot be verified because Duursma did not supply data on primary productivity or on grazing rates or standing zooplankton stocks. Harvey *et al.* (1935), Clarke (1939), and others claim that the standing stock of phytoplankton in the open ocean is regulated mainly through grazing by zooplankton, and therefore only a small proportion of the phytoplankton will remain long in a stationary phase, or will die a natural death.

A different situation occurs in estuaries which are relatively fertile and support a large standing stock of phytoplankton not appreciably controlled by zooplankton grazing, for example, in Great South Bay and Moriches Bay (Ryther, 1954; Ryther *et al.*, 1958). In such places the relative amounts of dissolved organic carbon, contributed by the excretion of healthy algae and by degradation of algae, may be quite different from those in the open ocean.

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LITERATURE CITED

- ANTIA, N. J., C. D. McALISTER, T. R. PARSONS, K. STEPHENS, and J. D. H. STRICKLAND, 1963. Further measurements of primary production using a large-volume plastic sphere. *Limnol. Oceanogr.*, 8:166-183.
- BIDWELL, R. G. S., G. KROTKOV, and G. B. REED, 1952. Paper chromatography of sugars in plants. *Can. J. Botany*, 30:291-305.
- CLARKE, G. L., 1939. The relation between diatoms and copepods as a factor in the productivity of the sea. *Quart. Rev. Biol.*, 14:60-64.
- DUURSMA, E. K., 1961. Dissolved organic carbon, nitrogen and phosphorus in the sea. *Neth. J. Sea Res.*, 1:1-148.
- DUURSMA, E. K., 1963. The production of dissolved organic matter in the sea, as related to the primary gross production of organic matter. *Neth. J. Sea Res.*, 2:85-94.
- FOGG, G. E., 1958. Extracellular products of phytoplankton and the estimation of primary production. *Rapp. Cons. Explor. Mer.*, 144:56-60.
- FOGG, G. E., 1963a. Extracellular products. In *Physiology and Biochemistry of Algae*, edited by R. A. Lewin; pp. 475-489. Academic Press, New York.
- FOGG, G. E., 1963b. The role of algae in organic production in aquatic environments. *British Phycol. Bull.*, 27(4):195-205.
- GARDER, T., and H. H. GRAN, 1927. Investigations of the production of plankton in the Oslofjord. *Cons. Perm. Intern. Explor. Mer., Rapp. Proc.-Verb.* 41:1-48.
- GILLBRICHT, M., 1952. Untersuchungen zur Produktionsbiologie des Planktons in der Kieler Bucht II: Die Produktionsgrössse. *Kiel. Meeresforsch., Board 8*: 51-61.
- GUILLARD, R. R. L., and J. H. RYTHER, 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt, and *Detonula congener* (Cleve). *Can. J. Microbiol.*, 8:229-239.
- GUILLARD, R. R. L., and P. J. WANGERSKY, 1958. The production of extracellular carbohydrates by some marine flagellates. *Limnol. Oceanogr.*, 3:449-454.
- HARVEY, H. W., L. H. N. COOPER, M. V. LABOUR, and F. S. RUSSELL, 1935. Plankton production and its control. *J. Marine Biol. Assoc. U.K.*, 29: 407-441.
- HELLEBUST, J. A., 1965. Excretion of some organic compounds by marine phytoplankton. *Limnol. Oceanogr.*, 10:192-206.
- MARSHALL, S. M., and A. P. ORR, 1936. A study of the spring diatom increase in Loch Striven. *J. Marine Biol. Assoc. U. K.*, 16:853-878.
- MENZEL, D. W., 1964. The distribution of dissolved organic carbon in the Western Indian Ocean. *Deep Sea Res.*, 11:757-765.
- MENZEL, D. W., and J. H. RYTHER, 1961. Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production. *J. Cons. Intern. Explor. Mer.*, 26:250-258.
- NALEWAJKO, C., N. CHOWDHURI, and G. E. FOGG, 1963. Excretion of glycolic acid and the growth of a planktonic *Chlorelia*. In *Microalgae and Photosynthetic Bacteria*; pp. 171-183. Japan. Soc. Plant Physiol., Univ. of Tokyo Press, Tokyo.
- RYTHER, J. H., 1954. Ecology of Phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, N. Y. *Biol. Bull. Woods Hole*, 106:198-209.
- RYTHER, J. H., 1956. Interrelation between photosynthesis and respiration in the marine flagellate, *Dunaliella salina*. *Nature*, 178:861-862.
- RYTHER, J. H., C. S. YENTSCH, E. M. HULBURT, and R. E. VACCARO, 1958. The dynamics of a diatom bloom. *Biol. Bull. Woods Hole*, 115:257-268.
- STEWART, W. D. P., 1963. Liberation of extra-cellular nitrogen by two nitrogen-fixing blue-green algae. *Nature*, 200:1020-1021.
- TOLBERT, N. E., and L. P. ZILLI, 1957. Excretion of glycolic acid by *Chlorella* during photosynthesis. In *Research in Photosynthesis*, edited by H. Gaffron; pp. 228-231. Interscience, New York.
- WANGERSKY, P. J., and R. R. L. GUILLARD, 1960. Low molecular weight organic base from the dinoflagellate *Amphidinium carteri*. *Nature*, 185:689-690.

Dissolved Organic Material as a Nutritional Source for Marine and Estuarine Invertebrates

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Marine invertebrates, like any other heterotrophs, depend on reduced carbon compounds as an energy source. Such compounds derive from photosynthesis, with a few exceptions. The usual picture of the trophic structure of marine communities is derived from analyses of terrestrial ecosystems where herbivores are nourished by the primary producers and, in turn, provide sustenance for a complex pyramid or web of carnivores. This is somewhat complicated by saprotrophs and omnivores, but the basic structure remains pyramidal.

In this conceptual scheme a great deal of organic material, beyond that represented by the biomass of the various trophic levels of the community, is present in the environment. In an inshore marine community, this material would include particulate detritus, material of colloidal dimensions, and organic material in solution in sea water. The question is whether this organic material requires us to modify our concept of the trophic structure of marine and estuarine communities. This paper summarizes some recent evidence concerning a possible nutritive role of organic material in true solution.

The idea that dissolved organic material may contribute to the nutrition of aquatic animals is not new. The hypothesis is usually associated with Pütter (1909), and it received a great deal of attention in the first three decades of this century, but Krogh (1931) concluded that there was no substantial evidence for Pütter's idea.

Collier *et al.* (1953), however, reported the presence of an unidentified carbohydrate material in high concentrations which was removed from sea water by oysters. The extremely high concentrations reported (about 100 mg/l), apparently represented a local situation, since other investigators (Lewis and Rakestraw, 1955) have been unable to find carbohydrate in comparable amounts. Collier's work, which apparently has not been extended and pursued, stands as the isolated demonstration of the removal of a naturally occurring organic material from solution by a metazoan.

Fox and his co-workers (1952, 1953) suggested that leptopel is a potential source of organic material for filter-feeding organisms. Leptopel consists of micelles of organic material adsorbed on inorganic particles of colloidal dimensions. These authors presented evidence that much of the "dissolved" organic material was actually present in this form and suggested

that this might be available to filter-feeding animals as a nutritive supplement.

Cheesman (1956) reported on the ability of snails to feed on material denatured at the air-water interface, using their foot as a "Langmuir funnel". More recently, Baylor and Sutcliffe (1963) raised *Artemia* on particulate organic material produced by bubbling air through filtered sea water, and Riley (1963) reported flakes of particulate material which may be derived in a fashion comparable to a natural constituent of the waters of Long Island Sound.

It may be noted that these studies, with the possible exception of the work of Collier *et al.*, deal with pathways for using organic material after it has been concentrated by adsorption or some other physical process in the environment. Clearly, these pathways may contribute in a quantitative way to the normal nutrition of some aquatic animals, although whether they do remains to be established. Can aquatic animals remove organic material directly from solution? This paper attempts to explore this question.

UPTAKE OF ORGANIC MATERIAL FROM SOLUTION

Several points in the possibly significant nutritional role of organic material obtained from true solution should be established. Dissolved organic carbon in sea water typically does not exceed a few milligrams per liter (Hood, 1963). It is clear, therefore, that a prior condition for a serious discussion of the direct nutritive role of this material is the demonstration of a physiological mechanism for supplying significant amounts of at least some organic compounds to the animal from extremely dilute solutions.

Stephens and Schinske (1961) presented qualitative evidence of the ability to remove amino acids from solution among marine invertebrates. Of 35 genera in 11 phyla which were examined, only six arthropods failed to remove amino acids supplied in dilute solution. However, much of this work was at concentrations of 1 to 2 mM/l, or about two orders of magnitude higher than any likely natural concentration. However, it was demonstrated that at least some of these organisms could remove glycine at concentrations of 2×10^{-5} M/l—a much more reasonable figure. Later, a series of papers appeared (Stephens, 1960, 1962, 1963, 1964; Virkar, 1963) in which C^{14} -labeled compounds were used in studying the ability of marine and estuarine forms to take up

Table 1. Some species studied using C^{14} to show the ability of marine and estuarine forms to take up several small organic compounds.

Organism and compound	V_{\max} (moles/g/hr)	K_m (moles/l)	Q_{eq} (ml/g/hr)	Amount of compound equivalent to Q_{eq} (moles/g/hr)
<i>Fungia</i> glucose	2×10^{-7}	1×10^{-4}	0.005 0.01	3.3×10^{-9} 6.7×10^{-9}
<i>Clymenella</i> glycine	1×10^{-5}	2×10^{-4}	0.090	1.2×10^{-8}
phenylalanine	3.7×10^{-6}	5×10^{-5}		5.5×10^{-7}
lysine	3.6×10^{-6}	1.2×10^{-4}		6.0×10^{-7}
valine	4.4×10^{-6}	2.7×10^{-4}		7.7×10^{-7}
<i>Nereis succinea</i> glycine	1.6×10^{-6}	1.1×10^{-4}	(0.026)*	3.5×10^{-7}
<i>Nereis limnicola</i> glycine	1.3×10^{-7}	3.7×10^{-5}		
<i>Golfingia</i> glycine	1.0×10^{-7}	1.0×10^{-4}		

* Value for *N. virens* from Bosworth *et al.* (1936).

several small organic compounds. Table 1 lists some species for which published information is available. In addition, several other genera have provided material for casual examination and detailed study in our laboratory. A partial list includes the bivalve brachids, *Mercenaria* (= *Venus*) *mercenaria*, *Mytilus edulis*, and *Solemya velum*; the echinoderms, *Asterias forbesi*, *Thyrsone briareus*, and *Leptosynapta inhaerens*; and several annelid and cnidarian genera. A similar extension of the list of compounds used is justified, since most forms examined were tested with glucose and several amino acids. It is fair to state that any soft-bodied marine invertebrate examined, regardless of its apparent primary mode of feeding, has exhibited some ability to remove glucose and amino acids from solutions of a concentration of about 10^{-5} to 10^{-6} M/l.

The conclusion is justified that at least some organic compounds are available to a wide variety of soft-bodied marine invertebrates from solutions of very modest concentration. It is reasonable, therefore, to discuss whether or not such an uptake of dissolved organic material may be a significant source of reduced carbon for these organisms under natural conditions. This problem may be outlined in a series of questions:

1. What is the evidence that the uptake of small organic molecules occurs from solution rather than by adsorption on particulate matter? Is the uptake initially by bacteria or by passage of the medium through the digestive tract?

2. What is the relationship between ambient concentration of organic compounds and the rate at which they are removed from solution?

3. What is the expected concentration of such compounds in the normal environment of the animals? When this concentration is determined, how much material can be supplied to the organism by this method?

4. What fraction of the total energy budget of the organism is provided by reduced carbon supplied in this fashion?

5. What is the evidence for significant participation of material acquired in this fashion in the metabolism of the organism?

Answers to such a series of questions depend on the initial designation of an experimental organism and the designation of a particular compound or class of compounds. When these questions are answered they may provide some evidence for attaching nutritional significance to certain dissolved organic materials. A broader ecological significance would rest on the demonstration of the need of a number of different forms for a fraction of the total requirement of reduced carbon supplied in this way.

It is possible to approximate the answers to all these questions in one animal, the maldanid worm, *Clymenella torquata*, and to provide answers to some of the questions in a few other cases.

CHARACTER OF THE UPTAKE PROCESS

The evidence for interpreting the uptake of glucose and amino acids as a process occurring directly across the body wall is presented in detail elsewhere, but perhaps the most cogent evidence rests on procedures which occlude the digestive tract. When this is done in *Fungia* (Stephens, 1962), *Clymenella* (Stephens, 1963), *Nereis succinea*, and *N. limnicola* (Stephens, 1964), no decrease in the rate of disappearance of such compounds from the ambient medium is observed.

In most of the studies, antibiotics have been used in control procedures. Rates of uptake are not modified. Wherever sufficient data are available for analysis, the rate of uptake is an exponential function of the animal's weight. This suggests in another way that the uptake process is related to the surface of the organism.

In those cases where data are available (*Clyme-*

nella, *N. succinea*, and *N. limnicola*), the uptake of amino acids represents an accumulation of these compounds in the free amino acid pool of the organism. Chromatography has shown that the radioactive alcohol-soluble material extracted from these worms after exposure to C^{14} -labeled amino acids remains in the same chemical form. It is interesting to note that the exchange of amino acids from the organism to the environment is negligible. If an organism such as *Clymenella* is permitted to accumulate C^{14} -labeled glycine or phenylalanine, and then is placed in sea water containing these compounds unlabeled and at concentrations of 10^{-5} or 10^{-4} m/l, no significant amounts of labeled amino acids appear in the medium. Hence, for practical purposes, this is a one-way accumulation system.

RELATION OF UPTAKE TO AMBIENT CONCENTRATION

Five organisms have been examined and a general account may be given for all of them. At low ambient concentrations, uptake is linearly related to concentration. As the concentration of the material concerned is increased, a point is reached where further increase no longer modifies the rate at which the material is removed from solution. This suggests that some rate-limiting step is involved which is adsorptive in its formal character (i.e., adsorption on a surface, saturation of a rate-limiting carrier, etc.). This suggestion is also supported by the relation between concentration and uptake which follows the prediction for kinetics of an enzyme-catalyzed reaction: that a plot of the reciprocal of the velocity against the reciprocal of concentration should give a straight line if the enzyme concentration is fixed. This, of course, does not mean that the uptake is necessarily enzymatic, but is merely a further consequence of some surface-limited step.

As a result of this relationship between concentration and rate, it is possible to estimate the maximum velocity of uptake (V_{max}) for a particular compound and a particular animal. It is also possible to estimate the concentration at which the velocity is half-maximal (K_m). These values are listed in Table 1. This straightforward relationship between uptake velocity and ambient concentration makes it possible to calculate expected uptake at any predicted concentration.

AVAILABILITY OF MATERIAL IN ENVIRONMENT

It is necessary to confine our attention to estimates of free amino acids in sea water. Although a number of investigators have estimated total carbohydrate (Hood, 1963), it has been shown that carbohydrates other than glucose are not available to *Fungia* (Stephens, 1962) and *Mercenaria* (Stephens, unpublished) from solution. Hence, these estimates are not useful in the present context.

Belser (1959, 1963) studied the free amino acids of seawater samples using a bioassay procedure which depended on the growth of amino acid-requiring mutants of *Serratia marinorubra*. Lower limits of

concentration detectable were about 10^{-5} m/l. He reported arginine, glycine, histidine, isoleucine, methionine, threonine, and tryptophan as occurring at these levels in at least some samples of Seitz-filtered sea water. He was not able to detect cystine, leucine, and proline—the remaining amino acids for which mutants were available. He also reported (personal communication) finding arginine, glycine, histidine, isoleucine, and threonine in some inshore sediment samples.

Stephens (1963) reported the presence of twelve neutral and acidic amino acids in interstitial sea water of a mud flat at concentrations ranging from 2.5×10^{-5} m/l to trace amounts. Total concentrations of free amino acids reported for several samples range from 6×10^{-5} to 10^{-4} m/l.

Tatsumoto *et al.* (1961) and Park *et al.* (1962) have reported the presence of free amino acids in surface sea water and at depths as great as 3,500 meters. Ferric hydroxide coprecipitation was used to concentrate the material for analysis. Since this technique would not be expected to give quantitative recovery, these reports should probably be interpreted as further qualitative evidence for the presence of free amino acids in sea water.

It is reasonable to assume that free amino acids may be present in total concentrations ranging between 10^{-5} and 10^{-4} m/l in inshore waters. But how much organic material can be supplied to metazoan invertebrates at such concentrations? Stephens (1963) calculated that the mixture of amino acids observed in the habitat of *Clymenella* could provide approximately 135 micrograms of amino acid per gram wet weight per hour at the rates of accumulation measured in the laboratory.

It is clear that calculation of the amount of material available to animals in the environment must involve a number of assumptions, some of which can be directly checked. It can be shown, for example, that amino acids are removed from both raw and filtered samples of interstitial sea water at the same rate as from artificial sea water (Stephens, unpublished). This indicates that there are no significant naturally occurring inhibitors in the environment, and it also indicates that interactions between amino acids are not a major factor. Other necessary assumptions remain unsupported. For example, one must assume that the solution is exchanged at the surface of the animals at a rate sufficient to supply new material. One can calculate that this rate is comparatively modest. No direct information is available, however.

COMPARISON WITH TOTAL ENERGY BUDGET

Oxygen consumption is often used as a measure of an organism's energy budget. It is consequently interesting to compare the amount of organic material which can be obtained from solution with the amount of material necessary to support the oxygen consumption of the animal concerned. Such a calculation does not imply that the material obtained in this way is,

in fact, the substrate for oxidation. An aerobic animal may require, however, about three times the amount of reduced carbon necessary to support its oxygen consumption in order to allow for growth and reproduction (Jørgensen, 1955). Hence, any material available directly from solution may spare the total requirement, even though it does not all directly enter oxidation pathways.

This comparison may be made by calculating the concentration necessary to provide an amount of material sufficient to support the observed oxygen consumption. Thus, Stephens (1960, 1962) estimated that solutions of glucose of a few mg/l would suffice to support the oxygen consumption of *Fungia*. Of more interest is a comparison based on amounts available in the normal environment. Stephens (1963) reported that *Clymenella* may obtain amino acids equivalent to 150 percent of its observed oxygen consumption. This figure is based on estimates of free amino acids present in the environment. This is the only organism for which such an estimate is available, but, if this is approximately correct, dissolved organic material represents a major supplemental source of food for these worms.

Examination of Table 1 permits some further speculation concerning the potential significance of this process. The last column of the table presents the amount of the organic compound equivalent to the oxygen consumption reported for the animal. When this is compared with the V_{max} for these compounds, it is apparent that the maximum rates of uptake measured exceed the respiratory requirements of *Fungia*, *Clymenella*, and *Nereis succinea* (accepting oxygen consumption for *N. virens* as an approximation). The K_m 's listed indicate that reasonable amounts of material can be supplied at modest concentrations. Hence, dissolved compounds might possibly contribute effectively to the supply of reduced carbon in these three cases. On the other hand, the figures for *N. limnicola* and *Golfugia* indicate a V_{max} which is low compared with probable energy requirements, suggesting a more modest contribution of dissolved material to the energy budget.

Perhaps the most serious criticism of this speculation is in the use of oxygen consumption as an index of food requirements. This assumes that the organism concerned is aerobic in its metabolism, but this may be only partly true. To the extent that an animal derives energy by anaerobic pathways with a loss of partially oxidized material, its requirement for reduced carbon will increase. This implies a corresponding decrease in the calculated percentage contribution made to its nutrition by a measured level of uptake of organic material from solution. No information is available in the forms studied which would permit an estimate of the extent of anaerobic metabolism under normal conditions. Both *Clymenella* and *N. virens* survive exposure to deoxygenated water for periods of 24 hours or more. It is interesting that their capacity to accumulate amino acids is not impaired by the absence of oxygen.

PARTICIPATION OF ACCUMULATED MATERIAL IN METABOLISM

At least some of the compound taken from solution enter oxidation pathways. Significant amounts of C^{14} -labeled carbon dioxide are produced by *Fungia*, *Clymenella*, and *Golfugia* after exposure to labeled glucose and amino acids. These observations are qualitative in character and do not permit calculation of the fraction of oxidative metabolism dependent on these compounds. It is also the case that C^{14} -labeled material is found in alcohol-insoluble form in all of the organisms studied, even after brief exposures to labeled amino acids. The fraction of alcohol-insoluble radioactivity has been shown to increase with time in *Clymenella*. There seems to be no reason to suspect that, generally, material accumulated from solution in the surrounding medium may not be fully available to the organism and enter any of the relevant oxidative or synthetic pathways.

Oxygen consumption as a measure of the potential significance of material which has been obtained from solution is merely a device. There is no implication that all the amino acid obtained in this way is ultimately burned. However, if the material which can be obtained directly from solution is roughly equal to the reduced carbon necessary to support the oxygen consumption of the organism, it is probably significant as a nutritive supplement.

UPTAKE OF ORGANIC MATERIAL IN BRACKISH-WATER ENVIRONMENTS

Numerous attempts have been made to demonstrate uptake of amino acids and glucose by soft-bodied freshwater invertebrates in our laboratory. The experiments do not permit the conclusion that no material can be obtained by such organisms from solution. However, the rate at which such uptake may proceed is very much lower than that observed for marine organisms. Of twelve genera in six phyla (Stephens, 1964), none is capable of removing more than a few percent of added labeled glucose or amino acids over a period of 24 hours. Where labeled material does disappear from solution, the addition of antibiotics markedly reduces the observed rate. Although it cannot be claimed that any of the freshwater forms employed is closely related to the marine forms studied, these uniformly extremely low rates stand in sharp contrast to the apparent widespread ability of marine forms to remove such compounds from solution rapidly.

The relationship between salinity and rate of uptake in forms which can tolerate considerable changes in the osmotic concentration of the environment is interesting. Two species of brackish-water nereids have been studied (Stephens, 1964) with respect to their ability to accumulate glycine at different salinities. Both *Nereis succinea* and *N. limnicola* are capable of accumulating this compound at permissive chlorosities of the medium. When this capacity is exhibited, it follows the pattern which has been de-

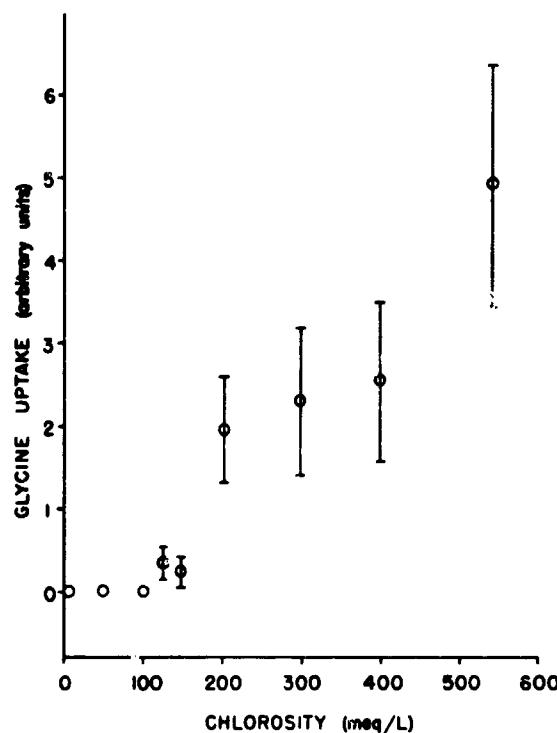


Fig. 1. Rate of uptake of glycine by *Nereis limnicola* as a function of the chlorosity of the ambient medium. Glycine concentration ranges from $1-2.5 \times 10^{-4}$ moles/liter. Uptake is expressed in arbitrary units, bars represent standard deviations.

scribed above. However, when the chlorosity of the medium falls below permissive levels, accumulation stops. Figure 1 exhibits this relationship for *N. limnicola*; the behavior of *N. succinea* is closely comparable.

If one examines previous data concerning the regulation of osmotic concentration of chloride in these animals (Smith, 1959), both organisms merely adapt to declining salinity by a decrease in chloride and in osmotic concentration of the coelomic fluid at chlorosities greater than about 225 meq Cl⁻/l. In more dilute media, osmoregulation and regulation of chloride concentration appear. There is a striking correlation between the onset of these regulatory phenomena and the decline of the ability to accumulate glycine from the medium.

It may be that the processes that underlie osmotic regulation are incompatible with the rapid accumulation of amino acids from the ambient medium, and essentially all marine invertebrates examined (with the exception of arthropods) exhibit such accumulation; none of the freshwater metazoans examined show this ability.

At permissive salinities, the rate of glycine accumulation by *N. succinea* exceeds that shown by *N. limnicola* (Table 1). The two species may be compared with respect to their distribution and their ability to regulate at extremely low salinities. *N. limnicola*

regulates extremely well at very low salt concentrations and may be found in true freshwater environments as well as in brackish water. The osmoregulatory ability of *N. succinea* declines at low salinities and the organism is found in mixopolyhaline or mixomesohaline habitats. The two species seem not to overlap in distribution where both are present in an estuarine system, *N. succinea* replacing *N. limnicola* in brackish waters of higher salinity (Felice, 1958). These data support the assumption that osmoregulation and accumulation of amino acids are not compatible. They also suggest the speculation that the ability to accumulate amino acids may confer an adaptive advantage on organisms which inhabit marine or more saline brackish-water habitats. (Since this manuscript was submitted, studies have been carried out to relate amino acid uptake to the process of "isosmotic regulation" which characterizes many marine and brackish-water invertebrates. The large free amino acid pool in such animals is reduced in response to lowered salinity. This spares changes in critical inorganic constituents and is consequently interpreted as a regulatory response by several authors. Stephens and Virkar (1966) have studied the rate of uptake and the rate of assimilation of amino acids by the brittle star, *Ophiactis arenosa*, as it is related to the modification of the free amino acid pool at various salinities. These authors also give a balance sheet for uptake, assimilation, and oxidation of glycine by these organisms. Additional references can be found in their paper.)

CONCLUSIONS

The uptake of organic compounds of low molecular weight appears to be a significant supplemental source of reduced carbon for several marine animals. Comparison of the material available to the animals at concentrations characteristic of their environment, and the amount of material necessary to account for oxidative metabolism supports this position. Finally, there is qualitative evidence that such material can enter oxidative and synthetic pathways in the animals studied.

This is a general position, but some additional remarks should be made:

First, it is clear that the calculations which permit the assessment of the potential significance of this process can offer nothing more than order-of-magnitude estimates. Our data concerning naturally occurring concentrations of specific organic compounds in sea water are limited. Even in the most carefully studied animal, the bamboo worm, *Clymenella*, we cannot provide a complete description of the rates at which all amino acids are accumulated. Finally, work should be done, not with one class of compounds but with many. Recognizing the limitations of our information, we have made every effort to avoid overestimating the amount of organic material available by this pathway. It is fair to describe this work as pseudo-quantitative in the sense that calculations are based on incomplete information. Never-

theless, one arrives at the conclusion that significant amounts of material are involved in terms of the overall budget of the organism. A more intensive study of this possibility is needed—particularly because the work which has been undertaken strongly suggests the potential importance of dissolved organic material in ecosystem dynamics.

Second, it should be emphasized that in defending the potential significance of dissolved organic material, there is no intent to deny the significance of other means by which marine invertebrates obtain organic material. There is not the slightest doubt that *Clymenella* is indeed a detritus feeder and passes material through the gut. There is no reason to doubt that this contributes to its nutrition. Similarly, *Fungia* functions as a carnivore. It may also derive organic compounds of nutritive significance from symbiotic algae. What is being proposed is that uptake of organic material from solution may supplement other pathways. If this is the case, it may serve the animals in several ways: organic material derived from this process of uptake from solution may quantitatively spare other feeding mechanisms; it may provide a qualitative supplement to food derived from other sources by providing compounds not normally present in the diet; it may increase survival time during periods of scarcity of other food material. If dissolved organic material is indeed significant in one or more of these ways, this has implications of ecological interest. The biomass supported at a particular trophic level may be increased by such contributions. The last point suggests a corresponding decrease in efficiencies calculated on the assumption that all nutrition is derived directly from the adjacent lower trophic level. This would also imply a further relaxation of physical limitations on communities. Distant primary producers may contribute in yet another way to the support of a limited area under study. If we extend the term "detritus" to include dissolved organic material, then soft-bodied marine invertebrates at all trophic levels may to some extent be detritus feeders.

A third point concerns reservations about using oxygen consumption as a measure of food requirements of marine animals. Some marine invertebrates are capable of tolerating anaerobic conditions for considerable periods. That such conditions are characteristic of aquatic environments has been pointed out by several investigators (Weiser and Kanwisher, 1959; Gordon, 1960). It is possible that products of anaerobic metabolism may accumulate during brief periods of oxygen deficit and may subsequently undergo complete oxidation. However, it is likely that partially oxidized products of anaerobic metabolism may be transferred to the medium. Thus, if one calculates the reduced carbon required by a facultative anaerobe based on measurements of oxygen consumption in the laboratory, an underestimate will result. This correspondingly modifies the relationship between available dissolved organic material and the energy budget of the organism. Another pathway by which

material is lost is that slime-producing animals must certainly be less than 100 percent efficient in the recovery of mucus and other material secreted at the body surface. This represents a loss of reduced carbon which is not reflected in oxygen consumption or in biomass measurements, but which must be replaced by synthesis from organic precursor materials. The quantitative significance of such losses of reduced carbon has yet to be assessed.

The complex of questions which may be raised about the role of organic material in aquatic environments cannot be approached meaningfully by such techniques as measurements of total organic carbon. It is likely that some materials are available to organisms and may function as nutritive supplements. Other organic materials may represent losses of one sort or another injected into the medium, perhaps to the ultimate benefit of other members of that community or some downstream association. Study of the exchanges of organic material between animals and an aquatic environment can be pursued with increased profit when we know more about qualitative and quantitative organic analysis. Additional studies will produce systems of great interest to the general and comparative physiologist. They may also lead to information which will amplify and clarify ecological analysis of aquatic communities.

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LITERATURE CITED

- BAYLOR, E. R., and W. H. SUTCLIFFE, Jr., 1963. Dissolved organic matter in seawater as a source of particulate food. *Limnol. Oceanog.*, 8:369-371.
- BELSER, W. L., 1959. Bioassay of organic micronutrients in the sea. *Proc. Nat. Acad. Sci.*, 45:1533-1542.
- BELSER, W. L., 1963. Bioassay of trace substances. In *The Sea, Ideas and Observations*, edited by Goldberg et al.; vol. 2, pp. 220-231. John Wiley and Sons, New York.
- BOSWORTH, M. W., H. O'BRIEN, and W. R. AMBERSON, 1936. Determination of the respiratory quotient in marine animals. *J. Cellular Comp. Physiol.*, 9: 77-87.
- CHEESMAN, D. F., 1956. The snail's foot as a Langmuir trough. *Nature*, 178:987-988.
- COLLIER, A., S. M. RAY, A. W. MAGNITSKY, and J. O. BELL, 1953. Effect of dissolved organic substances on oysters. *U. S. Fish Wildlife Serv. Fishery Bull.*, 51:167-185.
- FELICE, F. P., 1958. Invertebrates from the estuarine portion of San Francisco Bay and some factors influencing their distributions. *Wasmann J. Biol.*, 16: 159-211.
- FOX, D. L., J. D. ISAACS, and E. F. CORCORAN, 1952. Marine leptocephalids, their recovery, measurement and distribution. *J. Marine Res.*, 11:29-46.
- FOX, D. L., C. H. OPPENHEIMER, and J. S. KITTREDGE, 1953. Microfiltration in oceanographic research. II. Retention of colloidal micelles by adsorptive filters and by filter-feeding invertebrates; proportions of dispersed organic to dispersed inorganic matter and to organic solutes. *J. Marine Res.*, 12:233-243.
- GORDON, M. S., 1960. Anaerobiosis in marine sandy beaches. *Science*, 132:616-617.
- HOOD, D. W., 1963. Chemical oceanography. *Oceanog. Marine Biol. Ann. Rev.*, 1:129-155.

- JØRGENSEN, C. B., 1955. Quantitative aspects of filter feeding in invertebrates. *Biol. Rev.*, 30:391-454.
- KROGH, A., 1931. Dissolved substances as food of aquatic organisms. *Biol. Rev.*, 6:412-442.
- LEWIS, G. J., JR., and N. W. RAKESTRAW, 1955. Carbohydrate in sea water. *J. Marine Res.*, 14:253-258.
- PARK, K., W. T. WILLIAMS, J. M. PRESCOTT, and D. W. HOOD, 1962. Amino acids in deep-sea water. *Science*, 138:531-532.
- PUTTER, A., 1909. *Die Ernährung der Wassertiere und der Stoffhaushalt der Gewässer*. Fischer, Jena, Germany.
- RILEY, G. A., 1963. Organic aggregates in sea water and the dynamics of their formation and utilization. *Limnol. Oceanogr.*, 8:372-381.
- SMITH, R. I., 1959. Physiological and ecological problems of brackish waters. *Marine Biol., Proc. Biol. Colloq.*; pp. 59-69. Oregon State College, Corvallis, Oregon.
- STEPHENS, G. C., 1960. Uptake of glucose from solution by the solitary coral, *Fungia*. *Science*, 131:1532.
- STEPHENS, G. C., 1962. Uptake of organic material by aquatic invertebrates. I. Uptake of glucose by the solitary coral, *Fungia scutaria*. *Biol. Bull.*, 123:648-659.
- STEPHENS, G. C., 1963. Uptake of organic material by aquatic invertebrates. II. Accumulation of amino acids by the bamboo worm, *Clymenella torquata*. *Comp. Biochem. Physiol.*, 10:191-202.
- STEPHENS, G. C., 1964. Uptake of organic material by aquatic invertebrates. III. Uptake of glycine by brackish water annelids. *Biol. Bull.*, 126:150-162.
- STEPHENS, G. C., and R. A. SCHINSKE, 1961. Uptake of amino acids by marine invertebrates. *Limnol. Oceanogr.*, 6:175-181.
- STEPHENS, G. C., and R. A. VIRKAR, 1966. Uptake of organic material by aquatic invertebrates. IV. The influence of salinity on the uptake of amino acids by the brittle star, *Ophiactis arenosa*. *Biol. Bull.*, 131:172-185.
- TATSUMOTO, M., W. T. WILLIAMS, J. M. PRESCOTT, and D. W. HOOD, 1961. Amino acids in samples of surface sea water. *J. Marine Res.*, 19:89-96.
- VIRKAR, R. A., 1963. Amino acids in the economy of the sipunculid worm, *Golfingia gouldii*. *Biol. Bull.*, 125:396-397.
- WEISER, W., and J. KANWISHER, 1959. Respiration and anaerobic survival in some sea weed-inhabiting invertebrates. *Biol. Bull.*, 117:594-600.

The Organic Detritus Problem

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This volume represents a major effort to summarize and synthesize our present knowledge in the various disciplines of estuarine science so that it may form a true point of departure for future research. In a very real sense these considerations apply to the role of organic detritus in estuaries. Literature dealing with the organic detritus problem is diffuse, widely scattered, and written in a variety of languages so that it is difficult for the individual worker to gain an overall insight into the complexities of the subject. Much of the important detritus work has not been carried out in estuaries. It is, therefore, necessary to transpose and translate this knowledge into the estuarine context. In addition, the actual critical work on the problem appears to be very small, and one is forced to deal with voluminous reports in which the significance of organic detritus is inferred from several types of circumstantial evidence.

Traditionally organic detritus has been thought of as including only the particulate decomposing organic material. It is quite clear, however, that biological degradation basically involves reduction of the formed bodies through a continuous spectrum of particle sizes down to the level of small molecules. In addition, certain secondary processes are now known which result in an increase in particle size. In either case no sharp dividing lines exist. Therefore, it seems appropriate to redefine organic detritus as *all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species*. By this definition organic detritus includes all dead organisms as well as the secretions, regurgitations, excretions, and egestions of living organisms, together with all subsequent products of decomposition which still represent potential sources of energy. According to this definition, proteins, amino acids, and methane gas, for example, would still be considered as organic detritus, whereas carbon dioxide, water, etc. would not. For convenience we may distinguish between particulate organic detritus (that material retained by filters with apertures of one micron diameter) and subparticulate organic detritus (material which passes through such filters). Many forms of microbiota are intimately associated with the decomposing substrata.

The history of human thought regarding organic detritus may be traced back to antiquity. Many of the ancient peoples believed that the muds and slimes represented both the source and sustenance of aquatic life. Major recorded inferences regarding the matter

began after the advent of the microscope, and the problem has really achieved prominence only during the past century, beginning with the observation by Möbius (1871) of Germany that oysters may consume detritus particles. Later Rauschenplot (1901) and Lohmann (1908, 1909, 1911) pointed out that other "plankton feeders" also consume quantities of this material. Petersen and Jensen (1911) put forth convincing evidence to support their hypothesis that in the shallow Danish wadden area the basic source of nutrition of the animal populations, especially the benthic invertebrates, is the organic detritus derived chiefly from the decay of shallow-water rooted vegetation (especially *Zostera marina*). Blegvad (1915) gave further evidence in support of this hypothesis, and Jensen (1915) concluded that, whereas the communities of open marine waters might be supported chiefly by phytoplankton, as suggested by Hensen (1887) and others of the "Kiel school", the communities of the more enclosed coastal waters, in general, are largely dependent upon particulate organic detritus derived principally from the decay of rooted vegetation. Other early workers who stressed the significance of particulate organic detritus include Naumann (1918, 1921, 1923) in Europe, and Baker (1916) and MacGinitie (1932, 1935) in the United States.

Another aspect of the organic detritus problem is the significance of the subparticulate matter. Historically, study of this may be said to have originated at the turn of the century with the work of Knorr (1901) who postulated that *Daphnia* is able to derive nourishment from dissolved nutrients. This notion was greatly expanded by Putter (1908, 1909a, b) who theorized that many aquatic animals (including fish) can utilize dissolved organic material present in the surrounding water. This topic became the center of lively debate during the ensuing years, but up to the present decade, at least, Putter's basic hypothesis remained neither proven nor conclusively disproven. It is not possible to devote time to the details of the debate here. Historical summaries may be found in the papers of Krogh (1931), Bond (1933), Alice and Frank (1949), and Edmondson (1957).

During the past two decades a number of significant papers have appeared dealing with the topics of biological decomposition, consumption of particulate detritus, ingestion and utilization of specific organic compounds (biochromes, vitamins, amino acids, sugars, gases, etc.), as well as the environmental concentrations of these materials. With the advent of

radioactive tracer techniques and germ-free procedures it is now possible to approach these matters experimentally, to sort out the variables, and to provide quantitative data in place of speculative hypothesis. The study of organic detritus has just entered the analytical phase, and for the first time we stand on the threshold of real knowledge.

Considering the tremendous bulk of organic matter which annually passes through the processes of biological decomposition, and recognizing the existence of a number of thriving communities which apparently receive energy from no other source, this relatively unexplored field must stand as one of the major frontiers of aquatic science.

In conclusion, it should be noted that consumer nutrition is only one aspect of the organic detritus problem. Many organic compounds released into the aquatic environment have been shown to exert specific influences upon various species. Such influences include growth stimulation or inhibition, attraction or repulsion, etc. Through its contributions to turbidity, sedimentation, and chemical alteration of the environment, organic detritus must influence every major process active in aquatic communities.

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LITERATURE CITED

- ALLETT, W. C., and P. FRANK, 1949. Utilization of minute food particles by goldfish. *Physiol. Zool.*, 22: 346-358.
- BAKER, F. C., 1916. The relations of mollusks to fish in Oneida Lake. *New York State Coll. of Forestry, Tech. Publ.*, 16(21):1-36.
- BLEGVAD, H., 1915. Undersøgelse over Næring og Ernæringsforhold hos Havbundens Invertebrater Dyresamfund i Danske Farvande. *Ber. f. Dansk. Biol. Sta.*, 22: 37-132.
- BOND, R. M., 1933. A contribution to the study of the natural food cycle in aquatic environments. *Bull. Biolog. Oceanogr. Coll.*, 4(4):1-89.
- EDMONDSON, W. T., 1957. Trophic relations of the zooplankton. *Trans. Am. Microscop. Soc.*, 76:225-245.
- HENSEN, V., 1887. Ueber die Bestimmung des Planktons oder des im Meere treibenden Materials an Pflanzen und Thieren. *Ber. Komm. Wiss. Unters. deutschen Meere, Kiel*, 5:1-107.
- JENSEN, P. B., 1915. Studier over Havbundens organiske Stoffer. *Ber. f. Dansk. Biol. Sta.*, 22:1-36.
- KNÖRRICH, F. W., 1901. Studien über Ernährungsbedingungen einiger für die Fischproduktion wichtiger Mikroorganismen des Süsswassers. *Forschungsber. Biol. Sta. z. Plon.*, 8:1-52.
- KROGH, A., 1931. Dissolved substances as food of aquatic animals. *Biol. Rev.*, 6(4):412-442.
- LOHMANN, H., 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des meeres an plankton. *Wiss. Meeresunters. Komm. Wiss. Unters. deutsch. Meere, Kiel, u. Biol. Anst. Helgoland, Abt. Kiel, Bd. 10*:129-370.
- LOHMANN, H., 1909. Ueber die Quellen der Nahrung der Meerestiere und Putter's Untersuchungen hierüber. *Intern. Rev. Hydrobiol.*, 2:10.
- LOHMANN, H., 1911. Ueber das Nannoplankton und die Zentrifugierung Kleinster Wasserproben zur Gewinnung derselben im lebenden Zustande. *Intern. Rev. Hydrobiol.*, 4:1.
- MCGINTIE, G. E., 1932. The role of bacteria as food for bottom animals. *Science*, 76:490.
- MCGINTIE, G. E., 1935. Ecological aspects of a California marine estuary. *Am. Midland Naturalist*, 16: 629-765.
- MÖBIUS, K., 1871. Die Austern und die Austernwirtschaft. (Berlin transl., 1890.) The oyster and oyster culture. *Rept. U. S. Fish. Comm.*, 1890:683-751.
- NAUMANN, E., 1918. Ueber die natürliche Nahrung des limischen Zooplanktons. Ein Beitrag zur Kenntnis des Stoffhaushalts im Süsswasser. *Lunds Univ. Arsskr., N. F.*, Bd. 2, Bd. 14, 31:1-48.
- NAUMANN, E., 1921. Spezielle Untersuchungen über die Ernährungsbiologie des Tierischen Limnooplanktons. I. Über die Technik des Nahrungserwerbs bedien Cladoceren und ihre Bedeutung für die Biologie der Gewässertypen. *Lunds Univ. Arsskr., N. F.*, Avd. 2, Bd. 17:3-27.
- NAUMANN, E., 1923. Spezielle Untersuchungen über die Ernährungsbiologie des Tierischen Limnooplanktons. *Lunds Univ. Arsskr., N. F.*, Avd. 2, 19(6):3-17.
- PETERSEN, C. G. J., and P. B. JENSEN, 1911. Valuation of the sea. I. Animal life of the sea bottom, its food and quantity. *Ber. f. Dansk. Biol. Sta.*, 20:1-76.
- PUTTER, A., 1908. Die Ernährung der Wassertiere. *Z. Allgem. Physiol.*, 7:283-368.
- PUTTER, A., 1909a. Die Ernährung der Fische. *Z. Allgem. Physiol.*, 9:147-242.
- PUTTER, A., 1909b. *Die Ernährung der Wassertiere und der Stoffhaushalt der Gewässer*. Fischer, Jena, Germany.
- RAUSCHENPLOT, E., 1901. Ueber die Nahrung von Thieren aus der Kieler Bucht. *Wiss. Meeresunt. Kiel, N. F.*, Bd. 1, vol. 5.

Organic Detritus in Relation to the Estuarine Ecosystem

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Our aim is to examine the state of knowledge of the estuarine detritus problem in order to place the various aspects in perspective as an orientation for future research. To accomplish this, we shall first explore the processes of biological decomposition, then examine the non-nutritive as well as the nutritive roles, and finally reach some tentative conclusions regarding the general role of organic detritus in estuaries. Since estuaries are variable and many gaps exist in our present knowledge, it will sometimes be necessary to deal in generalities.

NATURE OF ESTUARINE DETRITUS

We have defined organic detritus as all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species, and, for convenience, we have recognized two states: the particulate and subparticulate (Jørgensen, 1952). Many forms of microflora are intimately associated with the decomposing substrata.

BIOLOGICAL DECOMPOSITION

A generalized scheme of biological decomposition based upon particle size is presented in Figure 1. Organic material entering this scheme represents the total gross primary and secondary production of the community, exclusive of that material which is temporarily tied up in the protoplasm of producer, consumer, and decomposer species, and that material which has been oxidized to the low-energy state through respiration. Organic matter may enter the scheme either as large particles: carcasses, feces, shed exoskeletons, leaves, etc.; as smaller particles: fragments of organisms, regurgitations, smaller fecal particles, etc.; or as colloids or smaller molecules: secretions, excretions, etc. Regardless of the form in which it enters the decomposition scheme, if it is not lost to the sediments it will subsequently be broken down to smaller size until it reaches the end-molecule low-energy state.

For convenience, we think of the particulate organic detritus as being composed of large and small particles. The source of large particles is generally recognizable, and the particles tend to precipitate rapidly. Smaller particles generally cannot be identified with a specific source, and they usually precipitate more slowly (the relatively larger surface area of small particles results in sufficient friction with the surrounding water molecules to offset much of the gravitational force).

Subparticulate organic detritus includes the colloidal micelles as well as the chemically reduced organic molecules. Colloids, which often remain in suspension almost indefinitely, may include molecular aggregates or large molecules, such as proteins, carbohydrates, lipids, etc. Smaller molecules may exist as dissolved liquids (biochromes, vitamins, amino acids, sugars, urea, nitrates, nitrites, etc.) or as dissolved gases (methane, ammonia, hydrogen sulfide, etc.). All of the above materials represent potential energy sources for some consumer species, and, therefore, they are referred to here in the broader context of organic detritus. The fully oxidized end-molecules (carbon dioxide, water, etc.) can neither supply energy to any known consumer species nor enter into any calculations of the Lindemanian energy scheme. Hence, they are excluded from our definition of organic detritus.

Although organic decomposition basically involves a reduction in particle size, a number of factors in aquatic environments increase the size of particles. In marine environments, at least, colloidal organic micelles tend to adhere to exposed surfaces by the processes of adsorption, agglomeration, and coacervation, thus forming larger dispersed particles (leptopel), oozes and slimes on surfaces of small objects and particles (pelogloea), and thin organic sludges on the muddy ocean floor (sapropel) (Fox *et al.*, 1952; Fox *et al.*, 1953). In addition, particles may be formed in marine waters by denaturation of dissolved organic molecules on surface films such as the air-water interfaces of bubbles (Baylor *et al.*, 1962; Ramsey, 1962; Riley, 1963; Sutcliffe *et al.*, 1963). The operation of these phenomena in estuaries has yet to be studied in detail. Many aquatic consumers are known to produce fecal pellets which are larger than the individual particles ingested (Moore, 1931a, b)—a factor which clearly operates in estuaries as elsewhere.

Biological decomposition involves both mechanical and chemical simplification. Mechanical breakdown must occur primarily through the repeated shaking and rolling action of waves and water currents which affect materials that have been structurally weakened through chemical action. The tearing and grinding processes of many consumer species must likewise play a significant role in the reduction of particle size.

Chemical simplification of organic detritus must be brought about primarily through the processes of hydrolysis and oxidation. Three agents are likely to be

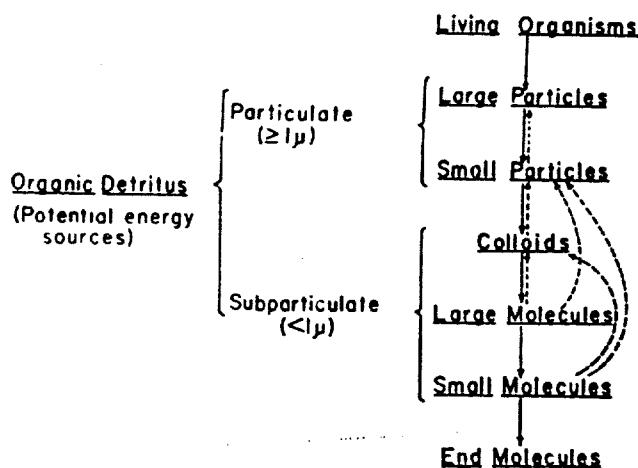


Fig. 1. Biological decomposition and organic detritus formation. Primary processes of particle size reduction are indicated by unbroken arrows. Secondary processes which increase the size of the particles are shown by broken arrows.

involved: autolysis—the breakdown of tissues by their own enzymes; chemical effects of passage through the guts of consumers; and the chemical activities of the saprophytic bacteria and fungi. Autolysis may be of some initial importance, especially in destruction of the cell membranes (Golterman, 1964). It is probable that enzymes of consumer species continue to hydrolyze fecal components after passage from the gut, but little work seems to have been carried out on this matter (Anderson *et al.*, 1958). Undoubtedly, the bacterial and fungal decomposers account for the greatest share of the chemical breakdown of organic material in most natural aquatic systems. The first visible evidence of such a breakdown is a rupture of the cell membrane with a subsequent release of cell components into the environment. Peripheral cells undoubtedly are attacked first. In plant cells, the cellulose walls may trap some of the larger protoplasmic constituents, and microorganisms which invade the cell wall structures must decompose this material *in situ*. Some workers have postulated that particulate organic detritus must be composed primarily of the structural components of vegetation, and, as such, must represent primarily a carbohydrate rather than a nitrogen source (Darnell, 1964). This may be true of smaller particles in later stages of breakdown, but, initially at least, the large particles must contain much nitrogenous matter in the form of trapped protoplasmic structures and invading microorganisms. Surface adsorption phenomena undoubtedly increase the nitrogen content of particles of all sizes (Krey, 1961), but they may play an especially prominent role in the enrichment of smaller particles which tend to have a higher surface to volume ratio (Fig 2). Plant detritus, which appears to persist longest, includes structural materials composed largely of cellulose and lignins as well as certain other large molecules, such as the biopigments. Persisting animal detritus includes certain hard parts,

such as chitinous structures, teeth, bones, scales, eye lenses, etc. These chemically resistant materials, which tend to remain after loss of the softer matter, have been collectively referred to as "humus" (Odum, 1959).

It has been pointed out that some nutrients become immediately available for consumer use and others persist longer. It is also clear that subparticulate material is more readily transported by water currents to other areas than is particulate material. Therefore, organic detritus may be an important source of stored energy and building materials, part of which may be used locally and immediately, and part of which is available elsewhere later. The long-persisting structural elements may eventually prove to be among the chief energy sources of productive areas during off-seasons, and of nonproductive areas (such as the sea bottom) during all seasons (Krey, 1961).

COMPOSITION AND SOURCES OF ORGANIC DETRITUS

Since primary production far exceeds secondary production in most environments, it is not surprising to find that the great bulk of organic detritus in estuaries is derived from vegetation. The original sources of such material have been described as:

1. Autochthonous sources
 - a. Phytoplankton (including algae and auto-trophic bacteria).
 - b. Marginal submerged vegetation.
 - c. Mud-flat diatoms and filamentous algae (especially blue-greens).
 - d. Periphyton growing on stems of emergent plants and other surfaces.
2. Allochthonous sources
 - a. Marginal marsh vegetation.
 - b. Marginal swamp vegetation.
 - c. River-borne phytoplankton and organic detritus.
 - d. Beach and shore material washed in during storms or other times of high water.
 - e. Windblown material, especially leaves and pollen grains.

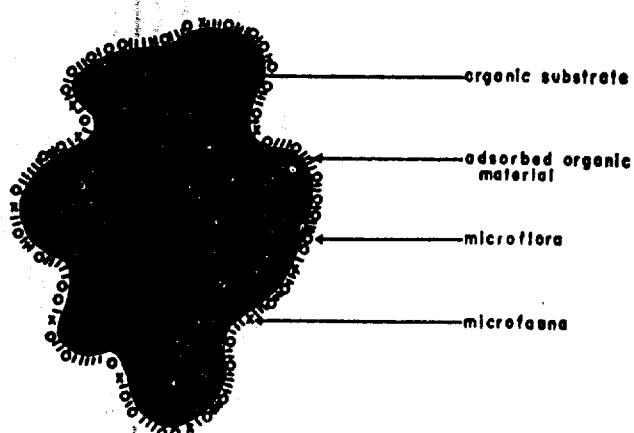


Fig. 2. Organic detritus particle showing living and non-living components (schematic).

f. Phytoplankton and other material originating in the adjacent marine environments.

A comparable list of sources showing materials of animal origin might be drawn up, but the only notable addition would be a category for organic sewage derived from human settlements, upstream or adjacent to the estuary.

Quantitative data on the significance of each source of estuarine detritus have seldom been given, but estimates of relative importance clearly indicate that the sources differ in abundance from one estuary to another, and within a given estuary they vary in relation to the season and to the position in the salinity gradient. Sources of estuarine detritus have been discussed by many workers, including MacGinitie (1932, 1935) and Fox (1950) in California; Darnell (1961, 1964) in Louisiana; Burkholder (1956), Burkholder and Burkholder (1956), Burkholder and Bornside (1957), Starr (1956), and others in Georgia; Darnell (1964) in North Carolina; Rees (1940) in England; Petersen and Jensen (1911) in Denmark; Day (1952), Day *et al.* (1952), Macnae (1956, 1957), and Scott *et al.* (1952) in South Africa.

Rivers entering most estuaries carry a load of negatively charged organic particles which are precipitated by the positively charged metallic ions of the salt water. As noted by Day (1952) and others, however, positively charged organic particles may not be precipitated in this fashion, but may persist for some time suspended even in the salt water. Materials swept into the estuary by saltwater currents from the adjacent marine environments are also precipitated within the estuary. Among autochthonous phytoplankton populations, surface-floating blue-greens such as *Anabaena* (Darnell, 1961) and various species of diatoms have been mentioned by some workers. The dominant vegetation of marginal marshes often progresses from species inhabiting relatively fresh water (*Typha*, *Scirpus*, *Phragmites*, etc.) near the head of the estuary to more salt-tolerant species (*Spartina*, *Salicornia*, *Juncus*, and the mangroves, *Rhizophora* and *Avicennia*) nearer the ocean. *Zostera* and *Ruppia*, among the submerged vascular plants, and *Enteromorpha* and *Polysiphonia*, among the filamentous algae, have also been suggested as important sources. Little attention seems to have been given to the potentially important matter of periphyton which, although small, is often ubiquitous in marsh areas. The rates of production, destruction, and transport of this material are likely to be high in certain environments. It is clear that organic detritus from one source or another is abundant in most estuaries, but, before the study of the estuarine detritus problem can make much headway, it will be necessary to define the sources on a quantitative basis. Such figures will have to take into account seasonal aspects of availability as well as the importance of the various sources in each region of the estuary. A good beginning in this direction has been made by the workers in the Georgia salt marshes (Odum and de la Cruz, elsewhere in this volume).

ESTUARINE DETRITUS IN RELATION TO TURBIDITY AND SEDIMENTATION

TURBIDITY

The turbidity of estuaries is variable, but on the average, far higher than in neighboring marine environments (Day, 1952). This is due in some measure to suspended silt and other inorganic materials, but it is also due in no small measure to the amount of particulate organic detritus present. Important estuarine processes are erosion, transport, and deposition. These phenomena are reversible and depend largely upon the strength of the currents (Day, 1952). High turbidity, in turn, limits the growth of autochthonous vegetation, both the phytoplankton (Darnell, 1961; Day, 1952; Rees, 1940) and the rooted vegetation (Cooper and Milne, 1938; Milne, 1938). Darnell (1961) noted that among the most successful phytoplankton species of the very turbid Lake Pontchartrain community were the surface-floating blue-green algae (*Anabaena* spp., *Microcystis* spp., etc.). To some extent the reduction in photosynthesis and dispersal of bacteria-laden detritus particles reduce the oxygen tension of the estuary. Because of waves and water movement, however, low oxygen conditions are rare in estuaries, except where the flow rate is low. This sometimes occurs near the bottom, especially at low tide and at night (Day, 1952). High turbidity may also affect the animal populations adversely (presumably through gill clogging), but it may also conceal certain benthic species from attack by predators (Darnell, 1958, 1961).

SEDIMENTATION

Day (1952) has pointed out that if sedimentation is too slow the mud-fauna is restricted, whereas too rapid sedimentation may smother certain plants and animals. Whether through the action of turbidity, sedimentation, or other associated factors, the fauna and flora of muddy, high-organic environments tend to be different from the biota of other areas. Many morphological adaptations have been noted among the inhabitants of such areas (MacGinitie, 1932), and certain groups are known to be especially successful here (sciaenid fishes, penaeid shrimp, certain annelids, etc.), whereas others are reduced or absent.

NUTRITIVE ASPECTS OF ESTUARINE DETRITUS

CRITERIA FOR DEMONSTRATING THE NUTRITIVE ROLE OF ORGANIC DETRITUS

A large share of the literature concerning the actual role of organic detritus in the nutrition of aquatic animals has involved speculation based upon incomplete knowledge. To date, most of our conclusions are really opinions based upon personal experience with one environment or another. Therefore, before initiating the discussion of the state of present knowledge, it seems wise to put forth a statement of the types of information required for a rigorous demon-

stration of the nutritive role. These include the following four criteria:

1. Availability of organic detritus in the natural environment of the organism.
2. Ability of the organism to procure and handle the material (i.e., demonstration of appropriate morphological, physiological, and behavioral adaptations).
3. Actual utilization of the detritus under field conditions (i.e., in relation to the physical environment and in competition with other species of the community). This is especially important. The work of Stephens (1964) has pointed out that certain estuarine species may take in dissolved organic matter only if the salinity is sufficiently high.
4. Nutritive value of the consumed detritus for the consuming species. Ingestion alone does not demonstrate a nutritive role. Tests of survival and growth on detritus diets help, but the convincing evidence must come from the utilization of C¹⁴-labeled organic detritus and the demonstration of its incorporation into the consumer's protoplasm. Ideally, these tests should be run under germfree conditions.

NUTRITIVE ROLE OF PARTICULATE ORGANIC DETRITUS

As indicated earlier, particulate organic detritus of one sort or another is an almost universally abundant commodity in the estuaries of the world. If it plays a nutritive role anywhere, it must do so here. Unfortunately, few investigators have actually reported particle sizes of this material, but all visible organic detritus, of course, falls within this category. Edmondson (1957) has noted that, although many freshwater zooplankton species show particle size selectivity, practically all particulate matter suspended in the water is subject to ingestion by one species or another. This is undoubtedly true for the benthic feeders as well. Actually much of the matter which passes through the guts of the consumers is reingested and may be recycled over and over again, perhaps allowing microbial decomposition and surface adsorption to take place between passages.

Morphological and behavioral adaptations for detritus procurement are obvious, and it would be a remarkable feat of selection for most estuarine species to avoid ingesting this material in quantity. Even the most carnivorous species of the estuarine community often take in a certain amount of organic detritus (Darnell, 1958, 1961), and, while they probably derive little caloric value from the small amounts consumed, the significance of this material as a source of vitamins and other micronutrients remains a distinct possibility. From the nutritional standpoint it makes little difference whether the consumers ingest such material through choice or not. Jørgensen (1952) has demonstrated that the rate of filtration of certain marine filter feeders is probably great enough to provide the animals with sufficient amounts of particulate food for maintenance, and the same is true for their estuarine counterparts. Research supports the conclusion that particulate organic detritus is in-

gested in fairly high quantities by most estuarine consumers, whether they are vertebrate or invertebrate, large or small, suprabenthic or benthic.

The actual nutritive roles of the particulate organic substrata have yet to be clearly demonstrated. A number of freshwater species are known to consume particulate detritus regularly (Poddubnaya, 1961; Smirnov, 1958, 1959a, b, 1962), and laboratory feeding experiments indicate growth and reproduction of cladocerans maintained on detritus particles (Richman, 1958; Smirnov, 1962). Most estuarine consumers and most estuarine workers unfortunately have not distinguished between the decomposing substrata and the associated microbiota. Several workers on the Georgia salt marshes have noted the availability of major categories of organic matter from degradation of the annual *Spartina* crop, and some have suggested the nutritive importance of this material for the various consumer species. The actual pathways of consumer utilization have yet to be established.

In our own studies on the Lake Pontchartrain community, we have been able to demonstrate that particulate organic detritus is everywhere abundantly available, that it is ingested in quantity by zooplankton, fishes, and benthic invertebrates, and that areas of zooplankton abundance are correlated with centers of detritus abundance rather than with phytoplankton abundance. Such results lead one to suspect that nutrition is derived therefrom, but whether the relation is direct or indirect is not yet known.

Edmondson (1957) pointed out specific cautions in the interpretation of such circumstantial evidence which might well be reviewed here:

1. The presence of unrecognizable organic material in the guts of zooplankters does not necessarily indicate that they have been feeding on organic detritus because many phytoplankters, and especially small flagellates, break down rapidly.
2. Low phytoplankton-zooplankton ratios do not necessarily mean much because the more rapidly reproducing phytoplankters may be kept at relatively low levels by the grazing activities of the zooplankters.
3. Much detritus in the water may only represent the fecal matter of the zooplankton which is well fed from the phytoplankton, or it may represent fecal matter forced from the zooplankton during the process of sample preservation.
4. Plankton is self-renewing, whereas detritus is not. Hence the real production rate of each is not revealed in "standing crop" estimates.

Some of these same general cautions may be applied to the benthic species as well.

Taking these considerations into account, there can still be little doubt that in most estuaries particulate organic detritus is abundant and is consumed in great quantities. In some cases, at least, the substrata of the particles appear to contain readily utilizable forms of organic matter, but the critical feeding experiments have not yet been carried out.

NUTRITIVE ROLE OF COLLOIDAL ORGANIC MATERIAL

From the abundance of particulate detritus in the estuary, it may be inferred that the level of colloidal matter is also high, but, again, the literature is incomplete. One may assume that such material is several orders of magnitude higher than in the ocean where some measurements have been made. Many invertebrate species of diverse feeding mechanisms (cilia, setae, mucus, etc.) are known to be able to concentrate colloidal materials in the digestive tract (Fox *et al.*, 1953), and evidence suggests that fishes may do likewise (Allee and Frank, 1948, 1949). Increased survival and growth on colloidal diets have been reported for invertebrates as well as vertebrates in the laboratory, but most field studies have not eliminated the possibility of microbial intervention.

NUTRITIVE ROLE OF DISSOLVED ORGANIC MATERIAL

Little can be added to the presentation of Stephens (elsewhere in this volume). I might reemphasize, however, the importance of defining quantitatively the vertical, horizontal, and seasonal distribution of each molecular species within the estuarine waters and in the sediment interstices. Our new knowledge of physiological uptake mechanisms, although quite exciting, is still preliminary. Other species and other environmental complexes must be analyzed before broad generalizations are justified.

NUTRITIVE ROLE OF THE MICROFLORA

Many authors have suggested that aquatic organisms may be nourished wholly or in part by bacteria. ZoBell and Feltham (1942) reported that enormous numbers of bacteria are present on marine mud flats. Although high bacterial populations have been reported for some estuarine environments, this has not been uniformly the case. Bacteria tend to be associated with sediments, exposed surfaces of leaves, etc., and with suspended particles (Jannasch, 1954). They may themselves be nourished by the substratum of the detritus particle or by dissolved organic matter of the medium. In some cases they may act as competitors with the larger consumers, but it is equally true that they may serve an important function in converting organic matter from a relatively unavailable to a relatively available form.

(A comment by Dr. P. Koringa, after one of the lectures of this symposium, is pertinent: A lecture was presented in the "Symposium on Living Molluses", organized by the Zoological Society of London on March 4-5, 1964, by Dr. R. C. Newell from Westfield College, Hampstead, London, on the topic, "The role of detritus in the nutrition of *Hydrobia ulvae* and other deposit feeders." In his lecture, Dr. Newell explained that the snail *Hydrobia* feeds on detritus it finds on the mud flat. The fecal pellets of *Hydrobia* are virtually devoid of nitrogen

(i.e., proteins), but are still rich in carbohydrates such as cellulose. If these fecal pellets are kept for some days in filtered sea water the nitrogen content rises quickly. This is because marine bacteria develop on the organic material and produce bacterial protein utilizing atmospheric nitrogen dissolved in the sea water. When such pellets are reingested by *Hydrobia*, the snail readily digests the bacterial bodies, and the subsequent fecal pellets are again free of nitrogen, but still contain a fair quantity of carbohydrates. This process may be repeated several times. Apparently *Hydrobia* and other deposit feeders can readily digest proteins from the bodies of microorganisms, but cannot themselves digest such carbohydrates as cellulose. Bacteria, on the other hand, are capable of utilizing the carbohydrates and dissolved atmospheric nitrogen in the production of bacterial protein (Newell, 1964).)

A wealth of evidence points to the fact that most invertebrate groups and some fishes are capable of growth and long-term survival when fed diets of pure bacteria (Allee and Frank, 1949; Banta *et al.*, 1939; Burbank, 1942; Rodina, 1950; Stuart *et al.*, 1931; ZoBell and Feltham, 1938). Most such experiments have been based upon diets of the bacterium *E. coli*, and they should be repeated with other naturally occurring strains of bacteria.

An interesting series of experiments carried out by Soviet workers has recently been cited by Sorokin (1964). By bubbling C¹⁴-labeled methane gas through an aqueous bacterial suspension, these investigators were able to obtain labeled bacteria. These were then fed to cladocera, which, in turn, picked up the labeled carbon, thus demonstrating a food chain involving dissolved gas, bacteria, and crustaceans. It is not clear from this series of experiments, however, that the methane-oxidizing bacteria themselves were the food source of the cladocera. The methane-oxidizers may have released identified CO₂ into the environment, where it could have been picked up by another species of bacterium which was subsequently ingested by the crustaceans.

It must be assumed, therefore, that the usually abundant estuarine bacteria probably afford a considerable food source for many consumer species. It seems unjustified to assume that they are the primary or only food source for detritus feeders. Curiously, fungi which are also sometimes abundant appear not to have been investigated in relation to consumer nutrition.

NUTRITIVE ROLE OF MICROFAUNA

When one examines particulate organic detritus fresh from the estuary, he is impressed by the fact that such particles are often inhabited by myriads of small invertebrates (protozoa, nematodes, rotifers, etc.). Detritus feeders cannot avoid ingesting them

along with the particles. Many are probably nutritious, but specific feeding experiments appear to be lacking.

CONCLUSIONS

A number of points may summarize the present state of our knowledge of the role of estuarine organic detritus.

1. Alsterberg (1925) referred to the mud as a "trophic environment", but it is now clear that the whole aquatic system may be so characterized. Let us face the fact that the aquatic medium is really vegetable soup! Due to the availability of large quantities of dead protoplasm, shallow bottoms, and moving water, the estuary especially may be thought of as a thin mud containing many nutritious opportunities for the consumer species.

2. The estuarine environment has placed a premium upon the iliophage (= detritus feeder). As pointed out by Darnell (1958, 1961, 1962, 1964), these forms, including both the transients and the permanent residents, are among the most successful inhabitants of the estuary.

3. Because of the complex origin of organic detritus and because of the associated microbiota, all larger detritus feeders must be considered omnivores.

4. Organic detritus represents a major storage, transport, and buffer mechanism for the estuarine ecosystem: *storage*—organic matter produced at one time is released later; *transport*—downstream away from the point of production; and *buffer*—availability during seasons of low primary production.

5. Relations with Lindemanian trophic scheme:

- Most of the organic detritus is of vegetable origin.
- Since few of the larger estuarine consumers feed upon vegetation alone, the real primary consumers of the community are the microbial species (decomposers).
- Some energy is lost in passage through the microbial scheme, although it remains to be demonstrated what the trophic efficiency of microbes may be.
- Since most of the larger consumers of the estuarine community are omnivores, their relative trophic positions can be assigned only by determining the percentage of contribution of energy from each food source.

It must be concluded that the estuarine community is one of the most complex known to mankind, and this is largely because of the prevalence of organic detritus. Elaboration of all the nutrient pathways will be an undertaking of some magnitude. Fortunately, the number of major contributing species appears to be reasonably low, and many, such as *Zostera*, *Spartina*, etc., have a worldwide distribution. Even so, the tasks of elaborating pathways of biochemical degradation and of investigating the ecological role of each intermediary product should occupy researchers for some years to come.

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LITERATURE CITED

- ALLEE, W. C., and P. FRANK, 1948. Ingestion of colloidal material and water by goldfish. *Physiol. Zool.*, 21:381-390.
- ALLEE, W. C., and P. FRANK, 1949. Utilization of minute food particles by goldfish. *Physiol. Zool.*, 22: 346-358.
- ALSTERBERG, G., 1925. Die Nahrungszykulation einiger Binnenseetypen. *Arch. Hydrobiol.*, 15:291-338.
- ANDERSON, A. E., E. C. JONAS, and H. T. ODUM, 1958. Alteration of clay minerals by digestive processes of marine animals. *Science*, 127:190-191.
- BANTA, A. M., T. R. WOOD, L. A. BROWN, and L. INGLE, 1939. Studies on the physiology, genetics, and evolution of some *Cladocera*. *Carnegie Inst. Wash., Dept. Genetics Paper*, 39:1-285.
- BAYLOR, E. R., W. H. SUTCLIFFE, JR., and D. S. HIRSCHFIELD, 1962. Adsorption of phosphate onto bubbles. *Deep-Sea Res.*, 9:120-124.
- BURBANK, W. D., 1942. Physiology of the ciliate *Colpodium colpoda*. I. The effect of various bacteria as food on the division rate. *Physiol. Zool.*, 15:342-362.
- BURKHOLDER, P. R., 1956. Studies on the nutritive value of *Spartina* grass growing in the marsh areas of coastal Georgia. *Bull. Torrey Botan. Club*, 83(4):327-334.
- BURKHOLDER, P. R., and G. H. BURNSIDE, 1957. Decomposition of marsh grass by aerobic marine bacteria. *Bull. Torrey Botan. Club*, 84(5):366-383.
- BURKHOLDER, P. R., and L. M. BURKHOLDER, 1956. Vitamin B₁₂ in suspended solids and marsh muds collected along the coast of Georgia. *Limnol. Oceanog.*, 1(3):202-208.
- COOPER, L. H. N., and A. MILNE, 1938. The ecology of the Tamar Estuary II. Under-water illumination. *J. Marine Biol. Assoc. U. K.*, 22(2):509-527.
- DARNELL, R. M., 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, an estuarine community. *Publ. Inst. Marine Sci. Univ. Texas*, 5:353-416.
- DARNELL, R. M., 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology*, 42(3):553-568.
- DARNELL, R. M., 1962. Ecological history of Lake Pontchartrain, an estuarine community. *Am. Midland Naturalist*, 68(2):434-444.
- DARNELL, R. M., 1964. Organic detritus in relation to secondary production in aquatic communities. *Verh. Intern. Ver. Limnol.*, 15:462-470.
- DAY, J. H., 1952. The ecology of South African estuaries. I. A review of estuarine conditions in general. *Trans. Roy. Soc. S. Africa*, 33:53-91.
- DAY, J. H., N. A. H. MILLARD, and A. D. HARRISON, 1952. The ecology of South African estuaries. III. Knysna: a clear open estuary. *Trans. Roy. Soc. S. Africa*, 33:367-413.
- EDMONDSON, W. T., 1957. Trophic relations of the zooplankton. *Trans. Am. Microscop. Soc.*, 76:225-245.
- FOX, D. L., 1950. Comparative metabolism of organic detritus by inshore animals. *Ecology*, 31(1):100-108.
- FOX, D. L., J. D. ISAACS, and E. F. CORCORAN, 1952. Marine leptopel, its recovery, measurement and distribution. *J. Marine Res.*, 11(1): 29-46.
- FOX, D. L., C. H. OPPENHEIMER, and J. S. KITTREDGE, 1953. Microfiltration in oceanographic research: II. Retention of colloidal micelles by adsorptive filters and by filter-feeding invertebrates; proportions of dispersed organic to dispersed inorganic matter and to organic solutes. *J. Marine Res.*, 12(2):233-243.
- GOLTERMAN, H. L., 1964. Mineralization of algae un-

- der sterile conditions by bacterial breakdown. *Verh. Intern. Ver. Limnol.*, 15:444-448.
- JANNASCH, H. W., 1954. Ökolog. Unters. d. planktischen Bakterienflora im Golf v. Neapel. *Naturwissenschaften*, 41.
- JØRGENSEN, C. B., 1952. On the relation between water transport and food requirements in some marine filter feeding invertebrates. *Biol. Bull.* 103(3):356-363.
- KREY, J., 1961. The balance between living and dead matter in the oceans. In *Oceanography*, edited by Mary Sears; pp. 539-548. American Association for the Advancement of Science, Washington, D. C.
- MACGINITIE, G. E., 1932. The role of bacteria as food for bottom animals. *Science*, 76:490.
- MACGINITIE, G. E., 1935. Ecological aspects of a California marine estuary. *Am. Midland Naturalist*, 16: 629-765.
- MACNAE, W., 1956. Aspects of life on muddy shores in South Africa. *S. African J. Sci.*, 53(2):40-43.
- MACNAE, W., 1957. The ecology of the plants and animals in the intertidal regions of the Zwartkops Estuary near Port Elizabeth, South Africa. I and II. *J. Ecol.*, 45:113-131, 361-387.
- MILNE, A., 1973. The ecology of the Tamar Estuary. III. Salinity and temperature conditions in the lower estuary. *J. Marine Biol. Assoc. U. K.*, 22(2):529-542.
- MOORE, H. B., 1931a. The muds of the Clyde Sea area. III. Chemical and physical conditions: rate and nature of sedimentation and fauna. *J. Marine Biol. Assoc. U. K.*, 17:325-358.
- MOORE, H. B., 1931b. The specific identification of faecal pellets. *J. Marine Biol. Assoc. U. K.*, 17:359-365.
- NEWELL, R. C., 1964. The role of detritus in nutrition of *Hydrobia ulvae* and other deposit-feeders. *Symposium on Living Molluscs*. Zoological Society of London, London.
- ODUM, E. P., 1959. *Fundamentals of Ecology*; 2nd ed., p. 20. W. B. Saunders Co., Philadelphia, Pennsylvania.
- PETERSEN, C. G. J., and P. B. JENSEN, 1911. Valuation of the sea. I. Animal life of the sea bottom, its food and quantity. *Ber. f. Dansk. Biol. Sta.*, 20:1-76.
- PODDUBNAYA, T. L., 1961. Materialy po pitaniyu massovykh vidov tubifitsid Rybinskogo vodokhranilishcha. (Materials on nutrition of mass species of Tubificidae of the Rubinsk Reservoir.) *Trudy Instituta biologii vodokhranilishch. A N SSSR*, 4(7):219-231.
- RAMSEY, W. L., 1962. Dissolved oxygen in shallow near-shore water and its relation to possible bubble formation. *Limnol. Oceanogr.*, 7:453-461.
- REES, C. B., 1940. A preliminary study of the ecology of a mud-flat. *J. Marine Biol. Assoc. U. K.*, 24:185-199.
- RICHMAN, S., 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monographs*, 28(3):273-291.
- RILEY, G. A., 1963. Organic aggregates in sea water and the dynamics of their formation and utilization. *Limnol. Oceanogr.*, 8(4):372-381.
- RODINA, A. G., 1950. Eksperimental'noe issledovanie pitaniya dafniy. (Experimental investigation of nutrition of *Daphnia*.) *Trudy Vsesoyuznogo Gidrobiologicheskogo Obshchestva*, 2:169-193.
- SCOTT, K. M. F., A. D. HARRISON, and W. MACNAE, 1952. The ecology of South African estuaries. II. The Klein River Estuary, Hermanus, Cape. *Trans. Roy. Soc. S. Africa*, 33:283-331.
- SMIRNOV, N. N., 1958. Some data about the food consumption of plant production of bogs and fens by animals. *Verh. Intern. Ver. Limnol.*, 13:363-368.
- SMIRNOV, N. N., 1959a. Rol' vysshikh rasteniy v pitaniyu zhivotnogo naseleniya bolot. (Role of higher plants in nutrition of animal populations.) *Trudy Moskovskogo Tekhnicheskogo Instituta Rybnoy Promyshlennosti i Khozyaystva*, 10:75-87.
- SMIRNOV, N. N., 1959b. O privalzhennom kolichestvennom issledovanii sostava pishchi vodnykh bespozvonochnykh pri vskrytii. (On approximately quantitative evaluation of gut contents of aquatic invertebrates.) *Byull. Inst. Biol. Vodokhranilishch AH SSSR*, 5:43-47.
- SMIRNOV, N. N., 1962. *Eurycericus lamellatus* (O. F. Muller) (Chydoridae, Cladocera): field observations and nutrition. *Hydrobiol.*, 20:280-294.
- SOROKIN, J. I., 1964. On the trophic role of chemosynthesis in water bodies. *Intern. Rev. d. gesamt. Hydrobiol.*, 49(1):307-324.
- STARR, T. J., 1956. Relative amounts of vitamin B₁₂ in detritus from oceanic and estuarine environments near Sapelo Island, Georgia. *Ecology*, 37(4):658-664.
- STEPHENS, G. C., 1964. Uptake of organic material by aquatic invertebrates. III. Uptake of glycine by brackish water annelids. *Biol. Bull.*, 126:150-162.
- STUART, C. A., M. McPHERSON, and H. J. COOPER, 1931. Studies of bacteriologically sterile *Moina macrocopa* and their food requirements. *Physiol. Zool.*, 4:87-100.
- SUTCLIFFE, W. H., E. R. BAYLOR, and D. W. MENZEL, 1963. Sea surface chemistry and Langmuir circulation. *Deep-Sea Res.*, 10:233-243.
- ZOBELL, C. E., and C. B. FELTHAM, 1938. Bacteria as food for certain marine invertebrates. *J. Marine Res.*, 4:312-327.
- ZOBELL, C. E., and C. B. FELTHAM, 1942. The bacterial flora of a marine mud flat as an ecological factor. *Ecology*, 23(1):69-78.

Particulate Organic Detritus in a Georgia Salt Marsh-Estuarine Ecosystem

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In Georgia estuaries which are dominated by *Spartina alterniflora* marshes, organic detritus is the chief link between primary and secondary productivity, because only a small portion of the net production of the marsh grass is grazed while it is alive. The major energy flow between autotrophic and heterotrophic levels is by way of the "detritus food chain", rather than through the "grazing food chain" (Odum,

1962, 1963; Odum and de la Cruz, 1963; Teal, 1962). Seven aspects of detritus are being studied in the extensive salt marshes and estuaries that lie between Sapelo Island and the mainland of Georgia: (1) the seasonal picture of the standing crop of detritus in the water of tidal creeks; (2) the distribution of size and the composition of detritus particles; (3) the tidal transport of detritus in and out of a ten hectare

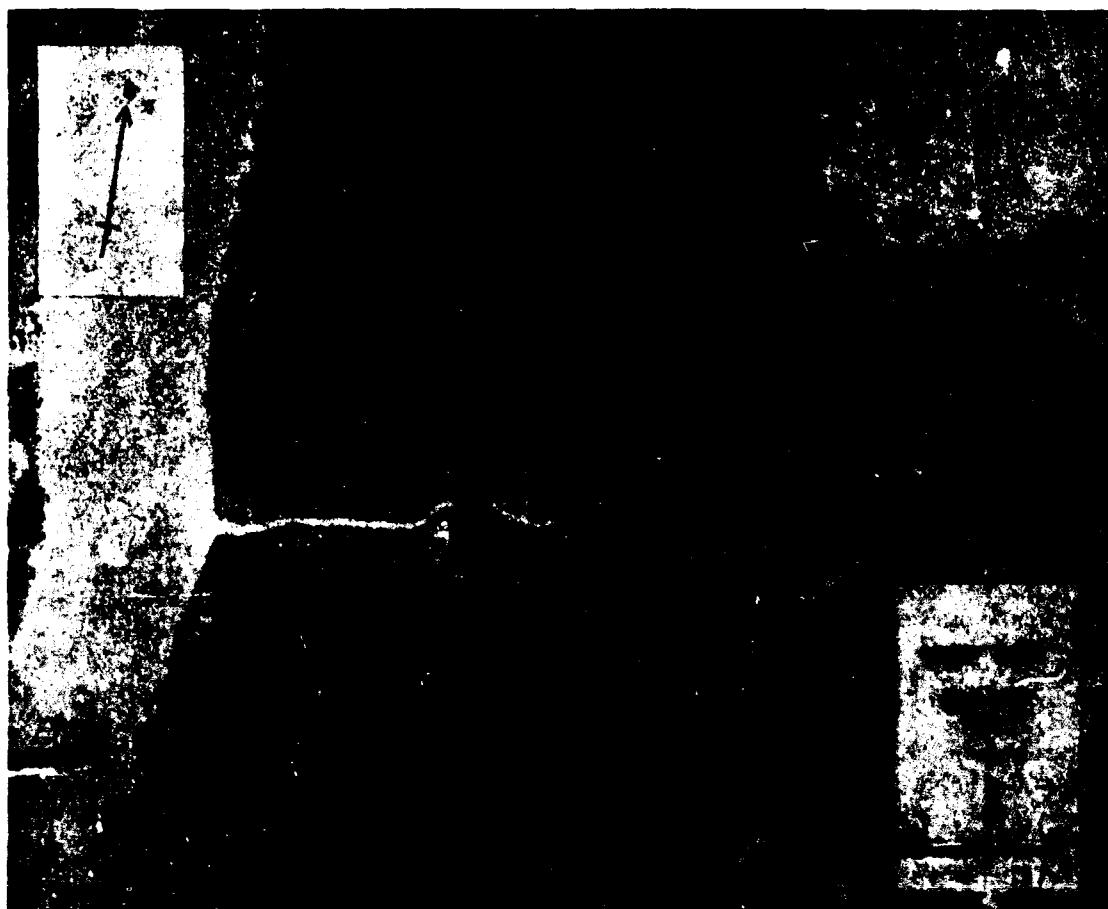


Fig. 1. Aerial photograph of the study area showing the creek at the center of the picture and the *Spartina* marshes it drains. Small lateral tributaries of the creek interconnect with branches of other creeks at right and top. Light areas along the edges of the creek outline the tall and medium *Spartina* marshes while the dark areas between the larger creeks are the short *Spartina* high marsh. At the left of the picture is the Duplin River, a large tidal channel running parallel to Sapelo Island, a small portion of which may be seen at the top right corner.

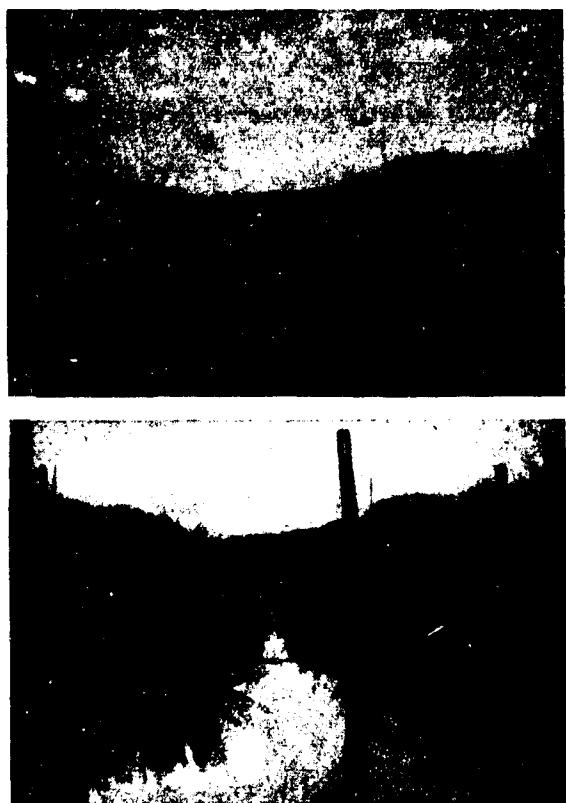


Fig. 2. Mouth of the tidal creek study area, showing tall *Spartina* grass at high (A) and low (B) tide levels during a neap tide. During spring tides, the creek is almost dry at low water and the tall grass is practically submerged at high water. The temporary weir seen across the creek was used to trap dead floating *Spartina* stalks to determine net transport of large floating organic detritus. The main sampling station is located in the immediate foreground.

marsh area which is drained by a single small creek; (4) the origin of the particles; (5) the decomposition of marsh grass in nylon "litter bags" placed at different tide levels in the field; (6) the nutritive values of different age and size components; and (7) the metabolism of detritus particles. The principal study area is shown in the aerial photograph of Figure 1. The mouth of the main creek under study, the tall *Spartina* grass, and the high and low tide levels under neap tidal conditions are shown in Figure 2. The chief sampling station was located just outside the temporary weir shown in the foreground of Figure 2.

METHODS

Suspended particles were separated into size classes in this way: known volumes of water were strained successively through a No. 6 plankton net (74 meshes/inch; 0.239 mm aperture), a No. 25 net (200 meshes/inch; 0.064 mm aperture), and a HA millipore filter. Particles retained by the No. 6 net were labeled "coarse fraction", particles strained by the No. 25

net, "fine fraction", and particles collected by the membrane filter, the "nanno fraction". Dry weight and ash-free dry weight (loss on ignition at 550° C. after one hour) were determined for each fraction. The number of particles (counted in a 45 × 45 × 10 mm chamber with 5 mm² grids) was also determined for the net fractions. The metabolic rate of detritus samples was determined in the laboratory as follows: net fractions were resuspended in millipore-filtered water while the filtrate was saved for the nanno fraction. All three fractions were collected on millipore filters which were then placed in filtered water in 300 ml bottles. After shaking to redisperse particles, the bottles were incubated in the dark at 29.5, 19.5, and 9.5° C. (representing the range of seasonal temperature of the study area) for 6, 12, and 18 hours respectively. Dissolved oxygen consumption was determined by the Winkler method.

To obtain an estimate of the exchange of detritus between the marsh and the tidal creek (Figs. 1 and 2), water samples were collected at the mouth of the creek every hour for 12 hours starting at either high or low slack water. It was estimated that the creek drains ten hectares of marsh at neap tidal levels and 24 hectares at spring tidal levels. Current velocity measurements and cross-sectional area of the creek were estimated as a basis for calculating exchange of detritus between the marsh and the estuarine creek system.

The decomposition rate of four species of marsh plants was determined by enclosing plant samples in litter bags of nylon net (2.5 mm mesh) which were placed at various tide levels in the marsh.

The successive decomposition stages of *Spartina* grass collected in the field for nutritive analyses were: living *Spartina*, dead standing, floating dead, decomposed samples in litter bags, and coarse, fine, and nanno fractions of suspended detritus. The analyses were carried out by Law and Company, Atlanta, Georgia.

Table 1. Suspended particulate detritus in mg dry weight per liter at mid-tidal levels at the mouth of a small tidal creek draining a *Spartina* salt marsh at Sapelo Island, Georgia. Each is based on two samples taken on different days.

Season	Tide levels	Spring		Neap	
		Total	Ash-free	Total	Ash-free
Summer	Mid-flood	35.44	6.59	21.28	5.12
	Mid-ebb	112.41	20.75	32.47	6.59
Fall	Mid-flood	41.72	7.36	24.80	6.72
	Mid-ebb	110.32	16.50	57.92	13.54
Winter	Mid-flood	29.82	5.68	10.68	1.99
	Mid-ebb	71.77	10.10	36.91	3.90
Mean	Mid-flood	35.66	6.54	18.92	4.61
	Mid-ebb	98.17	15.78	42.43	8.01

RESULTS

STANDING CROP AND SIZE DISTRIBUTION OF DETRITUS

Table 1 compares the standing crop of suspended particulate matter at mid-flood and mid-ebb tidal levels. The greater amount at the mid-ebb level at all seasons is indicative of the net export of detrital material from the marsh, especially since the velocity of the water is greater at the mid-ebb than the mid-flood level.

The standing crop of 2-20 mg ash-free dry organic matter per liter is much greater than that reported for open sea water, or such fertile locations as Plymouth Bay and Long Island Sound, where particulate organic matter is approximately 1-3 mg/l (Armstrong and Atkins, 1950; Riley, 1959; Corner, 1961; Cowey and Corner, 1963).

We do not yet have sufficient data to determine the extent of seasonal differences. We can say, however, that organic detritus is being produced and exported at all seasons.

The percentage of organic matter content of the various fractions photographed (Fig. 3) revealed that coarse, fine, and nanno fractions made up 1, 4, and 95 percent respectively. It appeared then that the highly decomposed, unrecognizable nanno fraction might be of the greatest importance.

COMPOSITION AND ORIGIN

Microscopic analysis of net seston composition revealed a high percentage of detritus particles. The mean values (Table 2) showed that about 90 percent of total seston was net detritus and only about 10 percent net plankton. More organic detritus was present during the mid-ebb flow which, again, strongly suggested a net export of organic material to the estuarine system. Plankton density was also greater at mid-ebb than mid-flood even though the percentage composition was lower (Table 2), indicating that the marsh was exporting plankton, but not as much as detritus. Much of the phytoplankton coming out of the marsh may be of benthic origin (Williams, 1962). The ratio of zooplankton to phytoplankton (in terms of numbers) was approximately 1:3 at mid-ebb and 1:4 at mid-flood.

Even though the total seston is much lower in most coastal seas, and especially in the ocean, than in Sapelo estuaries, detritus seems to make up a large percentage of seston in marine waters in general (Krey, 1961; Riley, 1963; Strickland, 1963).

Table 3 gives three estimates of the percentage of net detritus originating from *Spartina*, algae, and animals. Almost 95 percent of these larger suspended particles originated from decaying *Spartina* grass. Algal detritus consisted mostly of broken pieces of large diatom shells and dinoflagellate cases. Animal detritus included fragments of crustacean integument, pieces of chitinous appendages, fragments of molluscan shell, scales of fish, fecal pellets, shells of ostracods and foraminiferans, pieces of insect wings, bits of mammalian hair, bird feathers, etc.



Fig. 3. Photomicrographs of detritus particles collected from the salt marsh tidal creek. A—"Coarse Detritus" collected with a coarse net (74 meshes inch; 0.239 mm aperture), approximately 90X. B—"Fine Detritus" collected with an extra fine net (200 meshes inch; 0.064 mm aperture), approximately 70X. C—"Nanno Detritus", aggregates of highly decomposed particles sedimented from water previously strained through the extra fine net, approximately 80X.

Table 2. Numerical composition of net seston in estuarine waters collected at the mouth of a small tidal creek at mid-tidal levels.

Dates	Tidal level	Total number seston particles per liter	Detritus		Phytoplankton		Zooplankton	
			No. / l	%	No. / l	%	No. / l	%
6/20/63	Mid-flood	3,148	2,984	94.8	104	3.3	60	1.9
	Mid-ebb	28,653	28,452	99.3	115	0.4	86	0.3
7/3/63	Mid-flood	1,625	1,378	84.8	219	13.5	28	1.7
	Mid-ebb	5,411	5,065	93.6	271	5.0	76	1.4
7/29/63	Mid-flood	1,805	1,518	84.1	218	12.1	69	3.8
	Mid-ebb	7,242	6,952	96.0	217	3.0	73	1.0
9/26/63	Mid-flood	1,169	960	82.1	134	11.5	75	6.4
	Mid-ebb	2,928	2,293	78.3	477	16.3	158	5.4
10/1/63	Mid-flood	18,128	16,170	89.2	1,722	9.5	236	1.3
	Mid-ebb	71,196	69,914	98.2	1,068	1.5	214	0.3
11/22/63	Mid-flood	5,258	4,950	94.5	267	5.1	21	0.4
	Mid-ebb	32,264	31,554	97.8	387	1.2	323	1.0
Mean	Mid-flood	5,185	4,660	89.9	444	8.5	81	1.6
	Mid-ebb	24,015	24,038	97.7	422	1.7	155	0.6

TIDAL TRANSPORT

Smoothed curves (Fig. 4) are typical of a number of measurements of tidal transport for both spring and neap tides. As would be expected, spring tide transport of water, total particulate matter, and ash-free organic matter greatly exceeded that of neap tide. The maximum rate of discharge from the marsh occurred at the mid-ebb level, which was about 2-3 hours after the high slack water.

A preliminary calculation, based on data in Figure 4, resulted in an estimated net export of about 140 kg and 25 kg of organic matter for spring and neap tides, respectively, from the 10-25 hectare marsh area in one tidal cycle.

DECOMPOSITION OF MARSH PLANTS

Figure 5 traces the rate of decomposition of four species of marsh plants and, for comparison, decomposition of animal biomass (Fiddler crabs, *Uca pugnax*). The curves are based on the mean weight loss of two litter bags for *Distichlis*, *Juncus*, and *Salicornia*, nine bags for *Spartina*, and three bags for *Uca*. The litter bags were staked down in the marsh at the same tidal levels, where each species occurred naturally. After 300 days, residues expressed as the percentage of initial dry plant tissue were: *Distichlis* - 47 percent, *Juncus* - 65 percent, *Salicornia* - 6 percent, and *Spartina* - 42 percent. *Uca* decomposed completely after about 180 days in the field.

It may be pointed out that "dead standing" plant material was placed in the bags to simulate the stage when the detritus formation begins in nature. The decomposition curves indicate the rate of release into the water of soluble material and particles small enough to pass through the 2.5 mm mesh nylon litter bags.

NUTRITIVE VALUE OF DETRITUS

The percentage of protein, fat, crude fiber, and nitrogen-free extract of *Spartina* grass and detritus are compared in Figure 6, as a preliminary analysis based on single large pooled samples of each item. Although the small suspended particles were 70-80 percent ash, the organic matter in them proved to be rich in protein, up to 24 percent on an ash-free basis as compared with 10 percent in living grass and 6 percent in dead grass, as it enters the water. A buildup of microbial populations is presumed to account for the enrichment of decomposing *Spartina*. Thus, detritus rich in bacteria may be a better food source for animals than the grass tissue that forms the base for most of the particulate matter.

METABOLISM OF DETRITUS

The results of oxygen consumption measurements of the three size fractions of detritus at three temperatures are summarized in Figure 7. The 9.5 to 29.5° C. range approximates the seasonal range of temperatures in Sapelo waters. Milliliters of O₂ hr were calculated in terms of fresh weight of detritus and ash-free dry weight (i.e., actual organic matter). Analysis of variance indicates that both size and temperature have a highly significant effect on the weight-specific oxygen consumption. The rate of oxygen consumption of nano-detritus proved to be five to six times greater than that of coarse net detritus. A rate of metabolism of 10 ml O₂ gm ash free dry weight is comparable to the respiration rate of zooplankton. The results of the metabolism measurements provide further evidence of the importance of microbial activity in determining the important role played by detritus in the ecology of estuaries. The suspended particles are by no means "dead" or "inert."

bodies, and the detritus particles and the attendant microorganisms make up a highly active heterotrophic micro-ecosystem.

SUMMARY

Estuaries in Georgia dominated by *Spartina alterniflora* marshes have organic detritus as the chief link between primary and secondary productivity, since

Table 3. Percentage of detritus particles originating from three major sources as determined by microscopic examination of three samples of the net fractions strained from tidal creek water.

Date	Tidal level	<i>Spartina alterniflora</i> (Macrophytic) (%)	Algae (Macrophytic) (%)	Animals (Zootic) (%)
6 20 63	Mid-flood	97.7	2.0	0.3
7 3 63	Mid-ebb	90.5	7.6	1.6
7 26 63	Mid-ebb	93.4	4.5	2.1
Mean		93.9	4.8	1.3

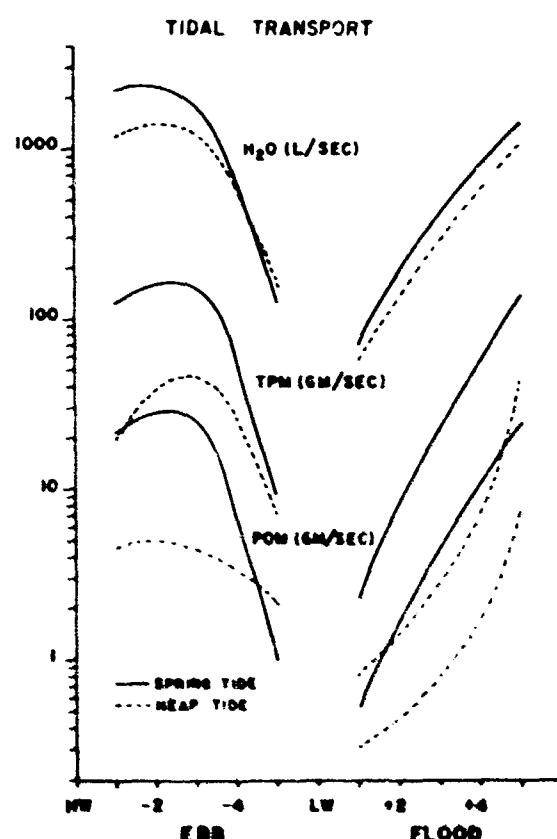


Fig. 4. Comparison of tidal transport during spring and neap tidal phases. Abscissa represents hours of tidal cycle after high water (HW) to and after low water (LW). TPM = Total particulate matter; POM = Particulate organic matter.

only a small portion of the net production of the marsh grass is grazed while it is living. Seven aspects of detritus are being studied at the University of Georgia Marine Institute at Sapelo Island: (1) the seasonal picture of the standing crop of detritus in water; (2) size distribution and composition of detritus particles; (3) tidal transport of detritus in and out of a ten-hectare marsh area drained by a single small creek; (4) origin of the particles; (5) decomposition of marsh grass in nylon litter bags; (6) nutritive values of different age and size components; and (7) metabolism of detritus particles.

In creeks draining Sapelo marshes, organic detritus ranges from 2 mg/l at mid-flood tide to 20 mg/l at mid-ebb tide, and makes up about 90-99 percent of the total seston. The small suspended particles are 70-80 percent ash, but the organic portion is rich in protein, up to 24 percent on an ash-free basis, as compared with 10 percent in living grass and only 6 percent in dead grass as it enters the water. Oxygen consumption (B.O.D.) per gram is more than five times as

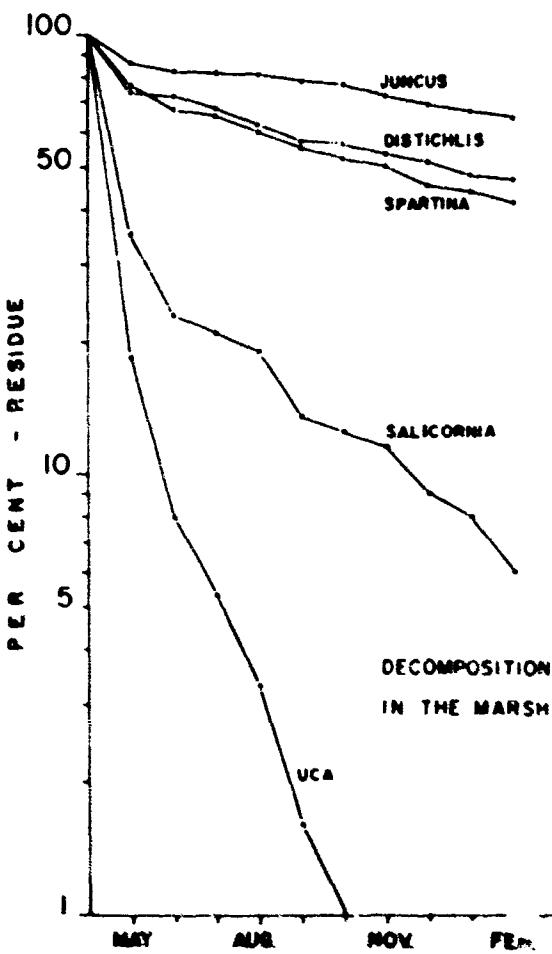


Fig. 5. Decomposition rate expressed as percentage of residue. Curves dry weight of samples of dead individuals of four species of salt marsh plants (*Distichlis*, *Juncus*, *Salsicornia*, and *Spartina*) and crabs (*Uca*).

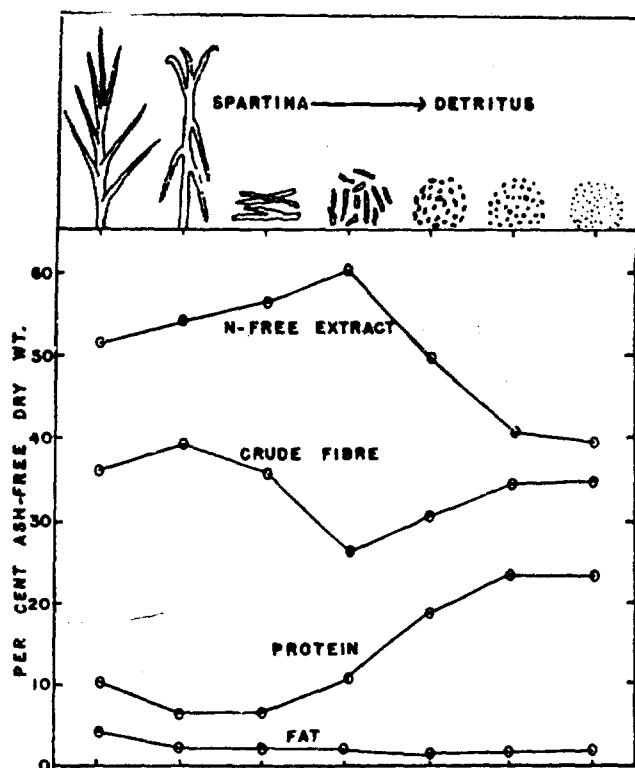


Fig. 6. The nutritive composition of successive stages of decomposition of *Spartina* marsh grass, showing increase in protein and decrease in carbohydrate with increasing age and decreasing size of detritus particles.

great in "nanno detritus" (that which passes through a No. 25 net—200 meshes per inch; 0.064 mm per aperture) as compared with coarse detritus (that retained by a No. 6 net—74 meshes per inch; 0.239 mm per aperture) indicating increasing microbial activity with age. The nanno fraction comprises 95 percent of the total particulate organic matter. Thus, the bacteria-rich detritus is nutritionally a better food source for animals than is the *Spartina* tissue that forms the original base for most of the particulate matter.

Authors' Note: This paper is Contribution No. 118 from the University of Georgia Marine Institute.

LITERATURE CITED

- ARMSTRONG, F. A. J., and W. R. G. ATKINS, 1950. The suspended matter of sea water. *J. Marine Biol. Assoc. U. K.*, 29:139-143.

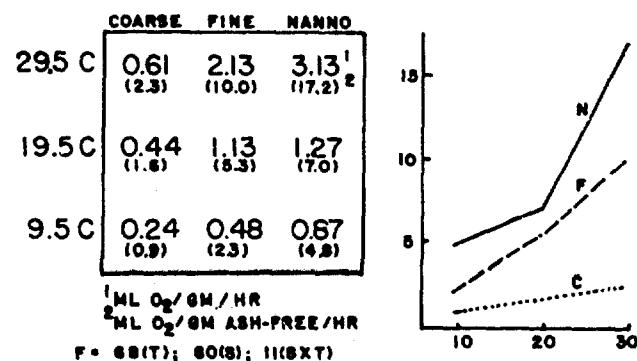


Fig. 7. Oxygen consumption of the three size fractions of detritus under constant temperature conditions in darkness in the laboratory. Means for each size-temperature category (10 replications) are shown in the table and temperature-respiration rate (in terms O₂/gm ash-free) curves are shown in the graph. F values for analysis of variance are shown below the table. Both temperature and size affect O₂ consumption to a highly significant degree at the 99 percent level.

- CORNER, E. D. S., 1961. On the nutrition and metabolism of zooplankton. I. Preliminary observations on the feeding of the marine copepod, *Calanus helgolandicus* (Claus). *J. Marine Biol. Assoc. U. K.*, 41:5-16.
- COWEY, C. B., and E. D. S. CORNER, 1963. On the nutrition and metabolism of zooplankton. II. The relationship between the marine copepod, *Calanus helgolandicus*, and particulate material in Plymouth sea water, in terms of amino acid composition. *J. Marine Biol. Assoc. U. K.*, 43:495-511.
- KREY, J. 1961. Der Detritus im Meere. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 26:263-280.
- ODUM, E. P., 1962. Relationship between structure and function in the ecosystem. *Japan. J. Ecology*, 12:108-118.
- ODUM, E. P., 1963. Primary and secondary energy flow in relation to ecosystem structure. *Proc. XVI Intern. Congr. Zool.*, 4:336-338.
- ODUM, E. P., and A. A. DE LA CRUZ, 1963. Detritus as a major component of ecosystems. *AIBS Bull.*, 13:39-40.
- RILEY, G. A., 1959. Note on particulate matter in Long Island Sound. *Bull. Bingham Oceanog. Coll.*, 17:83-86.
- RILEY, G. A. (Editor), 1963. *Marine biology I. First Intern. Interdisciplinary Conf. on Marine Biol.* Am. Inst. Biol. Sci., Washington, D. C.
- STRICKLAND, J. D. H., 1963. Phytoplankton and primary production. *AIBS Bull.*, 13:58-59.
- TEAL, J. M., 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, 43:614-624.
- WILLIAMS, R. B., 1962. *The ecology of diatom populations in a Georgia salt marsh*. Ph. D. Dissertation, Harvard Univ., Cambridge, Massachusetts.

Detritus in the Ocean and Adjacent Sea

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Since the classical work of Lohmann (1908) the question of the role of detritus as food for filter-feeding organisms of the sea has arisen repeatedly. Comprehensive literature has now been published on the detritus of both fresh water and the sea. A considerable part of it is included in recent reviews (Krey, 1961; Parsons, 1963). New observations on the quantity of detritus in the ocean are presented in this paper. The question of the role of detritus in metabolism is deferred, because a clarification of the nutritive value of detritus is not available.

METHODS OF ANALYSIS

The methods for determining detritus are varied and include methods relying exclusively on microscopic observations and countings as well as purely chemical and combined microscopic-chemical methods. The pure microscopic observations have the disadvantage of being too slow; an experienced observer can count and measure no more than two samples a day. All three dimensions of a single detritus particle should be measured, because calculations of volume based on the two-dimensional form of the detritus particle are subject to error. The pure chemical methods have the advantage of permitting an analysis of a large number of samples per day with a comparatively small amount of equipment. Chemical methods are based on two different processes. In one, the dry weight of the total particulate matter collected on a filter is determined. From this particulate substance the content of chlorophyll can be determined (Parsons, 1963), and the proportion of living matter calculated (assuming that the zooplankton and bacteria amount to only a small share). The quantity of detritus is obtained as the difference between the total dry weight and the dry live weight. In the other process the amount of living matter can be determined by the biuret method (Krey *et al.*, 1957) by means of variable conversion factors, ranging between 2.5, for pure dinoflagellates and zooplankton, and 5.0 for pure diatomaceous plankton. One can also calculate the content of detritus by finding the difference. These two methods are uncertain because only average conversion factors are used.

A third group of methods combines the microscopic and chemical processes by determining the total weight of the particulate substance and ascertaining the living proportion of the particulate matter by microscopic examination of the number and size of phyto- and zooplankton. The quantity of

detritus is then calculated by finding the difference. This last group of analyses has been enhanced by a photomicrographic method, in which the content of phyto-, zooplankton, and detritus can be determined by means of a particle-size analyzer. Until recently, microscopic and microscopic-chemical determination of detritus have not permitted evaluation of the population of bacteria on detritus, though the group is of primary importance in all questions concerning the metabolism in the sea.

RESULTS AND DISCUSSION

During our work in IGY 1958, supported by the Deutsche Forschungsgemeinschaft, we were able to collect and examine 1,600 water samples from the northern North Atlantic for detritus content (Fig. 1). These samples were taken largely in the surface layer from 0–200 m, although deeper water layers were also sampled (530, 1,530, and 4,000–5,000 m). The chemical method was employed in the analyses.

The results are summarized in Figure 2, based on observations made during late winter and late summer. The mean values indicate that an extraordinarily high percentage of total particulate matter is found as detritus in late winter, as well as in late summer. A high percentage of total particulate matter was found at depths, as expected, but also at the surface and in the surface layer. It appears that at most 20–30 percent of the total particulate matter is found as living substance, although it is generally less. These diagrams suggest the important role of detritus in the metabolism of the ocean, especially if one accepts the theory that detritus acts as an adsorber of dissolved organic matter, found in this area in the quantity of 0.2–2 mg C/l (Duursma, 1960).

The mean values have been further divided into separate areas (Table 1), which appear to be of special interest for productivity. We have differentiated calm areas, where only a small oceanic upwelling must be taken into consideration, from oceanic areas where there is an increased upwelling of deep water and, consequently, an increase in primary production can be expected. The core areas situated within the Gulf Stream, in which there is only a small direct exchange of water from the depths, are also differentiated. In Table 1 examples are given of the mean values of the concentration of living substance and detritus for different depths. In the core area the proportion of living material in the upper 50 m is found to be more than 50 percent of the total particles,

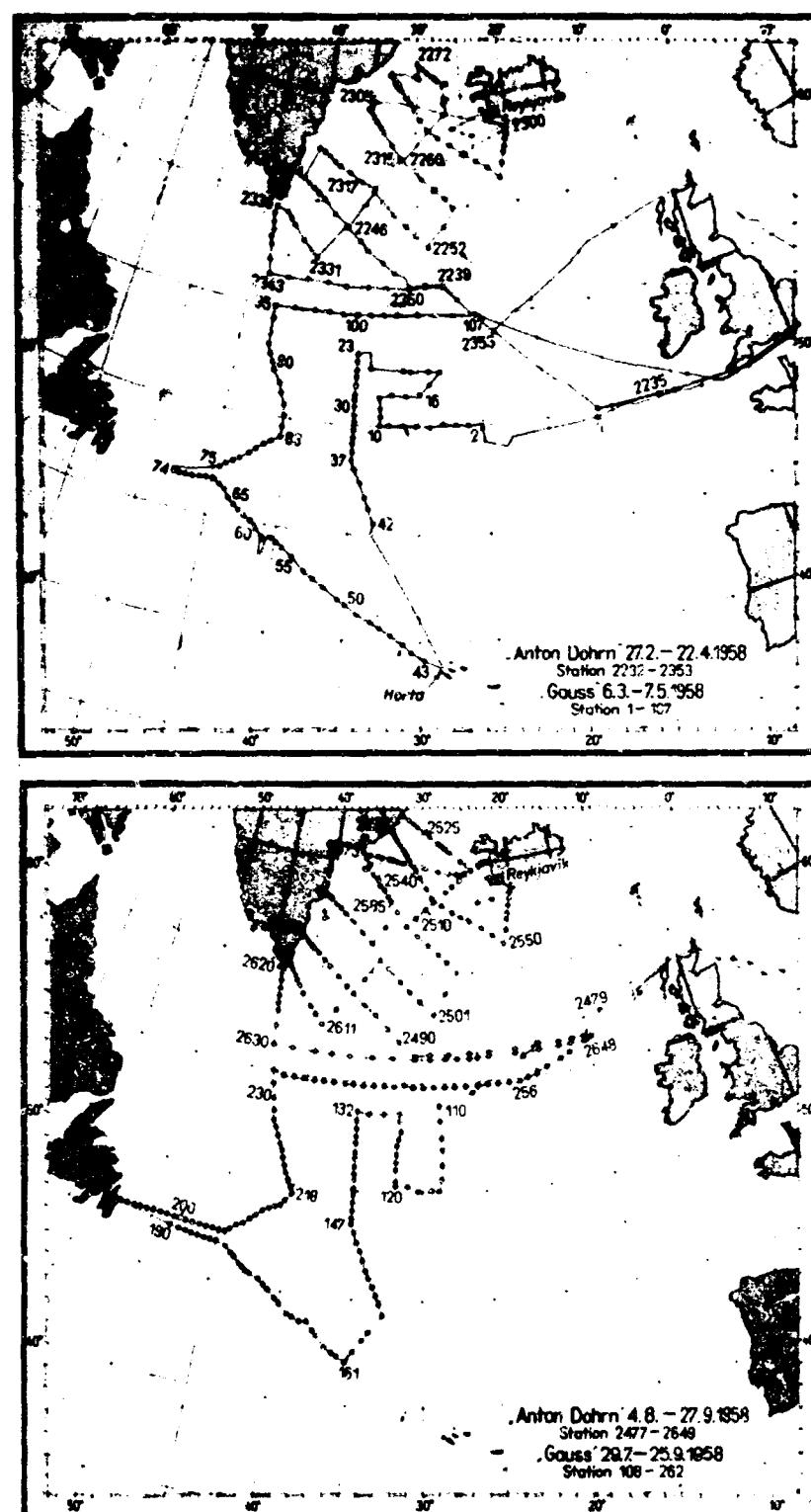


Fig. 1. Oceanographic stations where samples for determination of microbiomass and detritus were taken.

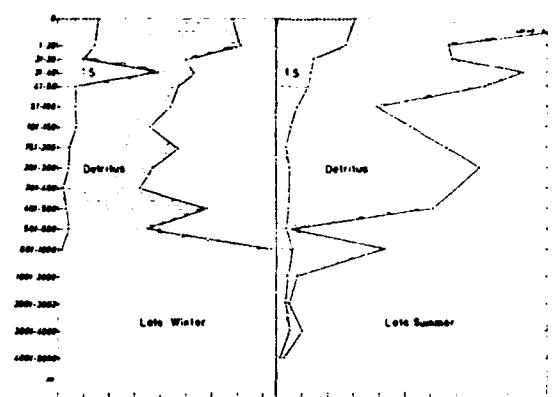


Fig. 2. Average depth distribution of detritus in late winter and in late summer in the northern North Atlantic.

indicating a lower content of detritus. The absolute value for living substances varies considerably in all areas. These examples of single groups of stations are presented to suggest the very heterogeneous distribution of detritus, but are also applicable to the vertical distribution of detritus.

In June, 1960, Körte (1962, unpublished manuscript) investigated the vertical distribution of detritus in the area between the Faroe Islands and Iceland (Table 2) using a pure microscopic-photographic method. He found a relatively high concentration of detritus. The mean particle volume increased from $80 \mu^3$ at the surface to $159 \mu^3$ at 394 m and diminished to $134 \mu^3$ in 476 m. The weight of detritus (determined chemically) is in relatively good agreement with that counted and measured microscopically assuming a specific weight of 1.00.

Earlier Hagnieier (1960) determined the content of detritus in the area around Iceland, based on a combined microscopic-chemical method. In the example chosen here (Fig. 3) a very high percentage of the total particulate matter for surface samples, mostly more than 60 percent, was found to be detritus. A considerable part originated from offshore areas

following the spring bloom of phytoplankton. The surface waters contained a mean weight of seston, ranging between 0.4-2.0 mg/l; about 0.2-1.8 mg represented detritus. Hagneier observed that the proportion of detritus increased considerably in deeper water layers, although its absolute quantity remained the same or even decreased.

In a study on the content of seston and plankton in the Indian Ocean, Hagmeier (1964) reported similar high values for the areas west and northwest of Australia, where certainly no coastal influences are to be expected. He employed the pure chemical method in evaluating the different components and his results were similar to those already reported for the North Atlantic Ocean. Figure 4 summarizes his observations to a depth of 500 m. Here it is again evident that detritus in the surface layer, with only a few exceptions, constitutes more than 50 percent of the total particulate matter. The absolute values are considerably lower than those found in the northern North Atlantic. Hagmeier's detritus values range between 44 and 96 $\mu\text{g/l}$, with a maximum of 105 $\mu\text{g/l}$ living substance. This comparatively low value can be explained by the trophic condition of the area during the time the observations were made. It might be expected that this value would be considerably higher, and perhaps even lower, during other seasons.

Only portions of the detritus distribution have been studied closely, but it is without doubt that annual detritus cycles can be expected in most parts of the ocean and adjacent seas. We do have some knowledge of such cycles in the adjacent seas, but in the oceanic environment only a few data are available on annual cycles of specific biological components and environmental factors, largely from the basic investigations of primary production near Bermuda (Menzel and Ryther, 1960). Recently, seasonal observations on biological and environmental parameters over a distance of 24° were carried out in the Indian Ocean by a team of Australian scientists during cruises aboard the Australian vessel, "Diamantina". These studies also indicate considerable seasonal differences. As far as I know no previous measurements on the

Table 1. Mean values for detritus and living substance (as dry material) in $\mu\text{g/l}$ (IGY 1958).

Table 2. Mean vertical distribution of detritus in the area between Faroe Islands and Iceland in June, 1960 (From Körte, 1962).

Mean values of depth .n	No. of samples	Volume of detritus mm ³ /l	Mean volume of particle μ ³	Weight of detritus (dry material) mg/l
0	50	0.78	88	1.10
4	21	0.77	78	
49	12	0.63	91	
107	8	0.83	104	
180	20	0.57	100	0.76
296	6	0.43	130	
394	9	0.38	159	0.68
476	11	0.32	134	0.55

annual cycle of the content of detritus are available. During a six-year period (1958-1963) the cycle was followed in Kiel Bay at two different stations (Krey, 1964). For a water depth of 28 m (Fig. 5c) the average results, obtained by the pure chemical method, are summarized for this period of observation. The conversion factors used provided minimum and maximum values, but there is comparatively little deviation. There is a considerable shift in the maxima,

in contrast to the distribution of microbiomass (Fig. 5a) and to chlorophyll content. While these latter two elements show a four- and three-peaked curve, the mean content of detritus follows a two-peaked curve with maximum values in April and November. This distribution closely parallels the mean seasonal distribution of seston (Fig. 5b). It is apparent that the detritus distribution is influenced, in part, by bottom materials. According to Zeitzschel (1964) who also worked in this area, the annual quantity of seston deposited to the sediments amounted to 500 g dry weight per m². Only 75 g of the 500 g was organic material and, of that, 15 g was living substance. Accordingly, the amount of organic detritus was only 60 g dry substance; that of inorganic detritus, 425 g/m². Unfortunately no further information is available on the organic detritus. One must consider that a part of the substance included as organic detritus was present in the form of dissolved or colloidal and adsorbed materials associated with fine inorganic particles such as clay.

The distribution of size of the detritus particles in the different water layers for one station of the Kiel Bight has been reported recently (Krey, 1961). The curves of distribution indicate that the mean particle size of the detritus particles increased from the surface to the bottom. This factor can be explained by

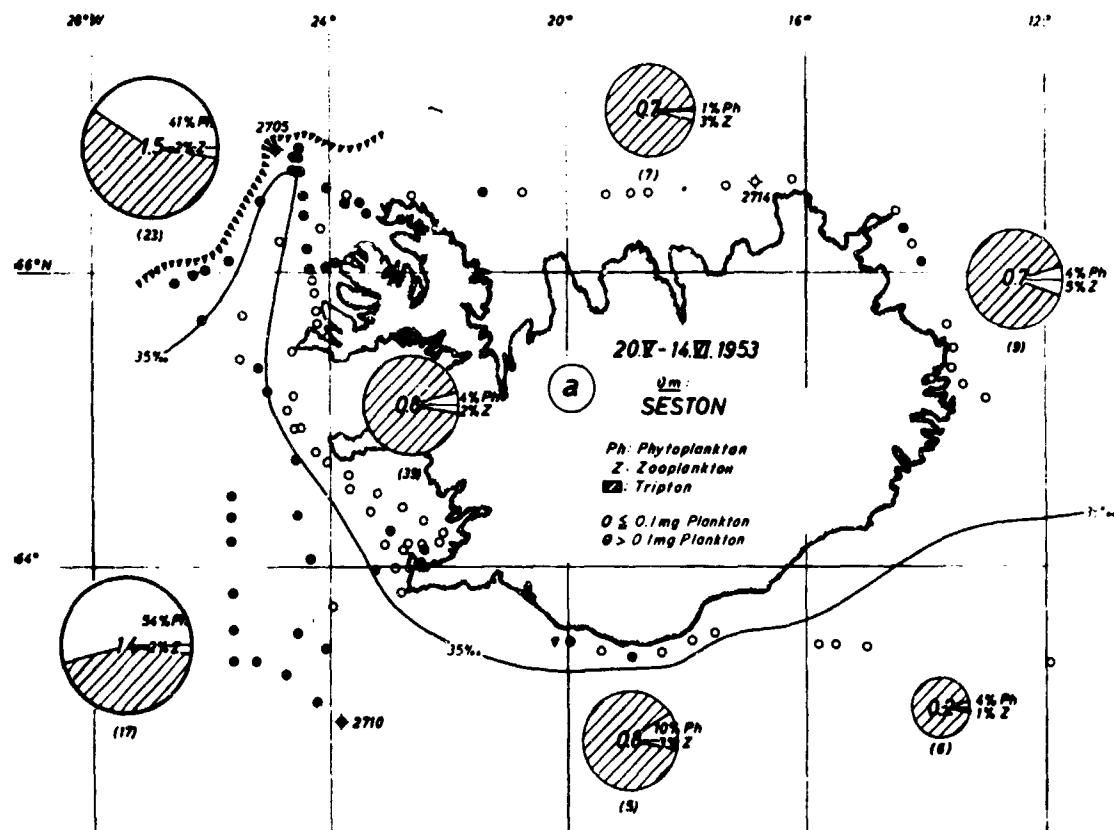


Fig. 3. Average surface distribution of detritus (mg dry weight/l) around Iceland in early summer 1953 (From Hagmeier, 1960).

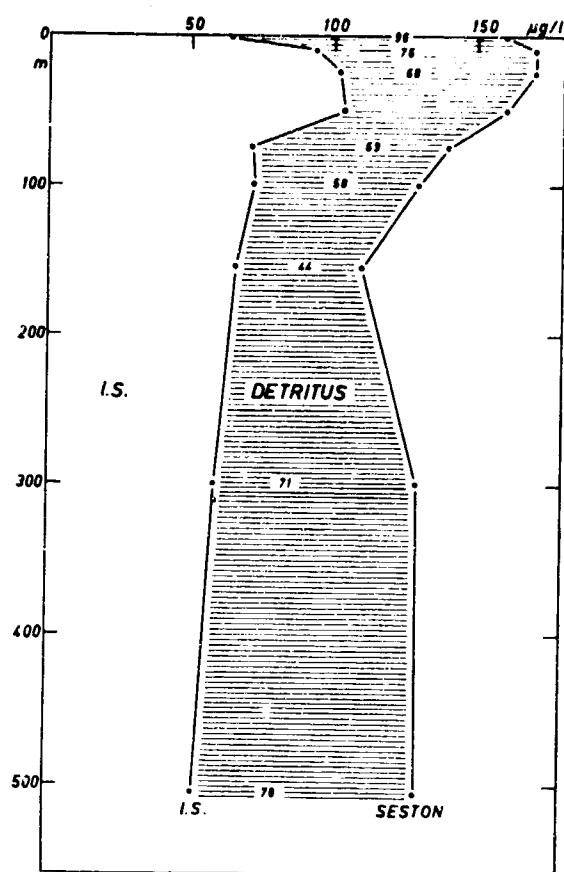


Fig. 4. Average depth distribution of detritus (dry weight) W and NW of Australia in summer, 1961 (From Hagmeier, 1964).

the considerable quantity of detritus mixed from the bottom.

In Table 3, mean values for one year of observation (1963) are summarized for the total water column and include detritus, seston, protein, and living substance calculated from protein values using conversion factors of $F = 5$ and $F = 2.5$. Using two different conversion factors for calculating the minimum and maximum value of detritus, very large proportions are found, ranging between 30–90 percent of the seston. Only in May, 1963, was a relatively small quantity of detritus observed (2 percent).

The vertical distribution of detritus is shown in the isopleth diagram of Figure 6. The water was comparatively low in detritus from April to December in different water layers, but during other periods the detritus values increased beyond 50 percent. The absolute values of detritus demonstrated a seasonal distribution. During the months between April and December values were generally 500 μg and less, with a minimum in May. The low values in May were associated with comparatively little water turbulence and the end of the spring bloom of the phytoplankton. In contrast, the early spring bloom can be

clearly recognized at the beginning of April with a subsequent increase in detritus.

Table 4 gives the monthly and annual mean values of seston, living substance, and detritus for the years 1958–1963. Again, the minimum and maximum values for detritus were calculated. The minimum mean value of detritus was found in May, ranging between 340 μg ($F = 5$) and 550 μg ($F = 2.5$). Immediately before, in April, the highest annual value of detritus was found, estimated to range between 3,310 μg and 3,630 μg . The annual mean value of detritus, calculated to be between 1,290 and 1,540 μg , seems to be astonishingly high. The high value can be accounted for by a considerable addition of bottom material. The portion of organic detritus in the total particulate matter amounted to 12 percent.

The foregoing is a contribution to our knowledge of the quantity of detritus in the sea, with particular reference to the annual cycle in the adjacent seas. We must investigate the nutritional role of detritus, as we now know it occurs in marine waters in extremely large quantities. In future work, we must also distinguish between young detritus of high nutritive value and old detritus, reduced by bacteria, which has small nutritive value for filter-feeding animals. Techniques of the bacteriologist will assist us, especially in direct observations of bacteria attached to the detritus. The solution of the question of the nutritive value of detritus will provide a key to the

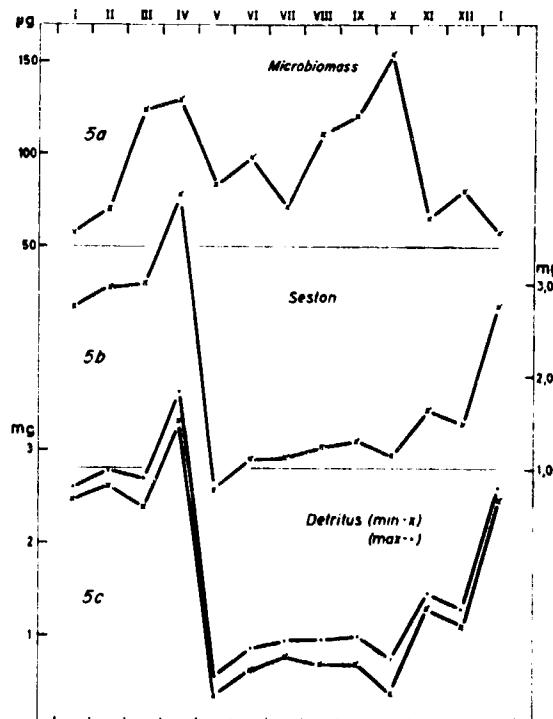


Fig. 5. Seasonal changes of mean concentration of microbiomass, total particulate material (=seston), and detritus in Kiel Bay, 1958–1963.

Table 3. Mean values of seston, protein, living substance, and detritus in $\mu\text{g/l}$ Kiel Bay, 1963.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Seston	-	-	1,590	3,790	470	730	730	790	1,250	-	830	830
Protein	-	-	88	155	92	56	77	111	138	-	76	102
Living Substance (F = 5)	-	-	440	775	460	280	385	555	690	-	380	510
Detritus (min.)	-	-	1,140	3,020	10	450	350	240	560	-	450	320
% of seston	-	-	72	80	2	62	48	30	45	-	54	39
Living Substance (F = 2.5)	-	-	220	388	230	140	193	278	345	-	190	255
Detritus (max.)	-	-	1,360	3,400	240	590	540	510	900	-	640	570
% of seston	-	-	86	90	51	81	74	65	72	-	77	69

Table 4. Mean values of seston, protein, living substance and detritus in $\mu\text{g/l}$ 1958-1963.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Yearly average values
Seston	2,750	2,960	3,000	3,960	760	1,100	1,120	1,230	1,290	1,130	1,620	1,480	1,790
- Living substance (max.)	290	350	620	650	420	490	360	550	600	770	330	400	500
= Detritus (min.) %	2,460	2,610	2,380	3,310	340	610	760	680	690	360	1,290	1,080	1,290=72%
- Living substance (min.)	150	180	310	330	210	250	180	280	300	390	170	200	250
= Detritus (max.) %	2,600	2,780	2,690	3,630	550	850	940	950	900	740	1,450	1,280	1,540=86%

understanding of life of filter-feeding organisms in the deep sea. We can expect with some optimism to resolve many of the questions regarding the metabolism in the sea by comprehensive investigations of the detritus. Our work should be stimulated by the agricultural sciences, especially in their study of the soil. It can be expected that detritus plays a role in the ocean similar to that of humus in our arable soils and those in uncultivated areas of tropical regions.

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LITERATURE CITED

- DUURSMA, E. K., 1960. Dissolved organic carbon, nitrogen and phosphorus in the sea. *Neth. J. Marine Res.*, 1:1-148.
 HAGMEIER, E., 1960. Untersuchungen über die Menge und die Zusammensetzung von Seston und Plankton in Wasserproben von Reisen in die Nordsee und nach Island. *Diss. Kiel*, pp. 168-355.
 HAGMEIER, E., 1964. Zum Gehalt an Seston und Plankton im Indischen Ozean zwischen Australien und Indonesien. *Kiel. Meeresforsch.*, 20:12-17.
 KÖRTE, F.R., 1962. Plankton- und Detritusuntersuchungen zwischen Island und den Färöer im Juni 1960. *Kiel. Meeresforsch.*, 22:4-30.
 KREY, J., 1961. Der Detritus im Meere. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 24:263-280.
 KREY, J., 1964. Die mittlere Tiefenverteilung von Seston, Mikrobiomasse und Detritus im nördlichen Nordatlantik. *Kiel. Meeresforsch.*, 20:18-29.
 KREY, J., K. BANSE, and E. HAGMEIER, 1957. Über die Bestimmung von Eiweiß im Plankton mittels der Biuretreaktion. *Kiel. Meeresforsch.*, 13:35-40.
 LOHMANN, H., 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Wiss. Meeresuntersuch., Abt. Kiel, N.F.*, 10:129-370.
 MENZEL, D. W., and J. H. RYTHER, 1960. The annual cycle of primary production in the Sargasso Sea off Bermuda. *Deep-Sea Res.*, 6:351-367.
 PARSONS, T. R., 1963. Suspended organic matter in sea water. *Prog. Oceanogr.*, 1:205-239.
 ZEITZSCHEI, B., 1964. Zur Sedimentation von Seston, eine produktions-biologische Untersuchung von Sinkstoffen und Sedimenten der Westlichen und Mittleren Ostsee. *Diss. Kiel*, pp. 1-95.

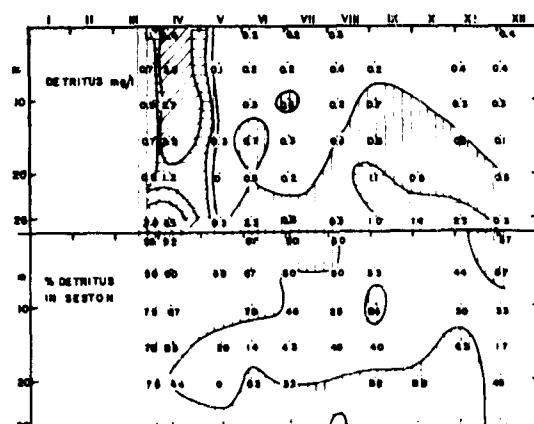


Fig. 6. Isopleth diagram of absolute concentration of detritus (upper) and of percentage of detritus of total particulate material (lower) as observed in Kiel Bay, 1963.

VII. ECOLOGY AND POPULATIONS

The Biology of Knysna Estuary, South Africa

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The currents, the salinity, the temperature of the water, and the nature of the bottom sediments each has its own effect on estuarine fauna. But in a natural habitat environmental factors do not act independently as a laboratory physiologist would wish them to do. An estuary is a single, unified ecosystem with all the environmental factors interacting to determine the nature and distribution of the fauna.

Knysna is an ordinary estuary with a normal salinity regime and a rich fauna. This will provide a basis for comparison with other estuaries; it is hoped that the interaction of the various environmental factors will become apparent.

THE FACTORS WHICH DETERMINE THE RICHNESS OF AN ESTUARINE FAUNA

The ecology of Knysna Estuary was described by Day *et al.* (1952), and full details of topography, environmental conditions, and a list of the fauna were given. Since then, we have studied several other estuaries along the coasts of southern Africa and have learned more about the distribution and biology of the typical estuarine animals. We have revisited Knysna very recently and can now see much more clearly why Knysna has such a rich fauna and why many of the other estuaries are impoverished.

THE SIGNIFICANCE OF CLIMATE

Knysna is situated on the southern coast of Africa roughly half way between Port Elizabeth and Mossel Bay. The climate is temperate throughout the year and frosts are unknown. The Knysna River arises in the Outeniqua Mountains and the drainage basin receives an average rainfall of 36.3 inches per year spread evenly over the seasons. Thus the maximum of 11.03 inches which falls during the three spring months (September, October, and November) is not very different from the minimum of 7.03 inches which falls in the winter months of June, July, and August. As a result there is a steady flow of river water into the estuary throughout the year; the salinity remains fairly stable and the mouth remains permanently open.

The importance of this even rainfall is shown by comparison with the St. Lucia Estuary described by Day *et al.* (1954). Here the annual rainfall is much the same (54.4 inches) but 16.04 inches, or almost half the rain, falls in the three summer months, and during the whole of the winter there is only 1.82 inches. As a result there are floods and low salinities in summer while in the winter the rivers stop flowing.

As evaporation proceeds, sea water is drawn up the estuary and it gradually becomes more and more saline until the headwaters of the estuary are more saline than the sea. It is not surprising that St. Lucia has a much poorer fauna than Knysna.

EROSION OF THE DRAINAGE BASIN

The banks of Knysna are well wooded and there is little or no erosion. The river water is clear, though peat-stained, and the estuary itself is sufficiently clear for a Secchi disc to be visible at a depth of six feet in the mixing basin. There is vigorous plant growth at this depth and, as a result, the fauna is rich.

The contrast may be seen in many South African rivers where bad farming and overgrazing to the water's edge have removed the plant cover. The Umzimvubu, which flows through the Transkei and enters the sea at Port St. Johns, is a pitiful example. This once-beautiful estuary with a mouth sufficiently deep to provide a port for steam coasters is now a morass of porridgey mud. Each rain brings down enormous masses of chocolate-brown silt so that a Secchi disc disappears three inches below the surface. There is no vegetation below the mid-tide mark and the fauna is reduced to the barest minimum. During the dry season, when the water clears, some benthic species re-establish themselves, but the next floods cover them with a blanket of fine silt. This is merely one example among many and one can appreciate why the fauna of Knysna Estuary is one of the richest in South Africa.

THE VARIETY OF SUBSTRATUM TYPES

Knysna has an interesting geological history. Apparently the coastal plain across which the river runs has undergone many changes in level relative to the sea. During the Pleistocene it was submerged and the sea lapped at the Outeniqua Mountains which are now twenty miles inland. During the subsequent period of elevation the young rivers cut deeply into the coastal plain so that the latter is now transected by a whole series of deep gorges (Fig. 1). Elevation must have continued until the coastal plain was much higher than it is at present, for the bedrock below Knysna Estuary is about 100 feet below sea level.

A period of subsidence followed and the drowned valley which now forms Knysna Estuary started to fill with sediments. The present height of the coastal plain is about 200 feet. Its seaward edge is a steep cliff, and when one enters Knysna Estuary from the



Fig. 1. Knysna Estuary (Photo: South African Railways).

sea one passes through a narrow channel between two impressive rocky headlands. Then the estuary suddenly widens into a broad lagoon with low-lying banks of sandy mud. Farther up, the banks become steeper, but the tidal flats become more and more muddy with the main channel winding through them. Twelve miles from the mouth is the head of the estuary at the Old Drift where there is a series of rapids and sandy pools. Thereafter the banks close in and the river runs through a deep rocky gorge.

As this description suggests, there is a wide range of substratum types along the estuary: rocky banks and clean sand at the mouth, sandy mud in the lagoon, soft mud in the upper reaches, and coarse sand and rock at the head of the estuary. Also, rocky road embankments and piers abut the channel in many places. Each substratum type has its own characteristic fauna. About one-third of the Knysna fauna is associated with rocks, and in particular with the rocks at the mouth which are not covered by a layer of silt. Most of the other species prefer sandy mud, but some are confined to soft mud or clean sand. When one compares the variety of the Knysna fauna with the restricted number of species in estuaries which lack rocks at the mouth or muddy sandbanks farther up, the importance of a broad range of substratum types becomes very obvious.

THE SIGNIFICANCE OF THE OPEN MOUTH

Knysna has a deep mouth which is permanently open throughout the year. This has two important effects; the first concerns wave action and the second the tidal range.

Waves with an amplitude up to two feet penetrate the mouth and there is a continual surge on the rocky shores between the headlands. This is sufficient to prevent the deposition of silt, and there is a fairly good algal growth on the rocks and a variety of halophytic angiosperms on the mud banks. Many seashore animals also extend into the mouth of the estuary and then disappear where the lagoon widens and the strength of the waves is dispersed.

The effect of the tidal range is not appreciated until one visits a blind estuary, where the water level

becomes static as soon as the bar closes. Hermanus Estuary, described by Scott *et al.* (1952), is a good example, for it maintains a normal salinity gradient, and the changes which occur when the bar closes in spring cannot be ascribed to this factor. Yet many species die and others are stunted. The shore fauna becomes restricted to a narrow band at the air-water interface. Burrowing forms, in particular, disappear, with the notable exception of *Callianassa kraussii*, the sand prawn. When one digs into the sandy mud at the water's edge, the black deoxidized layer is found just below the surface and deeper digging often produces a smell of H₂S. This suggests that the rise and fall of the tides is one of the main methods whereby oxygen is carried to subsurface levels (Brafield, 1964). When the bar closes and the water level is stabilized, many burrowing forms cannot survive. *Callianassa* maintains very vigorous respiratory currents, and the sandy walls of its burrow are never black and deoxidized. Work on the oxygen tolerance of this species is now in progress.

The tidal range has another important effect. As the water of a falling tide seeps into the porous sand, any plankton or suspended organic matter it contains must be caught on the surface like a precipitate on a filter paper. The wet sand banks at low tide must, therefore, be covered by a layer of food, and they provide a rich feeding ground for detritus feeders which form the bulk of an estuarine fauna.

SEA TEMPERATURES

Stephenson (1944) and Ekman (1953) have discussed the distribution of marine fauna along the coasts of southern Africa on the basis of sea temperature. The figures used by Ekman are too high, because they are based on the temperature of the Agulhas Current which runs along the edge of the continental shelf. The neritic water which bathes the coasts and enters the estuaries is somewhat cooler. Thus, the surface water of the Mozambique Current is about 26° C. off Lourenco Marques, while the in-shore temperatures fall to 20° C. As Macnae and Kalk (1958) have shown, this is the southern limit of coral reefs and many other species from the tropical Indian Ocean.

Temperatures along the coasts of Natal and Transkei vary between 18° and 25° C., and the fauna is sub-tropical, with individual corals on the shore and a few mangroves in the estuaries. Knysna Estuary opens onto the south coast of the Cape Province where the sea temperature varies between 15° and 20° C., and the marine fauna has been termed warm temperate by both Stephenson and Ekman. To complete the picture, it may be mentioned that the whole of the west coast from Cape Point in the south to Cape Frio in the north is bathed by the cold Benguela Current, with coastal temperatures between 12° and 15° C. The marine fauna is cold temperate.

As usual, the diversity of the marine fauna is related to the sea temperature. There is a wealth of species along the tropical shores and relatively few

on the cold shores. Temperatures in estuaries vary more widely than they do on the open shore, but the number of species in estuaries seems to vary in the same way as do the marine ones. It is difficult to obtain reliable figures for comparison, for the richness of an estuarine fauna depends on many factors other than temperature, and the number of species recorded depends on the intensity of collecting which is seldom the same in different estuaries. For this reason, only striking differences are worth discussion. With these reservations the figures from three similar estuaries may be compared. The first is Morumbene Estuary on the tropical coast of Mozambique: 470 species have been recorded, including 66 polychaetes, 67 crabs, and 115 fishes. The second is Knysna Estuary on the warm temperate coast of South Africa: 350 species have been recorded, including 69 polychaetes, 12 crabs, and 40 fishes. The third is the Olifants Estuary on the cold temperate coast of South Africa: 53 species have been recorded, including 10 polychaetes, 3 crabs, and 9 fishes.

The first point of interest is that the composition by taxonomic groups changes markedly. There are proportionately far more crabs and fishes in the tropical estuary than in the colder ones. It is suspected that there are similar differences between the other taxonomic groups, but further collections are necessary before the figures may be regarded as reliable.

The second point is the very great difference between the total fauna of Olifants Estuary on the cold Atlantic coast and the warm or tropical estuaries on the south and east coasts. There is no doubt at all that these differences are valid, because the Olifants is the richest of all the estuaries on the cold Atlantic coast. It was suspected that there would be a reduction in the number of species here in conformity with the reduction of seashore species, but it was not expected that the reduction would be so marked. Brown (1959) has discussed possible reasons for the virtual absence of any estuarine fauna in the estuary of the Orange River farther north on the Atlantic coast, but none of his explanations cover all of these estuaries. The only environmental factor they all share is that the rivers are all warm and they all open into a cold sea, but it is hard to believe that this is the only factor at work.

The foregoing is an attempt to evaluate what factors are responsible for the richness or poverty of an estuarine fauna. Taking Knysna as an example of an average estuary it is suggested that the following are the controlling factors:

1. The climate, particularly the rainfall, and its seasonal changes, which determine the salinity regime
2. The amount of erosion in the drainage basin, which determines the amount of silting and hence the richness of the aquatic vegetation.
3. The geology of the estuary basin and the variety of substrata in the estuary.
4. The width and permanence of the estuary mouth, which affects the tidal range and the strength of wave action in the estuary.

5. The sea temperature, which determines the variety of marine species which may colonize the estuary.

THE ORIGIN AND DISTRIBUTION OF THE FAUNA

The fauna of an estuary is derived partly from the river and partly from the sea, and it is common practice to separate the different faunistic components by their salinity tolerance. In an earlier paper, Day (1951) recognized five components:

1. The freshwater component comprising a few salt-tolerant species derived from the river. These are found in waters of low salinity.
2. The stenohaline marine component, restricted to water of high salinity near the mouth of the estuary.
3. The euryhaline marine component, extending from the sea throughout the estuary.
4. The estuarine component which has evolved from marine forms but is now restricted to estuaries and is never found in the sea.

5. The migratory component, which includes a variety of active forms such as birds, fish, prawns, and cephalopods which move in and out of the estuary on feeding and spawning migrations.

These five components stress the great importance of salinity, and there is a tendency among researchers to regard salinity as the only important factor in determining the origin of an estuarine fauna. But this is certainly not the case. Work in Durban by Day and Morgans (1956) showed that in this landlocked bay where there is no reduction in salinity from the normal seawater range, there are many species which are characteristic of estuaries. These findings were confirmed by Day (1959) working on Langebaan Lagoon, another sheltered bay with no reduction in salinity. It has become evident that many so-called estuarine species are really calm-water species, and that the ability to survive in sheltered waters is just as important as tolerance to reduced salinity in determining an estuarine population. Bearing these points in mind, we may now examine the composition and distribution of the Knysna fauna to see how the two factors interact.

In work of this sort it is most convenient to deal with the benthic fauna which is easily surveyed and assigned to definite localities, but there is every indication that the findings derived from the benthic fauna are applicable both to fishes and other nekton and to the plankton which is now being investigated.

Since 1952, when Knysna was first surveyed, we have returned to this estuary many times and have greatly increased our knowledge of the fauna. Not only have we found many more species and gained a better knowledge of their distribution within the estuary, but we have also determined their distribution in other estuaries, bays, open shores, and in dredgings. We have culled the whole South African literature for records, and in this way we are able to assign a faunistic category to each species. It is the analysis of these faunistic categories that provides the basic data set out in Table I.

Table 1. Distribution of faunistic components along Knysna Estuary.

	Mouth	Lagoon	Middle reaches	Head	Total species
Salinity range	34.5 - 35.7%	29.1 - 34.8%	18.9 - 26.5%	1.1 - 14.0%	
Fresh water	0	0	0	7 = 18.7%	7 = 2.3%
Estuarine only	3 = 1.7%	20 = 10.0%	12 = 18.7%	12 = 36.4%	27 = 8.6%
Euryhaline and marine	80 = 44.6%	108 = 54.2%	46 = 71.9%	14 = 42.4%	137 = 44.1%
Stenohaline marine	96 = 53.7%	71 = 35.8%	6 = 9.4%	0	139 = 45.0%
Total species	179	199	64	33	310

The last row of Table 1 shows the number of species recorded in each section of the estuary. The mouth and lagoon have rich and diverse faunas while the upper reaches have less and the head of the estuary has a poor and restricted fauna. This pattern is common to all normal estuaries.

The last column shows a total of 310 species recorded from the whole estuary and the relative weight provided by each faunistic component. The distribution of each component may now be discussed.

The *freshwater component* is very small, comprising only seven species or 2.3 percent of the total fauna. It includes six insects and one small gastropod, and it will be noted that all of them are restricted to the head of the estuary where the salinity seldom rises above 5%, and is usually less.

The *estuarine component*, those species which occur in estuaries but have never been found in the sea, includes 27 species or 8.6 percent of the total fauna. It shows what a small proportion of an estuarine fauna is truly estuarine. Most of the animals are small crustaceans and there are very few annelids or molluscs. While this component extends along the full length of the estuary it will be noted that it becomes progressively more important higher up the estuary and forms 36.4 percent of the small fauna at the head of the estuary.

The *euryhaline marine component* includes those species which have been recorded from the sea and from other estuaries besides Knysna. There is a total of 137 species, making up 44.1 percent of the total fauna. It is slightly less important than the marine component at the mouth, but along the rest of the estuary it is the most important component of the fauna.

Table 2. Tolerance of euryhaline marine component to wave action.

	Restricted to exposed seashores	Present on sheltered seashores	Total species
Restricted to estuary mouth			
mouth	11 = 8%	12 = 8.8%	23 = 16.8%
Extending farther up estuary			
19 = 13.8%	95 = 69.2%	114 = 83.2%	
Totals	30 = 21.8%	107 = 78.2%	137 = 100%

The *stenohaline marine component* includes those species which are known from the sea but have never been recorded in any other estuary except Knysna. Knysna records have been excluded from consideration when deciding whether a species should be included in either the euryhaline marine or the stenohaline marine category, since this estuary is the subject of the analysis. Probably some of the "stenohaline marine" species will later be found in other estuaries and they will then be transferred to the "euryhaline marine" component, but in the meantime it is better to leave the figures as they stand.

The stenohaline marine component as defined here includes 139 species or 45 percent of the total fauna. It is the most important component at the mouth of the estuary, but is reduced upstream and is completely absent from the head of the estuary.

THE IMPORTANCE OF SALINITY AND WAVE ACTION

It is not easy to determine the independent effects of salinity and shelter on the distribution of an estuarine fauna. At the mouth there is a high salinity and strong wave action; inside the estuary there is a reduced salinity and no wave action, and the observed differences in the fauna may be ascribed to either factor.

One possible way of disentangling the effects of these two environmental factors is by comparing the distribution within an estuary of those species which are restricted to surf-beaten shores with those which occur in sheltered bays. Table 2 is an analysis of the euryhaline marine component and Table 3 is a similar analysis of the stenohaline marine component.

It will be seen that only 21.8 percent of the eury-

Table 3. Tolerance of stenohaline marine component to wave action.

	Restricted to exposed seashores	Present on sheltered seashores	Total species
Restricted to estuary mouth			
mouth	34 = 24.3%	37 = 26.6%	71 = 51%
Extending farther up estuary			
20 = 14.4%	48 = 34.5%	68 = 49%	
Totals	54 = 38.9%	85 = 61.1%	139 = 100%

haline component is restricted to surf shores, as compared with 78.2 percent which is not restricted and extends into calm bays; 83.2 percent of the euryhaline component extends into the calm parts of the estuary. It is evident that the bulk of the euryhaline species are also calm-water species.

An analysis of Table 3 does not show any very strong contrasts. In general the stenohaline species which are characteristic of surf-beaten shores show a greater tendency to be limited to the mouth of the estuary (24.5 vs 14.4 percent), while those which extend into calm bays are more liable to extend up the estuary (26.6 vs 34.5 percent). A comparison of Table 3 with Table 2 shows that the two components differ in their tolerance of wave action or the lack of it. In particular, only 16.8 percent of the euryhaline marine component is restricted to the mouth of the estuary as compared with 51 percent of the steno-haline marine component.

When one examines the distribution of individual species further interesting points appear. Like all estuaries, Knysna is mainly populated by mud dwellers, for the few rocky banks within the estuary have a very poor fauna. The banks of sandy mud are rich, and one might presume that the component species have been derived from the sandy shores along the coast. But this is not the case. Exposed sandy beaches have a very poor fauna, and hardly any of the species found there penetrate farther than the mouth of the estuary. Typical species like *Bullia rhodostoma* and *Dicarax serra* are absent and in their place are *Bullia annulata*, *Bullia laevissima*, *Tivela compressa*, and *Mactra adansonii*, which are characteristic of dredgings in the open sea. As has been shown, the fauna found on the sandbanks of calm landlocked bays form the bulk of an estuarine population, with burrowing forms such as *Callianassa kraussii*, *Upogebia africana*, *Arenicola loveni*, and *Marphysa sanguinea*, and surface forms such as *Cleistostoma edwardsii*, *Hymenosoma orbiculare*, and *Nassa kraussiana*. The rocky shores at the mouth of the estuary have a fauna similar in composition to that of an exposed reef, but poorer in species. Barnacles such as *Octomeris angulosa*, which depend on the waves to produce a feeding current, disappear early, and so do a variety of herbivorous gastropods such as limpets (*Patella* spp.) and periwinkles (*Oxystele* and *Turbo*) as soon as their encrusting algal food is smothered in silt. It would appear that the importance of wave action to an animal is that it provides a food current for lazy filter feeders, or keeps rocks clean for the growth of algal food. It is suggested that oxygenation effects are indirect. It has been noticed that on wave-washed rocky shores the lower surfaces of stones are clean and free from encrusting silt. Stones sufficiently heavy to remain stable carry a rich cryptic fauna. On very calm shores similar stones are embedded in black and obviously deoxygenated silt. Such stones have a limited fauna of worms such as *Cirriformia tentaculata* and *Capitella capitata* which tolerates low oxygen concentrations.

VERTICAL ZONATION AND ESTUARINE SHORES

The vertical zonation of the impoverished fauna of the rocky shores of Knysna Estuary does not call for comment. It is basically similar to that on open seashores, and further details will be found in Day *et al.* (1952). Zonation on soft substrata, however, is much more complex and the picture changes along the length of the estuary. This is illustrated by four transects.

The Knysna River issues from a steep gorge at Charlesford Farm. At each high tide, the water at that point becomes saline, so that it represents the head of the estuary. As the tide falls, the bed of the river is revealed as a series of sandy pools linked by stony runs and rapids, the last of which is known as the Old Drift. Figure 2 is a surveyed transect immediately below this point.

The outflowing current has cut so deeply into the soft alluvium of the flood plain that the banks of the estuary are almost vertical down to the low tide mark. Here the contours flatten out and the bed of the estuary is a flat bank of coarse sand. The steep banks are covered with salt marsh vegetation which keeps the surface moist. Marsh crabs (*Sesarma*) and talitrid amphipods (*Parorchestia*), both capable of aerial respiration, are fairly common, but do not extend out onto the open sands. The coarse sands are very porous and at low tide the water table falls eight or ten inches below the surface. As a result, the surface is dry and barren, and the burrows of the sand prawn, *Callianassa kraussii*, extend down well below the permanent water level.

In the upper reaches the flow of the river is reduced, and the tidal currents are weak except during the middle of the ebb. Soft silt is deposited during the slack period of high tide. This has formed extensive flats which are now overgrown with halophytic plants, particularly the sedge, *Juncus kraussii*, whose roots consolidate the soil. The fine-grained compacted mud is not very porous and drainage is over the surface. A network of minor seepage channels meanders through the muddy salt marsh to the main estuary channel, where the ebb current has cut a vertical step at the lower edge of *Juncus* to form a salting cliff. This is continually eroding. Towards the low tide mark the currents are slower, and in consequence the shore flattens out. A typical transect through these upper reaches is reproduced in Figure 3.

The salt marsh near the high tide mark has a scanty epifauna similar to that at the head of the estuary. The same marsh crab (*Sesarma*) makes most of its burrows in the eroding salting cliff. During the day it feeds in the shelter of the *Juncus* near high tide, but at night it feeds at low tide levels, spooning up the surface silt with its chelae, sucking out the detritus, and discarding the silt as pseudo-faecal pellets. In tropical estuaries *Uca* and *Dotilla* have similar habits.

The rest of the fauna is found near the low tide

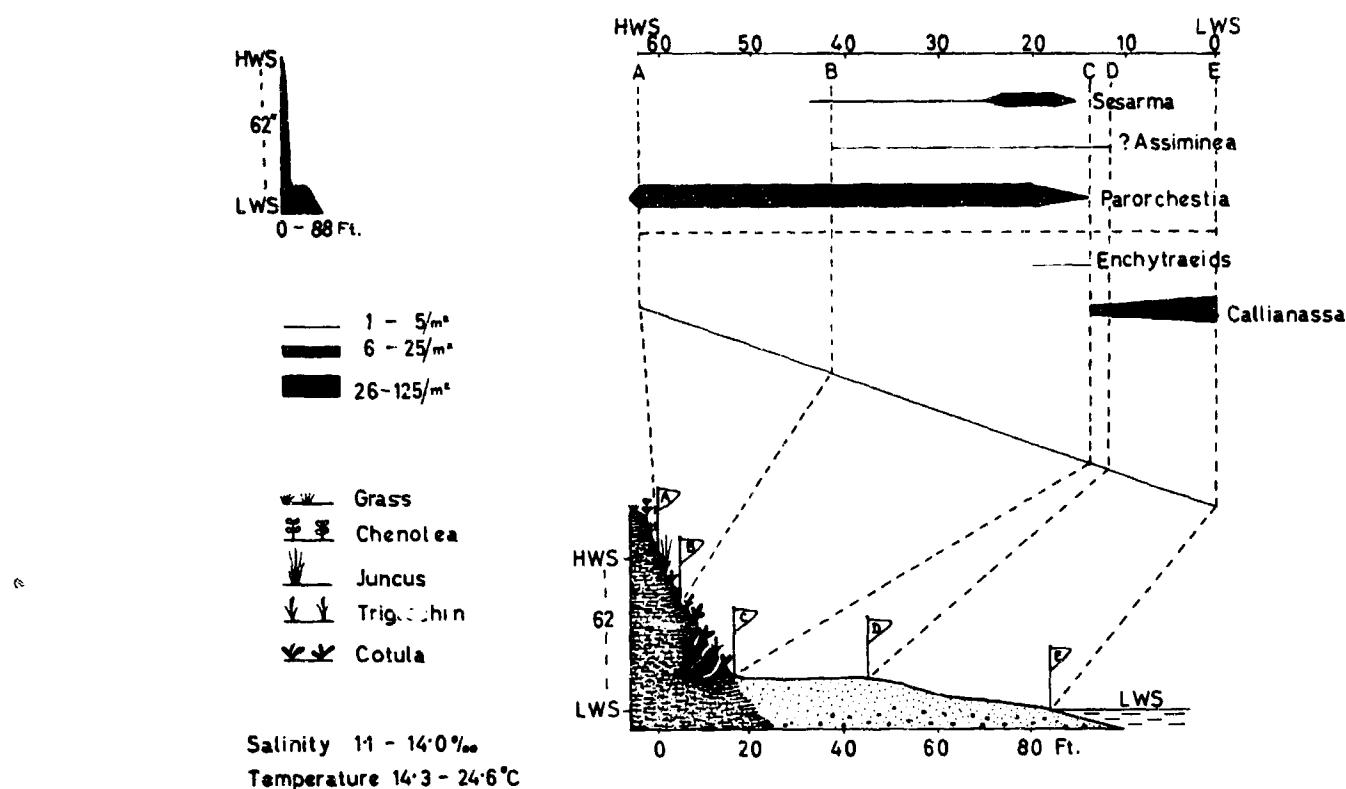


Fig. 2. Transect at Old Drift, head of the Knysna Estuary.

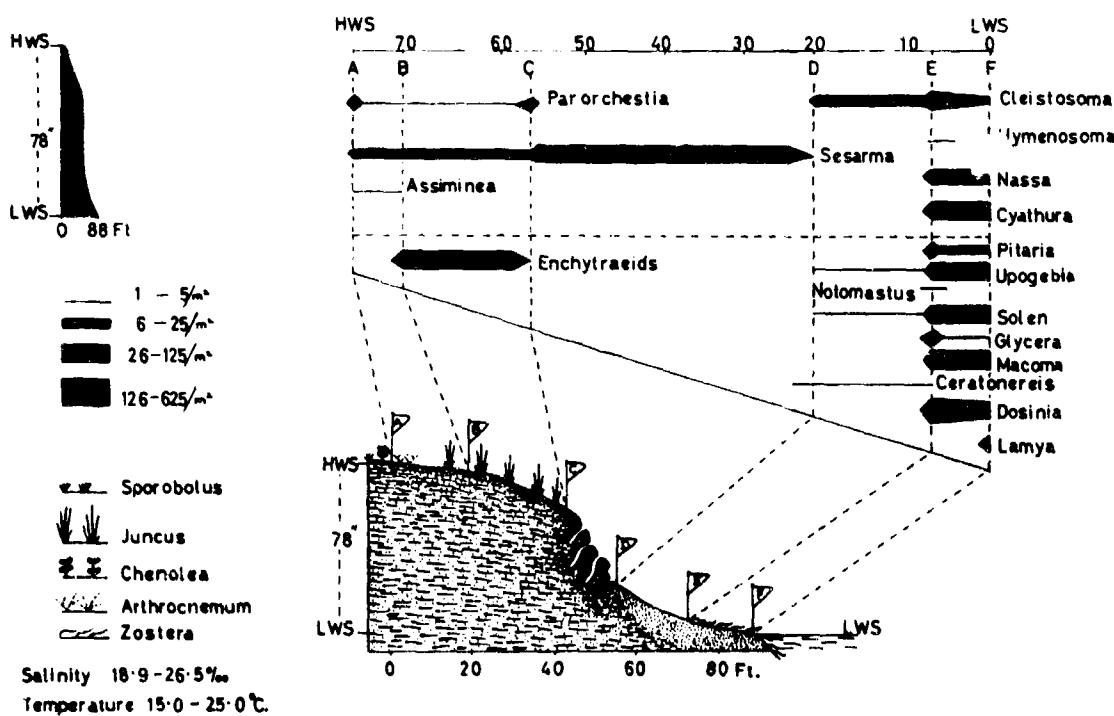


Fig. 3. Transect at Ashford, Knysna Estuary.

mark, where the water table is always at the surface due to seepage from higher levels. The substratum is mud with a thin covering of *Zostera*. The fauna is rather more diverse than that at the head of the estuary, and includes surface forms such as the crab, *Cleistostoma edwardsii*, the whelk, *Nassa kraussiana*, and a fair number of burrowing types—the mud prawn, *Upogebia africana*, bivalves such as *Solen capensis*, *Dosinia hepatica*, and *Macoma littoralis*, and a few polychaete worms (*Ceratonereis erythraeensis*). The most notable feature in this vertical zonation is the gap or bare zone at mid-tide levels between the air-breathing epifauna of the high tidal flats and the aquatic-breathing fauna at low tide.

Below Ashford the estuary widens out into a lagoon; along the edges of the main channel the salting cliff gradually disappears and the shore becomes wider and more evenly sloping. The substratum is rather more sandy and the whole shore is covered with vegetation from above the high tide mark to below the low tide. At the highest levels there are only a few tufts of *Juncus* but *Arthrocnemum*, *Chenolea*, and the sea thrift, *Limonium*, form a fairly dense carpet. Farther down this is replaced by the rice grass, *Puccinella*, and from mid-tide this is replaced by *Zostera*, which is at first scanty but later becomes more luxuriant and mixed with patches of *Halophila*. The surface is always moist under cover of the vegetation and from mid-tide down the free water table is within half an inch of the surface. A transect across the shore near the rail bridge which shows these conditions is reproduced in Figure 4.

In comparison with the transect at Ashford it will be noted that the fauna is much richer and more evenly spread over the width of the shore. Among surface forms the crabs, amphipods, and periwinkles capable of aerial respiration extend farther up so that there is no mid-tide gap such as was seen at Ashford. Among burrowing forms many now extend well up towards mid-tide and there is not the sharp cutoff that was seen seven inches above the low tide mark at Ashford. Vertical distribution is far more varied, with each species increasing in abundance at its optimum level. There are no obvious changes in substratum type or plant cover, and it is presumed that the main factor which controls vertical distribution is the tidal level.

Towards the mouth the tidal currents increase in the main channel and the swells coming from the open sea are now appreciable. The intertidal banks are very broad and distinctly more sandy than upstream. There is still an abundance of mud and a luxuriant salt marsh vegetation in the backwaters around Leisure Isle, but the shore along the main channel is mainly bare sand with scattered patches of *Arthrocnemum* or *Puccinella*.

An offshore sandbank separates Leisure Isle from the main channel, and between the two there is a waterlogged area of sandy mud which is just uncovered at low tide. It is known as the "false channel". The transect illustrated in Figure 5 runs from the point of Leisure Isle across the false channel and over the offshore sandbank to the main channel. It is an extremely wide transect of 1,450 feet across two

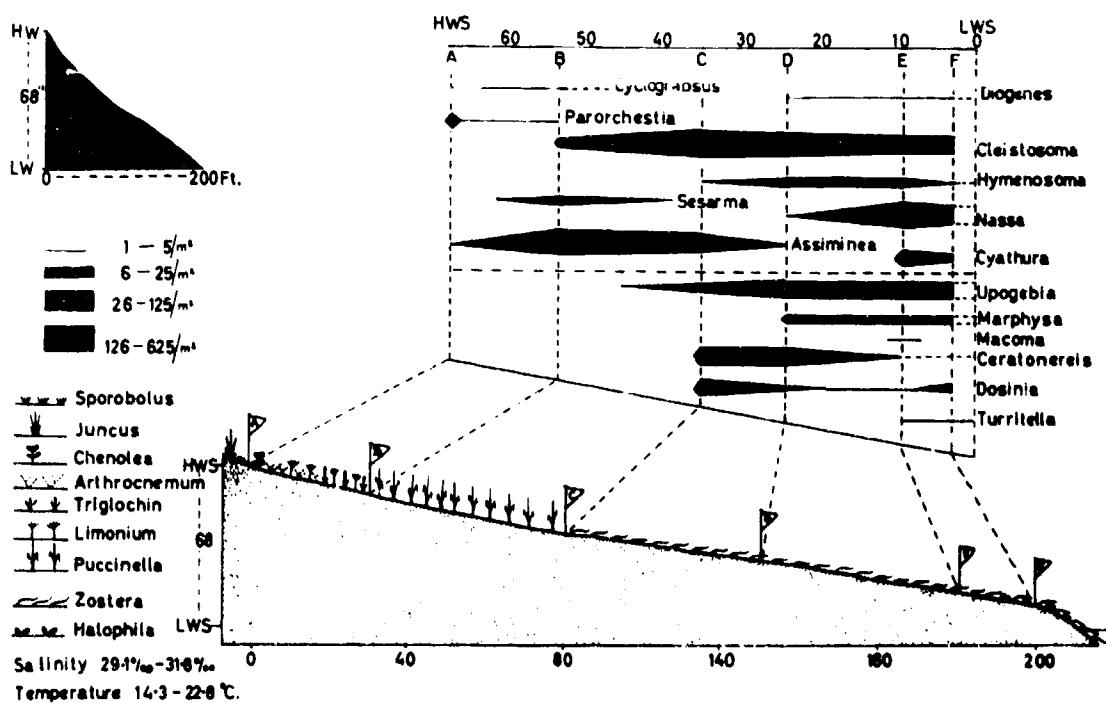


Fig. 4. Transect at Rail Bridge, Knysna Estuary.

different types of substrata, muddy sand from Leisure Isle to the false channel and clean unconsolidated sand from there to the main channel. Each has its own distinctive fauna. Only the vertical zonation across the muddy sand is shown. It will be evident that the upper level of the shore is relatively steep and sandy, and in the section the free water table is well below the surface at the time of low tide. Thus it is over 24 inches at stake A, 15.5 inches at stake B and eight inches at stake C. From there on, seepage from the porous sand at higher levels maintains the water table at or just below the surface, and from stake E (30 inches above low water springs, or LWS) every depression has a permanent pool of water. The vegetation on the upper shore is scanty. There is lawn grass (*Sporobolus virginicus*) at and above high water springs, but below this there are mere patches of salt marsh. The transect was purposely laid across a patch of *Puccinella*, since this provided support of *Littorina knysnaensis* and shelter for *Cyclograpus punctatus* (not shown in Fig. 5). *Zostera* appeared at stake E and continued down to LWS at stake L.

The interesting features shown by this transect include the restriction of talitrid amphipods (*Parorchestia*) to the decaying vegetation at the high tide drift line and the absence of any except air-breathing surface forms from the upper levels. Almost all in-

fauna is restricted to the levels where the water table reaches the surface, except *Upogebia*, which makes deep burrows, and *Ceratonereis*, the depth of whose burrows is unknown. It is surprising to find it so high up the shore both here and at Ashford.

The upper limit at which an animal can live on the shore is mainly determined by an animal's ability to resist desiccation. On a smoothly sloping rocky shore where the rocks dry out at low tide, the animals live in well-defined belts related to tidal levels, though the bands tend to be tilted upward in shaded areas or in situations where dense algal growth reduces evaporation. On a sandy or muddy shore there are many complicating factors. The animal may live on the surface or in a burrow; parts of the shore may be kept moist by dense vegetation; or the substratum may be porous so that the water sinks as the tide falls to seep out at a lower level, particularly where there is a sudden drop in the contour. For an animal living on the shore the most important feature is the depth of the water table, however this may be determined. Only when the whole shore is uniform from the high tide mark to the low tide mark will the upper limits of distribution be related directly to tidal levels. This has been illustrated during a description of four transects, and the variability of vertical distribution is summarized in Table 4.

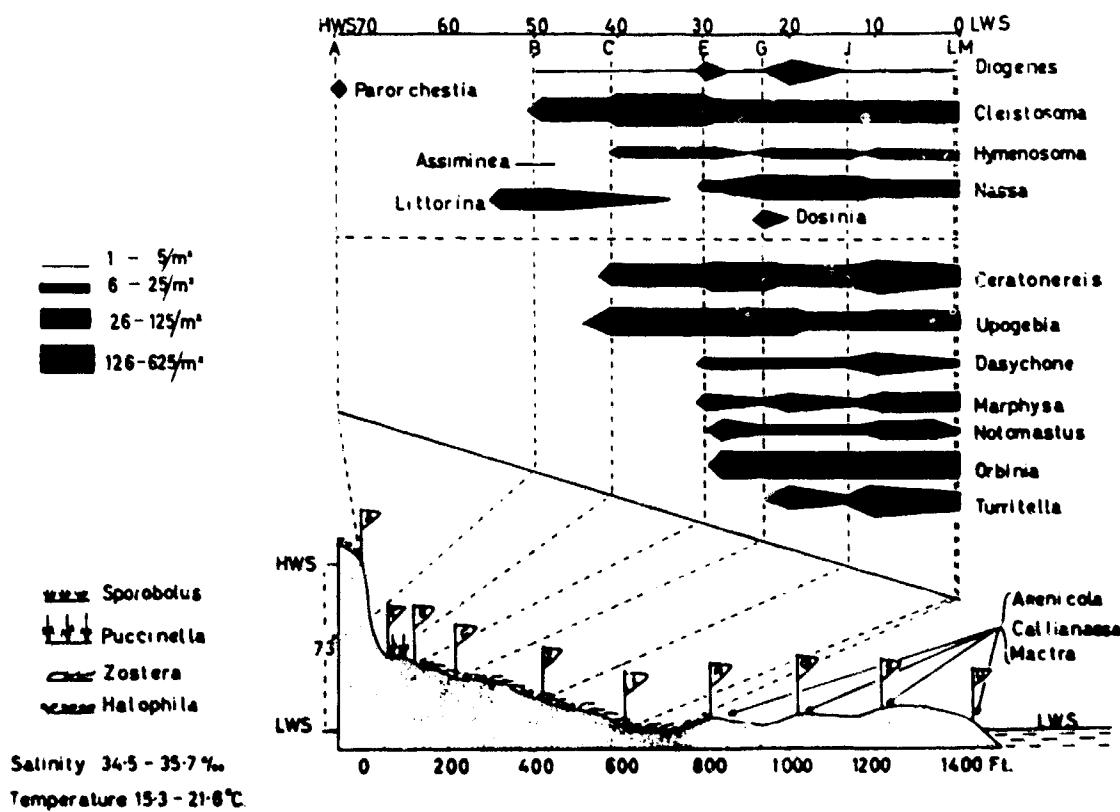


Fig. 5. Transect at Leisure Isle, Knysna Estuary.

Table 4. Heights in inches above low water springs of the upper limits of common members of the epifauna and the infauna on three transects across muddy sand.

Species	Leisure Isle	Rail Bridge	Ashford
EPIFAUNA			
<i>Cleistostoma edwardsii</i>	50	53	22
<i>Hymenosoma orbiculare</i>	40	33	7
<i>Nassa kraussiana</i>	30	23	7
INFANIA			
<i>Upogebia africana</i>	43	43	22
<i>Ceratonereis erythracensis</i>	40	33	23
<i>Dosinia hepatica</i>	23	33	7

TROPHIC RELATIONS BETWEEN THE COMMON SPECIES IN KNYSNA ESTUARY

PLANKTON

Unpublished work by John Grindley shows that the mouth of Knysna Estuary is inhabited by neritic plankton and that farther up there are a number of small estuarine species. Among the copepods, genera such as *Pseudodiaptomus*, *Acartia*, and *Paracalanus* are dominant, but no dense plankton swarms have been found and it is suggested that plankton is not a major source of food in the estuary. By the same token, there are relatively few plankton feeders. The mussel, *Perna perna*, the barnacle, *Tetraclita serrata*, and the oyster, *Crassostrea margaritacea*, are the main ones at the mouth and the mud mussel, *Lamyia capensis*, is the dominant plankton feeder in the upper mud channels; it is suspected that all of these depend on detritus to some extent. Among fishes the only common species are the mullet, *Hyporhamphus knysnaensis*, and the wintebait, *Atherina breviceps*, but these are not abundant.

ATTACHED PLANTS

Knysna has a luxuriant aquatic vegetation from high water of spring tide down to low water springs and below. Most of the plants are angiosperms, but there is a fair amount of *Enteromorpha* and *Ulva* between tide marks and loose *Zostera* below.

Relatively few animals feed directly on the macroscopic vegetation, but periwinkles (*Gibbula* sp.) do and certain crabs and fishes crop living plants when hungry. Thus the crab, *Sesarma catenata*, has been observed to feed at times on living *Arthrocnemum* and the stomachs of juveniles of the fish, *Rhabdosargus globiceps*, are occasionally packed with *Zostera*. Probably more species feed on minute filamentous algae or the film of attached unicellular forms which discolors stable sand flats. *Littorina knysnaensis*, *Oxystele variegata*, and *Siphonaria* spp. feed in this way on rocky shores and *Assiminea* spp. and *Bursatella leachii* find similar food on the surface of sand banks.

DETITUTUS FEEDERS

The decomposition products of the plants plus the dead or stranded plankton form the basic source of food in the estuary. It may be ingested while drifting or lying on the surface or extracted from the sediments. Deposit feeders include polychaetes such as *Thelepus plagiostoma*, amphipods such as *Parorchestes rectipalma* and *Melita zeylanica*, shrimp (*Palaeomon pacificus*), prawns (*Upogebia africana*), crabs (*Cleistostoma edwardsii* and *Sesarma catenata*), bivalves (*Dosinia hepatica*), and the fish *Mugil* spp. Mud swallowers include such polychaetes as *Orbiniangrapaequensis*, *Notomastus fauvillii*, and *Arenicola lorenzi*; and sand sifters include the prawn, *Calianassa kraussii*, as well as numerous minute animals.

BENTHIC CARNIVORES

A number of predaceous polychaetes such as *Glycera concolor*, and the giant nemertine, *Gorgonorrhynchus* sp., feed on *Upogebia africana* and *Morphysa sanguinea*. There are also numerous whelks such as *Thais dubia* which feeds on *Littorina knysnaensis* and barnacles on rocky shores, and *Natica genuana* on various bivalves on sandy shores. Possibly the ubiquitous *Nassa kraussiana* belongs to this group, but it must feed on very minute animals for it occurs in enormous numbers crawling over the fronds of *Zostera*.

PREDACEOUS FISHES

The fishes usually form the last link in the food chain, and examination of stomach contents shows that their preferred food changes with age. Merely the main outlines can be given here. *Rhabdosargus globiceps*, or white stumpnose, is one of the commonest bream-like fishes found along the coasts of the Cape Province. A study by Talbot (1955) and the records in the Zoology Department of the University of Cape Town are the sources of the present summary.

In the adult stage *R. globiceps* is about 25 cm long and weighs about 3 lb. It lives in the sea and feeds on mussels, small crustaceans such as amphipods, and a variety of other foods from submerged reefs. This part of its life cycle requires further study. It breeds in November and December and juveniles about 20 mm long shelter in rock pools along the coast or enter estuaries. Up to this stage it feeds on plankton. When it is 5 cm long it starts feeding on the epifauna of the benthos including amphipods and isopods (*Melita zeylanica* and *Exosphaeroma hylecoetes*). As its molariform teeth develop it is able to take shelled molluscs (*Assiminea* and *Nassarius kraussiana*) and at times its stomach is filled with algae, particularly *Enteromorpha*. It grows rapidly and at 10 cm length it takes larger crustaceans such as *Hymenosoma* and *Upogebia* and small mussels (*Lamyia capensis*). By the end of a year it has reached a length of about 15 cm and its gonads are beginning to develop. It now leaves the estuary and does not return. It is an ex-

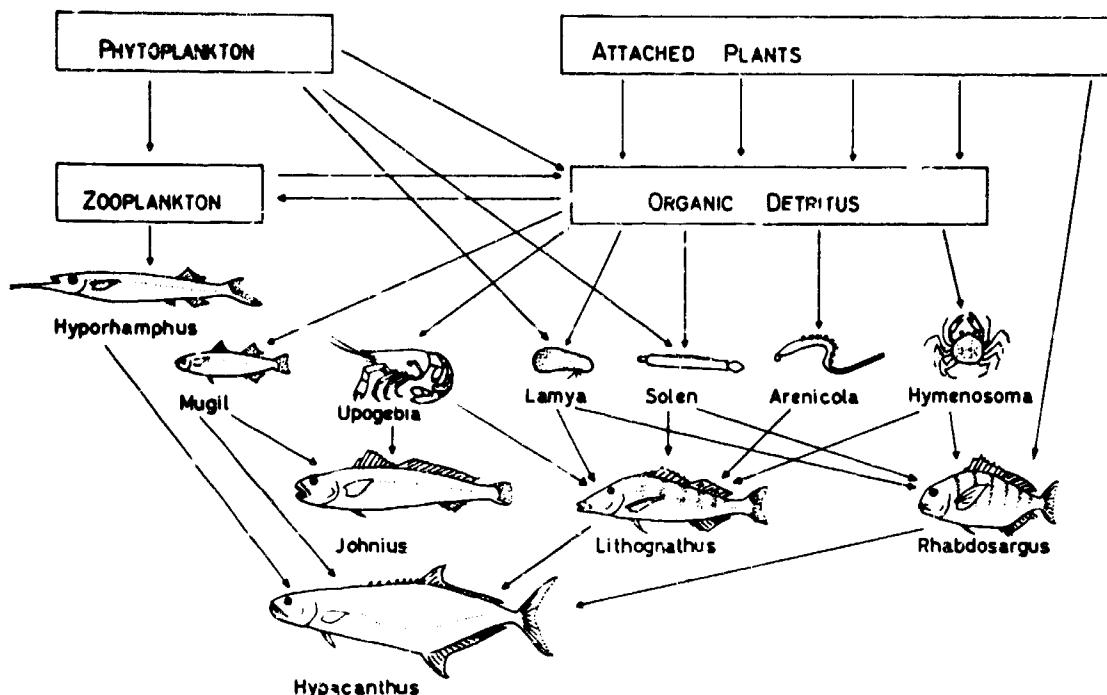


Fig. 6. Trophic relations within Knysna Estuary.

ample of one of the many fishes which breed in the sea, but shelter in estuaries as juveniles.

Lithognathus lithognathus, the white steenbras, reaches a weight of about 30 lb and a length of about three feet. Its biology has never been studied in detail, though it is a common game fish all around the Cape Province and is of some importance to commercial fishermen as well. It breeds in the sea and the juveniles enter estuaries at a length of 4 cm. At this stage they are still feeding on planktonic crustaceans, probably snapping up individual copepods, since they are not adapted for filter feeding. They shelter from predaceous fish in sandy shallows; the elongated snout and thickened lips are adapted to grubbing in the sand for polychaetes (*Orbiniella* and *Nephtys* sp.) and small crustaceans, particularly *Pontogeneleides* and *Urothoe*. As they grow they take larger food organisms and develop the capacity of blowing holes in the sand to feed on *Upogebia* and *Arenicola*. Adult *Lithognathus* are one of the main angling fishes in Cape estuaries but the roes are never ripe. For this reason it is presumed that they spawn in the sea and return to estuarine waters in the summer to feed.

Johnius hololepidotus, the kabeljauw or kob, reaches a weight of 150 lb and a length of six feet. Its biology has not been studied, though it is an important game fish and commonly taken by trawlers. Fingerlings are never found in estuaries or along the shore and it is concluded that spawning takes place in the sea in fairly deep water. A ripe female measuring 88.5 cm was trawled off Cape Infanta in 40 fathoms. Young kob appear in the estuaries when they are about 15 cm long. They feed on a variety of small

crustaceans, including mysids, shrimp, prawns (*Upogebia*), and crabs (*Hymenosoma*), but there is no evidence that they are adapted to feed on the infauna of muddy bottoms. Larger specimens of 30 cm or more become predaceous and, in addition to the larger crustaceans, they feed on cuttlefish (*Sepia*) and mullet (*Mugil* and *Liza* spp.). Adult kob extend the whole length of the estuary and are often taken in the upper reaches.

Hypacanthus amia, the leervis or garrick, extends from Natal to False Bay both in the sea and in estuaries. It reaches a weight of about 40 lb and is highly esteemed as a game fish. Its biology has not been studied in detail. Fish with ripe roes are not found in estuaries, so it presumably breeds in the sea, but small juveniles only 4 cm long do occur in estuaries. Even at this stage they are vicious predators and feed on shoals of postlarval mullet in the shallows. They extend into the upper reaches of the estuary and as adults they feed on all types of small fish, particularly mullet, halfbeaks (*Hyporhamphus*), and juvenile *Lithognathus* and *Rhabdosargus*. They are swift predators and form the final link in the food web.

Figure 6 summarizes the trophic relationships between the main elements of the Knysna biota. It is suggested that phytoplankton, zooplankton, and plankton feeders are of minor importance in the economy of the estuary. Macroscopic vegetation such as *Zostera*, *Entromorpha*, and *Ulva* provides food, while alive, for a few herbivores such as periwinkles and some fish. The main source of basic food in the estuary is organic detritus, which feeds most of the benthic fauna and a few important swimming forms such

as mullet. A variety of benthic carnivores feed on these in turn, but the ultimate consumers are predatory fish. Some of these are adapted to prey on burrowing invertebrates, some feed on the epifauna, and a few on fish. All of them leave the estuary to breed in the sea.

LITERATURE CITED

- BRAFIELD, A. E., 1964. The oxygen content of interstitial water in sandy shores. *J. Animal Ecol.*, 33 (1): 97-116.
- BROWN, A. C., 1959. The ecology of South African estuaries. Part IX: Notes on the estuary of the Orange River. *Trans. Roy. Soc. S. Africa*, 35(5):463-473.
- DAY, J. H., 1951. The ecology of South African estuaries. Part I: General considerations. *Trans. Roy. Soc. S. Africa*, 33:53-91.
- DAY, J. H., 1959. The biology of Langbaan Lagoon: a study of the effect of shelter from wave action. *Trans. Roy. Soc. S. Africa*, 35:475-547.
- DAY, J. H., and J. F. C. MORGANS, 1956. The ecology of South African estuaries. Part VII: The biology of Durban Bay. *Ann. Natal Mus.*, 13:259-312.
- DAY, J. H., N. A. H. MILLARD, and A. D. HARRISON, 1952. The ecology of South African estuaries. Part III: Knysna, a clear open estuary. *Trans. Roy. Soc. S. Africa*, 33:367-413.
- DAY, J. H., N. A. H. MILLARD, and G. J. BROEKHUYSEN, 1954. The ecology of South African estuaries. Part IV: The St. Lucia system. *Trans. Roy. Soc. S. Africa*, 34:129-156.
- EKMAN, S., 1953. *Zoogeography of the Sea*. Sidgwick and Jackson, London.
- MACNAE, W., and M. KALK, 1958. *A natural history of Inhaca Island, Mozambique*. Witwatersrand Univ., Johannesburg, Republic of South Africa.
- SCOTT, K. M. F., A. D. HARRISON, and W. MACNAE, 1952. The ecology of South African estuaries. Part II: The Klein River estuary, Hermanus. *Trans. Roy. Soc. S. Africa*, 33:283-331.
- STEPHENSON, T. A., 1944. The constitution of the intertidal fauna and flora of South Africa. Part II. *Ann. Natal Mus.*, 10:261-358.
- TALBOT, F. H., 1955. Notes on the biology of the white stumpyose, *Rhabdosargus globiceps* (Cuvier), and on the fish fauna of the Klein River estuary. *Trans. Roy. Soc. S. Africa*, 34:387-407.

Ecological Aspects of the Laguna Madre, A Hypersaline Estuary

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The Laguna Madre of Texas is a series of coastal lagoons, consisting of a long narrow outer lagoon separated from the Gulf of Mexico by Padre Island, and divided into northern and southern parts by extensive, barren flats, and an inner tributary, Baffin Bay, extending westward like an elbow from the lower part of the main Laguna (Fig. 1). Baffin Bay has a large branch, Alazan Bay, extending northward and somewhat parallel to the axis of the main Laguna. The main part of the Laguna Madre begins near the city of Corpus Christi at the southern part of Corpus Christi Bay and ends just south of Port Isabel. This is a distance of about 120 miles between latitudes 27°45' N and 26° N. The total area of this system of bays is slightly more than 600 square miles. The maximum depth in Baffin Bay is about 12 feet, but most of the Laguna is very shallow (Table 1).

The flats which divide the Laguna Madre into two parts extend from a few miles south of the confluence of Baffin Bay to just south of Mesquite Rincon (from about 27°10' N to 26°49' N). It is thought that this filling in has occurred within the last century, but this segmentation of a long narrow lagoon may be an equilibrium phenomenon inherent in the shape, so that the lagoon tends to segment at the nodes of oscillation. There was apparently considerable sanding over in this area during the 1919 hurricane. At the present time this area is covered by a few inches of water at times of high tides and strong winds; since the construction of the Intracoastal Waterway in 1949 the two parts of the Laguna have been connected by the channel. This does not appear to have much effect on the salinity exchange except during winter when highly saline water is moved into the southern Laguna by the action of northerns.

Another lagoon with similar characteristics and about the same size lies south of the Rio Grande in the Mexican state of Tamaulipas. The Laguna Madre de Tamaulipas extends from about 25°30' N to 23°30' N and has an area of about 1,000 square kilometers (Hildebrand, 1958).

The Laguna Madre lies in a region characterized as semiarid, with annual rainfall about 27 inches a year and evaporation about 21 inches; however, the rainfall average is skewed by the occasional heavy cloudbursts that may contribute as much as six inches of rain in a comparatively small area in a few hours. "Average" conditions are usually more arid than indicated by the climatological data. No streams of consequence flow into the Laguna Madre, and, until recently, the Laguna was closed off from the sea except across a sill at Corpus Christi Bay in the north and through Brazos Santiago Pass in the south. Salinities in excess of 80‰ were frequent, and in some years they exceeded 100‰. Extremely high salinities occurring during high summer water temperatures were associated with fish mortalities. Cloudbursts in the area would bring about abrupt reductions of surface salinity to as low as 2‰. In very cold winters there have been spectacular mass mortalities of fish in various parts of the Laguna Madre when low temperatures coincided with circumstances of wind and tide that made it impossible for fish to escape into the Gulf of Mexico. In spite of these environmental extremes, the Laguna Madre has been an important source of fish—contributing as much as 50 percent of the total catch from Texas coastal waters in some years.

On the basis of extensive sediment studies, Rusnak (1960) estimates that the Laguna Madre was formed about 5,000 years ago, and that hypersaline conditions have been prevalent for perhaps 4,000 years. However, it is obvious that Baffin Bay is the remnant of a former stream drainage, and the presence of old oyster shells, possibly from Indian middens, suggests less saline conditions in this part of the Laguna Madre system at some time in the past (Breuer, 1957). Recent preliminary sonoprobe studies of the area indicate a Pleistocene channel in Baffin Bay perhaps 60 to 80 feet below present sea level (Behrens, 1963). Conditions were apparently less saline in the not too remote past in the Mexican Laguna Madre; Hildebrand (1958) notes the presence of oyster shell deposits there which he suggests may have been accumulated at a time when the Rio Grande carried more water and entered the Gulf of Mexico in Tamaulipas instead of Texas.

In the more recent past various alterations of the physical conditions in the Laguna Madre have been brought about by the activities of man. There is a long history of deliberate attempts to alleviate salinity conditions by digging artificial channels across Padre Island. Efforts to construct an artificial pass have been conducted by the Texas Game and Fish Commission at the instigation of fishermen, primarily at the lower end of the northern part of the Laguna Madre, south of the junction with Baffin Bay. This pass, known as Yarborough Pass, has been dredged

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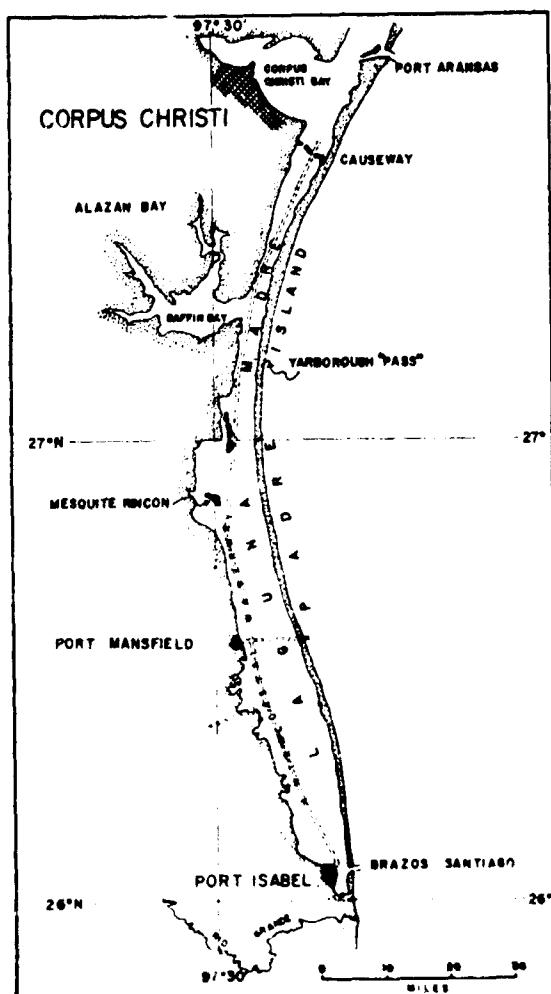


Fig. 1. The Laguna Madre of Texas. (Intracoastal Waterway not to scale.)

out several times, but has never materially reduced the salinity within the Laguna Madre. The pass was opened in 1941, 1942, and 1944, but quickly filled in again because there is no natural flow of water from the mainland to maintain it. In 1949 the Intracoastal Waterway, a channel about 125 feet wide and 12 feet deep, was completed along the entire length of the Laguna Madre. This ship canal has alleviated salinities somewhat, but this action has been offset to the north by the construction of a causeway from Corpus Christi to Padre Island. While the salinity exchange with Corpus Christi Bay has therefore been limited, the waterway has provided an escape channel for fish during high summer temperatures and salinities and during winter cold periods and mass mortalities have apparently been greatly reduced. The cold spell of 1962, however, caused as much loss to trout (*Cynoscion nebulosus*) as that of 1951, although only about a tenth as destructive to drum (*Pogonias cromis*) (E. G. Simmons, personal correspondence). During

the drought years of the late 1940's and early 1950's salinities increased and fishermen continued to agitate for an artificial pass; Yarborough Pass was reopened again in February, 1952. It remained open for about three weeks (Breuer, 1957).

The changes in the salinity regime of the northern part of the Laguna Madre, as a result of the construction of the waterway and the causeway, have been discussed by Simmons (1957). He noted that, in spite of the Intracoastal Waterway, salinities have at times been higher than they were before dredging just below the causeway because of the reduced exchange with Corpus Christi Bay. Simmons also observed that a "block" of high-salinity water tends to shift back and forth in the Laguna in the region of Baffin Bay during the summers according to wind direction without being completely exchanged with less saline waters to the north. As a result of the various improvements by man and the prolonged drought, it appeared that the upper eight miles of the Laguna could become dry land in a comparatively short time (Simmons, 1957).

The dry winter of 1963-1964 has resulted in salinities in excess of 40‰ and "red water" conditions in the upper Laguna Madre in the spring of 1964, and agitation for passes into the Gulf of Mexico has sprung up anew. A group of consulting engineers has proposed a plan which provides for two passes across Padre Island in the upper Laguna area, some channel dredging, and the removal of some of the spoil banks. The two passes and the channel would provide for a circulating system for control of salinity and would restore several square miles of habitat for fishes. It would provide not only for the circulation of water, but for the circulation of men and of fishermen in their boats. The total cost of this project is estimated at \$715 million. What the cost of maintenance may be is unknown, but the history of the Port Mansfield Pass suggests substantial annual costs. If the Laguna Madre is such a valuable recreational resource, it would probably be considerably less expensive to dig up the present spoil banks and convert the causeway separating the Laguna from Corpus Christi Bay to an open trestle bridge structure.

Warnings of the potential effect of a solid fill causeway were clearly voiced before it was built (Hedgpeth, 1947), but, since navigation would not be interfered with, the project was approved by the Corps of Engineers. It is obvious that remedial measures, if indeed they could remedy the situation, will cost

Table 1. Dimensions, Laguna Madre (from Ruskak, 1960).

	Northern	Baffin Bay	Southern	Total
Area (sq. mi.)	124	85	400	609
Area (water only)	120	75	270	475
Length (mi.)	50	15	55	120
Avg. width (mi.)	2.5	3.0	3.0	
Avg. depth (ft.)	2.5	5	2.5	

more than the projects which have exacerbated the original conditions.

Modifications by the activity of man have also occurred in the southern part of the Laguna Madre. A large, permanently jettied and protected pass has been cut across Padre Island to enable ships to enter Port Mansfield. This pass was completed in 1962 after a preliminary one failed to remain open. It is a smaller opening than the Brazos Santiago Pass opposite Port Isabel, and, except during strong north winds, the water flows northward from Port Isabel and out into the Gulf of Mexico through this pass. Salinities in the southern Laguna Madre are now "stabilized" nearer Gulf of Mexico values and the faunal assemblage is being altered by the invasion of species from the Gulf.

As a result of these changes, older data for temperature, salinity, and community assemblages are no longer indicative. Unfortunately, data are somewhat sporadically offered. Evidently the temperature-salinity characteristics of Laguna Madre waters have changed somewhat, primarily by the reduction of salinities in the lower Laguna and the increase of salinities in the upper Laguna by obstructions to water exchange. Baffin Bay does not seem to have been altered much by the recent changes, but the data presented by Breuer (1957) are summarized in terms of stations rather than months and cannot be compared with other data—the original data are not available. Various temperature and salinity conditions in the Laguna Madre are summarized in Figure 2.

Active studies of biological problems in the Laguna Madre have been carried out by various investigators since the 1940's. The initial reconnaissances are summarized by Gunter (1945a, b). The basic hydrographic data were obtained during 1946-1947 (Hedgpeth, 1947; Collier and Hedgpeth, 1950), and have been added to by others, notably Simmons (1957). Since about 1951 there have been several different types of studies made in various parts of the Laguna Madre. Biologists for the Texas Game and Fish Commission have conducted surveys of the biota in various regions of the Laguna Madre, geologists have studied the sediments and the potential fossil assemblages, and ecosystematists have measured photosynthesis. In all, more than 20 papers with some information about the Laguna Madre have been published in the past twenty years. In addition, studies have been made of the similar Laguna Madre de Tamaulipas in Mexico, south of the Rio Grande (Hildebrand, 1958; Odum *et al.*, 1963).

The earlier biologists who were concerned with the Laguna Madre were interested in determining the identity and, to some extent, the abundance of species, and related this information to environmental variables, but more recent investigators have been concerned with such matters as chlorophyll, photosynthesis, and net respiration. While this information is useful, many questions of peculiar interest for our understanding of the Laguna Madre still remain to be investigated. This is especially true for the prob-

lems of salinity physiology and no one seems to have made a detailed analysis of the composition of the water itself. Yet the Laguna Madre is a unique environment in many ways, not the least being its comparative accessibility. No other such extreme environment except the salterns of San Francisco Bay or Great Salt Lake is so near a large city and a research station.

FLORA AND FAUNA

The Laguna Madre lies between the dunes of Padre Island and the barren mainland flats. Isolated clumps of salt cedar grow on the mainland shore, but the oak-covered ridges of the northern bay shores are absent. The bottom of the Laguna is sand or mixed sand and silt for the most part, grading into clay in Baffin Bay. In the northern and southern parts of the Laguna there are extensive patches of *Diplantheria t Wrightii*, and meadows of *Thalassia testudinum*.

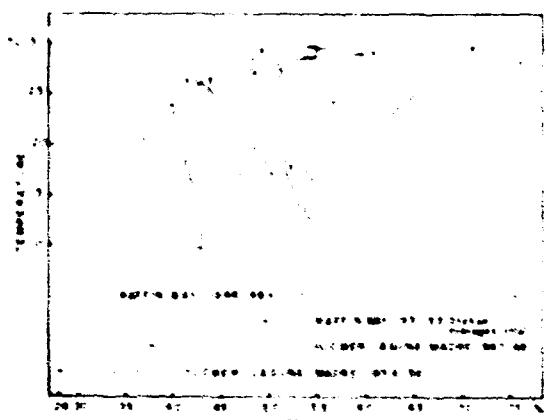
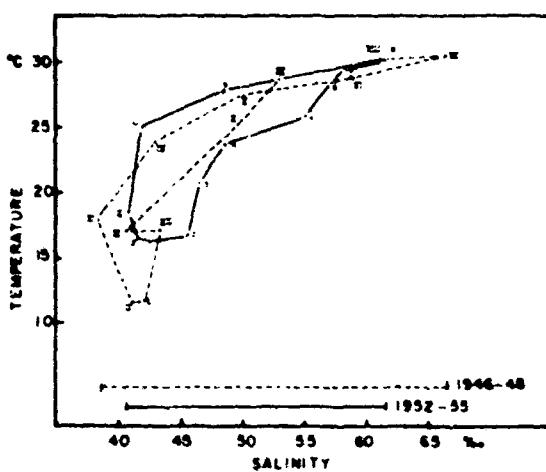


Fig. 2.—(Above) Temperature-salinity conditions in the upper Laguna Madre. Data for 1946-1948 from Collier and Hedgpeth (1950); for 1952-1955 from Simmons (1957). (Below) Temperature-salinity conditions in Baffin Bay (data from Collier and Hedgpeth, 1950) and the lower Laguna Madre. Data for 1947-1948 from Collier and Hedgpeth (1950); for 1954-1956 (without temperature data) from Breuer (1962).

occur in the southernmost part (South Bay) of the Laguna. *Ruppia maritima* is common along the Intra-coastal Waterway. In Baffin Bay, however, rooted spermatophytes were not observed in the 1950's although *Diplantheria wrightii* is sparsely present at this time (1964); algae are also apparently sparse there and the principal plant life is microscopic. The flats in many parts of the Laguna Madre, especially along the Padre Island side, are covered with algal mat communities consisting mostly of the blue-green *Lyngbya confervoides* (Sorensen and Conover, 1962). A community of this type also occurs in parts of the Laguna Madre de Tamaulipas (Hildebrand, 1958). When such algal mats occur on fine calcareous sediments in hyperhaline environments, stromatolite structures may be formed, as in Shark Bay, Western Australia (Logan, 1961). This combination of conditions has not been observed in Texas.

In the southern part of the Laguna *Gracilaria blodgettii* is the most conspicuous macroscopic alga; there are also extensive stands of *Penicillus capitatus* in the Port Isabel area when temperatures and salinities are sufficiently high (Sorensen, 1963). *Acetabularia crenulata* occurs in scattered patches throughout the lower Laguna (Breuer, 1962). *Enteromorpha* and *Cladophora* occur sporadically.

The plant life of the Laguna is highly seasonal, dying down during the high summer temperatures in August and September, and remaining dormant until spring. The macroscopic algae begin to appear in February and the grasses start to grow in March. The algae are restricted to the southern part of the Laguna.

The diatom flora of Texas bays, as represented in fresh sediment samples, has been studied by Ferguson Wood (1963). A preliminary tabulation of his list indicates 183 species in the bays adjacent to the Laguna Madre (principally in Aransas and Corpus Christi Bays). Since the listings for the Laguna Madre do not always specify which part of the Laguna, all such records were combined, producing a total of 129 species. In Baffin Bay, however, only 33 species were recorded, of which 22 were found in all the bays of the area. In addition, seven species were recorded from Baffin Bay and from such bays

as Aransas and Corpus Christi but not the Laguna Madre. Ferguson Wood calls attention to the frequent occurrence of species of *Rhopalodia* in Baffin Bay, which also occur in fresh water. These species are found in all of the three environmental categories tabulated. Species of *Amphora* are abundant and frequently dominant in the upper Laguna Madre, Aransas Bay, and Redfish Bay.

There is an abundant and varied fish fauna in the various parts of the Laguna, and our best faunal information concerns fishes. This is primarily due to the work of Gunter (1945 and later papers), and more recent studies by biologists of the Texas Game and Fish Commission (now the Parks and Wildlife Department). Among the resident species in the Laguna Madre are the tenpounder or skipjack (*Elops saurus*), anchovies (*Anchoa* spp.), three species of cyprinodontids (*Fundulus similis*, *F. grandis*, and *Cyprinodon variegatus*), the silversides (*Menidia beryllina peninsulae*), mullet (*Mugil cephalus*), the spotted sea trout (*Cynoscion nebulosus*), and the black drum (*Pogonias cromis*). These species are known to spawn in the Laguna, and most of them (except the anchovies and possibly the cyprinodontids) are winter or early spring spawners. While complete data are lacking, it appears that most of these species do not spawn in concentrations of salinity in excess of 45‰. Some of them, however, probably spawn in higher salinities; an atherinid (*Atherinops affinis affinis*) can spawn in concentrations of 72‰, but the young die within four months (Carpelan, 1955). Many other species of fish spend considerable time in the Laguna, but do not spawn there and usually leave in summer during temperature and salinity rises. Other fish are occasional visitors. Simmons (1957) listed more than 70 species of fishes occurring in the upper Laguna Madre. Two of the most important species in terms of species mass and representation in both sports and commercial fisheries are the redfish, *Sciaenops ocellatus*, and the black drum, *Pogonias cromis*. The life histories of these species in the Laguna have been reviewed by Simmons and Breuer (1962). The redfish is not a permanent resident, and does not spawn in the Laguna, while the black drum does. The black drum also seems to withstand higher temperatures and salinities, although older fish tend to become deformed and blind in the highest salinities. Both of these species are sciaenids; another fish of this family, the sea trout, *Cynoscion nebulosus*, is also an important game fish in these waters. Simmons (1957) has pointed out the occurrence of larger sizes in the saltier waters of the Laguna Madre (Fig. 3), indicating that the larger fish remain in the Laguna longer or that they grow larger in higher salinities, or perhaps simply that they tolerate the higher salinities. Gunter (1961a, b) has summarized some of the aspects of relationships of organisms to salinity, including the relationships between size and the environmental salinity gradient. He is of the opinion that in some cases there may be a direct relation between salinity and size, with the larger individuals at higher salinities.

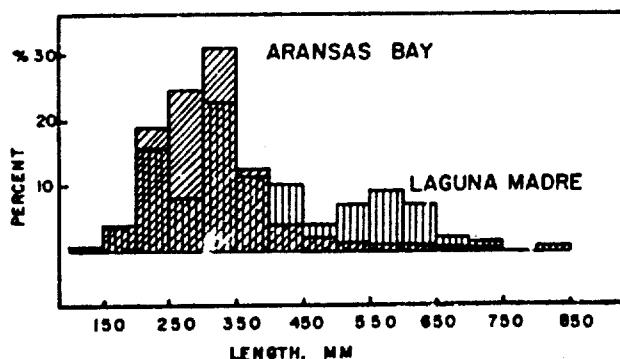


Fig. 3. Size distributions of spotted sea trout, *Cynoscion nebulosus*, in upper Laguna Madre (Simmons, 1957).

The living invertebrates of the Laguna have not been so thoroughly studied as the fishes. Crustaceans of several species are abundant, and make up a significant part of the food for several species of fishes, especially the redfish. Young blue crab, *Callinectes sapidus*, and the small mud crab, *Neopanope texana*, are the important crabs. Young penaeids, especially *Penaeus aztecus*, and the small resident grass shrimp, *Palaeomonetes intermedius*, are the most important shrimp. The copepod, *Acartia tonsa*, is apparently the most abundant plankton organism in many parts of the Laguna, including Baffin Bay, where it occurs in salinities as high as 80‰. Simmons (1957) reported a concentration of 7 million to a liter on one occasion. (In view of the difficulty that some workers have in identifying copepods, it can be pointed out that the identification of *Acartia tonsa* has been confirmed by Bowman (1961). No other species of this genus has been identified from Laguna waters. The occurrence of *A. tonsa* in high salinities in Texas is interesting in the light of its distribution as a bay and coastal water species as far north as Cape Cod.) *A. tonsa* is apparently the dominant copepod of the Laguna waters, and feeds on some "reddish submicroscopic plankters". It is important as a food item for small fish. Another copepod, *Metis japonica*, is common, but not so abundant (although one sample contained about 1 million per liter, according to Simmons). It does not seem to be as important as a food.

Several small bivalves are common in various parts of the Laguna, and constitute a major element in the diet of the black drum. The commonest species are *Anomalocardia cuneimeris* and *Mulinia lateralis*; evidently these occur in extensive beds although there is no clear information on the locations of these beds or the density of molluses per unit area. Other species mostly associated with the grassy areas of the Laguna are *Brachidontes exustus*, *Aequipecten irradians amplicostatus*, *Lacvicardium mortoni*, and, especially in the Port Isabel area, *Chione cancellata*. Little attention seems to have been paid to gastropods, and even less to worms and other invertebrates. It is obvious that a thorough quantitative study of the benthic organisms in the Laguna would be of considerable value, especially in view of costly proposals to rehabilitate certain areas as nursery and feeding grounds for desirable species of fishes.

Parker (1959, 1960) has described molluscan assemblages for various regions of the Laguna Madre as potential indicator groups for certain ecological conditions. Since these studies were carried out primarily for the benefit of paleontologists, those organisms most likely to contribute to the fossil record, especially the molluses, were studied. The distribution of several species is indicated as characteristic of certain environments in both these papers. No reason is given for extending the environment of *Amygdalum papyria* some twenty-five miles beyond the indicated records for living specimens, while at the same time the distribution of *Laevicardium mortoni* is at least ten miles short of the posted occurrence of living ani-

mals (compare Figures 25a and b in Parker, 1959). The lower Laguna is characterized by Parker as "open hypersaline lagoon" although it is abundantly populated by two species (*Anomalocardia cuneimeris* and *Tellina tampaensis*) indicated on his Figures 27 a and b as "characteristic of enclosed hypersaline environment", and the environment is indicated as more or less continuous with the northern Laguna Madre, but also exclusive of extensive areas in the southern Laguna from which living specimens have been taken. These species may well be characteristic of the environments suggested, but they are evidently also characteristic of slightly different conditions, or perhaps, the subdivisions suggested are not as well defined ecologically as geographically. Examination of lists of "characteristic" species (Table 2) suggests that the differences indicated by these characteristic species may be subjective, if these lists have been compiled from essentially the same data.

It is unfortunate that more detailed studies of living communities could not have been made before the recent changes in the Laguna Madre, as it is now difficult to assess the significance of the somewhat divergent results set forth in the papers of Parker (1959, 1960), Breuer (1957, 1962), and Simmons (1957) (Table 3). While it is probable that these various authors were studying the same place, it is obvious that different types of collecting and different interests can produce results which are not complementary. Part of the difficulty is, of course, the reliance upon dead or "freshly dead" material that may be carried to other areas by winds and currents, or possibly by fish. Ernest G. Simmons (personal correspondence) writes: "I am highly suspicious of 'dead' shells as I have seen too many small shells pass undisturbed through the digestive tract of large drum."

BAFFIN BAY

In both persistence of higher salinities and in sediment characteristics, Baffin Bay is somewhat apart from the two main parts of the Laguna Madre. It is in this part of the Laguna Madre system that organisms meet the greatest environmental stress; while the flora and fauna are reduced in numbers, the abundances of some of the species present are very high.

Observations were made by Breuer (1957) in the Baffin Bay-Alazan Bay area during 1951-1953 as part of the Texas Game and Fish Commission's environmental studies of the Laguna Madre complex. Salinities during that period ranged from a low of 1.40 to a high of 75.05‰; the mean during the period of the study was 51.68‰. The extremes were for the same station at the head of Alazan Bay. Breuer considered the following organisms to be "normal residents of the area":

Diatoms	Pisces
<i>Navicula</i> sp.	Ariidae
<i>Amphiprora apaludosa</i>	<i>Galeichthys felis</i>
Dinoflagellates	Cyprinodontidae
<i>Ceratium hirundinella</i>	<i>Cyprinodon variegatus</i>

Coelenterata	Atherinidae
<i>Phortis</i> sp.	<i>Menidia beryllina</i>
Ctenophora	<i>peninsulae</i>
<i>Beroe ovata</i>	Mugilidae
Mollusca	<i>Mugil cephalus</i>
<i>Mulinia lateralis</i>	Sparidae
Copepoda	<i>Lagodon rhomboides</i>
<i>Acartia tonsa</i>	Sciaenidae
Cirripedia	<i>Cynoscion nebulosus</i>
<i>Balanus eburneus</i>	<i>Sciaenops ocellatus</i>
Amphipoda	<i>Micropogon undulatus</i>
<i>Gammarus mucronatus</i>	<i>Pogonias cromis</i>
Decapods	Bothidae
<i>Penaeus aztecus</i>	<i>Paralichthys</i>
<i>Callinectes sapidus</i>	<i>lethostigma</i>

Most of these species are known to occur in salinities in excess of 60‰, although Simmons (1957) stated of the redfish, *Sciaenops ocellatus*, that "populations were severely limited by salinity of 50‰ or above." Breuer found few living *Mulinia lateralis* and apparently no living *Anomalocardia cuneimeris* during his study. Breuer (1957) suggested that the absence of living molluscs during the period of his survey was due to pollution from a large celanese plant whose effluent drained into Baffin Bay.

According to earlier observations (Hedgpeth, 1953), at least two species of polychaetes, *Nereis pelagica occidentalis* and *Polydora ligni*, occurred in Baffin Bay, as well as two species of amphipods, *Podocerus brasiliensis* and *Grandidicella bonnieroidea*, not mentioned by Breuer. A green alga, possibly *Chaeto-*

morpha, has been observed on pilings at various parts of the Laguna; Breuer mentions the occurrence of "Enteromorpha and Cladophora", but does not consider them part of the "normal residents" as he states they "are kept down by radical changes in salinity." As noted above, at least 33 species of diatoms occur in Baffin Bay, some of them abundantly. On a map published in Odum and Hoskin (1958), but without further explanation in the text, Baffin Bay is labeled a "nannoplankton-clay" ecosystem. Nannoplankton as such, however, does not appear to have been studied.

A most interesting puzzle is the frequent occurrence of considerable numbers of the Leptomedusan "*Phortis*" or *Eirena*. This medusa has a hydrozoan stage, but no hydroids have been observed in the adjacent Laguna Madre or Baffin Bay. It could be a small hydroid epizoic on other hydroids or some substrate. What can this medusa be feeding on? It is also worthy of comment that *Nemopsis bachei* has been found in the Laguna up to salinities of 75–80‰; the hydroid of this medusa is a *Bougainvillea*. Hydroids of this genus are common in Texas coastal waters, and *B. niobe* (det. by C. Cutress) was collected in the upper Laguna in 1958 and 1959 (*fide* E. G. Simmons).

The absence of *Artemia* from Baffin Bay has been attributed by Hedgpeth (1957) to possible predation by fishes, since salinities would seem favorable for this organism. It seems more likely, however, that the dietary needs of the brine shrimp are not met in Baffin Bay. Brine shrimp were also absent from the Laguna Madre de Tamaulipas, according to Hilde-

Table 2. Species considered characteristic of environments of the Laguna Madre.

Inlet-influenced, hypersaline lagoon		Open hypersaline lagoon	
(a) Parker, 1959	(b) Parker, 1960	(c) Parker, 1959	(d) ¹ Parker, 1960
GASTROPODA			
<i>Anachis avara semiplicata</i>	<i>Bittium varium</i>	<i>Bittium varium</i>	<i>Caecum pulchellum</i> ²
<i>Anomia simplex</i>	<i>Caecum pulchellum</i> ³	<i>Haminoea succinea</i> ³	<i>Cerithidea pliculosa</i> ³
<i>Bulla striata</i> [= <i>occidentalis</i>] ⁴	<i>Cerithidea pliculosa</i> ³	<i>Mitrella lunata</i>	<i>Cerithium variable</i> ³
<i>Crepidula glauca convexa</i>	<i>Haminoea succinea</i> ³	<i>Truncatella pulchella</i> ^{3,4}	<i>Haminoea succinea</i> ³
<i>Littorina nebula</i>	<i>Modulus modulus</i> ³		<i>Modulus modulus</i> ³
<i>Nassarius vibex</i>	<i>Tegula fasciata</i>		<i>Vermicularia fargoi</i> ³
<i>Neritina virginea</i>	<i>Vermicularia fargoi</i>		
<i>Turbonilla interrupta</i>			
PELECYPODA			
<i>Abra aequalis</i>	<i>Amygdalum papyria</i>	<i>Amygdalum papyria</i>	<i>Amygdalum papyria</i>
<i>Acquipecten i. ampliostatus</i>	<i>Anomalocardia cuneimeris</i> ³	<i>Brachidontes citrinus</i>	<i>Anomalocardia cuneimeris</i>
<i>Anadara transversa</i>	<i>Laevicardium mortoni</i>	<i>Laevicardium mortoni</i>	<i>Laevicardium mortoni</i>
<i>Atrina seminuda</i> ³	<i>Phacoides pectinatus</i>	<i>Macoma brevicornis</i>	<i>Phacoides pectinatus</i>
<i>Chione cancellata</i>	<i>Pseudocardium floridanum</i> ³	<i>Mactra fragilis</i>	<i>Pseudocardium floridanum</i>
<i>Cyrtopleura costata</i>		<i>Tagelus divisus</i> ³	<i>Tellina tampaensis</i>
<i>Macoma tenta</i> ³		<i>Tellina tampaensis</i>	
<i>Nuculana acuta</i>			
<i>Ostrea equestris</i>			

¹This column has been developed from the caption for Plate 3, Figure 1 in Parker, 1960, because there is no text for this environment. Parker (1960, p. 316) stated that some of the characteristic species listed for (b) are illustrated on this plate. This leaves only two species in (d) not listed in (b).

²Not listed as found in this environment by Parker (1959, Table II, pp. 2164–2166).

³Listed only as dead shells in Parker's Table II (above) for the environment stated.

⁴A maritime or halophilic, but not aquatic, species (Clench and Turner, 1948).

Table 3. Common or "characteristic" molluscs of the Laguna Madre.

"Open hypersaline" species listed as "characteristic" by Parker (1959); found in "lower Laguna" (north of Three Islands) by Breuer (1962)		Listed for "enclosed hypersaline" by Parker (1959); "upper Laguna" by Simmons (1957)	
Parker	Breuer	Parker	Simmons
<i>Bittium varium</i>			<i>Bittium varium</i> (<i>fide</i> Parker) ¹
<i>Hamiroca succinea</i> ²		<i>Cerithium variabile</i>	
<i>Mitrella lunata</i>			
<i>Truncatella pulchella</i> ³ *			<i>Odostomia bisuturalis</i> ("")
<i>Amygdalum papyria</i>			
[<i>Anomalocardia</i>			
<i>cuneimeris</i> ⁴			
<i>Brachidontes cirratus</i>	<i>Anomalocardia cuneimeris</i>	<i>Anomalocardia cuneimeris</i>	<i>Anomalocardia cuneimeris</i>
<i>Laevicardium mortoni</i>	<i>Esis minor</i> ⁵ *		
<i>Macoma brevifrons</i>	<i>Laevicardium mortoni</i>		
<i>Mactra fragilis</i>			
[<i>Mulinia lateralis</i>] ⁶			
<i>Pseudocyrene floridana</i>	<i>Mulinia lateralis</i>	<i>Mulinia lateralis</i>	<i>Mulinia lateralis</i>
<i>Tagelus divisus</i>	<i>Polymesoda floridana</i> ⁷		<i>Pseudocyrene floridana</i>
<i>Tellina tampaensis</i>		<i>Tellina tampaensis</i>	<i>Tellina tampaensis</i>

Notes, on basis of listing in Parker (1959, Table II, pages 2164-2166).

¹ Listed only as dead shells.

² This is not a marine mollusc; it lives on land near shore.

³ These species not included in Parker's list, p. 2144, as "characteristic" of this environment, but given equal abundance rating in Table II for both regions.

⁴ Not recorded by Parker as living or dead for either environment.

⁵ *Polymesoda* is a synonym of *Pseudocyrene*.

brand (1958), but they have since made their appearance. Concerning changes in the Mexican Laguna, Hildebrand informed me (in a letter dated June 11, 1964): "Conditions are far different than during my earlier work reported in 1958. In the fall of 1960, Eighth Pass closed and it has remained closed except for a brief period after Carla [the hurricane of 1961]. The Laguna now produces no commercial fishes and on my last trip on January 9, 1964, it contained a number of brine shrimp. Somewhat, *Cyprinodon variegatus* and the silverside, *Menidia beryllina*, have been able to maintain a population around Punta Piedras despite salinities ranging above 100 parts per thousand for more than two years." It is possible that suitable algae for *Artemia* are not usually present in these coastal hypersaline lagoons; Carpelan (1964) has pointed out the interrelationships between salinity and other factors in limiting algal distribution. The brine fly, *Ephydria*, has not been reported from Baffin Bay, but Hildebrand found it abundant in the northern, most saline part of the Laguna Madre de Tamaulipas.

As previously noted (Hedgpeth, 1953, 1959) the Laguna Madre has several similarities to the Sivash or Putrid Sea lying to the southwest of the Sea of Azov (Zenkevitch, 1963). In the more saline regions of the Sivash the macroscopic biota is reduced to *Artemia*, *Chironomus*, and *Cladophora*. The Sivash, however, adjoins a body of water whose average salinity is about one-third that of sea water. Less saline parts of the Sivash, like Baffin Bay, may have dense stands of small molluscs, which support large

fish populations. Possibly, as suggested by Vorobieff (1940), the annual production of this mollusc biocoenosis in the Sivash is consumed by fish.

The Faunal Gradient Related to Salinity

In the Laguna Madre there are at least 25 species of animals that persist or withstand concentrations of 75-80%. Some of these also occur in salinities as low as 15% (e.g. *Nemopsis bachei*, *Acartia tonsa*, *Balanus eburneus*, and most of the fishes). Above 80% there is a small hardy group of organisms that may withstand even higher salinities. The environmental salinity ranges of those species commonly occurring above 45% are indicated in Table 4. The lower distribution limits are those actually recorded for south Texas waters from San Antonio Bay southward; a number of the species are known to occur in lower salinities than stated, but with the exception of the fish (Gunter, 1945a, b; Simmons, 1957), field salinities have not been recorded in several cases. There are probably more species with such field tolerances; what is particularly interesting is the broad range in which the species have been observed in nature. With the possible exception of the as yet unidentified medusa, *Eirene*, no endemic species restricted to higher salinities have been found in the Laguna Madre.

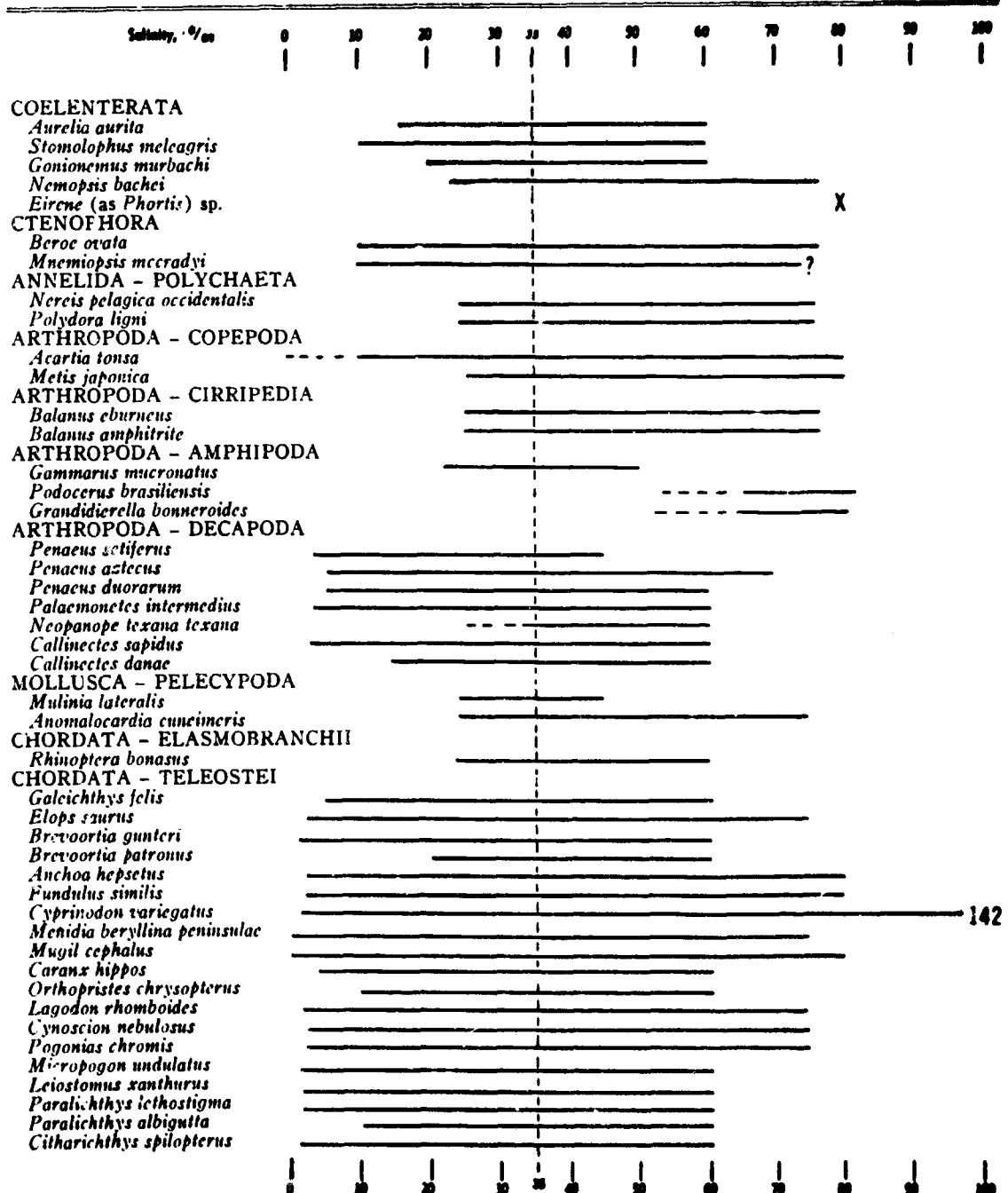
The field data also indicate that within the range of 50-70% more species are found in lower temperatures (Fig. 4). However, this is probably more an indication of migration out of the hypersaline areas during high summer temperatures than of a

physiological relationship between temperature and salinity tolerance. As Carpelan (1964) has emphasized, organisms in a natural salinity gradient may distribute themselves according to salinity optima, and further, salinity *per se* is not the only—or possibly even principal—factor in many distributions in nature.

In saltrens and landlocked inland saline waters

there are organisms that may occur in nearly saturated brine (Hedgpeth, 1959). A few of these may run the gamut from fresh water to saturation, as was originally suggested by Remane in 1934 in the "holoeuryhaline" part of his diagram. This diagram has often been quoted without the solid black bar for "holoeuryhaline species" across the bottom (Remane

Table 4. Recorded occurrence in salinities of 45‰ and above, of certain metazoa in bays and lagoons of the northwestern Gulf of Mexico.



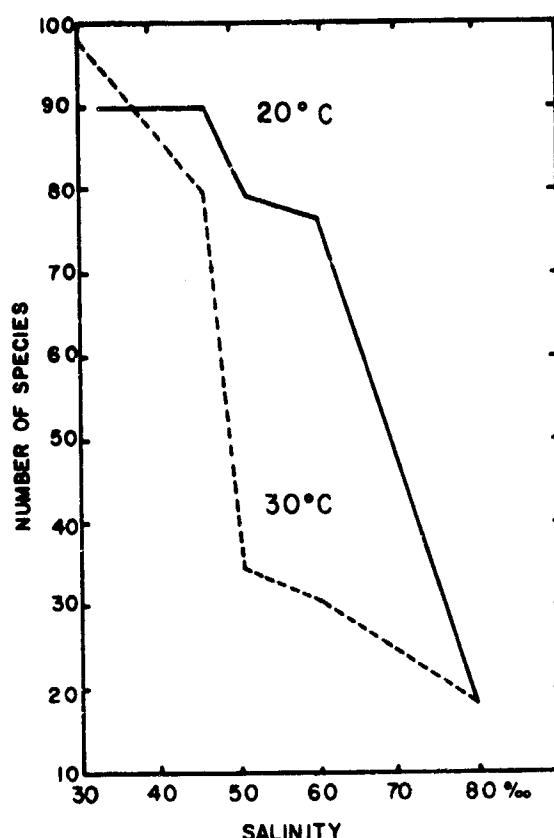


Fig. 4. Species abundance in various temperatures and salinities (Simmons, 1957).

and Schlieper, 1958). Such species do exist, although there are probably very few that occur from 0 to 31%; many of these are flagellates and other small organisms and it is difficult to be certain of their precise identity in every case. These holoeuryhaline species may, however, be absent from sea water, and therefore represent a different group than the "ultrahaline" species in such places as the Laguna Madre and the Sivash, which range from fairly low salinities through oceanic concentrations (and, in many cases in the ocean) to the hypersaline bays and lagoons. Some of these species are in turn distinct from the "brackish water" species, primarily endemics of the Baltic and similar areas. Thus it appears that Remane's diagram should be modified, or amended, somewhat in the manner suggested in Figure 5. (For another modification of this diagram, for the Caspian basin fauna, see Fig. 10, p. 166 in Mordukhai-Boltovskoi, 1964.)

ECOSYSTEMATICS

For the past several years (1956 through 1962) the ecosystem approach to problems of estuarine ecology has been emphasized by Odum and his students at the Institute of Marine Science at Port Aransas. Measurements of light, oxygen, pH, chlorophyll, and similar variables have been made in various bays

and ponds, including the upper Laguna Madre and Baffin Bay (Odum and Hoskin, 1958; Odum *et al.*, 1958; Park *et al.*, 1958; Wilson, 1961; Odum and Wilson, 1962; Odum, Cuzon *et al.*, 1963). An attempt to correlate such measurements with biomass data, especially of the fish, was made by Hellier (1962), and small-scale experimental systems were set up as analogues (Odum, Siler *et al.*, 1963).

This work has consisted principally of various kinds of measurements at various seasons and conditions of weather. These have usually been runs for a period of time, perhaps 24 hours, to indicate diurnal variations. While the individual sets of observations may cover an entire day, it appears that there are few periods of sustained observation. In the Baffin Bay data, for example, there are two eight-month gaps in data for a four-year period, and a total of 18 sets of observations for the entire four years. The upper Laguna Madre is represented by thirty such sets of observations from late 1956 to the end of 1960. These data are summarized in terms of photosynthesis and respiration.

The Laguna Madre is characterized as a "thin grass system": the data summarized are those for the upper Laguna Madre. The biological system of this area is described by Odum and Wilson (1962) as follows:

"The upper Laguna Madre in the study area is carpeted with a firm bottom and fine grass in water about one meter in depth. In the dry years with the salinity above 40% this grass was almost exclusively composed of *Diplanthera wrightii*, but during the relatively wet year of 1959 considerable *Ruppia maritima* developed, diminishing again in 1960.

"Only in summer 1960 were dense mats of dead grass observed accumulating. In general, consumption and production were closely correlated. There was an immense difference between the winter and the summer. Whereas 96,000 foot candle-hours were received on a representative summer day July 25, 1960, only 4500 foot candle-hours were received on a cloudy winter day Dec. 8, 1960, and 19,500 foot candle-hours on a clear day in winter, Dec. 28, 1961. The low

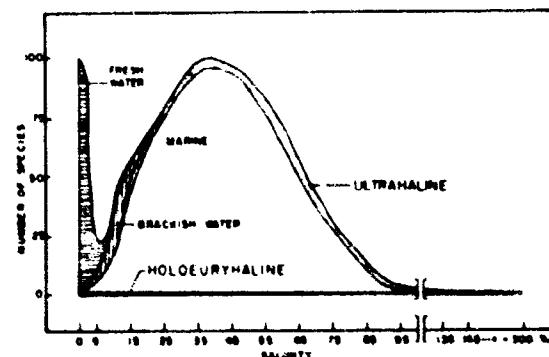


Fig. 5. Suggested extrapolation of Remane's curve through the entire salinity spectrum.

winter photosynthetic productivities thus were correlated with winter cloudiness and short days. Unlike Florida at a similar latitude, the cloudiness in Texas was maximal in winter. There was thus a tremendous annual pulse in the energy entering the biological system. The observed photosynthesis reflects this cloudiness. The close correspondence of respiration with photosynthesis without lag suggests that the life cycles of the organism are sufficiently adjusted to provide almost simultaneous increase and decrease of consumer populations to maintain equivalence of P [Photosynthesis] and R [Respiration]. The migration of mullet, shrimp, crabs and other consumers from the Laguna (Hellier, 1962) is a part of this system which diminishes winter metabolism as the photosynthesis drops. There is relatively little lag.

"The temperature sequence parallels photosynthesis only in part. Productivities fall rapidly after July whereas temperature does not diminish appreciably until November. Although the decrease in salinity produced some differences in plant type, gross photosynthesis was little affected."

Although Odum and Hoskin (1958) labeled the Baffin Bay area as a "nannoplankton-clay" system, this terminology is not referred to in the later paper by Odum and Wilson (1962). The situation in Baffin Bay is referred to in the following terms: "Baffin Bay is in a very arid area and was observed with an excess of respiration over photosynthesis for extended periods. The bay was continuously turbid suggesting a runoff of organic matter after cloudbursts over the arid lands of the surrounding King Ranch, little-covered with vegetation. Whereas the rains coming in floods were not frequent enough to equal evaporation, runoff was apparently adequate to supply the bay with enough particulate and other organic matter to maintain consumption in excess of photosynthesis" (Odum and Wilson, 1962). High concentrations of organic matter in Baffin Bay are accompanied by this excess of respiration over photosynthesis. The observed data are summarized in Figure 6.

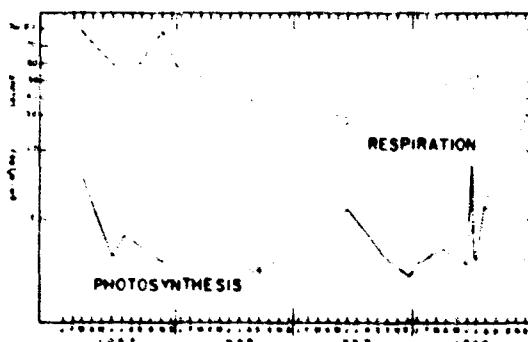


Fig. 6. Photosynthesis, respiration, and salinity in Baffin Bay, based on a series of 18 sets of observations (Odum and Wilson, 1962).

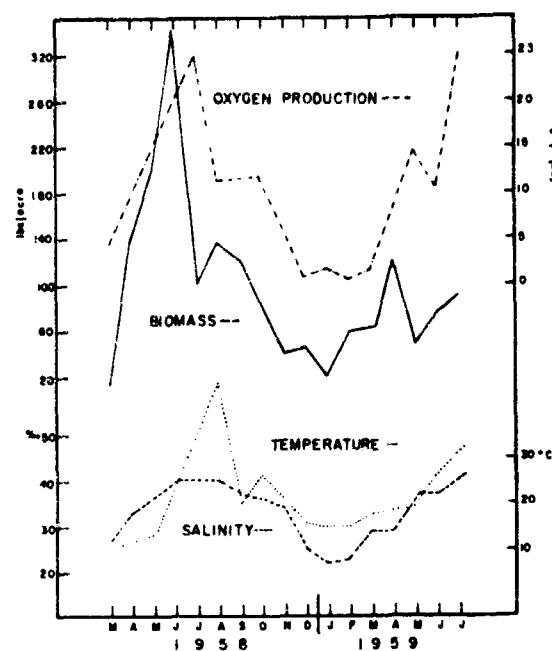


Fig. 7. Biomass and production, upper Laguna Madre (Hellier, 1962).

According to these authors there is also a recycling of nutrients in highly saline bays with limited circulation.

Hellier's (1962) study is a comparison of data on fish catches and metabolic measurements at monthly standard stations in the upper Laguna Madre. The fishes were caught by a large drop net which provided some data per unit area, although small fish, young shrimp, and jellyfish were not included in the catches. No effort was made to sample the infauna. The basic information from this study is presented in Figure 7.

Concerning these curves, Hellier states:

"The curves show a comparison of fish biomass to gross plant production. A correlation between the biomass of fishes present and gross plant production is illustrated by these curves. In examining the curves, one can see a tendency for the biomass of fishes to follow the curve of photosynthesis without much lag during the spring months. This tendency was primarily due to a rapid influx of young of the year fishes. Thus the extreme decline in biomass after the spring peak may at least in part be a function of the availability of food as expressed by the rate of photosynthesis. The biomass is also correlated with the temperature and salinity curves. Therefore it is possible that several factors interact to control fish biomass and production. In other years curves of gross photosynthetic production in the Laguna Madre, taken as the area under the curve

"Gross annual photosynthetic production in the Laguna Madre, taken as the area under the curve

of photosynthesis was $4177 \text{ g/m}^2/\text{yr}$ wet weight or $3.1 \text{ g/m}^2/\text{yr}$ dry weight. The calculated efficiency of conversion of gross plant production into fish production on a dry weight basis would then be 0.074 percent.

The most obvious thing about these ecosystem data is that the values of the various variables rise and fall with the progression of the seasons. Thus it cannot be stated whether temperature or salinity *per se* have any control over the system; indications are that the systems are not directly dependent upon temperature, and they also seem independent of salinity. Although there are many gaps in the data which must be filled before we have a picture of the whole seasonal process in the ecosystem, Odum and his colleagues are obviously of the opinion that the best index of the ecosystem is gross photosynthesis. Undoubtedly it tells us something about what is going on, but it is doubtful that it is the entire story. Certainly the old-fashioned naturalist would like to have a more complete range of information, no matter how much he may agree that "spreading over the earth in vast variety are endless ecosystems making ecological magic from sunbeams." After all, as another poet so eloquently put it, other things are going on in the ocean, that,

". . . unfathom'd waste of agony,
Where millions live their horrid lives by making
other millions die."

On the assumption that photosynthesis is indeed the measure of an ecosystem and that increasing photosynthesis will improve the ecosystem for our anthropocentric purposes, Odum and Wilson (1962) suggest: "To produce maximum total photosynthesis in all of the waters of Texas, measures for management should include: reducing turbidity, eliminating irregular flushing of flood waters, developing grass bottoms, retaining wind driven circulation, and adjusting water depths of shallow and deep areas towards an average depth of 0.5 m."

This has inspired an indignant protest from Rounsefell (1963), who states: "Interpreted realistically this means removing the most important cog from the estuarine-continental shelf complex and substituting therefor a polluted basin of green slime. The best current example of such a basin is the upper Laguna Madre, with a salinity higher than the oceans, vast schools of unfishable slime-eating mullet and schools of black drum (*Pogonias cromis*) that the state must contract to have removed (Simmons and Breuer, 1962). About every four or five years a cold 'norther' kills most of the fish in this shallow 'ideal' fish pond."

Perhaps we are taking these recommendations more seriously than they were intended to be taken, for there are inevitable gaps between theory and practice in most lines of human endeavor. In this case the gap between the ideal and the practical is also accompanied by a large gap in our knowledge. So large, in fact, that we cannot concede that photosynthesis is

¹R. F. Burton, *The Kestrel*. The other ecological poets are Odum, McConnell, and Abbott, 1958.

the ideal measure of the practical. Certainly an ecosystem in which nothing much more besides photosynthesis and plant respiration is going on is not the most interesting system ecologically, whether it proceeds at the optimum efficiency for maximum output or not. (Odum and Pinkerton (1955) have elaborated on this idea.) Furthermore, it would not appeal to public interest to spend \$7,150,000 to "improve" such an ecosystem by increasing output of plant material at the expense of ecological diversity.

None of this is intended to imply that this work is not valuable or that it should not be done. It is part of what should be done, but it needs to be done more consistently for longer consecutive periods of time, in conjunction with biomass studies of both plankton and benthos and with quantitative studies of the nektonic elements of the system. This is a large order, but until it is done we cannot say that one index number is more valid than the other for characterizing a complex natural system. The Laguna Madre has certain simple features in spite of, or because of, its salinity; it is an ideal place for such a complex and detailed pilot study.

SUMMARY

Since this paper is a summary of work done in and around the Laguna Madre in the last two decades, it seems in order to emphasize what still remains to be done.

1. While the works of man have made it possible for fish and motile invertebrates to escape extremely high salinities, these high salinities still occur, and in some cases have been increased as a result of other works of man.

2. Further works of man are proposed to improve salinity exchange and habitats in the upper Laguna Madre. There appears to be no adequate field study that would demonstrate that these proposals are based on sound biological criteria. It may be better to undo what has been done than to add further complications.

3. No adequate study has been made of the living benthos of any part of the Laguna in terms of frequency, mass per unit area, or seasonal fluctuation.

4. With the exception of recent work on diatoms, the phytoplankton and smaller heterotrophic nanoplankton are unstudied.

5. A number of intriguing life cycles have not been worked out, and many others are inadequately known.

6. No laboratory studies have been made of the salinity tolerances and osmoregulatory abilities of the species from the Laguna Madre although the field data suggest many interesting problems.

7. These gaps in our information have led to conclusions concerning the manipulation of the ecosystems of the Laguna Madre which are of questionable validity.

8. The estimated costs for engineering improvements to enhance the value of the present ecological system for recreational and commercial fishing interests are about \$7 million. Since architect's fees for

designing and superintending a large building may run around ten percent, it would seem advisable, by analogy, to consider a ten percent investment in research and supervision by biologists of the proposed project if it is improved. While money is not the entire answer, the magnitude of work and talent needed that is represented by a sum of \$700,000 is real and some approximation of this investment in time and personnel is imperative if the \$7 million is not to be wasted.

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LITERATURE CITED

- BEHRENS, E. W., 1963. Buried Pleistocene river valleys in Aransas and Baffin Bays, Texas. *Publ. Inst. Marine Sci., Texas*, 9:7-18.
- BOWMAN, T. E., 1961. The Copepod genus *Acartia* in Chesapeake Bay. *Chesapeake Science*, 2(3-4):206-207.
- BREUER, J. P., 1957. Ecological survey of Baffin and Alazan Bays, Texas. *Publ. Inst. Marine Sci., Texas*, 4(2):134-155.
- BREUER, J. P., 1962. An ecological survey of the lower Laguna Madre of Texas, 1953-1959. *Publ. Inst. Marine Sci., Texas*, 8:153-183.
- CARPELAN, L. H., 1955. Tolerance of the San Francisco Topsmeat, *Atherinops affinis affinis*, to conditions in salt-producing ponds bordering San Francisco Bay. *Calif. Fish and Game*, 41(4):279-284.
- CARPELAN, L. H., 1964. Effects of salinity on algal distribution. *Ecology*, 45(1):70-77.
- CLENCH, W. J., and R. D. TURNER, 1948. The genus *Truncatella* in the western Atlantic. *Johnsonia*, 2(25):149-164.
- COLLIER, A., and J. W. HEDGPETH, 1950. An introduction to the hydrography of tidal waters of Texas. *Publ. Inst. Marine Sci., Texas*, 1(2):123-194.
- GUNTER, G., 1945a. Studies on marine fishes of Texas. *Publ. Inst. Marine Sci., Texas* 1(1):1-190.
- GUNTER, G., 1945b. Some characteristics of ocean waters and the Laguna Madre. *Texas Game and Fish*, 3(11):7, 19, 21-22.
- GUNTER, G., 1961a. Some relations of estuarine organisms to salinity. *Limnol. and Oceanogr.*, 6(2):182-190.
- GUNTER, G., 1961b. Salinity and size in marine fishes. *Copeia*, 1961(2):234-235.
- HEDGPETH, J. W., 1947. The Laguna Madre of Texas. *Trans. 12th North Am. Wildlife Conf.*; pp. 364-380.
- HEDGPETH, J. W., 1953. An introduction to the Zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Publ. Inst. Marine Sci., Texas*, 3(1):107-224.
- HEDGPETH, J. W., 1957. Estuaries and Lagoons, II. Biological aspects. In *Treatise on Marine Ecology and Paleoecology*; vol. 1, pp. 693-729. *Geol. Soc. Am. Memoir 67, Vol. 1*.
- HEDGPETH, J. W., 1959. Some preliminary considerations of the biology of inland mineral waters. *Arch. Oceanogr. Limnol.* 11 (Suppl.):110-141.
- HELLIER, T. R., JR., 1962. Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. *Publ. Inst. Marine Sci., Texas*, 8:1-22.
- HILDEBRAND, H. H., 1958. Estudios biológicos preliminares sobre la Laguna Madre de Tamaulipas. *Cárcamo (Mexico)*, 17(7-9):151-173.
- LOGAN, B. W., 1961. Cryptozoon and associate Stromatolites from the Recent, Shark Bay, Western Australia. *J. Geol.*, 69 (5):517-533.
- MORDUKHAI - BOLTOVSKOI, F. D., 1964. Caspian fauna beyond the Caspian Sea. *Intern. Rev. Ges. Hydrobiol.*, 49(1):139-176.
- ODUM, H. T., and C. M. HOSKIN, 1958. Comparative studies on the metabolism of marine waters. *Publ. Inst. Marine Sci., Texas*, 5:16-46.
- ODUM, H. T., and R. C. PINKERTON, 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *Am. Scientist*, 43(2):331-343.
- ODUM, H. T., and R. F. WILSON, 1962. Further studies on reaeration and metabolism of Texas bays, 1958-1960. *Publ. Inst. Marine Sci., Texas*, 8:23-55.
- ODUM, H. T., W. McCONNELL and W. ABBOTT, 1958. The chlorophyll "A" of communities. *Publ. Inst. Marine Sci., Texas*, 5:65-96.
- ODUM, H. T., R. P. CUZON DU REST, R. J. BEYERS, and C. ALLBAUGH, 1963. Diurnal metabolism, total phosphorus, Oble anomaly, and zooplankton diversity of abnormal ecosystems of Texas. *Publ. Inst. Marine Sci., Texas*, 9:404-453.
- ODUM, H. T., W. SILER, R. J. BEYERS, and N. ARMSTRONG, 1963. Experiments with engineers of marine ecosystems. *Publ. Inst. Marine Sci., Texas*, 9:373-403.
- PARK, K., D. W. HOOD, and H. T. ODUM, 1958. Diurnal pH variation in Texas bays, and its application to primary production estimation. *Publ. Inst. Marine Sci., Texas*, 6:47-64.
- PARKER, R. H., 1959. Macro-invertebrate assemblages of central Texas coastal bays and Laguna Madre. *Bull. Amer. Assoc. Petrol. Geologists*, 43(9):2100-2166.
- PARKER, R. H., 1960. Ecology and distributional patterns of marine macro-invertebrates, northern Gulf of Mexico. In *Recent Sediments, Northwest Gulf of Mexico, 1951-1958*; pp. 302-337. Am. Assoc. Petrol. Biologists Publ., Tulsa, Oklahoma.
- REMANE, A., and C. SCHLIEPER, 1958. Die Biologie des Brackwassers. *Die Binnengewässer*, Band 22; viii - 348.
- ROUNSEFELL, G. A., 1963. Realism in the management of estuaries. *Marine Resources Bull. 1*, Alabama Marine Resources Lab., Dauphin Island, Alabama.
- RUSNAK, G. A., 1960. Sediments of Laguna Madre, Texas. In *Recent Sediments, Northwest Gulf of Mexico, 1951-1958*; pp. 153-196. Am. Assoc. Petrol. Biologists Publ., Tulsa, Oklahoma.
- SIMMONS, E. G., 1957. An ecological survey of the upper Laguna Madre of Texas. *Publ. Inst. Marine Sci., Texas*, 4(2):156-200.
- SIMMONS, E. G., and J. F. BREUER, 1962. A study of Redfish, *Sciaenops ocellatus* Linnaeus and Black Drum, *Pogonias cromis* Linnaeus. *Publ. Inst. Marine Sci., Texas*, 8:184-211.
- SORENSEN, L. O., 1963. Growth and decay of *Penicillius capitatus* Lamarck in the lower Laguna Madre of Texas. *Publ. Inst. Marine Sci., Texas*, 9:106-111.
- SORENSEN, L. O. with J. T. CONOVER, 1962. Algal mat communities of *Lymbyxa confervoides* (C. Agardh) Gomont. *Publ. Inst. Marine Sci., Texas*, 8:61-74.
- VOROBIEFF, V., 1940. "Hydrobiological outline of the Eastern Sivash and its possible utilization for economic fisheries." *As-Cher. NIRO*, 12:69-164. (In Russian)
- WILSON, R. F., 1961. Measurement of organic carbon in sea water. *Limnol. and Oceanogr.*, 6(3):259-261.
- WOOD, E. J. FERGUSON, 1963. A study of the diatom flora of fresh sediments of the south Texas bays and adjacent waters. *Publ. Inst. Marine Sci., Texas*, 9:237-310.
- ZENKEVITCH, L., 1963. *The Sivash, or Putrid, Sea*; Ch. 10, S. VI, pp. 528-537. *Biology of the Seas of the U.S.S.R.* George Allen and Unwin, London.

An Ecological Study of a Hawaiian Mangrove Swamp

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In 1902 the American Sugar Company introduced seedlings of the red mangrove, *Rhizophora mangle*, from Florida into Hawaii. The seedlings were planted on the mudflats of the southwest portion of the island of Molokai to prevent erosion of the area. A second introduction of mangrove occurred in 1922 when the Insular Bureau of Forestry of the Philippine Islands shipped seedlings of *Rhizophora mucronata*, *Bruguiera sexangula*, and *Sonneratia caseolaris* to Hawaii.

At the present time, the mangroves *R. mangle* and *B. sexangula* are extending their ranges on the various islands of the Hawaiian group by invading sheltered bays and estuaries now occupied by *Hibiscus tiliaceus*. One such invasion has resulted in a small intertidal swamp forest in the Heeia District on the island of Oahu. The forest is dominated by *R. mangle*, but *B. sexangula* is also present. Except for a few dying specimens of *H. tiliaceus*, these are the only tree species present.

An extensive literature exists on the ecology of mangroves (Bowman, 1917; Chapman, 1940; Davis, 1940, 1942; Egler, 1948; Golley *et al.*, 1962; Guppy, 1906; Maenae and Kalk, 1962; Orr and Moorehouse, 1933; Warming and Vahl, 1925). None of the reports include comprehensive diurnal, monthly, or seasonal data on physical and chemical factors, nor do they consider the physiological adaptations or food interrelationships of the fauna. These parameters provided the basis for the present study, an ecological analysis and integration of the physical, chemical, and biological aspects of the Heeia Mangrove Swamp.

DESCRIPTION OF THE STUDY AREA

Heeia Mangrove Swamp occupies about 35 acres where Heeia Stream, one of the main drainage arteries of the Ko'olau Mountain Range, enters the ocean (Fig. 1). The swamp is bordered on its eastern edge by a pond which communicates with the ocean through a channel at its northern border. The pond is bounded to the west by mangrove and to the east by the stone wall of Heeia Fish Pond. Inland, the swamp adjoins a freshwater, grassy marsh. As it enters the marsh, Heeia Stream overflows and covers the muddy substrate to a depth of about ten centimeters of water which passes directly into the swamp. Water flow through the swamp proceeds by two main drainage arteries, namely, Heeia Stream and a subsidiary channel formed by water from the marsh. In the center of the swamp these two arteries merge to form the main drainage channel. It is mainly by these

channels that the tide has access to the swamp. Indentation occurs each high tide, leaving a thin layer of brown sediment on the swamp floor.

METHODS

Six sampling stations were established along the watercourses of Heeia Swamp. Station 1 was a pool at the inland edge where the water depth ranged between 10 and 15 cm. The water originated as overflow from Heeia Stream, entered the station from the marsh, and flowed slowly into the subsidiary channel. The substratum was composed of loose, fine-grained, black mud.

Station 2 was located 56 m downstream from Station 1. Here, the width of the subsidiary channel was 2.5 m and water depth ranged between 15 and 60 cm. The substratum was loose, fine-grained, black mud.

Station 3, 70 m downstream from Station 2, was a pool formed by the junction of Heeia Stream and the subsidiary channel. It was 5.0 m long and 2.5 m wide. Water depth ranged between nine and 94 cm. The substratum was pebbles, shells, and pieces of coral.

Station 4 was located 96 m downstream from Station 3. The width of the channel was 5 m, and the water depth ranged between 15 and 105 cm. The substratum in the center of the channel was similar to that of Station 3, but also contained a small amount of black mud of fine grain. The banks were formed of black mud which accumulated around mangrove roots.

At Station 5, 52 m downstream from Station 4, the width of the channel was 7 m. Water depth ranged between 60 and 120 cm, and the substratum was composed of well-packed mud overlain by about 20 cm of extremely fine-grained flocculent sediment.

Station 6, 80 m downstream from Station 5, was a pond measuring 40 m in length with an average width of 25 m. Water depth varied between 30 and 130 cm. The substratum in the center was composed of pebbles, shells, and pieces of coral, while that of both edges was a similar material overlain by 10 cm of black mud.

Water samples were taken at mid-depth at all stations each month at the time of highest and lowest tide, over a 16-month period, from August, 1961, to November, 1962. The water was analyzed for total salinity, dissolved oxygen, pH, and temperature. Air temperature was also taken. In addition, from October, 1961, to the end of the testing period, monthly

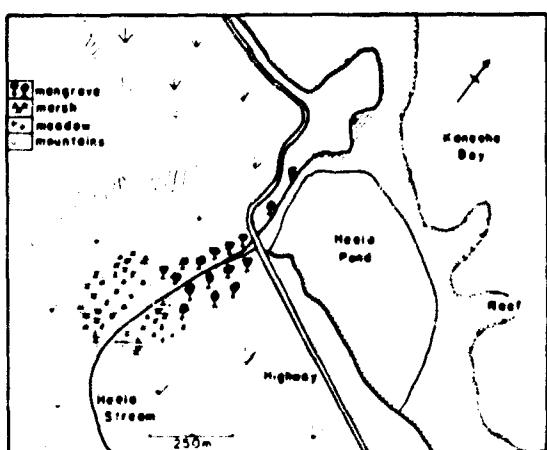


Fig. 1. Map illustrating the topographical relationship between Heeia Swamp, Heeia Pond, Kaneohe Bay, and reef.

measurements were made of Eh of the water and of humidity. In the last three months of the testing period, assays were performed for dissolved nitrate and phosphate.

In addition to the monthly sampling, five studies were made over a 24-hour period at various tidal cycles and seasons. Water samples were taken at Stations 1, 3, and 6 at two-hour intervals from noon on the first day to noon on the second day. Analyses were similar to those performed on a monthly basis. The data from one typical diurnal study are presented in this paper.

Tidal fluctuation was measured by tide staffs permanently fixed at each station. Readings of water level were made to the nearest centimeter.

Salinity was measured by titration with silver nitrate; dissolved oxygen by the Winkler technique; dissolved phosphate by the method of Robinson and Thompson (1948); and dissolved nitrate by the method of Mullin and Riley (1955). Measurements of pH and Eh were made in the field with a Beckman Model G portable pH meter using glass and calomel or platinum and calomel electrodes. Eh readings were corrected to pH 7 as suggested by Mortimer (1941).

Humidity was determined by the wet bulb temperature depression method.

Intensity of light was measured at each station in association with productivity studies at a depth of about 30 cm by the method of Friend (1961). This method uses the principle that paper coated with a light-sensitive diazo compound is bleached upon exposure to light. Light penetration through a stack of diazo paper follows Lambert's Law of Absorption. Paper used was Ozalid 64021T. Underwater light measurements were made by a modification of the method using a watertight Mason jar fitted with a clear plastic cap and sealed with waterproof tape. A calibration curve was obtained by exposing the meter to a light source of known intensity for various in-

tervals of time. Light intensity is expressed as the average number of foot candles of light impinging upon the area over a three-hour period.

Substratum sampling and pH and Eh measurements were performed by the methods suggested by Jackson (1958). Each sample was composed of 15 subsamples taken at regular distances from each other. Organic matter content of the substratum was determined by drying at 110°C. for 24 hours and ashing at 600°C. for six hours. Values obtained were reduced by 15 percent because the clays halloysite, kaolinite, and allophane, which are components of the substratum, retain that amount of water up to 120°C. (Moberly, personal communication).

Water content of the substratum was determined by drying at 110°C. for 24 hours. Values obtained were adjusted upward by 15 percent to compensate for retention of water by the clays.

Particle size analysis was performed by the use of a graded series of geological sieves.

Uptake of dissolved nitrate and phosphate by substratum deposits was determined by the method of Macpherson *et al.* (1958). Twenty-five grams of dried substratum were mixed with 150 ml of phosphate or nitrate solutions of 4.2 $\mu\text{g-at/l}$ and 7.2 $\mu\text{g/l}$ respectively. After continuous shaking for one hour the supernatant fluids were filtered through Whatman #1 filter paper and analyzed as described above for dissolved nitrate and phosphate.

Qualitative faunal and stomach-content analyses were made at each station for determination of food webs.

Determination of the number of primary producer organisms was made by adding 150 ml of 38 percent formaldehyde to each of two one-gallon samples of water from each station. The samples were allowed to settle for 24 hours, after which the water was siphoned off, leaving 15–40 ml of water containing the settled material. Four aliquot samples were taken from each plankton suspension and the primary producers counted at 430X using a Spencer Bright-Line hemacytometer.

Three primary productivity studies were made by the light and dark bottle method at high and low tide respectively at all swamp stations. Light and dark bottles were incubated for three hours at a depth of about 30 cm in the water at the site of collection.

Studies were made of certain animal species to learn if they could survive at stations where they were not found. These were carried out by placing animals in non-toxic, galvanized wire cages (45 cm long and 11 cm square) at each station at a time of spring tide and observing the degree of survival or death.

The role of salinity as a limiting factor was determined for several species by maintaining animals in the laboratory in waters ranging in salinity from fresh water collected from Heeia Stream to full strength sea water. Before an experiment was begun, the animals were kept in the laboratory for at least 24 hours in aerated water from the station at which they were captured.

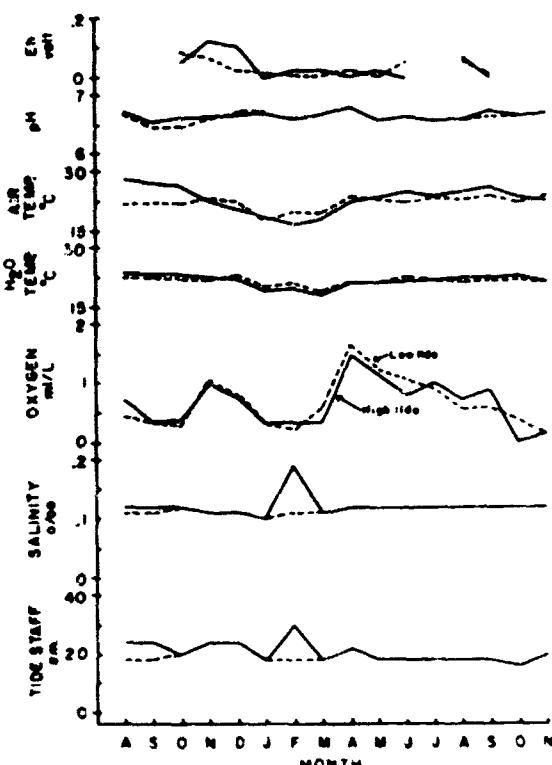


Fig. 2. Monthly physical and chemical data obtained at high and low tide at Station 1; August, 1961–November, 1962. Continuous line designates high tide; dotted line designates low tide.

Low oxygen partial pressure was characteristic of swamp water at low tide. Experiments were performed to determine the partial pressure of oxygen at which selected swamp species began to show symptoms of oxygen lack (surfacing, rolling on side). One to five animals were placed in 400 ml of water in a 500-ml glass-stoppered bottle. Over this was layered 100 ml light mineral oil and the bottle stoppered, care being taken that no air bubbles remained in the oil. At the onset of symptoms of oxygen lack, water was carefully siphoned from the experimental bottle and the oxygen measured.

RESULTS

Station 1

Physical and Chemical Factors

Physical and chemical data collected at Station 1 are presented in Figure 2. This station was influenced by tidal action in August and September, 1961, and February, 1962. Small monthly variations in water level were due to fluctuations in rainfall, with greatest depth after periods of heavy rain.

Salinity at Station 1 was low due to the influx of fresh water from the marsh. The highest salinity, 0.19%, was recorded in February, 1962, the time of highest tide. At all other times salinity of the water varied between 0.11 and 0.12%. Because fresh

Table 1. Average concentration of dissolved nitrate and phosphate at six stations in Heeia Swamp at high and low tide, September–November, 1962.

Station	Nitrate $\mu\text{g/l}$		Phosphate $\mu\text{g-at/l}$	
	High tide	Low tide	High tide	Low tide
1	1.45	1.43	0.70	0.68
2	0.81	1.39	0.62	1.03
3	0.73	1.47	0.92	1.69
4	0.82	1.83	1.11	1.63
5	0.46	0.74	0.56	0.79
6	0.38	1.36	0.57	1.36

water of Heeia Stream gave the same salinity readings, the water of Station 1 may be regarded as fresh.

Oxygen content of the water was that of a dystrophic body, averaging 0.67 ml/l throughout the sampling period. The highest figure, 1.69 ml/l, was recorded in April, 1962. No oxygen was detected in October, 1962. Likewise, pH and Eh values were low and not subject to large diurnal or monthly variation.

Concentration of dissolved phosphate at the stations is given in Table 1. At Station 1 no significant difference was found between the times of high and low tide on the same sampling day, but monthly variation did occur. Table 2 shows that substratum from Station 1 removed over 90 percent of the phosphate from solution.

As did phosphate, the concentration of dissolved nitrate fluctuated monthly, but the concentration was low and substratum deposits from Station 1 removed over 90 percent of the nitrate from solution.

Table 3 gives data obtained by analyses of the substratum of the six stations. At Station 1 black mud extended to a depth of 73 cm and was underlain by coarse sand, pebbles, and shells. The surface was formed by sedimentary deposits and detritus of mangrove origin and was of such an extremely loose nature that no animals were supported by it. Benthic animals were found only along the firmer banks.

The results of a study performed from noon, February 3, to noon, February 4, 1962, are given in Figure 3. In this period occurred the highest tide reported during the sampling months. Tide staff readings throughout the period were constant at 29 cm except at 4:00 a.m. High tide occurred at that time and the tide staff reading rose to 35 cm. The evanescent tidal effect upon Station 1 is illustrated by the

Table 2. Uptake of phosphate and nitrate from water by sedimentary deposits in Heeia Swamp

Station	pH	Eh mV	Phosphate % taken up	Nitrate % taken up
1	4.20	0.061	93.7	93.3
2	4.81	0.062	80.8	53.2
3	5.58	0.074	127	48.0
4	5.90	0.029	106	46.8
5	4.37	0.061	100.0	94.7
6	4.90	0.065	39.2	79.7

Table 3. Composition and physical measurements of superficial sediments in Heeia Swamp.

Station	Composition	pH	Eh volts	% Organic matter	% Water content	Percent retained in sieves; pore size in mm				
						3.35	1.91	0.70	0.45	0.23
1	Black mud	6.80	-0.116	16.25	77.6	0.0	0.0	0.0	0.0	0.0
2	Black mud	6.85	-0.266	28.52	78.1	0.0	0.0	0.0	0.0	0.0
3	Pebbles, coral, gravel, shells	7.53	+0.088	0.48	39.4	52.1	14.0	2.5	19.6	4.9
4	Pebbles, gravel, black mud	7.32	+0.077	5.81	45.2	39.4	12.5	4.6	34.2	5.1
5	Black mud	7.01	-0.135	9.43	92.9	0.0	0.0	0.0	0.0	0.0
6-Center	Pebbles, coral, gravel, black mud	7.64	+0.113	4.14	48.1	74.6	1.4	0.7	5.4	2.5
6-Edge	Black mud	6.95	-0.235	14.12	69.6	0.0	0.0	0.0	0.2	1.1

return of the staff reading to 29 cm at 6:00 A.M. and by the transient rise in salinity at high tide.

Biological Factors

Average values of three light and dark bottle experiments performed upon the water of Station 1 between June and November, 1962, are given in Table 4. No primary productivity was found and no primary producer organisms were ever observed.

The animals found in the water of Station 1 were:

- Pisces
 - 1) *Electrodes sandwicensis*
 - 2) *Lebiasina reticulatus*
 - 3) *Xiphophorus helleri*

Mollusca

- 1) *Melania undulata*
- 2) *Prisium sp.*

Arthropoda

- 1) *Procambarus clarkii*
- 2) *Tendipes tenens* larvae
- 3) Mosquito larvae

The simple food web at Station 1 is shown in Figure 4, with the electrid *E. sandwicensis* as the top carnivore, a position it holds at all stations.

STATION 2

Physical and Chemical Factors

Physical and chemical data collected at Station 2 are given in Figure 5. Mean high tide mark was 44 cm and mean low level was 25 cm. The difference of 19 cm between mean high tide and mean low tide, and 40 cm between highest and lowest water, illustrate the greater influence of the tide upon Station 2 than upon Station 1. This influence is further emphasized by fluctuations of the physical and chemical parameters with tidal flux. Salinity ranged from 0.11‰ at low tide in December, 1961, to 38.75‰ in September, 1961.

Dissolved oxygen, pH, and Eh were similar to those of Station 1 but were generally highest at high tide. As at all stations, a seasonal variation in dissolved oxygen was noted, with highest values in the spring and late fall.

The dissolved phosphate and nitrate content of the water (Table 1), highest at low tide, was low. Similar results were obtained at all other stations affected by the tide. Table 2 shows that at Station 2 80.8 percent of the phosphate and 53.2 percent of the ni-

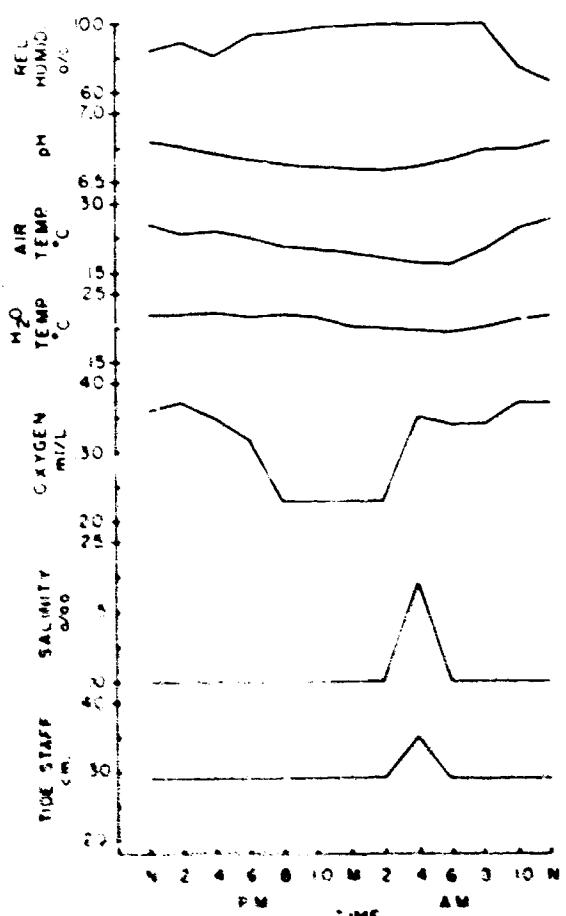


Fig. 3. Diurnal changes in physical and chemical conditions at Station 1 from noon, February 3, to noon, February 4, 1962.

Table 4. Average of quantities of carbon assimilated during the light and dark bottle experiments performed at high and low tide respectively in the water at six stations in Heeia Swamp between April and November, 1962.

Station	Tide	Carbon assimilated g/l/hr	Average light intensity, foot candles
1	High	0.00	398
	Low	0.00	388
2	High	0.01	200
	Low	0.01	289
3	High	0.03	355
	Low	0.00	141
4	High	0.97	310
	Low	0.00	207
5	High	0.21	1,180
	Low	0.11	678
6	High	0.25	1,000
	Low	0.22	5,835

trate were removed from solution by mud. This could partly account for the low concentrations found. The diminution of the amount of phosphate at high tide was most likely due to dilution by tidal water. It is also possible, however, that changes of a physical and chemical nature with ebb and flow could affect the equilibrium constant of phosphate and mud. The experiments of Mortimer (1941), Macpherson *et al.* (1958), and Helper (1958) lend credence to this possibility.

Data obtained from analyses of the substratum are given in Table 3. These are similar to those of Station 1 except that the Eh was lower and the percentage of organic matter higher. Mud extended to a depth of 97 cm and was underlain by substratum similar to that underlying the mud of Station 1.

Biological Factors

Three light and dark bottle experiments were performed at high and at low tide between June and November, 1962. Average results of these tests are given in Table 4, where it is shown that no appreciable primary productivity occurred at Station 2. In addition to this, although many searches were made, no primary producer organisms were found in the water.

With the exception of the bivalve, *Pisidium*, the fauna and food web at Station 2 were identical to those of Station 1.

STATION 3

Physical and Chemical Factors

Figure 6 illustrates the physical and chemical data obtained at Station 3. Mean high tide level was 74 cm and the mean low tide reading was 19 cm. Associated with this tidal fluctuation was great variation in salin-

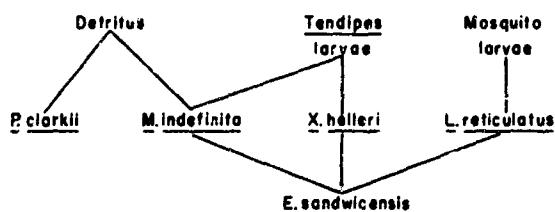


Fig. 4. Food web at Station 1. The first trophic level is shown at the top.

ity, which ranged from 0.14‰ at low tide in June, 1962, to 37.83‰ at high tide in September, 1961. Similarly, dissolved oxygen, pH, Eh, and water temperature fluctuated widely with tidal penetration. Dissolved phosphate and nitrate content of the water, lowest at high tide, was low (Table 1).

Results of sediment analyses are given in Table 3. A substratum of shells, coral, and pebbles predominated. Station 3 differed from the others by the absence of mangrove roots around which sediment accumulates. Due to this and tidal flushing, the substratum was similar to that underlying the sedimentary deposits at the other stations.

Figure 7 illustrates the results of a diurnal study performed at Station 3 from noon, September 15, to noon, September 16, 1962, a period in which two high tides of almost equal amplitude occurred. Salinity

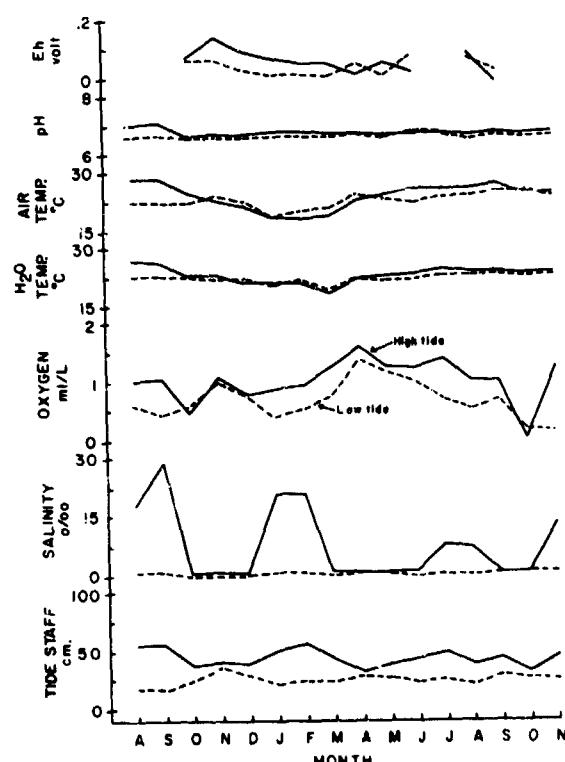


Fig. 5. Monthly physical and chemical data obtained at high and low tide at Station 2; August, 1961–November, 1962.

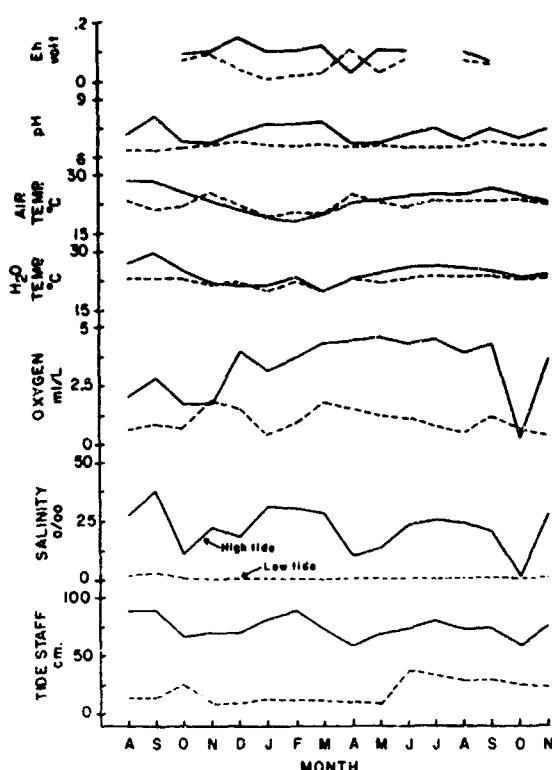


Fig. 6. Monthly physical and chemical data obtained at high and low tide at Station 3; August, 1961–November, 1962. Continuous line designates high tide; dotted line designates low tide.

fluctuated with the degree of tidal penetration. In general, fluctuation of oxygen content and pH of the water paralleled that of the tide. An exception was found at 10:00 P.M. and midnight when oxygen and pH rose slightly. Heavy rains began to fall at 8:00 P.M. Increasing dissolved oxygen and pH after a heavy rain were often noted. Higher oxygen values at 2:00 A.M. and 4:00 A.M. resulted from the effect of high tide and rain.

Biological Factors

Table 4 gives average values for three light and dark bottle experiments performed at high and at low tide at Station 3. No measurable primary productivity occurred at low tide, but a very small evolution of oxygen was found at high tide. Microscopic analysis of the water revealed only an occasional diatom.

The number of animal species collected at Station 3 was small:

Pisces

- 1) *Eleotris sandwicensis*
- 2) *Lebistes reticulatus*
- 3) *Xiphophorus helleri*
- 4) *Chonophorus genivittatus*
- 5) *Kuhlia sandvicensis*

Mollusca

- 1) *Neritina tahitiensis*

Arthropoda

- 1) *Metopograpsis messor*
- 2) Copepods
- 3) Mosquito larvae

Several species not found at Station 2 were added to the list. These are the common estuarine forms, *Kuhlia sandvicensis*, *Neritina tahitiensis*, and *Metopograpsis messor*. Also added to the list was the freshwater goby, *Chonophorus genivittatus*. Missing were *Melania indefinita*, which disappeared a short distance upstream from Station 3, *Procambarus clarkii*, and *Tendipes tentens* larvae.

The food web at Station 3 is given in Figure 8.

STATION 4

Physical and Chemical Factors

Physical and chemical data obtained at this station are given in Figure 9. Mean high tide reading was 81 cm and mean low reading was 22 cm, a tidal amplitude 4 cm greater than at Station 3.

In general, all factors measured were slightly higher than at the previous station because of greater tidal influence.

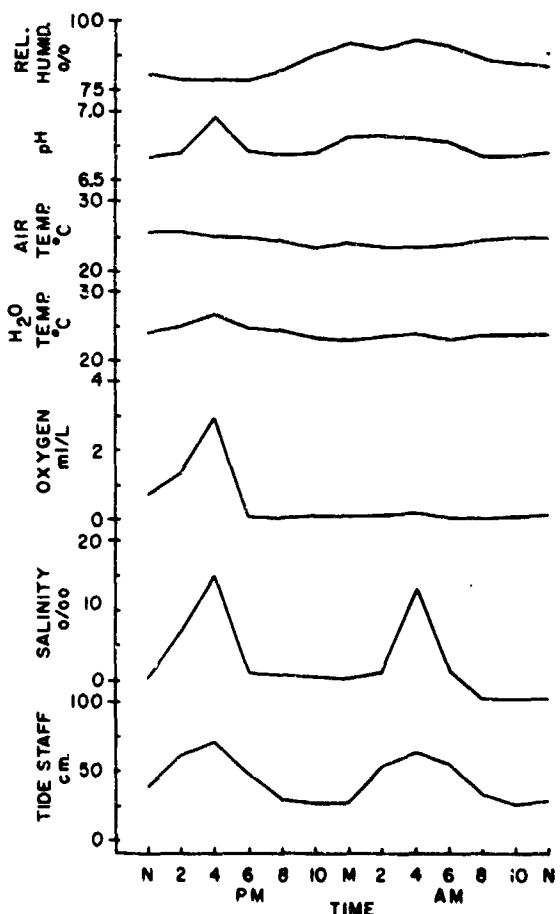


Fig. 7. Diurnal changes in physical and chemical conditions at Station 3 from noon, September 15, to noon, September 16, 1962.

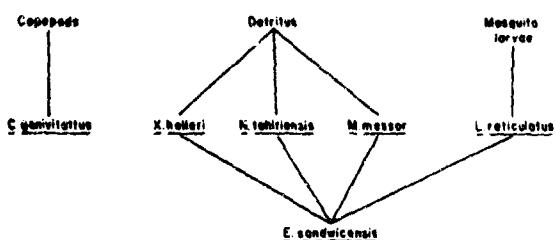


Fig. 8. Food web at Station 3. The first trophic level is shown at the top.

Substratum data (Table 3) were similar to those of Station 3 except for black flocculent mud which was present along the banks.

Biological Factors

Tables 5 and 6 show that no primary producers were found at Station 4 at low tide, but that a small number were present at high tide.

Average results of three light and dark bottle experiments performed at high and low tide are given in Table 4. These indicate that at low tide, no primary productivity was found, while at high tide a small amount of carbon was assimilated.

Species of animals found at Station 4 are shown in the following list:

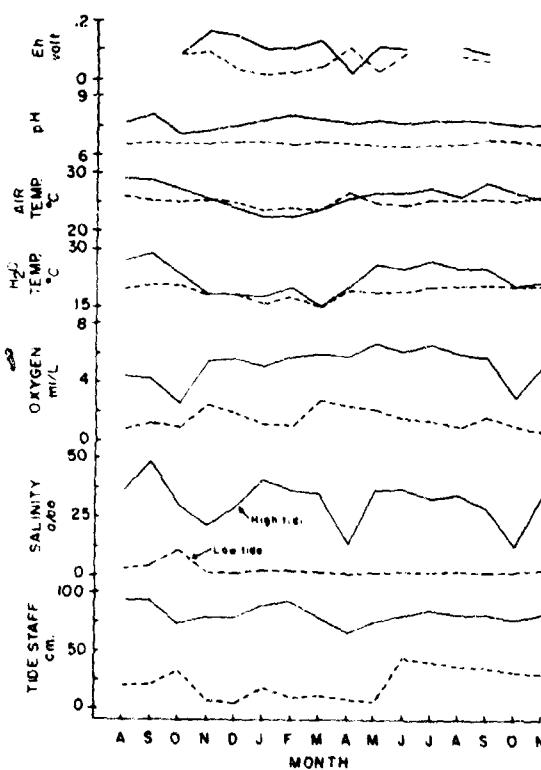


Fig. 9. Monthly physical and chemical data obtained at high and low tide at Station 4; August, 1961–November, 1962. Continuous line designates high tide; dotted line designates low tide.

Pisces

- 1) *Eleotris sandwicensis*
- 2) *Lebistes reticulatus*
- 3) *Kuhlia sandvicensis*
- 4) *Tilapia mossambica*
- 5) *Conger marginatus*

Arthropoda

- 1) *Scylla serrata*
- 2) Copepods

A striking aspect of Station 4 is that very few individuals of each species were collected and each was of a motile type which could move easily into or out of the area. Stomach analyses indicated that the fauna was composed of transient forms and no evidence for a permanent local food web was found.

STATION 5

Physical and Chemical Factors

Figure 10 illustrates physical and chemical data obtained at Station 5. Mean high tide was 77 cm and mean low tide was 8 cm, a tidal variation of 10 cm greater than that at Station 4. Dissolved oxygen, pH, Eh, and temperature were higher here at comparable stages of the tide than at the previous stations.

Dissolved phosphate and nitrate concentrations were lower than elsewhere (Table 1). It is shown in Table 2 that 100 percent of the phosphate and 94.7 percent of the nitrate were removed from solution by the sub-

Table 5. Changes in abundance of phytoplankton with tide at three stations in Heeia Swamp in 1962.

Month	Tide	Phytoplankters per liter (Station)		
		4	5	6
September	High	3,128	162,170	180,020
	Low	0	76,028	86,122
October	High	0	185,100	175,332
	Low	0	103,414	93,542
November	High	31,872	191,856	197,758
	Low	0	81,007	102,722

Table 6. Relative abundance of primary producer organisms found at high tide at Stations 4–6 in Heeia Swamp in November, 1962.

Organism	Station Percent of total		
	4	5	6
<i>Navicula</i>	12.0	23.1	25.2
<i>Chaetoceros</i>	70.0	33.9	43.7
<i>Nitzschia</i>	10.0	23.3	17.7
<i>Surrella</i>	8.0	7.7	5.0
<i>Pleurostigma</i>	0.0	4.6	1.7
<i>Gyrostigma</i>	0.0	1.5	1.7
<i>Grammatophora</i>	0.0	0.0	0.9
<i>Ulothrix</i>	0.0	3.1	2.5
<i>Chlamydomonas</i>	0.0	3.1	1.7

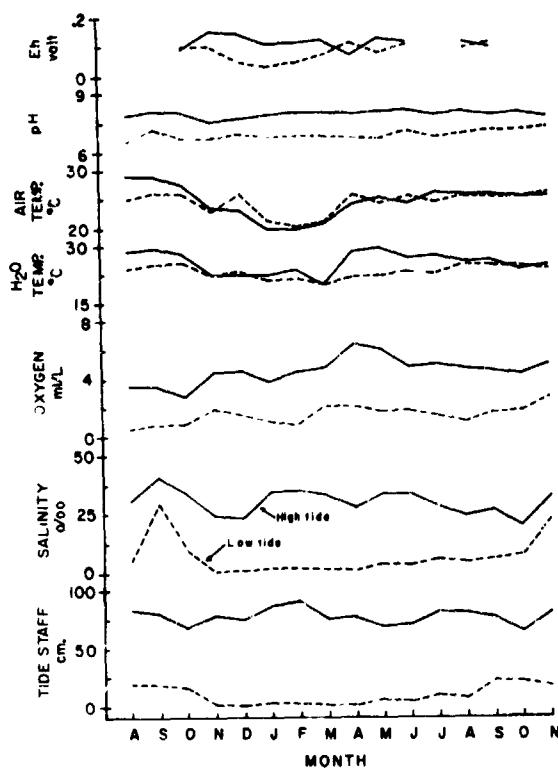


Fig. 10. Monthly physical and chemical data obtained at high and low tide at Station 5: August, 1961–November, 1962. Continuous line designates high tide; dotted line designates low tide.

stratum. This could account for the low concentrations of these substances there.

The substratum (Table 3) was composed of black mud overlain by about 20 cm of suspended matter of very fine grain.

Biological Factors

Data presented in Table 5 show that a large number of primary producers existed at both high and low tides at Station 5. Differential counts of these producers taken at high tide November, 1962, are presented in Table 6; diatoms comprised 93.8 percent of the total.

Average results of three light and dark bottle experiments performed at high and low tide are given in Table 4. A measurable primary productivity occurred at both high and low tide. The greater carbon assimilation at high tide was probably due to the presence of a larger number of producer organisms.

The animals found at Station 5 were:

Pisces

- 1) *Eleotris sandwicensis*
- 2) *Kuhlia sandricensis*
- 3) *Tilapia mossambica*
- 4) *Oxyurichthys longhotus*
- 5) *Mugil cephalus*

Arthropoda

- 1) *Charybdis orientalis*
- 2) *Metopograpsis messor*
- 3) *Palaeomonetes sp.*
- 4) *Macrobrachium sp.*
- 5) Copepods

Mollusca

- 1) *Littorina scabra*
- 2) Unidentified nematode

Although a greater number of animal species was found at Station 5 than at the previous four stations, their numbers were small, and no food web could be drawn. The lack of an extensive estuarine fauna at Station 5 may have resulted from the flocculent nature of the substratum in the center. It is significant that no animals were captured when traps were placed in the center of the station, although many attempts were made. The banks of the channel were firm, however, and it was there that all animals were taken.

STATION 6

Physical and Chemical Factors

Data for this station are given in Figure 11. Mean high tide reading was 80 cm and mean low tide reading was 8 cm, with a difference of 95 cm between maximum and minimum tides. This is slightly less

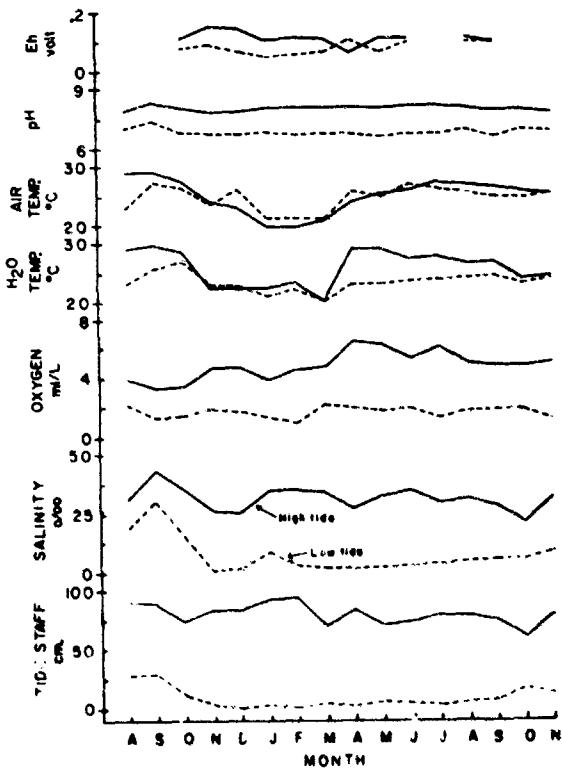


Fig. 11. Monthly physical and chemical data obtained at high and low tide at Station 6: August, 1961–November, 1962. Continuous line designates high tide; dotted line designates low tide.

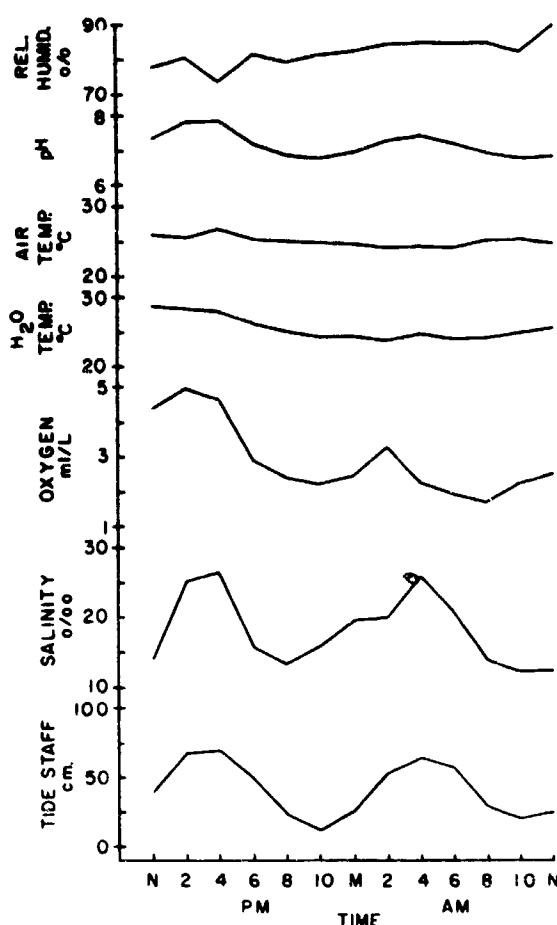


Fig. 12. Diurnal changes in physical and chemical conditions at Station 6 from noon, September 15, to noon, September 16, 1962.

than that found in Kaneohe Bay, where a difference of 101 cm between maximum and minimum tides was found during the 16-month sampling period. Because of its proximity to Kaneohe Bay, physical and chemical conditions at Station 6 at high tide approached those of the bay, where salinity fluctuated between 34.38 and 35.88 ‰, and oxygen between 4.02 and 6.07 ml/l.

Table 3 gives data from analyses of the substratum. On the east and west sides of Station 6 the substratum was composed of black mud, while the central portion was shells, coral, and pebbles. The data show that the center and edges were considerably different environments. This was caused by rapid tidal movement of water over the central portion and at low tide by slightly brackish channel water.

Figure 12 illustrates the results of a 24-hour study performed at Station 6 from noon, September 15, to noon, September 16, 1962. At this time two high tides of almost equal amplitude occurred in the afternoon and early morning. The tide staff reading during the first high tide was 70 cm at 4:00 p.m. At 4:00 a.m. the staff reading was 65 cm. Salinity and pH values

fluctuated with the tide, but there was a decrease in dissolved oxygen in the water before each high tide. This decrease was greater during the early morning tide, indicating that the oxygen content of the water at Station 6 was regulated by factors in addition to those associated with the tide. Absence of an oxidized microzone in the substratum and the greater loss of oxygen at night suggest the loss was due to uptake by organisms.

Biological Factors

Table 5 shows that a large number of primary producer organisms existed in the water at Station 6. Results of differential counts of these organisms taken at high tide in November, 1962, are given in Table 6; diatoms comprised 95.8 percent of the total population.

Table 4 gives the average results of three light and dark bottle experiments performed at high and low tide at this station. A measurable quantity of primary production occurred at both high and low tides. At high tide this was considerably greater than at any other station, and at low tide was equal to that at Station 5.

Station 6 supported a larger fauna than did any other station:

Pisces

- 1) *Elecotris sandwicensis*
- 2) *Kuhlia sandvicensis*
- 3) *Oxyurichthys longchotus*
- 4) *Mugil cephalus*
- 5) *Conger marginatus*
- 6) *Tilapia mossambica*
- 7) *Chonophorous genivittatus*
- 8) *Lebistes reticulatus*
- 9) *Xiphophorous helleri*

Arthropoda

- 1) *Scylla serrata*
- 2) *Charybdis orientalis*
- 3) *Metopograpsis messor*
- 4) *Podophthalmus vigil*
- 5) *Portunis sanguinolentus*
- 6) *Macrobrachium sp.*
- 7) *Palaemonetes sp.*
- 8) *Alpheus fabricius makayii*
- 9) *Limnoria lignorum*
- 10) Copepods
- 11) Unidentified shrimp of tribe Carida
- 12) Ostracods

Mollusca

- 1) *Littorina scabra*
- 2) *Melampus parvulus*
- 3) *Scissulina dispar*

Polychaeta

- 1) *Scolelepus sp.*

Coelenterata

- 1) *Mastigias ocellata*

Nematoda

- 1) Unidentified nematode

A diagram of the food web at Station 6 is given in Figure 13. Of the permanent residents, *Eleotris sandwicensis* and *Scylla serrata* are the top carnivores. Most of the animals of Station 6 are typical estuarine forms. Of those which are not, *Conger marginatus* is an occasional visitor at high tide, while *Chonophorus genivittatus*, *Lebistes reticulatus*, and *Xiphophorus helleri* occur there after having been swept downstream.

ANIMAL EXPERIMENTS

FIELD

Table 7 gives the results of the experiment designed to test the capacity of several animal species to live at all of the six stations. *Eleotris sandwicensis*, the only species found at all stations, was also the only one to survive for seven days at all stations. The crayfish, *P. clarkii*, survived at all stations for five days, but became cannibalistic after that time and prematurely terminated the experiment. Other animals collected at Station 6 failed to survive at Stations 1-4. The goby, *O. longirostris*, and the portunid crab, *C. orientalis*, succumbed within one day at Stations 1-4. The

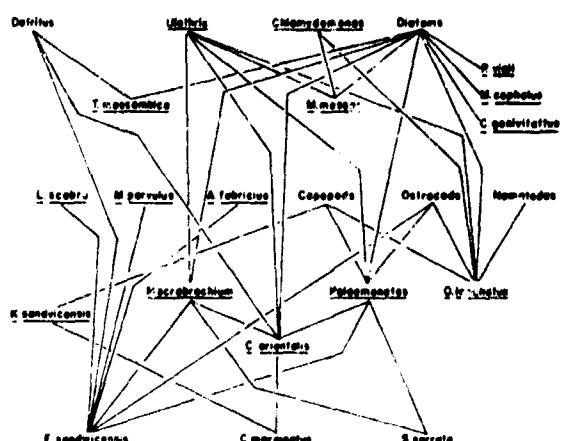


Fig. 13. Food web at Station 6, with primary producers at the top and leading downward to terminal carnivores.

shrimp, *Palaeomonetes* and *Macrobrachium*, both of which are highly tolerant to salinity change, lived longer, but failed to survive one week.

Table 7. Survival time in days of animals in wire baskets at six stations in Heeia Swamp. Figures show the number of animals surviving.

	<i>E. sandwicensis</i> (10 tested)	<i>O. longirostris</i> (10 tested)	<i>Palaeomonetes</i> (10 tested)	<i>Macrobrachium</i> (10 tested)	<i>P. clarkii</i> (8 tested)	<i>C. orientalis</i> (3 tested)	<i>S. serrata</i> (3 tested)
<i>Station 1</i>							
Day 1	10	0	0	0	8	0	0
2	10	0	0	0	8	0	0
3	10	0	0	0	-	0	0
5	10	0	0	0	6	0	0
7	10	0	0	0	-	0	0
<i>Station 2</i>							
Day 1	10	0	0	3	8	0	0
2	10	0	0	0	7	0	0
3	10	0	0	0	-	0	0
5	10	0	0	0	6	0	0
7	10	0	0	0	-	0	0
<i>Station 3</i>							
Day 1	10	0	1	5	7	0	0
2	10	0	1	4	7	0	0
3	10	0	0	3	-	0	0
5	10	0	0	0	7	0	0
7	10	0	0	0	-	0	0
<i>Station 4</i>							
Day 1	10	0	5	6	7	0	1
2	10	0	2	6	7	0	1
3	10	0	0	6	-	0	1
5	10	0	0	3	6	0	0
7	10	0	0	0	-	0	0
<i>Station 5</i>							
Day 1	10	10	10	10	8	3	3
2	10	10	10	10	6	3	3
3	10	10	10	10	-	3	3
5	10	9	10	10	4	3	3
7	10	9	10	10	-	3	3
<i>Station 6</i>							
Day 1	10	10	10	10	8	3	3
2	10	10	10	10	8	3	3
3	10	10	10	10	-	3	3
5	10	10	10	10	8	3	3
7	10	9	10	10	-	3	3

Table 8. Salinity tolerance of several animal species from Heeia Swamp.

Animal	Range of salinity tolerance %
<i>Electris sandwicensis</i>	0-35.1
<i>Orynnichthys longhotus</i>	0.5-35.1
<i>Palaemonetes</i>	3.9-35.1
<i>Macrobrachium</i>	0.5-35.1
<i>Charybdis orientalis</i>	9.2-35.1
<i>Chonophorus genivittatus</i>	0-35.1
<i>Scylla serrata</i>	9.2-35.1

LABORATORY

Table 8 shows that all animals tested tolerated wide ranges of salinity and *E. sandwicensis* and *C. genivittatus* were capable of surviving in both fresh and full-strength sea water.

Experiments upon the tolerance to low oxygen partial pressure in the water showed that *E. sandwicensis* could survive for two hours in water in which no oxygen could be detected. However, *O. longhotus*, *Palaemonetes*, and *Macrobrachium* showed signs of distress at oxygen concentrations of 1.31, 1.33, and 1.02 ml oxygen/l respectively.

DISCUSSION AND CONCLUSIONS

Heeia Swamp was found to be an estuarine environment with sharp gradients in hydrographic conditions associated with tidal penetration. At the landward edge, where tidal effect was slight and evanescent, hydrographic conditions fluctuated little, both diurnally and seasonally. Proceeding oceanward, the degree of tidal amplitude increased. Because of the sharp drop in contour of the land toward the sea, the water in the channels at low tide was almost wholly fresh from Heeia Stream; at high tide water from Kaneohe Bay dominated hydrographic conditions. The role of the large marsh behind the swamp was significant, especially at low tide. Water from Heeia Stream as it entered the marsh contained large amounts of dissolved oxygen, nitrate, and phosphate. As it emerged from the marsh and entered the swamp, these substances almost disappeared. Thus, except at the landward edge, the swamp was subjected to large tidal changes of salinity, dissolved oxygen, pH, and temperature. In addition, the area was one of deposition and decay. Sedimentary and organic detritus accumulated around the prop roots of the trees, producing a fine-grained substratum with considerable organic matter, alkaline pH, low Eh, and containing hydrogen sulfide. Under such circumstances it is not surprising that the most striking aspect of Heeia Swamp was its paucity of animal species, particularly at Stations 1-5. Of great importance was the lack of an appreciable primary productivity at Stations 1-4. This was probably due to the combined effects of hydrogen sulfide and low concentrations of nitrate and phosphate. At the seaward edge (Station 6) hydrographic and substratum conditions were less extreme

and the fauna contained elements similar to those reported for mangrove stands at Low Isles (Stevenson et al., 1931), Puerto Rico (Golley et al., 1962), Mozambique (Macnae and Kalk, 1962), and Venezuela (Rodriguez, 1963). These included portunid and grapsoid crabs, littorine snails, polychaetes, *Neritina*, and gobies. Absent, however, were oysters, barnacles, holothurians, tunicates, sponges, amphipods, and isopods. The zooplankton of Station 6 was composed of adult and larval copepods and the larvae of fish, shrimp, crabs, and barnacles, but was extremely impoverished compared to that of the brackish-water mangrove areas of southern Florida (Davis and Williams, 1950). However, the plankton was similar to that reported by Mattox (1949) for the mangrove swamps of Puerto Rico, where phytoplankters predominated and zooplankters were relatively scarce.

Stevenson et al. (1931), in a study of the mangrove forest at Low Isles, reported that the roots of *Rhizophora mucronata* support a large epifauna in some areas, while elsewhere in the same stand they are clean and bare, but no data were presented to explain this. Rodriguez (1963) stated that mangroves of mesohaline and oligohaline waters commonly support fewer species on the roots than do those of euhaline waters, and that the fauna of the mud is also relatively impoverished. In Heeia Swamp all species tested were tolerant to large changes in salinity, and as would be expected, freshwater species lived at the inland edge and brackish and euhaline forms lived nearer the bay. Conspicuously absent were oysters, and it is probable that low saline conditions in Heeia Swamp would inhibit their early development. It is possible that the same is true for barnacles, and that the adults of holothurians, tunicates, and sponges could not survive in the reduced salinities at low tide. It is significant that another, more euhaline, Hawaiian mangrove swamp located in Pearl Harbor supported large oyster and barnacle populations.

Field studies described in this paper show that the animals tested were incapable of living for extended periods outside the areas where they were normally found. Laboratory data presented show that these species were intolerant to low salinities present at low tide at inner stations where they were not found and indicate that salinity was a main factor limiting distribution. In addition to this, studies upon oxygen requirements of several swamp species showed that the amount of dissolved oxygen present in the water at low tide at the inland stations was incapable of supporting them. If placed in water from the inland stations when salinity was not too low, animals from Station 6 showed almost immediate symptoms of oxygen lack (e.g., surfacing). If air was bubbled through the water, however, such symptoms disappeared. Conversely, *E. sandwicensis*, the only animal found at all stations, could survive in the absence of detectable oxygen for periods of time as long as two hours. It is possible that low salinity and reduced oxygen acted together as limiting factors in Heeia Swamp.

The nature of the substratum was also an important

limiting factor. At Stations 1, 2, 4, and 5, it consisted of a loose, flocculent sediment, incapable of supporting benthic animals except along the banks. At Station 6 the substratum was firm enough to support a relatively large benthic fauna, and substratum preference at this station was evident from the fact that no animals lived on the stony portion, all animals preferring the adjacent muddy sections.

It would seem that, as sediment accumulates along the ocean edge and mangrove trees migrate bayward, hydrographic conditions will stabilize and new euhaline species will move in while others are lost. A long-term study of this and other similar areas would contribute greatly to our knowledge of the mangrove habitat and its evolution.

SUMMARY

Ecological conditions in Heeia Swamp, an intertidal mangrove forest on the island of Oahu, Hawaii, are described. Mangrove species present were *Rhizophora mangle* and *Bruguiera sexangula*. Six hydrographic stations were established along watercourses extending from the seaward to the landward edges of the swamp. At the landward edge salinity varied between 0.10 and 0.19 %, and oxygen from an undetectable amount to 1.69 ml/l. The conditions of pH and Eh of both water and substratum were those of a dystrophic body of water, and no primary productivity was found. The fauna at the inland edge was composed of eight freshwater species. At the ocean edge of the swamp hydrographic conditions were influenced greatly by tidal flux, with salinity ranging from 1.00 to 43.30 %, and oxygen from 0.92 to 6.53 ml/l. Twenty-seven animal species lived at the ocean edge, and a large primary productivity was found.

The types of animals present and their distribution in the swamp were regulated by gradients in salinity and oxygen and by the flocculent nature of the substratum in some sections.

Author's Note: This paper is Contribution No. 203, Hawaii Institute of Marine Biology. It is a portion of a thesis submitted in partial fulfillment of the requirement for the degree of Doctor of Philosophy in Zoology.

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LITERATURE CITED

- BOWMAN, H. H. M., 1917. Ecology and physiology of the red mangrove. *Proc. Am. Phil. Soc.*, 56:589-672.
- CHAPMAN, V. J., 1940. The botany of the Jamaica shoreline. *Geograph. J.*, 96:312-323.
- DAVIS, C. C., and R. H. WILLIAMS, 1950. Brackish water plankton of mangrove areas in southern Florida. *Ecology*, 31:519-531.
- DAVIS, J. H., JR., 1940. The geologic role of mangroves in Florida. *Papers from the Tortugas Lab.*, 32:303-412. Carnegie Inst., Washington, D. C.
- DAVIS, J. H., JR., 1942. The ecology of the vegetation and topography of the sand keys of Florida. *Papers from the Tortugas Lab.*, 33:113-195. Carnegie Inst., Washington, D. C.
- EGLER, F. E., 1948. The dispersal and establishment of the red mangrove, *Rhizophora*, in Florida. *Caribbean Forester*, 9:299-319.
- FRIEND, D. T. C., 1961. A simple method of measuring integrated light values in the field. *Ecology*, 42:577-580.
- GOLLEY, F., H. T. ODUM, and R. F. WILSON, 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology*, 43:9-19.
- GUPPY, H. B., 1906. Observations of a naturalist in the Pacific between 1896 and 1899. *Plant Dispersal*; vol. 2. Macmillan, London.
- HELPHER, B., 1958. On the dynamics of phosphorus added to fish ponds in Israel. *Limnol. Oceanogr.*, 3:84-100.
- JACKSON, M. L., 1958. *Soil chemical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.
- MACNAE, W., and M. KALK, 1962. The ecology of the mangrove swamps at Inhaca Island, Mozambique. *J. Ecology*, 50:19-34.
- MACPHERSON, L. B., N. R. SINCLAIR, and F. R. HAYES, 1958. Lake water and sediment, III. The effect of pH on the partition of inorganic phosphate between water and oxidized mud or its ash. *Limnol. Oceanogr.*, 3:318-326.
- MATTOX, N. T., 1949. Studies on the biology of the edible oyster, *Ostrea rhizophorae* Guilding, in Puerto Rico. *Ecol. Monographs*, 19:341-356.
- MORTIMER, C. H., 1941. The exchange of dissolved substances between mud and water in lakes. *J. Ecology*, 29:280-329.
- MULLIN, J. B., and J. P. RILEY, 1955. The spectrophotometric determination of nitrate in natural waters with particular reference to sea water. *Anal. Chem. Acta*, 12:464-480.
- ORR, A. P., and F. W. MOOREHOUSE, 1933. Physical and chemical conditions in mangrove swamps. Great Barrier Reef Expedition, 1928-1929. *Sci. Rept.*, 2:102-110.
- ROBINSON, R. J., and T. G. THOMPSON, 1948. The determination of phosphate in sea water. *J. Marine Res.*, 7:33-41.
- RODRIGUEZ, G., 1963. The intertidal estuarine communities of Lake Maracaibo, Venezuela. *Bull. Marine Sci. Gulf and Caribbean*, 13:197-218.
- STEVENSON, T. A., A. STEVENSON, G. TANDY, and M. SPENDER, 1931. The structure and ecology of Low Isles and other reefs. Great Barrier Reef Expedition, 1928-1929. *Sci. Rept.*, 3:17-112.
- WARMING, E., and M. VAHL, 1925. *Oecology of plants*. Oxford Univ. Press, London.

Zonation Within Mangroves Associated with Estuaries in North Queensland

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This paper is concerned with the mangrove swamps near Townsville, Australia, and compares them with others along the Hinchinbrooke Channel, Innisfail, and Cairns, to explain the succession and distribution of both plants and animals. The study is concerned, primarily, with the estuaries in Queensland, Australia, between Townsville at 19° S and Mossman at 17° S, around Gladstone at 24° S, and in the vicinity of Brisbane at 26° S.

The word mangrove has an obscure origin; it is a combination of the Portuguese "mangue" and the English "grove". It describes an association of trees which grow in the sea or it may describe the individual species which make up the association. In this paper the word will be used in either sense.

DESCRIPTION OF MANGROVE AREAS IMMEDIATELY TO THE SOUTH OF TOWNSVILLE

Townsville lies on the banks of Ross Creek, a tributary of the Ross River. North and south of the city, along the shores of Cleveland Bay, are several square miles of low-lying terrain, much of which is only some 10 m above sea level. These flats are deltaic deposits laid down in embayments during Pleistocene interglacial periods when the sea level was higher than it is today (Jardine, 1928). Aerial photographs indicate that the old courses of the Ross River once crossed the region over a wide area north of Townsville. The present river mouth seems to be a southern extension of the series. The movement of the river channel may not yet have ceased. Meandering across the flat lands to the south are several creeks, some of which are, at times of heavy spates in the river and at extreme flood tides, connected to the main stream of the river.

The estuarine portions of these creeks and the main river channel are lined with mangroves (Figs. 1, 2). Most of the mangroves have been cleared from Ross Creek in Townsville.

The intertidal portion of these low-lying flats is extensive, as might be expected in a region where the tidal range is up to 3.5 m.

The annual rainfall in the Townsville district is around 1,000 mm (40 inches), the bulk of which falls between December and March (Fig. 3). The soils are well drained; hence, the vegetation of the flats consists of drought-resistant grassland and sparse thorn trees.

THE MANGROVE FLORA

On the landward side of the flats, at the level of extreme high tides, *Sporobolus virginicus* (L.) Kunth (an almost cosmopolitan grass in warm temperate and tropical regions) is dominant, and around high-water mark it becomes mixed with *Sesuvium portulacastrum* L., *Arthrocnemum leiosachyum* (Benth.) Paulsen, and *A. halimoides* Nees var. *pergranulatum* J. M. Black, which gradually displace the grass and extend to the flats below. (The Australian species of *Arthrocnemum* and *Sesuvium* must be considered to be *sub judice* and in need of revision. According to Moss (1954), the Australian *A. leiosachyum* is *A. indicum* (Willd.) Moq., a species which extends from Natal, in South Africa, to Timor.) They do not go much lower than the level of ordinary spring tides. Locally, bushes of *Suaeda* are common.

In many places along the upper beach a "salting cliff" is found; it is about 20 cm high. High waters of ordinary spring tides lap the base of the little cliff and extreme high tides pass just above it. Below the cliff is a bare flat of fine, sandy mud, which is slimy when wet, and criss-cross cracked and salt-encrusted when dry. This flat is covered by only 117 tides annually (Fig. 4), ranging from as few as four in May and June to 21 in March. Occasional higher "islands" in the flats support the flora mentioned above.

In the absence of a salting cliff the upper beach slopes gently, and the sward of *Sesuvium* and *Arthrocnemum* may be invaded by quite widely spaced trees of *Acacia marina* (Forst.) Vierh. to form an *Acacia* parkland or a landward *Acacia* fringe. Occasional sprawling shrubs of *Aegialitis annulata* R. Br. and bushes of *Eucalyptus agallocha* L. also occur here. This parkland eventually gives way to thickets of *Ceratopetalum* (Perr.) C. B. Rob., beyond which vegetatively bare areas lie.

Seaward or toward the creeks, one passes from the bare areas into *Ceratopetalum* thickets. Where these bare flats extend to the high water mark, crabs are first encountered near the periphery of the thickets. None of the bushes of *Ceratopetalum* are tall (1.5 to 3 m) near Townsville.

The *Ceratopetalum* give way to a mixed community dominated by *Braggiera gymnorhiza* (L.) Lam. Common associates include *B. exaltata* Ding Hou, *Xylocarpus granatum* Koenig, and occasional trees

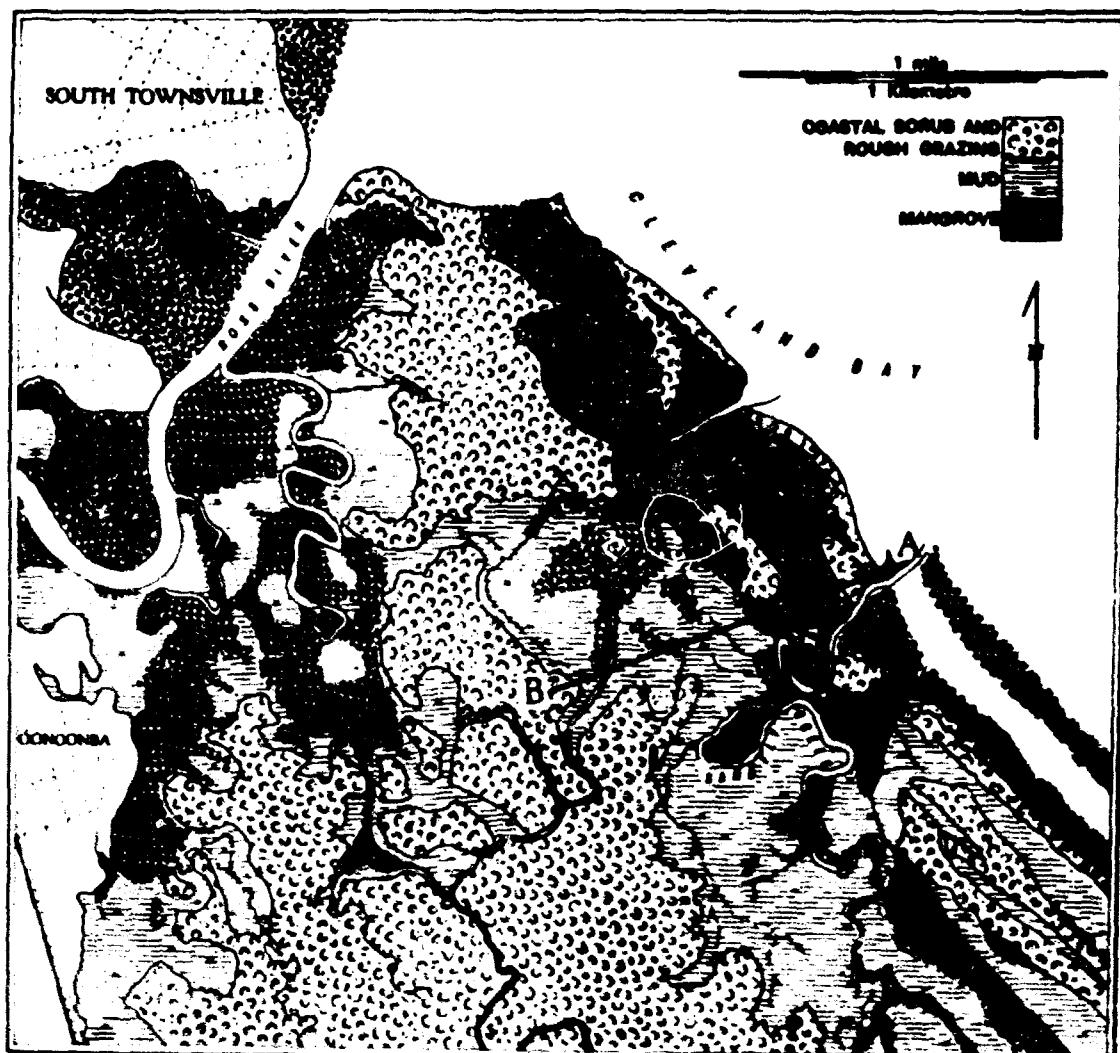


Fig. 1. Map of the mangroves south of Townsville. It should be noted that the mangroves are creek-based and that there are extensive bare areas of mud. The line A-B is the line of transect in Fig. 3A.

of *Rhizophora stylosa* Griff. and *Aegiceras marina*. This mixed community extends to the margin of the creek, which is fringed by either *Rhizophora* or *Aegiceras*.

Along the shore of the bay, ranges of low sand dunes are found. Where the mangrove extends to the inner slope of a dune, a richer flora of mangrove trees occurs. *Obiornia petiolaris* F. Muell. (a myrtaceous shrub restricted to Australia), *Eucoccyxa agallocha*, and *Lumnitzera racemosa* Willd. occur at and around the high-water mark. The lianas, *Cynanchum corneum* (R. Br.) Domke, and *Pteris trifoliata* Lour. tie everything together. *Obiornia*, *Pemphis acidula* Forst., and *Sarcocolla laevigata* (Gerts.) Roxb. ($= S. sericea$ Vahl) dominate the higher levels of the dune.

Seaward of the dunes, *Ceriops tagal* and *Aegiceras* extend to a level just below the high water of the neap tides. *Aegiceras* forms the seaward fringe. Oc-

casional trees of *Rhizophora stylosa* and the two species of *Bruguiera* occur among the *Ceriops*. Transect A-B, located in Figure 1, is also diagrammed for the Townsville area in Figure 4.

It is interesting that two varieties of *Ceriops tagal* occur within the area. Along the shore of the bay the flowers of this species have five fringes on the tips of the petals and smooth radicles. These constitute the variety *australis*; those in the mangroves landward of the dunes have three fringes on the petal tips and prominently ridged radicles; they constitute the variety *tagal*. *Ceriops tagal* var. *australis* was not observed north of Townsville but was the only variety seen near Brisbane.

This mangrove flora is an impoverished one, restricted to the immediate vicinity of creeks because of the conjunction of high evaporation and seasonal rainfall.

THE FAUNA

Around the high-water mark the hooded burrows of *Sesarma meinerti* de Man and *S. smithi* H. M. Edw. were found; these crabs extend downward almost to the level of the lowest mangrove trees.

Among the pneumatophores of *Avicennia* in the *Avicennia* parkland, large numbers of *Cleistostoma wardi* Rathbun were common to abundant, and specimens of three species of small robber crabs, *Sesarma* (*Chiromantes*) spp. (one closely resembling *S. semperi* and one, *S. guttata*) were common. Sheltering under the samphires in the more open areas, e.g., along the edges of man-made paths, were a few specimens of *Uca lacustris* (de Haan). The snail, *Cerithidea anticipata* Iredale, occurred on the trees.

The bare flats were only sparsely inhabited near their periphery by *Uca bellator* (White) (= *U. nigrolineata* (Hess)), which was also common in areas shaded by the outermost bushes of *Ceriops*. It would appear that this crab is tolerant of low humidities, exposure to bright sun, and highly saline soil water.

The fauna of the densely shaded portions of the mangrove is more or less uniform throughout, in spite

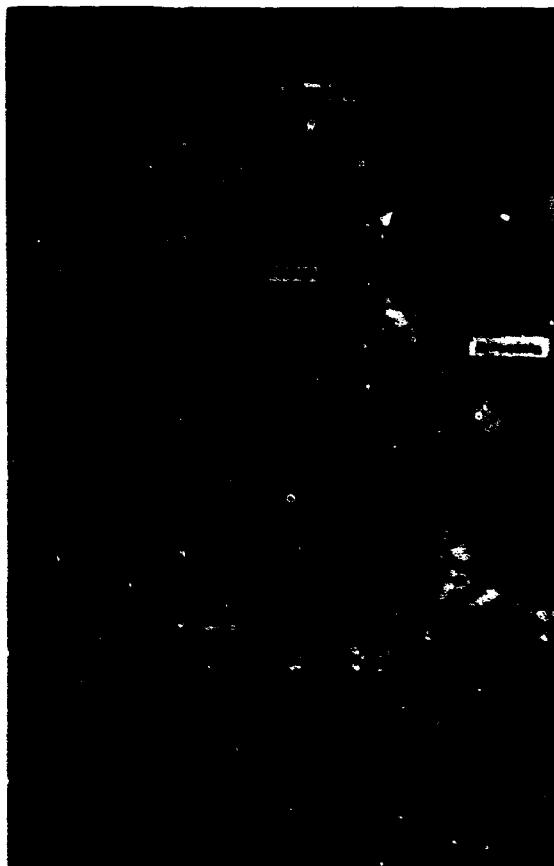


Fig. 2. Aerial photograph of mangroves south of Townsville. Compare with the region of Fig. 1 created by the intersect A-B. (Reproduced by permission of Townsville's Town Clerk.)

of differences in elevation. It is comprised of species which are intolerant of bright sunlight or very dry air. Faunal changes, as one passes down-slope through the inangrove forests, may be related to changes in the drainage pattern of the soil, to the degree of soil consolidation, or to the considerable soil turnover resulting from the activities of the strange thalassinidean mud prawn, *Thalassina anomala* (Herbst). The burrows of this prawn have one entrance surmounted by a mound of soil which is often three feet high.

The following animals were encountered within the shade of the *Ceriops* thickets and down-slope to the edge of the steep creek bank. In the list below a = abundant; c = common; p = present; and l = locally:

Crustacea

<i>Alpheus</i> sp. or spp.	c-a
<i>Cleistostoma wardi</i> Rathbun	la
<i>Euplas tridentata</i> (H. M. Edw.)	c
<i>Eurycarcinus integrifrons</i> de Man	p
<i>Helice haswellianus</i> (Whitelegg)	c
<i>Helice leachi</i> Hess	c
<i>Ilyoplax dentata</i> Ward	c
<i>Metapogoprus gracilipes</i> de Man	c-a
<i>Metapogoprus pacificus</i> Dana	c
<i>Sarmatium crassum</i> Dana	p
<i>Sesarma</i> (<i>Chiromantes</i>) sp. (cf. <i>semperi</i>)	c-a
<i>Sesarma</i> (<i>Chiromantes</i>) sp. (cf. <i>guttata</i>)	c-a
<i>Sesarma</i> (<i>Chiromantes</i>) sp.	c-a
<i>Sesarma meinerti</i> de Man	c-a
<i>Sesarma smithi</i> H. M. Edw.	p-c
<i>Thalassina anomala</i> (Herbst)	c
<i>Uca bellator</i> (White)	p
<i>Uca dussortieri</i> (H. M. Edw.)	c
<i>Uca lacustris</i> (de Haan)	p

Mollusca

<i>Cassidula angulifera</i> Petit	a
<i>Cassidula rugata</i> Menke	c
<i>Cerithidea anticipata</i> Iredale	a
<i>Cerithidea fluctuosa</i> (P. & M.)	c
<i>Ellobium austensudae</i> L.	c
<i>Ellobium austensudae</i> L.	p
<i>Oncidium tamela</i> Semper	la
<i>Ophiocardia sulcata</i> H. & A. Ad	a
<i>Terebralia palustris</i> L.	c-a
<i>Terebralia sulcata</i> Born	a
<i>Gelona costata</i> Gmelin	la

Of the crustaceans in this list, some are burrowers, and some merely seek shelter under fallen logs, bark, etc., or among the knee roots of *Braguiera* trees. In the early morning, one may encounter forms which are not seen later in the day. The burrowing species of *Sesarma* are rarely observed during the heat of the day or during the afternoon.

The larger *sesarmas*, being mainly vegetarian, graze the seedlings of *Avicennia*, *Braguiera*, and *Ceriops* and may profoundly affect regeneration of

the mangroves. This has been commented on by Watson (1928). The smaller sesarmas often feed upon leaves or dead animals. *Metopograpsus gracilipes* is a carnivore which usually feeds on smaller crabs or, occasionally, carcasses of other animals.

This species ranges widely and has frequently been confused with *M. messor* of open sea beaches.

Fiddler crabs are not normally seen deep within the mangrove forests, but at Townsville, where the forests are not extensive, they may be observed

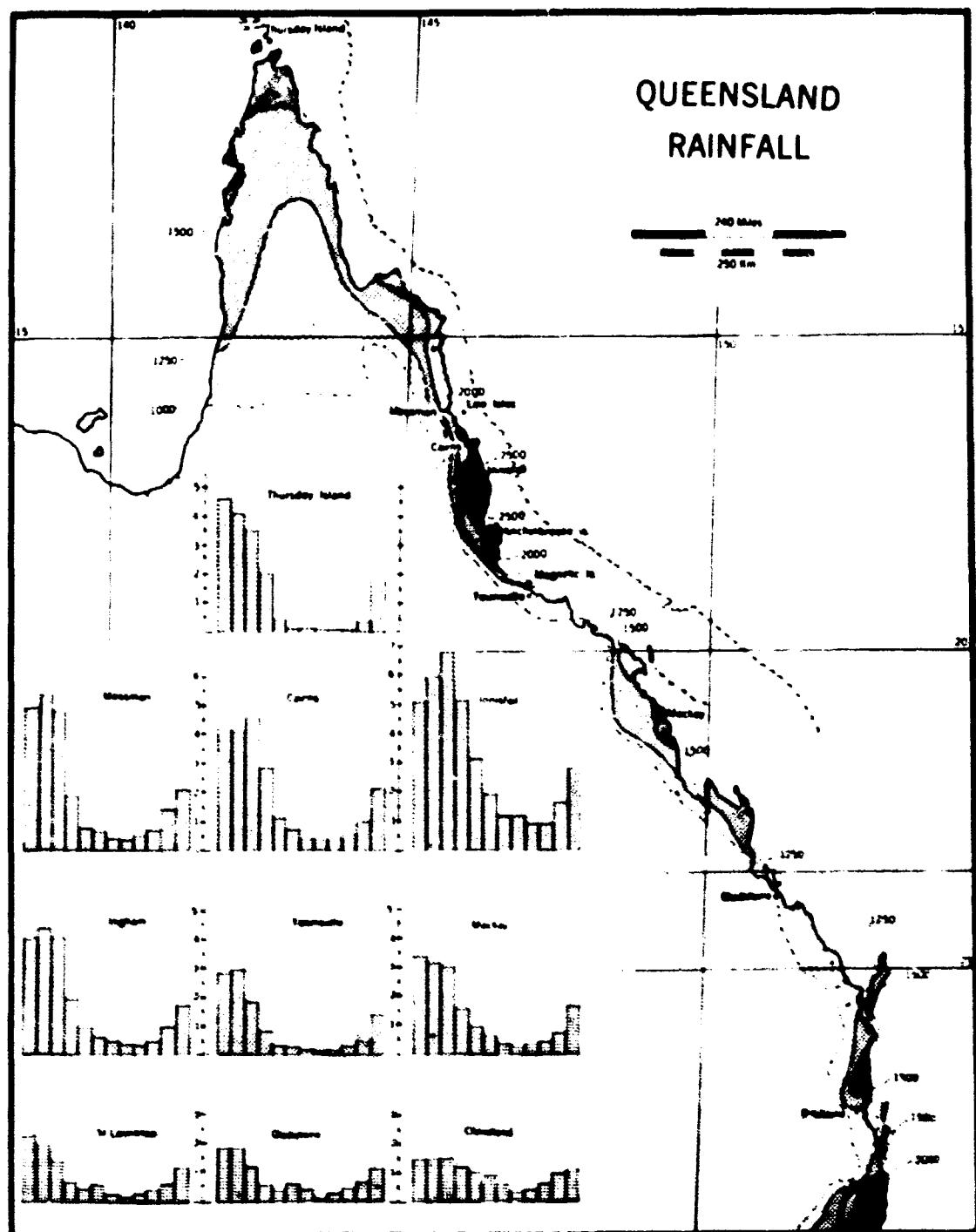


Fig. 3. Rainfall in the coastal regions of Queensland. Measurements are in mm. The histograms are scaled in cm. Notice the markedly seasonal rainfall.

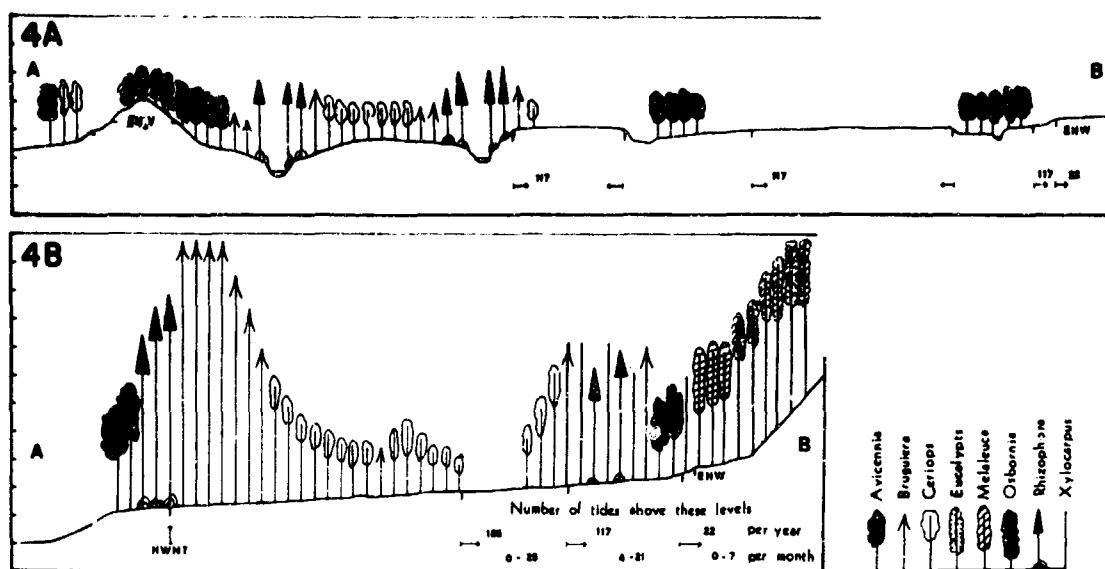


Fig. 4. Transects across mangrove areas. 4A (above), south of Townsville; 4B (below), on Magnetic Island. The divisions in the scale at left represent $1\frac{1}{2}$ m; the trees are drawn to scale. The numbers of tides above certain levels are indicated.

throughout. *Uca dussumieri* is a large species and almost always occurs in the shelter of the mangroves which line the creeks. *Uca bellator* and *Uca lactea* frequent the margins of the mangrove forests.

Thalassina anomala makes huge burrows. Heaps of mud often up to 75 cm high alternate with sub-conical pools of water. The animals have been seen pushing mud out at the top of the volcano-like mound. Whether the burrow is simple, with one entrance as Verwey (1930) describes, or a U-shaped structure like that of most thalassinideans is uncertain, but both types may occur. As a result of this animal's presence, there is a great turnover of the mud on the forest floor. Occasionally the ground level in an isolated clump of *Ceriops* may be about 25–30 cm above the general level of the bare area around it, because of the burrowing activities of *Thalassina anomala*.

The molluscs mentioned may all be seen crawling over the surface of the mud. They are less common where *Thalassina* is abundant and more abundant in its absence. The two species of *Terebralia* seem to prefer muddy substrata and are most common in and around shallow-water pools on the forest floor. *Cassidula* spp. crawl among the decaying vegetation. *Cerithidea* spp. climb up the tree trunks and rest just above high-water level. *Oncidium* tends to bury itself in the mud and is seen only just after the ebb tide. *Geloina coarctans* is a large subspherical bivalve which may be found on the surface, but more probably, normally lives some 10–15 cm below the surface.

Steep creek banks form the characteristic habitat of *Uca coarctata* (H. M. Edw.). This species has conspicuous white meropodites on the last pair of legs and is very similar in size to *Uca dussumieri*. Both species belong to the same subgroup of the genus but

always appear to be separable, taxonomically, on ecological grounds. *U. dussumieri* was never seen on steeply sloping banks. *U. coarctata* was rarely observed on level ground, and then only in the absence of the other species.

The large crab, *Macrophthalmus latreillei* H. M. Edw., was abundant on the creek banks at the low tide water level. It is also characteristic of the muddy flats, around mean sea level, of sheltered bays. Off the esplanade at Cairns they were found to be more or less evenly distributed at intervals of 50 cm. The smaller *M. pacificus* was also found on the upper portion of these banks.

Scuttling round the prop roots of *Rhizophora* were many large, blue *Metapograpsus latifrons* (White). This species was never observed on the floor of the mangrove forests nor was it seen together with *M. gracilipes*. Oysters (almost certainly a form of *Crassostrea cucullata* (Born.)) grew on the roots of *Rhizophora*. Barnacles were uncommon.

Where the floor of the creeks was exposed many specimens of *Telescopium telescopium* L. crawled over the mud. They moved up among the pneumatophores of the lowermost mangroves and into the forests, provided the surface mud was semifluid and the creek banks were not steep, meeting with the species of *Terebralia*.

Two mudskippers were common. One, *Periophthalmus kalolo* Lesson, was abundant and ranged in size up to 10 cm; the other, *Periophthalmodon australis* Castelnou, ranged up to 25 cm in length. These species were identified by G. P. Whitley. Where *Avicennia* grows near the water's edge, forming a "seaward fringe", there are holes among the pneumatophores made by the siphons of *Glauconome*



Fig. 5. Map of mangroves on the western shore of Magnetic Island. Notice the distinctly zoned mangrove area and the presence of a bare area within the thickets of *Ceriops*. The landward fringe is so narrow that it does not show on this scale. The heavy line lower right is the line of transect A—B in Fig. 4B.

virens (L.). Shells of *G. virens* lie among the mass of *Avicennia* roots some 5–10 cm below the surface.

Where the bank below the mangrove area contains spits of sand, *Uca vocans* (Latr.) (= *U. marionis* (Desm.)) and an undescribed species with a tuft of hair at the base of the finger and thumb commonly occur. At a slightly lower level, but extending up into the most seaward mangroves if the bank is sandy or of sandy mud, armies of *Myctyrus longicarpus* Latr. mill around.

Worms were scarce and were rarely found by casual digging. The few specimens I collected were identified by Mrs. P. Mather, University of Queensland, as *Marphysa sanguinea* (Montagu). On one occasion numerous egg masses of a *Marphysa* were found scattered, about a foot apart, among the pneumatophores of *Avicennia* in the seaward fringe.

COMPARISON WITH OTHER MANGROVE AREAS IN NORTH QUEENSLAND

MAGNETIC ISLAND

I have stated above that the mangroves around Townsville are impoverished, albeit extensive. In some ways they are remarkably like those of Inhaca Island off Lourenco Marques at 26° S, described by Macnae and Kalk (1962a). To look at a more typical tropical mangrove one does not have to travel far from Townsville. Some 6 km across the bay lies Magnetic Island, which rises steeply from the sea to a maximum height of about 500 m. There are no records of rainfall for the island, but it is probably close to double that of Townsville.

The map (Fig. 5) and the transect (Fig. 4) indicate that the mangroves are more continuous laterally, with restricted bare areas, and are quite distinctly zoned.

The mountainside is clothed by a forest of eucalypts; the swampy flat between this forest and the sea is dominated by species of *Melaleuca*, the paperbark tea tree.

Quite abruptly, one then enters the mangrove area where the following zones are clearly defined:

The Landward Fringe—Within this fringe of mangroves *Avicennia marina* is the most conspicuous tree, but with it occur *Aegialitis annulata*, a sprawling shrub; *Aegiceras corniculatum* (L.) Blanco, *Bruguiera gymnorhiza*, *Excoecaria agallocha*, *Hibiscus tiliaceus* L., *Lumnitzera littorea* (Jack) Voigt, *L. racemosa*, *Osbornia octodonta*, *Rhizophora stylosa*, and *Xylocarpus granatum*, with the lianas *Cynanchum carnosum* and *Derris trifoliata*. Occasional clumps of the samphire, *Tecticornia cinerea* (F. Muell.) F. M. Bail, occur on drier ground. During my visit in February, the whole of this area was covered by about 2 cm of water.

Ceriops Thickets—The landward fringe thins out as bushes of *Ceriops tagal* become common and eventually take over as an almost pure stand with only occasional trees of *Avicennia*, *Bruguiera gymnorhiza*, and *B. exaristata*. The height of the bushes decreases until finally a bare area is encountered; on the opposite side the *Ceriops* bushes increase in height until, as trees of some 7–8 m, they merge with the *Bruguiera* forest.

Bruguiera Forest—The dominant tree is *Bruguiera gymnorhiza* with *Xylocarpus australasicum* Ridl. (? = *X. molluccensis* (Lam.) M. Roem.) common. The ground is firm and muddy.

Rhizophora Forest—*Rhizophora stylosa* gradually displaces *Bruguiera* on extremely soft ground.

Seaward Avicennia Fringe—This is a fringe of *Avicennia marina* rarely more than one tree deep. The ground is muddy but the mat of nutritive roots lying some 20–30 cm below the surface gives support to a walker. This fringe is just below the level of ordinary neap high waters.

The animals listed above showed the same type of distribution within the mangroves on Magnetic Island.

HINCHINBROOKE CHANNEL

This stretch of coast, beginning some 150 km north of Townsville, was by far the largest mangrove area visited. The mangroves stretch along some 40 km of the continental shore and are up to 6 km deep. The Hinchinbrooke Channel is a rift valley with steep sides and a narrow coastal plain along the continental shore. It is a drowned valley and represents the old lower course of the Tully River.

The zones recognized on Magnetic Island were again visible (Fig. 6). A slight variation is present at the landward edge of the *Ceriops* thickets, for these are invaded locally by *Scyphiphora hydrophyllacea* Gaertn. Bare areas are rare. A road (Fig. 6) has



Fig. 6. Aerial photograph of the southern end of the Hinchinbrooke Channel at Lucinda. Note the encroachment of sugar cultivation and that bare areas are uncommon. One distributary of the Herbert River crosses the picture. (Crown copyright reserved; reproduced by permission of the Honorable Minister of Lands, Queensland.)

been cut through from Halifax to a sugar loading station at Lucinda, and along the roadside there have developed *ad hoc* communities consisting mainly of *Aegiceras corniculatum*, indicating strong freshwater influence. *Ceriops tagal*, *Lumnitzera littorea* and *L. racemosa*, and *Ceriops decandra* (Griff.) Ding Hou, which was seen nowhere else.

The disturbed areas are colonized by thick, almost impenetrable, masses of the fern *Acrostichum speciosum* Willd. and the spiny-leaved *Acanthus ilicifolius* L. These two plants are always opportunists. They normally occur in the landward fringe, but take advantage of any clearing. On occasion they may grow so thickly as to inhibit regeneration by preventing the seedlings of the mangrove trees from reaching the soil. In the Hinchinbrooke stretch these two form part of the field layer in the *Bruguiera* forests.

In the wetter parts of the area the *Ceriops* thickets become overgrown and straggly and are replaced by forests of *Bruguiera parviflora* (Roxb.) Arn., a tall slender tree with abundant regeneration and several age groups.

Rhizophora apiculata Blume becomes associated with *R. stylosa* in the *Rhizophora* forests, occurring about 1 in 50 near Lucinda at the southern end of the channel; it increases northwards and is present in 1 in 5 at the northern Cardwell end.

The fauna comprises the same animals as have been listed above.

INNISFAIL TO CAIRNS

Innisfail lies within one of the wettest districts of Queensland and has a rainfall of approximately 3,480 mm (137 inches). Furthermore, there is an appreciable fall in the drier winter months.

The rain forest comes down to the sea level and merges with the mangroves. These conditions also apply at Cairns and Mossman, where rainfall is around 2,000 mm (80 inches).

The landward fringe of the mangrove, in addition to scattered specimens of each tree species characteristic of a mangrove swamp, also contains several of the epiphytes from the neighboring forests: ferns, orchids, ant-plants, and others. All the trees are tall, reaching what is probably their maximum size.

Forests of *Bruguiera parviflora* dominate in the middle stretch and reach heights of more than 30 m, but the trunks remain slender with a diameter of about 25–35 cm. The *Ceriops* thickets are often absent.

A zone of *Sonneratia alba* J. Sm. may be found outside of the seaward *Avicennia* zone, which is still present. Such a *Sonneratia* zone is only locally developed, and it is difficult to adduce a reason for either its presence or absence.

On most beaches throughout the world, there is a strong seepage of fresh water at a level close to, or somewhat above, mean sea level. Where this occurs in front of a mangrove, e.g., just north of Cairns and near Port Douglas, a strong growth of saplings of *Avicennia marina* and *Aegiceras corniculatum* develops. (*Aegiceras corniculatum* is a species of mangrove which favors areas with reduced salinity. Hence, it is the one which penetrates farthest upstream on the permanent banks of rivers. In Australia it occupies the position taken up by *Barringtonia racemosa* Roxb. in East African mangroves.)

DISCUSSION

ZONATION WITHIN THE UPPER INTERTIDAL REGION

The zonation of plants and animals within the upper intertidal region is associated with rising ground level and the consequent drop in frequency of tidal flooding. Assuming a hypothetical sheltered shore which slopes gradually downwards, five zones would be recognizable. But such gentle slopes are rare; there is a tendency on any shore for the beach to flatten out at one level or another, and then the zone characteristic of that level is the most conspicuous one (Macnae and Kalk, 1962b). Modifications will also follow from the entry of a creek, and will result from the interference of rainfall, evaporation, and salinity. No zone is exempt from interference.

The Landward Fringe

It has been shown that this fringe assumes either of two forms: (1) If the landward vegetation is

wooded this zone will contain any tree which one may expect to find in a mangrove. If the terrain has water close to the surface *Aegiceras corniculatum* or *Bruguiera gymnorhiza* will predominate. Where there are only scattered bushes or "wallum" (Coadlak, 1961), this fringe will tend to be *Avicennia marina* or *Lumnitzera* spp. (2) If the landward vegetation is grassland, then a sward of species of *Arthrocnemum*, *Susuvium portulacastrum*, and *Sporobolus virginicus* will occur, and this may or may not be shaded by an *Avicennia* parkland.

The landward fringe is colonized by few animals; *Sesarma meinerti* and *S. smithi* will burrow in shaded areas. *Uca lactea* and *U. bellator* will occur in more open sunny places.

Pools left by the tide are occupied by mosquito larvae. Five species are common at Mackay, some 300 km south (Marks, 1947), and these species are common along the Queensland coast. *Aedes vigilax* (Skuse) lays its eggs in pools left by high tides: they hatch, and larvae and pupae develop through their life cycle before the next high tide. The pools chosen for oviposition and in which larvae have been found are almost always in full sunlight. *Aedes alternans* (Westwood) is a large mosquito exceeding one cm long which breeds in both salt- and freshwater pools. *Aedes scutellaris* (Walker) breeds in rot holes in *Avicennia* trees. *Culex sitiens* Wiedemann breeds in tidal pools, both in the open and in the deep shade of the landward fringe of mangroves. *Anopheles farauti* Laveran breeds in shaded pools among the roots of the mangroves and in more open areas. *Anopheles amictus* Edwards subsp. *hilli* Woodhill and Lee breeds in open sunny pools on the mud flats.

Ceriops Thickets

In many mangrove areas this is the zone of greatest extent; in others it is absent; and again, it may be interrupted by extensive bare areas.

Where rainfall is high and well distributed over the year, thickets of *Ceriops tagal* are not found; the landward fringe and the *Bruguiera* forest meet and occupy the area where *Ceriops* would be expected. As rainfall decreases and rate of evaporation rises, the moisture-loving species of *Bruguiera* become restricted and *Ceriops* increases its distribution. As the rainfall decreases further, the trees become stunted into bushes and bare areas develop. These bare areas increase in extent with decreasing rainfall and increasing evaporation rate. As a corollary, the salinity of the soil increases. Few other trees grow with *Ceriops* in these thickets.

The animal population varies with the degree of cover. *Thalassina anomala* may range from common under cover to absent where there is none. Burrowing crabs are always present; non-burrowers are less frequent. In open spaces the fiddler crab *Uca bellator* may be very abundant. This species seems to be the most tolerant of all fiddlers. It appears to be able to withstand hot, dry areas as efficiently as the south-

east African *Uca universa* (Hoffman), but unlike this species it penetrates into the shade of the trees.

As elsewhere in the Indo-West Pacific, *Ceriops tagal* is a favorite nesting tree of the weaver ant, *Ocophyila* sp.

Bruguiera Forests

These have their greatest extent and development in the "ever-wet". With decreasing rainfall and increased evaporation the *Bruguiera* forests become narrowed and trees less tall. *Bruguiera parviflora* is the tallest mangrove known to me. It forms dense stands and the trees are close together; there is also considerable regeneration and several age groups of saplings occur. *B. gymnorhiza*, usually associated with *Xylocarpus australasicum*, forms a more open forest. *Bruguiera* forests tend to be most extensive and grow best in areas where there is abundant fresh water. This is in agreement with their Malayan distribution (Watson, 1928). An occasional, very tall, aged tree of *Sonneratia alba* may be encountered.

There are more crabs and snails on the floor of these forests than anywhere else in the mangrove. Large colonies of a black ant are common on low mounds on the forest floor; the ants seal the entrances from within as the tide rises.

Creeks are the home of *Scylla serrata* (Forskal), one of the best of all edible crabs. They live in large burrows some 3-4 m long and grow to a carapace width of about 14 cm.

Rhizophora Forests

I have mentioned two species of *Rhizophora*, *R. stylosa* and *R. apiculata*, though *R. mucronata* is the common *Rhizophora* of the bulk of the Indo-West Pacific region. In Malaya *R. apiculata* tends to occur in water of lower salinity; *R. mucronata* is dominant in water approaching normal salinity; *R. stylosa* is rarer and occurs only in the shelter of coral reefs and on stony ground. I found no *R. mucronata* in Australia, and all previous records seem to apply to *R. stylosa*. Only *R. stylosa* was seen on a visit to Low Isles, and this was recorded as *R. mucronata*.

In the Australian swamps, *R. apiculata* occurred abundantly only in places with a high rainfall and consequent high level of ground water, probably of reduced salinity. *R. stylosa* occurred in all situations where one would expect to find a *Rhizophora*. Whereas in southeast Asia it appears to have ecological preferences, it shows no peculiarities of habitat nor preferences in Australia.

The fauna depends on the degree of fluidity of the mud. If the terrain is firm, it is occupied by the animals characteristic of the upper mangrove zones. If the terrain is soft, the zone is dominated by species of *Alpheus*, and few crabs run on the surface. They are confined, like *Metopograpsus latifrons*, to running over and around the prop roots.

The Seaward Fringes

The extension of a mangrove area out to sea and the colonization of recently formed banks of sand, mud, gravel, or a mixture of them depends, as far as observation suggests, on either *Sonneratia alba* or *Avicennia marina*. *Sonneratia* develops into well-formed trees at a level only a little above mean sea level. Seedlings of both trees are frequently far out on the flats, but they die within their first year. Death is partly the result of being chewed, partly the result of shading by encrustation with mud.

The fringe normally consists of only a few rows of mature trees fronted by a dense growth of saplings. Observations at Richards Bay in Natal, South Africa (Macnæ, 1963), indicate that *Avicennia* cannot grow in dense shade. Its roots run horizontally at a depth of about 50–75 cm; from them rise pneumatophores which give off numerous nutritive roots. Hence, a dense mat of thread-like roots is formed some 25–30 cm below the surface. *Sonneratia* has a similar root system (Backer and Van Steenis, 1951). These two species are capable of holding the surface soil firm and protecting the seedlings of *Rhizophora* which germinate in their shade. These, in turn, will grow to shade out the *Avicennia* fringe trees, and the advance goes on steadily out to sea.

Unlike *Avicennia*, some trees of *Sonneratia* persist when surrounded by *Rhizophora* and *Bruguiera*, and an occasional stag-headed tree may overtop the forests of *B. gymnorhiza*. Saplings of *Aegiceras corniculatum* occur with the saplings of *Avicennia* and *Sonneratia* only along the line of seepage.

Animals are rare in the soft mud at this level, except for colonies of *Glaucome virens* and crabs, *Macrobrachium pacificus*. *Littorina (Melarapha) scabra* is abundant on the leaves of the trees at this level, and becomes scarcer towards the landward fringe.

MODIFICATIONS DUE TO AN ESTUARY ENTERING THE SEA

The fringe species are first visibly affected as the shore turns from the sea into the estuary mouth. There is a tendency for the seaward fringe to disappear and for the *Rhizophora* forest to border the stream bank. If the rivermouth is wide the fringe of *Avicennia* or *Sonneratia* will go upstream for some way, but sooner or later it will drop out. There is a tendency for one bank of an estuary to be an erosion bank and the other, a bank of deposition. The latter will be colonized by *Avicennia*, *Sonneratia*, or *Rhizophora*, but more usually by one of the first two. The vegetation on the erosion bank will depend on the type of forest being invaded. Such erosion banks are colonized by *Uca coarctata*, *Metopograpsus gracilipes*, and *M. latifrons*; the banks of deposition, by *Macrobrachium pacificus* and *Macrobrachium latreillei*.

Xylocarpus granatum, *Avicennia marina*, and particularly *Aegiceras corniculatum* extend farthest upstream into that part of the estuary which is under predominantly freshwater influence.

INFLUENCE OF SALINITY AND DESICCATION

Studies at Manly, just south of Brisbane, by Miss Judy Badham (unpublished), and at Inhaca Island off Lourenco Marques by myself and others indicate that salinities of the soil waters in the bare areas may reach levels of over 100 %. *Avicennia marina* grows in soils of over 90%, but then it forms copses rarely more than waist high. Such copses are common at Inhambane in south central Mozambique, but were not seen in Queensland. *Ceriops tagal* at Inhaca grows well in soils of salinity around 70%, but not above this. *Uca longidigitum* (Kingsley) (perhaps a southern form of *U. bellator*) occurs on these hypersaline flats near Brisbane and *U. inversa* at Inhaca. It is equally clear that *U. bellator* is capable of living under conditions of similar high salinity, since it occurs commonly on salt-encrusted flats.

INFLUENCE OF SOIL FERTILITY

The regions of best development of mangroves seen were Lucinda, Innisfail, Cairns, and Mossman. The rivers responsible for the deposits along the estuaries, and alongshore in these regions, drain areas of basaltic rocks of comparatively recent lavas. Such soils are known to possess a high fertility, and when this is combined with an ample rainfall, conditions would appear to be right for maximum development of mangroves.

Along the foot of the Cardwell ranges the soils are quartzitic and poor. In spite of a good rainfall the development is mediocre.

Along the shores of Cleveland Bay on the deltaic deposits associated with the Ross River, development of mangroves is marginal—the result of poor soils derived from quartzites and an inadequate rainfall.

CAUSATION OF ANIMAL DISTRIBUTION

The mangroves of Natal and Pondoland in southeastern Africa indicate (Macnæ, 1963) that the fauna associated with mangroves is one characteristic of sheltered shores on which grow some shade-giving plants, either mangroves or grasses such as *Spartina* and an ample cover of samphires (*Arthrocnemum* spp.). This is confirmed by the basic similarity between the faunas of the mangroves described here. But biogeographic factors interfere and the fauna described here is restricted to Queensland. Mangroves occur in central New South Wales, near Melbourne, and in the southern Australian Gulfs; their fauna is that typical of sheltered shores in these regions.

Comparing Queensland mangroves with those of the eastern coasts of Africa, we find no parallel to the African *Sesarma culmene* and *S. ortmanni* which are restricted to the supralittoral fringe, just around the high-water mark of ordinary spring tides. The other sesarmas occur on firm ground. When the ground becomes soft, *Alpheus* spp. and *Macrobrachium* spp. dominate. These two statements refer to any intertidal level within the mangrove zone. Most other animals listed show little or no predilection for a particular level.

LITERATURE CITED

- BACKER, C. A., and C. G. G. J. VAN STEENIS, 1951. *Sonneratiaceae in Flora Malayana*, 1(4):280-289.
- COALDRAKE, J. E., 1961. The ecosystem of the coastal lowlands ("wallum") of southern Queensland. *Bull. C.S.I.R.O.*, Melbourne, Australia.
- JARDINE, F., 1928. The topography of the Townsville littoral. *Rep. Gt. Barrier Reef Committee*, 2:70-87.
- MACNAE, W., 1963. Mangrove swamps in South Africa. *J. Ecol.*, 51:1-25.
- MACNAE, W., and M. KALK, 1962a. The ecology of the mangrove swamps at Inhaca Island, Mozambique. *J. Ecol.*, 50:19-34.
- MACNAE, W., and M. KALK, 1962b. The fauna and flora of the sand flats at Inhaca Island, Mozambique. *J. Animal Ecol.*, 31:93-128.
- MARKS, E. N., 1947. Report of a mosquito survey of Mackay and portions of the Pioneer Shire, Queensland. Dept. of Health, Brisbane, Australia.
- MOSS, C. E., 1954. The species of *Arthroracnemum* and *Salicornia* in southern Africa. *J. S. African Botany*, 20:1-22.
- VERWEY, J., 1930. Einiges über die Biologie ost-indischer Mangrovekrabben. *Treubia*, 12:169-201.
- WATSON, I. G., 1928. Mangrove forests of the Malay peninsula. *Malayan Forest Rec.*; vol. 6, 275 pp. Kuala Lumpur, Malaysia.

Ecology of Estuarine Benthic Invertebrates: A Perspective

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It is a singular fact, in view of man's proximity to coastal resources and his dependence on them, that intensive investigation of the biological aspects of estuaries did not commence until early in the present century (Hedgpeth, 1957a). Since then, however, the number, breadth, and depth of such researches has increased at an accelerating rate (Day, 1951, 1964; Gislén, 1930; Gorsline, 1962; Hedgpeth, 1957e; Hesse *et al.*, 1951; Moore, 1958; Pearse, 1950; Redeker, 1933; Reid, 1961; Remane, 1934, 1958; Rochford, 1951; Yonge, 1949a).

This perspective is an attempt to provide an overview of major trends and advances in the field of estuarine ecology as it applies primarily to estuarine benthic invertebrates, and to point out some neglected aspects which suggest avenues for further research. The benthos will be considered in the categories of infauna, sessile epifauna, slowly moving epifauna (Petersen, 1913), and mega-, meio-, and microbenthos (Mare, 1942). The prefix mega- (meaning large, great) is preferred to macro- (meaning long, large) and is employed in this perspective.

The largest volumes of fresh water meeting the sea enter the Atlantic and Arctic Oceans which receive all the European, and the most important African, North American, and South American rivers (Hesse *et al.*, 1951). These estuaries range in form from broad, open, relatively shoal, dendritic indentures like the Miramichi Estuary (Bousfield, 1955a), Delaware Bay (Shuster, 1959), Chesapeake Bay (Pritchard, 1952b), Crouch and Roach Estuaries (Waugh, 1957), Baltic Sea (Segerstraale, 1957, 1964), Knysna Estuary (Day *et al.*, 1952), Australian estuaries (Rochford, 1951), and Mangoku-Ura Inlet (Imai *et al.*, 1951), to series of shallow anastomosing sounds and lagoons buffered from the ocean by narrow barrier bars of sand breached intermittently by inlets like the eastern New Jersey estuaries (Carricker, 1961a), North Carolina estuaries (Roelofs and Bumpus, 1954), Louisiana estuaries (Mackin and Hopkins, 1962), Texas estuaries (Collier and Hedgpeth, 1950), to embayments with deep basins and steep shores like the fjords of Scandinavia, Greenland, and New Zealand (Gaarder and Spärck, 1933; Fleming, 1950; Thorson, 1933; Gislén, 1930). Under certain circumstances the mouths of estuaries may close to form blind embayments (Day, 1964; Scott *et al.*, 1952). Day (1951, 1964), Emery and Stevenson (1957a), Pritchard (1952a, 1955, 1960a, b), and Rochford (1951) include reviews of general classifi-

cations of the physical features of estuaries. The geological origin of the estuary is important as it determines the character of the water and sediment (Ferguson Wood, 1962), the degree of exposure, and other physical factors (Day, 1964).

Attempts to define the term "estuary" have provoked spirited discussions, primarily because of the physiographic and hydrodynamic variability of estuarine systems. Some (e.g., Ketchum, 1951) would include the entire spectrum of measurably diluted sea waters ranging from drowned river mouths, sounds, lagoons, straits, and broadly open embayments, to open coastal waters, or any region in which sea water is measurably diluted by land water drainage; while others (Day, 1951, 1964; Pritchard, 1960b; Rochford, 1951) employ Pritchard's (1955) more limiting definition as "a semi-enclosed coastal body of water having a free connection with the open sea and within which the sea water is measurably diluted with fresh water runoff". Pritchard's definition excludes the zone of very slightly diluted sea water along many open coasts and thereby excludes many physical problems which are not found within semi-enclosed coastal embayments. His definition implies an estuarine circulation pattern resulting from vertical and horizontal distribution of density, a range of reversing tidal currents and tidal amplitudes and other tidal effects, and partial protection from winds and oceanic waves by semi-enclosure. Day (1951) omits reference to tidal effects and so includes blind estuaries, which are common in South Africa. Because of the uniqueness and profound biological significance of physical conditions within partially enclosed estuaries, Pritchard's definition is adopted in this perspective. Main emphasis will be placed on positive or true estuaries in which freshwater flow exceeds evaporation (Pritchard 1960a, b). Neutral estuaries, in which neither evaporation nor freshwater inflow dominates (Carricker, 1961b); inverse estuaries (hypersaline lagoons, Day, 1964; Hedgpeth, 1957e; Parker, 1959) in which evaporation exceeds freshwater inflow; and blind estuaries (Day, 1964) periodically blocked from the sea are given less attention. The word "tidal" in the phrase "tidal estuary" is redundant, as tidal effects, albeit rather negligible at times, are implicit in the definition of a true estuary.

As a consequence of the great variety of sizes and forms of estuaries, it is difficult to provide a precise classification of the physical divisions of a generalized estuary. Table 1 is, however, a general classification

Table 1. Classification of approximate geographic divisions, salinity ranges, types, and distribution of organisms in estuaries (Adapted from Day, 1951, 1964; and Venice System, Symposium on the Classification of Brackish Waters, 1959).

Venice system			Ecological classification		
Divisions of estuary	Salinity ranges %	Zones	Types of organisms and approximate range of distribution in estuary, relative to divisions and salinities		
River	0.5	limnetic	↑	limnetic	
Head	0.5 ~ 5	oligohaline		oligohaline	
Upper Reaches	5 ~ 18	mesohaline	mixohaline		
Middle Reaches	18 ~ 25	polyhaline		↑ true estuarine	
Lower Reaches	25 ~ 30	polyhaline			↑ euryhaline marine
Mouth	30 ~ 40	euhaline	↓ stenohaline marine		↑ migrants

with only roughly approximate divisional limits, patterned after Day's geographic divisions in an ideal estuary (1951, 1964). It includes most of Day's ecological classification, and is based on the Venice System of approximate ranges of salinities in coastal waters (Symposium on the Classification of Brackish Waters, 1959). Because of the spectrum of genotypic variation and variable rates of speciation, modern estuarine biotas fall into broad ecological categories with diffuse and sometimes overlapping boundaries, as can be seen in the ecological classification in Table 1. The phrase "oligohaline organisms" is substituted for Day's "freshwater organisms" at the head of the estuary, and "limnetic" replaces "freshwater organisms" in rivers. Day (1951) divided the basin of the ideal estuary into four major divisions based on three common biotically important physical characteristics, namely salinity, water movement, and substrate. In Table 1 these have been extended to five divisions to accommodate the broader lower (frequently lagoonal) reach often present in larger estuaries. Because of the diversity of types of estuarine basins and the range of fluctuations of these factors in them, these divisions are only roughly proportionate and are not intended to have precise boundaries. Central regions of these physical divisions are described below:

Head of estuary—where fresh water enters the estuary from streams, and salinity during high spring tides may reach a maximum of 5 %. Currents and substrate vary broadly, and are dependent on the physiography of the region.

Upper reaches of estuary—muddy bottoms, slow movement of water, and salinities roughly in a range of 5 to 18 %.

Middle reaches of estuary—sandy mud bottoms, fairly fast movement of water, with salinities from 18 to 25 %.

Lower reaches of estuary—sandy mud to clean sand or gravel bottoms, fast movement of water, and salinities from 25 to 30 %.

Mouth or inlet of estuary—clean sand, gravel, or rock bottom, very rapid flow of water, with salinities above 30 % and depending on the salinity of neritic waters outside.

Dimensions of the divisions are generally in proportion to the size of the estuary, both in length and width (Stroup and Lynn, 1963; Barlow, 1955; Carricker, 1959; Day, 1951; Hedgpeth, 1957e). The sides of an estuary are designated as "left" and "right" as viewed from the head of the estuary toward the inlet (Pritchard, 1951).

The biotic categories in the ecological classification of Table 1 are further characterized as:

Oligohaline organisms—The majority of animals living in rivers probably do not tolerate variations in salinity greater than 0.1 % and disappear at the head of the estuary; but there are some of these, the oligohaline species, which persist until salinities rise to 5 %, and a few have been recorded as high as 19 %.

True estuarine organisms—A few broadly eurytopic species are restricted to estuaries and do not occur in the sea or in fresh water; they are best represented in low salinities in the upper and middle reaches of estuaries. They have marine affinities, but have become adapted to the greater range of ecological amplitudes found in central regions of the estuary rather than in marine or fluvial environments, and are said not to be able to compete with marine animals in the sea nor to tolerate conditions there. These are the true estuarine species whose distribution, form, and variation in European estuaries have been reviewed by Remane (1958), Robertson (1964), Schlieper (1958), and Segerstraale (1957). The term "true estuarine" is reserved for species in this category, to avoid confusion with the more general term "estuarine" which is used to refer to all species dwelling in or migrating into estuaries without regard to geographical or ecological location in the estuary. Hedgpeth (1957e) suggests that true estuarine species are conservative forms with a long history and

may have left the ocean in remote times, and that there seems to have been no striking change in the stocks giving rise to them. Depletion of one such stock seems to have been followed by replacement from a similar stock.

Euryhaline marine organisms—Some species extend from the sea into the upper reaches of the estuary, and tolerate reduction in salinity often as low as 15 %, and a few even to 5 %. The acclimation of some of these to low estuarine salinities has been described by Schlieper (1955, 1957). Euryhaline marine species constitute the majority of total estuarine taxa.

Stenohaline marine organisms—These live on open seashores and at the mouths of estuaries. They do not penetrate into estuaries below salinities of about 25 % in the lower reaches.

Migrants—Certain euryhaline marine migrants spend only a part of their lives in estuaries. Some depend to a limited degree on the bottom, and many are predators subsisting on resident estuarine benthic populations (Gunter, 1961; Hartley, 1940, 1947; Williams, 1955). These species, for instance blue crabs (*Callinectes*) and flatfish (*Pleuronectes*), may move up the estuary through the entire mixohaline range of salinities before returning to the sea.

Other classifications of estuarine biota have been proposed (Bousfield, 1955b; Hedgpeth, 1957e; Kinne, 1963a, 1964; Remane, 1958; Segerstraale, 1957). Kinne classified crustaceans into four groups on the basis of their capacity to osmoregulate: oligostenohaline, euryhaline, polystenohaline, and haloeuryhaline. These correspond more or less as follows, respectively, to the estuarine faunal groups given in Table 1: oligohaline, true estuarine-euryhaline marine, stenohaline marine, and mixohaline. Remane (1934) presents a schematic diagram representing the comparative distribution of the limnetic, true estuarine, and euryhaline marine species in the Bay of Kiel.

METHODS IN ESTUARINE BENTHIC ECOLOGY

GENERAL APPROACHES

An inclusive study of estuarine benthic ecology should involve comparative investigations of density and distribution of the benthos; ecological life histories; species interactions and intraspecies populations; and biotic community structure, function, origin, and development—all in relation to the estuarine ecosystem and to ecosystems in adjoining fresh water and seas. Overall emphasis should be on the interplay among living organisms and the total interrelated environment examined both in the field (Redfield, 1958) and in the laboratory (Simpson, 1963). Maximum advancement in such studies can be expected by providing broadly trained biologists the opportunity to attack these problems in a basic fashion with modern tools, taking their studies to whatever reasonable experimental and descriptive level is required, even to molecular (Vallentyne, 1954, 1957)

and ultrastructural studies (Hathaway and Robertson, 1961), to gain an understanding of the function of the benthos at all levels of organization. The approach, then, becomes essentially an interdisciplinary one, using the applicable methodologies of the physical and chemical sciences, thus benefiting from partnerships both of investigators and of disciplines (Riley, 1964); and of sufficient duration on a day-and-night and year-round scale to gain meaningful results (Doty, 1957; Ingle, 1962; Loosanoff *et al.*, 1955; Segerstraale, 1960).

FIELD AND LABORATORY METHODS

Environmental Factors

Development of instruments for recording a number of the aquatic environmental factors, though not yet perfected, has far surpassed that of biological sampling devices, and in some cases a considerable degree of electronic sophistication has been achieved (Johnston, 1964), permitting continuous recording of several factors simultaneously in the field and telemetering the information to the laboratory. Weakness of these instruments are the relatively short life of operation before failure, the incapacity to function reliably and accurately in sea water at thermal ranges as low as -2° C., and their mechanical inability to monitor microhabitats on and in the bottom. A continuous census of factors *in situ* is now limited to the more obvious ones like temperature, turbidity, light penetration, current velocity, salinity, water level, oxygen, pH, and Eh. Equally important ecologically, if not more critical, are many of the less obvious factors such as the micronutrients, external metabolites, and other dissolved substances (Buzzati-Traverso, 1958; Rae, 1958). Instruments for continuous recording of these, not only in ambient estuarine water but in interstitial fluids of sediments, have not yet appeared. A useful manual (Strickland and Parsons, 1960) on standardized laboratory seawater analyses is available.

The physical nature of sediments, especially among the diversity of types characteristic of estuaries, has been more difficult to analyze ecologically (Drach, 1958; Longhurst, 1964; Moore, 1931a; Morgans, 1956; Parsons, 1963; Sanders, 1956, 1958) and has yet to be done realistically. Standard mechanical-chemical analysis of sediments, for example, requires disruptive removal of samples from the field to the laboratory and destroys the very aggregations which constitute the microenvironment of infauna. There is serious need in the near future, therefore, for a more rapid, less laborious method for determination in the laboratory of such sedimentary characteristics as inorganic particle size, porosity, compactness, and organic content. Eventually a kind of sediment mapper may be developed which can be used directly in the field for at least gross analysis of sediments without disturbing the substratum and its resident biota. A means is also necessary for measuring quantitatively in the laboratory, and ultimately in the field, the range

of size and nature of organic and organic-inorganic sediment aggregates.

The Benthos

Excisive sampling of the bottom (Petersen, 1913) is still at the heart of most benthic research, and until the advent of underwater diving, represented an indirect or "blind" approach (Drach, 1958; Longhurst, 1964; Riedl, 1958). The primitive level of development of modern sampling gear (Drach, 1958) and its inefficiency (Birkett, 1958; Holme, 1964; Longhurst, 1964), is in a sense a measure of the slow progress in this field (Riedl, 1958). Recent papers reviewing present benthic sampling instruments and methods express concern over their inadequacies, and point out the serious need of innovations (Birkett, 1958; Cummins, 1962; Drach, 1958; Hedgpeth, 1957c; Holme, 1964; T. Hopkins, 1964; Longhurst, 1964; McIntyre, 1956). Longhurst (1964) urges that, before better samplers are devised, more be done on assessment and standardization of current gear, relating kinds and density of fauna caught in the gear to those actually present in the bottom (Barnard and Jones, 1960; Birkett, 1958; Drach, 1958; McIntyre, 1956; and R. Wood, 1963). Buzzati-Traverso (1958) reemphasizes the need for quantification. Special problems are the sampling of hard surfaces (Doty, 1957; Drach, 1958; Pequegnat, 1964), large scattered infauna, and sparse widely ranging motile epifauna (Van Cleave and Ting, 1962). Unquestionably the most promising innovation in the study of the benthos has been the adaptation of underwater diving (Drach, 1948, 1958; Forster, 1953, 1954; Gislén, 1950; Haas, 1948; Morgans, 1959; Pequegnat, 1964; Turner *et al.*, 1965; R. Wood, 1963). Excessively turbid conditions in many estuaries, however, somewhat reduce its potential value there. Underwater photography and underwater television (Barnes, 1958, 1963; Owen, 1951; Veevers, 1952) are coming into common use in clear waters, but turbidity limits their use in estuaries. Barnes (1963) reports that placement of a cone of fresh water held in a rigid container in front of the lens overcomes the difficulty to some extent.

In the pursuit of quantitative estuarine benthic studies we are still left with some unsatisfied critical needs: (1) collectors to excise quantitative units of bottom of comparable volume and depth for all types of sediment, in a range of sizes and types geared to the gradient of morphological size, fragility, and density of organisms, and including large, more sparsely distributed animals living deeply in the sediment; it is evident that simultaneous sampling of all groups with the same size and type of gear is impractical (MacFadyen, 1962), and that the required number of samples depends on the demands of the investigator for precision and the inherent variability of the population being sampled (D. W. Hayne, personal communication); (2) reliable metered trawl-like collectors which will operate in the confining areas of smaller estuaries, for censusing accurately large, more widely ranging epifauna; (3) quantitative methods

for sampling hard surfaces which will supplement, or, in difficult habitats, substitute for SCUBA divers; (4) quantitative laboratory methods for extraction, without disrupting, the meiobenthos and small megabenthos from sediments (Anderson, 1959; Hedgpeth, 1957c; Jonasson, 1955; Longhurst, 1964; MacFadyen, 1962; Reish, 1959); current methods are time consuming, inexact, and destructive especially to soft-bodied forms; (5) a universal standard for pore sizes of screens for sieving and sorting benthic organisms of various sizes—though some workers prefer to employ pore sizes which most efficiently segregate organisms from the range of sizes of sedimentary grains present in the samples without reference to a universal standard; and (6) standards which will provide accurate data on density and distribution for representative volume and number of samples per unit area of bottom, for various sizes of organisms, and acceptable factors for extrapolation of densities thus obtained to the common denominator of square and cubic meter (Longhurst, 1964).

These requirements direct attention to the need for uniform sampling and processing methods which will, in turn, permit universal comparison of resulting data (Longhurst, 1964; Sanders, 1956; Thorson, 1957, 1958). It should be stressed, however, that standardization should not be so inflexible as to prevent use of variations in investigating different basic questions. The troublesome problems of sampling design and of treatment of census data persist (Barnard and Jones, 1960; Glover, 1961; Longhurst, 1964; MacFadyen, 1962; Thorson, 1957, 1958; Williams and Lambert, 1960); they appear to have no simple solutions, and they should be reevaluated in a sound biostatistical framework before application in future estuarine benthic work. Whether units of biomass or numbers of individuals is the more meaningful way of handling biotic data likewise is still debated (Buzzati-Traverso, 1958; Longhurst, 1964; McNulty *et al.*, 1962; Sanders, 1958, 1960), and until the concept of biomass is better defined, it may be expedient to use both units in estuarine benthic studies.

It is not difficult to see that current excisive sampling of bottom sediments is grossly inefficient and inadequate. Hopefully more ecologically realistic methods will be devised which will permit study of the benthos *in situ* with minimum disturbance. Continuous benthic sampling in one area by present methods, especially with large, frequently collected samples, soon alters catastrophically the resident biota and its environment, making results dubious at best.

Analysis, integration, and interpretation of the diversity and magnitude of variables accumulated in modern benthic populational and community investigations can seldom be done accurately by inspection alone. Recent application of electronic computer techniques in storing, retrieval, and analysis of data on offshore bottom communities (Parker, 1964, b; MacFadyen, 1962; Williams and Lambert, 1960) demonstrates the usefulness of the method for estuarine benthic community studies, provided it is employed pri-

marily to facilitate manipulation of the data; but final analysis and interpretation is still a function of the investigator.

MODELS OF ESTUARIES

Large-scale model estuaries have been used for many years to facilitate analysis of hydrographic phenomena and solution of problems relating to pollution and to securing and maintaining navigational facilities in tidal waterways (Barnes *et al.*, 1957; Pritchard, 1954; Simmons, 1960). The Delaware River and Bay model, for example, is constructed of concrete on a horizontal scale of 1:1,000 and a vertical scale of 1:100 (Pritchard, 1954). Considerable accuracy has been attained in the quantitative reproduction of amplitudes and phases of the tides, mean cross-sectional velocities of tidal currents, density, and freshwater forces which affect the dispersion, dilution, and flushing of wastes.

These prototypes provide the estuarine ecologist with a ready-made estuarine model for controlled ecological research on a large scale (Rae, 1958; Ingle, 1962). Models should be located in coastal areas sheltered from storms, and in close proximity to clean high-salinity sea water and clean fresh water (preferably from springs). With the use of automatic continuously monitoring electronic instruments and appropriate feedbacks, a number of the prominent environmental factors could be effectively controlled in such a model. Technically easy analyses of a wide variety of substances by means of spectrophotometric techniques should facilitate periodic monitoring of salts and organic substances in the resulting gradient of estuarine water. Non-toxic substances would have to be eliminated from all parts of the model. The prototype would permit carefully controlled experiments on a large scale for testing the relative importance of physical and chemical environmental factors (Rae, 1958), and the experimental use of an increasing number of species (Rae's marine equivalents of the "laboratory guinea pig") to explore some of the untested hypotheses extant on estuarine benthic ecology. Many taxa of estuarine invertebrates and unicellular food organisms are now being cultured under controlled laboratory conditions (Costlow and Hookhout, 1958, 1959, 1961; Kinne, 1964; Loosanoff and Davis, 1963; Provasoli 1958; Provasoli and Pinner, 1953; Ray, 1958; Walne, 1958) and could be produced in large numbers for such investigations.

There is also a need for small laboratory models of designs and sizes suited to the particular requirements of specific laboratory observations and experimentation. These could be erected in special rooms (like "biotrons") in marine laboratories very near clean high-salinity sea water, and provide independent control for such variables as temperature, salinity, pH, oxygen, current velocity, turbulence, tidal drifts, and light. The commercial availability of transparent, easily cut, drilled, and cemented non-toxic plastic sheets, rods, and tubing, as well as an assortment of non-toxic pumps and valves, make the construction

of such models a reasonable possibility. The excellent summary of seawater systems for experimental aquaria by Clark and Clark (1964) is an admirable source of ideas and plans. Experimentation with organic substances will require working with artificial sea water, now available commercially. To avoid accumulation of concentrations of metabolites and microorganisms, which inevitably result when animals are held in closed systems—usually with unpredictable consequences—it is necessary that running (rather than closed) water systems be employed. Small models make this practical. Laboratory models are especially useful in the study of the behavior and ecological tolerances of pelagic, settling, and juvenile benthic invertebrates (Haskin, 1954).

ROLE OF SYSTEMATICS IN ESTUARINE BENTHIC ECOLOGY

The uniqueness of ecology is its emphasis on living organisms in relation to each other and to the physical environment, and their responses and adaptations to the environmental labyrinth. It follows, therefore, that rigorous identification and classification of these biotic units is fundamental to ecological research. Thus ecologists should have some facility in the use of taxonomic keys and manuals and familiarity with nomenclature and classification. Hedgpeth (1953), in fact, would go as far as to suggest that the first procedure in ecological research is exercise in systematics—and it is not hard to agree with him. Because of the significance of the concept of the niche in ecology as a basic functional unit of the biotic community (Hutchinson, 1953), it is imperative that organisms be properly identified to species, and in some cases to subspecies and race (Buzzati-Traverso, 1958; Gilover, 1961; Kinne, 1964; Kohn, 1958; Kohn and Orians, 1962; Loosanoff, 1958; Loosanoff and Nomejko, 1951; Prosser, 1955). With research in ecology expanding rapidly on a worldwide basis there is serious question whether the present limited number of taxonomists will be in a position to help ecologists except with the most difficult systematic problems, and the burden of the nomenclatural aspects of ecology will fall increasingly on the ecologist. Not only for these important reasons, but more urgently because there is so much yet to be done in basic systematics as a whole (Blackwelder, 1962, 1964), there is critical need for more young biologists to enter systematics professionally (Barnard, 1962; Barnard and Jones, 1960; Buzzati-Traverso, 1958; Hedgpeth, 1953, 1961; Redfield, 1958). The line of advance in taxonomic knowledge is held by a veritably thin force of specialists (Redfield, 1958). There is also an impressive necessity for a central repository, preferably in a national or international institution whose base is systematics, where relatively complete, carefully classified and indexed collections of identified organisms will be available to ecologists for study and comparison with their specimens; where current scientific names of organisms and their synonyms will be accessible in a computerized system which will be kept up to date and will permit rapid

retrieval of generic and specific names; and where a complete library on the systematics of the world will be housed and its contents indexed by computerized means for rapid use. A major bottleneck in systematics and ecological research is the scattered literature on groups of most organisms, and the present stupendousness of the task of bringing together a catalog of major taxa, especially of invertebrates.

Adults of species of megascopic estuarine benthic invertebrates are relatively well known systematically, except in little-populated geographical areas, but not much has been done to study them comparatively on a broad scale in estuaries of the world. This study could be extended with profit, in time, to investigations based on laboratory-reared organisms and field analyses of comparative morphological, physiological, and behavioral variations within and among populations of representative species and subspecies (Kinne, 1964; Schlieper, 1958).

Early stages in the life history of estuarine benthic invertebrates are generally less well known than the adult, and thus provide an unusually fertile field for systematic researches. Investigations would be enhanced by inclusion of as many representative stages in ontogenies as feasible. In most cases this would require raising these populations in the laboratory, because working backwards, step by step in the field, from identified juveniles to larval stages is not always a reliable method of identifying early stages (Carricker, 1961b).

Least known, systematically, in estuaries are the micro-, meio-, and small megabenthos, and these groups therefore pose insurmountable taxonomic barriers to most ecologists. For some of these taxa there are no living systematic specialists, and all the benthic ecologist can do is to assign arbitrary codes to potential species until such time as they have been investigated systematically. This problem is especially thwarting now that benthic ecologists recognize more clearly the profound ecological significance of the smaller benthic organisms (Sanders, 1956; Wieser, 1960).

Lastly there is a conspicuous lack of checklists, illustrated keys, handbooks, atlases, and monographs for estuarine organisms of the world. The seriousness of this void to ecologists is apparent.

Although some of the recent biochemical (Buzzati-Traverso and Rechmire, 1953; Fox, 1956; Kirk *et al.*, 1954), cytological (Burch, 1960; Staiger, 1954), and numerical (Michener, 1963; Rogers, 1963) approaches may enhance the systematics of estuarine benthic organisms, there is so much to be done first at fundamental morphological and biogeographic levels that these other approaches on a large scale might better be delayed for a time.

ESTUARINE ENVIRONMENTAL FACTORS AND BENTHIC ORGANISMS

LATITUDE

It is recognized that the total number of coastal marine invertebrate species, especially epifaunal, increases markedly from higher latitudes to the tropics

(Day, 1964; Fischer, 1961; Hunter, 1964; Nicol, 1935; Panikkar, 1950; Parker, 1964a, b; Thorson, 1957); and that of these, species with pelagic larvae increase from a few to about 85 percent from the poles to the tropics (Thorson, 1961). How much, if any, of the global biotic gradient is effected by geographic position alone relative to the poles remains to be investigated. Whether latitudinal position, per se, of an organism on the globe, exclusive of the effects of temperature, day length, and biotopic instability (Fischer, 1961; Brongersma-Sanders, 1957), can be considered an ecological factor is uncertain.

Most latitudinal studies have compared animal activity with particular reference to temperature, and show that within a species, rates of metabolism in marine poikilotherms are about the same in individuals from northern and southern seas at their own native temperatures; and that at any given temperature metabolic activity is greater in individuals from colder waters (Bullock, 1955; Dehnel, 1955; Thorson, 1950).

Exclusion of all environmental effects, if possible, will be necessary to determine whether a specific latitudinal influence exists. Perhaps true estuarine species with their broad eurytopic proclivities and extensive latitudinal ranges may offer good experimental subjects. In a provocative study of growth as a function of latitude in populations of shallow-water euhaline gastropods of the same species separated latitudinally by approximately 1,900 miles, Dehnel (1955) held temperature and other obvious factors constant. He concluded that rates of growth of encapsulated embryos and larvae from northern populations were two to nine times greater than for southern populations at a given comparable temperature. Nothing was said about a possible ecological-latitude effect, per se; he speculated that better quality of yolk and growth promoters in the northern water may have explained the difference.

ESTUARINE WATERSHED

The variables of size, climate, geology, and vegetation of watersheds constitute an important, sometimes critical, complex of remote estuarine factors, in that they determine the volume and chemical nature of fresh water, the kinds and particle size distribution of unconsolidated sediments, the quality and quantity of organic matter, and living organisms discharged into the heads of estuaries, and the seasonal abundance of these properties.

Fresh water (Bernal and Fowler, 1933; Dussey, 1940; Klotz, 1962) flows into estuaries primarily as drainage areas from watersheds, and only to a minor degree as precipitation and underwater springs. Stream water functions as a vehicle for potential transport of (1) dissolved minerals and gases (Day, 1951, 1954; Hayes, 1954; Hutchinson, 1952; Nelson, 1945; Reid, 1961; Rockford, 1951; Russell, 1953); (2) silt (Hayes and Austin, 1951; Wells, 1961) and other organic substances in solution (Hood, 1963); (3) clays, salts, and lands (Menard, 1950a, b;

Nelson, 1959, 1962); (4) organic colloids and clay-organic complexes (Bader, 1962; Carritt and Goodgal, 1954); (5) detritus (Fox, 1957; Hjulström, 1955; Nevin, 1946; Parsons, 1963); (6) debris; (7) microscopic and larger drift organisms (Dendy, 1944); and (8) heat in summer in non-tropic latitudes (Nelson, 1947). The degree of survival of freshwater organisms as they drift into increasingly saline waters is poorly known.

Despite the purity of rainwater, its pH may range from 3.0 to 7.2, its Eh from 300 to 800 mv, and soluble constituents of $\text{SO}_4^=$, Cl^- , HCO_3^- , NO_3^- , Na^+ , Ca^{++} , and NH_4^+ may often exceed one milliequivalent per liter. Water originating in rivers and lakes has a pH range of 4.8 to 9.5 and Eh of -100 to 600 mv, in peat bogs a pH of 2.8 to 8.0 and Eh below 500 mv, in limestone caves a pH of 5.9 to 9.0 and Eh of 100 to 455 mv, and in mineral soils a pH of 2.8 to over 10 and Eh of -350 to 750 mv (Baas Becking *et al.*, 1957, 1960). Thus at one physiographic extreme a sandy pine barrens with its acid bogs and swamps drains an acid water low in minerals and high in stains (Carriker, 1961b). At another, a limey densely vegetated upland contributes clear alkaline water (Brust and Newcombe, 1940; Day, 1964). At still a third, a grossly deforested degenerating terrain loses excessive quantities of sediment which become deposited primarily in the head of the estuary (Emery and Stevenson, 1957b), accelerated by electrolytic flocculation (Day, 1951; Rochford, 1951), suffocating fixed benthic organisms, reducing photosynthetic activity, and rapidly filling the basin (Day, 1951, 1964; Hunter, 1912; Newcombe, 1952; Shepard, 1953). Man, at an advancing rate commensurate with the explosive growth of the human population, pipes domestic and industrial pollution into estuaries (Pearson, 1960a); releases aerial pollutants which wash into them; and ditches, dredges, and fills them (Allen, 1964; Bourn and Cottam, 1950; Thomas, 1956). A true estuary can exist only in climates with some rainfall, and inverse estuaries result in dry regions (Heigpeth, 1957c).

The characteristics and movements of factors contributed by watersheds to estuaries have been inadequately studied and offer many profitable avenues for investigation. A few of these are suggested in the following outline.

1. Examine the origin, nature, and temporal distribution of dissolved (Collier, 1953), and colloidal organic materials such as biocolloids and leptopel (Fox, 1957) originating in watersheds of various substrate and vegetational types; correlate the kind, quantity, and temporal and spatial distribution of these organic fractions with the seasonal decay cycles of vegetation in forested and swampy watershed areas, contrasting freezing and warm conditions; and investigate the potential of these fractions as nutrients and as stimulants for spawning and settling of estuarine benthic invertebrates. These organic substances assume increased significance now that it has been indicated that invertebrates

remove organic compounds from solution (Erdman *et al.*, 1956; Stevens, 1963) and fix carbon dioxide (Hammen, 1964); dissolved organic matter can be formed into particulate food (Bernal, 1961; Riley, 1953; Sutcliffe *et al.*, 1963) which can be utilized by certain invertebrates (Baylor and Sutcliffe, 1963; MacGinitie, 1945).

2. Determine the source pathways and rates of movement under varying seasonal conditions of selected inorganic molecules and clays from given sites in the watershed into the estuary (Carritt and Goodgal, 1954; Carritt and Harley, 1957; Hevesi, 1956; Nelson, 1962) by means of radioactive tracers (Mauchline and Templeton, 1964; Pearson, 1960b).

3. Study the possible role of free metabolites derived from the watershed as ectocrines in estuarine benthic communities (Lucas, 1961). Loosanoff *et al.* (1951), for example, in laboratory culture of bivalve larvae in water taken during the winter and spring from the Milford Estuary obtained inconsistencies in growth possibly attributable to unknown trace substances in this water (Ito and Imai, 1955; Provasoli *et al.*, 1959).

4. Consider the role of naturally occurring clays and silts in adsorption and transport of naturally occurring organic substances from the watershed into the estuary (Carritt and Goodgal, 1954; Bader, 1962; Nelson, 1962), and the use of these complexes by benthic filter and deposit feeders (MacGinitie, 1945).

5. Examine the capacity of estuarine benthic organisms to withstand the range of concentration of suspended sediments usually encountered in estuaries. Inter- and intraspecific variations in tolerance and adaptations to these are relatively unknown (Carriker, 1963; Day, 1951, 1964; Loosanoff and Davis, 1963; Yonge, 1953).

ESTUARINE BASIN, INLET, AND OFFSHORE AREA

Sea water (Hood, 1963; Lyman and Fleming, 1940; Sverdrup *et al.*, 1942; ZoBell, 1963) transports a rich admixture of dissolved gases, minerals, organic molecules (Hood, 1963; Parsons, 1963), clays, silts, sands (Van Straaten and Kuenen, 1958), organic aggregates, debris, and microscopic and macroscopic organisms (including predators) into estuaries. Although generally freer of organic fractions and suspended sediments than fresh drainage water, sea water carries a heavier load of dissolved minerals and organisms; as a consequence of its conservative thermal properties (Sverdrup *et al.*, 1942), it provides a buffer against extreme fluctuations of temperature (Clarke, 1954). Denser than fresh water, sea water moves into partially and completely stratified estuaries as a more or less distinct wedge along the bottom. In these circumstances its impact on benthos, especially in the lower reaches of these estuaries, is more immediately significant than that of the overlying fresh water whose mixing bottomward is delayed to the degree that the estuary is stratified vertically along its course (Bowden, 1964; Pritchard, 1960a). Ex-

ploration of the nature, seasonal distribution, and role of organic fractions of marine origin as nutrients, growth materials, and behavior-stimulating substances for the benthos (Lucas, 1961; Provasoli *et al.*, 1959), and the extent to which live marine plankters are killed on contact with less saline estuarine water and added to the load of dead benthic organic matter, provides a basis for an extended series of important investigations. The biological implications of chemical and biological interactions occurring in the estuary between organic and inorganic substances derived from the watershed and the ocean, especially in view of the fact that dissolved organic matter may be aggregated (Riley, 1963), are worth investigating, and may lend credence to the suggestion (Bernal, 1961) that polymerization of organic substances leading to the origin of life may have taken place primarily on estuarine muds.

In addition to the physical variability provided by volume and swiftness of flow of fresh water and rate of terrigenous erosion relative to the shape and capacity of the principal basin, the diversity of estuaries is further augmented by the shape and minimal cross-sectional area of the inlet (Bruun and Gerritsen, 1958; Day, 1951), tidal amplitude and type of tides (Marmer, 1926; Rossiter, 1963), height of shores, stability of bottoms and shore lines, longshore circulation, and degree of exposure to the ocean (Kuenen, 1950). In the Mediterranean, where the sea is relatively calm and tidal range is negligible, estuaries gradually broaden towards their mouths, and deltas are common. In England, where tidal action is considerable and wave action moderate, many estuaries broaden and tidal mudbanks appear, but main channels are kept open by the outflow of the river assisted by tidal currents. In South Africa, where wave action is usually extreme and tidal range seldom more than five feet, a sand bar is rapidly built up at the mouth and behind this the estuary spreads out as a wide shallow lagoon (Day, 1951). Estuaries are characteristically muddy coastal regions, exaggeratedly so on coastal plains (Day, 1951, 1964; Emery and Stevenson, 1957b) which are typical of the eastern coast and Gulf Coast of the United States. The estuarine basin constitutes a reservoir for concentration of sediment from both land and ocean (Van Straaten and Kuenen, 1958). Volume of water in the estuary, which is related to capacity of the basin, tidal amplitude, and volume of freshwater inflow, influences the size and depth of the inlet and other channels on sedimentary coasts. Unconsolidated sediments of barrier bars of bar-built estuaries are readily shifted by severe storms (Hite, 1924; Raymont, 1949), and inlets may be temporarily closed in the case of estuaries with minimal freshwater inflows (Day, 1964), or shifted along the barrier beach in those receiving more fresh water (Carriker, 1959; Shepard, 1952). This is in contrast to rocky shores which support relatively stable inlets. Oceanic shorelines of loose sediment are likewise readily worn by wave action and contribute suspended sediment which is transported into neighboring estuaries on flooding

tides (Emery and Stevenson, 1957b). High shores afford protection from wind and thus from wave action, and contribute to quiet estuarine habitats. Extremely high fjord shores may provide considerable shade to the disadvantage of photosynthesizing organisms.

Pervading longshore coastal currents are important not only in transporting coastally eroded suspended sediments, organic detritus, and debris (Zeigler, 1964), but probably also pelagic larvae of benthos (Bousfield, 1955b; Thorson, 1961) over long distances from one estuary to the next. During the ebbing tide the mass of water in lower reaches of the estuary flows out of the inlet, carrying plankters with it (Ayers, 1956; Barlow, 1955; Carriker, 1959, 1961b), and portions of this water fail to return to the same estuary, being transferred along the shore eventually to enter a neighboring estuary on a subsequent flood tide. In this manner it is likely there is substantial mixing among estuaries along many coasts of benthic biota equipped with dispersal stages. Information on this interesting biogeographic problem could result from tracing the movement of large numbers of laboratory-reared pelagic larvae of benthic invertebrates (Loosanoff and Davis, 1963) tagged with radioisotopes (Mauchline and Templeton, 1964), in a manner analogous to that being used to measure the transport of sediments with radioactive and fluorescent tracers (Zeigler, 1964).

In time, the estuary is shortened spatially by sedimentary deposition at the head and by wave erosion at the mouth, and filled by sediments. Rate and degree of fill corresponds principally with the rate of erosion of the watershed and inlet areas and amplitude of eustatic movements of the coastline (Emery and Stevenson, 1957a; Kuenen, 1950; Russell, 1957). Estuarine benthos are generally unaffected by imperceptible geological coastal movements induced by fluctuations of the shore relative to mean sea level. Furthermore, motile infauna and epifauna accommodate rapidly to gradual short-range vertical physiographic alterations imposed by removal or deposition of sediments (Carriker, 1961b). But the capacity and behavior of less motile estuarine benthos in adjustment to relatively rapid fluctuations of the bottom level are little known. Fixed epifauna, like oysters and barnacles, perish when covered by sediment, adjustment occurring only indirectly through later repopulation of the area from elsewhere.

ESTUARINE CIRCULATION

Estuaries range from vertically more or less stratified two-layered systems with opposing net (residual) non-tidal flows (drifts) of sea and fresh water to more or less well-mixed vertically homogeneous systems with unidirectional seaward flow. They grade from the idealized condition of the former to the homogeneous extreme of the latter as river flow decreases, tidal current velocities increase, width increases, and depth decreases (Bousfield, 1955a; Pritchard, 1955). No theoretical model yet takes into consideration the

possible effects of imperfect mixing of the fresh and sea water (Rossiter, 1963). Tidal currents shift the density stratification pattern up and down the estuary and contribute to vertical mixing. Winds may impose further mixing patterns (Bowden, 1964), especially in shallow estuaries (Barlow, 1956; Roelofs and Bumpus, 1954). Comparatively little mixing occurs between the fresh and salt layers of stratified systems (Pritchard, 1960a), so that dissolved and inert buoyant particulate substances entering in the salt wedge probably move very slowly up the estuary over the benthos in the landward drift, mix upward slowly across the level of no net motion and the halocline (Nelson and Perkins, 1931) into the surface freshwater stratum, and are transported fairly rapidly seaward in the surface drift. Thus substances entering in land drainage may never come directly in contact with estuarine benthos. In homogeneous estuaries distribution is uniform from surface to bottom, and the benthos probably are affected directly by the products of both watershed runoff and sea water. Although no statistics are available on this point, probably the majority of open estuaries of the world are of the partially mixed types. Pelagic larvae of benthic parents in stratified estuaries tend to be blocked from swimming into the freshwater stratum by the chemical ceiling imposed by the halocline (Nelson and Perkins, 1931; Bousfield, 1955a, b), a little-understood behavioral mechanism which appears to provide protection from osmotic stress.

Although duration of the complete tidal cycle in an estuary is the same as that in the ocean, duration of ebb is greater than that of flood tide, and time of low and high tide at the head of an estuary is later than that at the mouth. In estuaries with relatively small inlets the volume of water entering during flooding spring tides does not leave before the next flood tide, and consequently neap tides expose more of estuarine bottoms than spring tides. The effect of these phenomena on the benthos is unknown.

A major biological significance of the net circulation pattern in partially to completely stratified estuaries is the vehicle it provides for potential retention of pelagic larvae, and for mixing and concentrating inorganic and organic nutrients and other biotically important substances. Tidal currents and estuarine drifts also aid in mingling and dispersing gametes, spores, larvae, and minute older stages; in removal of metabolic products from, and bringing food and oxygen to, fixed benthos; and in flushing from the sediment metabolic products of benthic microbiological activity (Ferguson Wood, 1962). It is significant that current velocity is reduced to negligible rates immediately above many bottoms, because of resistance, and is difficult to measure accurately there with available current meters. Estuarine currents, furthermore, may aid predators in locating prey by means of chemical clues (Blake, 1960; Carriker, 1955a, 1957), in distributing benthos floated off the substratum and intertidal invertebrates crawling under the surface film of water on the incoming tide (Carriker, 1957;

Nelson, 1928), and in guiding rheotactically oriented mobile benthic organisms. The consequences of stagnation in the absence of estuarine circulation are seen in the bottom stratum of deep estuaries with sills (Gaarder and Spärck, 1933) and in periodically blocked, relatively shallow estuaries (Day, 1964).

One of the most obvious differences between an estuary and the open sea, and greatly modified by the width of the inlet, is the decrease in strength of wave action brought about by terrestrial semi-enclosure (Day, 1951, 1959, 1964). The impact of this on sediments and distribution of estuarine biota will be discussed later.

ESTUARINE SALINITY AND TEMPERATURE

Because of the relative ease of measurement of these factors, their vertical and horizontal distribution in estuaries is well known (Bassindale, 1943b; Bousfield, 1955a; Carriker, 1951b, 1959, 1961b; Day, 1951, 1964; Gunter, 1961; Hopkins, 1957; Kinne, 1964; Milne, 1938; Pearcy, 1962; Rochford, 1951; Segerstraale, 1957; Stroup and Lynn, 1963; Wells, 1961). Superimposed upon the broad salinity gradient from mouth to head is a series of salinity oscillations of varying duration and amplitude at any point along the estuary (Yonge, 1949a) corresponding with daily and lunar tidal cycles, seasons, rainfall, and melting snow and ice. Land drainage during periods of heavy precipitation forces salt water down the estuary, and spring tides move high-salinity water farther up the estuary than do neap tides. Although salinity is generally credited with setting the upper limit of penetration of estuarine species (Fischer-Piette, 1931), it is a complex interaction of many factors, any one or combination of which, exclusive of osmoregulatory problems (Prosser, 1955), could act as sources of this barrier. For the majority of benthic estuarine species the minimum survival salinity imposes a restraint which oscillates up and down the estuary with changes in freshwater inflow (Bousfield, 1955b; Carriker, 1955a; Gunter, 1961; Hopkins, 1957, 1962; Milne, 1940a; Segerstraale, 1957; Wells, 1961). At summer temperatures in temperate latitudes mortality rates of some molluscs increase as salinities fall, but this rate is reduced at lower temperatures so that in winter they may withstand low salinities for protracted periods (Amemiya, 1928; Carriker, 1955a). In the case of certain transient shrimp and crabs survival at low salinities is greater at higher temperatures (Kinne, 1964; Pearse and Gunter, 1957). Kinne (1964) reviews the effect of low limiting salinities on reproduction in estuarine invertebrates. Benthos which can retreat into burrows or exclude exchange of water by closure of exoskeletal parts are thought to be more resistant to low salinities than exposed "naked" species (Kinne, 1964; Moore, 1958). Thus the concentration, magnitude, and rate of change of salinity, and duration of exposure to these, are all ecologically significant (Bassindale, 1943b; Day, 1951; Smith, 1959). Furthermore, as dilution of estuarine water varies with fluctuations of freshwater inflow,

the proportion of salts in estuarine waters, generally slightly different from that of sea water to begin with (Carpenter, 1957; Kinne, 1964; Pearse and Gunter, 1957), and a function of the mineral composition of the hinterland (Day, 1951), may oscillate still further. On the whole there is a higher ratio of carbonate and sulfate to chloride and of calcium to sodium in estuarine waters than in sea water (Emery and Stevenson, 1957a; ZoBell, 1963). The effect of these ionic fluctuations on the behavior and distribution of estuarine benthos has not been reported in any detail (Kinne, 1964; Segerstraale, 1964). Day (1951) notes that the concentration of salt in sea water may be higher than essential so marine animals will tolerate passively a limited and slow reduction of salts, remaining isotonic throughout the change; possibly the same is true of changing proportions of minerals.

In vertically well-mixed estuaries the higher portions of the intertidal zone will be inundated only by the high salinity of high tide, and in the lower portions greater salinity fluctuations may occur as fresher water from the upper estuary flows seaward each ebb tide, whereas in stratified estuaries the intertidal zone may be subject to extremes of dilution. These variations undoubtedly influence the intertidal distribution of benthos (Day, 1951).

Thermal oscillations accompany those of salinity in estuaries, though not necessarily correlated with them, and result from the seasonal warming and cooling of the land and similar, more conservative, cyclical thermal changes in surface oceanic waters. Thus temperature conditions at the mouth are more stable than those higher up the estuary (Day, 1951). Within normal limits of subtidal distribution in a given estuary, heat is not normally lethal to benthos because of their relative independence of temperature (Bousfield, 1955b; Bullock, 1955; Kinne, 1963b; Prosser and Brown, 1961). As the density of the water varies with temperature, thermal differences in the two-layered estuarine circulation system can enhance its stratification and rate of residual circulation. This occurs in the late spring and early summer in temperate latitudes, when freshwater runoff is warmer and lighter than the colder, heavier sea water irrespective of salinity differences; the converse obtains in the fall. No one has attempted to relate these phenomena to the fact that most spawning of benthos occurs in the late spring and early summer in temperate and boreal regions. The migration of animals, including predators of estuarine benthos, in and out of estuaries in relation to temperature is not completely understood (Day, 1951), though migrations of invertebrates and fishes into warmer water in winter have been reported (Kinne, 1963b).

Drost-Hansen (1956; Oppenheimer and Drost-Hansen, 1960) has suggested that a number of more or less abrupt changes in the properties of water and aqueous solutions occur when the temperature is increased from 0° to 60° C., these changes or "kinks" occurring at approximately 15, 30, 45, and 60° C. The kinks are believed to be caused by structural

changes in water, and it is postulated that these changes influence the behavior and activity of biological systems. Thus optimal conditions for growth occur somewhere near the middle of the interval between two consecutive kinks, or approximately at 7–8, 22–23, and 37–38° C. where the liquid is structurally most stable to thermal changes and consequently where the most stable conditions for biological activity are present. This further suggested to Oppenheimer and Drost-Hansen (1960) the possibility that an organism may have more than one optimal temperature in nature, that this may account for increase in activity at certain periods of the annual cycle corresponding to the predicted optimal temperature, and that microorganisms which are optimally active in arctic environments may also be active in tropical environments at temperatures between the kinks. The implications of these aspects of molecular and quantum biology (P. Person, personal communication) are worth examining in terms of ciliary, locomotory, growth, spawning, predatory, feeding, and other activities of estuarine benthos with reference to the seasons, location along the estuarine gradient, and in estuaries located along the latitudinal range. For example, is it possible that there is a null point in the vicinity of 15° C. at which minimal activity in terms of spawning, feeding, and locomotion may be expected on a seasonal and latitudinal scale?

In upper latitudes benthic intertidal organisms may freeze and ice may scour and gouge them away (Bousfield, 1955b; Madsen, 1936). Kanwisher's pioneer studies on the effect of freezing on intertidal organisms (1955, 1957, 1959) should stimulate further work along these productive lines. Amplification of this approach with reference to the estuarine salinity gradient and the capacity of organisms physiologically to adjust or regulate (Prosser, 1955) also bears consideration. Also worth pursuing are similar investigations in the estuary on the effect of heat in warmer seasons and regions of the globe. Little has been done on the seasonal vertical migrations of motile benthos within sediments and the correlation of this with temperature (Carriker, 1955b). It is not surprising that year-round studies of estuarine benthos in higher latitudes have received much less attention than summer investigations; reports on long-range studies which have appeared (Sanders, 1960; Thorson, 1946a, b) attest the substantial productivity of the over-winter approach.

Heat distribution in sediments can be determined readily by means of thermal probes. Changes in the sediment reflect those of the overlying water, but the rate is more conservative and is dependent on the thermal buffering capacity of the sediment (Johnson, 1965; Linke, 1939; MacGinitie, 1935). Because of the cooling effect of evaporation, an exposed bottom is cooler than a submerged one at a similar constant air and water temperature.

Distribution of interstitial salinity is considerably more difficult to study and consequently is less well understood (Alexander *et al.*, 1932; Emery and Ste-

venson, 1957a, b; Jansson, 1962; Johnston, 1964; Nelson, 1962; Smith, 1956). Jansson (1962) and Cox (1963) strongly recommend study of the salts of interstitial estuarine water by means of electrical conductivity, which is directly proportional to total salinity, though the ionic composition may vary from that of sea water of the same salinity. Jansson (1962) has demonstrated in the laboratory that certain oligochaetes will choose a preferred interstitial salinity over another.

Kinne (1963b) emphasizes the combined ecological and physiological importance of temperature and salinity, and thus the need to consider the effects of these factors jointly. Temperature can modify the effects of salinity and change the salinity range of an organism, and salinity can correspondingly modify the effects of temperature.

Hydroclimographs (Hedgpeth, 1951) may present a useful means of comparing salinity-temperature conditions in varying estuarine sediments. Stauber's (1943) haligraph, which combines a map and graph on which are plotted the geographic points at which salinities are determined, the value of these salinities, and the total range of salinity as it varies with tide and depth of water, might be a useful way of recording the salinity dynamics of estuarine sediments.

Although no one appears to have suggested the possibility, it is reasonable to suppose that warm cooling water from atomic energy plants along estuaries could be released at the surface and in the vicinity of sewage outfalls in order to accelerate the flushing of this pollution out to sea in the surface drift.

LIGHT ENERGY IN ESTUARIES

Intensity of penetration of solar energy in water is reduced by absorption and scattering, while stains and suspended particles further attenuate its intensity and modify the degree of penetration of each part of the spectrum (Clarke, 1954; Clarke and James, 1939; Clarke and Oster, 1934; Cooper and Milne, 1938). Because of the seasonal discharge of muddy streams and rivers, variations in plankton blooms, and seasonal changes of light intensity, the quantity of solar energy reaching the benthos is highly variable. Suspended matter absorbs the blue and green wave lengths of light, and, because of the lower salinity, less of the infrared and visible red is absorbed by dissolved salts (Cooper and Milne, 1938). The predominantly turbid nature of most estuarine waters makes their bottoms considerably more shaded than those of clear sea water. These conditions directly affect photosynthetic microorganisms dwelling on or near the surface of the sediments. The marked contrast in primary productivity between subtidal bottoms and intertidal flats has been investigated by Sanders (1958, 1960) and Sanders *et al.* (1962). Little information is available on penetration of light into different types of estuarine sediments; depth at which photosynthesis ceases is unknown, though photosynthetic cells may be found as deep as 12 cm and

can migrate vertically at least a centimeter in the mud with rise and fall of the tide (Ferguson Wood, 1962). Motile benthos are generally negatively phototactic to strong illumination (Carriker, 1957), and thus may benefit from the shaded estuarine conditions, coming out into more exposed areas in daylight during periods of heavy turbidity. Conversely, infaunal invertebrates with light-sensitive organs at the sediment-water interface (Light, 1930) may be at a disadvantage in the dimmer estuarine environment when relying on shadows cast by passing predators to escape by withdrawal. This interesting possibility has not been investigated. A number of investigators suggest that light plays an important role in the behavior and distribution of pelagic larvae of benthic organisms (Carriker, 1961b; Haskin, 1964; Nelson, 1916; Nelson, 1926; Thorson, 1957). Except for Haskin's significant discovery that in the laboratory oyster larvae do not respond to changing salinities except under light passing through a yellow-grain filter with maximum transmission at 575 μ , little is recorded on the specific effects of light and which frequencies of the spectrum are effective. Much has been written on photoperiodicity, but little is recorded on the effect of light periods (exclusive of temperature effects) on, for example, gonadal development and hibernation in estuarine benthos at different latitudes. Finally, Friedrich (1961) summarized information that suggests that penetration of marine organisms into estuarine waters depends not only on temperature and oxygen content of the water, but also on light, penetration being facilitated by the absence of light. This bears further study in terms of a possible higher rate of penetration of marine predators into estuaries during periods of high estuarine turbidity.

SUSPENDED SEDIMENTS AND SEDIMENTATION IN ESTUARIES

The characteristically turbid nature of estuarine waters is a product of the interplay of: (1) the particulate matter from the watershed, off-inlet shores and bottoms, reworking and scouring of estuarine bottoms by tidal currents and waves, loosening of bottom sediments by burrowing animals, and decomposition of pelagic and benthic estuarine organisms; (2) the net two-layered opposing estuarine circulation pattern; (3) the mixing of fresh and sea water and consequent flocculation of finer particles; and (4) the presence of relatively quiet sedimentation areas provided by semi-enclosures and widening of the estuarine basin. The original bulk of sediment in most estuaries is derived from the watershed, in some from the sea, and in some probably from both; it is this which makes determination of origin difficult. In all estuaries the quantity of sediment is generally greater than 1% accumulating on the watershed and off-inlet areas (Bassindale, 1943a; Burt, 1955; Cooper and Milne, 1938; Emery and Stevenson, 1957a, b; Guilcher, 1958; Kuenen, 1950; Salomon, 1962).

Suspended estuarine sediments consist of particles and aggregations of particles floating in a complex

solution, and, though having affinities with terrigenous and marine sediments, they retain their own unique character and complexity (Nelson, 1962). In open surface waters the organic component of suspended sediments consists of zooplankton 3 percent or more, phytoplankton seasonally up to 50–60 percent, and organic detritus up to 90 percent (Hayes, 1964). Similar data are not available for estuaries. The original structure and texture of terrestrial soils are broken up and the components transported into the estuary by forces of water flow. Sediments may there be transformed by ion exchange reactions, recrystallization, assumption of new bulk properties, and changes in associated microbiota. Drifts and tidal currents distribute the gradient of particle sizes, and tidal currents and wave action locally redistribute and rework these particles and sort them into well-differentiated, more or less homogeneous sediment types (Inman, 1949; Sanders, 1958). It is thus that the textural variations typical of estuarine substrates, of such significance to benthic ecology, are formed (Nelson, 1962).

Coarsest particles drop out at, and immediately beyond, the mouths of streams and in the vicinity of inlets. The proportion of sand decreases from the head and inlet toward the upper region of the estuary, finer sands settling out roughly as water motion decreases (Day, 1951; Inman, 1949). In strong channel currents abrasive forces of waterborne sands may be sufficiently harsh to remove even oyster larvae which may have settled there on exposed rock surfaces (Shelbourne, 1957). Larger silt particles also probably sink directly from suspension; successively finer particles accumulate in the deeper, quieter areas and toward the high water line in areas where wave turbulence and current velocity are minimal, leading to the formation of flats, tidal marshes, and mangrove swamps (Day, 1951; Emery and Stevenson, 1957b; Guilcher, 1958; Kuenen, 1950; Kurz and Wagner, 1957; Rochford, 1951).

The problem of deposition of colloidal particles in estuaries is complicated and not entirely resolved (Kuenen, 1950; Sverdrup *et al.*, 1942). According to Rochford (1951), electrolytic flocculation of colloidal clay-silt fractions takes place at a fairly low chlorinity figure, and the rate of sedimentation is balanced between gravity and vertical turbulence developed by water movement. Thus maximum deposition occurs in quiet sheltered areas where water is nearly motionless. Coarser materials larger than 15 μ may not be flocculated and will settle approximately at the computed velocity; but finer flocculated materials settle with a velocity equivalent to that of quartz spheres between 5 and 15 μ in diameter, or 1 to 20 m per day (Sverdrup *et al.*, 1942). Coloring matter from decomposition of vegetable matter in the watershed is a positive-charged colloid and is deposited in the presence of colloidal silt which is negatively charged; but it is not coagulated by metallic ions of sea water. In some South African estuaries the brown color persists even in salinities of 30 %

(Day, 1951). Flocculated particles, organic and inorganic and mixtures of these, caught in vertical turbulence, will be held in suspension for a long time or until transported out into neritic waters, where they are dispersed and sedimented as turbulence decreases. Some may be returned to the estuary later in the bottom drift. Nelson (1959) reported that freshwater streams discharge into estuaries both dispersed sedimentary particles and floccular aggregates originating in weathering horizons of the watershed. The dispersed particles are carried in relatively permanent suspension, while floccular aggregates are transported by saltation and temporary suspension, later settling in quieter areas. Concentration of dispersed suspended sediment in low salinities at the head of the estuary exceeds that in the freshwater discharge. He attributed this increase to deflocculation of floccular aggregates in the lowest salinity zone. Concentration of dispersed suspended sediment decreases down the estuary as a result of progressive dilution of fresh water by neritic water, and not significantly by flocculation and subsequent settling out.

It appears, then, that what fractions do settle out are deposited mainly in quiet areas relatively free of waves where the water is at rest for a sufficient length of time at each turn of the tide for settling to take place (Häntzschel, 1955; Nelson, 1959; Rochford, 1951); field observations confirm this. It is probable that more sedimentation occurs during the ebb than during the flood, as current velocities are lower and duration of flow is greater during the ebb; and more during neap than spring tides, because of lower tidal amplitudes and correspondingly lower current velocities during neap tides.

The literature stresses the role of physical and chemical factors in sedimentation of colloids and larger particles, but it is the writer's untested observation that biotic activity may be more important in this regard than has been suggested to date (Kuenen, 1950). Estuarine bottoms are paved by a wide variety of in- and epifaunal filter feeders (Barker Jørgensen, 1955, 1962; Marshall, 1960), a number of which are well known as sediment consolidators (Lund, 1957; Maas Geesteranus, 1942; Verwey, 1952). Furthermore, the epidermis of external soft parts in the mantle cavity and other gill chambers of many invertebrates consists of mats of mucous and ciliated cells that function in trapping and removing the settling particles (Carriker, 1963). The volume of estuarine water from at least the lower vertical stratum which is pumped through these organic filtering devices, or moves over these ciliated cleansing surfaces, must be substantial (Barker Jørgensen, 1960) and accumulation of bottom sediments by defecation and ciliary concentration could account for a major percentage of the sedimentation process. In a more passive way rooted estuarine plants (tidal marsh vegetation, mangroves, *Zostera*, *Ruppia*, and similar forms) accelerate sedimentation by providing quiet zones for settlement (Ferguson Wood, 1962).

Bader (1962) demonstrated experimentally in the

laboratory that naturally occurring dissolved organic molecules are absorbed from aqueous solution by naturally occurring clay minerals to form clay-organic complexes, controlled primarily by the crystallographic structure of the mineral and the molecular weight, functional group, and structure of the organic compound. There is a preferential order of association of both minerals and organic compounds. The clay montmorillonite removed the most organic molecules from solution, then illite, kaolinite, and quartz, in that order; alanine was most readily and consistently removed by all the minerals, then sucrose, fructose, succinic acid, and oxalic acid, in this order. Expressed on a relative scale based on 100 for quantity of soluble organic matter in the sea (average of 1 mg/l), Parsons (1963) gave the following proportions of total organic materials: soluble organic matter, 100; particulate organic matter (minimum size 1 μ), 10; phytoplankton, 2; zooplankton, 0.2; and fish, 0.002 (R. Wood, 1963). For coastal offshore waters Barker Jørgensen (1955, 1962) reported concentrations ranging from 2 to 5 mg/l; and for coastal bodies of water in the U.S.S.R., Skopintsev (1959) recorded a range of 3 to 13 mg/l. Negligible information on the concentration of dissolved organic matter in estuaries is available but because of biological activity there and the amounts brought down in stream water (Hood, 1963), it should be higher than in the sea. Dissolved organic substances identified in sea water are listed by Hood (1963). The potential significance of sorption to clays in making the substantial reserve of dissolved organic matter available to benthic filter and deposit feeders is clear (Fox *et al.*, 1952), and in this sense it is a favorable circumstance for estuarine benthos that both dissolved organic matter and suspended clays are especially abundant in estuaries. Fox (1957) called these finely particulate fractions leptopel, and found that concentration of organic (protein, lipid, polysaccharide) and inorganic (silicates, insoluble carbonates, phosphates, hydrous oxides) portions and proportions between the two classes were highly variable even in temperate waters in nature (Hood, 1963). Their disposition depends upon depth, temperature, light, relative densities, water movements, seasons, and proximity to land. In surface neritic waters the concentration may approach several mg/l and increase tenfold or more immediately beneath surface slicks. The amounts of organic matter may rise by a hundred thousand times their values when adsorbed to fine inorganic particles or bottom muds.

Coarser to macroscopic organic-inorganic complexes have been known for some time as detritus. In suspension they occur mainly in the form of loosely aggregated, flaky, sometimes frothy mixtures of organic molecules, including vitamins, organic colloids, and organic fragments intermixed with various proportions of clay, silt, fine sand, and living microfauna (Parsons, 1963; Starr, 1956; Zhukova, 1963; Zhukova and Fedosov, 1963). Many of these detrital aggregates have a specific gravity approaching that

of estuarine water and may be carried for a long time in suspension before they settle or come close enough to filter-feeding organisms to be taken in by them. Once deposited on the bottom, detritus adheres there, bound by organic matter in various stages of decomposition. It is these mucoid binding materials that give fine estuarine deposits (Kuenen, 1950; Macnae, 1956) their specific properties and are the main cause of the mixing of finer and coarser fractions in the same deposit (exclusive of rhythmic stratification imposed by fluctuations in water motion). Only relatively strong water action or activities of animals can then dislodge the surface layers (Kuenen, 1950). Parsons (1963) reviews a number of recent methods, some of which when further developed may facilitate the study of suspended detritus. These methods involve photography, particle size analyzers, distinction of phytoplankton and other particles by means of red fluorescence of chlorophyll, and estimating the total living portion of particulate matter. As detritus is readily fragmented when removed from its natural environment, it is best studied *in situ*; the viewing devices of Nishizawa *et al.* (1954), and the television microscope (Barnes, 1958) may be helpful. For the study of distribution and patchiness of suspended detritus, Tonolla's (1958) apparatus might be considered.

Guilcher (1958) suggested that certain mudbanks seem to have reached a state of equilibrium in spite of the presence of suspended sediment over them. This is of ecological significance to benthic community stabilization, and is worth further study. Such an investigation would be difficult inasmuch as determination of the rate of accumulation of sediment in the sea presents formidable difficulties (Kuenen, 1950).

Owing to the unconsolidated nature of estuarine sediments, the subtidal and intertidal banks of channels (including those of marshes, but less so through mangrove swamps), are continuously eroded along the outer bank of a curve by waves and currents, and simultaneously built up on the opposite bank; meanders are cut off; abandoned channels are filled; and other physiographic alterations are very slowly but constantly occurring (Kuenen, 1950; Ragotzkie *et al.*, 1959). Fecal and pseudofecal pellets formed by benthos (Moore, 1955) and sedimentary particles released by animals burrowing for shelter or food are further added to the load of suspended materials. This resuspension of sediment takes place most actively during the flood of spring tides. As a consequence of estuarine tidal mixing, sedimentation, and reworking processes, turbidity of the water is higher at a given point in the estuary at low than at high tide. This is particularly evident in the lower reaches of the estuary (Cooper and Milne, 1938), where water is clearest and most saline during high spring tides (Carricker, 1959).

Although it is known that the presence of significant amounts of fine suspended particles decreases perceptibly the rate of fall of large particles (Hjul-

ström, 1955), there is a scarcity of information on the mechanical effect of these particles on pelagic larvae of benthic parents. Studies performed on estuarine bivalves suggest that their larvae display a considerable tolerance to suspended sediments. Loosanoff and Davis (1963) found that oyster larvae (*Crassostrea virginica*) may live as long as 14 days in concentrations of 2 g/l of silt and up to 4 g/l of either kaolin or Fuller's earth under laboratory conditions, demonstrating the ability of the larvae to withstand the highly turbid conditions of its natural estuarine environment. Clam larvae (*Mercenaria mercenaria*) apparently do not utilize detritus for food and, as they are capable of selective feeding and controlling the volume of intake up to a certain level of concentration of available food cells, sedimentary particles may be selectively eliminated from the diet. Loosanoff's further observation, that growth of straight-hinged larvae of oysters and clams was often considerably more rapid than that of controls when small quantities of sediment were introduced to the cultures, suggested to him that these particles adsorbed toxic substances present in the cultures. The heavy loads of clays and silts which enter estuaries may conceivably adsorb the increasing quantities of toxic pollutants flowing into these embayments, and may account for survival of these and other similar larval species of invertebrates, who do not ingest inert particles, in the face of increasing pollution. The greater the degree of selective elimination from the diet of inert particles by filter-feeding adult benthos, the greater the chance of escape from these adsorbed poisons; correspondingly, non-selective deposit and suspension feeders would be most vulnerable to poisoning. Loosanoff's experiments provide the basis for many more studies on the role of sedimentary particles in the lives of pelagic larval stages of estuarine benthos. Furthermore, there is much more to be known of the capacity of different larval species to ingest and utilize the available spectrum of suspended organic particles, the concentrating mechanisms by means of which this is done, and whether finest mineral particles may not themselves be ingested to satisfy physiological mineral requirements.

ESTUARINE BOTTOM SEDIMENTS

These differ importantly from terrestrial soils as a result of physical alteration and redistribution and chemical adjustments in the estuary; they are unique assemblages of matter retaining their own character and complexity (Nelson, 1962). They constitute a massive ecological complex of factors of significance to benthic organisms; as Longhurst (1964) points out, the nature of sediments should receive almost as much attention as the fauna in them. Until a decade or so ago emphasis in the ecological study of marine sediments was placed on gross texture and total organic carbon (Barnes, 1959). In recent years stress has shifted to a closer examination and interpretation of the dynamics of benthic phenomena at ionic, molecular, micro-, and smaller megabenthic levels

(Bader, 1962; Burkholder, 1963; Hayes, 1964; Kanwisher, 1962; Kohlmeyer, 1963; Nelson, 1962; Oppenheimer, 1963; Sanders, 1960; Sears, 1959; Wieser, 1960; Ferguson Wood, 1962; Zhukova and Fedosov, 1963). The field is far from exhausted, but results so far indicate that this has been a rewarding trend.

The most characteristic and best known estuarine substrate consists of clays and silts and organic matter, and is found principally in the upper reaches and quiet lateral areas of estuaries. This substrate assumes a distinctive profile to a depth of a decimeter or so, and, being an integrated spectrum of all the physical, chemical, and biological factors there, serves to distinguish many of the microenvironments in quieter areas of estuaries (Nelson, 1962). Ecologically, the upper layer very roughly 5 to 10 cm deep, which is inhabited by burrowing invertebrates and re-worked by them, grades into the bottom or "historical" unworked zone; below the burrowing line there is a decline with depth in the number of bacteria (Hayes, 1964).

There is no fundamental textural differentiation among horizons of the clay-silt-organic sediment profile. It is primarily a chemical and biological adjustment between the oxygenated mobile overlying water and the de-oxygenated and immobile sediment at depth in which diffusion and exchange proceed upward toward the free water and vary seasonally, at least, in non-tropic regions. At the sediment-water interface (Hayes, 1964) there is a thin layer of semi-fluid brown oxidized sediment which is swept temporarily into suspension by the stronger currents. Below this is a thin layer of olive gray sediment and then one of very dark gray or black mud. Where water movements above the bottom are sluggish and there is minimum diffusion of molecules from the water to the sediment, these zones may compress close to the surface. Nutrients and trace elements diffuse across the second and third layers from the sediment into the overlying water. Below them all is a layer, typically medium to light gray in color, which represents sediment that has passed beyond maximum microbial decomposition and chemical activity. The depths of the various horizons below the sediment-water interface are a function of ventilation in the overlying water, and their positions shift with changes in these conditions. Varying degrees of water movement will erode the surface of the profile or may admix fine sand, and in shallow water the mud may be swept away, leaving a sand which does not exhibit the typical estuarine sediment profile (Nelson, 1962). Moore (1930), in a mud profile in Bristol Channel, distinguished an upper dark layer containing a high organic content, an intermediate reduced stratum with less organic matter, and an anaerobic layer with very little organic matter. Sanders (1960), in the high salinity silty-clay sediment of Buzzards Bay, noted a top 2-3 cm brown unconsolidated flocculent layer, and a lower gray consolidated zone. The amount of organic matter present in the two layers was about equal, but detectable quantities of free sugars were

present only in the surface zone. Although in general no basic textural distinctions in particulate matter among horizons at the macro- and microscopic levels of the profile have been recognized, these may exist at the low ultrastructural level. In view of the relationship of microorganisms which dwell on and among sedimentary particles and aggregates, it may be useful to examine these particles with the electron microscope (Hathaway and Robertson, 1961).

Although clays, silts, and organic matter constitute the distinctive and predominant sediments in estuaries, admixtures of sands and coarser particles occur in the direction of inlets and wave-exposed shallow and intertidal zones; bottoms under strong currents and wave action may be predominantly sand (Day, 1951). Particularly in small shallow exposed estuaries the proportion of sandy bottom may be substantial (Carricker, 1959; Parker, 1960). Hedgpeth's detailed review of sandy beaches (1957d) suggests what may be looked for in estuarine sandy beaches and clean sand flats (Pearse *et al.*, 1942; Stephen, 1953; Yonge, 1950), though such extrapolation should be pursued cautiously until further work is done on estuarine intertidal areas.

Rocky substrates, oyster reefs, shell deposits, and other hard surfaces (except at water-scoured inlets and wave-exposed intertidal zones) seldom exist as clean surfaces in estuaries because of sedimentation (Day, 1959; Percival, 1929). Colonizing organisms are thus presented with a mat of sediment of varying thickness overlying hard surfaces (Carricker, 1961b; Korringa, 1951; Percival, 1929). The character of such sediments, in most respects, is probably similar to that of deeper sediments in the bottom, but the effect of the presence of the underlying shallow solid floor and thus minimal anaerobic conditions is not known (Chapman and Newell, 1949; Glynne-Williams and Hobart, 1952). Most studies of colonization of rocky surfaces have been conducted on relatively clean exposed non-estuarine hard surfaces (Doty, 1957). Worth pursuing is the effect of salinity and sedimentation on settling and excavation by organisms boring into mollusc shell and calcareous rocks (Goreau and Hartman, 1963; Hopkins, 1958, 1962; Yonge, 1963) and the degree to which up-estuary penetration occurs.

As Nelson (1962) points out, it is apparent that complexities of estuarine sediments determine many of the subtleties of ecological relationships among the benthos; and that the major effect of the sedimentary substrate is its role in maintaining unique chemical conditions in the bottom and immediately overlying water. The chemical complex consists of the interdependent factors of texture and structure, organic content, pore-water chemistry, ion-exchange equilibria, gas equilibria, and microbiological activity. The structure and texture of sediment *in situ* establishes the framework within which chemical and biotic processes operate. Determination of particle size distribution of disaggregated sediments has been accomplished routinely for some time; but much more

needs to be done on the characterization, started by Moore (1931a), of the natural size range and nature of particles and aggregates, and porosity in undisturbed sediments. To be examined are such physical properties of sediments as thixotropy (quicksand) and dilatancy, as they affect the speed of burrowing and probably other activities of burrowers, especially intertidally (Chapman, 1949). The ecological significance of these structures and their properties to micro- and meiobenthos, especially, must be profound, as it is these which constitute their biotope.

Only a rudimentary knowledge exists of the chemistry of interstitial water. Nelson (1959, 1962), working on sediments within a salinity gradient of 0-20‰ in a long estuarine distributary of Chesapeake Bay, contributed significant information on water content, ion exchange, pH, chlorinity, major ion composition, alkalinity, NH_3 , H_2S , and CO_2 . Water content of the profile was about 80 percent by weight at the surface, and then decreased regularly to about 50 percent at a depth of some three feet. Calcium was the dominant exchange ion in fresh water; in brackish water sodium began to occupy the exchange sites and as salinity increased, sodium replaced calcium. In brackish water the concentration of magnesium and potassium apparently was too low to have any effect on the exchange complex, but with increasing salinity down the estuary they became about equivalent to exchangeable calcium, while sodium remained the dominant ion. The change in chemical character of estuarine sediments along the salinity gradient was most generally reflected by a change in sediment pH. Freshwater sediments were slightly acidic in reaction; as clay materials were moved progressively into more saline water, their pH rose until it became moderately more alkaline as a result of saturation of the negative surface charges with basic cations. Vertically, pH within an estuarine sediment profile, determined first by cation exchange and then by gaseous equilibria, generally increased slightly with depth to a maximum, then decreased very slightly.

The chlorinity of interstitial water increased down the estuary commensurate with that in overlying water. Normally, chlorinity of pore-water at the sediment surface slightly exceeded that of the adjacent overlying water, though this feature may vary with the type of estuary. In the upper reaches of the estuary chlorinity was uniform with profile depth, but in the lower, more saline reaches interstitial chlorinity increased slightly with depth (Nelson, 1962). Laevastu and Fleming (1959) found that replacement of fresh interstitial water with salt water in an estuary was rapid, but replacement of salt interstitial water by overlying fresh water was a much slower process. This confirms the earlier observations of Alexander *et al.* (1932), that water retained in the muddy foreshore of an estuary at low tide is more saline than estuarine water itself at the same distance from the sea, and those of Reid (1932), that sand likewise tends to retain higher interstitial salinity. This condition may be of considerable ecological

import, as it permits infauna to penetrate a greater distance up the estuary than epifauna of similar osmotic tolerances (see also Milne, 1940a; Moore, 1958; Kinne, 1964), presumably providing a more stable saline environment than the ambient water for burrowing organisms and roots of plants (Emery and Stevenson, 1957b). The quantitative relationship between salinity in the substratum and the variable salinity of the overlying water is still not completely understood; bottom dwellers, by irrigation of their burrows, may profoundly influence the speed of adjustment of interstitial salinities to variations in the overlying ambient salinities (Smith, 1956).

Occasionally groundwater flows into estuaries by way of springs either in the salt marsh or subtidally, creating unique ecological conditions in sediments in the close vicinity of the freshwater inflow (Burbanck *et al.*, 1956). The details of this interesting ecological phenomenon have not been reported.

Nelson (1962) reports that one of the most useful potential ecological factors for detecting significant changes in the sediments is the titration alkalinity of interstitial water. At the sediment surface this generally increased from fresh to saline water just as did the alkalinity of the estuarine water itself, but whereas that of sea water seldom exceeds 2 meq/l, pore-water alkalinites commonly reached 5 or even 10 meq/l, increasing from well-ventilated to poorly ventilated sediments. A pronounced increase occurred with depth in all sediment profiles, but apparently independently of chlorinity.

In a stimulating report on gas exchange in shallow marine sediments, Kanwisher (1962) records that gas exchange measurements of a bottom provide an indirect means of determining the overall biological rate in the benthic community, and indicate that shallow marine sediments constitute essentially an anaerobic biotope. In this regard, Hayes (1964) cautions that there are difficulties in using oxygen consumption as a useful and sensitive measure of the biochemical activity of sediments, as each mud, by reason of the historical activity of anaerobic organisms, forms reduced compounds which oxidize spontaneously when aerobic conditions are provided; at the same time aerobic bacteria increase in numbers to reach a steady state; and in nature, oxygen uptake is a surface phenomenon and, depending on the season, the circulation, and the demand, the sediment-water interface may be more or less deprived of oxygen. He concludes that study of the biology of marine sediments is largely a problem of microbiology. In obtaining energy through respiration under aerobic conditions, organisms use molecular oxygen as the hydrogen acceptor. Under anaerobic conditions, nitrogen, sulfur, and carbon, in this ascending order of efficiency, are used, and then primarily only by bacteria which are capable of such biochemistry. Below a thin surface layer of a centimeter or so, bottom sediments are anaerobic; thus the alternate hydrogen acceptors are used, and NH_4^+ , H_2S , and CH_4 occur in the sediment if nitrogen, sulfur, and carbon are available. The

general anaerobicity in the bottom results from the *in situ* demand for oxygen exceeding that supplied by diffusion from the overlying water, and from the fact that there is little vertical movement of the interstitial water and of dissolved gases, except from burrowing animals (Brafield, 1964). In the absence of oxygen the most general chemical factor of the sediment is the state of oxidation-reduction, which seems useful only as a general guide in estimating the types of organisms to be expected (Baas Becking *et al.*, 1957, 1960; Hayes, 1964). Eh decreases with depth, measurements of -200 mv being common in organically rich sediments. Much of anaerobic respiration involves sulfur reduction, because nitrogen is present only in small amounts and sulfur is abundant; this accounts for the conspicuous quantities of H_2S in anaerobic sediments. Formation of H_2S by bacteria is a ubiquitous and common microbiological process (Gunkel and Oppenheimer, 1963; Moore, 1931a) and seems to exert a marked influence on the biology of sediments (Ferguson Wood, 1962; ZoBell, 1946b). Methane is also common as carbon-reducing bacteria are also abundant. As respiration usually predominates over photosynthesis, oxygen passes into the sediments from the overlying water, and CO_2 emerges. Insoluble compounds such as elemental sulfur and FeS will be held at the level where formed. As H_2S diffuses upward it reaches the oxygenated layer, where it either oxidizes spontaneously or is utilized by bacteria; some also passes freely into the water. All biological and chemical activity involving sulfur occurs in the upper 1 or 2 cm of the profile. Photosynthetic oxidation is limited to the depth of light penetration, but some diatoms are also heterotrophic (Lewin, 1963; Ferguson Wood, 1962) and thus may move deeper into the sediments. Kanwisher calculates that a little over 10 percent of the productivity of the overlying waters is consumed by the bottom community; and notes that in spite of lack of oxygen in the bottom and greater production of CO_2 than O_2 consumption, there is an extensive infauna which must live temporarily or permanently without this gas (Wieser and Kanwisher, 1961). The reduced products produced by this anaerobiosis are oxidized in the thin aerated surface layer of the sediment. Kanwisher did not relate his observations to specific types of sediment or strata in the substrate profile, so it is difficult to relate his results spatially to those of Nelson (1962).

Oppenheimer and Ward (1963) investigating intertidal mud flats of Texas estuaries where rapid sedimentation occurred, found an annual cycle of redox potential, in which the oxygen transition zone was at the surface of the sediment during the summer with high bacterial activity and oxygen consumption, but a few centimeters within the sediment in the winter when bacterial activities declined. In contrast, pH went through a diurnal change from approximately 6.5 to 8.0, during respiration and photosynthesis, respectively, to the depth of light penetration (about 0.5 cm in fine sediments, and to 1.5 cm in sandy sediments). Under circumstances of high temperatures,

deep sluggish water, and a highly reducing bottom, free oxygen may disappear from the zone of water immediately over the bottom (Carpenter and Cargo, 1957; Nash, 1947) with lethal consequences to epifaunal and aerobic infauna.

In his studies of estuarine sediments, Nelson (1962) found CO_2 , NH_3 , and H_2S the most abundant and reactive gases. The relative proportion of total NH_3 , H_2S , and CO_2 was 1:10:100. All showed maximum concentration at some horizon a few inches below the sediment surface; in addition NH_3 showed a gradual increase with depth, H_2S remained essentially constant, and CO_2 decreased with depth. Shishkina (1959), from a study of the composition of salts in interstitial water in deep, quiet, undisturbed marine sediments, suggests that in some regions this pore-water may remain unchanged for hundreds of thousands of years; studies of the age of interstitial water in estuarine sediments have not been reported, but because of the geological instability of these profiles, it is unlikely that they are ever very old.

Because of their significance as plant nutrients, the distribution and cycling of phosphorus and nitrogen in estuaries has received considerable attention (Harvey, 1955; Jeffries, 1962; Jitts, 1959; Rochford, 1951). Jeffries (1962) notes that the summer increase in phosphate phosphorus found in estuarine waters contrasts with a decrease in the sea during this period coincident with a sharp drop in the $\text{NO}_3 : \text{PO}_4$ ratio, and that this seems to be characteristic of estuaries along the northeast coast of the United States. Jitts (1959) showed that fine suspended estuarine sediments can trap 80 to 90 percent of the large amount of PO_4 present during periods of high runoff, and later release it as conditions become more stable, thereby contributing to the high level of production characteristic of the estuary. Jeffries (1962) adds that metabolism of benthic organisms (see also tidal marshes, Ragotzkie *et al.*, 1959) may also contribute to these nutrients, promoting higher initial regeneration rates of PO_4 and NO_3 .

Organic matter in the sediments is derived primarily from decomposition of dead organisms, their fecal matter, and secretions and runoff from the land (Fox, 1950; Hood, 1963). Rooted aquatics such as *Zostera* and *Spartina* may be the chief producers in shallow water (Fawcett, 1928; Hayes, 1964). This matter serves as an energy source for a broad gradient of heterotrophic bacteria and of larger sizes of benthic organisms dependent on it for food, as a modifier of inorganic chemical reactions through complex formation and chelation phenomena, and as a reacting system itself (Hood, 1963; Nelson, 1962; Ferguson-Wood, 1962). Recent researches indicate that amino acids may also be evolved abiotically (for example, by photosynthesis from paraformaldehyde involving the fixation of nitrogen in the presence of the catalyst, colloidal molybdenum oxide, Bahadur *et al.*, 1958), and then polymerized. Glycine has been polymerized on a clay base with ultraviolet light to produce polyglycine (Bernal, 1963). Estuaries may

be in a unique position for the abiotic formation of organic molecules, in that they provide a rich milieu of charged clay minerals and potential elemental carbon, hydrogen, nitrogen, and oxygen. The process may occur continuously, accelerated by the fluctuating mixing gradients of fresh and sea water in relatively shallow basins.

Suitable methods for determination of total organic carbon in sediments have been in use for some time (Barnes, 1959; Trask, 1955), but only in the last few years has research on the composition of this organic matter been undertaken. With the currently available analytical techniques, the presence of hydrocarbons, cellulose, hemicellulose, humus, carbohydrates, rhamnosides, simple sugars, proteins, amino acids, fatty acids, organic acids, wax, lignin, lipids, chlorophylls, vitamins, and many other organic compounds have been demonstrated in sediments (Bader, 1956, 1962; Hood, 1963; Plunkett, 1957; Vallentyne, 1957; Zhurkova and Fedosov, 1963). It has been postulated that dissolved amino acids and proteins may form carbamino carboxylic acid complexes with molecular CO_2 , thereby increasing the solubility of calcium carbonate and phosphate in sea water (Hood, 1963).

In shallow coastal seas, organic substances produced by phytoplankton are unstable and decompose rapidly; for example, one day after death of cells, 20 percent of their phosphorus and 30 percent of their nitrogen is released and decomposition is complete in five days. Dead plankters sink slowly to the bottom, beginning to decompose in the water column. Thus in the sediments is found, in addition to the labile organic molecules produced there by benthic organisms, mainly organic matter that is difficult to decompose. Hemicellulose decomposes most rapidly in the sediments, the lignin-humus complex most slowly. Of the total quantity of carbon in the sediment, 18 to 38 percent is of soluble compounds (less sugars and cellulose), 5-10 percent is of sugars and hemicellulose, 5-14 percent of cellulose, and 47-63 percent of lignin-humus (Hayes, 1964; Zhurkova and Fedosov, 1963). Loeffblom (1963) reported a wide variation in ratios as well as absolute amounts in the local concentration of proteins, carbohydrates, and ether-extractable lipids within different marine sediments of open waters. In some areas, he found an interesting trend in the decrease of protein and carbohydrate, and an increase of lipid, with depth. Sanders (1961), in preliminary measurements, discovered free small chain sugars in the upper 2 cm of the sediment.

Starikova (1959) found in strongly reducing marine sediments that the organic content (a total range of 0.08 to 1.11 percent, and a variation in the surface zone, 0-25 cm thick, of 10 to 21 mg/l) of the interstitial water increased from the surface downward; contrary conditions were observed in oxidized sediments elsewhere. Mironov and Borodovsky (1959), investigating Recent sediments in the western Bering Sea, found that organic carbon content increased with a decrease in the average diameter of sedimentary

particles, and amounted to 0.32 percent for sands of average grain size, 0.51 percent for fine sands, and 0.72 percent for coarse silt. A maximum concentration was found in silty clay muds, 1.46 percent; fine silty muds, 1.08 percent; and in clay muds, 0.92 percent. They noted that sediments include humus (characterized by a low carbon and a high hydrogen and nitrogen content; see also Skopintsev, 1959) which is proportional to the organic carbon concentration. Humus is thought to arise autochthonically. Whether disposition of organic matter in sediments of true estuaries is similar is not known. In the shallow estuaries of Texas (Oppenheimer and Ward, 1963), where water is highly turbid and sedimentation rates are relatively high (up to 19 cm per 100 years), intertidal sediments may contain a maximum of 5 percent organic matter in the summer, and a winter low of 0.8 percent.

The suggested availability of a large concentration and variety of dissolved organic molecules in estuarine interstitial water assumes importance not only to heterotrophic microorganisms, but to higher forms of invertebrate life which may be able to utilize them directly (MacGinitie, 1945; Stevens, 1963). Whether dissolved organic matter can be aggregated in interstitial estuarine water by adsorption to the surface or by other means, as has been demonstrated in open sea water (Baylor and Sutcliffe, 1963; Riley, 1963; Sutcliffe *et al.*, 1963), has not been shown. It is nonetheless an important area for research, in view of the ease of utilization of non-living particulate organic matter by suspension and deposit benthic feeders, whether as organic aggregates or bound to mineral particles (Carraker, 1959; Fox, 1957; Fox *et al.*, 1952; Wieser, 1960; Wilson, 1956). It would be useful to have further information on the series of fractions resulting from degradation of dead bodies of plants and animals; the composition of particulate organic fractions and organo-mineral complexes; and the transformation to particulate organic matter from compounds in solution, through sorption to clay, silts, and larger surfaces, through abiotic chemical action, and through incorporation into the protoplasm of microorganisms (Zhukova, 1963). Ecologically such knowledge is fundamental, not only because of the nutritive value of such organic fractions, but because of what they might contribute in integration of benthic microcommunities.

The color of finer sedimentary fractions in estuaries is generally black or dark gray. The significance of this color to benthos is unknown, and it would be interesting to learn whether the color pattern of true estuarine species is universally uniform or varies with that of the substratum. Comparison of organisms of a typically colored estuarine sediment with that of estuarine portions of the Bay of Fundy where fine sediments are red (Giglach, 1958) would afford an opportunity to investigate the matter.

Microorganisms

These are extraordinarily abundant and very active

in estuarine sediments and must play a most important role in shaping the overall sedimentary environment of larger benthic organisms. Exploration of their effect on the chemistry and biology of the benthic biotope is a recent undertaking, but rapid and encouraging progress is being made in these studies (Oppenheimer, 1960, 1963; Ferguson Wood, 1962, 1963; Zhukova and Fedosov, 1963; Zel'Bell, 1946a, b). Ferguson Wood has provided excellent reviews.

Photosynthetic benthic microorganisms include diatoms, flagellates, filamentous green, brown, and red algae, and blue-green algae, and in reducing sediments photoautotrophic purple and green sulfur bacteria. Photosynthetic processes raise the pH of the interstitial and near bottom water by removing CO_2 from bicarbonate, and raise Eh by the production of free O_2 . Almost all the microorganisms represented at the surface are autotrophs which do not require organic substances for development; but they constitute only a small percentage of the total number of microorganisms in sediments, which is dominated by the heterotrophs. Heterotrophic (phagotrophic) benthic microorganisms include the colorless (and some of the colored) algae (diatoms), flagellates, bacteria, fungi, yeasts, ciliates, rhizopods, and some other protozoa. Many of the diatoms found in sediments are facultative heterotrophs, and flagellates are frequently both autotrophic and heterotrophic. Anaerobiosis in the sediment results from the consumption of available O_2 during the decomposition of organic matter by bacteria and the release of microbially produced reducing substances; aerobiosis occurs in the presence of dissolved O_2 and oxidized substances, these resulting largely from microbial activities such as photosynthesis, oxidation of sulfides to sulfate and ammonia to nitrite or nitrate. CO_2 is reduced by the energy of photosynthesis or by photoreduction in the absence of free O_2 . Inorganic material is converted to organic matter by plants and reconverted by the bacteria and fungi; the former is most complete under anaerobic conditions; aerobic conversion proceeds to such intermediate organic products as lactic or pyruvic acids. Nitrate is reduced to ammonia by most plants, though some require ammonia or amino acids. Heterotrophs tend to reduce nitrates, though there are oxidizing bacteria. Many bacteria and some of the algae can fix dissolved nitrogen forming ammoniacal compounds or amino acids. Organic forms of phosphorus are converted into inorganic forms by heterotrophic bacteria, and are frequently precipitated in the sediment as calcium or ferric phosphate. Except where the organic content is very high, the whole sulfur cycle seems to control the biology of the sediments (Ferguson Wood, 1962); this occurs because pH and Eh are governed by the activity of the sulfur bacteria (Ferguson Wood, 1962). Baas Becking *et al.* (1957) have presented a model to explain the chemical control of the biological reactions within an estuary. The lower Eh limits of the anaerobic reactions are set by equilibria between H_2S sulfur and sulphydryls, the alkaline limit of photosynthesis is set

by equilibria between CO_2 , bicarbonate, and carbonate; the acid limit is controlled by sulfur bisulfate. In the acid range the upper limit of redox potential is probably due to equilibria between ferrous and ferric sulfate. These limits are considerably outside those of the estuarine environment, except for Eh and carbonate-bicarbonate.

From detailed microbiological studies of the upper sediment layers of shallow coastal seas, Zhukova (1963) and Zhukova and Fedosov (1963) conclude that heterotrophic bacteria constitute the major percentage of bacteria in sediments there, functioning in the decomposition and regeneration of organic matter. The uppermost silt layer of 1 to 1.5 cm at the sediment-water interface is the most active bacteriologically, and consumes from 1.5 to 3 times more O_2 than lower strata. Accumulation of bacteria at the surface is so great that it often forms a dense bacterial film, bacterial biomass ranging from 2 to 57 g/m²/cm layer. This mass under natural conditions is increased five- to six-fold in 24 hours. The fact that this concentration maintains a rather constant level indicates active consumption of bacteria by higher organisms. These heterotrophs are actively involved in production of organic detritus and are a part of it, one gram of detritus containing up to five billion cells. The number of bacteria decreases noticeably with depth to one meter. In the formation of its cell a bacterium expends three times its own weight in organic matter. The biomass of heterotrophic microorganisms in the sediment fluctuates primarily with the presence of organic matter and thus with the seasons. Diurnal production of microorganisms at surface of the sediment varies from 1.2 to 6.2. Percentage of dividing cells increases from 4.7 in the spring to 8 in the summer. It is estimated that quantity of organic matter in the surface sediments nearly meets the requirements of microorganisms in summer conditions. The high rate at which demineralization of organic matter can occur has also been described by Gunnerson (1963). Thus across the sediment-water interface is a micro-organismically controlled exchange of organic materials, stimulated by added substrate, such as plankton fallout, and by oxygen (Hayes, 1964). The effect of the estuarine gradient on the taxonomic and physiological composition and activities of heterotrophic microorganisms has not been given in any detail, but in view of the findings of Zhukova and Fedosov in marine environments, there should be substantial microorganismic activity at least in the lower reaches of estuaries.

Burkholder (1963), discussing co-actions among microautotrophic and heterotrophic plants of shallow water sediments, reports that important growth-regulating and antibiotic substances are synthesized, excreted, and used by them in different ways. Among auxotrophic algae and bacteria, requirements for biotin, thiamine, cobalamine, and nicotinic acid are common. These and other metabolites are formed by primary microproducers, but their direct availability may

often be regulated by selective inhibitory action of microorganismically produced antibiotic substances. Furthermore, the metabolites of some of these microorganisms are utilized in sequence by others, and simultaneous exchanges of metabolites can occur among these microorganisms. The impact of these interactions at the microorganismic level on larger benthos in the estuarine gradient can only be guessed at now, but leaves the impression that if this degree of interdependence exists at this level of biotic organization, it may not be far-fetched to speculate about it between this and higher levels.

Benthic viruses (Spencer, 1963), yeasts (Fell and van Uden, 1963), fungi (Kohlmeyer, 1963; Johnson and Snarow, 1961), ciliates (Faure-Fremiet, 1951a, b), and other microinvertebrates are being studied intensively (Ferguson Wood, 1963), but little can be said at present of the ecological relationships of these to higher estuarine benthic organisms.

It has often been stressed that the composition of the sediment is important in determining the distribution of benthic organisms (Baas Becking and Wood, 1955; Bearland, 1940; Day, 1951; Holme, 1949; Morgans, 1956; Parker, 1956, 1960; Pratt, 1953; Rockford, 1951; Sanders, 1959; Thorson, 1958; Wieser, 1959; Zhukova and Fedosov, 1963). This relationship will probably be explained fundamentally at the ionic, molecular, particulate, aggregative, and microbiological levels, and the research reviewed here establishes a pattern for continued productive investigations of the physical, chemical, and biological environment of estuarine benthic invertebrates.

Effect of Meio- and Megabenthos on the Sediment

Estuarine sediments are also modified to a conspicuous macroscopic degree by meio- and megabenthos (Moore and Scruton, 1957). Estuarine invertebrates, more or less adapted to living in a turbid environment, are often highly specialized, not only to feed on sediments (Sanders *et al.*, 1962; Wells, 1945; Yonge, 1949b), but to entangle in mucus the particles settling on their internal and external free surfaces and to remove these by ciliary currents and muscular movements (Graham, 1957). These loose aggregates then accumulate on the surface or in the sediment near the consolidators. The oyster (Lund, 1957; Gallo, 1964) and the mussel (Verwey, 1952) are especially well known in this regard; ciliated meio- and microbenthos may function similarly and just as efficiently, but have not been investigated with this in mind. Heterotrophic microorganisms probably soon decompose the mucus and liberate the particles, though there are no supporting reports on this problem.

More conspicuous and perhaps of greater ecological significance is the capacity of animals with complete alimentary canals to consolidate undigested residues into more or less compact, resistant, sometimes ornately sculptured, often long-lived fecal pellets of characteristic form (Edge, 1934; Moore, 1955) and of systematic value (Moore, 1931b, c). The pel-

lets are molded in the ciliated intestine by mixing inorganic particles and undigestible organic residues with mucus and coating the resulting pellets with further mucus as they are voided. Sculptured pellets result from corresponding ridges and grooves in the walls of the intestine.

These fecal pellets are characteristic of most deposits in quiet estuaries. Depending upon the degree of circulation of the water over the bottom, sediments may consist of 30 to 50 percent, and in very quiet deep bottoms close to 100 percent pellets (Moore, 1931a, 1955; Carriker, 1959). Moore (1931a) noted that with increasing depth within the bottom the friable pellets of planktonic organisms break up and are no longer recognizable, whereas those formed by the mud dwellers are extremely firm and may last for a hundred years or more. On the average, carnivorous animals tend to produce feces of loose consistency, vegetable eaters firmer ones, and deposit feeders the most resistant of all. Exceptions to the latter are sand-swallowing forms whose feces may be insufficiently bound with mucus to survive the action of water. In some species pellets form as homogeneous rods; in others, as heterogeneous structures with definite sorting of coarser from finer material into specific tracts in the pellet (Moore, 1955). Fox *et al.* (1952) report that leptopellic organic matter is present in rich concentration in the fecal pellets of filter-feeding invertebrates, suggesting that this material passes through the digestive tract with only minor modification or that it accumulates in the pellets after voiding.

In some interesting studies, Zhukova (1963) found that bacteria ingested as nutriment by invertebrates may either be digested with other components of food or passed through the intestine unchanged. In the polychaete, *Nereis*, and the amphipod, *Portogammarus*, it was noted that the number of microbial cells sharply decreased as the food passed from the mouth to the mid-gut, but in passage to the anus the number increased slightly, there being no active enzymes there and thus an opportunity for undigested cells to multiply. In the mollusc, *Monodacna*, a different intestinal physiology brought about a continuing decrease in the microbiota throughout the intestine. Fecal pellets, then, depending on the species, will contain varying concentrations of microorganisms at the time of release; but there is no information on the ecological succession, if any, of microorganisms or physical and chemical changes occurring within the pellets after voidance. Such phenomena will undoubtedly vary with the species of pellets and the substances contributed by the guts of the invertebrates. In a study of the nature of the food of deposit feeders, R. C. Newell measured the carbon and nitrogen removed by the snail, *Hydrobia*, from test foods, and concluded that microorganisms are much more important as food than the organic debris of fine sediments (Kohn, 1964). These problems are worth studying further in view of the abundance of fecal pellets in estuaries, and because of their role in the recycling of matter

and the nutrition of benthic deposit and suspension feeders.

Should fecal residues be voided into the environment in the finely particulate form resulting from digestion, and often from mechanical trituration in the mid-gut, it is certain that estuaries would be considerably more turbid than they are and that filter feeders might recycle fecal particles ad infinitum. Accordingly, the almost universal habit of compacting and cementing excrement of animals possessing complete alimentary canals helps at least to reduce the load of finely suspended sediment about them. This may explain the survival and elaborate development of the mechanism in the course of organic evolution.

Infaunal burrows in estuarine bottoms range from temporary spaces pressed out as animals move about in the sediments to elaborately lined, more or less stable tubes, in which they live permanently with little movement (Yonge, 1953). In heavily populated bottoms (Fox, 1950), certain active infaunal inhabitants undoubtedly assume a dominant role in vertical mixing of the sediments (Emery and Stevenson, 1957a, b; Hayes, 1964; Moore and Scruton, 1957; Rhoads, 1963), and in contributing to the vertical homogeneity of the physical aspects of the profile described by Nelson (1962). The rate of biological reworking, the species involved, and the relationship of these to the rate of sedimentation and erosion bear further quantitative investigation. The fact that sediments vary so widely in horizontal composition (Salomon, 1962) suggests that much of the mixing is a vertical process where organisms work sediments primarily in a vertical or oblique direction. Pumping of water over gills and food-gathering ciliated structures accounts for a substantial movement of estuarine water through the sediments, but this matter has not received the quantitative attention it deserves. The rapidity of reworking of most estuarine bottoms with their often high degree of colonization suggests that microbenthos are concomitantly shifted freely about, and that vertical microbiological and chemical readjustment occurs continuously to provide the rather clear-cut gross vertical stratification described by microbiologists. Finally, it is doubtful that estuarine sediments, to the depth commonly inhabited by estuarine infauna, are very old and thus that the chemistry of their interstitial waters has been altered by any mechanism requiring long periods of time for their operation.

Counteracting the biological and physical forces of horizontal shifting and vertical mixing and erosion of sediments are the stabilizing effects of estuarine plants (Fasset, 1928) like blue-green algae (Conover, 1962), *Spartina* (Miller and Egler, 1950), *Zostera* (Ostenfeld, 1908), *Diplanthera*, *Thalassia*, *Ruppia*, and others (Aleem, 1955; Day, 1951; Ferguson Wood, 1962), which further greatly modify the aspect of the community by imposition of root systems in the sediment and of circulation-reducing conditions over the bottom. According to Ferguson Wood (1962), macroscopic algae do not often have extensive growths

of epiphytes, possibly because of the production of antibiotics (Allen and Dawson, 1960), whereas the sea grasses are usually covered with diatoms, blue-green algae and associated bacteria, ciliates, and flagellates. The effect of these ecological differences, if any, on underlying sediment and fauna are unknown. Little has been reported on the biochemical effect of the root systems of flowering sea grasses on the sedimentary biotope, and the ecological relationship particularly of micro- and meiobenthos to these subterranean plant systems and their possible gaseous and fluid secretions. Root hairs and more tender rootlets may be utilized for food by mandibulate burrowers; and certainly the greater availability of decaying organic matter in the vicinity of these plants should serve to catalyze the multiplication of microorganisms and concomitantly that of deposit feeders. The most densely populated portions of the estuary are the bottoms of muddy sand overgrown by *Zostera*. These provide shelter for small benthic organisms, sufficient silts to allow construction of permanent burrows, and ample detritus for food (Day, 1951).

A VANISHING ESTUARINE HOMEOSTASIS

Although variation of environmental factors in estuaries is a permanent feature of the estuarine complex (Hedgpeth, 1957e), maximal biological and physical constancy will prevail in those geologically stable estuaries where the watershed is blanketed by climax vegetation, the inlet is fixed structurally and its level is relatively constant with that of the sea, and there is freedom from destructive storms. Under such idyllic circumstances, approached by Knysna Estuary in South Africa (Day *et al.*, 1952), the amplitude of seasonal flows of fresh water from the watershed will be small, gross erosion and catastrophic salinity fluctuations will be nonexistent, maximum opportunity for adaptation of marine organisms to the estuarine environment should prevail, and an optimal setting for evolution of the estuarine life should be available. Even though estuaries are considered to be geologically ephemeral structures, they may be comparatively permanent (Hedgpeth, 1957e; Hunter, 1964) in the sense that "the aggregate rate of change in the estuarine environment may actually be less than in the geographical province in which it occurs over the same period of time" (Hedgpeth, 1957e).

Unfortunately, undisturbed mature estuaries are becoming increasingly rare as man mutilates and scars coastal areas and dumps a potpourri of ions and particles into their basins. It may be suggested that protoplasm, with its basic property to respond (Bullock, 1958), may regulate and continue to exist even in the harsh man-altered estuarine milieu; but even if this is true, many of the more stenotopic estuarine species would be eliminated. There is consequently an urgency to study estuaries before unenlightened defacement obliterates them and before it becomes expedient

to investigate them primarily as outdoor pollution laboratories.

RECAPITULATION OF ENVIRONMENTAL FACTORS

Up to this point this perspective clarifies the existence in estuarine waters and sediments of certain physical, chemical, and microbiological structures, actions, and interdependences which collectively constitute a unique, true estuarine environment, and describes something of the impact of larger organisms on the sediments. The hypothesis also emerges that inherent in the nature of true estuaries certain factor complexes, or common ecological denominators, occur which are similar in true estuaries around the world. They are: (1) presence of well-aerated, constantly moving, relatively shallow water, mostly free from wave action and excessively rapid currents; (2) a salinity gradient, and accompanying chemical gradients, of near zero to about 32‰; (3) a range of sedimentary particle sizes from colloids to sands and detritus, resulting from terrigenous weathering, water transport, impact of the estuarine gradient, and other estuarine processes; and (4) complex molecular interactions in both water and sediments in an abundance of dissolved and particulate organic matter, microorganisms, and fine sedimentary particles.

DISTRIBUTION OF BENTHIC INVERTEBRATES IN ESTUARIES

ESTUARINE FAUNAL REGIONS

The most favorable environment for life, which arose in the ocean, is provided by many littoral areas of tropical seas where salinity is subject to little variation, temperature is nearly constant at about 25° C., and an abundant supply of nutrients and particulate food comes in from the land. As a result, the fauna there represents all the phyla and is more diverse than elsewhere. Unfavorable conditions requiring special adaptations are relatively few, and rank growth with a high tendency to variation, combined with the severe struggle for existence, has produced maximum differentiation. Wherever environmental conditions deviate from such an optimum a reduction occurs in the diversity of the fauna, as "under the stress of conditions that urgently demand adaptation, the number of species diminishes" (Hesse *et al.*, 1951). Patrick's (1949) studies in streams where pollutants decrease the number of species and the remaining species occur in great abundance confirm this.

This concept explains in broad terms the smaller number of benthic species within estuaries than in equivalent depths in the adjacent shallow sea (Gunter, 1961; Hedgpeth, 1957e; Segerstrale, 1964; Thorson, 1957), the lesser diversity in estuaries of higher latitudes than those of the tropics (Fischer, 1961; Hunter, 1964), and deeper marine faunal invasion of estuaries in the tropics than in temperate regions (Annandale, 1922; Burbank *et al.*, 1956). The fact that the number of individuals in estuaries is often great (Hedgpeth, 1957c) is explained at least in part

by the reduction in number of total species and thus a diminution of the number of taxa competing for the food supply (Hesse *et al.*, 1951), and exemplifies the capacity of some organisms to adapt to extremes of environmental stresses (Brown, 1957).

Repopulation of benthic taxa in most estuaries occurs from season to season primarily by reinforcement from the sea, to a lesser extent from parents in the estuary itself, and least from fresh water (Day, 1951; Gunter, 1950, 1961; Hedgpeth, 1957e; Nicol, 1935, 1960; Pearcy, 1962; Pearse, 1950; Pearse and Gunter, 1957; Percival, 1929; Remane, 1958; Wells, 1961; Yonge, 1949a). The details of how recruitment occurs at the level of most individual species remain to be studied (McDougall, 1943; Wells, 1961). Many studies show that the number of marine species is most abundant at the mouth of the estuary and decreases and finally disappears in the upper reaches of the estuary, while the number of freshwater species disappear as the estuary is descended (Alexander *et al.*, 1935; Annandale, 1922; Bassindale, 1938; Day, 1951; Hedgpeth, 1957e; Kinne, 1963a; Milne, 1940a, b; Nicol, 1935; Parker, 1955; Percival, 1929; Remane, 1934, 1958; Segerstraale, 1964; Stopford, 1951). Animals reach maximum size in the sea, and species widely distributed in the estuary generally decrease in size up the estuary (Kinne, 1964; Milne, 1940b; Remane, 1958; Segerstraale, 1957), their complete elimination up the environmental gradient frequently being preceded by the production of stunted individuals at the upper extreme (Hesse *et al.*, 1951). Some genera in estuaries are represented by two or more species geographically distributed in different regions of the estuarine gradient (Hedgpeth, 1957c), while a few individual species may be found along the greater part of the gradient (Kinne, 1964). For example, the amphipod, *Gammarus locusta*, inhabits the region from the inlet to upper reaches, and *Gammarus pulchra* the head of the estuary; the carid, *Palaeomonetes varians*, the middle and upper reaches, and *Palaeomonetes antennarius* the head; the gastropod, *Neritina virginea*, the mouth and middle reaches, and *Neritina reclivata* the middle reaches and head; and the bivalve, *Rangia flexuosa*, the mouth to upper reaches, and *Rangia cuneata* the upper reaches and head. As Hedgpeth points out, these may be environmental variations (ecotypes) rather than genotypes; and it will require the approach employed by Kinne (1964) to determine which is the case.

This distribution results in minimum diversity of species in the zone of steepest gradient between the marine and freshwater regions, a moderate increase of taxa into fresh water, and maximal increase into sea water (Remane, 1958; Segerstraale, 1964). Marine organisms occur much farther up the estuary, and conversely, freshwater organisms much nearer the sea, in estuaries where tidal amplitude is small and the up-estuarine gradient is relatively stable, than in estuaries with large tidal ranges and rapidly changing gradients (Alexander *et al.*, 1935; Day, 1964;

Hedgpeth, 1957e; Odum, 1954; Remane, 1958; Segerstraale, 1957). There also appears to be minimal density of individuals (Hedgpeth, 1957e) and of productivity (Caspers, 1948, 1954; Lundbeck, 1926) in the estuarine transitional zone between marine and fresh water. A number of benthic species with wide tolerances for estuarine gradients, and consequently widely distributed up the long axis of the estuary, has been studied in some detail: hydroids (Kinne, 1956, 1958), green crab (Broekhuysen, 1936), gammarids (Bassindale, 1942; Spooner, 1947), boring sponge (Hopkins, 1962), mud crabs (McDermott and Flower, 1952), neritid snails (Russell, 1941), and nereid worms (Smith, 1955, 1956, 1964). Intertidally, more species occur at the lower than at the upper level (Spooner and Moore, 1940); and on the whole, infauna are more abundant up the estuary than epifauna (Alexander *et al.*, 1932). Nonetheless, estuaries are productive regions: Spärck (1935) reported that maximum densities of benthic organisms per square meter of bottom are found in rather shallow water with ample water renewal and surrounded by a region of high precipitation (Thorsen, 1957).

In the course of geological time, marine animals have repeatedly invaded fresh water and land through estuaries and other routes, and then reinvaded estuaries and the sea; colonization probably began in the Devonian period, and may still continue under suitable circumstances (Nicol, 1935, 1960; Pearse, 1950). The resulting distribution of organisms within the estuary in time and space is a product of the physical, chemical, and biological gradients of the estuary and the limits imposed by these gradients on the genotypic physiological tolerance and behavior of the total available number of species from all sources (Day, 1951; Hedgpeth, 1957e; Nicol, 1960; Potts, 1954; Prosser, 1955; Robertson, 1964; Schlieper, 1958; Smith, 1959). Distribution cannot be based on a single factor, as such prominent estuarine factors as salinity variation, current strength, and degree of turbidity, when adverse in the field, may collectively impose more stringent limits to distribution than would the individual factors alone in laboratory experiments (Bassindale, 1943b). Conversely, an animal's tolerance of a few factors may be extended where most of the factors are optimum (Day, 1951).

During the past decade, Day and his associates have investigated the origin and distribution of estuarine benthic animals in South African estuaries and provide new information with broad applications for estuaries in other regions of the world (Day, 1964). Using Knysna Estuary (Day *et al.*, 1952) as a base of reference, they examined benthic fauna in several other types of estuaries and compared these with the fauna of the open coasts in the region. Knysna Estuary receives a continuous flow of clear fresh water from a well-wooded watershed with minimal erosion, low evaporation rate, and sufficient inflow of fresh water to maintain a normal salinity gradient and keep the mouth open and deep throughout the year. The result is a clear estuary which supports a rich and

varied fauna and in which *Zostera* and other plants extend one to two meters below low tide mark.

As the investigations progressed, it was recognized more clearly that estuaries differ from the open shores not only in salinity but in strength of wave action and type of substratum. This was tested in two embayments (Day and Morgans, 1956; Day, 1959, 1964) which have effectively the same salinity as the sea and contain many species common to neighboring estuaries but not to the open sea. Some 26 percent of the fauna of sheltered sand flats and 13 percent of that of sheltered rocks had never been recorded outside estuaries before. The effects of wave action appeared to be indirect: silt-covered rocks in the quiet lagoon lacked half of the common species living on clean exposed reefs outside the bay, and the stable flats of fine sandy mud in the lagoon had 20 times as rich a fauna as the coarse shifting sands of surf beaches outside. It was concluded that distribution of these faunas was determined, not by salinity, but by the strength of wave action.

Analysis of distribution of the benthos on rocky, sandy, and muddy shores, and at stations in bottom sediments in the inlet, lagoon, upper reach, and head of Knysna Estuary revealed that:

1. Animals extending from the open sea into the estuary were abundant only in the lower parts of the estuary; those adapted to life at intertidal levels were much more numerous than those restricted to the bottom, though infauna penetrated farther up the estuary than epifauna, possibly as a result of less variability of salinity within the sediments.

2. Species colonizing sandy shores of the estuary were not derived from fauna of open surf beaches, but from sandy pools and crevices among the rocks. This may be more marked in South Africa where open shores are more battered by surf than the quiet shores of the Mediterranean.

3. True estuarine fauna, whether species from rocky, sandy, or muddy shores or subtidal sediments, were never important at the mouth of the estuary, but formed a larger and larger percentage of the benthos farther up the estuary until they dominated the fauna in waters of low and variable salinity in the upper reaches.

4. Stenohaline marine species dominated the fauna of rocky shores and were important at the entrance where the mouth is wide and wave action fairly strong.

5. Those euryhaline marine species which can tolerate calm water and reductions in salinity formed the most important element within the estuary, and many of them never occurred on exposed seashores, being found commonly in sheltered areas or below tide mark.

Day (1964) found further that whereas Knysna Estuary has a deep mouth into which waves penetrate, in almost all the other estuaries the mouth is shallow and sandy, and wave action is eliminated. As a result there was no gradual change from an open shore fauna to an estuarine lagoonal fauna in most

estuaries, but a very abrupt one, and true marine species were very poorly represented in the lower estuary. In heavily silted, extremely turbid embayments, as in the Umkomaas Estuary, the whole estuary is foreshortened biologically; stenohaline marine forms were entirely absent, euryhaline marine forms were rare, and even true estuarine species were not abundant. In blind estuaries like the Hermanus Estuary, the fauna inside the mouth and lagoon was poor and the main species were the same as those in the middle and upper reaches and headwaters of the Knysna system. In larger, more saline, blocked estuaries euryhaline marine species were better represented.

The observations of Day, his associates, and many others define in a general way the role of such factors as salinity, turbidity, sediments, and water movements in the distribution of estuarine organisms, and provide a fundamental basis for further observations and experimentation on the specific causal roles of these and other factors. Expression of these factors, particularly wave action (Zeigler, 1964), in quantitative units will be required before their impact can be examined precisely. Many other possible factors have been listed in the literature (Milne, 1940b), but precise information on their function in limiting distribution of estuarine species is scarce. Their effects will have to be examined experimentally, as distribution records do not fix the causal relationship between the factor and the organism (Wells, 1961). Not only will factors in estuaries have to be explored in depth, but also the physiological limits of tolerance of estuarine benthic species to single and multiple factors. In the case of motile benthos, the sensory receptors and behavior patterns affected by these factors will also bear detailed investigation.

ROLE OF SALINITY AND SEDIMENTS IN DISTRIBUTION

Salinity

This is one of the most studied environmental factors in the estuary, and is cited as a major factor in limiting distribution of estuarine organisms (Gunter, 1961). As sea water becomes more dilute up the estuary species drop out in part, apparently in the order of decreasing ability to regulate hyperosmotically. Which mechanisms fail, or what processes are modified as dilutions become more extreme are little known (Schlieper, 1958), and vary in different species, but are significant in determining distribution (Hunter, 1964; Kinne, 1964; Nicol, 1960; Prosser and Brown, 1961; Robertson, 1964). As Milne (1940a) emphasizes, there are differences in up-estuary penetration even among species belonging to the same genus, and the problem of distribution with reference to salinity must be approached at the species level (Kinne, 1964). Elimination of taxa with decrease in salinity up the estuary is presented graphically for Randers Fjord, Firth of Tay, Tamar Estuary, and Tees Estuary by Alexander *et al.* (1935); and Hedges (1957c) lists the distribution of geminate pairs

of species relative to salinity distribution in various estuaries of the world.

Wells (1961), in a comprehensive study of the distribution of the epifauna of oysters in the Newport River, found that the 303 species investigated declined up the estuary in direct relationship to reduction of salinity. Twenty of these species were tested in the laboratory for tolerances to low salinities, and a ranking of their death points with their distribution in the estuary disclosed that only two species deviated widely from the predicted distribution (see also Fischer-Piette, 1931; Gunter, 1961; Kinne, 1964). Ionic composition of estuarine water is not necessarily proportionate to that of sea water and may vary measurably from estuary to estuary (Baas Becking *et al.*, 1957, 1960; Kinne, 1964) and from season to season, so influence of estuarine salinities on biotic distribution may be more than an osmotic effect. The effect of estuarine waters (not dilutions of sea water) and their chemical constituents on estuarine benthos bears intensive investigation.

Sediments

Considerable attention has also been given to the role of constituents of sediments in the distribution of infaunal invertebrates in coastal level bottoms (Beanland, 1940; Brett, 1963; Davis, 1925; Holme, 1949; McNulty *et al.*, 1962; Parker, 1956, 1959, 1960; Pratt, 1953, 1956; Remane, 1933; Sanders, 1956, 1958, 1959, 1960; Swan, 1952; Thorson 1957, 1958; Wieser, 1959, 1960; Williams, 1958). The significance of sediments as a complex of limiting values determining distribution of benthic fauna is fully recognized (Brett, 1963; Sanders, 1959; Thorson, 1957, 1958). Unfortunately, few comparative studies relating the nature of bottom sediments to distribution of benthos along the gradient of the estuary have been undertaken (Parker, 1960). Detailed investigations of animal-sediment relationships by several recent workers (Brett, 1963; McNulty *et al.*, 1962; Sanders, 1956, 1958, 1960; Sanders *et al.*, 1962) in what would correspond roughly to bottoms in the seaward end of estuaries form an important base for future comparative estuarine studies.

Sanders (1956, 1958) showed, in subtidal bottoms in central Long Island Sound and Buzzards Bay, that small deposit feeders (individuals weighing 0.2 g dry weight or less and retained on a 0.2 mm pore screen) numerically dominated in mud, and filter feeders dominated in sand sediments. In Buzzards Bay, primary consumers (herbivores and detritus feeders) comprised 80 to 99 percent by number of the benthic fauna. He suggested that clay is the most valid sediment correlate for the distribution of deposit-feeding organisms living on organic matter in or on fine-grained sediments (muds), as clays are much smaller than silt particles and therefore have a relatively much larger surface area to bind organic matter which is probably a primary source of food for deposit feeders (Bader, 1962; Grim, 1953). The largest populations of benthos were found in Long Island

Sound in sediments containing 13 to 25 percent silt and clay; percentage deviation upward and downward gave lower values of biomass. Whereas detritus tends to accumulate on muddy sediment and provides a further source of food, large concentrations of organic matter may reduce the oxygen content within the sediments and eventually limit the profile for feeders not tolerating anaerobic conditions. Bader (1954) found that up to a concentration of 3 percent organic matter in sediments, infaunal bivalves increased in density, but beyond this level products of bacterial decomposition and decline in available oxygen became limiting and population density declined. Sanders concluded (1958) that distribution of filter feeders in fine sandy sediments was controlled by the hydrodynamic processes which determine the character of the sediment, rather than directly by the nature of the sediment. Densest populations were found where sediments were relatively well-sorted with a median grain size of fine sand ranging from 0.15 to 0.26 mm and an optimal size of 0.18 mm. He noted that these fine particles are most easily moved by currents, thus their presence in large concentrations is indicative of a feeble, relatively constant current over the bottom, little active sediment transport, and a stable environment; and that currents of this intensity must be adequate to support the large populations of filter feeders found in such sediments. Components of benthic species in Buzzards Bay (Sanders, 1960) constituted a continuum varying with the gradual change in sediment composition, but at a given point in the sediment spectrum the species structure of the association was similar even when the sampling was done at various times of the year.

Further studies by Sanders *et al.* (1962), in Barnstable Harbor, demonstrated that intertidally the deposit feeder may be the dominant feeding type in both mud and stable sand sediments, in contrast to findings in the subtidal regime in Long Island Sound and Buzzards Bay. Despite the fact that sediments at stations in Barnstable Harbor consisted almost entirely of fine sand with very little organic matter, most of the biomass (78 percent) consisted of animals that were primarily deposit feeders. The presence or absence of large populations of deposit feeders in sandy sediments was correlated with the stability of the sediment surface. In stable sediments where ripple marks were absent, dense concentrations of benthic diatoms (Faure-Fremiet, 1951a) and dinoflagellates were found which provided the major food source for the large biomass of deposit feeders. Chlorophyll values obtained from sediments to a depth of 1 cm ranged from 147 to 770 mg m⁻². Sanders concluded that the sediment should be considered an indicator of food, and not a factor directly determining the distribution of feeding types.

In an examination of some relationships between the infauna of subtidal level bottoms and sediments in Biscayne Bay, south Florida, McNulty *et al.* (1962), compared populations in terms of their dry tissue weight (retained on a 1.0 mm pore screen).

and classified the infauna as deposit, detritus (at sediment surface), and filter feeders. They found detritus feeders most abundant in the finest sediments, and suggested that in such bottoms little detritus may be expected from outside and that infauna may subsist on the rich algal surface film present. Deposit and filter feeders predominated in intermediate sedimentary grades, the latter being most abundant in sediments with a median grain size of 0.3 to 0.4 mm, whether calculated on a dry weight or numbers basis. They found no apparent differences in sorting coefficient preference among the feeding types. Deposit feeders were most abundant at a median grain size of about 0.25 mm, and the fine fraction of the sediment did not seem to play a role in the distribution of deposit feeders, probably because clays constituted such a small percentage of the fine grains there. Comparison of a number of selected bottom communities demonstrated a close correlation between body size of deposit feeders (but not detritus and filter feeders) and particle size, regardless of the type of animal concerned, there being an almost linear increase in size of animal with increasing particle size. Very coarse sediments did not support a large population of any feeding type.

In an investigation of the relationships between distribution of megabenthos and sediment types in Bogue Sound, North Carolina, Brett (1963) characterized sediments by means of phi mean diameter, sorting coefficient, percentage of clay-size particles and readily oxidizable organic matter. He related these to densities of dry weights of animals retained on a 3 mm pore screen. With an increase in current velocity there was a generally corresponding increase in mean grain size and decrease in organic matter clay, and coefficient of sorting. As current velocity increased there was a loss of fine sediments from the environment, and with fewer sediment grades the sorting coefficient became smaller. As was also shown by Sanders and McNulty, Brett found that feeding habits of animals were related to prevailing hydrodynamic characteristics of the environment and the resulting sediment types: (1) detritus feeders predominated in areas of slow currents with sediments having a mean diameter less than 0.09 mm; (2) filter feeders exceeded detritus feeders in all areas where the mean grain size exceeded 0.09 mm, the largest populations being supported in sediments of mean diameters ranging from 0.12 to 0.14 mm, not necessarily well sorted; and (3) the largest standing crop of predators occurred in high-energy environments where the mean sediment size surpassed 0.15 mm and contents of clay and organic matter were generally low—and here also the density of filter feeders was low as compared to bottoms where density of predators was minimal. Thus the sediments of Bogue Sound which supported the largest populations of filter feeders had mean diameters of 0.12 to 0.14 mm, somewhat less than the 0.18 mm of Buzzards Bay and considerably less than the 0.4 mm of Biscayne Bay. Brett noted that the Bogue Sound

and Buzzards Bay sediments are noncarbonate, while those of Biscayne Bay are carbonate. This, in addition to adaptations occurring in the evolution of these organisms in different ranges and proportions of grain sizes, may explain the variations in relation of infauna to particle size observed by Brett, McNulty, and Sanders; and stresses the need for more comparative studies of this nature.

Comparison of results of investigations in Buzzards Bay, Biscayne Bay, and Bogue Sound emphasizes the existence of a rather close relationship between infaunal feeding habits and gross organic content and the mechanical nature of sediments; and these partially mirror the degree of movement of the overlying water. More significantly though, they suggest the important role of the sediment as a source of food. This relationship underscores the necessity of comparability of methods for studying not only the characteristics of the sediments but the associated organisms themselves, at least as to size range, number, weight, behavior, and feeding types. Because those benthic animals (generally of small size) which are restricted in their movements may most lucidly reflect the physical and chemical attributes of their environment, benthic researchers can profit materially by investigating the smallest organisms practical to handle. For example, the minimum size of benthos retained in the Bogue Sound studies was 15 times larger than that in Buzzards Bay and three times larger than that in Biscayne Bay. One wonders what differences in interpretation may have resulted had the smallest size fraction of animals been retained in all areas. These studies provide a stimulating beginning for similar ones along the estuarine gradient. They should include the effect of the chemical properties of the aqueous gradient and accompanying microbiological activities on the distribution and abundance of estuarine megabenthos relative to the mechanical qualities of the sediments.

The observations of Brett, McNulty, and Sanders explain in general terms the nature of the faunally rich "muddy sand" frequently mentioned in the literature (Beanland, 1940; Day, 1951; Holme, 1949; MacGinitie, 1935; Percival, 1929; Sanders *et al.*, 1962; Stopford, 1951; Yonge, 1953). In estuaries, these appear to be more or less "optimum" mixtures of clays, silts, fine sands, and organic matter which support greater densities of megabenthic populations than either clean coarse unstable sands and gravels at the mouth or soft slurry muds in the quiet sheltered reaches of estuaries.

The role of sediments in the distribution of meiofaunal benthos (foraminiferans, nematodes, kinorhynchs, ostracods, copepods, turbellarians, oligochaetes, halacarids, gastrotrichs, cephalocarideans, and others very roughly in the size range of 100 to 500 μ) has received much less examination than of the megafaunal benthos, and most of the research has been directed to marine interstitial metazoans (Mare, 1942; Wigley and McIntyre, 1964). The recent valuable paper by Wieser (1960) reviews earlier studies and

reports on investigations primarily of nematodes and kinorhynchs in sediments at three stations in Buzzards Bay, an environment grossly similar to that of the lower reaches of an open estuary. These two groups comprised 89 to 99 percent of the total meiofauna; dry weight of the total meiofauna ranged from 100 to 600 mg/m² of bottom, and wet weight from 0.4 to 2.5 g/m². In general, sediments rich in silts and clays supported a larger number of meiofaunal animals than those poorer in fine sediments, a relationship displayed by the deposit-feeding component of the macrofauna. Three ecological meiofaunal groups were found: (1) species with affinity for sand, (2) species with affinity for fine deposits, and (3) more eurytopic species. Thus the meiofauna at any point in the bay is determined by the degree of mixing of sediment types, to which it is quite sensitive, and consists of a subtle graded series of faunal assemblages. Most representatives of the meiofauna feed on the epigrowth of sand grains or on the fine deposits, which further affects their distribution. Whether meiofaunal sediment relationships change up the long axis of the estuary is not known, but the matter provides a stimulating area for research provided the associations are related to organisms identified to species, as has been done by Wieser (1960). A major drawback in the investigation of causes of distribution *in situ* lies in the difficulty of controlling environmental factors and the impossibility of singling out the specific effect of single and multiple factors. Because of their small size, inordinate abundance, and apparent hardness, nematodes might lend themselves admirably to studies in the laboratory. Investigations could include uni- and multifactorial variation of such factors as inert artificial particles in a range of sizes and angularities, synthetic dissolved and particulate organic material, salinity, and temperature.

WORLDWIDE DISTRIBUTION AND SPECIATION OF ESTUARINE BENTHIC INVERTEBRATES

A striking feature of estuarine faunas is that they resemble each other in estuaries in various parts of the world (Burbanck *et al.*, 1956), although estuaries may have little more in common than similar ranges of environmental variability (Hedgpeth, 1953). Species and genera having widely cosmopolitan representatives are listed by Redeker (1933), Hedgpeth (1953, 1957e), and Burbanck *et al.* (1956). These lists will probably grow longer as the systematics of estuarine taxa is developed on a worldwide basis. On the basis of Day's classification, the characteristic estuarine benthic fauna probably represent primarily euryhaline marine and true estuarine taxa, both of which are broadly eurytopic. Hesse *et al.* (1951) note that the common characteristics of animals living under similar conditions, which are the more striking the more closely the environmental conditions approach limiting factors, arise from the requirement for definite adaptations. These act "upon the fauna like a sieve of definite mesh, allowing only more or less similar forms to pass". Colonization of estuaries

by marine benthos has been taking place for long periods of geological time, and still continues primarily in the tropics (Hesse *et al.*, 1951; Hunter, 1964; Pearse, 1950; Segerstraale, 1964). Kinne (1964) writes that non-genetic adaptations to salinity are acquired during very early ontogeny, tend to be more stable and more complete than those acquired in older individuals, and may even be irreversible. He also discusses physiological and behavioral differences which are likely to represent genetic adaptations to life in lower salinities. Hedgpeth (1957e) suggests that typically estuarine benthos may represent a considerably earlier invasion of estuaries than that by euryhaline marine forms. The wide tolerance of estuarine organisms undoubtedly helps to explain their capacity to establish themselves in estuaries over the world, at least in similar latitudes (Parker, 1964a). As they may not be able to compete with marine organisms in the sea (Korringa, 1957), the advent of rapid means of oceanic transportation has facilitated their dispersal, both accidental and deliberate, to new estuaries (Elton, 1958; Hedgpeth, 1957e; Hesse *et al.*, 1951). Another factor which appears to contribute indirectly to the universal uniformity of appearance of estuarine benthos is their suggested origin from similar stocks of widely distributed organisms in the sea which may have been characterized by physiological euryhalinity to begin with (Hedgpeth, 1957e).

Carter (1961) speculates that in littoral regions where environments are locally highly variable, the rate of evolution should be rapid, since changing conditions lead to rapid adaptation if organisms can survive physiological alteration. After organisms have developed wide environmental tolerances, they would tend to continue unchanged (Hedgpeth, 1957e). Various theoretical aspects of speciation relating to coastal areas are considered by Buzzati-Traverso (1958), Bullock (1955), Hutchinson (1953), Kohn (1958), Nicol (1935, 1960), Prosser, (1955), and Smith (1959). Now that difficulties of rearing marine larvae in the laboratory are being overcome (Costlow and Bookhout, 1961; Losanoff and Davis, 1963; Ray, 1958), useful marine animals for genetic studies are becoming available (Ray, 1958), and suggestions of methods for elucidating some of the processes of speciation and for distinguishing between genotypic and phenotypic variations have been offered (Buzzati-Traverso, 1958; Kohn, 1958; Prosser, 1955). Experimental verification of the modern occurrence of speciation and invasion of estuaries by marine benthos from the shallow seas is a distinct possibility.

ORIGIN OF ESTUARINE BENTHIC INVERTEBRATE POPULATIONS

Repopulation of benthic invertebrate animals in estuaries takes place by means of free-swimming pelagic larvae arising sexually; non-pelagic larvae arising sexually and developing in brood pouches, capsules, and gelatinous masses; and asexual reproduction. The percentage of invertebrate species in open level bot-

tom communities having pelagic larvae is approximately 67 percent in temperate seas, and about 90 in the tropics (Thorson, 1957, 1958). Similar statistics for faunas of estuaries grading from temperate to tropical regions and of faunas along the longitudinal axes of these estuaries are not available, but would be instructive. With the exception of an unknown number of species of non-pelagic young which have special means of relatively long-distance dispersal (Carriker, 1957; Shuster, 1951), non-sessile benthic juveniles tend to remain in the area of their origin, although how much tidal currents may transport them passively back and forth over the bottom is unknown. As in true stratified estuaries where flood tidal currents are stronger near the bottom than those of ebb tide, there is a distinct possibility that some net up-estuary conveyance of benthic juveniles may occur unless counteracted behaviorally by use of such structures as byssi and tubes and by burrowing (Carriker, 1961b). The possibility is important and needs examination because juveniles might be carried into regions of lethal salinities.

Planktonic larvae originating in the estuary, on the other hand, are probably scattered widely over the estuary and, especially in short shallow estuaries, may be flushed out to sea before metamorphosis and settlement, primarily because of the overwhelming impact of estuarine water movements on them. Study of the unique means by which larval plankters are able to settle in certain estuaries has been in progress for the last half century, and information on a few species is accumulating (*Mya*: Ayers, 1956; *Mercenaria*: Carriker, 1961b; *Crassostrea*: Haskin, 1964; *Ostrea*: Korringa, 1941; *Balanus*, *Rhithropanopeus*: Bousfield, 1955b). The mechanism of retention, not yet entirely explained, provides a remarkable example of the capacity of organisms to adapt to and utilize every habitable biotope on earth.

SPAWNING OF BENTHIC INVERTEBRATES WITH PELAGIC LARVAE

As Bousfield (1955b; see also Carriker, 1961b) points out, the degree of settlement of larvae in an estuary is a function of the initial abundance, rate of mortality, and duration of planktonic existence of the larvae, circulation pattern of water at the depths at which larvae swim, and overall size and type of estuary. Thus environmental phenomena associated with release of gametes and larvae by benthic species are important in larval retention.

Although most of the factors that stimulate spawning under natural conditions in the field are still obscure, thermal stimulation is a major factor in temperate latitudes (Carriker, 1961b; Kinne, 1963b; Landers, 1954; Loosanoff and Davis, 1963; Thorson, 1946b). Both rising and falling temperatures play a part after a certain temperature level is reached. Whether this is also true in the tropics is not clear. In the laboratory, Loosanoff and Davis (1963) have been able to induce spawning in a number of coastal species of bivalves by thermal and chemical (sperm)

stimuli, independently of day length, tidal rhythm, precipitation, kinds of plankton, and other factors present in the late spring and early summer when gametogenesis normally occurs. The kind and quantity of food appearing in plankton blooms, and the resulting release of ectocrines, may also be important in stimulating spawning (Lucas, 1961; Thorson, 1950).

The time of discharge of planktonic sperm, ova, and larvae into the water relative to the phase of rhythmic environmental factors is a first consideration in terms of larval retention in the estuary. It is thought that a few males spawn first, releasing a cloud of sperm which tidal currents pass over other males and females, stimulating them to spawn (Galtsoff, 1964), thus better insuring mass fertilization of the ova (Thorson, 1950). Recent studies suggest that, at least in some cases, time of spawning may coincide with the particular periods of the tides and seasons, which tend to reduce dispersal of larvae seaward (Carriker, 1961b). In an investigation of the veliger larvae of *Mercenaria mercenaria* in a neutral homogeneously mixed estuary, this author noted that maximum density of swarms of early larvae predominated during neap tides, indicating that spawning occurred primarily during neap tides rather than during spring tides. The cause for this may have been the higher temperatures prevailing during neap tides, periods of lesser tidal amplitude and exchange with the cooler oceanic waters, or possibly periods of denser populations of food organisms, because of higher temperatures and less dilution of the plankton and nutrients with sea water. The observations also suggested that spawning was triggered principally at or just after low tide, coinciding with periods of maximum temperatures occurring as a result of heat brought down the estuary by the ebbing tide. Spawning at this phase of the tide is advantageous to the larvae, as they would be transported up the estuary from the spawning area rather than down the estuary toward the mouth resulting in possible loss at sea. Whether these responses also occur in stratified estuaries is not known. A further interesting coincidence is that in temperate latitudes, at least, much of the spawning in estuaries occurs in the summer during periods of reduced flushing because of minimal rainfall and river discharge. The survival value of this to all plankters both in stratified and homogeneously mixed estuaries is clear; though it should be pointed out that, up to a point, increased river discharge will accelerate the movement of the up-estuary bottom drift and pelagic larvae remaining below the halocline (level of no net motion) will be transported more rapidly up the estuary, as is the case with *Balanus crenatus* in Miramichi Estuary. Conversely, surface larvae will move more quickly out to sea as in the case of *Balanus balanoides* (Bousfield, 1955b). Study of these phenomena in a series of estuaries geographically distributed between the arctic and the tropics could yield much valuable information. It would be particularly instructive to know whether

the bulk of spawning in tropical estuaries occurs during the dry or the rainy season, and, in the absence of seasonal thermal fluctuations, what stimulus induces spawning.

MOVEMENT AND DISTRIBUTION OF ESTUARINE PLANKTONIC LARVAE

The activities of planktonic larvae of estuarine benthic invertebrates have been studied by many investigators, and reviews of this work have been provided by Bousfield (1955b), Carricker (1951b, 1959, 1961b), Haskin (1964), and Thorson (1946b). Nelson (1912) was the first to suggest that estuarine larvae (American oyster) may control their horizontal distribution by regulating their bathymetric distribution relative to direction of tidal currents. In his thorough report on the distribution and movements of larvae of barnacles and other benthic invertebrates in Miramichi Estuary relative to the hydrography of this water mass, Bousfield (1955b) theorizes that the mechanism by which the larvae are retained in the estuary consists of three main features: (1) a changing vertical distribution of successive planktonic stages of larvae; (2) a non-tidal drift seawards at the surface, and another landwards along the bottom, superimposed on tidal oscillation; and (3) a counter-clockwise circulation of the larvae completed within the planktonic duration in the outer estuary. With minor modifications, this theory applies to all estuarine species so far investigated, among which the American oyster, *Crassostrea virginica*, has been most thoroughly examined.

Studies by Nelson (1917), Nelson and Perkins (1931), Carricker (1951b), Manning and Whaley (1955), and Haskin (1964) on the larval biology of *C. virginica*, primarily an estuarine form, show clearly that early stages tend to remain more or less uniformly distributed vertically in the water column, and that as larvae mature they seek lower levels of the profile, with an increased proportion of older stages on the flood over that on the ebb tide. In some cases (Carricker, 1951b), large concentrations of older stages of these larvae were found on the bottom during ebb tide. This observation supports the hypothesis (Nelson and Perkins, 1931) that older stages drop on or close to the bottom during the falling salinities of ebb tide and are stimulated to rise by the increasing salinity of early flood tide, thus moving up the estuary by successive stages, in some instances far beyond the parents. Most recently, Haskin (1964), in controlled laboratory experiments, demonstrated a very close correlation between salinity change and swimming activity of mature and eyed oyster larvae. Therefore salinity variations may play an important role in the vertical movements of these larvae in nature, even in the absence of a prominent halocline. Other information suggests that in nature light tends to depress vertical distribution during daylight hours (Bousfield, 1955b; Carricker, 1961b; Haskin, 1964; Nelson, 1916; Rogers, 1940; Yasuda, 1952), and that turbulence from tidal currents and wave action may

stimulate the larvae to rise in the water column (Carricker, 1951b, 1961b; Nelson and Perkins, 1931). Carricker (1961b) observed that, even during hours of darkness when veligers of *Mercenaria mercenaria* assumed a broader vertical distribution, there was a scarcity of these larvae near the bottom. The same was observed for veligers of *Crassostrea virginica*, except for an occasional dense concentration of mature and eyed larvae near the bottom (Carricker, 1951b) during daylight hours. Whether this scarcity of younger stages near the bottom reflects the results of filter-feeding predation by bottom-dwelling organisms, or whether the larvae have evolved behavioral response that tends to keep them swimming away from the bottom, or both, is not known. The significance in terms of survival is clear: enemies are generally more abundant in the bottom than in the water column. Most maturing pelagic larvae of estuarine benthic parents probably become photonegative, geopositive, and positively thigmotactic as they approach metamorphosis. Aside from the work of Nelson and Perkins (1931) and Haskin (1964), very little has been done to examine experimentally the many potential causes for, and behavior involved in, the vertical distribution of pelagic larvae in estuaries; this is a serious gap in our knowledge of these embayments.

Elucidation of the physical hydrography of estuaries by Pritchard and associates was a major contribution to the study of estuarine plankton, and soon made clear that inherent in the circulation of stratified estuaries is the two-layered drift transport system which in itself can account for automatic transport up the estuary of larvae remaining below the level of no net motion. In Chesapeake Bay, for example (Pritchard, 1951), the net up-estuary bottom drift (0.2 to 0.4 knot) could transport larvae 130 miles up the estuary from the mouth in 20 days; and Bousfield (1955b) describes a similar drift of 0.128 knot in Miramichi Estuary. Contrary to the suggestions of Pritchard (1953), however, that these larvae can be considered theoretically the same as dissolved material, and of Emery and Stevenson (1957a) that vertical migrations are not necessary to account for their horizontal movements, it has been demonstrated beyond a doubt by many investigators that these larvae are active swimmers, and although they do not make appreciable progress horizontally, their vertical activity is conspicuous. It is reasonable to hypothesize that in the course of the evolution of the estuarine invertebrate form with planktonic larvae, behavioral mechanisms have evolved which make use of the estuarine circulatory system for retention within the estuary. Accumulating information suggests that this is so.

Not all species of larvae of benthic invertebrates behave similarly under estuarine hydrographic conditions. Their behavior undoubtedly reflects genotypic differences and limits of tolerance, and this affects the resulting distribution of the adults. In Miramichi Estuary, for example (Bousfield, 1955b),

adult *Balanus balanoides* and *B. crenatus* are found in the outer estuary, and *B. improvisus* is mainly within the estuary. The surface residual drift transports early larval stages of *B. improvisus*, found near the surface, to the mouth of the estuary, and as the larvae develop they move below the level of no net motion and are carried up the estuary to and beyond the original spawning sites by the landward drift. This species differs in this behavior, then, from the American oyster only in the distribution of the early stages, but the effect of up-estuary conveyance is the same. On the other hand, by means of the same two-layered opposing drifts the later deep-swimming larval stages of *B. crenatus* are carried into the estuary from the open water to the limit of their low salinity tolerance; but those of *B. balanoides*, all stages being near-surface swimmers, tend to be carried out of the estuary especially during periods of warm river flood. How the latter set in the estuary is not yet known, but Thorson (1957) notes that larvae of species like this which settle near the intertidal zone remain positively phototactic and in the surface stratum of water. The seaward transport of the three species of barnacle larvae in Miramichi Estuary is strongest on the right side, and the up-estuary movement strongest on the left side of the estuary as a result of Coriolis force. A similar horizontal drift circulation pattern exists in Delaware Bay (Nelson, 1947), resulting in heavier sets of oysters on the left than on the right side of the estuary.

Bousfield (1955b) suggests that active avoidance of low salinities by estuarine and euryhaline marine planktonic larvae probably takes place only near lethal limits of salinity. He describes concentrations of cyprid larvae of *Balanus improvisus* found near the head of the estuary within the landward drift and under the fresh to brackish seaward drift, some 40 miles from the mouth of the Miramichi Estuary during an exceptionally dry summer and only 30 miles above it during a rainy summer. Nelson and Perkins (1931) observed in Barnegat Bay that, in the presence of more or less sharp haloclines, the maximum number of immature larvae of gastropods, and the pelecypods, *Crassostrea*, *Mya*, *Mercenaria*, *Mytilus*, and *Teredo*, tended to concentrate in the close vicinity of the discontinuity layer, while oyster larvae generally remained above it. Carriker (1951b) later observed a similar response on the part of oyster larvae in the same estuary. Nelson further reported that mature larvae of *Mya* occurred below the halocline and near the bottom; this suggests that like the mature stages of the larvae of *C. virginica*, these of *Mya arenaria* may also remain in the landward drift and be transported up the estuary. Distribution of adult *Mya* in estuaries supports this idea. The crowding of immature larvae in the vicinity of the sharp discontinuity layer between the surface and bottom drifts suggests minimal net up- or down-estuary movement, and may aid their retention in the estuary. In the presence of more gradual vertical gradients of salinity, immature stages of *C. virginica* are more uniformly

distributed, and up-estuary migration is left to the mature stages in the bottom stratum. On the basis of his experiments, Haskin (1964) suggested that continuous up-estuary transport of mature stages of *C. virginica* in the landward drift to the upper end of the estuary, where progressively diluted sea water crosses upward through the discontinuity layer to be entrained in the surface seaward drift, results in a "larval trap"; larvae are carried passively to this point, but are blocked from further transport by minimal salinity limits. He notes that heavy spatsfalls around the mouths of tributaries of estuaries may be partly due to such entrapment. Bousfield's discovery of similar concentrations of cyprid larvae contributes further support for the idea.

To what degree all planktonic larvae of estuarine benthic invertebrates respond to the non-tidal drift circulation of estuaries is not known, though limited available information suggests that the response may be widespread (Smith, 1964), and even extends to entirely pelagic estuarine species (Hulbert, 1957). Unfortunately studies of the larvae of *Mercenaria mercenaria* (Carriker, 1961b) and *Mya arenaria* (Ayers, 1956) were conducted in estuaries lacking noticeable non-tidal drifts, so that information on the response of these species to vertical stratification is not available, but distribution of adults indicates at least some response. Much more information is needed on the response of the larvae of freshwater, true estuarine, euryhaline marine, and marine species of estuaries, not only to vertical salinity stratification, but to that of turbulence, light, turbidity, pressure (Thorson, 1957; Haskin, 1964), and lesser known factors, in the entire range of types of estuaries. Such studies could well be conducted with profit in the laboratory and field models of estuaries. As Bousfield (1955b) has discovered for three species of barnacles, it may be that larvae of other benthic species along the gradient of the estuary may possess different behavioral responses in keeping with their positions relative to the gradient; and that these responses may also differ in estuaries towards the tropics. For example, larvae of oligohaline species, commonly in the brackish surface drift, might easily become entrained there and killed by increasing salinities encountered down the estuary, unless they could move downward into and tolerate the higher salinities just below the zone of no net motion and accordingly ride back up the estuary. In more or less homogeneously mixed estuaries they must be flushed into lethal salinities.

Biologists investigating the abundance of pelagic larval broods in coastal waters have been impressed by the wide range of number and density of broods encountered from year to year and from one embayment to another (Carriker, 1961b; Cole, 1957; Loosanoff et al., 1955; Thorson, 1957; Wilson, 1958). Whether this results initially from variation in availability of unspawned gametes, fluctuations in the quantity of spawning as determined by environmental factors, loss of larvae to predators (Carriker, 1961b;

Thorson, 1946b), failure to encounter appropriate substrate for metamorphosis and settlement (Wilson, 1952), or loss to the sea is not known. All of these are undoubtedly important at one time or another, and may differ from embayment to embayment. Accumulating information, however, indicates that exclusive of the rates of non-tidal residual drifts and thus of stream discharge, variations in the rate of tidal exchange alone may, in certain cases, be more critical than all other factors in relation to retention (Ketchum, 1954). In Barnstable Harbor, for example, where exchange in each tidal excursion may amount to 90 percent and residual drifts are negligible, *Mya arenaria* is unable to maintain itself without larval recruitment from Cape Cod Bay (Ketchum, 1954; Ayers, 1956); and similarly in Home Pond, a small shallow estuary with an exchange rate varying from 22 to 73 percent, recruitment of *Crassostrea virginica* and *Mercenaria mercenaria* is obtained almost entirely from Gardiners Bay (Carriker, 1959). In Little Egg Harbor, where the exchange rate varies from 20 to 47 percent, a curious eddy circulation and the spawning behavior of *Mercenaria mercenaria* insure a high retention rate when veligers coincide with periods of little or no rainfall and medium to low tidal amplitudes (Carriker, 1961b). At these times, survival rates of veligers from the straight-hinged to the setting stage approximated 2.6 percent. During periods of heavy rainfall and high spring tidal exchanges, however, the occasional large swarms of young larvae disappear from the water before settlement. An exchange rate of 15 percent in Miramichi Estuary (Bousfield, 1955b) in addition to the residual drifts, is apparently adequate to insure settlement of barnacles there. Very low exchange rates, such as the 4 percent of the Oosterschelde (Korringa, 1941, 1952) greatly minimize losses of larvae of *Ostrea edulis* by exchange. Rate of dispersal of larval plankters at sea by exchange is difficult to calculate because of variable mixing of water moving out of the inlet on the ebb tide with longshore or offshore currents. Ayers (1956) calculated for Barnstable Harbor the theoretical size of larval populations of *Mya arenaria* which would survive and remain in the estuary under various flushing and mortality rates.

As short duration of the pelagic phase of the life cycle appears to have value in retaining more or less immobile estuarine benthic species within the estuary, it would be desirable to discover whether these species have shorter planktonic stages than littoral marine species. A limited survey of the duration of pelagic stages suggests this, but a broader study must be made before conclusions can be reached. Of the 19 species of larvae of benthic bivalves reared in the laboratory by Loosanoff and Davis (1963), for example, 16 species which are primarily true estuarine or euryhaline marine have larval stages ranging in duration minimally from one to two weeks (see also Carriker, 1961b), whereas the remaining three genera which are more typically marine (*Spisula*, *Arca*, *Teredo*) begin to metamorphose after about three

weeks. *Balanus improvisus* (Bousfield, 1955b) and *B. amphitrite* (Costlow and Bookhout, 1958) which also inhabit estuaries, began to settle after about one to two and a half weeks (Thorson, 1957). On the other hand, the typically marine outer beach sand crab, *Emerita*, is said to take four to five months (Johnson, 1939). It would be interesting to know the duration of the pelagic phase of its close neighbor, the beach clam, *Donax*. In the case of the widely ranging motile epibenthic forms like the crab, *Callinectes*, which moves actively about as an adult, remaining within the estuary is not difficult and its long pelagic phases of five to six weeks (Costlow and Bookhout, 1959) may have added dispersal value. This discussion raises the question of whether there may not exist ecological races of estuarine benthic species with a longer pelagic phase in long stable estuaries like the Miramichi (Bousfield, 1955a) than in shorter less stable ones like Great Bay (Carriker, 1951b); and whether larvae of tropic, temperate, and arctic estuarine species have planktonic periods of similar or dissimilar duration (Thorson, 1957).

It is a fair assumption that larvae originating from true benthic parents in middle and upper reaches of the estuary are retained to settle in greater numbers than those spawned from euryhaline marine stocks farther down the estuary. Thus a natural selection for behavioral patterns which promote retention may be taking place among the euryhaline marine species, and probably gave rise in the beginning to true estuarine species with planktonic larvae. It is further possible to conjecture that the larvae of true estuarine species have retained a widely euryhaline (or better, eurytopic) tolerance to the extremes of the estuarine environmental gradients, perhaps more so than adults, and thus can tolerate transport into neritic waters and up and down the coast to adjacent estuaries. If true, this would help explain the similarity of true estuarine species in different estuaries. The studies of Loosanoff and Davis (1963), Bousfield (1955b), Costlow and Bookhout (1961), and Carriker (1951b) indicate a wide euryhalinity of the larvae of certain estuarine species. Kinne (1964) reports that salinity tolerance in many species is narrowest during very early ontogeny, then increases in young stages, and finally decreases again in the senile adult. On the other hand, larvae of at least some species from different salinity regimens, like *Nereis diversicolor* (Smith, 1964), bear an apparently adaptive relationship to the prevailing salinity of the habitat. Thorson (1946b) writes that most species of planktonic larvae in coastal waters are restricted to specific horizontal strata. This suggests that true estuarine species may have been derived primarily from those open-water marine species whose larvae are characteristic of the surface rather than the deep layers of continental shelf waters.

SETTLEMENT OF ESTUARINE PLANKTONIC LARVAE

Planktonic larvae of many species of benthic coastal invertebrates explore the bottom to which they are

exposed when ready to metamorphose. If they find it attractive they will settle there; if not, metamorphosis is delayed for an extended time and the alternation of bottom searching and swimming continues, probably greatly enhancing the possibility that a suitable substratum is encountered (de Blok *et al.* 1959; Lynch, 1959; Scheltema, 1961; Thorson, 1957, 1958; Wilson, 1952, 1958). To what extent the observed behavior of alternation of crawling and swimming is an indication of searching has not been tested experimentally, though circumstantial information suggests that this is so. In estuaries where ready-to-set larvae may be transported by both tidal currents and landward drifts, the opportunity for settling in appropriate substrates should be considerable, the nature of each estuary and its tidal and drift circulation dictating the magnitude. In spite of the number of estuarine pelagic larvae which have been reared in the laboratory, there is little information on how long metamorphosis may be postponed, and the range of duration of larval life given in the literature (Loosanoff and Davis, 1963) for each species may in part reflect a variation in delay of metamorphosis under the conditions of culture. The chemical nature of estuarine waters (Lynch, 1959), exclusive of attractive properties from the sediments or benthos, may also exert a delaying or an accelerating effect on metamorphosis. The point is worth pursuing. As Wilson (1952) points out, it has been easier to establish the facts that metamorphosis can be delayed and that larvae can choose their substratum than to determine the actual qualities of the substratum to which they react. In general, particle size of the sediment, quality (and possibly quantity) of organic matter, and species and activity of microorganisms may all be important factors in attracting or repelling, and different species may metamorphose in response to different factors or combinations of factors. It has been suggested that searching larvae discover suitable substrata only by actual contact (Thorson, 1957). This may be true for some species, but Scheltema (1961) demonstrated experimentally that metamorphosis-inducing properties of the substratum for *Nassarius obsoletus* are probably water soluble and may be transferred to the adjacent water. Consequently, sensitive chemo-reception may be involved, and, because this snail is primarily a deposit feeder, selection of a favorable substratum would have survival value. To what extent a distance response to properties of sedimentary substrates occurs among pelagic larvae of most estuarine deposit feeders remains to be investigated, but it may be more widespread than Thorson (1957) believes, especially in estuaries where organic matter is such a conspicuous component of sediments and where microbiological activity and release of organic substances is correspondingly high. Whether estuarine infauna emit intraspecific ectocrines which mediate preferential settlement of larvae of the same species in the close vicinity of adults, much as gregarious settlement of certain epifaunal invertebrates is induced by a substance secreted into the water by individuals al-

ready settled (Knight-Jones and Stephenson, 1950; Knight-Jones and Moyse, 1961), is still to be determined. Little is known of the capacity of widely scattered juvenile bottom states of true estuarine benthic species to migrate and aggregate in the area populated by adults, as is done by such euryhaline marine species as *Mytilus edulis* (Newell, 1964). Finally, it is possible that stimuli other than chemical signals may cue ready-to-set pelagic larvae to accumulate in specific bottom areas. Carriker (1961b), for example, observed that pediveligers ("swimming-crawling stage") of *Mercenaria mercenaria* seem to be stimulated to set below water masses exhibiting steep gradient or turbulence (Bowden, 1964); and Turner (1953) suggested that distribution of certain species of juvenile bivalves may be influenced by the same hydrographic features that affect the zonation and sorting of the particles of the substratum.

These facts imply, as Thorson (1957) has noted for level bottom communities, that recruitment for estuarine benthic communities is something of a selective process—just how much, only further study can tell us.

Thorson (1957) discusses in detail the balance between predators and newly settled benthic young in level bottom communities of the shelf and how species of new recruits are able to survive in the face of interspecific and intraspecific competition. Insofar as benthic predators, similar to those on the shelf, are involved in the high-salinity regions of the inlets of estuaries (sea stars, brittle stars, gastropods, crabs, and fish) Thorson's observations may well apply there, too. As the composition of the benthic fauna changes up the estuary with decreasing salinity, however, certain predators are eliminated (Hutchinson, 1953). It was this which led Korringa (1957) to state that it is not the low salinities of the estuary as such which bring advantages to estuarine fauna, but the biological richness of estuarine waters and the escape from many parasites and predators. In this regard, *Asterias forbesi* (Loosanoff, 1945; Loosanoff *et al.*, 1955) and *Urosalpinx cinerea* (Carriker, 1955a, 1957), both serious predators especially of molluscs, and highly predacious as early juveniles, are not able to migrate up the estuary much beyond an approximate salinity zone of 15 %. This may account, in part, for the extraordinary densities of *Crassostrea virginica* and *Mya arenaria* occurring in the upper reaches of Chesapeake Bay. On the other hand, other predators, highly tolerant of low salinities (for example: *Pleuronectes*, Hartley, 1947; xanthid mud crabs and *Callinectes*, Carriker, 1959, 1961b; *Carcinides*, Broekhuysen, 1956; and *Limulus*, Shuster, 1950), even as early juveniles begin preying on very young benthic fauna. Though a reduced number of species of predators may exist in estuaries, the number of individuals may be astronomic (as is *Callinectes* in Chesapeake Bay where it supports a major crab fishery; and the major oyster pest, *Urosalpinx*, on oyster beds). Thus, mechanisms must exist, perhaps similar to those Thorson (1957) speaks of,

which permit estuarine prey populations to survive, often in large densities. A partial explanation may be the fact that settling infauna soon burrow into the sediment (Carriker, 1961b) and thus achieve protection. This does not explain, though, the vulnerability of newly settled forms which temporarily rest superficially in the sediment, where they are subject to the depredations not only of wandering juvenile predators but of detritus-feeding grazers like *Nassarius obsoletus*, which probably inadvertently ingest them with detritus (Scheltema, 1961). Epifaunal forms like oysters achieve a measure of protection as their valves increase in thickness, but newly set populations of spat may be decimated by dense populations of newly emerged crawl-away stages of oyster drills and newly metamorphosed crabs which appear more or less concurrently. The presence of alternative prey species may provide something of a buffer, but little is known of this in the invertebrates. An apparent difficulty in oyster culture is that shellfishermen cultivate essentially a unispecies bivalve crop, quite unbuffered from predators by other prey species. Finally, Buzzati-Traverso's (1958) point that substances having antibiotic activity (as for example, in macroscopic algae which lack extensive growth of epiphytes due perhaps to production of antibiotics, Ferguson Wood, 1962) may be responsible for survival of very delicate early stages is worth keeping in mind. There is unquestionably a dearth of information in this area of estuarine biology, and the important contributions of Thorson and his colleagues in this field suggest avenues for further research.

THE ESTUARINE BENTHIC BIOCENOSE

REALITY OF THE ESTUARINE BENTHIC BIOCENOSE

Estuaries, although enduring biotopes, are regions of distinct ecotonal gradients, and the question logically arises whether, in the transitional environment of the estuary, and in the absence of catastrophic environmental changes, there does indeed exist an overall estuarine benthic biocenose, a discrete functional aggregation of interdependent, regularly recurring, reproducing dominant, benthic population strongly represented numerically. The concept of the benthic biocenose is broadly accepted, though whether as a biotic reality or as a useful statistical unit, and to what degree intrinsically regulated, is still widely debated (Barnard and Jones, 1960; Bodenheimer, 1958; Dexter, 1947; Ehrlich and Holm, 1962; Engelmann, 1961; Gislén, 1944; Hairston, 1959; Hedgpeth, 1953, 1957b; Jones, 1950; Longhurst, 1964; MacFadyen, 1957; McIntosh, 1963; Muller, 1958; Péres, 1961; Thorson, 1957). This is a matter which may not be resolved until much more is known of the ecological life histories of constituent populations and their collective nutritional, reproductive, competitive, and cooperative interactions, and there is more information on Lucas's (1961) important suggestion that the appearance of integration of interdependencies of organisms

in biocenoses may be mediated in part by external metabolites. There is a crippling shortage of comprehensive monographs on the biology of individual species, such as the excellent Liverpool Marine Biology Committee Memoirs (see Dakin, 1909, on *Pecten*, for example), which unfortunately were discontinued many years ago; and Galtsoff's (1964) fine treatment of the American oyster. The benthic biocenose will be better understood only as its constituent taxa become better known.

It has already been indicated in this perspective that the estuarine biotope is not just a simple overlapping of factors extending from the sea and the land, but is characterized by a unique set of its own factors arising within the estuary from the materials and forces contributed by its bordering environments. This has made possible the evolution of a benthic biota which included the unique true estuarine, and peripherally the euryhaline marine and freshwater components. Thus the potential does appear to exist for a distinct estuarine biocenose in the middle reaches of at least larger gradient-type estuaries. Where the landward and seaward boundaries of this biocenose might occur and the extent of their diffuseness are not known, but are probably functional characteristics of different estuaries. These boundaries in themselves could constitute ecotones between the estuarine biocenose and the freshwater and marine biocenoses.

Dominant macroscopic benthic estuarine organisms such as *Spartina alterniflora*, *Zostera marina*, *Ruppia maritima*, *Cymodocea manatoria*, *Rhizophora mangle*, *Avicennia nitida*, *Nereis diversicolor*, *Balanus improvisus*, xanthid mud crabs, *Uca pugnax*, *Callianectes sapidus*, *Mya arenaria*, *Mytilus edulis*, *Modiolus demissus*, and *Crassostrea virginica* are well known, as is their heterogeneous distribution in estuaries (Dexter, 1947). Tidal marshes (Chapman, 1961), mangrove swamps (Dansereau, 1947, 1957), eel grass mats, oyster reefs (Grave, 1905), mytilid beds (White, 1937), and soft clam-clam worm flats (Dexter, 1947) exemplify the dominancy of these species and their patterned distribution. As conspicuous as are these macroscopic organisms as indicators of estuarine conditions, it is certain, as shown by Sanders (1956, 1960) and by Wieser (1960), that meiobenthos and small megabenthos will provide a more workable correlation of numbers of individuals and species and biomass to the estuarine environment. Furthermore, the structure of invertebrates makes possible deduction from the animals themselves of certain characteristics of the sedimentary environment which are difficult to assess by means of physiographic procedures alone (Wieser, 1958). In estuaries, the oscillating gradient of water-borne factors is superimposed on that of the pattern of the sediments, and the degree of exchange of ambient water with interstitial water varies with the nature of the sediment and degree of exposure at low tides. Little is known of the sum of these effects on community structure, but they do emphasize the need to consider benthic organisms in the context of the total ecosys-

tem rather than as an independent benthic biocenose (see also Hedgpeth, 1957b).

There is a clear need for broad, intensive, estuary-wide investigations to determine more about the higher biological levels of organization in the estuary and whether the estuarine community does, in fact, exist as a discrete functional biocenose, or is only a purely statistical conception (Bodenheimer, 1958). The matter is important not only as an ecological principle, but as a theoretical basis for continuing estuarine studies. Detailed quantitative plotting of distribution and density of benthic species, including small sizes, with reference to gradients of sediments and other operationally significant factors, at different seasons of the year, over a period of years, although a herculean undertaking, should provide a fundamental beginning (see Barnard and Jones, 1960, for methods in large scale censuses; and MacFadyen, 1957; Fager, 1957, 1963; and Sanders, 1960, for methods on statistical analyses of recurrent species groups and faunal similarity). Another step, though decidedly more difficult and probably requiring some new conceptual and experimental methods, would be multi-factorial studies under controlled environmental laboratory or field model conditions, employing a series of increasingly complex biotic organizations culminating in model biocenoses. Because of the ecotonal characteristics of estuaries, and the complexity and number of factors involved, data collected in these studies would be more manageable if stored and analyzed by means of computers. Especially bothersome to the concept of the biocenose is the often diffuse nature of its geographical boundaries; this should receive special attention. Research planned on this scale and depth might well contribute new insights on interactions of benthic biota and environment, and specifically on limiting effects of multiple factors at both extremes of the estuarine system through the rhythmic change of the seasons. Repetition of the censuses in arctic and in tropic estuaries would enhance their worth.

COHESIVENESS AND FUNCTIONING OF THE ESTUARINE BENTHIC BIOGENOSE

Assuming that the estuarine biocenose is a reality within non-catastrophic environmental conditions, it is necessary to demonstrate the mechanisms by which its overall discreteness and integration are perpetuated. Unquestionably, inherent tactic and kinetic behavior of estuarine organisms as related to food-getting, mating and reproduction, space and surfaces, and in some cases shelter-seeking, and physiological adaptation to, as well as dependence on or repulsion by, certain aspects of the physicochemical habitat, may all be significant at one time or another in the ecological life history of component species (Fraenkel and Gunn, 1961; Klopfer, 1962). Some of this has already been indicated in this perspective. Fundamental to the aspect of behavior dependent upon chemical signals, though mostly unsubstantiated, is the potential role of exocrines in mediating symbiotic

interrelationships and other community integrations (Blake, 1960; Buzzati-Traverso, 1958; Carricker, 1951a, 1957; Crisp and Meadows, 1962; Dales, 1957; Davenport, 1955; Johnston, 1955; Kohn, 1961; Lucas, 1947, 1949, 1955, 1961; Yonge, 1957). Berrie and Visser (1963) demonstrated the productiveness of such studies when taken to the molecular level. There is little doubt that in the final analysis we should look primarily to chemical rather than to physical explanations for biocenotic unity. The autecological life history of at least the dominant faunas is also important (Cole, 1954), in that different developmental stages express various requirements and exhibit distinct behaviors. Thus the complexion of biocenotic structure, organization, and function will vary seasonally, giving rise to overall community periodicities (Allee *et al.*, 1949). Especially critical are early stages which are generally the most motile, in contrast to mature individuals of some species such as the oyster, which become fixed in position and cannot migrate even in the face of lethal environmental changes (Galtsoff, 1964; Grave, 1905; Verwey, 1952). The following are suggested as some fruitful beginning lines of research in the quest for information on integrative conditions in the estuarine benthic biocenose:

1. Explore sources and methods of use of representative types of nutrient, including dissolved and particulate organic matter and whole organisms, by representative ontogenetic stages of both autotrophic and heterotrophic populations in terms of the possible contribution of nutrient procurement to the unity of the biocenose. There appears to be little value in determining only total organic carbon available, as different species and different life history stages may consume quite different molecular, aggregative, and organic fractions. It has been indicated that organic coatings on sedimentary grains consumed by deposit feeders may be important sources of food (Fox *et al.*, 1948; Fox, 1950; Wilson, 1958), that zoning of burrowing species may be related to microscopic benthic organisms as well as to their capacity to utilize sediment fractions of various magnitudes (McNulty *et al.*, 1962; Sanders, 1956; Wilson, 1958; Wieser, 1959, 1960; ZoBell and Feltham, 1942), and that the microbenthos are a significant portion of the diet of many benthic invertebrates (Belser, 1958; Kohn, 1964; Mare, 1942; Ferguson Wood, 1953; ZoBell, 1946a; ZoBell and Feltham, 1942; Zhukova, 1963). Ample, probably stable, reserves of dissolved organic matter and detritus are available in estuaries and these are now thought to form a flexible system of reversible reactions with plankton, so that a relatively uniform source of sustenance may be available to the benthos (Riley, 1963). Consequently, from at least a nutritional aspect, estuarine species have had a highly favorable advantage in evolution toward establishment of a steady state of taxa able to fulfill the trophic functions of the estuarine biocenose on a continu-

ing basis (Dunbar, 1960; Riley, 1963). Incorporation of radioisotopes in nutrients and food organisms would facilitate quantitative tracing of nutritional relationships and interdependencies (see for example, Mauchline and Templeton, 1964; Odum and Kuenzler, 1963). More of this should be done. Following the nutritional relationships may also be fruitful (Odum and Odum, 1959; Slobodkin, 1962).

2. Investigate positive and negative intra- and interspecies interactions of representative stages in the life cycle of benthic invertebrates with special reference to possible cohesive and dispersive activities involved in food-getting, the sum of which may contribute to overall cohesion of the biocenose. A sizeable descriptive literature is accumulating in this field (Blake, 1960; Bullock, 1953; Carriger, 1957; Crisp and Meadows, 1962; Dales, 1957; Davenport, 1955; Johnson, 1952; Kohn, 1961; Thorson, 1957; van Dongen, 1956; Yonge, 1957). In addition, however, to the important descriptive investigations, it is critical that such researches be approached experimentally with a view to elucidating molecular-behavioral mechanisms (Blake, 1960; Bullock, 1953; Johnson, 1952; van Dongen, 1956) which in the sum may be integrative. Very little has been done at the molecular level.

3. Consider the function of populational reproduction and behavior of early larval stages as a source of organic integrity. In estuaries this is especially important in benthic species with pelagic larvae, and has already been discussed in this perspective. Certainly, larvae which tend to seek and to settle on or close to specific types of ancestral bottoms (Thorson, 1957), or to specific species (Knight-Jones and Moyse, 1961), or to aggregate after settlement (Verwey, 1952) may be perpetuating extant biocenotic structure and function. To what extent crawl-away juveniles, already within the biocenose, bear a part in this can only be conjectured. Shelter-seeking and maintenance may also support biocenotic cohesion, and bears exploration, but it may be troublesome, especially among infauna, to determine to what degree this aggregative behavior represents response to gravity, contact, particle size, light, and chemical clues (of all kinds) in the sediment, and if the summation of such responses is contribution to the discreteness of the estuarine biocenose.

In theory, according to Elton (1927), nearly all animals tend during the course of evolution to become more or less specialized for life in a narrow range of environmental conditions, and thereby more efficient. The more stable, efficient species tend to replace and to outlast the less stable ones (MacArthur, 1955). As is particularly true in estuaries, a rather high constant percentage of genera occur with only one species, there being a strong tendency for species of any genus to be distributed as ecotypes in different habitats (Elton, 1946). An increase in the number of links in the food web of a community confers augmented stability to the community (MacArthur,

1955), a constancy defined by Elton (1958) as ecological resistance to invaders and to explosions in native populations. Thus conservation of ecological variety insures biotic stability of the biocenose (Elton, 1958; Hutchinson, 1959). Simultaneously, relative uniformity of optimal physical conditions will support a wider range of species than environments approaching limiting conditions (Hesse *et al.*, 1951).

From these and earlier observations in this perspective it follows that most estuarine species are stable and efficient; that the estuarine biocenose is characterized by less diversity than those in the adjacent neritic littoral and sublittoral, resulting in the aperiodic occurrence of unusually heavy sets of estuarine benthic invertebrates; but that enough ecological stability appears to exist in the estuarine biocenose, in spite of the stresses of the physical environment, to maintain a relatively constant continuing complexion of estuarine species. A test of the substance of these considerations awaits long-range experimental investigations, in controlled estuaries, in the field, and in field models of estuaries.

ECOLOGICAL SUCCESSION IN THE ESTUARINE BENTHIC BIOGENOSE

Given a relatively constant estuarine biotope, that is, one where factors fluctuate about an average, and exclusive of seasonal changes and alterations imposed by varying catastrophic physiographic conditions, do benthic communities along the course of the estuary undergo predictable biotically induced succession as characterized by taxonomic change? Under such conditions do these communities reach maturity (climax) in which taxonomic stability is manifest? These questions have no simple answer because of the multifactorial intricacy and oscillatory nature of estuarine systems and frequent catastrophic interruptions, but deserve serious research in light of the consequences of such principles, if they operate, on the structure and function of the total estuarine benthic biocenose and its possible management by man (Hardy, 1958).

That irreversible biotic changes and not simply populational fluctuations (Coe, 1957) occur in coastal epifaunal communities is evident (Cole and Knight-Jones, 1949; Hewatt, 1935, 1937; Redfield and Deevy, 1952; Reish, 1961; ZoBell and Allen, 1935), suggesting short ecological successions. The usual excessive siltation in estuaries, however, complicates and tends to obscure epifaunal formations except in the case of such associations as tidal marshes, mangroves, and mussel and oyster reefs where much longer-range successions occur. Although questioned by Miller and Egler (1950), it seems that at a constant sea level and continuing sheltered physiographic conditions, tidal marshes constitute a series of stages in the sere leading to a terrestrial climax. Mangroves (Danseveau, 1947) and oyster reefs (Galtsoff, 1964; Grave, 1905; Hedgpeth, 1957e), if primarily biotic rather than physiographic changes can continue to operate, are thought to culminate in land communities. Mussel

associations, although appearing to pass through short serial stages, are much shorter lived.

Occurrence of succession in infaunal associations is more debatable. Reish (1961), basing his observations on a study of sediments in a freshly excavated small boat harbor, reports that it did not take place there. Conversely, Thorson (1957) noted that a well-established population of clean sand-dwelling *Spisula* will increase the quantity of silt on the bottom by accumulation of feces and will be able to tolerate this; but searching, less tolerant *Spisula* pediveligers may not settle there. Thus the bottom is made more attractive by the present suspension-feeding residents to young of deposit feeders, and a step in the succession will have taken place. In view of the remarkable abundance and activity of microorganisms, meiofauna, and small megafauna, especially in the finer-grained sediments of coastal waters, the degree of vertical working and reworking of sediments that takes place there, and the probable resulting complexity of the molecular sedimentary environment, it is hard to believe that succession may not be found there.

In the field, the problem of succession and climax may be approached by studying representative communities down the axis of a relatively small, carefully selected homeostatic estuary situated in a forested area, surrounded by high ground, and protected by sturdy man-made flood gates at both head and mouth. In this manner excessive fresh flood waters and high storm tides could be controlled and a normal representative estuarine gradient could be maintained. Excess fresh water could bypass the estuary through a special lateral conduit. In these circumstances sedimentation would be minimal because of the forested estuarine watershed. By commencing with sterile hard surfaces and introduced blocks of sediment planted down the axis of the estuary, preliminary observations on sere formation could be undertaken. Subsequently, by manipulation of the gates the aqueous gradient of the estuary could be varied experimentally, and this effect noted on succession. Eventually as a control, the water in the whole estuary could first be made uniformly saline, and subsequently, uniformly fresh water, and succession followed. Field investigations should be complemented by laboratory studies in models, described earlier in this perspective, in which environmental factors would be closely and quantitatively controlled. Perhaps by the time such investigations are feasible, substantial progress will have been made in the development of *in situ* environmental factor- and organism-monitoring instruments, and therefore many of the suggested investigations could be facilitated by the use of such instrumentation.

SUMMARY AND CONCLUSIONS

Estuarine sediments and waters are characterized by specific and complex physical, chemical, and microbiological properties, interactions, and interdependences which collectively constitute a unique estuarine

environment for benthic invertebrates. Meio- and megabenthos in turn modify these properties.

The hypothesis is advanced that true estuaries are distinguished by certain ecological factor complexes which are present and similar in true estuaries around the world: (1) presence of well-aerated, constantly moving, relatively shallow water, relatively free from wave action and excessively rapid currents; (2) a salinity gradient, and accompanying chemical gradients, of near zero to about 32‰; (3) a range of sedimentary particle sizes from colloids to sands and detritus, resulting from terrigenous weathering, water transport, effect of estuarine gradient, and other estuarine processes; (4) intricate molecular interactions in both sediments and water in an abundance of dissolved and particulate organic matter, microorganisms, and fine sedimentary particles.

It is suggested that the estuarine biotope is thus not a simple overlapping of factors extended from the sea and the land, but a unique set of its own factors arising within the middle reaches, especially of larger gradient estuaries, from materials and forces contributed by its bounding environments. This biotope has provided the environment for evolution of the true estuarine, and peripherally the euryhaline marine and oligohaline, benthic biota; the potential for a distinct estuarine biocenose appears to exist in the resulting organization of benthic populations in the middle reaches of at least larger estuaries.

The estuarine biocenose is characterized by less diversity than those in the neritic littoral and sublittoral, and this seems to result in the occurrence of aperiodic unusually heavy sets of estuarine benthic invertebrates. Enough ecological stability seems to exist in the estuarine biocenose, however, and in spite of stresses of the physical environment, to maintain a relatively constant continuing overall complexion of estuarine species.

A test of the substance of these considerations awaits long-range descriptive and experimental interdisciplinary investigations in estuarine models and in the field, drawing on the methods and points of view of both the physical and chemical sciences.

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LITERATURE CITED

- ALEEM, A. A., 1955. Structure and evolution of the sea grass communities *Posidonia* and *Cymodocea* in the southern Mediterranean. In *Essays in the natural sciences honoring Captain Allan Hancock*; pp. 279-298. Univ. So. Calif. Press, Los Angeles, California.
ALEXANDER, W. B., B. A. SOUTHGATE, and

- R. BASSINDALE, 1932. The salinity of the water retained in the muddy foreshore of an estuary. *J. Marine Biol. Assoc. U. K.*, 18:297-298.
- ALEXANDER, W. B., B. A. SOUTHGATE, and R. BASSINDALE, 1935. Survey of the River Tees. Part II. The estuary—chemical and biological. *Dept. Sci. Indust. Res., Water Pollution Res. Tech. Paper No. 5*.
- ALLEE, W. C., A. E. EMERSON, C. PARK, T. PARK, and K. P. SCHMIDT, 1949. *Principles of animal ecology*. W. B. Saunders Co., Philadelphia, Pennsylvania.
- ALLEN, G. W., 1964. Estuarine destruction—a monument to progress. *Trans. 29th N. Am. Wildlife Nat. Res. Conf. 1964*; pp. 324-331.
- ALLEN, M. B., and E. Y. DAWSON, 1960. Production of antibacterial substances by tropical marine algae. *J. Bacteriol.*, 79:459-460.
- AMEMIYA, I., 1928. Ecological studies of Japanese oysters with special reference to the salinity of their habitats. *J. Coll. Agr. Tohoku Imperial Univ.*, 9: 333-382.
- ANDERSON, R. O., 1959. A modified flotation technique for sorting bottom fauna samples. *Limnol. Oceanogr.*, 4:223-225.
- ANNANDALE, N., 1922. The marine element in the fauna of the Ganges. *Bijdrag. Dierk. Amsterdam*, 22: 143-154.
- AYERS, J. C., 1956. Population dynamics of the marine clam, *Mya arenaria*. *Limnol. Oceanogr.*, 1:26-34.
- BAAS BECKING, L. G. M., and E. J. FERGUSON WOOD, 1955. Biological processes in the estuarine environment. I., II. Ecology of the sulphur cycle. *Proc. Koninkl. Ned. Akad. Wetenschap. Ser. B*, 58: 160-181.
- BAAS BECKING, L. G. M., E. J. FERGUSON WOOD, and I. R. KAPLAN, 1957. Biological processes in the estuarine environment. X. The place of the estuarine environment within the aqueous milieu. *Proc. Koninkl. Ned. Akad. Wetenschap. Ser. B*, 60:88-102.
- BAAS BECKING, L. G. M., I. R. KAPLAN, and D. MOORE, 1960. Limits of the natural environment in terms of pH and oxidation-reduction potentials. *J. Geol.*, 68:243-284.
- BADER, R. G., 1954. The role of organic matter in determining the distribution of pelecypods in marine sediments. *J. Marine Res.*, 13:32-47.
- BADER, R. G., 1956. The lignin fraction of marine sediments. *Deep-Sea Res.*, 4:15-22.
- BADER, R. G., 1962. Some experimental studies with organic compounds and minerals. In *Symposium on the Environmental Chemistry of Marine Sediments*, edited by N. Marshall; Occ. Publ. No. 1:42-57. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- BAHADUR, K., S. RANGANAYAKI, and L. SANTAMARIA, 1958. Photosynthesis of amino acids from paraformaldehyde involving the fixation of nitrogen in the presence of colloidal molybdenum oxide as catalyst. *Nature*, 182:1668.
- BARKER JØRGENSEN, C., 1955. Quantitative aspects of filter feeding in invertebrates. *Biol. Rev.*, 30:391-454.
- BARKER JØRGENSEN, C., 1960. Efficiency of particle retention and rate of water transport in undisturbed lamellibranchs. *J. Conseil Perm. Intern. Exploration Mer.*, 26:94-116.
- BARKER JØRGENSEN, C., 1962. The food of filter feeding organisms. *Rapp. Proc. Verb. Conseil Perm. Intern. Exploration Mer.*, 153:99-107.
- BARLOW, J. P., 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biol. Bull.*, 109:211-225.
- BARLOW, J. P., 1956. Effect of wind on salinity distribution in an estuary. *J. Marine Res.*, 15:193-203.
- BARNARD, J. L., 1962. Final report on the first shallow water oceanographic conference. In *The First National Coastal and Shallow Water Research Conference*, edited by D. S. Gorsline; pp. 803-896. Sponsored by Nat. Sci. Found., Office Naval Res., Tallahassee, Florida.
- BARNARD, J. L., and G. F. JONES, 1960. Techniques in a large scale survey of marine benthic biology. In *Proceedings of the First International Conference on Waste Disposal in the Marine Environment*, edited by E. A. Pearson; pp. 413-447. Pergamon Press, New York.
- BARNES, H., 1958. The future of underwater television. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 105-116. Univ. Calif. Press, Berkeley, California.
- BARNES, H., 1959. *Apparatus and Methods of Oceanography. Part 1: Chemical*. Interscience Publishers, New York.
- BARNES, H., 1963. Underwater television. *Oceanogr. Marine Biol. Ann. Rev.*, 1:115-128.
- BARNES, C. A., J. H. LINCOLN, and M. RATTRAY, JR., 1957. An oceanographic model of Puget Sound. *Proc. Pacific Sci. Congr., Pacific Sci. Assoc.*, 3:686-704.
- BASSINDALE, R., 1938. The intertidal fauna of the Mersey estuary. *J. Marine Biol. Assoc. U. K.*, 23: 83-98.
- BASSINDALE, R., 1942. The distribution of amphipods in the Severn Estuary and Bristol Channel. *J. Animal Ecol.*, 11:131-144.
- BASSINDALE, R., 1943a. Studies on the biology of the Bristol Channel. XI. The physical environment and the intertidal fauna of the southern shores of the Bristol Channel and Severn Estuary. *J. Ecol.*, 31:1-29.
- BASSINDALE, R., 1943b. A comparison of the varying salinity conditions of the Tees and Severn estuaries. *J. Animal Ecol.*, 12:1-10.
- BAYLOR, E. R., and W. H. SUTCLIFFE, JR., 1963. Dissolved organic matter in seawater as a source of particulate food. *Limnol. Oceanogr.*, 8:369-371.
- BEANLAND, F. L., 1940. Sand and mud communities in the Dovey Estuary. *J. Marine Biol. Assoc. U. K.*, 24:589-611.
- BELSER, W. L., 1958. Marine microorganisms: some generalizations concerning their importance to marine life. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 405-408. Univ. of Calif. Press, Berkeley, California.
- BERNAL, J. D., 1961. Origin of life on the shores of the ocean. Physical and chemical conditions determining first appearance of biological processes. In *Oceanography*, edited by Mary Sears; Publ. No. 67, pp. 95-118. American Association for the Advancement of Science, Washington, D. C.
- BERNAL, J. D., and R. H. FOWLER, 1933. A theory of water and ionic solution, with particular reference to hydrogen and hydroxyl ions. *J. Chem. Physiol.*, 1: 515-548.
- BERKIE, A. D., and S. A. VISSER, 1963. Investigations of a growth-inhibiting substance affecting a natural population of fresh water snails. *Physiol. Zool.*, 36:167-173.
- BIRKETT, L., 1958. A basis for comparing grabs. *J. Conseil, Conseil Perm. Intern. Explor. Mer.*, 23:202-207.
- BLACKWELLDER, R. E., 1962. Animal taxonomy and the new systematics. *Surr. Biol. Progr.*, 4:1-57.
- BLACKWELLDER, R. E., 1964. Phyletic and phenetic versus omnisspective classification. In *Phenetic and Phylogenetic Classification*, edited by V. H. Heywood and J. McNeil; pp. 17-28. Systematics Assoc., London.
- BLAKE, J. W., 1960. Oxygen consumption of bivalve prey and their attractiveness to the gastropod, *Urosalpinx cinerea*. *Limnol. Oceanogr.*, 5:273-280.
- BODENHEIMER, F. S., 1958. Is the animal community a dynamic or a descriptive (statistic) conception? In *Animal Ecology Today. Monograph. Biol.*, 6:164-201 (Den Haag).
- BOURN, W. S., and C. COTTAM, 1950. Some biologi-

- cal effects of ditching tidewater marshes. *U. S. Fish Wildlife Serv., Res. Rept.*, 19:1-30.
- BOUSFIELD, E. L., 1955a. Some physical features of the Miramichi Estuary. *J. Fisheries Res. Board Can.*, 12:342-361.
- BOUSFIELD, E. L., 1955b. Ecological control of the occurrence of barnacles on the Miramichi Estuary. *Bull. Nat. Museum Can.*, No. 137.
- BOWDEN, K. F., 1964. Turbulence. *Oceanogr. Marine Biol. Ann. Rev.*, 2:11-30.
- BRAFIELD, A. E., 1964. The oxygen content of interstitial water in sandy shores. *J. Animal Ecol.*, 33: 97-116.
- BRETT, C. E., 1963. *Relationships Between Marine Invertebrate Infrafauna Distribution and Sediment Type Distribution in Bogue Sound, North Carolina*. (Doctoral Thesis) Univ. of N. Carolina, Chapel Hill, North Carolina.
- BROEKHUYSEN, G. J., JR., 1936. On development, growth and distribution of *Carcinides maenas* (L.). *Arch. Neerl. Zool.*, 2:257-399.
- BRONGERSMA-SANDERS, M., 1957. Mass mortality in the sea. *Geol. Soc. Am. Mem.*, 67(1):941-1010.
- BROWN, F. A., JR., 1957. The rhythmic nature of life. In *Recent Advances in Invertebrate Physiology*, edited by B. T. Scheer et al.; pp. 287-304. Univ. of Oregon Publ., Eugene, Oregon.
- BRUST, H. F., and C. L. NEWCOMBE, 1940. Observations on the alkalinity of estuarine waters of the Chesapeake Bay near Solomons Island, Maryland. *J. Marine Res.*, 3:105-111.
- BRUUN, P. M. ASCE, and F. GERRITSEN, 1958. Stability of coastal inlets. *J. Waterways and Harbors Div., Proc. Am. Soc. Civil Engrs.*, Paper 1644 (WW3): 1-49.
- BULLOCK, T. H., 1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. *Behavior*, 5:130-140.
- BULLOCK, T. H., 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.*, 30:311-342.
- BULLOCK, T. H., 1958. Homeostatic mechanisms in marine organisms. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 199-210. Univ. Calif. Press, Berkeley, California.
- BURBANK, W. D., M. E. PIERCE, and G. C. WHITELEY, JR., 1956. A study of the bottom fauna of Rand's Harbor, Massachusetts: an application of the ecotone concept. *Ecol. Monographs*, 26:213-243.
- BURCH, J. B., 1960. Chromosome studies of aquatic pulmonate snails. *Nucleus*, 3:177-208.
- BURKHOLDER, P. R., 1963. Some nutritional relationships among microbes of sea sediments and waters. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 133-150. Charles C. Thomas, Springfield, Illinois.
- BURT, W. V., 1955. Distribution of suspended materials in Chesapeake Bay. *J. Marine Res.*, 11:47-62.
- BUZZATI-TRAVERSO, A. A., 1958. Perspectives in marine biology. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 613-621. Univ. Calif. Press, Berkeley, California.
- BUZZATI-TRAVERSO, A. A., and A. B. RECHNITZER, 1953. Paper partition chromatography in taxonomic studies. *Science*, 117:58-59.
- CARPENTER, J. H., 1957. A study of some major cations in natural waters. *Tech. Rept. XI, Chesapeake Bay Inst., Ref. 57-7*, pp. 1-80.
- CARPENTER, J. H., and D. G. CARGO, 1957. Oxygen requirement and mortality of the blue crab in the Chesapeake Bay. *Tech. Rept. 13, Chesapeake Bay Inst., Ref. 57-2*, pp. 1-22.
- CARRIKER, M. R., 1951a. Observations on the penetration of tightly closing bivalves by *Buoycon* and other predators. *Ecology*, 32:73-83.
- CARRIKER, M. R., 1951b. Ecological observations on the distribution of oyster larvae in New Jersey estuaries. *Ecol. Monographs*, 21:19-38.
- CARRIKER, M. R., 1955a. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. *U. S. Fish Wildlife Serv., Spec. Sci. Rept. Fisheries* No. 148, pp. 1-150.
- CARRIKER, M. R., 1955b. Seasonal vertical movements of oyster drills (*Urosalpinx cinerea*). *Proc. Nat. Shellfisheries Assoc.*, 45:190-198.
- CARRIKER, M. R., 1957. Preliminary study of behavior of newly hatched oyster drills, *Urosalpinx cinerea* (Say). *J. Elisha Mitchell Sci. Soc.*, 73:328-351.
- CARRIKER, M. R., 1959. The role of physical and biological factors in the culture of *Crassostrea* and *Mercenaria* in a salt-water pond. *Ecol. Monographs*, 29: 219-266.
- CARRIKER, M. R., 1961a. Use of a floating laboratory for ecological estuarine research. *Ward's Nat. Sci. Bull.*, 34:3-7, 26-27.
- CARRIKER, M. R., 1961b. Interrelation of functional morphology, behavior, and autecology in early stages of the bivalve *Mercenaria mercenaria*. *J. Elisha Mitchell Sci. Soc.*, 77:168-241.
- CARRIKER, M. R., 1963. Suspended sediment as a factor in the ecology of the marine snail *Urosalpinx cinerea*. In *Research Problems in Biology: Investigations for Students*; Ser. 2, pp. 51-60. Anchor Books, Doubleday and Co., New York.
- CARRITT, D. E., and S. GOODGAL, 1954. Sorption reactions and some ecological implications. *Deep-Sea Res.*, 1:224-243.
- CARRITT, D. E., and J. H. HARLEY, 1957. Precipitation of fission product elements on the ocean bottom by physical, chemical, and biological processes. In *The Effects of Atomic Radiation on Oceanography and Fisheries*. Nat. Acad. Sci.-Nat. Res. Council Publ. 551:60-68.
- CARTER, G. S., 1961. Evolution in the deep seas. In *Oceanography*, edited by Mary Sears; Publ. No. 67, pp. 229-237. American Association for the Advancement of Science, Washington, D. C.
- CASPERS, H., 1948. Ökologische Untersuchungen über die Wattentierwelt im Elbe-Estuari. *Verhandl. Deut. Zool. Kiel* 1948, pp. 350-359.
- CASPERS, H., 1954. Biologische Untersuchungen über die Lebensräume der Untereile und des Vormündungsgebietes des Nordsee. *Mitt. Geol. Staatsinst. Hamburg*, 23:76-85.
- CHAPMAN, G., 1949. The thixotropy and dilatancy of a marine soil. *J. Marine Biol. Assoc. U. K.*, 28:123-140.
- CHAPMAN, G., and G. E. NEWELL, 1949. The distribution of lugworms (*Arenicola marina* L.) over the flats at Whitstable. *J. Marine Biol. Assoc. U. K.*, 28: 627-634.
- CHAPMAN, V. J., 1961. *Salt Marshes and Salt Deserts of the World*. Interscience Ser., New York.
- CLARKE, G. L., 1954. *Elements of Ecology*. John Wiley and Sons, New York.
- CLARKE, G. L., and H. R. JAMES, 1939. Laboratory analysis of the selective absorption of light by sea water. *J. Opt. Soc. Am.*, 29:43-55.
- CLARKE, G. L., and R. H. OSTER, 1934. The penetration of the blue and red components of daylight into Atlantic coastal waters and its relation to phytoplankton metabolism. *Biol. Bull.*, 67:59-75.
- CLARK, J. R., and R. L. CLARK (Editors), 1964. Seawater systems for experimental aquaria. A collection of papers. *U. S. Fish Wildlife Serv., Res. Rept. No. 63*:1-192.
- COE, W. R., 1957. Fluctuations in littoral populations. *Geol. Soc. Am. Mem.* 67(1): 935-939.
- COLE, H. A., and E. W. KNIGHT-JONES, 1949. The setting behaviour of larvae of the European flat oyster *Ostrea edulis* L., and its influence on methods of culti-

- vation and spat collection. *Gt. Brit. Min. Agr. Fisheries. Fisheries Invest. Ser. 2*, 17:1-39.
- COLE, L. C., 1954. The population consequences of life history phenomena. *Quart. Rev. Biol.*, 29:103-137.
- COLLIER, A., 1953. On the significance of organic compounds in sea water. *Trans. 18th N. Am. Wildlife Conf.*, 1953; pp. 463-472.
- COLLIER, A., and J. W. HEDGPETH, 1950. An introduction to the hydrography of tidal waters of Texas. *Publ. Inst. Marine Sci. Texas*, 1:121-194.
- CONOVER, J. T., 1962. Algal crusts and the formation of lagoon sediments. In *Symposium on the Environmental Chemistry of Marine Sediments*, edited by N. Marshall; Occ. Publ. No. 1; pp. 69-76. Univ. Rhode Island, Kingston, Rhode Island.
- COOPER, L. H. N., and A. MILNE, 1938. The ecology of the Tamar Estuary. II. Underwater illumination. *J. Marine Biol. Assoc. U. K.*, 22:509-527.
- COSTLOW, J. D., JR., and C. G. BOOKHOUT, 1958. Larval development of *Balanus amphitrite* var. *denticulata* Broch reared in the laboratory. *Biol. Bull.*, 114:284-295.
- COSTLOW, J. D., JR., and C. G. BOOKHOUT, 1959. The larval development of *Callianectes sapidus* Rathbun reared in the laboratory. *Biol. Bull.*, 116:373-396.
- COSTLOW, J. D., JR., and C. G. BOOKHOUT, 1961. The larval development of *Eurypanopis depressus* (Smith) under laboratory conditions. *Crustaceana*, 2:6-15.
- COX, R. A., 1963. The salinity problem. *Progr. Oceanogr.*, 1:243-261.
- CRISP, D. J., and P. S. MEADOWS, 1962. The chemical basis of gregariousness in cirripedes. *Proc. Roy. Soc. London Ser. B*, 136(965):500-520.
- CUMMINS, K. W., 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *Am. Midland Naturalist*, 67:477-504.
- DAKIN, W. J., 1909. Pecten. The edible scallop. *Liverpool Marine Biol. Comm., L.M.B.C. Mem.*, 17:333-468. (*Proc. Trans. Liverpool Biol. Soc.*, 23:1-136).
- DALES, R. P., 1957. Interrelations of organisms. A. Commensalism. *Geol. Soc. Am. Mem.*, 67(1):391-412.
- DANSEREAU, P., 1947. Zonation et succession sur la Restinga de Rio de Janeiro: I. Halosère. *Rev. Can. Biol.*, 6:448-477.
- DANSEREAU, P., 1957. *Bioogeography: an ecological perspective*. The Ronald Press Co., New York.
- DAVENPORT, D., 1955. Specificity and behavior in symbioses. *Quart. Rev. Biol.*, 30:29-46.
- DAVIS, F. M., 1925. Quantitative studies on the fauna of the sea bottom. 2. Results of the investigation in the southern North Sea, 1921-1924. *Gt. Brit. Fisheries Invest. Ser. 2*, 8(4):1-50.
- DAY, J. H., 1951. The ecology of South African estuaries. Part I. A review of estuarine conditions in general. *Trans. Roy. Soc. S. Africa*, 33:53-91.
- DAY, J. H., 1959. The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. *Trans. Roy. Soc. S. Africa*, 35:475-547.
- DAY, J. H., 1964. The origin and distribution of estuarine animals in South Africa. *Monograph. Biol.*, 10:159-173. (Den Haag).
- DAY, J. H., and J. E. C. MORGANS, 1956. The ecology of South African estuaries. Part VIII. The biology of Durban Bay. *Ann. Nat. Museum*, 13:259-312.
- DAY, J. H., N. A. H. MILLARD, and A. D. HARRISON, 1952. The ecology of South African estuaries. Part III. Knysna: a clear open estuary. *Trans. Roy. Soc. S. Africa*, 33:367-413.
- DE BLOK, J. W., J. HANNIE, and F. M. GEELEN, 1959. The substratum required for the settling of mussels (*Mytilus edulis* L.). *Arch. Neerl. Zool., Suppl. 1 to 13*:446-460.
- DEHNEL, P. A., 1955. Rates of growth of gastropods as a function of latitude. *Physiol. Zool.*, 28:115-144.
- DENDY, J. S., 1944. The fate of animals in stream drift when carried into lakes. *Ecol. Monographs*, 14:333-357.
- DEXTER, R. W., 1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: a study in bioecology. *Ecol. Monographs*, 17:261-294.
- DORSEY, E. N., 1940. *Properties of ordinary water substances—in all its phases: water vapor, water, all the ices*. A. C. S. Monograph No. 81. Reinhold Pub. Corp., New York.
- DOTY, M. S., 1957. Rocky intertidal surfaces. *Geol. Soc. Am. Mem.*, 67(1):535-585.
- DRACH, P., 1948. Premières recherches en scaphandre autonome sur le peuplement des facies rocheux de la zone littorale profonde. *C. R. Acad. Sci. Paris*, 227:1176-1178.
- DRACH, P., 1958. Perspectives in the study of benthic fauna of the continental shelf. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 33-46. Univ. Calif. Press, Berkeley, California.
- DROST-HANSEN, W., 1956. Temperature anomalies and biological temperature optima in the process of evolution. *Naturwissenschaften*, 43:512.
- DUNBAR, M. J., 1960. The evolution of stability in marine environments. Natural selection at the level of the ecosystem. *Am. Naturalist*, 94:129-136.
- EDGE, E. R., 1934. Faecal pellets of some marine invertebrates. *Am. Midland Naturalist*, 15:78-84.
- EHRLICH, P. R., and R. W. HOLM, 1962. Patterns and populations. Basic problems of population biology transcend artificial disciplinary boundaries. *Science*, 137(3531):652-657.
- ELTON, C. S., 1927. *Animal Ecology* (1962, 9th Impression). Sidgwick and Jackson, London.
- ELTON, C. S., 1946. Competition and the structure of ecological communities. *J. Animal Ecol.*, 15:54-68.
- ELTON, C. S., 1958. *The Ecology of Invasions by Animals and Plants*. Methuen and Co., London.
- EMERY, K. O., and R. E. STEVENSON, 1957a. Estuaries and lagoons. I. Physical and chemical characteristics. *Geol. Soc. Am. Mem.*, 67(1):673-693.
- EMERY, K. O., and R. E. STEVENSON, 1957b. Estuaries and lagoons. III. Sedimentation in estuaries, tidal flats and marshes. *Geol. Soc. Am. Mem.*, 67(1):729-749.
- ENGELMANN, M. D., 1961. The role of soil arthropods in the energetics of an old field community. *Ecol. Monographs*, 31:221-238.
- ERDMAN, J. G., E. M. MARLETT, and W. E. HANSON, 1956. Survival of amino acids in marine sediments. *Science*, 124(3230):1026.
- FAGER, E. W., 1957. Determination and analysis of recurrent groups. *Ecology*, 38:586-595.
- FAGER, E. W., 1963. Communities of organisms, composition of sea water, comparative and descriptive oceanography. In *The Sea*, edited by M. N. Hill; vol. 2, pp. 415-437. Interscience, New York.
- FASSETT, N. C., 1928. The vegetation of the estuaries of northeastern North America. *Proc. Boston Soc. Nat. Hist.*, 39:73-130.
- FAURÉ-FREMIET, E., 1951a. The marine sand-dwelling cliates of Cape Cod. *Biol. Bull.*, 100:59-70.
- FAURÉ-FREMIET, E., 1951b. The tidal rhythm of the diatom *Hantzschia amphioxys*. *Biol. Bull.*, 100:173-177.
- FELL, J. W., and N. VANT'DEN, 1953. Yeasts in marine environments. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 329-340. Charles C. Thomas, Springfield, Illinois.
- FISCHER, A. G., 1961. Latitudinal variations in organic diversity. *Am. Scientist*, 49:50-74.
- FISCHER-PIETTE, E., 1931. Sur la pénétration des diverses espèces marines sessiles dans les estuaires et sa limitation par l'eau douce. *Ann. Inst. Océanogr. Monaco* n. s., 10:213-243.
- FLEMING, C. A., 1950. The molluscan fauna of the fjords of western Southland, New Zealand. *J. Sci. Tech.*, 31, Sect. B:20-40.

- FORSTER, G. R., 1953. A new dredge for collecting burrowing animals. *J. Marine Biol. Assoc. U. K.*, 32: 193-198.
- FORSTER, G. R., 1954. Preliminary note on a survey of stoke point rocks with self-contained diving apparatus. *J. Marine Biol. Assoc. U. K.*, 33: 341-344.
- FOX, A. S., 1950. Comparative metabolism of organic detritus by inshore animals. *Ecology*, 31: 100-108.
- FOX, A. S., 1956. Application of paper chromatography to taxonomic studies. *Science*, 123: 143.
- FOX, D. L., 1957. Particulate organic detritus. *Geol. Soc. Am. Mem.* 67(1): 383-389.
- FOX, D. L., S. C. CRANE, and B. H. McCONAUGHEY, 1948. A biochemical study of the marine annelid worm, *Thoracophelia mucronata*, its food, biochromes, and carotenoid metabolism. *J. Marine Res.*, 7: 567-585.
- FOX, D. L., F. D. ISAACS, and E. F. CORCORAN, 1952. Marine leptocephal, its recovery, measurement and distribution. *J. Marine Res.*, 11: 29-46.
- FRAENKEL, G. S., and D. L. GUNN, 1961. *The Orientation of Animals; Kineses, Taxes and Compass Reactions*. Dover Publ., New York.
- FRIEDRICH, H., 1961. Physiological significance of light in marine ecosystems. In *Oceanography*, edited by Mary Sears; Publ. No. 67, pp. 257-270. American Association for the Advancement of Science, Washington, D. C.
- GAARDER, T., and R. SPÄRCK, 1933. Hydrographisch-biochemische Untersuchungen in Norwegischen Austern-Pollen. Bergens Mus. Aarb. 1932. *Naturv. tek.*, 1: 1-144.
- GALTSCOFF, P. S., 1964. The American oyster *Cassostrea virginica* Gmelin. *U. S. Fish and Wildlife Serv. Fishery Bull.*, 62: 1-480.
- GISLÉN, T., 1930. Epibioses of the Gullmar Fjord, I. II. *Kristinebergs Zoologiska Station 1877-1927*, Nos. 3, 4.
- GISLÉN, T., 1944. Physiographical and ecological investigations concerning the littoral of the northern Pacific. II-IV. Regional conditions of the Pacific Coast of America and their significance for the development of marine life. *Lunds Univ. Arsskrift*, N. F. (2), 40 (8): 1-91.
- GLOVER, R. S., 1961. Biogeographical boundaries: the shapes of distribution. In *Oceanography*, edited by Mary Sears; Publ. No. 67, pp. 201-228. American Association for the Advancement of Science, Washington, D. C.
- GLYNN-WILLIAMS, J., and J. HOBART, 1952. Studies on the crevice fauna of a selected shore in Anglesey. *Proc. Zool. Soc. London*, 122: 797-824.
- GOREAU, T. F., and W. D. HARTMAN, 1963. Boring sponges as controlling factors in the formation and maintenance of coral reefs. In *Mechanisms of Hard Tissue Destruction*, edited by R. F. Sognnaes; Publ. No. 75, pp. 25-54. American Association for the Advancement of Science, Washington, D. C.
- GORSLINE, D. S., 1962. *Proceedings of the First National Coastal and Shallow Water Conference, October 1961 (Baltimore, Tallahassee, Los Angeles)*, sponsored by Nat. Sci. Found. and Office Naval Res., Tallahassee, Florida.
- GRAHAM, A., 1957. The molluscan skin with special reference to prosobranchs. *Proc. Malacological Soc. London*, 32: 135-144.
- GRAVE, C., 1905. Investigations for the promotion of the oyster industry of North Carolina. *Rept. U. S. Fish Comm. for 1903*, pp. 247-327.
- GRIM, R. E., 1953. *Clay Mineralogy*. McGraw-Hill Co., New York.
- GUILCHER, A., 1958. *Coastal and submarine morphology*. Translation by B. W. Sparks and R. H. W. Kneese. John Wiley and Sons, New York.
- GUNKEL, W., and C. H. OPPENHEIMER, 1963. Experiments regarding the sulfide formation in sediments of the Texas Gulf Coast. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 674-684. Charles C. Thomas, Springfield, Illinois.
- GUNNERSON, C. G., 1963. Mineralization of organic matter in Santa Monica Bay, California. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 641-653. Charles C. Thomas, Springfield, Illinois.
- GUNTER, G., 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. *Unit. Texas Inst. Marine Sci. Publ.* 1(2): 7-51.
- GUNTER, G., 1961. Some relations of estuarine organisms to salinity. *Limnol. Oceanog.* 6: 182-190.
- HAIRSTON, N. G., 1959. Species abundance and community organization. *Ecology*, 40: 404-416.
- HAMMEN, C. S., 1964. Carbon dioxide fixation in marine invertebrates: a review. In *Symposium on Experimental Marine Ecology*; Occ. Publ. No. 2, pp. 48-50. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- HÄNTZSCHEL, W., 1955. Tidal flat deposits (watterschlick). In *Recent Marine Sediments, a Symposium*, edited by P. D. Trask. Soc. Econ. Paleontologists Mineralogists Spec. Publ. 4: 195-206.
- HARDY, A. C., 1958. Toward prediction in the sea. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso. Univ. Calif. Press, Berkeley, California.
- HARTLEY, P. H. T., 1940. The Saltash tuck-net fishery and the ecology of some estuarine fishes. *J. Marine Biol. Assoc. U. K.*, 24: 1-58.
- HARTLEY, P. H. T., 1947. Observations on flounders *Pleuronectes flesus* L. marked in the estuaries of the Tamar and Lynher. *J. Marine Biol. Assoc. U. K.*, 27: 53-64.
- HARVEY, H. W., 1955. *The Chemistry and fertility of sea waters*. Cambridge Univ. Press, Cambridge, England.
- HASKIN, H. H., 1964. The distribution of oyster larvae. In *Symposium on Experimental Marine Ecology*; Occ. Publ. No. 2; pp. 76-80. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- HAAS, H., 1948. Beitrag zur Kenntnis der Reteporiden mit besonderer Berücksichtigung der Formbildungsge setze ihrer Zoarien und einem Bericht (1948) über die dabei angewandte neue Methode für Untersuchungen auf dem Meersgrund. *Zoologica (Stuttgart)* 37: 1-138.
- HATHAWAY, J. C., and E. C. ROBERTSON, 1961. Microtexture of artificially consolidated argonitic mud. *U. S. Geol. Surv. Prof. Paper* 424-C: 301-304.
- HAYES, F. R., 1964. The mud-water interface. *Oceanog. Marine Biol. Ann. Rev.*, 2: 121-145.
- HAYES, H. L., and T. S. AUSTIN, 1951. The distribution of discolored sea water. *Texas J. Sci.*, 3: 530-541.
- HEDGPETH, J. W., 1951. The classification of estuarine and brackish waters and the hydrographic climate. *Rept. Comm. on a treatise on marine ecology and paleoecology No. 11*: 49-56. Nat. Res. Council, Div. Geol. Geogr., Washington, D. C.
- HEDGPETH, J. W., 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Publ. Inst. Marine Sci. Texas*, 3: 109-224.
- HEDGPETH, J. W., 1957a. Introduction. *Geol. Soc. Am. Mem.* 67(1): 1-16.
- HEDGPETH, J. W., 1957b. Concepts of marine ecology. *Geol. Soc. Am. Mem.* 67(1): 29-52.
- HEDGPETH, J. W., 1957c. Obtaining ecological data in the sea. *Geol. Soc. Am. Mem.* 67(1): 53-86.
- HEDGPETH, J. W., 1957d. Sandy beaches. *Geol. Soc. Am. Mem.* 67(1): 587-608.
- HEDGPETH, J. W., 1957e. Estuaries and lagoons. II. Biological aspects. *Geol. Soc. Am. Mem.* 67(1): 693-729.
- HEDGPETH, J. W., 1961. Taxonomy: man's oldest profession. Lecture. 11th Ann. Univ. Pacific Faculty Res.

- HESSE, R., W. C. ALLEE, and K. P. SCHMIDT, 1951. *Ecological animal geography*, 2nd ed. John Wiley and Sons, New York.
- HEVESY, G., 1956. Path of atoms through generations. *Sci. Monthly*, 83:238-241.
- HEWATT, W. G., 1935. Ecological succession in the *Mytilus californianus* habitat as observed in Monterey Bay, California. *Ecology*, 16:244-251.
- HEWATT, W. G., 1937. Ecological studies on selected marine intertidal communities of Monterey Bay, California. *Am. Midland Naturalist*, 18:161-206.
- HITE, M. P., 1924. Some observations of storm effects on ocean inlets. *Am. J. Sci. Ser. 5/7*, 319-326.
- HJULSTRÖM, F., 1955. Transportation of detritus by moving water. In *Recent Marine Sediments, a Symposium*, edited by P. D. Trask. Soc. Econ. Paleontologists Mineralogists Spec. Publ. No. 4:5-31.
- HOLME, N. A., 1949. The fauna of sand and mud banks near the mouth of the Exe Estuary. *J. Marine Biol. Assoc. U. K.*, 28:198-237.
- HOLME, N. A., 1964. Methods of sampling the benthos. *Adv. Mar. Biol.*, 2:171-260.
- HOOD, D. W., 1963. Chemical oceanography. *Oceanogr. Marine Biol. Ann. Rev.*, 1:129-155.
- HOPKINS, S. H., 1957. Notes on the boring sponges in Gulf Coast estuaries and their relation to salinity. *Bull. Marine Sci. Gulf Caribbean*, 6:44-58.
- HOPKINS, S. H., 1958. The planktonic larvae of *Polydora websteri* Hartman (Annelida, Polychaeta) and their settling on oysters. *Bull. Marine Sci. Gulf Caribbean*, 8:268-277.
- HOPKINS, S. H., 1962. Distribution of species of *Cliona* (boring sponge) on the eastern shore of Virginia in relation to salinity. *Chesapeake Sci.*, 3:121-124.
- HOPKINS, T. L., 1964. A survey of marine bottom samplers. *Progr. Oceanogr.*, 2:213-256.
- HULBURT, E. M., 1957. The distribution of *Neomysis americana* in the estuary of the Delaware River. *Limnol. Oceanogr.*, 2:1-11.
- HUNTER, J. F., 1912. Erosion and sedimentation in Chesapeake Bay around the mouth of Choptank River. *U. S. Geol. Surv. Prof. Paper* 90-B.
- HUNTER, R. W., 1964. Physiological aspects of ecology in nonmarine molluscs. II. Estuarine molluscs. In *Physiology of Mollusca*, edited by K. M. Wilbur and C. M. Yonge; vol. 1, pp. 84-85. Academic Press, New York.
- HUTCHINSON, G. E., 1953. The concept of pattern in ecology. *Proc. Acad. Nat. Sci. Phila.*, 105:1-12.
- HUTCHINSON, G. E., 1957. *A Treatise on Limnology*. Vol. I. Geography, Physics, and Chemistry. John Wiley and Sons, New York.
- HUTCHINSON, G. E., 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *Am. Naturalist*, 93:145-159.
- IMAI, T., M. HATANAKA, R. SATO, and S. SAKAI, 1951. Ecology of Mangoku-Ura Inlet with special reference to the seed-oyster production. *Sci. Rept. Res. Inst. Tohoku Univ. D.* 1-2:137-156.
- INGLE, R. M., 1962. Potential research benefits to be derived from estuarine heterogeneity. *Tulane Studies Zool.* 9:295-299.
- INMAN, D. I., 1949. Sorting of sediments in the light of fluid mechanics. *J. Sediment. Petrol.*, 19:51-70.
- ITO, S., and T. IMAI, 1955. Ecology of oyster bed. I. On the decline of productivity due to repeated cultures. *Tohoku J. Agr. Res.*, 5:251-268.
- JANSSON, B., 1962. Salinity resistance and salinity preference of two oligochaetes *Aktedrilus monospermatocerus* Knöller and *Marionina precitellochaeta* n. sp. from the interstitial fauna of marine sandy beaches. *Oikos*, 13:293-305.
- JEFFRIES, H. P., 1962. The atypical phosphate cycle of estuaries in relation to benthic metabolism. In *The Environmental Chemistry of Marine Sediments*, edited by N. Marshall; Occ. Publ. No. 1:58-68. Narragansett Marine Labs, Univ. Rhode Island, Kingston, Rhode Island.
- JITTS, H. R., 1959. The adsorption of phosphate by estuarine bottom deposits. *Australian J. Marine Freshwater Res.*, 10:7-21.
- JOHNSON, I. S., 1952. The demonstration of a "host-factor" in commensal crabs. *Trans. Kansas Acad. Sci.*, 55:458-464.
- JOHNSON, M. W., 1939. The correlation of water movement and dispersal of pelagic larval stages of certain littoral animals especially the sandcrab, *Emerita*. *J. Marine Res.*, 2:236-245.
- JOHNSON, R. G., 1965. Temperature variation in the infaunal environment of a sand flat. *Limnol. Oceanogr.*, 10:114-120.
- JOHNSON, T. W., and F. K. SPARROW, 1961. *Fungi in Oceans and Estuaries*. Hafner Publ. Co., New York.
- JOHNSTON, R., 1955. Biologically active compounds in the sea. *J. Marine Biol. Assoc. U. K.*, 34:185-195.
- JOHNSTON, R., 1964. Recent advances in the estimation of salinity. *Oceanogr. Marine Biol. Ann. Rev.*, 2:97-120.
- JONASSON, P. M., 1955. The efficiency of sieving techniques for sampling freshwater bottom fauna. *Oikos*, 6:183-207.
- JONES, N. S., 1950. Marine bottom communities. *Biol. Rev.*, 25:283-313.
- KANWISHER, J. W., 1955. Freezing in intertidal animals. *Biol. Bull.*, 109:56-63.
- KANWISHER, J. W., 1957. Freezing and drying in intertidal algae. *Biol. Bull.*, 113:275-285.
- KANWISHER, J. W., 1959. Histology and metabolism of frozen intertidal animals. *Biol. Bull.*, 116:258-264.
- KANWISHER, J. W., 1962. Gas exchange of shallow marine sediments. In *The Environmental Chemistry of Marine Sediments*, edited by N. Marshall; Occ. Publ. 1:13-19. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- KETCHUM, B. H., 1951. The exchanges of fresh and salt waters in tidal estuaries. *J. Marine Res.*, 10:18-38.
- KETCHUM, B. H., 1954. The relation between circulation and planktonic populations in estuaries. *Ecology*, 35:191-200.
- KINNE, O., 1956. Über den Einfluss des Salzgehaltes und der Temperatur auf Wachstum, Form und Vermehrung bei dem Hydrozoopoden *Cordylophora caspia* (Pallas). Thecata, Clavidae. *Zool. Jahrb. Abt. Physiol.*, 66:565-638.
- KINNE, O., 1958. Adaptation to salinity variations—some facts and problems. *Physiological adaptations*; pp. 92-106. Am. Physiol. Soc., Washington, D. C.
- KINNE, O., 1963a. Salinity, osmoregulation, and distribution in macroscopic crustacea. In *Marine Distributions*, edited by M. J. Dunbar; Roy. Soc. Canada Spec. Publ. No. 5:95-105.
- KINNE, O., 1963b. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanogr. Marine Biol. Ann. Rev.*, 1:301-340.
- KINNE, O., 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. *Oceanogr. Marine Biol. Ann. Rev.*, 2:281-339.
- KIRK, R. L., A. R. MAIN, and F. G. BEYER, 1954. The use of paper partition chromatography for taxonomic studies of land snails. *Biochem. J.*, 57:440-442.
- KLOPFER, P. H., 1962. *Behavioral aspects of ecology*. Prentice-Hall, Englewood Cliffs, New Jersey.
- KLOTZ, I. M., 1962. Water. In *Horizons in Biochemistry*, edited by Pullman and Kasha; Albert Szent-Gyorgyi dedicatory volume. Academic Press, New York.
- KNIGHT-JONES, E. W., and J. MOYSE, 1961. Intraspecific competition in sedentary marine animals. In *Mechanisms in Biological Competition*, Symp. Soc. Exptl. Biol.
- KNIGHT-JONES, E. W., and J. P. STEPHENSON,

1950. Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *J. Marine Biol. Assoc. U. K.*, 29:281-297.
- KOHLMEYER, J., 1963. The importance of fungi in the sea. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 300-314. Charles C. Thomas, Springfield, Illinois.
- KOHN, A. J., 1958. Problems of speciation in marine invertebrates. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 571-588. Univ. Calif. Press, Berkeley, California.
- KOHN, A. J., 1961. Chemoreception in gastropod mollusks. *Am. Zool.*, 1:291-308.
- KOHN, A. J., 1964. Mollusks. *Science*, 145:518-519.
- KOHN, A. J., and G. H. ORIANS, 1962. Ecological data in the classification of closely related species. *Systematic Zool.*, 11:119-127.
- KORRINGA, P., 1941. Experiments and observations on swarming, pelagic life and setting in the European flat oyster, *Ostrea edulis* L. *Arch. Neerl. Zool.*, 5:1-249.
- KORRINGA, P., 1951. The shell of *Ostrea edulis* as a habitat. *Arch. Neerl. Zool.*, 10:31-152.
- KORRINGA, P., 1952. Recent advances on oyster biology. *Quart. Rev. Biol.*, 27:266-308, 339-365.
- KORRINGA, P., 1957. On the supposed compulsory relation between oviparous oysters and waters of reduced salinity. *Ann. Biol.*, 61, Ser. 33:109-116.
- KUENEN, P. H., 1950. *Marine Geology*. John Wiley and Sons, New York.
- KURZ, H., and K. WAGNER, 1957. *Tidal marshes of the Gulf and Atlantic coasts of northern Florida and Charleston, South Carolina*. Studies No. 24, Florida State Univ., Tallahassee, Florida.
- LAEVASTU, T., and R. H. FLEMING, 1959. Chlorinity of the interstitial waters in sediments from Lake Washington Ship Canal and the flow of fresh and salt water through the sediments. In *International Oceanographic Congress—Preprints*, edited by Mary Sears; pp. 967-969. American Association for the Advancement of Science, Washington, D. C.
- LANDERS, W. S., 1954. Seasonal abundance of clam larvae in Rhode Island waters, 1950-52. *U. S. Fish & Wildl. Serv. Spec. Sci. Rept.—Fish.* No. 117:1-29.
- LEWIN, J. C., 1963. Heterotrophy in marine diatoms. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 229-235. Charles C. Thomas, Springfield, Illinois.
- LIGHT, V. E., 1930. Photoreceptors in *Mya arenaria* with special reference to their distribution, structure, and function. *J. Morph.* 49:1-41.
- LINDBLOM, G. P., 1963. The distribution of major organic nutrients in marine sediments. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 205-212. Charles C. Thomas, Springfield, Illinois.
- LINKE, O., 1939. Die Biota des Jadebusenwattes. *Holgaarders Wiss. Meeresuntersuch.*, 1:201-348.
- LONGHURST, A. R., 1964. A review of the present situation in benthic synecology. *Bull. Inst. Oceanogr. Monaco*, 63(1317):1-54.
- LOOSANOFF, V. L., 1945. Effects of sea water of reduced salinities upon starfish, *Asterias forbesi*, of Long Island Sound. *Trans. Conn. Acad. Arts Sci.*, 36:813-835.
- LOOSANOFF, V. L., 1958. Challenging problems in shellfish biology. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 483-495. Univ. Calif. Press, Berkeley, California.
- LOOSANOFF, V. L., and H. C. DAVIS, 1963. Rearing of bivalve mollusks. *Advan. Marine Biol.*, 1:1-136.
- LOOSANOFF, V. L., and C. A. NOMEJKO, 1951. Existence of physiologically different races of oysters, *Crassostrea virginica*. *Biol. Bull.*, 101:151-156.
- LOOSANOFF, V. L., J. B. ENGLE, and C. A. NOMEJKO, 1955. Differences in intensity of setting of oysters and starfish. *Biol. Bull.*, 109:75-81.
- LOOSANOFF, V. L., W. S. MILLER, and P. B. SMITH, 1951. Growth and setting of larvae of *Venus mercenaria* in relation to temperature. *J. Marine Res.*, 10:59-81.
- LUCAS, C. E., 1947. The ecological effects of external metabolites. *Biol. Rev.*, 22:270-295.
- LUCAS, C. E., 1949. External metabolites and ecological adaptation. In *Selective Toxicity and Antibiotics. Symp. Soc. Exptl. Biol.*, 3:336-356.
- LUCAS, C. E., 1955. External metabolites in the sea. *Papers Marine Biol. Oceanogr. Deep-Sea Res., Suppl. to vol. 3*, pp. 139-148.
- LUCAS, C. E., 1961. Interrelationships between aquatic organisms mediated by external metabolites. In *Oceanography*, edited by Mary Sears; Publ. No. 67, pp. 499-517. American Association for the Advancement of Science, Washington, D. C.
- LUND, E. J., 1957. Self-silting by the oyster and its significance for sedimentation geology. *Publ. Inst. Marine Sci., Texas*, 4(2):320-327.
- LUNDBECK, J., 1926. Die Bodentierwelt Norddeutscher Seen. *Arch. Hydrobiol. Suppl.* 7, pp. 1-473.
- LYMAN, J., and R. H. FLEMING, 1940. Composition of sea water. *J. Marine Res.*, 3:134-146.
- LYNCH, W. F., 1959. Factors influencing metamorphosis of larvae of some of the sessile organisms. *Proc. 15th Intern. Congr. Zool., London*, pp. 239-241.
- MAAS GEESTERANUS, R. A., 1942. On the formation of banks by *Mytilus edulis* L. *Arch. Neerl. Zool.*, 6: 283-326.
- MACARTHUR, R., 1955. Fluctuations of animal populations and a measure of community stability. *Ecology*, 36:533-536.
- MACFADYEN, A., 1957. *Animal ecology, aims and methods*. I. Pitman and Sons, London.
- MACFADYEN, A., 1962. Soil arthropod sampling. *Advan. Ecol. Res.*, 1:1-34.
- MACGINITIE, G. E., 1935. Ecological aspects of a California marine estuary. *Am. Midland Naturalist*, 16: 629-765.
- MACGINITIE, G. E., 1945. The size of the mesh openings in mucous feeding nets of marine animals. *Biol. Bull.*, 88:107-111.
- MACKIN, J. G., and S. H. HOPKINS, 1962. Studies on oyster mortality in relation to natural environments and to oil fields in Louisiana. *Publ. Inst. Marine Sci., Univ. Texas*, 7:1-131.
- MACNAE, W., 1956. Aspects of life on muddy shores in South Africa. *South African J. Sci.*, 53:40-43.
- MADSEN, H., 1936. Investigations of the shore fauna of East Greenland with a survey of the shores of other Arctic regions. *Medd. Grönland*, 100:1-79.
- MANNING, J. H., and H. H. WHALEY, 1955. Distribution of oyster larvae and spat in relation to some environmental factors in a tidal estuary. *Proc. Nat. Shellfisheries Assoc.*, 45:56-65.
- MARE, M. F., 1942. A study of a marine benthic community with special reference to the microorganisms. *J. Marine Biol. Assoc. U. K.*, 25:517-554.
- MARMER, H. A., 1926. *The Tide*. D. Appleton and Co., New York.
- MARSHALL, N., 1960. Studies of the Niantic River, Connecticut, with special reference to the bay scallop, *Argyocion irradians*. *Limnol. Oceanogr.*, 5:86-105.
- MAUCHLINE, J., and W. L. TEMPLETON, 1964. Artificial and natural radioisotopes in the marine environment. *Oceanog. Marine Biol. Ann. Rev.*, 2:229-279.
- McDERMOTT, J. J., and F. B. FLOWER, 1952. Preliminary studies of the common mud crabs on oyster beds of Delaware Bay. *Proc. Nat. Shellfisheries Assoc.*, 1952, pp. 47-50.
- McDOUGALL, K. D., 1943. Sessile marine invertebrates of Beaufort, North Carolina. *Ecol. Monograph*, 13: 321-374.
- MCINTOSH, R. P., 1963. Ecosystems, evolution and relational patterns of living organisms. *Am. Scientist*, 51:246-267.

- MCINTYRE, A. D., 1956. The use of trawl, grab, and camera in estimating marine benthos. *J. Marine Biol. Assoc. U. K.*, 35:419-429.
- MCMULTY, J. K., R. C. WORK, and H. B. MOORE, 1962. Some relationships between the infauna of the level bottom and the sediment in South Florida. *Bull. Marine Sci. Gulf Caribbean*, 12:322-332.
- MENARD, H. W., 1950a. Sediment movement in relation to current velocity. *J. Sediment. Petrol.*, 20:148-160.
- MENARD, H. W., 1950b. Transportation of sediment by bubbles. *J. Sediment. Petrol.*, 20:98-106.
- MICHENER, C. D., 1963. Some future developments in taxonomy. *Systematic Zool.*, 12:151-172.
- MILLER, W. R., and F. E. EGLER, 1950. Vegetation of the Wequetequock-Pawcatuck tidal-marshes, Connecticut. *Ecol. Monographs*, 20:143-172.
- MILNE, A., 1938. The ecology of the Tamar Estuary. III. Salinity and temperature conditions in the lower estuary. *J. Marine Biol. Assoc. U. K.*, 22:529-542.
- MILNE, A., 1940a. The ecology of the Tamar Estuary. IV. The distribution of the fauna and flora on buoys. *J. Marine Biol. Assoc. U. K.*, 24:69-87.
- MILNE, A., 1940b. Some ecological aspects of the intertidal area of the estuary of the Aberdeenshire Dee. *Trans. Roy. Soc. Edinburgh*, 60:107-139.
- MIRONOV, S. I., and O. K. BORDOVSKY, 1959. Organic matter in bottom sediments of the Bering Sea. In *International Oceanographic Congress—Preprints*, edited by Mary Sears; pp. 970-972. American Association for the Advancement of Science, Washington, D. C.
- MOORE, H. B., 1930. The muds of the Clyde Sea area. I. Phosphate and nitrogen contents. *J. Marine Biol. Assoc. U. K.*, 16:595-607.
- MOORE, H. B., 1931a. The muds of the Clyde Sea area. III. Chemical and physical conditions; rate and nature of sedimentation and fauna. *J. Marine Biol. Assoc. U. K.*, 17:325-358.
- MOORE, H. B., 1931b. The specific identification of faecal pellets. *J. Marine Biol. Assoc.*, 17:359-365.
- MOORE, H. B., 1931c. The systematic value of a study of molluscan faeces. *Proc. Malacological Soc.*, 19:281-290.
- MOORE, H. B., 1955. Faecal pellets in relation to marine deposits. In *Recent Marine Sediments, a Symposium*, edited by P. D. Trask; Spec. Publ. 4, pp. 516-524. Soc. Econ. Paleontologists Mineralogists.
- MOORE, H. B., 1958. *Marine ecology*. John Wiley and Sons, New York.
- MOORE, D. G., and P. C. SCRUTON, 1957. Minor internal structures of some Recent unconsolidated sediments. *Bull. Am. Assoc. Petrol. Geologists*, 41:2723-2751.
- MORGANS, J. F. C., 1956. Notes on the analysis of shallow-water soft substrata. *J. Animal Ecol.*, 25:367-387.
- MORGANS, J. F. C., 1959. The benthic ecology of False Bay. Part I. The biology of infratidal rocks, observed by diving, related to that of intertidal rocks. *Trans. Roy. Soc. South Africa*, 35:387-442.
- MULLER, C. H., 1958. Science and philosophy of the community concept. *Am. Scientist*, 46:294-308.
- NASH, C. B., 1947. Environmental characteristics of a river estuary. *J. Marine Res.*, 6:147-174.
- NELSON, B. W., 1959. Transportation of colloidal sediment in the freshwater-marine transition zone. In *International Oceanographic Congress—Preprints*, edited by Mary Sears; pp. 640-641. American Association for the Advancement of Science, Washington, D. C.
- NELSON, B. W., 1962. Important aspects of estuarine sediment chemistry for benthic ecology. In *Symposium on the Environmental Chemistry of Marine Sediments*, edited by N. Marshall; Occ. Publ. No. 1, pp. 27-41. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- NELSON, J., 1912. *Rept. Biol. Dept. New Jersey Agr. Expt. Sta.* 1911, pp. 267-309.
- NELSON, J., 1916. Report of the biologist. *Rept. Biol. Dept. New Jersey Agr. Expt. Sta.* 1915, pp. 239-260.
- NELSON, J., 1917. An investigation of oyster propagation in Richmond Bay, Prince Edward Island, during 1915. *Contrib. Can. Biol.*, 1915-1916, pp. 53-78.
- NELSON, T. C., 1926. Report of the Department of Biology. *Rept. Dept. Biol. New Jersey Agr. Expt. Sta.*, 1925, pp. 281-288.
- NELSON, T. C., 1928. Pelagic dissoconchs of the common mussel, *Mytilus edulis*, with observations on the behavior of the larvae of allied genera. *Biol. Bull.*, 55:180-192.
- NELSON, T. C., 1947. Some contributions from the land in determining conditions of life in the sea. *Ecol. Monographs*, 17:337-346.
- NELSON, T. C., and E. B. PERKINS, 1931. Annual report of the department of biology, July 1, 1929-June 30, 1930. *New Jersey Agr. Expt. Sta. Bull.* 522, pp. 1-47.
- NEVIN, C., 1946. Competency of moving water to transport debris. *Bull. Geol. Soc. Am.*, 57:651-674.
- NEWCOMBE, C. L., 1952. Aspects of water pollution study in the California and Great Basin area. *Sci. Monthly*, 74:9-13.
- NEWELL, G. I., 1964. Physiological aspects of the ecology of intertidal molluscs. In *Physiology of Mollusca*, edited by K. M. Wilbur and C. M. Yonge; vol. 1, pp. 59-81. Academic Press, New York.
- NICOL, E. A. T., 1935. The ecology of a salt-marsh. *J. Marine Biol. Assoc. U. K.*, 20:203-261.
- NICOL, J. A. C., 1960. *Biology of marine animals*. Interscience Publ., New York.
- NISHIZAWA, S., M. FUKUDA, and N. INOUE, 1954. Photographic study of suspended matter and plankton in the sea. *Bull. Fac. Hokkaido Univ.*, 5:36-40.
- ODUM, H. T., 1954. Factors controlling marine invasion into Florida fresh waters. *Bull. Marine Sci. Gulf Caribbean*, 3:134-156.
- ODUM, E. P., and H. T. ODUM, 1959. *Fundamentals of Ecology*, 2nd Ed. W. B. Saunders Co., Philadelphia, Pennsylvania.
- ODUM, E. P., and E. J. KUENZLER, 1963. Experimental isolation of food chains in an old field ecosystem with the use of phosphorus-32. In *Radioecology*, edited by V. Schultz and A. W. Klement; pp. 113-120. Reinhold Book Div., Washington, D. C.
- OPPENHEIMER, C. H., 1960. Bacterial activity in sediments of shallow marine bays. *Geochim. Cosmochim. Acta*, 19:244-260.
- OPPENHEIMER, C. H. (Editor), 1963. *Symposium on marine microbiology*. Charles C. Thomas, Springfield, Illinois.
- OPPENHEIMER, C. H., and W. DROST-HANSEN, 1960. A relationship between multiple temperature optima for biological systems and the properties of water. *J. Bacteriol.*, 80:21-24.
- OPPENHEIMER, C. H., and R. A. WARD, 1963. Release and capillary movement of phosphorus in exposed tidal sediments. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 664-673. Charles C. Thomas, Springfield, Illinois.
- OSTENFELD, C. H., 1908. On the ecology and distribution of the grass-wrack (*Zostera marina*) in Danish waters. *Rept. Danish Biol. Sta.*, 16:1-62.
- OWEN, D., 1951. Deep-sea underwater photography and some recent stereoscopic applications. *Photogrammetric Eng.*, 17:13-19.
- PANIKKAR, N. K., 1950. Physiological aspects of adaptation to estuarine conditions. *Proc. Indo-Pacific Fisheries Council, Bangkok*, 1950, Sect. 3:168-177.
- PARKER, R. H., 1955. Changes in the invertebrate fauna, apparently attributable to salinity changes, in the bays of central Texas. *J. Paleonto.*, 29:193-211.
- PARKER, R. H., 1956. Macro-invertebrate assemblages

- as indicators of sedimentary environments in east Mississippi Delta region. *Bull. Am. Assoc. Petro'. Geologists*, 40:295-376.
- PARKER, R. H., 1959. Macro-invertebrate assemblages of central Texas coastal bays and Laguna Madre. *Bull. Am. Assoc. Petro'. Geologists*, 43:2100-2166.
- PARKER, R. H., 1960. Ecology and distributional patterns of marine macro-invertebrates, northern Gulf of Mexico. In *Recent Sediments, Northwest Gulf of Mexico, 1951-1958*; pp. 302-381. Am. Assoc. Petro'. Geologists, Tulsa, Oklahoma.
- PARKER, R. H., 1964a. Zoogeography and ecology of some macro-invertebrates, particularly mollusks, in the Gulf of California and the continental slope off Mexico. *Vidensk. Medd. Dansk Foren.*, 126:1-178.
- PARKER, R. H., 1964b. Zoogeography and ecology of macroinvertebrates of Gulf of California and continental shelf of Western Mexico. In *Marine Geology of the Gulf of California—a Symposium*. Am. Assoc. Petro'. Geologists, Mem. 3: 331-376.
- PARSONS, T. R., 1963. Suspended organic matter in sea water. *Progr. Oceanogr.*, 1:205-239.
- PATRICK, R., 1949. A proposed biological measure of stream conditions, based on a survey of the Conestoga Basin, Lancaster County, Pa. *Proc. Acad. Nat. Sci. Philadelphia*, 101:277-341.
- PEARCY, W. G., 1962. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). *Bull. Bingham Oceanogr. Coll.*, 18:1-78.
- PEARSE, A. S., 1950. *The emigrations of animals from the sea*. Sherwood Press, Dryden, New Jersey.
- PEARSE, A. S., and G. GUNTER, 1957. Salinity. *Geol. Soc. Am. Mem.* 67(1):129-157.
- PEARSE, A. S., H. J. HUMM, and G. W. WHARTON, 1942. Ecology of sand beaches at Beaufort. *Ecol. Monographs*, 12:135-190.
- PEARSON, E. A. (Editor), 1960a. *Proceedings of the First International Conference on Waste Disposal in the Marine Environment*, Univ. Calif., Berkeley, 1957. Pergamon Press, New York.
- PEARSON, E. A., 1960b. Tracer methodology and pollution analysis of estuaries. In *Proceedings of the First International Conference on Waste Disposal in the Marine Environment*, edited by E. A. Pearson; pp. 556-568. Pergamon Press, New York.
- PEQUEGNAT, W. F., 1964. The epifauna of a California siltstone reef. *Ecology*, 45:272-283.
- PERCIVAL, E., 1929. A report on the fauna of the estuaries of the River Tamar and the River Lynher. *J. Marine Biol. Assoc. U. K.*, 16:81-108.
- PÉRES, J. M., 1961. *Océanographie biologique et biologie marine. I. La vie benthique*. Presses Universitaires de France, Paris.
- PETERSEN, C. G. J., 1913. The animal communities of the sea bottom and their importance for marine zoogeography. *Rept. Danish Biol. Sta.*, 21:1-44.
- PLUNKETT, M. A., 1957. The qualitative determination of some organic compounds in marine sediments. *Deep-Sea Res.*, 4:259-262.
- POTTS, W. T. W., 1954. The energetics of osmotic regulation in brackish- and fresh-water animals. *J. Exptl. Biol.*, 31:618-630.
- PRATT, D. M., 1953. Abundance and growth of *Venus mercenaria* and *Callocardia morrhuanus* in relation to the character of bottom sediments. *J. Marine Res.*, 12: 60-74.
- PRATT, D. M., and D. A. CAMPBELL, 1956. Environmental factors affecting growth in *Venus mercenaria*. *Limnol. Oceanogr.*, 1:2-17.
- PRITCHARD, D. W., 1951. The physical hydrography of estuaries and some applications to biological problems. *Trans. 16th North Am. Wildlife Conf.*, 1951, pp. 368-376.
- PRITCHARD, D. W., 1952a. Estuarine hydrography. *Advan. Geophys.*, 1:243-280.
- PRITCHARD, D. W., 1952b. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11:106-123.
- PRITCHARD, D. W., 1953. Distribution of oyster larvae in relation to hydrographic conditions. *Proc. Gulf. Caribbean Fisheries Inst.*, 5th Session, 1952, pp. 123-132.
- PRITCHARD, D. W., 1954. A study of flushing in the Delaware model. *Chesapeake Bay Inst. Tech. Rept.* 7, Ref. 54-5. Johns Hopkins Univ., Baltimore, Maryland.
- PRITCHARD, D. W., 1955. Estuarine circulation patterns. *Proc. Am. Soc. Civil Engrs.*, 81(717):1-11.
- PRITCHARD, D. W., 1960a. The movement and mixing of contaminants in tidal estuaries. In *Proceedings of the First International Conference on Waste Disposal in the Marine Environment*, edited by E. A. Pearson; pp. 512-525. Pergamon Press, New York.
- PRITCHARD, D. W., 1960b. Estuarine oceanography. *McGraw-Hill Encyclopedia Sci. Tech.*, pp. 79-83.
- PROSSER, C. L., 1955. Physiological variation in animals. *Biol. Rev.*, 30:229-262.
- PROSSER, C. L., and F. A. BROWN, Jr., 1961. *Comparative animal physiology, Second Edition*. W. B. Saunders Co., Philadelphia.
- PROVASOLI, L., 1958. Growth factors in unicellular marine algae. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 385-403. Univ. Calif. Press, Berkeley, California.
- PROVASOLI, L., and I. J. PINTNER, 1953. Ecological implications of in vitro nutritional requirements of algal flagellates. *Am. N. Y. Acad. Sci.*, 56:839-851.
- PROVASOLI, L., K. SHIRAISHI, and J. R. LANCE, 1959. Nutritional idiosyncrasies of *Artemia* and *Tigriopus* in monoxenic culture. *Ann. N. Y. Acad. Sci.*, 77: 250-261.
- RAE, K. M., 1958. Parameters of the marine environment. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 3-16. Univ. Calif. Press, Berkeley, California.
- RAGOTSKIE, R. A., L. R. POMEROY, J. M. TEAL, and D. C. SCOTT (Editor), 1959. *Proceedings salt marsh conference held at the Marine Institute of the University of Georgia, Sapelo Island, Georgia, March 25-28, 1958*. Marine Inst. Univ. Georgia, Sapelo Island, Georgia.
- RAY, D. L., 1958. Some marine invertebrates useful for genetic research. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 497-512. Univ. Calif. Press, Berkeley, California.
- RAYMONT, J. E. G., 1949. Further observations on changes in the bottom fauna of a fertilized sea loch. *J. Marine Biol. Assoc. U. K.*, 28:9-19.
- REDEKE, H. C., 1933. Über den jetzigen Stand unserer Kenntnis der Flora und Fauna des Brackwassers. *Verhandl. Intern. Ver. Angew. Limnol.*, 6:46-61.
- REFFIELD, A. C., 1958. The inadequacy of experiment in marine biology. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 17-26. Univ. Calif. Press, Berkeley, California.
- REDFIELD, A. C., and E. S. DEEVY, 1952. Temporal sequences and biotic successions. In *Marine Fouling and its Prevention*; pp. 42-47. Prepared for Bur. Ships, Navy Dept. by Woods Hole Oceanog. Inst., U. S. Naval Inst. Annapolis, Maryland.
- REID, D. M., 1932. Salinity interchange between salt water in sand and overflowing fresh water at low tide. II. *J. Marine Biol. Assoc.*, 18:299-306.
- REID, C. K., 1961. *Ecology of inland waters and estuaries*. Reinhold Publ. Corp., New York.
- REISH, D. J., 1959. A discussion of the importance of the screen size in washing quantitative marine bottom samples. *Ecology*, 40:307-309.
- REISH, D. J., 1961. A study of benthic fauna in a recently constructed boat harbor in southern California. *Ecology*, 42:42-91.
- REMANE, A., 1933. Verteilung und Organisation der benthonischen Mikrofauna der Kieler Bucht. *Wiss. Meeresunters.*, Abt. Kiel, n. f., 21:161-221.

- REMANE, A., 1934. Die Brackwasserfauna. *Zool. Anz.*, Suppl. 7; *Verhandl. Deut. Zool. Ges.*, 36:34-74.
- REMANE, A., 1958. Ökologie des Brackwassers. In *Die Biologie des Brackwassers*, edited by A. Thienemann. *Die Binnengewässer*, 22:1-216.
- RHOADS, D. C., 1963. Rates of sediment reworking by *Yoldia limatula* in Buzzards Bay, Mass., and Long Island Sound. *J. Sediment. Petrol.*, 33:723-727.
- RIEDL, R., 1958. An attempt to test the efficiency of ecological field methods and the validity of their results. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 57-65. Univ. Calif. Press, Berkeley, California.
- RILEY, G. A., 1963. Organic aggregates in seawater and the dynamics of their formation and utilization. *Limnol. Oceanogr.*, 8:372-381.
- RILEY, G. A., 1964. The role of basic sciences in the growth of modern ecology. In *Symposium on Experimental Marine Ecology*; Occ. Publ. No. 2, pp. 5-10. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- ROBERTSON, J. D., 1964. Osmotic and ionic regulation. In *Physiology of Mollusca*, edited by K. M. Wilbur and C. M. Yonge; vol. 1, pp. 283-311. Academic Press, New York.
- ROCHFORD, D. J., 1951. Studies in Australian estuarine hydrology. I. Introductory and comparative features. *Australian J. Marine Freshwater Res.*, 2:1-116.
- ROELOFS, E. W., and D. F. BUMPUS, 1954. The hydrography of Pamlico Sound. *Bull. Marine Sci. Gulf Caribbean*, 3:181-205.
- ROGERS, D. J., 1963. Taximetrics—new name, old concept. *Brittonia*, 15:285-290.
- ROGERS, H. M., 1940. Occurrence and retention of plankton within the estuary. *J. Fisheries Res. Board Can.*, 5:164-171.
- ROSSITER, J. R., 1963. Tides. *Oceanog. Marine Biol. Ann. Rev.*, 1:11-25.
- RUSSELL, H. D., 1941. The recent mollusks of the family Neritidae of the Western Atlantic. *Bull. Museum Comp. Zool. Harvard Coll.*, 88:345-404.
- RUSSELL, R. D., 1955. Effects of transportation on sedimentary particles. In *Recent Marine Sediments, a Symposium*, edited by P. D. Trask; Spec. Publ. 4, pp. 32-47. Soc. Econ. Paleontologists and Mineralogists.
- RUSSELL, R. J., 1957. Instability of sea level. *Am. Scientist*, 45:414-430.
- SALOMON, M., 1962. Soil chemistry—a tool for the analysis of marine sediments. In *The Environmental Chemistry of Marine Sediments*, edited by N. Marshall; Occ. Publ. 1, pp. 5-12. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- SANDERS, H. L., 1956. The biology of marine bottom communities. X. In *Oceanography of Long Island Sound, 1952-1954*. *Bull. Bingham Oceanog. Coll.*, 15: 345-414.
- SANDERS, H. L., 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.*, 3:245-358.
- SANDERS, H. L., 1959. Sediments and the structure of bottom communities. In *International Oceanographic Congress—Preprints*, edited by Mary Sears; pp. 583-584. American Association for the Advancement of Science, Washington, D. C.
- SANDERS, H. L., 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. *Limnol. Oceanogr.*, 5:138-153.
- SANDERS, H. L., E. M. GOUDSMIT, E. L. MILLS, and G. E. HAMPSON, 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.*, 7:63-79.
- SCHIELTEMA, R. S., 1961. Metamorphosis of the veliger larva of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. *Biol. Bull.*, 120:92-109.
- SCHLIEPER, C., 1955. Über die physiologischen Wirkungen des Brackwassers (Nach Versuchen an der Miesmuschel *Mytilus edulis*). *Kiel. Meeresforsch.*, 11: 22-33.
- SCHLIEPER, C., 1957. Comparative study of *Asterias rubens* and *Mytilus edulis* from the North Sea (30 per 1,000 S) and the western Baltic Sea (15 per 1,000 S). *Annales Biol.*, 61, Ser. 33:117-127.
- SCHLIEPER, C., 1958. Physiologie des Brackwassers. In *Die Biologie des Brackwassers*, edited by A. Thienemann; *Die Binnengewässer*, 22:217-330.
- SCOTT, K. M. F., A. D. HARRISON, and W. MACNAE, 1952. The ecology of South African estuaries. Part II. The Klein River estuary, Hermanus, Cape. *Trans. Roy. Soc. South Africa*, 33:283-331.
- SEARS, MARY (Editor), 1959. Sea water and sediment exchange. In *International Oceanographic Congress—Preprints*; pp. 956-991. American Association for the Advancement of Science, Washington, D. C.
- SEGERSTRAALE, S. G., 1957. Baltic Sea. *Geol. Soc. Am. Mem.*, 67(1):751-800.
- SEGERSTRAALE, S. G., 1960. Investigations on Baltic populations of the bivalve *Macoma balthica* (L.). *Soc. Sci. Fennica, Commentationes Biol.*, 23(2):1-72.
- SEGERSTRAALE, S. G., 1964. Marine zoology in the Baltic area in 1953-1962. *Oceanog. Marine Biol. Ann. Rev.*, 2:373-392.
- SHELBOURNE, J. E., 1957. The 1951 oyster stock in the Rivers Crouch and Roach, Essex, and the influence of water currents and scour on its distribution, with an account of comparative dredging experiments. *Gt. Brit. Min. Agr., Fish Food Fishery Invest., Ser. 2*, 21:1-27.
- SHEPARD, F. P., 1952. Revised nomenclature for depositional coastal features. *Bull. Am. Assoc. Petro. Geol.*, 36:1902-1912.
- SHEPARD, F. P., 1953. Sedimentation rates in Texas estuaries and lagoons. *Bull. Am. Assoc. Petro. Geol.*, 37:1919-1934.
- SHISHKINA, O. V., 1959. On the salt composition of the marine interstitial waters (solutions). In *International Oceanographic Congress—Preprints*, edited by Mary Sears; pp. 977-978. American Association for the Advancement of Science, Washington, D. C.
- SHUSTER, C. N., 1950. Observations on the natural history of the American horseshoe crab, *Limulus polyphemus*. Third Rept. Invest. Methods Improving Shellfish. Res., Mass., Commonwealth of Mass., Dept. Conserv., Div. Marine Fish., pp. 18-23.
- SHUSTER, C. N., 1951. On the migration of young Polynices. *Anal. Rec.*, 111:126.
- SHUSTER, C. N., 1959. Biological evaluation of the Delaware River Estuary. In *State of Delaware Intra-state Water Resources Survey*, edited by J. G. Smith et al.; vol. 21, pp. 1-73. William N. Cann, Wilmington, Delaware.
- SIMMONS, H. B., 1960. Application and limitations of estuary models in pollution analysis. In *Proceedings of the 1st International Conference on Waste Disposal in the Marine Environment*; pp. 540-546. Pergamon Press, New York.
- SIMPSON, G. G., 1963. Biology and the nature of science. *Science*, 139(3550):81-88.
- SKOPINTSEV, B. A., 1959. Organic matter in sea water. In *International Oceanographic Congress—Preprints*, edited by Mary Sears; pp. 953-954. American Association for the Advancement of Science, Washington, D. C.
- SLOBODKIN, L. B., 1962. Energy in animal ecology. *Advan. Ecol. Res.*, 1:63-101.
- SMITH, R. I., 1955. Comparison of the level of chloride regulation by *Nereis diversicolor* in different parts of its geographical range. *Biol. Bull.*, 109:453-474.
- SMITH, R. I., 1956. The ecology of the Tamar estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of *Nereis diversicolor*. *J. Marine Biol. Assoc. U. K.*, 35:81-104.
- SMITH, R. I., 1959. Physiological and ecological prob-

- lens of brackish waters. *Marine biology. Proc. 20th Ann. Biol. Coll., Oregon Sta. Coll.*, pp. 59-69.
- SMITH, R. I., 1964. On the early development of *Nereis diversicolor* in different salinities. *J. Morphol.*, 114:437-463.
- SPÄRCK, T., 1935. On the importance of quantitative investigation of the bottom fauna in marine biology. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 10: 3-19.
- SPENCER, R., 1963. Bacterial viruses in the sea. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 350-365. Charles C. Thomas, Springfield, Illinois.
- SPOONER, G. M., 1947. The distribution of *Gammarus* species in estuaries. *J. Marine Biol. Assoc. U. K.*, 27: 1-52.
- SPOONER, G. M., and H. B. MOORE, 1940. The ecology of the Tamar estuary. VI. An account of the macrofauna of the intertidal muds. *J. Marine Biol. Assoc. U. K.*, 24:283-330.
- STAIGER, H., 1954. Der Chromosomendimorphismus beim Prosobranchier *Purpura lapillus* in Beziehung zur Ökologie der Art. *Chromozoma*, 6:419-478.
- STARIKOVA, N. D., 1959. Organic matter of the liquid phase of marine muds. In *International Oceanographic Congress—Preprints*, edited by Mary Sears; pp. 980-982. American Association for the Advancement of Science, Washington, D. C.
- STARR, T. J., 1956. Relative amounts of vitamin B₁₂ in detritus from oceanic and estuarine environments near Sapelo Island, Georgia. *Ecology*, 7:658-664.
- STAUBER, L. A., 1943. Graphic representation of salinity in a tidal estuary. *J. Marine Res.*, 5:165-167.
- STEPHEN, A. C., 1953. Life on some sandy shores. In *Essays in Marine Biology*, edited by S. M. Marshall and A. P. Orr; pp. 50-72. Richard Elmhurst Memorial Lectures. Oliver and Boyd, Edinburgh.
- STEVENS, G. C., 1963. Uptake of organic material by aquatic invertebrates. II. Accumulation of amino acids by the bamboo worm *Clymenella torquata*. *Comp. Biochem. Physiol.*, 10:191-202.
- STOPFORD, S. C., 1951. An ecological survey of the Cheshire foreshore of the Dee Estuary. *J. Animal Ecol.*, 20:103-122.
- STRICKLAND, J. D. H., and T. R. PARSONS, 1960. A manual of sea water analysis (with special reference to the more common micronutrients and to particulate organic material). *Bull. Fisheries Res. Board Can.*, 125:1-185.
- STROUP, E. D., and R. J. LYNN, 1963. *Atlas of Salinity and Temperature Distributions, Chesapeake Bay 1952-1961 and Seasonal Averages 1949-1961. Graphical Summary No. 2*. Chesapeake Bay Inst., Johns Hopkins Univ., Baltimore, Maryland.
- SUTCLIFFE, W. H., E. R. BAYLOR, and D. W. MENZEL, 1963. Sea surface chemistry and Langmuir circulation. *Deep-Sea Res.*, 10:233-243.
- SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING, 1942. *The Oceans, Their Physics, Chemistry, and General Biology*. Prentice-Hall, Englewood Cliffs, New Jersey.
- SWAN, E. F., 1952. The growth of the clam *Mya arenaria* as affected by the substratum. *Ecology*, 33: 530-534.
- SYMPOSIUM ON THE CLASSIFICATION OF BRACKISH WATERS, 1959. Venice, 8-14th April, 1958. *Arch. Oceanog. Limnol. II, Suppl. (Simposio sulla classificazione delle acque salmastro)*. Venezia 8-14 Aprile, 1958.
- THOMAS, W. L., JR. (Editor), 1956. *Man's role in changing the face of the earth*. Univ. Chicago Press, Chicago, Illinois.
- THORSON, G., 1933. Investigations on shallow water animal communities in the Franz Joseph Fjord (East Greenland) and adjacent waters. *Medd. Grönland*, 100:1-69.
- THORSON, G., 1946a. Technique and future work in arctic animal ecology. *Medd. Grönland*, 144:1-40.
- THORSON, G., 1946b. Reproduction and larval development of Danish marine bottom invertebrates with special reference to the plankton larvae in the sound (Øresund). *Medd. Komm. Dansk. Fisk. Havunders., Serie Plankton* 1:1-523.
- THORSON, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25:1-45.
- THORSON, G., 1957. Bottom communities (sublittoral or shallow shelf). *Geol. Soc. Am. Mem.* 67(1):461-534.
- THORSON, G., 1958. Parallel level-bottom communities, their temperature adaptation, and their "balance" between predators and food animals. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 67-86. Univ. Calif. Press, Berkeley, California.
- THORSON, G., 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. In *Oceanography*, edited by Mary Sears; Publ. No. 67, pp. 455-474. American Association for the Advancement of Science, Washington, D. C.
- TONOLLI, V., and L. TONOLLI, 1958. Irregularities of distribution of plankton communities: considerations and methods. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 137-143. Univ. Calif. Press, Berkeley, California.
- TRASK, P. D., 1955. Organic content of recent marine sediments. In *Recent Marine Sediments, a Symposium*, edited by P. D. Trask; spec. Publ. 4, pp. 428-453. Soc. Econ. Paleontologists Mineralogists.
- TURNER, C. H., E. E. EBERT, and R. R. GIVEN, 1965. Survey of the marine environment offshore of San Elijo Lagoon, San Diego County. *Calif. Fish Game*, 51:81-112.
- TURNER, H. H., 1953. A review of the biology of some commercial molluscs of the east coast of North America. *Sixth Rept., Invest. Shellfisheries Mass., Div. Marine Fisheries, Dept. Nat. Res., Commonwealth Mass.*, pp. 39-74.
- VALLENTYN, J. R., 1954. Biochemical limnology. *Science*, 119:605-606.
- VALLENTYN, J. R., 1957. The molecular nature of organic matter in lakes and oceans, with lesser reference to sewage and terrestrial soils. *J. Fisheries Res. Board Can.*, 14:33-82.
- VAN CLEAVE, R., and R. Y. TING, 1962. A new bottom sampling mechanism. *Contr. Univ. Wash. Coll. Fish.*, 19:29-30.
- VAN DONGEN, A., 1956. The preference of *Littorina obtusata* for *Fucus*. *Arch. Neerl. Zool.*, 11:373-386.
- VAN STRAATEN, L. M. J. U., and PH. KUENEN, 1958. Tidal action as a cause of clay accumulation. *J. Sediment. Petrol.* 28:406-413.
- VEEVERS, H., 1952. A photographic survey of certain areas of sea floor near Plymouth. *J. Marine Biol. Assoc. U. K.*, 31:215-221.
- VERWEY, J., 1952. On the ecology of distribution of cockle and mussel in the Dutch Waddensee, their role in sedimentation and the source of their food supply with a short review of the feeding behavior of bivalve mollusks. *Arch. Neerl.* 10:171-239.
- WALNE, P. R., 1958. The importance of bacteria in laboratory experiments on rearing the larvae of *Ostrea edulis*. I. *J. Marine Biol. Assoc. U. K.*, 37:415-425.
- WAUGH, G. D., 1957. Oyster production in the Rivers Crouch and Roach, Essex, from 1950 to 1954. *Gr. Brit. Min. Agr. Fish Food, Fisheries Invest., Ser. 2* 21(1): 1-47.
- WELLS, G. P., 1945. The mode of life of *Arenicola marina*. I. *J. Marine Biol. Assoc. U. K.*, 26:170-207.
- WELLS, H. W., 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecol. Monographs*, 31:239-266.
- WHITE, K. M., 1937. *Mytilus*. Liverpool Marine Biol.

- Comm. Mem. Typical British Marine Plants Animals, 31:1-177 (Proc. Trans. Liverpool Biol. Soc., 50:1-177).
- WIESER, W., 1958. The particulate and the comparative concept in marine synecology. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 47-56. Univ. Calif. Press, Berkeley, California.
- WIESER, W., 1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnol. Oceanogr.*, 4:181-194.
- WIESER, W., 1960. Benthic studies in Buzzards Bay. II. The meiobenthos. *Limnol. Oceanogr.*, 5:121-137.
- WIESER, W., and J. KANWISHER, 1961. Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Massachusetts. *Limnol. Oceanogr.*, 6:262-270.
- WIGLEY, R. L., and A. D. McINTYRE, 1964. Some quantitative comparisons of offshore meiobenthos and macrobenthos south of Martha's Vineyard. *Limnol. Oceanogr.*, 9:485-493.
- WILLIAMS, A. B., 1955. A survey of North Carolina shrimp nursery grounds. *J. Elisha Mitchell Sci. Soc.*, 71:200-207.
- WILLIAMS, A. B., 1958. Substrates as a factor in shrimp distribution. *Limnol. Oceanogr.*, 3:283-290.
- WILLIAMS, W. T., and J. M. LAMBERT, 1960. Multivariate methods in plant ecology. II. The use of an electronic digital computer for association-analysis. *J. Ecol.*, 48:689-710.
- WILSON, D. P., 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Savigny. *Ann. Inst. Oceanogr.* N. S., 27:49-156.
- WILSON, D. P., 1958. Some problems in larval ecology related to the localized distribution of bottom animals. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 87-103. Univ. Calif. Press, Berkeley, California.
- WOOD, E. J. FERGUSON, 1953. Heterotrophic bacteria in marine environments of eastern Australia. *Australian J. Marine Freshwater Res.*, 4:160-200.
- WOOD, E. J. FERGUSON, 1962. The microbiology of estuaries. In *Symposium on the Environmental Chemistry of Marine Sediments*, edited by N. Marshall; Occ. Publ. No. 1:20-26. Narragansett Marine Lab., Univ. Rhode Island, Kingston, Rhode Island.
- WOOD, E. J. FERGUSON, 1963. Heterotrophic microorganisms in the oceans. *Oceanogr. Marine Biol. Ann. Rev.*, 1:197-222.
- WOOD, R. D., 1963. Adapting SCUBA to aquatic plant ecology. *Ecology*, 44:416-419.
- YASUDA, J., 1952. Tidal and diurnal changes of occurrence of molluscan larvae at Maeshida, Aichi Prefecture. *Bull. Japan. Soc. Sci. Fisheries*, 17(11):342-344.
- YONGE, C. M., 1949a. Life in estuaries. In *The Sea Shore*; pp. 259-268. William Collins Sons and Co., New York.
- YONGE, C. M., 1949b. On the structures and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. *Phil. Trans. Roy. Soc. London, Ser. B.*, 234(609):29-76.
- YONGE, C. M., 1950. Life on sandy shores. *Sci. Progr. (London)*, 38:430-444.
- YONGE, C. M., 1953. Aspects of life on muddy shores. In *Essays in Marine Biology*, edited by S. M. Marshall and A. P. Orr; Richard Elmhurst Memorial Lectures, pp. 29-49. Oliver and Boyd, Edinburgh.
- YONGE, C. M., 1957. Interrelations of organisms. C. Symbiosis. *Geol. Soc. Am. Mem.*, 67(1):429-442.
- YONGE, C. M., 1963. Rock-boring organisms. In *Mechanisms of Hard Tissue Destruction*, edited by R. F. Soginnae; Publ. No. 75, pp. 1-24. American Association for the Advancement of Science, Washington, D. C.
- ZEIGLER, J. M., 1964. Some modern approaches to beach studies. *Oceanogr. Marine Biol. Ann. Rev.*, 2: 77-95.
- ZHUKOVA, A. I., 1963. On the quantitative significance of microorganisms in nutrition of aquatic invertebrates. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 699-710. Charles C. Thomas, Springfield, Illinois.
- ZHUKOVA, A. I., and M. V. FEDOSOV, 1963. Significance of microorganisms of upper sediment layer of shallow water basin in transformation of organic matter. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 711-719. Charles C. Thomas, Springfield, Illinois.
- ZOBELL, C. E., 1946a. *Marine microbiology. A Monograph on hydrobacteriology*. Chronica Botanica Co., Waltham, Massachusetts.
- ZOBELL, C. E., 1946b. Studies on redox potential of marine sediments. *Bull. Am. Assoc. Petrol. Geol.*, 30: 477-513.
- ZOBELL, C. E., 1963. Domain of the marine microbiologist. In *Symposium on Marine Microbiology*, edited by C. H. Oppenheimer; pp. 3-24. Charles C. Thomas, Springfield, Illinois.
- ZOBELL, C. E., and E. C. ALLEN, 1935. The significance of marine bacteria in the fouling of submerged surfaces. *J. Bacteriol.*, 29:239-251.
- ZOBELL, C. E., and C. B. FELTHAM, 1942. The bacterial flora of a marine mud flat as an ecological factor. *Ecology*, 23:69-78.

Biological Zonation Related to Groundwater Discharge Along the Shore of Biscayne Bay, Miami, Florida

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Generally recognized parameters that contribute to biological zonation include turbidity, penetration of light, exposure to air, temperature, salinity, and sediment type. Although not commonly recognized, the discharge of fresh groundwater through the littoral bottom sediments of a bay or shallow sea may also produce a biological zonation. The overriding function appears to be that of dilution of the interstitial water and nearshore sea water. Zonation should exist along any shoreline where a fresh groundwater reservoir is hydraulically connected to a saltwater body through permeable bottom sediments. The purpose of this paper is to illustrate the hydrological factors leading to the zonation and to demonstrate the resulting gradation of flora and fauna at one site near Miami, Florida.

The interior of the Florida peninsula from Lake Okeechobee southward to Florida Bay is a vast freshwater swamp comprising the Everglades ("the river of grass") and Big Cypress Swamp (Fig. 1). The Atlantic Coastal Ridge (altitude 8 to 20 feet above mean sea level) consists of oolitic limestone in the Miami area. Numerous broad sloughs (altitude 5 to 8 feet) cut through the coastal ridge. Prior to the construction of drainage canals, the water level in the Everglades was high enough to cause discharge through these overflow channels to Biscayne Bay by poorly channelized sheet flow. In 1890 Alexander Agassiz commented, "To the damming up of the waters in the Everglades, and to the sudden outbursts of gigantic masses of water charged with organic matter and lime, we may trace the immense destruction of fishes which so frequently occurs on the shores of the Florida keys [sic] and the waters surrounding them." (Shaler, 1890).

In addition to the direct surface runoff, numerous freshwater springs occurred along the shore of Biscayne Bay (Parker *et al.*, 1955). Small springs, recognized by the birefringent mixing action of the waters, are reported by local residents to have existed as far as three-quarters of a mile seaward from the shoreline in the Cutler area. Near shore, freshwater springs welled up through the bottom of Biscayne Bay as large boils; one such potable spring just north of the study site is marked by the words "fresh water" on Coast and Geodetic Survey Navigation Chart No. 166, published in 1896. The early mariners and spongers customarily lowered kegs to the spring orifice to obtain fresh drinking water.

Starting in 1907 and continuing to the present, drainage canals were constructed westward from the coast through the Miami area into the Everglades to reclaim low-lying land for urban and agricultural use (Fig. 2). These canals lowered the water table about six feet in the Everglades. As a result of the reduction in freshwater head, many springs ceased flowing and these same orifices now serve as avenues by which salt water intrudes into the Biscayne aquifer. Near shore, however, some of the springs still exist, but their flows are greatly reduced. It is the intent of this paper to present evidence of a biological zonation related to the present, remnant conditions of groundwater discharge.

GEOLOGICAL AND HYDROLOGICAL CHARACTERISTICS

The locale of the study is the Cutler area shown in Figure 2. A mangrove swamp occupies a zone

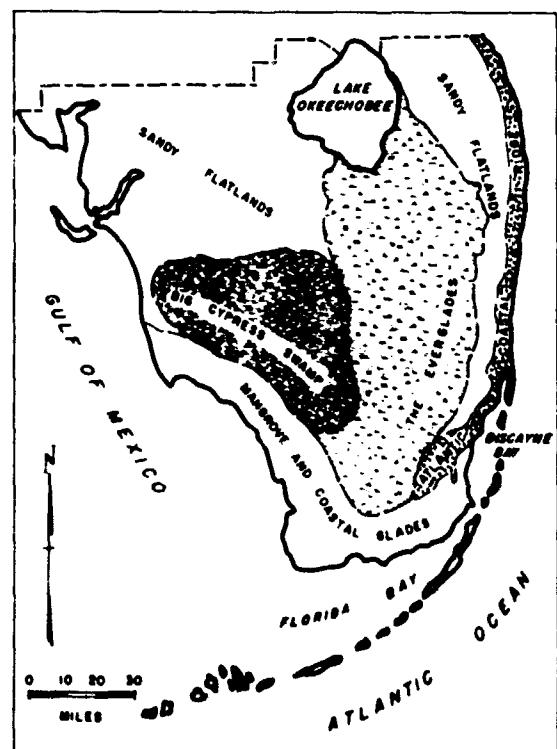


Fig. 1. Map of southern Florida showing physiographic divisions.

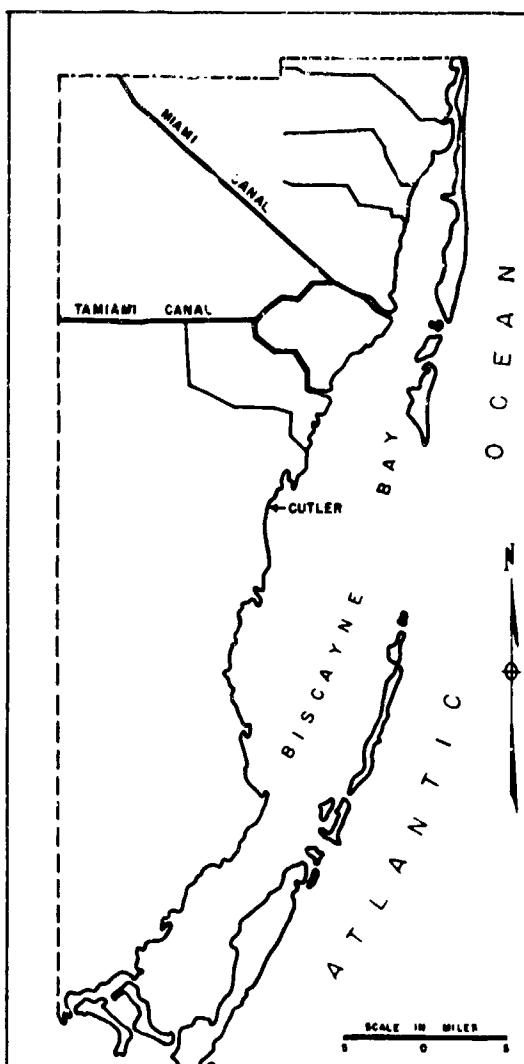


Fig. 2. Map of eastern Dade County showing location of the Cutler area.

about 200 feet wide between the pine- and deciduous-covered limestone of the coastal ridge to the west and the high tide mark to the east. Distance measurements are referred to the high tide mark, which approximately coincides with mean high-water altitude. At low tide, the tidal flat is uncovered 200 to 300 feet seaward from the high tide mark (Fig. 3). The bay bottom slopes gently to a depth of about ten feet below msl (mean sea level) at a distance of three miles from shore.

THE BISCAYNE AQUIFER

The Biscayne aquifer consists of highly permeable solution-riddled limestone and calcareous sandstone. It is a water-table aquifer and extends from land surface to an average depth of 100 feet below mean sea level where it is underlain by marl and clay. The marl and clay are of low permeability and effectively

isolate the aquifer from deeper circulation of groundwater. Rainfall infiltrates into the aquifer so rapidly that direct runoff is practically unknown except during flood times when the water table rises above land surface in low areas.

THE ZONE OF DIFFUSION

A cross section of the zone of diffusion in the Cutler area is shown in Figure 4. The chloride content in the zone of diffusion grades from 16 ppm (parts per million) (fresh water) to about 19,000 ppm (sea water). The isochlors are based on water samples from individual fully cased wells whose termini are represented by the black dots in the cross section. The blunt-nosed shape of the zone of diffusion is characteristic in the Miami area and results from the boundary requirement that no movement of salt can take place across the impermeable base of the aquifer; the salt moves horizontally landward from points of high concentration to points of low concentration and the individual isochlors approach the base of the aquifer perpendicularly.

Under low-head conditions, the sea water flows in a cycle, inland from the floor of the sea into the deep part of the aquifer, becoming progressively diluted with fresh water, thence upward across a line along which there is no horizontal component of flow, and seaward again as diluted salt water through the upper part of the aquifer (Kohout, 1960a). This cyclic flow pattern is shown in Figure 5 (Kohout, 1960b) and is similar in certain respects to the circulation of water in the Chesapeake Bay Estuary as demonstrated by Pritchard (1951).

DISCHARGE OF FRESH WATER

A comparison of Figures 4 and 5 shows that as the fresh groundwater in the upper part of the aquifer moves seaward, it gradually becomes more salty, i.e., the isochlor lines of less than 1,000 ppm swing upward and cross the flow lines. This is a consequence of the integration of salt into the seaward-flowing fresh water by dispersion and cyclic flow of salt water. The groundwater discharge at the shoreline, thus, is not completely fresh, but contains 1,000 to 2,000 ppm chloride.

Visual evidence of the discharge of groundwater through the bottom of the bay is provided by the photographs of a flowing well installed offshore in the Cutler area (see location of well G 934 in Figures 11 and 12). The photograph of Figure 6 was taken just after the casing which had been driven through the floor of the bay had been removed along with its contained rock core. At that time the well was developing itself by natural flow, causing the lime stain in the bay water. In Figure 7, the casing has been reinserted in the open hole and positioned just above the water surface of the bay. The picture shows that groundwater in the zone of diffusion, ten feet below sea level, is under sufficient head to rise above bay level and therefore to flow through the aquifer and discharge through the bottom sediments of the bay.



Fig. 3. Photograph showing groundwater seepage through the bay bottom of the Cutler area at low tide.

The chloride content of the well water at the time of the photograph was 10,700 ppm. Subsequent observations in 1958 showed that the chloride content of water in well G 934 ranged as low as 3,800 ppm; the same chloride content was obtained in a sample collected in February, 1964 (Fig. 12).

The uppermost flow tubes of Figure 4 contain relatively fresh water which discharges near the shoreline; the lower and most seaward flow tubes (above the zero-horizontal gradient line) contain the saltiest water which discharges farther from the shore. The importance of this to a biological study is that certain

plants and animals will zone themselves in response to the salinity of the upward percolating groundwater.

Frequently the presence of discharging groundwater can be recognized by visual inspection of the exposed bottom at low tide. For example, the patches of water on the sloping beach in Figure 3 are not normal "tidal pools". Rather, they are formed by the upward percolation of groundwater which occurs as a slow seepage throughout the exposed part of the bay bottom and extends into that part of the bottom still covered by bay water. In places, the discharge

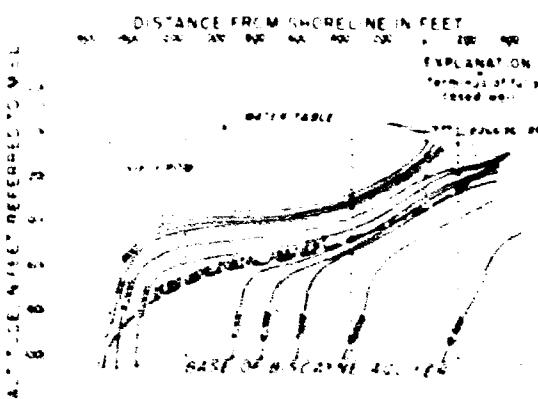


Fig. 4. Cross section through the Cutler area showing the zone of diffusion, September 18, 1958.

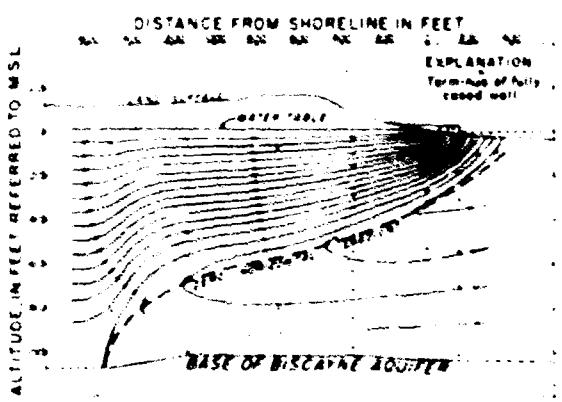


Fig. 5. Cross section through the Cutler area showing the flow pattern of fresh and salt water for a low-head condition, September 18, 1958.



Fig. 6. Photograph of well G 934 developing itself by natural flow.

breaks out in sufficient strength to be classified as a real spring. Thus, the subcircular ponds in Figure 3 are formed by the restricted growth of sea grass near small brackish-water springs in the Cutler area.

The discharge of groundwater is not unique to the limestone shore of Biscayne Bay, but may be recognized in a slightly different form on sandy beaches (Fig. 8). This photograph was taken at Jekyll Island, Georgia, the site of the Conference on Estuaries, looking southward from the Wanderer Motel toward the Aquarama. The Atlantic Ocean level at low tide can be seen at the extreme left; the high tide mark is at the right. The strip of water extending parallel to the shore is formed by groundwater seepage in a trough or runnel which lies landward from a small wave-constructed sand bar. The accumulated groundwater is discharged seaward through a small rivulet that extends down the sloping beach to the ocean. The chloride contents of several water samples collected at Jekyll Island at 6:15 p.m., April 3, 1964, are as follows:

Location on east shore of Jekyll Island, Georgia	Chloride content (in ppm)
Wanderer Motel—Inland edge of water strip shown in Figure 8, about 5 feet above ocean level	5,800
Wanderer Motel—Hole in beach, about 20 feet inland from the ocean and 1 foot above ocean level	12,600
Wanderer Motel—Ocean water, collected 4 feet seaward of ocean-level line, water about 0.3 foot deep	11,600
Aquarama—Collected in hole 1 foot deep, about 6 feet above ocean level	43

Jekyll Island is about seven miles long and one mile wide and is studded with large oak trees. The oak trees, along with the chlorinity gradient of water



Fig. 7. Photograph of flowing well G 934 with the casing positioned just above the water surface of Biscayne Bay.

on the oceanward strand, indicate that a freshwater lens underlies this small island. Clearly, the circumstances of groundwater discharge along the shore of Biscayne Bay cannot be considered unique.

SALINITY OF BISCAYNE BAY

The effect of groundwater discharge on the salinity of Biscayne Bay is significant. Figure 9 shows that the chloride content of water samples collected at the bottom of the bay at Stations 1 and 2 is occasionally less than 8,000 ppm (station locations Figs. 10 and 11). Station 1 is located in the intertidal zone, and at low tide the chloride content represents the admixture of residual bay water and groundwater discharge at one of the subcircular depressions shown in the foreground of Figure 3. The water at Stations 2 and 3 is about 0.5 and 1.5 feet deep at the lowest tide level. At high tide the bay water covers all stations and there may be a slight reversal of head so that near shore, the bay water may intrude slightly into the aquifer before being flushed out during the falling tide. The chloride contents of Figure 9 are random



Fig. 8. Photograph showing groundwater discharge on the exposed strand at the eastern side of Jekyll Island, Georgia, near low tide, April 3, 1964.

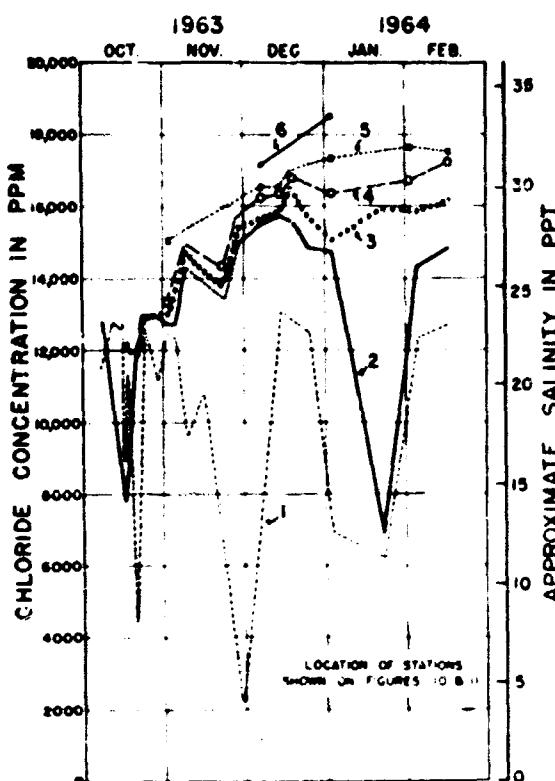


Fig. 9. Graph showing fluctuations of chloride content of water samples collected at the bottom of Biscayne Bay offshore from the Cutler area.

in relation to time, but it may be assumed that the lower values represent the conditions at low tide.

The seasonal character of the salinity fluctuations relates to the onset of the dry season after the rainy season ends in early November. A complete seasonal cycle for surface salinity near Chicken Key, slightly north of Stations 4 and 5 (insert map, Fig. 10), is given by Woodmansee (1958) for the year 1948. The salinity during that hurricane year ranged from a low of 15‰ (parts per thousand) in October to a high of 35‰ in March. The data of Figure 9 roughly indicate the salinity conditions antecedent to the present zonation study represented by species assemblages of February, 1964.

The chlorinity data of Figure 9 are plotted against distance in Figure 10. The envelope between the maxima-minima lines indicates the severe ranges of salinity fluctuation that fauna and flora near the shoreline must withstand. Desiccation does not appear to be a strong factor in the biological zonation because the upward seepage of groundwater maintains a sloping sheet of water over the exposed beach (Fig. 3). Animals capable of slight movement may easily find harbor by swimming or crawling into the grass—provided they can adjust or regulate osmotically to withstand the fluctuating salinities.

The average chloride-content line represents the arithmetic average of water samples collected at each

station from October, 1963, through February, 1964. Because the salinity fluctuations should decrease with distance from the shore, the infrequent sampling at the more seaward stations probably does not produce serious aberration of the average salinity curve. Though the data are sparse and obviously seasonal, the average values give an indication of the conditions under which the flora and fauna exist in the Cutler area.

BIOLOGICAL ZONATION

Under the definition that an estuary is a region of steep and variable gradients in environmental conditions, Biscayne Bay has been classified as a positive, shallow, tidal, bar-built estuary; the term positive indicates that the salinity is less than that of the connected seawater body (Hela *et al.*, 1957). The seasonal temperature range of the bay water is 19° to 32°C. with little vertical stratification (McNulty *et al.*, 1962). Fine calcareous sediments are brought into suspension by heavy wave action; transparency of the water is reduced, but generally the turbidity is not great enough to prevent penetration of light to the shallow bottom.

Maximum salinity fluctuations occur opposite the mouths of canals, and the biological distribution in the vicinity of the outlet of the Miami Canal has been studied intensively in connection with the decrease of sewage effluent after construction of the City of Miami sewage treatment plant in 1956 (Moore *et al.*, 1955; McNulty, 1961). From a hydrological viewpoint, a biological zonation should exist not only near the outlets of canals, but also along the shores of intercanal areas. Thorson's (1957) concept of level-bottom communities does not apply to the narrow region along the shore where groundwater discharge occurs.

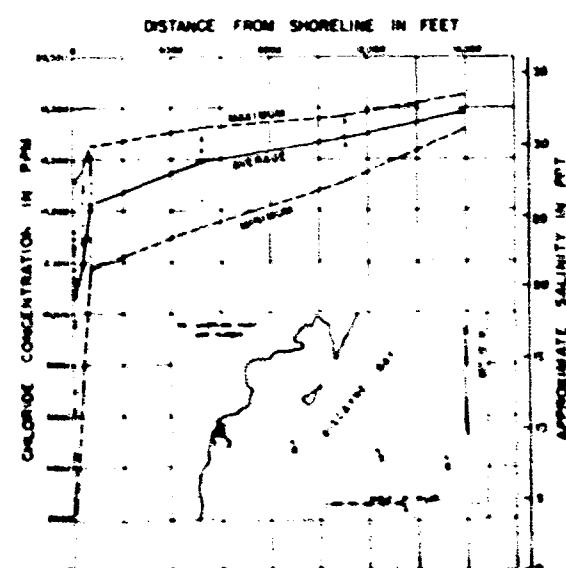


Fig. 10. Graph showing observed chlorinity profile in Biscayne Bay, October, 1963, to February, 1964.

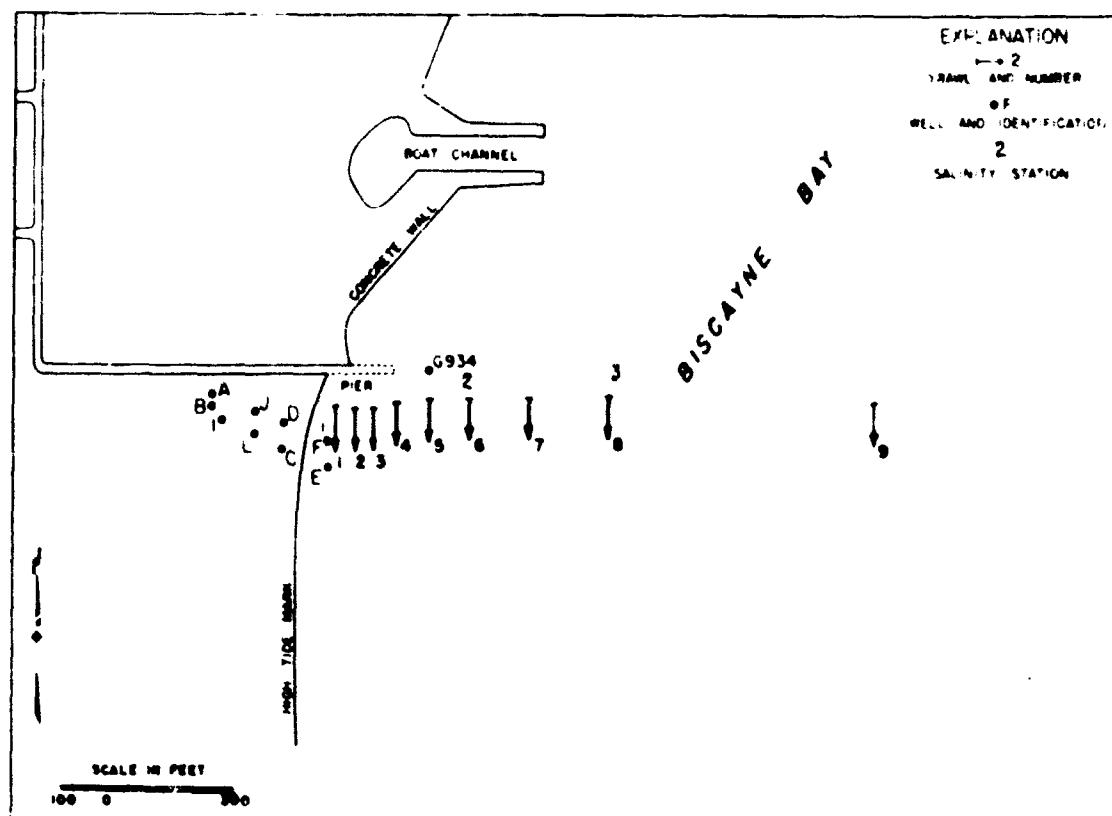


Fig. 11. Map of the Cutler area showing observation points

An incomplete search of the literature has yielded few references to the influence of groundwater discharge on the biological distribution in an estuary. Remane and Schulz (1934) clearly relate the presence of turbellarians (*Otoplana* zone) to brackish groundwater underlying the strand of the Kiel district of Germany. Emery and Cox (1956) mention that mullet and other brackish-water fish are cultivated in artificial ponds fed by artesian springs along the shore of Molokai, Hawaii. Abbott (1947) indicates that the fish ponds are fed by "subterranean wells" and correlates the algae growing in each of the ponds with the characteristic chlorinity for that pond. In discussing the evolutionary adaptations in the brackish inland water of the Florida peninsula, Odum (1953) notes that blue crabs are rarely observed in the main boil of Chassahowitzka Springs which has a chloride content of 50 ppm; but, in contrast, the crabs are abundant a few hundred feet downstream where water from a second boil with a chlorinity of 730 ppm mixes with the water of the first boil. This is an inverse example of the subject of this paper, in that the discharge of a salty spring is providing an inland habitat for a common marine form.

Stephenson and Stephenson (1950) and Voss and Voss (1955) found biological zonations along the shores of the Florida Keys. In general, the offshore keys are too small to develop a freshwater lens and

the biota represent the normal seawater salinity range. The concept of zonation has not been applied to the Florida mainland shore where the effect of groundwater discharge could produce significant differences in the distribution of the organisms.

SCOPE OF THE BIOLOGICAL STUDY

Semi-quantitative samples of the aquatic animals were collected by dragging a two-man trawl a distance of 100 feet parallel to the shore at the nine locations shown in Figure 11. The trawl had a metal-frame opening 4 feet wide by 2 feet high with a nylon window-screen collecting bag 4 feet long. Samples of the muddy-sandy sediment were shoveled up at selected intervals from the shore and were sifted through a quarter-inch mesh screen to collect the bottom fauna. The attached aquatic flora were mapped by direct observation. The abundance and zonation of species beyond 1,500 feet from shore (Table 1) were estimated visually by a face-mask-equipped diver who was pulled by a slow-moving boat along a section line perpendicular to the shore. The study can not be considered comprehensive as it was initiated and oriented to establish the effect of groundwater discharge on the biota in that part of the bay bottom where the effects would be most pronounced. Primary attention was given to the fauna and flora of the

Table 1. Comparative list of the fauna and flora collected at the Cutler Site. P—present; C—common; A—abundant.

	Distance from shoreline in feet												
	50 ^t	100 ^t	150 ^t	200 ^t	280 ^t	380 ^t	500 ^t	700 ^t	1,300 ^t	1,800	3,000	4,000	7,000
ALGAE													
<i>Batophora overstedii</i>	A	A	C	P		P							
<i>Enteromorpha</i> sp.		P											
<i>Digenia simplex</i>		P	C	C	C	C	C	C	C	C	C	C	A
<i>Laurencia</i> sp.			C	P	A								A
<i>Acetabularia crenulata</i>			P	P		P	C	C	C	C	C	C	
<i>Ulva</i> sp.				P			P	C	C	C	C	C	A
<i>Halimeda opuntia</i>					P	P	C	C	C	C	C	C	A
<i>Penicillus capitatus</i>					P	P	P	C	C	C	C	C	C
<i>Udotea conglutinata</i>					P	C	P	C	C	C	C	C	A
<i>Caulerpa</i> sp.													A
<i>Sargassum</i> sp.													
SEA GRASSES													
<i>Diplanthera wrightii</i>	A	A	A	C	P	A	A	A	A	P	A	A	A
<i>Thalassia testudinum</i>		P	C	A						C			
PORIFERA													
<i>Sphecospongia espuria</i>						P			C	C	C	A	A
<i>Haliclona</i> sp.								P	P	P	C	C	P
<i>Ircinia campanula</i>								P	P	P	C	C	P
<i>Tedania ignis</i>											C	P	P
CNIDARIA													
<i>Siderastrea sidercea</i> (Coral)								P		P	C	A	A
<i>Solenastrea hyades</i> (Coral)										A	P	C	P
<i>Antillogorgia acerosa</i> (Sea leather)													A
ANNELIDA													
Nereid worms	C	C	C	C	C	C			C	C			
ECHINODERMATA													
<i>Echinaster sentus</i>						1		1	1				
MOLLUSCA													
Gastropods													
<i>Melongena corona</i>	1	1											
<i>Neritina virginica</i>	39	4	2										
<i>Haminoea elegans</i>	33	23	2		1								
<i>Cerithium variabile</i>	144	6	3	4	1								
<i>Batillaria minima</i>	722	156	538	127	138	8	2						
<i>Cerithium muscarum</i>	54	28	35	71	57	60	54	35	3				
<i>Bulla occidentalis</i>	14	7	7	10	6	1	5		1				
<i>Prunum apicinum</i>	9	5	2	9	8	6	4		3				
<i>Nassarius vibex</i>	2	5	4	11	8	1	23	13	1				
<i>Thais haemastoma floridana</i>		1											
<i>Modulus modulus</i>	3	2	17	37	31	97	73	7	P				
<i>Fasciolaria tulipa</i>		1	1		2								
<i>Crepidula convexa</i>	3	21	16	16	12								
<i>Columbella rusticoides</i>					1	16	15	18					
<i>Vermicularia spirata</i>							2	2					
<i>Rissoa</i> sp.					P								
<i>Turbo castaneus</i>										P	A		
Pelecyopods													
<i>Anomia cardia concimeris</i>	3												
<i>Brachiodontes</i> sp.	3	5	5	7	52	56							
<i>Lacrycardium mortoni</i>	1	2	5	7			3	7	5				

Table 1 (continued)

	Distance from shoreline in feet												
	50'	100'	150'	200'	280'	380'	500'	700'	1,300'	1,800'	3,000'	4,000'	7,000'
MOLLUSCA (Continued)													
Pelecypods (Continued)													
<i>Chione cancellata</i>				2				6	2				
<i>Lima pellucida</i>				1		2	1			1			
<i>Aequipecten gibbus nucleus</i>					1			1	1		2		
<i>Tellina versicolor</i>							1						
<i>Anomia simplex</i>								1					
ARTHROPODA													
Palaeomimid Shrimps													
<i>Palaeomonetes intermedius</i>	121	137	100	13									
Penaeid Shrimps													
<i>Penaeus duorarum</i> (?)													
(juvenile)	8	91	26	26	14	2	2	2	7				
Hippolytid Shrimps													
<i>Toseuma carolinensis</i>	1							10					
<i>Hippolyte</i> sp.					1	90	200	550	680	620	96		
<i>Thor floridanus</i>					2	135	1,220	3,000	1,220	1,040	272		
<i>Hippolyte</i> sp.							30	240	340	340	128		
Mysids													
<i>Taphromysis bowmani</i>	2	91	4	70	50			1	20				
Hermit Crabs													
<i>Clibanarius vittatus</i>	C	C	P										
<i>Pagurus annulipes</i> , Provenzano			23	36	104	25	105	92	11	P			
Cancroid Crabs													
<i>Callinectes sapidus</i>	12												
FISHES													
<i>Cyprinodon</i> sp.	3												
<i>Lobotes surinamensis</i>	1												
<i>Spherooides testudineus</i>	2	1	1										
<i>Lucania parva</i>	262	356	150	94	24	40	10			3			
<i>Gobiosoma robustum</i>	1	1	2	13	7	4	5	5	5	3			
<i>Syngnathus</i> sp.		1	4				2	3	3	1			
<i>Hippocampus zosterae</i>					2	3	2	2					
<i>Lagodon rhomboides</i>					1	14	18	26					
<i>Chasmodes saburrae</i>							1						

¹ Trawls 1 through 9 are arranged in increasing distance from the shore. Each trawl was 100 feet long and the number in table represents the total count of specimens in the respective trawl. A blank in the column space indicates "not observed", but in the nearshore area, where observations were quite detailed, the blank indicates probable complete absence of the species. The table is arranged taxonomically and the species under each group are arranged to infer a zonation by the tapering pattern of numerical count or symbols.

wetted bottom extending to a distance of about 1,500 feet from shore.

BOTTOM TYPE

The nearshore bay bottom at Cutler may be classified as muddy, but it is more aptly described as consisting of sand and shell fragments with a matrix of organic mud. The substratum consists of consolidated limestone pitted with vertical solution holes up to four feet deep which are frequently filled with the sandy mud. Near shore, the bottom is extremely soft and wading is difficult, especially at low tide when upward percolation of groundwater tends to make the sediments quick.

ZONATION

Five of the 42 species that were captured in the trawls are graphed in relation to the underlying hydrological factors in Figure 12. Published information indicated that the distribution of these five animals

was more closely related to salinity than to other environmental factors. The vertical scale gives numbers of animals collected in each trawl and, as the first trawl was 50 feet from shore, the graph begins abruptly at that distance.

The strictly brackish gastropod, *Neritina virginea*, was most abundant near shore, especially around the springs, where the mean salinity was 19 %, but where a low of 5 % was observed. The first trawl contained 39 individuals, with the number decreasing rapidly to zero in the fourth trawl at 200 feet from shore. The only other recorded occurrence of this species in Biscayne Bay was at the mouth of the Miami River (McNulty, 1961). Russell (1941) describes the salinity range of this gastropod as follows: "*Neritina virginea* is a species of the mangrove swamps and is strictly a brackish water form. It appears to be most abundant around the mouths of creeks and rivers though it will not advance beyond the area of brackish waters."

Lucania parva, the rainwater killifish, is typical of swamps and brackish waters along the Atlantic coast from Cape Cod southward to Mexico (Eddy, 1957). It occurs at Cutler in hundreds per trawl near shore where the groundwater discharge is especially fresh. Although this species appears to prefer brackish waters, it tolerates hypersaline conditions. For example, Harrington and Harrington (1961) found *Lucania parva* to be abundant during the fall of 1956 in a subtropical marsh along the Indian River shoreline of Florida where the salinity in some of the smaller ponds rose to a maximum of 39‰. However, Tabb and Manning (1961), from work in the northern part of Florida Bay, describe *Lucania parva* as occurring most abundantly in low salinities. Though this species may be truly euryhaline, the distribution and the manner in which it congregates in spring ponds of the Cutler area suggests that this killifish has a definite preference for the brackish water of this nearshore region.

The recently described mysid, *Taphromysis bowmani* Bacescu, was concentrated in the low salinities near shore, but a few individuals were collected as far out as 700 feet from shore where the mean salinity was 26‰. Bacescu (1961), based on known habitats in Louisiana and Florida, described *T. bowmani* as characteristic of brackish water, but with occurrence in fresh water also.

The two marine forms (Fig. 12), the juveniles of the pinfish, *Lagodon rhomboides*, and the gastropod, *Columbella rusticoides*, extend shoreward into salinities of 22‰; the increasing numbers of these two forms seaward indicates their preference for higher salinity.

L. rhomboides has been recorded from waters along the east coast of the United States with salinities

ranging from approximately 0.1 to 37.2‰, but the larvae and post larvae have been found only in the relatively high salinities of the open sea (Caldwell, 1957). Only juveniles were collected at Cutler (the body lengths ranged from 11 to 28 mm), and their distribution suggests that they have not developed sufficient tolerance to withstand the low salinities in the region of groundwater discharge.

Apparently, the salinity tolerance of *Columbella rusticoides* is unreported, but Tabb and Manning (1961) found *C. rusticoides* common on *Thalassia* flats of Florida Bay in high salinities. Also, Robert C. Work (personal communication), who has collected extensively along the coasts of Florida, finds that this gastropod is absent from areas of low salinity.

Seventeen other animals were present in sufficient numbers to be plotted and their distributions are shown in Figure 13. The spatial arrangement of these forms shows a zonal effect but, because of their recognized intertidal occurrence or notoriously broad osmoregulatory abilities, these species may zone themselves in response to environmental factors other than salinity.

The most noticeable zonation in the Cutler area is reflected in the attached plants and sessile animals. For example, the transition between *Diplanthera* and *Thalassia* grass is plainly visible at the point of the arrow in Figure 14.

The dark zone at a distance of less than 200 feet from shore is almost a solid mat of *Diplanthera wrightii* grass along with a significant amount of the green alga, *Batophora oerstedii*. The light zone extending seaward from the transition line consists primarily of the marine turtle grass, *Thalassia testudinum*, and several marine algal species (Table 1).

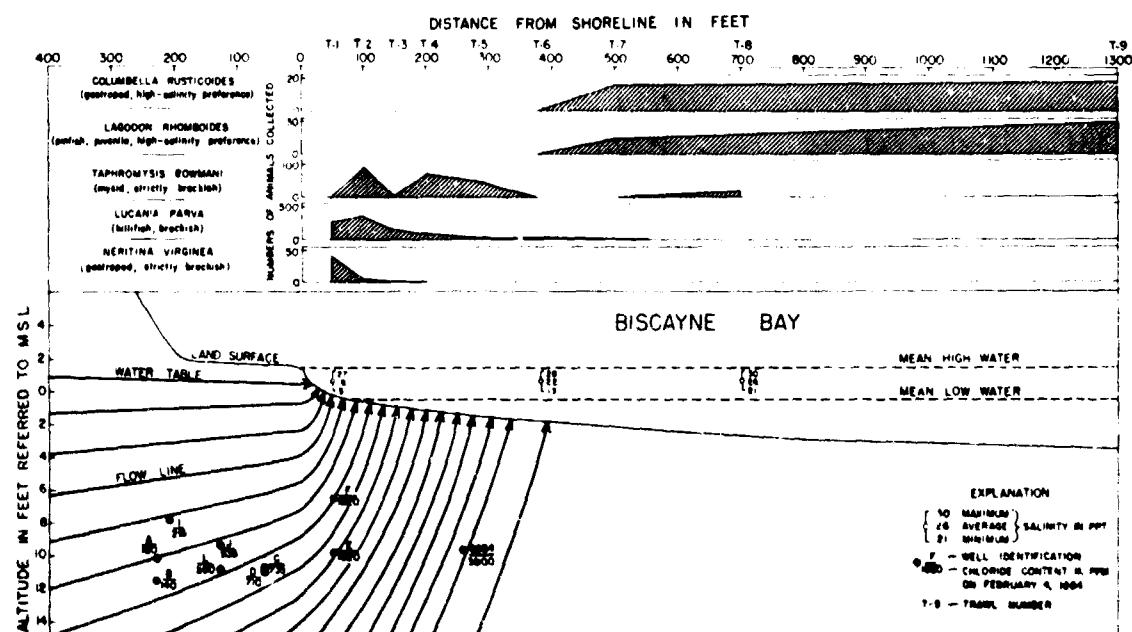


Fig. 12. Distribution of selected animals related to underlying hydrological factors in the Cutler area.

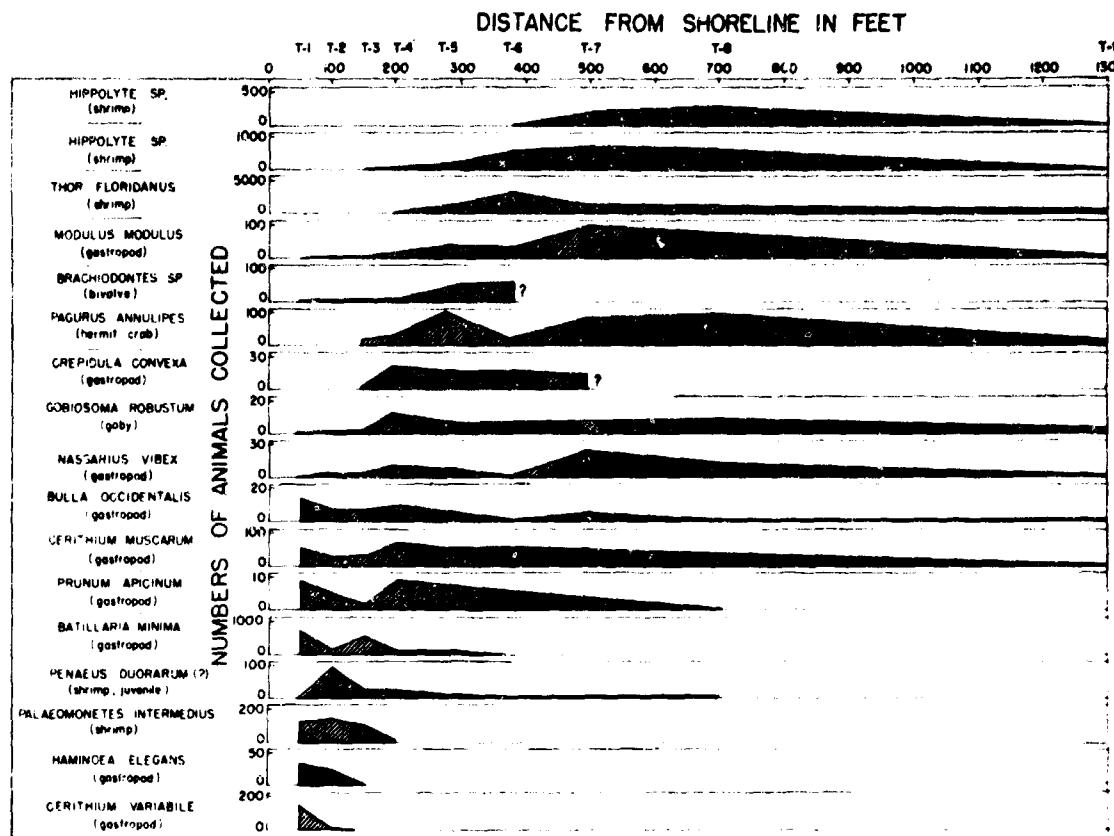


Fig. 13. Graph showing distribution of common animals related to distance from shore in the Cutler area.

B. overstedi is found throughout the West Indies and occurs in quite fresh water or in water of normal marine salinity but prospers in brackish water (Taylor, 1960). Tabb and Manning (1961) report that *Batophora* is uncommon in the high-salinity regions of Florida Bay, but is common in the brackish to fresh areas of the Everglades bay system.

Diplanthera grass occurs commonly in normal sea water, but the solid mat of this grass near shore suggests that *Diplanthera* is more tolerant to the low salinity of the upward percolating ground water than *Thalassia* grass. However, *Diplanthera* also has a lower salinity limit. Figure 15 is a closeup view of a spring pool about five feet in diameter located about 50 feet seaward from the shoreline in the Cutler area. The limestone detritus marks the points of two spring orifices. Live *Diplanthera* grass surrounds the spring pool, but is absent from the central part where the lowest salinities prevail. The dark material inside the pool is composed primarily of dead *Diplanthera* blades with a few washed-in *Thalassia* blades. In some of the other springs *Batophora* grows abundantly as an inner core surrounded by the outer ring of *Diplanthera*.

Several animals that were common in the near-shore trawls seek the low salinities of the spring pools. Until frightened into the surrounding grass, the killifish (*Lucania parva*) flit about the pools and tend to congregate near the spring orifices. Although

probably not distinguishable in Figure 15, examination of the original color transparency under a low-power microscope showed that specimens of *Neritina virginica* were present both in the dark central region and on the live grass surrounding the pool.

Exclusively marine forms such as echinoderms and corals were absent from the areas of low salinity near shore. Only one echinoderm, the starfish, *Echinaster sentus*, was encountered in the trawls. Its nearest approach to shore was in a *Thalassia* bed at a distance of 280 feet where the mean salinity was about 21‰. Lowell P. Thomas (personal communication) found the brittlestar, *Ophiophragmus filigranous*, to be common in the vicinity of the groundwater discharge in the soft bottom and *Diplanthera* roots about the year 1959. This brittlestar tolerates low salinities and was collected in the peripheral bays of the Everglades where the bottom salinities ranged from 7.7 to 14.0 ‰ (Thomas, 1961). The apparent absence of *O. filigranous* during the present study may indicate year-to-year and seasonal fluctuations in the biota.

HABITAT

The animals in the nearshore region live in a precarious environment. The mud underlying the grass reeks of hydrogen sulfide and in general is not habitable. As the tide floods over the nearshore region, the salinity of the water increases rapidly. Thus, the

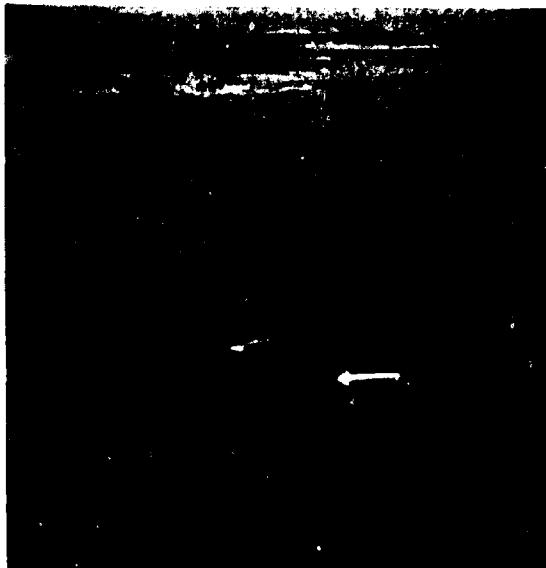


Fig. 14. Aerial photograph of the Cutler area showing the transition between *Diplanthera* (dark) and *Thalassia* grass (light). (Photograph by Richard A. Wade.)

brackish-water species probably cannot go downward into the sediments and presumably do not prefer the high salinity of the flooding tide. By feeling into the grass during the flood tide, the impression is obtained that the shelled animals are stratified under the upper

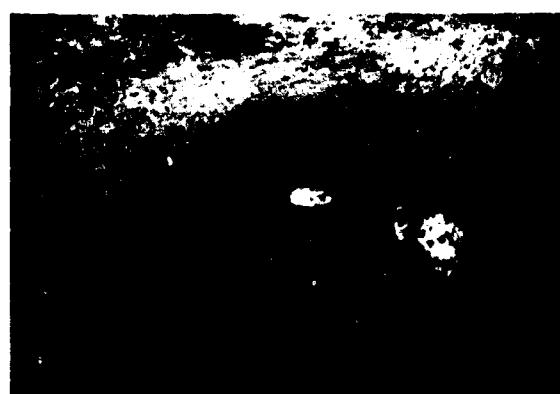


Fig. 15. Photograph of two spring orifices surrounded by live *Diplanthera* grass at the edge of a tidal pool.

layers of grass, but above the bottom. The observation may be of little merit but it seems reasonable that the best protection against the high salinity above and the hydrogen sulfide below would occur in this thin intermediate layer of grass.

Samples of water discharging from a spring orifice (Fig. 15) and from the edge of the pool were analyzed for hydrogen-sulfide content. The former contained 0.3 ppm and the latter 0.7 ppm, ± 50 percent. These low concentrations are consistent with the observations of Ostlund and Alexander (1963) that hydrogen sulfide is oxidized very rapidly as it diffuses

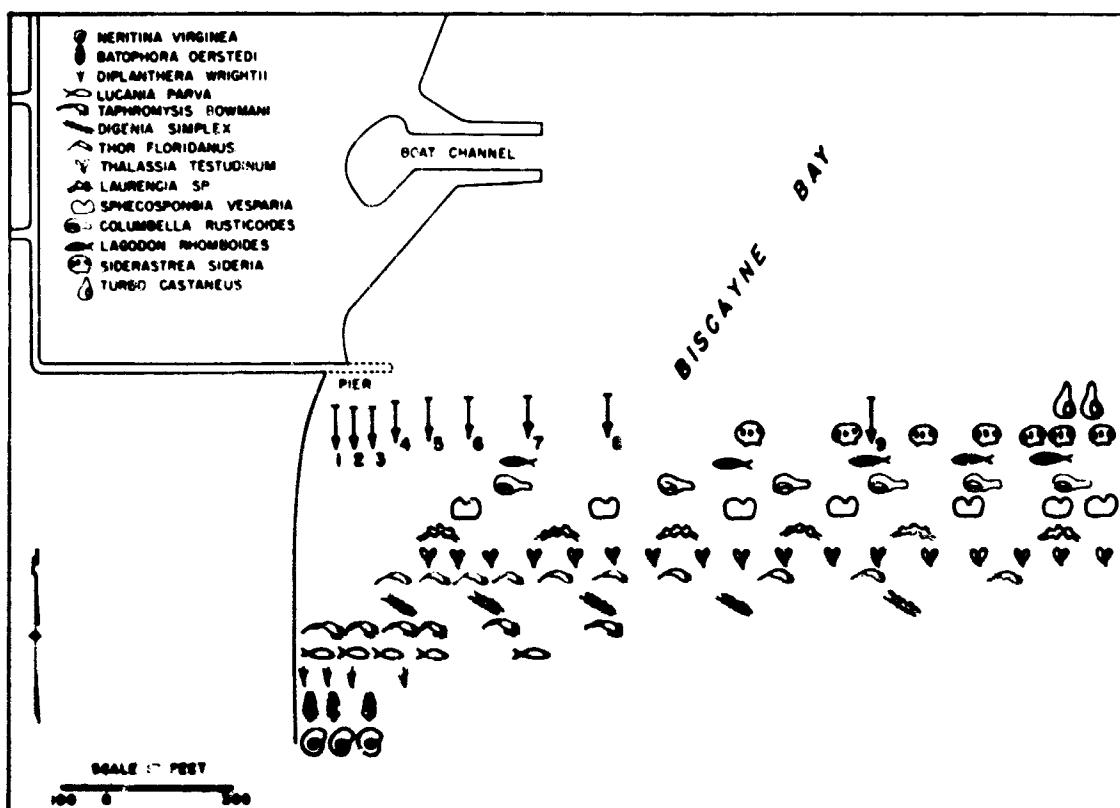


Fig. 16. Map of the Cutler area with superimposed résumé of the biological distributions.

upward from the sediments and is practically undetectable at distances greater than one cm above the sediment surface.

The bay water to a distance of 1,500 feet from shore was profiled with a Yellow Springs Model 51 oxygen meter. The oxygen content averaged about 5.7 ppm (4 ml/l) just after low tide with little deviation along the profile. The oxygen content of the groundwater from a flowing well was determined at about 4.0 ppm (2.8 ml/l) sufficient to sustain most animal life. The observations of hydrogen sulfide and oxygen content indicated that these were not limiting factors in the study area.

RÉSUMÉ OF BIOLOGICAL ZONATION

Figure 16 shows a schematic résumé of the biological distributions that were most noticeable. Among the marine forms the coral, *Siderastrea sideria*, dropped out landward at about 700 feet from shore, where the salinity ranged from 21 to 30 ‰, and the loggerhead sponge, *Spongia vesparia*, dropped out at 400 feet from shore where the salinity ranged from 13 to 28 ‰. The gastropods, *Turbo castaneus* and *Columbella rusticoides*, which were present beyond the ninth trawl, dropped out in the shoreward region of freshened bay water.

In contrast, the brackish forms, such as *Neritina virginea* and *Taphromysis bowmani*, fall out seaward (Fig. 16). These distributions focus at a distance of about 300 feet from shore, which is also the distance at which the main part of the groundwater discharge terminates.

Many factors influence the distribution of fauna and flora along a shoreline and it is difficult to positively assign one parameter such as salinity as the controlling factor. Nevertheless, the distribution of the organisms correlates so closely with the underlying hydrological factors that a conclusion appears justified: the distribution of the organisms is primarily a function of salinity related to groundwater discharge.

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LITERATURE CITED

- ABBOTT, I. A., 1947. Brackish-water algae from the Hawaiian Islands. *Pacific Sci.*, 1:193-214.
- BACESCU, M., 1961. *Taphromysis bowmani*, n. sp., a new brackish water mysid from Florida. *Bull. Marine Sci. Gulf Caribbean*, 11:517-524.
- CALDWELL, D. K., 1957. The biology and systematics of the pinfish, *Lagodon rhomboides* (Linnaeus). *Bull. Florida State Museum*, 2:77-173.
- COAST AND GEODETIC SURVEY, 1896. *Navigational Chart 166*. Environmental Sciences Services Administration, U.S. Department of Commerce, Rockville, Maryland.
- EDDY, S., 1957. *How to know the freshwater fishes*. William C. Brown Co., Dubuque, Iowa.
- EMERY, K. O., and D. C. COX, 1956. Beachrock in the Hawaiian Islands. *Pacific Sci.*, 10:384-402.
- HARRINGTON, R. W., and E. S. HARRINGTON, 1961. Food selection among fishes invading a high subtropical salt marsh: From onset of flooding through the progress of a mosquito brood. *Ecology*, 42:646-666.
- HELA, I., J. K. McNULTY, and C. A. CARPENTER, 1957. Hydrography of a positive, shallow, tidal bar-built estuary (Rept. on the hydrography of the polluted area of Biscayne Bay). *Bull. Marine Sci. Gulf Caribbean*, 7:47-99.
- KOHOUT, F. A., 1960a. Cyclic flow of salt water in the Biscayne aquifer of southeastern Florida. *J. Geophys. Res.*, 65:2133-2141.
- KOHOUT, F. A., 1960b. Flow pattern of fresh water and salt water in the Biscayne aquifer of the Miami area, Florida. *Publ. No. 52, Intern. Assoc. Sci. Hydrol. Comm. Subter. Waters*, pp. 440-448.
- MCNULTY, J. K., 1961. Ecological effects of sewage pollution in Biscayne Bay, Florida: sediments and distribution of benthic and fouling macro-organisms. *Bull. Marine Sci. Gulf Caribbean*, 11:394-447.
- MCNULTY, J. K., R. C. WORK, and H. B. MOORE, 1962. Level sea bottom communities in Biscayne Bay and neighboring areas. *Bull. Marine Sci. Gulf Caribbean*, 12:204-233.
- MOORE, H. B., I. HELA, E. S. REYNOLDS, J. K. MCNULTY, S. MILLER, and C. A. CARPENTER, Jr., 1955. Report on preliminary studies of pollution in Biscayne Bay. Rept. to Federal Security Agency, Public Health Service, National Institutes of Health, Washington, D.C.
- ODUM, H. T., 1953. Factors controlling marine invasion into Florida fresh waters. *Bull. Marine Sci. Gulf Caribbean*, 3:134-156.
- OSTLUND, H. G., and J. ALEXANDER, 1963. Oxidation rate of sulfide in sea water; a preliminary study. *J. Geophys. Res.*, 68:3995-3997.
- PARKER, G. G., G. E. FERGUSON, S. K. LOVE, and others, 1955. Water resources of southeastern Florida. *U. S. Geol. Surv. Water Supply Paper* 1255.
- PRITCHARD, D. W., 1951. The physical hydrography of estuaries and some applications to biological problems. *Trans. 16th No. Am. Wildlife Conf.*, Wildlife Manag. Inst., Washington, D. C.; pp. 368-376. (Chesapeake Bay Inst. Coll. Reprints, 1951-52, Contrib. No. 3).
- REMANE, A., and E. SCHULZ, 1934. Das Küstengrundwasser abs. Lebensraum. *Schriften Naturw. Ver. Schleswig-Holstein*, 20:399-408.
- RUSSELL, H. D., 1941. The recent mollusks of the Family Neritidae of the western Atlantic. *Bull. Museum Comp. Zool. Harvard Univ.*, 88:347-404.
- SHALER, N. S., 1890. The topography of Florida, with a note by Alexander Agassiz. *Bull. Museum Comp. Zool. Harvard Univ.*, 16:139-158.
- STEPHENSON, T. A., and A. STEPHENSON, 1950. Life between tide-marks in North America. I. The Florida Keys. *J. Ecology*, 38:354-402.
- TARB, D. C., and R. B. MANNING, 1961. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July 1957 through September 1960. *Bull. Marine Sci. Gulf Caribbean*, 11:552-649.
- TAYLOR, R. W., 1960. *Marine algae of the eastern tropical and subtropical coasts of the Americas*. The Univ. of Michigan Press, Ann Arbor, Michigan.
- THOMAS, L. P., 1961. Distribution and salinity tolerance in the amphipod brittlestar, *Ophiophragmus filigranous* (Lyman, 1875). *Bull. Marine Sci. Gulf Caribbean*, 11:158-160.
- THORSON, G., 1957. Bottom communities (sublittoral or shallow shelf). In *Treatise on Marine Ecology and Paleoecology*, edited by J. W. Hedgpeth; vol. 1, pp. 461-534. Geol. Soc. Am. Mem. 67.
- VOSS, G. L., and N. A. VOSS, 1955. An ecological survey of Solier Key, Biscayne Bay, Florida. *Bull. Marine Sci. Gulf Caribbean*, 5:203-229.
- WOODMANSEE, R. A., 1958. The seasonal distribution of the zooplankton off Chicken Key in Biscayne Bay, Florida. *Ecology*, 39:247-262.

Saturation of Estuarine Zooplankton by Congeneric Associates

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Zooplankton can be divided into two major categories, the holoplankton and the meroplankton, separated according to characteristics in the life cycle. All stages in the development of a holoplanktonic animal live in the water above the substrate; meroplankters spend only part of their lives in the water as free-swimming larval stages. A third group, the tychoplankton, is usually of minor importance and consists primarily of organisms accidentally swept from the bottom.

Estuarine holoplankton is a monotonous assortment of calanoid copepods. The meroplankton has numerous classes representing several phyla. Diversity, both from a specific and a phylogenetic point of view, is consequently much higher in the meroplankton than in the holoplankton, probably because marine sediments offer several different kinds of habitats which buffer physical variations in the water. Various niches are available within sediments to support a diverse benthic fauna. The only major groups that have been able to cope with the vicissitudes of brackish water throughout the life cycle are the Copepoda and Cladocera. Calanoid copepods are clearly the dominant members, constituting all but a fraction of the total except for brief periods in confined areas where a cyclopoid copepod and a cladoceran sporadically bloom. From Virginia through southern New England, the area covered in this review, the estuarine copepods of real consequence belong to the genera *Acartia*, *Eurytemora*, and *Oithona*. Because of their significance, the biology of the three genera or their counterparts along other coasts must be understood before the economy of an estuary can be worked out. They have received little attention, probably because of a combination of practical difficulties encountered in the study of ecology.

For each of these three genera, two species are generally represented in abundance. I attempt here to: (1) document the importance of congeneric associates in estuarine plankton and nearshore neritic waters; (2) relate their interactions to the high levels of productivity characteristically maintained in estuaries; (3) speculate on their evolutionary significance; (4) cite examples where similar phenomena exist in the benthos; and (5) examine the biochemical and physiological bases for relationships between interacting populations that meet in various ways within the lattice of space and time.

RELATIVE AND ABSOLUTE POSITIONS OF CONGENERIC ASSOCIATES

Seasonal abundances of the larval benthos and holoplanktonic copepods are shown in Figure 1A for Raritan Bay, New Jersey. In three estuaries, copepods usually comprise over 60 percent of the total zooplankton from spring through fall (Fig. 1B). Pelagic larval stages of benthic invertebrates make rela-

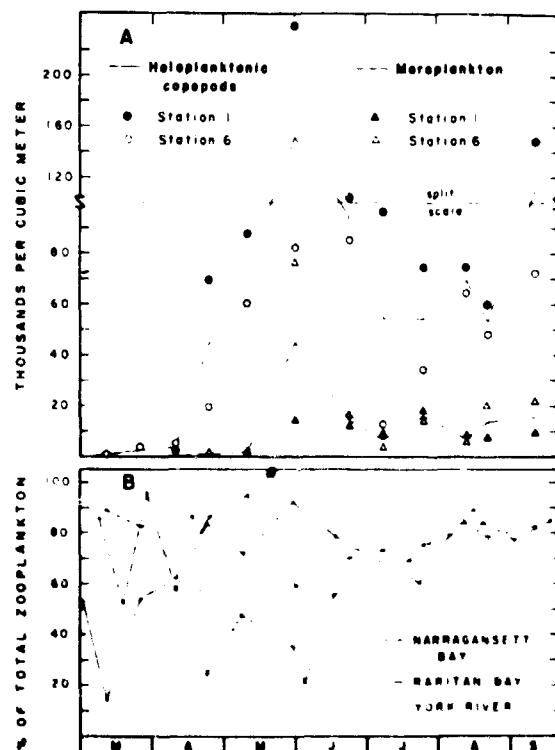


Fig. 1. Seasonal abundance of the zooplankton in East Coast estuaries. A. Raritan Bay, New Jersey. Average concentrations m^3 at Stations 1 and 6 shown for the holoplanktonic copepods (solid line) and meroplankton (broken line). Stations 1 and 6 represent the low and high salinity extremes of the bay. B. Density of holoplanktonic copepods relative to total zooplankton (holoplankton, meroplankton, tychoplankton; excluding fish and copepod eggs, forams and nematodes). Narragansett Bay, Rhode Island, Raritan Bay, New Jersey (averages for Stations 1 and 6), and the York River, Virginia, 1958.

tively large contributions in the York River, Virginia (a tributary of Chesapeake Bay), but in general the numerically important group is obviously the holoplankton.

In Table 1 the major species are classified according to their abilities to reproduce and maintain populations in brackish water. The categories are based on salinities which permit population growth, not isolated instances where a certain species occurred at an exceptional salinity. The categories are represented diagrammatically in Figure 2, showing the influence of the net circulation pattern. Note in Table 1 that there are usually two major species per genus. The species in each pair better able to withstand diluted sea water is listed first in the table. For *Eurytemora*, *Acartia*, and *Oithona*, at least, the more euryhaline member is also more southern in overall distribution and thus the more thermophilic species in the genus. It occurs during or following vernal warming, whereas the second listed member of the pair usually augments

when water is cooler, reflecting its more northern limit and center of distribution (Fig. 3). Within the area studied, this relationship does not hold for *Centropages*, although *hamatus* is less affected by reduced salinity than *typicus*, and neither species is estuarine. From the totals in each category, note that all but three of the 23 species are paired. In *Acartia* and *Eurytemora* there are three species, but the most halophilic members (*A. danae* and *E. herdmani*) are very scarce. The exceptions, genera represented by

Table 1 (continued)

Species	True estuarine	Estu- arine and marine	Eury- haline marine	Steno- haline marine
Copepod congeneric associates				
<i>Eurytemora</i>				
<i>affinis</i>	X			
<i>americana</i>	X			
(<i>herdmani</i>) ^a	X			
<i>Acartia</i>				
<i>tonsa</i>		X		
<i>clausi</i>		X		
(<i>danae</i>)				X
<i>Oithona</i> ^b				
<i>brevicornis</i>	X			
<i>similis</i>			X	
<i>Tortanus</i>				
<i>setacaudatus</i>	X	X		
<i>discaudatus</i>				
<i>Paracalanus</i>				
<i>crassirostris</i>				
<i>parvus</i>			X	
<i>Temora</i>				
<i>stylifera</i> ^c		X		
<i>longicornis</i>		X		
<i>Centropages</i>				
<i>hamatus</i>			X	
<i>typicus</i>				X
Important single species				
<i>Labidocera aestiva</i>			X	
<i>Pseudocalanus minutus</i>			X	
<i>Calanus finmarchicus</i>				X
Cladocera				
<i>Podon</i>				
<i>polyphemoides</i>	X			
<i>intermedius</i>				X
<i>Eucadne</i>				
<i>nordmanni</i>		X		
<i>spinifera</i>			X	
Total species	5	5	8	5
Members of congeneric associates	5	5	6	4

^a Modified from Day (1951), Spooner and Moore (1940).

^b Occurs in small numbers near the mouth of Narragansett Bay, Rhode Island.

^c *Oithona* none and *O. spinifera* may also be represented.

^d Observed on only two occasions in Raritan Bay, New Jersey.

^e *Pseudocalanus coronatus*, a calanoid copepod, might be included here because it is a common member of the plankton. Adult and late copepodite stages appear so intimately associated with the bottom (Jacobs, 1961) that it is better classified in the benthic plankton.

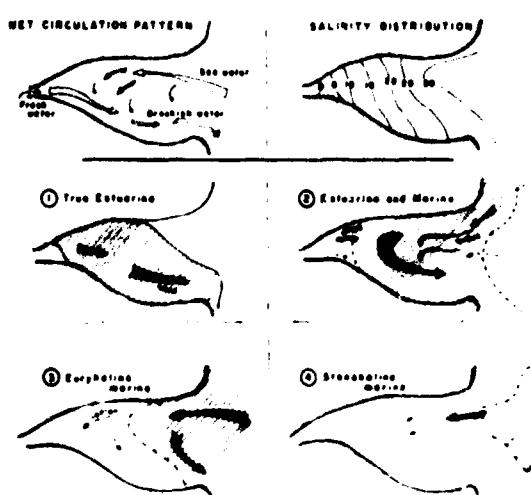


Fig. 2. Stylized distributions of four categories of holoplanktonic copepods (Table 1) in a hypothetical estuary. Darkened arrows indicate the drift of animals produced in areas shown by diagonal lines; the lines are closely spaced in the centers of propagation. Relative development of each component in an estuary is a function of salinity distribution and net circulation.

only a single species, are not estuarine; they do not propagate in brackish water. Consequently, they are usually insignificant except in the marine zone of an estuary. In the lower portion of Narragansett Bay and near the mouth of Raritan Bay, the marine copepod, *Pseudocalanus minutus*, is a frequent visitor during late winter and spring (Jeffries, 1962a). Throughout a major portion of the year congeneric associates account for 85 to 100 percent of the holoplankton. Although relative proportions change along the estuary's axis in relation to spatial distributions of salinity (Jeffries, 1962b) and flushing characteristics (Barlow, 1955), dominance of holoplanktonic copepods by these associated species generally becomes more pronounced upstream. The two major *Acartia* species, *clausi* and *tonsa*, are not members of the same subgenus (Farran, 1948). This suggests that direct genetic relationship is lacking in some "ecological species-pairs". In order to avoid confusion with strict taxonomic usage of the term "species-pair", M. S. Wilson (personal communication) suggested that I use "congeneric associates" to denote ecological association of two species belonging to the same genus.

With the possible exception of *Eurytemora*, these combinations of species may reflect vestiges of evolutionary patterns that radiated from warm waters to colonize temperate estuaries, part of a general tendency exhibited by many marine faunas (Ekman, 1953). A northern origin is indicated for *Eurytemora* by the diverse assemblage of species in Alaskan waters (Wilson and Tash, 1966). It appears that genera penetrated osmoregulatory barriers independently, forming a chain of species with overlapping distributions along the salt gradient. Each member of the chain probably had a better ability to tolerate lower

salinity. Between the Chesapeake and Cape Cod, *Eurytemora* populations do not have a species linking their distributions with propagation in the sea. In the Arctic, *herdmani* occurs several miles offshore (Wilson, personal communication). The three *Eurytemora* species in northeastern estuaries, *herdmani*, *americana*, and *affinis*, probably have consecutively lower salt tolerances. This has not yet been proved experimentally, but is apparent from distributions along salt gradients in several estuaries. An uninterrupted chain extending from salt to fresh water could be the result of intraspecific competition. Mayr (1963) called this kind of species relationship a powerful centrifugal force in promoting adaptive radiation; it favors speciation, driving a genus into new areas and niches where one member can escape from the other. Thus, a chain of related species portrays ascent of the estuary; the pattern is not always complete as we see it today because adaptive specialization can lead to extinction when animals overspecialize in a changing environment. Exchanges of congeneric species from one estuary to another could account for the fact that present-day chains are composed of different subgenera.

Remembering that the origin and maintenance of interspecific relationships are inseparable because "the ecological history of the species is to some extent

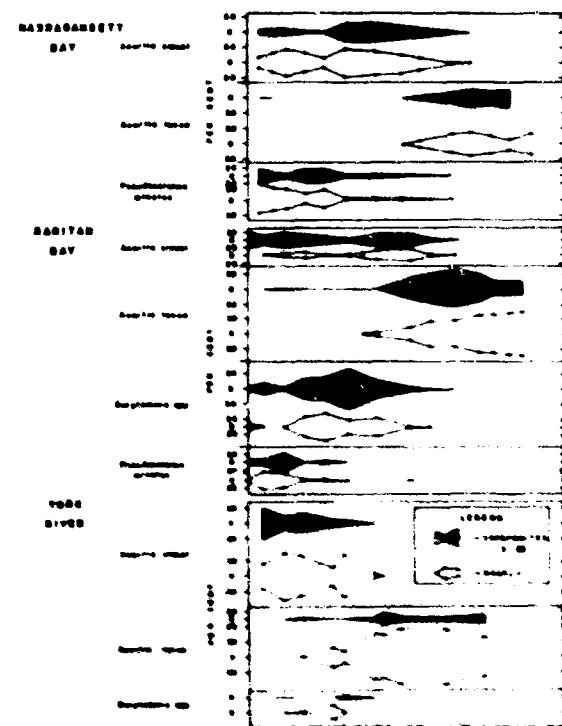


Fig. 3. Seasonal distribution of congeneric associates and *Pseudocalanus minutus* shown as percent of the total holoplanktonic copepods. Narragansett Bay, Raritan Bay (mean, Stations 5 and 6 at the mouth of the bay), and the York River, Virginia. Symmetrical plot around the time axis for visual emphasis. 1958.

preserved by the evolutionary process" (Slobodkin, 1962), it is appropriate to consider the biological processes sustaining competitive struggles for survival. Interactions often result when closely related species populations develop in the same place at the same time.

INTRAGENERIC RELATIONSHIPS

Classical competition theory—the Volterra-Gause-Lotka model—applies to the succession of *Acartia* populations during spring and early summer. At this time *A. clausi*, the winter-spring form, and *A. tonsa*, its summer replacement, reproduce at the same rate. These species are adapted for the specialized circumstances imposed by the estuarine environment, but they have different sensitivities to low salinity. *A. tonsa*, the less affected by low salinity (Larice, 1962, 1963), eliminates *clausi*, its northern counterpart, from the niche when temperature is still low enough for *clausi* to reproduce (Jeffries, 1962c). Because of the susceptibility of *clausi* to low salinity (11–16‰), succession starts well within an estuary when temperature becomes 13–17° C. Succession spreads seaward into more saline water where osmoregulatory burdens are less. Thus, changeover occurs progressively later, moving toward the ocean. Beyond the headlands, *tonsa* does not have an advantage until temperature becomes about 22° C. Since the ocean warms more slowly than an estuary during spring and summer, the lag between the two areas in species change-over can be considerable. It amounted to two and a

half months at two stations in Narragansett Bay separated by only ten miles. In the middle reaches of the bay, *clausi* was eliminated in July, but near the mouth succession did not start until September. Absolute temperature-salinity values for the interaction period differed between estuaries, but in all cases the higher the salinity, the greater the temperature necessary for *tonsa* to replace *clausi*.

Evolutionary implications can be drawn from these ecological distributions (Jeffries, 1962c), but the actual basis of the interaction—what the two species are competing for—is not understood. A clear-cut relationship with the phytoplankton in Raritan Bay was not apparent. A nutritional basis would be especially difficult to detect because phytoplankton and zooplankton populations differ greatly in generation times.

A very subtle interaction within a genus of copepods was shown by two species of *Eurytemora*. In Raritan Bay, specific differences in distribution indicated slight dissimilarities in fundamental niches, but, once again, only numerical relationships were seen, not the underlying biological mechanism which brought about the elimination of one species from a portion of the biotope where the niches intersected. Two species appeared in the Raritan during December, *E. americana* and *E. affinis*. The latter was identified as *hirundinoides* by Jeffries (1962b) from C. B. Wilson's (1932) account of the genus. This is wrong according to M. S. Wilson (personal communication), who kindly identified *affinis* in samples from two Rhode Island estuaries. Other records for *hirundinoides* on the East Coast of North America should probably be redesignated *affinis*, as suggested by M. S. Wilson (1959), leaving *americana* and *herdmani* as the only other representatives of the genus in this region. Structurally, the Rhode Island material sent to M. S. Wilson resembled specimens from both brackish and fresh waters in various parts of the United States. Engel (1962) recently found *affinis* in Lake Erie, the first recorded occurrence in the Great Lakes and their closely connected waters.

Even though the immature stages could not be distinguished, distribution of *Eurytemora* adults in Raritan Bay showed that *americana* outnumbered *affinis* during the first augmentation, which extended through February as water temperature dropped to the annual minimum (Fig. 4). *E. affinis* then began to proliferate in great numbers, overshadowing the previous *americana* generation. The *affinis* population in the mouth of the Raritan River (Station 1 in Fig. 4) became denser than in the more saline areas (Stations 5 and 6). Consequently, competition within the genus was most intense in low-salinity water, explaining the absence of a second *americana* generation. Downbay at Station 5, on the course of the net ebb current directed along the western shore (Jeffries 1962d), *affinis* did not become quite so abundant as it did in the head—the bay and *americana* persisted longer, developing a sizable second generation. In an even more saline area (Station 6) the influence of *affinis* on *americana* in the second generation was insig-

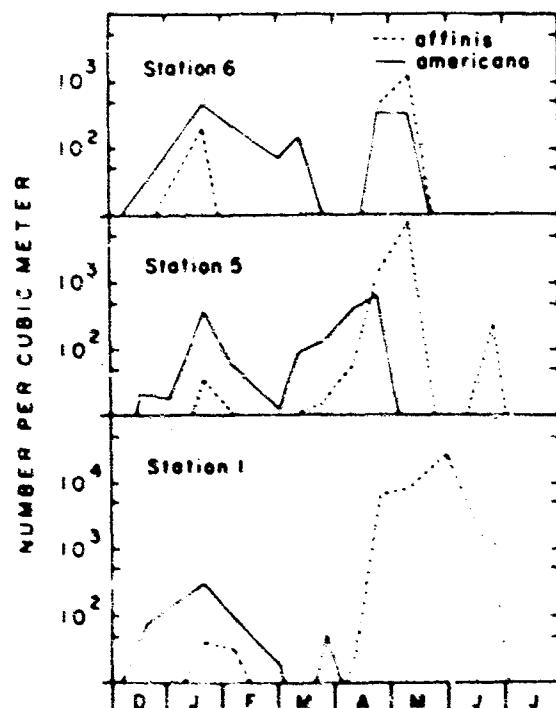


Fig. 4. Seasonal distribution of *Eurytemora americana* and *E. affinis* adults in Raritan Bay, New Jersey.

Table 2. Aspects of *Eurytemora* populations in Raritan Bay, New Jersey. Mean bottom temperature ($^{\circ}\text{C}$) and bottom salinity (‰) 1958. Critical ratios for the relative abundances of *affinis* and *americana* are indicated in boldface.

Property	Station		
	1	5	6
<i>E. americana</i> —order of last occurrence	1st (4/10)	2nd (4/24)	3rd (5/10)
Bottom temperature on above dates	7.0	12.2	10.1
Mean temperature, spring	13.4	12.4	11.6
Mean salinity, spring	16.5	19.8	20.7
Maximum population size attained (total copepodites and nauplii m^{-3})	205,500	117,300	48,960
Relative abundances <i>affinis</i> <i>americana</i> adults			
March 11	0.1	0.13	0.1
March 25	0.1	0.13	0.1
April 10	3.67	0.14	0.45
April 24	1.0	1.86	1.03
May 10	1.0	1.0	3.50
May 30	1.0	1.0	0.0

ther reduced. Here, both species produced similar numbers in the second generation.

Table 2 further demonstrates the pattern of succession. It started in the head of Raritan Bay (Station 1) in early April. Weeks later, when *americana* finally disappeared at the more saline downbay Stations 5 and 6, the water had warmed considerably. Consequently, succession took place at higher temperatures near the mouth of the bay than within its inner reaches. Relative abundance of the two species immediately before the disappearance of *americana* suggested an interaction with the rapidly developing *affinis* population. After the *affinis*-*americana* ratio increased to 1.9-3.7, a critical figure (indicated by boldface type in Table 2), *americana* was no longer seen. This ratio was attained on April 10 in the head of the bay and successively later in the progressively more saline areas. Salinity thereby damps the differential effect of rising temperature on the two species.

The spread of seasonal succession from the head of the bay toward the ocean did not appear related to phytoplankton distribution nor dynamics. *Skeletonema costatum*, the dominant late-winter diatom in Raritan Bay (Patten, 1962), was extremely abundant during the interaction period. Similarly, at the mouth of the bay, persistence of *americana* in the northern sector (Station 6) after it had disappeared from the southern sector (Station 5) could not be explained by the type nor amount of phytoplankton that occurred during the interaction period. *Leptocylindrus danicus*, *Rhabdonema setigerum*, *Thalassionema nitzschiae*, and *Asterionella radiata* had similar cell densities in both sectors during the critical period from April 10 to

May 10. Local factors, such as regional differences in currents, flushing, and stratification, apparently work with vernal warming and the spatial distribution of salinity to influence the rate at which the critical ratio is attained. However, the basic mechanism is not understood.

A schematic representation of this succession of events is shown in Figure 5. The four diagrams indicate progressive stages: (1) the initial *americana* population develops in the head of the estuary and spreads oceanward; (2) *affinis* then appears in the same general area and competes with *americana*; (3) *americana* is eliminated from low-salinity waters, and interaction enters a final phase in the more saline area near the mouth of the embayment; and (4) succession is complete, leaving *affinis* throughout the embayment. These stages take place from December through June. In late spring, following stage (4), the *affinis* population retreats toward the inner end of the estuary, where salinities of from 5 to 15 ‰ are optimal for *Eurytemora* (Jeffries, 1962b). When summer begins, continuous warming, coupled with changes in the phytoplankton from a predominantly diatom community to a chlorophyte-flagellate association, probably cause the rapid death shown in Figure 4.

This pattern has many points in common with the *Acartia* interaction. *E. americana* and *A. clausi* occur during winter. As temperatures rise, the second member of each pair, *E. affinis* and *A. tonsa*, augments near the inner end of an estuary. Competition results from the simultaneous propagation of congeneric species. The "pioneer" species in each genus is eliminated because the successors are better adapted to low salinity. Downbay, in more saline waters, this advantage is cancelled, causing a delay until high temperatures bring about succession. This mechanism insures that production remains high at the secondary level in spite of drastic fluctuations in the phytoplankton.

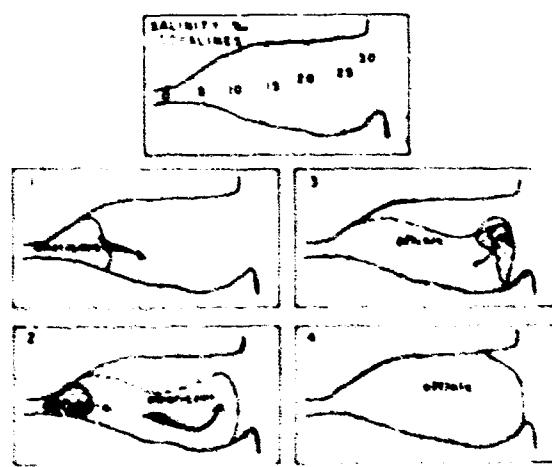


Fig. 5. Succession of *Eurytemora* species in a hypothetical estuary. Stages 1 to 4 represent progressively later phases, starting in December and terminating in late June.

COMPETITION BETWEEN CLOSELY RELATED SPECIES RESULTING IN EFFICIENT UTILIZATION OF THE BIOTYPE

A successful competitor extracts raw materials and energy from the environment with greater overall effectiveness (but not necessarily greater efficiency in a metabolic sense) than the loser. The mechanism used to exploit an environment and maintain a product in a competitive situation is bounded by two extremes, applying in principle to a manufacturing corporation in a free economy as well as to a population in nature. At one extreme, the system conserves raw material and processes it with maximum efficiency. At the opposite extreme, the system devours basic substances with no regard for supply, extracting small amounts from large quantities. Somewhere between these extremes, cost of supply and efficiency of utilization strike a balance. Here, the successful system achieves maximum effectiveness or optimum efficiency. For example, when food is scarce for a copepod or iron ore is expensive for a steel mill, efficiency should be increased to obtain the optimum balance; when raw materials are abundant, it is cheaper to run the machinery at a lower efficiency with more raw materials. In a manner analogous to a successful corporation, a natural population achieves the balance by a "decision-making process" which evolutionary experience under complex conditions has proved rewarding. From the stratification of phytoplankton, Patten (1963a, b) deduced a "profit motive" related to maximum energy gain; plankton communities exhibit goal-seeking, "the goal being biomass maximization".

Thus, a balance between the cost of acquisition and the cost of utilization results in maximum power output from the niche. According to Odum and Pinkerton (1955), "natural systems tend to operate at that efficiency which produces maximum power output". A system producing a lot for its size will gain the advantage in competition. Congeneric pairs of species do exactly this; they extract the raw materials of life from their environment with minimum waste. The optimum efficiency for power output in a rich environment is probably quite low. Consequently, sources of supply must be constant as well as abundant. But they are neither qualitatively nor quantitatively constant in an estuary. Congeneric associates compensate for this, however, by competing for common resources at times of the year when the biotope is least stable, wasting a minimum in acquiring the maximum. A good method of acquisition supplies metabolic machinery, operating at a relatively low efficiency with sufficient raw materials to develop tremendous power output. Congeneric associates have been preserved through evolution because struggles for a common resource help to meet the demands of an expensive but highly adapted metabolism.

Hutchinson's (1937) application of set theory to the niche concept further illustrates the way in generic associates derive maximum benefit with minimum waste in acquisition. In Patten's (1962) nota-

tion, applied to the phytoplankton of Raritan Bay, the physical space of a biotope, β , is subdivided into separate portions called "realized niches" by the ecological requirements of the species it supports. The hyperspace occupied by an individual of a species s_i is $\Delta\beta$, the specific biotope; thus, the total space occupied by a population with n individuals is $n_i\Delta\beta$. The "fundamental niche" encloses a multidimensional phase space in which every point represents some need the organism places upon the biotope for its continued existence. The realized niche can be smaller than the fundamental niche when: (1) the biotope is marginal, or (2) the intersection subset of points common to s_1 and s_2 is sizable. Competition for this portion of the biotope terminates in the elimination of one species.

Populations shift back and forth in space and abundance as seasons change and long-period cycles exert their influence. Throughout these changing conditions, maximum power output from the ecosystem will be attained when the specific biotopes add up to the volume of the entire biotope, that is, there are no interstices or void spaces going to waste between the specific biotopes. The most convenient way to minimize the chance of gaps along a biotope gradating from marine to fresh water and from summer to winter is achieved when two species compete for a niche. For example, when a seasonal change in temperature slows the reproductive rate of one member of the pair, diminishing its utilization of the biotope and thereby decreasing its overall power efficiency, the other species in the genus responds to conditions that have now become favorable for it to proliferate. A high level of production is thereby maintained in the richly endowed yet very demanding estuarine environment.

The biotope achieves equilibrium when all the usable sites are occupied (Patten, 1962). The biotope universe is then "perfectly partitioned into non-overlapping subsets by the m species present," and thus:

$$\beta = \sum_{i=1}^m n_i \Delta \beta$$

Perfect equilibrium may represent the limit a natural system can attain in generating power. Dominance by congeneric associates is the most practical and efficient way to achieve maximum power output, from the aspect of supplying raw materials to living systems. It is significant that neritic and estuarine zooplankton show the property to such a marked degree. Within the segment of the biotope available to filter-feeding zooplankton, the energy sites are saturated with organisms in spite of constant environmental change.

Success and preservation of congeneric associates are ultimately the expression of selective pressures on genetic mechanisms. When a single genetic combination could not provide sufficient variation for wide scale exploitation of the environment and still maintain a system efficient enough to cope with competitors, additional types adapted to segments of the range evolved. A chain of related species populations

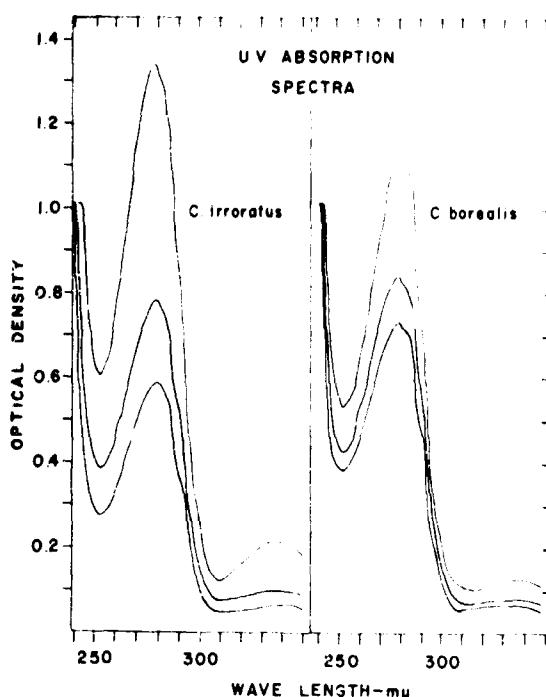


Fig. 6. Ultraviolet absorption spectra of sera from *Cancer irroratus* and *C. borealis*; 1/100 dilutions of clear supernatant from centrifuged samples, 1 cm light path; maximum absorbance at 278 m μ . Typical spectra; crabs obtained during summer, 1962.

resulted, one member interconnecting with another along the axis of the gradient. Greater opportunity for continued success was achieved when a species was able to diversify genetically throughout a heterogeneous environment and utilize additional portions of the total biospace. Genetic variability can, therefore, increase the specific biotope and power output of an estuarine species to a marked extent. An ecological mosaic, discussed by Mayr (1963), is formed by the spread of separate genotypes into new habitats. According to Ludwig's (1950) theorem, a newly formed ecological variety fares better in a newly invaded portion of the biotope than it would in the fundamental niche of the parent species; that is, in the original habitat the new genotype would be repressed, but in the absence of competition in another portion of the environment, it would prosper. Penetration of inland lakes by *Eurytemora affinis* might represent radiation of this sort. Even though morphologically similar to estuarine specimens from Rhode Island, freshwater populations may have a different genotype.

MEASURES OF ECOLOGICAL DIFFERENCE

It is appropriate to consider the structural, chemical, and behavioral differences that permit coexistence under various environmental conditions. Situations in nature where interactions regulate distribution and abundance are common. Readily measured rates and

densities document the phenomenon, but these numbers are abstractions—gross reflections of individual properties. Subtle differences can collectively culminate to make one species perform better than its competitor in a particular situation. Slobodkin (1962) states: "What is not yet clear is the degree of ecological difference required to permit coexistence, and we are not even sure how this difference should be measured."

Measuring these differences in marine copepods is hard. Maintenance of a holoplanktonic copepod species in culture has not been reported. Thus, all experimental laboratory work has been done on dying populations, hardly an appropriate system for studying phenomena intimately associated with life. In addition, a copepod's small size makes many physiological approaches impractical. Phytoplankton must be grown and presented in living condition, a further difficulty complicating practical investigation. A temporary expedient that may tell something about the problem is to use benthic crustaceans.

Several comparisons were made with *Cancer* crabs from Narragansett Bay. Morphological, physiological, and biochemical characteristics allow the two species to partition the environment spatially; they co-exist on distinctly different bottoms in the same general area. *C. borealis*, the slow-moving, heavy-clawed member of the pair, occurs in rocky areas where it leads a reclusive life hiding between stones. In this habitat it is admirably suited to fight a defensive role with its powerful claws. On sandy sediments, a flat, exposed tract requires that an epibenthic form possess a high degree of mobility to scurry in, out, and around the bottom to seek food and escape predators. *C. irroratus* can exploit this habitat; it has (1) an ability to walk for prolonged periods; (2) relatively light but efficient claws suitable for tearing tissues, but not sufficiently heavy to cause a burden when the crab is fleeing; and (3) high concentrations of serum phosphate, possibly supporting high levels of muscular activity.

The sera of both species are qualitatively very similar. Figure 6 shows ultraviolet absorption spectra of 1/100 dilutions in distilled water. Both species have a peak at 278 m μ , probably caused by aromatic amino acid moieties (Sizer and Peacock, 1947). Serum from both species was lyophilized, cast in KBr pellets, and examined for infrared absorption. Freshly caught specimens of both species had identical spectra (Fig. 7A, C), but a crab obtained during winter and held in a live-car for a month produced an atypical pattern (Fig. 7B). This crab also had very low serum nitrogen and an abnormal ultraviolet spectrum, showing greater absorption at 270 m μ than at 280 m μ .

Locomotor abilities of the two species were compared by forcing them to walk for prolonged periods in rotating jugs. Motor-driven rollers turned a 12-gallon jug in a water bath at 2.73 rpm, equal to a linear distance of 3.45 m/min. Locomotor ability was determined by the percentage of a 5-min observation period during which the crab actively walked.

Overall performances for 96-hr trials were compared by calculating integral mean activities. *C. irroratus*, the species restricted to an exposed habitat, had integral mean activities from 5 to more than 1,000 times greater than *borealis* (Fig. 8). *C. irroratus* walked best at 14° C. while *borealis* probably had a lower optimum near 6° C. The difference agrees with distributions in nature. Although latitudinal ranges of the two species are the same, extending from Newfoundland to Florida (Rathbun, 1930), *irroratus* appears to congregate in warmer waters than *borealis*. In keeping with the generally recognized fact that warm temperatures favor osmoregulation in decapods (Williams, 1960; Panikkar, 1940), *irroratus* is also the more estuarine member of the pair, especially in the southern portion of its range where it penetrates lower Chesapeake Bay, while *borealis* is limited to the cooler offshore waters.

In Narragansett Bay, *irroratus* rarely strays off a sand substrate. If *borealis* and perhaps the lobster, another heavy-clawed recluse, could be removed from the bay, *irroratus* would extend its range from sandy sediments into rough bottom. The opposite situation, removing *irroratus* from the bay, might not extend the range of *borealis* into sandy areas unless predatory fish were also taken away.

Seasonal change and major events in the life cycle modify this relationship. One example occurs in winter after the major portions of the two populations have moved offshore, leaving behind weak individuals with low serum nitrogen concentrations and one or more appendages missing. In this condition, *borealis* moves to sandy sediments and digs in, emerging occasionally to feed. With the exception of these brief periods of activity, low winter temperatures keep populations in a dormant condition, eliminating interac-

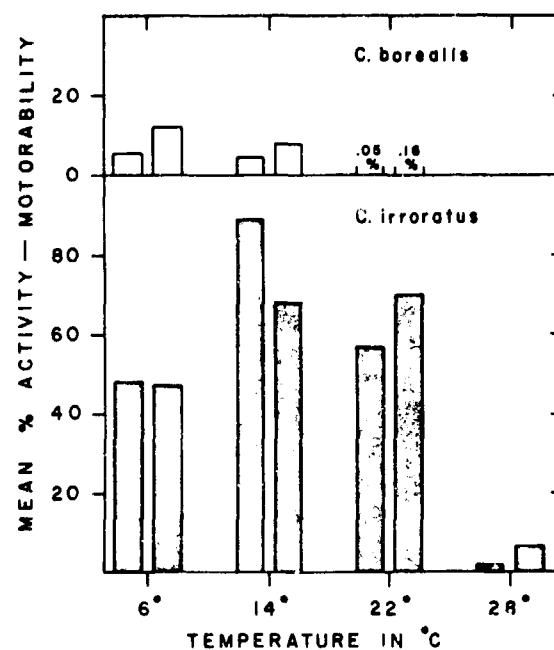


Fig. 8. Relative abilities of *Cancer irroratus* and *C. borealis* to walk for prolonged periods at various temperatures. Integral means summarize individual activity determinations during a 96-hr period; throughout the course of an experiment, activity was measured as the percent of a 5-min observation period during which the crab actively walked.

tion. During early spring, molting and reproduction by *borealis* occur. The few *irroratus* overwintering in the bay either die before spring or do not molt. By the time the first wave of *irroratus* returns from the ocean, *borealis*, which spent the winter dug into the sand, has molted and moved back to rocky substrates where it will be joined by migrants from the ocean. Perhaps this is an "escape in time" (Slobodkin, 1962) during the winter, but more important, the two species partition the fundamental *Cancer* niche into separate realized niches during the important phases of their life cycles. Low temperature may favor *borealis* in winter, but sluggish metabolism at this time precludes any tendency for a temperature-induced instability to become established between species.

The opposite holds for the *Acartia* populations as they alternate between summer and winter cycles of abundance. In an actively mixed water column, escape in space is not possible, and since 3-6 generations of *A. tonsa* are produced from late spring through fall (Jeffries, 1962c), the periodicity of environmental fluctuation is considerably longer than the generation time. As a result, competition leads to an escape of *A. clausi* in time until early winter, when *A. tonsa* becomes very scarce and temperature once again favors the northern member of the genus.

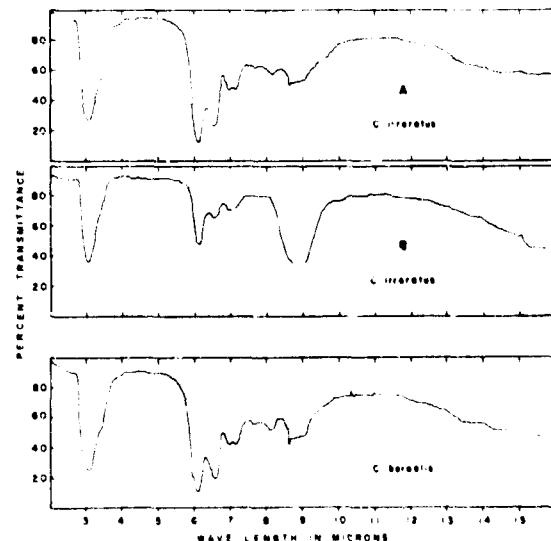


Fig. 7. Infrared absorption spectra of lyophilized *Cancer* sera. Crab B, the middle graph, had an atypical ultraviolet spectrum showing greater absorption at 270 m μ than at 280 m μ .

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LITERATURE CITED

- BARLOW, J. P., 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biol. Bull.*, 109:211-225.
- DAY, J. H., 1951. The ecology of South African estuaries, Part 1. A review of estuarine conditions in general. *Trans. Roy. Soc. S. Africa*, 33:53-91.
- DEEVEY, G. B., 1948. The zooplankton of Tisbury Great Pond. *Bull. Bingham Oceanog. Coll.*, 12:1-44.
- DEEVEY, G. B., 1952a. A survey of the zooplankton of Block Island Sound, 1943-1946. *Bull. Bingham Oceanog. Coll.*, 13:65-119.
- DEEVEY, G. B., 1952b. Quantity and composition of the zooplankton of Block Island Sound, 1949. *Bull. Bingham Oceanog. Coll.*, 13:120-164.
- DEEVEY, G. B., 1956. Oceanography of Long Island Sound, 1952-1954. V. Zooplankton. *Bull. Bingham Oceanog. Coll.*, 15:113-155.
- DEEVEY, G. B., 1960. The zooplankton of the surface waters of the Delaware Bay region. *Bull. Bingham Oceanog. Coll.*, 17:5-53.
- EKMAN, S., 1953. *Zoogeography of the Sea*. Sidgwick and Jackson, London.
- ENGEL, R. A., 1962. *Eurytemora affinis*, a calanoid copepod new to Lake Erie. *Ohio J. Sci.*, 62:252.
- FARRAN, G. P., 1948. Genus: *Acartia*. Fiches d'Identification du Zooplankton. Zooplankton Sheet 12. *Conseil Perm. Intern. Exploration Mer.*
- FISH, C. J., 1925. Seasonal distribution of the plankton of the Woods Hole region. *Bull. U. S. Bur. Fisheries*, 41:91-179.
- HUTCHINSON, G. E., 1957. Concluding remarks. Cold Spring Harbor Symposium. *Quant. Biol.*, 22:415-427.
- JACOBS, J., 1961. Laboratory cultivation of the marine copepod *Pseudodiaptomus coronatus* Williams. *Limnol. Oceanogr.*, 6:443-446.
- JEFFRIES, H. P., 1962a. Copepod indicator species in estuaries. *Ecology*, 43:730-733.
- JEFFRIES, H. P., 1962b. Salinity-space distribution of the estuarine copepod genus *Eurytemora*. *Intern. Rev. Hydrobiol.*, 47:291-300.
- JEFFRIES, H. P., 1962c. Succession of two *Acartia* species in estuaries. *Limnol. Oceanogr.*, 7:354-364.
- JEFFRIES, H. P., 1962d. Environmental characteristics of Raritan Bay, a polluted estuary. *Limnol. Oceanogr.*, 7:21-31.
- LANCE, J., 1962. Effects of water of reduced salinity on the vertical migration of zooplankton. *J. Marine Biol. Assoc. U. K.*, 42:131-154.
- LANCE, J., 1963. The salinity tolerance of some estuarine planktonic copepods. *Limnol. Oceanogr.*, 8:440-449.
- LUDWIG, W., 1950. Zur Theorie der Konkurrenz. Die Annidation. (Einnischung) als fünfter Evolutionsfaktor. *Neue Ergeb. Probleme Zool.*, pp. 516-537. Klatt-Festschrift, 1950.
- MAYR, E., 1963. *Animal Species and Evolution*. Harvard Univ. Press, Cambridge, Mass.
- ODUM, H. T., and R. C. PINKERTON, 1955. Time's speed regulator: the optimum efficiency from maximum power output in physical and biological systems. *Am. Scientist*, 43:331-343.
- PANIKKAR, N. K., 1940. Influence of temperature on osmotic behavior of some Crustacea and its bearing on problems of animal distribution. *Nature*, 146:366-367.
- PATTEN, B. C., 1962. Species diversity in net phytoplankton of Raritan Bay. *J. Marine Res.*, 20:57-75.
- PATTEN, B. C., 1963a. Plankton: optimum diversity structure of a summer community. *Science*, 140:894-898.
- PATTEN, B. C., 1963b. The information concept in ecology: some aspects of information-gathering behavior in plankton. In *Information Storage and Neural Control*, edited by W. S. Fields and W. Abbott; pp. 1-33. C. C. Thomas, Springfield, Illinois.
- RATHBUN, M. J., 1930. The cancerid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. *Bull. U. S. Natl. Museum*, 152:1-609.
- SIZER, I. W., and A. C. PEACOCK, 1947. The ultraviolet absorption of serum albumin and of its constituent amino acids as a function of pH. *J. Biol. Chem.*, 171:767-777.
- SLOBODKIN, L. B., 1962. *Growth and Regulation of Animal Populations*. Holt, Rinehart and Winston, New York.
- SPOONER, G. M., and H. B. MOORE, 1940. The ecology of the Tamar estuary. VI. An account of the microfauna of the intertidal muds. *J. Marine Biol. Assoc. U. K.*, 24:283-330.
- WILLIAMS, A. B., 1960. The influence of temperature on osmotic regulation in two species of estuarine shrimps (*Penaeus*). *Biol. Bull.*, 119:560-571.
- WILSON, C. B., 1932. The copepods of the Woods Hole region, Massachusetts. *Bull. U. S. Natl. Museum*, 158:1-635.
- WILSON, M. S., 1959. The Calanoida. In *Ward and Whipple's Freshwater Biology*, (2nd Ed.), edited by W. T. Edmonson; pp. 738-794, 858, 859. John Wiley and Sons, New York.
- WILSON, M. S., and J. C. TASH, 1966. The euryhaline copepod genus *Eurytemora* in fresh and brackish waters of the Cape Thompson region, Chukchi Sea, Alaska. *Proc. U. S. Natl. Museum*, 118(3534):553-576.

Mathematical Models for the Interpretation of Inshore Plankton Communities

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The general concepts discussed in this paper are applicable to almost any ecological situation, and not merely to estuarine plankton. The data I have available, however, are mostly concerned with inshore or estuarine plankton, since most of my experimental work has been carried out in that sphere of study. The basic mathematical models are not new; they have been used for many years in other fields, notably psychology and taxonomy, but only very recently in ecology.

When an old model is applied to a new situation, it is almost inevitable that some adjustments will have to be made, and the application of multivariate analysis in ecology is very much in its infancy. Suitable exploratory data are not always easy to collect, and theory and speculation are often ahead of information.

For many years, quantitative ecologists have sought means of digesting complex ecological data so that it can be interpreted in terms of communities or other ecological units, rather than as individual species. Broadly speaking, diversity and affinity are the two approaches to this problem. The diversity approach has been used in terrestrial ecology by many workers, notably in the famous mathematical model of Fisher *et al.* (1943), though Margalef (1961) seems to be among the few who have successfully applied diversity indices to plankton populations. My own experience is that diversity is rather difficult to interpret in plankton ecology, because the index is very sensitive to the influence of those dense monospecific blooms which come and go rapidly. Thus a diversity index is not a "conservative property" of a population as it has appeared to be in some terrestrial work (Williams, 1944).

The second approach, based on affinity, seems to be more compatible with the community concept in ecology. Fager and McGowan (1963) have used a non-parametric method to distinguish "concurrent groups"; that is, groups of species which are found together in the same sample more often than not. This method is particularly useful for large-scale geographic investigation, since it is relatively insensitive to variations in the quantitative accuracy of samples, so that data from different sources can be synthesized. My own preference has been for quantitative records in which the actual numbers per unit space of each species or form are used in the analysis. I also prefer to use relatively small samples, and to count the entire sample. This is theoretically satisfactory if one assumes that rare species are relatively unimportant to

the analysis. However, it does raise the difficulty that a species which is numerically rare may be relatively large and, therefore, abundant in its contribution to the biomass.

Diversity and affinity analyses are not necessarily incompatible methods for handling the same set of data. Margalef (1962) and I (Cassie, 1961a) have both analyzed some plankton data collected by Vittorio Tonolli for Lake Maggiore, and I hope we have made useful and complementary contributions to its interpretation.

MATHEMATICAL MODELS

The response of organisms to ambient variations in the physicochemical properties of their environment usually seems to follow an exponential relationship, $Y = a \exp(\beta x) + \epsilon$, where Y is the number of organisms per unit space, x is a physicochemical property of the environment, a and β are constants, and ϵ is an error term. This is a reasonable sort of relationship which has analogies with the physical laws. Thus, for example, a warmth-loving animal will increase its reproductive rate in a warmer location, or increase its rate of immigration to a warmer location, and hence increase its numbers by a fixed proportion rather than by a fixed number for any given increase in temperature. This relationship cannot be extrapolated indefinitely because few, if any, organisms can live in boiling water, but, within the normal ambient range of the temperature equation above, it is probably true more often than not.

Environments are seldom, if ever, strictly homogeneous, so that what passes for a uniform body of water is actually a mosaic of physical properties, all of which vary continuously and randomly, both in space and time. The pattern, though random, will not be wholly indeterminate, but, if measuring techniques were available, it could be described by fixed parameters. For example, Liebermann (1951) has shown that the temperature of ocean water varies continuously with a mean amplitude of the order of 0.04°C , and a correlogram which decays to $1/e$ in about 60 cm. Taking the whole gamut of physical properties and compounding the effect of their ambient fluctuations on the physiology and behavior of plankton, we have what might be described as a "dispersion factor". Generalizing the temperature equation above, we can make x represent this factor. Since there is no absolute scale for x , it is convenient to treat it as a standardized deviate, that is, to make the mean zero,

and the standard deviation unity. The spatial scale presents another problem, particularly in estuarine waters, where the correlogram may not present the same simple exponential decay curve as in the open ocean. For the time being we will make the simplest assumption—that x , being composed of a large number of small random factors, will be normally distributed.

If the dispersion factor influences the plankton in the manner of the above equation, it may be shown that the actual dispersion of organisms will have the negatively skewed distribution commonly described as "log-normal", because a logarithmic transformation is necessary to convert it to normal. The actual dispersion will not be exactly log-normal, because of the error component, ϵ . If the environment is the only causal factor influencing dispersion, ϵ will be a Poisson variate. Both the log-normal and Poisson components arise from random causes, and it would be reasonable to describe both of them as random distributions. In dealing with small samples, the superimposition of these two patterns produces considerable statistical difficulties (Cassie, 1961b), but provided we can think in terms of relatively large numbers of individuals, the Poisson effect can be ignored, and I will do so for the remainder of my discussion. The term "random variation" will then apply to the log-normal distribution induced by the dispersion factor, while "determinate variation" will refer to variation induced by non-random changes in the environment, taking the form of gradients, discontinuities, or a combination of both.

If $\log y$ is the standardized form of $\log Y$, we find that: $\log y \sim x$, that is, the standardized log transform of the sample count is an estimate of the dispersion factor. The log transform implies that a given geometric change in population density has the same significance regardless of absolute population density.

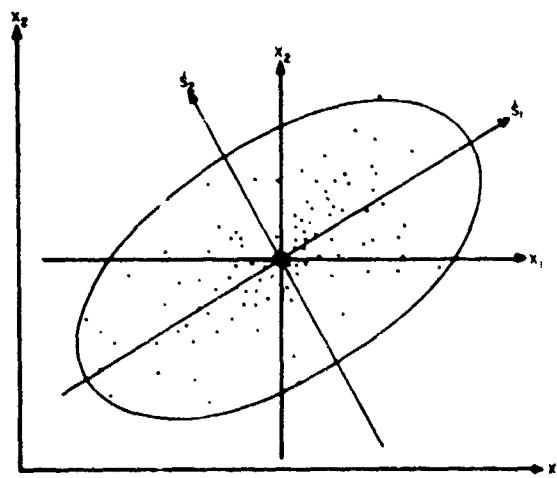


Fig. 1. Scatter diagram of the distributions of two correlated dispersion factors X_1, X_2 representing the distribution of two species of plankton, and showing the two new axes f_1, f_2 derived by principal component analysis. (From Cassie, 1963).

Standardization implies that the significance of a given change in population density is inversely proportioned to the overall variability of the species. The first of these two concepts is fairly easy to accept; the second a little less so, particularly when the relative allocation of random and determinate components is in doubt. There might be some argument for using non-standardized logarithms, or some form of weighting factors, but only experience will tell which is most effective.

Since the most powerful and comprehensive branch of statistical theory deals with normal distributions, it is appropriate to think in terms of the transformed rather than the raw data. Having derived the distribution of an individual species, we must now look for a means of representing a "community". Whether the mathematically defined community will correspond exactly to the terrestrial or benthic ecologist's concept remains to be seen, but we will retain this as an objective.

Figure 1 shows the dispersion factors, x_1 and x_2 (estimated in practice by $\log y_1, \log y_2$) of two species. Mathematically it is almost as easy to consider three or more species, but we are confined to two dimensions for graphic representation. The normal distribution still exists, not only along the x axes, but along any linear section through the scatter diagram. The elliptical envelope enclosing the points is the 99 percent probability level. We could, if necessary, draw a whole series of concentric probability contours at other levels. If the two species were distributed independently, that is, if they belonged to two separate communities, the envelope would be circular. As it is, the species are positively correlated, so that the ellipse has its major axis tilted upward to the right. We thus have some grounds for saying that the two species form a single community, and we could represent fluctuations in the density of this community by measurements along the longer axis of the ellipse. It is not clear what we should say if the correlation was negative, but so far I have found so few cases of negative correlation that the problem scarcely exists. If we have n species in the ecological complex, these can be represented by an imaginary diagram in n dimensions, or by an $n \times n$ correlation matrix. By principal component analysis (Kendall, 1957) we can define a new set of n axes, in such a way that axis 1 is the longest possible, axis 2 the next longest, and so on. Each community is represented by an axis. We could, of course, have n communities, but this would not simplify our data at all. In practice some of the smaller axes contain so little useful information that we can ignore them. There is no real statistical criterion of how many axes to reject, but a decision can usually be made on the basis of how much meaningful biological information is contained. The mathematical description of an axis is shown below by a "latent root" and a "latent vector":

[3.0] [.40 .49 .56 .52 .02 .13]

The root, 3.0, measures the variance; its square root

is proportioned to the length of the axis between given probability levels. The original x axes all have a variance of 1, so that this particular axis represents three times as much information as would be given by any single species. The vector elements are scaled so that the sum of their squares is 1, and their magnitudes with respect to each other give the relative importance of the various species members of the community. The decision as to which of the species can be considered dominant members of the community is partly subjective, but in practice I have found this decision fairly easy. For example, it is evident that species 1 to 4 are dominants, while 5 and 6 can be ignored. There is no reason why any species should not be dominant in more than one community, but it would usually seem unnecessary to use more dimensions than are required to ensure that no species remains unassigned to at least one community. If the physical structure of the environment is known in sufficient detail, it is possible to establish a second significant category by correlating communities with physical factors. Williamson (1961) found that in a 23-species complex of plankton, four components, or communities, accounted for 83 percent of the total variance, and that three of these four components were highly correlated with known hydrological features of the North Sea.

APPLICATION TO ESTUARIES

How does the foregoing apply to an estuarine population? Going back to the original model, we find that we have postulated a random dispersion factor. The most significant physical feature of an estuary is the determinate gradient of properties between river and sea. In some cases there may also be abrupt discontinuities in this gradient produced by the interaction of tides and topographical features. Such discontinuities produce sampling problems because they are dynamic and move with the tidal cycle. Non-random features such as these cannot be thrown indiscriminately into a random model. At this point we are faced with some of the difficulties of procedure which I have previously mentioned. I have used two approaches:

1. To pool all data and proceed directly with the principal component analysis, leaving the extraction of determinate effects to a later stage. This is a risky procedure, but sometimes it works.
2. To extract, as far as possible, the determinate effects from the raw data and then to proceed with principal component analysis. At present this separation is done after the data have been collected, but it appears that special sampling programs may be necessary to achieve the best results.

To illustrate the two methods, I will give the examples of Port Nicholson (Wellington Harbor) (Fig. 2) where there is an abrupt transition from oceanic to harbor water, and Pelorus Sound (Fig. 3) where the gradient of salinity and related properties is more gradual. In both cases sampling commenced at the

mouth of the estuary and continued in approximately a straight line towards the headwaters. The results of the two principal component analyses appear in Table 1.

We will refer to "forms" rather than species, because in some cases the different life stages of the same species are listed separately. Method 1 shows several features in common between the two examples. In both examples, all forms can be represented by three vectors, and (coincidentally) the roots of these three vectors represent 83 percent of the total variance. The first vector shows the dominants (in bold type) to be about two-thirds of the total number of forms, and the root is about half of the total variance. It is also the only vector showing a strong negative correlation with salinity: -0.92 for Port Nicholson and -0.82 for Pelorus Sound. The second and third vectors represent two single-form communities for Port Nicholson, and two two-form communities for Pelorus Sound. The single-form communities in Port Nicholson are interesting in that both of them are almost entirely independent of all other species, as well as of salinity. This is quite consistent with their biological nature, as one is a polychaete larva, the other a shorter-lived phytoplankton bloom; both of them are relatively ephemeral members of the plankton and they have not had time to be exposed to the same factors controlling the dispersal of the permanent species. The first two-form community in Pelorus Sound is a fairly obvious association of the adult and juvenile stages of the same species. The second is less predictable, since it contains two entirely different taxonomic groups, a polychaete, and a cirripede; the only common feature is that both are larvae of sedentary species.

In the second method, the determinate effects are removed by converting the zero-order correlation matrix to a partial correlation matrix, independent of salinity for Port Nicholson, and independent of salinity and temperature for Pelorus Sound. Of the latent vectors, only the first seems meaningful for our present discussion. In both cases the latent root has been substantially reduced, but the same elements are still recognizable. For Port Nicholson we find exactly the same four-form community as before, indicating that, although salinity preference is one factor uniting these forms, there are other common factors even when the salinity effects are removed. We cannot decide what these factors are without further information—they may be environmental or they may be a direct biological association between the forms. For Pelorus Sound the situation is a little different. The first vector now combines the nine forms which were previously divided between the first two vectors. The two forms, previously appearing as dominants in the second vector, are adults and copepodites of *Paracalanus parvus*. All but two of the seven forms from the original first axis are copepod adults and larvae. I have found in previous investigations that *Paracalanus* usually is most abundant in higher-salinity water, in contrast to the other species which are usu-

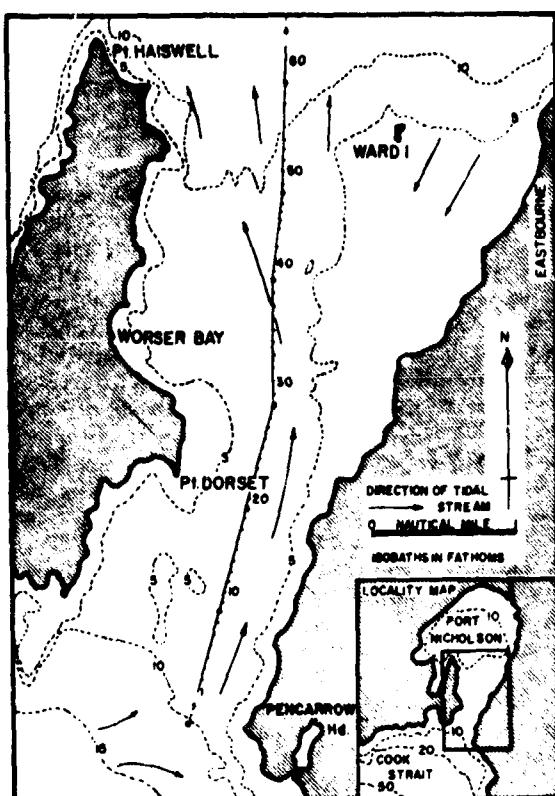


Fig. 2. Locality map showing the position of samples in Port Nicholson. Dots indicate the beginning and end of samples, and the lines joining them represent the course of the ship. Circled dots are radar fixes (From Cassie, 1960).

ally located inshore and are associated with lowered salinities. This has recently been confirmed in a personal communication by Jillett of the Zoology Department, University of Auckland, working in Auckland Harbor. *Paracalanus* is known as an oceanic species and is only an occasional visitor to harbor waters. It is relatively common in these two estuaries, mainly because both open almost directly into the deep oceanic waters of Cook Strait, with little intervening continental shelf. Though *Paracalanus* and the other copepods have different reactions to salinity, it seems that, perhaps because of their taxonomic relationship, all have similar reactions to other factors.

Which is the correct answer—the first or the second method? I feel that neither is completely right or wrong and that both give useful and complementary information. This emphasizes that a community cannot be reliably defined without reference to the nature and extent of the environment. Within a body of water either of uniform salinity or of such small dimensions that salinity changes are slight, *Paracalanus* might be indistinguishable from the general copepod community. However, when the survey area contains both oceanic and harbor waters of sufficiently contrasting properties, the semi-oceanic *Paracalanus*

will inevitably form a distinct community, at least in the terms of our mathematical definition. The affinity with other copepods remains, but is masked by the predominant salinity effect.

It is often a useful expedient when interpreting complex data to present the information in graphic form. In a multivariate distribution it is not possible to present all the information in a single two-dimensional graph. However, in the two examples (using the first method) two-thirds of the information is contained in the first two vectors, and this information may be plotted as a scatter diagram (Rao, 1952). Owing to the influence of non-random factors, the scatter of points cannot be contained within any single elliptical envelope (Figs. 4 and 5). There is, however, a clustering of points into distinct groups of approximately elliptical shape. For Port Nicholson (Fig. 4) there are three such clusters, corresponding respectively to samples 1-34, 35-45, and 46-60. Cluster 2 is attributable to a discontinuity along the second (ζ_2) axis and can be traced to a swarm of *Polydora* larvae embracing these samples. Along the first (ζ_1) axis, clusters 2 and 3 overlap considerably and can be treated as a single cluster which is entirely separate from cluster 1. The discontinuity between samples 34 and 35 can be traced to the boundary between oceanic and harbor waters.

In Pelorus Sound there are no such natural bound-

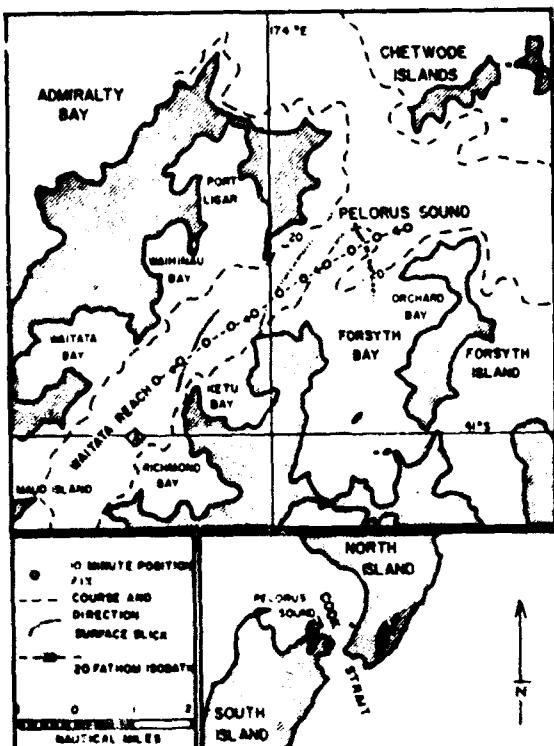


Fig. 3. Locality map showing the position of samples in Pelorus Sound. The circles represent fixes, taken at every tenth sample. The opening of Pelorus Sound is adjacent to arrow.

Table 1. Latent roots and vectors from a principal component analysis of correlation matrices of log transformed plankton counts from samples in Port Nicholson and Pelorus Sound, New Zealand. In Method 1, roots and vectors are computed from zero-order matrices; in Method 2, from partial correlation matrices independent of salinity (and of temperature for Pelorus Sound).

Port Nicholson				
LATENT ROOTS:	Method 1		Method 2	
LATENT VECTORS	3.0	1.0	1.0	1.8
1. <i>Paracalanus parvus</i>	.40	-.10	-.04	.57
2. <i>Elminius modestus</i> nauplii	.49	.01	-.12	.32
3. <i>Oithona similis</i>	.56	-.02	-.04	.59
4. <i>Coscinodiscus wailesii</i>	.52	.01	-.04	.43
5. <i>Polydora polybranchiata</i> larvae	.02	.99	-.13	-.20
6. <i>Melosira granulata</i>	.13	.13	.98	-.01
r.	-.92	-.06	.09	
Pelorus Sound				
LATENT ROOTS:	Method 1		Method 2	
LATENT VECTORS	6.3	1.7	1.1	4.6
1. <i>Paracalanus parvus</i> adult	.18	.64	.02	.38
2. <i>Paracalanus parvus</i> copepodites	.17	.61	-.16	.34
3. <i>Temora turbinata</i> adults	.36	.04	-.03	.38
4. <i>Temora turbinata</i> copepodites	.36	-.20	-.08	.23
5. <i>Temora turbinata</i> nauplii	.34	-.26	-.17	.24
6. <i>Acartia clausi</i>	.32	-.12	-.19	.40
7. <i>Euterpina acutifrons</i>	.38	-.07	-.17	.30
8. <i>Coscinodiscus wailesii</i>	.33	.08	-.14	.35
9. <i>Mytilus canaliculus</i> larvae	.34	-.02	-.11	.00
10. <i>Polydora polybranchiata</i> larvae	.26	-.23	.50	.05
11. <i>Elminius modestus</i> nauplii	.16	.16	.77	.33
r.	-.82	.39	-.17	

aries defined by the salinity or temperature pattern, but there is, nevertheless, a clustering of points in the diagram (Fig. 5). Only in clusters 2 and 3 do two consecutive clusters overlap, and even here there is no difficulty in distinguishing the two. Thus there appear to be four natural boundaries in the plankton

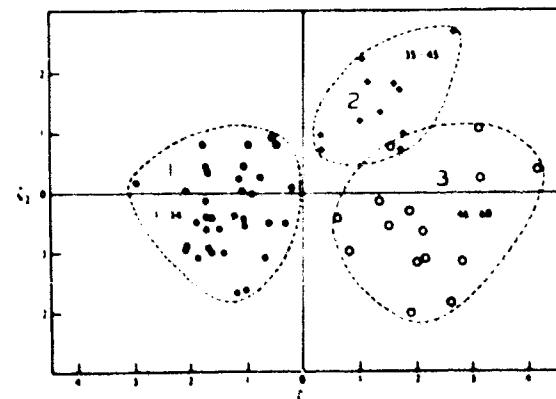


Fig. 4. Scatter diagram showing the sampling distributions ζ_1 , ζ_2 for the first two latent vectors—Port Nicholson. The points fall into three distinct clusters: 1, 2 and 3.

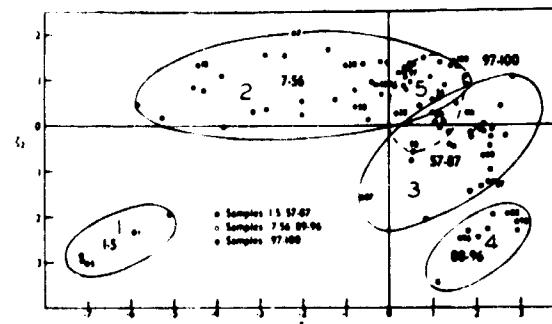


Fig. 5. Scatter diagram showing the sampling distributions, ζ_1 and ζ_2 for the first two latent vectors—Pelorus Sound. The points fall into five clusters: 1-5.

distribution which are not reflected by any obvious hydrological discontinuities. The salinity pattern, for example, though irregular, follows the same general trend throughout. Whether this "stepped" condition of the plankton population is attributable to some unknown environmental factor, perhaps to some past hydrological condition which has since vanished, must remain a matter for speculation.

CONCLUSION

I have shown only one method of eliminating determinate factors from the distribution—by partial correlation on known environmental factors. But sometimes this method fails because the environment is not sufficiently well mapped and other expedients must be adopted. The fitting of artificial trend lines may be appropriate in some cases, but the application is limited because many non-random trends are so complex that they cannot be fitted except by unrealistically high-order polynomials. Here serial correlation methods may help. I am investigating this possibility, but this leads into a rather esoteric field of statistics with features almost identical with time-series analysis, which often baffles even the professional mathematician.

Although complex sampling programs at sea present considerable technical difficulties, it may still be better to develop these specialized programs. I have recently experimented with a plan by which each sample is replicated ten times, and thus a correlation matrix can be computed for each set of 10 subsamples. The matrices for all samples are then pooled and subjected to principal component analysis. If replication is adequate, the vectors so derived will be independent of determinate trends, but their origins will vary from sample to sample and will reflect the pattern of these trends. Thus the pattern of change of one or more communities can be charted, even if it cannot be accounted for by any specific mathematical model.

Author's Note. I am not the first to use multivariate methods for ecological purposes. Other works, not mentioned in the text, which have helped to inspire the present contribution include Goodall (1954) (plant ecology), Reymond (1963) (paleoecology), and Williams and Lambert (1959) (plant ecology—using non-parametric methods).

Most of my ideas on this subject were developed while I was on the staff of the New Zealand Oceanographic Institute, Department of Scientific and Industrial Research. Thanks are due to the Director and all members of the staff who have collaborated with me, and to the Editor, *New Zealand Journal of Science*, for permission to republish Figures 1 and 2.

LITERATURE CITED

- CASSIE, R. M., 1960. Factors influencing the distribution pattern of plankton in the mixing zone between oceanic and harbour waters. *New Zealand J. Sci.*, 3: 26-50.
- CASSIE, R. M., 1961a. The correlation coefficient as an index of ecological affinities in plankton populations. *Mem. Ist. Ital. Idrobiol.*, 13:151-177.
- CASSIE, R. M., 1961b. Frequency distribution models in the ecology of plankton and other organisms. *J. Animal Ecol.*, 31:65-92.
- CASSIE, R. M., 1963. Multivariate analysis in the interpretation of numerical plankton data. *New Zealand J. Sci.*, 6: 36-59.
- FAGER, E. W., and J. A. McGOWAN, 1963. Zooplankton species groups in the North Pacific. *Science*, 140: 453-460.
- FISHER, R. A., A. S. CORBET, and C. B. WILLIAMS, 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Animal Ecol.*, 12:42-58.
- GOODALL, D. W., 1954. Objective methods in the classification of vegetation. III. An essay in the use of factor analysis. *Australian J. Botany*, 2:304-324.
- KENDALL, M. G., 1957. *A course in multivariate analysis*. Griffin, London.
- LIEBERMANN, L., 1951. The effect of temperature inhomogeneities in the ocean on the propagation of sound. *J. Acoust. Soc. Am.*, 23:563-570.
- MARGALEF, R., 1961. Communication of structure in planktonic populations. *Limnol. Oceanogr.*, 6:124-128.
- MARGALEF, R., 1962. "Diversità" dello zooplankton nel Lago Maggiore. *Mem. Ist. Ital. Idrobiol.*, 15:137-152.
- RAO, C. R., 1952. *Advanced statistical methods in biometric research*; pp. 370-378. John Wiley and Sons, New York and London.
- REYMENT, R. A., 1963. Multivariate analytical treatment of quantitative species associations: an example from paleoecology. *J. Animal Ecol.*, 32:535-547.
- WILLIAMS, C. B., 1944. Some applications of the logarithmic series and the index of diversity to ecological problems. *J. Ecol.*, 32:1-44.
- WILLIAMS, W. T., and J. M. LAMBERT, 1959. Multivariate methods in plant ecology. I. Association-analysis in plant communities. *J. Ecol.*, 47:83-101.
- WILLIAMSON, M. H., 1961. A method for studying the relation of plankton variations in hydrography. *Bull. Marine Ecol.*, 5:224-229.

Laboratory Analogues of Estuarine Plankton Systems

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The purpose of laboratory analogues is not to duplicate or imitate nature, but to have simple situations that make it easy to identify operational mechanisms, first in the experiment and later in nature. Useful data on the ecology of estuarine populations can be gathered through the customary flask culture, in which selected organisms are grown under different conditions of water quality, water turbulence, temperature, and light; the experimenter records the rates of growth and tries to find correlations with nutritional and other factors.

But the experimental approach must vary with the focus of interest. We may be more interested in clouds than in the behavior of definite molecules of water or of atmospheric gases; we may be more interested in plankton patches than in the destiny of particular algal cells. In this paper we are more interested in the estuary as a phenomenon in space than in the life and behavior of its individual inhabitants.

The design of the experiments reported here started from the consideration of estuaries as self-regulatory systems. A promising approach was the substitution of ordinary flask cultures by flow cultures, where stationary populations are the expression of equilibrium in dynamic processes that are made more or less independent of time. The vessels in a system of flow cultures are like a frame of geographic coordinates, that is, a rigid reference for the study of populations. The populations themselves are transient or stationary states, and express the processes of cell multiplication, diffusion, and flow.

The immediate purpose of these experiments was to understand the particular quantitative values found in estuaries, or in analogous situations, of certain characteristics pertaining to the structure and function of ecosystems. The selection of parameters to be used in the study of mixed populations or communities is dependent on the purpose of the worker; an assessment of resources calls for estimates of biomass and projects of exploitation need an estimate of production. In any consideration of the ecosystem as a cybernetic system, one has to overvalue certain synthetic and dynamic properties that include some reference to time, as time rates (primary production per unit of total biomass), or as structures resulting from historical developments (biotic diversity of populations; or plant pigment diversity, expressed in practice by the ratio D_{430}/D_{660} of the absorbancies, at the stated wavelengths, and of acetone extracts).

THE CHEMOSTAT

A chemostat is a culture vessel where conditions remain constant, traversed by a continuous flow of a medium. The principle and theory of the chemostat have been discussed by several authors. The following are a few especially useful references: Bulder, 1960; Herbert, 1961; Monod, 1950; Novick, 1959; Novick and Szilard, 1950; Pfennig and Jannasch, 1962; Watts and Harvey, 1963.

In a chemostat the population is suspended in a constant environment that can be selected or changed at will. The density of the population is controlled by a density-dependent factor. The culture vessel receives a constant input of fresh medium of definite composition, and the same amount of the well-mixed contents of the vessel is taken away. Losses of the population are proportional both to the flow and to the density of the population. The rate of growth decreases with increasing density; in consequence, their combined effects are density-dependent and effective in regulation.

Let N be the density of the population, r the rate of growth, and F the flow, that is, the fraction of the total volume of the culture that is exchanged in unit time. In stationary state we should have

$$N = N e^r - F N$$

$$r = \log_e (1 + F).$$

The regulation of the population density is very noticeable in a simple chemostat with a unialgal culture. When flow (= exploitation, = exchange) is increased, the ratio of production to biomass must become higher, since

$$\text{production/biomass} = e^r - 1 = F.$$

This is a relation of fundamental importance in general ecology and, of course, in the ecology of estuaries.

If we have a chemostat in a steady state, and the light or nutrient input is reduced or the rate of flow is increased, the value of r in a unispecific culture, or of any of the species in a mixed culture, can become insufficient to cope with exploitation. If such a situation develops, biomass will decrease until a new stationary level is reached, or until the population vanishes, and the ratio of production to biomass always goes up until the last moment. If the species becomes extinct, it can be said, because of the conditions of the experiment, that its potential turnover was too low to allow the passage of a certain energy flow.

Conditions of competition in a chemostat vessel may be practically reduced to differences in the rates of increase in definite conditions. Since it is highly improbable that two organisms will have exactly the same rates of increase, a chemostat inoculated with a mixed culture usually leads to a unispecific population, demonstrating Gause's law. The situation is more complex if the issue of competition is not decided by prolificness alone.

The merits of the chemostat for the simulation of situations found in estuaries increase when several chemostats are connected in a row, so that the outflow of the first chemostat is the inflow of the second, and so on. We can describe such a device as a compound chemostat. Malek (1952) and others have described such devices. The writer has been using compound chemostats for several years, with very stimulating results, of which only a short account of a particular experiment has been published (Margalef and Ryther, 1960).

Like a single chemostat vessel, under constant environmental conditions a system of many vessels approaches a stationary state. The basic expression for equilibrium resembles the one for the simple chemostat, except that the loss of cells due to the flow is not dependent on the density attained in the particular vessel under consideration (N_t), but of the difference between this density and the density in the preceding container (N_{t-1}).

$$N_t = N_{t-1} e^r - F (N_t - N_{t-1}) .$$

The composition of medium remains constant in time, changing in a progressive and directional way in space. Going from one flask to the next, the concentration of nutrients decreases and metabolites accumulate.

The theoretical limit in the construction of a linear compound chemostat would be the substitution of a series of flasks by a simple tube of uniform diameter, the ideal analogue of a river or of a layer in an estuary. The writer has experimented with plastic tubes up to 40 m long, but it has been found that such a device is less convenient than a multichambered chemostat. First, a flow system divided into chambers separately stirred and interconnected by rather narrow tubes is more appropriate for sampling purposes. Second, under conditions of laminar flow, any suspended population is washed away. The turbulence in the model made up by a row of chambers, separately stirred and with exchange in one direction, is more easily understood and managed by the biologist not familiar with hydrodynamics.

Any system of chemostats affords an ideal way for mapping time series into space; going down the row of flasks is equivalent to progressing along an ecological succession.

We may speculate about how to construct an ideal chemostat for the study of plankton populations. It might consist of any high number of culture vessels, to be interconnected in topological relations proper for forming a tridimensional lattice. An appropriate

control of the flow of liquid between the separate culture chambers could be attained by using tubes of elastic material. Such tubes would act as elements of peristaltic pumps. The adequately programmed pumps could forward the liquid in either direction and by this mechanism the effects of turbulent mixing could be simulated by pumping fluid from one vessel to another, stirring, pumping the same volume back again to the first, and so on. One can recognize the interest of a big system of about $10 \times 10 \times 10$ vessels, every one with appropriate conditions of light and temperature. It would be possible to lead into a given vessel, representing a point in a tridimensional system, a continuous flow representing a local upwelling or a spot source of nutrients. It would also be possible to program the exchanges between the different vessels according to selected conditions of flow and turbulence, and wait for a steady state. We could gain a dynamic insight on how spatial patterns develop. Such an approach is contemplated, but enthusiasm has been somewhat dampened for reasons explained later. The presence of walls soon becomes a nuisance.

THE CHEMOSTAT UNIT

After considerable trial and error, the unit now in use is satisfactory for many purposes (Fig. 1).

The compound chemostat is assembled from standard units. The elementary flasks are conical and 500 to 600 ml in capacity. The fluted sides increase turbulence when the contents are stirred. At a level containing a volume of 300 to 400 ml, there are one or two simple inlets, with ground-glass receiving joints. An outlet that starts above the bottom as a tube ends with a tapering male glass joint. High above, another opening equilibrates the atmospheric pressure. The contents of every vessel can be stirred magnetically, using iron bars covered with Teflon.

Two types of ground-glass stoppers have been used: simple or with conduction. The stoppers of the last

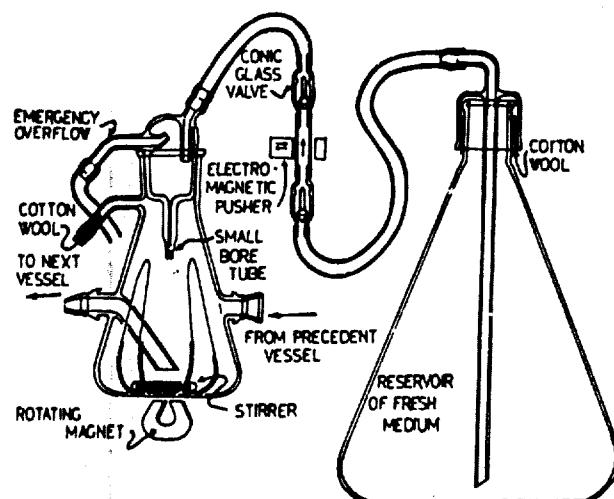


Fig. 1. The glass vessel used as a unit in the assembly of compound chemostats. It is represented with the hollow conducting stopper connected to the feeding system.

type are hollow, have an inflow, an interior vertical outlet made of small-bore tube (about 0.7–0.9 mm diameter) and an emergency overflow that serves to equilibrate atmospheric pressure and to allow the accumulated liquid to escape, in case the small-bore tube should become stopped up. The chamber in the hollow stopper provides a better equilibration of the temperature of the medium, when necessary. The small-bore tube insures a slow incorporation of the fresh medium to the contents of the culture vessel. The discontinuous feeding mechanism fills the stopper from time to time, but the passage of the liquid from the interior of the stopper to the culture vessel approaches or attains continuity. The end of the small-bore tube lies high above the level of the culture medium to prevent any ascending contamination.

The culture vessels can be sterilized separately after closing the lateral openings with stoppers or by using connecting segments with taps. The units can be assembled in rows or, in more complex patterns that include convergences, there is a provision for flasks with two inlets and one outlet. In these experiments the flasks have always been placed at the same level, and are connected by the simple glass joints. A certain amount of diffusion and contamination "upstream" has been permitted, as in natural systems. But no elaborate equipment is required for making the exchange between successive flasks rigorously unidirectional; it suffices to insert special connecting pieces and place the flasks at different levels.

The special hollow stoppers used as inlets of fresh medium are inserted at the head of the rows, or in an intermediate position, if the effect of a dilution or a special addition in definite stages of the development of a population is to be investigated. The other flasks receive simple stoppers.

The feeding mechanisms give considerable trouble, because they must resist sterilization. A discontinuous mechanism is much simpler to construct and is more reliable than a continuous feeding system. Solenoid-operated valves in connection with automatic measuring burettes have been tried and rejected. Long segments of capillary tubes also have been tested as flow regulators, but without satisfaction. Slow peristaltic pumps seemed promising, but they are expensive. Finally, a very sturdy, sure, and cheap device was adopted. Two glass valves, each one consisting of a ground tapered plug in its casing, are connected by a piece of elastic tubing. The whole is made sterile easily, together with the reservoirs of fresh medium. An electromagnetically activated pusher compresses the elastic tube and the whole acts as a pump. Selecting the diameter and the length of the compressible segment makes it possible to determine approximately the amount of fluid displaced at each stroke, but it is a difficult trick to make it coincide with a prefixed amount. The best thing to do is to measure *a posteriori* the amount of liquid actually flowing, and introduce the value found in the computations. Fortunately, the device is very stable; the delivered fluid, in ml/day, remains constant over

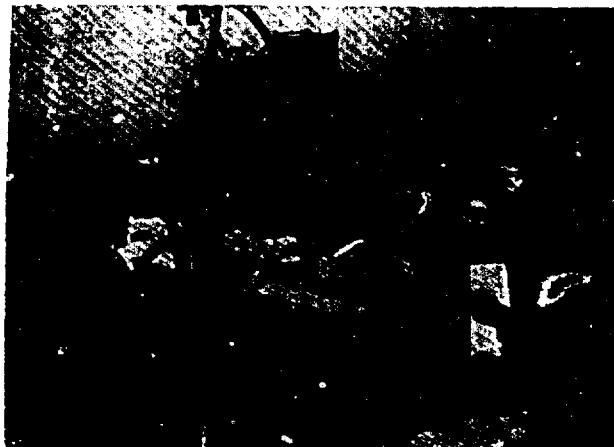


Fig. 2. Photograph of one assembled compound chemostat. The culture vessels are held in position in a frame that also supports the light sources and the other equipment. In the lower left corner are two reservoirs of fresh medium and, above them, the feeding mechanism. Above, right, is the motor of the stirring system. The chemostats are kept in a constant temperature room.

weeks. An electrical timer controls the electromagnetic pusher and further regulates the flow.

In the course of experiments, it has been found convenient to have a flow of about 100 ml/day. The electromagnetic pusher was activated every 20 minutes, and the amount of fluid introduced by every stroke was around 1.5 ml. Stirring was discontinuous, acting about half the time, and was linked to the same timer that controls the input of fresh medium. Stirring started before the injection of fresh medium and stopped after the chamber in the stopper emptied completely.

The final outflow of the whole system, through the outlet of the last culture flask, was led to a measuring cylinder. This reservoir was prepared with a few drops of a fixative (saturated solution of iodine in saturated solution of potassium iodide in water, plus 20 percent of sodium acetate). Every day, or more frequently if convenient, the amount of fluid collected in this reservoir was measured and the cell concentration counted—a good check of the regularity of flow, general behavior of the system, and a test for stability. In a few days, after the initial changes, the density of organisms in the discharge approached a stationary state. Only then has the system reached equilibrium. At this point the vessels should be disconnected and an analysis may be made of the partial populations enclosed in the different flasks. The system is illustrated in Figure 2.

OPERATION OF COMPOUND CHEMOSTATS

LINEAR COMPOUND CHEMOSTATS WITH ONE PLANKTONIC SPECIES

In a compound chemostat made up of a single row of culture vessels, with unidirectional flow, uniform

conditions of temperature and light, and populated by one true planktonic, non-sticking species of alga, we observe in the steady state (going in the direction of flow): (1) an increase of the biomass, (2) a decrease of the ratio primary production/biomass, and (3) an increase of the ratio D_{430}/D_{665} of plant pigments. The steady state is maintained during long periods and the system attains an almost total independence from time.

It should have a single inlet of fresh medium in the first vessel. If its inflow is increased, the entire pattern moves downstream; if the inflow decreases, the pattern is displaced upstream.

If, in a compound linear chemostat, inflow of fresh medium is not limited to the first vessel, or if many, or all, flasks receive an input of fluid, the flow and diffusion are accelerated along the system, as in an estuary with a wide mouth, and the population reacts by maintaining a high ratio of production to the biomass. One can speak of an "expansion" of the population in a void medium, and that expansion is associated with immaturity.

Another possible, but untested, variant of this sort of experiment would be to use several inflows of water of different salinities, increasing the salinity down the system. This model would duplicate situations often found in estuaries.

LINEAR COMPOUND CHEMOSTATS WITH SEVERAL PLANKTONIC SPECIES

If we have a single row of flasks, with an input in the first vessel of fresh medium containing several phytoplankton species, experiments demonstrate the simplification of structure (= drop of biotic diversity) of the mixed population when flow (= exploitation) is sustained or increased.

But flasks placed downward can accommodate more species, so that it can be said that going from the first to the last culture vessel there is an increase in species diversity. Distributions of biomass, of ratio primary production/biomass, and the index D_{430}/D_{665} give the same pattern as that in the case of unicellular populations.

LINEAR COMPOUND CHEMOSTATS, USING SPECIES WHICH STICK TO THE WALLS

When experiments are performed with a wide assemblage of species taken from natural populations, the systems develop a flaw—a fortunate flaw, because it throws light on the dynamics of populations in estuaries and in other natural environments. Species able to attach themselves to the walls of the culture vessels become more successful in competition. The same fact was observed by bacteriologists working with flow cultures. Graziosi (1959) states that in continuous cultures there is a positive selection for mutants which grow on the wall of the vessel. The increased probability of remaining in the vessel is a selective advantage that can be expressed quantitatively.

The adherence of organisms to the walls is a most serious inconvenience in the use of chemostats as

analogues of plankton systems. Species that are used often as models of planktonic algae, as *Nitzschia closterium*, and even some small species of *Chaetoceros*, are found attached in some way. Propensity to attachment seems to be different according to conditions of nutrition, to accompanying bacterial flora, and to the time elapsed from the start of the experiment. The role of possible mutants cannot be excluded. Stirring does not check attachment of algae to the walls. The design of a reliable chemostat for experimenting with complex planktonic populations awaits the improbable discovery of a bottle without walls. Ice walls do not help.

Several runs have been made in compound linear chemostats with *Tetraselmis* (attaching easily) associated with *Nitzschia* and/or *Skeletonema*. The results are almost opposite to those found in the case of a mixed population of non-adhering species. The biomass becomes abnormally higher in the first vessels and the usual regularity in the distribution of the ratio of production to biomass is distorted. The ratio D_{430}/D_{665} of plant pigments behaves in an interesting way. Its value is between 2 and 4 in healthy and normally growing cultures of *Tetraselmis*, and between 3 and 6 in comparable cultures of *Skeletonema*. In an experiment with a mixed culture of both species, *Tetraselmis* dominates in the first vessels, not by a higher rate of increase (it has not), but by a strong adherence to the glass. But *Skeletonema* makes up a higher proportion of the population in the flasks placed downwards in the flow. Thus, the customary pattern of increasing values of the ratio D_{430}/D_{665} is soon reduced with the flow. But one or two weeks later, populations of *Tetraselmis*, which have accumulated in the vessels at the head of the series, profit from the flow of the medium (the so-called "eutrophic effect of running water"), but, nevertheless, their relative rate of increase declines as cells accumulate, and the ratio D_{430}/D_{665} increases as in old and senescent populations. The populations of *Skeletonema*, on the contrary, are relatively more abundant in the vessels towards the tail of the system; being free or unattached, they are subjected to a strong exploitation that maintains a high ratio of production to biomass, and a relatively low ratio D_{430}/D_{665} . In consequence, at a certain stage of the experiment the distribution of the ratio D_{430}/D_{665} is reversed for the mixed populations in the successive vessels, and this is probably also true of the ratio of primary production to biomass; in fact, the ratio decreases from the first to the last flask. For instance, in an experiment with *Tetraselmis*, *Skeletonema*, and some bacteria, after 15 days of a flow of 130 ml/day, the ratios D_{430}/D_{665} in the mixed populations of four consecutive vessels were, respectively, 17.5, 13.9, 7.2, and 5.5.

In experiments with one species, described above, a similar decrease was observed, but here decrease of the value of the ratio is not related to an exaggerated dilution of the population downwards, but to an exaggerated concentration or contraction of the population upwards.

Table 1. Distribution of environmental and population parameters in different vessels of a compound chemostat.¹

Fresh medium inflow (2)	μg phosphate-P/l (1)	pH	Flow	Cells/ml	mg chlorophyll a/m ²	μg C fixed/m ² /hour	Probability of escape	D_{10}/D_{∞}
	(a) 47.0	7.67	0.304	107,800	39.22	11.55	0.046	4.2
↓	(b) 19.8	8.05	0.253	31,600	30.93	13.58	0.380	3.9
↓	(c) 26.2	7.68	0.288	138,300	71.46	25.52	0.084	3.5
↓	(d) 9.7	8.35	0.271	50,070	27.54	11.41	0.340	4.3
↓	(e) 4.8	8.58	0.444	37,700	15.66	15.36	0.280	3.6
↓	(f) (outflow) 9.0	8.68	0.575	13,450 2,920	11.00	13.01	0.935	3.3

¹ Inflow of fresh medium at inlet (1) was 103 ml/day; at inlet (2), 88 ml/day. Inorganic P and pH were measured in the flasks at the end of the experiment. Flow, expressed as volume per day, is dependent upon the useful capacity of the vessels. Density of cells was measured after suspension of the attached cells. The experiment was terminated when cell concentration in the outflow remained stationary for 5 days. The biotic diversity was between 0.91 and 1.12 bits per cell at the end of the experiment, without significant difference between vessels.

Conditions of the experiment were as follows: Duration: 3-17 August, 1963; Temperature: 15.5-16.5° C.; Illumination: continuous at approximately 5,000 lux; Medium: sea water diluted with distilled water to 30 %, and enriched with 1 mg nitrate-N and 0.2 n.g phosphate-P/l, plus a few drops of a solution of silicate and trace metals. Organisms: *Tetraselmis*, *Stichococcus*, *Amphora*, *Stauroneis* and *Nitzschia*.

The attached species progressively invade all the flasks as time advances. The concentration of organic matter on the walls and the absorption of light are new factors and the whole pattern becomes blurred. The elegant simplicity of the experiments with free-floating algae is lost. The brutal competition for dominance based on the rates of increase has given way to more subtle and interminable processes and the chemostat is prevented from attaining a stationary state. The situation is interesting as an example of development of more organization than the experimenter desires.

An attempt has been made to measure the degree of adherence of cells by counting cells in suspension, then detaching, suspending, and counting the cells which settled on the walls, and checking the data obtained with measurements of the production, the flow, and the final output of the system.

The results cannot be accurate and are expressed as an average probability (P) for an average cell to move with the water going through the flasks. $P = 1$ in the true planktonic and passive algae, non-attached and running with the medium; $P = 0$ if all the cells are solidly attached. Some examples of values found can be seen in Table 1. Mobile organisms pose special problems, but no special experiments have been performed with them.

The introduction of P in an expression describing a steady state would be

$$N_t = N_t e^t - F (N_t P_t - N_{t-1} P_{t-1}).$$

Since no true stationary state is reached, this expression is given with reluctance. Although the output of the final outlet of the system may remain approximately constant for days, there are rearrangements going on in the populations of the separate flasks.

CONVERGENT COMPOUND CHEMOSTATS USING SPECIES WHICH STICK TO THE WALLS

In other experiments with complex populations, the flasks have been assembled in two rows converging in a single final row, as an analogue of two water masses that meet and mix in a boundary. The same problems as in the previous experiment have been present. In the vessel placed just in convergence (e) in the experiment of Table 1, input is twofold and flow higher than in preceding vessels. It leads to a sharp increase of the ratio of production to biomass if attachment of organisms to the walls is not excessive. When the two converging flows consist of water of different composition, the success of attached species in front of suspended ones seems to be less decisive than in other circumstances.

CORRELATIONS IN CHEMOSTAT POPULATIONS

Selected quantitative characters of populations grown in chemostats show interesting correlations that are maintained over a wide range of conditions of flow, temperature, and species composition (Table 2).

Expected positive correlations were found between the number of cells counted in a sedimentation chamber, the number of particles counted with an electronic dimensional particle counter, and the chlorophyll content.

There is a significant positive correlation between the ratio of production to biomass and the average probability of being carried away by the flow. The probability of being washed away is unrelated to the intensity of flow. Production was measured by fixation with C^{14} at the end of the experiment, after interrupting the flow and disconnecting the flasks. Both the ratio of production to biomass and P are nega-

Table 2. Simple statistical correlations between untransformed values of some parameters of populations in compound chemostats.¹

	(B)	(C)	(D)	(E)	(F)
(A)	+0.608*	+0.960*	-0.063	-0.132	-0.407
(B)		+0.693*	+0.079	+0.054	-0.473
(C)			+0.006	-0.052	-0.454
(D)				+0.851*	-0.588*
(E)					-0.514

¹ The populations (17) were sampled in the separate vessels at the end of three experiments. Conditions of flow, temperature, nutrition, and organisms present were different. The position of each vessel in the chain of chemostats was not taken into consideration.

* $p < 0.01$.

** $p < 0.001$.

(A) Number of cells/ml, direct counts.

(B) Number of particles/ml, electronic dimensional particle counter.

(C) Concentration of chlorophyll *a*, $\mu\text{g/l} = \text{mg/m}^3$.

(D) C₁₄ fixation, $\mu\text{g C}/\text{million cells/hour}$.

(E) Probability of the average cell being carried away by the average flow (≥ 1).

(F) Ratio D_{430}/D_{665} in extracts of pigments.

tively correlated with the ratio D_{430}/D_{665} in plant pigments. There were hopes of finding in a general way, as in some experiments with several planktonic species in linear compound chemostats, a positive correlation between ratio D_{430}/D_{665} and species diversity. But biotic species diversity behaved rather disappointingly, since no significant differences were found in most runs between different vessels; it is true that assortment of species was artificially limited and bacteria were not considered in making diversity computations.

Correlations are lacking or poor between the quantitative instantaneous measure of biomass, in number of cells or in chlorophyll, and the second group of properties correlated between them. The properties included in this second group (ratio production/biomass, ratio D_{430}/D_{665} , perhaps diversity) are those considered especially relevant when the ecosystem is equated to a cybernetic system with regulation.

INTERPRETATION OF ESTUARIES

Estuarine ecosystems exhibit regulatory feedbacks at different levels. An increase of the inflow of fresh water in the head of an estuary may augment the flow of denser sea water over the bottom in the opposite direction. Any intensified exchange, by tides or other causes, means a heavy loss of suspended organisms, but in certain situations new nutrients are introduced into the system; selection is then active in favor of planktonic species endowed with a high rate of increase and capable of sustaining important losses, or of fixed organisms.

An estuary rarely can be studied as a nearly closed system; most of the time it receives materials from fresh water and exports production to neighboring systems, contributing to their maintenance with algae, detritus, and food. These contributions are more important when the flow of energy (primary production) per unit of biomass is high—a condition obviously fulfilled if flow and water exchange remain strong.

In populations organized under such constraints there is usually a dominance of one or a few species and a high ratio of primary producers to animals. Compound chemostats illustrate how the rate of exchange limits the increase of organization in communities, because low diversity is related to a high turnover of populations. Several authors have remarked that estuarine plankton populations have a low biotic diversity when compared with coastal and oceanic populations, and concrete evidence has been furnished (Hulbert, 1963; Margalef, 1958; Patten, 1962). Low diversity may be associated with a high density of populations. It is an indicator of poor organization under the influence of flow and of changing conditions.

When exchange is reduced, floating organisms with a relatively lower rate of increase can maintain themselves, the ratio of production to biomass drops and the planktonic community attains a higher organization. Mobility of organisms is an asset, and in conditions of reduced flow blooms of dinoflagellates may be apparent.

This applies especially to suspended and drifting populations, but, as we have seen in our models, populations are controlled by the capacity of keeping a position and not only by the rate of increase. In natural estuarine ecosystems, the benthic mode of life reduces the probability of losing position. Fixed plants are dominant in some situations, if the time necessary for development is not interrupted by drastic changes in the environment, and if light is sufficient.

Another resource leading to a decrease of the probability of being carried away is a special form of behavior, as in euryhaline animals that migrate vertically and are alternatively found in layers flowing in opposite directions (Cronin *et al.*, 1962). Such populations compete with advantage or exploit with success the less stable, truly planktonic or passively drifting populations.

The more or less fixed communities gather and preserve organization (information) better than passively vagrant communities. Their higher organization is linked with higher homeostasis and with lower energy flow (primary production per unit of total biomass). An increased water exchange or another form of heavy exploitation leads to a restructuring and simplification of the system, and the new structures, without loss of an already simple organization, can be subjected to further changes.

The compound chemostat is able to present didactically many situations that reflect the general ecology of estuaries. Operation of chemostats is an extremely instructive experiment and should be included in ecology courses. But probably the usefulness of the approach does not stop here. Compound chemostats facilitate the quantitative knowledge of correlated structures of ecosystems, their function or metabolism, and the identification of regulatory feedback circuits at work. Carefully conducted experiments can answer questions regarding nutrition, competition, and the

importance of certain adaptations in the maintenance of a population against dispersal by the flow.

Only experiments of an exploratory nature have been performed so far, and in too few replicates to allow a sound quantitative analysis of the results. But the approach looks promising.

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LITERATURE CITED

- BULDER, C. J., 1960. A simple device for steady state cultures of microbes. *Experientia*, 16:565-566.
- CRONIN, L. E., J. C. DAIBER, and E. M. HULBURT, 1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. *Chesapeake Sci.*, 3:63-93.
- GRAZIOSI, F., 1959. (Symposium VI held at the VII Intern. Congr. for Microbiology.) In *Recent Progress in Microbiology*; pp. 418-420. Almqvist and Wiksell, Stockholm.
- HERBERT, D., 1961. A theoretical analysis of continuous culture systems. *Soc. Chem. Ind., Monograph*, 12: 21-53.
- HULBURT, E. N., 1963. The diversity of phytoplankton populations in oceanic, coastal and estuarine regions. *J. Marine Res.*, 21:81-93.
- MALEK, I., 1952. Kultivierung von Bakterien in einem mehrstufigen strömenden Milieu. *Tchécoslovenska Biologija*, 1:35-38.
- MARGALEF, R., 1958. Temporal succession and spatial heterogeneity in phytoplankton. In *Perspectives in Marine Biology*; pp. 323-349. University of California Press, Berkeley, California.
- MARGALEF, R., and J. H. RYTHER, 1960. Pigment composition and productivity as related to succession in experimental populations of phytoplankton. *Biol. Bull.*, 119:326-327.
- MONOD, J., 1950. La technique de culture continue. Théorie et applications. *Ann. Inst. Pasteur*, 79:390-410.
- NOVICK, A., 1959. Experimentation with the chemostat. In *Recent Progress in Microbiology*; pp. 403-415. Almqvist and Wiksell, Stockholm.
- NOVICK, A., and L. SZILARD, 1950. Description of the chemostat. *Science*, 112:714-716.
- PATTEN, B. C., 1962. Species diversity in net phytoplankton of Raritan Bay. *J. Marine Res.*, 20:57-75.
- PFENNIG, N., and H. W. JANNASCH, 1962. Biologische Grundfragen bei der homokontinuierlichen Kultur von Mikroorganismen. *Ergebnisse der Biologie*, 25:93-135. Springer Verlag, Berlin.
- WATTS, J. R., and R. S. HARVEY, 1963. Uptake and retention of Cs¹³⁷ by a blue-green alga in continuous flow and batch culture systems. *Limnol. Oceanog.*, 8: 45-49.

VIII. PHYSIOLOGY AND EVOLUTION

Physiology of Estuarine Organisms with Special Reference to Salinity and Temperature: General Aspects

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Estuaries are areas of transition between the more stable conditions of the neighboring sea and fresh waters, which exhibit increased gradients and fluctuations of abiotic and biotic factors. Being in essence the mouth of a river, an estuary harbors bodies of water in which the seawater component is diluted and modified in various degrees by river water. The most important entities determining the physico-chemical conditions and their fluctuations are the tide, the volume and contents of the river water discharged, and the morphology of the estuarine area.

Though there are a number of different types of estuaries, these basic physical characteristics apply to the majority of them, and characterize an estuary physiologically as a stress habitat, strongly challenging its inhabitants and any potential immigrants from sea or river. Ecologically, most estuaries represent zones of reduced competition, areas in which physical factors, rather than biotic ones, determine population dynamics. Many estuarine organisms appear to have been forced out of physically more suitable conditions in sea or fresh water; for them, the estuary represents a refuge with suboptimal or even subnormal physico-chemical conditions, which protects them from predators, competitors, or parasites. The number of different forms of life or of species per space unit is usually much smaller in estuaries than in the neighboring marine or freshwater habitats. However, the number of individuals may be quite large, especially if the estuary is eutrophic, which is often the case. Consequently, intraspecific competition is frequently more pronounced than interspecific competition. Estuaries may have tremendous rates of primary production, especially in subtropical and tropical regions, and thus be important feeding and nursery grounds for euryhaline marine organisms.

Physiologically, few organisms seem to find optimum conditions in estuaries during their life cycles. To exist under estuarine conditions, an organism must be euryplastic, that is, it must be able to endure extreme ranges and intensity fluctuations of environmental factors. The availability of mechanisms for protection and increase of tolerance, as well as for regulation and acclimation, is therefore a necessary prerequisite for a successful establishment in estuarine waters.

It is usually not a single environmental factor which governs the physiological responses and population dynamics in an estuary, but a combination of

numerous factors counteracting, supporting, and modifying each other's physiological effects. At the present time it is not possible to measure all environmental components properly. If suitable techniques become available, the complexity of an estuary's physico-chemical conditions can probably be fully appreciated only by monographing or tabulating simultaneously the numerous factor intensities relative to space and time. In view of this, and our limited knowledge of physiology of estuarine organisms, I shall restrict myself here to the consideration of changes in salinity and temperature. Together with water movement, turbidity, light, dissolved gases, substrate, and nutrients, these two factors are of particular physico-ecological importance.

Several recent papers and reviews have been concerned with life in estuaries. The majority deal with ecological or physiographical aspects (Caspers, 1948, 1955, 1958, 1959; Day, 1951; Emery *et al.*, 1957; Girms, 1961; Kothe, 1961; Kötter, 1961; Reid, 1961; Schulz, 1961; Schumacher, 1961; Smith, 1956).

SALINITY AND TEMPERATURE IN ESTUARIES

The salinity of estuaries often undergoes considerable fluctuation. It is usually lower than that of sea water, but in regions with high evaporation and little rain, estuarine bottom-level salinities may exceed 100‰. The ion composition and the relative proportions of other solutes may be subject to significant modifications. In general, there is a higher ratio of carbonate and sulfate to chloride and of calcium to sodium than in sea water; extreme evaporation, however, causes these ratios to be lower (Clarke, 1924). Local modifications may be due to the type of soil of the river, its vegetation and fauna, and industrial or other products discharged into the river water. As a result of the tendency of the inward-flowing sea water and the outward-flowing fresh water to be displaced to their respective right sides, salinities are usually higher on the left side of larger estuaries in the northern hemisphere. Thus Pritchard (1952) found the salinity on the left side of the James River to be an average of 1‰ higher than on the right side. Such differences may, in some cases, be important for physiological reactions as well as for distribution of estuarine organisms.

Water temperatures in estuaries usually exhibit greater annual and diurnal fluctuations than in the

sea, especially if the estuary is shallow and if the water comes into contact with previously exposed areas of substrate. At the entrance of the estuary the temperature is nearly the same as in the open sea; upstream, however, the difference usually increases rapidly (Sumner *et al.*, 1914). In addition to horizontal temperature variations, considerable vertical variation may be produced, for example, by warm or cold river water flowing out over the more dense brackish or sea water.

While pronounced environmental variation is a basic characteristic of an estuary, the variability is also a rather constant feature in terms of phylogenetic considerations. Such a "concept of permanency of estuarine variation" carries with it the idea that the few species which have succeeded in inhabiting estuaries are phylogenetically rather conservative forms with a long history. The euryplasticity of estuarine organisms is probably a genetic trait "not easily come by and, once attained, is very conservative" (Emery *et al.*, 1957). Estuaries often contain an accumulation of genotypes exhibiting similar physiological characteristics. It is the purpose of this contribution to consider the present-day aspects of these physiological characteristics.

PHYSIOLOGICAL COMPENSATIONS FOR CHANGES IN SALINITY AND TEMPERATURE

Like other animals or plants which must encounter rigid and greatly varying environmental conditions, estuarine organisms possess a number of physiological mechanisms which assist them in compensating for the ill effects of their environment. Some of the studies devoted to these mechanisms will be considered here under four subheadings: escape, reduction of contact, regulation, and acclimation.

ESCAPE

Escape into more suitable conditions of salinity or temperature is restricted to vagile organisms and to situations in which such conditions are available and accessible. Both vertical and horizontal migration may be of assistance to some estuarine organisms in avoiding critical factor intensities. Salinity fluctuations are usually less pronounced in the substrate than in the free water above, and average salinity intensities may be different. This is particularly true for the zone in which the relative proportions of sea water and river water change rhythmically as a function of the tides. The substrate, therefore, may represent an important refuge for various estuarine forms. Permanent bottom dwellers frequently enjoy more stable conditions than their pelagic counterparts and may show quite different distribution patterns.

Various environmental factors of a given estuarine body of water may counteract, support, or modify each other's physiological effects. Jorgensen (1952), Lewin and Guillard (1963), McCombie (1960), others have shown this for plants; Kinne (1960) has reviewed the pertinent information for inverte-

brates and fishes. In addition to the direct escape mentioned above, therefore, indirect escape may be available as a means of compensation for the ill effects of a given environmental entity. Thus, for example, if salinity reaches extreme values, and more favorable salinities are not available at the time, the ill effects of that extreme salinity could be reduced if a suitable temperature or light condition were selected. No clear-cut case of indirect escape has come to the reviewer's attention, but the mounting evidence on factor interactions strongly suggests such a possibility.

REDUCTION OF CONTACT WITH THE ENVIRONMENT

Reduction of direct contact with an adverse environment is a temporary rather than a permanent measure. It may occur in response to sudden pronounced changes as well as to temporarily maintained extreme conditions of salinity or temperature.

Adverse conditions of salinity may cause a variety of responses: (1) Production of slime, mucus, or other protective substances covering sensitive body surfaces; such reactions are known for various types of organisms, especially annelids, molluscs, and fishes. (2) Retreat into holes or burrows, which may sometimes be plugged, e.g., polychaetes and crabs. (3) Muscle contractions leading to a reduction in surface to volume ratios of sensitive organs or the whole body, e.g., hydroids, annelids, and molluscs. (4) Withdrawal of sensitive body parts. (5) Closure of shell- or comparable structures; certain clams or barnacles may, for example, live indefinitely in extreme low or high average salinities, which per se would be lethal if the length of the active periods allowed by salinity fluctuations is sufficient for feeding and defecating. (6) Actual changes in body form and other structural properties may occur if a given stress is maintained for longer periods of time. Examples are colonial hydroids, such as *Cordylophora caspia*, *Perigonimus megas*, and *Laomedea locrensi*, which respond to maintained extreme salinities by reducing their hydranth size, e.g., reduction in length and number of tentacles and in surface to volume ratio of the hydranth body. Other examples can be found among protozoans, sponges, and certain crustaceans. (7) Transitions into resting stages are known to occur, for example, in bacteria, fungi, protozoans, sponges, hydrozoans, bryozoans, rotifers, nematodes, tardigrades, and crustaceans. They lead eventually to the formation of spores, cysts, or menonts, which often separate the organism to a considerable degree from its environment. Spore, cyst, or menont formation is usually accompanied by an increase in environmental resistance and by a reduction in activity and metabolic rate. The organisms involved may thus endure more extreme factor intensities than in the state of full activity and immediate contacts with the surrounding environment. After improvement of the adverse conditions the resting stages may re-transform into the active condition.

Adverse conditions of temperature may cause simi-

lar responses. The most frequent and apparently most efficient reduction-of-contact responses to extreme temperature intensities are transformation into resting stages during the cold season. Organisms incapable of forming resting stages often enter the substratum during the most severe winter months.

REGULATION

The regulatory devices for counteracting detrimental effects of salinity may be considered under three aspects: ion regulation, volume regulation, and osmoregulation. Recent pertinent reviews have been published by Beadle (1957), Brown and Danielli (1955), Kinne (1963b, 1964a, b, c), Lockwood (1962), Prosser and Brown (1961), Remane and Schlieper (1958), and Robertson (1957, 1960a, b).

Ion regulation presumably has a longer evolutionary history than volume or osmoregulation. All aquatic organisms appear to possess some capacity for regulating the ionic composition of their body, tissue, and cell fluids.

Ion regulation has been shown or suggested to exist in a number of aquatic plants (Bergquist, 1958a, b; Biebl, 1956; Blinks, 1951; Eppley, 1958a, b, 1962; Eppley and Cyrus, 1960; Guillard, 1962; Hope and Walker, 1960; MacRobbie and Dainty, 1958a, b; Scott and Hayward, 1953, 1954, 1955). There is little information available, however, on ion regulation in algae during osmotic stress. In *Porphyra perforata*, survival in diluted and concentrated sea water is affected by the amount of Ca present. Ca seems especially important in maintaining membrane selectivity toward K and Na. Over a wide range of salinities (about 3.5 to 70‰) cells of *P. perforata* accumulate K and partially exclude Na. Rain is potentially a more serious threat to survival, due in part to breakdown of ion transport, than are high salinities. By washing away the seawater film normally present between and around the blades even during emergence, heavy rain would "almost certainly abolish membrane selectivity, decrease respiration, induce loss of cellular cations, and result in high mortality if the blades were exposed long enough" (Eppley and Cyrus, 1960).

The same holds true for *Chaetomorpha linum*, an intertidal green alga, which often thrives in great numbers along the German coast. *C. linum* is well adapted to osmotic stress. It compensates for changes in the osmotic potential of the surrounding medium by regulating its turgor pressure (Kesseler, 1959). This regulation is achieved mainly by active accumulation or extrusion of KCl. Accumulation of KCl against strong diffusion gradients requires energy, which is, according to Kesseler (1962), obtained by respiration. In isoosmotic artificial sea water with Ca, the cells rapidly become permeable to accumulated KCl and lose turgidity (Kesseler, 1964). In distilled water containing small amounts of CaCl_2 and NaHCO_3 (establishing a pH of about 8), however, the cells—after having adjusted to the new condition—can survive for many days without a significant loss

of ions. Adjustment occurs within 24 hours (Kesseler, 1959). In most algae from Naples and Helgoland so far tested, K is the main intracellular cation. Only in the Siphonales is Na present in a concentration exceeding that of sea water, while Cl dominates among the intracellular anions (Kesseler, verbal communication). An exceptional case has been reported for some species of the genus *Desmarestia*; they accumulate sulfuric acid in their vacuoles, the sulfate ion acting as the main intracellular anion and electro-neutrality being curiously established by hydrogen ions (Eppley and Bovell, 1958).

In a number of algae Na is involved in "ion pump" systems (Eppley, 1962; Eppley and Cyrus, 1960; Hope and Walker, 1960). For recent reviews on the physiology and biochemistry of algae, consult Lewin (1962).

A series of papers demonstrates the importance of the ionic composition of the surrounding water for growth and reproduction of algae, and has been reviewed by Guillard (1962), Lewin and Guillard (1963), and Provasoli (1958). In recent years, growth rates have been determined, for example, by Droop (1958), Guillard and Ryther (1962), Provasoli *et al.* (1954), Schmitz (1959), and Williams (1962). Vollenweider (1950) studied the requirements for Ca and Mg in three diatoms. He found (1) needs for high Ca concentrations, (2) limited interchangeabilities between Ca and Mg, and (3) that a certain balance between the two ions may be required; addition of higher concentrations of Mg is necessary with high concentrations of Ca. Provasoli *et al.* (1954) tested a series of algae flagellates in order to find out how closely the mineral requirements of marine and freshwater forms reflect the composition of their natural environment. The experiments were so designed as to vary the salinity, the monovalent-divalent ratios (M/D), and the Ca/Mg ratios, permitting an evaluation of the relative or absolute importance of these factors for growth. As is well known, aside from total solid concentration, Mg/Ca ratios represent the most obvious differences between sea and fresh water. It may be expected therefore that marine organisms would prefer a Ca/Mg ratio close to that in sea water (1:3) and freshwater organisms, the 6:1 ratio characteristic for that medium. While this may hold at salinities and M/D ratios similar to habitat conditions, it was shown that for each of the tested phytoflagellates, at a specific total salt concentration and M/D ratio, Ca and Mg are widely interchangeable and that deviations from this particular condition may still allow maximum growth but only at restricted Ca/Mg ratios. In general, the preliminary data obtained by Provasoli and his collaborators indicate a great ionic plasticity.

In 1958, Droop established that the Ca/Mg ratios yielding best growth in the extremely euryhaline chrysomonad, *Monochrysis lutheri*, the cryptomonad, *Hemiselmis virescens*, and the chlorophycean, *Nannochloris oculata*, are more similar to the Ca/Mg ratio found in sea water than the ratio preferred by

Table 1. Proportions of major ions in the body fluid of the starfish, *Asterias rubens*, exposed to sea water of 31‰ salinity (After Cole, 1940) and to brackish water of about 16‰ (After Remane and Schlieper, 1958 and Seck, 1958). All concentrations are given in mM/l.

Medium	Na ⁺	K ⁺	Ca ⁺⁺	Mg ⁺⁺	Cl ⁻	SO ₄ ²⁻
31‰ S	417	9.10	9.41	50.1	483	30.3
Body Fluid	412	9.56	9.31	50.0	488	30.1
16‰ S	215	4.98	5.56	24.05	252.8	13.08
Body Fluid	216	5.40	5.60	24.22	255	13.05

the less euryhaline marine diatom, *Skeletonema costatum*. The tolerances of the species tested by Droop cover nearly all the Ca/Mg ratios that are characteristic of both sea and fresh water. *S. costatum*, however, differs from the more euryhaline species in having a narrower range of Na tolerance. Droop points to information obtained on some neritic dinoflagellates by Braarud (1951) and Braarud and Papas (1951), indicating that marine neritic species might be expected to have a lower Na limit of about 3,000 mg/l, whereas the limiting concentration for supralittoral species may be as low as 300 mg/l (there is also indication in Provasoli *et al.* (1954) that oceanic *Rhodomonas lens* has a lower Na limit of not less than 4,000 mg/l). Na tolerance may therefore be an important limiting factor for growth in water of reduced salinities or modified ionic composition. In *Thalassiosira weizietii* a variation of the sulfate to chloride ratio causes maximum growth rates to occur at different total salt concentrations (Schmitz, 1959). The information at hand indicates that significant changes in the ionic composition of the surrounding water may modify lethal limits and salinity preferences as well as capacities for growth, reproduction, and competition and, hence, may affect the abundance and distributional range of estuarine species.

Ion regulation in aquatic animals has received much attention. The most recent reviews have been written by Kinne (1963b; 1964a, b). In general, saltwater animals tend to accumulate higher proportions of potassium and hydrogen ions in their body fluids and tissues than are present in undiluted sea water; at the same time they tend to keep the internal sodium and chloride levels lower and to exclude magnesium and sulphate, which are both abundant in sea water. If exposed to diluted sea water, many estuarine invertebrates are capable, to some extent, of maintaining their original ionic proportions, while their marine counterparts usually exhibit considerably poorer capacities for ion regulation. Thus in echinoderms—which are sparsely represented in estuaries—body fluids conform closely to ionic ratios in the external medium, both in sea water and in brackish water. An example is the starfish, *Asterias rubens* (Table 1). However, intracellular ionic ratios of echinoderms (cells of blood, muscles, and body wall) are different from those of the surrounding sea water and so is

the ionic composition of their eggs (Rothschild and Barnes, 1953). Cnidarians, annelids, and molluses are somewhat better regulators. Most estuarine crustaceans exhibit a significant capacity for ionic regulation (Robertson, 1957, 1960a), and so do the fishes. In fact, estuarine teleosts show less variation in ionic ratios of their blood if exposed to salinity variations than do most invertebrates.

Ion regulation in aquatic animals occurs, essentially, between external medium and blood and between blood and tissues. Most of the estuarine species tested show significant differences between the ionic composition of their body fluids and that of their cell fluids. The cell fluids appear to be quite isoosmotic to coelomic and circulatory fluids; their total osmoconcentration, however, is the result of both inorganic and organic substances. In contrast, total osmoconcentration of coelomic and circulatory fluids results largely from inorganic ions only, especially from sodium and chloride. In *Gammarus duebeni*, for example, tissue chloride amounts to only a fraction of blood chloride over a salinity range from sea water to fresh water (Beadle and Cragg, 1940a, b), and in *Mytilus edulis* tissue chloride (foot tissue) amounts to less than half that of the blood, both in sea and brackish water (Table 2).

High capacities for ion regulation, tissue tolerance to fluctuations in ionic ratios, and, possibly, osmotic stabilization by means of dissolved organic substances represent important physiological prerequisites for successful establishment under estuarine conditions. The molecular mechanisms involved in active ion transport are not yet well understood. It has been demonstrated, however, that active transport depends ultimately on metabolic energy (Ackerman, 1962).

Volume regulation is known to occur in a variety of estuarine organisms. In fact, the ability to regulate body volume appears to be an important characteristic of most estuarine species. Upon a sudden change in salinity, volume regulators not only lose or gain water but also lose or gain salts. A change in volume is indicative of a distortion in the steady state balance of the continuous inflow and outflow of water and salt. In volume regulators, such distortion initiates a whole series of responses and adjustments leading to changes in permeability and excretory processes, and

Table 2. Chloride levels in blood and muscle tissue (foot) of the lamellibranch, *Mytilus edulis*. (1) Individuals kept in normal sea water; (2) 24 hours after transfer into diluted sea water; (3) 48 hours after transfer into diluted sea water. All concentrations are given in mM/kg H₂O (After Krogh, 1938).

Experimental condition	Blood Cl	Muscle Cl	External medium
(1) Sea water	526	109	532
(2) Diluted sea water after 24 hours	263	100	264
(3) Diluted sea water after 48 hours	224	55	229

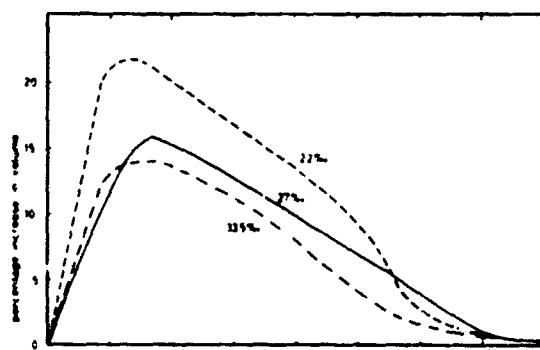


Fig. 1. Volume regulation in larvae of the polychaete, *Marphysa griseolyti*. Smoothed curves show percentage of increases of volume in waters of lowered salinity (After Krishnamoorthi, 1951).

finally to a new steady state balance between the organism and its external medium. The adjustments involved may take minutes, hours, or even days. Some euryhaline protozoans exhibit volume regulation when exposed to changing salinities. Their major regulatory mechanism appears to be the contractile vacuole (Kitching, 1938, 1948, 1951, 1952, 1954; Müller, 1936; Oberthür, 1937). On the other hand, some protozoan species are capable of regulating their volume in the absence of a contractile vacuole. The apparent osmotic volume in the red alga, *Porphyra perforata*, is nearly constant between about 17 and 35 %. This volume regulation is assumed to be due to differential shrinking and swelling of structural polysaccharides and not to active water secretion (Eppley and Cyrus, 1960). Further examples of volume regulators are *Nereis diversicolor* (Beadle, 1931, 1937; Ellis, 1937, 1939; Schlieper, 1929a, b),

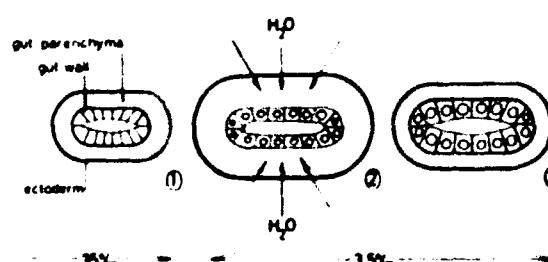


Fig. 3. Schematic cross sections through the turbellarian, *Procerodes ulvae*. (1) Condition during exposure to undiluted sea water of approximately 35 %. (2) A few hours after transfer into 3.5 %; water has entered through the ectoderm and caused considerable swelling of parenchyma; gut cells begin to collect the water in the form of intracellular vacuoles. (3) About 12 hours after transfer; gut cells have removed most of the water and thus decreased in body volume (After Beadle, 1934).

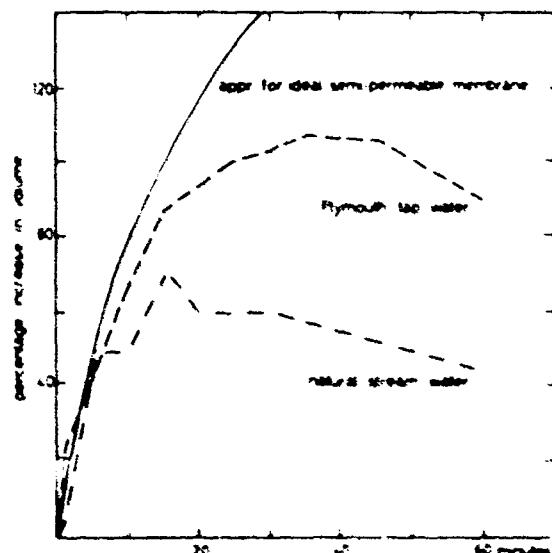


Fig. 2. Volume regulation in the triclad turbellarian, *Procerodes ulvae*, in tap and natural stream water (After Pantin, 1931b; from Pearce and Gunter, 1957).

Nereis diversicolor (Topping and Fuller, 1942), *Marphysa griseolyti* (Fig. 1) (Krishnamoorthi, 1951), *Physcosoma japonicum* (Koller, 1939), *Procerodes ulvae* (Beadle, 1934; Pantin, 1931b; Weil and Pantin, 1931), *Carcinus maenas* (Bethe et al., 1935; Nagel, 1934), *Gasterosteus leucurus* (Gueylard, 1925), *Pleuronectes platessa* (Henschel, 1936). Two examples may be presented in more detail. The triclad turbellarian, *Procerodes* (formerly *Gunda*) *ulvae*, lives in Devonshire estuaries, which are characterized by considerable diurnal salinity fluctuations. *Procerodes* is most abundant about halfway between high and low tide levels, and twice daily has to tolerate a decrease in salinity. If these worms are exposed to distilled water or soft Plymouth tap water, they rapidly increase in volume and finally burst. If exposed to natural, hard stream water, the volume increases about 70 percent and after a while begins to decrease (Fig. 2). Under these conditions survival is possible for several days (Weil and Pantin, 1931). The regulatory mechanisms involved include changes in membrane permeability, which are related to the state of acclimation as well as the calcium content of the surrounding water. Another aspect of the regulatory mechanisms is the removal of excess water by the gut epithelium (Fig. 3). Part of this water seems to be stored in gut cells during the low salinity phase (Pantin, 1931a, b). The estuarine polychaete, *Nereis diversicolor*, uses a combination of different regulatory methods. After exposure to reduced salinities, body volume increases temporarily, but urine flow from the nephridia is subsequently augmented, and as a result body volume declines again (Beadle, 1937); at the same time, reduction in salinity causes salt loss, which is compensated for by an increase in active salt uptake (Fretter, 1955; Jørgensen and Dales, 1957). In very low salinities *N. diversicolor* may be able to reabsorb some salts in its nephridial tubules and thus produce a urine hypoosmotic to the surrounding water (Potts and Harry, 1963).

Closely related to changes in body volume are changes in body weight. Increase in volume due to

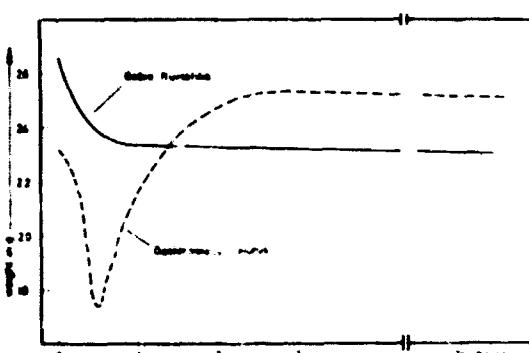


Fig. 4. Changes in body weight in the freshwater living fish, *Gobio fluviatilis*, after transfer into brackish water of $\Delta = 0.65^{\circ} \text{C}$. and in the euryhaline fish, *Gasterosteus leucurus*, after transfer into sea water of $\Delta = 20.2^{\circ} \text{C}$. (After Gueyland, 1925).

osmotic water uptake is, of course, always combined with increase in body weight; however, weight increase is not always paralleled by volume increase. Hard-shelled estuarine animals, for example, may exhibit osmotic water uptake and weight increase when exposed to hypoosmotic water, but their hard outer surfaces restrict volume changes. An example of weight changes in fishes is presented in Figure 4. In the freshwater-living fish, *Gobio fluviatilis*, transfer into hyperosmotic brackish water leads to loss of water and weight which is irreversible and soon becomes lethal. The euryhaline fish, *Gasterosteus leucurus*, on the other hand, is capable of compensating for the initial water loss and, thus, of surviving a sudden increase in salinity (Gueyland, 1925).

Osmoregulation is a capacity found in the majority of estuarine organisms. Most of the aquatic algae investigated tend to maintain an internal osmocconcentration somewhat higher than that of the surrounding water. Their ability to withstand osmotic stress depends ultimately on the resistance of their protoplasm to alterations in salt concentration (Gullard, 1962). Marine algae vary considerably in their osmocconcentration. Some are barely turgid, others maintain values almost twice those of sea water. Brackish-water forms usually are quite hyperosmotic, and freshwater algae often have very high osmotic values of about 5 atm (Blinks, 1951). The capacity to maintain turgor, even in abnormally high salinities, may be surprisingly great; *Elachista*, for example, maintained turgor in sea water concentrated to the point of salt crystallization (Bunning, 1934). In *Chaetomorpha linum* turgor remained almost constant at 14.8 to 16.5 atm over a salinity range (balanced artificial sea water) from fresh water to 35% (Kesseler, 1959). The physiology and biochemistry of algae and their osmoregulatory mechanisms have been reviewed by Blinks (1951) and Lewis (1962).

In aquatic invertebrates and fishes the most efficient osmoregulators may exhibit a considerable degree of osmostability over salinity ranges of up to 20 or 30%, resulting in an appreciable relative inde-

pence of salinity variations. High osmoregulatory capacities, however, are not a necessary prerequisite for a successful existence under estuarine conditions. Euryhalinity may also be based on high tissue tolerance to reduced or increased salt concentrations or may simply involve low permeability.

With respect to their regulatory capacities, osmoregulators can be subdivided into euryhaline, holeuryhaline, and oligohaline regulators. Euryhaline osmoregulators can regulate sufficiently in waters of fluctuating, reduced, or increased salinities, but over longer periods require more salt than is available in pure fresh water. Examples are the polychaetes, *Vereis diversicolor* (Schlieper, 1929a, b, 1930; Smith, 1955a, b, c, 1956); *Vereis limnicola* (formerly *lighti*) (Smith, 1957, 1959); the crustaceans, *Gammarus locusta*, *G. obtusatus* (Beadle and Cragg, 1940a), *G. duebeni* (Beadle and Cragg, 1940a; Kinne, 1952), *G. oceanicus*, *Marinogammarus finmarchicus* (Werntz, in Prosser and Brown, 1961), *Carcinus macrurus* (Daval, 1925; Nagel, 1934; Schlieper, 1929a, b), *Rhithropopaeus harrisii* (Kinne and Rotthauwe, 1952), *Palaeomonetes varians*, *Palaeomon serratus*, *Palaeomon squilla*, *Panaculus indicus*, *P. carinatus*, *Metapenaeus dobsoni* (Panikkar, 1939, 1940, 1941, 1950), *Metapenaeus monoceros* (Panikkar and Viswanathan, 1948), *Uca crenulata* (Jones, 1941), *Crangon crangon* (Broekema, 1941; Flügel, 1959), *Artemia salina* (Croughan, 1958a, b), *Pachygrapsus crassipes* (Jones, 1941); the fishes, *Gasterosteus* (Gueyland, 1924; Koch and Heuts, 1942), *Anguilla* (Callamand, 1943); various cyprinodonts; and many others (Black, 1957; Krogh, 1939; Nicol, 1960; Pearse and Gunter, 1957; Prosser and Brown, 1961) (Fig. 5).

Holeuryhaline osmoregulators are able to regulate sufficiently in media ranging from pure fresh water to full-strength sea water or higher. Examples are the crab, *Eriocheir sinensis* (Koch, 1954); Koch and Evans, 1956a, b; Schlieper, 1935; Scholles, 1933; Schwabe, 1933); the fishes, *Cyprinodon macularius* and *Fundulus heteroclitus*; and presumably many turbellarians, rotifers, and oligochaetes (Kinne, 1964b).

Oligohaline osmoregulators can regulate in pure fresh water, but collapse in salinities exceeding a few parts per thousand. Their body fluids are hyperosmotic to the surrounding water. To this group belong most of the typical freshwater animals (Fig. 6).

Among the fishes the elasmobranchs and the osmolyte hagfishes are unique in having blood which is about isosmotic with sea water. In elasmobranchs the actual salt content of the blood, however, is usually considerably below that of sea water and is not very different from that of the hypoosmotic marine teleosts; elasmobranchs make up the difference by maintaining a high content of urea in their blood. Upon entering an estuary, euryhaline elasmobranchs lower the urea content of their blood and thus reduce their internal osmocconcentration quickly and effectively (Pearse and Gunter, 1957).

The mechanisms employed in osmoregulation have received much attention, particularly those of crusta-

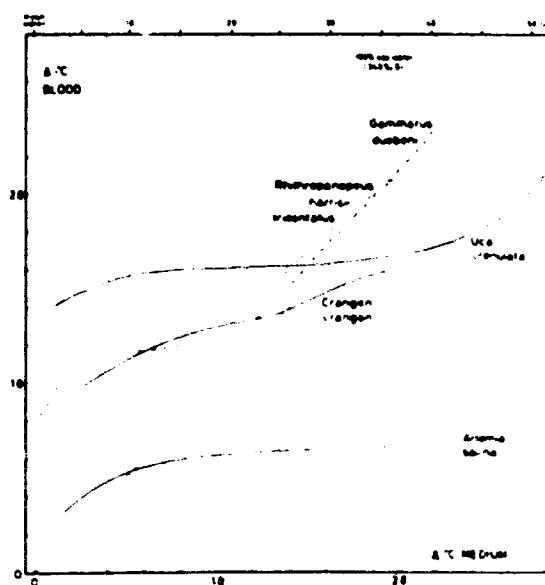


Fig. 5. Examples of osmotic responses (changes in blood osmoconcentration) in euryhaline osmoregulators exposed to variations in salinity (fresh water to about 50‰). *G. duebeni* and *K. horrisii tridentatus* are hyperosmotic regulators, being hyperosmotic in diluted sea water but more or less isosmotic in higher salinities. *U. cruentata*, *C. crangon*, and *A. salina* are hyperosmotic and hypoosmotic regulators, being hyperosmotic in diluted sea water and hypoosmotic in higher salinities (After various authors, from Kinne, 1963b).

ceans and fishes. In these two groups the mechanisms are complex, often involve several organs or organ systems, and may be under endocrine and nervous control. For extensive recent reviews and discussions on osmoregulatory capacities and mechanisms in Crustacea, consult Kinne (1963b, 1964b), Lockwood (1962), Nicol (1960), Prosser and Brown (1961), Robertson (1957, 1960a), and Shaw (1960). The main osmoregulatory organs are gills (often responsible for salt balance), gut (often responsible for water balance), antennal glands (in some crustaceans), nephridial canals, and body surfaces.

Estuarine invertebrates and fishes lack effective mechanisms for temperature regulation and are, in essence, thermo-conformers. Temperature fluctuations thus, affect their basic life processes directly and with considerable impact, unless escape by locomotion or transformation into resting stages is available.

ACCLIMATION

Acclimation (synonymy: acclimatization, non-genetic adaptation) is visualized here as an ecological phenomenon comprising adjustments of organisms to alterations in the intensity patterns of variables in their environment, which ultimately result in a relative increase in their capacity to survive, reproduce, or compete. Such adjustments are advantageous in an objective sense and can be assessed quantitatively by measuring differences in performance of individ-

uals with different environmental experiences. The net result of acclimation is compensation for adverse aspects of environmental circumstances, often leading to an increase in stability and in homeostasis and hence, in organismic independence (Kinne 1963b, 1964a, b, c). This definition separates "acclimation" from the more general term "response", which refers to any reaction to an environmental stimulus, whether it be adaptive or not. A major difference between acclimation and regulation is that regulation is a rather fast process, resulting primarily from routine activities of specific, pre-existing regulatory organs, while acclimation results in actual changes in the response mechanisms, requires time to develop, and may involve all levels of organismic functions and structures. In organisms under stress, regulation and acclimation may both occur simultaneously and may not be completely separable in all cases. Nevertheless, it appears necessary for the physiologist to differentiate between these two types of compensatory means in order to make a proper analysis. For further details concerning recent considerations on the concept of non-genetic adaptation, consult Adolph (1964), Kinne (1964a, b, c), Precht (1964), and Prosser (1964).

In estuarine organisms acclimation to environmental variations appears to be of greater importance than acclimations to extremely low or high intensities. Most of the experimental work on physiological aspects of non-genetic adaptation, however, has been carried out by exposing the test organism to constant low, normal, or high factor intensities; information on acclimation to fluctuating conditions is lacking. Furthermore, most of the work has been done by

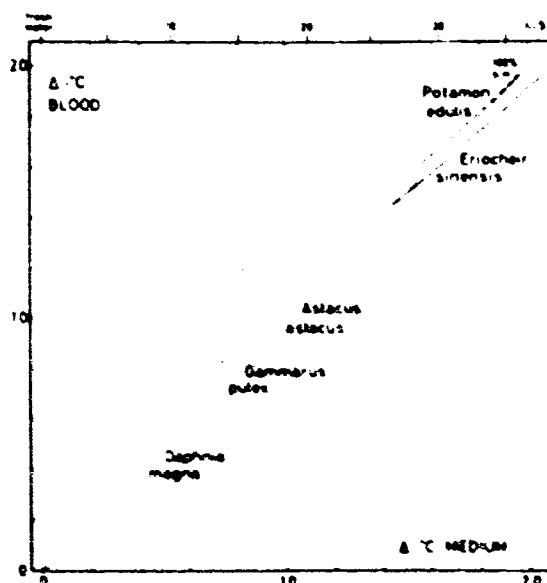


Fig. 6. Examples of osmotic responses (changes in blood osmoconcentration) in heterohaline osmoregulators (*E. sinensis*) and in oligohaline osmoregulators (*P. adamsi*, *A. astacus*, *G. pulex*, and *D. magna*). (After various authors, from Kinne, 1963b.)

vating one factor only, a situation which hardly occurs in estuaries. There is urgent need for new studies on non-genetic adaptation in estuarine organisms, performed under conditions simulating nature. Such studies are likely to add significantly to our incomplete knowledge concerning the importance of acclimation as a means of physiological compensation for estuarine conditions.

The literature on non-genetic adaptation to salinity variations is scanty. Next to nothing is known about acclimation to alterations in solute composition, although several investigations on ionic requirements have been carried out, for example, on aquatic plants (Elinks, 1951; Guillard, 1962; Lewin and Guillard, 1963; F. ovosoli, 1958); crustaceans, a fish, and other animals (Berger, 1929); and the cnidarians, *Cordylophora caspia* (Fulton, 1960, 1962; Roch, 1924) and *Hydra littoralis* (Lenhoff and Bovaard, 1960; Loomis, 1954). Acclimations to salinity appear to involve primarily functional and structural adjustments concerning water and salt balances. The simplest and presumably most ancient type of non-genetic adaptation to salinity is overall tissue acclimation in osmoconformers lacking specific organs for effective regulation. Osmoregulators employ specialized regulatory organs such as gills, gut, or excretory glands, which then presumably tend to represent the primary sites of acclimation.

The literature on acclimation to temperature in euryhaline invertebrates and fishes comprises several hundred papers. The present status of our knowledge with respect to life in estuaries will therefore be documented here only by referring to a few examples and previous reviews.

In the time course of non-genetic adaptation to changed conditions of salinity or temperature, three phases may be distinguished: (1) immediate responses, such as shock-type reactions or over- and undershoots of performance; they begin seconds or minutes after a significant environmental change and often have a positive survival value; they may not constitute, however, an integral part of the subsequent acclimation process per se in all cases; (2) the process of stabilization, which begins with decreasing fluctuations in performance and ends with the attainment of the new steady state; and (3) the new steady state of performance.

In estuarine organisms, the duration of the stabilization period, or the time between a substantial long-lasting change in salinity or temperature conditions and the completion of the respective acclimation processes, seems of special interest. In the organisms tested so far the process of stabilization lasts anywhere from several hours to several weeks. More than 50 percent of the total resulting amount of acclimation is often achieved within the first portion of the stabilization period, immediately following latency; towards its end, the gain in acclimation decreases progressively. The duration of the stabilization period tends to decrease with increasing metabolic rate. It depends on the amount and dynamics of the change in

salinity or temperature, on the parameter measured, and on other simultaneously effective environmental factors. Possibly the period of stabilization is shorter in organisms normally exposed to pronounced long-term environmental fluctuations. In microorganisms, stabilization may last only minutes or hours. In the stickleback, *Gasterosteus leucurus*, transferred from fresh water into blood-hyperosmotic brackish water, acclimation appears to be largely accomplished within a few hours (Gueyland, 1925). The crayfish, *Astacus astacus*, if transferred from its normal freshwater medium into blood-isosmotic brackish water of 15‰, reaches a new steady level of blood osmoconcentration after 12 days; simultaneously, O₂ consumption decreases and reaches a new steady level at 60 percent of the original values after 20 to 30 days (Herrmann, 1931; Schwabe, 1933). In the mud crab, *Hemigrapsus oregonensis*, measurable acclimation to approximately 51‰ required more than five days, strong acclimation, 22 days (Gross, 1963). The mussel, *Mytilus edulis*, exhibits a higher metabolic rate in the Baltic Sea at 15‰ than in the North Sea at 30‰; if North Sea individuals are transferred into water from the Baltic, tissue O₂ consumption increases 20 percent within a few hours; further increase is slow so that the steady state consumption of Baltic Sea mussels is reached only after four to seven weeks (Schlieper, 1955).

In crayfish exposed to a change in temperature from 4° to 23° C., acclimation to the higher temperatures is apparently completed in less than 24 hours (Spoor, 1955). The crabs, *Hemigrapsus nudus* and *H. oregonensis*, can regain their tolerance to high temperatures after a low temperature history within less than one week (Todd and Dehnel, 1960). In the shore crab, *Pachygrapsus crassipes*, respiratory acclimation to a temperature change of 7.5° C. was found to require a half-time of about 6 days (Roberts, 1957). In various fishes metabolic acclimation to a different temperature level takes four to five days (Precht, 1949). The marine fish, *Girella nigricans*, gains about 50 percent of the total resulting change of cold tolerance in two days; complete acclimation (constant cold tolerance) is achieved in about 20 days (Doudoroff, 1942). In American lobsters, *Homarus americanus*, previously kept at 14.5° C. and then transferred into an acclimation temperature of 23.0° C. for periods ranging from 1 to 31 days, survival time was determined at 30° C. These experiments demonstrated that thermal acclimation began only after a latent period of some ten days and was complete after about 22 days (McLeese, 1956). Intertidal molluscs, *Acmaea limatula*, when transplanted from low-level to high-level localities, exhibit a subsequent decrease in heart pumping rate, within 29 days the heart beat becomes finally equal to that of the high-level individuals, when measured at a given temperature (Segal, 1956).

Obviously, quick adjustments to new salinity or temperature intensities are advantageous to estuarine organisms. However, too fast adjustments may be

detrimental. They may gear the organism into a fast, endless series of "on-off responses" without ever reaching a new steady level (at which, energy requirements may be considered most economical under the circumstances).

THE NEW STEADY STATE AFTER A CHANGE IN SALINITY

The new steady state following a change from one salinity level to another has been studied with emphasis on lethal salinity limits, rates of metabolism and activity, and osmoregulatory capacity. In general, acclimation to subnormal salinities tends to shift the lower lethal limit downward, and acclimation to supranormal salinities tends to shift the upper lethal limit upward. Although there are many examples available from literature to illustrate this relationship, the mention of McLeese's work (1956) on the lobster, *Homarus americanus*, may suffice here.

The new steady level of metabolism may be (1) higher in subnormal salinities and/or lower in supranormal salinities, (2) higher both in subnormal and supranormal salinities, (3) lower both in sub- and supranormal salinities, or (4) essentially unaffected. Most species tested belong to type (1); the polychaete, *Nereis diversicolor* (Schlieper, 1929a, b); the crustaceans, *Carcinus maenas*, *Eriphia spinifrons* (Schlieper, 1929a, b; Schwabe, 1933), *Gammarus locusta* (Schlieper, 1929a, b), *Potamon edulis* (Raffy, 1934), *Gammarus duebeni* (Kinne, 1952), *Uca* spp. (Gross, 1957), and *Hemigrapsus oregonensis* (Dehnel, 1960); the mollusc, *Alderia modesta* (Friedrich, 1937); unfertilized eggs of the starfish, *Asterias glacialis* (Borei, 1936); and the fish, *Petromyzon marinus* (Fontaine and Raffy, 1935). Examples for type (2) are the crustaceans, *Ocypode quadrata* (synonym: *O. albicans*) (Flemister and Flemister, 1951), *Palaeomonetes varians* (Lofts, 1956), and *Metapenaeus monoceros* (Rao, 1958). Examples for type (3) are the anthozoan, *Metridium marginatum* (Schoup, 1932); the mollusc, *Mytilus edulis* (Bouxin, 1931; Beliaev and Tschugunova, 1952; see, however, the criticism by Remane and Schlieper, 1958); and various species of starfish, *Asterias* (Maloeuf, 1938; Meyer, 1935; Schlieper, 1929a, b). Examples for type (4) are the wool-handed crab, *Eriocheir sinensis* (Schwabe, 1933; Krogh, 1939); and the fishes, *Sargus* and *Scorpaena* (Raffy, 1932a, b), *Fundulus heteroclitus* (Maloeuf, 1938), and *Anguilla anguilla* (Raffy, 1933).

In *Metapenaeus monoceros*, increase of O_2 consumption due to transfer into sub- or supranormal salinities is, after prolonged exposure to the new salinity, followed by a gradual lowering of respiratory rate towards the original level (Rao, 1958). Complete acclimation of the freshwater living crayfish, *Astacus astacus*, to increased salinity results in a reduction of the osmotic gradient and fall in urine output by half in 8 % and to negligible amounts in 15 to 20 % (Herrmann, 1931; Schwabe, 1933). The breakpoint of the blood-medium curve in *Callinectes sapidus* collected in dilute sea water occurs at lower

salinity values than it does in individuals collected in full-strength sea water; after acclimation of crabs from dilute sea water to full-strength sea water, however, the breakpoint shifts towards higher salinities (Anderson and Prosser, 1953). Individuals of *Hemigrapsus oregonensis*, which had been exposed for more than 20 days to about 51 % salinity (150 percent sea water), exhibited a greater capacity for osmoregulation in high salinities than individuals that were previously exposed to approximately 34 % (100 percent sea water). This acclimation occurred both after a sudden or a gradual salinity increase (Gross, 1963).

Salinity changes may affect not only the rate but also the efficiency of metabolic processes. In the fish, *Cyprinodon macularius*, for example, a given amount of food is converted into different amounts of body substance, depending on the salinity history of the individuals (Kinne, 1960, 1963c). Osmoregulation in sub- or supranormal salinities might be expected to use extra energy (Croghan, 1961). Acclimations leading to an increase in efficiency of regulation would decrease the energy requirement for maintenance (reduction of food requirements) and, hence, afford a significant competitive advantage.

In addition to the functional acclimation to salinity mentioned above, there is some evidence of structural acclimation. Thus, in the hydroid, *Cordylophora caspia*, prolonged exposure (days to weeks) to different constant salinities results in a number of structural adjustments involving the shape of whole colonies, the number, length, and diameter of tentacles, size and shape of hydranth bodies, number of cells per hydranth, shape of individual cells (depth and width), as well as the size of nuclei and nematocysts. At a given normal temperature, transfer into a new salinity level will be followed by a gradual reorganization of structures until certain conditions are attained; this structural status will be modified again after a further change in salinity (Kinne, 1956, 1958a, b). Such continuous adjustments have been produced experimentally even in specimens with identical genotypes. Their most obvious net results are changes in surface area and in surface to volume ratios in hydranths and single cells, implying quantitative alterations in metabolic performance. In the euryplastic Pacific pink salmon, *Oncorhynchus gorbuscha*, individuals raised in sea water have somewhat fewer kidney glomeruli than individuals raised in fresh water (Ford, 1958). If exposed to diluted sea water, the Indian euryhaline fish, *Etroplus maculatus*, decreases the diameter of its glomeruli and shows structural changes in its kidney tubule. With acclimation to higher salinities, *E. maculatus* increases the thickness of the tunica propria of its gut wall and the number of goblet cells in the lining gut epithelium (Virabhadrachari, 1961). In the herring, *Clupea harengus*, hatching length and some meristic characters vary as a function of the salinity conditions effective during incubation (Blaxter and Hempel, 1961; Holliday and Blaxter, 1960), and in the pupfish, *Cyprinodon*

macularius, incubation salinity has been shown to affect the body form of newly hatched individuals (Kinne and Sweet, 1964; Sweet and Kinne, 1964). Similar structural consequences of salinity have been reported in a number of other fish species, particularly with respect to alterations in numbers of vertebrae and fin rays, gill structure, and surface area. They may be of adaptive value and significantly modify the performance of an individual.

THE NEW STEADY STATE AFTER A CHANGE IN TEMPERATURE

There is much information concerning the new steady state of performance (relative to the original one) after a defined change in constant temperature. Many of the pertinent contributions have been reviewed by Bullock (1955), Fry (1947), Kinne (1963a, b, 1964a, b, c), Precht (1958, 1961), Precht *et al.* (1955), Prosser (1955, 1958a, b), and Prosser and Brown (1961). A few examples will be presented below, first at the functional level, with special reference to lethal temperature and metabolic rate, then at the structural level.

Functional acclimation to extreme cold and heat is well documented. Acclimation to subnormal temperatures generally tends to shift the lower lethal limit downward, and acclimation to supranormal temperatures tends to shift the upper limit upward. Examples are the crustaceans, *Homarus* (McLeese, 1956), *Streptocephalus* (Moore, 1955) and *Artemia* (Grainger, 1958); the green fish, *Girella nigricans*, had a lower lethal temperature of 13° C. after acclimation to 28° C. and of 4.5° C. after acclimation to 12° C. (Doudoroff, 1942); for further examples consult Brett (1946, 1952), Christoffersen and Precht (1952a, b, 1953, 1956), Doudoroff (1942, 1945), Fry *et al.* (1942, 1946), Hart (1947), Hathaway (1927), Krüger (1962), Loeb and Wasteneys (1912), and Precht (1963, 1964). Non-genetic resistance adaptation to cold or heat seems to be correlated to changes in intermolecular forces leading to different degrees of stabilization of protoplasmic components. In many cases a gain in cold or heat resistance appears to be paralleled not only by increased protoplasmic stability, but also by a relative decrease in biochemical activity. Unspecific increase in general resistance to environmental stress as a by-product of acclimation to a given single factor has been reported in several cases. Thus, acclimation to extreme temperatures may result in concomitant increase in resistance to low oxygen concentration, radiation, and chemical poisoning. The upper lethal temperature is a useful tool in assessing intra- and interspecific (genetic) differences in thermostability (Brett, 1956; Fry, 1947, 1957; Fry *et al.*, 1942; Fry *et al.*, 1946; McLeese, 1956; Todd and Dehnel, 1960). It can also be used to assess the amount and speed of non-genetic adaptation. Experimental heat death—particularly when measured as protein denaturation at extreme high temperatures—appears, however, to be indicative of qualitative differences in basic properties such as primary protein structures, rather than of more subtle quantitative divergencies.

Non-genetic adaptation of metabolic rate to new levels of temperature has received much attention. All possible quantitative differences between the original level of performance and the new steady state that may follow a defined change in temperature have been considered and classified by Precht (1949, 1958), Precht *et al.* (1955), and later in a modified version by Prosser (1958b). Precht distinguishes five types: (1) overcompensation; (2) perfect or "ideal" compensation, resulting in constant rate functions after complete acclimation to different experimental temperatures; (3) partial compensation, the most frequent case; (4) no compensation; and (5) inverse compensation. Prosser distinguishes four basic patterns: (1) little or no compensation, indicated by little or no change in the position of rate temperature curves (log rate plotted against temperature); (2) shift in position (translation) of rate curves without change in Q_{10} ; (3) change in Q_{10} (rotation) of rate curves without shift in position; (4) translation combined with rotation. Little is known about what these different types and patterns imply in terms of the underlying physiological mechanisms. According to Prosser and Brown (1961), translation implies a change in activity (in the thermodynamic sense) of some enzyme system, and rotation implies a change in Q_{10} and hence in activation energy. Factors most likely to cause translation are alterations in enzyme concentration, in relations among enzymes (in series or parallel), and in external factors other than temperature (salinity, pH, etc.). Factors most likely to cause rotation are alterations in enzymatic protein, in enzymatic pathways and some cofactor.

Acclimation to changes in temperature expresses itself not only in alterations and shifts of lethal limits and metabolic rate, but it may also affect the temperature preferendum (Pitt *et al.*, 1956; Zahn, 1962), intra- and interspecific competition, behavior, orientation, and biological rhythms and quantitative changes in biologically important substances. In wool-handed crabs, *Eriocheir sinensis*, kept in fresh water, exposure to low temperatures of 1° to 3° C. results in a marked decrease of free proline concentration in the intracellular pool of amino acids in muscles, compared with individuals kept at 15° C. (Duchateau and Florkin, 1955). In *Daphnia* supranormal temperatures—at constant O_2 pressure—augment the amount of hemoglobin (Florkin, 1960). In the fishes, *Platypoecilus* and *Xiphophorus*, temperature decrease from 28° to 22° C. causes a significant rise in the level of amino acids (Anders *et al.*, 1962).

Structural acclimation to temperature is documented by relatively few reports. In various crustaceans, changes in temperature have been shown to cause morphological color changes involving differences either in the amount of pigment per pigment cell or in number of chromatophores per unit area, or both (Brown, 1934). In poeciliid fishes, temperature decrease may accelerate and intensify the forma-

tion of pigment cells. Thus, a decrease from 28° to 22° C. resulted within eight days in an increase in the number of scale melanophores 50 times that of the controls (Anders *et al.*, 1962). Changes in body size and shape, number, length, and diameter of tentacles, cell dimensions, cell number per hydranth, and size of nuclei and nematocysts due to acclimation to different constant temperatures have been demonstrated in the hydroid, *Cordylophora caspia* (Kinne 1956, 1958a, b). Structural adjustments of body size and shape are furthermore documented by the phenomenon of cyclomorphosis in Cladocera (Brooks, 1946, 1947, 1957; Lieder, 1951; Ostwald, 1904; Wessenberg-Lund, 1900; Wolterec, 1913) and Copepoda (Margalef, 1955). *Daphnia cucullata* and *D. retrocurva* exhibit the most spectacular changes of helmet, head crest, and spines, particularly if the parthenogenetic young developed at high temperatures of at least 18° C. to 20° C. Such structural adjustments, however, may not have an adaptive value. They may largely represent incidental expressions of a functional acclimation to the overall seasonal conditions, especially to high temperature and increased water turbulence. These two factors appear to affect relative growth of the different body parts through an increase in metabolic rate (Brooks, 1957; Hrbacek, 1959). In many invertebrates and fishes, final body size tends to be larger in individuals exposed to slightly subnormal temperatures than in those living at normal or supranormal temperatures. In stickleback, *Gasterosteus aculeatus*, various meristic characters vary as a function of incubation temperature (Lindsey, 1962). In another euryhaline fish, *Cyprinodon macularius*, body length (Kinne and Kinne, 1962) as well as body form (Kinne and Sweet, 1964; Sweet and Kinne, 1964) of newly hatched fry are significantly affected by the temperature conditions during incubation. Similar effects have been reported for other marine and estuarine fishes such as the herring (Blaxter and Hempel, 1961; Holliday and Blaxter, 1960). Such structural modifications may be of adaptive value for the individual involved.

CONCLUSIONS AND SUMMARY

Estuarine organisms exhibit a variety of compensatory measures reducing the impact and potential ill effects of their rough osmotic and thermal environment. Our present knowledge concerning physiological compensations for extreme conditions of salinity and temperature has been reviewed under four subheadings, namely, escape, reduction of contact, regulation, and acclimation. It should be especially emphasized that the latter three aspects may occur simultaneously in one individual and may not always be clearly distinguishable to the last detail; nevertheless, such subdivision makes it possible to present the multiplicity of physiological responses described in literature in some order, and may prove a useful tool for further analyses.

With respect to salinity, regulation (ion, volume, osmoregulation) and reduction of contact appear to

be most important. With respect to temperature, acclimation represents the essential means for compensation; winter conditions are also met by escape into deeper water or the substrate, and by transformation into resting stages. The information on hand indicates that compensatory means for adverse salinity conditions are more immediately available and better developed than those for temperature. Adverse temperatures are tolerated rather than compensated for and, thus, greatly affect activity, metabolic rate, reproduction, and other functions, as well as structural aspects.

In future studies on the physiology of estuarine organisms, more attention should be paid to the effects of environmental fluctuations (factor amplitude, rate of change, and duration of extreme intensities) and to polyfactorial analyses. Monofactorial approaches based on experiments employing different constant intensities of a single environmental factor are insufficient. There is a great need for long-term experiments using fully acclimated, healthy individuals and measuring ecologically important end points, such as growth, food conversion efficiency, and rate of reproduction.

LITERATURE CITED

- ACKERMAN, E., 1962. *Biophysical Science*. Prentice-Hall, Englewood Cliffs, New Jersey.
- ADOLPH, E. F., 1964. Perspectives of adaptation: some general properties. In *Handbook of Physiology*, edited by D. B. Dill, E. F. Adolph, and C. G. Wilber; sect. 4, pp. 27-35. Am. Physiol. Soc., Washington, D. C.
- ANDERS, F., F. VESTER, K. KLINKE, and H. SCHUMACHER, 1962. Genetische und biochemische Untersuchungen über die Bedeutung der freien Aminosäuren für die Tumorgenese bei Art- bzw. Gattungsbastarden lebendgebärender Zahnkarpfen (Poeciliidae). *Biol. Zb.*, 81:45-65.
- ANDERSON, J. D., and C. L. PROSSER, 1953. Osmoregulating capacity in populations occurring in different salinities. *Biol. Bull.*, 105:369.
- BEADLE, L. C., 1931. The effect of salinity changes on the water content and respiration of marine invertebrates. *J. Exptl. Biol.*, 8:211-227.
- BEADLE, L. C., 1934. Osmotic regulation in *Gunda ulvac*. *J. Exptl. Biol.*, 11:382-396.
- BEADLE, L. C., 1937. Adaptation to changes of salinity in the polychaetes. I. Control of body volume and of body fluid concentration in *Nereis diversicolor*. *J. Exptl. Biol.*, 14:56-70.
- BEADLE, L. C., 1957. Comparative physiology: osmotic and ionic regulation in aquatic animals. *Ann. Rev. Physiol.*, 19:329-354.
- BEADLE, L. C., and J. B. CRAGG, 1940a. Studies on adaptation to salinity in *Gammarus* spp. I. Regulation of blood and tissues and the problem of adaptation to fresh water. *J. Exptl. Biol.*, 17:153-163.
- BEADLE, L. C., and J. B. CRAGG, 1940b. Osmotic regulation in fresh water animals. *Nature (London)*, 146:588.
- BELIAEV, G. M., and M. N. TSCHUGUNOVA, 1952. Die physiologischen Unterschiede zwischen den Mytilen (*Mytilus*) der Barentsee und der Ostsee. *Vortr. Akad. Wiss. USSR, Ökol. [Russ.]*, 85:233-236.
- BERGER, E., 1929. *Unterschiedliche Wirkungen gleicher Ionen und Ionengemische auf verschiedene Tierarten. Ein Beitrag zur Lehre vom Ionenantagonismus*. (Kiel, Phil. Diss.) Springer, Berlin.
- BERGQUIST, P. I., 1958a. Evidence for separate

- mechanisms of sodium and potassium regulation in *Homosira banksii*. *Physiologia Plantarum*, 11:760-770.
- BERGQUIST, P. L., 1958b. Effect of potassium cyanide on apparent free space in a brown alga. *Nature (London)*, 181:1270.
- BETHE, A., E. VON HOLST, and E. HUF, 1935. Die Bedeutung des mechanischen Innendrucks für die Anpassung gepanzelter Seetiere an Änderungen des osmotischen Aussendrucks. *Pflügers Arch. Ges. Physiol.*, 235:330-334.
- BIEBL, R., 1956. Zellphysiologisch-ökologische Untersuchungen an *Enteromorpha clathrata* (Roth) Greville. *Ber. Deut. Botan. Ges.*, 69:75-86.
- BLACK, V. S., 1957. Excretion and osmoregulation. In *The Physiology of Fishes*, edited by M. E. Brown; vol. 1, pp. 163-205. Academic Press, New York.
- BLAXTER, J. H. S., and G. HEMPEL, 1961. Biologische Beobachtungen bei der Aufzucht von Heringsbrut. *Helgolander Wiss. Meeresunters.*, 7:260-283.
- BLINKS, L. R., 1951. Physiology and biochemistry of algae. In *Manual of Phycology*, edited by G. M. Smith; pp. 263-291. Chronica Bot. Co., Waltham, Massachusetts.
- BOREI, H., 1936. Über die Einwirkung des Salzgehaltes auf den O₂-Verbrauch des Echinodermeneies. *Zeit. Morphol. Ökol. Tiere*, 30:97-98.
- BOUXIN, H., 1931. Influence des variations rapides de la salinité sur la consommation d'oxygène chez *Mytilus edulis* var. *galloprovincialis* (Lmk.). *Bull. Inst. Océanog. Monaco*, 569: 1-11.
- BRAARUD, T., 1951. Salinity as an ecological factor in marine phytoplankton. *Physiol. Plantarum*, 4:28-34.
- BRAARUD, T., and I. PAPPAS, 1951. Experimental studies on the dinoflagellate *Peridinium triquetrum* (EHRB.) Lebour. *Arbhandl. Norske Vidensk.-Akad. Oslo, I. Mat.-Naturv. Kl.* 1951(2):1-23.
- BRETT, J. R., 1946. Rate of gain of heat-tolerance in goldfish (*Carassius auratus*). *Univ. Toronto Biol. Scr.* 52:9-28.
- BRETT, J. R., 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *J. Fisheries Res. Board Can.*, 9:265-323.
- BRETT, J. R., 1956. Some principles in the thermal requirements of fishes. *Quart. Rev. Biol.*, 31:75-87.
- BROEKEMA, M. M. M., 1941. Seasonal movements and the osmotic behavior of the shrimp, *Crangon crangon* L. *Arch. Néerl. Zool.*, 6:1-100.
- BROOKS, J. L., 1946. Cyclomorphosis in *Daphnia*. I. An analysis of *D. retrocurva* and *D. galatea*. *Ecol. Monographs*, 16:409-447.
- BROOKS, J. L., 1947. Turbulence as an environmental determinant of relative growth in *Daphnia*. *Proc. Natl. Acad. Sci. Washington, D. C.*, 33:141-148.
- BROOKS, J. L., 1957. The species problem in freshwater animals. In *The Species Problem*, edited by E. Mayr; pp. 81-123. American Association for the Advancement of Science, Washington, D. C.
- BROWN, F. A., JR., 1934. The chemical nature of the pigments and the transformations responsible for color changes in *Palaeomonetes*. *Biol. Bull.*, 67:365-380.
- BROWN, R., and J. F. DANJELLI (Editors), 1955. *Active transport and secretion*. Symp. Soc. Exptl. Biol., No. 8. Academic Press, New York.
- BULLOCK, T. H., 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.*, 30:311-342.
- BÜNNING, E., 1934. Zellphysiologische Studien an Meeressalgen. *Protoplasma*, 22:444-456.
- CALLAMAND, O., 1943. L'anguille européenne (*Anquilla anguilla* L.) les bases physiologiques de sa migration. *Ann. Inst. Océanog. (Monaco)*, 21:361-440.
- CASPERS, H., 1948. Ökologische Untersuchungen über die Wattentierwelt im Elbe-Ästuar. *Zool. Ans. (Suppl. Bd.)*, 13:350-359.
- CASPERS, H., 1955. Limnologie des Elbaestuars. *Verh. Intern. Ver. Limnol.*, 12:613-619.
- CASPERS, H., 1958. Biologie der Brackwasserzonen im Elbeästuar. *Verh. Intern. Ver. Limnol.*, 13:687-698.
- CASPERS, H., 1959. Die Einteilung der Brackwasser-Regionen in einem Ästuar. *Arch. Oceanogr. Limnol. (Suppl.)*, 11:153-169.
- CHRISTOPHERSEN, J., and H. PRECHT, 1952a. Untersuchungen zum Problem der Hitzeresistenz. I. Versuch an Karauschen (*Carassius vulgaris* Nils.). *Biol. Zb.*, 71:313-326.
- CHRISTOPHERSEN, J., and H. PRECHT, 1952b. Untersuchungen zum Problem der Hitzeresistenz. II. Versuch an Hefezellen. *Biol. Zb.*, 71:585-601.
- CHRISTOPHERSEN, J., and H. PRECHT, 1953. Die Bedeutung des Wassergehaltes der Zelle für Temperaturanpassungen. *Biol. Zb.*, 72:104-119.
- CHRISTOPHERSEN, J., and H. PRECHT, 1956. Über die Kälteresistenz von Hefezellen. *Biol. Zb.*, 75:612-624.
- CLARKE, F. W., 1924. The data of geochemistry. *Bull. U. S. Geol. Surv.*, 770.
- COLE, W. H., 1940. The composition of fluids and sera of some marine animals and of the sea water in which they live. *J. Gen. Physiol.*, 23:575-584.
- CROGHAN, P. C., 1958a. The survival of *Artemia salina* (L.) in various media. *J. Exptl. Biol.*, 35: 213-218.
- CROGHAN, P. C., 1958b. The osmotic and ionic regulation of *Artemia salina* (L.). *J. Exptl. Biol.*, 35:219-233.
- CROGHAN, P. C., 1961. Competition and mechanisms of osmotic adaptation. *Symp. Soc. Exptl. Biol.*, 15: 156-167.
- DAY, J. H., 1951. The ecology of South African estuaries. I. A review of estuarine conditions in general. *Trans. Roy. Soc. S. Africa*, 33:53-91.
- DEHNEL, P. A., 1960. Effect of temperature and salinity on the oxygen consumption of two intertidal crabs. *Biol. Bull.*, 118:215-249.
- DOUDOROFF, P., 1942. The resistance and acclimation of marine fishes to temperature changes. I. Experiments with *Girella nigricans* (Ayers). *Biol. Bull.*, 83: 219-244.
- DOUDOROFF, P., 1945. The resistance and acclimation of marine fishes to temperature changes. II. Experiments with *Fundulus* and *Atherinops*. *Biol. Bull.*, 88: 194-206.
- DROOP, M. R., 1958. Optimum relative and actual ionic concentrations for growth of some euryhaline algae. *Verh. Intern. Ver. Limnol.*, 13:722-730.
- DUCHATEAU, G., and M. FLORKIN, 1955. Influence de la température sur l'état stationnaire du pool des acides aminés non protéiques des muscles d'*Eriocheir sinensis* Milne-Edwards. *Arch. Intern. Physiol. Biochim.*, 63:213-221.
- DUVAL, M., 1925. Recherches physico-chimiques et physiologiques sur le milieu intérieur des animaux aquatiques. Modifications sous l'influence du milieu extérieur. *Ann. Inst. Océanog. (Monaco)*, 2:233-403.
- ELLIS, W. G., 1937. The water and electrolyte exchange of *Nereis diversicolor* (Mueller). *J. Exptl. Biol.*, 14: 340-350.
- ELLIS, W. G., 1939. Comparative measurements of water and electrolyte exchange in a stenohaline and a euryhaline polychaete. *J. Exptl. Biol.*, 16:483-486.
- EMERY, K. O., R. E. STEVENSON, and J. W. HEDGPETH, 1957. Estuaries and lagoons. *Geol. Soc. Am., Mem.* 67(1):673-739.
- EPPLER, R. W., 1958a. Sodium exclusion and potassium retention by the red marine alga, *Porphyra perforata*. *J. Gen. Physiol.*, 41:901-911.
- EPPLER, R. W., 1958b. Potassium-dependent sodium extrusion by cells of *Porphyra perforata*, a red marine alga. *J. Gen. Physiol.*, 42:281-288.
- EPPLER, R. W., 1962. Major cations. In *Physiology and Biochemistry of Algae*, edited by R. A. Lewin; pp. 255-266. Academic Press, New York.
- EPPLER, R. W., and C. R. BOVELL, 1958. Sulfuric acid in *Desmarestia*. *Biol. Bull.*, 115:101-106.

- EPPELEY, R. W., and C. C. CYRUS, 1960. Cation regulation and survival of the red alga, *Porphyra perforata*, in diluted and concentrated sea water. *Biol. Bull.*, 118:55-65.
- FLEMISTER, L. J., and S. C. FLEMISTER, 1951. Chloride ion regulation and oxygen consumption in the crab *Ocypode albicans* (Bosq.). *Biol. Bull.*, 101: 259-273.
- FLORKIN, M., 1960. Ecology and metabolism. In *The Physiology of Crustacea*, edited by T. H. Waterman; vol. 1, pp. 395-410. Academic Press, New York.
- FLÜGEL, H., 1959. Zum Problem der Osmoregulation im tropischen Brackwasser. *Naturwissenschaften*, 46: 213.
- FONTAINE, M., and A. RAFFY, 1935. Sur la consommation d'oxygène de la lampre marine (*Petromyzon marinus* L.). Influence de la salinité. *Bull. Assoc. Franc. Advan. Sci.*, 59:330-333.
- FORD, P., 1958. Studies on the development of the kidney of the Pacific pink salmon (*Oncorhynchus gorbuscha* Walbaum). II. Variation in glomerular count of the kidney of the Pacific pink salmon. *Can. J. Zool.*, 36: 45-48.
- FRETTER, V., 1955. Uptake of radioactive sodium (^{24}Na) by *Nereis diversicolor* Mueller and *Perinereis cultrifera* Grube. *J. Marine Biol. Assoc. U. K.*, 34: 151-160.
- FRIEDRICH, H., 1937. Einige Beobachtungen über das Verhalten der *Alderia modesta* Lov. im Brackwasser. *Biol. Zb.*, 57:101-104.
- FRY, F. E. J., 1947. Effects of the environment on animal activity. *Univ. Toronto Biol Ser. No. 55*, pp. 1-62.
- FRY, F. E. J., 1957. The lethal temperature as a tool in taxonomy. *Ann. Biol. (Copenh.)*, 33:205-219.
- FRY, F. E. J., J. R. BRETT, and C. H. CLAWSON, 1942. Lethal limits of temperature for young goldfish. *Rev. Can. Biol.*, 1:50-56.
- FRY, F. E. J., J. S. HART, and K. F. WALKER, 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis*. *Univ. Toronto Biol. Ser. No. 54*, pp. 9-35.
- FULTON, C., 1960. Culture of a colonial hydroid under controlled conditions. *Science*, 132:473-474.
- FULTON, C., 1962. Environmental factors influencing the growth of *Cordylophora*. *J. Exptl. Zool.*, 151:61-78.
- GARMS, R., 1961. Biozönotische Untersuchungen an Entwässerungsgräben in Flussmarschen des Elbe-Astuars. *Arch. Hydrobiol. (Suppl.)*, 26:344-462.
- GRAINGER, J. N. R., 1958. First stages in the adaptation of poikilotherms to temperature change. In *Physiological Adaptation*, edited by C. L. Prosser; pp. 79-91. Am. Physiol. Soc., Washington, D. C.
- GROSS, W. J., 1957. An analysis of response to osmotic stress in selected decapod Crustacea. *Biol. Bull.*, 112:43-62.
- GROSS, W. J., 1963. Acclimation to hypersaline water in a crab. *Comp. Biochem. Physiol.*, 9:181-188.
- GUEYLARD, F., 1924. Paris, Ph.D. Thesis (quoted in Black, 1957).
- GUEYLARD, D., 1925. De l'adaptation aux changements de salinité. Recherches biologiques et physico-chimiques sur l'épinoche (*Gasterosteus leiuurus* Cur. et Val.). *Arch. Phys. Biol.*, 3:79-187.
- GUILLARD, R. R. L., 1962. Salt and osmotic balance. In *Physiology and Biochemistry of Algae*, edited by R. A. Lewin; pp. 529-540. Academic Press, New York.
- GUILLARD, R. R. L., and J. H. RYTHER, 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustadt, and *Detonula conservacea* (Cleve) Gran. *Can. J. Microbiol.*, 8:229-239.
- HART, J. S., 1947. Lethal temperature relations of certain fish of the Toronto region. *Trans. Roy. Soc. Can.*, 41:57-71.
- HATHAWAY, E. S., 1927. Quantitative study of the changes produced by acclimation on the tolerance of high temperatures by fishes and amphibians. *Bull. Bur. Fish., Wash.*, 43:169-192.
- HENSCHEL, J., 1936. Wasserhaushalt und Osmoregulation von Scholle und Flunder. *Wiss. Meeresunters. Abt. Kiel*, 22:89-121.
- HERRMANN, F., 1931. Über den Wasserhaushalt des Fluskskrebses (*Potamobius astacus* Leach). *Z. Vergleich. Physiol.*, 14:479-524.
- HOLIDAY, F. G. T., and J. H. S. BLAXTER, 1960. The effects of salinity on the developing eggs and larvae of the herring. *J. Marine Biol. Assoc. U. K.*, 39: 591-603.
- HOPE, A. B., and N. A. WALKER, 1960. Ionic relations of *Chara australis*. III. Vacuolar fluxes of sodium. *Australian J. Biol. Sci.*, 13:276-291.
- HRBAČEK, J., 1959. Circulation of water as a main factor influencing the development of helmets in *Daphnia cucullata* Sars. *Hydrobiologia*, 13:170-185.
- JONES, L. L., 1941. Osmotic regulation in several crabs of the Pacific coast of North America. *J. Cellular Comp. Physiol.*, 18:79-92.
- JØRGENSEN, C. B., and R. P. DALES, 1957. The regulation of volume and osmotic regulation in some nereid polychaetes. *Physiologia Comp. Oecol.*, 4: 357-374.
- JØRGENSEN, E. G., 1960. The effects of salinity, temperature and light intensity on growth and chlorophyll formation of *Nitzschia ovalis*. *Yearbook, Carnegie Inst. Wash.*, 59:348-349.
- KESSELER, H., 1959. Mikrokryoskopische Untersuchungen zur Turgorregulation von *Chaetomorpha linum*. *Kiel. Meeresforsch.*, 15:51-73.
- KESSELER, H., 1962. Beziehungen zwischen Atmung und Turgorregulation von *Chaetomorpha linum*. *Helgolander Wiss. Meeresunters.*, 8:243-256.
- KESSELER, H., 1964. Die Bedeutung einiger anorganischer Komponenten des Seewassers für die Turgorregulation von *Chaetomorpha linum* (Cladophorales). *Helgolander Wiss. Meeresunters.*, 10:73-90.
- KINNE, O., 1952. Zur Biologie und Physiologie von *Gammarus aubeni* Lillj. V. Untersuchungen über Blutkonzentration, Herzfrequenz und Atmung. *Kiel. Meeresforsch.*, 9:134-150.
- KINNE, O., 1956. Über den Einfluss des Salzgehaltes und der Temperatur auf Wachstum, Form und Vermehrung bei dem Hydroidpolypen *Cordylophora caspia* (Pallas), Athecata, Clavidae. *Zool. Jahrb. Abt. Allgem. Zool.*, 66:565-638.
- KINNE, O., 1958a. Über die Reaktion erbglichen Coelenteratengewebes auf verschiedene Salzgehalts- und Temperaturbedingungen. *Zool. Jahrb. Abt. Allgem. Zool.*, 67:407-486.
- KINNE, O., 1958b. Adaptation to salinity variations—some facts and problems. In *Physiological Adaptation*, edited by C. L. Prosser; pp. 92-106. Am. Physiol. Soc., Washington, D. C.
- KINNE, O., 1960. Growth, food intake and food conversion in a euryplastic fish exposed to different temperatures and salinities. *Physiol. Zool.*, 33:288-317.
- KINNE, O., 1963a. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanogr. Mar. Biol. Ann. Rev.*, 1:301-340.
- KINNE, O., 1963b. Adaptation, a primary mechanism of evolution. In *Phylogeny and Evolution of Crustacea*. Mus. Comp. Zool. Harvard Coll., Cambridge, Mass. (Special Publication), pp. 27-50.
- KINNE, O., 1963c. Über den Einfluss des Salzgehaltes auf verschiedene Lebensprozesse des Knochenfisches *Cyprinodon macularius*. *Veröff. Inst. Meeresforsch. Bremenhaven, Sonderbd. Drittes Meeresbiol. Symposium*, pp. 49-66.
- KINNE, O., 1964a. Animals in aquatic environments: crustaceans. In *Handbook of Physiology*, edited by D. B. Dill, E. F. Adolph, and C. G. Wilber; sect. 4, pp. 669-682. Am. Physiol. Soc., Washington, D. C.
- KINNE, O., 1964b. The effects of temperature and salin-

- ity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. *Oceanogr. Mar. Biol. Ann. Rev.*, 2:281-339.
- KINNE, O., 1964c. Non-genetic adaptation to temperature and salinity. *Helgolander Wiss. Meeresunters.*, 9: 433-458.
- KINNE, O., and E. M. KINNE, 1962. Rates of development in embryos of a cyprinodont fish exposed to different temperature-salinity-oxygen combinations. *Can. J. Zool.*, 40:231-253.
- KINNE, O., and H. W. ROTTHAUWE, 1952. Biologische Beobachtungen und Untersuchungen über die Blutkonzentration an *Heteropanope tridentatus* Maitland (Decapoda). *Kiel. Meeresforsch.*, 8:212-217.
- KINNE, O., and J. G. SWEET, 1965. Die Umwelt-abhängigkeit der Körperform frischgeschlüpfter *Cyprinodon macularius* (Teleostei). *Z. Naturforsch.*, 52: 69-70.
- KITCHING, J. A., 1938. Contractile vacuoles. *Biol. Rev.*, 13:403-444.
- KITCHING, J. A., 1948. The physiology of contractile vacuoles. VI. Temperature and osmotic stress. *J. Exptl. Biol.*, 25:421-436.
- KITCHING, J. A., 1951. The physiology of contractile vacuoles. VII. Osmotic relations in a suctorian, with special reference to the mechanism of control of vacuolar output. *J. Exptl. Biol.*, 28:203-214.
- KITCHING, J. A., 1952. Contractile vacuoles. *Symp. Soc. Exptl. Biol.*, 6:145-146.
- KITCHING, J. A., 1954. Osmoregulation and ionic regulation in animals without kidneys. *Symp. Soc. Exptl. Biol.*, 8:63-75.
- KOCH, H. J., 1954. Cholinesterase and active transport of sodium chloride through the isolated gills of the crab *Eriocheir sinensis* (M. Edw.). In *Recent Developments in Cell Physiology*, edited by J. A. Kitching; pp. 15-27. Academic Press, New York.
- KOCH, H. J., and J. EVANS, 1956a. On the absorption of sodium from dilute solutions by the crab *Eriocheir sinensis* (M. Edw.). *Mededel. Koninkl. Vlaam. Acad.*, 18:3-15.
- KOCH, H. J., and J. EVANS, 1956b. Influence of a basic dye, thionine, on the absorption of sodium by the crab *Eriocheir sinensis* (M. Edw.). *Mededel. Koninkl. Vlaam. Acad.*, 18:3-11.
- KOCH, H. J., and M. J. HEUTS, 1942. Influences de l'hormone thyroïdienne sur la régulation osmotique chez *Gasterosteus aculeatus* L. forme *gymnurus* Cuv. *Ann. Soc. R. Zool. Belg.*, 73:165-172.
- KÖLLER, G., 1939. Über die Nephridien von *Physcosoma japonicum*. *Zool. Anz. (Suppl. Bd.)*, 12:440-447.
- KOTHE, P., 1961. Hydrobiologie der Oberelbe. *Arch. Hydrobiol. (Suppl.)*, 26:221-343.
- KÖTTER, F., 1961. Die Pflanzengesellschaften im Tidegebiet der Unterelbe. *Arch. Hydrobiol. (Suppl.)*, 26: 106-184.
- KRUSHNAMOORTHI, B., 1951. Studies on the osmotic properties of the eggs and larvae of a brackish-water polychaete, *Marphysa gravelyi* Southern. *Proc. Indian Acad. Sci. Sect. B.*, 34:199-209.
- KROGH, A., 1938. The salt concentration in the tissues of some marine animals. *Skand. Arch. Physiol.*, 80: 214-222.
- KROGH, A., 1939. *Osmotic Regulation in Aquatic Animals*. Cambridge Univ. Press, London.
- KRÜGER, G., 1962. Über die Temperaturadaptation des Bitterlings (*Rhodeus amarus* Bloch). *Z. Wiss. Zool.*, 167:87-104.
- LENHOFF, H. M., and J. BOVAIRD, 1960. The requirement of trace amounts of environmental sodium for the growth and development of *Hydra*. *Exptl. Cell. Res.*, 20:384-394.
- LEWIN, R. A. (Editor), 1962. *Physiology and biochemistry of algae*. Academic Press, New York.
- LEWIN, R. A., and R. R. L. GUILARD, 1963. Diatoms. *Ann. Rev. Microbiol.*, 17:373-414.
- LIEDER, U., 1951. Der Stand der Zyklomorphoseforschung. *Naturwissenschaften*, 38:39-44.
- LINDSEY, C. C., 1962. Experimental study of meristic variation in a population of three spine sticklebacks, *Gasterosteus aculeatus*. *Can. J. Zool.*, 40:271-312.
- LOCKWOOD, A. P. M., 1962. The osmoregulation of Crustacea. *Biol. Rev.*, 37:257-305.
- LOEB, J., and H. WASTENEYS, 1912. On the adaptation of fish (*Fundulus*) to higher temperatures. *J. Exptl. Zool.*, 12:543-557.
- LOFTS, B., 1956. The effects of salinity changes on the respiratory rate of the prawn *Palacmonetes varians* (Leach). *J. Exptl. Biol.*, 33:730-736.
- LOOMIS, W. F., 1954. Environmental factors controlling growth in hydra. *J. Exptl. Zool.*, 126:223-234.
- MACROBBIE, E. A. C., and J. DAINTY, 1958a. Sodium and potassium distribution and transport in the seaweed *Rhodymenia palmata* (L.) Grev. *Physiol. Plantarum.*, 11:782-801.
- MACROBBIE, E. A. C., and J. DAINTY, 1958b. Ion transport in *Nitellopsis obtusa*. *J. Gen. Physiol.*, 42: 335-353.
- MALOEUF, N. S. R., 1938. Studies on the respiration (and osmoregulation) of animals. *Z. Vergleich. Physiol.*, 25:1-42.
- MARGALEF, R., 1955. Temperatura, dimensiones y evolución. *Publ. Inst. Biol.apl. (Barcelona)*, 19:13-94.
- McCOMBIE, A. M., 1960. Actions and interactions of temperature, light intensity and nutrient concentration on growth of the green alga, *Chlamydomonas reinhardtii* Dangeard. *J. Fisheries Res. Board Can.*, 17:871-894.
- MCLEESE, D. W., 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. *J. Fisheries Res. Board Can.*, 13:247-272.
- MEYER, H., 1935. Die Atmung von *Asterias rubens* und ihre Abhängigkeit von verschiedenen Außenfaktoren. *Zool. Jahrb., Abt. Allgem. Zool. Physiol. Tiere.*, 55: 349-398.
- MOORE, W. G., 1955. Observations on heat death in the fairy shrimp, *Streptocephalus scaliger*. *Proc. La. Acad. Sci.*, 18:5-12.
- MÜLLER, R., 1936. Die osmoregulatorische Bedeutung der kontraktilen Vakuolen von *Amoeba proteus*, *Zoothamnium hiketense* und *Frontonia marina*. *Arch. Protistenk.*, 87:345-382.
- NAGEL, H., 1934. Die Aufgaben der Exkretionsorgane und der Kiemen bei der Osmoregulation von *Carcinus macrurus*. *Z. Vergleich. Physiol.*, 21:468-491.
- NICOL, J. A. C., 1960. *The biology of marine animals*. Interscience Publ., New York.
- OBERTHÜR, K., 1937. Untersuchungen an *Frontonia marina* Fabre-Dom. aus einer Binnenland-Salzquelle unter besonderer Berücksichtigung der pulsierenden Vakuole. *Arch. Protistenk.*, 88:387-420.
- OSTWALD, W., 1904. Experimentelle Untersuchungen über den Saisonpolymorphismus bei Daphnien. *Arch. Entwicklungsmicoh. Org.*, 18:415-451.
- PANIKKAR, N. K., 1939. Osmotic behavior of *Palacmonetes varians* (Leach). *Nature (London)*, 144: 866-867.
- PANIKKAR, N. K., 1940. Osmotic properties of the common prawn. *Nature (London)*, 145:108.
- PANIKKAR, N. K., 1941. Osmoregulation in some palaeomimid prawns. *J. Marine Biol. Assoc. U. K.*, 25:317-359.
- PANIKKAR, N. K., 1950. Physiological aspects of adaptation to estuarine conditions. *Proc. Indo-Pacific Fisheries Coun.*, 2:168-175.
- PANIKKAR, N. K., and R. VISWANATHAN, 1948. Active regulation of chloride in *Metapenaeus monoceros* Fab. *Nature (London)*, 161:137-138.
- PANTIN, C. F. A., 1931a. The adaptation of *Gunda ulvae* to salinity. I. The Environment. *J. Exptl. Biol.*, 8:63-72.
- PANTIN, C. F. A., 1931b. The adaptation of *Gunda*

- ulvae* to salinity. III. The electrolyte exchange. *J. Exptl. Biol.*, 8:82-94.
- PEARSE, A. S., and G. GUNTER, 1957. Salinity. *Mem. Geol. Soc. Am.*, 67(1):129-157.
- PITT, T. K., E. T. GARSIDE, and R. L. HEPBURN, 1956. Temperature selection of the carp (*Cyprinus carpio* Linn.). *Can. J. Zool.*, 34:555-557.
- POTTS, W. T. W., and G. PARRY, 1963. *Osmotic and ionic regulation in animals*. Pergamon Press, London.
- PRECHT, H., 1949. Die Temperaturabhängigkeit von Lebensprozessen. *Z. Naturforsch.*, 4b:26-35.
- PRECHT, H., 1958. Concepts of the temperature adaptation of unchanging reaction systems of cold-blooded animals. In *Physiological Adaptation*, edited by C. L. Prosser; pp. 50-78. Am. Physiol. Soc., Washington, D. C.
- PRECHT, H., 1961. Temperaturanpassungen bei wechselwarmen Tieren. *Zool. Anz. (Suppl. Bd.)*, 24:38-60.
- PRECHT, H., 1963. Anpassungen wechselwärmer Tiere zum Überleben extremer Temperaturen. *Naturw. Rundschau.*, 16:9-16.
- PRECHT, H., 1964. Über die Resistenzadaptation wechselwärmer Tiere an extreme Temperaturen und ihre Ursachen. *Helgolander Wiss. Meeresunters.*, 9:392-411.
- PRECHT, H., J. CHRISTOPHERSEN, and H. HENSEL, 1955. Wechselwärme Tiere und Pflanzen. In *Temperatur und Leben*; pp. 1-177. Springer, Berlin.
- PITCHARD, D. W., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11:106-123.
- PROSSER, C. L., 1955. Physiological variation in animals. *Biol. Rev.*, 30:229-262.
- PROSSER, C. L. (Editor), 1958a. *Physiological Adaptation*. Am. Physiol. Soc., Washington, D. C.
- PROSSER, C. L., 1958b. General summary: the nature of physiological adaptation. In *Physiological Adaptation*, edited by C. L. Prosser; pp. 167-180. Am. Physiol. Soc., Washington, D. C.
- PROSSER, C. L., 1964. Perspectives of adaptation: theoretical aspects. In *Handbook of Physiology*, edited by D. B. Dill, E. F. Adolph, and C. G. Wilber; sect. 4, pp. 11-25. Am. Physiol. Soc., Washington, D. C.
- PROSSER, C. L., and F. A. BROWN, JR., 1961. *Comparative animal physiology*. (Second Ed.) Saunders, Philadelphia.
- PROVASOLI, L., 1958. Nutrition and ecology of protozoa and algae. *Ann. Rev. Microbiol.*, 12:279-308.
- PROVASOLI, L., J. J. A. McLAUGHLIN, and I. J. PINTNER, 1954. Relative and limiting concentrations of major mineral constituents for the growth of algal flagellates. *Trans. N. Y. Acad. Sci. (Ser. 2)*, 16:412-417.
- RAFFY, A., 1932a. Variations de la consommation d'oxygène dissous au cours de la mort de poissons marins sténohalins passant de l'eau de mer à l'eau douce. *Compt. Rend.*, 191:1522-1524.
- RAFFY, A., 1932b. Recherches physiologiques sur le mécanisme de la mort des poissons sténohalins soumis à des variations de salinité. *Bull. Inst. Océanog. Monaco*, 602:1-11.
- RAFFY, A., 1933. Recherches sur le métabolisme respiratoire des poikilothermes aquatiques. *Ann. Inst. Océanog. (Monaco)*, 13:259-393.
- RAFFY, A., 1934. Influence des variations de salinité sur l'intensité respiratoire de la télphuse et de l'écrevisse. *Compt. Rend.*, 198:680-681.
- RAO, K. P., 1958. Oxygen consumption as a function of size and salinity in *Metapenaeus monoceros* Fab. from marine and brackish-water environments. *J. Exptl. Biol.*, 35:307-313.
- REID, G. K., 1961. *Ecology of inland waters and estuaries*. Reinhold, New York.
- REMANE, A., and C. SCHLIEPER, 1958. Die Biologie des Brackwassers. In *Die Binnengewässer*, edited by A. Thienemann; pp. 1-348. Schweizerbart, Stuttgart.
- ROBERTS, J. L., 1957. Thermal acclimation of metabolism in the crab *Pachygrapsus crassipes* Randall. II. Mechanisms and the influence of season and latitude. *Physiol. Zool.*, 30:242-255.
- ROBERTSON, J. D., 1957. Osmotic and ionic regulation in aquatic invertebrates. In *Recent Advances in Invertebrate Physiology*; pp. 229-246. Publication of the University of Oregon, Eugene, Oregon.
- ROBERTSON, J. D., 1960a. Osmotic and ionic regulation. In *The Physiology of Crustacea*, edited by T. H. Waterman; vol. 1, pp. 317-339. Academic Press, New York.
- ROBERTSON, J. D., 1960b. Ionic regulation in the crab *Carcinus maenas* (L.) in relation to the moulting cycle. *Comp. Biochem. Physiol.*, 1:183-212.
- ROCH, F., 1924. Experimentelle Untersuchungen an *Cordylophora caspia* (Pallas) (= lacustris Allman) über die Abhängigkeit ihrer geographischen Verbreitung und ihrer Wuchsformen von den physikalisch-chemischen Bedingungen des umgebenden Mediums. *Z. Morphol. Ökol. Tiere*, 2:350-426.
- ROTHSCHILD, L., and H. BARNES, 1953. The inorganic constituents of the sea-urchin egg. *J. Exptl. Biol.*, 30:534-544.
- SCHLIEPER, C., 1929a. Über die Einwirkung niederer Salzkonzentrationen auf marine Organismen. *Z. Vergleich. Physiol.*, 9:478-514.
- SCHLIEPER, C., 1929b. Neue Versuche über die Osmoregulation wasserlebender Tiere. *Sitzber. Ges. Befoeder. Ges. Naturw. Marburg*, 64:143-156.
- SCHLIEPER, C., 1930. Die Osmoregulation wasserlebender Tiere. *Biol. Rev.*, 5:309-356.
- SCHLIEPER, C., 1935. Neuere Ergebnisse und Probleme aus dem Gebiet der Osmoregulation wasserlebender Tiere. *Biol. Rev.*, 10:334-360.
- SCHLIEPER, C., 1955. Über die physiologischen Wirkungen des Brackwassers (Nach Versuchen an der Miesmuschel *Mytilus edulis*). *Kiel. Meeresforsch.*, 11: 22-33.
- SCHMITZ, W., 1959. Zur Frage der Klassifikation der binnendämmischen Brackwasser. *Arch. Oceanogr. Limnol. (Suppl.)*, 11:179-226.
- SCHOLLES, W., 1933. Über die Mineralregulation wasserlebender Evertebraten. *Z. Vergleich. Physiol.*, 19: 522-554.
- SCHOUP, C. S., 1932. Salinity of the medium and its effect on respiration in the sea anemone. *Ecology*, 8: 81-85.
- SCHULZ, H., 1961. Qualitative und quantitative Planktonuntersuchungen im Elbe-Ästuar. *Arch. Hydrobiol. (Suppl.)*, 26:5-105.
- SCHUMACHER, A., 1961. Die biologischen Verhältnisse in Nebenflüssen der Unterelbe. *Arch. Hydrobiol. (Suppl.)*, 26:185-219.
- SCHWABE, E., 1933. Über die Osmoregulation verschiedener Krebse (Malacostraca). *Z. Vergleich. Physiol.*, 19:183-236.
- SCOTT, G. T., and H. R. HAYWARD, 1953. Metabolic factors influencing the sodium and potassium distribution in *Urtica lactuca*. *J. Gen. Physiol.*, 36:659-671.
- SCOTT, G. T., and H. R. HAYWARD, 1954. Evidence for the presence of separate mechanisms regulating potassium and sodium distribution in *Urtica lactuca*. *J. Gen. Physiol.*, 37:601-620.
- SCOTT, G. T., and H. R. HAYWARD, 1955. Sodium and potassium regulation in *Urtica lactuca* and *Valonia macrophysa*. In *Electrolytes in Biological Systems*, edited by A. M. Shanes; pp. 35-64. Am. Physiol. Soc., Washington, D. C.
- SECK, C., 1958. Untersuchungen zur Frage der Ionenregulation bei in Brackwasser lebenden Evertebraten. *Kiel. Meeresforsch.*, 13:220-243.
- SEGAL, E., 1956. Microgeographic variation as thermal acclimation in an intertidal mollusc. *Biol. Bull.*, 111: 129-152.
- SHAW, J., 1960. The mechanisms of osmoregulation. In

- Comparative Biochemistry*, edited by M. Florkin and H. S. Mason; vol. 2, pp. 479-518. Academic Press, New York.
- SMITH, R. I., 1955a. Comparison of the level of chloride regulation by *Nereis diversicolor* in different parts of its geographical range. *Biol. Bull.*, 109:453-474.
- SMITH, R. I., 1955b. On the distribution of *Nereis diversicolor* in relation to salinity in the vicinity of Tvärminne, Finland, and the Isefjord, Denmark. *Biol. Bull.*, 108:326-345.
- SMITH, R. I., 1955c. Salinity variation in interstitial water of sand at Kames Bay, Millport, with reference to the distribution of *Nereis diversicolor*. *J. Marine Biol. Assoc. U. K.*, 34:33-46.
- SMITH, R. I., 1956. The ecology of the Tamar estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of *Nereis diversicolor*. *J. Marine Biol. Assoc. U. K.*, 35:81-104.
- SMITH, R. I., 1957. A note on the tolerance of low salinities by nereid polychaetes and its relation to temperature and reproductive habit. *Ann. Biol.*, 33:93-107.
- SMITH, R. I., 1959. Physiological and ecological problems of brackish waters. In *Marine Biology*; pp. 59-69. Proc. 20th Ann. Biol. Coll., Oregon State Univ., Corvallis, Oregon.
- SPOOR, W. A., 1955. Loss and gain of heat tolerance by the crayfish. *Biol. Bull.*, 108:77-87.
- SUMNER, F. B., G. D. LOUDERBACK, W. L. SCHMITT, and E. C. A. JOHNSTON, 1914. A report upon the physical conditions in San Francisco Bay. *Univ. Calif. (Berkeley) Publ. Zool.*, vol. 14. Univ. of Calif., Berkeley, California.
- SWEET, J. G., and O. KINNE, 1964. The effects of various temperature-salinity combinations on the body form of newly hatched *Cyprinodon macularius* (Teleostei). *Helgolander Wiss. Meeresunters.*, 11:49-69.
- TODD, M. E., and P. A. DEHNEL, 1960. The influence of temperature and salinity on heat tolerance in two grapsoid crabs, *Hemigrapsus nudus* and *Hemigrapsus oregonensis*. *Biol. Bull.*, 118:150-172.
- TOPPING, F. L., and J. L. FULLER, 1942. The accommodation of some marine invertebrates to reduced osmotic pressures. *Biol. Bull.*, 82:372-384.
- VIRABHADRACHARI, V., 1961. Structural changes in the gills, intestine and kidney of *Etorplus maculatus* (Teleostei) adapted to different salinities. *Quart. J. Microscop. Sci.*, 102:361-369.
- VOLLENWEIDER, R. A., 1950. Ökologische Untersuchungen von planktischen Algen auf experimenteller Grundlage. *Schweiz. Z. Hydrol.*, 12:1-75.
- WEIL, E., and C. F. A. PANTIN, 1931. The adaptation of *Gunda silvae* to salinity. II. The water exchange. *J. Exptl. Biol.*, 8:73-81.
- WESENBERG-LUND, C., 1900. Von dem Abhängigkeitsverhältnis zwischen dem Bau der Planktonorganismen und dem spezifischen Gewicht des Süßwassers. *Biol. Zb.*, 20:606-619, 644-656.
- WILLIAMS, R. B., 1962. *The ecology of diatom populations in a Georgia salt marsh*. Doctoral Thesis, Harvard Univ., Cambridge, Massachusetts.
- WOLTERECK, R., 1913. Über Funktion, Herkunft und Entstehungsursachen der sogen. "Schwebefortsätze" pelagischer Cladoceren. *Zoologica, Stuttg.*, 26:475-550.
- ZAHN, M., 1962. Die Vorzugstemperaturen zweier Cypriniden und eines Cyprinodonten und die Adaptionsarten der Vorzugstemperaturen bei Fischen. *Zool. Beitr.*, Berlin, 7:15-25.

Osmotic and Ionic Regulation in Estuarine Crabs

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The decapod Crustacea have developed a wide variety of regulatory processes to maintain osmotic and ionic stability, and these processes permit considerable lability in physiological response. Most marine Crustacea are osmotic conformers; the blood is isoosmotic with the medium. Estuarine and coastal Crustacea maintain hyperosmotic blood in dilute media, but isoosmotic in concentrated media. Terrestrial and semi-terrestrial animals respond to variations in salinity by regulating their blood concentration to hyperosmotic in dilute media and hypoosmotic in concentrated media.

The processes responsible for the maintenance of an osmotic or ionic imbalance between the blood and the external media relate to permeability of the exoskeleton, regulation of water volume, active uptake or extrusion of ions, reabsorption of water and ions by the kidney, and regulation of osmotic and ionic concentrations at the cellular level!

For blood to be regulated with regard to an external salinity, a rather delicate balance must be established between the blood and renal and extra-renal routes of excretion. These latter routes not only concern the removal of water and ions from the blood, but involve active processes against concentration gradients which reduce loss of water and ions. Blood which is hyperosmotic tends to lose salts from the body and gain water. Hypoosmotic blood tends to lose water and gain salts. Production of hypoosmotic urine by hyperosmotic animals, and hyperosmotic urine by hypoosmotic animals tends toward salt and water balance. Recent reviews (Lockwood, 1962; Potts and Parry, 1964) give further details on these aspects of osmoregulation.

The research reported in this paper concerns the physiological responses of an estuarine shore crab, *Hemigrapsus nudus*, to seasonal variations in the environment, and to a series of temperature and salinity combinations during a given season. The responses concern electrolytic imbalances of the blood, urine, and muscle with respect to external media concentrations and water movement between tissues. The electrolytes studied are sodium, potassium, calcium, magnesium, and chloride.

The area in which these crabs were collected is subject to considerable seasonal fluctuation in temperature and salinity. Summer animals (June through August) were collected during a period of relative temperature and salinity stability, which is characterized by a high temperature (20°C) and a low

salinity (11‰ or 35 percent sea water). Winter animals (December through March) were collected during an extended period of low temperature (5°C .) and high salinity (24‰ or 75 percent sea water). All experimental salinities were based on a standard sea water (100 percent), 31.88‰ salinity, 17.65‰ chlorinity. Concentrations of the five major electrolytes in 100 percent sea water were determined: sodium, 439 meq/l; potassium, 10.7 meq/l; calcium, 24.9 meq/l; magnesium, 100 meq/l; chloride, 497 meq/l. Experimental temperatures were 5°, 15°, and 25° C., and experimental salinities were 6, 12, 25, 75, 100, 125, 150, and 175 percent sea water. Ionic fluxes for summer and winter animals were determined at all combinations for the experimental temperatures and salinities.

OSMOTIC REGULATION

Osmotic regulation, as expressed by total osmotic pressure of blood and urine, showed that blood and urine concentrations fall in dilute, and rise in concentrated, media at rates directly related to the gradients between media and equilibrated body fluid concentrations, and are influenced by the seasonal adaptation of the animals and the experimental temperature. Major changes in body fluids occurred within 48 hours. Hyperosmotic regulation in summer-adapted animals resulted in isoosmotic blood and urine, suggesting extra-renal mechanisms. The production of hypoosmotic urine in winter-adapted animals indicated the participation of the antennal glands. Summer and winter adaptation tended to favor stronger hyperosmotic regulation at the seasonal temperatures than at temperatures foreign to the seasons. Seasonal adaptation of osmoregulatory mechanisms in *Hemigrapsus* is shown to alter the balance of active processes, so that for a given range of experimental conditions urine is lower in winter than in summer, both in absolute concentration and relative to the blood (Dehnel, 1962; Dehnel and Stone, 1964).

CATIONIC REGULATION—BLOOD

Ion concentration in blood of summer and winter *H. nudus* as a function of salinity is shown in Figure 1 (sodium and potassium) and Figure 2 (calcium and magnesium). These seasonal values are presented at experimental temperatures (15° C . and 5° C .) approximating field temperatures in summer and winter (17° C . and 5° C .). In salinities of from 12–100 percent sea water, sodium and potassium are maintained

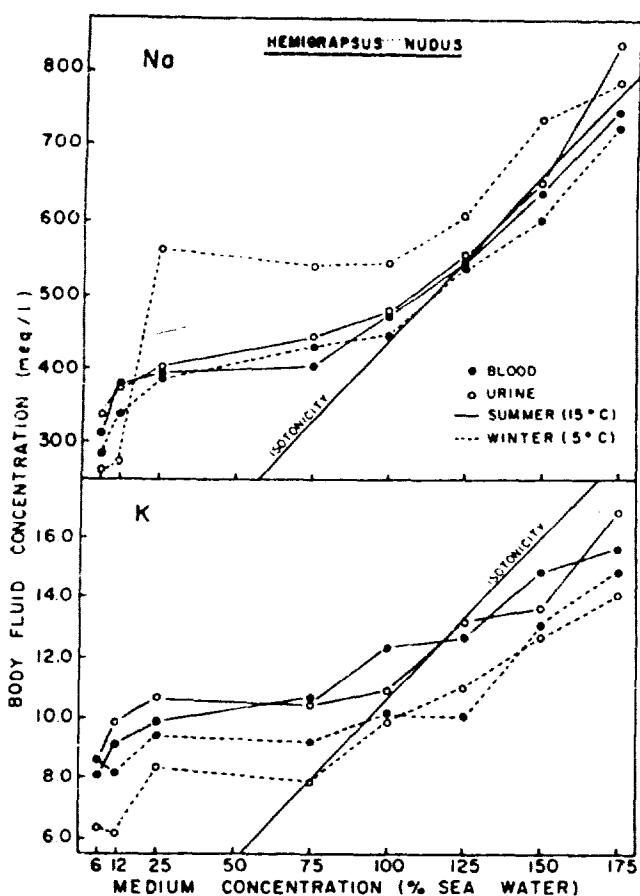


Fig. 1. Sodium and potassium ion concentrations in the body fluids of winter ($5^{\circ}\text{ C}.$) and summer ($15^{\circ}\text{ C}.$) *Hemigrapsus nudus* as a function of salinity. Each point represents the mean value of ten measurements after exposure for 24 hours to each experimental salinity.

at relatively constant blood levels, hypertonic to the media. In salinities above and below this range, regulation becomes less effective and concentrations approach those of the media. In concentrated salinities (above 100 percent sea water), sodium concentrations in blood of summer animals are isotonic with the media. Winter animals in concentrated salinities, however, exhibit a limited hypotonic regulation of sodium. Similarly, potassium concentrations in blood of summer and winter animals in salinities above 100 percent sea water are maintained hypotonic to the media. This hypotonic regulation, however, can be of little adaptive importance to these animals since field salinities greater than 75 percent sea water are rarely encountered in this area. The constancy of hypertonic calcium regulation in dilute salinities is demonstrated by animals in both seasons (Fig. 2). Considerable hypotonicity is maintained for magnesium over most of the salinity range: the values increase from only 19 to 52 meq/l after exposure to a change in external magnesium concentration from 6 to 176 meq/l. In media above 25 percent water, blood magnesium is regulated at about one-third the medium concentration.

Statistical comparisons of seasonal blood ion concentrations indicate that over the entire salinity range for sodium and over most of the salinity range for potassium, there is no significant seasonal difference (Fig. 1). In salinities from 100–150 percent sea water, summer potassium levels are significantly higher than winter levels. For calcium, however, winter crabs have a significantly higher blood concentration over the entire salinity range than summer crabs (Fig. 2). This winter calcium level, in dilute salinities in which the blood is hypertonic, is equivalent to seawater concentrations of 125–145 percent. Comparable summer calcium values are 95–115 percent. Magnesium concentrations in blood are maintained at almost the same level regardless of the season (Fig. 2). Statistically significant seasonal differences in the dilute salinities reflect the lack of variation in the regulation of this ion, for the absolute magnitude of difference is small. Such slight differences are probably not meaningful from a biological standpoint.

The effect of temperature (5° , 15° , and $25^{\circ}\text{C}.$) on blood ion concentrations of summer and winter *H. nudus* over a range of salinities shows that in dilute salinities, concentrations of sodium, potassium, and calcium are maintained hypertonic to the media, apparently independent of experimental temperature or season. In concentrated salinities, limited hypotonic

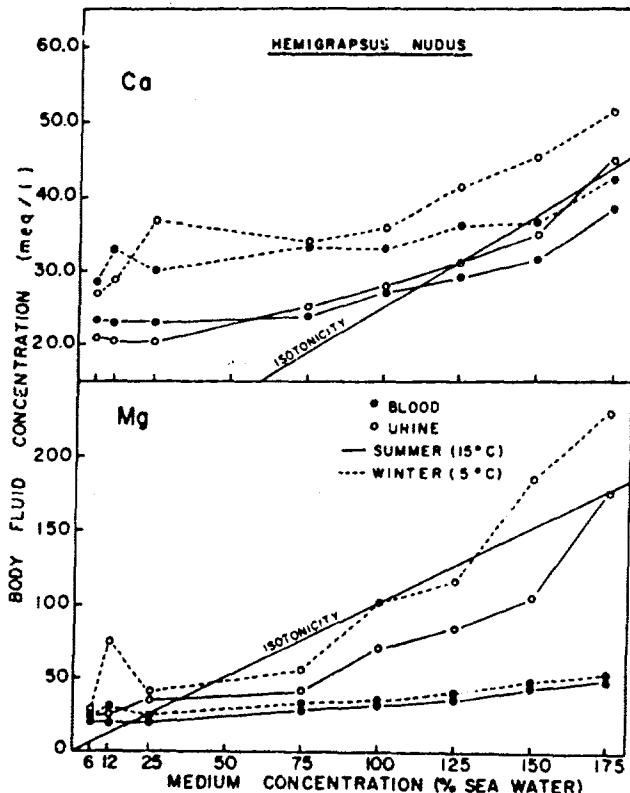


Fig. 2. Calcium and magnesium ion concentrations in the body fluids of winter ($5^{\circ}\text{ C}.$) and summer ($15^{\circ}\text{ C}.$) *Hemigrapsus nudus* as a function of salinity. Each point represents the mean value of ten measurements after exposure for 24 hours to each experimental salinity.

regulation is effective in maintaining the concentration of these ions slightly below the media concentrations at almost all combinations of temperature and season. Potassium alone shows a consistent seasonal difference at the three temperatures, winter values tending to be lower than summer values in media above 25 percent sea water. Since no consistent effect of temperature on seasonal animals could be demonstrated, it appears that the mechanisms important in maintaining ion hypertonicity in a dilute environment are remarkably tolerant to wide temperature variation.

This is not altogether true for the response of magnesium to temperature at each season. The range of magnesium concentrations in the blood (measured in 6 and 175 percent sea water) increases with increasing temperature in both seasons. In 175 percent sea water the total variation in magnesium concentration for all combinations of temperature and season is only from 49 to 68 meq l.

Urine ion concentrations of summer and winter *H. nudus* in relation to salinity are depicted in Figure 1 (sodium and potassium) and Figure 2 (calcium and magnesium). Winter urine sodium concentrations are significantly higher than summer values in most of the salinities (25–150 percent sea water). Also, in media above 12 percent sea water, winter urine sodium concentrations are hypertonic to winter blood sodium concentrations. This suggests that the antennary glands actively rid the blood of sodium, contributing to a winter blood sodium condition that is hypotonic to the medium in the concentrated salinities. This is presumably advantageous in that excessive concentration of the blood in high salinities is lessened. In dilute media, however, sodium excretion by kidneys tends to increase sodium loss by supplementing the passive outward diffusion of this ion (in salinities of 25–100 percent sea water, the blood sodium concentration is 400–450 meq l, equivalent to sea water of 85–100 percent). Thus, selective extra-renal sodium uptake from a dilute environment in order to maintain blood hypertonicity is opposed by a sodium loss due to antennary gland activity. Summer urine sodium concentrations show no significant difference from summer blood concentrations, indicating that hypertonic sodium regulation in the blood in this season is by extra-renal mechanisms. The antennary glands are ineffective in hypertonic potassium regulation in summer animals, because the urine concentrations are essentially isotonic with the blood concentrations. In winter crabs, however, maintenance of a blood potassium concentration hypertonic to the media is assisted by the production of a dilute urine. Hypotonic potassium regulation in media above 100 percent sea water is accomplished in both seasons extra-renal, for the urine is essentially isotonic with the blood. Urine potassium concentration is significantly higher in summer than in winter over most of the salinity range. Hypertonic regulation of blood calcium is accomplished solely by extra-renal mechanisms in the summer because the urine concentrations

are equal to the blood in most of the experimental media (Fig. 2). In winter animals, however, there is at least some participation of the kidneys in hypertonic calcium regulation in salinities of 100–150 percent sea water, for the urine is hypertonic to the blood. Thus, extra-renal absorption of calcium in dilute media appears to be gradually replaced in these concentrated salinities by calcium excretory activity of the kidneys. Winter urine calcium levels are significantly higher than summer levels over the entire salinity range.

Whereas regulation of the other ions appears to be largely a result of extra-renal processes, the hypotonic regulation of blood magnesium is effected almost entirely by antennary gland activity. Data presented in Figure 2 indicate that urine magnesium concentrations are significantly higher in both winter and summer crabs in salinities above 25 percent sea water than comparable blood magnesium values. Thus, regulation of magnesium in these salinities is by excretion in the urine. In salinities below 25 percent sea water, blood magnesium concentrations are hypertonic to the medium. Although urine-blood isotonicity minimizes magnesium loss in these dilute salinities, it is possible that absorptive processes also contribute to the maintenance of hypertonicity. In salinities above 25 percent sea water, summer urine magnesium is markedly hypotonic to the media, becoming isotonic in 175 percent sea water, and winter urine magnesium is slightly hypotonic, becoming hypertonic between 125–150 percent sea water.

Winter urine magnesium concentrations are significantly greater than summer values over most of the salinity range, even though the seasonal blood levels are almost identical. Possibly winter crabs, because of their seasonal acclimatization to higher environmental magnesium levels, are more effective in excreting magnesium when exposed to an excess in the experimental media. Summer animals, however, because they are accustomed to lower environmental levels of magnesium, must rely on accessory organs of excretion. Thus, summer urine is less concentrated.

The seasonal urine values for sodium, potassium, and calcium are comparable in magnitude and variation to those presented for blood. No consistent effect of temperature on urine ion concentrations could be demonstrated.

Seasonal variation with temperature in urine magnesium concentration shows that, in media above 25 percent sea water, the urine is consistently hypertonic to the blood. Although an effect of temperature on this ion is not demonstrated, the variability in urine magnesium concentration at the three temperatures is twice that of the blood at a given season. Values for the other ions did not exhibit this difference in variability between the two body fluids.

The urine blood ion ratio is indicative of the extent of kidney activity in the regulation of a blood ion. Thus, if the U:B ratio for an ion equals or approximates unity, there can be no participation of the kid-

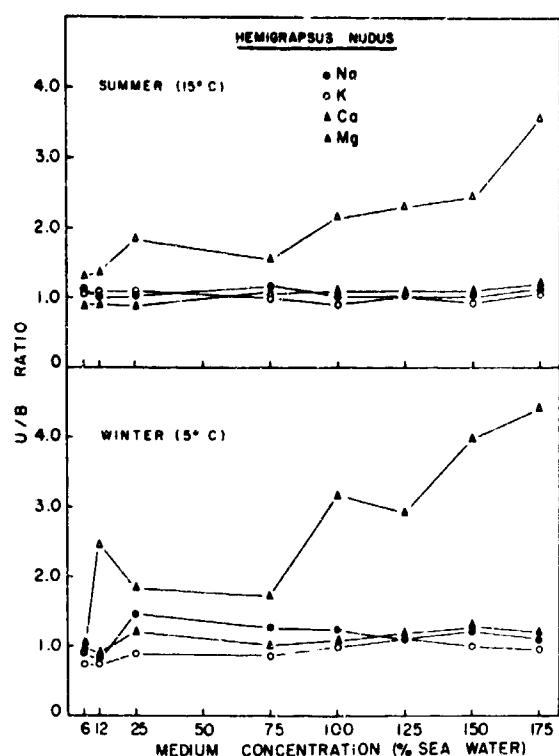


Fig. 3. Relationship of urine-blood (U/B) ion ratios of summer and winter *Hemigrapsus nudus* to a range of salinities. Each point represents a ratio of the means of ten measurements for blood and urine after exposure for 24 hours to each experimental salinity.

neys, for the urine and blood are isotonic. Ratios greater than unity, however, indicate urinary excretion; ratios markedly less than unity suggest renal absorption.

The U/B ion ratios for summer and winter *H. nudus* are shown in Figure 3. As expected, U/B magnesium ratios deviate markedly from unity in both seasons. The higher winter ratio for magnesium, as noted previously, may reflect a greater potential for magnesium excretion in the winter population—a necessity because the field concentration of magnesium in this season is twice that of the summer. If the absolute quantity of magnesium ion diffusing into summer and winter crabs when immersed in a comparable salinity (above 25 percent sea water) is equivalent, then the difference in the amount of magnesium excreted by summer crabs must be eliminated extra-remally, since the blood magnesium concentration is identical in the two seasons.

The maintenance by winter crabs of a constant hypertonic blood sodium level in dilute salinities (Fig. 1) is accomplished even though the urine has a significantly high concentration of this ion, represented here by U/B sodium ratios greater than unity. Hypertonic sodium regulation in summer animals is effected by extra-renal mechanisms, since U/B ratios are near unity. A limited hypotonic sodium regulation

in concentrated media by urinary excretion in winter crabs is suggested by the presence of ratios greater than unity. Hypertonic potassium regulation by winter crabs in dilute salinities is aided by production of urine less concentrated than the blood, indicated by U/B ratios less than unity. In summer, hypertonic regulation of potassium and calcium is only by the kidney. Hypotonic calcium regulation by winter crabs in concentrated media is assisted by calcium excretion in the urine (Dehnel and Carefoot, 1965).

CHLORIDE REGULATION—BLOOD

Blood and urine response curves for 1, 3, and 7 days (summer) and 3 days (winter) at a series of salinities and at 10° C. shows that major changes in blood chloride concentrations result during the first 24 hours. Following this, blood is regulated at levels which are significantly hypertonic from the lowest salinities to 100 percent sea water, and then summer blood becomes hypotonic. Winter blood is isotonic between 100 and 125 percent sea water, and subsequently becomes hypotonic (Fig. 4). The seasonal difference in the chloride concentration of the blood is evident at the lower experimental media. At 75 percent sea water and above winter and summer blood are isotonic, except at 125 percent. There is, however, a tendency for winter blood to have a higher concentration throughout the range of experimental media. The slopes of the hypertonic curves for summer and winter blood concentrations show that blood

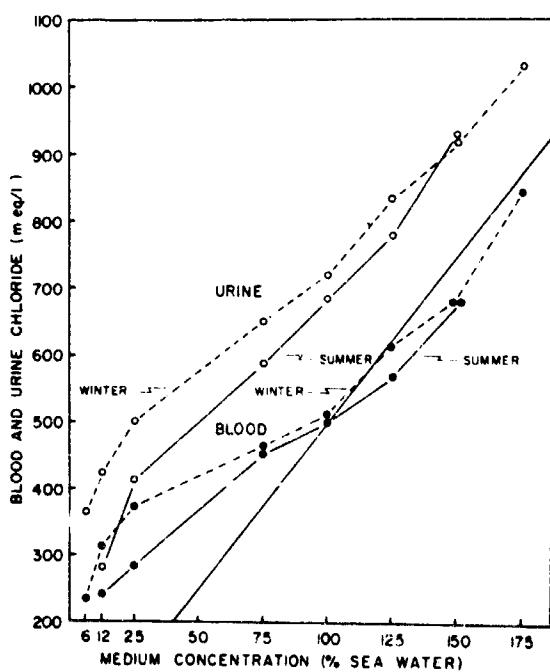


Fig. 4. Chloride ion concentration in the body fluids of winter and summer *Hemigrapsus nudus* as a function of salinity. Each point represents the mean value of twenty measurements after exposure for 72 hours to each experimental salinity.

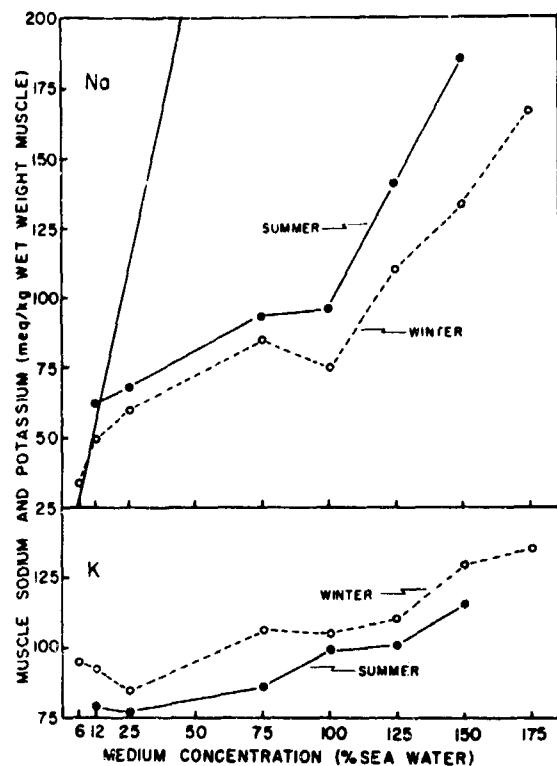


Fig. 5. Sodium and potassium ion concentrations in muscle of winter and summer *Hemigrapsus nudus* as a function of salinity. Each point represents the mean value of twenty measurements after exposure for 72 hours to each experimental salinity.

chloride concentrations are relatively dependent upon the concentration of the experimental media, although sizable gradients exist when the actual concentration of the blood is compared with the line of isotonicity. For instance, at 25 percent sea water, summer blood maintains a gradient of 160 meq/l., and winter blood, 250 meq/l. At 125 percent sea water, winter blood is isotonic and summer blood maintains a minus 50 meq/l. gradient.

Urine chloride concentration changes show a similar time response to that of the blood, except for the higher salinities (125–150 percent sea water). Major changes are effected during the first 24 hours. At the higher salinities, even after 7 days, changes occur at 125 percent sea water. After 24 hours, urine chloride concentration is significantly hypertonic to the experimental media as well as to the blood. This hypertonicity of the urine exists for both seasons. Comparison of winter and summer urine shows that winter urine is significantly higher than its summer counterpart at up to 100 percent sea water.

Comparison of the chloride gradients between urine and blood generally show that winter gradients are significantly higher than summer ones. This results from the fact that urine chloride concentration is hypertonic to blood and parallels the line of isotonicity, whereas the blood concentration becomes hypotonic at the higher salinities. Further, winter urine concentration is hypertonic to summer urine.

If winter U:B ratios are compared at three selected salinities, 25, 75, and 125 percent sea water, there is considerable agreement. Ratios range between 1.33 and 1.40. Similar comparison for summer values gives a range from 1.31 to 1.46. Summer values tend to have the greater range, based on the fact that summer blood concentrations are more hypotonic at higher salinities. The significant consideration of these ratios is that they demonstrate renal excretion of chloride. But the magnitude of deviation from unity would suggest that there is an extra-renal route (Dehnel, 1966).

CATIONIC REGULATION—MUSCLE

Sodium, potassium, and calcium ion concentrations in muscle are hypotonic to medium concentrations of the respective ions except at 6 percent sea water. Muscle magnesium is hypertonic at the lower salinities, but then maintains a hypotonic concentration as the external medium concentration increases. Concentrations of sodium and calcium are higher in summer, but are significantly different only at salinities above 100 percent sea water. Concentrations of potassium and magnesium are higher in winter, and are significant throughout the range of salinities (Figs. 5 and 6).

Comparison of the concentrations of the cations of the blood and muscle show that blood sodium is about five times greater than that of muscle, whereas muscle potassium is approximately eight times greater than the blood. Muscle potassium tends to be slightly higher than muscle sodium, except at higher salinities, where the sodium concentration rises sharply. Blood calcium concentration is three times higher than that of the muscle, and muscle magnesium is somewhat higher than the blood at low salinities; it becomes lower in concentration as salinity increases (Dehnel, 1967).

CHLORIDE REGULATION—MUSCLE

Muscle chloride concentration (Fig. 7) is hypotonic to the experimental media concentrations, except at the lowest salinities, where it is isotonic. Over the range 6 to 100 percent sea water, muscle chloride maintains a concentration of approximately 100 meq/l. Above 100 percent sea water there is a steady increase, until at 175 percent sea water the concentration is doubled. Blood chloride concentration is approximately four to five times greater than that of the muscle. There is a general trend for chloride to be higher in the summer than in the winter (Dehnel, 1967).

MUSCLE AND BLOOD WATER

Reference to Figure 8 shows that the water content of the blood ranges approximately from 880 to 930 mg/kg wet weight. Further, it should be noted that water content of summer blood tends to be higher. A regression line fitted by the method of least squares,

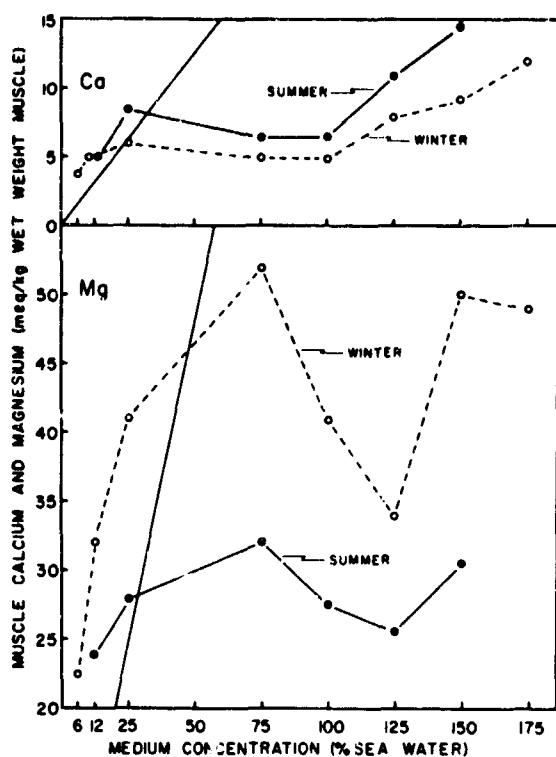


Fig. 6. Calcium and magnesium ion concentrations in muscle of winter and summer *Hemigrapsus nudus* as a function of salinity. Each point represents the mean value of twenty measurements after exposure for 72 hours to each experimental salinity.

but not indicated on the figure, describes the data as a straight line at 920 mg/kg wet weight tissue. These data show that as medium concentration increases water content of the blood is constant.

Water content of muscle tissue ranges from 690 to 800 mg/kg wet weight. As with the blood, water content of summer muscle tends to be higher. The regression line, again not shown, demonstrates that, as salinity increases, water content of muscle decreases 15 to 20 mg/kg wet weight for each 25 percent increase in salinity (Dehnel, 1967).

SUMMARY AND CONCLUSIONS

In low salinities (6–75 percent sea water), sodium, potassium, and calcium ion concentrations in the blood of *Hemigrapsus* were shown to be considerably hypertonic to the media. In high salinities, ion regulation became less effective and concentrations approached isotonicity. Blood concentration of magnesium was found to be regulated at a precise hypotonic level, approximately one-third that of the medium concentration. Seasonal differences in ability to regulate sodium and potassium were not consistent, whereas calcium ion concentrations in the blood in low salinities are higher in winter, and this suggests that winter animals are more effective regulators of this ion. Concentrations of magnesium in the blood are almost

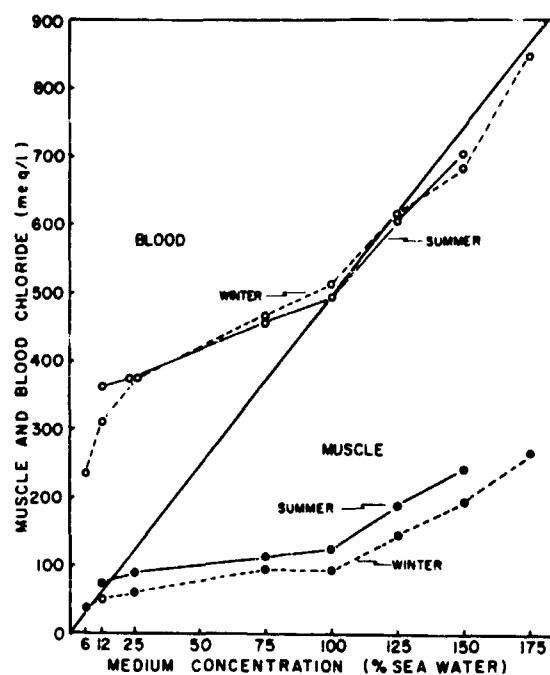


Fig. 7. Chloride ion concentrations in muscle and blood of winter and summer *Hemigrapsus nudus* as a function of salinity. Each point represents the mean value of twenty measurements after exposure for 72 hours to each experimental salinity.

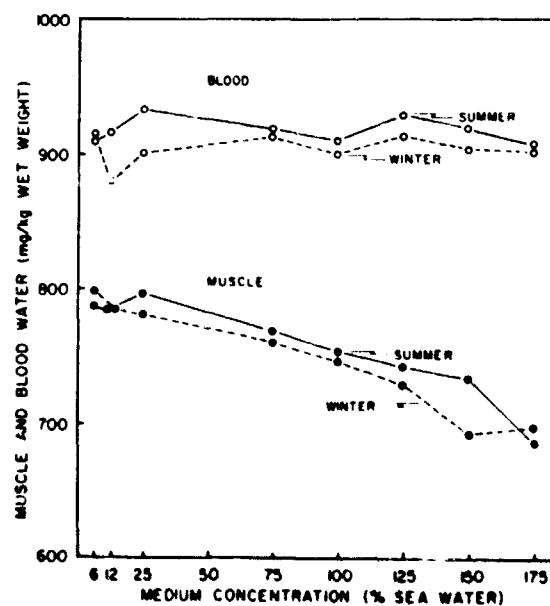


Fig. 8. Water content of muscle and blood of winter and summer *Hemigrapsus nudus* as a function of salinity. Each point represents the mean value of twenty measurements after exposure for 72 hours to each experimental salinity.

identical, seasonally. Hypertonic regulation of sodium, potassium, and calcium ions was shown to be primarily effected by extra-renal processes. The principal site may reside in the lamellar epithelium of the gills. The major function of the antennary glands is the maintenance of blood magnesium, and there is limited hypotonic regulation of sodium and calcium ions in high-salinity media by excretion of these ions in the urine. In dilute salinities, there is active reabsorption of potassium ions in the kidney tubules in the winter, contributing to the maintenance of potassium hypertonicity to the media. It is suggested that the hypotonic regulation of blood magnesium ion concentration is necessary to facilitate neuromuscular impulse transmission, and appears to be a characteristic feature of ion regulation in active decapod Crustacea.

Blood chloride regulation is a predominant feature of ionic regulation in these estuarine crabs, but the degree to which chloride is regulated is not so great as that of sodium; that is, the slopes of the chloride regulation curves, at 100 percent sea water and below, are not as flat as those for sodium.

Major gradients are maintained between muscle cations and the blood. Blood sodium and calcium are higher than that of the muscle, and muscle potassium and magnesium are higher than the blood. All muscle

cations are hypotonic to medium concentrations, with minor exceptions.

Muscle chloride is maintained at a relatively constant level, hypotonic to the blood as well as to the experimental salinities.

Changes in muscle water with respect to experimental salinity changes suggest a movement of water between blood and muscle, but the maintenance of a constant blood water content would indicate changes in filtration rate of the antennary gland.

LITERATURE CITED

- DEHNEL, P. A., 1962. Aspects of osmoregulation in two species of intertidal crabs. *Biol. Bull.*, 122:208-227.
DEHNEL, P. A., 1966. Chloride regulation in the crab, *Hemigrapsus nudus*. *Physiol. Zool.*, 39:259-265.
DEHNEL, P. A., 1967. Ion regulation in the muscle of an estuarine crab, *Hemigrapsus nudus*. (Manuscript)
DEHNEL, P. A., and T. H. CAREFOOT, 1965. Ion regulation in two species of intertidal crabs. *Comp. Biochem. Physiol.*, 15:377-397.
DEHNEL, P. A., and D. STONE, 1964. Osmoregulatory role of the antennary gland in two species of estuarine crabs. *Biol. Bull.*, 126:354-372.
LOCKWOOD, A. P. M., 1962. The osmoregulation of Crustacea. *Biol. Rev.*, 37:257-305.
POTT'S, W. T. W., and G. PARRY, 1964. *Osmotic and ionic regulation in animals*. Pergamon Press, Oxford, England.

Physiological Response of Estuarine Animals from Different Latitudes

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Studies concerned with latitudinal physiological variation in marine animal populations of the same or closely related species have been numerous and instructive. Discourse, both original and review, is available in Scholander *et al.* (1953), Prosser (1955), Bullock (1955, 1958), Segal (1961), Vernberg (1962), Kinne (1963), Precht *et al.* (1955), and Precht (1958).

If we now move out of the strictly marine realm and search for studies concerned with latitudinal physiological variation in brackish-water or estuarine populations of the same or closely related species, we find that little work has been carried out in this area. Smith (1959) and Kinne (1964) summarize the available information within reviews more generally concerned with the physiology of brackish-water animals. In original and comprehensive programs on the subject, one name stands out—that of Carl Schlieper (see Remane and Schlieper, 1958, for a complete bibliography of the earlier work from Schlieper's laboratory). It is Schlieper's contention that the subject matter of the present paper is the main problem to be analyzed in the field of brackish-water physiology. It is from the study of brackish-water and estuarine populations that we will gain insights into the question of the migration of species from marine to brackish waters and from brackish to fresh waters. Whether one agrees with Schlieper or not, it is an area of study which has been badly neglected.

Why has it been neglected? Distance is readily recognized as a formidable deterrent. But distance is equally formidable if one is studying strictly marine populations, and such studies are certainly not at a loss for contributors. The answer must lie in the analysis one must undertake in an attempt to interpret the response of estuarine organisms in terms of their environment. The most fundamental difference between high latitude and low latitude seas is temperature. As Kinne (1963) has concluded, many of the pertinent reports comparing the physiology of marine populations from different latitudes stress that temperature appears to be acting as an ecological master factor. Brackish-water and in particular estuarine populations, on the other hand, are living in a cycling temperature-salinity environment so complex that many of the experts in the field of estuarine research cannot come to common agreement as to what an estuary is and what an estuary is not. It is no wonder that the ecological physiologist has shied away from this area of study.

In the present paper I shall survey the few pertinent studies comparing various physiological responses of brackish-water and estuarine populations from different latitudes. Then I shall comment upon the interpretations of these data relative to the genotypic or phenotypic basis for the observed differences. Lastly, I shall attempt to relate these data to the current theories concerning the penetration of brackish waters by marine species and the penetration of fresh waters by brackish-water species.

LATITUDINAL VARIATION

As I have previously indicated, a significant body of work comes from the laboratory of Carl Schlieper at Kiel (Schlieper, 1957). Schlieper and his co-workers have been studying the North Sea (30‰) and western Baltic Sea (15‰) forms of the mussel, *Mytilus edulis*, and the starfish, *Asterias rubens*. The western Baltic, or low-salinity, forms of *Asterias rubens* are smaller, have a softer, more weakly sclerotized integument, more slowly developing gonads, a higher rate of tissue metabolism, and a longer latent period and longer turning-over time when displaced from their normal position. *Mytilus edulis*, which is more euryhaline than *Asterias rubens*, similarly shows various physiological differences in the low- and high-saline populations. The western Baltic forms have a higher gill respiration, regardless of the temperature and condition of the gonads, slower heart beat, reduced ciliary activity, and a lowered resistance to heat.

When North Sea *Mytilus edulis* were transferred from 30‰ to 15‰, the oxygen consumption of the gill tissue rose quickly and reached the level of the Baltic forms in four to seven weeks. When the Baltic animals were transferred from 15‰ to 30‰, there was a reduction in gill respiration. Schlieper has concluded that the physiological differences shown by the two populations are neither hereditary nor directly dependent on the lower osmotic concentration of the animals in the Baltic Sea. He believes there has been a lengthy process of adaptation to the lower salinity of the Baltic. Further tests are under way to determine whether the North Sea and Baltic Sea populations do, in fact, represent physiological races (Schlieper personal communication). *Asterias rubens*, *Mytilus edulis*, and a third species, the anemone, *Metridium senile*, are under investigation in terms of their cellular responses to heat, cold, varying salinities, and varying pressures. In addition, these work-

Table 1. Comparison of blood concentration (as percent sea water) of *Cyathura polita* from Pocasset River, Massachusetts, and Silver Glen Springs, Florida.

Pocasset River, Mass.				Silver Glen Springs, Fla.				P
Medium (percent sea water)	Blood concen- tration (percent sea water)	Standard devia- tion	No.	Medium (percent sea water)	Blood concen- tration (percent sea water)	Standard devia- tion	No.	
Distilled H ₂ O	59.4	3.90	8	Distilled H ₂ O	29.1	2.78	4	.01
1.5 ^a	59.2	4.53	9	—	—	—	—	—
1.5	64.0	3.97	10	—	3.0	50.5	2.78	3
—	—	—	—	3.5 ^b	57.6	1.92	6	—
3.5	64.8	3.59	11	24.0	67.0	2.76	10	.01
24.0	67.0	2.76	10	25.5	62.8	5.10	4	N.S.
57.0	72.8	1.90	10	53.0	71.4	1.59	6	N.S.
73.0	72.0	0.77	10	75.5	82.1	4.44	5	.01
104.0	104.0	1.73	10	96.5	100.8	3.75	5	N.S.
130.0	128.3	4.03	8	123.5	123.7	4.63	5	N.S.
155.0	153.6	3.02	11	—	—	—	—	—

Experimental temperature was 22° C.; blood samples taken after 48 hours at the various salinities; 100 percent sea water = 32.00 ‰.

^a River water.

^b Spring water.

P = significance of difference between means.

N.S. = no significance.

ers are subjecting the populations of each of these species to different stresses, and recording the time needed for a complete adaptation or readaptation.

In an earlier study Beliaev and Birstein (1944), compared the osmoconcentration of the body fluids of the amphipod, *Dikerogammarus haemobaphes*, from the Volga River and the Caspian Sea at a common temperature. The Volga population showed a higher level of regulation in dilute media and a shift in the point of isotonicity. These authors have concluded that their populations belong to different physiological races, although a test of this hypothesis has never been carried out.

Landers and Toner (1962) studied the righting reflexes, at various temperatures and salinities, of a population of the polyclad, *Stylochus ellipticus*, living in Milford Haven, Connecticut. Earlier, Pearse and Wharton (1938) had carried out a similar study on a population of the same species living at Apalachicola Bay, Florida. Comparing the results of the two populations revealed that, at the same temperatures, locomotion rates of Connecticut worms were consistently faster than those of Florida worms. Landers and Toner suggest that each group was working with a different physiological race. Their conclusions, in my opinion, are not warranted on the meager data available.

The oxygen consumption of *Uca pugilator* from Woods Hole, Massachusetts, and Florida was studied by Demeusy (1957). The Woods Hole animals showed obviously faster O₂ consumption at 1.4° C. but not at 15° C. The differences between the populations were not abolished after eight weeks at a common temperature. The populations also differ in color. Demeusy believes these differences between the populations might warrant their separation into

two subspecies. However, she is well aware that breeding tests are very much needed.

Segal and Burbanck (1963) carried out a series of studies on *Cyathura polita*, a ubiquitous amphipod inhabiting estuaries and tidal marshes from Maine to Louisiana. The range of temperature and salinity conditions under which *C. polita* can live (0.5 ‰ to 17 ‰ salinity with a temperature variation of about 2° to 23° C. in the Pocasset River on Cape Cod, Massachusetts, to a virtual thermo- and chemostat of approximately 1 ‰ salinity and 21–23° C. in Silver Glen Springs, Florida) means that the osmoregulatory demands placed upon each population are quite different.

When individuals from both populations are tested over a series of salinities at a temperature common to both at the time of collection, it is clear that each population regulates at a different level, particularly at 50 percent sea water and below (Table 1 and Fig. 1). Further, although there is no significant difference in the level of osmoregulation in these populations in their natural media (Pocasset animals in river water at low tide, 1.5 percent sea water; Silver Glen Springs animals in 3.5 percent sea water), there is a striking difference in salinities below 3.5 percent sea water. The osmoregulatory ability of Silver Glen Springs animals breaks down below 3.5 percent sea water, while Pocasset animals can regulate for at least a week in distilled water. The populations also differ in their osmoregulatory behavior at low temperature and this will be dealt with in more detail shortly. At intermediate and high salinities and at intermediate temperatures *C. polita* from both localities behave as typical brackish-water animals—hypertonic in dilute media and essentially isoosmotic in more concentrated media.

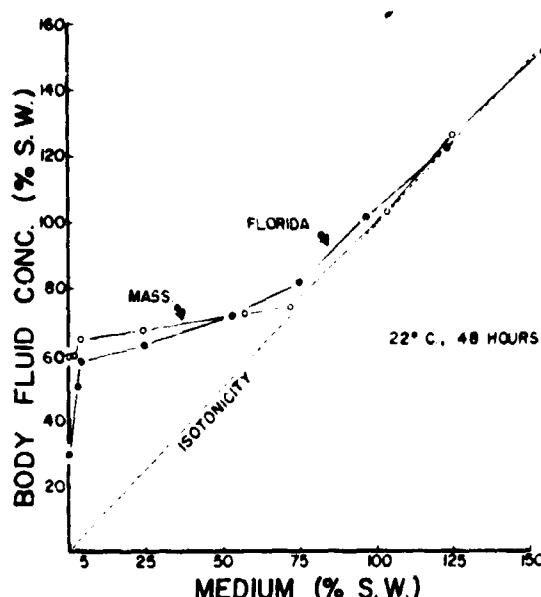


Fig. 1. Relation between blood concentration and concentration of medium at 22° C. in *C. capitata polita* from Massachusetts and Florida (Segal and Burbanck, 1963).

In all the studies cited, the latitudinally separated populations differ in one or more physiological activities. Except for Schlieper's studies in the western Baltic and North Sea where the obvious main difference in the environment is salinity, there is no single common denominator operating as a function of the difference in latitude. Although temperature, over short or long term, is a prime suspect because of its impact on physiological variation in marine forms, it is most doubtful that physiological variation between estuarine or brackish-water populations is caused by a single environmental parameter. The estuarine or brackish-water environment is too complex and the present stage of our knowledge too meager to permit a generalization.

On the basis of one or more physiological differences in latitudinally separated populations, many of the workers cited have concluded that the populations they dealt with were "physiological races" of each species. Postulation of physiological races assumes a genetic difference between populations. Although it is true that physiological races can only come about through the operation of environmental factors, it does not automatically follow that estuarine or brackish-water populations, which are products of discontinuous and widely divergent ecological conditions, are necessarily genetically different—at least not without some adequate tests. Smith (1959) has discussed this problem at length. He feels that one must not only ask the right questions of organisms, but rule out acclimation phenomena by the proper tests and carry out breeding experiments over at least two generations before one can claim that he is dealing with genetically distinct physiological races. Schlieper's studies on *Mytilus edulis* from the North Sea

and Baltic Sea bear this out. Reciprocal transplantation of mussels between the two areas eliminates the differences in oxygen consumption between the two populations. In other words, a phenotypic acclimation was responsible for the initial difference, since the physiological activity was reversible with transplantation. It seems, then, that unless we can show that a physiological difference is not phenotypic we should be cautious in invoking physiological races, particularly when our information is purely descriptive although of a physiological nature.

PENETRATION

Related to the problem of physiological variation in latitudinally separated populations of species is the question of whether penetration of brackish waters by marine species and penetration of fresh water by brackish-water species is more likely or would be easier when the temperature is high than when it is low—thus at the lower as compared with the higher latitudes. Whether on experimental or on purely philosophical grounds, numerous authors have agreed with the dictum of von Martens (1858) that migration from the sea occurred in tropical regions where the temperature of rivers and seas is nearly uniform and generally warm. The comparative richness of the fauna of tropical and subtropical estuaries, as compared with temperate and northern estuaries, suggests that the invasion of estuaries is easier in warm waters.

Segerstråle (1949, 1950) lists a number of species which are not found in fresh water in the Baltic region, although these species have freshwater "races" farther south. Milne (1940), comparing the penetration of the same species (*Vittorina littorea*, *Pectella vulgata*, *Balanus balanoides*) in various estuaries in France and England (Lat. 48°-57°N.), found a greater penetration of populations of the same species in French estuaries. This suggests a temperature effect, but since no salinity data are given, the situation merits further study. Pannikar (1951) accepts the thesis that penetration is more likely in the warmer parts of the range of a species or in a species living in warmer waters and suggests that it may be correlated with increased osmoregulatory ability at higher temperatures.

Studies in which the organisms have been asked a specific question in the laboratory have led to conflicting results. (Do you osmoregulate at a higher level or at lower salinities when the temperature is high or when it is low?)

Smith (1956) measured the chloride-regulating ability of the polychaete, *Nereis diversicolor*, from six European localities. The animals regulated over a range of salinities from about 6‰ to 15‰ Cl (1 g^{-1} sea water). *Nereis* from marine-dominated habitats died in fresh water while animals from water of low salinity did not die in fresh water regardless of the latitude. But for all populations the plateau of Cl regulation was very much at the same level regardless of the origin of the worms. As Smith suggests, he

may not have asked his animals the right question. However, *N. diversicolor* does drop out at higher salinities in the Gulf of Finland where the temperature is lower than it does in Danish and British rivers where the temperature is higher. This is not to say that Danish and British rivers are tropical or subtropical but merely that they are at the upper end of the temperature gradient for the populations that were studied. It is interesting that a related estuarine species, *N. limnicola*, contains a population inhabiting the fresh water of Lake Merced in San Francisco (Smith, 1959). Although Smith did not study the effects of low temperature on chloride regulation in *N. diversicolor* from the different parts of its range, he did ask the question of *N. limnicola* from central California estuaries. *N. limnicola* was unable to regulate volume or maintain its chloride level at temperatures near zero. It is clear that the question was not a fair one since the stress was obviously too great.

In another study, Broekema (1941) worked with the shrimp, *Crangon crangon*, off the Dutch coast. These animals migrate into high salinity waters in winter and brackish waters in summer. In the laboratory it seemed that the osmoregulatory capacity was greater at higher temperatures (21°C.) than at lower temperatures (4°C.) in low salinities. More recent work by Flügel (1959), using a more refined technique on the same species, did not clearly show the same relationship reported by Broekema.

There is also evidence to suggest that higher temperatures could not assist at least some brackish-water species to move towards fresh water. This is probably the case with *Gammarus duebeni* which in nature has an optimal salinity between 5-15‰ and osmoregulates at a higher level at lower (7°C.) as compared with higher (20°C.) temperatures (Kinne, 1952). In support, Lockwood (1961) reports that in *G. duebeni* the temperature coefficient of loss and uptake of sodium bears an inverse relationship to those found in the freshwater *Asellus aquaticus*. *A. aquaticus* can maintain the physiologically necessary concentrations of Na and Cl in fresh water more readily if the temperature is high than if it is low.

Also, the brackish water crab, *Rhithropanopeus harrisi*, which is usually found in salinities as low as 1.5-5‰, shows the same response to temperature as *G. duebeni*, that is, stronger hyperosmotic regulation at 7°C. than at 20°C. (Kinne and Rotthauwe, 1952).

What is difficult to equate from the data on *G. duebeni* is the fact that in nature this species actually is found in less saline waters in the more southern parts of its range (marine in the Barents Sea, brackish in the Baltic, and fresh water in Ireland and England). There is the possibility, as suggested by Segersstraale, that the freshwater populations of this species represent distinct physiological races. If so, it makes the analysis of the data most complex.

With the foregoing conflicting results in mind, I asked *Cyathura polita* from Massachusetts and Florida the same question: Is regulation stronger or weaker when the temperature is low and the salinity is also

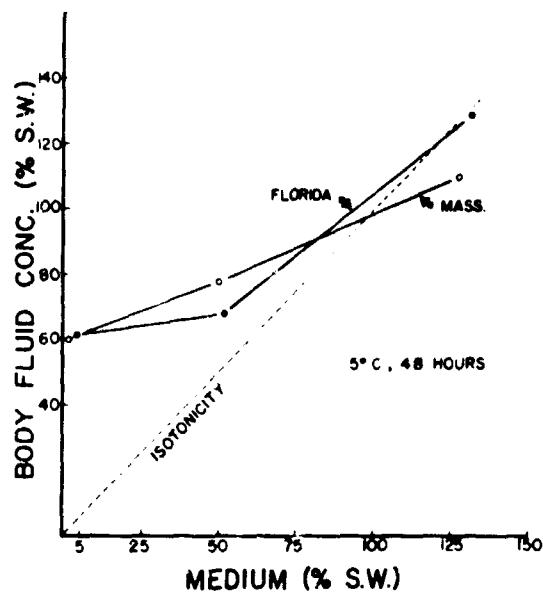


Fig. 2. Relation between blood concentration and concentration of medium at 5° C. in *Cyathura polita* from Massachusetts and Florida (Segal and Burbanek, 1963).

low? Northern animals from the Pocasset River in Massachusetts showed no regulatory impairment over a 27° C. range in temperature, although there was a temporary interference with the regulatory mechanism at high temperatures (32° C.) and low salinity (1.5 and 50 percent sea water). When one compares the response at low temperature (5° C.) with that at the higher temperatures (22° and 32° C.), it is clear that the northern animals show a higher level of hyperosmotic regulation in 50 percent sea water, the approximate salinity level during high tide in the estuary. This response is similar to that obtained by Kinne on *Gammarus* and *Rhithropanopeus*. In a way, what was more surprising was the response of Pocasset set animals at 5° C. and 125 percent sea water. The animals were hypoosmotic in hypersaline media, thus flattening the curve along its entire length. The meaning and significance of hypoosmotic regulation is not apparent. Whether the more effective regulation at low temperature and high salinity can properly be considered a steady state or merely reflects a transition period is not known.

To return to the point at hand, Figure 2 shows that Pocasset and Silver Glen Springs *Cyathura* do not respond in the same way to low temperature. Silver Glen Springs animals maintain the same level of internal osmotic concentration at 5° C. as at 22° C. The differences between the two populations are statistically significant. Further, the Silver Glen Springs animals were not able to regulate properly at either low or high salinities when subjected to high temperature (32° C.).

Thus, we have two populations of a species from radically diverse ecological habitats. One is from the higher latitudes, in an estuary that has ontogenetically

been adapted to a daily cyclic salinity regime (1.5-50 percent sea water) and an annual temperature change of from approximately 2°-23° C. The other population, from the lower latitudes, is adapted to the relatively constant salinity (3.5 percent sea water) and temperature (20°-23° C.) of a natural springs. The northern population tolerates a wider range of salinity and temperature, but osmoregulates more efficiently in the cold, at least in moderately diluted and hyper-saline media.

It is clear that the populations of *C. polita* answered the question asked of them. But, as is so often true, the inadequacy of the question is revealed by the answer. The differential response of the two populations must be a reflection of the thermal and salinity histories of the populations. It is clear that at least the Silver Glen Springs *Cyathura* could not survive in fresh water and it is unlikely that penetration would occur here. Although they live at almost constant 3.5 percent sea water, they were unable to osmoregulate properly at 3 percent sea water, and died quickly in distilled water at their own temperature (22° C.). The Pocasset River *Cyathura*, on the basis of these short-term experiments, might survive in fresh water, or at least be on the way to penetration of fresh water. Those animals did maintain the normal gradient between inside and out in 1.5 percent sea water and in distilled water for at least 48 hours. It is of interest that Frankenberg and Burbanck (1963) report a population of *C. polita* in South River, Marshfield, Massachusetts, extending as far as eight miles from the mouth of the river and subjected to a salinity cycle from a low of 0.1 percent (fresh water) to a high of 28.9 percent (close to sea water). Although the authors attach no significance to it, the South River population shows a higher level of internal osmotic concentration at lower temperature (15-17° C.) than at higher temperature (27° C.). In addition, a population from Sapelo Island, Georgia, collected in December shows a more rapid fall in internal osmotic concentration at lower temperature (1.9° C.) and very low salinities (about 1‰) than did the Massachusetts population collected in April.

Obviously, the entire matter of latitudinal physiological variation in brackish-water and estuarine populations needs extended attention. The available information, in its meagerness, gives us little insight into the questions that have been posed. It is an area of study which would benefit greatly from cooperation of scientists at high- and low-latitude coastal laboratories. We particularly need investigations of animals from tropical and arctic estuaries.

LITERATURE CITED

- BELIAEV, G. M., and J. A. BIRSTEIN, 1944. A comparison between the osmoregulatory ability in Volga River and Caspian Amphipods. *Compt. Rend. (Doklady) de l'Acad. d. Sci. d. URSS.*, 45(7):304-306.
- BROEKEMA, M. M. M., 1941. Seasonal movements and the osmotic behaviour of the shrimp *Crangon crangon*. *L. Arch. Neerl. Zool.*, 6:1-100.
- BULLOCK, T. H., 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.*, 30:311-342.
- BULLOCK, T. H., 1958. Homeostatic mechanisms in marine organisms. In *Perspectives in Marine Biology*, edited by A. A. Buzzati-Traverso; pp. 199-210. Univ. Calif. Press, Berkeley, California.
- DEMEUSY, N., 1957. Respiratory metabolism of the fiddler crab *Uca pugilator* from two different latitudinal populations. *Biol. Bull.*, 113:245-253.
- FLUGEL, H., 1959. Zum problem der osmoregulation im tropischen brackwasser. *Naturwissenschaften*, 46:213.
- FRANKENBERG, D., and W. D. BURBANCK, 1963. A comparison of the physiology and ecology of the estuarine isopod *Cyathura polita* in Massachusetts and Georgia. *Biol. Bull.*, 125:81-95.
- KINNE, O., 1952. Zur biologie und physiologie von *Gammarus duebeni* Lillj. V. Untersuchungen liber Blutkonzentration, Herzfrequenz und Atmung. *Kiel. Meeresforsch.*, 9:134-150.
- KINNE, O., 1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. In *Oceanog. Marine Biol. Ann. Rev.*, edited by H. Barnes; vol. 1, pp. 301-340. George Allen and Unwin Ltd., London.
- KINNE, O., 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. In *Oceanog. Marine Biol. Ann. Rev.*, edited by H. Barnes; vol. 2, pp. 281-339. George Allen and Unwin Ltd., London.
- KINNE, O., and H. W. ROTTTHAUWE, 1952. Biologische beobachtungen Über die Blutkonzentration an *Heteropanope tridentatus* (Maitland) (Dekap.). *Kiel. Meeresforsch.*, 8:212-217.
- LANDERS, W. S., and R. C. TONER, 1962. Survival and movements of the flatworm, *Stylochus ellipticus*, in different salinities and temperatures. *Biol. Bull.*, 123: 146-153.
- LOCKWOOD, A. P. M., 1961. The urine of *Gammarus duebeni* and *G. pulcr.* *J. Exp. Biol.*, 38:647-658.
- MARTENS, E. VON, 1858. On the occurrence of marine animal forms in fresh water. *Ann. and Mag. Nat. Hist.*, 1:50-63.
- MILNE, A., 1940. Some ecological aspects of the intertidal area of the estuary of the Aberdeenshire Dee. *Roy. Soc. Edinburgh, Trans.* 40:107-139.
- PANNIKAR, N. K., 1951. Physiological aspects of adaptation to estuarine conditions. *Proc. Indo-Pacific Fisheries Council*, 2 (Sects. II and III), Bangkok, Thailand.
- PEARSE, A. S., and G. W. WHARTON, 1938. The oyster "leech" *Stylochus inimicus* Palombi, associated with oysters on the Coast of Florida. *Ecol. Monographs*, 8:605-655.
- PRECHT, H., 1958. Concepts of the temperature adaptation of unchanging reaction systems of cold blooded animals. In *Physiological Adaptation*, edited by C. L. Prosser; pp. 50-78. Am. Physiol. Soc., Washington, D. C.
- PRECHT, H., J. CHRISTOPHERSEN, and H. HENSEL, 1955. *Temperatur und Leben*. Springer-Verlag, Berlin.
- PROSSER, C. L., 1955. Physiological variation in animals. *Biol. Rev.*, 30:229-262.
- REMANE, A., and C. SCHLIEPER, 1958. *Die Biologie des Brackwassers*. E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart, Germany.
- SCHLIEPER, C., 1957. Comparative study of *Asterias rubens* and *Mytilus edulis* from the North Sea (30‰ S) and the Western Baltic Sea (15‰ S). *Ann. Biol.*, 33:117-127.
- SCHOLANDER, P. F., W. FLAGG, V. WALTERS, and L. IRVING, 1953. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.*, 26:67-92.
- SEGAL, E., 1961. Acclimation in molluscs. *Am. Zoologist*, 1:235-244.

- SEGAL, E., and W. D. BURBANCK, 1963. Effects of salinity and temperature on osmoregulation in two latitudinally separated populations of an estuarine isopod, *Cyathura foliacea* (Stimpson). *Physiol. Zool.*, 36:250-263.
- SEGERSTRAALE, S. G., 1949. The brackish-water fauna of Finland. *Oikos*, 1:127-141.
- SEGERSTRAALE, S. G., 1950. The amphipods on the coasts of Finland—some facts and problems. *Comm. Biol. Soc. Sci. Fennica*, 10:1-28.
- SMITH, R. L., 1956. Comparison of the level of chloride regulation by *Nereis diversicolor* in different parts of its geographical range. *Biol. Bull.*, 109:453-474.
- SMITH, R. L., 1959. Physiological and ecological problems of brackish waters. In *Marine Biology*, edited by J. Pratt and J. E. McCauley; pp. 59-69. 20th Ann. Biol. Colloq. Oregon State College, Corvallis, Oregon.
- VERNBERG, F. J., 1962. Comparative physiology: latitudinal effects on physiological properties of animal populations. In *Ann. Rev. Physiol.*, edited by V. E. Hall; vol. 24, pp. 517-546. Annual Reviews, Inc., Palo Alto, California.

Some Future Problems in the Physiological Ecology of Estuarine Animals

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Studies on the physiology and ecology of estuarine animals have encompassed a number of different approaches involving various disciplines of biology. A first investigation may be classified as descriptive and qualitative; this type of investigation need not be restricted to compiling a checklist of organisms with accompanying ecological or natural history notes, nor need it be limited to a description of the physical and chemical characteristics of an estuary, but it may include studies on certain physiological parameters of estuarine animals. In addition to descriptive qualitative studies, a second approach has been quantitative in nature where an attempt is made to estimate the amount of a specific ecological factor or to determine the rate of a specific physiological function which is associated with the estuarine environment. A third approach deals with the problem of describing mechanisms involved in biological phenomena in estuaries and formulating conceptual schemes. The need for additional studies using this third method is obvious, as evidenced by the limited number of published studies. The verification of conceptual schemes, however, must be based on careful qualitative and quantitative investigations. There is a need, therefore, for all three research methods.

As problems become more complex a greater need for interdisciplinary studies has resulted in investigations involving two or more fields. One such hybridization has taken place between ecology and physiology.

The field of physiological ecology is not new; it dates back to the early work of V. E. Shelford who first taught a course in Physiological Ecology in the early 1920's. Before this date, numerous studies emphasized this biological viewpoint, and Davenport (1897) summarized many of the pertinent published papers. Since Shelford's early efforts, this field has expanded until it is now taught in over 20 schools; the Ecological Society of America recently established a Committee on Physiological Ecology which has a mailing list of over 200 investigators.

Studies in physiological ecology of estuarine animals involve a number of unstereotyped approaches. It is suggested that future studies might include some of the following points:

1. An ecological survey of species under study to include both abiotic and biotic factors.
2. Physiological studies to assess the role of the environmental complex on the organism. Although investigations might involve various levels of biological organization, such as metabolism of the whole organism or cell, the prime objective is to keep in sight the adaptive nature of the response to the success of the whole organism.
3. A study of all stages of the life cycle to understand the influence of the environment.
4. The correlation of laboratory results with ecological observations. The physiological capabilities of an animal under controlled laboratory conditions might not reflect the ecological distribution of an animal.

This paper will deal with only a few of the problems in the physiological ecology of estuarine animals.

Few environments can equal an estuary in terms of the great number of physiological and ecological problems that an organism must solve. By its very nature an estuary is a region of marked change, not only in salinity but in many other biotic and abiotic environmental factors, such as temperature, moisture, food, competition, pollutants, etc. Changes occur rapidly over a regular tidal time sequence as well as on an irregular basis, i. e., extraordinary rainfall. Long-term fluctuations of environmental factors result from marked seasonal changes. All these changes profoundly influence the organisms living in an estuary.

When confronted with marked changes in the environment, various responses have been shown by animals:

1. Some can migrate to a more favorable environment. This migration might be in a vertical direction into the bottom or toward the surface of the estuary, or it might be a horizontal movement out to the ocean or toward fresh water.
2. Some become inactive. If this is the case, the organism might enter a resistant stage, such as a spore, or withdraw its soft parts, or the animal might become immobilized without any apparent special modifications.
3. Some remain active. To remain active in an estuary, organisms may be expected to possess some means of compensating for the stress brought on by the variable environment in an attempt to return to some physiological norm.

One of the basic problems in the physiological ecology of estuarine animals is to understand the mechanisms by which organisms compensate for alterations in their environment. This is not a new problem, nor one restricted to estuarine animals, but rather a persistent one of general biological significance.

cance as emphasized earlier by Bullock (1955), Prosser (1955), Precht (1958), Vernberg (1962), and others.

The influence of a changing environment on an organism may be discussed under two general types of adaptations according to the terminology of Precht (1958): resistance adaptation and capacity adaptation. Resistance adaptation is concerned with adaptive changes to extreme conditions, while capacity adaptation refers to adaptive responses to the normal range of an environmental factor.

Before discussing these two types of adaptations it would be well to distinguish between phenotypic and genotypic variation. It is extremely important to differentiate between a response which is the result of environmental conditioning and is labile, and a response which is genetically fixed.

When a given function of an organism is measured, the response is most frequently the result of a complex polygenic system which reflects the adaptive state of the organism to a given set of conditions. This response may be called a phenotypic expression. Under slightly different experimental conditions the same organism may give a different response—a second phenotypic expression—and in this manner a number of different responses may be obtained. There are limits, however, beyond which the response of the organism does not change appreciably with experimental manipulation. These upper and lower limits delineate the genotypic boundaries of expression while between them various phenotypic expressions are possible. This distinction must be considered especially when making intra- or interspecific comparisons. Dissimilarities might be various phenotypic expressions of overlapping genotypic limits, and hence, observed differences would not reflect basic differences.

It is not simple to determine experimentally the degree of phenotypic and genotypic variation. Two methods are used: (1) acclimating animals to various environmental conditions; and (2) rearing animals under controlled conditions.

For a more detailed discussion of these points consult Precht (1958), Prosser (1955), and Waddington (1957).

RESISTANCE ADAPTATION

The lethal effect of an environmental factor is expressed in terms of the duration of exposure and of intensity. The actual lethal point of an organism is subject to a number of variables and must be described in terms of the experimental conditions. The lethal effect of temperature has been studied in some detail (Fry, 1957, 1958). Working on freshwater fish, Fry (1957) has clearly shown that one important experimental variable is the thermal history of an organism. Animals that were maintained at higher temperatures survived elevated temperatures better than animals acclimated to lower temperatures. Data from recent studies on *Pagurus longicarpus* (Schneider and Vernberg, unpublished observation) show a

Table 1. Resistance adaptation of *Pagurus longicarpus*. Each value listed is based on a median taken from all animals under experiment (From Schneider and Vernberg, unpublished observation).

Group	Acclimation		Survival after temperature change	
	Temper- ature (in °C.)	Duration (in days)	Temper- ature (in °C.)	Duration (in minutes)
1	10	82	32	41
2	15	72	33	92
3	20	73	34	641
4	15	—	34	16

similar relationship in an estuarine hermit crab (Table 1).

The ability to shift survival limits with changing environmental temperatures would have great adaptive value to an organism, but information on the rate of change in survival limits with fluctuating environmental temperatures is needed. The speed with which an organism can compensate for rapid temperature changes would have as much biological significance as the long-term (seasonal) shift in survival limits. This is not an easy problem to study as the rate of change in limits would depend on which portion of the thermal gradient is being studied and the amount of temperature change to which the organism is being subjected. Preliminary work by Schneider and Vernberg (unpublished observation) on *Pagurus longicarpus* has demonstrated that shifts in thermal limits take place within three hours. A greater difference in response occurs in animals originally acclimated to 15° C. than forms acclimated to 5° C. when the environmental temperature was raised 5° C., 10° C., or 15° C. above the original acclimation temperature. High lethal temperature limits did not appear to be changed appreciably in animals acclimated to temperatures lower than 15° C. Comparative studies of these problems involving animals from different estuarine habitats undoubtedly would help explain animal distribution in an estuary.

Other variables influencing thermal limits which have received attention are discussed below.

STARVATION

Specimens of the intertidal zone isopod, *Ligia exotica*, which had been fed, survived high temperatures longer than animals starved for two days. Both of these groups survived longer than animals starved for seven days (Vernberg, Segal, and Schneider, in preparation).

SIZE AND SEX

Larger *Ligia exotica* survived low temperatures longer than medium-sized or small individuals. This trend is reversed when considering the response of newly hatched young who are very resistant to extreme high temperatures. Interestingly, the gravid

female is more thermal-resistant than either non-gravid females or males (Vernberg, Segal, and Schneider, unpublished observations).

PARASITISM

Estuarine intertidal zone snails, *Nassarius obsoleta*, parasitized with larval trematodes were less resistant to high temperatures than non-parasitized individuals (Vernberg and Vernberg, 1963).

LATITUINALLY SEPARATED POPULATIONS

Population samples of *Ligia exotica* from Galveston, Texas, treated in the same manner as animals of the same species from Beaufort, North Carolina, survived high temperatures better (Vernberg, Segal, and Schneider, in preparation).

There is a great need for detailed studies of the influence of environmental factors on the physiological ecology of estuarine forms. As indicated for temperature, many variables must be considered to assess the role of any factor in limiting an animal's distribution. The methodology for comprehensive studies is now available, and it is hoped that the studies will be undertaken soon.

Another problem in the field of physiological ecology which warrants additional study deals with the investigation of the relationship of the response of the whole organism and the response of its component tissues. The analysis of surviving tissue pieces can be of great value as the levels of resistance to such environmental factors as temperature and salinity of an animal may be largely based on the local qualities in the cells. This approach is illustrated by studies on the response of isolated pieces of gill tissue of molluscs from oceanic and estuarine waters. The cilia of gill tissue from intertidal zone species, *Crassostrea virginica* and *Modiolus americanus*, continued active at higher temperatures and lower salinity than the sublittoral species, *Aequipecten irradians*. These results correlated well with the response of the whole organism. Interestingly, the response of the intertidal zone forms, but not that of the scallop, could be shifted markedly by acclimation (Vernberg *et al.*, 1963). Schlieper *et al.* (1960) found that gill tissue of deep (100 m) water species were less tolerant of temperature and salinity change than species found in the intertidal zone or to a depth of one meter.

CAPACITY ADAPTATION

Many excellent examples of capacity adaptations are presented in Dr. Kinne's paper (elsewhere in this volume), and only a few additional points need be made.

Both Precht (1958) and Prosser (1958) have proposed a classification of patterns of acclimation. There is a need to apply these methods to studies involving estuarine organisms in order to determine whether the types vary in a systematic way with the distribution of animals. Distribution in this case is not restricted to organisms found in various parts of one distinct estuary, but includes a comparison of animals

from different latitudes. In one genus, *Uca* (fiddler crabs), different patterns of acclimation have been reported for adult and larval stages of tropical and temperate zone species. Not only does the pattern vary throughout the life cycle of a species, but different patterns are observed in the five tissues studied (Vernberg and Vernberg, 1964).

Some studies on the whole organism have demonstrated marked capabilities of organisms to compensate for environmental stress. Investigations are needed to elucidate the intra-organismic mechanisms responsible for adaptation.

Finally, the rate of acclimation to various environmental factors needs to be accurately described for estuarine species. Do intertidal species acclimate at the same rate or to the same degree as do deepwater forms? What role does rate of acclimation have in interspecific competition? These are only a few questions which need to be explored.

MULTIPLE FACTORS

Another problem related to the physiological ecology of estuarine animals which needs further study is the interaction of multiple environmental factors. A considerable amount of literature is accumulating concerning the influence of a single factor on an organism; it is obvious that in nature a complex of factors is operative on an organism. A second variable may markedly influence the response observed when a single factor is studied (McLeese, 1956). The second factor may increase or decrease the survival of an organism, or it may have no apparent effect. Two factors may interact to produce an effect which is not equal to the sum of either factor acting independently. The complexities of experimental design and of interpretation of data are greatly increased when three or more factors are to be studied; the technical advances in instrumentation and computer analyses are beginning to make this approach feasible, but expensive. It should be emphasized that these studies need to observe the influence of both exposure to a given constant complex of factors and, perhaps of more importance, exposure to regulated but fluctuating factors. There is some evidence that the response of animals under fluctuating conditions is much different from response under exposure to constant conditions (Heath, 1963). Fluctuation of environmental factors is a characteristic of the estuarine habitat and the speed with which an organism can adjust to its total environment is important to its survival.

In addition to these problems, numerous other lines of investigation need active study. A few are listed and briefly described below:

CORRELATION OF THE RESPONSES OF OCEANIC AND ESTUARINE POPULATIONS

This problem deals with two groups of animals: those that spend a portion of their life cycle in either an estuary or the open ocean, and those found almost exclusively in either an estuary or the open ocean.

In respect to the first group, it is not only important to understand why animals move from one region to another, but what mechanisms enable these organisms to make the adjustments required for this migration.

Even less data are available on the ecological-physiological factors restricting organisms to either an oceanic mode of life or to an estuarine existence. Recently expanded cooperative programs in biological oceanography should provide the necessary shipboard and land-based laboratory facilities needed for these studies.

NUTRITION

The feeding mechanisms, nutritional requirements, and rate of turnover of food materials are some of the problems needing further investigation.

REPRODUCTIVE BIOLOGY

Giese (1959) has emphasized the lack of extensive studies on the reproductive biology of estuarine animals. Additional information would be valuable to ecosystem ecologists as well as physiological ecologists.

CYCLED PHENOMENA

As a result of the fluctuating environment in an estuary, it is expected that pronounced cyclic phenomena would be observed in animals residing there. Relatively few animals, however, have been studied in detail. Seasonal investigations have been particularly neglected, possibly as a result of the traditionally seasonal activity at most marine laboratories.

CORRELATION OF LABORATORY AND FIELD STUDIES

In order not to lose sight of the importance of the total response of the organism to an environment, it is necessary to correlate the results of laboratory and field investigations. As a result, a feedback mechanism could develop which would bring into clearer focus the important factors influencing estuarine animals.

LITERATURE CITED

- BULLOCK, T. H., 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.*, 30:311-342.
- DAVENPORT, C. B., 1897. *Experimental Morphology*. The Macmillan Co., New York and London.
- FRY, F. E. J., 1957. The lethal temperature as a tool in taxonomy. *Annu. Biol.*, 33:205-219.
- FRY, F. E. J., 1958. Temperature compensation. *Ann. Rev. Physiol.*, 20:207-224.
- GIESE, A., 1959. Comparative Physiology: Annual reproductive cycles of marine invertebrates. *Ann. Rev. Physiol.*, 21:547-576.
- HEATH, W. G., 1963. Thermoperiodism in sea-run cutthroat trout (*Salmo clarki clarki*). *Science*, 142:486-488.
- MCLEESE, D. W., 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. *J. Fisheries Res. Board Can.*, 13:247-272.
- PRECHT, H., 1958. Concepts of the temperature adaptation of unchanging reaction systems of cold blooded animals. In *Physiological Adaptation*, edited by C. L. Prosser; pp. 50-78. Am. Physiol. Soc., Washington, D. C.
- PROSSER, C. L., 1955. Physiological variation in animals. *Biol. Rev.*, 30:229-262.
- FROSSE, C. L., (Editor), 1958. *Physiological Adaptation*. Am. Physiol. Soc., Washington, D. C.
- SCHLIEPER, C., H. FLUGEL, and J. RUDOLF, 1960. Temperature and salinity relationships in marine bottom invertebrates. *Experientia*, 16:1-8.
- VERNBERG, F. J., 1962. Comparative physiology: latitudinal effects on physiological properties of animal populations. *Ann. Rev. Physiol.*, 24:517-546.
- VERNBERG, W. B., and F. J. VERNBERG, 1963. Influence of parasitism on thermal resistance of the mud-flat snail, *Nassarius obsoleta* Say. *Exptl. Parasitol.*, 14:330-332.
- VERNBERG, F. J., and W. B. VERNBERG, 1964. Metabolic adaptation of animals from different latitudes. *Helgolander Wiss. Meeresunters.*, 9:476-487.
- VERNBERG, F. J., C. SCHLIEPER, and D. E. SCHNEIDER, 1963. The influence of temperature and salinity on ciliary activity of excised gill tissue of molluscs from North Carolina. *Comp. Biochem. Physiol.*, 8:271-285.
- WADDINGTON, C. H., 1957. *The strategy of the genes: a discussion of some aspects of theoretical biology*. Allen and Unwin, London.

Some Problems Facing the Ecologist Concerning Races and Subspecies of Brackish-Water Animals

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Many biologists deal with what Hedgpeth (1957) calls "the anatomy of ecology". They perform faunistic surveys, study the composition of animal communities, and make standing crop investigations on a broad scale. Sooner or later they usually have to rely upon specialists when identifying the often vast collections of animals sorted out of the samples. Also, physiologists often depend on other people's identifications of animals used for experiments. It is reasonable to apply for help to the taxonomists—one cannot cover all fields—and, in Europe, at least, the estuarine fauna has been the object of so many comprehensive investigations during the last 80 years or so that one feels justified in assuming that at least the predominant benthic animals are well defined as species.

I have been working mainly with the ecology of the Danish brackish-water fauna of quite shallow water. It has been my experience that, even in northern Europe, which is supposedly the most thoroughly investigated region of the world, one has to be extremely careful when identifying collections, because the assumption that abundant animals are well defined as species is not always true.

In order to convince skeptics that this is not mere talk, I can mention some examples, partly from my own experience and partly from recent literature, restricting myself to abundant and well-known animals.

RECENT REVISIONS IN THE MOLLUSCA

The common European cockle, *Cardium edule*, is a wide-spread, shallow-water species along all European coasts, ranging from the Black Sea and the Mediterranean to northern Europe. In Danish waters about 200 specimens per square meter are often found. A few years ago I performed some growth experiments, marking cockles in various parts of Danish estuaries and placing them in open wire baskets dug down in shallow water. To prevent the cockles from escaping, the edges of the baskets were 10 cm above the sea floor. I intended to demonstrate the different growth conditions, but did not succeed for a peculiar reason. A month later all the cockles had escaped from the inner baskets placed at low salinities. Only very few escaped from baskets placed near the entrance of the estuary where the salinity was approximately 24 ‰. In control experiments, cockles which had been dug up in the inner parts of the estuary and

placed in baskets near the entrance, had all disappeared. As I saw no reason why only cockles from low salinities should be able to crawl out of wire baskets, we made some additional experiments in the laboratory. We now found that cockles from mesohaline habitats escaped using byssus threads while cockles from polyhaline habitats have no byssus gland. My assistant, Höpner Petersen, tackled the problem and finally demonstrated that *Cardium edule* is not one but two closely related species (Petersen, 1958) (Fig. 1).

Many papers have been written about the growth, oxygen consumption, filtering abilities, feeding, etc. of the cockle. Much of the literature on *C. edule* has now lost a great deal of its value as it is often impossible to tell exactly which of the two species is treated. All that can be said with certainty is that cockles from polyhaline marine habitats are identical with *C. edule*, and that the Baltic seems to hold only one species, *C. lamarcki*. But all transitional areas, as found in the Danish Belt Sea and the great delta districts of Holland or the estuaries of England, are likely to hold both species.

The hydrobines are another group of animals extremely abundant in estuaries and lagoons. Looking through a collection of hydrobines, one is struck immediately by the amazing variation of shell form. A review of literature reveals that only *Hydrobia ulvae* and *H. ventrosa* are recognized in the brackish waters of northern Europe (Krull, 1935; Ankel, 1962). In spite of the copious literature on these two species, I recently experienced great difficulty identifying a certain part of my *Hydrobia* collections. Finally, I made an outline drawing of each shell, crushed it, investigated the radula and genitalia, and found that all my material fell into three distinct groups, two comprising the "old" species *H. ulvae* and *H. ventrosa*, and a third species apparently undescribed (Fig. 2). I have named it *H. neglecta* (Muus, 1963)—and neglected it must have been by several dozens of students, as the species is hardly endemic to Denmark, where I have found it at numerous places in numbers up to 3,000 per square meter. It has for years, no doubt, been confused with both *H. ulvae* and *H. ventrosa*, and it has contributed considerably to the enormous shell variation postulated for these snails. All three species have different, though overlapping, areas of distribution and behavior.

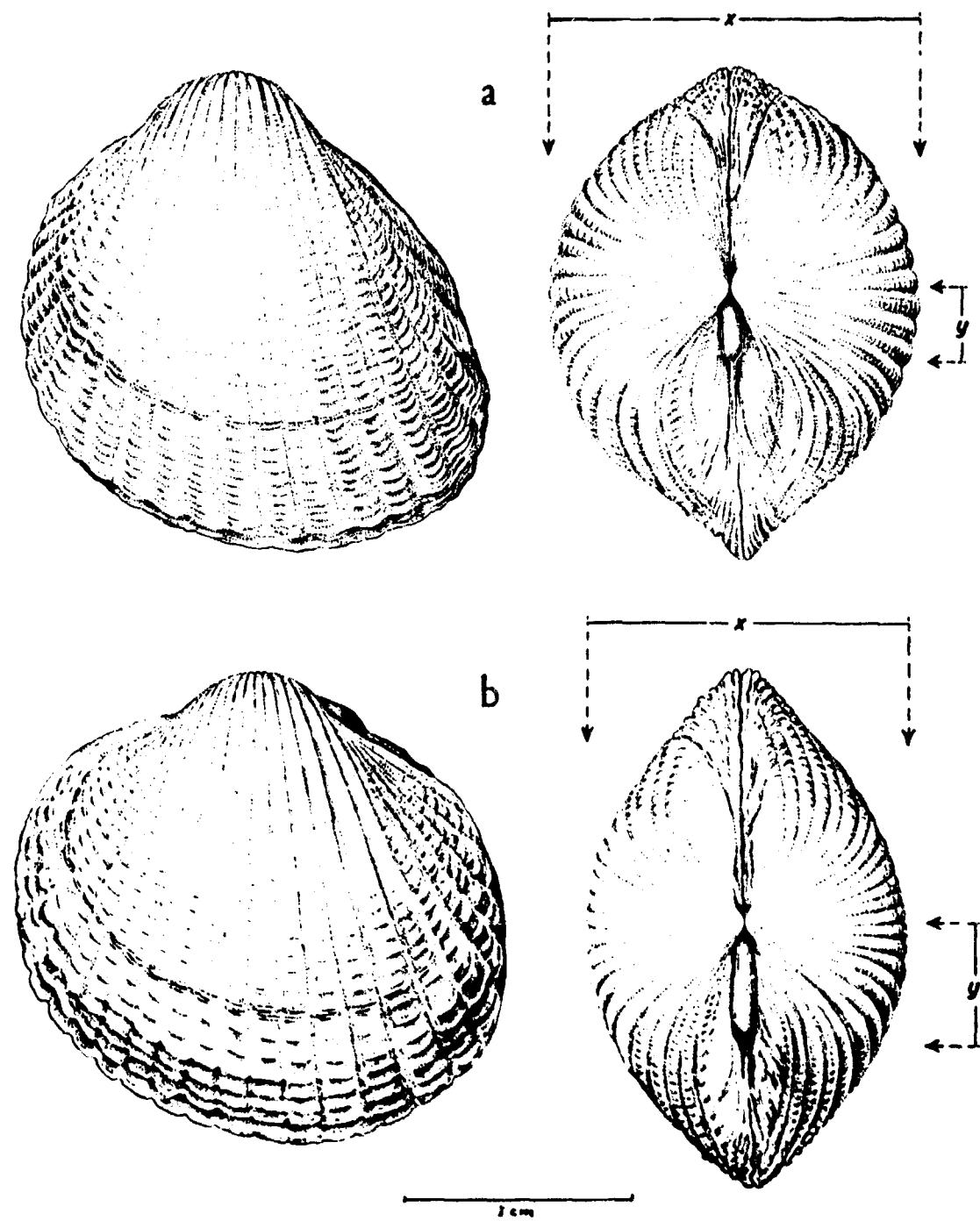


Fig. 1. a. *Cardium lamarki* Reeve. b. *C. edule* L. (From Petersen, 1958).

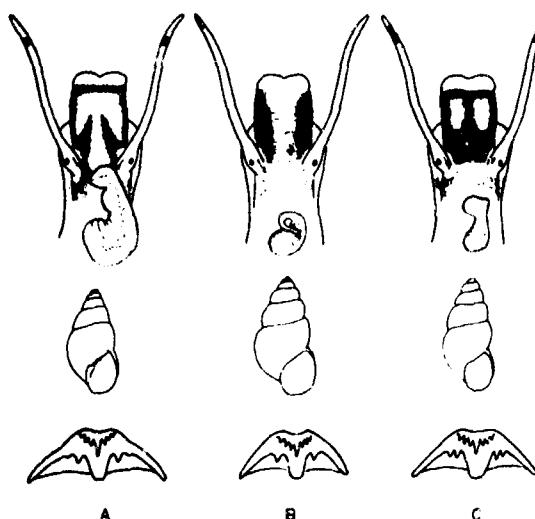


Fig. 2. Head, penis, shell, and central tooth of radula in:
 A—*Hydrobia ulvae* (Pennant).
 B—*H. ventrosa* (Montagu).
 C—*H. neglecta* Muus.

Warwick, in Edinburgh (1952), discovered that the famous hydrobiid snail *Potamopyrgus jenkinsi* also occurs in three different strains which probably are true species. The amazing variability of this "species" in fresh and brackish waters thus seems to be the sum of shell variation in three different, though very closely related, parthenogenetic species.

I have mentioned only three of many different examples among the molluscs where an apparently great shell variation turns out to be imperfect perception of the species. All the animals I have mentioned have played a title role in many doctoral theses and numerous other papers dealing with ecological or physiological problems, while the authors were unaware that the animals had been properly identified. This can be an annoying fact in studies of estuarine zoogeography. Zenkevitch (1947) mentions a *Cardium edule-Hydrobia ventrosa* community in the Sea of Azov, but the identity of both species is now open to doubt. Ecologists, in particular, should appreciate that this is not a mere dispute regarding names, but a question of recognizing species occupying different positions in an ecosystem, or their respective position in different ecosystems.

DOES *NEREIS DIVERSICOLOR* FORM LOCAL RACES?

On the subspecies level also, much taxonomic and zoogeographical work should be done as a prerequisite to experimental work.

A prominent member of the polychaete group may be taken as an example because it has been the object of many physiological investigations. The dominating polychaete in Danish brackish-water habitats is *Nereis diversicolor*, often occurring up to about 50 g/m². Though this species is euryhaline, it is, peculiarly, re-

stricted exclusively to mesohaline localities in the inner parts of bays and estuaries at salinities of 4–21‰. In the polyhaline zone it is replaced by its close relatives, *N. virens* and *N. succinea*.

The family Nereidae forms a very uniform group. Among the important characteristics used for identification of the species is the denticulation of the proboscis. On the outstretched, turned proboscis are seen some zones armed with chitinous denticles and paragnaths, the number and pattern of which have taxonomic value (Fig. 3). During the identification of my large quantitative collections from various Danish estuaries, I noticed that the paragnath number of the different zones varies a good deal, but that this variation remains within different ranges at different localities.

A look at histograms (Fig. 4) showing numerical variation of paragnaths of animals from different localities shows the peaks being displaced in relation to each other; the bases, however, overlap. One gets the clear understanding that the paragnath pattern in *N. diversicolor* is not stable, and that this polychaete forms local tribes or races. On account of the far more stable paragnath pattern known from other nereids, the variation found in *Nereis diversicolor* is such that a traditional taxonomist would probably not hesitate to rank the two extremes as two species.

The osmoregulation of *N. diversicolor* has been the object of several interesting investigations, including Smith's research (1956) on the chloride regulation of animals from English, Danish, and Finnish localities. He did not succeed, however, in demonstrating physiological races. The differences he found were small, and Smith explained that the better ability to regulate chloride found in specimens from marine-dominated (English) localities might be due to their high mortality during adaptation to low salinities; probably the best regulating specimens survived the experimental conditions.

The high mortality among specimens from marine-dominated habitats is unclear, because *N. diversicolor* from Danish mesohaline localities is considered to be an extremely hardy animal, not only against sudden alterations of salinity, but also against heavy pollution and great fluctuations of temperature and oxygen

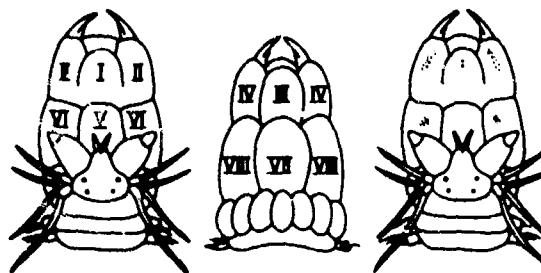


Fig. 3. Proboscis of *Nereis*. The left figures show the zonation used by taxonomists. The right figure demonstrates the position of paragnaths on the upper side of the proboscis of *N. diversicolor*.

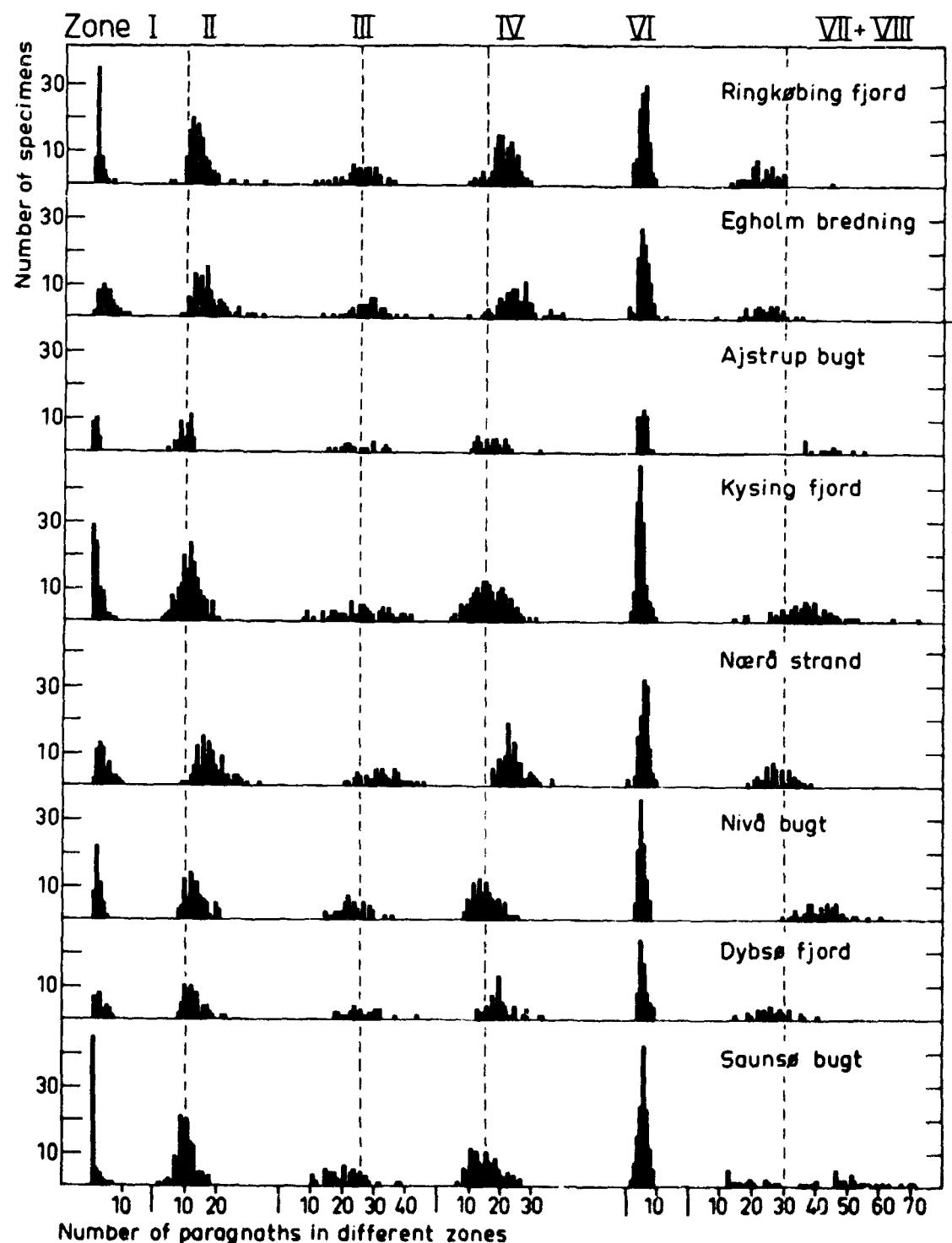


Fig. 4. Numerical variation of paragnaths in *Nereis diversicolor* Müller in eight Danish localities.

tension. Smith pointed out that though a comparative study of chloride regulation after slow adaptation does not point towards the existence of physiological races, other types of responses to environmental factors still remain to be considered. These may reveal that the isolated populations actually develop genetically founded physiological adaptations.

My own investigations have shown clearly that *Nereis* is found in isolated races or entities. The theoretical possibility exists that the variation of the number of paragnaths is due to environmental influence, but it is not likely, because a clear correlation has not been found between the number of paragnaths and salinity, though there is a cline towards a decreasing number of paragnaths going from the North Sea to Finnish waters. Rearing and interbreeding experiments might clarify the problem.

The pattern of paragnaths is used in taxonomy, however, because their position and number have been found to be genetically rather stable. In the case of *Nereis diversicolor*, the local paragnath patterns must be taken as the proof of the existence of local isolated populations slowly stabilizing their pattern of paragnaths.

The mature *N. diversicolor* does not swarm and has no epitokous phase, the larvae are non-pelagic, and the species does not easily spread over long distances. As already mentioned, the species is euryhaline. It is also eurytopic, found in all kinds of bottoms except in black, stinking mud. It is omnivorous. When food is scarce, it swallows sand like the *Arenicola* species. It devours all sorts of meiobenthic animals, young *Corophium*, other amphipods, and worms, and is a passionate carrion-feeder. Thus, there is no obvious reason found in its life habits why it should not thrive well in polyhaline and euhaline habitats.

The limited occurrence of *N. diversicolor* is, no doubt, due to competition with the much greater and stronger *N. virens* which takes up exactly the same ecological niche in the polyhaline and euhaline habitats. I have planned, but have not yet performed, aquaculture experiments which may throw light upon the nature of this competition.

Thus, *N. diversicolor* lives in isolated populations, inwardly barred off by fresh water and coasts, outwardly by its competition with a more potent relative.

No doubt, this type of selective forces plays a role in many other euryvalent species. Ecological omnivulence as a passive means of defense in competition with close, but more stenovalent, relatives is known from *Gammarus duebeni*. This species is euryhaline, eurythermal, omnivorous, and endures low oxygen tensions to such a degree that it is able to occupy habitats where it is left alone by such strong competitors as *G. zaddachi* and *G. salinus*. Kinne (1953, 1954) has shown that an important part of the competition in this case is a complete sterile mating, the female *G. duebeni* being unable to mate with the stronger *G. zaddachi* and *G. salinus* males.

Although the very active, abundant, and hardy

gammarids have better chances of dispersal over long distances than have many other amphipods, they seem to form local varieties characterized by quantitative differences in setation. *Gammarus duebeni* has developed a freshwater race in Ireland (Hynes, 1954).

The genus *Corophium* resembles the genus *Gammarus* in that both genera comprise species in brackish as well as fresh waters. The rather uniform appearance of the *Corophium* species and their ability to adjust themselves to a multitude of different habitats in brackish or fresh waters suggest that this group is in a state of development, and that it might be worthwhile to look out for races when dealing with one of the species. Already Chevais (1937) has shown through biometric studies that *Corophium volutator* forms local, isolated races along the French coast.

CONCLUSIONS

Though much fundamental experimental work may be carried out successfully without bothering too much about the exact identity of the species involved, it is advisable to make a reliable identification, and in the cases of comparative physiology or ecology, it is imperative. Since very few professional morphologists are engaged with the commonplace animals of brackish waters, taxonomic revisions are left to the ecologists. Through their field work they are in a better position than most taxonomists to reach a balanced perception of species and races. Small morphological deviations of preserved specimens may easily be thought of as being the effect of individual variation, but when seen in relation to ecological peculiarities, they may be clearly recognized as group variations, demanding a closer study.

The examples mentioned seem to indicate that many cases of sibling species may be found disguised under familiar names, and that we need information concerning the subspecific variation in euryhaline animals.

The study of speciation in recent decades has profited much from entomology and ornithology, but apart from the racial investigations of commercially important fish, we do not have a similar fund of knowledge about speciation in marine animals.

An understanding of the selective forces which are supposed to act in speciation is obtained by combining a knowledge of morphology, variation, and distribution of the species with a knowledge of biological and physical environmental factors. The morphology and variation of brackish-water animals are not too well known, and, consequently, the distribution is also incompletely known. Among the biological environmental factors, competition plays an important part and competition is probably why euryhaline species are restricted to habitats where stenovalent species have poor chances. Our concept of competition, however, is usually based on imagination rather than actual observations.

Many papers consider but a single physical environmental factor, for instance, the composition of the sub-

stratum. At the same time several physical factors exist which do not enter our description of the animals' surroundings in a satisfactory way, for instance, the concept of exposure. Generally, the ecologists seem satisfied by referring to a habitat as "exposed" or "sheltered", lotic or lentic. No doubt animals make more elaborate distinctions between environments, and water movements greatly influence the local distribution, but we do not know how. We need, however, a means of measuring exposure, turbulent water movements, and also a unit of measurement.

We are still a long way from a reasonable analysis of the occurrence and variation of euryhaline animals, though not so long as when Darwin wrote (1859): "In determining whether a form should be ranked as a species or a variety, the opinion of the naturalists having sound judgment and wide experience seems the only guide to follow."

LITERATURE CITED

- ANKEL, F., 1962. *Hydrobia ulvae* Pernant und *Hydrobia ventrosa* Montagu als Wirte larvaler Trematoden. *Uid. Medd. Dansk. Naturh. Foren.*, 124:1-100.
- CHEVAIS, S., 1937. Croissance et races locales de *Ceropagium volutator*. *Trav. Stat. Biol. Roscoff. Fasc.*, 15:99-133.
- HEDGPETH, J. W., 1957. Concepts of marine ecology. *Geol. Soc. Am. Mem.*, 67(1):29-52.
- HNES, H. B. W., 1954. The ecology of *Gammarus duebeni* Lilljeborg and its occurrence in fresh water in western Britain. *J. Animal Ecology*, 23(1):38-84.
- KINNE, O., 1953. Zur Biologie und Physiologie von *Gammarus duebeni* Lillj. VI. Produktionsbiologische Studie. *Veroeffentl. Inst. Meeresforsch. Bremerhaven*, 2:125-145.
- KINNE, O., 1954. Interspezifische Sterilpaarung als konkurrenzökologischer Faktor bei Gamariden (Crustacea, Peracarida). *Naturwissenschaften*, 41:434.
- KRULL, H., 1935. Anatomische Untersuchungen an einheimischen Prosobranchiern und Beiträge zur Phylogenie der Gastropoden. *Zool. Jahrb. Abt. Anat.*, 60: 399-464.
- MUUS, B. J., 1963. Some Danish Hydrobiidae with the description of a new species, *Hydrobia neglecta*. *Proc. Malacol. Soc.*, 35:131-138.
- PETERSEN, G. H., 1958. Notes on the growth and biology of the different *Cardium* species in Danish brackish water areas. *Medd. Danmarks Fiskeri- og Havunders. N.S.*, 2, No. 22.
- SMITH, R. I., 1956. Comparison of the level of chloride regulation by *Nereis diversicolor* in different parts of its geographical range. *Biol. Bull.*, 109:453-474.
- WARWICK, T., 1952. Strains in the mollusc *Patomopygus jenkinsi* (Smith). *Nature*, 169:551.
- ZENKEVITCH, L., 1947. Fauna and biological productivity of the seas. *Seas of U.S.S.R.*, 2. (In Russian) Moscow, U.S.S.R.

Evolutionary and Ecological Implications of the Zoogeography, Physiology, and Morphology of *Cyathura* (Isopoda)

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Twelve or more species of *Cyathura* are described herein. They range from 3 to 27 mm in length and burrow into the substratum which may be exposed at low tide, or they may be under water from a few centimeters to as much as 60 meters. The salinity of the water in which they live varies. Three species live in fresh water; several species are found offshore on the ocean bottom; but the most widespread species are estuarine, living chiefly in oligohaline and mixohaline zones and are capable of existing under both limnetic and marine conditions. Salinity, therefore, does not seem to be a limiting factor for the geographic distribution of the genus nor of the estuarine species. Rather, because of their mode of life, a stable substratum is the critical factor for the establishment of a population of *Cyathura*. As far as is known, their whole life cycle is completed in the substratum since there is no free-swimming larval stage. The tiny juveniles are shed directly into the substratum and are truly interstitial animals. Adults are able to swim, but are rarely observed doing so. Populations tend to maintain a constant density, gradually spreading into adjacent areas.

The genus *Cyathura* has a worldwide distribution in spite of limited methods of dispersal. The species with the widest distributions are estuarine forms: *C. carinata* from Europe, Africa, China, and Asiatic Russia; *C. estuaria* (=*C. estuarium*) which may be synonymous with *carinata* from South Africa; and *C. polita* from eastern and southern coastal United States. An analysis of the zoogeography, physiological tolerances, morphological variations, and habitat niches of the estuarine species of *Cyathura* should yield valuable information on the past and present evolution of species of *Cyathura*, and the peculiar conditions which obtain in an estuarine habitat. Eurykous estuarine species, capable of surviving in a characteristically fluctuating environment, are traditionally conservative from an evolutionary standpoint. How, then, have cyathurans spread around the world and differentiated into so many species?

ZOOGEOGRAPHY

No one knows for certain the exact number of valid species of *Cyathura*, a genus of the subtribe Anthuroidea in the order Isopoda. The anthurid genera have not always been adequately described—as K. H. Barnard said in his revision of the Family in 1925, "In

the old days species were dumped into "*Anthura*" or "*Paranthura*", and consequently both genera became jumbles of widely differing forms." The recently established species, *C. polita* (Miller and Burbanck, 1961), was at one time or another designated as three different species of *Anthura*. The following discussion of the distribution of species of *Cyathura* deals with species generally recognized at this time, but the author realizes that new species may be discovered, further study may result in redefining the present species, and more intensive investigation may show the need for a critical study of the generic concepts within the Anthuroidea.

The genotype species, *C. carinata*, as delineated by Miller and Burbanck (1961) has been reported from type locality in Copenhagen Harbor, Denmark (Krøyer, 1847; Smidt, 1944); northward along the Swedish coast (Löwegren, 1937; Lundström, 1937) of the Baltic and eastward to the Bay of Danzig (Dahl, 1944; Segerstråle, 1957); the Netherlands (Burbanck and Burbanck, 1964); both the English (Spooner and Moore, 1940) and French (Cléret, 1960) sides of the English Channel; the western coast of France (Salvat, 1962); several locations along the shores of the Mediterranean Sea (Monod, 1925; Stammer, 1932; Larwood, 1940; Amar, 1951; Burbanck and Burbanck, 1964); China (Tattersall, 1922); and Asiatic Russia (Gurjanova, 1936). Animals reported as *C. carinata* from South Africa (Barnard, 1925; Day et al., 1952; Scott et al., 1952) may be a distinct species, *C. estuaria* (Miller and Burbanck, 1961). The cyathurans from eastern North America which formerly were included in the species *C. carinata* have now been put into the reestablished species, *C. polita* (Miller and Burbanck, 1961). Since these three estuarine species, *C. carinata*, *C. estuaria*, and *C. polita*, are similar in size, physical and chemical habitat characteristics, and general morphology, but almost circumglobal in distribution, it is suggested that they be considered a species complex, the *C. carinata* complex.

Other than the members of the *C. carinata* complex, the widest ranging species of *Cyathura* is the 3.5–8 mm-long *C. indica* (including *C. pusilla* Stebbing, according to Miller and Burbanck, 1961) which has been reported from British East Africa, southwest India, Ceylon, Singapore, and Siam, from depths ranging from 1 to 14 fathoms (Barnard, 1925). Almost indistinguishable from *C. indica* morphologically, and from a similar depth (4 fathoms), is *C.*

crucis from the Virgin Islands, West Indies (Barnard, 1925). Other marine species with very limited distribution are eyeless *C. siamensis* from Siam (Barnard, 1925), *C. munda* from 10–30 fathoms off the southern coast of California (Menzies and Barnard, 1959), a new species from near the mouth of the Altamaha River, Georgia (Frankenberg, 1965), and an unnamed species found at 3–8 fathoms two miles off the coast of Accra, Ghana (Buchanan, 1958). In addition to estuarine and marine species, there are two species which live in freshwater springs, *C. curassavica* from the island of Curaçao, just north of Venezuela (Stork, 1940), and *C. milloti* from Réunion Island east of Madagascar (Delamare Deboutteville, 1960), and a new species, *C. specus*, reported from a freshwater lake in a cave in eastern Cuba (Bowman, 1965).

Three anthurids from western and northwestern Africa of uncertain taxonomic status are *C. cremophila*, of which only a few imperfect specimens are known, and *C. robertiana* and *C. liouvillei*, the last two probably belonging to the genus *Anthelura* (Monod, 1925; Miller and Burbank, 1961). Also assigned to the genus *Anthelura* by Barnard (1925) and Menzies (1962) is the abyssal form from Davis Strait, Canada, *Cyathura truncata*.

The widespread distribution of the genus *Cyathura* and of the *carinata* complex may be significant when considering the evolution of species. It is generally conceded that an organism having a worldwide distribution is ancient, or a descendant of a widely dispersed ancestor (Willis, 1949). It is possible that the *C. carinata* complex represents an "old species". The less widely distributed species may have arisen in either of two ways, by being relict species isolated long ago from the main population of *Cyathura* but lacking the genetic makeup to colonize adjacent areas, or by speciation having taken place in modern times and not yet having had time to occupy a large area.

Several facts of physical and historical geology are appropriate to consider at this point. According to Snodgrass (1938), Crustacea are at least Cambrian in origin "being contemporaneous with the oldest known trilobites". By the Permian period, therefore, it is possible that animals very similar to modern cyathurans could have evolved. The modern distribution of *Cyathura* shows a marked correlation with areas under the influence of the Tethys Sea which played an important role from the Permian period to the middle of the Cenozoic era. Rudistid pelecypods from the late Cretaceous show a horizontal distribution of fossils from the Gulf of Mexico across western Europe and the shores of the Mediterranean Sea to northern India, and finally to the East Indies (Kummel, 1961). Geological evidence supports the hypothesis that transgressions of the Tethys Sea during the Triassic, Jurassic, and Cretaceous periods could have provided pathways for the distribution of a cyathuran or cyathuran progenitor from the region of the present Mediterranean Sea to the Gulf of Mexico, to the Baltic Sea and Denmark and England,

to the south along the eastern coast of Africa, and to the east where the Tethys Sea extended to the present Himalayan Mountain area and interconnected with waters to the north and south of modern China (Moore, 1933; Kummel, 1961). Indications are that during this time warm or temperate climates prevailed in the area covered by the Tethys Sea. No fossil cyathurans are known, but this is not surprising since they disintegrate quickly. Fossils of *Limulus*, which is found with *Cyathura* in some modern habitats, and of the crustacean, *Cyclosphaeroma*, whose modern counterparts are found with *Cyathura*, are known from the Jurassic period (Easton, 1960); so it is not unreasonable to suppose that cyathurans were evolving during the Mesozoic era.

To return to the idea of a *C. carinata* complex, it is possible that a *C. carinata*-like cyathuran with habitat requirements similar to those of modern *C. carinata* evolved in Permian or early Triassic times and populated parts of the Tethys Sea. That segment of the population which reached American shores and the Gulf of Mexico differentiated into *C. polita*. Those that migrated down the east coast of Africa to South Africa became *C. estuaria*. Others may have migrated from the eastern limits of the Tethys Sea north of the South China massif and now are found on the coast of China and at the mouth of the Amur River in Asiatic Russia. A part of the *carinata* complex may have penetrated southward from the eastern limits of the Tethys Sea and differentiated into *C. indica* and *C. siamensis*.

The above concept of a *C. carinata* complex assumes that the animals were benthic forms in relatively shallow waters. Thus, as the waters rose and fell on the wide coastal plain of eastern North America in Cenozoic times, the *C. polita* element of the complex could have spread northward and southward from the Gulf of Mexico (Ray *et al.*, 1963). *C. crucis* and *C. curassavica*, from shallow sea water and a freshwater spring, respectively, in the Caribbean area, may represent populations of the euryhaline *C. carinata* complex which became geographically isolated during the middle or late Cenozoic era and developed morphological characters distinct enough to be given species rank today. Although there is no geological evidence of a land bridge across the Caribbean Sea from Florida to South America, it is possible that small land masses were alternately emergent or submerged and allowed some migration of shallow-water and terrestrial animals. There are modern estuarine crustaceans in Florida which are closely related to South American species, and fossil bones of a flightless bird, armadillo-related animals, and sloths with South American affinities that have been found in streams and springs in Florida (Brodkorb, 1963; Sparks, 1963).

Estuarine forms are traditionally conservative (Hedgpeth, 1957), and the *C. carinata* complex animals are typically found in estuaries, but there is some evidence of migration and evolution of species in modern times. A warming trend in northern lands

may account for the movement of *C. polita* up the eastern coast of the United States and of *C. carinata* into Sweden (Burbanck, 1959). Not only low temperatures, but the molar effects of ice moving downstream in the spring and its rising and falling with the tides could make northern habitats unsuitable for cyathurans. The finding of a new species, *C. burbancki*, eight and one-half miles east of a population of *C. polita* on Sapelo Island near the mouth of the Altamaha River, Georgia (Frankenberg, 1965), raises the possibility of a marine species derived from the estuarine *C. polita*. The distribution of cyathuran populations in the St. Johns River system in Florida indicates how freshwater species now found in springs may have arisen from estuarine forms in the past and may continue to do so in the future. As long as there is the possibility of interbreeding between populations which occur the length of the St. Johns River from its brackish mouth to the springs 120 miles upstream, a single species will be maintained. If the populations adjacent to those in the springs, however, were destroyed by predation, physical changes in the environment, or disturbance by man, the animals living in fresh (or almost fresh) water would be isolated from other cyathuran populations and in time might differentiate into a new species.

Although *C. polita* is present in every state along the Atlantic coast of the United States, it has a disjunct distribution rather than a continuous one since it is an estuarine species. Thus the destruction of all the cyathurans in an estuary would widen the gap between neighboring populations. Hurricanes destroyed populations of *C. polita* in the Ashepoo River, South Carolina (Burbanck, 1961a), and at Naushon Island, one of the Elizabeth Islands between Buzzards Bay and Vineyard Sound, Massachusetts (Burbanck, 1962a). Man destroys populations by building dams which cut off the flow of fresh water, by dredging estuaries to build boat harbors, by filling lowlands, and by rendering environments anaerobic by the introduction of industrial and fecal contamination (Burbanck, 1962a).

On the positive side, man may aid in the distribution of cyathurans and may create habitats for them. *C. polita* has been successfully transplanted from the warmer south to the colder north side of Cape Cod, Massachusetts (Burbanck, 1962a), a distance of 10-15 miles overland but much farther by coastal waters. During the days of sailing vessels which used rock ballast, cyathurans may inadvertently have been carried great distances, and currently they have been included in shipments of the aquatic plant, *Vallisneria*. In the United States, the depositing of rocks as railroad ballast or to support highway bridges, and the use of sand, gravel, and shell to build launching ramps for small boats have created stable substrata where cyathurans have been found (Burbanck, 1961a; Miller and Burbanck, 1961). In the Netherlands, *C. carinata* is found in estuaries under rocks (Burbanck, 1962b) and along the sandy-mud margins of newly made land.

Altogether, the present zoogeography of the *C. carinata* complex offers various opportunities for continued evolution of *Cyathura*. The many estuarine populations of *C. polita* on Cape Cod (Burbanck, 1962a) are not widely separated from each other, and there may be occasional interchange between populations. According to Dobzhansky (1937), a species in such a situation "is in a most advantageous position for an evolutionary change". Potentially *C. polita* on Cape Cod could differentiate into distinguishable, geographically separated races, or there could be a Cape Cod variant of the species distinct from other populations of the *C. carinata* complex.

PHYSIOLOGY

Since cyathurans are so widely distributed both temporally and geographically, it is to be expected that within the *C. carinata* complex there would be physiological differences, perhaps even physiological races. One of the most striking characteristics which *C. carinata* and *C. polita* have in common, however, is that they are both eurykous. These estuarine cyathurans living in creeks, rivers, bays, and marshes are subjected to stresses of salinity, pH, and temperature which change not only with the tides but also with seasons, latitude, and local storm conditions.

Among all of the environmental characteristics of estuaries, salinity has received the greatest attention. This is not the place to review the voluminous literature pertaining to the reactions of estuarine animals to salinity, but it is appropriate to cite recent works on the osmoregulatory capacities of *C. polita* which are pertinent to our present discussion. As Hedgpeth (1957) suggests, euryhalinity "may be a physiological characteristic not of a species or a genus alone, but of a phyletic stock", and thus be of evolutionary significance.

At the northern end of their range, *C. polita* live in habitats where the water, according to the Venice System (Am. Soc. Limnol. Oceanog., 1958), is (mixo-) polyhaline. About 1,500 miles to the south in Florida, the same species lives far up the St. Johns River in (mixo-) oligohaline springs flowing into Lake George and in a limnetic habitat (0.2%) in the runoff of Weeki Wachee Spring on the Gulf side of the state (Burbanck, unpublished). In contrast to these, *C. polita* 250 miles farther south near Flamingo at the southern tip of Florida live, at certain times of the year, under hyperhaline conditions (up to 70%) (Segal and Burbanck, 1963) which are caused by high radiation and rapid evaporation. Under all of these conditions of salinity, reproducing populations of *C. polita* occur, as evidenced by females bearing embryos or juveniles in their marsupia. Since the survival of young is usually considered the critical stage in the life history of an organism, thorough tests should be made of the salinity tolerance of juvenile forms of *Cyathura*. Nikitin and Turpaeva (1959) have reported a narrow range of tolerance for larval stages of Black Sea benthic invertebrates and state

that "the true euryhalinity of species is determined by the critical stage of their development which shows the least ecological valency as regards salinity". Juvenile forms of *C. polita* shed at a salinity of 32‰ in a laboratory aquarium in Massachusetts, lived and grew at this salinity in finger-bowl cultures until their food was exhausted. More laboratory studies of survival of juveniles need to be made, but present evidence suggests that *C. polita* is a truly euryhaline species.

Latitudinal studies of osmoregulation of *C. polita* have revealed that the salinity characteristics of the ecosystem may affect the osmoregulatory ability of geographically separated populations, however. Animals from a tidal creek at Marshfield, Massachusetts, and from a beach at Sapelo Island, Georgia, had essentially the same osmoregulatory abilities; at lower salinities the animals were hyperosmotic and above 87 percent sea water they were isoosmotic, regardless of temperature changes (Frankenberg and Burbanck, 1963). The results were different when a comparison was made of animals from Pocasset, Massachusetts, and Silver Glen Springs, Florida (Segal and Burbanck, 1963), two places about the same distance apart as Marshfield and Sapelo Island. The estuarine Pocasset animals were hyperosmotic over a salinity range from distilled water to 70 percent sea water, isoosmotic at about 70 percent, and regulated to remain approximately isoosmotic up to 155 percent. Differences in temperature did not affect their osmoregulatory ability. Silver Glen Springs animals were not able to osmoregulate over as wide a salinity range; experimental animals (at 22°C.) died at salinities less than those of their natural habitat (3.5 percent) but were isoosmotic at high concentrations. Their osmoregulatory ability in both high and low salinities was impaired at temperatures of 5° and 22°C.

The results of these experiments cannot be explained on the basis of latitudinal difference alone, since the two southern populations did not react in the same way. The physiological difference of the Silver Glen Springs animals may be explained by the fact that their natural environmental conditions are more constant than are those of the other populations and they may, therefore, have lost some ability to adjust to changes in temperature and salinity. Tidal salt water does not penetrate as far up the St. Johns River as the runoff of Silver Glen Springs, but the water is alkaline, and the combination of mild climate and constant-temperature spring water (21°C.) keeps temperature variation at a minimum. The two northern populations have year-round temperature variations of from 2° to 23°C. and with each tidal change the salinity varies from 0.5‰ to 17‰. The temperature range of the water at the Sapelo Island habitat is at least 18°C., and although the salinity remains fairly constant during tidal cycles, there are seasonal variations related to increased or decreased discharge of fresh water by the Altamaha River. Thus there

may be phenotypic differences in the cyathuran populations in Florida spring waters that could result in physiological races.

Temperature has been shown to play a part in the ability of cyathurans to osmoregulate (Segal and Burbanck, 1963), but comparative tolerance tests of northern and southern cyathurans subjected to extreme temperatures have not been made. *C. polita* collected in Massachusetts exhibited a wide range of tolerance when subjected to temperature changes in the laboratory. When exposed for 12 hours (a tidal cycle) to the extremes of -8°C. and 45°C., half of the animals died, but those which survived appeared to recover completely. On the basis of the results of the osmoregulation studies of *Cyathura*, it might be expected that cyathurans from the more constant temperature conditions of Florida spring waters would be less tolerant of temperature extremes than those from Massachusetts.

To further complete the picture of a eurykous animal, cyathurans appear to be omnivorous in their feeding habits. Diatoms and detritus have been found in their alimentary tracts, but in the laboratory we have seen them attack and eat *Gammarus tigrinus*, injured and young cyathurans, and dead *Fundulus* (Burbanck, 1961b). Whether or not cannibalism may occur in the field is debatable because cyathurans do not normally leave their burrows in pursuit of prey. Both *C. estuaria* (Barnard, 1925) and *C. polita* do possess a setigerous, chitinous stomach which might serve to strain out foreign or indigestible substances if they ingested larger particles of food than the finely divided detritus usually consumed. Whether or not cyathurans are carnivorous, it is probable that they are both herbivorous and carnivorous detritus eaters (Blegvad, 1914). *C. polita* have been kept in the laboratory in plastic boxes containing a mixture of sand and mud about 2 cm in depth shallowly covered with brackish water for from 3-8 months. As unfed animals moved through the flocculent surface material composed of detritus and some diatoms, their empty alimentary tracts became filled, as could readily be seen under a microscope with transmitted light. The ability to use such a non-specific food as finely divided detritus enables cyathurans to live under a great variety of conditions and, therefore, raciation with respect to food requirements is not probable.

Although *C. polita* can tolerate a wide range of environmental factors, there are certain ones which must obtain for the species to maintain vigorous, reproducing populations and which appear to limit the extension of the present range of the species or account for its absence from certain habitats. These limiting factors fall into the same general categories that Savilov (1959) listed as affecting the bottom fauna groupings of invertebrates of the North Okhotsk Sea:

- 1—Water movement as a factor in the food supply of sessile and semi-sessile animals;
- 2—the quantity of plankton and suspended

detritus in the water itself, as the main food of marine bottom animals; 3—the rate of deposition accumulation and the nature of the distribution of the deposited detritus on the bottom; 4—the mechanical composition of the ground as a substance for the support of animals; and 5—the degree of vertical mixing and of aeration of the bottom water."

In the truly estuarine habitats, there is always sufficient water movement to distribute detritus over the "semi-sessile" tubicolous cyathurans, but the quantity of the food may be insufficient to support both cyathurans and associated animals. There are usually small numbers of animals of the species which live with *C. polita* along the coast of the United States, but at both Arcachon, France (Salvat, 1962), and in Maine on the east coast of the United States, populations of *Corophium* appear to replace *Cyathura*, perhaps because of competition for food. If detritus were to be deposited at such a high rate that aeration of the water above cyathurans was reduced, or at such a low rate that the food supply was insufficient, populations might be reduced in size or even eliminated. In general, however, detritus supplies are adequate, but not excessive, throughout the range of the *C. carinata* complex. As has been pointed out already, food is not usually a critical factor in the survival of cyathurans nor in the prevention of the extension of their range.

Savilov's fourth point concerning "the mechanical composition of the ground" in which benthic animals live is a much more important factor than food in relation to cyathuran populations. *C. polita* is found only where there is a stable substratum. Shifting sandy beaches, estuaries where silting conditions are extreme, and shores or stream beds where swift currents scour the bottoms cannot support populations of *C. polita*. The texture of the soil must be suitable; young cyathurans live interstitially and adults may live in the tubes of other animals or make tubes of their own, and the soil particles must be of the proper size for such modes of life (Delamare Deboutteville, 1960). Not only is the structure of the substratum important, but it must always be saturated with water. *C. polita* cannot survive even a little drying. This factor may prevent the colonization of the Texas coast of the Gulf of Mexico and be one of the reasons why there is not an estuarine species of *Cyathura* on the coast of California, because in both places the creeks and rivers either dry up or are intermittent during periods of severe drought. Related to the composition of the substratum is the factor of competition for space. It may be advantageous for cyathurans to be associated with a population of tube-building worms, but disadvantageous to compete with a more closely related form, such as the benthic *Corophium*.

As for the invertebrates of the North Okhotsk Sea, aeration and mixing of the water may be a limiting factor for *Cyathura*, which must have an adequate supply of dissolved oxygen. It was recognized early

(Burbanck, 1959) that *C. polita* occurs only where there is sufficient water movement to insure proper aeration.

In addition to physical environmental factors, there is an important biotic one which may affect evolution in *Cyathura*. Predation may act as a limiting factor in the extension of the range of the species, as an isolating mechanism by destroying part of a continuous population, or as a stimulant for protective adaptation and selection within the species which might become fixed genetically and produce local variants. In Europe, eel, sea scorpion (Larsen, 1936), and plaice are known to eat *Cyathura*. In the United States they are eaten by black duck, brook trout, and flounder in Massachusetts (Burbanck, 1962a), by white perch, striped bass, and spot in Chesapeake Bay (Frank I. Schwartz, personal communication), by large-mouth bass and blue gills in Florida (McLane, 1947), and by many fish in Lake Pontchartrain (Darnell, 1958; Burbanck, 1963). In conversations and correspondence with biologists and fishermen here and abroad, the statements were repeatedly made that numbers of cyathurans fell off in the summer because of predation by fish. This would seriously reduce the size of a population if the height of predation took place during the season when females were carrying young, but such a depletion of numbers has not been observed in the large population at Pocasset, Massachusetts, where I have made year-round studies. Wading birds may also prey on *Cyathura*. We do not have any direct evidence for this except the example of the black duck, but attached to the alimentary tract of *C. polita* from Massachusetts and Sapelo Island have been seen metacercaria which have been tentatively identified as a parasite having as its final host such birds as plovers and gulls (Burbanck, 1962a).

While predation may cause geographic isolation which might eventually lead to raciation and speciation in *Cyathura*, reproductive isolation is another mechanism frequently involved in speciation. There are several significant gaps in our knowledge of reproduction of *Cyathura*, however. Cyathurans have never been reported in a clasping condition nor *in copula*, either by the present author or by other workers with the genus. Observations of *C. polita* have revealed females carrying young in Florida at all seasons of the year; gravid females are found in Massachusetts only in the summer; sperm have been found in the vasa deferentia of male *C. polita* whenever and wherever collected. A series of smear preparations of testes of Massachusetts animals made during March, April, May, and June, however, and spot checks at other times of year and at other places have not given a complete picture of spermatogenesis. Field observations suggest that *C. polita* individuals live at least three years, increasing in size each year, but the time of sexual maturation of animals is not known. Very young animals are externally undifferentiated as to sex, but by the time they reach medium,

two-year-old size, males can be identified by the brush-like flagellum of the first antenna and the appendix masculina on the second pleopod. Yet large animals that superficially appear female have been observed to undergo a metamorphosis and acquire external male characteristics late in life. In Massachusetts, when gravid females appear in June, large dead or dying males appear above ground as if they had come to the surface and died, a phenomenon which suggests the completion of a sexual cycle. The whole picture is not clear, however, and until more positive evidence of copulation and fertilization is found, the possibility exists that cyathurans may produce offspring parthenogenetically.

Regardless of whether or not there is sexual reproduction in *C. polita*, there is evidence of physiological variation in the reproductive cycle correlated with difference in latitude. In the warmer southern climate, young are produced several times during a year. In Massachusetts, young are produced only once a year, while at the most northern station for *C. polita* in the United States, Chewonki Creek, Maine, young may not be produced every year since sometimes there are only large and medium-sized, but no small animals present in mid-November.

MORPHOLOGY

To many biologists today, a comparative study of homologous structures in different species of *Cyathura* or between populations of the *C. carinata* complex is neither as exciting as the study of their zoogeography nor as modern as a study of physiological differences among cyathurans. It must be pointed out, however, that although the former is indeed absorbing, much of the evidence from the geological past is speculative. Also, although modernity is the fetish of our day, our lack of information on the physiology of juvenile cyathurans all but nullifies any conclusions drawn from adults alone. For these reasons, morphological evidence of evolutionary change is still of paramount importance.

Perhaps one of the most careful and painstaking studies of morphological differences among cyathurans is the comparative study by Miller (Miller and Burbanck, 1961) of *C. carinata* and *C. polita*. This study resulted not only in the untangling of a taxonomic enigma, but also confirmed and extended our precise knowledge of the comparative anatomy of cyathurans. In his study, Miller reiterated the importance of the usual diagnostic characters such as size, the first antenna, mouth parts, segmentation of the pleon, the shape of the telson, and cited additional significant structures. He discovered a heretofore unrecognized sex dimorphism in the gnathopods of *C. carinata*, and emphasized for the first time the importance of the appendix masculina on the second pleopod, calling it a "valuable diagnostic character" and of "great systematic importance". We propose to examine here certain morphological characters of *Cyathura* in the light of their evolutionary and eco-

logical significance, namely size, the structure of the abdomen, the appendix masculina, and the dorsal chromatophoral pattern. None of these show such striking correlation of structure and adaptation to habitat, however, as do the generic modifications of the anthurid telson cited by Barnard (1925).

Unless large numbers of cyathuran specimens are available for comparison, size (an obvious characteristic) is not a very useful one for separating races and species. After collecting hundreds of *C. polita* and scores of *C. carinata*, it seems apparent to me that the American species is larger than the European and perhaps the African one; however, there is a great overlap in the size distribution of the two species and only by using statistical comparisons involving measurement of large numbers of cyathurans would any useful information emerge. In such a study it would be necessary to take into consideration such seasonal factors as predation of cyathurans and size classes related to age of animal and time of production of young. There appears to be no correlation of animal size with geographic distribution. The largest *C. polita* in North America are found from Cape Cod northward and from the mouth of the St. Johns River, Florida, southward, but at the edge of the Everglades in the often highly saline waters at the southern tip of Florida, cyathurans are small. Cyathurans from the Hudson River, an intermediate latitude with almost completely fresh water, were unusually small. Other populations, such as those in Chesapeake Bay and those of *C. carinata* in the Baltic and Mediterranean Seas, are not characterized by "large" or "small" animals, but are made up of individuals of all sizes. Size, therefore, has only a limited use in distinguishing ecotypes, races, subspecies, and species of *Cyathura*, at least within the *C. carinata* complex.

Similarly, the degree of fusion of the pleonites of *C. polita*, earlier suggested as a possible specific difference (Burbanck *et al.*, 1956), is not a good diagnostic character to use as a basis for possible raciation. In *C. polita*, the anterior five pleonites are fused dorsally and usually laterally, but there may be only partial lateral fusion. The number and extent of visible, lateral suture lines varies throughout the range of *C. polita* and within any given population; "... variants are just as apt to occur in New England populations as in cyathurans in Florida" (Miller and Burbanck, 1961). Segmentation of the pleon is important, however, in distinguishing anthurid genera (Barnard, 1925; Menzies and Barnard, 1950).

It has long been recognized by entomologists (Ross, 1956) that "structural differences in the copulatory organs furnish excellent taxonomic characters in many groups of insects; for the differentiation of families, genera, or species". Miller (Miller and Burbanck, 1961), in his emphasis upon the importance of the appendix masculina in *Cyathura*, accepts this principle, but he adds an evolutionary significance to it when he says, "The taxonomic importance of in-

herently stable genital structures is generally recognized since they presumably are not subject to environmental modification, and, in some instances, may actively determine by their structural conformations whether or not interbreeding can take place."

Barnard (1925) noted that the complexity or simplicity of the structure of the appendix masculina was characteristic of some cyathuran species, and Miller (Miller and Burbanck, 1961) found an easily recognized and consistent difference between the complex appendices of *C. polita* and *C. carinata* based on the point of origin of the crowned process which arises from the laterally projecting, subterminal lobe of the stylet in each species. This difference is always evident, although there are many minor variations in the structure of the appendix masculina throughout the range of *C. polita* which appear to fall within the normal range of variability and are in no way correlated with habitat.

From the point of view of evolution and speciation, the structure of the appendix masculina is of primary importance, assuming, of course, that it is a copulatory organ. The differences that do exist might prevent interspecific breeding if the ranges of the species overlapped, and if the present minor variations of *C. polita* should prevent intraspecific breeding within populations, the resultant reproductive isolation would encourage raciation. This matter must remain speculative, however, since "presumably these appendices serve as copulatory organs (as in isopods generally), but the details of the process and the function of the constituent parts is unknown" (Miller and Burbanck, 1961).

Superficially, the dorsal chromatophoral patterns of *C. polita*, *C. carinata*, and *C. estuaria* that we have seen resemble each other to a remarkable degree (Burbanck and Burbanck, 1961, 1964; Cléret, 1960). Small variations in the distribution of the chromatophores occur in all populations, but regional differences can be detected particularly between northern and southern populations of *C. polita* (Burbanck and Burbanck, 1961). In populations near the limits of the range of *C. polita* in Maine, Louisiana, and Mississippi, and in populations somewhat isolated geographically from the species as a whole, as in Martha's Vineyard, Massachusetts, and in Alabama, there was a fusion of parts of the pattern that distinguished the animals. Regional differences were evident in specimens of *C. carinata* collected in the Netherlands, two locations in France, and in Italy (Burbanck and Burbanck, 1964). Sufficient numbers of animals from South Africa have not yet been examined to discover the degree of variation in that area. None of these differences are absolute and there is some overlapping of types. Whether or not these differences are genetic and may be correlated with other geographical variations such as the north-south difference in osmoregulatory ability is a question which cannot be answered until breeding experiments or more transplants are performed. The dorsal

patterns of at least four other crustacea are genetically controlled: *Sphaeroma serratum* (Bocquet *et al.*, 1950); *Tisbe reticulata* (Battaglia, 1958; Bocquet, 1951); *Jaera marina* (Bocquet, 1953); and *Cambarus shufeldtii* (Volpe and Penn, 1957).

Following the method published by Clausen and Hiesey (1958) for studying four levels of variability in ecological races of the plant *Potentilla glandulosa* complex, the available information on populations of *C. polita* was similarly analyzed by Burbanck and Burbanck (1961). There seemed to be close agreement between the types of variability for the first three levels as cited by Clausen and Hiesey, and more recent information on *Cyathura* supplements the earlier data. To summarize: (1) There is variation within local populations. This is true for *C. carinata* as well as *C. polita*. (2) There are varying, isolated, local populations within the same climatic range. *C. polita* shows examples of this type of variation in the populations living along the Gulf of Mexico and on Cape Cod. In Europe this is also true for *C. carinata* in populations living in estuaries and étangs along the Mediterranean and is very likely true for populations living on either side of the English channel, in the Tamar River (between Cornwall and Devon), and in Brittany and Normandy. (3) Ecotypes with physiological differences are sometimes accompanied by morphological differences. The latitudinal differences in osmoregulation between Cape Cod and Silver Glen Springs, Florida, animals and the northern and southern patterns of *C. polita* are examples of this. Further study may reveal similar correlations with differences in the appendix masculina and differences in latitudinal-seasonal variations in the reproductive cycle. *C. carinata* also shows differences in pattern that may be of this level of variability. (4) Concerning the establishment of morphologically and physiologically distinct taxonomic sub-species within the *C. carinata* complex, it does not seem to us at all impossible that with more zoogeographical evidence, by the use of serological tests, and with additional work on cyathuran physiology and morphology, the American forms (both brackish-water and marine) and the South African, Chinese, and Russian forms may all be recognized eventually as subspecies of the "old" species, *C. carinata* (Kroyer, 1847).

As something of an appendix or postscript, the question might well be asked, "Why has not more been done on the study of cyathuran chromosomes?" Why, indeed? The fact is that they are very difficult to study because of their small size, and there are peculiarities in their meiotic stages that have not, as yet, been fathomed. Because of difficulty in dissecting out female reproductive tissue, meiotic studies were made of spermatogenesis rather than of oogenesis. Tentative chromosome counts can be made, but some stages appear to be missing and a coherent picture has not yet evolved. We have found tissues with apparently haploid, diploid, and tetraploid nuclei. The present working hypothesis is that $n = 12$. When the

chromosome number for a particular population of *C. polita* has been determined and the details of the male and female meiotic stages discovered, we can make an efficient cyto-taxonomic approach to the problems of raciation and evolution in *Cyathura*.

CONCLUSIONS

The picture that we have presented is that of a truly estuarine, benthic animal, an indicator species, which presents unlimited opportunities for further evolutionary development. There are populations of *Cyathura* of every size and in many countries around the world. In small, geographically isolated populations, phenotypic adaptations may lead to genetic differences and more rapid speciation than in large populations (Wright, 1940); but there is the constant danger that small populations may become extinct by a catastrophic event or deleterious inbreeding. In larger populations there is opportunity for gene flow and the maintenance of a vigorous species; from an estuarine habitat, a large cyathuran population may invade adjacent fresh- and saltwater habitats and become physiologically, and eventually morphologically, differentiated into new species.

There are indications that raciation may already be taking place in some populations. Now that it has been proved that cyathurans can be labeled with Zn⁶⁵ (Burbanck *et al.*, 1964), it may be possible to perform transplant experiments to test whether the observed differences are truly genetic or merely non-heritable adaptations to environmental conditions. One transplant experiment was attempted from Florida to an apparently suitable site in Massachusetts where there were no cyathurans, but the population survived only a few weeks (Burbanck, 1962a), apparently due to predation by *Uca pugnax*. With labeled animals, transplants could be made to areas where cyathurans were already established, thus avoiding the hazard of predation by or competition with other genera. Various types of intraspecific crosses would also need to be made before races or subspecies could be postulated within a species of *Cyathura*.

The foregoing propositions are based on the assumption that there is sexual reproduction in *Cyathura*. Cyathurans do have morphologically distinguishable males and females; sperm are produced in the male gonads and are found in the vasa deferentia; there is a seasonal dying of males correlated with the appearance of gravid females. However, males and females have never been seen clasping nor *in copula*; there have been no cytological observations of meiosis during oogenesis nor of fertilization; there are chromosomal irregularities during spermatogenesis. Sexual reproduction occurs in other isopods, but it has been noted that cyathurans are relatively conservative with respect to adaptive speciation. If some or all of the populations were parthenogenetic, this might be one explanation of their conservatism. In a study of brackish-water pereids in California, Smith (1958) has found reproductive differences which can be used

as specific characters and suggests that the hermaphroditic species has been derived from a form with sexual reproduction.

There is at least one genus of Tanaid, *Apscudes*, which is similar to *Cyathura* with respect to geographic distribution, tolerance of a wide range of salinities, and opportunity for further evolutionary development. In connection with a survey of the depths at which *Apscudes* is found, Wolff (1956) lists four fresh- or brackish-water species, 12 littoral, 31 at depths of 10–20,000 m, and six truly abyssal species. The genus is cosmopolitan with more than half of the species being reported from the Atlantic Ocean and the Mediterranean Sea.

It is possible that the investigation of evolutionary trends in animals associated with *Cyathura* might reveal that they, also, are in the process of differentiating into distinct races. Benthic animals which we and others have frequently found with *Cyathura* are *Nereis*, *Hypniola*, *Macoma*, *Nassarius*, *Leptochelia*, sphaeromids, *Corophium*, and *Gammarus tigrinus*. Given a certain set of environmental conditions such as those of an estuary, there may be a mutual interdependence among the members of the biocoenosis whereby they give similar responses and tend to evolve in the same direction. It is significant that it has been stated that both *Cyathura* and *Apscudes* need further taxonomic revision and that Smith (1958) suggested the physiological process of reproduction as a taxonomic character. The ecological approach could be a synthesizing agent to bring together physiology, taxonomy, and genetics to differentiate species and analyze evolutionary trends in estuarine animals.

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LITERATURE CITED

- AMAR, R., 1951. Isopodes marins de Banyuls. *Vie et Milieu*, 2:529–530.
- AMERICAN SOCIETY OF LIMNOLOGY AND OCEANOGRAPHY, 1958. The Venice System for the classification of marine waters according to salinity. *Limnol. Oceanogr.*, 3:346–347.
- BARNARD, K. H., 1925. A revision of the Family Anthuridae (Crustacea Isopoda), with remarks on certain morphological peculiarities. *J. Linn. Soc. (Zoology)*, 36:109–160.
- BATTAGLIA, B., 1958. Balanced polymorphism in *Tisbe reticulata*, a marine copepod. *Evolution*, 12: 358–364.
- BLEGVAD, H., 1914. Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. *Rept. Danish Biol. Sta.*, 22:45–78.
- BOCQUET, C., 1951. Recherches sur *Tisbe* (= *Idyoa*) *reticulata*, n. sp. *Arch. Zool. Exp. Gen.*, 37:337–416.
- BOCQUET, C., 1953. Recherches sur le polymorphisme naturel des *Jassa marina* (Fabr.) (Isopodes Assellotes). *Arch. Zool. Exp. Gen.*, 40:187–450.
- BOCQUET, C., C. LEVI, and G. TEISSIER, 1950. Recherches sur le polychromatisme de *Sphaeroma serratum* (F.). *Arch. Zool. Exp. Gen.*, 37:245–297.
- BOWMAN, T. E., 1965. *Cyathura speciosa*, a new cave isopod from Cuba (Anthroidea: Anthuridae). In *Stud-*

- ies on the Fauna of Curaçao and other Caribbean Islands*, edited by P. W. Hummelinck; vol. 22, pp. 87-97. Martinus Nijhoff, The Hague, Netherlands.
- BRODKORB, P., 1963. A giant flightless bird from the Pleistocene of Florida. *The Auk*, 80:111-115.
- BUCHANAN, J. B., 1958. The bottom fauna communities across the continental shelf off Accra, Ghana (Gold Coast). *Proc. Zool. Soc. London*, 130:1-56.
- BURBANCK, W. D., 1959. The distribution of the estuarine isopod, *Cyathura* sp., along the eastern coast of the United States. *Ecology*, 40:507-511.
- BURBANCK, W. D., 1961a. The disappearance of *Cyathura polita* from the Ashepoo River, South Carolina, after hurricane "Gracie" in 1959. *Ecology*, 42:606-607.
- BURBANCK, W. D., 1961b. The biology of *Cyathura* sp., an estuarine isopod of eastern North America. *Verh. Intern. Verein. Limnol.*, 14:968-971.
- BURBANCK, W. D., 1962a. An ecological study of the distribution of the isopod *Cyathura polita* (Stimpson) from brackish waters of Cape Cod, Massachusetts. *Am. Midland Naturalist*, 67:449-476.
- BURBANCK, W. D., 1962b. Further observations on the biotope of the estuarine isopod, *Cyathura polita*. *Ecology*, 43:719-722.
- BURBANCK, W. D., 1963. Some observations on the isopod, *Cyathura polita*, in Chesapeake Bay. *Chesapeake Science*, 4:104-105.
- BURBANCK, W. D., and M. P. BURBANCK, 1961. Variations in the dorsal pattern of *Cyathura polita* (Stimpson) from estuaries along the coasts of eastern United States and the Gulf of Mexico. *Biol. Bull.*, 121:257-264.
- BURBANCK, W. D., and M. P. BURBANCK, 1964. A comparison of dorsal patterns of the estuarine isopods *Cyathura polita* of North America and *C. carinata* of Europe. *Verh. Intern. Verein. Limnol.*, 15:865-870.
- BURBANCK, W. D., R. GRABSKE, and J. R. COMER, 1964. The use of the radioisotope, Zinc 65, in a preliminary study of population movements of the estuarine isopod, *Cyathura polita* (Stimpson, 1855). *Crustaceana*, 7:17-20.
- BURBANCK, W. D., M. E. PIERCE, and G. C. WHITELEY, JR., 1956. A study of the bottom fauna of Rand's Harbor, Massachusetts: an application of the ecotone concept. *Ecol. Monographs*, 26:213-243.
- CLAUSEN, J., and W. M. HIESEY, 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. *Carnegie Inst. Wash. Publ.*, 615:iv-312.
- CLÉRET, J.-J., 1960. Etude de *Cyathura carinata* (Krøyer) (Isopode Anthuridae) I. Redescription de l'espèce et discussion systématique. *Cah. Biol. Mar.*, 1:433-452.
- DAHL, E., 1944. The Swedish brackish water Malacostraca. *K. Fysiol. Sällsk Lund Förh.*, 14:1-17.
- DARNELL, R. M., 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. *Inst. Marine Sci.*, 5:353-413.
- DAY, J. H., N. A. H. MILLARD, and A. D. HARRISON, 1952. The ecology of South African estuaries. Part III. Knysna: A clear open estuary. *Trans. Roy. Soc. S. Africa*, 33:367-413.
- DELAMARE DEBOUTTEVILLE, C., 1960. *Biologie des Eaux Souterraines Littorales et Continentales*. Hermann, Paris.
- DOBZHANSKY, T., 1937. *Genetics and the Origin of Species*. Columbia Univ. Press, New York.
- EASTON, W. H., 1960. *Invertebrate Paleontology*. Harper and Bros., New York.
- FRANKENBERG, D., 1965. A new species of *Cyathura* (Isopoda, Anthuridae) from coastal waters off Georgia, U.S.A. *Crustaceana*, 8:206-212.
- FRANKENBERG, D., and W. D. BURBANCK, 1963. A comparison of the physiology and ecology of the estuarine isopod *Cyathura polita* in Massachusetts and Georgia. *Biol. Bull.*, 125:81-95.
- GURJANOVA, E. F., 1936. Isopodes des mers orientales. In *Faune de l'URSS. Crustacées*; vol. 7, no. 3. (*Inst. Zool. Acad. Sci. U.R.S.S., N.S.*, 6:126-127.)
- HEDGPETH, J. W., 1957. Estuaries and Lagoons. II. Biological aspects. In *Treatise on Marine Ecology and Paleoecology*, vol. 1, Ecology, edited by J. W. Hedgpeth. (*Geol. Soc. Am. Mem.*, 67:693-729.)
- KRØYER, H., 1847. Karcinologiste Bidrag. *Naturh. Tidsskr.*, 2:1-123, 366-446.
- KUMMEL, B., 1961. *History of the Earth*. W. H. Freeman and Co., San Francisco.
- LARSEN, K., 1936. The distribution of the invertebrates in the Dybsø Fjord, their biology and their importance as fish food. *Rept. Danish Biol. Sta.*, 41:3-35.
- LARWOOD, H. J., 1940. The fishery grounds near Alexandria. XXI. Tanaidacea and Isopoda. *Fouad I Inst. Hydrobiol. Fish., Notes and Mem.*, 35:1-72.
- LÖWEGREN, Y., 1937. Ein für die Fauna Schwedens neuer Isopoden *Eurydice pulchra* Leach, sowie ein neues Lokal für den Isopoden *Cyathura carinata* (Krøyer). *K. Fysiol. Sällsk Lund Förh.*, 7:182-185.
- LUNDSTRÖM, A., 1937. Neue Fundorte für *Cyathura carinata* (Krøyer) und *Polydora ligni* Webster. *K. Fysiol. Sällsk Lund Förh.*, 7:172-174.
- MCLANE, W. M., 1947. The seasonal food of the largemouth black bass, *Micropterus salmoides floridanus* (Lacepede), in the St. Johns River, Welaka, Florida. *Quart. J. Florida Acad. Sci.*, 10:103-138.
- MENZIES, R. J., 1962. The Isopods of abyssal depths in the Atlantic Ocean. *Abyssal Crustacea (Vema Research Series)*, 1:83-206.
- MENZIES, R. J., and J. L. BARNARD, 1959. Marine Isopoda on coastal shelf bottoms of southern California: Systematics and ecology. *Pacific Naturalist*, 1(11-12):3-35.
- MILLER, M. A., and W. D. BURBANCK, 1961. Systematics and distribution of an estuarine isopod crustacean, *Cyathura polita* (Stimpson, 1855), new comb., from the Gulf and Atlantic seaboard of the United States. *Biol. Bull.*, 120:62-84.
- MONOD, T., 1925. Tanaïdacea et Isopodes aquatiques de l'Afrique occidentale et septentrionale (I. Tanaïdacea, Anthuridea, Valvifera), with appendix by W. M. Tattersall: "New Tanaïdacea and Isopoda from the west coast of Africa"; (II. Tanaïdacea, Anthuridae, Stenothriidae, Jaeridae (Janirini), Munnidae (Munnini), Asellidae, Limnoriidae). *Bull. Soc. Nat. Maroc.*, 5:61-85, 233-247.
- MOORE, R. C., 1933. *Historical Geology*. McGraw-Hill, New York.
- NIKITIN, V. N., and E. P. TURPAEVA, 1959. The euryhalinity of some species of the Black Sea benthos and the possibility of their settlement in the Sea of Azov. In *Marine Biology*, edited by B. N. Nikitin; pp. 45-66. Am. Inst. Biol. Sci., Washington, D. C.
- RAY, C. E., S. J. OLSEN, and H. J. GUT, 1963. Three mammals new to the Pleistocene fauna of Florida, and a reconsideration of five earlier records. *J. Mammal.*, 44:373-395.
- ROSS, H. H., 1956. *A Textbook of Entomology*. 2nd ed. John Wiley and Sons, New York.
- SALVAT, B., 1962. Faune des sédiments meubles intertidaux du Bassin d'Irréachon. *Cah. Biol. Mar.*, 3:219-244.
- SAVILOV, A. I., 1959. Biological aspect of the bottom fauna of the North Okhotsk Sea. In *Marine Biology*, edited by B. N. Nikitin; pp. 67-136. Am. Inst. Biol. Sci., Washington, D. C.
- SCOTT, K. M. F., A. D. HARRISON, and W. MACNAE, 1952. The ecology of South African estuaries. Part II. The Klein River Estuary, Hermanus, Cape Trans. Roy. Soc. S. Africa, 33:283-331.
- SEGAL, E., and W. D. BURBANCK, 1963. Effects of

- salinity and temperature on osmoregulation in two latitudinally separated populations of an estuarine isopod, *Cyathura polita* (Stimpson). *Physiol. Zool.*, 36:250-263.
- SEGERSTRAALE, S. G., 1957. Baltic Sea. In *Treatise on Marine Ecology and Paleoecology*, vol. 1, Ecology, edited by J. W. Hedgpeth. (*Geol. Soc. Am. Mem.*, 67:751-800.)
- SMIDT, E. L. B., 1944. Biological studies of the invertebrate fauna of the harbour of Copenhagen. *Vidensk. Medd. Fra Dansk Naturh. Foren.*, 107:235-316.
- SMITH, R. I., 1958. On reproductive pattern as a specific characteristic among nereid polychaetes. *Systematic Zool.*, 7:60-73.
- SNODGRASS, R. E., 1938. Evolution of the Annelida, Onychophora, and Arthropoda. *Smithsonian Misc. Coll.* No. 6, 97:1-159.
- SPARKS, A., 1963. Skin divers discover a monster bird. *Atlanta Journal and Constitution Magazine*, 8:20-21.
- SPOONER, G. M., and H. B. MOORE, 1940. The ecology of the Tamar Estuary. VI. An account of the macrofauna of the intertidal muds. *J. Marine Biol. Assoc.*, 24:283-330.
- STAMMER, H. J., 1932. Die fauna des Timavo. *Zool. Jahrb. Abt. Syst. Ökol. Geogr. Tier.*, 63:521-656.
- STORK, H. A., 1940. A new fresh-water isopod from Curaçao. In *Studies on the Fauna of Curaçao, Aruba, Bonaire and the Venezuelan Islands*, edited by P. W. Hummelinck; vol. 10, pp. 147-150. Martinus Nijhoff, The Hague, Netherlands.
- TATTERSALL, W. M., 1922. Zoological results of a tour in the far east. Amphipoda with notes on an additional species of Isopoda. *Mem. Asiatic Soc. Bengal*, 6:435-459.
- VOLPE, E. P., and G. H. PENN, 1957. Dimorphism of chromatophore patterns in the dwarf crayfish. *J. Heredity*, 48:91-96.
- WILLIS, J. C., 1949. *The Birth and Spread of Plants*. Chronica Botanica Co., Waltham, Massachusetts.
- WOLFF, T., 1956. Crustacea Tanaidacea from depths exceeding 6000 meters. *Galathea Report*, 2:187-241.
- WRIGHT, S., 1940. Breeding structure of populations in relation to speciation. *Am. Naturalist*, 74:232-248.

Genetic Aspects of Benthic Ecology in Brackish Waters

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Other papers in this volume have dealt with many aspects of estuarine benthic ecology. Attention has been given to problems concerning the evolutionary patterns of estuarine communities, species, and populations, particularly the important question of subspecific differentiation in brackish waters and the responsible selective factors.

I would like to emphasize the potential contribution that evolutionary genetics could bring to the solution of some problems the marine ecologist may face when studying such a peculiar milieu as the estuary, and the contribution of these environments and their living inhabitants to the better knowledge of evolutionary mechanisms in the sea. From this viewpoint, the importance of estuaries lies in the fact that these brackish-water environments, as well as other marginal areas of marine habitat such as intertidal regions, interrupt the continuity and the relative stability of marine environments. In estuaries, the fluctuations of ecological conditions themselves may act as selective factors. Moreover, the discharge into estuaries of fresh water of various temperatures laden with sediments—a typical feature of the estuarine environment—creates patches of different temperatures and salinities, thus forming habitat niches similar but not completely comparable to the number of microenvironments offered by a rocky bottom. Therefore, the relation between genetic structures of estuarine populations, especially those which are sedentary, can be expressed at a microgeographical level, and a partial control of physical and chemical conditions and of animal populations may be feasible.

As our knowledge of the benthic estuarine fauna increases, the number of bottom species suitable for laboratory culture, and therefore for the experimental analysis of the above relations, is becoming increasingly greater. On the basis of the more recent advances in the field of population ecology we may also be able, in the near future, to analyze the factors controlling the establishment of special benthic facies at all possible levels of integration, namely from the level of Mendelian populations up to the level of complex communities whose members are kept together by the interaction of environmental factors.

INTERSPECIES AND INTRASPECIES SELECTION IN BRACKISH WATERS

Much is known about the non-genetic adaptation to the variable brackish-water environment, in other words, about the great physiological homeostasis

achieved by the inhabitants of this fluctuating milieu. Although our information on the genetic background of this adaptation is very scanty, some examples are already available. They have been drawn mainly from the results of work carried out in the Lagoon of Venice during the last few years. This lagoon, as well as the other ones situated along the Adriatic coast from Grado to Comacchio, has polyhaline waters and most of its inhabitants are of marine origin. However, the great variability of its conditions in time and space does not allow the permanent settlement of many marine forms. A first selection takes place among marine species the moment they enter the lagoon from the sea. Few of them are able to survive in the new environment and, therefore, the lagoon, compared with the adjacent sea, is inhabited by a remarkably reduced number of species. Crustaceans, molluses, echinoderms, fishes, and other organisms provide good evidence of this situation (D'Ancona and Battaglia, 1962). To quote a few examples, of the 358 species of fish recorded in the Adriatic Sea (Soljan, 1948) only 85 are found in the Lagoon of Venice, and most of them are occasional or temporary inhabitants. Of the 67 species of echinoderms found in the Adriatic Sea, only 15 live in the lagoon (Vatova, 1950). Among the Decapoda, only six of the 33 brachyurans found in the sea are common in the lagoon.

A strong selection occurs also inside the lagoon. This applies especially to some sedentary forms which gradually decrease both in number of species and individuals as they approach the inner parts of the lagoon, that is, those farthest from the sea. For example, the Adriatic fauna includes 18 species of cirripedes representative of nine genera, whereas in the lagoon there live four species belonging to two genera, some of them, however, can be found only in those areas which are nearest the sea (Righi, 1942). A similar situation occurs with the Syllidae (Polychaeta). All the 22 species recorded for the lagoon can be found in the areas closer to the sea. In three stations situated along a line which goes from the sea toward the inner margin of the lagoon, their numbers drop to 9, 5, and 0 (Cognetti, 1958). In the Adriatic lagoons, no endemic species have been discovered so far, probably because of the comparatively recent origin of these environments.

Natural selection in the lagoons may act at a specific as well as at an intraspecific level. Research, for the purpose of detecting the survival in the lagoons of

those genotypes within a species which possess the necessary requirements, has recently been carried out, especially utilizing some benthic copepods showing adaptive genetic polymorphism.

ADAPTIVE POLYMORPHISM IN MARINE AND BRACKISH-WATER ORGANISMS

A species which proved to be profitable material for the genetic study of adaptive processes and of intra-specific differentiation is the harpacticoid copepod *Tisbe reticulata* Bocquet. This species exhibits a striking polychromatism which, for the population of the Lagoon of Venice, is under the control of a series of multiple alleles. The species occurs also in Roscoff (France) and Plymouth (England), but the Atlantic populations differ from the Adriatic ones in many respects. The main differences are in the frequencies of the genes responsible for polymorphism and in the ability to withstand low salinities. Moreover, there is a certain degree of incompatibility to crossing between the two populations, as revealed by the low survival of the F₁ hybrids and by the upsetting of the sex ratio among them. This differentiation is likely to be the result of the ecological divergencies between the marine and brackish-water biotopes (Battaglia, 1957). We have also obtained experimental evidence of the adaptive nature of the polymorphism in *Tisbe*. In fact, the different forms show different norms of reaction when confronted with varying salinities and temperatures. Some components of their fitness appear to be affected, to a varying extent, by differences in these ecological parameters. For instance, the form *violacea* is favored by lower salinities and higher temperatures, and it is also the form best able to tolerate a wide range of conditions. An attempt has been made recently to see whether the different abilities to stand diluted sea water of the homozygotes *violacea* and *trifasciata* were due to different osmoregulatory powers (Battaglia and Bryan, 1964). The two genotypes compared have exhibited a significantly different rate of uptake of Na²², K⁴², and Cs¹³⁷, which adds further evidence to the physiological importance of these genetic differences.

One of the main mechanisms which maintains polymorphism in *T. reticulata* is the higher viability of the heterozygotes compared to the homozygotes. The importance of the role played by heterosis in the maintenance of this polymorphism is stressed by the results of experiments carried out with laboratory populations which permit the investigation of all the components of fitness of the various genotypes (Battaglia, 1962).

Another interesting aspect of the adaptation in *T. reticulata*, and in other species of the same genus, concerns their peculiar genetic sex determination. In Tisidae sex determination is multifactorial, and this involves a remarkable variability of the sex ratios according to the kind of mating. Moreover, any increase of heterozygosity leads to an increase of females, whereas an increase of homozygosity—which in nature could result from a decrease in the size of

the population—implies a shifting of sex ratio in favor of males. It has been shown that at least some of the various sex genotypes have different selective values. Without going into details, it can be recognized easily how such a mechanism of sex determination, combined with natural selection operating on the different genotypes, may be of great adaptive importance. In other words, a mechanism of the kind just described can make an environmental choice of the fittest sex ratio highly probable. The advantages of such a situation are quite clear, especially in a varying environment like that of estuarine brackish waters.

Another case of genetic polymorphism is given by the colonial ascidian *Botryllus schlosseri* (Sabbadin, 1959), a species which is abundant and widespread in the Lagoon of Venice. This animal has several types of vacuolar cells containing pigments of various colors and chemical natures. The different distribution of these cells permits the distinguishing of three main discontinuous characters, whose presence or absence is under the control of three pairs of independent factors. The variety of patterns in nature is due to the various combinations of these factors. Sabbadin believes that the polymorphism of *Botryllus* is adaptive. Actually, it was recently found (Sabbadin, personal communication) that the frequencies of certain forms vary according to depth. This case deserves further investigation.

ESTUARINE ENVIRONMENT AND GENETIC STRUCTURE OF POPULATIONS

Another problem concerning the relation between environment and genetic structure of populations, which might be attacked in estuarine benthic habitats, is that of the degree of polymorphism, the number of forms by which a polymorphic species may be represented in these peculiar environments. From many observations carried out in the brackish waters of the Lagoon of Venice, we have found that the copepods, *Tisbe reticulata* and *Porcellidium fimbriatum*, and the isopod, *Sphaeroma serratum*, are represented by fewer forms than in typical marine habitats, such as Plymouth, Roscoff, or the Bay of Naples. This apparently suggests that the same mechanisms which control the establishment of different species in the lagoon operate also at an intraspecific level. If the degree of polymorphism is a function of the variety of the ecological niches available, the reduced degree of polymorphism in the lagoon populations could be ascribed to the smaller number of niches offered by this environment as compared to marine ecosystems. Such a possibility is suggested by the relatively monotonous vegetal substratum associated with these benthic forms. Another important factor is provided by the exacting lagoon environment where the chances of survival depend primarily on the ability to tolerate the inconstancy of the medium. A reduced degree of visible polymorphism, however, does not necessarily imply a drop in genetic variability. For their inhabitants of marine origin, lagoons and estuaries present a high variability in time that must somehow be faced. In

environments of this sort a reduced polymorphism may in part be replaced by an enforced individual homeostasis. A nonspecific genic variability enabling the species to confront unpredictable environmental changes (in oxygen, temperature, nutrients, etc.) could be of great advantage (Battaglia, 1964). We are therefore investigating if, in *Tisbe*, there are other possible sources of genotypical plasticity which can endow the species or the population with potential adaptability.

GEOGRAPHIC DIFFERENTIATION IN PHYSIOLOGICAL CHARACTERISTICS

Another aspect concerns the adaptation of the brackish-water organisms of marine origin to varying salinities. The cases of homeostatic adaptation in the physiology of populations or subspecies known to be genetic are so few that Prosser was led to conclude that on the whole "physiological races are scarce and adaptations are either phenotypic or their bearers are properly separable as good species" (Bullock, 1958). In my opinion, this is merely due to the paucity of marine forms which have so far proved suitable for genetic investigations.

For the study of inherited physiological differences, Tisidae offer excellent material. We have seen earlier that the populations of *Tisbe reticulata* from Roscoff and from the Lagoon of Venice differ in their ability to stand low salinities. The problem has been attacked utilizing another benthic copepod, *Tisbe furcata*, which is far more suitable for this kind of research.

Three geographical populations of *T. furcata*, one from Plymouth and the others from two brackish-water localities in the Adriatic Sea (Chioggia, in the Lagoon of Venice and the Lake of Varano, Gargano, Apulia), have been compared as to their tolerance of diluted sea water. The mean salinities in the three localities show remarkable differences. They decrease in the following order: Plymouth, Chioggia, and Gargano, the latter two places also show wide salinity fluctuations. The experiments consisted of transferring samples of adults of the same age from the standard laboratory sea water (34‰) into diluted sea water (18‰). At the moment of the transfer the animals suffered a sudden shock from which, after a certain time, they recovered. The times of recovery for the three populations were recorded and the mean values (in minutes), together with their standard errors, are as follows:

Gargano	43.19 ± .82
Chioggia	54.42 ± 1.16
Plymouth	81.58 ± 1.86

The differences between the three populations are significant, being in all cases $P < .01$. The populations at the moment of the experiment were thoroughly acclimated, having been kept in the laboratory under standard salinity and temperature conditions for over two years (more than 60 generations), and therefore, the observed differences must be genetically controlled. A further evidence of the genetic nature

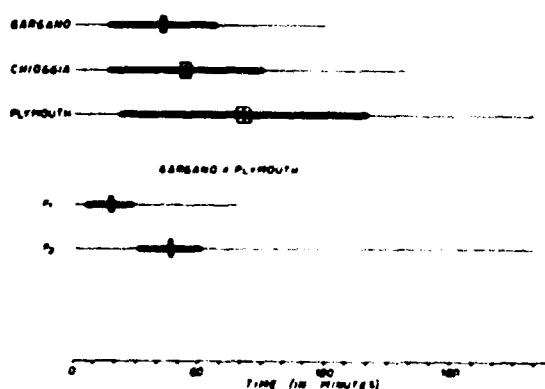


Fig. 1. Times of recovery from the shock suffered by individuals belonging to three geographical populations of *Tisbe furcata*, and by hybrids of the cross Gargano X Plymouth, transferred into diluted sea water. The straight line indicates the field of variation; the vertical bar, the value of the mean; the solid band, a standard deviation on each side of the mean; the empty rectangle, twice the standard error on each side of the mean.

of these differences has been obtained by testing the tolerance to dilution of the F_1 and F_2 of the cross Plymouth X Gargano. The greater tolerance of the F_1 hybrids, compared to the parental populations, shows that they are strongly heterotic. In the F_2 there is an increase of variance which is clearly due to segregation (Fig. 1).

The three populations compared are therefore genetically different as to their degree of tolerance of diluted sea water. The more tolerant population is the one from Gargano, followed in order by the populations from Chioggia and Plymouth. The adaptive meaning of these differences is obvious, since they can be related to the average salinities of the places from where the populations come. It seems, however, that the differential tolerance to salinity variations might be caused not only by the effect of specific genes—not necessarily many—but also by the degree of heterozygosity.

From the examples and the considerations reported above, we may draw the conclusion that the benthic component of the fauna living in estuaries and brackish-water lagoons offers a most interesting research field both to the ecologist and the geneticist. These environments, characterized by remarkable fluctuations in space and time, subject their living inhabitants to selective pressures which may induce differentiation at various levels. These environments therefore, disclose unique opportunities for the study of evolution and adaptation in the sea.

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LITERATURE CITED

- BATTAGLIA, B. 1957. Ecological differentiation and incipient intraspecific isolation in marine copepods. *Int. Rev. Zool.* 27: 299-308.

- BATTAGLIA, B., 1962. Osservazioni preliminari sugli equilibri di popolazioni sperimentali a diversa composizione iniziale, nel Copepode *Tisbe reticulata*. *Rend. Accad. Nazl. Lincei, Ser. 8*, 32: 1-5.
- BATTAGLIA, B., 1964. Advances and problems of ecological genetics in marine animals. *Genetics Today. Proc. Eleventh Intern. Congr. Genet.*, 2: 451-463.
- BATTAGLIA, B., and G. W. BRYAN, 1964. Some aspects of ionic and osmotic regulation in Harpacticoid Copepods of the genus *Tisbe* in relation to polymorphism and geographical distribution. *J. Marine Biol. Assoc. U. K.*, 44: 17-31.
- BULLOCK, T. H., 1958. Homeostatic mechanisms in marine organisms. In *Perspectives in Marine Biology*, pp. 199-210. Univ. Calif. Press, Berkeley, California.
- COGNETTI, G., 1958. I Sillidi della Laguna di Venezia. *Atti. Ist. Veneto Sci., Lettere Arti*, 116: 167-177.
- D'ANCONA, U., and B. BATTAGLIA, 1962. Le Lagune salmastre dell'Alto Adriatico, ambiente di popolamento e di selezione. *Pubbl. Staz. Zool. Napoli (Suppl.)*, 32: 315-335.
- RIGO, L., 1942. Ricerche sistematico-ecologiche sui Cirripedi della Laguna Veneta. *Arch. Oceanogr. Limnol. Venez.*, Mem. 291, 2: 13-44.
- SABBADIN, A., 1959. Analisi genetica del policromatismo di *Botryllus schlosseri* (Pallas) Savigny (Ascidacea). *Boll. Zool.*, 26: 221-243.
- SOLJAN, T., 1948. *Fauna et flora adriatica*. Vol. 1. Pisces, Split, Yugoslavia.
- VATOVA, A., 1950. Gli Echinodermi della Laguna Veneta. *Nova Thalassia*, 1: 1-13.

IX. FISHERIES

Estuarine Nekton

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The term "nekton" belongs to a system of classification which characterizes certain aquatic organisms according to their structure and habits. The definition given in Webster's Dictionary is as succinct and accurate as any definition in the scientific literature: "The actively swimming pelagic organisms." This imparts to the nekton some characteristics unique in this system of classification of living things, for it describes a group of organisms from which all plants are excluded and which is dominated in numbers and biomass by fishes.

The nekton of estuaries is much more difficult to define. Most fishes are migratory and can tolerate wide variations in salinity. The commonly accepted definitions of an estuary, although they are not entirely in agreement, describe a restricted zone which does not encompass the entire geographic or environmental range of most nekton found in estuaries. Webster (Second Edition) describes an estuary as: "A passage, as the mouth of a river or lake, where the tide meets the river current; more commonly, a narrow arm of the sea at the lower end of a river; a frith." Or in terms of physical geography (Webster, Second Edition): "A drowned river mouth, caused by the sinking of the land near the coast." Obviously, the popular concept of an estuary has been determined on the basis of physical features. Even the biologists have accepted this concept, as illustrated by the definition given in a recent ecological text (Odum, 1959): "An estuary is a river mouth where tidal action brings about a mixing of salt and fresh water."

Most definitions of an estuary are based on two sets of criteria. On the basis of mixing of water from river and sea, an estuary should be delimited approximately by the salinity range 0 to 35 %. This definition is narrowed, however, by geographic restrictions which are related only remotely to the processes that create estuarine conditions. This does not necessarily fix a rigid landward boundary, but it does place an arbitrary seaward boundary on the estuary, represented by a line across a river mouth, like the mouth of the Columbia River on the west coast of North America, or across the points of land marking the entrance to a larger estuarine system like Chesapeake Bay on the Atlantic coast.

This system of classification may be suitable for sessile organisms, for their distribution is determined by average, or minimal, environmental conditions.

But for actively moving, largely euryhaline animals like fishes, such a definition is not particularly useful. It is not necessary to cite literature references to call attention to the fact that many estuaries extend their influence far to sea. It is well known that the Amazon, the Mississippi, the Congo, and many other rivers influence the marine environment for many miles offshore. At the surface the horizontal gradients from fresh water to oceanic salinity usually are fairly gradual, with few sharp permanent boundaries or fronts. Indeed, in most estuaries the boundary between river water and ocean water usually is much more sharply defined with depth than along the surface. The sharpest surface salinity fronts often occur in the ocean well away from shore, under the influence of the rotation of the earth and the courses of the great permanent ocean currents.

Usually there is a surface salinity front within many estuaries near the upper limit of the estuarine zone. Its position is related to the magnitude of the river runoff and to the amplitude of the tidal cycle. In a large estuarine system like Chesapeake Bay, this front usually occurs at salinities well below 18 %. Massmann (1963) has described this as the "critical zone" of an estuary, rich in adults, but especially in young, of many fish species, and with abundant plankton populations. This is a fluctuating boundary, also, with respect to fixed geographic points, for its geographical position and its gradient depend on the interaction of opposing and fluctuating forces.

It is not surprising that man, a land animal, should view the ocean in the context of a system of land-based coordinates. The definitions of an estuary currently in vogue were determined largely by geographers. Yet many leading oceanographers also prefer a relatively restricted definition, like that expressed by Cameron and Pritchard (1963): "An estuary is a semi-enclosed coastal body of water having a free connection with the open sea and within which the sea-water is measurably diluted with fresh water deriving from land drainage." For many purposes this is a reasonably satisfactory view. To understand the distribution and migrations of nektonic organisms, however, the only logical point of reference is a system of oceanographic coordinates which make allowance for the fact that the estuarine environment is highly variable with respect to fixed points on land. Our present knowledge is quite inadequate to describe

these coordinates precisely, but our understanding of the biology of nekton will be imperfect until we can do so.

THE NEKTONIC ESTUARY

It is interesting to consider the estuarine environment of the North American Continent as a zone bounded by salinity fronts rather than by land barriers. On the Atlantic coast the Gulf Stream immediately becomes important as the seaward boundary. A roughly triangular area bounded by the coastline, the Gulf Stream, and the Arctic seas, extending northeastward from Cape Hatteras, becomes a part of the Northwest Atlantic Estuary (Fig. 1). South of Cape Hatteras, in the South Atlantic Bight, land drainage is rather thoroughly mixed with oceanic water before it leaves the landbound estuaries and the extensive system of channels between the mainland and the coastal chain of islands. Consequently, there is no extensive offshore estuarine zone over the continental shelf in this region. North of Cape Hatteras the offshore estuarine system must be described in three dimensions, because there is a more or less horizontal front beneath the surface which is even more sharply defined. When the third dimension is brought into consideration the Northwest Atlantic Estuary becomes a vast lens of brackish water, extending to the bottom only near the shore, and underlain by a wedge of water of oceanic characteristics.

Off the Pacific coast of North America an estuarine system of even more gigantic proportions emerges under this definition. Many large rivers pour fresh water into the Bering Sea, Gulf of Alaska, and coastal areas of the Pacific Northwest. The Yukon River; the river systems draining into Bristol Bay; the many rivers of rainy Central and Southeastern Alaska; the Nass, Skeena, Fraser, and many other rivers of British Columbia; the Columbia, Sacramento, and other rivers of the United States coast all contribute

to the greatest estuarine system in the world. This lens of low-salinity water extends across the entire Bering Sea and North Pacific Ocean to the shores of Kamchatka and Sakhalin where it is fed by large Asian rivers. It dips to a point southwest of the entrance of San Francisco Bay on our west coast and extends to the subarctic boundary in mid-Pacific, reaching south almost to 40° N. latitude. Under this definition the entire North Pacific Ocean, northward from 40° to 45° N. latitude, is an estuary. This has already been recognized by Tully and Barber (1960).

Parts of the Gulf of Mexico also have estuarine characteristics. The great flow of the Mississippi River system, veering to the westward as it leaves the delta under the influence of the earth's rotation, creates a lens of brackish water over much of the northwestern Gulf. The influence of the northwesterly flowing equatorial current, which carries oceanic water of relatively high salinity into the Gulf, restricts the offshore estuarine zone in the Gulf to a surprisingly narrow band, considering the great flow of the Mississippi River. It is obvious that Mississippi River water and other land drainage into the Gulf of Mexico must mix rather rapidly with oceanic water flowing into the Gulf from the Caribbean Sea and leaving again through the Strait of Florida. The relatively small influence that this great river has on the waters of the Gulf can be understood when the magnitude of the two flows is considered. The total transport through the Yucatan Channel is about 26×10^6 cubic meters per second (Sverdrup *et al.*, 1942). The average runoff into the Gulf of Mexico is about 877 cubic kilometers per year (Fleming and Elliott, 1956) or about 28×10^3 cubic meters per second, only about one-tenth of one percent of the total oceanic flow through the Gulf. A simple calculation will demonstrate that if all the freshwater runoff from the North American Continent into the Gulf were mixed thoroughly with the oceanic water entering the Gulf

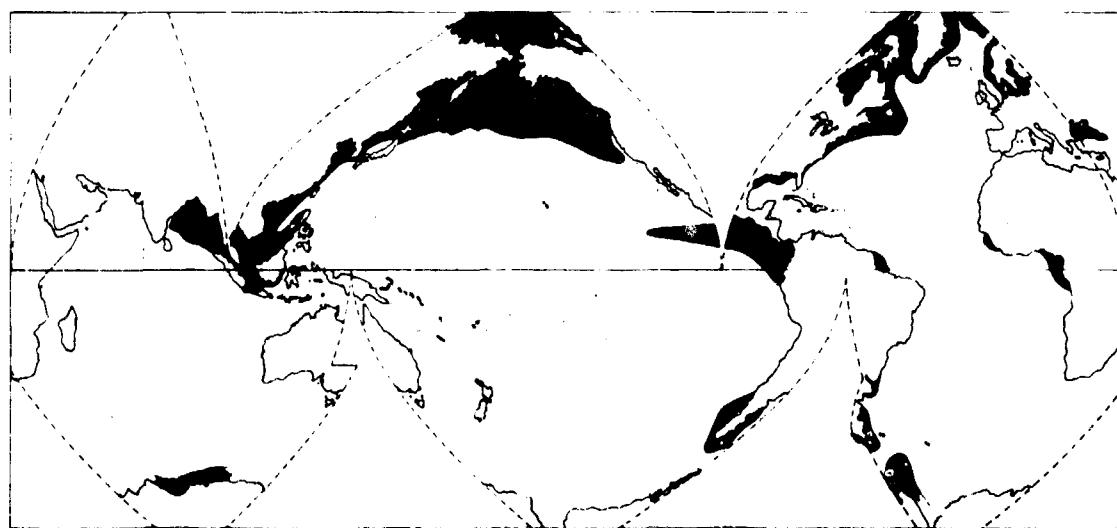


Fig. 1. Offshore estuarine zones of the world ocean bounded by the 33.5‰ isohaline.

through the Yucatan Channel and flowing out through the Florida Strait, it would reduce the salinity by less than 0.04%.

The roughly triangular temperate offshore estuarine zone in the western North Atlantic is continuous with a body of subarctic estuarine water off the Labrador coast and in Hudson and James Bays. Thus, there are three major estuarine zones off the coasts of North America, the vast North Pacific zone, an extensive Northwest Atlantic zone, and a smaller zone in the northern Gulf of Mexico (Fig. 1). Contiguous with the North Pacific estuary is an extensive estuarine zone that lies in an apparently continuous band from the Okhotsk Sea along the coasts of Korea, China, and Southeastern Asia into the Bay of Bengal.

In the eastern tropical Pacific, a tongue of relatively low salinity surface water extends in a very thin layer more than a thousand miles westward from a stretch of coast off Central and South America. The surprising extent of this body of relatively low-salinity water, in a region that has no major rivers, is explained by the local climate and oceanic circulation. The fresh water that generates this offshore estuary arises principally from two sources, land drainage into the sea along at least 1,000 miles of coast from El Salvador to Ecuador, and the direct effects of precipitation. The discharge of these rivers closely follows the seasonal cycle of rainfall, with a minimum in April or May and a maximum in October or November. The flow of the Rio Tempisque, Costa Rica, in 1952 ranged from about 2,500 cubic feet per second in October to about 300 cubic feet per second in April. The average amount of fresh water contributed to the Gulf of Nicoya directly by precipitation is estimated at 5,670 cubic feet per second (Peterson, 1960). Thus, from this small gulf alone, the average contribution of fresh water to the sea probably is at least 7,000 cubic feet per second. An even greater body of low salinity water apparently originates in the Gulf of Panama (Bennett, 1963). If the entire stretch of coast from El Salvador to Ecuador contributes equivalent amounts of fresh water to the sea, the average total runoff in this region will amount to about 300,000 cubic feet per second, about half the flow of the Mississippi River. The prevailing currents in this part of the Pacific Ocean are conducive to convergence of this broadly based runoff and attenuation toward the west (Fig. 2). Peterson (1960) notes that the Gulf of Nicoya is a positive estuary, at least from May to December, for land drainage plus precipitation exceeds evaporation during this period. Moreover, at such times there is entrainment of water from below as the runoff moves seaward. Therefore, in order to maintain the salinity distribution, a compensatory flow of deeper saline water must enter the Gulf. This is the typical circulation pattern of an estuary like the subarctic region of the North Pacific (Tully and Barber, 1960). The detailed dynamics of this Central American offshore estuary is not well understood. It is likely that it varies considerably in extent in response to variations in precipitation (Bennett, 1966). Such a lack of sta-

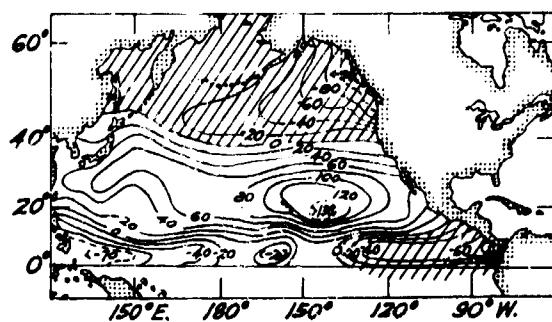


Fig. 2. Mean annual excess of evaporation over precipitation in the North Pacific Ocean (After Jacobs, 1951). The shaded zones, where precipitation exceeds evaporation, correspond closely with the two major offshore estuarine zones in the eastern Pacific (Fig. 1). The difference in the western Pacific from the pattern exhibited in Fig. 1 is related to the distribution of currents.

bility would have adverse effects upon its estuarine-dependent nekton.

In the northeastern Atlantic the only extensive estuarine system includes the Baltic Sea, the southeastern part of the North Sea, and a narrow band off the Norwegian coast. In the tropical Atlantic there are three offshore estuaries, one off the mouth of the Amazon, a second off the mouth of the Niger and Congo Rivers, and a third off the West Coast of Africa from Senegal to Liberia. This third offshore estuary is not fed by any major rivers. It probably is generated by a set of circumstances similar to the climatic and oceanographic phenomena that give rise to the offshore estuarine zone in the tropical eastern Pacific off Central America. Much greater and more concentrated flows from streams like the Magdalena, Orinoco, Nile, Euphrates, Zambezi, and other major world rivers create insignificant offshore estuaries because prevailing ocean currents oppose the accumulation of fresh water at the surface, or because evaporation and mixing quickly dissipate land drainage.

The Southern Hemisphere is remarkably devoid of offshore estuarine waters. The only exceptions are a zone surrounding the southern end of South America, extending from the south coast of Chile around Tierra del Fuego and north along the southern coast of Argentina, and a band around the Antarctic Continent.

Many other estuaries exist in the world, but apparently none extends its influence far to sea. Most of the world's major river systems flow into the regions designated as offshore estuaries (Fig. 1), but there are some notable exceptions. With few exceptions the offshore estuarine zones are in regions where precipitation exceeds evaporation. Almost all major rivers which do not contribute to substantial estuarine areas enter the sea in latitudes where evaporation exceeds precipitation. These rivers include the Nile, Zambezi, and Orange Rivers in Africa; the Indus, Euphrates, Tigris, and Narbada Rivers in Asia; the Darling and Murray Rivers in Australia; and the Colorado River in North America. On the other

hand, at least 35 of the 50 major world rivers flow into the zones marked as offshore estuarine zones in Figure 1.

Many of the major rivers of the world empty into the Arctic Ocean. Southward flow of this water into the North Pacific and North Atlantic must contribute substantial quantities of fresh water to the two major offshore estuaries.

Any attempt to describe the distribution and intermingling of land drainage in the ocean is quickly handicapped by a lack of information. The runoff from even the Amazon, the world's greatest drainage system, is poorly known. Studies in 1963 by scientists of the United States Geological Survey, in cooperation with the Government of Brazil, have improved our knowledge (W. B. Langbein, personal communication), but these observations were made hundreds of miles upstream, and did not include the flow of three major and many lesser tributaries. The flow of many important world rivers has never been gauged.

The general distribution of surface salinity in the world ocean is influenced primarily by precipitation, evaporation, and the effects of the major currents. From north to south, and averaged for the entire world ocean (Defant, 1961), surface salinity rises from a minimum in the Arctic regions (32.66‰ between 55° and 60° N. latitude) to a maximum of 35.76‰ between 25° and 30° N. latitude, falls to a minimum in the tropics (34.43‰ between 5° and 10° N. latitude), rises to a maximum between 20° and 25° S. latitude, and falls again toward Antarctica (33.96‰ between 50° and 55° S. latitude). This distribution corresponds very closely to the distribution of the mean sum of evaporation and precipitation, which shows excess precipitation in the Arctic, the tropics, and the Antarctic, and excess evaporation in mid-latitudes at about 20°–25° N. latitude and 20°–25° S. latitude. The offshore estuarine zones illustrated in Figure 1 fall almost entirely in the arctic or subarctic, and tropical regions, characterized by relatively low mean ocean salinities and an excess of precipitation over evaporation.

Seasonal and annual variations in land drainage are tremendous, and we know that these variations have important effects on estuarine life. We can only speculate on the biological effects of such variations in the open sea, but they must have a great influence on the movements and abundance of nekton, especially fishes. Our understanding of these relationships will require improved knowledge of the details of the earth's water budget and of the behavior of estuarine nekton.

ADAPTATIONS FOR NEKTONIC EXISTENCE

The term "nekton" identifies one group of organisms in an ecologically oriented system of classification of aquatic life based on form or habits. The benthos is composed of plants and animals attached to, or resting on, the bottom, or more or less buried in the bottom. Periphyton or aufwuchs includes organisms that are attached or cling to stems and leaves of

plants or other surfaces projecting above the bottom. Plankton are usually small animals and plants which, although they may be able to swim to some extent, and can maintain or change their position between surface and bottom, essentially drift passively with the currents. Neuston includes those organisms which rest or swim on the surface. In the marine environment a simplified classification often is used: benthic life includes the benthos and periphyton; pelagic forms include the nekton, plankton, and relatively unimportant marine neuston.

To these living organisms might be added a sixth category, tripton, composed of detritus of biological origin and inorganic particulate matter. The role of this non-living suspension in the aquatic environment is not well understood (Krey, 1961). It certainly plays an important role in marine ecology, especially in the inshore estuarine environment, and its importance to estuarine nekton deserves greater attention.

The principal adaptations for truly nektonic existence are the possession of swimming organs, a smooth streamlined body, and a specific gravity reasonably close to that of the surrounding medium. Most fishes have achieved these objectives successfully by developing smooth, terete, flexible bodies covered with mucus. The bodies of most fishes can be flexed laterally but not vertically. This provides propulsive power which allows the relatively large and flexible caudal fin to move the fish forward. Many pelagic fishes are able to adjust their specific gravity by controlling the amount of gas in the swim bladder and can maintain and alter their equilibrium and direction by appropriate movements of the median and paired fins. Another important requirement for truly nektonic existence is the ability to extract oxygen at a relatively rapid rate from the surrounding water. The gills of fishes are well adapted to this mode of life, which permits active and sustained movement.

Fishes also are well adapted to withstand the rigors of the estuarine environment. Their skin, scales, and coat of mucus minimize osmotic changes associated with changes in salinity. Their capacity for active movement allows them to avoid the unfavorable effects of variations in salinity, temperature, dissolved oxygen, suspended silt, and other environmental variables. Nevertheless, the tiny young of many marine species, in which these protective mechanisms apparently are not well developed, migrate in large numbers to water of very low salinity in estuaries, where they thrive. It is generally agreed that the bony fishes originated in fresh water (Romer, 1945), and it is understandable that the young are more tolerant of low salinity. At these early stages, like young salmon, these fishes have not developed salt-secreting cells. June and Chamberlin (1958) concluded that young menhaden (*Brevoortia tyrannus*) must undergo their early development in waters of low salinity. Their experiments showed that mortality was high and development abnormal in sea water.

Most invertebrates lack this precise combination of adaptations for nektonic life. The squids are the only

invertebrates that rival the fishes in this respect. Most squids have firm, terete, smooth, and relatively inflexible bodies. They swim by quite a different process, however, by a form of jet propulsion so adapted that they can move backwards as well as forwards with great speed. Squids cannot adjust to reduced salinities, however. They are important members of the oceanic nekton and enter the offshore estuary in abundance at certain places and times, but they are not typical estuarine animals.

Another molluscan group that enters the nekton occasionally is the scallop family. Normally members of the benthos, scallops are able to swim short distances by convulsive movements of the two valves of the shell. Like most of the more powerful invertebrates, however, they are prevented from adopting an exclusively nektonic existence by the presence of a heavy exoskeleton, which is necessary for attachment of the musculature.

The Crustacea are divided into two subclasses, Reptantia, the creeping forms, and Natantia, the swimmers. Some members of the Reptantia, although they do not possess true swimming organs, are able to propel themselves through the water out of contact with the bottom for limited periods. The swimming crabs, exemplified by the commercially important blue crabs of the Atlantic and Gulf coasts of the United States, have developed this capacity to a remarkable degree. This has been achieved by a modification of the fifth pair of thoracic legs to form paddle-like swimming organs, with powerful muscles. The legs and carapace are relatively smooth, slender, and light in weight, and are free of bulky spines and protuberances. By reason of these modifications, these crabs are capable of swimming off the bottom for extended periods and they perform extensive seasonal migrations.

Other Reptantia capable of swimming are the lobsters, characterized by the American lobster (*Homarus americanus*) of New England and the spiny lobsters (*Panulirus* spp.) of Florida and California. These crustaceans do not have true swimming organs, but can propel themselves with surprising agility by convulsive movements of the powerful abdomen. However, the bulky carapaces and heavy spines of *Panulirus* and the large chelipeds of *Homarus* are not conducive to extended movements off the bottom, and these occasional swimmers can hardly be termed nektonic.

Many members of the subclass Natantia are very active swimmers, although they also may crawl on, or even bury in, the substrate. Important members of this group are the shrimps, some of which, like the penaeid shrimps of the South Atlantic coast of the United States and the Gulf of Mexico, are of great commercial importance. These shrimps spawn in the ocean, but the tiny young soon congregate in the inshore estuarine areas, where they spend several months of their first year of life. The pink shrimp of southern Florida (*Penaeus duorarum*), which use the estuarine environment of the Everglades as a nursery

ground, have been shown to migrate at least 120 miles from Florida Bay to the fishing grounds north of the Dry Tortugas (Costello and Allen, 1961). During this migration, and at other times, they are primarily nektonic.

All vertebrate members of the nekton other than fishes are limited in their capacity to become truly nektonic by the need to come to the surface periodically to breathe air. Whales and porpoises have been the most successful in adapting to aquatic life. They never leave the water and can remain submerged for surprisingly long periods, but they, also, must return periodically to the surface to obtain oxygen. Pinnipeds also have become well adapted to life in the water. They do need, however, to return to land to breed and some spend considerable periods resting on land. Some birds have developed remarkable capacities to dive beneath the surface and swim underwater. The rhythmic, organized mass-feeding movements of cormorants are particularly interesting (Bartholomew, 1942). Turtles and certain snakes also can swim beneath the surface for various periods. But birds, turtles, and snakes, like all air breathers, are not permanent members of the nekton.

Man is a special case. His capacity for learning to swim allows him to become a temporary member of the nekton. His ability to think, and to design, build, and operate artificial devices for catching aquatic animals makes him an important member of the nektonic community. By reason of these same abilities he possesses a tremendous capacity to modify the nektonic environment. Since he is a land-based animal, who lives mainly near rivers, lakes, and the seacoast, his influence on the estuarine environment is particularly important. Moreover, as already pointed out, his rapidly increasing numbers and evolving technology are causing him to exert an ever-increasing influence on the physical and chemical environment and on the nekton as a whole.

THE ESTUARINE ENVIRONMENT

In the enclosed or land-bound portion of the estuary, estuarine water usually can be considered as extending to the bottom. This is especially true in estuaries where strong tidal mixing usually prevents the formation of a sharp vertical salinity gradient. In some estuaries like Chesapeake Bay, however, a pronounced salinity front exists between the surface and the bottom, and the environments above and below this boundary may differ sharply. The zone of sharp transition is known as the level of no net motion (Pritchard, 1951, 1952a). Above this level the water is relatively low in salinity and has a net transport toward the sea. Below this level the water is denser and saltier, with a net transport up the estuary. This deeper water also is diluted to some extent by fresh water from the land, and its salinity is reduced gradually as it moves up the estuary.

In the offshore estuary the salinity of the deeper water usually is the same as, or not much less than, the salinity of the surface water of the open ocean

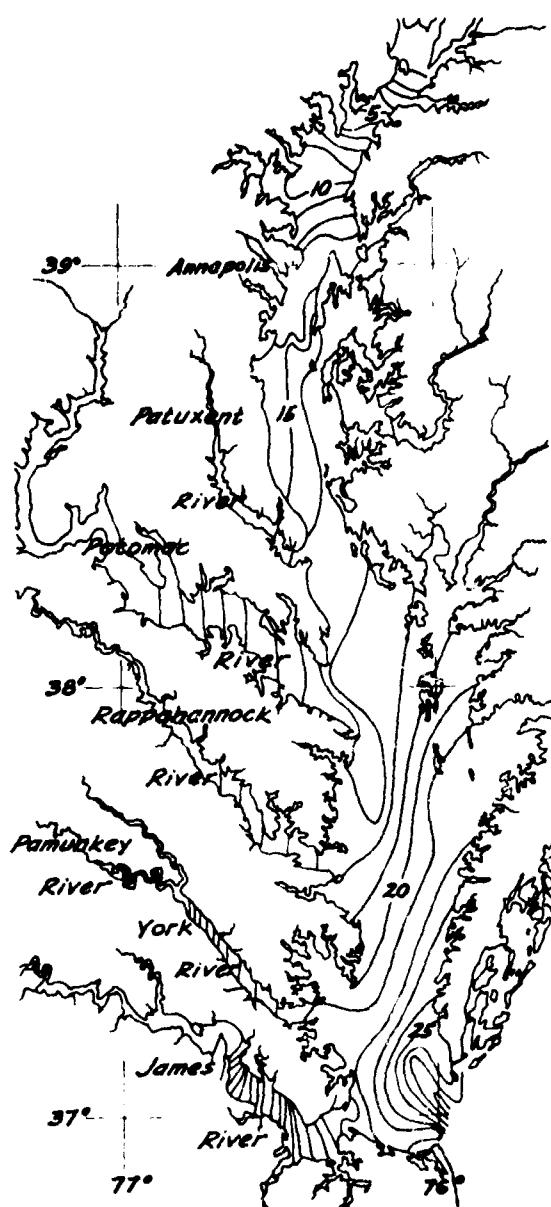


Fig. 3. Typical distribution of salinity at the surface in Chesapeake Bay.

beyond the estuarine salinity front. Details of the horizontal and vertical circulation are less well understood, but evidence is accumulating in the North Atlantic that there is an onshore transport of water near the bottom from as far out as the edge of the continental shelf, as there is in the North Pacific (Tully and Barber, 1960) and in the eastern tropical Pacific (Peterson, 1960). The outflowing surface water of reduced salinity, under the influence of the earth's rotation, is diverted to the right as it leaves the mouth of the landbound estuarine zone in the Northern Hemisphere. Hence, the surface water leaving Chesapeake Bay flows south along the coast in the direction

of Cape Hatteras (Joseph *et al.*, 1960). Apparently, the Gulf Stream interposes a barrier at this point, and little if any of the low-salinity surface water passes farther south. Instead, it turns to the northward and follows the inshore edge of the Gulf Stream.

The effect of the earth's rotation is shown in the surface salinity patterns of the inshore estuaries also. In Chesapeake Bay, for example, the northerly flowing water from the sea is diverted toward the eastern side of the Bay and the southerly flowing river runoff holds to the western side. This produces a pronounced surface salinity gradient across the Bay, especially in its lower part (Fig. 3). Measurable average salinity gradients exist across the major tributaries also, with the higher salinity on the left side of the estuary looking downstream. Even the depth of the level of no net motion is affected. Careful measurements have shown that this boundary is deeper on the right side of the tributaries of the Chesapeake (Pritchard, 1952b). These general principles will apply to the structure and circulation of estuaries in other parts of the world ocean also. It should be remembered, of course, that the rotation of the earth causes the flow to veer to the right in the Northern Hemisphere and to the left south of the Equator. On the west coasts of the continents in the Northern Hemisphere, this throws river runoff to the north.

In the North Pacific the details of the structure and circulation of the offshore estuary are better understood (Dodimead *et al.*, 1963). Dodimead (1961), using the salinity structure to define major oceanographic regions in the North Pacific, described subarctic water on the basis of the presence of a well-developed halocline (Fig. 4). The boundary between subarctic and subtropic waters is identified by an almost vertical 34‰ isohaline extending from the surface to depths of 200 to 400 meters. This boundary, at the surface, corresponds rather closely with the northern edge of the North Pacific Drift. In the subarctic region a permanent halocline exists at a depth between 100 and 200 meters and at a salinity of about

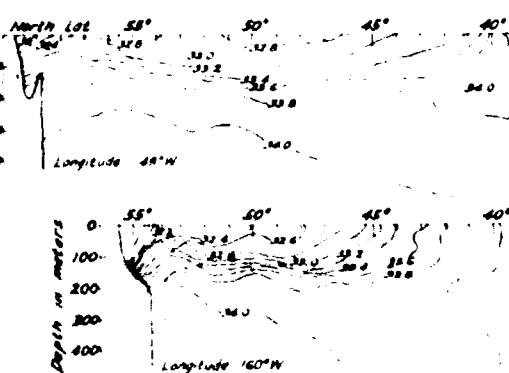


Fig. 4. Typical cross sections of the lens of low salinity water which forms the vast North Pacific offshore estuary (After Dodimead *et al.*, 1963).

33.8 ‰. As already mentioned, Tully and Barber (1960) recognized in this salinity structure the features of a simple estuarine system.

The great abundance and widespread distribution of anadromous fishes in the Northern Hemisphere, particularly in temperate and subarctic waters of the North Pacific and northwestern Atlantic, probably are related to this extensive development of oceanic estuaries. The long migrations of Pacific salmonids become somewhat less of a mystery if it is conceded that they never entirely leave the influence of their home streams. Their great abundance undoubtedly can be attributed at least partially to the vast extent and high biological productivity of their offshore estuarine feeding grounds. Shad (*Alosa sapidissima*), introduced on the Pacific coast three-quarters of a century ago, are still increasing in abundance. There is good reason to believe that already this species is more abundant in the Pacific than in the Atlantic. If its oceanic feeding grounds are more extensive in the Pacific, as Figure 1 suggests, this superiority in numbers is not surprising. Striped bass (*Morone saxatilis*) probably are prevented by temperature barriers from utilizing much of the offshore estuary in the North Pacific. Figure 1 also suggests that it would be folly to expect successful establishment of Pacific salmonids or other wide-ranging anadromous species in the Southern Hemisphere in any great abundance, except perhaps along the southern coasts of Chile and Argentina.

SALINITY

At any fixed point in the inshore estuary great changes in salinity occur. These changes have a greater influence on sessile or slowly moving organisms than they do on nekton, but the nekton sometimes is affected, too. Rapid salinity changes, of course, are caused primarily by variations in rainfall or in the rate of melting of snow. The direct effects of precipitation are perhaps of little importance to nekton, but the indirect effects can be great. The major estuaries of the world receive runoff from vast areas of land. The drainage basin of the Mississippi River system, for example, covers an area of almost 1.25 million square miles. This is about 13 percent of the total area of the North American Continent. The mean flow of the Mississippi and its tributaries is about 620,000 cubic feet per second (Langbein and Harbeck, 1949) and the recorded maximum of about 1.9 million cubic feet was more than 30 times the minimum. The Amazon River system, the greatest drainage basin in the world, covers an area of about 2.7 million square miles, about 40 percent of the entire area of South America. The flow of this mighty river still has not been adequately measured, but some concept of its size may be gained from the fact that one of its major tributaries, the Rio Negro, has a volume of nearly 2.4 million cubic feet per second where it enters the main river. Thus, this tributary, which enters the Amazon 1,000 miles upstream from the sea, contributes more water than the entire Mississippi

system (Office of International Scientific Affairs, 1964). Flow measurements of the Amazon proper also were made far upstream. When the contributions of tributaries like the Tocantins, Tapajos, and Xingu Rivers, which enter the Amazon lower down, are added, there is little doubt that the volume of discharge into the Atlantic Ocean under flood conditions will be at least 8 million cubic feet per second, more than four times the flow of the entire Mississippi system at flood stage. The low-water measurement of the flow of the Amazon, also made well upriver, above its confluence with several important tributaries, was about 2.5 million cubic feet per second. Variations in precipitation and runoff tend to be seasonal, but there are often sudden great changes. The passage of a major storm over the watershed can have catastrophic delayed effects on marine life in the estuary when the maximum effect of runoff from the heavy rains is felt.

TEMPERATURE

Salinity gradients are not the only important features of the estuarine environment, although it can be said that intermediate salinities are the most characteristic feature. Temperature also is an important characteristic. The level of temperature is important biologically, because respiration and osmoregulation of animals (Pearse, 1950; Pearse and Gunter, 1957) are more difficult in waters of reduced salinity, and these processes also are functions of temperature. The effects of low salinity on respiration and osmoregulation are less adverse at high temperatures. This has been accepted as the reason why southern estuaries have richer faunas than northern estuaries. The difference in variety of fish faunas between northern and southern estuaries is certainly striking. Such temperature effects also could explain the migration of many fishes out of estuaries in fall and winter.

The relatively great range of temperature in most estuaries also has important biological effects. The diurnal temperature range in a shallow estuary is relatively great (Gunter, 1945; Beaven, 1960), for such waters are quite sensitive to changes in air temperature. In the lower York River, at Gloucester Point, Virginia, for example, at a point where the water is about 5 feet deep, the bottom water temperature can vary as much as 8° F. (4.4° C.) in 24 hours (McHugh, 1959a). Relatively large vertical temperature differences also occur. In summer the surface water usually is much warmer than the deeper layers, a common characteristic of all natural bodies of water. In winter the deeper waters usually are warmer, but, more important for nektonic organisms, the temperature is relatively stable in the deeper portions of the estuary. There are important lateral gradients in estuarine water temperature also. In summer the temperature typically decreases from the upper estuary to the sea. In winter the gradient is reversed. The gradients and changes in water temperature, rather than the general level of temperature, have the greatest influence on estuarine nekton. Consequently, sudden cold waves will immobilize or kill fishes in

shallow waters at temperatures that would not be lethal if the fishes were properly acclimated.

OXYGEN

In southern estuaries, especially, large variations in dissolved oxygen content of the water occur. These changes can have great effects on distribution and abundance of nekton. In Chesapeake Bay large volumes of water beneath the halocline become completely devoid of dissolved oxygen in late summer. This phenomenon affects a large area in the middle portion of the Bay and extends at times for miles up the Piankatank, Rappahannock, Potomac, and Patuxent Rivers. Its occurrence is related to the salinity structure of the water mass and the prevailing high summer temperatures. The abundant flora and fauna of the water beneath the layer of no net motion have a high oxygen demand which the natural rate of oxygen replacement is not sufficient to balance. In the absence of strong winds this deep water, once it leaves the surface outside the mouth of the Bay, can receive oxygen only by the very slow process of diffusion or advection from above. As the dissolved oxygen content of these waters approaches zero, the animals must die or move out. The only organisms that can survive are those that do not require oxygen, like anaerobic bacteria. At such times these waters contain hydrogen sulfide. Extensive mortalities of blue crabs in fishermen's pots are reported when these conditions prevail, but it is not known whether serious natural mortalities of crabs or other nekton occur. Mass fish kills occur in these areas at these and other times, but the causes are difficult to trace. There is no doubt, however, that these conditions drive nektonic forms out of the affected areas and effectively block reentry and that sometimes fishes may be trapped in restricted areas. Thus, substantial parts of Chesapeake Bay and some of its tributaries are rendered uninhabitable for fishes in late summer. The zone most seriously affected lies below the halocline or level of no net horizontal water movement, but substantial oxygen deficiencies sometimes extend to the surface. This undoubtedly affects the distribution and abundance in the Bay of densely schooling, active fishes like menhaden.

These conditions become especially acute after hurricanes deposit heavy rains over the area. Heavy runoff from the land washes large quantities of organic matter into the water, the large volumes of fresh water increase the stability of the water column, and the high summer temperatures speed up biological activity. In August, 1955, two hurricanes passed over the Chesapeake Bay area within a week of each other, with total precipitation of about 11 inches. On September 1, 1955, about ten days after the second hurricane, at a station 24 miles above the mouth of the Rappahannock River, the salinity gradient from surface to a depth of 20 feet was more than 7%. The boundary between the two water masses was so sharp that the salinity at this station rose from about 10.8‰ at a depth of 12.5 feet to about 15.3‰ at 15 feet. At

this time the dissolved oxygen content at 20 feet below the surface was less than 8 percent of the saturation value, and zero at 30 feet. Typical profiles of dissolved oxygen content in the Rappahannock River and Chesapeake Bay in late summer are illustrated in Figure 5.

Similar conditions undoubtedly prevail in other estuaries along the United States coast. The "jubilees" of the Gulf of Mexico are caused by similar phenomena. Brongersma-Sanders (1957) described similar conditions which caused mass fish mortalities in Walvis Bay on the southwest coast of Africa. She also cited conditions in the Sea of Azov that are similar to the phenomenon in Chesapeake Bay. Reliable quantitative estimates of fish mortalities caused by such natural oxygen deficiencies are not available. More information about the quantitative biological effects of these phenomena is needed.

OTHER FACTORS

Many other factors undoubtedly influence the distribution, abundance, and migrations of nekton in estuaries. Many authors have pointed out that nutrient-rich waters from the rivers support abundant stocks of food organisms. Others have said that these restricted, shallow waters afford a considerable degree of shelter from enemies. But it is difficult to escape the conclusion that we really know very little about the environment in which estuarine animals live. In planning "environmental" studies, we have made little progress since oceanographic research began. Measurements of temperature, salinity, dissolved oxygen, and one or two other variables usually are more or less standard practice. We measure "transparency", analyze for phosphate, and measure chlorophyll, because these are known to reflect certain aspects of biological productivity. Productivity measurements by the light and dark bottle method, and more recently by carbon-14 techniques, are frequently a part of "environmental" studies.

Odum (1950) and many other ecologists have

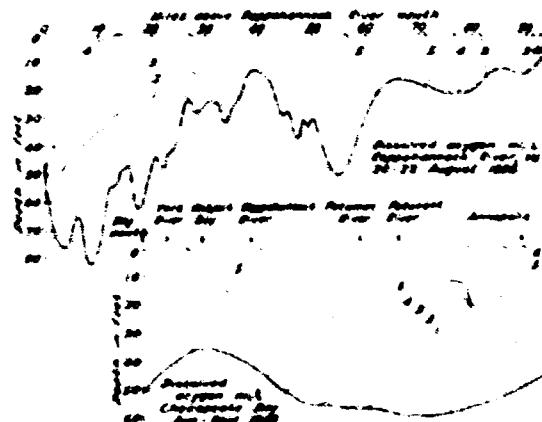


Fig. 5. Typical vertical distribution of dissolved oxygen in the Rappahannock River and Chesapeake Bay in late summer.

stressed the importance of the ecological "niche" as compared to the more general term "habitat". General measurements of environmental characteristics, like those described above, are only of limited value in describing the place where the biological community resides. By themselves these measurements do little to tell us why a variety of species can coexist in certain waters yet maintain their specific differences, or why abundance and distribution vary so greatly. We have done very little in fishery investigations to understand the microclimate in which each species lives. Yet we know from the work of Hasler (1958) and many others that fishes have acute vision, hearing, and olfactory senses by which they can orient themselves. For example, fishes apparently are able to discriminate extremely low concentrations of certain dissolved substances in the water.

Despite the fact that all biologists must have at least an elementary knowledge of the principles of ecology, a clear concept of the difference between habitat and niche has not been demonstrated in many field studies of fish distribution and abundance. The temptation is strong, when large quantities of biological observations have been made in the field, accompanied by measurements of temperature, salinity, and perhaps other characteristics of the surrounding water, to search for correlations between physical and biological variables; or, if concurrent measurements of physical and biological phenomena are not available, physical data from the same general area, collected for other purposes, have been used. Since apparent correlations often can be found by successive trials using various combinations of biological and physical data, or even with random numbers, it is not surprising that strong and apparently statistically significant correlations can be derived by trial and error from series of field observations. Now that electronic data processing facilities are so readily available, it can be expected that the search for correlations may increase. The fallacious reasoning that underlies such attempts to find relationships between variables arises from a misunderstanding of the nature of scientific hypotheses and how they should be tested. For example, it often is argued that such studies are useful in determining which observations should be continued and which should be dropped. This ignores the fact that mechanical searching for correlations can neither demonstrate nor disprove cause and effect. There is a need for more careful attention to research planning before field work begins.

We still do not know precisely what we mean by the "environment" of a nektonic individual or species. There is abundant evidence that the reactions of an organism to its environment and the influence of the environment on the organism or species are highly complex. On the other hand, at certain times unmistakable evidence of the direct and profound effects of single factors is brought forcibly to attention. Gunter (1945) has reviewed many such occurrences along the Florida and Texas coasts of the Gulf of Mexico,

which sometimes affect the future success of fishing. Brongersma-Sanders (1957) has reviewed the literature on mass mortalities of nekton in estuaries caused by sudden changes in salinity, in temperature, in dissolved oxygen content, and by other natural phenomena. These catastrophic single-factor effects occur because the organism reaches the limit of its tolerance for that particular factor. But in its ordinary relations with its environment, it is virtually certain that the animal usually is integrating the effects of a relatively large number of environmental pressures, probably reacting to each in different ways according to the strengths of the other stimuli. The spectacular decline in abundance of tilefish (*Lopholatilus chamaeleonticeps*) in the northwestern North Atlantic in 1882 probably was an example of a catastrophic single-factor effect (Bigelow and Welsh, 1925). Most natural fluctuations in abundance of fishes cannot be expected to have a simple cause. Thus, it would be naive to assume that variations in survival of fishes to commercial sizes could be explained adequately in terms of variations in only one, or even several, of the many variables in the surrounding medium, even if we knew what variables are important and how they operate. This question deserves much more careful attention than it has received in the past. Field studies must be accompanied, and often preceded, by controlled laboratory experiments.

DISTRIBUTION AND ABUNDANCE OF ESTUARINE NEKTON

Our knowledge of the distribution and abundance of estuarine nekton comes almost entirely from two sources: faunal surveys and fishery investigations. The literature is extensive and it would not be practical to attempt a thorough review here. Many comprehensive studies of the fish fauna of North American coastal areas have been published. Most of these, like Jordan and Evermann (1896-1900), Clemens and Wilby (1961), Barnhart (1936), and Bigelow and Welsh (1925), describe the entire marine fish fauna of an area and not estuarine species specifically. Others, like Smith (1907), Hildebrand and Schroeder (1928), and Gunter (1941, 1945) deal with the fishes of large estuarine systems. Many of the major works are cited at appropriate places in the text, and these, together with their literature citations, provide an extensive, although by no means complete, bibliography. Many of the major faunal surveys include abundance estimates, but the best estimates of absolute abundance have been derived from the fisheries or from scientific fishery investigations. Even these are not entirely satisfactory, for, by their very nature, nektonic organisms are difficult to sample quantitatively. Some of the best estimates, although they measure only the mature segment of a population, have come from a knowledge of fecundity and counts of eggs on the spawning grounds.

According to Odum (1959), although the individual range of nekton may be great, the geographic range of a species may be less than that of many in-

vertebrates. Nevertheless, some estuarine nektonic species have extensive geographical ranges. The Pacific herring (*Clupea pallasii*), for example, is distributed more or less continuously from the Bering Sea to San Diego Bay, a range of about 28 degrees of latitude and some 43 degrees of longitude. In a straight line between northern and southern limits, this is more than 2,000 miles. The Atlantic herring (*Clupea harengus*) also has a wide range, from the Arctic to temperate waters, and from one side of the Atlantic to the other. Within these ranges, however, both species are divided into subpopulations with more restricted ranges (Heineke, 1898; Rounsefell, 1930; Tester, 1937, 1946; McHugh, 1954).

Other nektonic estuarine fishes with wide ranges are some of the Pacific salmons, such as the red salmon (*Oncorhynchus nerka*). Alaskan red salmon from streams flowing into Bristol Bay in the Bering Sea have been caught on the high seas at least as far west as 167° E. longitude, not far from the east coast of Kamchatka, and chinook and steelhead salmon have been shown to travel even farther, from upper reaches of the Columbia River, far inland, to the vicinity of the Aleutian Islands, a distance of 2,500 miles (Hartt, 1960). Atlantic menhaden (*Brevoortia tyrannus*) occur from the Nova Scotia coast to the east coast of Florida, a range of at least 16 degrees latitude and 15 degrees longitude (Gunter and Christmas, 1960). Within this range there are apparently at least two subpopulations of *Brevoortia tyrannus* (Sutherland, 1963), but their ranges overlap considerably.

Other widespread nektonic estuarine species of the Atlantic coast of North America extend their range into the Gulf of Mexico and perhaps even farther south. Probably the most abundant of all Atlantic fishes is the bay anchovy (*Anchoa mitchilli*), which ranges from the Massachusetts coast to the Gulf. This is the most abundant species in Chesapeake Bay according to Massmann (his and personal communication). Although this is a small anchovy, which in the adult stage can easily slip through the meshes of the trawl used by Massmann, only one fish species was caught in greater numbers in many hauls made at all seasons. Gunter (1941) also found that this anchovy is present in greater biomass than any other species in the estuarine waters of the northern part of the Gulf of Mexico. Next in abundance are the menhaden, *Brevoortia tyrannus* on the Atlantic coast and *B. patronus* and *B. guntheri* in the Gulf. Certain abundant members of the family Sciaenidae have a similar distribution. The Atlantic croaker (*Micropogonias undulatus*) and the spot (*Leiostomus xanthurus*) are perhaps the most abundant members of this family among the estuarine nektonic community of the Atlantic and Gulf coasts of North America. They range from Massachusetts to Texas and support important commercial and recreational fisheries from New Jersey south. Gunter (1941) found that the mullet (*Mugil cephalus*) was the third most abundant species in Texas.

For comparison, the fish fauna of a New England

estuary can be cited. Stickney (1959) listed the more important nektonic organisms of the Sheepscot Estuary in Maine. He did not give the numbers of fish caught, but it is clear that herring-like fishes and cods were important. Fewer species were represented in his collections than in collections from the Chesapeake or the Gulf, and two notable differences were evident. Firstly, the Salmonidae, which are absent farther south, were important members of the estuarine nekton in northern New England. Two species were represented, the Atlantic salmon (*Salmo salar*) and the American smelt (*Osmerus mordax*). Secondly, the croaker family, an important group in southern Atlantic and Gulf coast estuaries, was apparently rare or absent along the New England coast.

Few estuaries of the types so common along the Atlantic and Gulf coasts of the United States are found on the Pacific coast of North America. The rivers of southeastern Alaska and British Columbia empty into deep fjords or protected inshore waters created by a barrier of islands and peninsulas that extend almost continuously from Puget Sound to Skagway, Alaska. Tidal amplitudes are so great in this region that the inshore waters mix rather quickly, and the estuarine nekton is quite different from that of the Atlantic. In other parts of Alaska the major rivers flow into fjords or directly into the sea. The Columbia River and other streams of the coasts of Washington, Oregon, and California have very small inshore estuaries or flow directly into the sea. San Francisco Bay is the only really large inshore estuarine body of water on the entire west coast of North America, and it is small in comparison with Delaware and Chesapeake Bays, the North Carolina sounds, and the coastal lagoons of Texas.

The typical native estuarine fishes of the Pacific coast are anadromous. They include the Pacific salmons (*Oncorhynchus*, *Salmo*, and *Salvelinus*), certain smelts of the family Osmeridae, lampreys (*Petromyzontidae*), and sturgeons (*Acipenseridae*). The introduced shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) are well established, and both species, especially shad, may now be more abundant in the Pacific than they are in their native Atlantic waters. Shad are being caught in increasing numbers by salmon gill-net fishermen in the Fraser River (Clemens and Wilby, 1961), and the numbers ascending the fishway at Bonneville Dam on the Columbia River now are close to half a million fish a year (L. E. Perry, personal communication). The extensive offshore estuary in the North Pacific is a vast and rich feeding ground which obviously contributes to the great abundance of the Pacific salmons of the genus *Oncorhynchus*, and it, perhaps, also could support larger populations of shad.

In estuaries like San Francisco Bay, clupeoid fishes and shrimp are important members of the nekton. An interesting method of collecting nekton in San Francisco and San Diego Bays is to dip fishes off the revolving screens that protect cooling water intakes of the power and light companies. Such col-

lections have shown that juveniles of several marine species enter these enclosed waters at times, as they do on the Atlantic coast (Herald and Simpson, 1955). The most abundant fishes, in decreasing order of total numbers caught in 248 collections from the intake in San Francisco Bay, were: surfperches (Embiotocidae, 10 species), many thousands; sculpins (Cottidae, 4 species), about 1,000; rockfishes (Scorpaenidae, 6 species), 951; herrings and anchovies (Clupeidae, Engraulidae, 3 species), 812; silversides (Atherinidae, 2 species), 387; toncod (*Micromugil proximus*), 354; lingcod (*Ophiodon elongatus*), 322; midshipman (*Porichthys notatus*), 280; sharks and rays (Squaliformes, Rajiformes, 8 species). Several anadromous species were caught: striped bass (*Morone saxatilis*), 168; smelts (Osmeridae, 2 anadromous, 1 marine), 19; lamprey (*Entosphenus tridentatus*), 7; and king salmon (*Oncorhynchus tshawytscha*), 2. Other groups, commonly found also in Atlantic coast estuaries, included flounders (4 species), white croaker, sticklebacks, pipefish, goby, and cusk-eel.

There is no counterpart on the Pacific coast of the mass inshore movement of larvae and young of offshore-spawning nektonic species into brackish nursery grounds that is such a striking feature of the ecology of most Atlantic coast and Gulf of Mexico estuaries. In British Columbia coastal waters, for example, Clemens and Wilby (1961) listed 272 species of fish. Only 21 of these species were described as entering the rivers, and 18 of these 21 were anadromous. The three marine species were the Pacific hake (*Merluccius productus*) which was described as a nuisance to salmon gill-net fishermen at the mouth of the Fraser River, the starry flounder (*Platichthys stellatus*), the young of which frequently move into streams, and the cockscomb prickleback (*Anoplarchus purpurescens*), a member of the family Stichaeidae, a common blenny which has been taken at the mouth of the Fraser River.

Aside from the anadromous species, which are much more abundant and important members of the estuarine community on the Pacific coast than in the Atlantic, the typical estuarine nekton of the Pacific coast is made up of the many species that inhabit the rocky intertidal zone, the fjords and channels between the coastal islands and the mainland, and the offshore estuary on the high seas. Important among these are the sharks, skates, and rays, especially the Pacific dogfish (*Squalus suckleyi*). This small, abundant shark is a great nuisance to fishermen, damaging their nets and greatly increasing their costs of operation. Many commercial and sport fishermen believe that dogfish are destructive of herring, salmon, and other species valuable to man. For these reasons, it has been proposed that a governmental bounty would encourage fishermen to destroy these pests.

The Pacific herring (*Clupea pallasi*) is an important member of the Pacific estuarine nekton. Adults spawn in the intertidal zone, where their adhesive eggs remain attached to eelgrass (*Zostera*) and other marine vegetation until hatching. The masses of eggs,

exposed on the beaches and rocks at low tide, attract large numbers of gulls and other birds. They are not protected from bird predation even when covered by the tide, for they are still vulnerable to ducks and other diving birds. The young remain in the bays and channels between the islands for most of their first year of life. Several flatfish species (Order Heterosomata) perform seasonal migrations from deep to shallow water. Others spend their entire lives in relatively shallow waters. Alverson *et al.* (1964) have made the interesting observation that a species of small-mouth flounder, which feeds on small benthic molluscs, crustacea, and echinoderms, always dominates the flounder population on the inner continental shelf; whereas large-mouth flounders, which feed on zooplankton and fishes, usually predominate on the outer continental shelf and slope. Other important members of the fish fauna near shore on the Pacific coast of Canada are the seaperches (Embiotocidae), sculpins (Cottidae), gobies (Gobiidae), and kelp-fishes (Clinidae). An important commercial fish of the inshore zone is the lingcod (*Ophiodon elongatus*). The Pacific cod (*Gadus macrocephalus*) makes a seasonal migration from deep to shallow water in spring.

Marine mammals are abundant members of the offshore estuarine community in the Pacific. They feed on many smaller forms of estuarine nekton, including some of commercial importance. Seals and sea lions sometimes are destructive to fishermen's nets and also damage fish in their catches. For these reasons it is commonly believed that these animals should be destroyed or that commercial uses should be developed to hold their numbers in check. Baleen whales are common in the Bering Sea and North Pacific Ocean at certain seasons, and some species come close to the coast. Sightings of baleen whales (Suborder Mysticeti) by vessels of the United States Navy (Fleet Intelligence Center, Pacific, 1961) give some idea of the distribution of these nektonic animals in the offshore estuary of the North Pacific (Fig. 6). Most of these plankton feeders do not consume other nektonic organisms directly, although they may take in eggs and small larvae, and some species do consume fish. Their gigantic food requirements, however, may limit the food supply of other nekton at certain times and places. The gray whale (*Rhachianectes glaucus*) migrates south in winter to calving grounds in shallow lagoons along the Baja California coast. Whales have no inherent need to favor brackish over saline waters, although the movement of gray whales and humpback whales (*Megaptera nodosa*) into coastal waters at the calving season may be because it is desirable for the young to be born in shallow water (Sliper, 1962). Their presence in estuarine waters must be principally a response to the presence of abundant food. The toothed whales, and especially porpoises, may consume large quantities of fishes.

Extremely interesting seasonal successions of nekton occur in most estuaries. In far northern waters the typical cycle swings from almost complete absence of life in winter to almost an incredible abundance of

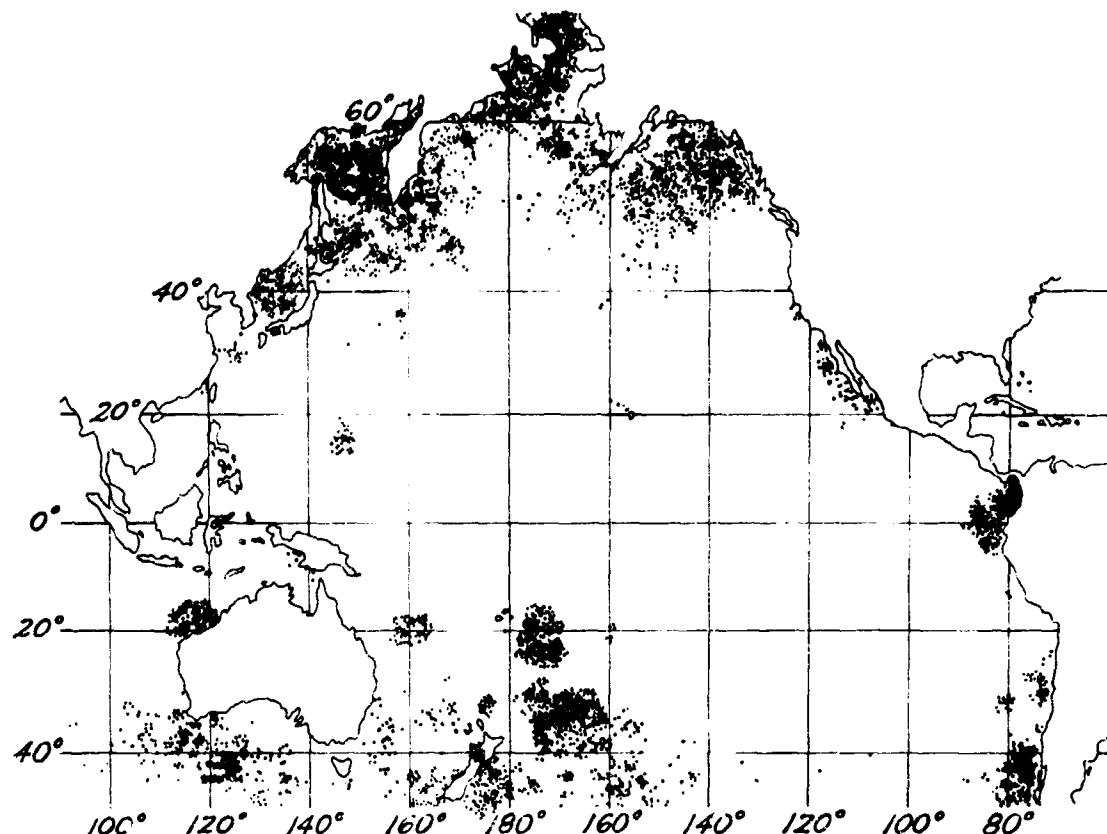


Fig. 6. Distribution of baleen whales in the Pacific Ocean, as indicated by sightings from U.S. Naval vessels.

nektonic life in spring and summer, as illustrated vividly by the following excerpt from a personal communication received in 1964 from Dr. William A. Smoker, Assistant Director of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. He was referring to Kitoi Bay on Afognak Island.

"In April the estuary was still in the grip of a severe winter. The bay would freeze over between snowstorms and then break up and clear with rain and tidal action. Temperatures were quite low, the water clear, and nothing was observed swimming in the water. Then very rapidly as the hours of daylight increased, temperatures rose, plankton blooms occurred, herring moved in from the ocean, salmon fry and fingerlings moved in from the streams, barnacle exuviae floated all over, hexagrammids were apparent, swarms of small cottids and flounders moved around in the littoral areas, seals moved in and first chased the herring schools around and then by midsummer chased the adult salmon right up the creek mouths. A vast school of pink salmon moved in and out of a creek mouth for weeks with the tides. One could stand on the dock at 10 o'clock at night and see all sorts of nekton activity as it broke the surface of the estuary. Such animals as puffins also might be called 'nekton'.

They occurred by the hundreds at Kitoi and dove and swam extensively for food, an occasional land otter would swim across the bay and dive for food, and even blooms of large jellyfish, which could be seen when the tide was slack, swimming with apparent purpose. With the decrease of daylight in late fall and winter, all of these forms disappear from the estuary and bay and again the water is cold, clear, and virtually devoid of nekton. On calm nights the skin of fresh water from the land runoff forms a layer of ice over the estuary which frequently breaks up in the tide and wind."

In temperate waters the variation in total biomass is less pronounced, but marked seasonal changes in species composition or size and age composition are common. For example, in Chesapeake Bay the smallest numbers of species are found in winter when the inshore estuarine community has been impoverished by migration of adults and most juveniles to the sea. These faunas are augmented through spring and summer by young fishes migrating downstream from nursery grounds in brackish water, and by adult fishes moving in from the ocean. The greatest diversity of species is reached late in the year (Fig. 7). Some northern forms, or deepwater species of the offshore zone, move into the Bay in winter, and some relatively non-migratory species concentrate in the chan-

Table 2. The major fishery products of the U. S. Gulf of Mexico ports for 1961 and 1962 in millions of pounds, as given by the U. S. Bureau of Commercial Fisheries.

	1961	1962
Menhaden	1,020.4	1,056.6
Shrimp ¹	133.8	141.7
Industrial Fishes (75% croakers)	78.0	96.0
Mullet	34.8	35.3
Crabs	36.3	26.8
Oysters	18.2	18.8

¹ Shrimp weights are on a heads-off basis and should be multiplied by 1.68 to give the total pounds.

and Texas waters in that order, but a few are taken in Alabama and Florida.

The shrimp catch is made up of four species: the brown shrimp, *Penaeus aztecus*; the white shrimp, *Penaeus flaviatilis*; the pink shrimp, *Penaeus duorarum*; and the seabob, *Xiphopenus kroyeri*. The pink shrimp is taken mostly in south Florida waters and the seabob amounts only to about one percent of the northern Gulf catch. During 1961-1962 Texas was the leading shrimp-producing state, but in 1963 a very fine crop of white shrimp brought Louisiana to the fore again.

"Industrial" fishes are made up of everything that the trawlers can catch after the fishes with hard bony parts are removed. The discarded species consist of the skates and rays, catfish, spiny boxfishes, cowfish and their relatives, and all crustaceans. Even so, two species of croakers make up approximately 75 percent of the catch. The common croaker, *Micropogon undulatus*, makes up approximately 50 percent and the flat croaker or spot, *Leiostomus xanthurus*, makes up 25 percent of the catch.

The striped mullet, *Mugil cephalus*, makes up most of the mullet catch, and the silver mullet, *Mugil curema*, comprises about 1.6 percent. Most of the mullet catch comes from Florida waters.

Over 98 percent of the crab catch reported consists of the common blue crab, *Callinectes sapidus*, the well-known species which extends from the Gulf of St. Lawrence to Uruguay. However, the stone crab, *Menippe mercenaria*, which is produced commercially mostly in Florida, has also been included in these figures, although its total contribution to the catch is only about 1.3 percent annually.

The oyster catch is made up totally of the common Virginia oyster, *Crassostrea virginica*. It is interesting that the center of production of this oyster is in two widely separated areas, the coast of Louisiana and Chesapeake Bay; their chief common characteristic is the estuarine nature of the waters.

Very few other species are taken in amounts greater than a million pounds and they are not given in detail in the table. Of the estuarine species in 1961 there were: 2.1 million black drum, *Pogonias cromis*; 2.2 million red drum, *Sciaenops ocellata*; 4.3 million

spotted weakfish, *Cynoscion nebulosus*; and 1.2 million pounds of whiting, *Menticirrhus* spp. Of the high-salinity fishes there were 6.8 million pounds of groupers of several species; 1.7 million pounds of king mackerel, *Scomberomorus cavalla* and *S. regalis*; 11.9 million pounds of red snapper, *Lutjanus blackfordi*; and 4.0 million pounds of Spanish mackerel, *Scomberomorus maculatus*.

The chief fisheries of the Gulf coast are based on one or two species of menhaden, one species of mullet, two species of croakers, three species of shrimp, one crab, and the oyster; or five fishes, four crustaceans, and one mollusc.

In 1961 the order of rank of the species was: menhaden, one billion pounds; brown shrimp, 39 million pounds; croakers, 39 million pounds; blue crabs, 35 million pounds; striped mullet, 33 million pounds; pink shrimp, 24 million pounds; flat croakers, 18.5 million pounds; oysters, 18.2 million pounds; and white shrimp, 14 million pounds. It should be noted that all shrimp weights are given on the heads-off basis and they should be multiplied by 1.68 to give the total figure of the catch.

During 1961 the fishery production of the Gulf States amounted to 1.377 billion pounds, of which 9.3 million pounds came from fresh water. Table 3 compares the catches of saltwater and estuarine species, using only those species which were taken in amounts of one million pounds or more. The catch of those fishes which have little or no connection with estuaries amounted to 24.4 million pounds, while the catch of estuarine species amounted to 1.332 billion pounds, including oysters and crustaceans. Every fish on the estuarine list has been included on the list of euryhaline fishes of North America (Gunter, 1956a), because they have been taken in fresh water when small; the same thing is true of the blue crab. The shrimp also enter water which is almost fresh, that is, 0.4 % salt for *Penaeus flaviatilis* and 0.8 % for *P. aztecus* (Gunter and Shell, 1958). In short, estuarine species make up about 97.5 percent of the total commercial fisheries catch of the Gulf States and saltwater species comprise about 2.0 percent, the remainder being freshwater species.

It should be stated that some of the catch of species listed here as estuarine takes place in the open sea in waters of oceanic salinities. This is particularly true of the shrimp and industrial fishes. Nevertheless, these animals are estuarine in the young stages. The largest fishery, however, that for menhaden, operates in estuarine waters. Christmas et al. (1960) showed that menhaden catches in Alabama, Louisiana,

Table 3. Gulf production of commercial fisheries in millions of pounds for those species taken in amounts of a million pounds and more (From Fishery Statistics of the United States 1961).

Freshwater species	9.3
Saltwater species	24.4
Estuarine species	1,332.2

and Mississippi were made in waters with salinities ranging from 6.2 to 31.6 ‰, and 88 percent of the catches were between salinities of 15 and 29 ‰. The average salinity for catches was 21.4 ‰, or about 60 percent sea water.

All production figures used were taken from various publications of the Branch of Statistics of the U. S. Bureau of Commercial Fisheries. (The 1962 figures had not been published at the time of writing. I am indebted to Mr. Hermes Hague, of the above office, for securing them for me.)

THE SPORTS FISHERY

Statistics on the sports fishery are scarce. During the years 1957-1958 and 1959-1960 Belden Associates (1961) made two studies of sports fishing on the Texas coast, restricted to red drum, speckled trout (squeteague), flounder, and black drum—all estuarine species and the most commonly taken sport fishes. The total catches for the two periods were 36,586,000 and 24,726,000 pounds, respectively. There are no similar estimates for Louisiana, Mississippi, and Alabama. The Florida State Board of Conservation and the University of Miami have published several surveys on sport fishing effort, the number of anglers, expenditures, charter boat catches, etc., but there are no total estimates by species. However, it may be surmised from the Texas figures that the annual sport fishing catch of estuarine fishes of the Gulf coast is at least 100 million pounds, and it may be considerably greater. Thus, the total catch of estuarine species on the United States Gulf coast now amounts to about 1.5 billion pounds.

TIDAL AND SALINITY CHARACTERISTICS OF GULF ESTUARIES

In Mobile Bay, the salty water comes in on the east side of the mouth and the fresh or low-salinity water apparently flows outward mostly on the west side of the opening, due to the Coriolis force. Thus, the east side of the bay up to about the middle reaches has a higher salinity than the west side of the bay. Several studies have shown that as the fresher waters flow out of the mouth of an estuary at the surface there is an inflow of saltier waters in the deeper layers (Bousfield, 1955; Ketchum, 1951; Pritchard, 1952; Riley, 1952).

American biologists have not paid much attention to the biotic and salinity divisions of brackish waters which have received considerable attention from the Europeans (Symposium on the Classification of Brackish Waters, 1959). The reasons for these two diverse views are fairly clear. The average bay system on the northern Gulf coast covers about 500 square miles or less and the same thing might be said of most bay systems of the United States except the Chesapeake Bay. The bays are comparatively small and the total salinity gradient from sea water to fresh water covers only a small distance. These bay systems also are subject to floods which may make them almost completely fresh, or to droughts and dry spells

when the salinity becomes quite high. The sudden influx of fresh water into Galveston Bay has been mentioned above. Nueces Bay was turned into a freshwater lake in 1935 (Collier and Hedgpeth, 1950). In the drier parts of the country, such as the south Texas coast, I have seen salinities rise to 64 ‰ in the upper bays which normally have low salinities, but this was during the greatest drought (1948-1957) recorded on this continent. Wide variations in salinity are fairly common, but less than the extremes of 1948-1957. For this reason American workers have not found it particularly helpful to use the oligohaline, mesohaline, and polyhaline terminology. Nevertheless, there are some waters to which these terms might be applied properly. Along parts of the Texas coast there is a double system of bays, commonly referred to as the front bay and the back bay. In Louisiana such waters as White Lake, Grand Lake, Lake Maurepas, and Lake Pontchartrain, are separated from the outside bays by narrow openings. During the big drought (Gunter and Shell, 1958) the waters of White and Grand Lakes did not rise above 4.5 ‰ salinity, while a great deal of the vegetation in the surrounding marsh was dying because of dryness. These waters are stable in the oligohaline condition. The same characterization may be applied to Lake Maurepas, and there are other small bodies of water along the Gulf coast that may be similarly characterized. The Bay of Biloxi, which is long and river-like, is always oligohaline in its upper reaches. Such situations are exceptions, however, and usually the salinity characteristics of the bay streams of the Gulf coast fluctuate to such an extent that oligohaline water may be completely obliterated except near the mouths of rivers, or it may extend over the whole bay. For these reasons American zoologists have been content to refer to the precise salinity at given stations without much reference to the European categories.

In addition to varying with rainfall and drainage, the salinity of the bays varies with the winds and tides. The clearest explanation of Gulf tides is given in Collier and Hedgpeth (1950). On the Gulf coast the maximum tidal variation is 26 inches with one maximum and one minimum a day. The maximum tide occurs only once a month. Every following day it declines a few inches and finally the variation is only two or three inches a day with the tide standing a little above mean low. It is further complicated by the fact that it changes over to two tides a day at the small fluctuation. In the bays these tides are damped, and they may come several hours later than they do on the outside beaches. When the winds blow hard from the south, water piles up on the coast and Chew (1964) has shown that the sea-level stand varies a foot or two even on the outside beach, depending on the direction of the prevailing winds over a period of a few weeks. In the winter when the winds blow hard from the north, a great many shallow areas in the bays are exposed and the water level drops considerably. The other extreme is when the hurricane tides come in at a maximum height of

about 16 feet. The highest lunar tides are only 26 inches on the outside beaches for a few days every month, and the tides are damped to lower heights in the bays; because of this, experienced boatmen pay very little attention to them. On the other hand they pay a great deal of attention to the way the wind is blowing and how hard, and how long it is supposed to last. It is even stated in the official tide tables that in the bays the periodic tide is negligible and the water levels depend principally on the wind. It is clear that wind conditions have considerable effect upon the salinity of the shallow waters of the estuarine areas of the Gulf.

Local heavy rains on the coast often raise the water level of the back bays and the relatively enclosed areas as the water drains quickly from the adjacent land. Tide gauge records have not proved this phenomenon, but it has been observed so many times by various people that there seems to be no doubt of the correctness of the observations.

In speaking of Texas bays, Collier and Hedgpeth (1950) made the following remarks concerning the relations of tides to the fisheries:

"The high levels observed during March and April for the spring months, and during September and October for the autumn, are spoken of as 'spring tides' and 'fall tides' respectively by coastal inhabitants.

"From the point of view of the coastal fisheries of the Gulf of Mexico this phase of tidal study is as important as any. Some of the principal fisheries are dependent upon the young gaining the protection and nourishment offered by the tidal flats during the early days of their lives. The degree to which a given year class is successful might depend upon the extent, both spatial and temporal, to which the tidal flats and low marshlands are flooded. This is variable from year to year, and, so far as the authors can learn, this factor has not been studied in connection with annual fisheries production. It is suggested here that such a study might prove fruitful on the Gulf Coast."

THE MARINE-ESTUARINE LIFE HISTORY

The general life history of most of the motile estuarine animals on the Gulf coast follows a similar pattern and, as was shown above, this includes most of the commercial species. The eggs are spawned at sea and the larvae somehow make their way into the low-salinity waters of the estuaries. The young animals develop in the estuaries and then return to or towards the sea. This is an extremely important phenomenon and constitutes a general law regarding most of the large motile estuarine organisms of the south Atlantic and Gulf coasts of the United States, and probably other estuarine coasts as well. Recognition of this phenomenon was so slow that no one deserves full credit for it, and appreciation of it came about so gradually that it stands as an example of how important generalizations are brought to light through the long laborious field work of a number of workers. Years ago marine biologists in the Chesapeake Bay area worked out the general life history of the blue

crab (Hay, 1905). They found that the fertilized females go to or towards the sea and spawn their eggs in high-salinity waters (Churchill, 1919). Later Sandoz and Rogers (1944) showed that the eggs and larvae would not survive in low-salinity water. The young crabs move back into low-salinity water and mature there, with the females finally returning to sea and completing the cycle. The same type of life history of the crab has been observed on the Gulf coast (Darnell, 1959; Gunter, 1950) and apparently it holds true over the whole range of the species. Darnell's paper gives an excellent summary of studies on the blue crab.

Viosca (1920) noted that post-larval white shrimp, *Penaeus flaviatilis*, on the Gulf coast enter the low-salinity waters and develop there, to return to sea as they mature, a fact which has been amply corroborated (Gunter, 1950; Lindner and Anderson, 1956; Weymouth *et al.*, 1933).

On the Atlantic coast Smith (1907) and Hildebrand and Schroeder (1928) noted such things as the fact that ripe mullet and croakers were not to be found in the bays, and that the very earliest larvae were found offshore. Pearson (1929) first showed specifically that important groups of fishes, the Sciaenidae, spawned offshore in high-salinity waters and the larvae entered the bays, sometimes "grimly" bucking the outflowing currents of the narrow passes of the Texas coast. Later research showed that on both the Louisiana and Texas coasts this general type of life history applies to nearly all the important motile species, especially those upon which the fisheries depend (Gunter 1938b, 1945, 1950).

Pearce and Gunter (1957) summarized the situation: "The young of many animals, usually thought of as marine, require areas of low salinity for nursery grounds. The distribution and abundance of the blue crab and of the commercial shrimp (*Penaeus setiferus*) on the South Atlantic and Gulf coasts are dependent on the presence of estuarine areas. The shrimp spawn in oceanic salinities; the early stages apparently require oceanic water, but the older larvae must reach bay waters or perish. The young shrimp grow up in the low-salinity bays and return to the sea. . . . roughly this cycle of spawning, growth, and movement in relation to salinity holds true for many important fishes and invertebrates on the Gulf coast. In general marine animals on such estuarine coasts move offshore as they grow older."

Additional remarks were made by Gunter (1961): "A number of workers on the Gulf coast have demonstrated that a great many of the important marine animals of that area have similar life histories. The adults spawn offshore and the young move back into the estuaries where they grow up in low-salinity waters; after a time they return to the sea and the larger adults of many species are found only in the sea.

"The preponderant macroorganisms, both in numbers of species and individuals, are mostly motile species which undergo the general type of life history

described above. In southern waters these are the mullet, menhaden, croakers, shrimp and crabs. Vast numbers of these animals may be found in estuaries at one time or another and in general the very smallest sizes are found in the lower salinities. Estuaries are predominantly nursery grounds."

There are some important organisms which are indigenous to bay and estuarine waters and never leave them. This includes a number of copepods and planktonic species, about which we know very little. It also includes several species of molluscs, of which the only commercially important one is the common oyster, and certain gobioid and cyprinodontid fishes and the palaemonid shrimp of the grass beds and shallows. Thus, populations of estuarine animals are broadly divisible into those that complete their life histories in the estuaries and those that use the estuaries as rearing grounds. The first group is generally sessile or small, and weakly motile; and the second is generally composed of larger, strongly motile species. It should be noted that the movements and life cycles of the second group have a resemblance to those of the catadromous fishes.

Striped mullet have even been recorded spawning 50 miles offshore from the mouth of the Mississippi River (Arnold and Thompson, 1958). This is a curious matter and it seems peculiar that the fish would find it necessary at times to go so far, since the young must develop in estuaries.

How the small delicate young of the offshore spawners move over the long distances from oceanic waters to the low-salinity estuaries, and what leads them to do so, are unanswered questions—we have general ideas only, but little specific information. The inflow of salt water along the bottom of the mouths of the bays indicates one way in which young enter the bays. Viosca observed that small shrimp entered Lake Pontchartrain in the upper layers of water of the two passes, the Rigolets and Chef Menteur, but they left the lake some months later in the bottom water layers. Pearson (1929) saw the larval sciaenid fishes struggling to enter Texas bays at the surface in the face of the outflowing tide.

The stages from the eggs to juveniles, during which transport from offshore waters to low-salinity areas is somehow effected, may be the most critical of all in the life histories of the important fishery animals of the Gulf coast. The problem may be broken down into three phases: (1) transport from the offshore waters to the vicinity of the passes or bay mouths; (2) transport through the passes into the bays, where currents are often quite strong; and (3) distribution within the bays after entrance has been obtained.

The first phase of the problem is most puzzling. The larvae must travel up to 50 miles in some instances and cross strong currents flowing parallel to the coast, and sometimes two of them going in opposite directions. The matter is further complicated by the fact that the eggs and larvae of mullet and sciaenids probably come in near the surface (Arnold and Thompson, 1958; Pearson, 1929), while the shrimp

have demersal eggs and the larvae apparently stay in the water layers below the surface. Groups of incoming larvae have never been traced satisfactorily and we do not know whether they touch land, so to speak, nearest to where they were spawned or many miles up or down the coast. If the adults spawn near their home bays and the larvae are carried far away, then there are curious aspects in the life histories of several common Gulf coast animals. But it would seem to be a matter of slim chance for larvae to reach the passes into Texas bays, which comprise less than two percent of the total coastline, unless they drift up or down the coast for some distance until they come to a pass.

The high tides, which come once a month, and the especially high tides of the spring and fall may have a great deal to do with the second phase, the movement of the young through the passes into the estuaries, as suggested by Collier and Hedgpeth (1950).

It should be mentioned here that contrary to the idea of the critical stages of life histories during inshore transport, there has never been any indication of a dearth of larvae coming into the estuaries. On the other hand, this apparent fact may be based on our ignorance of the true situation.

The third phase of larval or juvenile movement, distribution within the estuaries after entrance has been made, is probably as important as the first two phases, for the young must have living room and they cannot pile up, so to speak, near the entrances to the bays. Here, again, we have little knowledge. The movement of more saline water into the bays is certainly important with regard to larval transport within the bays. In addition, the young are growing in strength as they enter the bays and some of them swim quite well. On the Texas coast, young mullet, *Mugil cephalus*, after entering the passes in November or December, follow the shoreline to the back bays. It takes them approximately three weeks to cover a distance of sixty miles.

RELATIONS OF THE SALINITY FACTOR TO DISTRIBUTIONS OF ESTUARINE ORGANISMS

The lower salinity of estuarine waters is the outstanding difference between these waters and sea water, and salinity has an important influence on the life histories and distributions of estuarine organisms. One of the clearest indications of the salinity influence is the relationship of salinity gradient to numbers of species. The greatest numbers of marine species are to be found in high-salinity waters of the open ocean offshore from the bays and estuaries; as the salinity gradient falls through the sounds and bays and into fresh water, the numbers of species of organisms decline. This has been observed many times on many coasts; it is an example of the general phenomenon that numbers of species decline as the physical factors of the environment vary from the optimum. The optimum in ecological matters is generally defined as related in some manner to the maximum numbers of

organisms, and the maximum numbers are said to exist at the optimum, all of which is somewhat circular. Whatever the basic philosophy of the situation may be, the numbers of species of marine organisms decline with the salinity gradient or, conversely, increase with it.

The importance of salinity to the distribution of marine organisms may be illustrated by the case of the common American oyster, *Crassostrea virginica*. Some workers have noted that this animal will apparently live and reproduce at seawater salinities, but it grows, lives, and reproduces best under estuarine conditions. Amemiya (1926) came to the conclusion that the developmental stages of this oyster took place best at salinities from 25 to 29 %. That seems a little high, although it is lower than the range for the other two (European) oysters with which Amemiya worked. In any case, it is well recognized that the American oyster, *Crassostrea virginica*, is confined to estuarine salinities from about 10 to 30 % which extend over a horizontal distance of several miles. This oyster has left what are probably the largest and most voluminous remains of any species that ever existed on the North American continent in the form of buried reefs which are now being dredged up as important sources of calcium carbonate and for other purposes. At higher salinities a second species, *Ostrea equestris*, is found, and on the Gulf coast a third species (*O. frons*) is found at still higher salinities (Gunter, 1951), usually not in the bays. According to Nelson (1938), the oyster larvae maintain themselves in the bays by falling to the bottom during the falling tide and swimming upward with the rising tide. Thus, the larvae seem to select the salinities at which the oyster will do best. The distribution of the three Gulf coast oysters from the mouths of the bays to far inland in the estuarine waters is in a sense foreshortened on oil well platforms in the open Gulf some miles offshore (Gunter and Geyer, 1955). The surface waters are of low salinity, and here the common oyster, *Crassostrea virginica*, grows on the templates of the platforms. At a lower level *Ostrea equestris* is found, and overlapping it and extending down to waters of oceanic salinity is the tree oyster, *O. frons*.

The above observation and many others indicate that the Virginia oyster lives best at estuarine salinities, and, furthermore, that it selects areas in which to grow. This might be called a physiological adaptation or adjustment. In addition, there seems to be another adaptation to a lower salinity which may be called indirect. Nelson (1938) and several previous workers have noted that enemies of the oyster are less abundant at the low salinities of the estuaries than in sea water. This led Nelson to theorize that the oyster left the sea and populated the estuaries partly to avoid parasites and predators. A study of the distribution of oyster enemies (Gunter, 1955) seems to indicate that, both as predators and parasites, they increase with rising salinities. Whether or not the oyster genus *Crassostrea* arose in the sea and later

invaded the estuaries, as Nelson's theory implies, or originated in the estuaries, as seems to be quite possible, the benefit derived is the same in either case. This leads to another concept, namely, that organisms with a marine-estuarine life history, as outlined above, have the distinct advantage of avoiding most of their predators and parasites during the early stages of life; this idea was advanced in connection with the life history of the white shrimp, *Penaeus flaviatilis* (Gunter, 1956b). It has been said that this shrimp and the other members of the genus on the northern Gulf coast are prime prey of all the large animals that live in, over, or around the sea. Nevertheless, the younger stages avoid a great many of their enemies by living in the estuaries. Thus, it appears that the strong tendency of the young of many coastal organisms to seek the lower salinity of the estuarine waters is an adaptation to lead them into a nursery ground where there are few enemies, diseases, and parasites.

Most estuarine organisms can live in or withstand full seawater salinities, but they are limited by salinity decline (Gunter, 1945, 1950). This is not always the case, however, and salinity tolerance varies with the life history stage of the organism. For instance, June and Chamberlin (1959) reported that young menhaden larvae, *Brevoortia tyrannus*, develop normally only in very low salinities until past a certain stage of growth; if they are subjected to high salinities before this stage, they develop abnormally.

The lower salinity limit which an estuarine organism can tolerate depends a great deal upon the temperature. In general, the higher the temperature the lower the salinity that can be tolerated, and in conformity with this principle greater numbers of marine organisms invade fresh water in the warm parts of the earth than in the colder parts (Pearse, 1950). It has been reported by Remane and Schlieper (1958) that the low point in numbers of organisms is at about 5 % salinity in the waters of northern Europe. On the other hand, in the more southerly climes of the Gulf coast we find that the low point is at the lowest part of the salinity gradient, and, in fact, marine species predominate in low-salinity estuaries that are virtually fresh water (Gunter and Shell, 1958).

Moebius (1877) supplied the terms "stenohaline" and "euryhaline" for organisms that cannot withstand and can withstand variations in salinity. They are good terms, but it is difficult to apply them precisely because there are many degrees of euryhalinity. In the Laguna Madre region of Texas, I took some small fish (*Menidia beryllina*) in hyperhaline water of 71.3 % salinity. After a cloudburst, the salinity dropped to 2.2 % within several hours to a few days, the precise time being unknown. The *Menidia* remained, and a very few *Cyprinodon variegatus* also remained in greatly reduced numbers. The change in osmotic pressure of the medium was from about 45 to 1.5 atmospheres. There are very few aquatic organisms except the air breathers that can survive the abrupt change from fresh water to pure sea water or the reverse. Such organisms would be completely

euhaline. However, conditions where such abrupt changes occur naturally are quite rare and it seems rather extreme to set such conditions as the measure of complete euhalinity. Therefore, I have set the definition of complete euhalinity on a different base and call a euhaline animal one which during its life history is found in both fresh water and full sea water (Gunter, 1942a). A list has been compiled of 161 species of fishes from North America that fall in this category (Gunter, 1950; Gunter and Hall, 1963). Possibly there are several hundred such organisms in the world, and a complete list may be prepared some day.

The salinity limits at which many organisms have been taken have been recorded, and the ranges are broad. Nevertheless, the salinity range at which the organisms are most commonly taken may be small, compared to the total range over which they may be found. There are many examples of the percentages of fishes and invertebrates, taken at various salinities on the Texas and Florida coasts, which show greater abundance at various salinities. Work in the Laguna Madre of Texas has shown, for instance, that several organisms may be taken in this hypersaline area at salinities up to 80‰, although they are common only up to 60‰ and quite rare above that salinity (Simmons, 1957).

The most complete analyses of this situation, to this writer's knowledge, concern the three commercial penaeid shrimp of the South Atlantic and Gulf coasts of the United States. The data were collected by me in Texas about twenty years ago, by Dr. Harold Loesch in Mobile Bay some ten years ago, and during the past three years in all Texas bays by the Texas Game and Fish Commission personnel.

The known salinity limits of these shrimp on the northern Gulf coast are:

<i>Penaeus flaviatilis</i>	0.42–45.0‰
<i>Penaeus aztecus</i>	0.80–60.0‰
<i>Penaeus duorarum</i>	2.7–60.0‰

These figures are from various sources. The upper limits were derived from Simmons' (1957) studies in the Laguna Madre. Both Simmons and Breuer (1962) noted that the brown shrimp, *P. aztecus*, enters waters of higher salinities than the pink shrimp, *P. duorarum*, but these are within the hypersaline ranges. The white shrimp, *Penaeus flaviatilis*, seems to be less salinophilous than the other two species. Other information shows that the rank of these shrimp in order of their preference for low-salinity water is the white shrimp, the brown shrimp, and the pink shrimp. The pink shrimp is taken in greatest abundance in the Dry Tortugas area of Florida and the Bay of Campeche, both highly saline areas. The brown shrimp is taken in greatest abundance on the dry Texas coast, and the white shrimp is produced in greatest numbers about the vast estuarine area of the Mississippi River (Gunter, 1962). Salinity is a limiting factor to distribution of shrimp, but it is

certainly not the sole limiting factor. For instance, the pink shrimp, which is produced commercially in the smallest numbers of these three species, is the only one found continuously all around the coast from North Carolina to Yucatan. There are three discrete separated populations of the white shrimp. One extends from North Carolina to the St. Lucie Estuary on the east coast of Florida; another from about Apalachee Bay, Florida, to south Texas and northern Mexico; the third is in the lower part of the Bay of Campeche in Mexico. The brown shrimp extends from North Carolina to about Miami and then picks up again in the northern Gulf at about Apalachicola Bay and extends from there to Yucatan. Why the white and brown shrimp are not found in the estuaries of southwest Florida is unknown. Apparently their absence is not related to salinity.

The studies referred to above in Texas waters and Mobile Bay relate to the distribution of post-larval shrimp at various salinities within the bay systems. In Mobile Bay it was found that the white shrimp are most abundant at salinities from 1 to 5‰, and twice as many shrimp are taken at salinities below as above 15‰. In the same area the greatest abundance of brown shrimp was at 25 to 30‰ and practically none were taken at salinities below 5‰, although the shrimp were quite abundant between 5 and 15‰. In Texas waters, the greatest abundance of white shrimp was in the salinity range of 5 to 10‰, and below and above 10‰ the average numbers taken per haul in trawls were 107 and 20 respectively. The brown shrimp were most abundant in a salinity range of 10 to 20‰. Between the ranges of 1 and 10‰, the average catch per haul was 19.5 and above salinities of 10‰ the average catch was 60.9. In the Texas catches recorded by the Game and Fish Commission, 97.5 percent of the pink shrimp catch was taken at salinities above 18‰. It appears that the distribution of the young shrimp as they develop in the bays is quite different among the three species and follows a pattern of preference of low and high salinity.

Such preference may also be deduced by commercial production: in Texas waters the average salinity at which white shrimp were caught, including the open Gulf, was 16.00‰ (Gunter, 1950). In the Texas bay waters alone, the average salinity was 8.8‰. In Mobile Bay waters the average salinity at which white shrimp were caught was 12.7‰. In Mobile Bay brown shrimp were taken at an average salinity of 16.5‰; in Texas bays the mean salinity was 18.9‰. In Texas bays the average salinity where pink shrimp were caught was 25.0‰ (Table 4).

The salinities in which these animals are found in the greatest abundance are considerably more limited than the total range over which they live. The same thing has been shown many times for the invertebrates and fishes, especially in Caloosahatchee Estuary (Gunter and Hall, 1963). The situation revises Elton's idea (1927) of many years ago that an animal ordinarily does not invade an environment where it can-

Table 4. The salinity ranges, proportions above and below 15‰, and mean salinity at which three species of shrimp (Family Penaeidae) were caught in Mobile Bay, Alabama, and in Texas waters; 117,349 whites, 71,100 browns, and 882 pink shrimp were involved.

Known salinity range; ‰	Proportions										Mean salinity, all specimens (‰)	
	Mobile Bay					Texas					Mobile Bay	Texas
	Below 15‰	Below 18‰	Above 15‰	Above 18‰	Below 15‰	Below 18‰	Above 15‰	Above 18‰				
White shrimp	0.42-45.0	2	-	1	-	3	-	2	-	12.7	8.8	
Brown shrimp	0.80-60.0	4	-	7	-	2	-	4	-	16.5	18.9	< 18‰ >
Pink shrimp	2.7-60.0	-	-	-	-	-	1	-	32	-	25.0	

not survive well. This revision is contrary to some ideas that the wildlife biologists have gained in the past thirty years or so. They speak quite often of animals living in "submarginal areas", the inference being that such areas are not the optimum but certain individuals are forced to live there because the good environment is already occupied. I believe that the same thing holds true in the distribution of estuarine organisms in the bays with respect to salinity and other factors.

Although the three chief commercial shrimp have somewhat different seasons for invading the estuaries, they may all be found there during the warmer months, but with different distributions. The same thing holds true for various fishes. These animals are not spread evenly over the bays, but are somewhat separated because of salinity and other factors. Thus, there are no barren bottoms in the bays. They are all productive, and that is one reason why the whole estuarine area is fertile.

SOME CYCLIC PHENOMENA IN THE GULF ESTUARIES

Seasonal changes are among the first phenomena that man noted concerning animal life. Most animals have seasonal variations with more or less cyclic or rhythmical abundance and these are largely correlated with the breeding cycle, although other factors are involved. The changes in numbers in fishes in a given locality are brought about by an influx of young hatched and raised in the region, or a migration of young or old individuals from another locality. The young may be moving from or to the nursery grounds. The older animals may be moving to or from the spawning grounds, or on a seasonal migration brought about by changes in the environment.

These matters have been discussed and their importance concisely stated by Pearse (1926): "The annual cycle of many species of animals is made up of a series of stages in a characteristic life history or of a characteristic series of periods of rest and activity which are closely correlated with seasonal succession. Long established correlations operate in such a way that seasonal environmental changes serve to stimulate animals to appropriate activities or inactivities

and cyclical physiological changes within animals prepare them to react properly with recurring seasonal events."

Elton (1927) made the following statement: "The numbers of very few animals remain constant for any great length of time, and our ideas of the workings of an animal community must therefore be adjusted to include this fact."

After a count of the numbers of fishes taken in trawls in Louisiana between October, 1931, and March, 1934 (Gunter, 1938b), it was obvious that the greatest numbers of an animal species occur immediately after the breeding season when the young come into existence. However, the peak seasonal numbers of estuarine species detected depend on the type of collecting gear used in making the studies. Elton (1927) made some remarks related to succession which are applicable here: "It is almost impossible to make even a superficial study of succession in any large and complicated community, owing to the appalling amount of mere collecting which is required, and the trouble of getting the collected material identified. When one has to include seasonal changes throughout the year as well, the work becomes first of all disheartening, then terrific and finally impossible." This is a rather pessimistic philosophy and it is not much comfort to the marine ecologist or zoologist who must work in an area which is never simple.

In the face of the impossibility of working out these problems (Gunter, 1938b), such phenomena as seasonal variation in abundance should be studied and as many legitimate conclusions drawn from them as possible. I have stated (Gunter, 1938b): "It seems very probable that only by such forward inclining movements will the life histories of fishes and their interrelationships with their environment be worked out." It might now be more accurate to say that a great deal of information can be gathered by such methods. In any case, some interesting information was gathered in this initial attempt. It was found that, for 11 species of common fishes "... there was a recurrent, sequential phase in the life history or annual cycle of the fish, when there was a sharp abundance mode", and these fell at certain times of the year. Other fishes had wider periods of increased abun-

dance. Two species came and went at certain times of the year so that their arrivals and departures could be predicted with some accuracy. The smaller fishes were practically always found in bay waters, while the larger ones were taken in the Gulf, and it was quite evident that bay waters act as nursery grounds. It was also surmised that most species spawn in the Gulf and certain exceptions were listed. It was noted that young individuals of many species preferred or were able to stand low temperatures and salinities of the Louisiana bays during the winter better than the older fishes, and this writer (Gunter, 1938b) stated:

"A very clear seasonal cycle and seasonal biological succession was observed in this region. There is a period of low temperatures during the winter in the bay. In the winter and spring the salinities are quite low. At this time the water at the upper part of the bay is practically fresh. The condition extends somewhat to the outside. On two consecutive years in the late winter and early spring, *Cynoscion nebulosus* was taken in the gulf. The alligator gar was also taken in the gulf during these months. At the same time the fresh-water catfish, *Ictalurus furcatus*, and the river shrimp, *Macrobrachium ohionis*, appeared in the bay. The migration of the latter animal into brackish water has been recorded before by Gunter (1937). These animals are probably more influenced by salinity than temperature. On the other hand *Urophycis floridanus* came from deep water to the bay in winter and the only appearance of *Cynoscion nothus* in the bay was noted in the months of December, January and May. With these two fishes temperature and not salinity was probably the governing factor.

"During the winter sharks, jackfish and many of the *Carangidae* absented themselves from the bay as well as from that part of the gulf explored by the trawls. In the summer as *Urophycis floridanus*, the fresh-water catfish, and the river shrimp retreat to their respective abodes, the sharks, jacks, threadfins and others return to the shore waters of the gulf. As the summer progresses and the temperatures and salinity of the bay rise some of these fishes move into it and remain there until autumn and the return of low temperatures, whereupon they move back into the gulf and later depart for deep water as the river shrimp, fresh-water cat, and *Urophycis floridanus* return, thus completing a cycle."

In 1941 and 1942 more extensive studies were made on the south Texas coast over a period of eighteen months. This included both invertebrates and fishes collected by minnow seines, beach seines, trammel nets, and trawls. The area covered included two connecting bays, one behind the other, and the open Gulf and the Gulf beach. Considerably more information was collected (Gunter, 1945, 1950), and although in many ways the seasonal cycle problems were clarified, because of the increasing detail it becomes considerably more complicated to describe.

During the spring, many fishes which are taken only in the Gulf during the winter or which are absent entirely begin to come into the bays. Some of them

go only into the seaward bay and many that go into the back bay are taken there only rarely in the summer and fall. At the same time several fishes which do not enter the bay appear in the Gulf catches only in the summer. Many fishes which migrate largely into Gulf waters in the fall and are uncommon in the bays during the winter return in large numbers in the spring. This influx into the bays continues through the warm months and some species are not found in the bays until late summer or fall. Many fishes begin to leave the bays in the early fall and winter and some of these are found in the Gulf during periods varying from one to three months in midwinter. Some fishes disappear from the bays entirely, as well as from the shallow Gulf. With the exception of the stingaree, no sharks or rays are caught in the winter. Several of the beach fishes disappear in the winter, and species that are taken only a few times are caught only in the Gulf during summer. Taking all migrant species into consideration, the general movement to the Gulf starts in October and continues into December. Likewise, most fishes return to the bays from February to April. It has been noted repeatedly that when a fish species is present in both bays, it disappears from the back bay first and reappears there later than in the front bay. For instance, one flatfish was not found in the back bay from October to May but was absent from the front bay only from January to March.

The large general exodus of the fishes from the bays in the fall is the most noticeable aspect of the seasonal cycle. The exodus includes the commercial shrimp and other penaeids. However, there is a counter-movement of a few species. The Gulf hake appears in the Gulf and bays in the winter after a sudden drop in temperature. It remains until the spring when the temperature rises considerably. In mild winters the fish does not come into the bays at all. Similarly, a species of sand trout does not enter the bays except during the winter, and the tonguefish, *Synphurus plagiura*, is found there only during the November-April period. The seabob shrimp moves into the lower bay only in the winter. Mature mullet and redfish return to the bays after spawning in Gulf waters in early fall and they are followed until mid-winter by hordes of young mullet, croakers, and redfish.

Several species of fishes, the common shrimp, and the blue crab, spawn in the Gulf near the passes. The young of many fishes spawned in the shallow Gulf move into the bays in winter and spring and remain in the bays during the spring and summer. Most of the fishes which leave the bays when cool weather begins are the young which have been in this nursery area during the warm months. The other major component of the fall seaward migration is the spawners going to the Gulf.

"It appears that the temperature cycle is chiefly responsible for the seasonal movements and other recurrent cyclic activities of the fishes under discussion. The temperature cycle is definite while the general salinity changes are not nearly so regular. The win-

ter and spring in general are the times of greatest rainfall but this is not always the case. A salinity gradient from a very high to very low salinity is more or less maintained at all seasons and a migratory animal could presumably take its choice so far as salinity of the environment is concerned. Such a wide salinity gradient is on the other hand not present at any given season in the shallow Gulf waters. In a few instances there are indications that either temperature or salinity is clearly more operative than the other factor in influencing the movements or presence of a species in a given environment at a given time, but mass movements coincide with the temperature cycle. Both of these important physical factors, salinity and temperature, have definite limiting and differential effects, which are difficult to separate merely by observation. Nevertheless, it appears that temperature is the chief factor affecting and initiating seasonal migrations and other seasonal cyclic actions of the fishes of this coast" (Gunter, 1945).

Pearson (1929) worked on the life histories of fishes of the family Sciaenidae in Texas and gave some information on their cyclic movements. Weymouth *et al.* (1933) did the same thing with commercial shrimp in Gulf and south Atlantic waters. The earliest observations on the seasonal phenomena of marine organisms probably concern the oyster. On the Gulf coast the oysters get fat in winter and become very poor in the summer and fall after they have spawned and in October the Gulf coast oysters are in poorest condition (Gunter, 1942b). There is a steady improvement until spring. This situation is quite different from that in the northern part of the oyster's range, where it quits feeding and remains in a quiescent state during most of the winter. The greatest fatness of the oyster in those waters occurs in the spring and fall. It appears that the fatness of oysters corresponds to the peak bloom of plankton organisms which occurs during the winter on the Gulf coast with only one peak a year. The food of the oyster consists chiefly of small flagellates and we know little about them; they are virtually impossible to collect and handle because of their minute size and fragile nature. A great deal needs to be done in this field of basic production, and probably the best approach would be through analyses of chlorophyll or other plant pigments in the water. There is a suggestion that the peak season for diatoms also occurs in winter in southern waters. However, diatoms are probably not important as oyster food.

ESTUARINE POPULATIONS

Thirty-three years ago it was inconceivable that some day we might be able to arrive at reasonable estimates of the total populations of certain important marine species. In view of the accelerating increase in technological improvements this attainment may be possible at some time in the future. Nevertheless, those interested in the populations of marine animals could do no better at that time than to estimate what

were called the relative "species mass" of certain fishes. This means that the species which were most abundant were estimated as one being more plentiful than the other, without any estimates of the total species mass. (The term "species mass" is more appropriate than "biomass", which is so commonly used in ecology for the total mass of single species; it seems that biomass would be more appropriate to the total living component of all species within a given environment.) The first estimates were based on simple counts of the fishes taken in trawls on the Louisiana coast (Gunter, 1936, 1938a). It was concluded that the most abundant fish in the trawl catches was the common croaker, *Micropogon undulatus*. It was further shown that the most abundant families of fishes consisted of the Sciaenidae (croakers and drums), Engraulidae (anchovies), Ariidae (catfishes), and Clupeidae (chiefly menhaden). In a later paper (Gunter, 1941) these estimates were refined mostly on the basis of general observations, and consideration was given to the fact that mullet and menhaden are not often taken in trawls and that the anchovies are so small that they generally slip through the meshes of the nets. Thus, it was estimated that the order of greatest species mass of the most abundant fishes was (1) the anchovy, *Anchoa mitchilli*; (2) the menhaden, *Brevoortia patronus*; (3) the mullet, *Mugil cephalus*; and (4) the croaker, *Micropogon undulatus*. The bay anchovy is found mostly in low-salinity waters, as its name indicates, but *Anchoa hepsetus* is relatively just as abundant at higher salinities in the shallow Gulf.

Later, much more extensive work was done in Texas bays utilizing small minnow nets, trawls, train-mel nets, and large haul seines (Gunter, 1945). It is difficult to compare the relative abundance of the anchovy, which is taken in great numbers only in fine-mesh nets such as bobinet cloth, with that of the redfish, *Sebastes ocellatus*, which can be caught only by large-mesh nets. Therefore, the general observations of the commercial catch and schools of fishes were taken into consideration.

The estimates of relative abundance were the same as those given previously and there is little reason to revise the estimates during the ensuing years. Further, these estimates were made long before the menhaden industry which landed over a billion pounds from Gulf waters in 1961 and 1962 was established; nevertheless the menhaden probably is exceeded in species mass by the bay anchovy, *Anchoa mitchilli*. Attention should be called to the fact that the three top species as given are all feeders at the base of the food chain. The anchovy and the menhaden are plankton feeders, and the mullet eats the mud or surface of the sand and even sucks the slime from the sides of boats, pilings, etc. The croaker seems to be an omnivorous bottom feeder.

An attempt to get some idea of the relative abundance of shallow-water Gulf fishes was made by Haskell (1961), who concluded that the catch of the

trawlers for industrial fishes (those canned for cat food or reduced to meal) landing at Mississippi ports consisted of about 50 percent croakers.

The environment of the animals considered here may be classified or divided into several parts. The first large division is the Gulf and the bay or estuarine region (the inland salt waters). Apart from differences in salinity there are other differences between these two areas. The Gulf waters are deeper and are not subject to such extreme changes in temperature. The muds of the Gulf bottom are firmer than those of the bays, which in some places are ooze. The shallows of the Gulf beach are monotonous stretches of sand without macroscopic plant life or cover, while the shallows in the bays are covered in places with grass and algal growths. This does not hold true, however, for the waters around the mouth of the Mississippi, and I have never seen an algal bed in Louisiana. The great marshes of that state, on the other hand, cover some 15 to 18 thousand square miles and they are partially flooded by high tides.

The bay area may be divided into three parts, deep or offshore waters, oyster reefs, and the shallows or inshore waters. The offshore waters range from 4 to 12 feet in depth and are typically mud bottom without vegetation. The inshore shallows are commonly known as flats. These flats line the shores of all bays and may extend from a few yards to over a quarter of a mile in width. They are usually around two feet deep and drop off rather sharply to deeper water at the outer edge. Since the tidal exchange is small in this area, the flats are rarely uncovered, even in part, but during heavy northerns the flats may become partly dry. The bottoms of the flats are not alike; some places are covered with growth of algae and higher plants, while others are bare sand, ooze-like mud covered with decaying vegetation, or hard clay-like mud pitted so that the bottom resembles that of ponds waded and trampled by livestock. Oyster shells in various states of erosion form the bottoms in other places. Over most of the flats there is usually cover of some kind for small fishes and crustaceans.

The most numerous fishes on the bay flats, shown by minnow seine catches are the silverside, *Menidia beryllina*, the cyprinodontid, *Cyprinodon variegatus*, the anchovy, *Anchoa mitchilli*, the mullet, *Mugil cephalus*, and the cyprinodontid, *Fundulus similis*. Vast numbers of the shrimp, *Palaeomonetes* spp., are present, especially among vegetation. The fishes, *Brevoortia patronus* and *B. gracilis* (in the western Gulf only), *Menidia beryllina*, *Engraulis pictus*, *Fundulus grandis*, *Mugil curema*, *Lagodon rhomboides*, *Micropanchax undulatus*, and *Gobiosoma boscii* are common, but much less numerous. Pipefishes and small gobies are probably more abundant than the catches indicate because they live in vegetation and easily elude seines. The Gulf sardine, *Harengula macroura*, is taken only sporadically in the lower bay.

The two silversides, the cyprinodontids, and the palaeomnid shrimp are taken only on the compara-

tively narrow strip of flats next to shore. They do not inhabit deeper waters where the salinity and temperature are suitable. A chief requirement for these animals is ample cover and protection, which is not obtainable in the deep waters. The reactions of hiding and seeking cover are commonly observed when the small shore fishes are disturbed. The galaemonid shrimp and the cyprinodontids, with the rare exception of *Fundulus similis*, are not found on the Gulf beach. The silverside, *M. beryllina*, is uncommon there and these animals may be said to be typical of the bay flats. Certain gobies and pipefishes are occasionally taken in deep water in the bays, but they are rarely taken in the Gulf, and they, too, may be said to be typical inhabitants of the bay flats.

Mullet are largely shore and shallow-water fishes, but they are larger than the cyprinodontids and silversides and are occasionally found in deep waters, although the young probably do not normally leave the flats. The young of many species of fishes in the bay waters, as well as young blue crabs, young penaeid shrimp, small croakers, young menhaden, and the anchovy, *Anchoa mitchilli*, are found in the shallows and outnumber the purely shallow-water species. *Anchoa mitchilli*, *Lagodon rhomboides* and *Brevoortia patronus* were the only three species taken in about equal abundance in both deep and shallow waters. The smaller fishes of the last two species were taken in shallow water and the larger fishes in deeper water.

Large fishes and crabs also visit the flats to feed, and practically all commercial fishing for food fish is done here with trammel and gill nets, trotlines, and pole and line. Floundering with gigs is also done on the flats.

The bottom areas of deep water of the bays are inhabited by large numbers of croakers, *Micropanchax undulatus*, anchovies, *Anchoa mitchilli*, catfish, *Galeichthys felis*, and sand trout, *Cynoscion nebulosus*. Also common at times in this environment are *Bagre marina*, *Eucinostomus janthinus*, *Brevoortia*, *Polydactylus octonemus*, *Dorosoma cepedianum*, *Lagodon rhomboides*, *Squalidae mexicana*, and *Orthopristis chrysoptera*. Some of these fishes are present more or less seasonally. *Bagre marina* and *Polydactylus octonemus* are absent in the winter. It is clear that the distributions of fishes in deeper waters and the flats of the bays are quite different. The penaeid shrimp, *Penaeus setiferus*, is also very abundant in the deeper waters of the bays. The blue crab, *Callinectes sapidus*, is common.

The sardine, *Harengula macroura*, the anchovies, *A. mitchilli* and *A. hepsetus*, the threadfin *Polydactylus octonemus*, and small pompano, *Trachinotus carolinus*, are the chief fishes of the shallow Gulf beach. Small mullet and the rough silverside *Menidia beryllina* are also common at times. In offshore waters the chief bottom fishes are the sand trout, *Cynoscion nebulosus*, the croaker, *Micropanchax undulatus*, the threadfin, *P. octonemus*, the catfish, *G. felis*, the moonfish, *Limen tetragonum*, the star drum,

Table 5. The order of abundance of the families of fishes taken with various collecting gear in the Gulf and in the bays.

Trawls		Minnow Seines		Large Nets	
Gulf	Bays	Gulf	Bays	Gulf Shallows	Bay Shallows
Sciaenidae	Sciaenidae	Engraulidae	Atherinidae	Sciaenidae	Sciaenidae
Polynemidae	Engraulidae	Clupeidae	Cyprinodontidae	Mugilidae	Clupeidae
Ariidae	Ariidae	Polyenidae	Engraulidae	Carangidae	Mugilidae
Heterosomatidae	Clupeidae	Mugilidae	Mugilidae	Ariidae	
Carangidae	Polyenidae	Carangidae	Clupeidae		

Stellifer lanceolatus, two flatfishes, *Syacium gunteri* and *Syphurus plagiusa*, and two sciaenids, *Leiostomus xanthurus* and *Menticirrhus americanus*. The shrimp, *Penaeus setiferus*, and the crabs, *Callinectes sapidus* and *Callinectes danae*, are also very common.

The mullet, *Mugil cephalus*, the speckled trout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*, are the larger fishes taken most commonly on the bay flats. The most common larger fishes on the Gulf beach are the spot, *Leiostomus xanthurus*, the mullet, *M. cephalus*, and the stingaree, *Dasyatis sabina* (Table 5).

The fishes and crustaceans and other animals living on the oyster reefs have not been studied closely in this country. The fishes typical of oyster reefs are not active swimmers and are equipped for living in and under oyster shells. They attach their eggs to oyster shells so the developing eggs do not drift away from the reef. The chief oyster reef fishes are *Opsanus beta*, *Gobiosox strumosus*, and several blennies.

The common oyster, *Crassostrea virginica*, probably has the greatest mass of any molluse on the Gulf coast. Buried reef masses are quite extensive down to 30 feet; at deeper depths they become less abundant, but they are known to extend down to 80 feet. Carbon dating has shown that all beds at depths of about 30 feet are approximately 6,000 years old. It appears that there was a rather rapid rise in sea level about 6,000 years ago and from that time on the oysters began to flourish. On the other hand, there are vast beds of *Rangia cuneata* in Louisiana and also large buried deposits of this clam. It is found in lower salinity waters than the oyster and it is possible that, at least in Louisiana, it exceeds the oyster in species mass. My own explorations have indicated that *Rangia cuneata* and *Polymesoda caroliniana* are the two most abundant mud-dwelling molluses on the Gulf coast, but *Modiolia* has been reported in great abundance in the Gulf estuaries. These are the most numerous molluses in the Gulf estuaries, with the possible exception of *Littorina irrorata* which may be observed in thousands on the grass in the marshes. The best information on the general distribution of estuarine molluses is given in Ladd (1951) and Parker (1956, 1959, 1960).

No doubt the annelid worms form a considerable part of the macroscopic animals in the Gulf estuaries. Certain general remarks may be fog: (1) Hedgpeth

(1953), but quantitative information is almost totally lacking.

The abundant animals in the Gulf fisheries in the order of their rank are: menhaden, penaeid shrimp, fishes of the croaker family, mullet, oysters, and crabs. Although precise quantitative information on the abundance of these organisms is not yet available, general observations made years ago indicated that they are the organisms with greatest species mass in the Gulf estuaries, and these observations have been substantiated by the rank of these species in the commercial fisheries of recent years.

GENERAL FACTORS RELATED TO THE FERTILITY OF GULF ESTUARIES

Basic fertility of the Gulf estuarine waters is limited by the nutrients entering them and, presumably, these come largely from the land. Very few measurements have been made of the nutrients in the Gulf or in the rivers emptying into it. Fifty-two analyses of Mississippi River water by the New Orleans Sewerage and Water Board in 1905 and 1906 showed a nitrate content of 2.5 ppm and a silicate content of 11 ppm (Gunter, 1953). Riley (1937) indicated that nitrogen in all forms except the gas was present in the river at New Orleans in amounts of 575 mg/m³. Sixteen mg/m³ of dissolved phosphorus was found in waters around the mouth of the river and Riley estimated that 47,000 kilos of dissolved phosphorus and 4,700 kilos of combined phosphorus flowed from the river into the Gulf during a day. Riley also showed that there was a large standing crop of phytoplankton in the waters around the river and that the effect of river nutrients extended as far east as Alabama. If the significance of Riley's studies had been appreciated at the time they were published, the great increase in Gulf fisheries production since then would not have come as a surprise. One analysis of water coming through the Bonnet Carré Spillway in 1950 (Gunter, 1953) showed the following concentrations: nitrates, 0.4 ppm; phosphates, 1.25 ppm; and organic nitrogen, 2.1 ppm. On this basis it was calculated that 5,900 tons of nitrates, 18,500 tons of phosphates, and 31,100 tons of organic nitrogen were added to the Louisiana and Mississippi waters affected by the spillway. The waters flowing out of the mouth of the river ran about ten times the Bonnet Carré discharge over a

37-day period. Viosca (1938) and I observed independently that following the spillway openings, which are, in effect, man-made crevasses, there seems to be greater production of shrimp, oysters, crabs, and estuarine fishes in the following years, even if the floods kill some of the marine organisms. As far back as 1912, Louisiana Conservation Commission annual reports said that crevasses were sometimes "a blessing in disguise" because they were followed by increased oyster production (Gunter, 1952b).

In all likelihood the chief characteristic of any fertile area is the continuous supply of nutrients. The waters of the Mississippi are not so rich in nutrient salts as the upwelling waters from the oceans, but the supply is certainly continuous. On the other hand, it might not be safe to say that shallow Gulf waters are more productive than the offshore waters, at least to the bottom of the photic zone. Perhaps we are only fishing organisms which are easy to capture, and this apparent fertility is really based on availability.

Attempts have been made to study fertility or basic production by measurements of chlorophyll or measurements of carbon incorporated into organic material. There are some deficiencies in this approach, however. The chlorophyll system does not necessarily produce at the same rate all the time. It has always been applied to the upper-water layers, but it has recently been stated that, by using red light, there is some photosynthesis even at a few thousand feet. If this idea is correct, the accepted limits of the photic zone will have to be changed. Then, too, there are certain colorless flagellates and bacteria which can utilize chemical energy for organic synthesis in the absence of light, and we do not know how abundant these organisms are. The Institute of Marine Science in Port Aransas, Texas, has carried on work on productivity, but that region is probably not so fertile as the crescent around the mouth of the Mississippi River, where there have been only two quantitative studies. Dawson (unpublished data) found that in 3.5 to 20 fathoms of water the drained weights of bottom organisms taken with a Petersen grab averaged only 1.4 grams. We thought this figure was extremely low and that the trawl catches were completely different. However, calculations of the weight of fishes and crustaceans taken in trawls, which may be called the epifauna, were almost exactly the same. Sitaramiah (1963) estimated the common nutrient materials, the oxygen production per cubic meter, the chlorophyll content of phytoplankton and attached plants, the dry weights of zooplankton per liter, and the dry weight of the nekton taken over 60 square meters. The average dry weight taken was 72.5 g and the weight of shrimp alone was 12.8 g.

I mentioned above that we are not sure of the relative productivity of the inshore and offshore waters of the Gulf, but there is a little information indicating that the bottom fauna is richer inshore. In the work referred to above, Dawson found that the mean weight of living organisms in Petersen grabs from 3.5 to 4

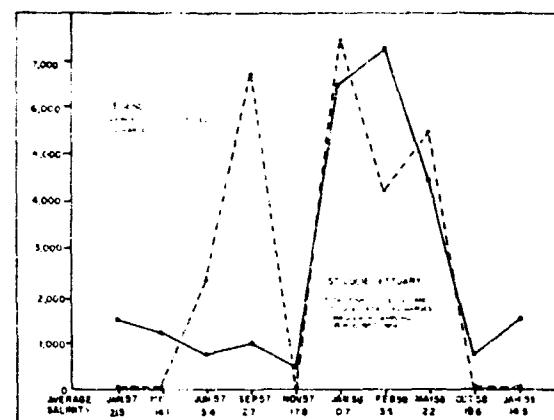


Fig. 2. The numbers of fishes caught in the St. Lucie Estuary during a biological investigation and the freshwater discharge into the area through the St. Lucie Canal (in cubic feet per second).

fathoms was 3.5 g, while at depths greater than 4 fathoms the figure was 0.8 g. Ragan (1962) found that the weight of bottom fish trawled over a three-mile distance averaged 213 pounds at 7½ fathoms, 151 at 15 fathoms, 163 at 25 fathoms, and 87 at 45 fathoms.

We are not sure what part salinity plays in the fertility of the coastal bays. The animals entering these waters, however, would probably have fewer predators during their earlier life stages than when they return to the sea. In this connection, Figure 3 illustrates an artificial situation in the St. Lucie Estuary on the east Florida coast. During certain years the Corps of Engineers is required to lower the level of Lake Okeechobee for the prevention of hurricane damage, and when this influx of fresh water corresponds with the breeding season of the anchovies, mullet, menhaden, and croakers, the abundance of the young of these fishes mounts in a striking manner. Probably both the lowered salinity and the influx of nutrient salts and organic nutrients play a considerable part in this phenomenon. In considering the matter of estuarine fertility, I should like to mention the recent remarks of Harvey R. Bullis, who has explored the northern coast of South America. He noted that the coastal waters between the Orinoco and the Amazon Rivers are estuarine to a hundred miles offshore, and that they are very shallow. This suggests that the area, whenever developed, is going to be in strong competition in fishery production with the northern Gulf of Mexico.

There are indications that animals such as the various species of penaeid shrimp develop in different areas in the estuaries. These animals seem to enter the bays at different periods and are thus somewhat isolated from one another, thereby avoiding competition. The bay bottoms are in continuous use, so to speak. It appears that a high rate of basic production continues over the whole year and is not limited by low temperatures.

It has been pointed out by ecologists that anaerobic bacteria could utilize food resources not available to other organisms. The supply of organic materials in the muds of the Gulf coast is tremendous. According to Priddy *et al.* (1955), the upper layer of sediments in the Mississippi Sound have an organic content of about 6.8 percent. The same authors found that in five samples with an organic content of 4.3 percent, the combined amino, nitrate, and nitrite nitrogen was 0.118 percent. Analyses of phosphates were not made. It is obvious there are millions of tons of organic materials and nitrogen compounds in the sediments of Gulf coast estuaries. The boring and tunneling action of the infauna and the scouring action of floods and storms permit this material to be reworked and brought to the surface. Man-made canals, channels, and dredge-cuts, as well as the disturbance caused by boats and trawls, enhance the reworking process. But what percentage of the sediment is reworked after burial is not known.

Knowledge of basic fertility on the Gulf coast is in a very primitive state. We have large fishery resources, some of which are used. We know that large amounts of organic and mineral nutrients are brought down by the rivers, but we do not know how much; we know little of seasonal characteristics but we suspect that the shallowness of the waters enhances the activity of photosynthetic organisms. Unfortunately, quantitative information on the most fertile part of the Gulf coast is practically nil. We suspect that the organic materials buried in the sediments act as a reserve food supply for estuarine organisms. We believe that we can perceive dimly most of the most important factors concerned with the richness of the Gulf estuaries, but most of the work which will lead to real understanding of the situation remains to be done.

LITERATURE CITED

- AMEMIYA, I., 1926. Notes on experiments on the early developmental stages of the Portuguese, American and English native oysters with especial reference to the effect of varying salinity. *J. Marine Biol. Assoc., Plymouth*, 14:161-175.
- ARNOLD, E. L., JR., and J. R. THOMPSON, 1958. Offshore spawning of the striped mullet, *Mugil cephalus*, in the Gulf of Mexico. *Copeia*, 2:130-132.
- BELDEN ASSOCIATES, 1961. The salt water fish harvest of Texas sportsmen, September 1959-August 1960. *Second Study for the Texas Game and Fish Commission*, 1-88.
- BOUSFIELD, E. L., 1955. Some physical features of the Miramichi Estuary. *J. Fisheries Res. Board Can.*, 12(3):342-361.
- CHEW, F., 1964. Sea-level changes along the northern coast of the Gulf of Mexico. *IG Bull.*; pp. 12-20. *Nat. Acad. Sci.*, Washington, D. C.
- CHRISTMAS, J. Y., G. GUNTER, and E. C. WHATELEY, 1960. Fishes taken in the menhaden fishery of Alabama, Mississippi and eastern Louisiana. *U. S. Fish and Wildlife Serv., Spec. Sci. Rept. Fisheries*; p. 369.
- CHURCHILL, E. P., 1919. Life history of the blue crab. *Bull. U. S. Bur. of Fisheries*, 36(870):95-128.
- COLLIER, A., and J. HEDGPETH, 1950. An introduction to the hydrography of the tidal waters of Texas. *Publ. Inst. Marine Sci., Univ. of Texas*, 1(2):120-194.
- DARNELL, R. M., 1959. Studies of the life history of the blue crab, *Callinectes sapidus* Rathbun, in Louisiana waters. *Trans. Am. Fisheries Soc.*, 88:294-304.
- DAWSON, C. E., 1955. A study of the oyster biology and hydrography of Crystal River, Florida. *Publ. Inst. Marine Sci., Univ. of Texas*, 4(1):279-302.
- ELTON, C., 1927. *Animal Ecology*. The Macmillan Co., New York.
- GUNTER, G., 1936. Studies of the destruction of marine fish by shrimp trawlers in Louisiana. *Louisiana Conserv. Rev.*, 5(4):18-46.
- GUNTER, G., 1937. Observations on the river shrimp, *Macrobrachium ohionis* (Smith). *Am. Midland Naturalist*, 18(6):1038-1042.
- GUNTER, G., 1938a. The relative numbers of species of marine fish on the Louisiana coast. *Am. Naturalist*, 72:77-83.
- GUNTER, G., 1938b. Seasonal variations in abundance of certain estuarine and marine fishes in Louisiana, with particular reference to life histories. *Ecol. Monog.*, 8:313-346.
- GUNTER, G., 1941. Relative numbers of shallow water fishes of the northern Gulf of Mexico, with some records of rare fishes from the Texas coast. *Am. Midland Naturalist*, 26(1):194-200.
- GUNTER, G., 1942a. A list of the fishes of the mainland of North and Middle America recorded from both fresh water and sea water. *Am. Midland Naturalist*, 28(2):205-326.
- GUNTER, G., 1942b. Seasonal condition of Texas oysters. *Proc. Trans. Texas Acad. Sci.*, 25:89-93.
- GUNTER, G., 1942c. Offatts Bayou, a locality with recurrent summer mortality of marine organisms. *Am. Midland Naturalist*, 28(3):631-633.
- GUNTER, G., 1945. Studies on marine fishes of Texas. *Publ. Inst. Marine Sci., Univ. of Texas*, 1(1):1-190.
- GUNTER, G., 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. *Publ. Inst. Marine Sci., Univ. of Texas*, 1(2):7-51.
- GUNTER, G., 1951. The West Indian tree oyster on the Louisiana coast, and notes on growth of the three Gulf coast oysters. *Science*, 113(2940):516-517.
- GUNTER, G., 1952a. The import of catastrophic mortalities for marine fisheries along the Texas coast. *J. Wildlife Management*, 16(1):63-69.
- GUNTER, G., 1952b. Historical changes in the Mississippi River and the adjacent marine environment. *Publ. Inst. Marine Sci., Univ. of Texas*, 2(2):119-139.
- GUNTER, G., 1953. The relationship of the Bonnet Carré Spillway to oyster beds in Mississippi Sound and the "Louisiana marsh"; with a report on the 1950 opening. *Publ. Inst. Marine Sci., Univ. of Texas*, 3(1):17-71.
- GUNTER, G., 1955. Mortality of oysters and abundance of certain associates as related to salinity. *Ecology*, 36(4):601-605.
- GUNTER, G., 1956a. A revised list of euryhaline fishes of North and Middle America. *Am. Midland Naturalist*, 56(2):345-354.
- GUNTER, G., 1956b. Principles of shrimp fishery management. *Proc. Gulf and Caribbean Fisheries Inst.*, 8:99-106.
- GUNTER, G., 1957. Wildlife and flood control in the Mississippi Valley. *Trans. N. Am. Wildlife Conf.*, 1957:191-196.
- GUNTER, G., 1961. Some relations of estuarine organisms to salinity. *Limnol. Oceanogr.*, 6(2):182-190.
- GUNTER, G., 1962. Shrimp landings and production of the State of Texas for the period 1956-1959, with a comparison with other Gulf states. *Publ. Inst. Marine Sci., Univ. of Texas*, 8:216-226.
- GUNTER, G., 1963. The fertile fisheries crescent. *J. Mississippi Acad. Sci.*, 9:286-290.
- GUNTER, G., and R. A. GEYER, 1955. Studies on

- fouling organisms of the northwest Gulf of Mexico. *Publ. Inst. Marine Sci., Univ. of Texas*, 4(1):37-67.
- GUNTER, G., and G. E. HALL, 1963. Biological investigations of the St. Lucie Estuary (Florida) in connection with Lake Okeechobee discharges through the St. Lucie Canal. *Gulf Res. Rept.*, 1(5):189-307.
- GUNTER, G., and W. E. SHELL, JR., 1958. A study of an estuarine area with water-level control in the Louisiana marsh. *Proc. Louisiana Acad. Sci.*, 21:5-34.
- HASKELL, W. A., 1961. Gulf of Mexico trawl fishery for industrial species. *Com. Fisheries Rev.*, 23(2):1-6.
- HAY, W. P., 1905. The life history of the blue crab, *Callinectes sapidus*. *U. S. Bur. Fisheries Rept.* (1904), Append.; pp. 395-413. Washington, D. C.
- HEDGPETH, J. W., 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Publ. Inst. Marine Sci., Univ. of Texas*, 3(1):110-224.
- HILDEBRAND, S. F., and W. C. SCHROEDER, 1928. Fishes of Chesapeake Bay. *Bull. U. S. Bur. Fisheries*, vol. 33, part 1.
- JUNE, F. C., and L. CHAMBERLIN, 1959. The role of the estuary in the life history of the Atlantic menhaden. *Proc. Gulf and Caribbean Fisheries Inst., 11th Annual Session*, pp. 41-45.
- KETCHUM, B. H., 1951. The exchanges of fresh and salt waters in tidal estuaries. *J. Marine Res.*, 10(1): 18-38.
- LADD, H. S., 1951. Brackish-water and marine assemblages of the Texas coast, with special reference to mollusks. *Publ. Inst. Marine Sci., Univ. of Texas*, 2(1):125-163.
- LINDNER, M. J., and W. W. ANDERSON, 1956. Growth, migrations, spawning and size distributions of shrimp, *Penaeus setiferus*. *Fishery Bull. U. S. Fish and Wildlife Serv.*, 56(106):555-645.
- LOESCH, H., 1960. Sporadic mass shoreward migrations of demersal fish and crustaceans in Mobile Bay, Alabama. *Ecology*, 41(2):292-298.
- LUND, E. J., 1957. Self-silting, survival of the oyster as a closed system, and reducing tendencies of the environment of the oyster. *Publ. Inst. Marine Sci., Univ. of Texas*, 4(2):311-319.
- MOEBIUS, K., 1877. *Die Austern und die Austernwirtschaft*. Berlin.
- NELSON, T. C., 1938. The feeding mechanism of the oyster. *J. Morphol.*, 63(1):1-61.
- PARKER, R. H., 1956. Macro-invertebrate assemblages as indicators of sedimentary environments in east Mississippi Delta region. *Bull. Am. Assoc. Petro. Geologists*, 40(2):295-376.
- PARKER, R. H., 1959. Macro-invertebrate assemblages of central Texas coastal bays and Laguna Madre. *Bull. Am. Assoc. Petro. Geologists*, 43(9):2100-2166.
- PARKER, R. H., 1960. Ecology and distributional patterns of marine macro-invertebrates, northern Gulf of Mexico. In *Recent Sediments, Northwest Gulf of Mexico, 1951-1958*; pp. 302-381. Am. Assoc. Petro. Geologists, Tulsa, Oklahoma.
- PEARSE, A. S., 1926. *Animal Ecology*. McGraw-Hill, New York.
- PEARSE, A. S., 1950. *The emigrations of animals from the sea*. The Sherwood Press, Dryden, New York.
- PEARSE, A. S., and G. GUNTER, 1957. Salinity. In *Treatise on Marine Ecology and Paleoecology*; vol. 1, pp. 129-157. Mem. 67. Geol. Soc. Am.
- PEARSON, J. C., 1929. Natural history and conservation of the red fish and other commercial sciaenids on the Texas coast. *Bull. U. S. Bur. Fisheries*, 44(1928): 129-214.
- PRICE, W. A., 1933. Role of diastrophism in topography of Corpus Christi area, South Texas. *Bull. Am. Assoc. Petro. Geologists*, 17(8):907-962.
- PRICE, W. A., 1947. Equilibrium of form and forces in tidal basins of coast of Texas and Louisiana. *Bull. Am. Assoc. Petro. Geologists*, 31(9):1619-1663.
- PRICE, W. A., 1954. Oyster reefs in the Gulf of Mexico. In *Gulf of Mexico, Its Origin, Waters, and Marine Life*. U. S. Dept. Interior Fish and Wildlife Serv. *Bull. 89*:491.
- PRIDDY, R. R., R. M. CRISLER, C. P. SEBREN, J. D. POWELL, and H. BURFORD, 1955. Sediments of Mississippi Sound and inshore waters. *Mississippi State Geol. Surv. Bull.* 82.
- PRITCHARD, D., 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *J. Marine Res.*, 11(2):106-123.
- RAGAN, J. G., 1962. Western Gulf bottomfish survey. Fishery Research Biological Laboratory, Galveston, Texas, Fiscal Year 1962. *U. S. Bur. Com. Fisheries, Cir. 161*:42-44.
- RAINWATER, E. H., 1964. Late Pleistocene and Recent history of Mississippi Sound between Beauvoir and Ship Island. *Mississippi Geol. Res. Papers*, 1963, *Bull. 102*:32-61. Mississippi Geol., Econ. and Topog. Surv., Jackson, Mississippi.
- REMANE, A., and C. SCHLIEPER, 1958. *Die Biologie des brackwassers*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- RILEY, G. A., 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. *Sears Found. J. Marine Res.*, 1(1): 60-74.
- RILEY, G. A., 1952. Hydrography of the Long Island and Block Island Sounds. *Bull. Bingham Oceanog. Collections*, 13 (Article 3):5-39.
- SANDOZ, M., and R. ROGERS, 1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab, *Callinectes sapidus*. *Rathbun. Ecology*, 25(2):216-228.
- SHEPARD, F. P., 1964. Sea level changes in the past 6000 years: Possible archeological significance. *Science*, 143(3606):574-576.
- SIMMONS, E. G., 1957. An ecological survey of the upper Laguna Madre of Texas. *Publ. Inst. Marine Sci., Univ. of Texas*, 4(2):156-200.
- SIMMONS, E. G., and J. P. BREUER, 1962. A study of redfish, *Sciaenops ocellatus* Linnaeus and black drum, *Pogonias cromis* Linnaeus. *Publ. Inst. Marine Sci., Univ. of Texas*, 8:184-211.
- SITARAMAIAH, P., 1963. Summer hydrography, productivity and fertility of Mississippi Sound. (Manuscript)
- SMITH, H. M., 1907. The fishes of North Carolina. *Geol. and Econ. Surv.*; vol. 2. Raleigh, North Carolina.
- SYMPOSIUM ON THE CLASSIFICATION OF BRACKISH WATERS, 1959. Venezia 8-14 Aprile 1958, 1959. *Archivio di Oceanografia e Limnologia*, 11: 1-248. (Suppl.)
- VIOSCA, P., JR., 1920. Fourth biennial report, April 1, 1918, to April 1, 1920; pp. 106-130. State of Louisiana, Dept. of Conserv., Baton Rouge, Louisiana.
- VIOSCA, P., JR., 1927. Flood control in the Mississippi Valley and its relation to Louisiana fisheries. *Trans. Am. Fisheries Soc.*, 57:49-61.
- VIOSCA, P., JR., 1938. Effect of the Bonnet Carré Spillway on fisheries. *Louisiana Conserv. Rev.*, 6: 51-53.
- WEYMOUTH, F. W., M. J. LINDNER, and W. W. ANDERSON, 1933. Preliminary report on the life history of the common shrimp, *Penaeus setiferus* (Linn.). *U. S. Bur. Fisheries Bull.* 14:1-26.

Estuarine Fisheries of West Africa

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The West African coast extending from Senegal in the west to Cameroun in the east (Fig. 1), approximately between 4° and 15° N and 10° E and 20° W, is indented by a number of rivers and lagoons. The salinity in the Gulf of Guinea is greatly affected by the effluents from these rivers and lagoons; dilution is at its maximum during the rainy season of May to October, the season being longer in certain areas in the eastern region of the coast. The greatest dilutions occur in the Bight of Biafra where there is very heavy precipitation, in the Bight of Benin in connection with the Niger effluents, and off the Liberia-Sierra Leone coast. Though information on salinity conditions is incomplete, it is clear that estuarine conditions exist in the Gulf of Guinea at varying distances from the shore, at least during the rainy season and the periods of flood in the rivers emptying into it. The effect is detected as far as the continental edge, even on the Guinea shelf where this is relatively far offshore (Postel, 1955). Longhurst (1963) gives the offshore salinity gradient west of Cape Sierra Leone as follows:

10 miles from shore	24.8 %
30 miles from shore	27.5 %
50 miles from shore	30.2 %
75 miles from shore	32.8 % (at continental edge)

A transect from Lagos to Calabar, around the Niger Delta, worked by HMNS Nigeria from July 19th to 20th, 1961, showed that salinities fell rather abruptly to the west of the Benin River from about 34.9 % to a minimum of 27.1 % off the Dodo River (Long-

hurst, 1962). There was increase in values farther east up to a maximum of 32.5 % off Brass and then a slow decline to 28.9 % off Calabar in the Bight of Biafra. The cruises of the *Ombango* in the Bight of Biafra and to the south of Fernando Po in October, 1959, recorded salinities of only 20 %. At Pointe-Noire, salinities between 25 and 26 % have been observed in March (Collignon, 1955). Watts (1958) recorded salinities below 20 % off Cape Sierra Leone in September.

ESTUARIES OF RIVER SYSTEMS

The Niger Estuary is the most extensive on the West African coast and covers about 3,400 square miles, of which about 2,815 square miles consist of saline mangrove swamps subject to tidal flooding. The total mean freshwater discharge through the estuary is estimated to be about 250,000 cubic feet per second, the maximum quantities flowing through the tributaries of the Ramos and Nun Rivers (25 and 24 percent respectively). Forcados and Sengana Rivers together convey 30 percent of the Niger discharge. The salinity regime in the estuary varies with the amount of freshwater discharge and the volume of tidal flow. During the months of heavy floods, the estuarine water has been observed to be essentially fresh even near the mouths of the distributaries of the river. The maximum salinity recorded in any part of the estuary is 28 % very near the river mouth at high tide. Dry and wet seasons account for the main variations in salinity.

The Volta Estuary is the other large estuarine area in the region and is associated with the Keta Lagoon. The estuary of the Rokel River in Sierra Leone, known as the Sierra Leone River, is about 100 square miles in area with a maximum depth of 98 to 132 feet near the southern shore. The upper reaches merge into a maze of creeks and channels fringed by large areas of mangrove swamps. Detailed studies have shown that the salinity in the estuary fluctuates between mean values of about 15 % in August-October and 33 % in April-May (Bainbridge, 1960; Watts, 1958). The vertical salinity gradient is correlated with the tidal range as well as the rate of river discharge. During the wet season, stratification is pronounced at neap tides and is slight during spring tides.

Studies have been made of the standing crop of phytoplankton in the Sierra Leone River (Bain-

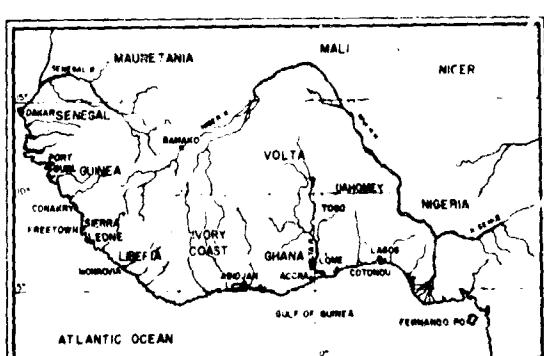


Fig. 1. Map of West Africa showing the major estuarine areas.

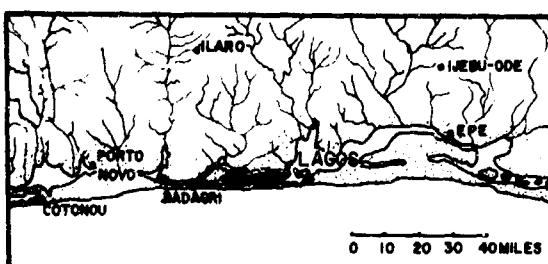


Fig. 2. The lagoons of the Guinea coast.

bridge, 1960). During and immediately after the wet season, from late July to the end of December, there was a dearth of phytoplankton within the estuary and the bulk of suspended vegetation consisted of small littoral diatoms. A high standing crop of phytoplankton developed during January, as the rate of river outflow diminished, and persisted until mid-July, after the onset of the rains, when it declined considerably. Large diatoms of the genera *Actinocyclus* and *Coscinodiscus* contribute the bulk of this standing crop. Assessments of pigment from net-caught phytoplankton gave a mean of 19,057 Harvey units/m³ for the period from January to July compared with a mean of 353 units/m³ from August to December.

Fluctuations in the quantity and composition of the zooplankton were clearly correlated with seasonal changes in the volume of freshwater discharge. The total numbers of zooplankton per unit volume were generally low from late July to the end of December. The copepods, *Temora turbinata* and *Schmackiria sericicaudatus*, were the two most common forms for much of the year. The larvae of benthic and littoral invertebrates constituted a relatively high proportion of the total zooplankton.

Longhurst (1959) has recorded a high production of benthic biomass in the Sierra Leone Estuary. As an example, he gives the concentration of the polychaete, *Pectinaria sourei*, as 7,680 m², which is far greater than that found on the Guinea shelf. Besides the estuaries mentioned above, there are extensive estuarine areas in Port Guinea, and the estuaries of the Gambia and Cassamance Rivers are of considerable importance from the point of view of fisheries. Very little is known about hydrobiological conditions of these estuaries.

LAGOONS

There are a number of fairly large lagoons on the coast of Liberia. In two main regions of the West African coast, one the Ivory Coast and the other extending from the Volta River to the Niger Delta, a lagoon system exists behind the barrier beach. These are located at an angle of about 45° to the dominant and prevailing southwest wind (Webb, 1958).

The extensive lagoon in the Ivory Coast, with Abidjan at its center, is fed by a number of large rivers. On the Ghana coast the more important ones are the Keta and Angaw Lagoons connected to the

Volta Estuary and the Juen Lagoon. The Keta Lagoon is about 8.5 square miles in area, is relatively shallow, and its area fluctuates considerably in relation to the water level in the Volta. To the east of this is the lagoon system traversing the Dahomey Gap—a region where the coastal forest belt is interrupted by savannah country with few rivers of any size. The most important of these are Lake Nacoue and the Porto Novo Lagoon. The largest of the lagoon systems on the coast extends for about 160 miles from Cotonou in Dahomey to the western edge of the Niger Delta in Nigeria (Fig. 2). The lagoon borders the forest belt and a number of fairly large rivers join it. It is in communication with the sea at Cotonou and at Lagos. The lagoons in areas where there are few rivers draining the mainland are generally greatly elongated and narrow, connected with the sea through shallow and widely separated inlets. Such lagoons are generally more brackish than those fed by large rivers. The river-fed lagoons, like those of the Ivory Coast and western Nigeria, form wide sheets of shallow water and extend farther inland. Water in these lagoons is practically fresh in areas beyond major tidal influence. Hill and Webb (1958) have made observations on the hydrological features of the Lagos Lagoon. The salinity shows both a diurnal fluctuation due to tidal effects and much greater seasonal changes caused by the influx of fresh water in the rainy months. During the dry season from November to March, the salinity in the Lagos Harbor is high, and brackish conditions extend up to about 20 miles inland from Lagos. From April to October, which is the rainy season, the salinity falls and almost freshwater conditions prevail.

FISH AND FISHERIES

ESTUARINE FISHES

Fishes commonly caught in West African estuaries are listed in Table 1. As a single species, the bonga (West African shad), *Ethmalosa dorsalis* (Cuvier and Valenciennes), probably accounts for the maximum production in the estuarine waters. Bainbridge (1964) has described the distribution and abundance of the species on the West African coast. It supports an important inshore fishery along the ria coastline with a network of wide shallow estuaries stretching from the Saloum Estuary, southern Senegal, to the Sherbro River, southern Sierra Leone. It is abundant at the mouth of the Senegal River (Postel, 1950), considerable catches being made from the Saloum, Djomboss, and Cassamance Estuaries. Hickling (1950) has reported it to be an abundant fish in the Gambia Estuary and confluent creeks. In Guinea it is caught in the coastal waters as well as in estuaries like those of the Dubreka, Konkoure, and Bofa Rivers. In Sierra Leone it is taken in the coastal waters off Shenge and in the Scarcies, Sierra Leone, and Sherbro Estuaries (Longhurst, 1960a, b). The species forms the mainstay of fishermen along the coast and the estuaries of the delta region of

Nigeria and is intensively fished in the wide estuaries of the Cameroun Republic. Even though the fish is scarce on the coastline from the Sierra Leone-Liberian border to the west of the Niger Delta, it provides fisheries of importance in areas where there are extensive brackish-water lagoon systems such as those found near Abidjan on the Ivory Coast, Cotonou in Dahomey, and Lagos in Nigeria. In Cameroun it is fished for mainly in the vicinity of the Sanaga Delta

(Dueroz, 1957). Bonga fishing is done throughout the year in most areas, except in certain regions like the coastal waters of Guinea and Cameroun. Reliable statistics of landings are not available for the whole region. Landings are estimated to be about 1,700 metric tons from the Joal area and roughly 3,000 tons from the Saloum-Djomboss area (Blanc, 1957; Main-guy and Doutre, 1958). At the Conakry market in Guinea about 400 tons of the bonga, comprising about

Table 1. Fishes commonly caught in West African estuaries.

PRISTIDAE <i>Pristis perotteti</i> Müller and Henle	BELONIDAE <i>Belone houttuyni</i> (Walbaum) <i>Strongylura crocodila</i> Le Sueur
TRYGONIDAE <i>Trygon pastinaca</i> (Linnaeus) <i>Trygon margarita</i> Günther	HEMIRAMPHIDAE <i>Hyporamphus socogechi</i> Bleeker
ELOPIDAE <i>Megalops atlanticus</i> Cuvier and Valenciennes <i>Elops lacerta</i> Valenciennes <i>Elops senegalensis</i> Regan	CYPRINODONTIDAE <i>Epiflatys sexfasciatus</i> Gill <i>Apocheilichthys spilenauchen</i> (Duméril) <i>Apocheilichthys macrurus</i> (Boulenger)
CLUPEIDAE <i>Pellonula vorax</i> Günther <i>Ethmalosa dorsalis</i> (Cuvier and Valenciennes) <i>Cynothrissa ansorgii</i> (Boulenger) <i>Hisha africana</i> (Bloch) <i>Sardinella aurita</i> Cuvier and Valenciennes <i>Sardinella eba</i> Cuvier and Valenciennes <i>Engraulis encrasicolus</i> Linnaeus	CENTROPOMIDAE <i>Lates niloticus</i> (Linnaeus)
OSTEOGLOSSIDAE <i>Heterotis niloticus</i> Ehrenbaum	SPHYRAENIDAE <i>Sphyraena sphyraena</i> (Linnaeus) <i>Sphyraena gauchancho</i> Cuvier and Valenciennes
CHARACIDAE <i>Hepsetus odoe</i> (Bloch) <i>Hydrocyon brevis</i> Günther <i>Alestes nurse</i> Rüppell	SYNGNATHIDAE <i>Dorichthys smithii</i> (Boulenger)
CITHARINIDAE <i>Citharinus citharus</i> Geoffroy <i>Citharinus latus</i> Müller and Troschel <i>Distichodus rostratus</i> Günther	MUGILIDAE <i>Mugil hocfieri</i> Steindachner <i>Mugil falcipinnis</i> Cuvier and Valenciennes <i>Mugil grandisquamis</i> Valenciennes <i>Mugil cephalus</i> Linnaeus <i>Mugil capito</i> Cuvier <i>Mugil auratus</i> Risso <i>Mugil brasiliensis</i> Agassiz
CYPRINIDAE <i>Labeo senegalensis</i> Cuvier and Valenciennes	POLYNEMIDAE <i>Galeoides decadactylus</i> (Bloch) <i>Polynemus quadrifilis</i> (Cuvier and Valenciennes) <i>Pentanemus quinquarius</i> Linnaeus
SILURIDAE <i>Tachysurus gambensis</i> Bowdich <i>Tachysurus hundeloti</i> Cuvier and Valenciennes <i>Tachysurus latiscutatus</i> (Günther)	BOTHIDAE <i>Citharichthys stampfii</i> (Steindachner)
BAGRIDAЕ <i>Chrysichthys auratus</i> <i>Chrysichthys walkeri</i> Günther <i>Chrysichthys nigrodigitatus</i> (Lacépède)	SOLEIDAE <i>Solea triopthalma</i> (Bleeker) <i>Synaptura lusitanica</i> Capello
SCHILBEIDAE <i>Schilbe mystus</i> (Linnaeus) <i>Eutropius niloticus</i> Rüppell <i>Eutropius mentalis</i> Boulenger <i>Eutropius micropteron</i> Trewavas <i>Physallia pellucida</i> Boulenger	CYNOGLOSSIDAE <i>Cynoglossus senegalensis</i> (Kaup)
CLARIIDAE <i>Clarias lazera</i> Cuvier and Valenciennes <i>Heterobranchus longifilis</i> Cuvier and Valenciennes	SERRANIDAE <i>Cephalopholis taeniops</i> (Cuvier and Valenciennes) <i>Epinephelus aeneus</i> Geoffroy Saint-Hilaire <i>Epinephelus goreensis</i> Cuvier and Valenciennes <i>Epinephelus gigas</i> Günther <i>Rypticus saponaceus</i> (Schneider)
MOCHOCIDAE <i>Synodontis melanopterus</i> <i>Synodontis schall</i> Bloch and Schneider	CARANGIDAE <i>Caranx hippos</i> (Linnaeus) <i>Caranx cryos</i> (Mitchell) <i>Caranx senegallus</i> Cuvier and Valenciennes <i>Scyrus alexandrinus</i> (Geoffroy Saint-Hilaire) <i>Vomer setapinnis</i> (Mitchell) <i>Chloroscombrus chrysurus</i> (Linnaeus) <i>Lichia glauca</i> Linnaeus <i>Lichia amnis</i> Linnaeus
ECHELIDAE <i>Paramyrus plumbeus</i> (Cope)	Trachinotus glaucus (Linnaeus) <i>Trachinotus fulcatus</i> (Linnaeus) <i>Trachinotus goreensis</i> Cuvier and Valenciennes
OPHICHTHIDAE <i>Ophichthus semicinctus</i> (Richardson) <i>Cæcula cephalopeltis</i> (Bleeker)	

(Continued on next page)

Table 1. (Continued)

LUTJANIDAE	CICHLIDAE
<i>Lutjanus agassizii</i> Bleeker	<i>Hemichromis fasciatus</i> Peters
<i>Lutjanus eutactus</i> Bleeker	<i>Hemichromis bimaculatus</i> Gill
<i>Lutjanus goreensis</i> (Valenciennes)	<i>Pelmatolochromis guentheri</i> Sauvage
<i>Lutjanus guineensis</i> Bleeker	<i>Tilapia melanopleura</i> Duméril
<i>Lutjanus dentatus</i> Duméril	<i>Tilapia heudelotii</i> (Duméril)
POMADASYIDAE	<i>Tilapia zillii</i> (Gervais)
<i>Pomadasys jubelini</i> (Cuvier)	TRICHIURIDAE
<i>Pomadasys peroteti</i> (Cuvier and Valenciennes)	<i>Trichiurus lepturus</i> Linnaeus
<i>Pseudopristipoma macrolepis</i> (Boulenger)	SCOMBRIDAE
<i>Brachydeuterus auritus</i> (Cuvier and Valenciennes)	<i>Scomberomorus maculatus</i> (Mitchill)
LOBOTIDAE	<i>Cybium tritor</i> Cuvier and Valenciennes
<i>Lobotes surinamensis</i> (Bloch)	ELEOTRIDAE
GERRIDAE	<i>Eleotris lebretoni</i> Steindachner
<i>Gerris melanopterus</i> Bleeker	<i>Eleotris senegalensis</i> Steindachner
<i>Gerris nigri</i> Günther	<i>Eleotris daganensis</i> Steindachner
<i>Gerris octatus</i> Bleeker	<i>Eleotris vittata</i> Duméril
SCIAENIDAE	<i>Hannoichthys africana</i> Steindachner
<i>Cynoscion senegallus</i> (Cuvier and Valenciennes)	GOBIIDAE
<i>Cynoscion macrognathus</i> (Bleeker)	<i>Bathygobius soporator</i> (Valenciennes)
<i>Sciaena epiperca</i> (Bleeker)	<i>Acentrogobius schlegelii</i> (Günther)
<i>Sciaena nigrita</i> (Cuvier and Valenciennes)	<i>Oxyurichthys occidentalis</i> (Boulenger)
<i>Umbrina cirrosa</i> (Linnaeus)	<i>Gobioides ansorgii</i> Boulenger
<i>Larimus elongatus</i> (Bowdich)	<i>Gobius casamancus</i> Rochebrune
<i>Pseudotolithus brachygaster</i> (Bleeker)	<i>Gobionellus lepturus</i> (Pfaff)
<i>Pseudotolithus senegalensis</i> (Valenciennes)	PERIOPHTHALMIDAE
NANDIDAE	<i>Periophthalmus koelreuteri</i> (Pallas)
<i>Polycentropsis abbreviata</i> Boulenger	BATRACHOIDIDAE
MONODACTYLIDAE	<i>Batrachoides liberiensis</i> (Steindachner)
<i>Psettus sebae</i> Cuvier	TETRODONTIDAE
EPHIPPIDAE	<i>Tetronodon pustulatus</i> Murray
<i>Chaetodipterus lippei</i> Steindachner	<i>Lagocephalus laevisgatus</i> Linnaeus
	POLYPTERIDAE
	<i>Polypterus endlechieri</i> Heckel

65 percent of the total landings by canoe fishermen, are landed (Moal, 1957; Sahrhage, 1961; Bainbridge, 1964). The annual production in Cameroun is estimated to be about 3,000 tons of dried bonga.

Next in importance to the bonga in many areas are prawns and shrimps. The extensive mudbanks of the Bight of Biafra support a rich prawn population and Cameroun derives its name from the important indigenous prawn fisheries of its coast and estuaries. *Penaeus duorarum* Burkenroad is the most common and important prawn of the estuarine waters. In the Niger Delta appreciable quantities of this prawn are caught in various traps, especially during the dry months. Another prawn of importance in the estuaries is *Parapenaeopsis atlantica* Balss. Small shrimps of the genus *Macrobrachium* are also landed in large quantities.

Miller (1957) has recorded the occurrence of large schools of *Sardinella* and other fishes in the lagoons and river mouths in Liberia, from November to January. Crabs are found in abundance throughout the estuarine area, especially in the swamps. The calling crab (*Gelasimus* spp.) and the hairy lagoon crab (*Sesarma* spp.) are not generally eaten, but the blue-legged lagoon swimming crab, *Callinectes latimanus* Rathbun, is caught in large numbers for consumption.

Even though the salinity of the waters in the Niger Estuary is very low for most of the year, species of

marine origin predominate in the catches throughout the year. The snappers (*Lutjanus* spp.), the barracuda (*Sphyraena* spp.), the grunter (*Pomadasys* spp.), the catfishes (*Tachysurus* spp.), croakers (*Otolithus* and *Sciaena* spp.), threadfins (*Galeoides* and *Pentanchus* spp.), and grey mullets (*Mugil* spp.) are predominant in the catches almost throughout the year. Longhurst reports (unpublished) that trawling in the Lagos Lagoon showed that in the dry season the demersal fauna is dominated by *Polynemus quadrifilis*, *Epinephelus aeneus*, *Elops lacerta*, *Sphyraena* sp., *Pomadasys jubelini*, and large numbers of freshwater catfish, *Chrysichthys nigrodigitatus*. Trawling in the same area during the height of the rainy season, when the water was virtually fresh, showed the same catch composition with the addition of the freshwater species, *Schilbe mystus*. In the estuarine waters of Ghana, also, the marine species predominate in the fish fauna. The horse mackerel (*Caranx hippos*) supports a fishery of some importance in the Volta Estuary and it migrates into the freshwater areas of the river. The grey mullets that migrate from and to the sea afford lucrative fishing in the Keta Lagoon in Ghana.

Tilapia spp., along with other cichlids that can tolerate variations in salinity, are caught from the estuaries and surrounding saline swamps throughout the year all over the West African coastal zone.



Fig. 3. Fishing with cast net in the Niger Estuary.

Many freshwater species of fishes like the tiger fish (*Hydrocyon brevis*), and catfishes (*Chrysichthys* spp. and *Eutropius* spp.), occur in the catches from the estuaries of the Niger and Volta, but not in significant quantities.

Two groups of shellfishes contribute significantly to food production in the estuarine areas of West Africa, especially in the Niger Delta and coastal areas of Liberia. In the mangrove swamps, the mangrove oyster (*Ostrea tulipa* Lamarck) grows in great profusion attached to the aerial roots of mangroves and other substrata. Miller (1957) has reported the occurrence of large "deep water oysters" in Liberian estuaries. These oysters are regularly collected for consumption by the local inhabitants. Similarly, at low tides innumerable numbers of periwinkles, *Tympanotonus fuscatus* Linnaeus and *Tympanotonus fuscatus* var. *radula* Linnaeus, can be found exposed on the mud flats and mangrove swamps in the estuaries. The collection of these and removal of the flesh from the shell provide employment and an income to many women and children. The cockle, *Arca senilis* Linnaeus, occurs in fairly large numbers in soft muddy areas where they are collected after locating them by feeling with the feet. The flesh is highly relished for eating and the shells are used in certain areas as weights for gill nets. No estimates of the production of the shellfishes are available, but judged by the heaps of empty shells that one comes across in every village in the area, the quantities collected annually must be considerable.

FISHING METHODS

Estuarine fishing in West Africa is mostly done from indigenous dugout canoes. Bonga fishing in the Sierra Leone Estuary utilizes cast nets and drift nets. Gill nets, long lines, and various types of traps are operated in estuarine areas of Liberia. In the lagoons of Dahomey, shoals of bonga are surrounded by a number of canoes, from each of which cast nets are operated. In western Nigeria, set nets, drift nets, encircling nets, and cast nets are used in the estuaries and in foreshore areas up to a distance of about five

miles. In recent years the fishermen have changed to synthetic fibers to make their nets, and this is reported to have resulted in an increase of their catches. In the Cameroun, cast nets, set gill nets, and encircling nets are used in the bonga fishery.

In the Niger Delta, cast nets are used for catching bonga, grey mullets, and other clupeid fishes; set gill nets and long lines are also operated throughout the year (Figs. 3 and 4). The long lines are operated from canoes and usually do not have more than 100 hooks, but many prized fishes like the barracuda, snapper, croaker, and grunter are caught in them. Traps of different design and size are operated in the Niger and other estuaries throughout the year. Large traps are made of walls of bamboo or raffia stalk slats set in a circle (the ends are involuted to form a V inside to permit fish to enter, but to prevent their escape); they have two diverging wing walls of fencing made of closely arranged long twigs stuck in the river bottom to serve as guide lines for fish, and usually can be seen in the eastern zone of the Niger Delta. In some, two or more trapping devices may be found (Fig. 5). When the trap is set near the river bank there may be only one guide wall; this is set at right angles to the bank with a wall of raffia slats set at right angles to it and trapping devices at either end of the latter wall. Prawns, shrimps, and miscellaneous fishes are caught in these traps and the catches are removed at low tide. Another very common method of fishing in the Niger Delta is to



Fig. 4. Long-line fishing in the Niger Estuary.



Fig. 5. The common fence trap in the Niger Estuary.

fence off portions of the marginal swamps or shallow mud flats with walls of closely set raffia slats (Fig. 6). At high tide, portions of the fencing are removed to allow the entry of fish with the tidal water. As the tide begins to turn, the fence is closed to prevent the escape of fish, and the stranded fish are picked up at low tide. Large catfish, along with other large fishes, are commonly caught from such traps. A similar method of weir trap fishing is practiced in the estuarine areas of Liberia. Set nets are used in the Cameroun for prawn fishing but most of the prawns and shrimps landed in the Niger Delta are caught in different types of traps. In the western zone of the Niger Delta, series of stakes can be found stuck at the river mouth. From each such stake a conical trap (Fig. 7) of about 3 to 4 feet in length and 1.5 to 2 feet in diameter at the mouth is operated against the tidal flow mainly at night, to catch prawns. In the eastern zone of the Niger Delta, larger conical traps are operated from stakes at river mouths. The trap is made of a webbing woven with the long and slender stem of a locally available creeper and shaped into a cone of about 26 feet in length and 17 feet in diameter at the mouth. The cod end is made of closely set bamboo slats of about 10 to 14 feet in length. The general design of the net is similar to the bag nets used in the estuarine waters in India (Pillay and Ghosh, 1964). The trap is operated against the tidal flow and the catches are removed at the turn of the tide. Prawns, along with small fishes, form the main catches of these traps. At the Imo River mouth, east of the main Niger Delta, conical raffia bag nets with circular frames are operated from long wooden stakes driven into the riverbed. The nets are about 5 feet in diameter at the mouth and about 15 feet long and catch largely prawns and shrimps. Another efficient device used for catching prawns during the night, and small grey mullet during the day, is the "onguro," which consists of a rectangular piece of close-set raffia stalk slats (8 to 10 ft. x 6 to 7 ft.) mounted on the gunwale of a canoe. One side of the onguro is lowered into the river and dragged some distance by two

fishermen or women wading along the shallow marginal areas of the river. It is raised at regular intervals and the catches tilted into the canoe. In Dahomey lagoons prawns are caught in traps using light as a lure.

Tilapia spp. are mostly caught in smaller traps of different shapes and made of raffia splits or chicken wire. In the Niger Delta cassava flour mixed with palm oil is generally used as bait for tilapia. The mudskipper is caught in large numbers from the Niger Delta swamps and estuarine margins by means of small traps. Gras (1958) describes the "Akadja" method of fishing in Porto Novo Lagoon in Dahomey to catch *Tilapia* spp., catfish, grey mullet, etc. Large circular or rectangular areas (as much as 2½ acres) are enclosed by driving long twigs or tree branches into the lagoon bed. Fishes take shelter among the foliage and in the enclosed area, feeding on the algal growth that develops. After a period of about four to six months the Akadja is enclosed by nets and the brush removed. Remarkably large quantities of fish are caught in this manner.

Crabs are generally caught with the hand or with small circular dip nets. Crab fishing is generally done by women or children who locate the crab holes at low tide and then, using a piece of rag for protection, insert the hand into the hole and pull out the crab. In the lagoons of Ghana the swimming crab is often caught using small fish tied to a long piece of thread as bait. As a crab takes the bait, it is drawn slowly to land where it is caught in a small hand net.

UTILIZATION OF CATCHES

Except for the limited use of fresh fish for consumption in the immediate neighborhood of the fishing areas, there appears to be no organized fresh fish trade in the estuarine areas. The catches are either dried or smoked. In the coastal zones of Cameroun and Nigeria, where the rainfall is heavy and the rainy season extended, fish are generally preserved only by smoking. They are placed on racks made by fastening supporting sticks to four bamboo poles which are



Fig. 6. Fence fishing in the mangrove swamps.



Fig. 7. Conical prawn traps operated in Brass area of the Niger Estuary.

driven into the ground and by laying slats across the supports to hold the fish. Four to five layers of fish separated by layers of sticks are spread on the rack leaving about a half-inch space for smoke to circulate. Sometimes individual fish are rolled and strung on sticks for smoking. Every smoking hut has one small and one big smoking rack. The small one is used for cooking fish on the first day; the large one is for smoke-drying the fish, which begins on the second day of the processing. Fires of mangrove wood are lighted below to produce smoke. Smoking is done for varying periods of time, from three to 14 days, depending on the type of fish and the type of product required for marketing locally or in distant places. In the western region of the coast where the rainy season is shorter, sun-drying of catches is often done without salting or after soaking the fish in sea water.

Transport and marketing arrangements are not very well organized. Smoked fish are generally stored in the fishermen's huts (usually in the smoking hut) for some days before they are transported in canoes (and in some cases in canoes) to distributing centers. During storage and distribution considerable loss and deterioration takes place. Re-smoking is seldom done. In a recent study (Piatek, 1963) it was found that the loss during a month of storage in the fishing villages amounted to 3 to 15 percent. The loss during transport has been estimated to be 8 to 12 percent.

POSSIBILITIES OF DEVELOPING ESTUARINE FISHERIES

CAPTURE FISHERIES

In the development of estuarine capture fisheries on the West African coast, the highest priority should go to improving the methods of processing, transport, and marketing of the catches. Piatek (1963) has demonstrated that bulk smoking of the bonga can be effectively done by following improved methods in smoking kilns which can be constructed locally at reasonable costs. Pilot experiments in storage, trans-

port, and marketing of smoked fish in the delta province of the midwestern region of Nigeria have clearly shown the possibility of organizing the industry on cooperative lines with great advantage. The government could also establish and maintain fish-curing yards and smoking kilns at appropriate centers and at reasonable charges for the use of fishermen.

The fishing gear used in the estuarine areas may be capable of improvement. For example, the large conical fish traps made of creeper stems, if made with nylon or cotton webbing in the form of bag nets may catch more fish and last much longer. The number of hooks on long lines could be greatly increased, and larger and more effective traps could possibly be introduced. For the use of larger nets and other fishing gear and for extending the area of fishing, larger and better boats would be required. Mechanization of at least fish transport boats is necessary for better organization of the fish trade.

Preliminary trawling experiments in the inshore areas of the Bight of Biafra opposite the Niger Estuary have given very encouraging results, and indicate that it may be possible to operate powered boats for fishing in the bay. The presence of sandbars across the mouths of rivers greatly handicaps the operation of such boats. For landing of catches, and for day-to-day maintenance, it is necessary for the boats to enter the estuaries and the sandbars make it difficult and dangerous in many areas.

CULTURE FISHERIES

The production of fish in most of the West African countries is much below the local requirements and every means of increasing production should be explored. Development of culture fisheries in estuarine areas appears to hold great possibilities. In the deltaic regions and along the margins of lagoons, there are very extensive mangrove swamps which are unsuitable for agriculture. Where an adequate tidal range is available, brackish-water fish ponds can be constructed for the culture of fishes like the grey mullet, tilapia, prawns, etc. A recent survey in the Niger Delta has shown that over 1,795,300 acres of the swamps are suitable for conversion into fish ponds. It is likely that most of swamps around the Keta Lagoon may also be suitable for reclamation. The peaty nature of the soil is a handicap, but experimental studies conducted by the author have shown that, if necessary precautions are taken, watertight dikes can be constructed with the mangrove soil, and tidal ponds can be successfully operated. Commercial brackish water fish ponds, if properly designed, can be constructed at a cost of about \$400 per acre; if a production of about 400 pounds of fish per acre can be obtained and marketed in the fresh state, the capital investment will be paid back in about four years' time. Considering the enormous area of mangrove swamps on the West African coast, the contribution that culture fisheries can make to increased fish production in the area is remarkably high, even if it is possible to reclaim only a fraction of the

swamps. The reclamation of the swamps is not likely to affect the commercial fisheries in any appreciable manner. It is true that culture in estuarine fish ponds will be largely based on spawn and fry obtained from the estuary which forms the nursery grounds of the species, but only a negligible percentage of juvenile stocks need be collected, as survival rate is greatly increased in the protected environment of fish farms. In many Asian countries this type of fish culture has been in existence for centuries and no adverse effect has been observed on the capture fisheries of the species concerned. However, even this possibility can be avoided if pond breeding of the cultivated species can be induced by suitable techniques.

Another possible means of developing culture fisheries in the estuaries is through the cultivation of oysters in suitable localities. The most common species of oyster in the area is *Ostrea tulipa* which grows to a size of over 12 cm. Preliminary observations have shown that the spat of the species can be obtained over an extended period, and their rate of growth, at least in the early stages, is fairly rapid.

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LITERATURE CITED

- BAINBRIDGE, V., 1960. The plankton of the inshore waters off Freetown, Sierra Leone. *Fish. Publ. London*, 13:1-48.
- BAINBRIDGE, V., 1964. The food, feeding habits and distribution of the Bonga, *Ethmalosa dorsalis* (Cuvier and Valenciennes). *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 28(2):270-284.
- BLANC, A., 1957. *La peche africains sur la petite cote du Senegal*. O.C.W. 27. C.S.A. Symposium. Luanda, Angola.
- COLLIGNON, J., 1955. Observations hydrologiques dans la baie de Pointe Noire. *Bull. Inst. Etud. Centrafricaines*, N. S. (10):153-166.
- DUCROZ, J., 1957. *La peche du Bonga - fish au Cameroun*. O.C.W. 8. CSA. Symposium. Luanda, Angola.
- GRAS, R., 1958. *Une annee de peche d'un acadja ora de la lagune de Porto-Novo; series D.R.*, vol. 4. C.S.A. Symposium. Luanda, Angola.
- HICKLING, C. F., 1950. *Report of the Fisheries Adviser on His Visit to the Gambia*. S. P. No. 9/51. H. M. Stationery Office, London.
- HILL, M. B., and J. E. WEBB, 1958. The topography and physical features of Lagos Harbour and Lagos Lagoon. *Phil. Trans. Roy. Soc. London (B)*, 683, 241: 319-333.
- LONGHURST, A. R., 1959. Benthos densities off tropical West Africa. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 25:21-28.
- LONGHURST, A. R., 1960a. *Fish landings in Sierra Leone during 1959*. Fish. Development and Research Unit. Freetown Occas. Paper, Sierra Leone.
- LONGHURST, A. R., 1960b. Local movements of *Ethmalosa fimbriata* off Sierra Leone from tagging data. *Bull. Inst. Franc. Afr. Noire*, Ser. A, 22:1337-1340.
- LONGHURST, A. R., 1962. A review of the oceanography of the Gulf of Guinea. *Bull. Inst. Franc. Afr. Noire*, Ser. A, 24(3):633-663.
- LONGHURST, A. R., 1963. The bionomics of the fisheries resources of the eastern tropical Atlantic. *Fish. Publ. London*, 20:1-66.
- MAINGUY, P., and M. DOUTRE, 1958. Variations annuelles de la teneur en matières grasses de trois Clupeides du Sénégal. *Rev. Trav. Off. Peche Marit.*, 22:303-321.
- MILLER, G. C., 1957. Marine fishery development in Liberia, 1952-1954. *U. S. Fish and Wildlife Service, Fish. Leaflet* 440:1-41.
- MOAL, R. A., 1957. *La peche autochtone en Guinéa*. O.C.W. 5, C.S.A. Symposium. Luanda, Angola.
- PIATEK, M., 1963. *Report to the Government of Nigeria on improvements in the bulk smoking of Bonga in Western Nigeria*. Rept. FAO/EPTA (1956). Food Agr. Organ., U. N., Expanded Technical Assistance Program, Rome, Italy.
- PILLAY, T. V. R., and K. K. GHOSH, 1964. The bagnet fishery of the Hooghly-Matlah estuarine system (West Bengal). *Indian J. Fisheries*, 9:71-99.
- POSTEL, E., 1950. Note sur *Ethmalosa fimbriata* (Bowdich). *Bull. Serv. Elev. Ind. Anim. A.O.F.*, 3(1): 49-59.
- POSTEL, E., 1955. Observations hydrologiques au large des côtes de Guinée Française. *Bull. Serv. Elev. Ind. Anim. A.O.F.*, 137:14-16.
- SAHRHAGE, D., 1961. Die seefischerei in der Republik Guinéa und einige Möglichkeiten zu ihrer Intensivierung. *Arch. Fisherenteiss.*, 12:38-74.
- WATTS, J. C. D., 1958. The hydrology of a tropical West African estuary. *Bull. Inst. Franc. Afr. Noire*, Ser. A, 20:697-752.
- WEBB, J. E., 1958. The ecology of Lagos Lagoon. 1. The lagoons of the Guinea Coast. *Phil. Trans. Roy. Soc. London (B)*, 683, 241:307-318.

Estuarine Fisheries of the Indian Ocean Coastal Zone

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The coastal zone of the Indian Ocean includes a number of bays and gulfs into which large and small rivers empty, creating estuarine conditions in the inshore areas. The extent of the estuarine zone in the sea varies according to the size of the river and the volume of its freshwater discharge, the steepness of the gradient, and the tidal range. The Bay of Bengal receives the large river systems of the Ganges, Brahmaputra, and Irrawaddy, and has estuarine conditions extending many miles from the shore. Waters of low salinity and high turbidity can be found far out in the sea during the rainy season. In the inshore waters, the salinity is considerably lower due to the influx of fresh water, and reaches its minimum in about November. Studies of plankton have indicated two periods of maximum production; the primary one in spring, and the other in autumn. In Sumatra and Java the color of estuarine water may be tea-brown or blackish, due to outflow from enormous peat forests—(Hardenberg, 1950). The pH of this water is reported to be as low as 5 or less. There is a marked increase in the number of planktonic organisms as a result of increase in nutrient salts. Copepods diminish to be replaced by an increased amount of diatoms and *Noctiluca*. Marine species are replaced by coastal forms.

ESTUARIES OF MAJOR RIVER SYSTEMS

The largest estuarine area of the Indian Ocean coastal zone is the Ganges-Brahmaputra Delta, generally referred to as the Sunderbans. The Sunderbans has an extensive and complicated system of interconnected distributaries. The delta area in West Bengal alone is about 3,100 square miles. Estuarine conditions extend about 100 miles upstream. Considerable fluctuation is observed in the salinity in most areas, between almost freshwater and marine conditions. Hydrobiological studies made in Hooghly River, one of the main distributaries of the Ganges, have shown that salinity zonations into marine, tidal, gradient, and freshwater zones are not clearly evident. Oag (1939) has recognized three distinct seasons in the tidal regime of the estuary: (1) the southwest monsoon season when the effect of flood tides is countered and nullified by freshets and when there is a strong predominance of ebb tides, (2) from November to February when the strength of the flood tide over the ebb tide is minimum, and (3) the hot and dry months (May to June) when the effect of flood tides is considerably stronger than that of the ebb tides.

with the salinity of the water consequently becoming very high.

A general trend of increase in salinity has been observed in the river in recent years and the migration of several marine species of bottom fish (Hora, 1943, 1953) and even pelagic fish (Pillay, 1953) which did not occur earlier have been noticed. There is a marked abundance of phytoplankton during the winter season with the peak period in about January. Growth of plankton is minimal during the rainy months, when the turbidity of the water is high. Both phytoplankton and zooplankton show a bimodal cycle, with one peak during June to August and the other during November to January (February in the case of zooplankton). Zooplankton are generally at their lowest level during the latter part of the monsoon season. Among the zooplankton, copepods form the dominant group. Though satisfactory quantitative data on productivity are not available, the Hooghly, like the rest of the Sunderbans, is highly fertile.

The Irrawaddy Delta in Burma is also very extensive and supports important fisheries. On the Indian coast there are a number of smaller rivers like the Mahanadi and the Krishna that have wide estuaries. Mahanadi Estuary on the east coast (in Orissa State) is particularly important as a source of fish production. The Indus in West Pakistan, emptying into the Arabian Sea, and the Euphrates and the Tigris, joining the Persian Gulf, have estuaries of fair size. On the east coast of Africa bordering the Indian Ocean coastal zone, the largest estuarine area is that of the Zambezi, even though there are many other rivers emptying into the Indian Ocean. The ecology of a number of smaller estuaries along the South African coast has been investigated. Some of these, like the estuary of the Klein River, are closed to the sea for most of the dry season. The water remains brackish throughout the year, though there is wide fluctuation in salinity depending on the season and tidal condition.

One feature common to all estuaries of the Indian Ocean coastal zone is the formation of sand bars at the river mouths. These bars generally are horseshoe-shaped; the open side facing the river is steep and that facing the sea has a very gentle slope. In spite of heavy tidal action, these bars maintain their shape and size. The bars and the heavy siltation in some of the estuaries often render them unnavigable. When navigational facilities are maintained, as in the Hooghly or the Sunderbans, constant and expensive dredging operations are required.

LAGOONS

Along the Indian Ocean coastal zone are numerous lagoons, or brackish-water lakes as they are sometimes called. They are generally connected with the sea during periods of flood, but may get cut off during drought. These lagoons may be connected to river systems, but the connection with the sea is often limited to a number of narrow channels.

Chilka Lake and Pulicat Lake on the east coast of India have received considerable attention because of their importance in fish production. Chilka Lake is roughly pear-shaped with a length of 40 miles (north-south) and width of 12.5 miles (east-west), covering an area of about 350 square miles in the dry season and about 450 square miles during the flood season. The lake has an outer channel 14 miles long with a sandy bottom. The lake proper is very shallow; the average depth in the dry season rarely exceeds eight feet over a large stretch of the northern sector, increasing during the flood season by five or six feet. During February-April, when the floods subside, ingress of sea water into the lagoon increases and the southern end of the lake is more saline. In May and June, the hottest months, the ingress of sea water increases, resulting in higher salinity. In September, during the monsoon floods, salinity is greatly reduced. The floodwaters of the Mahanadi River enter the lake at its northeast end and it becomes almost fresh in the course of time. Plankton studies made in the lake indicate high productivity. Zooplankters, predominantly copepods, constitute the bulk of plankton throughout the year. Copepods form 42 to 70 percent of the total plankton and have two seasons of abundance, coinciding with the periods of higher salinity. Diatoms form 41 to 50 percent of the total phytoplankton.

Pulicat Lake, near Madras, has an area of about 178 square miles and is shallow, being only about six feet deep in most areas. The lake receives fresh water from a large catchment area during the rains and the water becomes almost fresh. A narrow channel connects the lake with the sea through which tidal water and large numbers of marine fish and prawns enter the lake.

The chain of lagoons (or backwaters as they are locally called) along the coast of Kerala on the west coast of India, of which the largest is Vembanad Lake, is of considerable fishery importance. The lagoons are connected to the sea only at a few places and the salinity, which has been observed to range between 33.25 ‰ and 1.2 ‰, is always higher near the opening to the sea and progressively diminishes in areas away from the sea. Zooplankton, predominated by copepods, forms the bulk of plankton in the backwaters. Fluctuations in the volume of plankton have been found to be positively correlated with salinity changes.

Lagoons on the coast of Ceylon vary in extent from 100 to 70,000 acres and the total estimated area of such brackish waters in the country is about 350,000

acres. Salinity increases rapidly in shallow and isolated areas of the lagoons and their connected salt marshes during the dry months, often resulting in hypersaline conditions or even actual deposition of salt.

FISH FAUNA OF THE ESTUARIES

The estuaries of the Indian Ocean coastal zone support a varied fish fauna, but for a tropical region it is rather poor in species (Table 1). The fish fauna consists of species that spend all or a major part of their life in the estuaries, and marine or freshwater species which migrate seasonally into or through the estuaries. In the present state of our knowledge, a proper classification of the species based on their period of life in the estuaries is difficult.

In the Sunderbans area over 120 species are commonly caught by commercial fishermen. From Chilka Lake some 138 species have been recorded—many are only migrants or stray visitors. In the estuary of the Rokan River in Sumatra, Hardenberg (1950) has reported the occurrence of some 175 species, including occasional migrants. The number of individuals is, however, high.

The fish of muddy estuaries show affinities to deep-sea fauna in some of their features. Some genera of clupeids and polynemids have prolonged fin-rays, and others have small diminutive eyes. Hardenberg (1950) has recorded even a species of blind sole from the Rokan Estuary. The Bombay duck, *Harpodon nicherus*, is a species that has its nearest relatives in the deep sea and its appearance is very much like that of a deep-sea form. *Bregmaceros maccllellandii* cannot be distinguished from specimens from the deep sea.

In the Indian subcontinent the single species that constitutes a fishery of great importance is the hilsa, *Hilsa ilisha*. Though it was generally considered an anadromous fish, recent investigations have shown that some of the main stocks of this species are purely estuarine. It occurs from the Persian Gulf, along the coasts of West Pakistan, India, and East Pakistan to Burma, ascending the main river systems. The major fisheries are in Chilka Lake, and Irrawaddy, Sunderbans, Godavari, Narbada, and Indus Estuaries. The Bombay duck is a major constituent of the catches in the Sunderbans Estuary in India. Grey mullet (*Mugil* spp.), cock-up (*Lates calcarifer*), milk fish (*Chanos chanos*), threadfin (*Polynemids*), and pearl spot (*Etropus suratensis*) are the prime fishes caught from estuarine areas of the Indian subcontinent. Catfishes of the genera *Tachysurus*, *Osteogencosus*, *Pangasius*, and *Mystus* contribute very considerable catches. Sciaenids and smaller clupeids are abundant and landed in appreciable quantities, though their market value is considerably less than that of other species. Sharks, rays, and skates, though occasionally caught in the estuaries, are not abundant in any of the areas. Juveniles and young of several marine and coastal fishes may be found in the estuaries during certain seasons. In some of the lagoons of Ceylon, the cichlid

Tilapia mossambica was introduced with a view to increasing fish production. It is reported that the species has established itself and multiplied rapidly. The indigenous fauna is believed to have been very adversely affected by *Tilapia*, especially the prawns and shrimps.

In the estuarine fauna, the crustaceans, which include several species of commercially important shrimps and crabs, have a predominant position. The more important shrimps caught by commercial fishermen are the following:

- Penaeus indicus* H. M. Edw.
Penaeus semisulcatus de Haan
Metapenaeus brevicornis (H. M. Edw.)
Metapenaeus affinis (H. M. Edw.)
Metapenaeus dobsoni (Miers)
Parapenaeopsis sculptilis (Heller)
Parapenaeopsis stylifera (H. M. Edw.)
Macrobrachium mirabile (Kemp)
Macrobrachium malcolmsonii (H. M. Edw.)

(Continued, p. 652)

Table 1. List of common estuarine fishes of the Indian Ocean coastal zone.

SCYLIORHINIDAE	<i>Chiloscyllium indicum</i> (Günther)	<i>Selipinna phasa</i> (Hamilton)
CARCHARINIDAE	<i>Carcharhinus gangeticus</i> (Müller and Henle)	<i>Selipinna taty</i> (Cuvier and Valenciennes)
	<i>Carcharhinus melanopterus</i> (Quoy and Gaimard)	<i>Selipinna melanochir</i> (Bleeker)
	<i>Physodon mulleri</i> (Müller and Henle)	<i>Selipinna breviceps</i> (Cantor)
PRISTIDAE	<i>Pristis pectinatus</i> Latham	<i>Coilia borneensis</i> Bleeker
RHINOBATIDAE	<i>Rhynobatus djiddensis</i> (Forskaal)	<i>Coilia dussumieri</i> (Cuvier and Valenciennes)
TRYGONIDAE	<i>Dasyatis (Amphotistius) imbricata</i> (Schneider)	<i>Coilia ramcaratii</i> (Hamilton)
	<i>Dasyatis (Himantura) uarnak</i> (Forskaal)	<i>Coilia reynaldi</i> (Cuvier and Valenciennes)
	<i>Dasyatis (Pastinachus) sephen</i> (Forskaal)	
	<i>Trygon walga</i> Müller	
MYLOBATIDAE		
	<i>Aetobatis narinari</i> (Euphasin)	CHANIDAE
	<i>Aetomylaeus nichofii</i> (Bloch and Schneider)	<i>Chanos chanos</i> (Forskaal)
ELOPIDAE		CHIROCENTRIDAE
	<i>Elops saurus</i> Linnaeus	<i>Chirocentrus dorab</i> (Forskaal)
MEGALOPIDAE		<i>Chirocentrus hypselosoma</i> (Bleeker)
	<i>Megalops cyprinoides</i> (Broussanet)	
CLUPEIDAE		SYNODONTIDAE
	<i>Gadusus chapra</i> (Hamilton)	<i>Harpodon nehereus</i> (Hamilton)
	<i>Hilsa ilisha</i> (Hamilton)	
	<i>Hilsa toli</i> (Cuvier and Valenciennes)	NOTOPTERIDAE
	<i>Hilsa kamagurta</i> (Bleeker)	<i>Notoptrerus notopterus</i> (Pallas)
	<i>Hilsa macrura</i> (Bleeker)	
	<i>Corixa soborna</i> (Hamilton)	SIRRIDAE
	<i>Ilisha elongata</i> (Bennett)	<i>Bagarius bagarius</i> (Hamilton)
	<i>Ilisha indica</i> (Swainson)	<i>Glyptosternum telchitta</i> (Hamilton)
	<i>Ilisha motius</i> (Hamilton)	<i>Gagata cenia</i> (Hamilton)
	<i>Sardinella fimbriata</i> (Valenciennes)	<i>Gagata viridescens</i> (Hamilton)
	<i>Pellona ditchela</i> (Cuvier and Valenciennes)	
	<i>Opisthoterpus tardore</i> (Cuvier)	CYPRINIDAE
	<i>Racunda russeliana</i> Gray	<i>Catla catla</i> (Hamilton)
	<i>Kowala coral</i> (Cuvier)	<i>Chela cuchius</i> (Hamilton)
	<i>Anodontostoma chacunda</i> (Hamilton)	<i>Chela labuca</i> Hamilton
	<i>Nematalosa nasus</i> (Bloch)	<i>Crossocheilus latius</i> (Hamilton)
	<i>Dussumieri hasseltii</i> Bleeker	<i>Labeo rohita</i> (Hamilton)
STOLEPHORIDAE		<i>Osteobrama vigorsii</i> (Sykes)
	<i>Stolephorus baganensis</i> Hardenberg	<i>Oxygaster bacaila</i> (Hamilton)
	<i>Gilchristella aestuaria</i> (Gilchrist and Thompson)	<i>Esomus danicus thermoicos</i> (Valenciennes)
ENGRAULIDAE		<i>Puntius dorsalis</i> (Jerdon)
	<i>Anchoriella commersonii</i> (Lacépède)	<i>Puntius sophore</i> Hamilton
	<i>Anchoriella indica</i> (van Hasselt)	<i>Puntius ticto</i> Hamilton
	<i>Anchoriella tri</i> (Bleeker)	<i>Puntius vittatus</i> Day
	<i>Thrissocles annandalei</i> (Chaudhuri)	<i>Puntius javanicus</i> (Bleeker)
	<i>Thrissocles hamiltonii</i> (Gray)	<i>Rasbora daniconius</i> (Hamilton)
	<i>Thrissocles kempfi</i> (Chaudhuri)	
	<i>Thrissocles mystax</i> (Schneider)	TACHYSURIDAE
	<i>Thrissocles purava</i> (Hamilton)	<i>Ostegonciosus militaris</i> (Linnaeus)
	<i>Thrissocles kammalensis</i> (Bleeker)	<i>Tachysurus arius</i> (Hamilton)
	<i>Thrissocles rambhae</i> (Chaudhuri)	<i>Tachysurus coelatus</i> (Valenciennes)
	<i>Thrissocles malabaricus</i> (Bloch)	<i>Tachysurus falcirostris</i> (Richardson)

(Continued on next page)

Table 1. (Continued)

BAGRIDAE	POLYNEMIDAE
<i>Rita rita</i> (Hamilton)	<i>Eleutheronema tetractylum</i> (Shaw)
<i>Mystus aor</i> (Hamilton)	<i>Polydactylus indicus</i> (Shaw)
<i>Mystus carasius</i> (Hamilton)	<i>Poly nemus paradiseus</i> (Linnaeus)
<i>Mystus gulio</i> (Hamilton)	OPHICEPHALIDAE
<i>Mystus vittatus</i> (Bloch)	<i>Ophicephalus punctatus</i> Bloch
<i>Mystus seenghala</i> (Sykes)	<i>Ophicephalus striatus</i> Bloch
<i>Mystus tengara</i> (Hamilton)	CENTROPOMIDAE
<i>Mystus armatus</i> (Day)	<i>Ambassis nama</i> (Hamilton)
SCHILBEIDAE	<i>Ambassis ranga</i> (Hamilton)
<i>Eutropichthys vacha</i> (Hamilton)	<i>Ambassis ambassis</i> (Lacépède)
<i>Pangasius pangasius</i> (Hamilton)	<i>Ambassis gymnocephalus</i> (Lacépède)
<i>Pangasius polyuranodon</i> (Bleeker)	<i>Ambassis urotaenia</i> (Bleeker)
<i>Pangasius nasutus</i> (Bleeker)	<i>Lates calcarifer</i> (Bloch)
<i>Clupisoma garua</i> (Hamilton)	SERRANIDAE
<i>Ailia coila</i> (Hamilton)	<i>Epinephelus bleekeri</i> (Vaillant and Bocourt)
<i>Pseudatropius atherinoides</i> (Bloch)	<i>Epinephelus diacanthus</i> (Valenciennes)
<i>Silonia silondia</i> (Hamilton)	<i>Epinephelus tauzinai</i> (Forskaal)
HETEROPNEUSTIDAE	<i>Epinephelus sexfasciatus</i> (Cuvier and Valenciennes)
<i>Heteropneustes fossilis</i> (Bloch)	THERAPONIDAE
ANGUILLIDAE	<i>Therapon jarbua</i> (Forskaal)
<i>Anguilla australis</i> Richardson	<i>Therapon puta</i> Cuvier
<i>Anguilla bengalensis</i> Gray	APOGONIDAE
MURAENIDAE	<i>Apogon gymnocephalus</i> (Lacépède)
<i>Rhabdura macrura</i> (Bleeker)	<i>Apogon nigripinnis</i> Cuvier and Valenciennes
MURAENOSOCIDAE	SILLAGINIDAE
<i>Muraenesox cinereus</i> (Forskaal)	<i>Sillago sihama</i> (Forskaal)
OPHICHTHYIDAE	<i>Sillago panijus</i> (Hamilton)
<i>Ophichthys boro</i> (Hamilton)	CARANGIDAE
<i>Ophichthys microcephalus</i> Day	<i>Caranx (Carangoides) preustus</i> Bennet
<i>Pisodonophis chikensis</i> Chaudhuri	<i>Caranx (Caranx) caranx</i> (Bloch)
<i>Pisodonophis hijala</i> (Hamilton)	<i>Caranx (Selar) mate</i> Cuvier and Valenciennes
<i>Ophisurus serpens</i> (Linnaeus)	<i>Atropus atropus</i> (Bloch and Schneider)
BELONIDAE	<i>Megalaspis cordyla</i> (Linnaeus)
<i>Tylosurus strongylurus</i> (van Hasselt)	<i>Caranx (Caranx) sansum</i> (Forskaal)
HEMIRHAMPHIDAE	<i>Chorinemus tala</i> Cuvier
<i>Hemirhamphus limbatus</i> (Cuvier and Valenciennes)	<i>Chorinemus tol</i> Cuvier
<i>Hemirhamphus gaimardi</i> (Valenciennes)	<i>Chorinemus sancti petri</i> Cuvier and Valenciennes
<i>Hemirhamphus georgii</i> (Valenciennes)	<i>Hypanthus amia</i> (Linnaeus)
BREGMACEROTIDAE	<i>Trachinotus blochi</i> (Lacépède)
<i>Bregmaceros macclennandi</i> (Thompson)	POMATOMIDAE
SYNGNATHIDAE	<i>Pomatomus saltator</i> (Linnaeus)
<i>Hippocampus brachyrhynchus</i> Duncker	LUTIANIDAE
<i>Ichthyo campus corce</i> (Hamilton)	<i>Lutianus johni</i> (Bloch)
<i>Syngnathus acus</i> Linnaeus	<i>Lutianus argenteimaculatus</i> (Forskaal)
CYPRINODONTIDAE	LOBOTIDAE
<i>Aplodichthys panchax</i> (Hamilton)	<i>Lobotes surinamensis</i> (Bloch)
<i>Panchax lineatus</i> dayi (Steindachner)	<i>Cottus quadrifasciatus</i> (Sebastianof)
<i>Oryzias melastigma</i> (McClelland)	LEIOGNATHIDAE
SPHYRAENIDAE	<i>Leiognathus brevirostris</i> (Valenciennes)
<i>Sphyraena rajah</i> Chaudhuri	<i>Leiognathus blochii</i> (Cuvier and Valenciennes)
MUGILIDAE	<i>Leiognathus equidens</i> (Forskaal)
<i>Rhinomugil corsula</i> (Hamilton)	<i>Leiognathus fasciatus</i> (Lacépède)
<i>Mugil macrolepis</i> (A. Smith)	<i>Leiognathus ruconius</i> (Hamilton)
<i>Mugil cephalus</i> (Linnaeus)	<i>Scutor ruconius</i> (Hamilton)
<i>Mugil cuneatus</i> Valenciennes	<i>Scutor insidiosus</i> (Bloch)
<i>Mugil belanak</i> Bleeker	<i>Gazea minuta</i> (Bloch)
<i>Mugil borneensis</i> Bleeker	GERRIDAE
<i>Mugil troscheli</i> Bleeker	<i>Gerres oblongus</i> Cuvier
<i>Mugil sebili</i> (Forskaal)	<i>Gerres oyena</i> (Forskaal)
<i>Mugil persica</i> (Hamilton)	<i>Gerres punctatus</i> Cuvier
<i>Mugil tade</i> (Forskaal)	<i>Gerres setifer</i> (Hamilton)
<i>Mugil jerdoni</i> Day	<i>Gerreomorpha setifer</i> (Hamilton)
<i>Mugil subcordis</i> Valenciennes	<i>Pertica filamentosa</i> (Cuvier)
<i>Mugil wauwaeensis</i> (Quoy and Gaimard)	POMADASYIDAE
<i>Liza ramada</i> (Risso)	<i>Pristipoma hasta</i> (Bloch)
<i>Valamugil caeruleomaculatus</i> (Lacépède)	<i>Pristipoma operculare</i> Playfair
	<i>Pristipoma quoraka</i> (Russell)

(Continued on next page)

Table 1. (Continued)

SCIENIDAE	ELEOTRIDAE
<i>Pseudosciaena coitoides</i> (Hamilton)	<i>Butis butis</i> (Hamilton)
<i>Sciaena russelli</i> (Cuvier)	<i>Eleotris fusca</i> (Bloch and Schneider)
<i>Sciaena hololepidota</i> Lacépède	<i>Oxyeleotris marmoratus</i> (Bleeker)
<i>Sciaena albida</i> (Cuvier and Valenciennes)	GOBIIDAE
<i>Sciaena belangeri</i> (Cuvier and Valenciennes)	<i>Gobius sudanundio</i> (Hamilton)
<i>Sciaena glauca</i> Day	<i>Gobius nudiceps</i> Cuvier
<i>Sciaena vogleri</i> (Bleeker)	<i>Cryptocentrus gymnocephalus</i> (Bleeker)
<i>Johnius diacanthus</i> (Lacépède)	<i>Pammogobius knysnaensis</i> Smith
<i>Johnius osseus</i> (Day)	<i>Acentrogobius globiceps</i> (Hora)
<i>Johnius sina</i> (Cuvier)	<i>Bathygobius fuscus</i> (Rüppel)
<i>Johnius dussumieri</i> (Cuvier)	<i>Brachygobius natus</i> (Hamilton)
<i>Johnius coibensis</i> (Hamilton)	<i>Glossogobius biocellatus</i> (Valenciennes)
<i>Johnius exillaris</i> (Cuvier)	<i>Glossogobius giuris</i> (Hamilton)
<i>Johnius carutta</i> Bloch	<i>Glossogobius maculatus</i> (Hamilton)
<i>Sciaenoides bairdii</i> (Cantor)	<i>Glossogobius maculatus</i> (Hamilton)
<i>Poma pama</i> (Hamilton)	<i>Glossogobius maculatus</i> (Hamilton)
<i>Otolithus maculatus</i> (Cuvier)	<i>Glossogobius maculatus</i> (Hamilton)
<i>Atractoscion acutidens</i> (Cuvier)	<i>Glossogobius maculatus</i> (Hamilton)
LETHRINIDAE	ELEOTRIDAE
<i>Lethrinus reticulatus</i> Valenciennes	<i>Butis butis</i> (Hamilton)
<i>Lethrinus nebulosus</i> (Forskaal)	<i>Eleotris fusca</i> (Bloch and Schneider)
PSETTIDAE	<i>Oxyeleotris marmoratus</i> (Bleeker)
<i>Monodactylus argenteus</i> (Linnaeus)	GOBIIDAE
DREPANIDAE	<i>Gobius sudanundio</i> (Hamilton)
<i>Drepene punctata</i> (Linnaeus)	<i>Gobius nudiceps</i> Cuvier
SCATOPHAGIDAE	<i>Cryptocentrus gymnocephalus</i> (Bleeker)
<i>Scatophagus argus</i> (Bloch)	<i>Pammogobius knysnaensis</i> Smith
CICHLIDAE	<i>Acentrogobius globiceps</i> (Hora)
<i>Etroplus suratensis</i> (Bloch)	<i>Bathygobius fuscus</i> (Rüppel)
<i>Etroplus maculatus</i> (Bloch)	<i>Brachygobius natus</i> (Hamilton)
<i>Tilapia mossambica</i> Peters	<i>Glossogobius biocellatus</i> (Valenciennes)
NANDIDAE	<i>Glossogobius giuris</i> (Hamilton)
<i>Nandus nandus</i> (Hamilton)	<i>Glossogobius maculatus</i> (Hamilton)
BLENNIIDAE	<i>Glossogobius maculatus</i> (Hamilton)
<i>Petroscirtes bhattacharyae</i> Chaudhuri	<i>Gobius maculatus</i> (Hamilton)
SIGANIDAE	<i>Gobius maculatus</i> (Hamilton)
<i>Siganus oramin</i> (Bloch and Schneider)	<i>Odontombyopus rubicundus</i> (Hamilton)
<i>Siganus guttatus</i> (Bloch)	<i>Taenioides chilensis</i> Chaudhuri
<i>Siganus vermiculatus</i> (Cuvier and Valenciennes)	<i>Trypauchen vagina</i> (Bloch and Schneider)
<i>Teuthis sutor</i> Günther	TAENIOIDIDAE
ANABANTIDAE	<i>Gobiodon caeruleus</i> (Bloch and Schneider)
<i>Anabas testudineus</i> (Bloch)	<i>Gobiodon unguicularis</i> (Linnaeus)
KURTIDAE	<i>Odontombyopus rubicundus</i> (Hamilton)
<i>Kurtus indicus</i> Bloch	<i>Taenioides chilensis</i> Chaudhuri
TRICHIURIDAE	<i>Trypauchen vagina</i> (Bloch and Schneider)
<i>Trichiurus haemula</i> (Forskaal)	PERIOPHTHALMIDAE
<i>Trichiurus miticus</i> Gray	<i>Periophthalmus koelreuteri</i> (Pallas)
<i>Trichiurus savala</i> Cuvier	CLINIDAE
<i>Trichiurus glossodon</i> Bleeker	<i>Clinus superciliosus</i> (Linnaeus)
SPARIDAE	PLATYCEPHALIDAE
<i>Acanthopagrus berda</i> (Forskaal)	<i>Thysanophrys indicus</i> (Linnaeus)
<i>Rhabdosargus globiceps</i> (Cuvier)	<i>Platycephalus insidiator</i> (Forskaal)
<i>Rhabdosargus tricuspidens</i> Smith	<i>Platycephalus punctatus</i> (Cuvier and Valenciennes)
<i>Diplodus sargus</i> Linnaeus	BOTHIDAE
<i>Diplodus trifasciatus</i> (Rafinesque)	<i>Pseudorhombus ursinus</i> (Hamilton)
<i>Lithognathus lithognathus</i> (Cuvier)	<i>Typhlachinus caecus</i> Hardenberg
SCOMBEROMORIDAE	SOLEIDAE
<i>Indocypris guttatum</i> (Bloch and Schneider)	<i>Brachirus pan</i> (Hamilton)
<i>Cypris commersonii</i> (Lacépède)	<i>Brachirus orientalis</i> (Bloch and Schneider)
<i>Cypris kuhlii</i> Cuvier and Valenciennes	<i>Solea bleekeri</i> Boulenger
STROMATEIDAE	<i>Heteromycteris capensis</i> Kaup
<i>Parastromateus niger</i> (Bloch)	CYNOGLOSSIDAE
<i>Pampus argenteus</i> (Euphrasen)	<i>Cynoglossus brevis</i> Günther
<i>Pampus chinensis</i> (Euphrasen)	<i>Cynoglossus cynoglossus</i> (Hamilton)
	<i>Cynoglossus lingua</i> (Hamilton)
	<i>Cynoglossus monopterus</i> (Bleeker)
	<i>Cynoglossus puncticeps</i> (Richardson)
	MASTACEMBELIDAE
	<i>Macrogaster aculeatus</i> (Bloch)
	<i>Mastacembelus armatus</i> (Lacépède)
	TRIACANTHIDAE
	<i>Triacanthus brevirostris</i> (Temminck and Schlegel)
	TETRODONTIDAE
	<i>Chelonodon patoca</i> (Hamilton)
	<i>Torquigenes oblongus</i> (Bloch)
	<i>Chelonodon fimbriatus</i> (Hamilton)
	<i>Arotroton reticulatus</i> (Bloch)
	<i>Monopterus albus</i> (Hamilton)
	BATRACHOIDIDAE
	<i>Batrachus granulosus</i> (Linnaeus)

(Continued on next page)

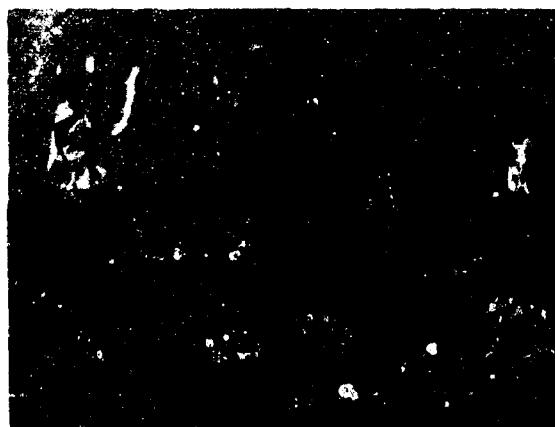


Fig. 1. Fishing with a fixed bag net in the Ganges Estuary.

(Continued from p. 649)

- Macrobrachium rude* (Heller)
- Macrobrachium scabrum* (Heller)
- Palaemon carcinus* (Linnaeus)
- Palaemon lamarrei* H. M. Edw.
- Palaemon styliferus* H. M. Edw.
- Palaemon tenuipes* (Henderson)
- Palaemon fluminicola* Kemp
- Caridina gracilirostris* de Man
- Acetes indicus* H. M. Edw.

Crabs belonging to different genera and species are abundant along the estuarine shores and swamps, but those of economic importance affording minor fisheries are the swimming crabs belonging to the genera *Scylla* and *Neptunus*. *Scylla serrata* (Forskaal), *Neptunus pelagicus* (Linnaeus), and *Neptunus sanguinolentus* (Herbst) are the most common forms. The oyster, *Ostrea virginiana*, occurs in Chilka Lake and *Ostrea madrasensis* and *Ostrea cucullata* in lagoons and minor estuaries on the Madras coast. *Meretrix* spp. are found abundantly in the channel area of Chilka Lake, and extensive clam beds occur in the backwaters of Kerala. Shells of these are collected in large quantities for manufacture of lime. In Tambegam Lagoon in Ceylon the windowpane oyster (*Placuna placenta*) is found in fishable numbers and from the shallow waters of many bays and lagoons sea cucumbers (*Holothuria* spp.) are collected for the preparation of beche-de-mer.

CAPTURE FISHERIES OF THE MAJOR ESTUARIES

FISHING METHODS

The commonest method of fishing in the estuaries of rivers in the Indian subcontinent is by means of fixed bag nets (Fig. 1). Bag nets of different sizes are set against the current in shallow areas by fastening the wings to wooden posts or bamboo poles driven into the bottom, the mouths of the nets being kept open by means of bamboo poles. In deeper waters

heavy wooden anchors are used instead of wooden posts or bamboo poles. In very deep waters, bag nets are operated in pairs from anchored boats, one net being set on either side of the boat or from wire ropes laid across the estuary. Tidal water is allowed to flow through the net and a variety of small-sized fish are caught.

In the Sunderbans Estuary, various types of gill nets, drift nets, cast nets, encircling, and drag nets are used for hilsa fishing. In the Sunderbans, as well as in the Mahanadi Estuary, narrow creeks are often fenced off at high tide with walls of bamboo slats or with netting. At low tide, if the creek is drained dry, the fish are caught by hand; if not, the stranded fish are caught with cast nets or smaller seines. In the Mahanadi Estuary, even wider creeks may be fenced off and the fish are driven towards the fence by beating the water with poles and caught with the help of a seine dragged towards the fence.

In the Chilka Lake, commercial fishing is generally done with nets for fish and traps for prawns and crabs. Gill nets and drag nets are used for catching hilsa, cock-up, and grey mullets. Special types of drag nets are used for catching smaller fish. The most common prawn trap is made of bamboo slats, and consists of a bamboo screen measuring about 40 by 4 feet which serves as a guide for directing the prawns into the prism-shaped trap also made of bamboo strips. Crabs are caught in cage traps. Barriecades of bamboo screens provided with openings are used for fishing in a low-lying area about a mile long and a few yards wide. During rains the enclosed area is filled as high as floodwater will permit and then the openings are blocked, thus trapping fish within the enclosure. Fishing takes place from the end of October to February, when the water level falls. The catches consist largely of immature fish.

In the estuaries of Krishna and Godavari, the most common fishing gear is the Rangoon net, a floating gill net in which large fish become entangled after gilling. The bulk of the catches of hilsa from these estuaries is landed with this net, incidental catches being the threadfin and the cock-up.

In Pulicat Lake drag nets or beach seines are commonly used. The Konda Valai is a peculiar fishing implement about 65 feet long and only about 24 inches deep in the form of a shallow bag, the mouth of which is kept open by means of short sticks along its length. It is operated like a shore seine or set in a semicircle and fish driven into it with the help of a scare line. Stake nets, set nets, gill nets, cast nets, and torches in conjunction with fish baskets, are also used extensively.

Very familiar landmarks along the backwaters of the Travancore-Cochin area in Kerala are the Chinese dip nets installed all along the banks (Fig. 2). The net is hung from a wooden framework and is dipped and raised with the help of a lever arrangement. At night lanterns are tied to the net frame to serve as lure and appreciable catches are obtained; the main advantage of the net is that it can be operated at any



Fig. 2. The Chinese dip net commonly used in the backwaters of Kerala.

time under any weather conditions and ensures some catch every day. Cast nets are extensively used in the backwaters and catch a good part of the prawns and shrimps landed from these areas. A striking sight in the backwaters is the enormous number of commercial rod-and-line fishermen. From a very small dugout canoe manned by a single fisherman, three or four rods may be operated and appreciable quantities of quality fish are thus caught. The right to operate fixed bag nets, generally called stake nets because of their being tied to stakes driven into the bottom at different spots in the backwaters, is leased out by the government and the catches, consisting mostly of small fish, are sun-dried. Besides these, a variety of gill nets with scare lines, encircling nets, etc., are also operated in the backwaters.

In Lake Negumbo, and other lagoons in Ceylon, a variety of fishing implements such as rod and line, hand lines, cast nets, barrier nets, prawn traps, crab nets, and brush pile traps are employed for fishing. A very effective fishing device, though considered very destructive to fish stocks, is the use of fish kraals or weirs built across tidal rivers and shallow estuaries.

LANDINGS

Owing to the scattered nature of the fisheries and the lack of specified landing places, the collection of fish landing statistics from most of the estuarine areas in the Indian Ocean coastal zone is difficult. Only in the Hooghly-Matlab estuarine system of Sunderbans in West Bengal has an attempt been made to collect statistics of catch and effort (Pillay, 1960; Pillay and Ghosh, 1964) by a stratified sampling survey. The total annual production from this area is estimated to average around 3,500 metric tons. The bag-net fishery normally accounts for about 70 percent of the catch and production was estimated to be 1,986 metric tons in 1958 and 2,471 in 1959. The catch per net (of 800 to 1,000 meshes along the periphery) per tide varies with the distance of the fishing spot from the sea. The maximum catches are

from November to January when the average catch per net was 175.2 kg. Prawns constitute between 16.6 and 28.9 percent and Bombay duck 19.5 to 38.8 percent. Miscellaneous fishes (small clupeids, catfish, sciaenids, scad, and gobies) form 18 to 22 percent of the catches. *Pama pama*, *Trichiurus* spp., *Setipinna* spp., *Sillago panijus*, *Osteogencosus militaris*, *Polynemus paradiseus*, *Coilia* spp., and *Ilisha* spp. are the other important species.

The production of fish from Chilka Lake has been estimated on the basis of export figures and the quantities of fish dried locally added to a rough estimate of local consumption (Jones and Sujansinghani, 1954). For 1948 the estimated total production was about 3,900 metric tons. The average production may be taken as about 3,300 metric tons, which is about 30.15 kg per hectare (ha.). Mullet, clupeids, catfish, sciaenids, perch, threadfin, beloniformes, and prawns form the main constituents of the catches. Marked fluctuations in production have been observed and it is suspected that the lake is being over-exploited.

The Mahanadi Estuary, till recent years, has been cut off from the main consuming centers and, probably because of this, fishing effort in the estuary has not been as intensive as in most other estuaries of the Indian subcontinent. It has not yet been possible to obtain a reliable estimate of the landings from this estuary, but the composition of catches is roughly the same as in Chilka Lake. Production figures for the whole of Pulicat Lake are not available, but landings from three important fishing centers in one year amounted to about 2,562 tons (Chacko *et al.*, 1953), mullets and prawns constituting the major part of the catches. Statistics of landings from other estuaries in India are not available. The production of prawns from the Travancore-Cochin backwaters, however, has been roughly estimated at 10,000 tons per year.

In Ceylon, the landings from Lake Negumbo are reported to be about 65 pounds per acre. Other lagoons in the country are estimated to have similar productivity.

UTILIZATION OF CATCHES

In the Indian subcontinent as a whole the preference of consumers is for large fish, except for fishes like *Polynemus paradiseus*, which are considered a delicacy though attaining only a small size. In the Sunderbans Estuary the main fishing season is in the winter; quality fish purchased from the fishermen by fish traders are preserved in ice on carrier boats and transported to landing centers up the estuary where they are repacked and transported to markets. The smaller fish are dried on specially constructed platforms, or, as in the case of Bombay duck, ribbon fish, etc., are hung on ropes (Fig. 3). Very small sciaenids and similar fish which have no market as food are dried on the beach for use as manure.

At Chilka Lake, fish preserved in crushed ice are brought to landing centers in boats. Here all fish meant for export—the majority of the catches are exported to Calcutta—are repacked in ice in bamboo



Fig. 3. Bombay duck being sun-dried in the Sunderbans.

baskets and transported by train. During the main fishing season in the winter months, railways operate "fish specials" for the transport of Chilka fish. In recent years the railways have introduced refrigerated rail vans. The less important varieties of fish, like engraulids and small clupeids as well as small shrimps, are dried with or without salting. The dried fish are transported to inland areas, mainly in the State of Orissa, for local consumption.

The bulk of the catches from the Mahanadi Estuary is dried. A small fresh fish trade has developed in recent years as a result of the installation of an ice plant. Fresh fish is now sent to Cuttack and, during the main fishing season, some quantities are transported by rail to Calcutta. The catches from Krishna, Godavari, and Cauvery Estuaries, especially the hilsa, are transported on cycles or horse-carriages to the nearest markets. Other fish are also sold fresh, but when catches are larger than can be marketed locally, they are dried, especially the small-sized fish. Catches from the Pulicat Lake are marketed fresh, mostly in Madras. The catches from the backwaters of Travancore-Cochin (Kerala) are also mostly sold fresh, except for very small shrimps and miscellaneous catches of stake nets. The bigger prawns are sold to freezing and canning companies in Cochin for processing and export.

TRENDS IN THE DEVELOPMENT OF CAPTURE FISHERIES

The existing world market for prawns and shrimps has encouraged intensive fishing. The establishment of large-scale freezing and canning industries in Cochin is partly to utilize the catches from the estuarine areas, including the rice fields. Establishment of such processing plants in other estuarine areas is either under way or planned. The trend is to utilize as much of the catch as possible fresh, iced, or frozen and as a consequence the dry fish trade is dwindling. There are certain fishes, however, like the Bombay duck which are not relished fresh and must be dried for marketing.

In the Sunderbans Estuary intensive fishing is re-

stricted to the winter season, when the estuary is calm and the local boats can operate safely. The use of mechanized boats suitable for operation during rough weather may help to extend the fishing season and thereby the production. Trawling experiments were recently conducted from a specially designed trawler. While the total landings by the trawler were not particularly low, very few quality fish were caught and the experiments did not indicate the possibilities of commercial trawling in the estuaries. Long lines, gill nets, and drift nets generally catch quality fish and the operation of such nets from safer mechanized decked boats may be feasible under conditions in Chilka Lake and other estuaries.

In Travancore-Cochin backwaters, operation of small shrimp trawls has also given encouraging results and it may be possible to establish a small trawl fishery there, at least for shrimps.

Preliminary trawling experiments in the estuarine areas of Kenya with a shrimp trawl have given encouraging results (Wilkinson, personal communication). The catches averaged about 91 kg per half hour.

As mentioned earlier, considerable fishing in the estuaries is done with fixed bag nets or stake nets, and a large percentage of the catches consists of young and immature fish, the market value of which is very low. Many workers have advocated regulation of this type of fishing to reduce the capture of immature fish. Experimental fishing with cover nets has shown that very few juveniles are able to escape from the cod ends of fixed bag nets when they are in operation. If nets of larger mesh could bring in catches of equivalent value, if not of equivalent weight, there may not be much difficulty in enforcing regulation of mesh size. There is a general belief that the Sunderbans Estuary, Chilka Lake, and Travancore-Cochin backwaters are being overfished. As yet, there is no evidence to prove this, but investigations are now under way. In Chilka Lake, however, the silting of the channel that connects it with the sea has been recognized as the one main cause for reduction of catches. The silt accumulation restricts the migration of juveniles and other young fish into the lake from the sea, and hinders movement of adult fish. Regular dredging of the channel has been suggested.

Except in restricted areas in the backwaters of Travancore-Cochin, no effect of pollution on estuarine fisheries has been noticed. But large-scale reclamation projects in estuarine areas, as those in progress in parts of Sunderbans and in Travancore-Cochin backwaters, are bound to affect the fisheries. Proper appraisal of the socio-economic aspects of such projects in relation to the fishing industry has not been made, and one cannot overemphasize the need for it.

CULTURE FISHERIES IN ESTUARINE AREAS LAND RECLAMATION AND FISH CULTURE

Very extensive saline swamps similar to those of the deltaic regions of rivers in the Indian Ocean



Fig. 4. A view of a brackish-water fish farm on the west coast of India.

coastal zone, as well as shallow mud flats, are also found along the margins of lagoons, bays, and creeks. A system of culturing fish as a phase in the reclamation of such swamps for agriculture has developed in this area from ancient times (Schuster, 1952; Pillay, 1958). The swamps are banked with dikes to take in water at high tide, and the suspended silt settles on the bottom, slowly raising its level. It may take several years for the land to be raised sufficiently for culturing paddy. During this period the area can be used for growing fish. The tidal water brings in the fry of commercially important fishes, including prawns, and by the provision of suitable sluice gates and by taking in tidal water regularly during the periods of abundance of fry, the areas can be stocked with adequate quantities of seed for rearing. Screens are provided in the sluice gates to prevent the escape of fish or the ingress of extraneous fish. Commercial brackish-water fish culture in the Indian Ocean coastal zone originated in this manner and original practice is still followed without much modification in many areas in India (Pillay, 1954) and Pakistan. When the land level is sufficiently raised, intake of tidal water is discontinued and rain water is collected to leach the salt from the soil. This may be done for two or three seasons, after which the paddy may be planted. The plot will, however, have the canal system inside the dike (dug for obtaining earth to construct the dike) and these canals are used for culturing brackish-water fishes. Many farmers, who have found fish culture to be more remunerative than growing paddy, utilize the embanked areas entirely for fish culture, and the silt deposited is regularly removed to maintain sufficient depth of water.

BRACKISH-WATER FISH FARMS

The incidental use of swampy land for raising fish promoted a system of intensive fish culture. Fish ponds of different design and shape began to be constructed for the sole purpose of culturing fish on a commercial scale (Fig. 4). Brackish-water fish cul-

ture has developed on a very large scale in Indonesia (particularly the islands of Java and Madura). About 200,000 acres of ponds, locally called "tambaks", have been constructed in the mangrove swamps and nearly 33 million pounds of fish are produced from these (Schuster, 1952). In Indonesia, as in some of the neighboring Asian countries, this industry is largely based on the milk fish, *Chanos chanos*, which is highly relished. As the fish does not breed in captivity, post-larvae and juveniles are collected from the inshore areas from September to December and April to May and transported to the fish pond areas in special containers (flat, watertight bamboo baskets). The collection, transport, and sale of fish seed constitute an industry of some magnitude. The annual requirements for the tambaks of Java and Madura are estimated to be about 190 to 200 million fry. The fry often pass through several hands before they reach the farmers. *Puntius javanicus* and *Tilapia mossambica* are also stocked in some of the brackish-water ponds in Indonesia. In India selective stocking of brackish-water fish ponds is done only in government-owned fish farms. Grey mullet, pearl spot, prawns, or milk fish fry are collected with close-meshed seines from nearby areas and transported directly to the farms. Different types of layouts are adopted for brackish-water fish farms. In Java the improved porong type of farm is considered the most satisfactory. On the average, they are about 7.5 ha in extent and consist of 3 to 10 irregularly shaped sections connected by secondary sluice gates, the whole being controlled by a main gate which is located in a deep portion having a channel in the middle. Each porong-type of farm has fry ponds (nursery ponds) of about 90 to 900 square meters, and rearing ponds of 200 to 4,500 square meters. The growing period ranges from 6 to 10 months, when the milk fish attains a weight of about 350 g. Prawns, mullet, catfish, and snapper gain access to the ponds and contribute to the production.

The production of adequate quantities of benthic algae of the desired type is the most important cultural technique. Nursery ponds are drained and dried to eradicate predatory and weed fishes and to hasten decomposition of organic matter. A depth of only 3 to 5 cm of tidal water is taken in and allowed to stand. Within 3 to 7 days a brownish, greenish, or yellowish layer of microorganisms (predominantly bacteria, unicellular and filamentous Myxophyceae, especially Oscillatoriaceae, fragments of filamentous green algae, and diatoms, as well as protozoans, copepods, ostracoda, free-living flat worms, round worms, and larval forms of molluscs and larger crustaceans) develops on the pond bottom. A good growth is essential for the survival of fry. Fertile soil, exposure of pond bed to intense light, low level of stagnant clear water of salinity ranging from 10 to 40‰, regular renewal of the pond water, and absence of browsing animals in the pond are believed to be the main factors in inducing the growth of such an algal complex (Rabanal *et al.*, 1951). Experimental studies

and observations in India have indicated that different algae have different ecological requirements for their growth (Pillay *et al.*, 1962). Higher temperature and salinity seem to be generally conducive to greater production of benthic algae, and the soil nutrients appear to be of greater significance in the production of benthic algae than nutrients in the water phase.

Chanos fry are planted in nurseries at the rate of 30 to 55 fry per square meter and are reared for a period of about 30 days when they attain a length of 5 to 7 cm. The average survival rate is about 50 percent, but experienced culturists may obtain a survival rate of 60 to 80 percent. In rearing, as well as stocking ponds, production of benthic algae is of great importance. While fry of milk fish or mullets are not able to consume tough filamentous algae, larger fish are able to forage on decaying or decayed algae. Higher levels of water in ponds encourage more profuse growth of Chlorophyceae. Limited green manuring with grass or mangrove leaves is practiced in Indonesia, and copra slime, at the rate of 450 to 900 kg per ha has also been used for the purpose. Growth and production of fish in the ponds depend on the growth of algae. It is estimated that the conversion ratio of wet algae to fish is approximately 25 to 30:1. Artificial feeding is not practiced except in brackish-water nursery ponds where rice bran may be used as a food.

As brackish-water ponds can generally be drained at low tide, capture of fish from the ponds does not present any great difficulty. The tendency of the fish to swim against the current is utilized for partial fishing. When tidal water is let into the pond, the fish swim against the current and can then be led into a catching pond or similar area for capture. In the "bheris" of India, special traps are installed near the sluice gates to trap the fish. Cast nets and seines are also often used in the ponds. The production of fish varies considerably according to the fertility of the soil, size of ponds, and other factors. The production of tambaks is estimated to vary between 50 and 450 kg per ha. The total annual fish production from tambaks in Java and Madura is estimated to be 8,962,500 kg (19,759,000 lbs.) of milk fish, 2,940,300 kg (6,482,300 lbs.) of penaeid prawns and 1,496,800 kg (3,300,000 lbs.) of other fish. The mortality of fry during growth to commercial size may be from 60 to 80 percent. In well-managed brackish-water ponds in India, a higher production of 1,000 kg per ha (900 lbs. per acre) has been obtained. In the less intensively cultivated bheris the production is generally between 150 and 250 kg per ha (between 130 and 220 lbs. per acre).

BRACKISH-WATER FISH CULTURE IN PADDY FIELDS

The practice of culturing brackish-water fishes in saline swamps after reclamation for paddy culture is generally prevalent in parts of India. Pillay and Bose (1957) have described the practice in the deltaic areas of West Bengal, where the canal system around the



Fig. 5. A paddy field in the Sunderbans, where fish are also cultured.

paddy field is used initially for rearing of fry taken in with the tidal water during the dry months. The water level in the canals is maintained at about 30 cm below the level of the paddy land until the onset of the southwest monsoons in June. The fields are then prepared by manuring and seedlings are planted. By August the water level in the canals has increased appreciably from the accumulation of rain water, and the salinity of the water is low. The bunds along the canals are then cut and the fish are able to migrate into the paddy plots and feed on the growth of algae and other microscopic organisms. Before harvesting of the paddy, the water level falls and the fish return to the canals where they are easily captured (Fig. 5). Grey mullet (*Mugil persia*, *M. tade*, and *M. corsula*), the cock-up (*Lates calcarifer*), catfish (*Mystus gulio*), and prawns (*Palaeomon carcinus*, *Macrobrachium rude*, *Metapenaeus monoceros*, *M. brevicornis* and *Penaeus semisulcatus*) are the major species cultured. The yield of fish is between 100 and 200 kg of fish per ha (about 90 to 180 lbs. per acre) of paddy field, without in any way affecting the yield of the paddy.

The paddy fields in the backwater areas of Travancore-Cochin produce considerable quantities of prawns. Panikkar (1937) and Gopinath (1955) have described the methods adopted. The paddy fields are single-crop lands and the interval between harvesting and the next planting is utilized for growing prawns. In October after the harvest, the embankments are strengthened and sluice gates installed. Water is let into the fields at high tide after allowing the water level in the feeder canal to rise to the maximum, so that the water flow will carry in large numbers of young prawns. A large part of the water is drained at low tide and again at next high tide the process is repeated. Generally a lamp is hung above the sluice gate at night to attract prawns. The sluices are finally closed and the prawns are allowed to grow for periods up to three months, after which they are captured. At neap tides, the water from the field is filtered through a conical bag net having a rec-

tangular frame at the mouth, which is fixed in the sluice gate. The water is allowed to flow with force so that the prawns will also be carried with it. The catches are removed from the eel end of the net at regular intervals. Fishing may continue for seven to eight days, and a lamp may be used at night to lure the prawns.

There are about 4,400 ha of such paddy fields in the Kerala area and the annual yield varies between about 785 and 2,135 kg per ha. The annual production is estimated to be 3,000 to 5,400 tons. Prawns and shrimps form about 80 percent of the catch and the species generally caught are *Penaeus indicus*, *P. semisulcatus*, *Metapenaeus monoceros*, *M. dobsoni*, *Macrobrachium rude*, *Palaemon styliferus*, *Caridina gracilirostris*, and *Aeetes* sp. Almost the entire production is exported to Rangoon, Singapore, and Hong Kong dried and shelled.

POSSIBILITIES OF EXPANDING CULTURE FISHERIES

In the estuarine areas of the Indian Ocean coastal zone there are extensive mud flats, saline swamps, and protected bays well suited for conversion into fish ponds, but only a very small percentage of them is being used now. Many hundreds of acres of mangrove swamps remain to be cleared and reclaimed into fish ponds.

In Ceylon it is estimated that there are some 117,000 ha of lagoons and estuaries suitable for fish culture. A very conservative estimate for India is about 121,200 ha of mangrove swamps and 264,400 ha of lagoons and estuaries. In Indonesia 6 million ha of mangroves and 8.5 million ha of lagoons and estuaries are estimated to be suitable for fish culture. Pakistan also has some 305,000 ha of mangrove swamps and 424,000 ha of lagoons and estuaries that can be brought into fish production. According to records, the total area of brackish-water fish ponds presently existing in these four countries is only about 137,300 ha.

Most of the countries in the area are in urgent need of increasing their fish resources and the utilization of these waste lands for fish production can be expected to make a very important contribution to the solution of the food problem. Some of the areas may also prove suitable for the culture of oysters, even though the markets for oysters in many of the countries in the region are limited.

LITERATURE CITED

- CHACKO, P. I., J. G. ABRAHAM, and K. R. ANDAL, 1953. Report on a survey of the flora, fauna and fisheries of Pulicat Lake, Madras State. Contrib. 8. Freshwater Biol. Station, Madras, India.
- GOPINATH, K., 1955. Prawn culture in the rice fields of Travancore, Cochin, India. Proc. Indo-Pacific Fisheries Council, 6(3):419-424.
- HARDENBERG, J. D. F., 1950. Estuarine problems in Southeast Asia. Proc. Indo-Pacific Fisheries Council (2nd meeting), pp. 175-180.
- HORA, S. L., 1943. Evidence of distribution of fishes regarding rise in salinity of the River Hooghly. Current Sci., (India), 12(3):89-90.
- HORA, S. L., 1953. Further evidence from fish distribution of the rise in salinity of the River Hooghly. Current Sci. (India), 21(2):49-50.
- JONES, S., and K. H. SUJANSINGHANI, 1954. Fish and fisheries of the Chilka Lake with statistics of fish catches for the years 1948-1950. Indian J. Fisheries, 1(1-2):246-344.
- OAG, T. M., 1939. Report on the River Hooghly and its headwaters. Commissioner for the Port of Calcutta, Calcutta, India.
- PANIKKAR, N. K., 1937. Prawn industry of the Malabar Coast. J. Bombay Nat. Hist. Soc., (39):343-353.
- PILLAY, T. V. R., 1953. Studies on the food, feeding habits and alimentary tract of the grey mullet, *Mugil tade* (Forskaal). Proc. Natl. Inst. Sci. India, 19(6):777-827.
- PILLAY, T. V. R., 1954. The ecology of a brackish-water bheri with special reference to the fish cultural practices and biotic interaction. Proc. Natl. Inst. Sci. India, 20(4): 399-427.
- PILLAY, T. V. R., 1958. Land reclamation and fish culture in the deltaic area of West Bengal, India. Progressive Fish Culturist, 20:99-103.
- PILLAY, T. V. R., 1960. On the occurrence of *Hilsa toli* (Cuv. and Va.). Current Sci. (India), 22:82-83.
- PILLAY, T. V. R., and B. BOSE, 1957. Observations on the culture of brackish-water fishes in paddy fields in West Bengal (India). Proc. Indo-Pacific Fisheries Council, 7(2-3): 187-192.
- PILLAY, T. V. R., and K. K. GHOSH, 1964. The bag net fishery of the Hooghly-Matla estuarine system (West Bengal). Indian J. Fisheries, 9:71-99.
- PILLAY, T. V. R., M. R. VIJAYARAGHAVAN, and S. C. THAKURTA, 1962. An ecological study of benthic flora in brackish-water bheris. Proc. Natl. Inst. Sci. India, 28 (B) (5):416-431.
- RABANAL, H. R., H. R. MONTALBAN, and D. K. VILLALUZ, 1951. The preparation and management of bangos fish pond nursery in the Philippines. Philippine J. Fisheries, 1(1):3-34.
- SCHUSTER, W. H., 1952. Fish culture in brackish-water ponds of Java. Indo-Pacific Fisheries Council (Spec. Publ.), No. 1.

Estuarine Fisheries in Europe as Affected by Man's Multiple Activities

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In this paper some typical examples of the variety of patterns which affect the potentiality of estuaries for fishery resources will be discussed with particular reference to the biological effects of man's activities in estuarine environments.

An estuary in the classical sense of the word is the more or less broadening seaward section of a river, through which the fresh water flows towards the sea, swiftly on the ebb tide, slowly, sometimes even in the reversed direction, during the flood. Here the intricate interaction of the river and the tides can be clearly observed. Where the estuary is deep enough, a salt wedge creeps landwards under the fresher river water; the wedge pulsates with the tides and tapers off as the distance from the sea increases, but it always shows a sharp halocline where it meets the fresh river water above it.

In such an estuary biological conditions are more or less inimical to fishes and invertebrates. Salinity changes abruptly and markedly in sections of the estuary, both vertically and horizontally. These changes can be observed from hour to hour, depending on the tides; but in addition, longer-term fluctuations also occur. These are caused by variations in the runoff of the river, by the sequence of springs and neaps, and by the influence of prevailing strong winds. It is clear that few fish species can endure these ever-changing conditions. And even if food were plentiful, such areas would not make good spawning grounds for fishes. Fish eggs and larvae attached to some type of substratum would not be able to stand the frequent and sharp changes in salinity, and pelagic fish eggs and larvae would be carried down to the sea by the residual current long before the larvae could develop into juveniles strong enough to swim to suitable habitats.

Even so, fishing can be good in such estuaries, for fishes may pass here in incredible numbers on their way from the sea to their spawning grounds in the fresher water. These are the anadromous fishes, of which the more important in the European waters are salmon, shad, sturgeon, and smelt.

The word salmon has an almost magical sound to both professional and sport fishermen. The river Rhine, in season, used to teem with salmon making their way to their spawning grounds in Germany, France, and Switzerland. Old paintings in art galleries reveal that salmon was on the tables of the poorest people in the Netherlands. In the Netherlands today, few people have ever seen a salmon which did

not come out of a tin, or was on display, smoked, in a fishmonger's shop. The salmon disappeared from the Rhine River in the first half of this century (Deelder and Van Drimmele, 1959). Several hydroelectric dams were built in the Rhine tributaries and the fish passes that were constructed were not always adequate. Even where they were, the fish that traversed them found the formerly swift-running upriver sections changed into a series of nearly stagnant pools, and the gravel beds where eggs were deposited turned into muddy bottoms. Meanwhile industrial and domestic sewage has poured into the river in such great quantities that the Rhine is now called Europe's open sewer. In the downriver section, especially, the water often has a very bad smell, and its oxygen supply is low to very low.

Thus man's rapidly increasing population and expanding industrial activities in this part of Europe have brought about profound ecological changes in the rivers which hurt the fishery resource. This does not mean, however, that the salmon is extinct in Europe, even though it has disappeared from the Rhine where it was once most plentiful. In other countries, such as Ireland, Iceland, Scotland, Norway, and Sweden, there remain rivers where ecological conditions have hardly changed, and salmon run there in considerable numbers.

The shad, too, is an anadromous fish, but it does not make its way upriver as far as the salmon. Of the two species once teeming in the Rhine River, *Alosa alosa* (L.) and *Alosa fallax* (Lac.), only the latter remains. The former, which is the larger variety, and used to be enjoyed as a smoked product, was formerly caught by the millions in the Rhine Estuary. It has disappeared from the Rhine as a result of overfishing and pollution. *A. fallax* still occurs there, some years in fair numbers, but it is a fish of little importance commercially because of its poor table qualities.

The third anadromous fish in European waters is sturgeon, of which there are several species, those from southeastern Europe being renowned for caviar. *Acipenser sturio* ascends the rivers of the Atlantic coast of Europe, although only in small numbers. In the Netherlands' estuaries, where this species was once common, it has become a rarity. Recent excavations uncovered a prehistoric village in the vicinity of Rotterdam. The numerous remains of sturgeon scales that were found indicate that sturgeon fishing must have been a major occupation of the people living there.

The fourth anadromous fish is the smelt *Osmerus eperlanus* (L.), a small salmonoid fish. It lives chiefly in brackish water, often in estuaries, and moves somewhat farther upriver to spawn in early spring. Its economic importance is limited.

Taking the meaning of the word estuary in a broader sense, we find a number of instances where fish and invertebrates occur in tremendous numbers and have supported great fisheries, often since time immemorial. In pounds of yield per surface area these estuaries are much richer than the open sea in food resources. Several ecological factors may contribute to their productiveness, as illustrated in examples described below.

ZUIDER ZEE

Some estuaries are characterized by a huge body of brackish water, with a fairly wide opening to the sea. In these, reduced salinity, higher summer temperatures as compared with the open sea, and abundance of food support large populations of fish species.

The old Zuider Zee was a good example of such an estuary until completion of its enclosure and separation from the Wadden Zee in 1932. Its main communication with the North Sea was the wide and deep Mars Diep, situated between the island of Texel and the mainland of the province of North Holland. The Mars Diep leads into the Wadden Zee behind the Frisian Islands; but to the south it was formerly continuous with the Zuider Zee. The funnel-shaped northern section of the Zuider Zee was some eight to nine meters deep, and had predominately a sandy bottom. It was an area of about 1,000 square kilometers. South of the narrowing between the old cities of Enkhuizen and Stavoren began the bag-shaped widening of the Zuider Zee, which was about three to four meters deep, with a predominantly muddy bottom, and here and there some sand banks and sections with a subsoil of peat. This area measured about 2,700 square kilometers. The river IJssel, a branch of the Rhine, poured its water into the Zuider Zee at the eastern coastline, not far from the city of Kampen.

In the funnel-shaped northern section tidal currents contributed to its furrowed sandy bottom. The salinity in the Wadden Zee fluctuated between 20 and 30‰; and the funnel-shaped northern section of the Zuider Zee had salinities roughly between 15 and 20‰. In the bag-shaped widening, salinities were lower, from 10 to 15‰ in the northern portions, slightly under 10‰ farther south, with minimum values in the vicinity of the river IJssel. Tides had a very modest range here, and wind was the important factor in bringing about water displacements. The bottom was predominantly muddy, leading to resuspension of sediments during strong winds, hence the greyish-green color of the water. In summer, water temperatures in the old Zuider Zee were several degrees higher than in the adjacent section of the North Sea; in winter they were several degrees lower, often leading to ice formation. Plankton was tremendously

abundant, since the productivity in this shallow body of water was continuously promoted by the nutrients brought in by the IJssel River, and by the mineralization of domestic sewage brought into the Zuider Zee by the city of Amsterdam and a number of smaller cities and villages fringing the coastline. Plankton was abundant, but it was comprised of few species, for only those adapted to mesohaline conditions could survive. Among the phytoplankters the diatom *Coscinodiscus biconicus* predominated; among the zooplankters copepods such as *Eurytemora* and *Acartia* were numerous. The bottom fauna included a variety of crustaceans, annelids, and molluscs. Redeke *et al.* (1922, 1936) gave a clear picture of the rich flora and fauna in this interesting estuary.

Among the Zuider Zee fishes, herring ranked first in economic importance. Spring spawners, with an average vertebrae number of 55.5, migrated into the Zuider Zee in March and April. Spawning took place from April to July, chiefly in the southwestern section of the bag-shaped widening, on the sandy bottom rich in molluscan shells and hydroids. Herring larvae were numerous in May and June in water of 5 to 10‰ salinity. They grew rapidly, mostly on a diet of copepods, and left the Zuider Zee in the autumn at a length of 8 to 9 cm. Two or three years later they returned to the Zuider Zee to spawn (Redeke, 1907).

The catches fluctuated around 13,500,000 kg per year. The Zuider Zee herring was excellent fresh and for smoking, but was unsuitable for the traditional salt-curing.

The enclosure of the Zuider Zee made it impossible for herring to enter the mesohaline Zuider Zee, and the salinity of the Wadden Zee was too high for the development of its larvae. In the first years after completion of the enclosure in 1932, the Zuider Zee herring still tried to reach the old spawning area. As the average age increased, the number of fish decreased, and within a few years this herring tribe, which once brought prosperity to the local fishing population, became virtually extinct.

Ranking second in importance was the anchovy *Engraulis encrasicholus* (L.). When pickled in brine, this little clupeoid fish develops an excellent flavor which it retains even with long storage. Formerly, eastern Europe was the main market for this product. Although the abundance of the anchovy fluctuated considerably, the anchovy merchants could store it successfully against periods of scarcity.

The anchovy entered the Zuider Zee as soon as the water temperature became higher there than in the open North Sea, usually during May. June was the best month for fishing. The anchovy spawned its large ellipsoid pelagic eggs in the funnel-shaped northern section of the Zuider Zee in water with a salinity of over 15‰. The larvae migrated into the bag-shaped widening of the Zuider Zee and developed there on the rich plankton in water of a salinity of about 10‰. After a period of rapid growth, they migrated in autumn to the open North Sea, to return the next year

to spawn in the Zuider Zee. Most of the spawning anchovies were only one year old. The anchovy catches in the northern section of the Zuider Zee fluctuated around 1,500,000 kg a year. Unlike the herring, the anchovy was not attracted by the lower salinities in the Zuider Zee, but by the higher water temperatures; for here it is at the northern fringe of its range, and the water in the open sea is usually too cold for its reproduction. The enormous year-to-year fluctuations of the catch were clearly associated with favorable or unfavorable weather conditions during June, the principal month of spawning. In the Oosterschelde, in the southwestern section of the Netherlands where salinity is much higher (averaging 28‰), the anchovy successfully reproduces because of the high water temperatures prevailing when the weather is favorable.

The enclosure of the Zuider Zee made it impossible for the anchovy to reach its old spawning area. It could still reproduce in the saltier Wadden Zee, however, though temperatures were somewhat lower there than in the Zuider Zee. With the loss of the Zuider Zee anchovy, the catch fell to 13 percent of its old level. The Oosterschelde catch was not affected by the enclosure of the Zuider Zee, which indicates that this kind of anchovy always returns to its home grounds for spawning (Korringa, 1963d).

The enclosure of the Zuider Zee crippled the traditional fishing in this estuary, but after the change of the blocked-off section into a freshwater lake, eels became so abundant there that a new type of fishing industry developed.

LAKE PATRIA

In Italy, Lake Patria, north of Naples, resembles the former Zuider Zee in some respects. Here, too, the Volturno River discharges into a lake-like estuary. This river discharges only moderate quantities of water, however, and the communication of the estuary with the sea consists of a narrow and very shallow watercourse. Moreover, in the Mediterranean Sea, the tidal range, and hence the effect of the tides in the estuary, is considerably less important than on the Atlantic coast of Europe. Still, the influence of the tides is strong enough to create mesohaline conditions, with a salinity of about 9‰.

Lake Patria teems with fish, predominantly mullet and eel. The intense green color of the water, observed by the author during a visit in April, 1954, indicated a high degree of productivity (Korringa and Postma, 1957). Analysis revealed that at that time free phosphate was virtually absent, and few phytoplankton could be caught with a fine-meshed net. The bottom fauna, among which *Chironomid* larvae and the brackish water polychaete *Mercierielia* predominated, appeared to be very rich. Free phosphate was found in great quantities in one of the wells discharging into the lake, and the quantity of organic phosphorus in the lake itself was very high. Though diatoms and larger green algae were virtually absent, the chlorophyll content of the water was very high.

being from 20 to 100 mg per m³. This could be ascribed to a superabundance of small flagellates, from 100,000 to 500,000 per cm³. Evidently this estuary is biologically much richer than the water of the Volturno River itself, or of the Mediterranean Sea into which the lake discharges. Nutrients, including considerable quantities of phosphate, enter the lake from the volcanic subsoil. Mesohaline conditions and the rich supply of plankton support large stocks of a few species of fish.

Other lakes communicate with the sea northwest of Naples, including the well-known Lake Fusaro and Lake Lucrine. Since less fresh water enters these two lakes than Lake Patria, and since the communication with the Mediterranean Sea is larger and deeper, salinities are considerably higher, leading to polyhaline conditions.

Man has learned to take advantage of this situation by growing mussels in hanging cultures in these lakes. The soft muddy subsoil makes mussel farming on the bottom impossible, but in hanging cultures the mussels grow and fatten rapidly. Consequently, these lakes are highly productive. Biological and chemical analyses revealed that the rich phytoplankton in these estuarine lakes makes large-scale mussel production feasible, and promotes a better growth of mussels than the sheltered sites in nearby coastal water. Here, too, nutrients, especially phosphates brought in by subterranean wells from the fertile volcanic subsoil, account for the increased productivity (Korringa and Postma, 1957).

Man has exerted a positive influence in these polyhaline estuaries by developing a system of mussel farming in mid-water and permitting this potential fisheries resource to be exploited in a rational way.

OOSTERSCHELDE

The Oosterschelde, situated in the southwestern section of the Netherlands in the province of Zealand, is an estuary with a very different pattern. The Oosterschelde is an embayment penetrating far into the land, but receiving little influx from the surrounding fertile arable land. Its salinity is rather high (28‰ on an average) comparable with the coastal water of the North Sea with which it is continuous. Still, there is every reason to regard the Oosterschelde as an estuary, for here, too, river water and sea water meet under the influence of tides. The Rhine, and to a lesser degree the Meuse and Scheldt Rivers, discharge fresh water rich in nutrients and organic matter into the North Sea. Tides and winds bring about a thorough mixing, and microorganisms mineralize the remains of freshwater organisms and other organic material. It is this mixed coastal water which pours into the Oosterschelde with the tides. The greater the discharge of fresh water by the Rhine, the lower the salinity of the Oosterschelde. It could be demonstrated that there is an inverse relationship, with a lag of about one month, between the level of the Rhine where it enters the Netherlands and the salinity of the bay-harbor widening of the Oosterschelde (Korringa, 1940).

The high and rather constant salinity, together with the discharge of nutrients conducive to a rich plankton development, makes good oyster water. Moreover, oysters require a stable bottom; they cannot live on soft mud or shifting sand. Therefore most of the sandy bottom of the coastal waters of the Netherlands is not suitable for oysters. In the bag-shaped eastern section of the Oosterschelde, part of which was inhabited land only 400 years ago, large areas have a subsoil of peat, which makes good oyster bottom. It is here that natural oyster beds were found. From those beds as many as one million oysters a year were harvested by the Zealand oyster fishermen.

The discovery and general adoption in the 1860's of culture techniques in France led to withdrawal of natural beds from the free fishery. The present French oyster industry was established, with a multiple increase in yield. This development was observed with much interest in the Netherlands, and in 1870 cultivation of oysters was started in the Oosterschelde (Korringa, 1953). In due course some 30 million marketable oysters were produced annually. This success demonstrates that nature left to itself does not always lead to the highest possible production.

The sparsity of oyster production was caused, evidently, by the lack of suitable substrate on which larvae could settle. Recent investigations have revealed that favorable water temperature and a high degree of larval retention, both attributable to the shape of this estuary and the oscillating movement of the tide, provide excellent conditions for a relatively high degree of larval survival (Korringa, 1940).

Not only has there been an increase in the number of oysters through providing suitable substrate, but growth and fattening have been stimulated by transferring the young from the beds where they have settled profusely to areas where feeding conditions are considerably better. Here, too, nature left to itself does not necessarily lead to the best results. The setting pattern reveals that numerous larvae settle only where current velocities are low for many hours in succession. Such a situation is found near the head of the estuary, and here and there in eddies. By trial and error, oystermen found these favorable places to put out their collectors (Korringa, 1951, 1955).

Poor fattening occurs in the easternmost section of the Oosterschelde; the marketable oysters are found on plots which receive the flood current directly from the west. The condition index of the oysters fans out and tapers off over the beds farther east (Drinkwaard, 1959, 1960, 1961; Korringa, 1956b, 1957, 1958).

Water analysis reveals that phytoplankton, total phosphorus, and total organic matter are consistently higher in the western section of the Oosterschelde. It is the true estuarine water of the coastal area which brings fertility to the oyster area on the firm bottom farther east. Efforts to fatten oysters in hanging culture in the rich waters of the western section of the Oosterschelde were unsuccessful. Here the oysters starved in the midst of plenty because of too strong a current. Laboratory experiments led to the conclu-

sion that in a continuous stream of water, growth and fattening were best at current velocities of only a few cm per second. On the other hand, too slow a current does not supply sufficient food.

Recent annual production of marketable oysters has been around 30 million a year. Since most of these oysters are four to five years old, the total population of adult oysters is estimated at about 150 million. The entire bag-shaped widening of the Oosterschelde contains about 600 million m³ of water at high tide, about 250 million m³ at low tide. Thus at high tide there are about four cubic meters of water for each adult oyster. Practical experience over many years has shown that one cannot increase the population of oysters to a significantly higher level. When, for example, the volume of water at high tide per adult oyster is reduced to two cubic meters, the effects of crowding become evident. Each oyster must share the available food with other filter feeders. The consequences are poor growth, poor fattening, and an increased mortality rate (Korringa, 1956a).

The Oosterschelde is a clear-cut case of an estuary in which man has exerted a beneficial effect. A rational exploitation of a natural resource by applying adequate techniques of cultivation has resulted in a 30-fold increase of production over what nature formerly yielded. Under natural conditions the oyster population was limited by a lack of cultch and also by failure of the oyster larvae to settle on beds where growth and fattening would be optimal.

Unfortunately, the Delta project threatens to cut the Oosterschelde off from the sea late in the 70's.

BAYS OF GALICIA

A most interesting situation is evident in the bays of Galicia in Spain. These bays, especially the estuary of the Vigo, the Pontevedra, and the Arosa are wide and deep, penetrate far into the land, and are well sheltered by ranges of hills. Salinity in these waters is high, for the amount of river water discharging into them is very limited. The bay water is rich in plankton and detritus because upwelling at the Galician coast brings to the surface nutrients which support an abundance of phytoplankton from March till November. The temperature ranges from a summer maximum of about 18° C. to a winter minimum of about 10° C. Such temperature conditions, combined with stable and high salinity and great quantities of phytoplankton and detritus, are excellent for mussels, *Mytilus edulis*. Wild mussels are found on the rocks in the intertidal zone. Here wave action and the intense light are inimical to their growth and fattening. In the early 1950's, experiments were carried out to take advantage of the favorable conditions in these estuaries by growing mussels in hanging culture, following experience gained in the Mediterranean Sea. Instead of racks, which are unsuitable where the tidal range is great, rafts were used. At first these were old boats equipped with outriggers. The success was tremendous; and now about 1,500 installations, consisting mainly of specially constructed

rafts, are in use in the bays of the Galician coast. Each raft carries about 800 ropes; each rope is about six meters long and carries about 50 to 60 kg of marketable mussels. It takes about eight months to rear a mussel seed to marketable size, that is, with a shell length of seven cm or over. The total annual production exceeds 80 million kg (Andreu, 1958).

The Galician bays are examples of estuaries in which shelter is a more important factor than discharge of nutrient-rich fresh water, since the sea water is sufficiently rich through the phenomenon of upwelling. Here, too, adoption of adequate cultivation methods has led to a rational exploitation of a potential natural resource, another example of a beneficial effect exerted by man.

WADDEN ZEE

Another type of estuary is the western section of the Dutch Wadden Zee, behind the Frisian Islands of Texel, Vlieland, and Terschelling. Its estuarine character may seem somewhat doubtful since no river discharges into it directly. Though the salinity is relatively high, approaching that of the coastal water of the North Sea nearby, it fluctuates to some extent in response to the sluicing out of fresh water from the IJsselmeer, the body of water into which the River IJssel discharges. This demonstrates that this section of the Wadden Zee has an estuarine character.

The Wadden Zee, with its extensive tidal flats and its ramifying channels of varying depth through which tidal currents run, is tremendously productive. The number of mussels, *Mytilus edulis*, and cockles, *Cardium edule*, to be found here reach astronomic figures. Brown shrimp, *Crangon crangon*, and polychaete worms of various species occur in countless numbers; young flatfishes such as plaice and sole use this area as nursing grounds. Birds, especially wading birds and various kinds of ducks, find a wealth of food here. Man fishes for shrimp and cultivates mussels on a great number of plots, all of which are under the low-water line. The production of marketable mussels occasionally surpasses 75 million kg a year.

Verwey (1952) estimates the number of cockles of two years and older living in this area at about 6 billion. He rightly states that the fauna of the Wadden Zee could not be that rich if it were an enclosed saltwater lake. Though the fresh water sluiced out from the IJsselmeer may bring in some nutrients, it is clear that the productivity of the Wadden Zee does not come from that source. The mechanism involved is an accumulation of rich nutrient material against a gradient, combined with an intensive carbon dioxide assimilation in this shallow water. The accumulation is partly mechanical. Postma demonstrated how suspended matter is carried into the Wadden Zee by the flood tide, and only part of this material is carried back by the ebb (Postma, 1957). A variety of filter feeders, chiefly cockles and mussels, filters off enormous volumes of water brought in on the flood from the North Sea. Thus, easily digestible matter of the plankton is readily transformed into molluscan flesh.

Less readily digestible material is deposited in fecal pellets and pseudofeces where it is utilized by micro-organisms. Waves and currents may resuspend such worked-over fecal pellets and the filter feeders and deposit feeders can digest the countless microorganisms intracellularly. Thus, part of the material of the phytoplankton and its debris becomes recomposed in the benthic organisms; and, of course, part of it is used to furnish energy during this process. The tremendous number of benthic organisms per unit of surface area can survive only through the continuous accumulation of organic material brought in from the North Sea by the flood tides. The figures for animal protein per square meter rank among the highest to be found in the world. Here and there entire sections may be completely paved with cockles (over 1,000 per m²) and, where mussel plots are well stocked and extensive natural mussel beds occur, hardly any space is free for other organisms of similar size.

One of the most valuable food resources in the Wadden Zee is the mussel. Before 1950 only seed mussels were harvested, to be transplanted to the Zeeland plots. But since cultivation started in 1950, production of market-sized mussels has increased rapidly to over 75 million kg per year. Fishing for brown shrimp is also a remunerative business, even though more money could be made per acre by mussel cultivation than by shrimp fishing. A clash between these two industries seems unavoidable, but, since there is a tendency to build bigger shrimp-fishing vessels which can work in the open North Sea, more ground may eventually become available for mussel farming. A negative side of shrimp fishing is that it unavoidably destroys many young flatfish; consequently it has a deleterious effect on the quantities of marketable sole and plaice to be caught in the North Sea, sometimes by the same fishermen who fish for the shrimp.

NORTH SEA

Though the statement may seem rather bold, one may consider the whole southern North Sea as a type of estuary. Geologically speaking, it was recently part of the land; at that time the Thames was a tributary of the Rhine. When the icecaps melted, the North Sea was gradually flooded, turning the Dogger Bank from a low hill into a shallow area of the sea.

The North Sea is rich in plankton, and this supports an abundance of fish and bottom invertebrates. Rivers discharging into the North Sea may contribute to its fertility, but it seems almost certain that a more important source is the supply of ocean water around the Shetland Islands. This water may be somewhat poorer than the true North Sea water, but just as has been discussed above for the Wadden Zee, an accumulation takes place against a gradient. The North Sea is comparatively shallow, and evidently few valuable materials become lost by sinking into the dark abyss. Various filter feeders live there in enormous numbers and consolidate organic matter contained in plankton and detritus. Thus, vast quantities of protein and other organic material accumulate in the bodies of

invertebrates living on and in the bottom, and many demersal fishes are supported by this supply. The quantity of fish in the North Sea is not limited by the quantity of available food (Korringa, 1960, 1961, 1963b). Immediately after the Second World War, when the fish stocks were more than twice what they are now, owing to the virtual interruption of fishing, the fish did not grow more slowly than now. Even if artificial fertilization were feasible it would probably not increase the production of fish. The principal adverse effect on the production of fish is the fishery itself, which exploits the stocks at excessive rates and persists in using gear that is unnecessarily destructive of young fish (Rollefsen, 1957). Thus, if the question is put as to what man's effect is on the productivity of the southern North Sea, the answer must be that it is negative. If man will only reduce his fishing effort and increase the size of the meshes of his nets, then he can harvest much more fish from this wonderfully fertile area with less effort and at less cost than now. It is to be hoped that these measures will be applied within the foreseeable future through international collaboration.

LITERATURE CITED

- ANDREU, B., 1958. Sobre el cultivo del mejillón en Galicia; biología, crecimiento y producción. *Rev. Ind. Pesqueras de Vigo*: 745-746.
- DEELDER, C. L., and D. E. VAN DRIMMELLEN, 1959. The decline of the fish stocks in the Netherlands section of the rivers Rhine and Meuse. *Athens Proc. I.U.C.N. Tech. Meeting 1959*, 4:185-190.
- DRINKWAARD, A. C., 1959. The quality of oysters in relation to environmental conditions in the Oosterschelde. *Ann. Biol., Conseil Perm. Exploration Mer.*, 14:217-223.
- DRINKWAARD, A. C., 1960. The quality of oysters in relation to environmental conditions in the Oosterschelde. *Ann. Biol., Conseil Perm. Exploration Mer.*, 15:224-233.
- DRINKWAARD, A. C., 1961. The quality of oysters in relation to environmental conditions in the Oosterschelde. *Ann. Biol., Conseil Perm. Exploration Mer.*, 16:255-261.
- KORRINGA, P., 1940. Experiments and observations on swarming, pelagic life, and setting in the European flat oyster, *Ostrea edulis* (L.). *Arch. Neerl. Zool.*, 5:1-249.
- KORRINGA, P., 1951. The shellfish industry in Holland. *Proc. U. N. Sci. Conf. Conserv. and Utilisation of Resources*, 7(1949):47-51.
- KORRINGA, P., 1953. Aan de wieg van de vaderlandse oestercultuur. *Maatschappijbelangen*, 117(2): 34-37.
- KORRINGA, P., 1955. Waarnemingen over de winning van oesterbroed met behulp van mosselschelpen in het jaar 1955. *Visserij-Nieuws*, 8(6): 88-96.
- KORRINGA, P., 1956a. Oyster culture and biological productivity. *Rapp. Proces-Verbaux Reunions, Conseil Perm. Intern. Exploration Mer.*, 140:30-31.
- KORRINGA, P., 1956b. The quality of marketable oysters from the Zealand waters. *Ann. Biol., Conseil Perm. Exploration Mer.*, 11:180-182.
- KORRINGA, P., 1957. The quality of marketable oysters from the Zealand waters. *Ann. Biol., Conseil Perm. Exploration Mer.*, 12:225-228.
- KORRINGA, P., 1958. The quality of marketable oysters from the Zealand waters. *Ann. Biol., Conseil Perm. Exploration Mer.*, 13:241-243.
- KORRINGA, P., 1960. Enkele aspecten van de overbevissing van de Noordzee. *Koninkl. Ned. Akad. Wetenschap., Akademiedagen*, 12:50-59.
- KORRINGA, P., 1961. *Voedsel uit water*. Inaugural Address, University of Amsterdam, Wolters, Groningen.
- KORRINGA, P., 1963a. De weervisserij in de Oosterschelde. *Zeeuws Tijdschrift*, 13(4):103-112.
- KORRINGA, P., 1963b. De Rijkdom van de Zee. *Visserij-Nieuws*, 16(5):137-140.
- KORRINGA, P., and H. POSTMA, 1957. Investigations into the fertility of the Gulf of Naples and adjacent salt water lakes, with special reference to shellfish cultivation. *Publ. Stas. Zool. Napoli*, 29:229-284.
- POSTMA, H., 1957. Hydrography in the Dutch Waddensea. *Arch. Neerl. Zool.*, 10:405-511.
- REDEKE, H. C., 1907. Rapport over de onderzoeken betreffende de visscherij in de Zuiderzee ingesteld in de jaren 1905 en 1906. *Den Haag, Gebr. van Kleef*, pp. 1-154.
- REDEKE, H. C. (Editor), 1922. Flora en Fauna van de Zuiderzee; monografie van een brakwatergebied. *Den Helder, de Boer*; pp. 1-460.
- REDEKE, H. C. (Editor), 1936. Flora en Fauna van de Zuiderzee; monografie van een brakwatergebied. *Den Helder, de Boer*; pp. 1-169. (Supplement)
- ROLLEFSEN, G., 1957. Report of the ad-hoc committee established at the Fourth Meeting of the Permanent Commission, September 1955. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 23:7-37.
- VERWEY, J., 1952. On the ecology and distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation and the source of their food supply. *Arch. Neerl. Zool.*, 10:171-239.

X. HUMAN INFLUENCES

The Role of Man in Estuarine Processes

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Vulnerability to human influence is a characteristic of estuaries. They lie in proximity to man's terrestrial habitat, produce large quantities of his food supply, and are doorways between the oceans and the land masses. Each receives the impact of many human activities throughout an entire watershed, and many are subjected to the most intensive levels of use applied to any marine water areas. It is, therefore, appropriate to identify and consider the past effects of man on the fundamental processes in estuaries and to contemplate future beneficial and detrimental influences on these fascinating, complex, and important waters.

Man's historical development has been closely linked with the estuaries. Humans have always exhibited a natural affinity for water and these bays and river mouths often present unique advantages. They are semi-enclosed and therefore provide natural harbors; they are effective nutrient traps and therefore are rich in food; they connect the oceans and the inland rivers so that they are natural transportation centers; and their often high rates of flux and flush permit disposal of great quantities of waste. The history of exploration, colonization, and settlement of the coasts of the North American continent illustrates the use of estuaries in the development of new populations and cultures.

The effect of human activity on these estuaries was probably unimportant prior to about 1850, and was limited to the effects of silt erosion from agricultural areas and the disposal of human wastes. The enormous expansion during the last century in industrial activity, production and use of power, diversity of manufactured materials, transportation, fishing intensity, and human population have all placed diverse and increasing pressures on these waters. They all affect the processes of the estuaries and their capacity for future use.

The uses of estuaries are described by others in this volume, but additional examples can be added:

1. The Rhine River, according to Bolomey (1959), is heavily polluted by the 40 million people who live along its course, as well as by the great industrial centers like the Ruhr and the Saar. The need to eliminate this pollution is so great that an international commission has been established. The estuarine areas near Rotterdam receive the net product.

2. In Baltimore Harbor, near the head of Chesapeake Bay, the equivalent of about 400 tons of con-

centrated sulfuric acid is released daily from a single large industrial operation (Stroup *et al.*, 1961).

3. The city of Washington, D. C., uses the upper Potomac Estuary as the final stage in its sewage treatment process (Auld, 1964). Brehmer (1964) has pointed out that this is a present average daily addition of 22,700 pounds of phosphorous and 68,100 pounds of nitrogen. This annual release of eight million pounds of phosphorous and 25 million pounds of nitrogen will nearly double by the year 2000, as treatment plant effluent increases from 200 million gallons a day to 360 million gallons a day. Brehmer further emphasizes that present knowledge of the effects of this pollution is insufficient to predict the effects on the estuary or even to establish rational limits.

4. Of the ten largest metropolitan areas in the world, seven border estuarine areas (New York, Tokyo, London, Shanghai, Buenos Aires, Osaka, and Los Angeles). They contain over 55 million people and enormous industrial activity. One-third of the population of the United States lives and works close to estuaries.

5. Bulkheading, dredging and filling to create waterfront real estate have already permanently changed the nature of some estuaries. The Branch of River Basin Studies of the U. S. Department of the Interior reviews and comments on federal projects which would affect fish and wildlife resources. They have reported on 426 different projects in five years which would affect coastal areas. They expect to start 100 more projects this year, 15 for flood control, 20 for navigation, 20 for beach erosion or hurricane protection projects, and 50 for private proposals.

6. Without waiting for inexpensive nuclear energy, man has begun to engineer vast estuarine changes. The 2,700 km² Zuider Zee has been enclosed for 32 years, essentially fresh for 27 years, and largely converted to sub-sea-level agricultural land. Holland has also begun to transform salt and brackish waters into lakes in the great Delta Project of southwest Holland (Vaas, 1963).

7. More than a billion pounds of biocidal chemicals have been used in the United States, and Butler *et al.* (1962) point out that many of these substances and their oxidation products reach the coastal waters and the estuaries. Cottam (1960) reported that 35 million pounds of arsenical salts, 45 million pounds of copper sulfate, six million pounds of organic phosphates, and 130 million pounds of chlorinated insecti-

cides and fungicides were used in one year. Six thousand brand-name biocidal materials are now available and almost unrestricted in use. Rachel Carson (1962) has cited specific and vivid examples of the results of application of control chemicals in the areas of the Miramichi in Canada, in the Indian River of Florida, in New Jersey, and at other sites.

These brief examples of the effect of human activities are further evidenced by experience in various parts of the world. They serve as reminders, not as an adequate review.

The future will bring very rapid increase in all the present uses of estuaries, and entirely new pressures and modifications are already taking shape: (1) California is studying alternate plans for damming, diverting, filling, and vastly modifying large areas in the Sacramento-San Joaquin region and elsewhere (Jones *et al.*, 1963). (2) There is a well-advanced plan to divert the waters of the Sabine River, the Neches, the Trinity, the Brazos, the Colorado, and the Nueces from east Texas to west Texas. No water would escape to the coastal estuaries (Thompson, 1961).

The development of inexpensive sources of power in unprecedented quantities may make these seem like mere practice sessions. In this compilation to assemble and assess our knowledge, constructive perspective can be gained by reviewing the effects of man on estuaries.

This review is presented to single out the most significant estuarine processes which man affects, to offer summary and partial assessment of the location and nature of human effects, to suggest the present benefits and losses from these effects, and to consider the future role of man in the estuaries.

No attempt will be made here to stress their importance in human welfare, or the economic and social values which they provide. The enormous diversity of systems, which results in highly significant individuality, is assumed. So, too, is the inherent dynamism of most estuaries. We must consider generalized effects by specific examples, and the net effects superimposed on vigorous rhythmic systems.

There are no physical, chemical, or biological processes unique to the estuary, but many are typical of this complex and distinctive mixture of sea and river. In the cases and discussions which follow, primary attention will be given to these questions:

1. What physical, chemical, and biological processes are unusually significant in the estuary and may be modified by man?

2. How have human activities affected these processes beyond the normal range of variation present in the virgin estuary?

3. What are the possibilities for future management of estuarine processes for optimal achievement of man values from estuaries?

The literature of estuaries contains many research reports, administrative summaries, and discussions dealing with specific problems, and many of these will be cited later. No previous general review was located, but several contributions have been especially

helpful and stimulating. They include the series of reports on estuarine hydrography by Pritchard (1951, 1952, 1955, 1959a, b, 1960); on flushing and biological effects by Ketchum (1950, 1951a, b, c, 1954); on the grand-scale effects of enclosing the Zuider Zee (Havinga, 1935, 1936, '41); on the biology of pollution by Hynes (1960); on biological aspects of estuaries by Hedgpeth (1957); on physical and chemical aspects by Emery and Stevenson (1957); Mansueti (1961) on the nature of man's effects; Nelson (1947) on enrichment; H. T. Odum and his students (1958, 1962) on estuarine processes; Rounsefell (1963) on the choices of management objectives; Sykes (1965) on multiple usage; and E. P. Odum (1961b) on imaginative and constructive approaches to new potentials. Baughman's valuable bibliography (1948) contains many pertinent annotations. Sverdrup *et al.* (1942) continues to serve as a splendid general reference.

The topics presented here are numerous and diverse, ranging from upland erosion to invertebrate toxicity and estuarine hydrography. The pertinent literature is, therefore, represented by illustrative examples rather than by exhaustive inclusion.

Certain processes have been chosen for emphasis here because they meet two criteria: (1) each is significant in many or most estuaries, at least of the coastal plain type; (2) each is now subjected to substantial (*i.e.*, beyond normal range) modification by man.

The physical attributes which will receive emphasis are salinity, temperature, river flow, and basin shape.

Chemical modifications which will be discussed include the addition of biocides, nutrient chemicals, pulp mill wastes, and certain exotics.

Geologically, only silt and siltation are considered.

Among the highly varied modifications of biological processes, human predation (more commonly called fishing!) and the introduction of new species have been chosen as illustrations.

The lists could be very long, but these may serve to summarize present knowledge and provide guidelines for the future.

ACTIVITIES IN THE WATERSHED

Since the estuary is the recipient of effects from changes throughout the watershed, a review of the pertinent human activities along the contributory waterways can be helpful. They vary and are important in the estuarine processes.

MODIFICATION OF RIVER FLOW

Many human activities affect the quantity of inflow of fresh water, its temporal distribution, and its contents. River flow can be reduced, especially by diversion of river water for human consumption (Nelson, 1960; Jones *et al.*, 1963; Ketchum, unpublished ms.; Thompson, 1961), for the vast increases in artificial irrigation of agricultural land (Mansueti, 1961), and by the intentional or accidental use of spillways or breaks in levees (Gunter, 1952, 1956). Conversely,

flow can be significantly increased in the basins receiving the diversion. More frequently, increase in the total annual output is the result of dredging the watershed by removing vegetation and by other activities that decrease the in-soak and subsurface retention. This is especially vivid in the paved urban areas (Renn, 1956) and along highways where as much as 30 acres per mile is paved or carefully sloped to maximize runoff. These also increase the flashiness of rivers, with greater flooding in high-flow periods and drought in low-flow seasons. Counteracting forces do exist, however, in the increasing number of small and large dams, many of which are specifically designed for moderation of the river flow and long-term release, and in improved general conservation practices.

Gross Effects

The gross estuarine effects of changed river flow are rather well understood, although more subtle effects have infinite local variation. The most pervasive effect is on the general hydrographic structure and behavior of the estuary. River flow is a prime factor in the determination of salinity distribution in the estuary (Ketchum, 1951a, c) and of the vertical and horizontal physical structure of the estuary (Pritchard, 1955). Pritchard has shown that increased river flow converts a homogeneous-type estuary through moderate stratification to strong and persistent stratification. Cronin *et al.* (1962) showed that this conversion occurs in the Delaware, following runoff variation. Pritchard (personal communication) has provided additional evidence of the power of flow. During most summers, the deeper waters of the central Chesapeake are severely depleted of oxygen as they are transported up-estuary. Stratification of cooler, saltier, denser deep water under warmer, fresher, lighter surface water may be very strong, and an increase in river flow during this period enhances stratification, enlarges the area of depleted oxygen, and may do extensive damage to estuarine organisms (Carpenter and Cargo, 1957).

More specific estuarine effects of change in river flow have been shown by Beaven (1946), Gunter and Hall (1963), Nelson (1960), and by others. Beaven documented the control by the Susquehanna River over salinity in the upper Chesapeake Bay, and provided excellent evidence that all major oyster mortalities recorded for the upper Bay from 1907 to 1946 were associated with and probably the direct result of periods of high runoff of the river.

Biological Effects

The intermittent controlled release of fresh water from Lake Okeechobee to the St. Lucie Estuary in Florida has probably enhanced the fisheries by nutrient supply, and may benefit croaker, mullet, anchovy, and menhaden, according to Gunter and Hall (1963). A better pattern of release could be of increased benefit to the fisheries.

Nelson (1931), in reviewing the arguments relat-

ing to diversion of Delaware River water to New York City in the Hudson River basin, cited many estimates of the ecological and biological effects. As an example, he predicted an up-bay movement of oyster drills, *Urosalpinx cinerea*, to invade several excellent oyster seed beds previously protected by low salinities. In more general terms, salinity is known to limit the distribution of oysters and many other estuarine species (Gunter, 1955; Galtsoff, 1960; Koringa, 1952). Davis (1958) and others have demonstrated from laboratory experiments that the eggs and larvae of clams, *Meretrix (Venus) mercenaria*, and oysters (*Crassostrea virginica*) have optimal salinity requirements for development and growth, and the optimal salinity for the eggs of the oyster may be governed by the degree of salinity at which the parent oysters develop gonads.

Additional biological effects of flow change are known. Diversion may disturb the migratory patterns of fish. Gauisse and Kelley (1963) found that flow reversal in the San Joaquin River, because of exportation of water through a power plant, has apparently affected salmon runs, presumably because "home stream" water was not present to stimulate ascent and spawning. The degree of dilution affects the decrease of bacteria in polluted estuaries, although Ketchum *et al.* (1952) found this to be a much smaller factor than the bactericidal effect of sea water. Ketchum (1954) also showed that the vigor of estuarine circulation, which is greatly affected by river flow, determines the reproductive rate necessary for maintenance of plankton populations. Pritchard (1951) suggested that the upstream movement of deep water, also affected by river flow, may transport young croaker, *Micropogonias undulatus*, from the spawning ground (off Chesapeake Bay) upstream at 2-4 knots, or 130 miles in less than 20 days. Our later experience in the Bay suggests that this is a primary and essential method of dispersion for the young of weakfish (*Cynoscion regalis*), spot (*Leiostomus xanthurus*), blue crab (*Callinectes sapidus*), and other species. Pritchard has also shown (1952) that similar movements may provide oyster larvae for the greatest seed oyster area of the world, in James River of Virginia. Housefield (1955) vividly related such flow-dominated circulation to the distribution of barnacles in the Miramichi Estuary. Odum and Wilson (1962) expressed the possibility that bays with little flushing may develop higher productivity and more effective regeneration of nutrients. Low river flow would obviously favor these effects.

Chemical Effects

Flow modification also affects the chemical content of waters entering the estuarine system. Carpenter (1957) found that the calcium content of the Susquehanna is broadly, but imprecisely, related to flow. Renn (unpublished), in preliminary scanning of the distribution of ABS (alkyl benzene sulfonate), principal ingredient of the non-biodegradable detergents, observed the effective reduction caused by dilution.

Laundry outfalls showed levels up to 140 ppm ABS, which was reduced by dilution, absorption, blow-off of foam, and degradation (about 5 percent per week) to .2-.3 ppm in rivers and estuaries. Agricultural or silvicultural pesticides would be similarly affected.

Siltation

Siltation in estuaries is caused by both natural and human factors. Deforestation, flashing runoff, and poor agricultural practices contribute. Burt (1955) showed that river discharge affects the distribution of the inorganic suspended load in the Chesapeake, as many others have seen from other estuaries. Wolman *et al.* (1957) calculated that 60 million cubic feet of silt per year are deposited in the estuary of the Potomac River near Washington. Mansueti (1961) estimated that half of the former upper estuary spawning areas for fish and shellfish beds for oysters have been destroyed or shifted downstream by sediments in the Chesapeake. He also pointed out the progressive filling of deeper channels by such silt. Gunter (1956) summarized the soil transport of the Mississippi River as 730 million tons of soil per year into the Gulf of Mexico—38 thousand acres, three feet deep. He deplores the narrow canalization of this transport, which formerly overflowed the basin.

Human countermeasures are again available, but not well utilized, in this country at least. Soil conservation is progressing. Small watershed dams and larger reservoirs also retain silt effectively.

ENRICHMENT

Organic enrichment of tributaries is an ancient problem. In direct relation to estuaries, Jeffries (1962) has described the nutritional contribution to Raritan Bay of nitrate-nitrogen and phosphate from sewage in the Raritan River and the resultant dense phytoplankton blooms. Renn (1956) cites human organic loading as being .4 lb person day. The quantities reaching the estuary will obviously vary greatly with distance, river flow, loading, and many other factors, so that generalizations here are inappropriate.

DAMS AND BARRIERS

Physical barriers in tributary streams create very special and important effects. Hynes (1960) and Mansueti (1961) pointed out that dams absolutely block anadromous fish migrations and may eliminate important runs unless fishways are provided. A series of dams on the Susquehanna has cut off migrations of the white shad (*Alosa sapidissima*) and reduced the spawning area of the striped bass (*Morone saxatilis*). Others have blocked herrings and other species. Whitney (1961) pointed out that, in addition to physical blockage, dams create reservoirs which differ greatly in circulation, temperature, and currents from the original stream, so that anadromous fish may not be successful even if they pass the wall. Fishways also introduce an artificial but effective factor for genetic selection. In addition, reservoir water can become depleted of oxygen, modified in temperature,

and changed in other ways (Whaley, 1960). The common practice of drawing relatively deep water through turbines can release undesirable conditions into the upper estuary. An aged fisherman pointed out other modifications in the upper Chesapeake. Before dams, the upper Bay was subject to annual ice scour alternating with heavy siltation. Dams prevent the ice movement, trap the silt, and produce much greater stability of the bottom. Heavy vegetation grows where it once could not.

SELECTED CASES

To illustrate the range and magnitude of watershed effects on estuaries, four vivid examples, past and future, will be briefly described. They are the leveeing of the lower Mississippi River, operation of the Bonnet Carré Spillway, plans for water management of the Potomac River, and diversion from the Delaware River to the Hudson River.

Levees—Gunter (1952, 1953, 1956, 1957a) describes the development of levees in the lower portion of the 1,257,000 square mile Mississippi basin (Fig. 1). First construction was in 1717, and a broader program was inaugurated in 1735 by private interests. The State of Louisiana assumed responsibility in 1828, the Mississippi Valley Commission in 1879, and the U. S. Army Corps of Engineers in 1928. Levees are now up to 35 feet high. Among the many results, runoff is faster and peakier; velocity increase transports more silt; alluviation, sedimentation, and flooding of the swamps, marshes, and estuaries have virtually ceased; and enormous quantities of silt are directly deposited in the Gulf of Mexico. These have brought serious, and usually detrimental, changes to the estuarine areas of Louisiana. Drainage of nutrients from land is reduced; salinity is increased and stabilized; island erosion is increased; and bays may move inland. Species appear to be responding to these changes and some oyster reefs are disappearing.

Bonnet Carré Spillway—In the same system, a great spillway, 7,700 feet wide, was completed in 1932 (Fig. 1). It was designed to protect New Orleans from Mississippi River floods, and can carry 250 thousand cubic feet per second (cfs). It diverts water into Lake Pontchartrain, thence through Lake Borgne and Mississippi Sound, and eventually to the Gulf of Mexico. Gunter (1953) describes the results of openings in 1937, 1945, and 1950. Since all of the receiving area is estuarine, the effects are of interest here. In Lake Pontchartrain, mobile organisms are driven out, and many non-mobile forms are killed by low salinities. A small area is covered by mud. Most or all of the oysters in certain beds are destroyed, with lower low over a wider area, although oyster pests and predators are killed out. Nutrient is added to the area, estimated in 1950 as 40 thousand tons. Following return to normal salinities, unusually great production of shrimp and other marine life is observed. In Gunter's opinion, the total beneficial economic effect out-weights the partial oyster mortalities which occur in some years.

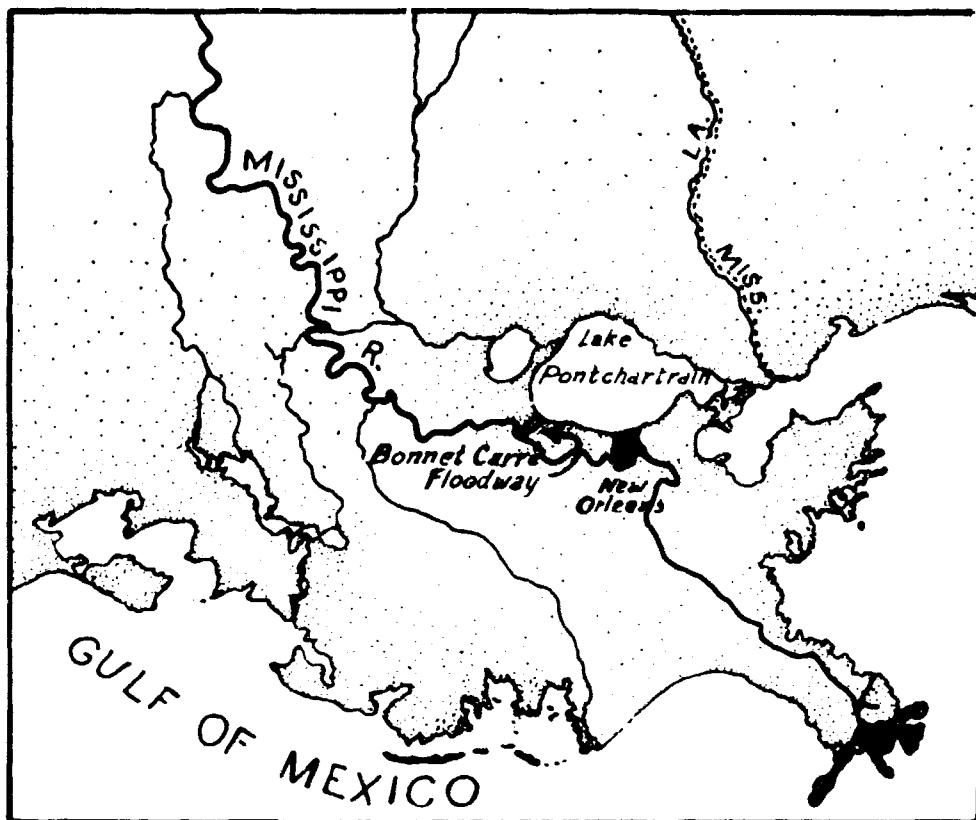


Fig. 1. Lower Mississippi River Basin, showing relation of Bonnet Carré Spillway to the estuarine areas bordering the Gulf of Mexico.

The Potomac—The Potomac is a very flashy river. With an average flow at Washington, D. C., of 11,000 cfs, it has an observed range from 800 cfs to 500,000 cfs. Droughts, floods, heavy siltation, massive enrichment, and increasing needs for sustained water supply all present problems in its control and use. Many partial or complete answers have been proposed (Wolman *et al.*, 1957), but the most recent suggestion is a dramatic example of efforts to manage a river and control its effects on an estuary.

The U. S. Army Corps of Engineers has developed four alternate plans, with primary interest in flood control, recreation, water supply, and water quality control (U. S. Army Engineer District, Baltimore, N. Atl. Div., 1963). The one recommended would include establishment of 418 headwater small reservoirs, 16 major reservoirs, 3 small flood control projects, and a general program of land management and reforestation. The cost is estimated at \$498 million, and it could be completed about 2010; the plan is now being reviewed.

Estuarine effects have been only partially estimated. Augmentation of low summer and fall flow is the obvious, and reduction of spring maxima is inevitable. Uncontrolled low-flow averages about 1,100 cfs, and would normally be expected to decline in 50 years to 800 cfs because of upstream irrigation and other con-

sumptive uses. If the plan is effected, minimal flow would be about 4,700 cfs, which is 42 percent of the annual average. Specific projection of all the effects of this change on the dynamics, populations, and character of the Potomac Estuary offers challenging problems. It has not even been attempted. It is already clear, however, that the upper estuary, at least, would be significantly and permanently different, especially during summer months. Physical circulation, nutrient availability, and biotic communities would all be significantly modified.

The Delaware diversion—New York City, on the Hudson River, has long sought to obtain water from the Delaware River watershed. Delaware Bay, principally through the State of New Jersey, fought such diversion in 1929-1931 and 1952-1954, primarily on the grounds that estuarine productivity would be decreased. Nelson championed this position and has summarized the estuarine argument (1960). Despite evidence which was more precise than usual, the Supreme Court allowed a diversion of 1,240 cfs (800 mgd). Part of this is already in effect. Part of the pattern provided will guarantee minimal flows at Trenton during low-flow periods. Nelson argued that the minimal flows would be ineffective in combating oyster drills, that drills would penetrate farther on to productive seed beds with higher average salini-

ties, and that the nutrient loss would be especially damaging.

Ketchum was asked to predict the effects, and provided estimates of channel salinities under normal flows and under diversion with controlled summer minima. The near future will test his precision, but his predictions provide an excellent example of the nature of the effects of intentional flow modification on estuarine conditions (Ketchum, unpublished).

The river in 1952 had a mean flow of 11,700 cfs, with usual lows near 2,000 cfs and highs near 29,000 cfs. With stipulated augmentation of flow at Trenton, and diversion of 1,240 cfs, Ketchum predicts that mean flow will be reduced from 11,700 to 10,530 cfs, low flow increased from 2,157 to 2,893 cfs, and high flow reduced from 28,900 to 21,950 cfs. Salinity will increase at mean flow a maximum of .85 %, decrease at low flow a maximum of 1.08 %, and increase at high flow a maximum of 3.2 %. Range would thus be reduced, with a maximum at the center of the estuary, where annual range of 16.46 % would become 12.85 %, a difference of 4.61 %. Isohalines would be moved upstream, except during augmented flow. Biologically, the important conditions which limit the viability or success of populations are generally the extreme conditions to which the populations are exposed. The proposed diversions should, therefore, be beneficial to the populations within the estuary.

At the hearings, other biologists expressed broad concern about the detrimental effects, but were unable to make and substantiate specific predictions of those effects.

It is interesting to compare these projections with the report of Segerstraale (1951) that average changes of .5-.75 % produced significant changes in the effective distribution of estuarine species.

Apparently, no one has made an effort to predict the effects of the addition of 1,240 cfs of water to the Hudson Estuary, perhaps because no one objects to the addition, or because the lower Hudson at New York City seems to be beyond reclamation.

ACTIVITIES IN THE ESTUARY

PHYSICAL PROCESSES

With increasing frequency and intensity, human activities are changing the physical conditions and processes in estuaries.

Thermal Addition

One dramatic and growing group of effects arises from the addition of heat on a continuous basis. The most important sources have been generating plants for electricity, using great quantities of water to cool condensers. Research on thermal effects in fresh water has been extensive, permitting summary by Ingram and Towne (1959), Hynes (1960), and others for the fluvial situation, where physical effects and the biological sequence produced are reasonably predictable. This is not so for estuaries, where tidal

flux and the presence of a different community of animal and plant species introduce complicating factors. Pannell *et al.* (1962) reported observations which illustrate the difficulties of predicting effects, and the types of effects which may occur. Specific predictions were used in designing the release of 26 million gallons per hour with a rise from intake to outfall of 12° F. The prediction was that warmed water would spread thinly on the surface. It was observed, however, that an area 1,000 feet in radius is warmed at least 5°, but most of it is between 3 and 9 feet below the surface, and the plume swings with tidal action.

It was predicted that little heat would be absorbed by the main body of the estuary, and observed that virtually all heat dispersion is by mixing. The most interesting observation was that most warmed water remained below cooler but fresh water and above cooler salt water. The interplay of salinity and temperature produced this unexpected vertical series, with salinity dominant.

Biologically, the heat appears to have extended the local breeding season of the boring gribble, *Limnoria*, and increased the incidence of the shipworm, *Teredo*. These sessile forms were affected, but no significant change in zooplankton was detected. Other effects remain to be evaluated.

In the United States, a valuable experiment may be provided by the construction of a 670 MW steam generating plant on the Patuxent Estuary, a tributary of the Chesapeake. The plant is now under construction and will warm 500,000 gallons per minute by 11.5° F. in warm months and half that quantity by 23° F. in winter. This volume is about 50 percent more than the average freshwater input of the watershed above this point, so that the estuary will be used as a tidal cooling lagoon. Fortunately, intensive studies are preceding and following the construction of the plant. The Chesapeake Biological Laboratory has established a research team and developed cooperation from about 40 scientists in a dozen institutions and agencies for pre- and post-operative studies of circulation, salinity, oxygen and thermal distribution, phytoplankton abundance and productivity, zooplankton distribution, bacterial density, fouling rates and species, benthic community composition, fish egg and larval distribution, adult fish distribution and migration, crab abundance, and other aspects of the area. Perhaps this will permit improved prediction and rational regulation of such activities. Present projections of the need for electric power call for demand to increase in this country from 60 billion gallons per day (bgd) in 1955, to 131 bgd in 1975, to 200 bgd in the 1980's (Picton, 1956). Against these figures, consider the estimates of total dependable surface runoff, 385 bgd at present increased to 630 bgd by 1975 or 1980. Power demand in this country and many others grows even more rapidly than populations, and increasing pressure to use estuaries for cooling is inevitable.

Otto Kinne at Helgoland has recently provided

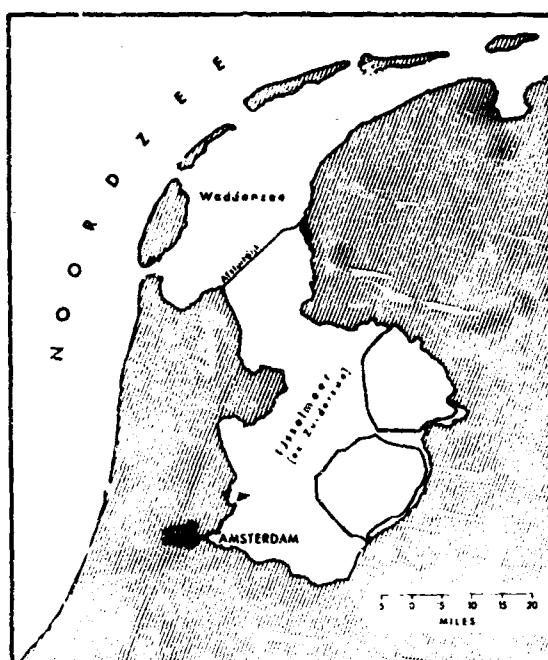


Fig. 2. The old Zuider Zee, cut off by an enclosure dike or "Afsluitdijk" to convert an estuary to a lake and dry land.

an excellent and valuable review of the effects of temperature on marine and brackish-water animals (1963) as part one of a survey of the effects of both temperature and salinity. The biological effects of thermal change, affecting all chemical and biological rates and processes, are profound. Kinne devotes portions of his review to temperature tolerance and lethal limits, effects on metabolism and activity, reproductive success, distribution, organism size, meristic characters and shape, and biotic adaptation to temperature.

Comprehension of these effects will be invaluable in efforts to prevent estuarine damage or to utilize heat to obtain optimal benefits.

Changed Salinity

Human activities in the estuary occasionally affect salinity. Examples are provided by pumping of large volumes of fresh water into the estuary (Wolman *et al.*, 1957) or by engineering changes affecting the fundamental pattern of circulation, such as major modifications of channel depth.

The great Dutch conversion of an estuarine area of the Zuider Zee to a freshwater lake was completed in 1932, when an enclosure dike was completed (Fig. 2), cutting off 2700 km² of rich, warm, shoal water with a salinity of 10–15‰ in the inner portion and 15–25‰ in the outer portion. The results, described and discussed by Havinga (1935, 1936, 1941, 1949, 1959), show a vivid example of man's impact.

Salinity decreased as the flow of the IJssel River continued while ocean water was almost completely

prevented from entering (Fig. 3). Stability was attained about 1937, and subsequent salt intrusion is limited to the water near two locks in the dike. The mero-estuarine species which had provided a large fishery (herrings, anchovy, and shrimp) and various non-commercial species were quickly and vastly reduced. Herring were seen in great numbers at the dike, but were unable to reach the low-salinity water. Anchovy sought a different estuarine condition, relatively high temperature, and were equally frustrated. Stenohaline marine and polyhaline organisms were killed, and eventually their predators starved. With varying periods of endurance, the edible mussel, *M. edulis*; the soft-shell clam, *Mya arenaria*; the green crab, *Carcinus maenas*; and other forms (*Cardium edule*, *Tellina balthica*, *Corophium sp.*, *Heteropanope tridentata*, *Gobius minutus*, and others) died out. Eventually, the predators dependent on intolerant forms also disappeared.

Most of the euryhaline forms passed out of existence more slowly in the IJsselmeer, but some survived. *Neomysis vulgaris* was highly successful in the new environment, and provides much of the food for larger species. Limnetic species spread slowly but effectively; the motile forms achieved wide dispersion.

As a result, the older fishery has been entirely replaced by freshwater production of pikeperch, bream, roach, and others. A striking survivor is the eel, *Anguilla vulgaris*, which lives as the principal commercial species. It is aided by nighttime locking of young elvers into the lake when they appear along the dike.

Havinga points out that the result is faunistic poverty, marked by adaptations and intrusions, although total human values have been greatly enhanced. Fish production of 16 million kilograms per year was replaced by 1959 with 7 million kg of fish plus 70 million kg equivalent of pork on the reclaimed land. This may treble when all the potential *polder* reclamation is completed.

The Netherlands has embarked on a second great program for modifying brackish-water areas (Fig. 4). Primarily for the control of highly destructive floods,

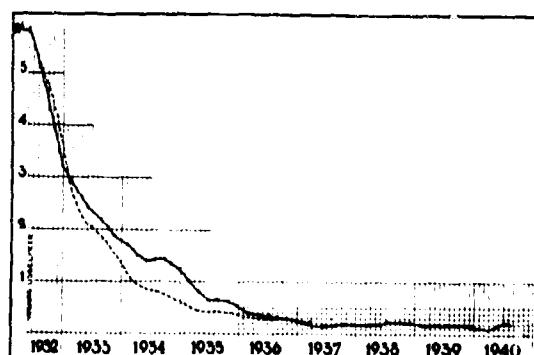


Fig. 3. Chlorinity in the IJsselmeer following enclosure. The broken line indicates the calculated chlorinity level. The solid line shows the observed level (After Havinga, 1941).

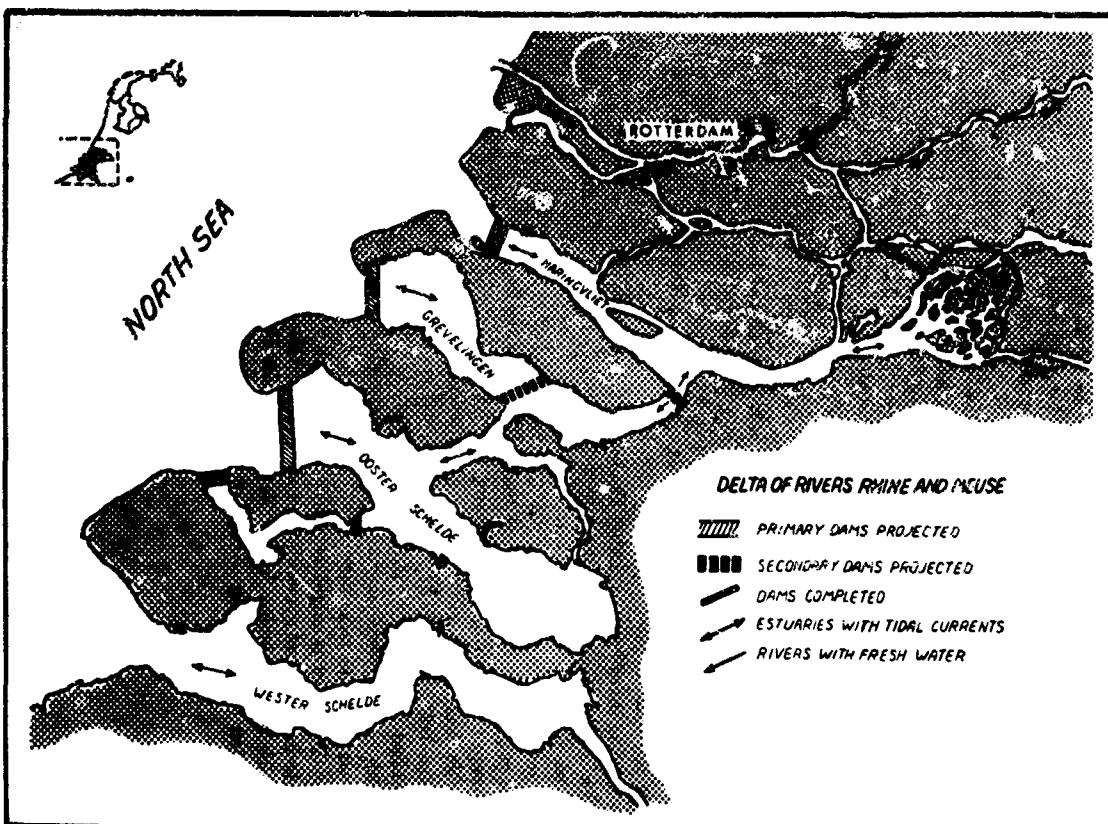


Fig. 4. The "Delta Plan" for modifying estuaries in southwest Netherlands (After Havinga, 1959, modified to show works completed by mid-1964).

they have begun the "Delta Plan" at the mouths of the Rhine, Meuse, and Scheldt Rivers, to be completed in 1978. Three arms of the sea will be cut off and a series of additional dams will modify flow and convert salt and brackish areas to fresh water. Thorough hydrographic study before, during, and after construction is being accompanied by intensive and extensive biological surveys (Hartog, 1963; Vaas, 1963). Present predictions of the effects are stimulating and instructive, in view of Dutch experience in other locations. Tidal action will cease for most of the region, and be reduced throughout the area. Salinity will decrease rapidly, modified by leaching of salt from *polders*, and is not expected to fall below .3 %. Stenohaline marine organisms will perish, although euryhaline species will persist for a long period and a brackish-water population will develop, then be succeeded by limnetic species.

Hartog has defined the euhalinicum, polyhalinicum, mesohalinicum, oligohalinicum, and freshwater conditions under the present regime, and published on some of the Amphipoda. Other studies are covering Hirundinea, Isopoda, Gastropoda, Gammaridae, turbellarians, fish, plankton, and vegetation.

Human safety will be gained, but it is most regrettable that part of Holland's important mussel industry and all of her Zeeland oyster industry may be

sacrificed. Korringa (1958) described the threat to these industries, in which cultivation and management have been brought to a high and intensive level. He pointed out that it might theoretically be possible to determine the allowable range of salinity, silt content, sand transport, current velocity, plankton, and other requirements and seek new oyster areas, but he was not optimistic. Artificial culture of seed would be required, and this is still a difficult technique, without demonstrated economic justification on a large scale.

Modifications of Basins

The shape of the basin of an estuary has many effects on hydrographic dynamics and, as a result, on other processes. Pritchard has expressed the effect of modification (1955) by pointing out that conversion from marked stratification to vertical homogeneity is favored by increasing the width and opposed by increasing the depth. Shore erosion, silting, channel dredging and spoil deposition would all have local effects. Skyes (1965) has noted that the establishment of cities on the shore is usually followed by an expanding pattern of reclamation, fills, causeways, and bridges, permanently altering the entire area. The premium which is placed on waterfront residences creates dramatic changes in basins

by a pattern of dredging and filling for housing and for industry. Thompson (1961) summarized the usual estuarine effects as reduction in the water area; denudation of the bottom as fill is removed; modification of currents and tidal exchange; alteration in salinity, temperature, and perhaps oxygen content; and sediment dispersion.

Boca Ciega Bay, on the west coast of Florida, is a clear example of the present and future magnitude of these changes (Fig. 5). Hutton *et al.* (1956) felt that the combined effects of sedimentation and basin change in Boca Ciega Bay might be to reduce or eliminate fishing, destroy breeding and nursery grounds, and create low oxygen areas. Woodburn has provided a guide (1963) for reviewing proposals to change shorelines, and suggests principles to be followed.

Comprehension of the relationships between the shape of the basin and various processes can be put to highly constructive uses. Scale models have been used in many parts of the world to study physical patterns of circulation and to test new possibilities. Simmons (1959) is enthusiastic about the potentials of using models in estuarine research. By using such techniques as single slug and continuous release, methylene blue chloride and other dyes, and artificial roughening, he is confident that models can produce accurate integration of the tidal, density, and fresh-water forces that affect dispersion, dilution, and flushing of introduced materials. However, present estuarine models usually cannot scale non-conservative, or interacting, or time-related materials and processes. Pritchard (1960) has called attention to possible limitations in model studies of processes involving diffusion phenomena. Present estuarine models include the Delaware Estuary, San Francisco Bay, Puget Sound, Thames Estuary, New York Harbor, Matagorda Bay, Galveston Bay, Narragansett Bay, and others. Additional models are planned.

Man has created a rather special change in the "shape" of estuaries by removing a portion of the land mass between them. In this country an inter-coastal waterway allows water, aquatic organisms, and people to move freely between bays along the entire East Coast and much of the Gulf Coast. The great canal systems of Europe and other areas provide similar interchanges. The greatest effects will probably involve biological exchanges and extensions.

CHEMICAL METHODS

Biocides

Many chemical compounds inhibit vital biological processes. Most compounds do so in excessive concentrations. In recent years, great industrial effort has gone into the development of compounds which could be used in small quantities to interfere with life processes in specific target species. The results are variously called weedicides, herbicides, bactericides, fungicides, and pesticides. Miss Carson has correctly termed the group "biocides" because of their

fundamental effect. They destroy life. Advantages and disadvantages from their use are both very great. These, and toxic substances never intended for use in control work, are present in estuaries in increasing amounts.

The U. S. Fish and Wildlife Service has been especially concerned with biocidal effects, and very valuable work has been done on two broad problems. What are the effects of these materials on estuarine species other than the original target? Can biocides be used constructively in the management of estuarine organisms? This research provides valuable guidance. It is, however, most regrettable that there has as yet been little support for research on the fundamental physiological mechanism of biocides, and on the effects of known toxins on the broad spectrum of non-commercial species.

Davis investigated the effects of 31 pesticides on the eggs and larvae of the oyster and clam (1961). He reported great variation in toxicity within each group of chemicals, ranging from 90 percent mortality of oysters in .05 ppm DDT to improved growth of clams in 5 ppm of lindane. Several apparently beneficial materials may have reduced bacterial action. Reduction in growth rate was identified as a useful indicator of toxicity. Davis felt that it will eventually be possible to select materials for highly specific control.

The effect of toxins on growth was more fully developed by Butler *et al.* (1962). They observed that change in growth rate provides a sensitive bioassay technique, allowing detection of differences in one or two days. Chlordane, heptachlor, and rotenone were observed to be inhibitory within 24 hours in concentrations as low as .01 ppm. All of the common agricultural pesticides tested were toxic, but there was some indication that they are released from internal storage in organisms when environmental concentration drops.

In efforts to utilize biocides constructively, Loosanoff (1960) and his associates have screened hundreds of compounds in a search for effective methods for controlling green crabs (*Carcinus maenas*) and other arthropod predators on molluscan shellfish. They identified a large number of effective compounds, which can also kill shrimp, prawns, copepods, and other crustaceans. Perhaps it is suggestive of the complexity and difficulties of this field to note that my own professional interest in the blue crab (*Callinectes sapidus*) and the copepods of the estuaries makes me regard this new knowledge with conflicting feelings. Loosanoff also reported that many of the materials tested adversely affect molluscs. 1.0 ppm of DDT caused the death of oyster larvae, and .025 ppm interfered with growth. He suggested combinations which might be effective chemical barriers to minimize the invasion of shellfish beds by arthropods, and urged thorough evaluation of every such possibility prior to use.

Additional efforts in the control of undesired species have been reported recently. Hanks (1963)

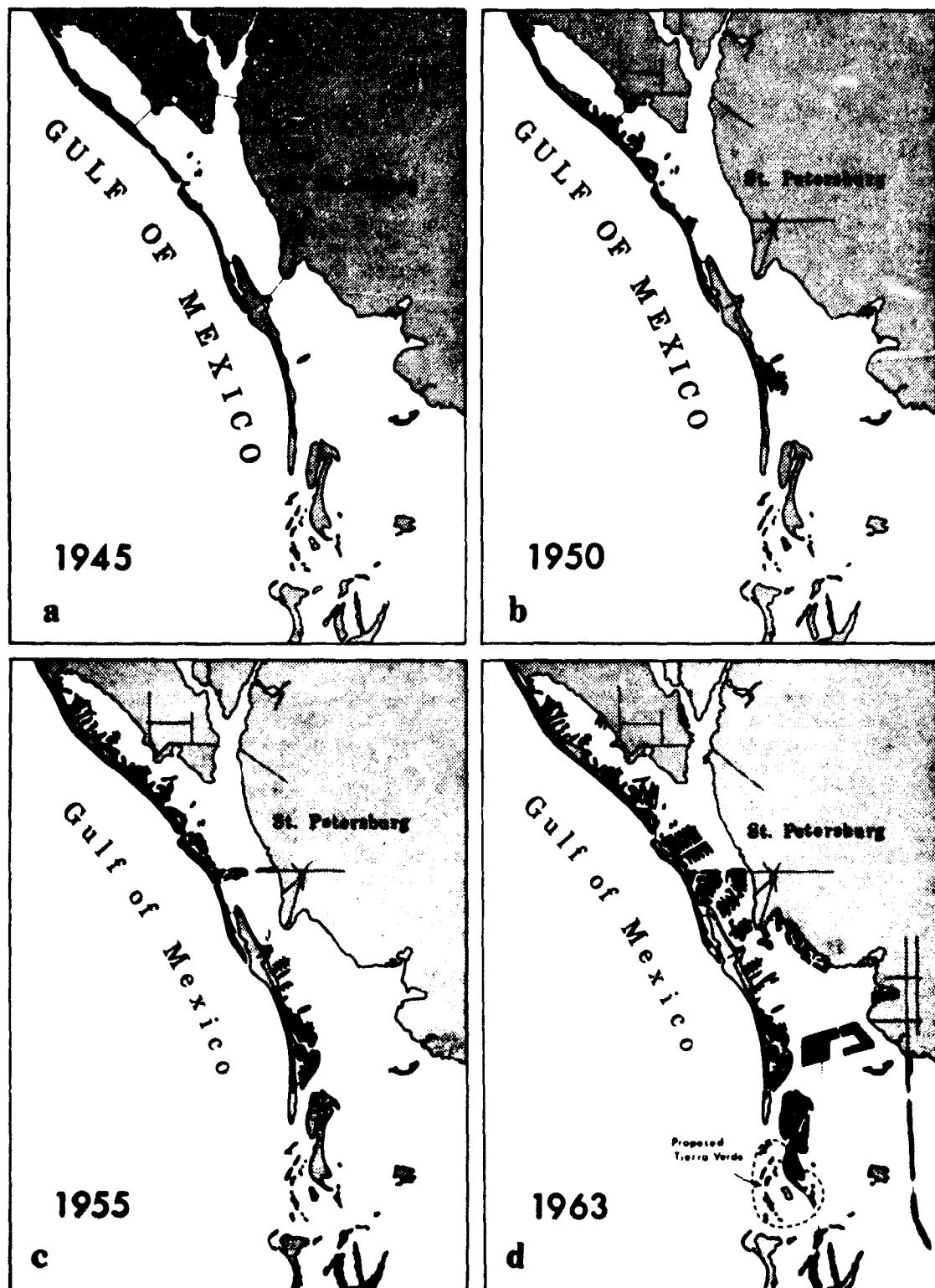


Fig. 5. Progressive development of land by dredging and filling in Boca Ciega Bay near St. Petersburg, Florida (Courtesy Mr. James Sykes and the U.S. Bureau of Sport Fisheries and Wildlife).

learned that baitfish could be soaked in lindane solution to reduce green crab populations and reduce crab immigration. Lindsay (1963) tested several materials for the control of ghost shrimp, *Callianassa* sp., and Japanese drills, *Ocinebra japonica*, in Puget Sound. Shrimp could be controlled and drills could be prevented from entering experimental plots, but Lindsay urged that the methods be avoided until long-term effects and public health problems could be fully understood. The use of DDT on oyster cultch to control barnacles (*Elminius*) was tested for the effects on oysters (Waugh and Ansell, 1956). This control technique had been discovered by Loosanoff and tested by others. The set of oysters doubled, initial growth was somewhat inhibited but followed by excellent growth, to reach 40 percent greater size than controls in 2½ months.

With reference to plants, estuarine research on biocides is extremely limited. 2,4-D was effective in killing Eurasian milfoil in the upper Chesapeake Bay (Rawls, 1964), and Beaven *et al.* (1962) showed that the effective concentration had no acute effects on crabs, oysters, clams, and fish. A secondary mortality occurred, however, when the dense mat of killed plants decayed on the bottom, producing anaerobic and toxic conditions.

An excellent summary of the results of research on pesticides has been prepared by Butler and Springer (1963). It brings together the present knowledge pertinent to coastal waters, including a number of individual reports which must be omitted in the present general discussion. Pesticides have been developed on a significant scale only since World War II, and research on effects still lags far behind the rapid growth of this economically valuable field of products. The review includes the results of laboratory and field studies on phytoplankton, crustaceans, molluscs, fish, reptiles, birds, and mammals. It is abundantly clear that there is significant variation between species, between chemical families of compounds, and between individual compounds. Irregularity in the results of field tests suggests the reasonable probability that actual toxicity might be affected by temperature, silt, flushing rates, salinity, and other environmental factors.

These authors also comment constructively on the special problems related to pesticide application. Chronic toxicity may be more subtle than acute toxicity, but as devastating. Acquired resistance has been demonstrated for some vertebrates. The specific capacities of organisms to concentrate pesticides are poorly known, but may be extremely important because oysters concentrated 96 percent of available DDT within two days and retained much of this for substantial periods. The possibilities of recycling and build-up were noted, citing freshwater experience in which original applications of .014-.02 ppm of TDE (DDD) eventually produced concentration of 2,500 ppm in fish and 1,600 ppm in fish-eating birds. The eventual use of chemicals which are specific for target

species and non-toxic to all others is cited as the most promising future avenue of effort.

During March, 1964, the British Government ordered withdrawal of the chlorinated hydrocarbons, aldrin and dieldrin, from use. Action was apparently based on evidence of accumulative contamination, and also on some uncertainty of the physiological human effects. Also in March, 1964, the U. S. Public Health Service and the State of Louisiana established endrin used for cane borers as the probable cause of the killing of 10 million fish in the Mississippi River basin, including brackish waters of the Gulf of Mexico. As compared with environmental concentrations, fish blood showed a thousandfold increase, and fatty tissue a ten-thousandfold accumulation.

In the estuarine studies which have been conducted, these chlorinated hydrocarbons are all dangerous to important estuarine species, but so are many others. Revelations of damage and restrictions on use are not yet ended.

Intensified attention to pesticides should not obscure the ever-present possibilities of other toxic elements and compounds. The paucity of such research in estuaries is impressive in view of the great industrial growth of recent years and the consequent threat to inshore waters. Alexander *et al.* (1936) illustrated one type of effect in that low levels of cyanide showed linear increase in toxicity with temperature, but nearly logarithmic increase in toxicity with decrease in oxygen concentration. Olson *et al.* (1941) and Davis (1948) explained the effects of flocculent copperas pollution on diatoms, and learned that precipitating particles carry some diatoms from the water. This would decrease productivity, although Davis found no evidence of substantial loss. Galtsoff (1960) observed that the precipitate can be dealt with by oysters, but suspects that it may be harmful to larvae. He also notes the absorption and storage of copper, mercury, lead, and arsenic by oysters and other bivalves.

Ideally, research on the effects of chemical additions to the estuary should precede or parallel industrial development, new brand production, and chemical process modification. Regrettably, this is not the present practice. Therefore, new damage and danger remain as continuous and growing threats in coastal waters.

Nutrient Chemicals

Human wastes, or their degradation products, are universally placed in the river, the estuary, or the sea (see Koch, 1959, for a comprehensive European summary), and provide a continuous source of nitrogen and phosphorous in various combinations, plus a variable and imperfectly understood mixture of many substances. The great human preference for concentrating near estuaries makes the impact even greater at that site. Nitrogen and phosphorous are essential for photosynthetic elaboration, and availability sometimes limits production, so that they must receive principal discussion.

Before examining some of the effects of human waste, it is of interest to note that other potential mixtures of waste are added to estuaries in significant quantities. Ryther (1954) and others of the staff of the Woods Hole Oceanographic Institution (Ryther *et al.*, 1958a; Guillard *et al.*, 1960) have studied the remarkable growth of algae in Great South Bay and Moriches Bay, on Long Island, New York. Broad study of hydrography, chemistry, and biology has demonstrated that heavy pollution from surrounding duck farms, with high organic nitrogen but unusually low N:P ratio, combines with the topography and hydrography of these bays to yield a very dense population of small algae, dominated by *Nannochloris atomus* and a species of *Stichococcus*. These have seriously reduced the oyster-producing capacity of these estuaries by unbalanced overenrichment.

Effects of nutrient addition, rather than tables of the prevailing quantities, are of interest here. Hynes (1960) has provided a valuable condensation of knowledge of the fluvial and lacustrine effects of organic pollution, and demonstrates that processes are rather well established (see also Ingram and Towne, 1959). Of about 45 pages on the biological effects of organic matter, Hynes was able to devote only two to estuaries because "there is little detailed information on the biological consequences of estuarine pollution". He cites tidal activity and rapid environmental changes as complicating factors. However, the general pattern of dense algal blooms, often accompanied by esthetically undesirable appearance and odor is very familiar (Bartsch, 1961).

Rational attempts must be made to understand these effects, in view of the certain growth of coastal populations. E. P. Odum (1961a) provides a constructive point of departure when he recognizes that the addition of large amounts of organic waste into natural waters creates a new ecosystem, and that an effective response to it is most likely to be found in studying the fundamental principles and processes involved. He includes a helpful analysis of the energy flow involved and the nutrient cycling which occurs, and suggests avenues of attack when the results are inconsistent with human wishes. Krause (1961) and others have outlined the fundamentals of algal physiology, and have urged a basic approach to these highly practical problems.

The distinctive problems and potentials of estuarine enrichment have already received attention. Mansueti (1961) stresses the widespread estuarine tendency to act as a nutrient trap, with tidal cycles and slow flushing to enhance the availability of nutrients for chemical or biological use. Pritchard (1959b) reviewed the physical mechanisms affecting the distribution of conservative materials introduced, and showed that: (a) oscillatory tidal motion produces longitudinal spread; (b) non-tidal dispersion will respond to the density of the material and the pattern of net motion in the estuary (vertically homogeneous, two-layer, three-layer, etc.); (c) net flushing will occur, and

usually be predominantly along the right side of the estuary; and (d) entrapment by lateral indentures can provide important reservoirs. He predicted that computation may eventually be feasible for predicting the distribution of conservative contaminants, but that non-conservative materials will be much more difficult. I would add that biological processes and sequences in estuaries rarely permit such broad-scale projections with useful accuracy as yet, although they merit continued effort.

Artificial enrichment has been essayed, but it is expensive because of the cost of fertilizers and of accompanying research. Pratt (1949) found that the addition of superphosphate could elevate phosphate levels in a salt pond, although not by calculated amounts. Repeated addition held levels well above pre-treatment concentrations. Nitrate additions, on the other hand, produced short spurts to predicted levels, but these could not be held. A net increase in the standing crop was obtained, and it lasted for a significant period. Earlier large-scale study of changes in a fertilized sea-loch by Raymont (1949) and others showed that plankton production increased, bottom fauna was enhanced, and fish production eventually responded favorably. Use of sewage for enrichment of freshwater ponds is an ancient technique.

Development of practical methods for profitable management of the enormous quantities of fertilizing materials available to estuaries offers a challenging field for further research and for contribution to human welfare. At present, these vast quantities are released in undirected patterns, without using their great potential for profitable selected improvement.

The specific effects at sewage outfalls into estuaries also need further study. Through the tidal cycle, the release plume will swing upstream and downstream, and cover a central area twice or continuously. Effects on planktonic and nektonic species may be ephemeral, and the best record of effect is often made on the benthic community. The affected zones are oval, circular, or semicircular, in contrast with the more linear fluvial effects noted by Gaufin and Tarzwell (1956), Hynes (1960), and Ingram and Towne (1959). Estuarine patterns have been observed by Blevgad (1932), Fraser (1932), Filice (1954a, b), Reish (1959a, b), and McNulty (1961). Successive zones away from the outfall may include an area of sludge or soft muck with no macroinvertebrates; a poor zone which may have characteristic species present, sometimes dwarfed; a relatively rich zone with heavy populations of molluscs, worms, diatoms, and other species; and normal communities. Effects of local circulation, substrate, salinity, and other variables would produce almost infinite variations. In broader terms, McNulty saw a small damaged area surrounded by a much larger enriched area, and could distinguish indicator organisms and communities for both. Galtsoff (1956), however, reported that sludge from domestic sewers has almost completely smothered the formerly productive shellfish beds in the vicinity of large cities, including New

York, Boston, and Norfolk. Hynes cited the reports of Pentelow (1955) that sewage causes severe de-oxygenation in some estuaries like the Thames to promote a condition which blocks the upstream and downstream migration of sea trout and salmon so that these runs have become extinct. There is need for additional research on the effects of sewage—and much room for improvement in handling it.

Radioactive Wastes

Radioactive wastes are entering coastal waters in increasing quantities from such activities as research, munitions, industry, and medicine. The estuaries are likely to receive, and retain, greater concentrations than the oceans. These are of concern because they may cycle and recycle until they enter human food supplies in significant quantities, and they may also affect the genetic structure of aquatic organisms.

Chipman (1958, 1960) has cited the complexity of obtaining complete answers, since the fate of radionuclides is dependent on many physical, chemical, and biological processes. Pritchard (1960) stated that the principal factors involved will usually be the form of the contaminant, dilution, advective transport, turbulent diffusion, uptake on sediments, and extraction by the biota from solution or from the sediments. Chipman and his associates (Chipman *et al.*, 1958) reported on a series of experiments designed to establish uptake rate of various probable radionuclides by common species and to track these materials through major food chains. Of all the suggested fates, Donaldson (1960) found biological activity to be the most important factor in the distribution and localization of radioactive products at Eniwetok. He found no evidence of biological effects of these products, probably because competition quickly eliminates injured individuals. The applicability of these generalizations to estuaries has not been tested. Extreme local situations may be dangerous and important, but apparently the total effect is not yet great.

Pulp Wastes

The wastes from plants that process wood into cellulose products by various processes are released into many estuarine areas. A great deal has been written which contains many conflicting observations and opinions. As an example, in 1947 Galtsoff *et al.* were satisfied that pulp-mill waste was the principal cause of decline of the productivity of oyster bars in the York River of Virginia. In a very different area, Waldichuk (1959) described a variety of releases in British Columbia, and noted that chemical and biological degradation may or may not be present, depending largely on the mechanics of release. The report offered by Gunter and McKee to the Washington Pollution Control Commission in 1960 appears to contain a rational summary: (1) sulfite waste is exceedingly complex, varying with species of wood, treatment, and digestion chemicals; (2) effects have been erratic and mixed, with investigational results including both stimulation and depression of the

biota; (3) physical dispersion and dilution are important aids in disposal; (4) interim regulations should be established; and (5) research is essential to study the effects of the liquor and method of rendering it non-destructive.

Exotic Chemical Effects

Wherever large quantities of chemicals are placed in estuaries, they cause change. Each case is local and specific. Some special instances are, however, potentially instructive and important.

Stroup *et al.* (1961) commented on the effects of adding large quantities of acid to the carbonate-buffered waters of Baltimore Harbor. They found that pH is decreased, and the partial pressure of CO₂ is increased. This increase in CO₂ tension may be significantly favorable to photosynthesis but unfavorable to the fauna.

Galtsoff (1960) emphasized the capacity of many organisms to concentrate elements and compounds from the environment. Bivalve molluscs, for example, absorb copper, mercury, lead, and arsenic near industrial areas. Oysters, clams, and scallops can contain concentrations of zinc over 100 thousand times that of surrounding waters (Chipman *et al.*, 1958).

Oil, motor exhaust fumes, ship bilge, unusual industrial wastes, garbage dumping, and a limitless variety of special chemical additions exist, and require comprehension and control where they are important.

Pollution-control efforts are universal, but extremely variable. It is improbable, however, that understanding and effectively controlling chemical pollution will ever catch up in the race against new products and processes. In most cases, regulations are created after damage occurs rather than with intelligent foresight.

GEOLOGICAL PROCESSES

Man has directly influenced geological processes, principally by changing silt production and distribution. Within the estuary, this is usually the result of shoreline construction (Sykes, 1965), dynamiting (Gunter, 1957b), cutting of waterways and canals, or certain specialized fishing operations such as hydraulic dredging for soft shell clams (Manning, 1957). Manning described the Maryland gear, developed since 1950; it jets a trench in the bottom about 30 inches wide and up to 18 inches deep. Heavy materials drop rapidly, but clams and other coarse materials are conveyed by belt to the surface; the fine silts and clays are dispersed, usually to no more than 50 feet on either side of the cut. Most material returns to the trench.

Effects of silt handling are usually relatively local, although Hellier and Kornicker reported in 1962 that hydraulic canal dredging deposited silt as deep as 27 cm, and as far as .5 miles from the dredge. Many factors affect dispersion. Bartosch (1960) has identified the sources and results of silt in fresh water. Turbidity obviously interferes with light transmission and photosynthesis, and usually increases oxygen demand (Odum and Wilson, 1962). After heavier ma-

terials settle quickly, turbidities rarely exceed the natural levels caused by wind. Galloff (1960) included sedimentation as one of the negative factors in the environment of the oyster, since even the capacity of this remarkably silt-tolerant species can be overcome by smothering loads. Although severe special cases exist, Gunter's comment seems to have general application—deleterious effects are real but localized, and nutrient release may offset the damage done.

BIOLOGICAL PROCESSES

All the modifying activities considered in earlier sections affect biological processes. They operate through effects on photosynthetic production, nutrient cycling, changed food supply, altered activity patterns, direct maiming or killing, and many other pathways in the ecosystem. None of these effects of man are understood fully for estuarine areas. Our basic knowledge of effect on biological processes is limited and most of our information is clustered around the economically important species. Two areas of human activity offer dramatic evidence that we are as powerful in influencing these effects as we are in causing physical and chemical changes. Fishing and the transplanting of species into new aquatic communities are stimulating examples for review.

Human Predation (Fishing)

In the Chesapeake Bay and the immediate coastal waters, about 500 million pounds of aquatic organisms are stripped annually from the total estuary-dependent biota by human predation. Sykes (1964) reports 1,104,000,000 pounds in 1960 for the north portion of the Gulf of Mexico. This is a very specialized predation, which is highly selective by species and by size; it is seasonal in its effects, and does not return the captured nutrients directly into the system. Not all the effects on the biological processes are yet known, but many can be cited or suggested.

The species preyed upon by humans in the estuaries of the Middle Atlantic coast of North America can be grouped into three categories: wild resident species, wild transient species, and cultured species. Man's predation has different effects on each of these groups, but there are several general effects which apply to all.

The wild resident species, which spend virtually all their life history in the estuary, were, obviously, present in the estuary prior to man's intensive use. Consider the oyster bed communities, soft shell clams, and striped bass of the Chesapeake: early harvest was light, with inefficient gear; power boats, nylon nets, better dredges, navigational aids, increased experience, and more efficient predatory techniques have placed increased pressure on these and other residents. Four known and possible changes could be made. First, the structures of the community can be substantially altered: for example, all utilized oyster beds could be changed in species composition, size, distribution for oysters, and physical structure. Secondly, the total abundance and distribution of the prey species can be substantially changed. Maryland's

oyster catch is about 10 percent of earlier levels, despite gear improvement and high price. Many old beds are barren, without oysters or their usual associates.) The size and age composition of prey species can be modified, which appears to have occurred in striped bass, where human predation is heaviest on young fish. A fourth possibility is that growth rates, distribution, and spawning success might be enhanced. (Soft shell clams may be growing more rapidly and densely on worked beds than on undisturbed areas.)

The transient wild species like shad, herrings, etc., which move into or through the estuary to breed or to feed, are exposed to intensive inshore predation for only part of their lives, but it may be under highly vulnerable circumstances. A principle of fishery biology was expressed by an experienced fisherman when he told me that "Fish are fairly safe from overfishing unless we can get at them in a bottleneck that they must pass through. Then, we can really murder them." Although increased fishing efficiency also contributes to the decreases, the bottlenecks like migration to limited spawning areas, offer the greatest opportunities for the depletion of stocks by overfishing and for a significant genetic selection. The sturgeon appears to be depleted, for example, but critical studies are lacking; it is rare in this area, and extirpation is imaginable. Significant genetic selection can be effected by size limits, net-mesh regulations, and controlled seasons if the entire stock is regularly exposed to selective predation. Fishways interposed on essential spawning migrations may select to favor strains which can pass ladders.

The cultured and semi-cultured species are particularly vulnerable to change. Complete culture, involving production of young or seed from selected parents and supervision until harvesting, apparently is not now possible for any estuarine species on a commercial scale. *Crassostrea virginica*, *Ostrea edulis*, *Mytilus edulis*, *Chanos chanos*, and *Penaeus setiferus* are all partially cultured, and these and others will probably be fully controlled in the future. Several important steps can be taken on behalf of these species, including provision of effective substrate for larvae of oysters and clams, transportation and concentrations in favorable growing areas, partial or complete protection from other predators, feeding, and intensive and thorough harvesting. All of these are violent modifications of the natural biological processes of the estuary, and may result in improved growth rate, survival and condition of the cultured species. Oysters on planted cultch, for example, when transplanted to good growing areas where food is more plentiful and natural predators absent, show improved survival and growth. Genetic selection may also result, as in the case of oysters which may have been modified by culture and by very wide scale transplanting along the entire Atlantic coast—the potentials in this field will be enormously enhanced when artificial breeding becomes practicable. Still another result may be increased parasitic and natural

predator damage; planted oyster beds can be wiped out by cow-nose rays, oyster drills decimate seed beds, and the intensive populations in planted beds may be more severely parasitized by microparasites.

The capture and permanent removal of large quantities of any of these species is in itself a radical interruption of biological processes. Under undisturbed conditions, each animal would compete, die, be consumed and digested, pass into the nutrient sequence, and continue as recycled elements and compounds. The only net losses to the system would come from flushing and sedimentation. When we extract large chunks of organized organic materials, it seems likely that the total production of the prey species is probably increased because the removal of some organisms provides space and food for their competitors; a substantial quantity of organic material leaves the estuary, at least temporarily, although much may return as sewage and industrial waste; species competing with the prey species are favored; and a broad spectrum of modifications affects the unused species, including those that feed the species directly captured, its parasites, natural predators, and the rest of the ecosystem.

Far too little attention has been directed to research on these effects of human activity in the estuary. Many of the possibilities have not been tested. The speculative comments here are only indication of the actions and reactions that are modified, and suggest some challenging avenues for future investigation.

Artificial Introduction of Species

Each species attains a distribution which balances its needs and its environment. Distributions normally change slowly, accompanied by constant adjustments in that balance. Man, however, has often violently disrupted this leisurely pattern by transplanting species to new areas. This has sometimes been done intentionally in estuaries to increase or improve yields of food, and it has often been done inadvertently, carrying species along with transplants, on ship hulls, or by carelessness.

Great benefit is possible from introductions. The oyster fishery on the west coast of North America depends primarily on seed transplanted each year from Japan. Four hundred thirty-five striped bass (1879-81) and 15 thousand white shad fry (1871) were carried laboriously from the East Coast to the West Coast, both are widely established, with substantial benefits and no known damage to the receiving waters.

On the other side of the economic balance are the parasites, predators, and competitors of species which have food value. The Portuguese oyster, *Gryphaea (Crassostrea) angulata*, was introduced to the coast of France, where it gradually drove out some of the superior *Ostrea edulis* (Galtsoff, 1946). The voracious screw borer, *Urosalpinx cinerea*, one of the worst of the oyster drills, was accidentally carried into English waters with American oysters, and is a serious and extensive predator (Korringa, 1952).

Urosalpinx has also been taken to the Puget Sound area, where it joined another immigrant, *Tritonais japonica*, an oriental species which is considered to be the most destructive drill of the area (Korringa, 1952). The extensive transplantations of oyster stocks among waters of the Atlantic and Gulf Coasts have been suggested as suspected mechanisms for introducing to new areas the fungus, *Dermocystidium marinum*, the microparasite called MSX, and other parasites. Oyster competitors have been observed to create serious problems in new waters. A mudworm, *Polydora ciliata*, was introduced into Australia about 1870 (Nelson, 1946). It changed the industry, forcing oyster culture off the bottoms and onto stakes or stone slabs. A small slipper limpet, *Crepidula fornicalis*, was taken to Europe from America. It grows to giant size there and has spread over many areas, especially in Holland and England (Korringa, 1952). It increased so vigorously that it actually threatened to replace the Dutch oyster. Korringa believes that it is a space competitor, harbors a serious shell disease as it decays, and destroys great numbers of oyster larvae.

The barnacle, *Elminius modestus*, accidentally brought from the Southern Hemisphere to England (Korringa, 1952), competes vigorously with oyster larvae for settling space and probably destroys larvae. As reported earlier, DDT applications appear to be useful in its control. The shell of an oyster provides a habitat for a remarkable variety of protozoans, algae, sponges, worms, coelenterates, bryozoans, snails, and the eggs and spores of other species. It is possible that the transplantation of oysters, oyster shells, and seed has modified the distribution of more aquatic species than any other human activity.

The drama and problems associated with artificial introductions in estuaries are not, however, limited to invertebrates. Like the starling and the English sparrow on land, carp, goldfish (*Carassius auratus*), the walleye or yellow pike perch (*Stizostedion vitreum*), catfish, and others have entered the Middle Atlantic area and other waters (Mansueti, 1961). The effects are not yet measured, but the carp and goldfish are regarded with serious concern.

Water chestnut, *Tropea natans*, was imported into the United States as a handsome ornamental plant. Accidental release near Washington, D. C. produced, within ten years, beds covering 10,000 acres (Rawls, 1964). It blocked navigation, provided a breeding site for mosquitoes, and produced devilish "caltrops" or hard-spined seed cases. Expensive mowing, hand-picking and chemical treatment have reduced it to a controlled threat.

Eurasian watermilfoil, *Myriophyllum spicatum*, is widely distributed in Europe, Asia, and Africa, where it is a modest member of the flora. In Chesapeake Bay, however, it has recently become a serious menace to many interests, blocking navigation, preventing boating and swimming, interfering with seafood harvesting, increasing siltation, and encouraging mosquitoes. It thrives over a wide salinity range from

0 % to 15 %, and can tolerate 20 %, reproduces effectively by fragmentation, and survives in all depths less than about 9 feet. At least 100 thousand acres are infested, and new tributaries are invaded each year. Control has been effective on an expensive local basis, applying 2,4-D in clay pellets. This, in turn, opens serious questions about the dangers of the control method. Beaven *et al.* (1962) showed that standard applications have no acute effects on clams, crabs, oysters, or some fish, but the possibilities of chronic effects, residues, accumulation, and human intake are not yet resolved. Perhaps all this unfinished story began with the emptying of a fish bowl containing this attractive plant.

These varied instances of introduction without comprehension of natural controls and without effective restraint convey their own point. One need only add that each is likely to be an irreversible act, with permanent effects.

ACTIVITIES IN THE OCEAN

The sea is still beyond man's control, and the strenuous efforts he makes to change his terrestrial environment still seem puny in comparison with oceanic forces. He can, however, successfully block the sea from its tributary bays, with results that are important to the estuary.

Pritchard and many others have stressed the power and importance of tidal currents, which provide the energy for horizontal translation and for mixing throughout the estuary. He showed in 1955, for instance, that increased tidal velocity tends to convert a stratified estuary to vertical homogeneity. When ocean barriers are constructed or removed, the change will have far greater importance than merely reducing or encouraging the intrusion of salt and of marine species. Ryther *et al.* (1958), in considering the algal problem in Great South Bay and Moriches Bay, attributed improvement in the entire area to the reopening of Moriches Inlet to restore effective exchange with the sea.

Hundreds, perhaps thousands, of coastal inlets and harbors have been modified by engineering efforts to stabilize, improve, or protect them for various human endeavors. Groins, breakwaters, channel dredging, bulkheading, and filling all change the natural patterns and processes. Each inlet is a specific and local case, and the concept that engineering changes should always be preceded by thorough consideration of all the physical, chemical, and biological results to be effected should be encouraged. This has not been the usual sequence, and most inlet engineering appears to have been single-purpose modification. Improved comprehension of the total effects of altering relations between ocean and estuary is desirable and will be increasingly valuable.

Important special problems appear when nearshore ocean waters are used for waste disposal. Wastes can be translocated into the estuaries by such mechanisms as the regular migration of anadromous fish and the

great inflow of oceanic water with tidal currents. Ketchum, in an unpublished paper, reviewed pertinent data for one area, the mouth of Delaware Bay. He concluded that discharge would be undesirable at any site within five miles of the coast, but showed the great variation in waste-receiving capacity at different locations. Further, he stressed the necessity for specific on-site studies prior to selection of waste sites. Pritchard (1960) effectively outlined the steps necessary in evaluating sites for disposing of radioactive wastes. He also stressed that this inshore environment comes into more intimate contact with man than any other marine waters. Therefore, it is most likely to receive wastes and, simultaneously, most in need of protection from excess wastes. He discussed many of the factors which influence the fate of these wastes. As understanding of estuarine processes grows, the probabilities of irreparable and massive damage from ignorance in waste disposal should decline.

ON THE RESILIENCY OF ESTUARIES

The reading necessary for the preparation of this review has deepened and clarified my personal concern with the future welfare of estuaries. It is clear that many destructive forces are being applied widely, that pressures are increasing at a very rapid rate, but that intelligent planning and control of estuarine changes are rare. Fundamental and practical understanding of estuaries is now increasing at an impressive rate, but this growth appears to be dangerously slow in comparison with the increase in disruption of estuarine systems.

Several of the characteristic physical, chemical, and biological features of the estuary provide an interesting and valuable resistance to change. Seas often heal quickly. The factors aiding resiliency have not yet been adequately investigated, but several illustrative and stimulating examples are known:

1. The vigor of the rhythmic and turbulent circulation pattern continuously and endogenously renews the supply of water, food, larvae, and other essential elements to any small damaged area. This aids in recovery and protects long-term net stability patterns.
2. The substantial buffering capacity of estuaries, usually operating through the carbonate system, is another element which resists changes imposed on estuaries. It is not so great as the buffering capacity of the open ocean, but it is greater than most rivers, and is enormously important in the estuaries where pollution is received.

3. Exogenous renewal is also normally continuous, because estuaries receive continuous input from rivers and from the ocean. Since the river-sourced and ocean-sourced populations are substantial components of the estuarine biomass, the addition of organisms from these sources is important in normal estuarine sequences and in recovery from damaging or toxic change.

4. Many species have biological characteristics

which provide special advantages in estuarine survival. These characteristics usually protect the species against the natural violence of estuaries, and they are often helpful in resisting external forces, like man.

Additional examples of contributors to estuarine resiliency include the oyster, the blue crab and the striped bass. The oyster, for instance, has been cited by Galtsoff (1960) for great tolerance to temperature (10° C. to about 35° C.), salinity (about 5‰ to 35‰), and for its remarkable ability to hermetically seal the valves of its shell to isolate the animal from unfavorable conditions for as long as three weeks. Nelson (1938) described the oyster's complex and effective mechanisms for dealing with the high silt content of coastal waters. The blue crab uses the net upstream flow of deep waters in estuaries to provide annual redistribution of juveniles to all the tributaries and upstream areas of the Chesapeake Bay. Mansueti (1961) stressed the remarkable resiliency of the striped bass in surviving the increased pressures and damages in the Chesapeake system. He suggested that the specific gravity of the eggs of this species may be crucially important to survival, since the semi-buoyant eggs released in nearly fresh water are buoyed by turbulence as the embryos develop, and protected from silt smothering. When the larvae emerge, they have been carried downstream by net surface flow to waters of higher salinity, past the zone of maximum turbidity, so that they can feed. A last example can be drawn from the copepod populations of estuaries. The mechanisms which permit maintenance of large planktonic populations in these turbulent and flushed systems are not yet fully understood but appear to be complex and effective. They may include vertical migrations (which could move populations downstream at night and upstream by day), reservoirs in marginal areas, and other attributes or patterns of individual or population behavior (Rogers, 1940; Bousefield, 1955; Barlow, 1955; Cronin et al., 1962).

These resilient forces, and the others which certainly exist, are welcome allies in the efforts to achieve optimal balance between man's effects on estuaries and their capacities.

THE FUTURE ROLE OF MAN

Man's past effects on estuaries have been poorly and incompletely planned, unimaginative, and frequently destructive. In view of the many important uses served by these waters, and the size of the growing pressures on them, it is imperative that a new major human force be utilized in the future—the force of intelligent management. It will require application of many kinds of tools and techniques, ranging from original fundamental oceanographic research to regulatory changes and public education. The yields can be great indeed. Some of the approaches necessary for intelligent management are now apparent, and it is perhaps timely to summarize them and the achievement which could be gained.

THE TOOLS FOR MANAGEMENT

Research

This review has illuminated the need for basic research at every possible level to identify the significant estuarine processes, quantify relationships, and resolve many complexities to predictable patterns. Despite the visible and valuable increase in attention to the estuaries in recent years, most of the controlling parameters are yet incompletely and inadequately comprehended.

Among the physical processes, only gross estimates can be provided for the patterns of flushing, circulation, vertical mixing, and diffusion, and for such specific factors as light absorption, sedimentation rates, and location, current direction and velocity, and salt distribution. The valuable contributions of Ketchum, Pritchard, and others permit some of these estimates to be made under certain highly specific or broadly generalized conditions, but each new estuary observed is still likely to require an extensive descriptive survey, trial-and-error fitting of computed relationships, and a relatively long period of correction by well-designed local observation before useful precise predictions can be made. Field studies of interesting phenomena, increased use and refinement of physical and mathematical models, and controlled laboratory studies are all urgently needed.

Similar urgency exists for growth in chemical and geological comprehensions. The fate of the most abundant natural terrigenous elements and compounds is partly known but the chemical sequences involving rarer materials are almost untouched. Others have reviewed, with greater detail and higher competence, the present state of chemical knowledge of estuaries, but it is relevant here to point out that such knowledge appears to be completely insufficient for understanding and intelligent judgment of many present and probable human activities with chemical implications. These include the introduction of vast quantities of complex industrial chemical mixtures, the release of stored materials from bottom sediments by dredging, the pouring of sewage chemicals into the system, and other violent modifications. As usual, practical resolution of the problems involved will be almost totally dependent on fundamental comprehension.

The insufficiency of present biological knowledge in estuaries is equally evident. Indeed, it is rather shocking, since the areas have been so heavily utilized for food production for centuries. The oyster, for example, is considered to be the most studied of invertebrate animals, and yet there are important unanswered questions on nutrition, genetics, general physiology, reproduction, and even the morphology of the group. Similar and greater ignorance exists about all other estuarine species. Principal attention has always been focused on the relatively small numbers of economically useful species, and there is urgent need for more knowledge of phytoplankton, zooplankton, a wide variety of benthic organisms, and the large array of vertebrates and invertebrates which are part of the

dynamic estuarine biota, but which are not consumed, sold, or otherwise directly exploited by humans. Interrelationships between and among species must be illuminated, the interplay between organisms and the estuarine environment is but vaguely known, and full understanding of estuarine biology lies many years of research ahead.

Only passing and superficial attention can be given here to other research needs which appear to exist in the field of economics and social and political science. Intelligent management of estuaries will require a valid estimation of the economic results of various alternate routes of action, and will require modification of existing patterns of human activity. Perhaps research is not the necessary addition which will make this feasible, but there do appear to be major unanswered problems. Evaluation of recreational use has been notoriously difficult, especially in the non-consumptive fields like beauty, cleanliness, and personal refreshment. In social and political areas, the total effects of modifying the strongly independent behavior of fishermen, for instance, appear to be complex and difficult to comprehend.

Public agencies carry almost all the cost of estuarine research, since the public interests are so large and diverse. This is totally appropriate for basic research on the processes and principles of estuarine phenomena, and equally fitting for uses which directly serve public fisheries, waste disposal, recreation, and similar interests. There is, however, another potential and proper source for the substantial supporting funds required. When use of the estuaries for financial profit is desired, the cost of research on the effect of use should often be placed where the profit will be realized. An industry which proposes to save the cost of alternative methods of waste disposal by placing waste into an estuary (or other public holding) should pay the costs of research necessary for evaluation of the proposal. Under many circumstances, these funds might be supplemented by public funds, since the findings will be useful in other problems of interest to the public. Many examples exist of such research support, without control, by the using industries, but the policy of increased assignment of research costs to the profit maker appears to be equitable and to be necessary as a source of needed funds.

Pragmatic Experiments

Direct practical experiments in management, in which gross and relatively uncomprehending efforts are made to achieve identified objectives, appear to offer substantial and valuable assistance toward the intelligent management of estuaries. These are usually far less desirable and effective than efforts which can be properly based upon adequate understanding of the principles involved, but several special circumstances argue for serious consideration and use of some pragmatic studies.

The pressures on estuaries are so great now and the threats are so urgent that there is not always

time to develop comprehension. The rate of increase in use is so much greater than the rate of increase in knowledge that shortcuts are sometimes fully justified. The alternative appears to be destruction of many areas while we await the results of lengthy and complex research.

When a substantial change in an estuary cannot be deferred (usually because the opposing arguments are excessively weak in data and evidence), it can often be turned to constructive use in terms of improved understanding. Every possible effort should be made to capitalize on these forced but usable opportunities. Suggestions for research expenditures often face resistance, especially on a project regarded as a *fait accompli*, but adequate and competent study before and after a change can be valuable. No normal research budget can afford the cost of enormous diversion, or pollutant release, or engineering change, or thermal addition, or wide-scale pesticide application, which political decisions may require. Thorough pre- and post-treatment study, based on statistically sound sampling techniques, and paired when possible with another untreated estuary, can be of great value. It is essential that these studies meet several criteria, however. The pre-study and post-study periods must be long enough to distinguish the effects of change from normal (and often great) variations. Skilled professional guidance must be provided and not entrusted to inexperienced staffs. Interpretations must be based on objective criteria, free from adverse political pressures.

Under such circumstances, valuable knowledge can often be obtained.

Administration

The operating control of the modification of estuaries is dispersed among state and federal legislative bodies, executive agencies, and the public will. The mechanisms and experience of the groups cannot be discussed here, but recent vivid examples are interesting and may be stimulating.

In Massachusetts, recent state legislation requires review and prior approval of all proposed modifications of marshland, shores, and coastal lands. This law overrides the privileges of private ownership, in recognition of the effects of such modifications on the public interest. Other states, towns, and small governmental bodies are essaying similar careful management.

Maryland established a committee of its Board of Natural Resources to consider the problem of disposing of the large quantities of sediment removed in channel creation, improvement, and maintenance. The Board has approved and effectuated a change in policy from simple dumping in deep water to creation of useful diked land whenever feasible. Sometimes expensive and destructive waste can be converted into constructive, and even profitable, real estate.

At the federal level, mention has already been made of the legal requirement that the Branch of River Basin Studies of the U.S. Department of the

Interior must review and comment on proposed federal projects which would affect fish and wildlife resources. This includes estuaries, but review and comment is not a substitute for proper review and control—which would include study of all the effects of such projects.

Many other governments have initiated similar efforts to control and to manage rationally the violent changes which are occurring. Local conditions are as varied as the estuaries themselves, but examples of good management do exist, and they merit consideration and emulation.

THE YIELD

The benefits which may be derived from proper management of coastal areas are great enough to merit the costs. The gains appear to include:

1. Substantial growth in basic knowledge of many significant physical, chemical, geological, and biological processes as the result of the major research efforts essential for such management. Paralleling this would be an important increase in the training of competent scientists in these fields.

2. Vast improvement in the ability to predict the effects of important proposed engineering or management changes. Such predictions could be made in terms of organic production, dollar value, and other criteria.

3. Development of rational and balanced objectives, based upon the real capacities and limitations of various estuarine systems. The possible alternatives would be comprehended and choices would be made for good reasons. As an interesting example of conflict, Rounsefell (1963) wishes to make maximum use of the high potentials of estuaries as nursery areas for commercially useful fish, and takes rather violent exception to suggestions by H. T. Odum and Wilson (1962) of techniques which would maximize photosynthetic production in estuaries. In this case and others, there may be genuine conflicts of interest. However, it seems more pertinent to emphasize that we do not now understand enough about the ultimate results of photosynthetic increase or about how to single out and achieve the optimal balance in use of the factors which determine fish density.

4. The greatest benefits to be gained lie in achieving positive and ultimate uses of estuaries as replacement for negative resistance to change, temporizing half-measures, and short-term patchwork in management. Balance by informed decision could be reached among uses of estuaries for food production, waste disposal, recreation, navigation, esthetic enjoyment, and research. Without any assumption of unerring wisdom, there is hope for remarkable improvement in long-term use of these areas.

ON POSITIVE THINKING

Much of this review has described the destructive or at least incomprehensible, estuarine changes through man's efforts. However, the cited literature also contains suggestions for the positive and profit-

able manipulation of rivers, bays, marshes, and other coastal areas. Some of these proposals are well supported by experiments or field evidence, and others will require rigorous investigation prior to acceptance and improvement. The following suggestions do not by any means exhaust these ideas, but they indicate the directions and vitality of some of the recognized possibilities.

Chemical additions could protect or enrich estuaries, if they were used intelligently to offset undesirable conditions or to supplement limiting elements. Hynes (1960) has pointed out that the most outstanding problem in disposing of sewage is the appalling waste of nutrients. Brehmer (1964) noted that the District of Columbia area spends \$2.1 million annually in the unmanaged release of \$3.2 million worth of fertilizing materials. Constructive techniques are not fully developed, but Føyn (1959), for instance, has learned to remove phosphorous from wastes entering the Oslo Fjord by electrolytic precipitation. E. P. Odum (1961a) pointed out six ways by which phytoplankton blooms might be controlled. No problem here is likely to be beyond the capacity of industrial ingenuity, if economic incentives become sufficiently high. An interesting example may be provided in the case of the detergents. Widespread public reaction against visible suds and reported detergent residues in natural waters produced serious possibilities of strict prohibitive legislation and regulations. Pertinent industries have made massive investment in the discovery and development of "biodegradable" and other degradable cleansing compounds, and now promise that the problem will be effectively solved. If the competitive interest of such industrial giants can be focused on other estuarine problems, magnificent achievements may result.

Thermal additions might be constructively used. Spawning of all species and photosynthetic production are controlled by temperature, and offer tantalizing opportunities for management. Huntsman (1950) suggested the use of warmed water in controlling the movement of fish to concentrate populations, or for other purposes. The present increase in attention to research on many thermal effects should suggest some desirable possibilities. Imaginative engineering and improved biological understanding might be fruitful partners in achieving useful hot spots.

Improved races and species can be selected and introduced. Galtoff (1956) has pointed out some of the variation that exists among races of oysters and the possibility of selection for desirable characteristics under intensive cultivation. Provenance research has been so widely successful in forestry and agriculture that its potentials are beyond question. The successful introduction of new species presents greater difficulties and requires very thorough preparation and, perhaps, a share of good luck. Korringa (1952) has, however, pointed out that success might sometimes be encouraged and accelerated by simultaneous importation of natural control mechanisms. The literature contains many records of introduction, with

both successes and failures, available to guide future efforts. A peculiar blending of conservative concern and imaginative daring may be necessary in improving upon present races and species.

Management—the intentional modification of the factors determining production by a species—can be carried to higher levels than have yet been achieved in estuaries. Maximum culture of oysters, clams, and other usable herbivores may offer the greatest potentials, since they are nutritionally supported near the broad base of the food chains. For instance, Glude (1951) outlined the sequence of seed production, predator control, mortality prevention, fattening, and controlled harvest which might increase oyster production substantially. Similar concepts of population comprehension and management should eventually be possible, not only for the species of fish and shellfish directly utilized, but also for the supporting zooplankton species, phytoplankton, and all the necessary parts of the complex biota of estuaries.

The gross ecology of the estuary can be manipulated to advantage. Present and probable engineering capacities are so great as to require new thinking about potential use of these capacities as well as the more usual effort to resist their application. It may, in some circumstances, be found desirable to store and release river water; divert huge volumes; radically alter channels, currents, and tides; or in other ways introduce major alterations. Those who oppose such suggestions are often expressing fear of the unpredictable consequences, and might alter their position if sufficient knowledge existed to permit accurate prediction and evaluation of all the results.

RECOMMENDATIONS

1. Every level of estuarine research should be supported and speeded to the maximum rate consistent with competence. Basic research in this challenging, complex, and available marine environment is critically needed. Applied research and pragmatic "experiments" must also be fully utilized to prevent the uses and abuses from destroying these areas. The development of research programs should be aggressive and opportunistic.

2. The full force of intelligent management should be brought to bear in man's role in estuarine processes. Research, public education, and wise management are vital to the optimal future use of estuaries, with appropriate and balanced policies and practices applied in each estuarine system.

3. Selected estuaries, as "typical" as possible, should be set aside in the public interest to provide undisturbed research centers. These must be protected from the creeping exploitation that has eventually destroyed the character and value of many estuaries, and reserved for esthetic enjoyment, for comparison with utilized estuaries, and for the many kinds of research which would yield increased comprehension without damage to the system studied.

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LITERATURE CITED

- ALEXANDER, W. B., B. A. SOUTHGATE, and R. BASSINDALE, 1936. Survey of the River Tees. II. The estuary—chemical and biological. *J. Marine Biol. Assoc U. K.*:717-724.
- AULD, D. V., 1964. Waste disposal and water supply. In *Problems of the Potomac Estuary*; pp. 13-18. Proc. Interstate Comm., Potomac River Basin, Washington, D.C.
- BARLOW, J. P., 1955. Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biol. Bull.*, 109(2):211-225.
- BARTSCH, A. F., 1960. Settleable solids, turbidity, and light penetration as factors affecting water quality. In *Biological problems in water pollution*. Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept., W60-3:118-127.
- BARTSCH, A. F., 1961. Introduced eutrophication, a growing water resource problem. In *Algae and Metropolitan Wastes*. Trans. 1960 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept., W61-3:6-9.
- BAUGHMAN, J. L., 1948. An annotated bibliography of oysters with pertinent material on mussels and other shellfish and an appendix on pollution. Texas A. and M. Res. Found., Agr. and Mechanical College of Texas, College Station, Texas.
- BEAVEN, G. F., 1946. Effect of Susquehanna River stream flow on Chesapeake Bay salinities, and history of past oyster mortalities on upper Bay bars. *Third Ann. Rept., Maryland Bd. Nat. Resources*:123-133.
- BEAVEN, G. F., C. K. RAWLS, and G. E. BECKETT, 1962. Field observations upon estuarine animals exposed to 2,4-D. *Proc. N. E. Weed Contr. Conf.*, 16: 449-458.
- BLEGVAD, H., 1932. Investigations of the bottom fauna at outfalls of drains in the Sound. *Rept. Danish Biol. Sta.*, 37:5-20.
- BOLOMEY, J. G. W., 1959. Effect of the Rhine on Netherlands beaches. *Proc. First Intern. Conf. on Waste Disposal in the Marine Environment*:164-174.
- BOUSEFIELD, E. L., 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. *Bull. Natl. Museum Can.*, 137:1-69.
- BREHMER, M. L., 1964. Nutrient enrichment in the Potomac estuary. In *Problems of the Potomac Estuary*; pp. 47-50. Proc. Interstate Comm., Potomac River Basin, Washington, D.C.
- BURT, W. V., 1955. Distribution of suspended materials in Chesapeake Bay. *J. Marine Res.*, 14(1):47-62.
- BUTLER, P. A., and P. F. SPRINGER, 1963. Pesticides—A new factor in coastal environments. *Trans. 28th N. Am. Wildlife and Natl. Resources Conf.*: 378-390.
- BUTLER, P. A., A. J. WILSON, JR., and A. J. RICK,

1962. Effect of pesticides on oysters. *Proc. Natl. Shellfisheries Assoc.*, 51:23-32.
- CARPENTER, J. H., 1957. A study of some major cations in natural waters. *Chesapeake Bay Inst. Tech. Rept.*, 15:1-75.
- CARPENTER, J. H., and D. G. CARGO, 1957. Oxygen requirement and mortality of the blue crab in the Chesapeake Bay. *Chesapeake Bay Inst. Tech. Rept.*, 13:1-22.
- CARSON, R., 1962. *Silent Spring*. Houghton Mifflin Co., Boston.
- CHIPMAN, W. A., 1958. Biological accumulation of radioactive materials. *Proc. First Ann. Texas Conf. Utilization Atomic Energy, Misc. Publ. Texas Eng. Exp. Sta.*, 36-41.
- CHIPMAN, W. A., 1960. Accumulation of radioactive pollutants by marine organisms and its relation to fisheries. In *Biological Problems in Water Pollution. Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept.*, W60-3:8-14.
- CHIPMAN, W. A., T. R. RICE, and T. J. PRICE, 1958. Uptake and accumulation of radioactive zinc by marine plankton, fish, and shellfish. *U.S. Fish and Wildlife Serv., Fishery Bull.*, 135:279-292.
- COTTAM, C., 1960. A conservationist's view of the new insecticides. In *Biological problems in Water Pollution. Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center W 60-3*:42-45.
- CRONIN, L. E., J. C. DAIBER, and E. M. HULBURT, 1962. Quantitative seasonal aspects of zooplankton in the Delaware estuary. *Chesapeake Sci.*, 3(2):63-93.
- DAVIS, C. C., 1948. Studies of the effects of industrial pollution in the lower Patapsco River area. II. The effect of copperas pollution in plankton. *Maryland Dept. Res. and Education, Chesapeake Biol. Lab. Publ.*, 72:1-12.
- DAVIS, H. C., 1958. Survival and growth of clam and oyster larvae at different salinities. *Biol. Bull.*, 114(3):296-307.
- DAVIS, H. C., 1961. Effects of some pesticides on eggs and larvae of oysters, *Crassostrea virginica*, and clams, *Venus mercenaria*. *Com. Fisheries Rev.*, 23(12):8-23.
- DONALDSON, L., 1960. Radiobiological studies at the Eniwetok test site and adjacent areas of the western Pacific. In *Biological problems in water pollution. Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept.*, W60-3:1-7.
- EMERY, K. O., and R. E. STEVENSON, 1957. Estuaries and lagoons. I. Physical and chemical characteristics. *Geol. Soc. Am. Mem.*, 67, 1:673-749.
- FILICE, F. P., 1954a. An ecological survey of the Castro Creek area in San Pablo Bay. *Wasman J. Biol.*, 12(1):1-24.
- FILICE, F. P., 1954b. A study of some factors affecting the bottom fauna of a portion of the San Francisco Bay estuary. *Wasman J. Biol.*, 12(3):257-292.
- FØYN, E., 1959. Chemical and biological aspects of sewage discharge in inner Oslofjord. *Proc. First Intern. Conf. Waste Disposal in the Marine Environment*:279-284.
- FRASER, J. H., 1932. Observations on the fauna and constituents of an estuarine mud in a polluted area. *J. Marine Biol. Assoc.*, 18(1):69-84.
- GALTSTOFF, P. S., 1946. Comment on the importation of foreign shellfish. *Com. Rept., Natl. Shellfisheries Assoc.*
- GALTSTOFF, P. S., 1956. Ecological changes affecting the productivity of oyster grounds. *Trans. 21st N. Am. Wildlife Conf.*, 408-419.
- GALTSTOFF, P. S., 1960. Environmental requirements of oysters in relation to pollution. In *Biological Problems in Water Pollution. Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept.*, W60-3:128-133.
- GALTSTOFF, P. S., W. A. CHIPMAN, JR., J. B. ENGLE, and H. N. CALDERWOOD, 1947. Ecological and physiological studies of the effect of sulfate pulp mill wastes on oysters in the York River, Virginia. *U. S. Fish and Wildlife Serv., Fishery Bull.*, 51:58-186.
- GAUFIN, A. R., and C. M. TARZWELL, 1956. Aquatic macroinvertebrate communities as indicators of organic pollution in Lytle Creek. *Sewage Ind. Wastes*, 28:906-924.
- GAUSSLE, D., and D. W. KELLEY, 1963. The effect of flow reversal on salmon. *Ann. Rept. Delta Fish and Wildlife Protection Study, Append. A*, A1-A16.
- GLUDE, J. B., 1951. The effect of man on shellfish populations. *Trans. 16th N. Am. Wildlife Conf.*:397-403.
- GUILLARD, R. R. L., R. F. VACCARO, N. CORWIN, and S. A. M. CONOVER, 1960. Report on a survey of the chemistry, biology, and hydrography of Great South Bay and Moriches Bay, conducted during July and September 1959, for the townships of Islip and Brookhaven, New York. *Woods Hole Oceanog. Inst. Ref.*, 60-15.
- GUNTER, G., 1952. Historical changes in the Mississippi River and the adjacent marine environment. *Univ. Texas, Publ. Inst. Marine Sci.*, 2(2):119-139.
- GUNTER, G., 1953. The relationship of the Bonnet Carré Spillway to oyster beds in Mississippi Sound and the "Louisiana Marsh" with a report on the 1950 opening. *Univ. Texas, Publ. Inst. Marine Sci.*, 3(1):17-71.
- GUNTER, G., 1955. Mortality of oysters and abundance of certain associates as related to salinity. *Ecology*, 36:601-605.
- GUNTER, G., 1956. Land, water, wildlife and flood control in the Mississippi Valley. *Proc. Louisiana Acad. Sci.*, 19:5-11.
- GUNTER, G., 1957a. Wildlife and flood control in the Mississippi Valley. *Trans. 22nd N. Am. Wildlife Conf.*, 189-196.
- GUNTER, G., 1957b. How does siltation affect fish production? *Natl. Fisherman*, 38(3):18-19.
- GUNTER, G., and G. E. HALL, 1963. Biological investigations of the St. Lucie estuary (Florida) in connection with Lake Okeechobee discharges through the St. Lucie Canal. *Gulf Res. Repts.*, 1(5):189-207.
- GUNTER, G., and J. E. MCKEE, 1960. A report on oysters, *Ostrea lurida* and *Crassostrea gigas*, and sulfite waste liquors. *Spec. Consultants Rept. to Pollution Control Comm., State of Washington*, February 1960. Olympia, Washington.
- HANKS, R. W., 1963. Chemical control of the green crab, *Carcinus macanas* (L.). *Proc. Natl. Shellfisheries Assoc.*, 52:75-86.
- HARTOG, C. DEN., 1963. The amphipods of the deltaic region of the Rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. I. Introduction and hydrography. *Neth. J. of Sea Res.*, 2(1):29-39.
- HAVINGA, B., 1935. Het Zuiderzegebied in zijn huidige phase van ontwikkeling. *Vakblad voor Biologen*, 17(4):64-73.
- HAVINGA, B., 1936. De veranderingen in den hydrographischen toestand en in de macrofauna van Zuiderzee en IJsselmeer gedurende de jaren 1931-1935. *Mededelingen van de Zuiderzee-Commissie*, 4:1-26.
- HAVINGA, B., 1941. De veranderingen in den hydrographischen toestand en in de macrofauna van het IJsselmeer gedurende de jaren 1936-1940. *Mededelingen van de Zuiderzee-Commissie*, 5:1-18.
- HAVINGA, B., 1949. The enclosing of the Zuyder Zee and its effect on fisheries. *U. N. Sci. Conf. Conserv. and Util. of Resources. (Wildlife 1(a)/5; Water 7(c)/3)*
- HAVINGA, B., 1959. Artificial transformation of salt and brackish water into fresh water lakes in the Netherlands and possibilities for biological investigations. *Arch. Oceanog. Limnol.*, 10:47-52. (Suppl.)
- HEDGPETH, J. W., 1957. Estuaries and lagoons. II. Biological aspects. In *Treatise on marine ecology and*

- paleoecology*; vol. 1, *Ecology*. *Geol. Soc. Am. Mem.*, 67:693-729.
- HELLIER, T. R., Jr., and L. S. KORNICKER, 1962. Sedimentation from a hydraulic dredge in a bay. *Univ. Texas, Publ. Inst. Marine Sci.*, 8:212-215.
- HUNTSMAN, A. G., 1950. Population dynamics in estuaries. In *A Symposium on Estuarine Ecology*. Atl. Estuarine Res. Soc. Yorktown, Virginia.
- HUTTON, R. F., B. ELDRED, K. D. WOODBURN, and R. M. INGLE, 1956. The ecology of Boca Ciega Bay with special reference to dredging and filling operations. *Florida Marine Lab., Tech. Ser.* 17:1-86.
- HYNES, H. B. N., 1960. *The biology of polluted waters*. Liverpool Univ. Press, Liverpool.
- INGRAM, W. M., and W. W. TOWNE, 1959. Stream life below industrial outfalls. *Public Health Repts.*, 74(12):1059-1070.
- JEFFRIES, H. P., 1962. Environmental characteristics of Raritan Bay, a polluted estuary. *Limnol. Oceanogr.*, 7:21-31.
- JONES, R. L., D. W. KELLEY, and L. W. OWEN, 1963. Delta fish and wildlife protection study. *Ann. Rept. No. 2. Resources Agr. Calif.*, Sacramento, California.
- KETCHUM, B. H., 1950. The exchanges of fresh and salt waters in tidal estuaries. *Proc. Colloq. Flushing of Estuaries, Office of Naval Res.*:1-23.
- KETCHUM, B. H., 1951a. The flushing of tidal estuaries. *Sewage Ind. Wastes*, 23(2):198-209.
- KETCHUM, B. H., 1951b. The dispersion and fate of pollution discharged into tidal waters, and the viability of enteric bacteria in the sea. *Progress Rept. Res.*, Grant No. 1249(C2), Period Dec. 1, 1949 to Feb. 1, 1951. *Woods Hole Oceanog. Inst. Ref. No. 5-11*.
- KETCHUM, B. H., 1951c. The exchanges of fresh and salt waters in tidal estuaries. *J. Marine Res.*, 10:18-38.
- KETCHUM, B. H., 1954. Relation between circulation and planktonic populations in estuaries. *Ecology*, 35: 191-200.
- KETCHUM, B. H., J. C. AYERS, and R. F. VACCARO, 1952. Processes contributing to the decrease of coliform bacteria in a tidal estuary. *Ecology*, 33(2): 247-258.
- KINNE, O., 1963. The effects of temperature and salinity on marine and brackish water animals. I. Temperature. *Oceanog. Marine Bio. Ann. Rev.*, 1:301-340.
- KOCH, P., 1959. Discharge of waste into the sea in European coastal areas. *Proc. First Intern. Conf. Waste Disposal in the Marine Environment*:122-130.
- KORRINGA, P., 1952. Recent advances in oyster biology. *Quart. Rev. Biol.*, 27:266-303, 339-365.
- KORRINGA, P., 1958. The Netherlands shellfish industry and the Delta plan. *Intern. Council Explor. Sea. C. M., Shellfish Comm.*, No. 60.
- KRAUSE, R., 1961. Fundamental characteristics of algal physiology. In *Algae and Metropolitan Wastes*. *Trans. 1960 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept.*, W-61-3:40-47.
- LINDSAY, C. E., 1963. Pesticide tests in the marine environment in the State of Washington. *Proc. Natl. Shellfisheries Assoc.*, 52:87-97.
- LOOSANOFF, V. L., 1960. Some effects of pesticides on marine arthropods and mollusks. In *Biological Problems in Water Pollution*. 1959 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept., W-60-3: 89-93.
- MANNING, J. H., 1957. The Maryland soft shell clam industry and its effects on tidewater resources. *Maryland Dept. Res. and Education Resource Study Rept.*, No. 11.
- MANSUETI, R. J., 1961. Effects of civilization on striped bass and other estuarine biota in Chesapeake Bay and tributaries. *Proc. Gulf Caribbean Fisheries Inst.*, November 1961:110-136.
- MCNULTY, J. K., 1961. Ecological effects of sewage pollution in Biscayne Bay, Florida: Sediments and the distribution of benthic and fouling macroorganisms. *Bull. Marine Sci. Gulf Caribbean*, 11(3):393-447.
- NELSON, T. C., 1931. Expert testimony in *New Jersey vs. New York et al.*; Master hearings, U. S. Supreme Court, 283 U.S. 336, No. 16, original. Argued April 13-15, 1931.
- NELSON, T. C., 1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of *Ostrea virginica*, *O. edulis*, and *O. angulata*, with comparisons with other species of the genus. *J. Morph.*, 63:1-61.
- NELSON, T. C., 1946. Comment on the importation of foreign shellfish. *Com. Rept. Natl. Shellfisheries Assoc.*
- NELSON, T. C., 1947. Some contributions from the land in determining conditions of life in the sea. *Ecol. Monographs*, 17:337-346.
- NELSON, T. C., 1960. Some aspects of pollution, parasitism and inlet restriction in three New Jersey estuaries. In *Biological Problems in Water Pollution*. *Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept.*, W-60-3:203-211.
- ODUM, E. P., 1961a. Factors which regulate primary productivity and heterotrophic utilization in the ecosystem. In *Algae and metropolitan wastes*. *Trans. 1960 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept.*, W-61-3:65-71.
- ODUM, E. P., 1961b. The role of tidal marshes in estuarine production. *The Conservationist*, 15(6):12-15.
- ODUM, H. T., 1959. Analysis of diurnal oxygen curves for the assay of reaeration rates and metabolism in polluted marine bays. *Proc. First Intern. Conf. Waste Disposal in the Marine Environment*:547-555.
- ODUM, H. T., and C. M. HOSKIN, 1958. Comparative studies on the metabolism of marine waters. *Univ. Texas, Publ. Inst. Marine Sci.*, 5:16-46.
- ODUM, H. T., and R. F. WILSON, 1962. Further studies on reaeration and metabolism of Texas bays. *Univ. Texas, Publ. Inst. Marine Sci.*, 8:23-55.
- OLSON, R. A., H. F. BRUST, and W. L. TRESSLER, 1941. Studies of the effects of industrial pollution in the Lower Patapsco area. I. Curtis Bay region, 1941. *Chesapeake Biol. Lab. Publ.*, 43:1-40.
- PANNELL, J. P. M., A. E. JOHNSON, and J. E. G. RAYMONT, 1962. An investigation into the effects of warmed water from Marchwood power station into Southampton water. *Proc. Inst. Civil Engrs.*, 23:35-62.
- PENTELOW, F. T. K., 1955. Pollution and fishes. *Verhandl. Intern. Ver. Limnol.*, 12:768-771.
- PICTON, W. L., 1956. Water use in the United States, 1900-1975. Water and Sewerage Industrial and Utilities Div., U. S. Dept. Commerce, Bus. Serv. Bull., 136. Washington, D. C.
- PRATT, D. M., 1949. Experiments on the fertilization of a salt water pond. *J. Marine Res.*, 8:36-59.
- PRITCHARD, D. W., 1951. The physical hydrography of estuaries and some applications to biological problems. *Trans. 16th N. Am. Wildlife Conf.*:365-375.
- PRITCHARD, D. W., 1952. The physical structure, circulation, and mixing in a coastal plain estuary. *Chesapeake Bay Inst., The Johns Hopkins Univ. Tech. Rept.* 3, Ref. 52-2.
- PRITCHARD, D. W., 1955. Estuarine circulation patterns. *Proc. Am. Soc. Civil Engrs.*, 81:1-11.
- PRITCHARD, D. W., 1959a. Computation of the longitudinal salinity distribution in the Delaware estuary for various degrees of river inflow regulation. *Chesapeake Bay Inst., The Johns Hopkins Univ. Tech. Rept.* 18, Ref. 59-3.
- PRITCHARD, D. W., 1959b. The movement and mixing of contaminants in tidal estuaries. *Proc. First Intern. Conf. Waste Disposal Marine Environment*:512-525.
- PRITCHARD, D. W., 1960. Problems related to disposal of radioactive wastes in estuarine and coastal waters. In *Biological Problems in Water Pollution*

- Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center Tech. Rept., W'60-3:22-32.
- RAWLS, C. K., 1964. Aquatic plant nuisances. In *Problems of the Potomac Estuary*; pp. 51-56. Proc., Interstate Comm. Potomac River Basin, Washington, D. C.
- RAYMONT, J. E. G., 1949. Further observations on changes in the bottom fauna of a fertilized sea loch. *J. Marine Biol. Assoc.*, 27(1):9-19.
- REISH, D. J., 1959a. An ecological study of pollution in Los Angeles-Long Beach Harbors, California. *Occasional Paper, Allen Hancock Foundation*, 22:1-119.
- REISH, D. J., 1959b. The use of marine invertebrates as indicators of water quality. *Proc. First Intern. Conf. Waste Disposal in the Marine Environment*:91-102.
- RENN, C. E., 1956. Man as a factor in the coastal environment. *Trans. 21st N. Am. Wildlife Conf.*:470-473.
- ROGERS, H. M., 1940. Occurrence and retention of plankton within the estuary. *J. Fisheries Res. Bd. Can.*, 5(2):164-171.
- ROUNSEFELL, G. A., 1963. Realism in the management of estuaries. *Marine Resources Bull. No. 1, Alabama Marine Res. Lab.* Dauphin Island, Alabama.
- RYTHER, J. H., 1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. *Biol. Bull.*, 106:196-209.
- RYTHER, J. H., R. F. VACCARO, E. M. HULBURT, C. S. YENTSCH, and R. K. L. GUILLARD, 1958a. Report on a survey of the chemistry, biology and hydrography of Great South Bay and Moriches Bay conducted during June and September, 1958, for the townships of Islip and Brookhaven, Long Island, New York. *Woods Hole Oceanog. Inst. Rept.*, No. 58-57.
- RYTHER, J. H., C. S. YENTSCH, E. M. HULBURT, and R. F. VACCARO, 1958b. Dynamics of a diatom bloom. *Biol. Bull.*, 115:257-268.
- SEGERSTRAALE, S. G., 1951. The recent increase in salinity off the coast of Finland and its influence upon the fauna. *J. Conseil Intern. Exploration Mer.*, 17: 103-110.
- SIMMONS, H. B., 1959. Application and limitations of estuary models in pollution analyses. *Proc. First Intern. Conf. Waste Disposal in the Marine Environment*:540-546.
- STROUP, E. D., D. W. PRITCHARD, and J. H. CARPENTER, 1961. Final report, Baltimore Harbor study. *Chesapeake Bay Inst., The Johns Hopkins Univ. Tech. Rept.* 26, Ref. 61-5.
- SVERDRUP, H. U., M. W. JOHNSON, and R. H. FLEMING, 1942. *The Oceans*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
- SYKES, J. E., 1964. Requirements of Gulf and South Atlantic estuarine research. *Proc. 16th Ann. Session, Gulf and Caribbean Fish. Inst.*, 1963:113-120.
- SYKES, J. E., 1965. Multiple utilization of Gulf Coast estuaries. *Proc. Southeast Game and Fish Comm.*, 17th Ann. Conf. 1963:323-326.
- THOMPSON, S. H., 1961. What is happening to our estuaries? *Trans. 26th N. Am. Wildlife and Nat. Resources Conf.*, 318-322.
- U. S. ARMY ENGINEER DISTRICT, BALTIMORE, N. ATLANTIC DIV., 1963. *Potomac River Basin Report. Summary*, 1-43.
- VAAS, K. F., 1963. Annual report of the Delta Division of the Hydrobiological Institute of the Royal Netherlands Academy of Sciences for the years 1960 and 1961. *Neth. J. Sea Res.*, 2(1):68-76.
- WALDICHUK, M., 1959. Effects of pulp and paper-mill wastes on the marine environment. *2nd Seminar Biol. Problems in Water Pollution, Robert A. Taft Sanitary Eng. Center*.
- WAUGH, G. D., and A. ANSELL, 1956. The effect, on oyster spatfall, of controlling barnacle settlement with DDT. *Annals Applied Biology*, 44:619-625.
- WHALEY, R. C., 1960. Physical and chemical limnology of Conowingo Reservoir. *Chesapeake Bay Inst., The Johns Hopkins Univ. Tech. Rept.* 20, Data Rept. 32, Ref. 60-2:1-140.
- WHITNEY, R. R., 1961. The Susquehanna fishery study, 1957-1960: A report of a study on the desirability and feasibility of passing fish at Conowingo Dam. *Maryland Dept. Res. and Education Contrib.*, 169:1-81.
- WOLMAN, A., J. C. GEYER, and E. E. PYATT, 1957. A clean Potomac River in the Washington metropolitan area. *Interstate Comm. Potomac River Basin, October 1957*, Washington, D. C.
- WOODBURN, K. D., 1963. A guide to the conservation of shorelines, submerged bottoms and saltwaters with special reference to bulkhead lines, dredging and filling. *Marine Lab., Florida Board Cons., Educ. Bull.*, 14:1-8.

Notes on Estuarine Pollution with Emphasis on the Louisiana Gulf Coast

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On March 19, 1964, the U. S. Public Health Service and the State of Louisiana jointly announced that water pollution involving toxic synthetic organic chemicals appeared to be the cause of massive and continuing fish kills in the Lower Mississippi drainage basin.

Concentrations of endrin, dieldrin, and two unidentified chlorinated hydrocarbons were found in the blood of dead and dying fish from the Mississippi and Atchafalaya Rivers and estuarine waters in Louisiana. The concentrations of endrin, alone, found in these fish represented lethal levels. These findings bear out the earlier contention of the authors that water degradation in this part of the nation's largest watershed has been a reality for many years.

The Louisiana Wild Life and Fisheries Commission's Eighth Biennial Report (1958-1959) records that, "Foremost among kills attributable to man-made causes have been those resulting from use of insecticides, primarily endrin, for control of cane borers, and heptachlor for control of fire ants. These kills were caused by direct introduction of insecticides into the affected water bodies during careless aerial application, and by insecticides borne by surface runoff from rains immediately following applications. Heptachlor has caused an occasional kill in the area affected by the fire ant control program, but the major cause of concern has been the widespread use of endrin for control of cane borers throughout the cane growing area. During the 1958 growing season frequent kills caused by endrin were reported, but during the 1959 growing season these kills reached alarming proportions, with complaints being received by the Division of Water Pollution Control on an almost daily basis."

Again in 1961, twenty-five recorded fish kills (U. S. Public Health Service, 1961), the severities ranging from "moderate" to "heavy", were blamed on the careless application of endrin. These kills occurred in the coastal and near-coastal sugarcane areas of Louisiana.

Attempts by the authors in 1959 to obtain passage of state regulations controlling the use of pesticides were thwarted by the inability of the Division's labo-

ratories to detect any level of pesticide in dead or dying fish. Needless to say, endrin was not detected in dead sugarcane borers (*Diatraea saccharalis*). Our recommendations for pesticide regulations were based on the judgment that, coincidental with the application of endrin, fish were dying in large numbers, and at that time of the year were dying only in or near the areas of application. The application season for cane borer control occurs in June, July, and August of each year.

In November, 1960, the Louisiana Division of Water Pollution Control called on the U. S. Public Health Service and the U. S. Fish and Wildlife Service for assistance in solving mysterious fish die-offs in both the Atchafalaya and Mississippi Rivers in Louisiana and in the estuarine areas of the Gulf influenced by these two rivers.

Because of the extensive levee systems, neither the Atchafalaya nor the Mississippi watersheds receive significant drainage from sugarcane-producing areas in Louisiana. Especially is this true in the upstream areas of the two rivers where the die-offs had been traced. In the freshwater areas of the Atchafalaya and the Mississippi Rivers, catfish, carp, freshwater drum, and two species of shad were being killed. In the estuaries, speckled trout and other marine forms were observed to be affected.

The two federal agencies reported negative results in their analyses for diseases, parasites, and pesticides. The Louisiana Division had already determined that dissolved oxygen, pH, water temperature, and inorganic salts were within ranges known to be normal for these areas. The bacteriologist for the Division prepared cultures utilizing parts of the affected fish and determined that "these cultures indicated the presence of *Aeromonas liquefaciens*, the causative organism for abdominal dropsy in fish" (Ninth Biennial Report, 1960-1961).

The fish kills recurred in 1961 and 1962 in the same areas as before, but to a lesser degree. A seasonal pattern was established when it was observed that in three successive years the phenomenon manifested itself in the fall and winter months only.

In mid-November, 1963, die-offs of freshwater fish

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in the lower Mississippi and Atchafalaya Rivers and marine fish in the estuarine areas of the Gulf fed by the Mississippi River had attained such proportions that Lafleur, Division Chief of the Louisiana Wild Life and Fisheries Commission, again requested assistance from the Public Health Service and the U. S. Fish and Wildlife Service. This time, entire schools of menhaden, mullet, and other commercial and game fish species were observed dying in the estuarine areas.

The U. S. Fish and Wildlife Service reported on the bacterial examination of 20 fishes, both freshwater and marine, comprising six species taken from the Mississippi River and its estuarine area. Their report stated, "The only fish which carried a known pathogen was that large buffalo collected from the Mississippi River and it harbored a *Pseudomonas* infection, but the organisms were unique to that fish. No single bacterium showed up consistently from the fish, even of one species, so I suspect that the disease was definitely not of bacteriological origin. Freshwater fish often harbor low-grade infections of *Aeromonas* or *Pseudomonas* so the occurrence of a pathogen in one fish is of little significance" (U. S. Fish and Wildlife Service, 1963).

In December, 1963, the U. S. Public Health Service sent to Louisiana a team of scientists, headed by Donald Mount, Research Fishery Biologist of the Robert A. Taft Sanitary Engineering Center in Cincinnati, Ohio. These men collected water, mud, and fish samples from the affected areas, and returned to Cincinnati to begin exhaustive researches on these materials. Louisiana's Division of Water Pollution Control continually sent fresh materials to Cincinnati from both the affected and non-affected areas. The investigations and researches conducted by the Public Health Service biologists and chemists in defining the fish-killing agents as organic pesticides are, in our judgment, classic. The story of epochal achievement through unique bioassay and analytical techniques rightfully remains to be told by the workers themselves.

We have related this background in order to bring into sharper focus the needs for continued and increased analytical scrutiny of our estuarine areas. True, man does not have to depend upon these geographical niches for his most vital water needs. Nevertheless, we have just encountered a new dimension in water pollution which bears significantly on man's every use of the water resource. We have discovered this by detecting toxic materials at levels down to parts per trillion and relating these concentrations of minutiae to animal mortality. Our estuaries are the receptacles of all those inland rivers and streams which, as separate entities, we are trying at great cost to protect from the ravages of pollution. In our efforts we are prescribing appropriate levels of treatment for municipal and industrial wastes; withholding entirely from the stream such wastes as we can; and supplementing stream flows with dilution water where practical.

ECONOMIC CONSIDERATIONS IN POLLUTION

Economically, our estuaries are vital. Louisiana's 422,400 acres of coastal marshes and attendant estuaries are abundantly productive as fishery, fur, and recreational areas. St. Amant (1964) of the Louisiana Wild Life and Fisheries Commission recently stated that these apparent wastelands furnish livelihoods for more than 50 thousand people and yield more than 100 million dollars annually to the state. He cites the 1963 shrimp catch, totaling 80 million pounds. Oyster production in this same year was 10 million pounds; and the catch of menhaden, a fish valuable for fertilizer, pet foods, and oils, was one billion pounds. It will be interesting to analyze these catches with those of previous and future years to find out if these animal populations are being affected by synthetic organic chemicals.

Through Louisiana, an average of 450 billion gallons of water a day are discharged into the Gulf of Mexico. Streams and tributaries bearing such tongue-tripping names as the Sabine, Calcasieu, Mermentau, Vermillion, Atchafalaya, Mississippi, Pontchartrain, and Pearl carry water to the Gulf from 31 states and two Canadian provinces. The Missouri, the longest river in the United States, and the unpredictable Ohio, and their vast tributary networks all contribute to Louisiana's estuaries.

Like a bullet through a rifle barrel, waters of the mighty Mississippi are thrust toward the Gulf between the confines of the flood control levees. Before the day of these man-made structures, these waters fanned out over tremendous reaches of the coast, intermingling with waters contributed by the Atchafalaya and other tributaries to the Gulf. Freshwater marshes (salinities averaging 4-6 %) were formed by deposited silts and vegetative covers of wire grass (*Spartina patens*), widgeon grass (*Ruppia maritima*), three-cornered grass (*Scirpus olneyi*), and other common marsh grasses held these masses together. Wildlife communities were established in the marshes, and seafoods flourished from the nutrients carried by the fresh water into these positive estuaries.

As man erected his flood protection devices, these marshes ceased to form as extensively as before. When oil was discovered in the offshore and bay areas, drilling rigs and barges channeled through them. The intruding higher-salinity Gulf waters killed much of the vegetation and these marshes started dissolving under the constant buffeting of the tides. Silt and decayed grasses soon covered up many oyster-producing areas. Valuable nursery areas for both the white shrimp (*Penaeus setiferus*) and the brown shrimp (*Penaeus aztecus*) were adversely affected by the highly saline concentrations which formed when fresh waters were channeled away from parts of the estuaries.

Oil and other mineral production, shell dredging, pollutants from inland municipalities and industries,

channel dredging for navigation, and insect control are constantly changing the water quality and physical character of these areas. One example of draft channeling is the Mississippi River Gulf Outlet Project, authorized in 1956, which provides shipping service from the Gulf to New Orleans. This channel is 36 feet deep, 500 feet wide at the bottom, and about 76 miles long. When fully completed, Louisiana will lose an estimated 10-14 million dollars annually because of fish and wildlife habitat destroyed where this project cuts across highly productive estuarine and marsh areas (Eighth Biennial Report, 1958-1959). Fringe deficits, such as the inward march of the southern oyster drill (*Thais*) and the oyster parasite (*Dermocystidium marinum*), are all related to man's rearrangement of Louisiana estuaries.

SUMMARY

We have examined but a few of the problems now being experienced in only one estuarine complex. We are concerned, however, that most estuaries and their marshes are being influenced all too constantly by man's outpouring of wastes and by his geographical alterations. The preservation of these estuarial land masses is important, not only to the sports public and the commercial harvester of food and fur, but also to those marine life forms requiring nursery grounds and suitable bedding habitats. We have techniques for marsh management which, properly used, can provide vital protection to our coastline ecologies. We should initiate projects using these methods without

delay. At the same time we must have a strong program to control the discharge of wastes and toxins from all sources, including industries, municipalities, and agricultural areas. It is equally important that every possible step be taken to prevent accidental spills of oils, chemicals, and other pollutants capable of restricting the maximum use of estuaries and their adjacent land masses, and the profitable harvesting of the desirable biological forms they produce. No single facet of restoration or prevention is outstanding—they are all equally important links in the chain essential to the preservation of our coastal wealth, and merit the undivided attention of all those concerned with its protection.

LITERATURE CITED

- LOUISIANA WILD LIFE AND FISHERIES COMMISSION, 1958-59. *Eighth Biennial Report*; pp. 39 and 187. New Orleans, Louisiana.
- LOUISIANA WILD LIFE AND FISHERIES COMMISSION, 1960-61. *Ninth Biennial Report*; p. 207. New Orleans, Louisiana.
- ST. AMANT, L. S., 1964. Mosquitoes-Insecticides-Wildlife. *Louisiana Conservationist*, 16:2-5.
- U. S. FISH AND WILDLIFE SERVICE, 1963. *Letter Report of November 8, 1963, to Louisiana Wild Life and Fisheries Commission*. U. S. Department of Interior, Fish Farming Experimental Station, Stuttgart, Arkansas.
- U. S. PUBLIC HEALTH SERVICE, 1951. *Pollution-caused fish kills in 1961*. Publ. No. 847; p. 16. U. S. Department of Health, Education, and Welfare, Washington, D. C.

Technical Approaches Toward Evaluating Estuarine Pollution Problems

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Pollution caused by the discharge of pulp and paper mill wastes into marine waters at Everett, Bellingham, Anacortes, and Port Angeles, Washington, has stimulated field investigations which have been undertaken to support the enforcement proceedings authorized by the Federal Water Pollution Control Act. The programs include field research and investigations to determine the effects of such wastes on water quality, water uses, and the marine environment. The total effort represents cooperative participation by the U. S. Public Health Service; the Washington State Water Pollution Control, Fish, and Game Departments; universities; and industries.

Although the project was initiated in the spring of 1962, numerous technical problems and delays were encountered in tooling up for the job; it was about the same as starting with nothing and organizing miniature departments of oceanography, engineering, and biology and equipping them to function. The initial goal, to have all phases of the field program begin together and progress simultaneously, was unattainable. Therefore, additional sampling was necessary along the way to provide sufficient supporting information for each phase of study.

The program consists of several major elements—in-plant surveys, oceanographic studies, biological studies, and economic studies. The findings at Everett, Bellingham, and Port Angeles illustrate several aspects of the oceanographic and biological studies (Fig. 1).

NATURE OF THE OCEANOGRAPHIC STUDIES

The oceanographic studies have three principal objectives: (1) determining the dispersion and persistence of pulp mill wastes at the surface and at depths related to the flushing characteristics of the areas; (2) determining the extent and thickness of sludge beds caused by industry, and (3) determining the effect of surface waste concentrations on light penetration. Another important objective is to provide project biologists with the necessary physico-

chemical background on which to design their studies. Plankton, productivity, and larva bioassay sampling stations, for example, were selected on the basis of oceanographic field data. Temperature, salinity, dissolved oxygen (DO), Pearl-Benson Index (PBI), pH, and light penetration by Secchi disk were routinely measured on monthly field trips. Equipment is now being used which is more refined than the Secchi disk.

(The Pearl-Benson Index (PBI), as used in this paper, is the dilution of sulfite waste liquor (SWL) containing 10 percent solids expressed as ppm by volume; determined by the Barnes *et al.* (1963) modification of the Pearl and Benson (1940) technique. Although not synonymous, the terms PBI and SWL will be used interchangeably. The term "spent sulfite liquor" (SSL) is used by some and is equivalent to SWL. A model GS Beckman meter was used for pH; the Alsterberg (azide) modification of the Winkler method (A.P.H.A., 1960) for dissolved oxygen (DO) was used.)

The location and depth of sampling in all three areas were governed by the following concepts:

1. Stations were selected to allow adequate coverage of conditions from maximum sulfite waste liquor (SWL) concentration to those of little or no SWL. Stations were close enough together to allow contouring of the data and dispersed only enough to permit sampling a given area in one day.

2. Although SWL concentrations and associated effects at the surface are important to juvenile salmonids, concentrations in deeper waters are also important, especially at Everett, for their potential influence on: (a) sessile bottom fauna, (b) bottom fisheries, such as crab, flounder, and other demersal fishes, and (c) plankton.

3. In areas where only surface discharges are made, vertical mixing and diffusion will occur and, consequently, deeper waters must be sampled.

4. Pulp and paper mills usually operate around the clock, 12 months a year. There are seasonal and diurnal fluctuations of water properties throughout the water column, and the sampling was designed to obtain enough data to reflect at least one year of mill operation in each area.

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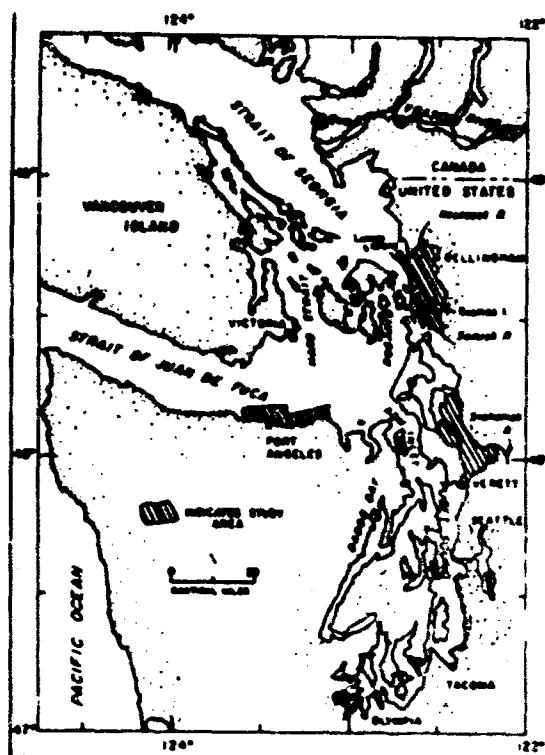


Fig. 1. Location map of Puget Sound area.

Oceanographic literature on Puget Sound and adjacent waters is voluminous, and no attempt is made to review it thoroughly here. The University of Washington (1953) has conducted long and extensive studies of Washington marine waters and has published a comprehensive literature review of the area. The Bellingham-Samish Bay system, in particular, has been investigated in regard to flushing characteristics and SWL distribution (Collas and Barnes 1962). The University of Washington has also completed a study of Bellingham Bay currents using Richardson meters supplied by the U. S. Public Health Service. The Pacific Oceanographic Group in Canada has also conducted numerous surveys in the Strait of Juan de Fuca and contiguous waters.

Because of the information already available on the Bellingham-Samish system, most of the present oceanographic work has been carried out in Everett and Port Angeles. These two areas have been studied by agencies of the State of Washington (Lindsay *et al.*, 1960; Orlob *et al.*, 1951; Peterson and Gibbs, 1957). Some of the pulp and paper companies concerned also have conducted field studies, but the resulting data are not generally available. Stein *et al.* (1963) published a report showing conditions existing in the Port Angeles area during a two-week survey.

NATURE OF THE BIOLOGICAL STUDIES

The objectives of the biological program are to detect and measure the influences of pulp and paper mill

wastes on significant marine organisms and their environment. Such information will help to determine whether damages have been caused by pollution and, if so, to define the necessary remedial steps. Eight separate activities are involved in doing this, as shown in Table I.

Other investigators have approached some of these objectives and a sizable literature has developed, especially relating to salmonids and shellfish (Lasater, 1954; Tolleson, 1963; Wagner *et al.*, 1957; Walidchuk, 1960). The toxic effects of SWL on young salmon have been studied intensely for several years. Mains *et al.* (1953), and Gunter and McKee (1960) thoroughly reviewed and evaluated current information on the effects of SWL on oysters.

Of the eight biological activities cited above, only three will be discussed in this paper: (1) oyster larva bioassays for the Bellingham-Samish and Port Angeles areas; (2) adult oyster mortality, growth, and condition index for the Bellingham-Samish area; and (3) live box bioassays with juvenile salmonids for the Everett area.

GROSS CHARACTERISTICS OF THE THREE AREAS

The three major areas under investigation have little in common, except that they are all bathed in salt water. Because Puget Sound itself is an estuary, waters adjacent to Everett may be considered an estuary within an estuary, since already dilute sea water at this point is freshened still more by entry of the Snohomish River. Bellingham Bay is similar, because it is fed at its northernmost end by the Nooksack River. Port Angeles harbor is not a true estuary, according to Pritchard's (1955) definition, because no large streams enter it. Indeed, its low-salinity water in the surface layer is mostly due to wastes from pulp and paper mills along the harbor shores.

It is customary to classify estuaries by their vertical and lateral salinity gradients. Because salinity is a result of an estuary's geomorphology, tides, and run-offs, its distribution reveals more about the type of estuary than any other single factor. Therefore, "typical" salinity, TBL, pH, and DO concentrations compared with depth-station curves are all used to exhibit the gross characteristics of each of the three areas.

OBSERVATIONS IN THE BELLINGHAM AREA

OCEANOGRAPHIC

Because of the extensive surveys conducted by the University of Washington in the Bellingham-Samish Bay system, the U. S. Public Health Service oceanographic field work was confined to a study of summer conditions in Bellingham-Samish Bay (Fig. 2). Sea water enters the system at depth primarily between Guemes and Lummi Islands, and is about two to four

Table 1. Type, area, and frequency of biological investigations.

Type	Areas	Frequency of invest	Initiation date
Vertical and horizontal tow collections of plankton	All	Monthly	July, 1963
Submerged microslides for attached organisms	Bellingham-Everett	10 days	Feb., 1964
Productivity and nutrient supply	Bellingham-Everett	Monthly	March, 1964
Adult oyster mortality, growth, and condition index—Phase 2	Bellingham-Samish	Monthly	March, 1964
Oyster larva bioassay	All	Monthly	May, 1963
Live box bioassay, juvenile salmonids	Bellingham, Port Angeles, Everett	Summer	April, 1963
Distribution-migration, juvenile salmonids	Bellingham, Port Angeles, Everett	Spring and Fall	March, 1963
Bottom fisheries, trawling	Bellingham-Samish, Port Angeles	Monthly	Dec., 1963

parts per thousand (‰) less saline than water in the Strait of Juan de Fuca near Port Angeles.

Figure 2 also shows that the 1960-1961 average surface PBI (Collins and Barnes, 1962) decreases with distance from the waste source, but extends as a detectable plume into Samish Bay. The percentage remaining with distance relative to the 200 parts per million (ppm) contour can be obtained by dividing

all values by two. Waters throughout the system are markedly turbid, with Secchi disk readings generally less than two meters. Low light transmission is caused by SWL, suspended fibers from the pulp and paper mill, plankton blooms, and silt transport from the Nooksack, Samish, and other smaller rivers. Effect of mill effluents in lowering DO levels is localized to within a one- to two-mile radius of the outfall, but oxygen saturation values of 120-140 percent are not uncommon in the upper 10 m during plankton blooms.

Figure 3 shows station curves at Stations A and B at two distances from the waste source. Station A, nearest the outfall, shows that PBI decreases rapidly with depth and is not found beneath the halocline. DO and pH are decreased in the upper 2 m. At a greater distance from the outfall, PBI values have diminished, and no effect on pH and DO is apparent. Surface salinity has also increased from 25.6 to 28.3 ‰ because of this station's position relative to the Nooksack River.

OYSTER STUDIES

Oyster culture was formerly one of the water uses in parts of Bellingham Bay, but it is now limited to the adjacent waters of Samish Bay. In that area, Pacific oysters (*Crassostrea gigas*) are cultivated from seed imported from Japan or Canada.

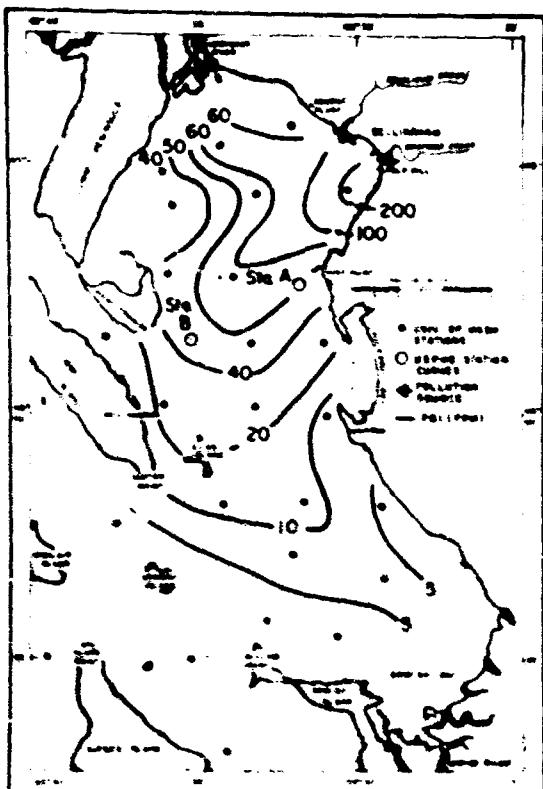


Fig. 2. Bellingham, Washington. Average surface Pearl-Benson Index (PBI) from University of Washington data (Collins and Barnes, 1962).

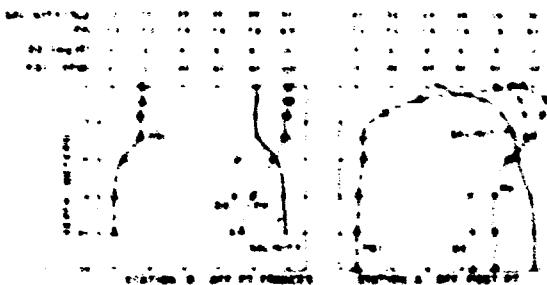


Fig. 3. Bellingham, Washington. Station curves, June 25, 1963.

Because wastes from the Bellingham mill are carried southward to the oyster-growing areas, it was necessary to devise a means of sensing the response of oysters to this factor of their environment. Two methods were developed: (1) larva bioassays of water samples were collected at key points in the area, and (2) *in situ* bioassay, were made of one- and two-year-old specimens of seed oysters to determine growth, survival, and condition index or fatness.

Each month one surface-water sample is collected by seaplane at each of 11 sampling points (Fig. 4). The samples are flown directly to the Point Whitney laboratory of the State of Washington Department of Fisheries to be processed. The time lapse from collection to processing never exceeds three hours. The technique is described by Loosanoff (1954) and has been modified by Woelke (1961). In brief, Pacific oysters are stimulated to spawn by raising their temperature to 25°–30°C. for three hours after having been held for four to six weeks at 20°C. At one and one-half hours or less after fertilization, about 25,000 larvae are added to each sample. After a 48-hour exposure to the test water, a sample containing 100–200 larvae is examined microscopically to determine the percent of "abnormal" larvae (those which are not fully shelled). Analyses are made for initial and ter-

Table 2. Oyster larva bioassay data for Bellingham-Samish area. Summary for period, May 13 to November 20, 1963.

Station	Kilometers from pollution source	Number of cultures	Mean percent abnormal larvae	Mean PBI	PRI range
1 & 2 (comb.)	0.1 & 3	42	95.9	1,087.8	6-3,840
3	5	9	67.8	105.0	1-222
11	7	15	72.2	70.2	4-250
4	8	15	44.2	26.8	1-91
5	12	12	27.5	10.1	1-25
10	16	21	19.5	12.3	2-35
6	17	21	17.8	3.7	0-22
9	18	21	16.1	14.0	0-28
8	19	15	23.3	3.2	1-7
7	20	15	22.9	3.6	0-9

minal PBI, and salinity concentration. Chlorophyll *a* is measured in the raw samples only.

Raw, unadjusted bioassay results for the first seven months are shown in Table 2. It is apparent that larval abnormalities increased with the decreasing distance from the pollution source, with all stations within 8 km showing abnormalities of 44 percent or greater. Similarly, high PBI and high abnormalities go together, which suggests a toxic influence of SWL from the Bellingham mill.

Long-term, *in situ* bioassays with seed stages and adult oysters are conducted at six locations (Fig. 4) to determine mortalities, growth rate, and condition index (Westley, 1959). When this program was initiated in June, 1963, the oysters were held in asphaltum-coated metal mesh baskets supported in 2.4 × 3 m anchored rafts. Test populations consisted of 50 pieces of seed cultch, 150 one-year-old and 100 two-year-old Pacific oysters. It was discovered shortly that violent tossing of the rafts in the open sweep of water during stormy weather caused the oysters to grind together, interrupted their feeding, and raised questions concerning other aspects of the test conditions.

The limited condition index data available at this point were sufficiently promising to justify continuing and improving the program. The first modification was to stabilize each raft by attaching two 35-foot-long Douglas fir saw logs in the manner of trailing rudders. Next, 4,000 test oysters were cemented with calcium aluminate and Portland cement to Fiberglas panels suspended vertically from the rafts 1 m deep at panel midpoint. It is now possible to remove each panel from the water for periodic examination and photographing. Oyster growth can be measured on the photograph by planimeter, and the growth history of each specimen can be followed individually. Quarterly, a sample consisting of 25 oysters on a panel will be taken to the laboratory to determine the

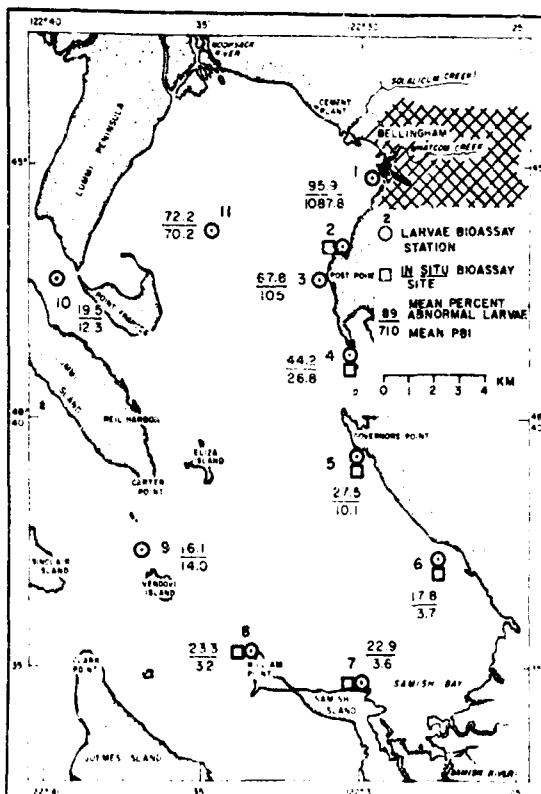


Fig. 4. Bellingham, Washington. Sampling stations for oyster larva bioassays and sites for *in situ* bioassays, May–October, 1963.

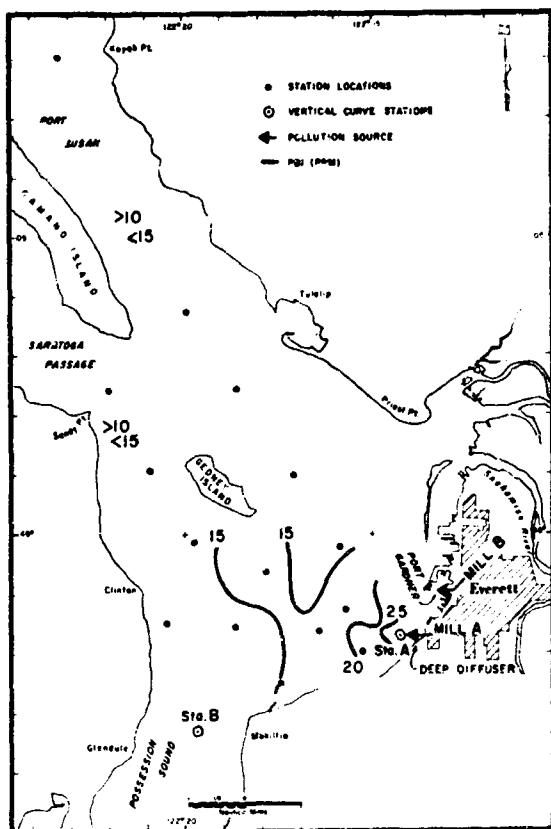


Fig. 5. Everett, Washington. Average surface PBI, May, 1962-May, 1963.

condition index. No data are yet available because the program was not revised until March of 1964.

OBSERVATIONS IN THE EVERETT AREA

OCEANOGRAPHIC

The City of Everett, located on Port Gardner at the mouth of the Snohomish River, is the site of two large sulfite pulp and paper mills (Fig. 5). Because of a thin freshwater layer at the top, surface effluents do not mix downward past the halocline. The bulk of the SWL from these mills is released through a deep diffuser, reported to be 91 m at its upper end and 104 m at its lower end. This being the case, there is an initial upward plume displacement of about 25 m, since the peak PBI is usually found at 75 m over the diffuser and at distance from it. The plume depth has been found to layer out at 50 m on occasion. Diurnal station data for the Everett area are not yet available, and significant variation in plume depth may occur over a tidal cycle.

Tides in the area under study are mixed and the mean diurnal range is 3.4 m. The tidal currents are described by the U. S. Coast and Geodetic Survey (1952) as "weak and variable", and the net current direction is northward along the bottom from Possession Sound. Considerable dilution of surface waters

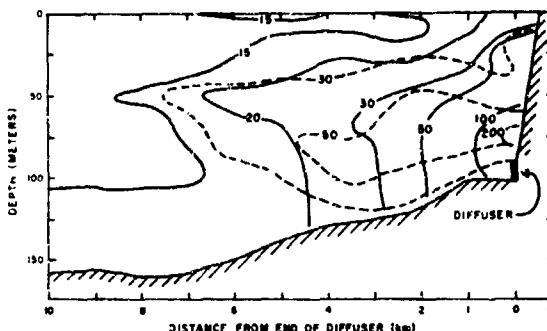


Fig. 6. Everett, Washington. Vertical section of PBI (ppm). Averaged for May, 1962-May, 1963 (solid lines) and for August 3, 1962 (dashed lines), diffuser to Saratoga Passage.

occurs because of precipitation and entry of the Snohomish River; net motion of surface waters is south. Sills are present where Possession Sound joins Port Susan. Their effect on water exchange with Port Susan and on oxygen consumption therein has been described by Barnes and Collias (1958). Since 1952, numerous hydrographic stations have been occupied in Possession Sound and adjacent areas by the University of Washington, which also operates a hydraulic model of Puget Sound, including the Everett area (Barnes *et al.*, 1954).

From May, 1962, hydrographic stations were occupied monthly at about one nautical mile intervals radially from the end of the deeper diffuser. Water samples for temperature, salinity, DO, PBI, and pH were collected by Nansen bottle at 0, 5, 10, 20, 30, 50, 75, 100, 125, and 150 m, depth permitting. Eleven cruises were completed from May, 1962, through May, 1963. Average surface PBI for this period is shown in Figure 5. There is a gradient of PBI directed into the inner harbor where surface outfalls are located. Concentrations of 10 ppm occur throughout the Everett area and in the entire Port Susan region.

Figure 6 shows a vertical section of PBI from the diffuser into Saratoga Passage. Indicated here are the

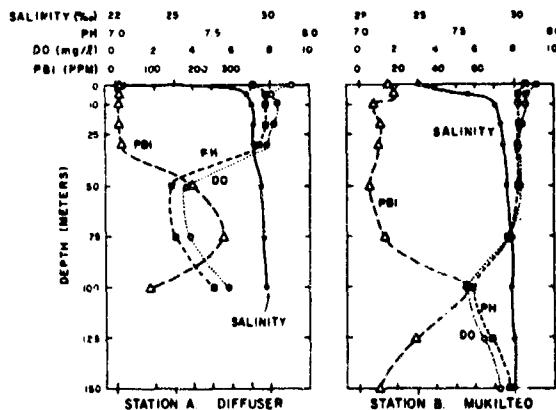


Fig. 7. Everett, Washington. Station curves, April 16, 1963.

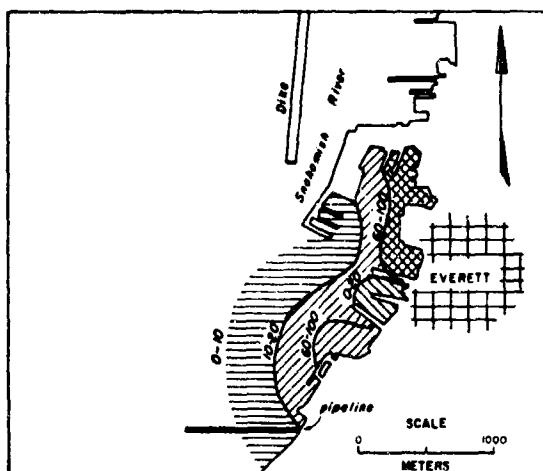


Fig. 8. Everett, Washington. Zones of toxicity to juvenile salmon as percentage of mortality in 24 hours. Composite of six tests.

11-cruise average PBI values and a single cruise (August, 1962) observation showing the 30 and 50 ppm contours only. This representation is somewhat analogous to the average and instantaneous configurations found in industrial smokestack meteorological studies (Pasquill, 1962).

The effect of SWL on DO concentrations and pH is illustrated in Figure 7. The data shown were obtained on April 16, 1963, and are typical of the consistent image effect correlation between SWL, pH, and DO. The station over the diffuser shows the more drastic reduction in DO and pH, as would be expected; the Mukilteo Station is 7.2 km distant from the pipeline, yet the effect of wastes is still present although at a greater depth than that of the station over the diffuser.

JUVENILE SALMONIDS

In the vicinity of Everett, the Snohomish River is used as a spawning stream by four species of salmon (*Oncorhynchus tshawytscha*, *O. kisutch*, *O. keta*, *O. gorbuscha*) and steelhead trout (*Salmo gairdnerii*). In addition, the adjacent waters of Port Gardner Bay, into which the river empties, are used as nursery and feeding grounds by juvenile salmonids and by bottom fish and crabs. The salmon, steelhead, and crab fishery of this area had an estimated 1962 commercial and sport harvest worth \$979,949.

The environmental conditions in the area are alarming because juvenile salmonids from the river have been found to invade waterfront areas where water quality conditions are known to be poor. Live box bioassays with juvenile chum salmon (*O. keta*) were made at 23 stations in this area. They revealed that environmental conditions were at times lethal to the test fish populations, as shown in Figure 8. On these occasions, temperature, salinity, and PBI were not at levels expected to be lethal. When mortalities occurred, they coincided with free chlorine concentra-

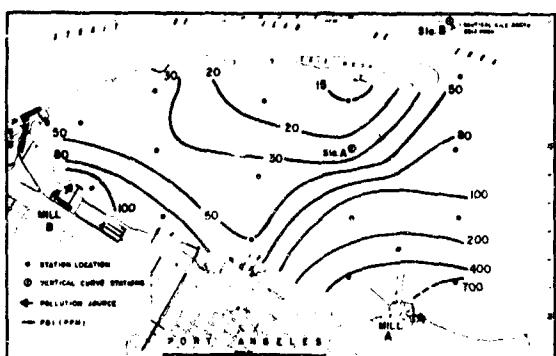


Fig. 9. Port Angeles, Washington. Average surface PBI, November, 1962-December, 1963.

tions of up to 50 ppm, pH below 6.5, sulfide concentrations of 0.5 ppm, or DO concentrations approaching zero. Fortunately, new waste-handling facilities now being provided by the mills will help eliminate these adverse waterfront conditions.

OBSERVATIONS IN THE PORT ANGELES AREA

OCEANOGRAPHIC

A 14-cruise average of surface PBI for November, 1962, through December, 1963, is shown in Figure 9. Two PBI sources are immediately apparent: a pulp and paper mill at the west end of the harbor, and another at the southeast. These are essentially point sources with fluctuating discharges.

On September 8, 1963, the PBI near the outfall of Mill A was greater than 3,500 ppm (Fig. 10). A Secchi disk reading one mile north of Ediz Point was 13.0 m, the highest obtained in this study. Contours of PBI at irregularly spaced concentrations and Secchi disk readings at 3-m contours show considerable agreement. Light penetration, as estimated by Secchi disk, has been reduced by 10 m in the immediate vicinity of both mills and by 4 m over most of the harbor. This is in contrast with the situation on August 30, 1963 (Fig. 11), when Mill A had been

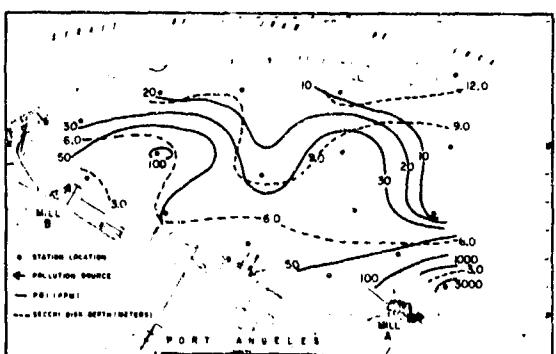


Fig. 10. Port Angeles, Washington. Surface PBI and Secchi disk depth, September 8, 1963.

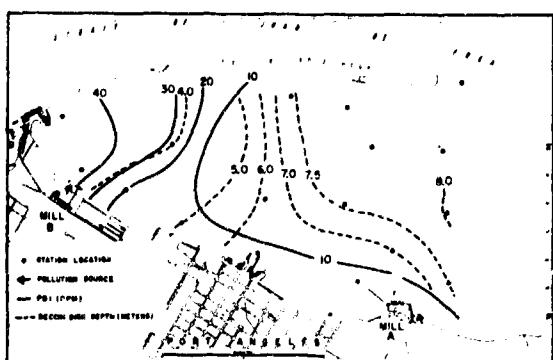


Fig. 11. Port Angeles, Washington. Surface PBI and Secchi disk depth, August 30, 1963.

shut down for a period of 11 days and the only PBI source was Mill B. Although the Secchi disk reading in the Strait was 8.0 m, concurrent with a plankton bloom, the only effect on light penetration was localized in the west end of the harbor; sharply reduced PBI was also noted throughout the harbor.

Station curves for Port Angeles Harbor (Station A) and the Strait of Juan de Fuca (Station B, one nautical mile due north of Ediz Hook Point) are shown in Figure 12. PBI values in the Strait of 2 ppm and less are background readings; this station is completely unaffected by mill wastes. There is a steady increase of salinity with depth to a maximum of 32.1‰ at 70 m and a decrease in pH and DO. In the harbor, PBI decreases from 50 ppm at the surface to 2 ppm at the bottom in 20 m of water. Surface salinity in the harbor is about 4‰ less than in the strait. There is no sharp halocline, as at Everett and Bellingham, and the PBI versus depth curves usually reflect this by decreasing more regularly in the top few meters.

OYSTER STUDIES

Oyster larva bioassays similar to those described

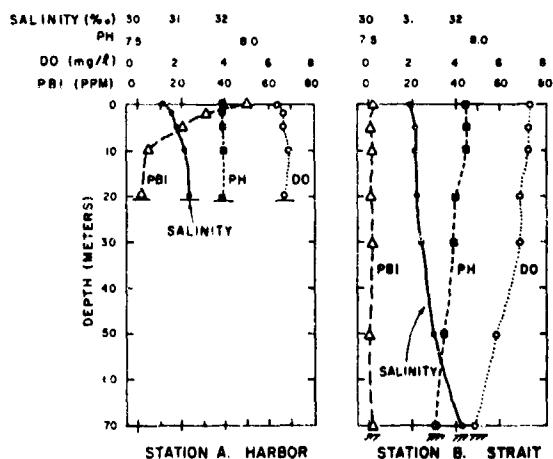


Fig. 12. Port Angeles, Washington. Station curves, October 29, 1963.

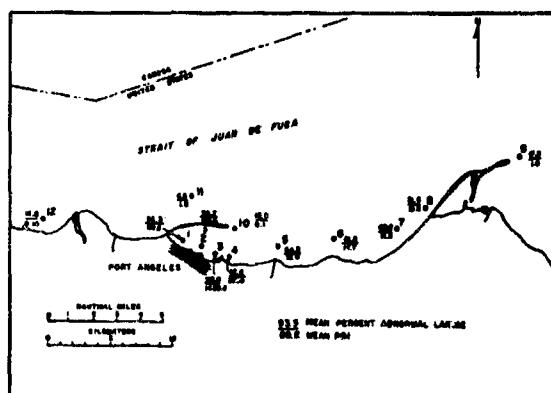


Fig. 13. Port Angeles, Washington. Stations for oyster larva bioassay samples.

for the Bellingham-Samish area also have been made at Port Angeles. Once each month, samples are collected by seaplane from 12 stations (Fig. 13), delivered to the laboratory, and processed in the same manner as the Bellingham-Samish samples.

Preliminary unadjusted results for the first seven months are shown in Table 3. Here, as at other pulp mill sites, larval abnormalities increase as distance to the waste source decreases.

SUMMARY

In situ studies of pulp and paper mill waste pollution, such as those in progress in Puget Sound and the Strait of Juan de Fuca, require the closely co-ordinated efforts of oceanographers, biologists, engineers, and others. Studies on the adverse effects of SWL and other mill wastes, carried out solely in the laboratory, do not sufficiently simulate field conditions and, therefore, cannot be projected directly to existing conditions in the marine environment. Hence, several "bioassay" techniques are used. They vary from di-

Table 3. Oyster larva bioassay data for Port Angeles Harbor and the Strait of Juan de Fuca. Summary for period, May 13 to November 20, 1963.

Station	Kilo-meters from pollution source	Number of cultures	Mean percent abnormal larvae	Mean PBI	PBI range
1	In harbor	21	93.3	89.2	19-420
2	In harbor	21	70.7	55.4	5-186
3	In harbor	21	98.6	1,429.8	23-14,750
4	In harbor	21	97.5	3,520.0	190-7,200
5	4 east	6	54.2	19.0	1-37
6	9 east	21	61.8	17.7	10-27
7	14 east	6	47.6	11.5	9-14
8	16 east	6	51.5	13.5	5-22
9	25 northeast	6	17.9	1.0	0-1
10	2 north	21	18.5	8.1	0-37
11	7 northwest	18	4.6	1.0	0-3
12	18 west	21	14.5*	0.14	0-1

* 100 percent mortality on one trip due to low salinity. Elimination of this sample puts mean percent abnormal larvae at 1.6.

rect examination of marine populations and the influence of pollutants on them, a) semi-natural *in situ* bioassays with maturing oysters, to laboratory bioassays with oyster larvae to test water collected at suspect points.

Oceanographic studies have traced the distribution and persistence of mill wastes. They also show that the wastes occur at points where oysters and juvenile salmon are of major concern. Although still incomplete, the bioassays with growth stages of salmon and oysters cast doubts on suitability of habitat near the waste sources.

LITERATURE CITED

- A.P.H.A., 1960. *Standard Methods for the Examination of Water, Sewage, and Industrial Wastes*, 11th ed.; pp. 309-311. American Public Health Association, New York.
- BARNES, C. A., and E. E. COLLIAS, 1958. Some considerations of oxygen utilization rates in Puget Sound. *J. Marine Res.*, 17:68-81.
- BARNES, C. A., J. H. LINCOLN, and M. RATTRAY, JR., 1954. An oceanographic model of Puget Sound. *Tech. Report No. 19*. Dept. of Oceanography, Univ. of Washington, Seattle, Washington.
- BARNES, C. A., E. E. COLLIAS, V. F. FELICETTA, O. GOLDSCHMID, B. F. HRUTFIORD, A. LIVINGSTON, J. L. McCARTHY, G. L. TOOMBS, M. WALDICHUK, and R. E. WESTLEY, 1963. A standardized Pearl-Benson, or nitroso, method recommended for estimation of spent sulfite liquor or sulfite waste liquor concentration in waters. *TAPPI*, 46: 347-351.
- COLLIAS, E. E., and C. A. BARNES (Compilers), 1962. An oceanographic survey of the Bellingham-Sanish Bay System. Vol. I, Physical and Chemical Data. *Special Report No. 32*. Dept. of Oceanography, Univ. of Washington, Seattle, Washington.
- GUNTER, G., and J. E. MCKEE, 1960. *On Oysters and Sulfite Waste Liquor*. Washington Pollution Control Commission, Olympia, Washington.
- LASATER, J. E., 1954. *A Biological Assay of Pollution in Port Gardner, Spring and Summer, 1954*. State of Washington Dept. of Fisheries, Olympia, Washington.
- LINDSAY, C. E., R. E. WESTLEY, and C. E. WOELKE, 1960. Reports on sulfite waste liquor in a marine environment and its effect on oyster larvae. *Research Bull. No. 6*. State of Washington Dept. of Fisheries, Olympia, Washington.
- LOOSANOFF, V. L., 1954. New advances in the study of bivalve larvae. *Am. Scientist*, 42:607-624.
- MAINS, R. W., W. E. ELDRIDGE, E. M. MAINS, J. E. LASATER, and G. A. HOLLAND, 1953. Toxic effects of sulfite waste liquor on young salmon. *Research Bull. No. 1*. State of Washington Dept. of Fisheries, Olympia, Washington.
- ORLOB, G. T., D. R. PETERSON, and J. R. JONES, 1951. A reinvestigation of pollution in Port Gardner and the lower Snohomish River. *Tech. Bull. No. 11*. Washington Pollution Control Commission, Olympia, Washington.
- PASQUILL, F., 1962. *Atmospheric Diffusion; The Dispersion of Windborne Material from Industrial and Other Sources*; 1st ed. D. Van Nostrand Co., New York.
- PEARL, I. W., and H. K. BENSON, 1940. A nitrosolignin colorimetric test for sulfite waste liquor in sea water. *Primer Trade J.*, 111:35-36.
- PETERSON, D. R., and C. V. GIBBS, 1957. Investigation of pollution in Port Angeles Area. *Tech. Bull. 23*. Washington Pollution Control Commission, Olympia, Washington.
- PRITCHARD, D. W., 1955. Estuarine circulation patterns. *Proc. Am. Civil Eng.* 81, Separate 717:1-11.
- STEIN, J. E., J. G. DENISON, and G. W. ISAAC, 1963. An oceanographic survey of Port Angeles Harbor. *Oregon State Univ. Eng. Exp. Sta. (Corvallis) Circular* 29:172-202.
- TOLLEFSON, R., 1963. Basic biological productivity in a marine industrial area. *J. Water Pollution Control Fed.* 35:989-1005.
- U. S. COAST AND GEODETIC SURVEY, 1952. Puget Sound, Northern Part. *Tidal Current Charts*. U. S. Dept. of Commerce, Washington, D. C.
- UNIV. OF WASHINGTON, 1953. *Puget Sound and Approaches, a Literature Survey*. Dept. of Oceanography, vol. III, Univ. of Washington, Seattle, Washington.
- WAGNER, R. A., C. D. ZIEBELL, and A. LIVINGSTON, 1957. Pollution investigation in Northern Puget Sound. *Tech. Bull. 22*. Washington Pollution Control Commission, Olympia, Washington.
- WALDICHUK, M., 1960. Effects of pulp and paper mill wastes on the marine environment. *Tech. Report W-60-3:160-176*. U. S. Public Health Service, Robert A. Taft Sanitary Engineering Center, Cincinnati, Ohio.
- WESTLEY, R. E., 1959. Selection and evaluation of a method for quantitative measurement of oyster condition. *Proc. Nat. Shellfisheries Assoc.*, 50:145-149.
- WOELKE, C. E., 1961. Bioassay—The bivalve larvae tool. *Proc. 10th Pacific Northwest Symp. on Water Pollution Research*; pp. 113-123. U. S. Public Health Service, Corvallis, Oregon.

The Estuary—Septic Tank of the Megalopolis

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This paper poses some questions relative to the problems that face the sanitary scientist in his attempt to meet the growing needs of the vast communities that populate our shorelines. The estuary in the United States, and in many other countries, has become the septic tank of the megalopolis.

As early as 1910, the Metropolitan Sewage Commission of the City of New York gave serious consideration to the possibility of installing a complete system of waste drainage by pumping the waste out to sea. Over the years many communities have built large trunk sewer systems. In the early 1900's the Passaic Valley Sewerage Commission built a trunk sewer system more than 20 miles in length, serving more than 25 communities in the Upper Passaic Valley area. These wastes were conveyed by a submarine outfall to Upper New York Harbor. Other trunk systems serve large areas of New Jersey, including the Elizabeth Joint Meeting and Middlesex County Sewerage Authority. Large trunk systems were installed in Westchester County, New York; these systems sent the sewage of a large suburban area of the county to the Hudson River and Long Island Sound. Nassau County, Long Island, diverts approximately one-third of the county's sewage to a large outfall located on the south shore of the Island. Trunk sewer systems have been projected and installed in many areas of the country, for example, in Boston, in the Blackstone Valley of Rhode Island, and in the Brandywine Valley of the Delaware. Disposal of sewage from upland areas to convenient estuaries where the wastes are discharged in large quantities after varying degrees of treatment presents many problems to the sanitary scientist in his search for the right combination of the degree of treatment, the location of outfall, and the volume of dilution necessary.

MANY SOURCES DEGRADE ESTUARIES

Additional problems are the development, in many of these communities, of large storm-water overflow systems, which drain sanitary sewage in combined systems and larger quantities of storm-water drainage in separate systems into the estuarine areas during times of high rainfall. Also, the drainage from many suburban areas may contain quantities of fertilizers and pesticides used by the suburban gardener on his quarter-acre grass farm. All of these wastes enter into the estuary where the tidal currents serve

to complicate and accentuate what in reality is a simple dilution problem in the usual river system. Of the 110 areas in the United States that are considered to be standard metropolitan statistical areas, more than 40 of these communities are located on estuaries. These communities represent a population total of fifty-five and one-half million people, or approximately one-third of the total population of the United States.

We have spent many years studying the effects of water pollution on the river systems of our country, and only within the last fifteen years has our attention turned to the estuary. What was once a bottomless pit, able to receive all that man could imagine, has now become, in many areas, a septic cauldron of man's wastes. Concentrated studies are underway in many estuaries, including those of California, Washington, Louisiana, Georgia, Maryland, Virginia, Delaware, Pennsylvania, New Jersey, New York, Connecticut, Rhode Island, and Massachusetts. My remarks will be confined to the estuaries on the continental shelf of the East Coast.

The majority of the estuaries on the East Coast are in the highly developed urban area from Boston to Washington, D. C.—an area referred to as the Megalopolis. These estuaries are the recipients of waste loadings from the upland non-tidal areas representing the upland development of these river systems. In addition, the communities that straddle the estuaries themselves place upon these estuaries the burden of municipal and industrial waste pollution from a population of approximately thirty-five million people.

Much is being done by the pollution control agencies of the local, state, interstate, and Federal governments to solve the problems associated with these waste discharges. Much research has been undertaken, and several large-scale engineering programs are underway involving the expenditure of hundreds of millions of dollars to abate the pollution of these estuaries. In the metropolitan area of New York City the communities have spent or are planning to spend in excess of a billion dollars for waste treatment.

POLLUTION LIMITS WATER USE

Pollution has taken its toll in the last half century. Many oyster and clam beds have disappeared or have been closed because of pollution. Many fishery areas, where the sports fisherman could depend on catching a variety of fish, have disappeared. Man must go farther and farther afield for his shellfishing, sport

¹ Since transferred, as the Federal Water Pollution Control Administration, to the U. S. Department of the Interior.

fishing, swimming, and boating. Bathing areas have moved farther and farther away from the center of the communities on the estuaries. Bathing beaches which were once convenient to the centers of population in New York, Philadelphia, and Boston have been closed, and the populace now must drive considerable distances in order to use the beaches. Commercial fishery prospects have also been dimmed by the specter of pollution. The runs of fingerlings have been hindered in many estuaries by oxygen blocks. Spawning areas have become polluted in many cases.

The sanitary scientist, in his fight to hold the ground against the incursion of pollution, finds a dearth of information in many areas in which he works. It is difficult to estimate the flow in an estuary. There is no readily available tool to enable the sanitary engineer to calculate easily the dilution factors. The sanitary chemist is faced with insufficient knowledge of the application of standard sanitary chemistry testing procedures in salt water. Many tests cannot be run at all because of high concentrations of salts interfering with the test procedures. Other tests have been modified, but few have been fully tested. Additionally, the effect of stratification of salt water or of thermal gradients may create serious problems in trying to obtain sufficient dilution of the waste even after treatment.

The sanitary microbiologist is faced with some serious questions about the growth cycles of various pollutant bacteria in salt waters. Much has been written which indicates the toxicity of salt water to many species of pollution organisms, but there are also conflicting suggestions which indicate that many species may exist in salt water for longer periods than may be expected.

The sanitary biologist, in turn, faces the problem that here, in the waters where the sea meets the land, many freshwater and saltwater species may exist, and what may appear to be in fresh water a preponderance of an organism due to pollution tolerance may in reality be a tolerance caused by saline conditions. The pollution-tolerant marine organisms have not been fully annotated or identified.

The use of dyes to measure dispersion in an estuary is of considerable interest to the sanitary engineer, although much needs to be done to enable the sanitary engineer to interpret the information when it is collected more accurately. Hydraulic models have been developed to a point where they may duplicate hydrological information for an estuary. The application of these models might provide valuable information if a more realistic method were available for evaluating the diffusion of the various types of estuarine materials.

WASTE AND WATER MAKE A COMPLEX MIXTURE

It must be remembered that the sanitary scientist is dealing with a mixture of materials which he commonly refers to as municipal or industrial waste. The admixture of this conglomeration with the mixture

of materials that exists in salt water compounds the problem even further, so that we have an extremely complex combination which is difficult to characterize. Removal from the system can be effected by sedimentation, possibly including coagulation and flocculation. It may be removed by diffusion, chemical interaction, or biochemical or biological conversion. Another possibility is that it may remain intact within the estuary. Materials entering the estuary may also act as nutrients to the animal or plant life present in the estuary and create noxious conditions such as the overgrowth of algae or other plantlike material. The sedimentation of large quantities of material in the estuary can create problems of silting-in of existing channels, sediment covering shellfish beds, or even possibly large quantities of organic materials which, as it degrades anaerobically, may in the future create a demand on the oxygen resources in the system.

Our theoretical knowledge of the estuaries is limited by the inadequate data that are available, and our empirical knowledge is limited by the difficulties in sampling and the small number of studies which have been conducted.

A considerable percentage of the work conducted by oceanographic institutions is in the ocean waters lying off the continental shelf, but very little work is being done in the estuary proper. If we might reorient some oceanographers to the problems we have here on our own shores, we might make a significant impression on the problems that face us in this area. We need active work in the area of tidal hydraulics of the estuary so that we may adequately concern ourselves with the volumes of water that are available for the movement of the waste materials to the sea. We need a comprehensive evaluation of bioassay techniques to determine the effects of the admixture of waste within the estuary. We also need an evaluation of what might naturally exist in the estuary prior to the defilement of the environment by man—by so doing we might be able to estimate the changes that have been brought about by the advent of man and his waste.

PROGRESS MADE IN METHODOLOGY

In spite of some lack of interest, we have been making gains with these problems over the past few years. We, in the Raritan Bay Project, have been faced with the problem of developing scientific data describing the pollution of the Raritan Bay area, an estuary of the Raritan River-Hudson River complex. In the process of our studies, we have developed and tested some modifications of existing testing procedures. In chemistry, a modified COD test as well as a modification for the nitrate-nitrite test is being used. We have also been exploring the possible use of ion-exchange resins for the concentration of trace materials.

Microbiologically, the use of the membrane filter in sea water has given us the same degree of accuracy previously attained in freshwater work. Biologically, our biologist has been able to separate and identify

some organisms which appear to be pollution-tolerant in marine waters. The species-numbers relationship appears to be highly significant in demonstrating whether polluted conditions exist or not. Studies conducted of sediments, sediment size, and geological makeup have been valuable in determining patterns of inflow into the bay system. The use of photo-fluorescent dyes and hydraulic models has also assisted in solutions to the hydraulic problems.

Other Public Health Service studies currently underway have developed a mathematical model of the dissolved oxygen system for that estuary which appears to permit forecasting of water quality conditions with sufficient accuracy so that remedial measures may be taken in time. Studies are under way on the Chesapeake Bay and the estuaries of the Southeast that will permit comprehensive planning for water pollution abatement in estuaries.

XI. SUMMARY

The Sense of the Meeting¹

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"Wend now thy way with brow serene, fear
not thy humble tale to tell:—
The whispers of the Desert-wind; the Tinkling
of the camel's-bell."

Burton: The Kasidah

"The best laid plans o' mice an' men gang aft agley", sometimes not so much for the worse as somewhat differently from what was anticipated. So it was with this conference, which was originally intended to be somewhat less formal and comprehensive in scope, and so understanding, I consented to attempt an *ad hoc* summary. However, interest in the meeting increased to such an extent during the organizational period that plans went into the exponential phase. Some 85 papers were arranged, many in concurrent sessions, with some sessions lasting late into the evening. No one person could absorb all this information in a week, and an adequate summary of all this would mean writing a book on the subject, which would be superfluous in a book already containing these papers.

Some people, among them perhaps those who would not attend for one reason or another, profess not to see much sense in large conferences, but there was a great deal of sense to, and sense of, this meeting. One thinks of this in the Quaker idiom, in which the sense of the meeting is conveyed by a spokesman or perhaps simply inferred by a bystander who has heard about what went on. The sense of this conference on estuaries is that of common interest and concern for the problems of estuaries—this is what brought us all together. At the same time, however, although we devoted a fair amount of time and thought to defining our terms, there was no feeling of need for a common term for a diverse and somewhat amorphous group of people. There is no term for a student of estuaries or the science of studying estuaries, and no one seriously proposed any word for it. This certainly suggests that we are still in the happy state of being more interested in what we are doing than in trying to build semantic empires.

We did have some difficulty in agreeing about what we were working in, that is, in defining an estuary. From a strict limitation to tidal influence—but not necessarily salt water, as Caspers proposed from the example of the Elbe—we ranged to the imperial (if

not empirical) assumption of the Atlantic Ocean as an estuary. We were reminded that from the fishes' eye view the estuary may extend as far into the ocean as a salmon might detect the influence of land. As McHugh pointed out, this could include an extensive part of the North Pacific Ocean. If an estuary must be tidal, then what is such a body of water as the Sea of Azov, the estuary of the Don, which flows into the essentially tideless Black Sea? Indeed, in all our good-humored differences about the definition of an estuary little consideration was given to the Sea of Azov, whose annual salinity regime is influenced by the removal of fresh water from the system by freezing in winter. In any event, we can have estuarine conditions without an estuary; the groundwater flow into parts of Biscayne Bay is an example of such a situation.

What is an ideal estuary? Is this something like trying to define "normal" climate? It has been pointed out by someone that the "normal" climate is the climate of your formative years. All other climates are different and therefore not "normal". From this it would follow that the ideal estuary is that of your own local experience. For me this would be that narrow tidal creek between Alameda and Oakland on the east side of San Francisco Bay called the Oakland Estuary. While it does have a sort of estuarine pond, Lake Merritt, and *Cordylophora* and *Mercierella* occur in it, it is really no one's idea of what an ideal estuary ought to be. After the first few definitions had been offered, some of us began to wonder if we had really come to the right conference. The best expression, however, was that of Margalef, who reminded us that estuaries are a special manifestation of the mixing process, and that to study estuaries by the ecosystem approach is a useful and essential way to bridge the gap between structure and function. There are contrary opinions and viewpoints that are inspired by the conviction that synecological and ecosystem approaches are too complicated for meaningful results as long as we do not understand enough about the individual species and factors in nature. But as far as estuaries are concerned, it is obvious that we must treat them as complex systems, especially in populated areas where they receive the greatest shock assault of man's increasing population and industrialization. They are indeed the septic tank of the megalopolis.

We cannot overestimate this problem of pollution in the future, although it may have been true in the

¹Editor's note: This summary was presented by Dr. Hedgpeth at the close of the Conference on Estuaries, Jekyll Island, Georgia—the Symposium on which this volume is based.

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past that a little pollution (at least of potentially nutrient material) is a good thing for an estuary. We are adding new pollutants, some of them of unknown long-term effects, at an exponential rate. In this context we should remind ourselves that any one who would have said in 1900 that the automobile would be a major source of pollution and would make a city the size of Los Angeles uninhabitable for many people would have been laughed at for his view of alarm. We no longer have 60 years to study these problems. [The Thames, for example, has been polluted for the last hundred years, but adequate study of the problem was not begun until 1949. After 15 years the report was published. "We are now at the point where it is possible to predict, with a fair degree of certainty, what the effect would be of making any of a wide variety of changes in the imposed conditions . . . For the first time in the United Kingdom, control of pollution in an estuary will be based on quantitative predictions of the effects of individual discharges." (Gamesson, 1964).]

It is obvious that we must approach the problems of estuaries in a reasonably holistic or synthetic way. This conference—and its published proceedings—should provide us with some idea of things we must know and do to understand estuaries. Of course, we need more attention to systematics, especially since we often seem to be dealing with pairs and complexes of closely related organisms, and we critically need some coordinated physiological studies of widely distributed species that may or may not have separate races in different estuaries. Of all the specialists involved in studying the estuarine system, the sedimentologists appear to be more satisfied with their conception of the processes they are studying than are many other people. This does not mean that they consider that their work is done—for sedimentation is as continuous as any other estuarine process. Everyone is looking for a better instrument, like a philosopher's stone. As expensive as they may be, however, fancy black boxes are not better than the watcher of the box. The temptation to leave it all up to the black box can lead into a circular situation in which it is not clear who has the upper hand—the black box or the observer of the box who modifies his observations according to the readings on the dials. In any event, there seems to be a limit to this, as anyone who tries to keep within reach of a speaker's microphone on a short cord soon realizes. Perhaps fish and copepods as well as ions and molecules will be more reasonable than men and obligingly present themselves to the sensor of the box in easily identifiable postures.

What we are looking for, whether in sediments, water mixing, copepods, physiology, diatoms, polychaetes, or honest natural history, is a way to understand the processes. While no two estuaries are identical, the ecosystem can be defined roughly as follows: The estuarine ecosystem is a mixing region between sea and inland water of such shape and depth that the net resident time of suspended materials exceeds the

flushing. Thus the system constitutes, as Ketchum has pointed out, a nutrient trap. It is furthermore a system in which control by the bottom materials is the dominant influence, as Ferguson Wood has pointed out at this conference and on a number of other occasions. Indeed the most interesting contributions to our understanding of estuarine processes made at this conference are in the fields of detritus and the physical processes of accumulation against a gradient, as elucidated by Postma.

It is in this context of dominant influence by sedimentary processes and the detritus cycle that the importance of benthic molluscs in estuarine ecosystems is best considered. We find indications of the significance of infauna bivalves in such diverse environments as the Sea of Azov (Zenkevitch, 1963) and the Laguna Madre of Texas. In other areas, such as marshlands, mangrove swamps, and the European waddens, the most significant, and potentially governing, factor of estuarine productivity (at least from man's viewpoint) are such organisms as detritus-feeding gastropods like Cerithiids and *Batillaria*, and the Hydrobiids, as well as such bivalves as oysters and molluscs. When one remembers the anaerobic condition of bottom sediments, it is easy to see why this should be so, and Kanwisher (1962) has put it most concisely. Molluscs, especially bivalves, are equipped not only to bring in oxygenated water but to close themselves off from the environment during periods of unfavorable conditions. Since they are not mobile, bivalves serve as biological integrators of the fluctuating processes of nutrient supply and regeneration in their environment, and the abundance of bivalves is doubtless a direct indication of the magnitude of the nutrient and detritus cycles of the estuary. The significance of the scum- and detritus-feeding gastropods is also great, and we had as a commentary during the detritus session the interesting story of recent observations on *Hydrobia* (*concreta?*) which can subsist in part on its own fecal pellets after microbial activity has increased the protein content of the pellets. Possibly Cerithiids can also do this. While it is not exactly perpetual motion, it is an interesting indication of how the food resources of the estuarine environment may be exploited to their maximum. It is, of course, a function of the comparatively shallow depth of estuaries and tidal flats that the major control of the ecosystem should be that of the activity of processes on and in the bottom sediments.

There are among us in every field of biology those who seek to simplify natural processes by numbers. It would be very useful if we could have a few magic numbers and equations to take the place of all this complexity and confusion. The search for a mystical index number, some neat and precise way to categorize a natural situation, has occupied many ecologists, and students of estuaries are not immune. It would be nice if we could agree on some such number—it would certainly save us from those slides with illegible columns of typewritten numbers of interest only to those with the instinct of bookkeepers, and

perhaps from listening to earnest young speakers who feel compelled to read pages of data to their audience.

However, there are dangers. We have yet to agree upon—or even understand—the meaning of P/R ratios, O₂ consumption, pH and Eh values, and chlorophyll and photosynthesis counts. At the present state of our knowledge, these are all useful as indications, and it was clear from the detritus discussion in particular that measurements of simple organic content do not necessarily tell us what is really going on in the sediments—these numbers that we get are by no means all the story. Yet when these numbers get in the hands of public officials they may cause difficulties, especially if the recommendations of the scientist are not too carefully considered. A case in point is the apparent overconfidence in photosynthesis as a measure of productivity and of potential economic value in an estuary, which leads to recommendations which Rounsefell (1963) considers would constitute "removing the most important cog from the estuarine-continental shelf complex and substituting therefor a polluted basin of green slime".

[In this context, see Ferguson Wood, 1956: "When we consider the limitations of our knowledge, it is obvious that the random fertilization of estuaries and lagoons to produce fish is likely to prove costly and wasteful, so that a thorough fundamental knowledge of the processes involved is essential to economic husbandry It will be a long time before the productivity of estuarine environments will be fully understood, and, though *ad hoc* measurements of productivity may be made by existing techniques adapted for the purpose, such measurements will not allow us to predict until we understand the dynamic forces of the problem." (In the example mentioned by Rounsefell, the faith in the significance of the numbers seems to be associated with ideas of efficiency and maximum power output of the biological system. Such abstract ideas are not necessarily related to actual systems, and the anthropocentric notion that they are is a gratuitous assumption that we understand the purpose of nature.)]

All our numbers at the present state of the art must be tempered with "intuition, imagination, and guesswork", and a sense of proportion. When a "simple-minded equation" gives an answer that is almost too pat, we should be skeptical of the answer, as Riley indeed said of his own results.

Nevertheless, we do need numbers, and good ones. Anyone who has had to appear at a public hearing or prepare a report for some commission realizes how useful a few concise numbers can be, and it is hoped that we will continue our search for them, but with realistic moderation.

Do estuaries have a future? Russell is of the opinion that "neither the past nor future of estuaries is very promising." This may be true from the viewpoint of a friend of the Pleistocene, but there must have been estuaries in other geological periods beyond even the moderately long view of those whose concern is with the transitory phenomena of the Quaternary.

[There is good evidence for estuarine conditions during a considerable part of mid-Pennsylvanian time, for example. Undoubtedly, there have been estuaries as long as salt water has been brought into lowlands by transgressions of the sea (Zangerl and Richardson, 1963).]

Several of those who have ventured to speculate upon the origin of life find the most plausible hypotheses to be those involving "habitats of low but perhaps variable salinity" (Hutchinson, 1961), or that surface-active molecules from which life may have become organized were most likely to be concentrated in a mud, "particularly on estuarine mud" (Bernal, 1961). Whether the estuaries of the present have had much past or have much future is a question, therefore, of concern to a geologist; it seems obvious to biologists, especially those who have studied euryhaline species and the distributions of inland or freshwater forms related to predominantly marine groups, that estuaries are not the peculiar phenomenon of our own epoch.

The greatest danger to our estuaries, as far as we are concerned, is not from the inexorable process of the earth, but from the activities of our own kind. The future of estuaries is indeed bleak if we do not reform our ways, as Cronin said so eloquently. In California we may be producing still another kind of estuary, by diverting all the streams of consequence in northern California to Los Angeles, where the water will pour out of the sewer into the ocean, loaded with undesirable materials. One proposal for the operation of this scheme would be the by-passing of already contaminated water into the headwaters of San Francisco Bay, thus concentrating the pollution of inflowing waters so that only polluted water would enter the bay, which could bring about a hyperpolluted system. Things are not much better in Texas, where a vast canal system which would divert water from all the coastal bays into the south is being considered. In this scheme, the relatively clean river water would be replaced by used—and polluted—water from cities and industries that would drain into the bays. These great canal systems of Texas and California should be visible to the people on Mars—or did they become extinct because they tampered with their planet in this way? We are not alone in such schemes; the Russians are evidently doing things to the Don and Volga systems which have already had a noticeable effect on the Sea of Azov. Any thoughtful ecologist must view these pretentious plans with horror. Certainly their immediate effect will be to hasten the demise of our estuaries.

Perhaps we do need a national estuary, dedicated for naturalists and for research, as Cronin suggested. However, which estuary, or which sort of estuary could we agree on? This leads us to some concluding remarks about the ideal estuary.

The ideal estuary should not be too small, nor too large. While a bight, which subtends slightly more than 100° and enables a square-rigged ship to leave on either tack, may have estuarine characteristics, a

square-rigged ship is not a useful research vessel these days. The size of the ideal estuary should be such that it can be studied with a vessel under the length of 64'11"—since at 65 feet the vessel must have a permanent captain and falls into a different budgetary category. The size should also be such that there is sufficient work for a coordinated team of half a dozen research workers (including at least one systematicist) and perhaps a dozen students and assistants.

There would have to be tides, of course, and an active mixing of fresh and sea water. All this should be carried out in a well-layered exchange system. The biota should include not too many species of diatoms and other autotrophes, replaced by successively smaller forms as the season progresses. Most of the invertebrates, especially the copepods, should occur in congeneric pairs. Fishes and motile invertebrates should find the ideal estuary a prime nursery ground, and the benthic organisms, especially molluscs, should occur in such numbers as to make the most of the detrital opportunities of the environment. It follows from this that there should be an interesting variety of sediments. From the viewpoint of those of us who have never learned to dive, it will not be unfortunate if the turbidity is such as to inhibit the activities of that recently developed facultative nektonic organism, the free diver.

Since we need money to continue our studies of this ideal system, there should be just a little pollution—enough to justify the budgets for personnel and black boxes—and we must conclude that this is unavoidable anyhow.

Who will work on such an ideal estuary? The present excellent company of such a conference as this, of course.

Author's Note: Some of the above remarks are essentially as given at the Conference, but a few changes have been inevitable for one reason or another. Several after-thoughts have been set off by brackets. It will also be noted that these concluding remarks do not have much resemblance to the abstract of the paper (which was prepared during a somewhat distracted period), and for this I have no real apology, as the paper supporting that abstract was never written. It is hoped that this note will at least explain to those who have already requested reprints (by postcards) why it is impossible for me to send them the paper they thought they were asking for.

LITERATURE CITED

- BERNAL, J. D., 1961. Origin of life on the shore of the ocean. In *Oceanography*, edited by Mary Sears; pp. 95-118. American Association for the Advancement of Science, Washington, D. C.
- GAMESON, A. L. H., 1964. Pollution of London's river. *New Scientist (London)*, 22:295-298.
- HUTCHINSON, G. E., 1961. The biologist poses some problems. In *Oceanography*, edited by Mary Sears; pp. 85-94. American Association for the Advancement of Science, Washington, D. C.
- KANWISHER, J., 1962. Gas exchange in shallow marine sediments. In *Report of the Symposium on the Environmental Chemistry of Marine Sediments; Occasional Publ. 1*:13-19. Graduate School of Oceanography, Univ. of Rhode Island, Kingston, Rhode Island.
- ROUNSEFELL, G. A., 1963. Realism in the management of Estuaries. In *Marine Resources Bull. No. 1*. Alabama Marine Resources Lab., Dauphin Island, Alabama.
- WOOD, E. J. FERGUSON, 1956. Some considerations on estuarine productivity. *Proc. Eighth Pacific Sci. Congr. Pacific Sci. Assoc.*, 3a:1107-1110.
- ZANGERL, R., and E. S. RICHARDSON, JR., 1963. The paleoecological history of two Pennsylvania black shales. In *Fieldiana, Geolmem.*, 4:xii-352.
- ZENKEVITCH, L., 1963. *Biology of the Seas of the U.S.S.R.*; chapter 10, pp. 465-537. Moscow, U.S.S.R.

SUPPLEMENTAL BIBLIOGRAPHY

Supplemental Bibliography

This compilation is based on references contributed by the authors of this volume and on additional selected references published since 1964. It is not intended as a comprehensive review of the literature, but is included to update the volume and enhance its effectiveness as a source book on estuaries.

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I BASIC CONSIDERATIONS

HANSEN, D. V., and M. RATTRAY, JR., 1966. New dimensions in estuary classification. *Limnol. Oceanogr.*, 11(3):319-326.

II PHYSICAL FACTORS

AYERS, J. C., 1965. A late summer heat budget of Barnstable Harbor, Mass. *Limnol. Oceanogr.*, 10: R9-R14.

GADE, H. G., 1963. Some hydrographic observations of the inner Oslofjord during 1959. *Hvalradets Skrifter*, No. 46.

GLENN, B., and T. SIMENSEN, 1963. Tidal current choking in the landlocked fjord of Nordævatnet. *Sarsia*, No. 11:43-73.

HANSEN, D. V., 1965. Currents and mixing in the Columbia River Estuary. *Ocean Science and Ocean Engineering*, 2:943-955.

HANSEN, D. V., and M. RATTRAY, JR., 1965. Gravitational circulation in straits and estuaries. *J. Marine Res.*, 23:104-122.

HARLEMAN, D. R., 1963. *Tidal Dynamics in Estuaries, Part II: Real Estuaries, Estuary and Coastline Hydrodynamics*, edited by A. T. Ippen; ch. J. Massachusetts Institute of Technology; pp. 1-21.

HICKS, STACEY D., 1964. Tidal wave characteristics of Chesapeake Bay. *Chesapeake Sci.*, 5(3):103-113.

KASHIWAMURA, M., 1963. Variation of surface-velocity in a tidal river. *J. Oceanog. Soc. Japan*, 19(1):1-5.

REDFIELD, A. C., 1965. Terrestrial heat flow through salt-marsh peat. *Science*, 148:1219-1220.

SNODGRASS, F. E., 1964. Precision digital tide gauge. *Science*, 146:198-208.

III GEOMORPHOLOGY

BLANC, J. J., and J. PICARD, 1954. Les schorres de l'estuaire du Stabbiaco (Corse). *Rev. Geomorphol. Dynam.*, 5:2-24.

CHRISTIANSEN, S., 1958. Bølgekraft og kystretning (Wave power and coastline orientation). *Geografisk Tidsskrift*, vol. 57.

CHRISTIANSEN, S., 1960. Wave power and the Djurstrand Coast. *Geografisk Tidsskrift*, vol. 59.

COLQUHOUN, D. J., 1966. Geomorphology of river valleys in the southeastern Atlantic Coastal Plain. *Southeastern Geol.*, 7:101-109.

IVERSEN, J., 1937. Undersøgelser over Litorina-transgressions i Danmark. (Investigations of Litorina transgressions in Denmark). *Mededel. Dansk. Geol. Foren.*, vol. 9.

IVERSEN, J., 1954. The zonation of the salt-marsh vegetation of Skallingen in 1931-1934 and in 1952. *Mededel. Skalling-Laboratoriet*, vol. 14.

JESPERSEN, M., 1961. Eiderstedt. Et stagnerende marskomrade. (Eiderstedt. A stagnant salt-marsh area). *Geografisk Tidsskr.*, vol. 60.

JOHANNESSEN, C. L., 1964. Marshes prograding in Oregon: aerial photographs. *Science*, 146:1575-1578.

MØLLER, J. T., 1964. Fladkystens og flodens morfologiske elementer i det tidevandsprægede landskab med dettes særlige vegetations og hydrografiske forhold. (Flatcoast and river morphology in tidal areas and the special vegetation and hydrology of these regions). *Folia Geograph. Danica*, vol. X, (1).

NIELSEN, N., 1935. The Scientific Investigation of the Peninsula of Skallingen. *Mededel. Skalling-Laboratoriet*, vol. 1.

SCHOU, A., 1950. The marine foreland. *Folia Geograph. Danica*, vol. 4.

SCHOU, A., 1960. The coastline of Djursland. A study in East-Danish shoreline development. *Geograf. Tidsskr.*, vol. 59.

VOLLBRECHT, K., 1966. The relationships between wind records, energy of longshore drift, and energy balance off the coast of a restricted body of water, as applied to the Baltic. *Marine Geology*, 4(2):119-147.

IV SEDIMENTS AND SEDIMENTATION

BARRASS, R., 1963. The burrows of *Ocypode ceratophthalmus* (Pallas) (Crustacea, Ocypodidae) on a tidal wave beach at Inhaca Island. *Mozambique J. An. Ecol.*, 32:73-85.

BENNETT, L. C., JR., and S. M. SAVIN, 1963. The natural history of the Hardangerfjord. 6. Studies of the sediments of parts of the Ytre Samlafjord with the continuous seismic profiler. *Sarsia*, 14:79-94.

BEYER, F., 1955. The spreading of sinking particles in the sea. *Sewage Ind. Wastes*, 27(9):1073-1078.

BOUCART, J., and H. CARLIER, 1959. The "tangue", a non-conforming sediment. *Bull. Geol. Soc. Am.*, 70: 565-568.

BRONFMAN, A. M., and A. N. ALEKSANDROV, 1965. The Don estuary as an example of sedimentation in marine shallows in part of an estuary. *Oceanology*, 5:68-75.

CAILLEUX, A., 1963. Forme des micas de l'estuaire de la Loire. *Sedimentology*, 2:90-92.

CARROLL, D., and H. C. STARKEY, 1960. Effect of sea water on clay minerals. *Proc. Seventh Natl. Conf. Clays, Clay Minerals*, 1958; pp. 80-101.

CONAGHAN, P. J., 1966. Sediment and sedimentary processes in Gladstone Harbour, Queensland. *Univ. of Queensland Papers, Dept. of Geology*, 6(1):1-52.

- CONE, R. A., N. S. NEIDELL, and K. E. KENYON, 1963. The natural history of the Hardangerfjord. 5. Studies of the deep-water sediments with the continuous seismic profiler. *Sarsia*, 44:61-78.
- CUTSHALL, N., and C. OSTERBERG, 1964. Radioactive particle in sediment from the Columbia River. *Science*, 144:536-537.
- DUNCAN, J. R., JR., 1964. The effects of water table and tide cycle on swash-backwash sediment distribution and beach profile development. *Marine Geology*, 2: 186-197.
- FAGER, E. W., 1964. Marine sediments: effects of a tube-building polychaete. *Science*, 143:356-359.
- FRANCIS-BOEUFF, C., 1943. Sur la constitution des sediments vaseux de l'estuaire de la Loire. *Bull. Inst. Océanogr.*, vol. 839.
- GADE, H., 1959. Notes on the effect of elasticity of bottom sediments to the energy dissipation of surface waves in shallow water. *Arch. Math. Natur. Oslo*, 55(3): 69-80.
- GIGLIOLI, M. E. C., and D. F. KING, 1966. The Mangrove Swamps of Keneba, lower Gambia River basin. III. Seasonal variations in the chloride and water content of swamp soils, with observations on the water levels and chloride concentration of free soil water under a barren mud flat during the dry season. *J. Applied Ecology*, 3(1):1-19.
- GORDON, D. C., JR., 1966. The effects of the deposit feeding polychaete *Pectinaria gouldii* on the intertidal sediments of Barnstable Harbor. *Limnol. Oceanogr.*, 11: 327-332.
- GRIFFIN, C. M., and R. L. INGRAM, 1955. Clay minerals of the Meuse River Estuary. *J. Sediment. Petrol.*, vol. 25.
- HANSEN, K., 1954. The sediments and the transport of debris in the Graadby tidal area. *Meddel. Skalling-Laboratoriet*, vol. 14.
- HAVEN, D. S., and R. MORALES-ALAMO, 1966. Use of fluorescent particles to trace oyster biodeposits in marine sediments. *J. Conseil, Conseil Perm. Intern. Exploration Mer*, 30:267-269.
- HAVEN, D. S., and R. MORALES-ALAMO, 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnol. Oceanogr.*, 11(4):487-493.
- HERON, S. D., I. S. JOHNSON, P. G. WILSON, and G. E. MICHAEL, 1964. Clay mineral assemblages in a South Carolina lake-river-estuary complex. *Southeastern Geol.*, 6(1):1-9.
- IKRAMUDDIN ALI, S., and D. J. C. LAMING, 1966. The Alma River intertidal delta in the Bay of Fundy at Alma, N. B. *Maritime Sediments*, 2:3-5.
- JACKSON, W. H., 1964. Effect of tidal range, temperature and fresh water on the amount of silt in suspension in an estuary. *Nature*, 201:1017.
- JOHNSTON, W. A., 1952. The character of the stratification of the silts in the recent delta of Fraser River, British Columbia, Canada. *J. Geol.*, 30:115-129.
- JONES, D., and M. S. WILLS, 1956. The attenuation of light in sea and estuarine waters in relation to the concentration of suspended solid matter. *J. Marine Biol. Assoc. U. K.*, 35:431-444.
- JOPLIN, A. V., 1963. Hydraulic studies on the origin of bedding. *Sedimentology*, 2:115-121.
- JORDAN, R. R., 1965. Notes on techniques for sampling suspended sediment. *Southeastern Geol.*, 7:9-13.
- JOSEPH, J., 1955. Extinction measurements to indicate distribution and transport of watermasses. *UNESCO Symp. Phys. Oceanogr. Tokio*; pp. 59-75.
- KEITH, M. L., and R. H. PARKER, 1965. Local variation of ^{13}C and ^{18}O content of mollusk shells and the relatively minor temperature effect in marginal marine environments. *Marine Geol.*, 3(4):115-130.
- KEITH, M. L., G. M. ANDERSON, and R. EICHLER, 1964. Carbon and oxygen isotopic composition of mollusk shells from marine and fresh-water environments. *Geochim. Cosmochim. Acta*, 28:1757-1816.
- KLEIN, G. DEV., 1966. Relating directional structures of modern sediments to the direction and velocity of tidal current systems, Five Islands tidal flat complex, Nova Scotia. *Maritime Sediments*, 2:19-21.
- KOFOED, J. W., and D. S. GORSLINE, 1966. Sediments of the Choptank River, Maryland. *Southeastern Geol.*, 7:65-82.
- KRINSLEY, D., T. TAKAHASHI, M. L. SILBERMAN, and W. S. NEWMAN, 1964. Transportation of sand grains along the Atlantic shore of Long Island, N. Y. An application of electron microscopy. *Marine Geol.*, 2:100-120.
- KUHL, H., and H. MANN, 1957. Beiträge zur Hydrochemie der unteren Weser. *Veröffentl. Inst. Meeresforsch. Bremerhaven*, 5:34-62.
- KULM, L. D., and J. V. BYRNE, 1966. Sedimentary response to hydrography in an Oregon estuary. *Marine Geol.*, 4:85-118.
- LAND, L. S., and J. H. HOYT, 1966. Sedimentation in a meandering estuary. *Sedimentology*, 6:191-207.
- LLOYD, R. M., 1964. Variations in the oxygen and carbon isotope ratios of Florida Bay mollusks and their environmental significance. *J. Geology*, 72(1):84-111.
- LUCHT, F., 1954. Geschiebe und Sinkstofftransport in der Elbe. *Mitt. Geol. Staatsinst. Hamburg*, 23:68-75.
- LUNEBURG, H., 1955. Beiträge zur Hydrographie der Wesermündung, IV. Die Verteilung der Sinkstoffe in den Seitenräumen der Wesermündung. *Veröffentl. Inst. Meeresforsch. Bremerhaven*, 3:228-265.
- LUNEBURG, H., 1961. Über die Erosion und den Sedimenttransport am Knechtsand und Eversand. *Veröffentl. Inst. Meeresforsch. Bremerhaven*, 7(H. 2):277-294.
- LUNEBURG, H., 1963. Wassermischvorgänge vor der Weser- und Elbmündung. *Veröffentl. Inst. Meeresforsch. Bremerhaven*, 8(H. 2):111-141.
- OLIVER, D. R., 1960. Sedimentation and effective viscosity. *Nature*, 185(4777):912-913.
- PETERSON, M. N. A., and C. C. VON DER BORCH, 1965. Chert: modern inorganic deposition in a carbonate-precipitating locality. *Science*, 149:1501-1503.
- PILKEY, O. H., and H. G. GOODELL, 1964. Comparison of the composition of fossil and recent mollusk shells. *Geol. Soc. Amer. Bull.*, 75:217-228.
- PILKEY, O. H., and R. C. HARRISS, 1966. The effect of intertidal environment on the composition of calcareous skeletal material. *Limnol. Oceanogr.*, 11(3): 381-385.
- POWERS, M. C., 1957. Adjustment of land derived clays to the marine environment. *J. Sediment. Petrol.*, 27:355-372.
- RANWELL, D. S., 1964. *Spartina* salt marshes in southern England. II. Rate and seasonal pattern of sediment accretion. *J. Ecol.*, 52:79-94.
- RANWELL, D. S., 1964. *Spartina* salt marshes in southern England. III. Rates of establishment, succession and nutrient supply at Bridgewater Bay, Somerset. *J. Ecol.*, 52:95-105.
- RASMUSSEN, K., 1956. Investigation on marsh soil and wadden sea sediments in the Tønder region. *Geogr. Tidskr.*, vol. 55.
- RAYNE, A., 1961. On the contribution of the Amazon River to accretion of the coast of the Guianas. *Geol. Mijnbouw*, 40:219-226.
- RIVIERE, A., 1948. Sur l'embouchure du Lay (Vendée). La sedimentation et la morphologie estuariennes. *Bull. Soc. Geol. France*, 18:139-151.
- RIVIERE, A., 1948. Observations sedimentologiques sur la côte Vendéenne. Sedimentation littorale et estuarienne, leurs lois générales. *Rev. Gen. Hydraul.*, 14: 283-306.
- SAKAGISHI, S., 1963. Investigation of the movement of mobile bed material in the estuary and on the coast by means of radioactive material. *J. Oceanogr. Soc. Japan*, 19:27-36.

- SALSMAN, G. G., W. H. TOLBERT, and R. G. VILLARS, 1966. Sand-ridge migration in St. Andrew Bay, Florida. *Marine Geol.*, 4(1):11-19.
- SANTEMA, P., 1953. Enkele beschouwingen over het slibtransport van de Rijn. *Ingenieur, B.* 3, nr. 7; pp. 37-40.
- SCHULTZ, E. A., and H. B. SIMMONS, 1957. Fresh water-salt water density currents a major cause of silting in estuaries. *Tech. Bull. Comm. Tidal Hydraul.*, U. S. Army, vol. 2.
- UCHIO, T., 1962. Influence of the river Shinano on Foraminifera and sediment grain size distributions. *Seto Marine Biol. Lab. Publ.*, 10(2):363-394.
- VOLPEL, F., 1960. Die bildung charakteristischer Sedimente in der Kustennahen Flachsee. *Deut. Hydrograph Z.*, 13(6):290-307.
- WOHLENBERG, E., 1954. Sinkstoff, Sediment und Anwachs am Hindenburgdamm. *Die Kuste*, 2(2):33-94.
- ZENKOVITCH, V. P., 1964. Formation and burial of accumulative forms in littoral and nearshore marine environments. *Marine Geol.* 1:175-180.

V MICROBIOTA

- BOLTOVSKY, E., 1964. Seasonal occurrences of some living Foraminifera in Puerto Deseado (Patagonia, Argentina). *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 29(2):136-145.
- DUTTA, N., J. C. MALHOTRA, and B. B. BOSE, 1954. Hydrology and seasonal fluctuations of the plankton in the Hooghly Estuary (Symposium on marine and freshwater plankton in the Indo-Pacific). *Proc. Indo-Pacific Fisheries Council, 5th meeting*; pp. 35-54.
- FREUDENTHAL, H. D., and J. J. LEE, 1963. *Glenodinium halli* n. sp. and *Gyrodinium instriatum* n. sp., dinoflagellates from New York waters. *J. Protozool.*, 10:182-189.
- GANAPATI, S. V., and V. S. R. MURTHY, 1955. Preliminary observations on the hydrography and in-shore plankton in the Bay of Bengal off Visakhapatnam Coast. *Indian J. Fisheries*, 2(1):84-95.
- GEORGE, M. J., 1958. Observations on the plankton of the Cochin backwaters. *Indian J. Fisheries*, 5(2):375-401.
- HOHN, M. H., and J. HELLERMAN, 1966. New diatoms from the Lewes-Rehoboth Canal, Delaware and Chesapeake area of Baltimore, Maryland. *Trans. Am. Microscop. Soc.*, 85:115-130.
- HOPKINS, J. T., 1963. A study of the diatoms of the Ouse Estuary, Sussex. I. The movement of the mud-flat diatoms in response to some chemical and physical changes. *J. Mar. Biol. Assoc. U. K.*, 43:653-663.
- HOPKINS, J. T., 1964. A study of the diatoms of the Ouse Estuary, Sussex. II. The ecology of the mud-flat diatom flora. *J. Mar. Biol. Assoc. U. K.*, 44:333-341.
- HOPKINS, J. T., 1964. A study of the diatoms of the Ouse Estuary, Sussex. III. The seasonal variation of the littoral epiphyte flora and the shore plankton. *J. Mar. Biol. Assoc. U. K.*, 44:613-644.
- HOPKINS, J. T., 1966. The role of water in the behavior of an estuarine mud-flat diatom. *J. Mar. Biol. Assoc. U. K.*, 46(3):617-626.
- JORDÉ, I., and N. KLAVESTAD, 1963. The natural history of the Hardangerfjord. 4. The benthonic algal vegetation. *Sarsia*, 9:1-90.
- PRAKASH, A., and A. H. VISWANATHA SARMA, 1964. On the occurrence of 'red water' phenomenon on the west coast of India. *Current Sci. (India)*, 33(6):168-170.
- PRATT, D. M., 1965. The winter-spring diatom flowering in Narragansett Bay. *Limnol. Oceanogr.*, 10(2):173-184.
- ROUNSEFELL, G. A., and A. DRAGOVICH, 1966. Correlation between oceanographic factors and abundance of the Florida red-tide (*Gymnodinium breve* Davis), 1954-1961. *Bull. Mar. Sci.*, 16(3):404-422.
- STEWART, W. D. P., and G. F. J. PUGH, 1963. Blue-green algae of a developing salt marsh. *J. Marine Biol. Assoc. U. K.*, 43:309-317.
- WELLS, J. B. J., 1963. Copepoda from the littoral region of the estuary of the river Exe (Devon, England). *Crustaceana*, 5:10.
- WIMPENNY, R. S., 1966. *The Plankton of the Sea*. Faber and Faber, Ltd., London.
- WOOD, E. J. F., 1966. A phytoplankton study of the Amazon region. *Bull. Mar. Sci.*, 16(1):102-123.
- ZANEVELD, J. S., and W. D. BARNE, 1965. Reproductive periodicities of some benthic algae in lower Chesapeake Bay. *Chesapeake Sci.*, 6(1):17-32.

VI NUTRIENTS AND BIOLOGICAL PRODUCTION

- BOTAN, E. A., J. J. MILLER, and H. KLEEKOPER, 1960. A study of the microbial decomposition of nitrogenous matter in fresh water. *Arch. Hydrobiol.*, 56(4):334-354.
- BRAND, T., N. W. RAKESTRAW, and J. W. ZABOR, 1942. Decomposition and regeneration of nitrogenous organic matter in sea water. V. Factors influencing the length of the cycle; Observations upon the gaseous and dissolved organic nitrogen. *Biol. Bull.*, 83:273-282.
- BURKHOLDER, P. R., 1959. Some microbial aspects of marine productivity in shallow waters. *Proc. Salt Marsh Conf., Marine Inst., Univ. Georgia, Sapelo Island, Ga.* (1958); pp. 70-72.
- BURSCHE, E. M., 1959. Untersuchungen über den Detritusgehalt in Seen und Flüssen. *Intern. Rev. Hydrobiol.*, 44:439-448.
- CASPERS, H., and H. SCHULTZ, 1960. Studien zur Wirkung der Saprobienstypen Erfahrungen an einem Stadtkanal Hamburgs. *Intern. Rev. Hydrobiol.*, 45(4):535-565.
- CASPERS, H., and H. SCHULTZ, 1962. Weitere Unterlagen zur Prüfung der Saprobienstypen. *Intern. Rev. Hydrobiol.*, 47(1):100-117.
- CHAPMAN, V. J., 1964. A submarine algal growth chamber for studies in benthic productivity. *Ecology*, 45:889-892.
- CUSHING, D. H., 1959. On the nature of production in the sea. *G. Brit. Min. Agr., Fisheries Food Tech. Bull.*, 22(6):1-40.
- FEILDY, L., and S. KALKO, 1958. Cellulosebontas merteke a Balaton különbozo biotopjaiban és annak merese antron reagenssel. (Decomposition of cellulose in different habitats of Lake Balaton and its measurement by anthrone reagent.) *Ann. Biol. Tihany*, 25:209-216.
- FOX, D. L., 1955. Organic detritus in the metabolism of the sea. *Sci. Monthly*, 80:256-259.
- FOX, D. L., 1960. Perspectives in marine biochemistry. *Ann. N. Y. Acad. Sci.*, 90(3):617-621.
- FURUKAWA, A., K. NOGAMI, M. HISAKO, Y. OGASAWARA, R. OKAMOTO, and U. KOBA-YASHI, 1961. A study of suspended matter in the sea and its importance as a factor characterizing the environment of shellfish culture grounds. *Bull. Nakai Regional Fish Res. Lab. No. 14 (Contr. No. 94)*.
- GILMARTIN, M., 1964. The primary production of a British Columbia fjord. *J. Fish. Res. Bd. Canada*, 21(3):505-538.
- JANNASCH, H. W., 1964. Microbial decomposition in natural waters as determined in steady state systems. *Verhandl. Intern. Ver. Limnol.*, 15:562-568.
- JEFFREY, L. M., and D. W. HOOD, 1958. Organic matter in sea water; an evaluation of various methods for isolation. *J. Marine Res.*, 17:247-271.
- JOHANNES, R. E., 1964. Uptake and release of dissolved organic phosphorus by representatives of a coastal marine ecosystem. *Limnol. Oceanogr.*, 9(2):224-234.

- JOHANNES, R. E., and K. L. WEBB, 1965. Release of dissolved amino acids by marine zooplankton. *Science*, 150(3692):76-77.
- KLEEREKOPER, H., 1952. The mineralization of plankton. *J. Fisheries Res. Board Can.*, 10:284-291.
- KRAUSE, H. R., 1959. Biochemische Untersuchungen über den postmortalen Abbau von totem Plankton unter aeroben und anaeroben Bedingungen. *Arch. Hydrobiol., Suppl.*, 24 (*Falkow-Schriften*, 3):297-337.
- KRAUSE, H. R., 1964. Zur Chemie und Biochemie der Zersetzung von Süsswasserorganismen, unter besonderer Berücksichtigung des Abbaus der organischen Phosphorkomponenten. *Verhandl. Intern. Ver. Limnol.*, 15: 549-561.
- KREY, J., 1961. Beobachtungen über der Gehalt an Mikrobiomasse und Detritus in der Kieler Bucht. *Kiel. Meeresforsch.*, 12:163-175.
- KREY, J., and K. BANSE, 1962. Quantitative Aspekte Kreislaufes der organischen Substanz im Meere. *Kiel. Meeresforsch.*, 18(13):97-106.
- KUHL, H., and H. MANN, 1960. Vergleich des Stickstoffabbaues in See- und Süsswasser-aquarien. *Vie et Milieu*, 11:532-545.
- MARSHALL, S. M., and A. P. ORR, 1955. On the biology of *Calanus finmarchicus*. VIII. Food uptake, assimilation, and excretion in adult and stage V. *Calanus*. *J. Marine Biol. Assoc. U. K.*, 34:495-529.
- MARSHALL, S. M., and A. P. ORR, 1964. Carbohydrate and organic matter in suspension in Loch Striven during 1962. *J. Mar. Biol. Assoc. U. K.*, 44:285-292.
- MENZEL, D. W., and J. H. RYTHER, 1964. The composition of particulate organic matter in the western North Atlantic. *Limnol. Oceanogr.*, 9(2):179-186.
- MENZEL, D. W., and R. F. VACCARO, 1964. The measurement of dissolved organic and particulate carbon in sea water. *Limnol. Oceanogr.*, 9:138-142.
- MOYSE, J., 1963. A comparison of the value of various flagellates and diatoms as food for barnacle larvae. *J. Conseil, Conseil Perm. Intern. Exploration Mer*, 28(2): 175-187.
- NEUSHUL, M., and J. H. POWELL, 1964. An apparatus for experimental cultivation of benthic marine algae. *Ecology*, 45:893-894.
- NEWELL, R., 1965. The role of detritus in the nutrition of two marine deposit feeders. The prosobranch *Hydrobia ulva* and the bivalve *Macoma balthica*. *Proc. Zool. Soc. London*, 144:25-45.
- OPPENHEIMER, C. H., E. F. CORCORAN, and J. VAN ARMAN, 1963. Method for the determination of organic carbon in seawater. *Limnol. Oceanogr.*, 8(4): 487-488.
- PARK, K., W. T. WILLIAMS, J. M. PRESCOTT, and D. W. HOOD, 1964. Amino acids in Redfish Bay, Texas. *Publ. Inst. Marine Sci. Univ. Texas*, 9:59-63.
- PARSONS, T. R., and J. D. H. STRICKLAND, 1962. Oceanic detritus. *Science*, 136:313-314.
- PATTEN, B. C., and B. F. CHABOT, 1966. Factorial productivity in a shallow estuary: Characteristics of response surfaces. *Chesapeake Sci.*, 7(3):117-136.
- PATTEN, B. C., D. K. YOUNG, and M. ROBERTS, 1963. Suspended particulate matter in the lower York River, Virginia. June 1961-July 1962. *Virginia Inst. Marine Sci. Special Sci. Rept.* No. 44.
- PATTEN, B. C., D. K. YOUNG, and M. H. ROBERTS, Jr., 1966. Vertical distribution and sinking characteristics of seston in the lower York River, Virginia. *Chesapeake Sci.*, 7(1):20-29.
- PATTEN, B. C., J. J. NORCROSS, D. K. YOUNG, and C. L. RUTHERFORD, 1964. Some experimental characteristics of dark and light bottles. *J. Conseil, Conseil Perm. Intern. Exploration Mer*, 28(3):335-353.
- POMEROY, L. R., 1959. Primary productivity of Boca Ciega Bay, Florida. *Bull. Marine Sci. Gulf Caribbean*, 10:1-10.
- POMEROY, L. R., 1960. Residence time of dissolved phosphate in natural waters. *Science*, 131:1731-1732.
- POMEROY, L. R., E. E. SMITH, and C. M. GRANT, 1965. The exchange of phosphate between estuarine water and sediments. *Limnol. and Oceanog.*, 10(2): 167-172.
- RODINA, A. G., 1963. Microbiology of detritus of lakes. *Limnol. Oceanogr.*, 8(4):383-393.
- SATOMI, M., and L. R. POMEROY, 1965. Respiration and phosphorus excretion in some marine populations. *Ecology*, 46:877-881.
- SEBESTYEN, O., 1949. Studies of detritus drifts in Lake Balaton. *Verhandl. Intern. Ver. Limnol.*, 10: 414-419.
- SEBESTYEN, O., 1959. Studie über das organische Sediment in Erosionstitor des Balatonsees. *Arch. Hydrobiol.*, 55:371-391.
- SEBESTYEN, O., 1964. Detritus problems in the ecosystem of Lake Balaton. *Verhandl. Intern. Ver. Limnol.*, 15:1006-1011.
- SHELSKE, C. L., and E. P. ODUM, 1962. Mechanisms maintaining high productivity in Georgia estuaries. *Proc. Gulf Caribbean Fisheries Inst.*, 14:75-80.
- SIMKISS, K., 1964. The inhibitory effects of some metabolites on the precipitation of calcium carbonate from artificial and natural sea water. *J. Conseil, Conseil Perm. Intern. Exploration Mer*, 29(1):6-18.
- SIU, R. G. H., and E. T. REESE, 1953. Decomposition of cellulose by microorganisms. *Botan. Rev.*, 19:377-416.
- SMIDT, E. B., 1952. Animal production in the Danish Wadden Sea. *Meddelelser fra Skalling-Laboratoriet*; vol. 6.
- SOROKIN, J. I., 1959. On the nutrition of aquatic invertebrates by autotrophic methane and hydrogen-oxidizing bacteria. *Microbiol.*, 27(6):916.
- STARR, T. J., and F. SANDERS, 1959. Some ecological aspects of vitamin B₁₂ active substances. *Texas Rept. Biol. Med.*, 17(1):49-59.
- STARR, T. J., M. E. JONES, and D. MARTINEZ, 1957. The production of vitamin B₁₂-active substances by marine bacteria. *Limnol. Oceanogr.*, 2:114-119.
- STEPHENS, G. C., and R. A. SCHINSKE, 1957. Uptake of amino acids from sea water by ciliary-mucoid filter feeding animals. *Biol. Bull.*, 111:356-357.
- STEPHENS, G. C., and R. A. SCHINSKE, 1958. Amino acid uptake in marine invertebrates. *Biol. Bull.*, 115:341-342.
- STEPHENS, G. C., and R. A. VIRKAR, 1966. Uptake of organic material by aquatic invertebrates. IV. The influence of salinity on the up-take of amino acids by the brittle star, *Ophiactis arenosa*. *Biol. Bull.*, 131: 172-185.
- STROSS, R. A., and J. R. STOTLEMEYER, 1965. Primary production in the Patuxent River. *Chesapeake Sci.* 6(3):125-140.
- VOLKMANN, C. M., and C. H. OPPENHEIMER, 1962. The microbial decomposition of organic carbon in surface sediments of marine bays of the Central Texas Gulf Coast. *Publ. Inst. Marine Sci. Univ. Texas*, 8:80-90.
- WANGERSKY, P. J., 1959. Dissolved carbohydrates in Long Island Sound, 1956-1958. *Bull. Bingham Oceanog. Coll.*, 17:87-94.
- WARD, R. W., V. VREELAND, C. H. SOUTHWICK, and A. J. READING, 1965. Ecological studies related to plankton productivity in two Chesapeake Bay estuaries. *Chesapeake Sci.*, 6(4):214-225.
- WILKINSON, L., 1963. Nitrogen transformations in a polluted estuary. *Intern. J. Air Water Pollution*, 7: 737-752.
- WILSON, R. F., 1963. Organic carbon levels in some aquatic ecosystems. *Publ. Inst. Marine Sci. Texas*, 9: 64-76.

VII ECOLOGY AND POPULATIONS

- ANDREWS, J. D., 1966. Oyster mortality studies in Virginia. V. Epizootiology of MSX, a protistan pathogen of oysters. *Ecology*, 47:19-31.

- ANSELL, A. D., 1963. *Venus mercenaria* (L.) in Southampton Water. *Ecology*, 44:396-397.
- ANSELL, A. D., 1964. Some parameters of growth of mature *Venus mercenaria* L. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 29(2):214-220.
- ANSELL, A. D., and F. A. LOOSMORE, 1963. Preliminary observations on the relationship between growth, spawning and condition in experimental colonies of *Venus mercenaria* (L.). *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 28(1):285-294.
- ANSELL, A. D., et al., 1964. Studies on the hard-shell clam, *Venus mercenaria*, in British waters. I. Growth and reproduction in natural and experimental colonies. II. Seasonal cycle in condition and biochemical composition. *J. Appl. Ecology*, 1:63-95.
- BARKER, D., 1963. Size in relation to salinity in fossil and recent euryhaline ostracods. *J. Marine Biol. Assoc. U. K.*, 43:785-795.
- BARNES, H., and M. BARNES, 1963. Salinity and the biometry of *Balanus improvisus*. *Soc. Scient. Fennica, Comment. Biol.*, 24(4).
- BARNES, H., FINLAYSON, D. M., and PIATIGORSKY, J., 1963. The effect of desiccation and anaerobic conditions on the behaviour, survival and general metabolism of three common cirripedes. *J. An. Acol.* 32: 233-252.
- BARTLETT, G. A., 1966. The significance of foraminiferal distribution in waters influenced by the Gulf of St. Lawrence. *2nd. Intern. Oceanog. Congr.*; pp. 22-23. (Abstracts)
- BATTY, M. E. J., 1965. Rocky shore ecology of a southern New Zealand fiord. *Trans. Roy. Soc. New Zealand*, 6(21):215-227.
- BENSON, R. H., and MADDOCKS, R. F., 1964. Recent Ostracodes of Krysia Estuary, Cape Province, Union of South Africa; *Univ. Kansas Paleont. Confr. Arthropoda*, 5:1-39.
- BRATTEGARD, T., 1966. The natural history of the Hardangerfjord 7. Horizontal distribution of the fauna of rocky shores. *Sarsia*, 22:1-54.
- BRINKHURST, R. O., 1964. Observations on the biology of the marine oligochaete *Tubifex costatus*. *J. Marine Biol. Assoc. U. K.*, 44:11-16.
- BROEKHUYSEN, G. J., and H. TAYLOR, 1959. The ecology of South African estuaries. Part VIII. Kosi Bay estuary system. *Ann. S. Afr. Mus.*, 44:279-296.
- CARGO, D. G., and L. P. SCHULTZ, 1966. Notes on the biology of the sea nettle, *Chrysaora quinquecirrha*, in Chesapeake Bay. *Chesapeake Sci.*, 7(2):95-100.
- CHANLEY, P. E., 1965. Larval development of the brackish mactrid clam, *Rangia cuneata*. *Chesapeake Sci.*, 6(4):209-213.
- CHANLEY, P. E., 1965. Larval development of a boring clam, *Barnea truncata*. *Chesapeake Sci.*, 6(3):162-166.
- COOPER, R. A., and N. MARSHALL, 1963. Conditions of the Bay scallop *Aequipecten irradians*, in relation to age and the environment. *Chesapeake Sci.*, 4(3):126-134.
- COUGHLAN, J., and ALAN D. ANSELL, 1964. A direct method for determining the pumping rate of siphonate bivalves. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 29(2):205-213.
- DARBY, D. G., 1965. Ecology and taxonomy of Ostracoda in the vicinity of Sapelo Island, Georgia. *National Science Foundation Project GB-26; Report No. 2*, pp. 1-76.
- DAVIS, C. C., 1965. A study of the hatching process in aquatic invertebrates: XX. The Blue Crab, *Callinectes sapidus*, Rathbun, XXI. The Nemertean, *Carcinonemertes carcinophila* (Kolliker). *Chesapeake Sci.*, 6(4): 201-208.
- DICKIE, L. M., and J. C. MEDCOF, 1963. Causes of mass mortalities of scallops (*Pecten magellanicus*) in the southwestern Gulf of St. Lawrence. *J. Fish. Res. Bd. Canada*, 20(2):451-482.
- DOVEL, W. L., 1964. An approach to sampling estuarine macroplankton. *Chesapeake Sci.*, 5:77-90.
- EDMONDSON, W. T. (Editor), 1966. *Marine Biology III. Proceedings of the Third International Interdisciplinary Conference*; pp. 1-313. New York Academy of Sciences, New York.
- ELLISON, R. M. NICHOLS, and J. HUGHES, 1965. Distribution of Recent Foraminifera in the Rappahannock River Estuary. *Virginia Inst. Marine Sci., Spec. Sci. Rept.* 47.
- ERIKSEN, C. H., 1963. A method for obtaining interstitial water from shallow aquatic substrates and determining the oxygen concentration. *Ecology*, 44:191-193.
- FEDER, H. M., 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. *Ecology*, 44:505-512.
- FRANK, P. W., 1965. The biodemography of an intertidal snail population. *Ecology*, 46:831-844.
- FRIEDRICH, H., 1959. Beiträge zu biologisch-ökologischen Untersuchungen in der Unter- und Außenweser. *Veroeffentl. Inst. Meeresforsch. Bremerhaven*, 6:1-12.
- GLEDHILL, D., 1963. The ecology of the Aberdeen creek mangrove swamps. *J. Ecology*, 51:693-704.
- GOODBODY, I., 1965. Continuous breeding in populations of two tropical crustaceans *Mysidium columbae* (Zimmer) and *Emerita portoricensis* Schmidt. *Ecology*, 46:195-197.
- GORE, R. H., 1966. Observations on the escape response in *Nassarius vibex* (Say), (Mollusca:Gastropoda). *Bull. Marine Sci.*, 16(3):423-434.
- GRANT, W. C., JR., 1963. Notes on the ecology and behavior of the hermit crab *Pagurus acadianus*. *Ecology*, 44:767-771.
- GREEN, J. P., 1964. Morphological color change in the fiddler crab, *Uca pugnax* (S. I. Smith). *Biol. Bull.*, 127:239-255.
- GUNTER, G., J. Y. CHRISTMAS, and R. KILLEBREW, 1964. Some relations of salinity to population distributions of motile estuarine organisms, with special reference to penaeid shrimps. *Ecology*, 45:181-185.
- HAAKE, F. W., 1962. Untersuchungen an der Foraminiferen-Fauna im Wattgebiet zwischen Langeoog und dem Festland. *Meyniiana*, 12:25-64.
- HALL, C. A., JR., 1964. Shallow-water marine climates and molluscan provinces. *Ecology*, 45:226-234.
- HANCOCK, D. A., 1965. Graphical estimation of growth parameters. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 29(3):340-351.
- HEDGPETH, J. W., 1950. Notes on the marine invertebrate fauna of salt flat areas in Aransas National Wildlife Refuge, Texas. *Publ. Inst. Marine Sci. Texas*, 1(2):103-119.
- HEINLE, D. R., 1966. Production of a calanoid copepod, *Acartia tonsa*, in the Patuxent River Estuary. *Chesapeake Sci.*, 7(2):59-74.
- HOPKINS, T. L., 1963. The variation in the catch of plankton nets in a system of estuaries. *J. Marine Res.*, 21:39.
- HOPKINS, T. L., 1965. Mysid shrimp abundance in surface waters of Indian River Inlet, Delaware. *Chesapeake Sci.*, 6(2):86-91.
- HOSOMI, A., 1966. On the growth of the bivalve, *Mytilus edulis* L. on the shore of Suma in Kobe City. *Japanese J. Ecology*, 16(3):109-113. [In Japanese]
- HOUGHTON, D. R., 1963. The relationship between tidal level and the occurrence of *Pinnotheres pinnum* (Pennant) in *Mytilus edulis* L. *J. Animal Ecol.*, 32: 253-257.
- HOUGHTON, D. R., and H. G. STUBBINGS, 1963. On the vertical distribution of *Elminius modestus* Darwin. *J. Animal Ecol.*, 32:193-201.
- HUGHES, D. A., 1966. Behavioral and ecological investigations of the crab *Ocypode ceratophthalmus* (Crustacea: Ocypodidae). *J. Zoology*, 150, part 1:129-143.
- IEFFRIES, H. P., 1964. Comparative studies on estuarine zooplankton. *Limnol. Oceanogr.* 9(3): 348-358.

- JEFFRIES, H. P., 1966. Partitioning of the estuarine environment by two species of *Cancer*. *Ecology*, 47(3): 477-481.
- JEFFRIES, H. P., 1966. Internal condition of a diminishing blue crab population (*Callinectes sapidus*). *Chesapeake Sci.*, 7(3): 164-176.
- JØRDE, I., and N. KLAVESTAD, 1963. The natural history of the Hardangerfjord. 4. The benthonic algal vegetation. *Sarsia No. 9*.
- LADD, H. S., J. W. HEDGPETH, and R. POST, 1957. Environments and facies of existing bays on the central Texas Coast. Chapter 22, in *Treatise on Marine Ecology and Paleoecology*, Vol. 2; pp. 599-640.
- LASSIG, J., 1965. The distribution of marine and brackishwater lamellibranchs in the northern Baltic area. *Soc. Scient. Fennica. Comment. Biol.*, 28(5).
- LIE, U., and M. M. PAMATMAT, 1965. Digging characteristics and sampling efficiency of the 0.1 square meter Van Veen grab. *Limnol. Oceanogr.*, 10: 379-384.
- LIVINGSTON, R., Jr., 1965. A preliminary bibliography with KWIC Index on the ecology of estuaries and coastal areas of the eastern United States. *U. S. Fish and Wildlife Service, Special Scientific Report—Fishes No. 507*. Washington, D. C.
- LOOSANOFF, V. L., 1965. Gonad development and discharge of spawn in oysters of Long Island Sound. *Biol. Bull.*, 129: 546-561.
- LOOSANOFF, V. L., and J. B. ENGLE, 1947. Effect of different concentrations of micro-organisms on the feeding of oysters (*O. virginica*). *U. S. Fish Wildlife Serv. Fishery Bull.*, 51: 31-57.
- MARKOWSKI, S., 1962. Faunistic and ecological investigations in Cavendish Dock, Barrow-In-Furness. *J. Animal Ecol.*, 31: 43-52.
- MARPLES, T. G., 1966. A radionuclide tracer study of arthropod food chains in a Spartina salt marsh ecosystem. *Ecology*, 47(2): 270-277.
- MARSHALL, N., and B. M. WHEELER, 1965. Role of the coastal and upper estuarine waters contributing phytoplankton to the shoals of the Niantic Estuary. *Ecology*, 46: 665-673.
- MCERLEAN, A. J., 1964. Characteristics of *Macoma balthica* populations in the Middle Patuxent Estuary. *Chesapeake Sci.*, 5(4): 200-208.
- MENZIES, R. J., and DIRK FRANKENBERG, 1966. *Handbook on the Common Marine Isopod Crustacea of Georgia*. Univ. of Georgia Press, Athens, Georgia.
- MILLAR, R. H., 1964. Breeding and gonadal cycle of oysters in Loch Ryan, Scotland. *J. Conseil, Conseil Perm. Intern. Exploration Mer.*, 28(3): 432-439.
- MILLARD, N. A., and A. D. HARRISON, 1954. The ecology of South African estuaries. Part V: Richard's Bay. *Trans. Roy. Soc. S. Africa*, 34: 157-174.
- MORGAN, E., 1965. The activity rhythm of the amphipod *Corophium volutator* Pallas and its possible relationship to changes in hydrostatic pressure related to the tides. *J. Animal Ecol.*, 34: 731-746.
- MURRAY, J. W., 1965. The Foraminifera of the Persian Gulf. 2. The Abu Dhabi region. *Palaeogeograph., Palaeoclimatol., Palaeoecol.*, 1(4): 307-332.
- MURRAY, J. W., 1966. The Foraminifera of the Persian Gulf. 3. The Halat al Bahrani region. *Palaeogeograph., Palaeoclimatol., Palaeoecol.*, 2(1): 59-68.
- NAGLE, J. S., 1965. Distributional aspects of the Cape Cod eelgrass epibiota. *Biol. Bull.*, 119: 417-418.
- OPPENHEIMER, C. G., and H. W. JANNASCH, 1962. Some bacterial populations in turbid and clear sea water near Port Aransas, Texas. *Publ. Inst. Marine Sci. Univ. Tex.*, 8: 56-60.
- PAINE, R. T., 1966. Food web complexity and species diversity. *Amer. Naturalist*, 100: 65-76.
- PAMATMAT, M. M., 1965. A continuous-flow apparatus for measuring metabolism of benthic communities. *Limnol. Oceanogr.*, 10: 486-489.
- PARKER, R. H., J. S. NAGLE, A. B. WILLIAMS, and R. KAUFMAN, 1965. Seasonal aspects of Hadley Harbor benthic ecology. *Biol. Bull.*, 129: 418.
- FATTEN, B. C., 1966. The biocoenetic process in an estuarine phytoplanktonic community. *ORNL-3946*; pp. 1-95. Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- PFITZENMEYER, H. T., 1965. Annual cycle of gametogenesis of the soft-shelled clam, *Mya arenaria*, at Solomons, Maryland. *Chesapeake Sci.*, 6(1): 52-59.
- PFITZENMEYER, H. T., and K. G. DROBECK, 1963. Benthic survey for populations of soft-shelled clams, *Mya arenaria*, in the lower Potomac River, Maryland. *Chesapeake Sci.*, 4(2): 67-74.
- PFITZENMEYER, H. T., and K. G. DROBECK, 1964. The occurrence of the brackish water clam, *Rangia cuneata*, in the Potomac River, Maryland. *Chesapeake Sci.*, 5(4): 209-215.
- PHILIPP, C. C., and R. G. BROWN, 1965. Ecological studies of transition-zone vascular plants in South River, Maryland. *Chesapeake Sci.*, 6(2): 73-81.
- REISH, D. J., 1964. Studies on the *Mytilus edulis* community in Alamitos Bay, California. II. Population variations and discussion of the associated organisms. *Veliger*, 6: 202-207.
- SAKUDA, H. M., 1966. Reproductive cycle of American oyster, *Crassostrea virginica*, in West Loch, Pearl Harbor, Hawaii. *Trans. Am. Fisheries Soc.*, 95: 216-218.
- SALMON, M., 1965. Waving display and sound production in the courtship behavior of *Uca pugnax*, with comparisons to *U. minax* and *U. pugnax*. *Zoologica*, 50(3): 123-151.
- SANDERS, H. L., P. C. MANGELSDORF, and G. R. HAMPSON, 1965. Salinity and faunal distribution in the Pocasset River, Mass. *Limnol. Oceanogr.*, 10: R216-R229.
- SANDISON, E. E., and M. B. HILL, 1966. The distribution of *Balanus pallidus stutsburi* Darwin, *Gryphaea gasar* (Adanson) Dautzenberg, *Mercierella enigmatica* Fauvel and *Hydroides uncinata* (Philippi) in relation to salinity in Lagos Harbour and adjacent creeks. *J. Animal Ecology*, 35(1): 235-250.
- SCHELTEMA, R. S., 1964. Feeding and growth in the mud-snail *Nassarius obsoletus*. *Chesapeake Sci.*, 5(4): 161-166.
- SCHOLL, D. W., 1965. High interstitial water chlorinity in estuarine mangrove swamps, Florida. *Nature*, 207: 284-285.
- SEGERSTRAALE, S. G., 1963. Investigations on Baltic populations of the bivalve *Macoma balthica* (L.). *Soc. Scient. Fennica. Comment. Biol.*, 24(7).
- SEGERSTRAALE, S. G., 1964. Literature on marine biology in the Baltic area published in the years 1953-1962. *Soc. Scient. Fennica. Comment. Biol.*, 27(3).
- SEGERSTRAALE, S. G., 1965. On the salinity conditions off the south coast of Finland since 1950, with comments on some remarkable hydrographical and biological phenomena in the Baltic area during this period. *Soc. Scient. Fennica. Comment. Biol.*, 28(7).
- SEIGLIE, G. A., and P. J. BERMUDEZ, 1963. Distribución de los Foraminíferos del Golfo de Cariaco. *Bol. Inst. Oceanogr. Univ. Oriente*, 2(1): 7-93.
- SHAW, W. N., 1962. Seasonal gonadal changes in the female soft-shell clam, *Mya arenaria*, in the Tred Avon River, Maryland. *Proc. Nat. Shellfisheries Assoc.*, 106: 53-121-132.
- SHAW, W. N., 1965. Seasonal settling patterns of five species of bivalves in the Tred Avon River, Maryland. *Chesapeake Sci.*, 6(1): 33-37.
- SMITH, R. I., 1964. The reproduction of *Nereis diversicolor* (Polychaeta) on the south coast of Finland—some observations and problems. *Soc. Scient. Fennica. Comment. Biol.*, 26(10).
- SYMONS, P. E. K., 1964. Behavioral responses of the crab *Hemigrapsus oregonensis* to temperature, diurnal light variation, and food stimuli. *Ecology*, 45: 580-591.
- TAYLOR, J. L., 1965. Bottom samplers for estuarine research. *Chesapeake Sci.*, 6(4): 233-234.

- TEAL, J. M., and W. WIESER, 1966. The distribution and ecology of nematodes in a Georgia salt marsh. *Limnol. Oceanogr.*, 11(2):217-222.
- VOGL, R. J., 1966. Salt-marsh vegetation of Upper Newport Bay, California. *Ecology*, 47(1):80-87.
- VOHRA, F. C., 1965. *Ecology of intertidal Zostera flats of Moreton Bay*. Ph. D. Thesis, Univ. of Queensland, Brisbane, Australia.
- WALTON, W. R., 1964. Ecology of benthonic Foraminifera in the Tampa-Sarasota Bay area, Florida. In *Papers in Marine Geology*; pp. 429-454. Macmillan, New York.
- WELLS, H. W., M. J. WELLS, and I. E. GRAY, 1964. Ecology of sponges in Hatteras Harbor, North Carolina. *Ecology*, 45:752-766.

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- BARNES, H., and M. BARNES, 1963. The relation of water uptake and oxygen consumption of body tissues to the moulting cycle in *Balanus balanoides* (L.) *Crustaceana*, 6:62.
- BARNWELL, F. H., 1963. Observations on daily and tidal rhythms in some fiddler crabs from Equatorial Brazil. *Biol. Bull.*, 125:399-415.
- BRUSCA, G. J., 1966. Studies on the salinity and humidity tolerances of five species of isopods in a transition from marine to terrestrial life. *Bull. South. Calif. Acad. Sci.*, 65(3):146-154.
- BRYAN, G. W., 1963. The accumulation of Cs¹³⁷ by brackish water invertebrates and its relation to the regulation of Potassium and Sodium. *J. Marine Biol. Assoc. U. K.*, 43:541-565.
- CARPELAN, L. H., 1961. Salinity tolerances of some fishes of a southern California Coastal lagoon. *Copeia* 1961, (1):32-39.
- CLÉRET, J. J., 1962. Sur un lot de "Cyathura carinata" (Kröyer) (Isopode, Anthuridae) provenant du Bassin d'Arcachon. Comparaison aux "C. carinata" vivant sur les cates de la Manche. *Bull. Soc. Linnaenne Normandie*, 3(10):142-144.
- DOUDOROFF, P., 1938. Reactions of marine fishes to temperature gradients. *Biol. Bull.*, 75:494-509.
- ELTRINGHAM, S. K., 1964. Blood concentrations of *Limnoria* (Isopoda) in relation to salinity. *J. Marine Biol. Assoc. U. K.*, 44:675-683.
- GECKLER, J. R., and T. A. WANDSTRAT, 1964. Uptake and retention of Rhodamine B by quahog clams, *Mercenaria mercenaria*. *Chesapeake Sci.*, 5(3):134-137.
- GROSS, W. J., 1964. Trends in water and salt regulation among aquatic and amphibious crabs. *Biol. Bull.*, 127:447-466.
- HAFFNER, P. A., Sr., 1964. Hemolymph calcium fluctuations as related to environmental salinity during ecdysis of the blue crab *Callinectes sapidus* Rathbun. *Physiol. Zool.*, 37(3):247-258.
- HAFFNER, P. A., Jr., and C. N. SCHUSTER, Jr., 1964. Length increments during terminal molt of the female blue crab, *Callinectes sapidus*, in different salinity environments. *Chesapeake Sci.*, 5(3):114-118.
- HAND, W. G., P. A. COLLARD, and D. DAVENPORT, 1965. The effects of temperature and salinity change on swimming rate in the Dinoflagellates, *Gonyaulax* and *Gyrodinium*. *Biol. Bull.*, 128:90-101.
- HILLMAN, R. E., 1965. Chromatographic studies of allopatric populations of the eastern oyster *Crassostrea virginica*. *Chesapeake Sci.*, 6(2):115-116.
- HUNTER, W. R., and R. T. NEADOWS, 1965. Aspects of water physiology in the salt-marsh pulmonate snail, *Melampus bidentatus*. *Biol. Bull.*, 129:409 (abs).
- KENDALL, A., and F. J. SCHWARTZ, 1964. Salinity tolerances of two Maryland crayfishes. *Ohio J. Sci.*, 64(6):403-409.
- KINNE, O., E. K. SHIRLEY, and H. E. MEEN, 1963. Osmotic responses of hermit crabs (*Pagurus longicarpus* Say) exposed to various constant temperatures and salinities. *Crustaceana*, 5:317.
- KRISHNAMOORTHI, B., 1963. Chloride regulation in *Marphysa grisea* Southern. *Current Science, India*, 32(10):463-464.
- LANCE, J., 1964. The salinity tolerances of some estuarine planktonic crustaceans. *Biol. Bull.*, 127:108-118.
- McFARLAND, W. N., and B. D. LEE, 1963. Osmotic and ionic concentrations of penaeidean shrimps of the Texas coast. *Bull. Marine Sci. Gulf Caribb.*, 13:391-417.
- MCLAREN, I. A., S. M. WOODS, and J. R. SHEA, Jr., 1966. Polyteny: a source of cryptic speciation among copepods. *Science*, 153:1641-1642.
- NELSON, K., 1964. The evolution of a pattern of sound production associated with courtship in the characid fish *Glandulocauda inequalis*. *Evolution*, 18:526-539.
- PALMER, J. D., 1964. A persistent light preference rhythm in the Fiddler Crab, *Uca pugnax* and its possible adaptive significance. *Am. Naturalist*, 98(903):431-434.
- RAO, K. P., and G. MADANMOHANRAO, 1963. Chloride regulation and its relation to oxygen consumption in the brackish water crab *Sesarma plicatum* (Latreille). *Crustaceana*, 5:188.
- REYMENT, R. A., 1964. Note on an upper salinity tolerance level for *Cypridopsis* (Ostracoda). *Crustaceana*, 7:75.
- SANDISON, E. E., 1966. The effect of salinity fluctuations on the life cycle of *Balanus pallidus stutsburgi* Darwin in Lagos Harbour, Nigeria. *J. Animal Ecology*, 35(2):363-378.
- SANDISON, E. E., 1966. The effect of salinity on the life cycle of *Gryphaea gasar* ((Adanson) Dautzenberg) in Lagos Harbour, Nigeria. *J. Animal Ecology*, 35(2):379-389.
- SCHELTEMA, R. S., 1965. The relationship of salinity to larval survival and development in *Nassarius obsoletus* (Gastropoda). *Biol. Bull.*, 129:340-354.
- SMITH, R. I., 1963. A comparison of salt loss rate in three species of brackish-water nereid polychaetes. *Biol. Bull.*, 125:332-343.
- STICKNEY, A. P., 1964. Salinity, temperature and food requirements of soft-shell clam larvae in laboratory culture. *Ecology*, 45:283-291.
- TAN, ENG-CHOW, and W. A. VAN ENGEL, 1966. Osmoregulation in the adult blue crab, *Callinectes sapidus* Rathbun. *Chesapeake Sci.*, 7(1):30-35.
- TARTAR, V., 1965. Fission and morphogenesis in a marine ciliate under osmotic stress. *J. Protozool.*, 12:444-447.
- TODD, M. E., 1964. Osmotic balance in *Littorina littorea* L. and *L. sulcata* (Littorinidae). *Physiol. Zool.*, 37(1):33-45.
- WATSON, D. G., J. J. DAVIS, and W. C. HANSON, 1963. Interspecies differences in accumulation of Gamma emitters by marine organisms near the Columbia River mouth. *Limnol. Oceanogr.*, 8(2):305-309.
- WEBB, H. M., and F. A. BROWN, Jr., 1965. Interactions of diurnal and tidal rhythms in the fiddler crab, *Uca pugnax*. *Biol. Bull.*, 129:582-591.
- WERNTZ, H. O., 1963. Osmotic regulation in marine and fresh-water Gammarids (Amphipoda). *Biol. Bull.*, 124:225-239.
- ZEIN-ELDIN, Z. P., 1963. Effect of salinity on growth of post-larval Penaeid shrimp. *Biol. Bull.*, 125:188-196.
- ZEIN-ELDIN, Z. P., and D. V. ALDRICH, 1965. Growth and survival of post-larval *Penaeus aztecus* under controlled conditions of temperature and salinity. *Biol. Bull.*, 129:199-216.

IX FISHERIES

- BAGENAL, T. B., 1963. The fecundity of plaice from the Bay of Biscay. *J. Marine Biol. Assoc. U. K.*, 43:177-179.

- BUREAU OF COMMERCIAL FISHERIES, 1966. *The Fisheries of Nort' Amer. The First North American Fisheries Conference: Canada, United States, Mexico;* pp. 1-72. Circular 250. Bureau of Commercial Fisheries, U.S. Dept. of the Interior, Washington, D.C.
- CHACKO, P. I., R. SREENIVASAN, S. GEORGE, and T. S. RAMACHANDRAN, 1954. Hydrology and fisheries of Vamsadara Estuary. *Contrib. Freshwater Biol. Sta. Madras*, 9.
- CHRISTY, F. T., and A. SCOTT, 1965. *The Common Wealth in Ocean Fisheries.* The Johns Hopkins Press, Baltimore, Maryland.
- CROKER, R. A., 1965. Planktonic fish eggs and larvae of Sandy Hook Estuary. *Chesapeake Sci.*, 6(2):92-95.
- CRUTCHFIELD, J. A., 1965. *The Fisheries: Problems in Resource Management.* Univ. of Washington Pre., Seattle, Washington.
- D'ANCONA, U., 1954. Fishing and fish culture in brackish-water lagoons. *FAO Fisheries Bull.*, 7(4): 2-28.
- DJAINGSASTRO, A. S., 1956. Experimentation in the brackish-water ponds at Polagan (Madura, East Java). *Indo-Pacific Fisheries Council, Proc., 6th Meeting*; pp. 202-209.
- GÖPINATH, K., 1955. Prawn culture in the rice fields of Travancore—Cochin, India. *Proc. Indo-Pacific Fisheries Council*, 6(III):419-424.
- HASLER, A. D., 1966. *Underwater Guideposts: Homing of Salmon.* Univ. of Wisconsin Press, Madison, Wisconsin.
- HEDGPETH, J. W., 1966. Aspects of the Estuarine Ecosystem. In *A Symposium on Estuarine Fisheries Am. Fisheries Soc., Spec. Publ. No. 3*:3-11.
- HERMAN, S. S., 1963. Planktonic fish eggs and larvae of Narragansett Bay. *Limnol. Oceanogr.*, 8(1):103-109.
- HORA, S. L., 1941. Life-history and wanderings of hilsa in Bengal waters. *J. Asiatic Soc. Bengal, (Sci.)*, 6: 93-112.
- HORA, S. L., and T. V. R. PILLAY, 1962. Handbook of fish culture in the Indo-Pacific Region. *FAO Fisheries Biol. Tech. Pap.*, 14:204.
- HORNELL, J., 1950. *Fishing in many waters.* Cambridge University Press.
- JOB, T. J., and V. R. PANTULU, 1953. Fish trapping in India. *J. Asiatic Soc. (Sci.)*, 19(2):175-196.
- JONES, S., 1951. Principal estuarine fisheries. *Handbook of Indian Fisheries*; pp. 48-54. Govt. Press, New Delhi.
- JONES, S., and K. H. SUJANSINGHANI, 1951. The hilsa fishery of the Chilka Lake. *J. Bombay Nat. Hist. Soc.*, 50(2):264-280.
- JOSEPH, E. B., J. J. NORCROSS, and W. H. MASSMAN, 1964. Spawning of the Cobia, *Rachycentron canadum*, in the Chesapeake Bay area, with observations of juvenile specimens. *Chesapeake Sci.*, 5:67-71.
- KEUP, L., and J. BAYLESS, 1964. Fish distribution at varying salinities in Neuse River Basin, North Carolina. *Chesapeake Sci.*, 5(3):119-123.
- KUTKUHN, J. H., 1966. The Role of Estuaries in the Development and Perpetuation of Commercial Shrimp Resources. In *A Symposium on Estuarine Fisheries. Amer. Fisheries Soc., Spec. Publ. No. 3*:16-36.
- LE MARE, D. W., 1950. Application of the principles of fish culture to estuarine conditions in Singapore. *Indo-Pacific Fisheries Council, Proc., 2nd meeting*; pp. 180-183.
- LEWIS, R. M., 1966. Effects of salinity and temperature on survival and development of larval Atlantic menhaden, *Brevoortia tyrannus*. *Trans. Am. Fisheries Soc.*, 95:423-426.
- MANSUETI, R. J., 1964. Eggs, larvae and young of the white perch, *Roccus americanus*, with comments on its ecology in the estuary. *Chesapeake Sci.*, 5:3-45.
- McHUGH, J. L., 1966. Management of estuarine fisheries. In *A Symposium on Estuarine Fisheries. Am. Fisheries Soc., Spec. Publ. No. 3*:133-154.
- McINERNEY, J. E., 1964. Salinity preference: an orientation mechanism in salmon migration. *J. Fisheries Res. Board Canada*, 21(5):995-1018.
- MENON, M. K., 1954. On the paddy field prawn fishery of Travancore-Cochin and an experiment in prawn culture. *Indo-Pacific Fisheries Council, Proc.*, 3(II): 80-93.
- MENON, M. K., and K. RAMAN, 1961. Observations on the prawn fishery of the Cochin backwaters with special reference to the stake net catches. *Indian J. Fisheries*, 8(1):1-23.
- MURPHY, G. I., 1966. Population biology of the Pacific sardine (*Sardinops sagax*). *Proc. Calif. Acad. Sci., 4th Ser.*, 34(1):1-84.
- PANIKKAR, N. K., and M. K. MENON, 1956. Prawn fisheries of India. *Indo-Pacific Fisheries Council, Proc., 6th session (II and III)*; pp. 328-344.
- PILLAY, T. V. R., 1958. Biology of the hilsa, *Hilsa ilisha* (Hamilton) of the River Hooghly. *Indian J. Fisheries*, 5:201-257.
- PILLAY, S. R., and K. V. RAO, 1964. Observations on the biology and fishery of the hilsa, *Hilsa ilisha* (Hamilton) of River Godavari. *Indo-Pacific Fisheries Council, Proc., 10th session (II)*; pp. 37-61.
- RAO, H. S., 1951. Research in fishery conservation. *Proceedings of the United Nations Scientific Conference on the Conservation and Utilization of Resources*, 7: 171-174.
- REINTJES, J. W., and A. L. PACHECO, 1966. The Relation of Menhaden to Estuaries. In *A Symposium on Estuarine Fisheries. Am. Fisheries Soc., Spec. Publ. No. 3*:50-58.
- SAROJINI, K. K., 1954. The food and feeding habits of the grey mullet, *Mugil persia* Hamilton and *M. speigleri*. *Indian J. Fisheries*, 1(1 and 2):67-93.
- SCHWARTZ, F. J., and R. JACHOWSKI, 1961. The age, growth, and length-weight relationship of the Patuxent River, Maryland Ictalurid White Catfish, *Ictalurus catus*. *Chesapeake Sci.*, 6(4):226-229.
- SHETTY, H. P. C., S. B. SAHA, and B. B. GHOSH, 1961. Observations on the distribution and fluctuations of plankton in the Hooghly-Matlab estuarine system, with notes on their relation to commercial fish landings. *Indian J. Fisheries*, 8(2):326-363.
- SMIDT, E. L. B., 1951. Animal production in the Danish Waddensea. *Medd. Komm. Danmarks Fisk. Haunders. Series Fisk.*, 11(6):1-151.
- SMITH, R. F., A. H. SWARTZ, and W. H. MASSMAN, 1966. A symposium on estuarine fisheries. *Trans. Am. Fisheries Soc., Spec. Publ. No. 3*:1-154 (Suppl. to Vol. 95, No. 4).
- TABB, D. C., 1966. The Estuary as a Habitat for Spotted Sea Trout *Cynoscion nebulosus*. In *A Symposium on Estuarine Fisheries. Am. Fisheries Soc., Spec. Publ. No. 3*:59-67.
- TALBOT, G. B., 1966. Estuarine Environmental Requirements and Limiting Factors for Striped Bass. In *A Symposium on Estuarine Fisheries. Am. Fisheries Soc., Spec. Publ. No. 3*:37-49.
- TAMPI, R. S., 1960. Utilization of saline mud flats for fish culture—An experiment in marine fish farming. *Indian J. Fisheries*, 7(1):137-146.
- WALLACE, D. H., 1966. Oysters in the Estuarine Environment. In *A Symposium on Estuarine Fisheries. Am. Fisheries Soc., Spec. Publ. No. 3*:68-73.
- WINBERG, G. G., 1956. *Rate of metabolism and food requirements of fishes (Intensivnost obmena i pishcherye potrebnosti ryb; Nauchnye Trudy Belorusskovo Gosudarstvennovo Universiteta imeni V. I. Lenina, Minsk.). Trans. Fisheries Res. Bd., Canada, Ser. No. 194.*

X HUMAN INFLUENCES

- ALABASTER, J. S., 1963. The effect of heated effluents on fish. *Intern. J. Air Water Pollution*, 7:541-563.

- BARLOW, J. P., C. J. LORENZEN, and R. T. MYREN, 1963. Eutrophication of a tidal estuary. *Limnol. Oceanogr.*, 8(2):251-262.
- BRAARUD, T., 1955. The effect of pollution by sewage upon the waters of Oslo-Fjord. *Verhandl. Intern. Ver. Limnol.*, 12:811-813.
- BREHMER, M., 1964. Nutrients. In Problems of the Potomac Estuary. *Proc. Interstate Comm. Potomac River Basin*, Washington, D. C.; pp. 47-50.
- BRUUN, P., 1960. Coastal Research and its Economic Justification. *Geografisk Tidsskrift*, Vol. 59.
- BUCK, D. H., 1956. Effects of turbidity on fish and fishing. *Trans. 21st N. Am. Wildlife Conf.*; pp. 249-261.
- BUTLER, P. A., 1963. Commercial fisheries investigations. Pesticide-wildlife studies: A review of Fish and Wildlife Service investigations during 1961 and 1962. *U. S. Fish Wildlife Serv., Circ.* 167; pp. 11-25.
- BUTLER, P. A., 1966. The Problem of Pesticides in Estuaries. In *A Symposium on Estuarine Fisheries*. Am. Fisheries Soc., Spec. Publ. No. 3:110-115.
- CARPENTER, J. H., 1961. *The Chesapeake Bay Institute study of the Baltimore Harbor*. 33rd Ann. Conf., Maryland-Delaware Water Sewage Assoc.
- CARRITT, D. E., 1956. Recent developments in the chemistry and hydrography of estuaries. *Trans. N. Am. Wildlife Conf.*, 1956; pp. 420-436.
- CAULFIELD, H. F., JR., 1966. Comprehensive Planning in Relation to the Use and Management of Estuaries. In *A Symposium on Estuarine Fisheries*. Am. Fisheries Soc., Spec. Publ. No. 3:121-126.
- CHAPMAN, C. R., 1966. The Texas Basins Project. In *A Symposium on Estuarine Fisheries*. Am. Fisheries Soc., Spec. Publ. No. 3:83-92.
- CHIN, E., and D. M. ALLEN, 1957. Toxicity of an insecticide to two species of shrimp, *Penaeus aztecus* and *Penaeus setiferus*. *Texas J. Sci.*, 9(3):270-278.
- COMMITTEE ON EFFECTS OF ATOMIC RADIATION ON OCEANOGRAPHY AND FISHERIES, 1957. The effects of atomic radiation on oceanography and fisheries. *Natl. Acad. Sci.-Natl. Res. Council, Publ.* 551.
- COMMITTEE ON OCEANOGRAPHY, 1959. Radioactive waste disposal into Atlantic and Gulf coastal waters. *Natl. Acad. Sci.-Natl. Res. Council, Publ.* 655.
- COOPER, R. A., S. B. CHENOWETH, and N. MARSHALL, 1964. Condition of the quahog, *Mercenaria mercenaria*, from polluted and unpolluted waters. *Chesapeake Sci.*, 5(4):155-160.
- COTTAM, C., 1965. The ecologist's role in problems of pesticide pollution. *Bioscience*, 15(7):455-463.
- DARSIE, R. F., JR., and F. E. CORRIDAN, 1959. The toxicity of malathion to killifish (Cyprinodontidae) in Delaware. *J. Econ. Entomol.*, 52(4):696-700.
- DAVIS, J. H., 1956. Influences of man upon coast lines. In *Man's role in changing the face of the earth*. Univ. of Chicago for the Wenner-Gren Foundation.
- DEAN, D., and H. H. HASKIN, 1964. Benthic repopulation of the Raritan River estuary following pollution abatement. *Limnol. Oceanogr.*, 9(4):551-563.
- DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH, 1964. Effects of polluting discharges on the Thames estuary. *Report, Thames Survey Comm. and Water Pollution Res. Lab.*; 609 pp. Her Majesty's Stationery Office, London.
- DE TURVILLE, C. M., and R. T. JARMAN, 1965. The mixing of warm water from the Uskmouth Power Stations in the Estuary of the River Usk. *Intern. J. Air Water Pollution*, 9:239-251.
- DOUDOROFF, P., B. G. ANDERSON, G. E. BURDICK, P. S. GALTSTOFF, W. B. HART, R. PATRICK, E. R. STRONG, E. W. SURBER, and W. M. VANHORN, 1951. Bioassay methods for the evaluation of acute toxicity of industrial wastes to fish. *Sewage Ind. Wastes*, 23(11):1380-1397.
- DUBROW, M. D., and J. E. GUIDRY, 1965. The new international Passamaquoddy tidal power project and the Saint John River hydroelectric power development. *Trans. N.Y. Acad. Sci. (Ser. II)*, 27(5):505-516.
- DUKE, T. W., J. N. WILLIS, and T. J. PRICE, 1966. Cycling of trace elements in the estuarine environment. I. Movement and distribution of Zinc 65 and stable zinc in experimental ponds. *Chesapeake Sci.*, 7(1):1-10.
- GAMESON, A. L. H., H. H. HALL, and W. S. PREDDY, 1957. Effects of heated discharges on the temperature of the Thames Estuary. *The Engineer*, Dec. 1957.
- GAMESON, A. L. H., and W. S. PREDDY, 1956. Factors affecting the concentration of dissolved oxygen in the Thames Estuary. *Water Pollution Res. Lab., Reprint* 297. Stevenage, England.
- GAMESON, A. L. H., M. J. BARRETT, and W. S. PREDDY, 1965. Predicting the condition of a polluted estuary. *Intern. J. Air Water Pollution*, 9:655-664.
- GEORGE, J. L., R. F. DARSIE, JR., and P. F. SPRINGER, 1957. Effects on wildlife of aerial applications of Stobane, DDT and BHC to tidal marshes in Delaware. *J. Wildlife Management*, 21(1):42-53.
- GLENN, T. R., JR., 1966. An Effective Estuarine Pollution Abatement Program. In *A Symposium on Estuarine Fisheries*. Am. Fisheries Soc., Spec. Publ. No. 3: 116-120.
- GOTTSCHALK, L. C., 1945. Effects of soil erosion on navigation in upper Chesapeake Bay. *Geograph. Rev.*, 35(2):219-238.
- GOTTSCHALK, L. C., 1947. Sedimentation in a great harbor. *Soil Conservation*, 10(1):3-12.
- GROSS, M. G., C. A. BARNES, and G. K. RIEL, 1965. Radioactivity of the Columbia River effluent. *Science*, 149:1088-1090.
- GUNTER, G., and J. MCKEE, 1961. On Oysters and Sulfite Waste Liquor. Part I. *Ind. Water Wastes*, 6:182-186.
- GUNTER, G., and J. MCKEE, 1962. On Oysters and Sulfite Waste Liquor. Part II. *Ind. Water Wastes*, 7: 7-9.
- HARRINGTON, R. W., JR., and W. L. BIDLINGMAYER, 1958. Effects of dieldrin on fishes and invertebrates of a salt marsh. *J. Wildlife Management*, 22(1):76-82.
- HERBERT, D. W. M., and D. S. SHURBEN, 1965. The susceptibility of salmonid fish to poisons under estuarine conditions. II. Ammonium Chloride. *Intern. J. Air Water Pollution*, 9:89-91.
- HERBERT, D. W. M., and A. C. WAKEFORD, 1964. The susceptibility of salmonid fish to poisons under estuarine conditions. I: Zinc sulphate. *Intern. J. Air Water Pollution*, 8:251-256.
- HOLLAND, G. A., 1953. Toxic effects of sulfite waste liquor on spring salmon. *State of Washington, Dept. of Fisheries Res. Bull.*, No. 1; pp. 1-111.
- HOOD, D. W., T. W. DUKE, and B. STEVENSON, 1960. Measurement of toxicity of organic wastes to marine organisms. *J. Water Pollution Control Federation*, 32(9):982-993.
- HULL, C. H. J., 1963. Photosynthetic oxygenation of a polluted estuary. *Intern. J. Air Water Pollution*, 7: 669-696.
- HULL, C. H. S., 1963. Oxygenation of Baltimore Harbor by planktonic algae. *J. Water Pollution Control Federation*, 35(5):587-606.
- ILES, R. B., 1963. Cultivating fish for food and sport in powerstation water. *New Scientist*, 17:227-229.
- JONES, B. F., C. E. WARREN, C. E. BOND, and P. DUODOROFF, 1956. Avoidance Reactions of Salmonid Fishes to Pulp Mill Effluents. *Sewage Ind. Wastes*, 28:1403-1413.
- JONES, J., and R. ERICHSEN, 1964. *Fish and River Pollution*; 203 pp. Butterworths, London.
- KEIGHTON, W. B., 1954. The investigation of chemical quality of water and tidal rivers. Quality Section. U. S. Dept. Interior, Geol. Surv., Aug. 1954.

- KELLEY, D. W., and J. L. TURNER, 1966. Fisheries Protection and Enhancement with Water Development of the Sacramento-San Joaquin Estuary. In *A Symposium on Estuarine Fisheries*. Am. Fisheries Soc., Spec. Publ. No. 3:78-82.
- KERSWILL, C. J., and P. F. ELSON, 1955. Preliminary observations on effects of D.D.T. spraying on Miramichi salmon stocks. *Progr. Rept. Atlantic Biol. Sta.*, 62:17-23.
- KETCHUM, B. H., 1955. Distribution of coliform bacteria and other pollutants in tidal estuaries. *Sewage Ind. Wastes*, 27(11):1288-1296.
- KETCHUM, B. H., 1960. Marine pollution problems in the North Atlantic area. In *Biological Problems in Water Pollution*. Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center, Tech. Rept. W60-3:212-217.
- KITAMORI, R., and K. FUNAE, 1959. The benthic community in polluted coastal waters. (III) Osaka Bay. *Island Sea Res. Biol. Sta. Bull.*, 12:215-222.
- KITAMORI, R., and S. KOBAYASHI, 1958. The benthic community in polluted coastal waters. (I) Fukuyama Inlet. *Island Sea Res. Biol. Sta. Bull.*, 11:1-6.
- KITAMORI, R., and Z. KOBE, 1959. The benthic community in polluted coastal waters. (IV) Kanzaki River. *Island Sea Res. Biol. Sta. Bull.*, 12:223-226.
- KITAMORI, R., S. KOBAYASHI, and K. NAGATA, 1959. The benthic community in polluted coastal waters. (II) Mikara Bay. *Island Sea Res. Biol. Sta. Bull.*, 12:201-214.
- LOOSANOFF, V. L., C. L. MACKENZIE, Jr., and L. W. SHEARER, 1960. Use of chemicals to control shellfish predators. *Science*, 131(3412):1522-1523.
- LOWE, J. I., 1965. Chronic exposure of blue crabs, *Callinectes sapidus* to sublethal concentrations of DDT. *Ecology*, 46:899-900.
- MACKENZIE, C. L., Jr., and L. W. SHEARER, 1959. Chemical control of *Polydora websteri* and other annelids inhabiting oyster shells. *Proc. Natl. Shellfisheries Assoc.*, 50:103-111.
- MALONEY, T. E., and E. L. ROBINSON, 1961. Growth and respiration of a green alga in spent sulfite liquor. *TAPPI*, 44:137-141.
- MANN, K. H., 1965. Heated effluents and their effects on the invertebrate fauna of rivers. *Proc. Soc. Water Treatment and Examination*, 14:45-53.
- MARKOWSKI, S., 1959. Cooling water of power stations. A new factor in the environment of marine and fresh water invertebrates. *J. Animal Ecol.*, 28(2):243-255.
- MARKOWSKI, S., 1960. Observations on the response of some benthonic organism to power station cooling. *J. Animal Ecol.*, 29(2):349-357.
- MARSHALL, S. M., 1947. An experiment in marine fish cultivation. III. The plankton of a fertilized loch. *Proc. Roy. Soc. Edinburgh*, (B)63:21-33.
- MCCABE, J. S., 1962. Organic pollution of New York Harbor—Application. *J. Water Pollution Control Federation*, 34(10):987-998.
- MC CRONE, A. W., 1966. The Hudson River Estuary: Hydrology, sediments, and pollution. *Geographical Review*, LV(2):175-189.
- MCKERNAN, D. L., V. TARTAR, and R. TOLLEFSON, 1949. An investigation of the decline of the native oyster industry of the State of Washington, with special reference to the effects of sulfite pulp mill waste on the Olympia oyster (*Ostrea lurida*). *Dept. Fish., State of Washington, Biol. Rept.*, 49A:115-165.
- MCNULTY, J. K., E. S. REYNOLDS, and S. M. MILLER, 1960. Ecological effects of sewage pollution in Biscayne Bay, Florida: Distribution of coliform bacteria, chemical nutrients, and volumes of zooplankton. *Trans. 2nd Seminar Biol. Problems in Water Pollution*. U. S. Public Health Serv.; pp. 189-202.
- MILLER, C. W., B. M. ZUCKERMAN, and A. J. CHARIG, 1966. Water translocation of Diazinol-C¹⁴ and Parathion-S³⁵ off a model cranberry bog and subsequent occurrence in fish and mussels. *Trans. Am. Fisheries Soc.*, 95:345-349.
- MOHR, J. L., 1960. Biological indicators of organic enrichment in marine habitats. In *Biological Problems in Water Pollution*. Trans. 1959 Seminar, Robert A. Taft Sanitary Eng. Center, Tech. Rept. W60-3:237-239.
- NADEZHIDIN, V. M., 1965. Hydrological regime of Pechora Bay and its possible variations when part of the discharge of the Pechora River is diverted. *Oceanology*, 5(3):47-55.
- NAYLOR, E., 1965. Effects of heated effluents upon marine and estuarine organisms. *Advan. Marine Biol.*, 3: 63-103.
- NEWELL, G. E., 1959. Pollution and the abundance of animals in estuaries. In *The Effects of Pollution on Living Material*; edited by W. B. Yapp; vol. 8, pp. 61-69. Inst. Biol. London Symposia.
- ODUM, H. T., 1963. Productivity measurements in Texas turtle grass and the effects of dredging an intra-coastal channel. *Publ. Inst. Marine Sci., Univ. of Texas*, 9:48-58.
- OLSEN, H. A., 1959. The influence of the Romo Dam on the sedimentation in the adjacent part of the Danish Wadden Sea. *Geograf. Tidsskr.*; Vol. 58.
- OLSON, T. A., and F. J. BURGESS, 1967. *Pollution and Marine Biology*. John Wiley and Sons, New York. (In press)
- PEARSON, E. A., 1959. Tracer methodology and pollution analyses of estuaries. *Proc. 1st Intern. Conf. Waste Disposal in Marine Environ.*; pp. 556-568.
- PRITCHARD, D. W., and H. H. CARTER, 1965. On the prediction of the distribution of excess temperature from a heated discharge in an estuary. *Chesapeake Bay Institute, The Johns Hopkins University, Technical Rept.* 33:1-45.
- RAWLS, C. K., 1965. Field tests of herbicide toxicity to certain estuarine animals. *Chesapeake Sci.*, 6(3): 150-161.
- RAWLS, C. K., 1965. Toxicity to certain estuarine animals in field tests of selected herbicides. *Proc. 18th Southern Weed Conf. (Dallas, Texas)* 18:574-575.
- RENN, C. E., 1957. Physical and chemical properties of wastes produced by atomic power industry. In *The effects of atomic radiation on oceanography and fisheries*; pp. 26-27. Natl. Acad. Sci.-Natl. Res. Council.
- RENN, C. E., 1960. Biological aspect of industrial waste problems. In *Biol. Problems in Pollution*, Robert A. Taft Sanitary Eng. Center Tech. Report W60-3:156-159.
- ROCHFORD, D. J., 1951. The application of studies on estuarine hydrology to certain problems in Australian oyster biology. *Rapp. Proc. Ver. Conseil*, 31:37.
- SCHMIDT, R. A., 1966. Needed—A Coastal Comprehensive Program for Development of Estuaries. In *A Symposium on Estuarine Fisheries*. Am. Fisheries Soc., Spec. Publ. No. 3:102-109.
- SCHUSTER, C. N., Jr., 1959. A biological evaluation of the Delaware River estuary. *Univ. Delaware Marine Lab. Info. Serv., Publ.* (3):1-77.
- SMITH, S. H., 1966. Effects of Water Use Activities in Gulf of Mexico and South Atlantic Estuarine Areas. In *A Symposium on Estuarine Fisheries*. Am. Fisheries Soc., Spec. Publ. No. 3:93-101.
- SPRINGER, P. F., and J. R. WEBSTER, 1951. Biological effects of DDT applications on tidal salt marshes. *Trans. 16th N. Am. Wildlife Conf.*; pp. 383-397. See also *Mosquito News*, 11(2):67-74.
- SPRINGER, P. F., G. F. BEAVEN, and V. D. STOTTS, 1961. *Eurasian Watermilfoil—a Rapidly Spreading Pest Plant in Eastern Waters*. Presented at Northeast Wildlife Conf., Halifax, Nova Scotia.

- TAYLOR, W. R., 1960. Some results of studies on the uptake of radioactive waste materials by marine and estuarine phytoplankton organisms using continuous culture techniques. *Chesapeake Bay Inst., The Johns Hopkins Univ., Tech. Rept. XXI, Ref. 60-3.*
- THAMDRUP, H., 1940. Nyere Undersøgelser over Vandhavets Betydning i praktisk-marinbiologisk Henseende. (Modern Studies of the Meaning of the Wadden Sea in practical-marine biological respect). *Meddelelser fra Skalling-Laboratoriet; Vol. 6.*
- THOMANN, R. V., 1965. Recent results from a mathematical model of water pollution control in the Delaware estuary. *Water Resources Res. 1(3):349-361.*
- TILLER, R. E., and E. N. CORY, 1947. Effects of DDT on some tidewater aquatic animals. *J. Econ. Entomol. 40(3):431-433.*
- TULLY, J. P., 1959. On structure, entrainment and transport in estuarine embayments. *Proc. 1st Intern. Conf. Waste Disposal Marine Environ., pp. 526-539.*
- UNDERHILL, A. H., 1966. Maintaining and Enhancing the Estuarine Environment. In *A Symposium on Estuarine Fisheries. Am. Fisheries Soc., Spec. Publ. No. 3:* 127-129.
- VAUGHN, M. W., and A. W. JONES, 1964. Bacteriological survey of an oyster bed in Tangier Sound, Maryland. *Chesapeake Sci., 5(4):167-171.*
- WHITE, J. C., Jr., and J. W. ANGELOVIC, 1966. Tolerances of several marine species to Co⁶⁰ irradiation. *Chesapeake Sci., 7(1):36-39.*
- WILSON, J., 1960. The effects of erosion, silt, and other inert materials on aquatic life. In *Biological Problems in Water Pollution. Robert A. Taft Sanitary Eng. Center, Tech. Rept. W60-3:269-271.*

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