1

ECOLOGY AND POPULATION DYNAMICS OF JUVENILE DUNGENESS CRAB IN GRAYS HARBOR ESTUARY AND ADJACENT NEARSHORE WATERS OF THE SOUTHERN WASHINGTON COAST

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This narrative on the life history, ecology and population dynamics of Dungeness crab is intended to provide background biological information for use in assessing potential impacts of the proposed U.S. Army Corps of Engineers (COE) Navigation Improvement Project in Grays Harbor, Washington. Much support for crab research has come from COE to fund research projects in the Grays Harbor estuary, often in concert with an ongoing University of Washington Sea Grant program, and much of the data derived from those projects are summarized in this document. The biological information collected to date on Dungeness crab has been used in a dredge impact model (Armstrong et al. 1987a) to estimate potential entrainment and mortality of crab according to various scenarios of construction proposed by COE. Of particular concern in

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Grays Harbor are large populations of juvenile Dungeness crab that reside in the estuary and may be affected by the Navigation project. Biological and life history information on the timing of occurrence of crab in the estuary, spatial distribution and abundance, movement to and from the estuary from the nearshore coastal zone, growth rates, and habitat requirements are all issues considered in this document, and these data have been used to attenuate any effects of the construction program to the greatest extent possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

S1. INTRODUCTION

This narrative on the life history, ecology and population dynamics of Dungeness crab is intended to provide background biological information for use in assessing potential impacts of the proposed U.S. Army Corps of Engineers (COE) Navigation Improvement Project in Grays Harbor, Washington. Much support for crab research has come from COE to fund research projects in the Grays Harbor estuary, often in concert with an ongoing University of Washington Sea Grant program, and much of the data derived from those projects are summarized in this document. The biological information collected to date on Dungeness crab has been used in a dredge impact model (Armstrong et al. 1987a) to estimate potential entrainment and mortality of crab according to various scenarios of construction proposed by COE. Of particular concern in Grays Harbor are large populations of juvenile Dungeness crab that reside in the estuary and may be affected by the Navigation project. Biological and life history information on the timing of occurrence of crab in the estuary, spatial distribution and abundance, movement to and from the estuary from the nearshore coastal zone, growth rates, and habitat requirements are all issues considered in this document, and these data have been used to attenuate any effects of the construction program to the greatest extent possible.

S2. LIFE HISTORY

Most major life history events of Dungeness crab occur along the open coast. Adult females molt to maturity, are bred by males, extrude and carry an egg mass, and hatch larvae along the open coast. Five larval zoeal stages and a last megalopal stage occur in coastal water between December and April. These larval populations are subject to a variety of biotic and abiotic processes that affect their distribution through transport, their survival in terms of predation and food supplies, and their eventual location at settlement and metamorphosis. Megalops larvae occur nearshore in shallow waters in April and May and settle to the benthos, but also directly enter estuaries such as Grays Harbor and, in certain years, settle in very high abundance. Siblings of a given year class that occur either in an estuary or nearshore grow at different rates and experience different rates of mortality. As a consequence, crab that recruit to estuarine or coastal areas may reach sexual maturity and the fishery at different ages and in substantially different proportions. In particular years it appears as though the majority of a year class that survives to age 1+ are primarily those that settle in an estuary, whereas in other years the coastal population represents the

the coastal population represents the larger proportion of the 1+ age class. Juvenile crab may reside in estuaries for one to two years and at this age or at a size of about 100mm carapace width (CW) or greater, emigrate from the estuary and reside along the coast through adulthood.

S3. THE FISHERY

Dungeness crab are Washington State's most valuable crustacean fishery and, as occurs elsewhere along the coast, landings cycle over a period of about 9-10 years and may range between 3 to 15 million pounds per year. The male only, pot fishery occurs for the most part nearshore although small fisheries take place in estuaries as well. The potential loss of juvenile crab during W&D may also pose some potential loss to future fisheries but this calculation must be made on the basis of natural mortality rates which have only recently been calculated for early life history stages (Armstrong et al. 1987a).

S4. HABITAT AND TIMING

Research done along Washington's southern coast has focused on three primary areas; Grays Harbor, Willapa Bay, and the nearshore coastal region adjacent to those two estuaries. Nearshore, most benthic substrate is composed of open sand/mud and offers relatively little refuge for newly settled 0+ crab. In certain regions gravel probably provides better habitat and also detrital eelgrass and other organic debris sometimes has been found to contain high densities of juvenile crab. Habitat and substrate is more complex in the estuaries and can be generally divided between those characteristic of subtidal channels where 1+ age class juveniles are most abundant, or in intertidal areas where 0+ juveniles dominate. Shell habitat composed primarily of cultured oysters and *Mya* sp. clams (shellhash) are the principal refuge habitat for 0+ crab in the intertidal. Densities of this stage are orders of magnitude higher in shellhash than found subtidally in open channels. The majority of the estuarine 0+ population through most of summer occurs in intertidal habitat but animals move from this location to subtidal channels when they reach a size generally greater than 25mm CW. 1+ juveniles are most abundant in shallow warm water channels of regions of the estuary inland from the mouth. Particularly North Bay in Grays Harbor has supported a majority of the 1+ population in most years between 1983 through 1986.

In the second summer after settlement there is a concerted immigration of nearshore 1+ crab into the estuary where they mix with larger siblings that settled directly to the estuary the previous year. Toward the end of the second summer, or as crab approach a size of about

Total estuarine populations of juvenile crab tend to be highest in the spring and summer because of both influx of megalopae that settle as the 0+ age class and also immigration of 1+ crab from the nearshore. Crab density is often substantially lower by winter because of outmigration of 1+ juveniles in the fall, and possibly because of burial behavior that results in lower estimates of true abundance due to reduced efficiency of sampling gear.

S5. POPULATION DYNAMICS AND MOVEMENTS

Most work done on analyses of Dungeness crab populations has been directed toward evidence of abundance seen in commercial fisheries landings. Because populations appear to cycle over a 9-10 year period, several attempts have been made to correlate these swings in abundance with physical processes such as upwelling, wind direction and water temperature as well as with biological processes such as density-dependent cannibalism, fish predation, and predatory worms. Because the fishery is a relatively imperfect way to assess population abundance and because of the uncertainty about size-at-age of individuals in the fishery, it is somewhat difficult to relate abundance of legal males to auspicious biological or physical processes operative within the year of settlement that might enhance survival.

Comprehensive studies of juvenile crab population dynamics in and nearshore of Grays Harbor are the most complete data on this life history stage, and indicate tremendous fluctuation of several orders of magnitude in abundance of new recruits in the spring of 1983 through 1986. Estimated population size in this period ranged from <60 million to more than 1.2 billion crab over an area of coast surveyed as part of the Washington Sea Grant Program. During summer, abundance of 0+ crab declines very quickly nearshore and estimates of population strength are regarded as more accurate when taken later in the summer (August, September) than near peak settlement in June/July. While initial density of 0+ crab can fluctuate inside Grays Harbor as well, long term summer population estimates tend to be relatively stable, particularly in the intertidal and most often range between 5 to 20 million 0+ crab depending on month and year.

Abundance of 1+ juveniles has usually been lower nearshore along the coast than in the estuaries. In all years except 1985, there is the appearance of immigration of 1+ juveniles into Grays Harbor where total population estimates have ranged between 7 to 12 million crab June through September. In 1985 however, a strong coastal population of 1+ juveniles (of the 1984 year class) that ranged between 15 to 25 million remained nearshore and did not enter an estuary. These crab were unique in part because they were substantially larger by September of their first year than seen for other year classes, and this larger size (apparently faster growth in 1984) may have resulted in much higher survival over winter.

Studies conducted on juvenile crab in Willapa Bay since 1985 indicate similar levels of population abundance and the two estuaries together support a substantially greater population of 1+ juveniles than occurs nearshore along the coast. Since water temperatures are significantly higher inside an estuary like Grays Harbor (5-6°C higher than nearshore), crab production tends to be high as well. Estimates of total energy/food requirements for resident juvenile populations in Grays Harbor during summertime are over 200 metric tons ash free dry weight of organic matter or about 800 metric tons wet weight (Gutermuth 1987), a substantial amount of food that attests to the high productivity of estuarine systems and the crabs' dependence on them.

S6. GROWTH AND MORTALITY

Summer growth rate of any juvenile crab age class is substantially higher in the estuary than nearshore in colder coastal waters. 0+ crab that settle in Grays Harbor in May are more than twice as wide across the carapace by September than are siblings nearshore and may be 5-6 times heavier. More rapid growth in the estuary imparts a survival advantage compared to nearshore siblings because estuarine crab more quickly reach sizes beyond the range of most predators. Slower growth and smaller size of siblings nearshore probably results in high mortality through the fall and winter. Extensive review is given in this document to analyses of growth rate, size-at-instar, and size-at-age. Such information is useful to estimate age at which a given year class will enter the fishery or over how many years a single year class might contribute to a fishery. Growth rate is also critical for calculating dredge impacts and showing the distribution of impacts over time since crab of several ages are involved.

Little work has been done to estimate survival/mortality rates of adult crab, but it is generally estimated to be .15-.20 per year. Analyses of the Grays Harbor juvenile crab data provides the first estimate of juvenile survival which for 0+ crab in the estuary is about 3.3% for the first year ($Z=3.047$/year), and an age-dependent Z has been calculated as $Z=2.49-0.43(\text{age})$. Annual survival estimates for various age classes have been calculated and range from about 16% between years 1 and 2 to 38% between years 3 and 4 (Armstrong et al. 1987a). These types of mortality estimates were used in the Dredge Impact Model to carry forward juvenile losses at any particular point in time to survivors remaining at sexual maturity or in the fishery. On this basis the loss of 0+ juveniles during W&D is relatively minor because the extent of natural mortality is so great that few would survive to adulthood anyway. Conversely, loss of 1+ and older age class juveniles can be important because survivorship is substantially better by this age so that more crab would be expected to reach maturity and the commercial fisheries.

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Washington Sea Grant (contract NA86AA-D-SG044) provided the basis of support for most research on juvenile crab ecology and we appreciate Director Louie Echols' enthusiasm for the program. Dr. Donald Gunderson has been Co-PI for the Sea Grant project and instrumental in its successful completion. Jan Armstrong and Dr. Jose Orensanz helped in organization of and editorial work on the manuscript, and Jenni Keith typed many versions of it. Many people have been key members of the field program and include R. McConnaughey, Y. B. Shi, B. Gutermuth, K. Carrasco, C. Rogers, R. Palacios, B. Dumbauld and R. Black, as well as a long list of hardworking student helpers. To all we express our sincere thanks.

Ecology and Population Dynamics of Juvenile Dungeness Crab in Grays Harbor Estuary and Adjacent Nearshore Waters of the Southern Washington Coast

1.0 INTRODUCTION

Use of estuaries and inland waters by juvenile Dungeness crab *(Cancer magister)* has been documented for a number of years along the Pacific Coast of the United States (Cleaver 1949; Tegelberg and Arthur 1977; Waldron 1958) and in British Columbia (Butler 1956, 1961; MacKay and Weymouth 1935), but only in the last decade have quantified studies of crab distribution and population dynamics been done to establish a time series longer than a single year (Armstrong and Gunderson 1985a; Armstrong et al. 1982, Collier 1983; Gotshall 1978; Stevens and Armstrong 1984, 1985; Tasto 1983). Most thorough studies of crab biology were conducted in the region of San Francisco Bay by Cal. Fish & Game for six years (Wild and Tasto 1983) and in Grays Harbor, Washington, since 1980 to the present (Armstrong and Gunderson 1985; Stevens 1981; Stevens and Armstrong 1984, 1985); in both cases potential or actual loss of fisheries through possible environmental perturbations gave impetus to the studies. Data indicate that a significant fraction of any Dungeness crab year class might use estuaries during early juvenile stages, and in this regard such systems serve as "nursery habitat" for juveniles that recruit to later adult populations and fisheries nearshore along the open coast.

Dungeness crab has historically been Washington state's most valuable crustacean fishery, exceeding in dollar value (if not pounds landed) that for pandalid shrimp (Nosho et al. 1980; PMFC 1985), although since 1980 several consecutive fishing years have been the worst on record since 1950 (PMFC 1985). This trend has intensified concern over coastal projects that might in some way exacerbate already low crab stocks and worsen the natural cycles of high and low abundance (Botsford and Wickham 1978; McKelvey et al. 1980).

1.1 PURPOSE

The Port of Grays Harbor requested the U.S. Army Corps of Engineers (COE) to study the feasibility of widening and deepening (W&D) the present navigation channel in Grays Harbor to accommodate larger ships in the future (details of the project are given in various environmental impact statements, EIS; see U.S. Army Corps of Engineers 1988). Among environmental impacts anticipated as a result of the project are direct entrainment and mortality of Dungeness crab, as well as possible alteration of important habitat during dredging and/or disposal, and a suite of more subtle perturbations based on sediment toxicity and chemosensory-linked avoidance of materials by several crab life history stages.

This report serves as a summary of species biology for *C. magister* and provides additional information to the impact assessment made elsewhere in the EIS (see Armstrong et al. 1987a, "Model of Dredging Impact on Dungeness Crab in Grays Harbor, Washington"). Emphasis is given to presentation of information on Dungeness crab ecology and population dynamics in the Grays Harbor estuary (and Willapa Bay to a limited extent) and along the adjacent nearshore coast, but a broad basis of other studies and analyses of Dungeness crab is used to augment the information required for modelling overall life history characteristics. Although impact calculations of entrainment and mortality of crab during dredging are not presented in this report, aspects of species ecology (e.g. habitat, growth rates, movement) that are germane and/or most susceptible to dredging impacts are highlighted.

1.2 NEED FOR ESTUARINE CRAB STUDIES

Although the majority of the commercial fishery and all reproductive events occur along the open coast (Cleaver 1949; Stevens and Armstrong 1985; Waldron 1958), there are several studies that point to the importance of estuaries in the life cycle of *C. magister*. During the life history of this species (Fig. 1.1), ovigerous females are found only along the open coast (Diamond and Hankin 1985) where eggs hatch and five zoeal stages develop (Lough 1976). Upon molt to megalopae, however, this last larval stage seems to move shoreward (Cal. Fish and Game 1981; Lough 1976; Reilly 1983a) and directly enters estuaries (Armstrong and Gunderson 1985a; Butler 1956; Gotshall 1978; Reilly 1983a). Newly metamorphosed first instars are abundant in estuaries (Butler 1956, 1961; Gotshall 1978; Stevens and Armstrong 1984; Tasto 1983) which has led to the notion that they serve as nursery grounds for young-of-the-year (YOY=0+) and 1+ age class crab (Fig. 1.1).

The present management plan for Dungeness crab can put no specific value on the importance of estuaries to the fishery other than to say in general terms that they may be significant. It is therefore difficult to argue to what extent estuaries like Grays Harbor and Willapa Bay should be protected, what sort of development should be allowed and where its location within the estuary might be compatible with habitat requirements of crab. During the last four years (1983 through 1986) of the University of Washington Sea Grant program on Dungeness crab in Grays Harbor, Washington Department of Fisheries (WDF) has interacted with university biologists to interpret data and is now in a better position to understand the species' ecology within the estuary. As a consequence of greater perception that estuaries are important to crab, WDF and other environmental agency representatives, as well as COE, have been instrumental in defining research

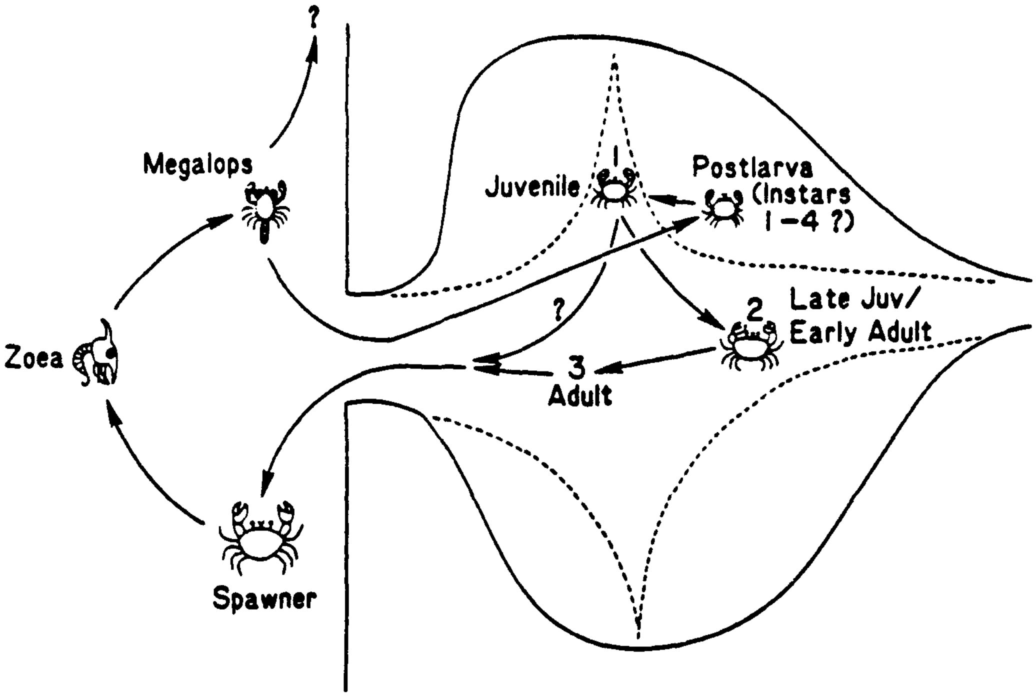


Figure 1.1. General hypothesis for early life history of *Cancer magister* in estuaries. Relative magnitude of postlarval settlement along coast is unknown. Numbers indicate predominant location of age groups. All spawning is oceanic.

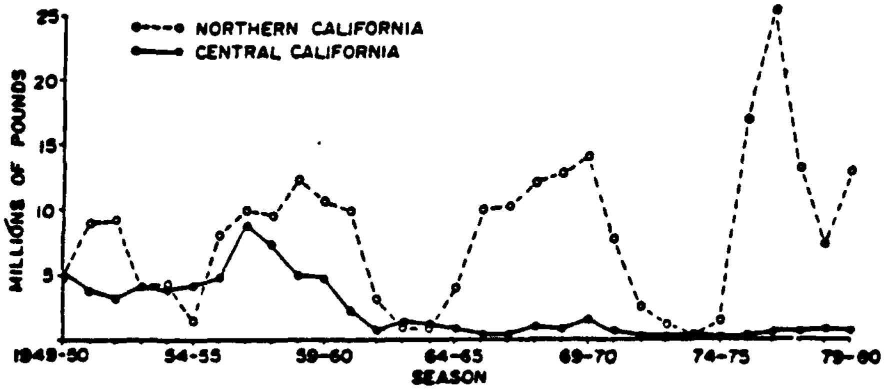


Figure 1.2. Dungeness crab commercial fishery landings for northern and central California by season since 1949.

programs required to answer specific questions of potential impact of W&D or to mitigate against loss.

Plans to alter and develop estuaries will be proposed for decades to come. A warning about the possible impact on Dungeness crab coming from extensive and poorly planned future development of Washington estuaries can be taken from San Francisco Bay. In 1957 landings of crab at San Francisco Bay, in central California, exceeded 9 million lb but by 1960 and for the last two decades landings have usually been about 0.5 million lb (Fig. 1.2). Hypotheses to account for the demise of this fishery include impacts to the bay caused by extensive dredging, landfill, municipal and industrial development and concommitant pollution, and the enormous agricultural drainage that enters the bay complex (see review by Armstrong 1983). The San Francisco estuary has been estimated to shelter more than 80% of incoming YOY in some years (Tasto 1983), which suggests that loss of vital habitat could significantly reduce recruitment to the nearshore coastal fishery.

1.3 BIOLOGICAL DATA FOR IMPACT ASSESSMENT

The dredge impact model (DIM) presented by Armstrong et al. (1987a) relies on a variety of life history information to calculate relative impact of several dredging scenarios to crab. A simplistic approach would be one in which the number of crab entrained and killed per cubic yard (cy) of material dredged was extrapolated to reflect the total cy of the project. The resultant number does not, however, provide any perspective of: 1) the loss relative to the total estuarine and nearshore population; 2) differences in distribution and abundance of crab over seasons; 3) variation in habitat type and crab utilization in and out of the project area; 4) differences in growth and mortality between habitats and; 5) the relative importance of different age classes of crab impacted by dredging and lost to future fisheries. These features of crab life history and age class were incorporated into the DIM by Armstrong et al. (1987a) for a more realistic and flexible (relative to COE construction scenarios) analysis of potential impact during W&D.

1.3.1 Total Population Abundance

Without a sense of the relative size of a local crab population in Grays Harbor it is difficult to judge whether or not an estimate of number killed during W&D (e.g. 10^4, 10^5, 10^6) is substantial. Regulatory agencies such as EPA and COE in concert with management agencies such as WDF may be better able to establish acceptable criteria of "significant" impact based on loss of a percentage of the population rather than on an absolute number, particularly since interannual variation in population abundance is high (see Figs 5.6, 5.7). Information on the magnitude of interannual variation of the total population, and of several age classes provides a basis for estimates of impact (mortality) based on mean, best and worst case population levels in the DIM, which also considers the loss to future fisheries in the context of variable population levels and multiple year classes. While impact to crab populations will come mainly in Grays Harbor estuary during W&D, the perspective of loss should include both estuarine and nearshore populations as the basis for estimating percentages. As discussed in Section 4.0, estuarine and nearshore coastal habitats generally accommodate different life history stages of crab and even age classes of juveniles. Population estimates to which dredging losses will be compared should include both coastal and estuarine stocks, although each system may differ in its relative value (e.g. temperature, food, refuge) to crab.

1.3.2 Temporal and Spatial Differences in Abundance

Because of pronounced seasonal and spatial shifts in abundance of several age classes within the estuary (not withstanding interannual variation) flexibility of dredging schedules and equipment for W&D has been considered in the DIM. Seasonal as well as spatial cycles of abundance have been documented for juvenile Dungeness crab (Armstrong and Gunderson 1985; Gotshall 1978; Stevens and Armstrong 1984) that reflect settlement of larval year classes in spring, and immigration and emigration of older juveniles between the estuary and nearshore, generally in spring and fall. The Corps has already made major adjustments to the W&D schedule because of biological data that provide managers the option of avoiding times and locations of high crab abundances. At this time, scheduling various dredging gear in accord with low temporal and spatial abundance of juveniles in the estuary is viewed as the principle means to attenuate crab losses during W&D.

1.3.3 Habitat

There are three general systems (regions) which are important to crab populations and focus concern on issues of potential dredge impact: the nearshore coastal system and, within the estuary, subtidal channels and intertidal flats. Each of the three systems contains different habitats in the form of variable substrate (e.g. rock, cobble, sand, shell, eelgrass, mixtures), that are of distinctly different quality for juvenile crab as a function of age and season. The relative strength of a given year class of crab will depend, in part, on whether or not larvae settle in an estuary or only nearshore, in sub- or intertidal areas, in shell or on open sand, and whether older juveniles immigrate to the estuary and move to warmer waters in small tidal channels beyond the Outer Harbor. Location of dredging and disposal sites significantly affect predicted losses by the DIM because of transient seasonal use of different habitats (see Pearson, 1987, for discussion of offshore disposal sites). Plans to mitigate for possible crab losses resulting from W&D have included habitat enhancement of intertidal (Dumbauld and Armstrong 1987) sites and, consistent with this approach, proposals to dispose of material in potentially critical habitat (e.g. intertidal; certain nearshore areas) have been abandoned over the years of planning for W&D.

An important measure of the habitats' (estuary, nearshore) importance to juvenile crab is relative growth and survival therein. The latter is difficult to calculate because crab shift between habitats as size, food, and refuge requirements change. Growth rate can be computed and is significantly greater for siblings of an age class within the estuary compared to those nearshore (see Section 6.1.2). As a consequence of W&D within the Grays Harbor estuary, losses resulting from the project will be more significant because larger, faster growing estuarine crab of several age classes will be disproportionately lost from the local population. These are animals that data indicate would reach sexual maturity and the fishery sooner than slower growing nearshore crab of equal age.

1.3.4 Age Classes

Although loss of male and female juvenile crab during W&D (and during subsequent years of maintenance dredging) equates to a loss from a future mature, reproducing adult population, it is loss of legal males from future fisheries that is addressed in the DIM. Age classes and relative numbers lost are important aspects of impact calculations because older crab (e.g. 2+ age class) have fewer remaining years to reach legal size and will experience less natural mortality than will younger (e.g. 0+) crab, and so are of greater value. Size frequency analyses are needed to equate size with age in order to predict number of intervening years to the fishery according to growth equations that distinguish estuarine from nearshore siblings. The combination of species information on age class abundance and also change in distribution between habitats, seasons, and years is used in the DIM to show substantial differences in estimated impact to future fisheries arising from variable loss of several age classes; in general fisheries are more perturbed by W&D when fewer older, rather than more younger crab are killed.

Species ecology and life history traits reviewed in this document have been used in the DIM to predict crab losses during W&D. Losses are given as absolute numbers (with *provisos* about accuracy) but also (and perhaps more usefully) are portrayed in the context of population dynamics measured in the field (e.g. Armstrong and Gunderson 1985a and b) and in terms of cycles in the commercial fishery (Botsford and Wickham 1978; Methot and Botsford 1982). The vagaries of natural levels of abundance and extent of mortality are important perspectives to have in reviewing losses predicted under several W&D scenarios.

1.4 HISTORY OF CRAB RESEARCH IN GRAYS HARBOR

Research on Dungeness crab in and nearshore of Grays Harbor was first reported by Cleaver (1949) who studied movement of tagged adult crab to and from the estuary and timing of settlement and growth rate of juvenile crab. Virtually no systematic work was done on *C. magister* in Grays Harbor until the COE maintenance dredging program necessitated environmental studies on a number of species including Dungeness crab (COE 1976). Limited work on distribution and abundance of crab in the estuary was reported by Tegelberg and Arthur (1977), but was not sufficient to allow forecast of dredge impacts or modification of dredging schedules. To acquire sufficiently detailed biological data to address these two points, and as a partial basis for the W&D EIS, a more systematic survey of crab populations was started in 1980 (Armstrong et al. 1982; Stevens and Armstrong 1984, 1985), as was a study of crab entrainment during dredging (Stevens 1981). In the former investigation, primary objectives were to characterize distribution of several age classes of Dungeness crab within the Grays Harbor estuary, note differences in density as a function of seasons between the inner and outer portions of the estuary, and predict whether or not entrainment mortality during dredging was likely to impact a significant part of the resident population.

Based on results from these investigations, a six-year study of juvenile Dungeness crab recruitment was conducted in 1983 through 1988, sponsored by Washington Sea Grant, that has as its primary objective a comparison of estuarine abundance and population dynamics of crab versus populations that reside nearshore along the Washington coast. In several respects this program was an improvement over previous investigations, primarily because of better survey design and methodology and improved gear (Gunderson et al. 1985). Due to NEPA requirements and concerns expressed by commercial fishermen's organizations as well as by WDF, COE has sponsored analyses of data given in this document as well as additional field programs that primarily address the following objectives:

1. Compare relative size of juvenile crab populations in Grays Harbor to those nearshore in the adjacent coastal area.
2. Determine size frequency and age class differences between populations in these two general areas.
3. Define smaller scale regional differences in distribution and age class structure within the estuary or nearshore, primarily in regards to the navigation channel proposed for W&D in Grays Harbor or specific nearshore sites for disposal of estuarine material.
4. Characterize attributes within the estuary (e.g. substrate, temperature, predators) that might benefit crab populations there compared to those nearshore.

5. Study population dynamics of 0+ crab within intertidal shell debris (shellhash) and test field plots for the purpose of future mitigation.
6. Determine the extent of fall emigration from the estuary, location of overwintering juveniles, and whether or not they bury in substrate.
7. Analyze crab samples from a series of nearshore site characterization studies (conducted by Battelle Northwest Laboratories; Pearson et al. 1987), to document seasonal crab distribution at proposed disposal sites.

Because of the direct applicability of data acquired during the University of Washington Sea Grant projects, COE sponsored analyses of 1983 field data that was reported by Armstrong et al. (1984) in a comprehensive review of literature on estuarine ecology of Dungeness crab as well as a summary of results from 1983. Subsequently, analyses of data collected in 1984 and 1985 were done by Armstrong and Gunderson (1985b) and Armstrong et al. (1986), respectively, and data taken in 1986 are incorporated into this review of crab ecology and the DIM analyses of Armstrong et al. (1987a). Other reviews of Dungeness crab life history and population dynamics can be found in the Alaskan Sea Grant Symposium on Biology and Management (1985), by Armstrong (1983), Hankin (1985) and Botsford (1986).

1.5 THE SEA GRANT PROGRAM IN GRAYS HARBOR

The majority of data acquired on crab in Grays Harbor that has been used in the DIM and to describe overall ecology of the species, comes from the University of Washington Sea Grant program which has been described in some detail (Armstrong and Gunderson 1985a and b; Carrasco et al. 1985; Gunderson et al. 1985). A stratified random survey established in 1983 divides the estuary into four strata (Fig. 1.3) that correspond to the Outer Harbour (Str 1), North Bay (Str 2), Inner Harbor (Str 3) and South Bay (Str 4), and cover only subtidal areas. Eighteen randomly selected stations were sampled beginning in April through September every two weeks (1983, 1984) or monthly (1985, 1986) during the spring tide series. In 1985, a similar survey design of 20 stations was initiated in Willapa Bay (Fig. 1.4) to compare crab populations between the estuaries, and to more closely compute estuarine crab abundance for contrast to that nearshore.

The nearshore survey design is based on five transect lines (three lines in 1983 and 1984) that are situated off Copalis Head in the north, Oyhut, Westport (just outside and south of the Grays Harbor jetty entrance), Cape Shoalwater (at the northern edge of Willapa Bay), and Leadbetter Point (Fig. 1.4). A series of seven stations arrayed according to depth are sampled on each transect line, and in 1984 replicate stations were added at 28 and 37 m (Fig. 1.4). These stations

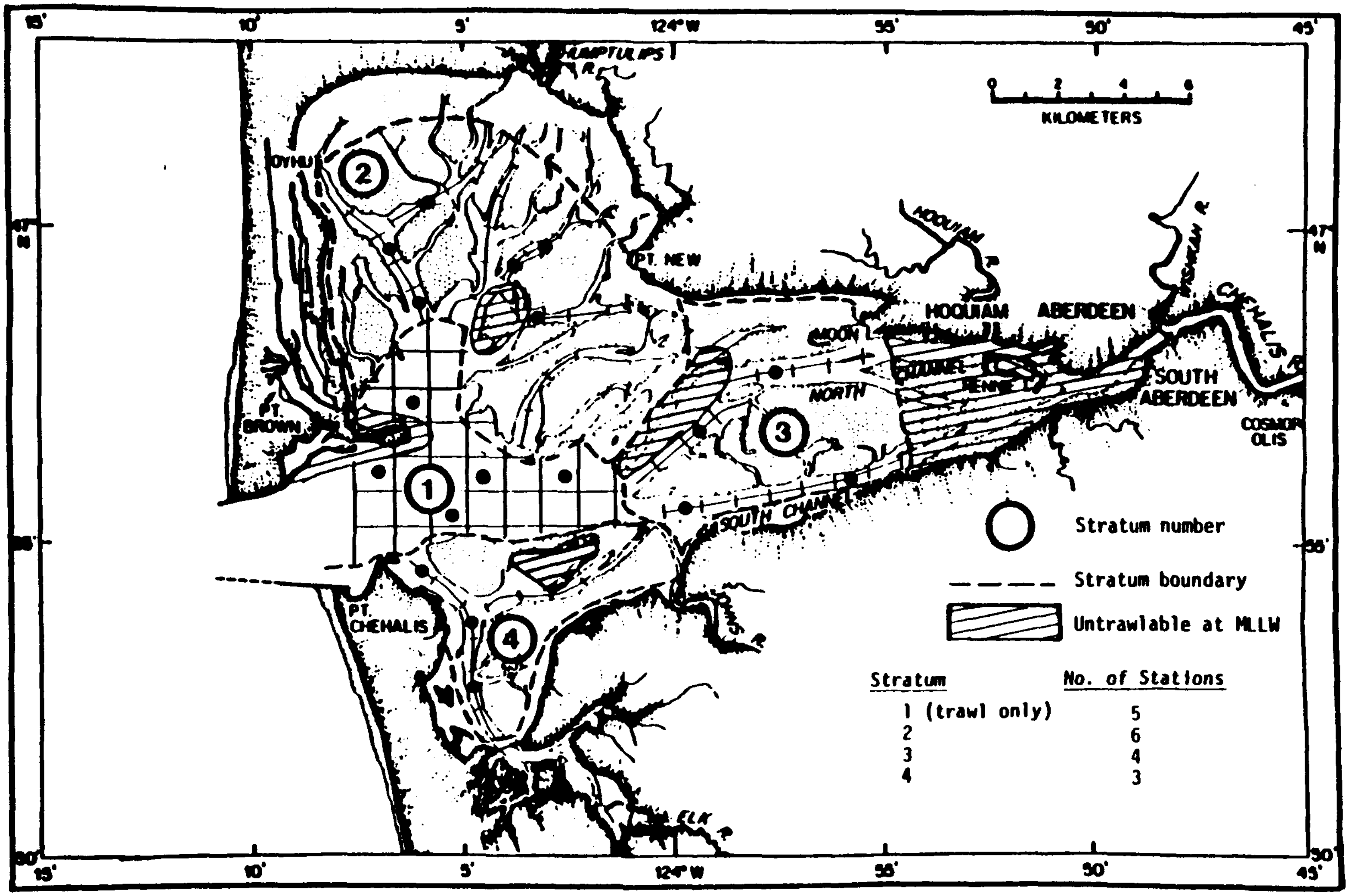


Figure 1.3. Survey design used to sample Dungeness crab density in 1983-1986. Four strata are shown, each divided into one kilometer grids for the subtidal areas only. Randomly selected stations are shown as dark circles and each is sampled bimonthly from April through September. The eastern portion of the estuary was deleted because of few crabs (Armstrong et al., 1982) and the difficulty of trawling.

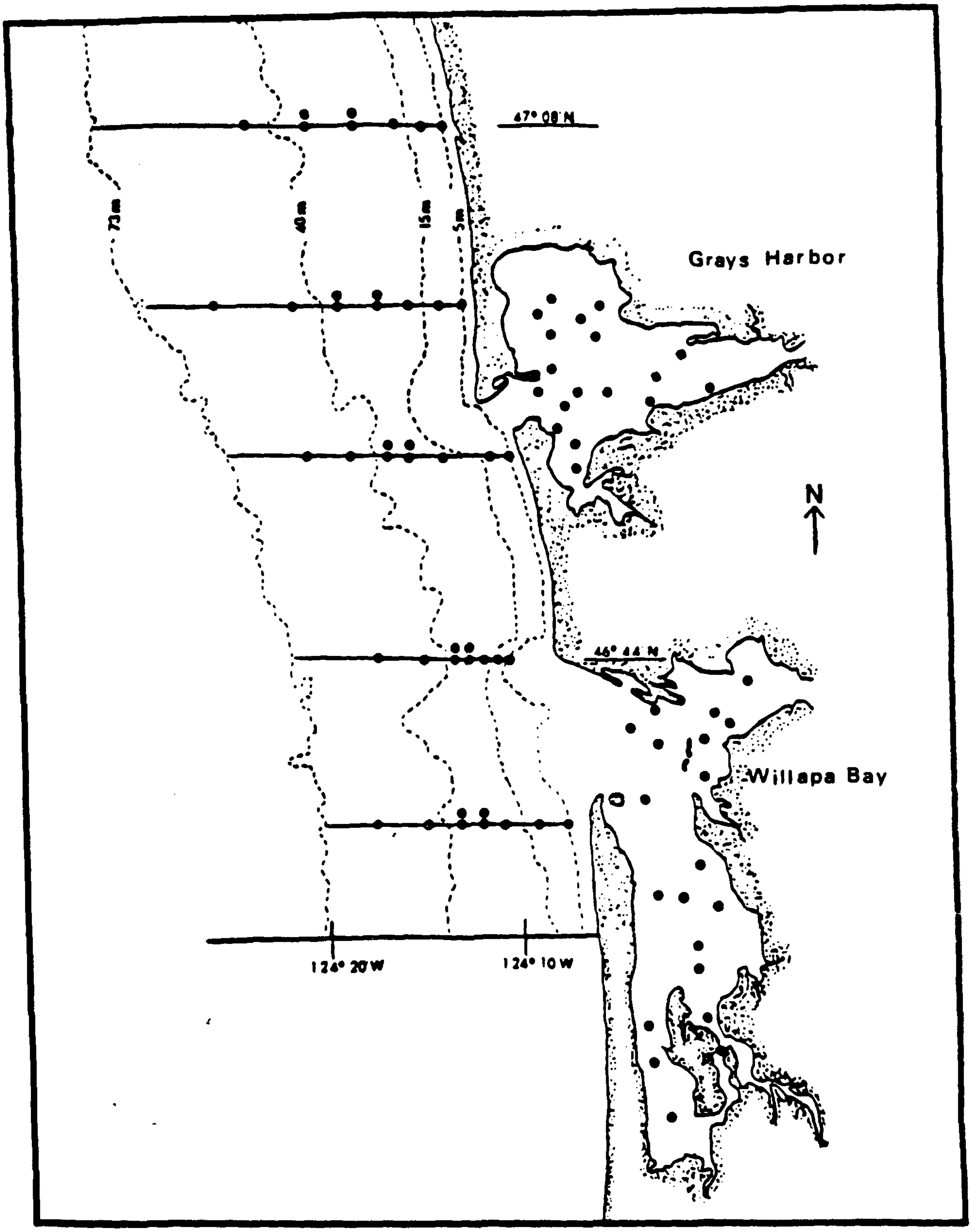


Figure 1.4. Dungeness crab survey design, 1983 through 1986. Dots represent sampling stations, solid lines represent nearshore transects. Willapa Bay and two of the transects were sampled only in 1985 and 1986. Each station was sampled at least monthly from May through September.

are sampled approximately monthly between May through September which encompasses the period of metamorphosis, settlement and first summer growth of a new year class.

The plumb-staff beam trawl used as the standard survey gear in this program (Gunderson et al. 1985; Fig. 1.5) is designed primarily to catch very small, newly settled instar crab in addition to the more typical one (1+) and two (2+) year old animals routinely surveyed in past investigations. Crab are measured to the nearest millimeter, sexed, and enumerated on computer files for subsequent calculation of station density and derivation of population estimates.

Population estimates are made by extrapolating station density within stratum to the total area of each strata digitized on computer, according to calculations described by Armstrong and Gunderson (1985a), and only the subtidal areas of estuaries are used for abundance estimates based on trawls. Nearshore stations are grouped into three strata that run north/south with east/west boundaries set at 5, 15, 40 and 73 m (Fig. 1.4). Population estimates of total crab in each system and stratum can be divided into three age classes (0+, 1+, >1+) according to size-at-age schedules derived from length frequency data (Section 6.1.2). The majority of crab in the >1+ age class are 2+ animals but it is sometimes difficult to separate large 2+ from small 3+, so the small fraction in the latter category are grouped into an inclusive >1+ age class.

A limited intertidal survey of 0+ crab density was done in 1983 and 1984 on the extensive mudflat that separates North and South Channels in Str 3 (Fig. 1.3), since abundance of this age class was more than expected. Because of high abundance found in those two years, COE funded a more comprehensive program in 1985-86 at three locations within the estuary (Str 2, 3, 4) to more accurately quantify 0+ populations and study the feasibility of mitigation through creation of optimal intertidal habitat for this age class (see Section 4.3.3 this report; Dumbauld and Armstrong 1987). At minus tides when the substrate was exposed, series of quadrat samples were taken to estimate crab density in relation to the presence or absence and type of epibenthic material (e.g. shell, eelgrass; see description by Armstrong and Gunderson, 1985). The results of these investigations indicate that shellhash (empty bivalve shells) composed of oyster and softshell clam, *Mya arenaria*, constitute the primary area of intertidal settlement and first-summer survival of an incoming 0+ age group of juvenile Dungeness crab in Grays Harbor. Population estimates were made by extrapolating density per m^2 to total area of several categories of habitat determined by aerial surveys (Coast Guard helicopter) and groundtruthing transects (Dumbauld and Armstrong 1987).

Through a combination of estuarine (sub- and intertidal) and nearshore surveys of crab density in spring through summer (plus a COE program in fall through winter 1985/86), a quantified time series of data has been obtained that enables a description of spatial and temporal population dynamics by age class, as well as a measure of interannual variability in abundance.

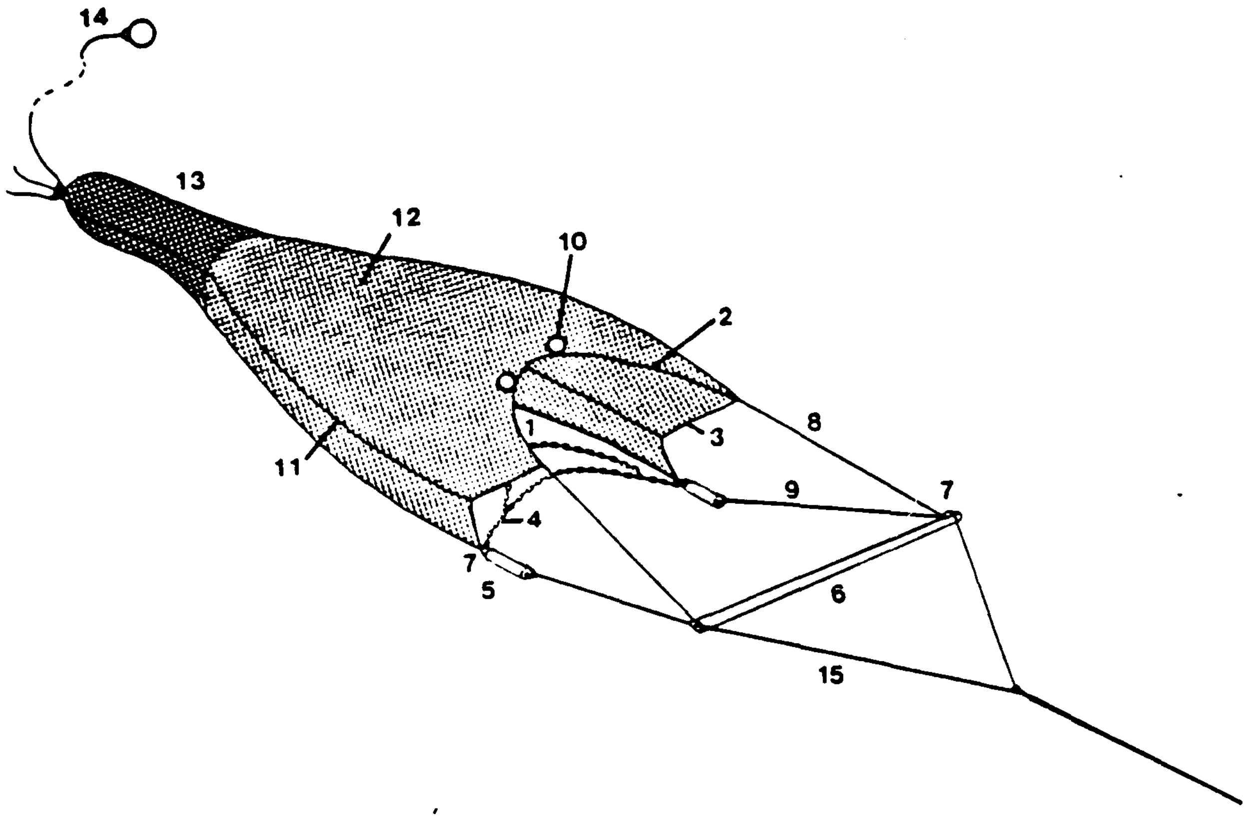


Figure 1.5. System developed for sampling juvenile Dungeness crabs and flatfish. 1, 5.1 m footrope; 2, 4.1 m headrope; 3, 1.0 m breastlines; 4, tickler chain arrays (4.3 and 4.9 m sections of 1.9 cm chain); 5, wingtip weight, 6.0 x 40.6 cm, 9.5 kg; 6, beam, 3.8 cm x 3.1 m aluminum conduit; 7, quick-release snap; 8, upper net bridle, 1.0 cm x 1.8 m; 9, lower net bridle, 1.3 cm x 1.4 m; 10, 7.6 cm cork float; 11, ribline; 12, main body of net, 7-9 mm (lumen) square knotless nylon; 13, cod-end, with 4.0 mm liner; 14, emergency retrieval line, with 20 cm float; 15, beam bridle, 1.3 cm x 3.1 m. Total length, wings to cod-end, is 7.9 m. Further information is available from Ellis Highliner Fishing Gear, P.O.Box 55028, Seattle, WA 98153, U.S.A. (after Gunderson et al., 1985).

1.6 PHYSICAL ENVIRONMENT OF GRAYS HARBOR

Grays Harbor estuary occupies a drowned portion of the Chehalis River mouth, extending 25.2 km (16 mi) east-west and 20 km (12.4 mi) north-south at its widest point. It covers an area of 223 km^2 (86 mi^2) at extreme high tide, and 99 km^2 (38 mi^2) at MLLW, exposing 124 km^2 (48 mi^2) of intertidal sand and mud flats (56% of total area). Water volume ranges from 10.5 x $10^8 m^3$ (13.7 x 10^8 cy) at extreme high tide to 3.9 x $10^8 m^3$ (5.1 x 10^8 cy) at MLLW. Most of the harbor is less than 5.5 m (18 ft) deep, but depths reach 18.5 m (60 ft) near Point Chehalis (COE 1976).

Grays Harbor receives 180-250 cm (70-100 in) of rainfall yearly, and has an annual average freshwater input of 10,500 cubic ft per sec (cfs) of which 80% comes from the Chehalis River. Tides are unequal semidiurnal with maximum spring ranges of -0.9 to +3.8 m (-3.0 to +12.5 ft) at Aberdeen, and an annual mean range of 2.1 m (7 ft). The harbor is a type B salt wedge estuary where tidal flow exceeds river flow, and tidal flow at surface and bottom are about equal. It is also classified as a positive estuary where influx (precipitation plus runoff) exceeds evaporation, and net surface flow is seaward. Strong tides cause the salt wedge to vary in position, and to reverse the direction of river flow as far upstream as Montesano on incoming tides. Such pronounced upriver exercusions of water on a flood tide, as well as pressure driven influx of ocean water into estuaries during upwelling periods (Duxbury 1979) provide mechanisms of larval crab transport discussed elsewhere in this report (Section 4.2).

A horizontal salinity gradient is maintained from Grays Harbor mouth to Aberdeen, with differences of 15 to 25 ppt between those points (Fig. 1.6). Vertical mixing is very strong, causing surface and bottom salinity differences of only 1 to 3 ppt in the Outer harbor, and about 5 ppt in the upper reaches, but occasionally reaching 10 ppt at the latter. Changes in salinity on a diurnal and, more significantly, seasonal basis may limit the distribution of crab within the estuary (Stevens and Armstrong 1984) because of osmoregulatory stress (Stevens and Armstrong 1985). Mean annual bottom water salinity was reported to range from 9 ppt near Aberdeen to 29 ppt in the estuary mouth (Stevens and Armstrong 1984). Annual water temperatures range from 3.3^{o} to $21.1^{o}C$ (38-$70^{o}F$, COE 1976), but in the spring and summer are more typically 10^{o} to $16^{o}C$ while nearshore temperatures are 8^{o} to $10^{o}C$ (Armstrong and Gunderson 1985a; Fig. 1.6).

Marine sediments occur from the harbor mouth to about halfway to Aberdeen, well into the South Bay, and about halfway into the North Bay. Fluvial deposits are present near the river mouths, and a zone of mixed sediments occurs in an area between the fluvial and marine deposits. Perhaps more important for juvenile crab are several types of epibenthic material present in the subtidal that may provide refuge and food. Paramount are bivalve (*Tresus* sp., *Crassostrea gigas, Clinocardium nuttalli)* and barnacle shell, sticks, eelgrass debris *(Zostera marina)*, and several species of macroalgae. In the intertidal, *Mya* sp. and oyster shell are more important habitat for 0+

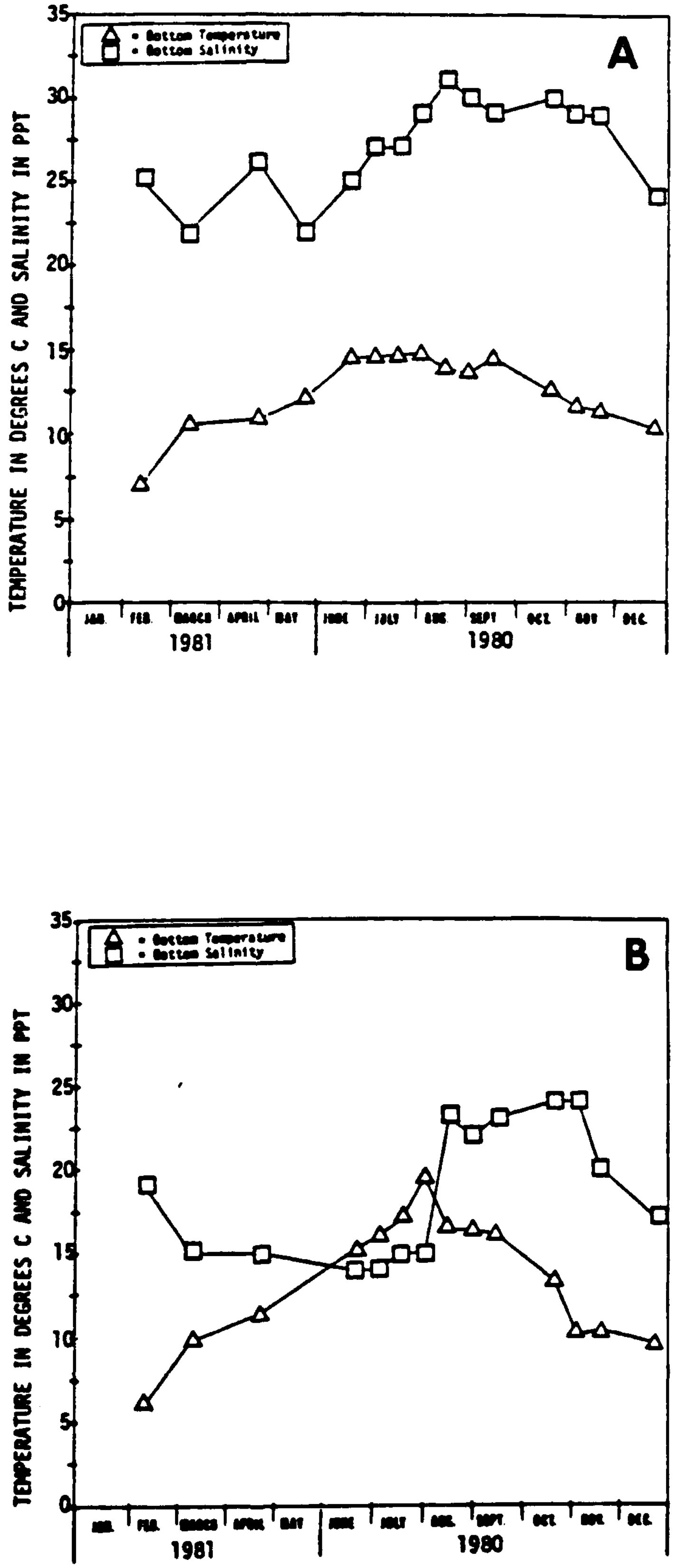


Figure 1.6. Seasonal change in bottom temperature and bottom salinity. A, South Reach; B, Cow Point. Years are reversed to present a continuous seasonal progression (from Armstrong et al., 1982).

crab (Dumbauld and Armstrong 1987) than is eelgrass as reported by Stevens and Armstrong (1984).

2.0 LIFE HISTORY

Much of the life history of *C. magister* occurs along the open coast and will not be directly impacted by W&D during actual construction operations, with the possible exception of perturbations caused by nearshore disposal of certain estuarine sediments. A general overview of crab life history should help to orient the reader as to which stages are most susceptible to estuarine impacts, but also to give a perspective of when and where other life history processes occur.

Dungeness crab life history is most easily portrayed as distinct stages of development shown as pelagic larvae, small benthic postlarvae (instars), older juveniles and mature adults (Fig. 2.1). The species is found nearshore along the open coast and in estuaries from central California through southeastern Alaska (see Symposium Proceedings, Alaska Sea Grant 1985; Dahlstrom and Wild 1983; Pauley et al. 1986). Mature crab and all reproductive events occur along the open coast (and throughout much of Puget Sound) and there is no evidence of reproductive activities in coastal estuaries including San Francisco and Humboldt Bays, California, and Grays Harbor, Washington (Armstrong and Gunderson 1985a; Stevens and Armstrong 1984, 1985; Tasto 1983). The general life history scenario presented in Figure 1.1 indicates that in the spring after an onshore migration females molt to maturity nearshore where they are bred by males, carry sperm for about six months and extrude an egg mass the following fall (Diamond and Hankin 1985). This egg mass is carried on the abdomen of the female (eggs not released into the water column) for approximately three months of embryonic development (Pauley et al. 1986; Reed 1969). Larvae hatch in the winter primarily between December and February and progress through five larval stages called zoeae which occur in the water column between December and March. There is evidence that larvae occur progressively farther offshore through the five developmental stages (Lough 1976; Reilly 1983a), and it is speculated that larvae might also be transported substantial distances alongshore during this period, particularly from south to north in the Davidson current (Johnson et al. 1986; Reilly 1983a). After five zoeal stages, larvae molt one last time to the final pelagic stage called a megalopa (see Fig. 2.1), and may return onshore by either directed swimming and/or in favorable current regimes (Johnson et al. 1986; Lough 1976; Reilly 1983a).

Movement of megalopae onshore is partially responsible for successful year class strength (see Section 4.2), and they are most prevalent within a few kilometers of shoreline where they settle to the benthos and metamorphose into first instar benthic juveniles (Figs 1.1, 2.1; Armstrong and Gunderson 1985a; Stevens and Armstrong 1985). Movement onshore may be coupled to chemosensory behavior and detection of lower salinity plumes nearshore associated with estuaries (Sugarman et al. 1983) and, indeed, megalopae directly enter the Grays Harbor estuary in high abundance (Armstrong and Gunderson 1985b; Armstrong et al. 1985a; Stevens and Armstrong

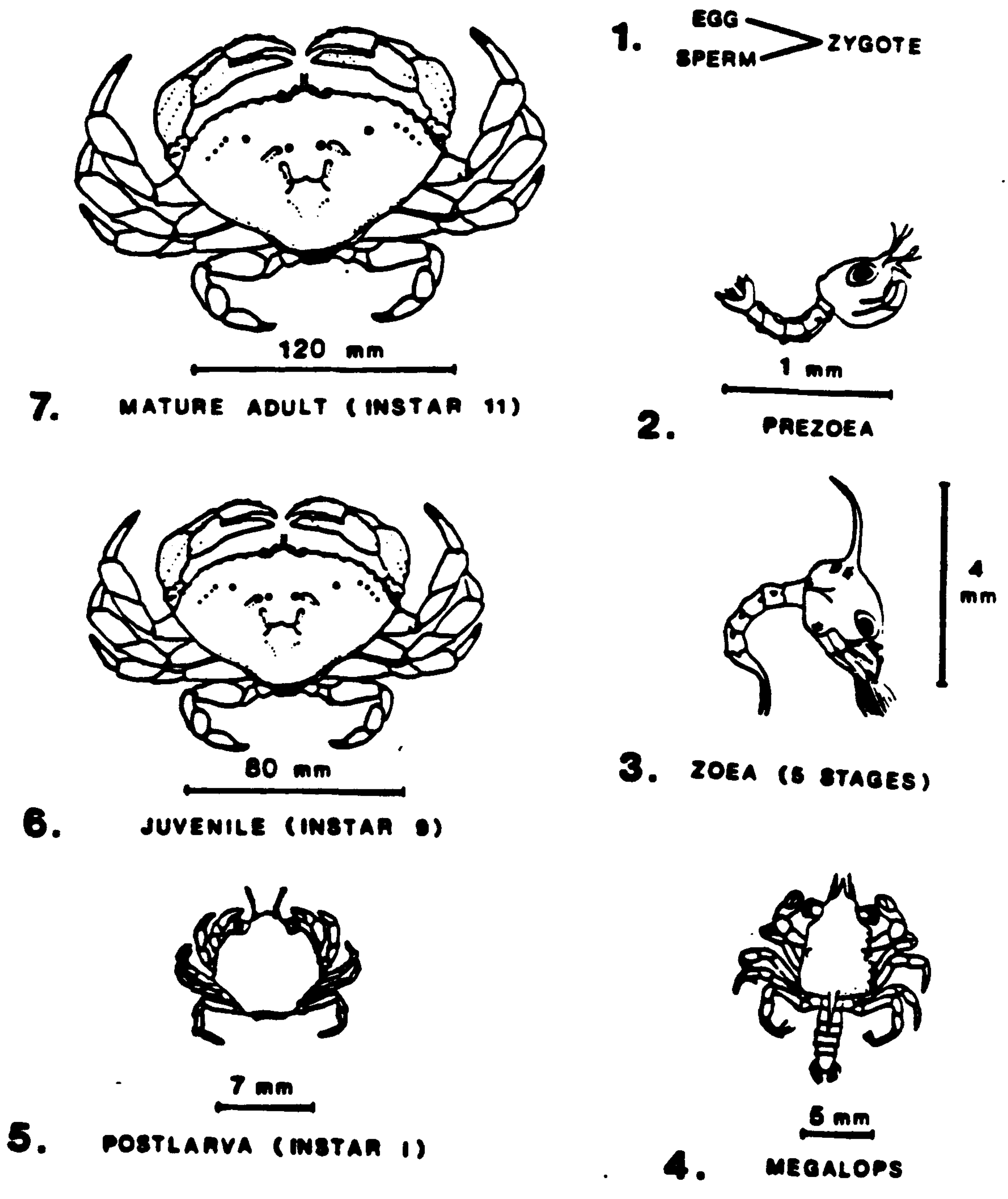


Figure 2.1. Life history stages of Cancer magister after various authors: prezoea (Buchanan and Milleman, 1969); zoea and megalops (Poole, 1966); postlarva, juvenile, adult (Mackay, 1942) (from Armstrong et al., 1982).

1984) although this does not seem to be the case off Central California where few megalopae enter San Francisco Bay (Reilly 1983a). After settlement and metamorphosis, growth of juvenile crab in estuaries (Armstrong and Gunderson 1985; Stevens and Armstrong 1984, 1985; Tasto 1983) is substantially faster than nearshore (Gutermuth and Armstrong 1989; Butler 1961; Poole 1967; Tasto 1983), which further underscores the importance of transport/movement onshore and entry into estuaries. Both male and female crab reach sexual maturity at about age two (Butler 1960; Hankin et al. 1985) although males probably do not breed until age three or older. Late juvenile and early adult crab leave coastal estuaries prior to reproductive events (Gotshall 1978; Pauley et al. 1986; Stevens and Armstrong 1984; Tasto 1983) which again all occur along the coast and complete the life cycle (Figs 1.1, 2.1).

2.1 RELEVANCE TO GRAYS HARBOR W&D

A summary of life history stages and the extent of their occurrence in estuaries (exclusive of Puget Sound) will give the reader a sense of that system's relative importance to each stage compared to the nearshore coastal system. Detailed information follows in subsequent sections.

Breeding Adults: There is no evidence that reproduction occurs in estuaries.
Eggs: Females extrude and carry fertilized eggs entirely nearshore, not in estuaries.
Zoeal Larvae: Eggs hatch and all five zoeal stages develop along the coast, not in estuaries. Occurrence of zoeae in estuaries should be considered superfluous to annual reproductive effort since these larvae would be relatively few of the annual hatch, and would not likely survive estuarine conditions in winter because of low salinities.
Megalopal Larvae: Zoeae molt to megalopae along the coast where most development of this last pelagic stage occurs. Advanced megalopae (near molt) may enter estuaries in spring (May, June) if the population occurs nearshore, but the magnitude of interannual estuarine populations varies substantially compared to megalopae that remain nearshore along the coast. Arrival of megalopae to estuaries is viewed as important for a strong year class.
Juveniles: Significant populations of several juvenile age classes use the estuary for one or two summers of growth. 0+ crab may recruit directly to the estuary at settlement in spring and remain through a second year as 1+, or 1+ crab immigrate to the estuary from nearshore in early summer of their second year. Use of estuaries enhances year class strength through faster growth and perhaps better survival of older 0+ and 1+ than occurs nearshore, but the relative proportion of any year class that reaches estuaries is highly variable.

3.0 THE FISHERY

The bulk of the fishery for Dungeness crab is located nearshore in relatively shallow water less than 50 m depth where only males >160 mm cw (variable by state) are taken in pots. The fishery generally opens in December and most of the annual landings occur by March (see series of reviews in Alaska Sea Grant 1985; Pauley et al. 1986), but open seasons may extend through summer. A closure is usually enforced in fall to provide legal males that have molted in September-October time to harden and fill out in meat before the winter opening of the fishery (Demory 1985). Washington State coastal landings have fluctuated between a low of about 2.6 million lb (1981/82) to a high of 18.4 million lb (1968/69), and most of these totals come from coastal fisheries landed at ports on the Columbia River, and in Grays Harbor and Willapa estuaries, primarily the latter; only about 10% of the seasonal catch is taken directly in the Grays Harbor and Willapa Bay estuaries (Barry 1985).

Most striking about the time series of annual landings of Dungeness crab along the coast from California through Washington have been the cycles of apparent abundance that show a period of about 9 to 10 years, approximately twice the mean age of male crab caught by the fishery (Fig. 3.1; PMFC 1985; Botsford 1986). Methot and Botsford (1982) estimated preseason abundance of male Dungeness crab from actual fisheries data and determined that the time series of population abundance and recruitment is not as smoothly cyclical as is the catch record (Fig. 3.2), and that the fishery can occasionally be dominated by single exceedingly strong year classes. Indeed, such a catch record may be highly imperfect as an indicator of actual population abundance for various age classes but does seem to highlight a trend in which occasional years of Dungeness crab recruitment along the coast are highly successful, probably for reasons of nearshore oceanographic features and processes (see Section 4.2.3).

3.1 INTERPRETATION OF CYCLES

The impact of W&D in Grays Harbor must be considered in the context of these cycles of abundance in the fisheries, both because of the potential effects of dredging on population dynamics, (and hence the cycles), and because the cyclic fluctuations of populations will limit the detectability of impacts from dredging. For these reasons, and because the research into causes of these cyclic fluctuations provides an additional perspective on crab life history and population dynamics, we present a brief review of that research here.

The first question of interest regarding the cycles in catch is whether they reflect fluctuations in abundance. Research on the northern California crab population indicates that cycles in catch do

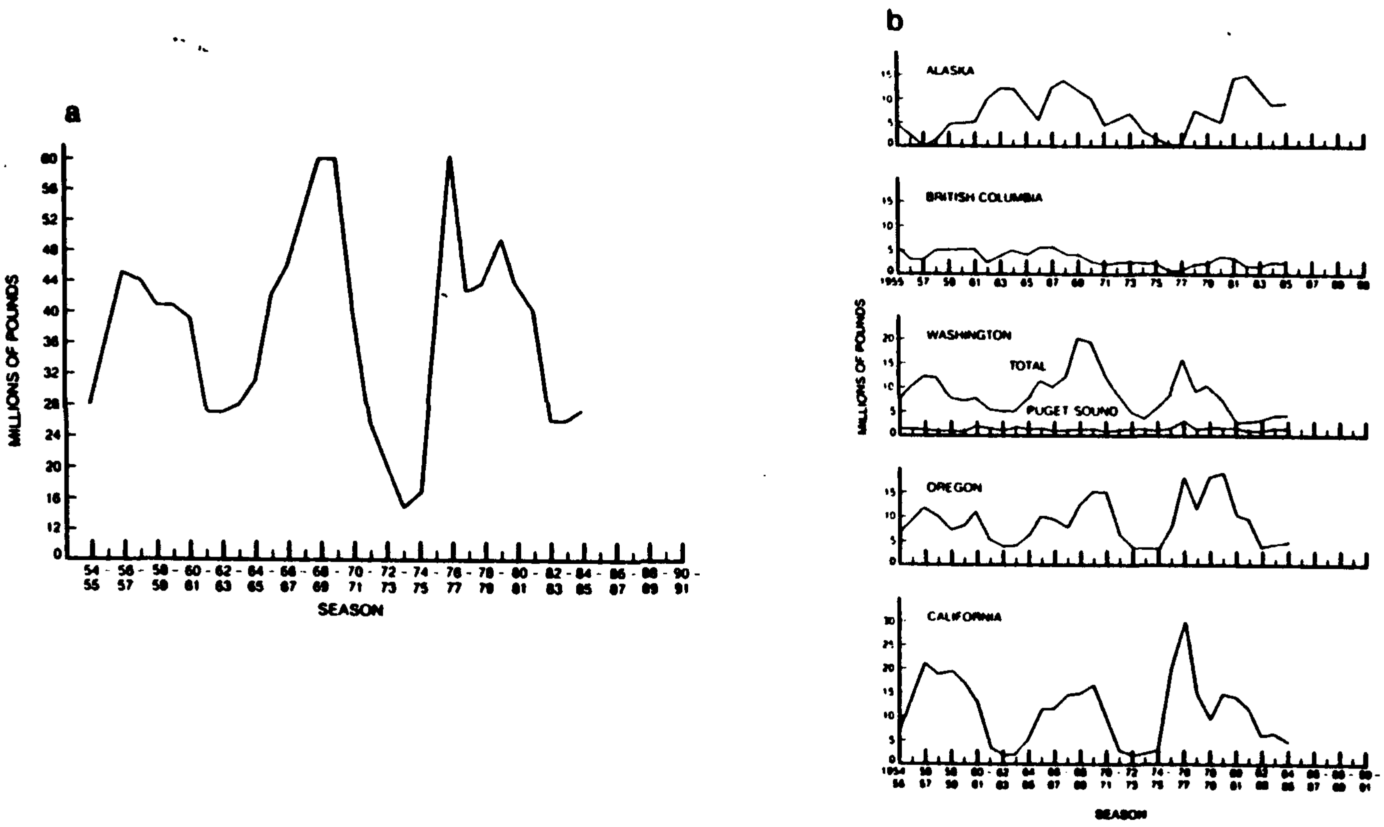


Figure 3.1. Pacific coast Dungeness crab landings by season, 1954-1985. a: coastwide total; b: by jurisdiction.

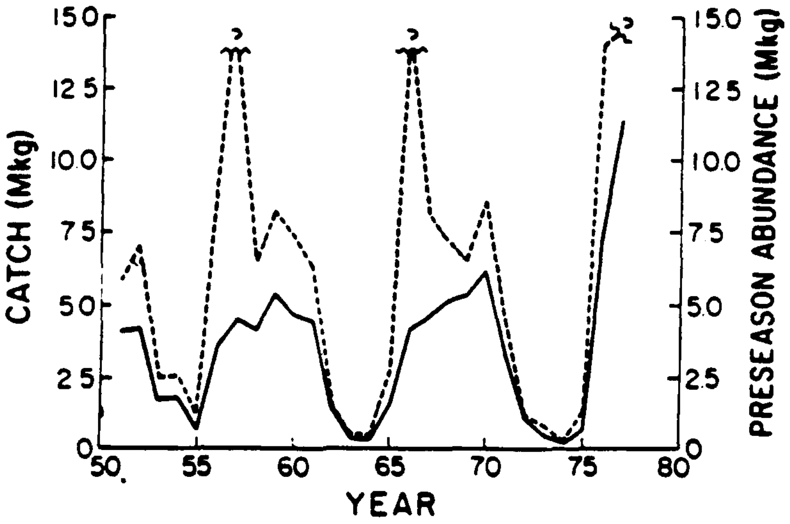


Figure 3.2. Catch (solid) and preseason abundance (broken line) in the northern California Dungeness crab fishery (from Methot and Botsford 1982).

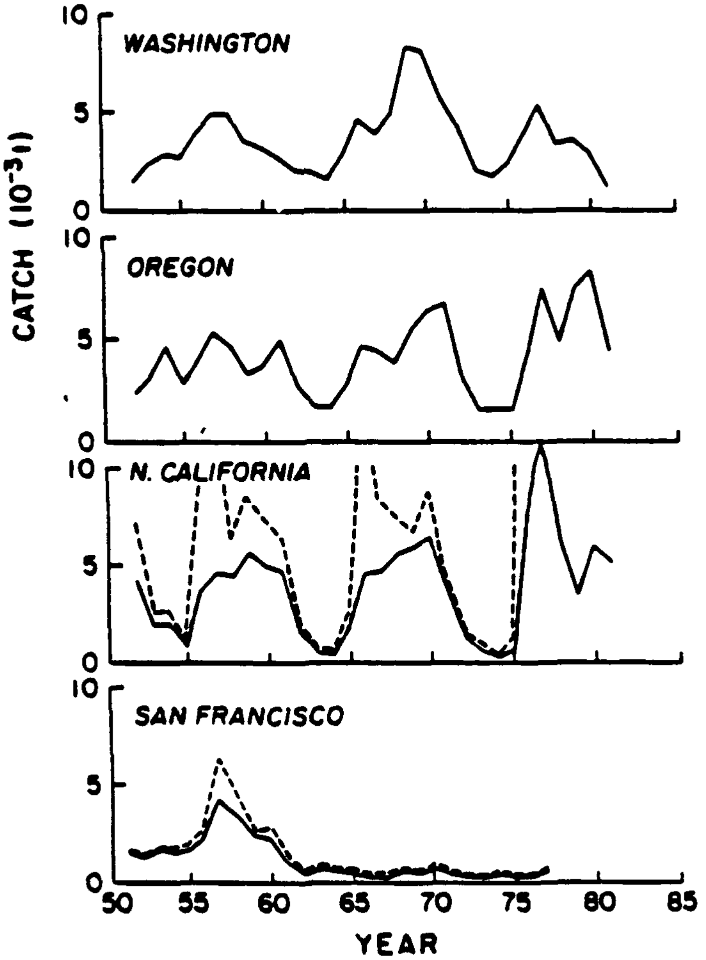


Figure 3.3. Catch series at various locations throughout the range of the Dungeness crab. Dashed lines are estimates of preseason abundance (Methot and Botsford 1982, points shown as offscale where extremely high their abundance could not be estimated). Only males greater than a certain carapace width are legally taken. N sustained decline off San Francisco since 1962.

reflect cycles in abundance, but that they are probably a distorted version of them (Methot and Botsford 1982; Botsford et al. 1983). This distortion is due to the fact that fishing effort has not remained constant, hence we do not sample a constant fraction of abundance each year. Fishing effort has increased over the past 30 years, and effort changes from year to year in response to changes in abundance, with a time lag of 1 to 2 years. This lag has decreased with the increase in real value of the crab over the years. The relationship between catch and estimated abundance for northern California is shown in Fig. 3.3 and is probably similar for Washington.

The fact that fishing effort varies in response to abundance has led to the proposal that the cycles are caused by this lagged response together with a lagged response of recruitment to reduced effort in a classical predator-prey cycle. However, since research has shown that the latter response is not present, this mechanism is not a likely cause (Botsford et al. 1983). A related suggestion is a predator-prey cycle with chinook or coho salmon, which feed on crab megalopae, as the predator (Thomas 1985). However, time series analyses has shown that covariation between salmon and crab have the wrong timing for this mechanism to be operating (Botsford et al. 1982).

One of the most important issues regarding the cycles in the fisheries in the context of the potential impact of work in Grays Harbor, is the point in the crab life history at which the cycles are caused. In all closed populations, the number in each year class declines continuously with time as the year class grows and ages. Although this happens in a random fashion, there is often one critical point at which year class abundance is determined. This point is of obvious importance in population dynamics in general and is an important issue in research on cycles of the crab. To detect this point researchers compare size or age distributions from different years, and attempt to follow year classes through time.

Consistent order of year classes after a certain age is taken as evidence that year class size is set before that age. Dungeness crab size distributions collected in the 1960s and 1970s in northern California do not show much year-to-year consistency, except in a couple of instances of extremely large year classes (i.e. the 1968 and 1973 year classes). These data suggest that year class size is set early in life, but are too "noisy" to be considered solid evidence. On the basis of other considerations, such as the vulnerability of early stages, year class size is assumed to be set within the first year of life and so, in turn, is the strength of a future fishery.

Some evidence of where this critical point occurs in the early juvenile stages comes from the Sea Grant crab population data base for Grays Harbor (see Sections 4.3, 5.4). Although estimated abundance of 0+ crab has varied by as much as a factor of 40x between 1983-1986 (Fig. 5.6), that for the 1+ age class has typically varied between 2-3x during the same time. This implies that the newly settled 0+ population is fairly labile each year, but that mortality rates have stabilized by the age of 1+.

3.2 IMPLICATIONS FOR DREDGING GRAYS HARBOR

There is considerable uncertainty regarding the cause of cycles in Dungeness crab catch (Botsford et al. 1989). The range of possible causes (see Section 5.1), from biotic to environmental hypotheses, includes mechanisms that would imply very different management by state fishery agencies. Unfortunately management, whether for better harvest in the fishery or assessing the impact of dredging, must take this uncertainty into account.

Because the uncertainty involves the relationship between adult stocks and the number of offspring they produce, the long term effects of dredging will be impossible to predict accurately. While we can predict the direct losses of crab entrained during the W&D that do not make it to the fishery (i.e. the short term effects), we cannot predict the results of lost reproductive effort. A possible rough indication of the impact on future stocks is to compute the relative effect on total egg production. However, this would not be a prediction of future reproduction but rather an indication of impact on stock safety. Another approach would be to assume a steady-state population in which the number of 2+ females (sexually mature) lost during W&D would have replaced themselves and an equal number of males a generation hence. Female loss could then be equated to lost production of males in a future fishery, in addition to the immediate loss of males during actual construction of the project.

A second implication of these random cyclic fluctuations is their effect on detectability of the impact of dredging. It is extremely unlikely that the effects of dredging on catch in the fishery will be detectable from a time series of catch records because the magnitude of the fisheries and their variability may be substantially greater than numerical loss of legal males caused by dredging. However, this should not be taken to imply that there is no demonstrable impact on catch. The fact that the magnitude of the impact is "down in the noise" may reflect the high magnitude of the noise, rather than justify a conclusion of low magnitude of impact. The protracted decline of the central California Dungeness crab fishery is a reminder that even "healthy" cycling populations are subject to dramatic change.

4.0 HABITAT AND TIMING

The three major life history stanzas of Dungeness crab - larvae, juveniles, adults - and stages therein have substantially different habitat requirements that vary temporally and spatially throughout the species life cycle. In the context of this report, "habitat" is inclusive of the geographical area of occurrence (e.g. estuary, nearshore, pelagic), abiotic (e.g. sediment composition, temperature) and biotic (e.g. food, predators, refuge) attributes of areas that typify locations of high abundance of life history stages. Access to these habitats for reasons of food and/or refuge, seasonal timing of movement to and from such habitats, and the extent of interannual variability in timing of use of habitats may significantly affect population dynamics of different age classes of crab and, in turn, commercial fisheries (see Section 5.0). Habitat and timing are paramount issues in analyses of the COE W&D project, and are critical components of the DIM used to calculate crab loss under various scenarios of dredging operations (see Armstrong et al. 1987a). So important are timing and habitat in the early life history of *C. magister*, that COE has already made major spatial and temporal adjustments to its dredging schedule as a means to reduce crab loss during construction (see summaries of Crab Study Panel meetings; W. Pearson Coordinator, Pacific Northwest Laboratory).

4.1 GENERAL CHARACTERISTICS OF HABITAT SUBSTRATE

While initial distribution in spring of newly settled, early instar crab reflects to a great extent transport patterns of larvae, later patterns of distribution and abundance of 0+ crab in summer depend, in part, on general features of the substrate that provide refuge and certain types of food (Stevens et al. 1982). Locations of older 1+ and 2+ juveniles in spring/summer is also influenced by characteristics of substrate, which vary substantially between habitats. A brief description of sediment composition for portions of the Grays Harbor estuary and nearshore are as follows:

4.1.1 Nearshore

Coastal substrate nearshore that typifies Dungeness crab habitat is composed of open, homogeneous sand/silt and small gravel. All benthic life history stages nearshore can be found on "sand" (as a general term that includes silts) including breeding adults (MacKay 1942; Waldron 1958) and newly metamorphosed juveniles (Carrasco et al. 1985; Gotshall 1978), and are not associated with large cobble and rock as are other species of *Cancer* (e.g. *C. oregonensis*, *C. productus*). Nearshore of Grays Harbor, general sediment characteristics have been noted along the five transect lines shown in Fig. 1.4. Most of the region from 5 m to 40 m depth is relatively smooth sand with areas of gravel intermixed. Deeper than 40 m, particularly to the north off Copalis Head, rock is more common and gravel is interspersed throughout. The boundaries between sand and gravel can be highly convoluted and the location of the latter is very patchy as shown in Fig. 4.1 for an area offshore of Grays Harbor mapped with side scan sonar by Williamson and Assoc. for COE. Information on the broad extent of sand substrate adjacent to Willapa Bay and Grays Harbor estuaries, gives the impression that little cover and refuge exists for early juvenile stages of crab following settlement and, as a consequence, mortality is likely high in the area.

Epibenthic material occurs over sand in some areas off Grays Harbor and may be important habitat for small juvenile crab although the quantity and extent varies interannually. At most sampling stations inside 15 m depth (Fig. 1.4), sand dollars (*Dendraster excenricus*) are very dense (Carrasco et al. 1985; video data, W. Pearson, Battelle NW) and may provide food and shelter to large and small crab, respectively. Perhaps more important for small crab, there are wide areas of marine and terrestrial plant material, which are assumably estuarine in origin. Along and over the Grays Harbor Bar, deciduous leaves, sticks and pine cones are commonly taken in trawls, and eelgrass (*Zostera marina*) in various stages of decomposition was taken in large quantity by trawl in 1983 and 1984, particularly off Willapa Bay (Carrasco et al. 1985). Eelgrass debris extended in depth from 18m to 46m (10 fm to 25 fm) with a peak at 37m (20 fm), and juvenile crab density was invariably greatest at stations with this epibenthic cover.

4.1.2 Estuary Subtidal

As previously described in Section 1.6, much of Grays Harbor is a mixture of marine and fluvial sand and silt. In the Outer Harbor (Str 1, Fig. 1.3) and along much of the main navigation channel, typical subtidal sediments are composed of fairly well consolidated sands, but in secondary and tertiary tidal channels of North Bay (Str 2) and South Channel (Str 3), softer sediments that contain a higher percentage of silts are common.

As noted for the coastal habitat, epibenthic material is certainly a more important determinant of crab distribution than is sediment *per se*, and a variety of such cover occurs throughout the subtidal of Grays Harbor based on numerous trawls of the U.W. Sea Grant program. Referring to Figs 1.3 and 4.2, much of the Outer Harbor and the main navigation channel from the Crossover through Aberdeen Reaches contain allochthanous leaf and stick debris in variable amounts in accord with seasonal river discharge, primarily from the Chehalis River. The South Channel of Str 3 (Fig. 1.3) also contains much wood debris and, in general, relatively high densities of 0+ and 1+ crab occur in such material (see Section 4.3.2).

A much more important and elaborate network of shallow (about 3 to 4 m) subtidal channels is inhabited by juvenile crab in North Bay (Str 2; Figs 1.3) where, in addition to leaf and wood

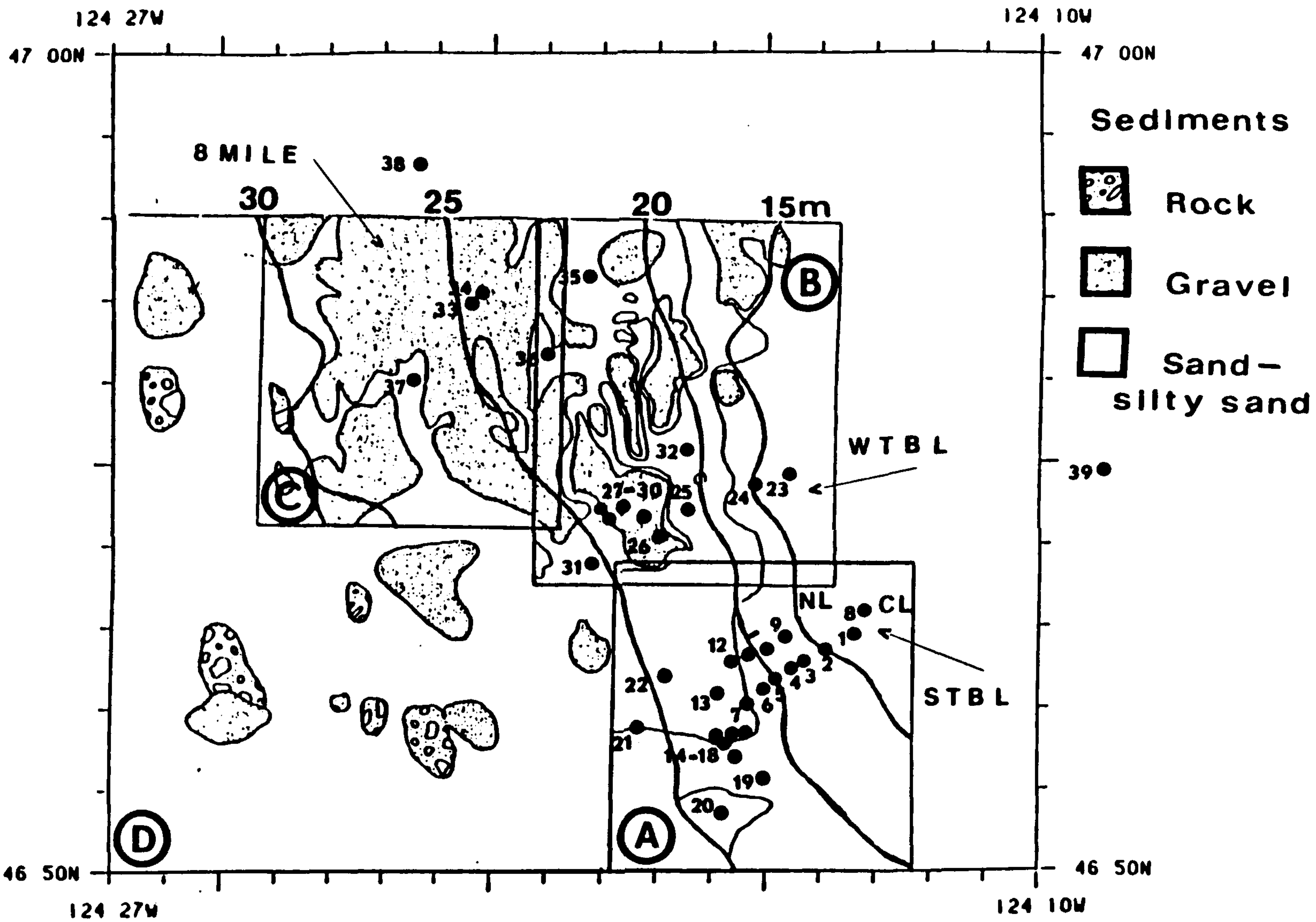


Figure 4.1. Offshore Grays Harbor trawl surveys in areas of proposed disposal sites showing sediments, depth contours and station locations for trawls in September 1985. Station numbers are UW Haul sequence (Table 1). STBL = Southwest Tow Boat Lane, WTBL = West Tow Boat Lane, and 8 MILE = 8 Mile Site. The STBL stations are grouped into a North Line (NL) and a Center Line (CL). Grids A, B, C, and D are strata for estimating relative extent of substrates and mean crab density (see Armstrong and Armstrong, 1985 a & b).

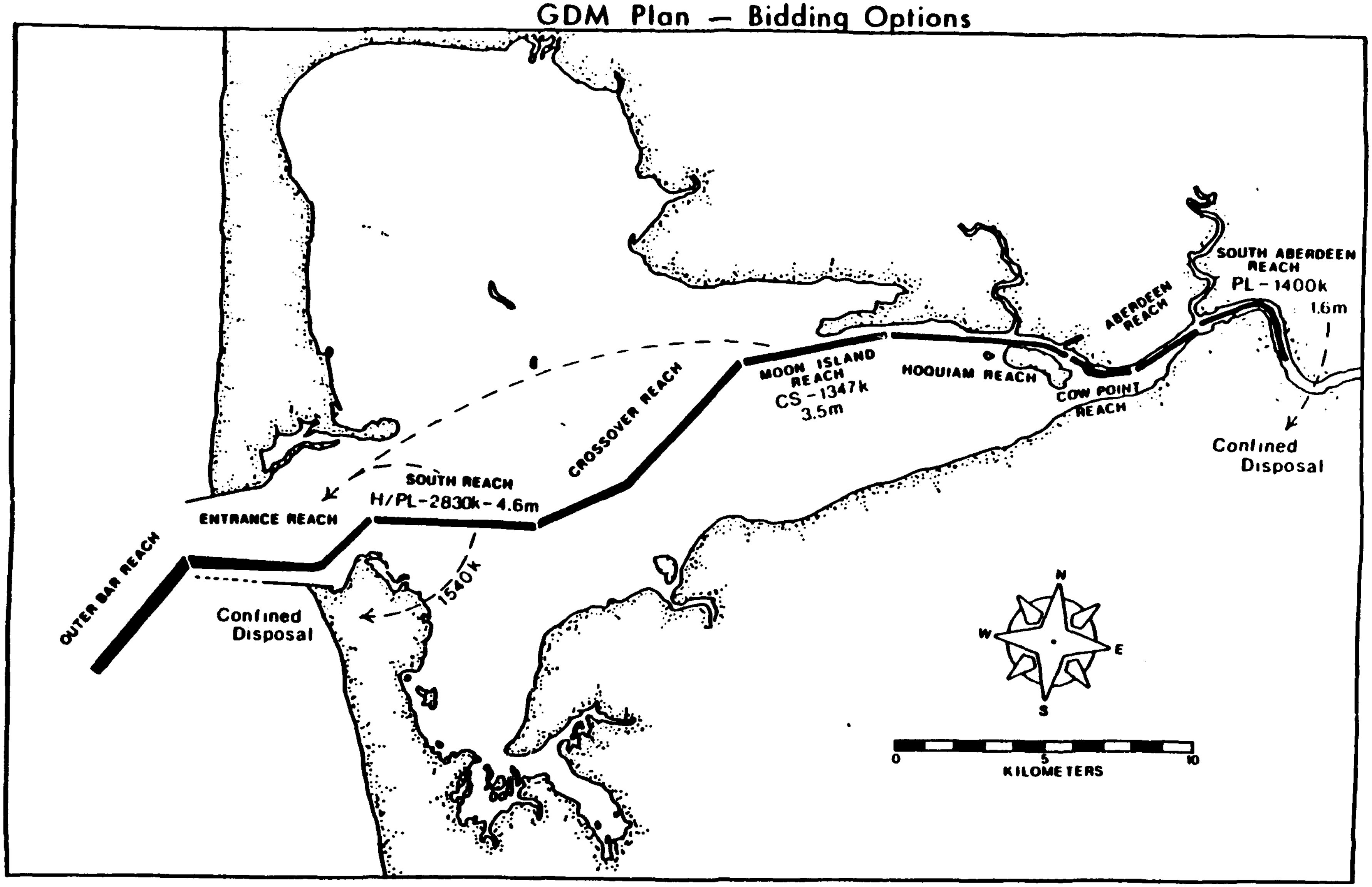


Figure 4.2. Diagram of proposed bidding options to be considered for inclusion in the Grays Harbor widening and deepening plan. Abbreviations: H= hopper dredge, PL = pipeline dredge; CS = clam shell; K = 1,000 cy; M = # months required for dredging.

debris from the Humptulips River, large quantities of bivalve shell also occur. Principal species of shell include cockle clam (*Clinocardium nuttali*), gaper clam (*Tresus capax*), *Macoma* spp., oyster (*Crassostrea gigas*; origins are probably decades old, now as unattended oyster plots around Ned's Rock, the Humptulips and Chenois River channels), and soft shell clam (*Mya arenaria*). Trawls of about 200 to 300 m length in the North Bay will commonly take from 10 to 40 kg of shell off the surface, and crab abundance in such habitat is always high between May through September (Armstrong and Gunderson 1985a,b; Armstrong et al. 1986).

In the South Bay (Str 4: Fig. 1.3), wood debris from the Elk River is not too common, nor is shell although oysters are cultured in the area. More common as epibenthic material are several species of macroalgae that are very seasonal in occurrence. Especially *Enteromorpha* sp. and *Ulva* sp. are taken by the trawl in large quantities in mid to late summer, and 0+ crab density is often high in such material if the year class entered the estuary in high abundance that spring (e.g. first instar abundance in the subtidal was high in 1983 and 1984 but low in 1985 and 1986; see Sections 4.3, 5.4).

4.1.3 Estuary Intertidal

Sediment composition ranges from well consolidated sand on Outer Harbor tidal flats such as Whitcom Flats, to loose sand and silt at many locations in Str 2, 3 and 4 (e.g. around Ned's Rock and the large flat between North and South Channel of Str 3 (Fig. 1.3). Eelgrass occurs intertidally throughout much of Grays Harbor (Fig. 4.3) and was reported by Stevens and Armstrong (1984) to be important cover for small 0+ crab, a finding consistent with that of Butler (1956) and Dinnel et al. (1986, 1987).

Further study of intertidal habitat and 0+ crab populations in Grays Harbor indicates that while young instar crab may occur in eelgrass soon after settlement, long term survival through the summer is maximal in shell debris (shellhash) (Armstrong and Gunderson 1985a, b;Armstrong et al. 1986; Dumbauld and Armstrong 1987). Type and extent of intertidal shellhash has been mapped in Grays Harbor (Fig. 4.4; helicopter, hovercraft and groundtruth surveys) and is composed almost entirely of either *Mya arenaria* or oyster. *Mya* shell is particularly dense in some areas of Str 2 and 3, and typically shelters small crab when the shell occurs in shallow (2-5cm) pools of water on the flats at low tide. In areas of Str 3 between North and South Channel, *Mya* shellhash occurs in piles (Fig. 4.5) up to 0.4m high, 1.0 m across and 2.0 to 30 m long. Intertidal density of 0+ crab is always high within shellhash even in years (1985, 1986) when recruitment of 0+ to the estuarine subtidal appears to be weak (see Section 4.3.2). The importance of shell to survival of juvenile crab has not been well studied although in Puget Sound small *C. magister* occur in shellhash and seem to prefer it to open sand (McMillan, Armstrong and Dinnel, U. of W., unpublished data). Mackay and Weymouth (1935) noted that small newly molted crab could be

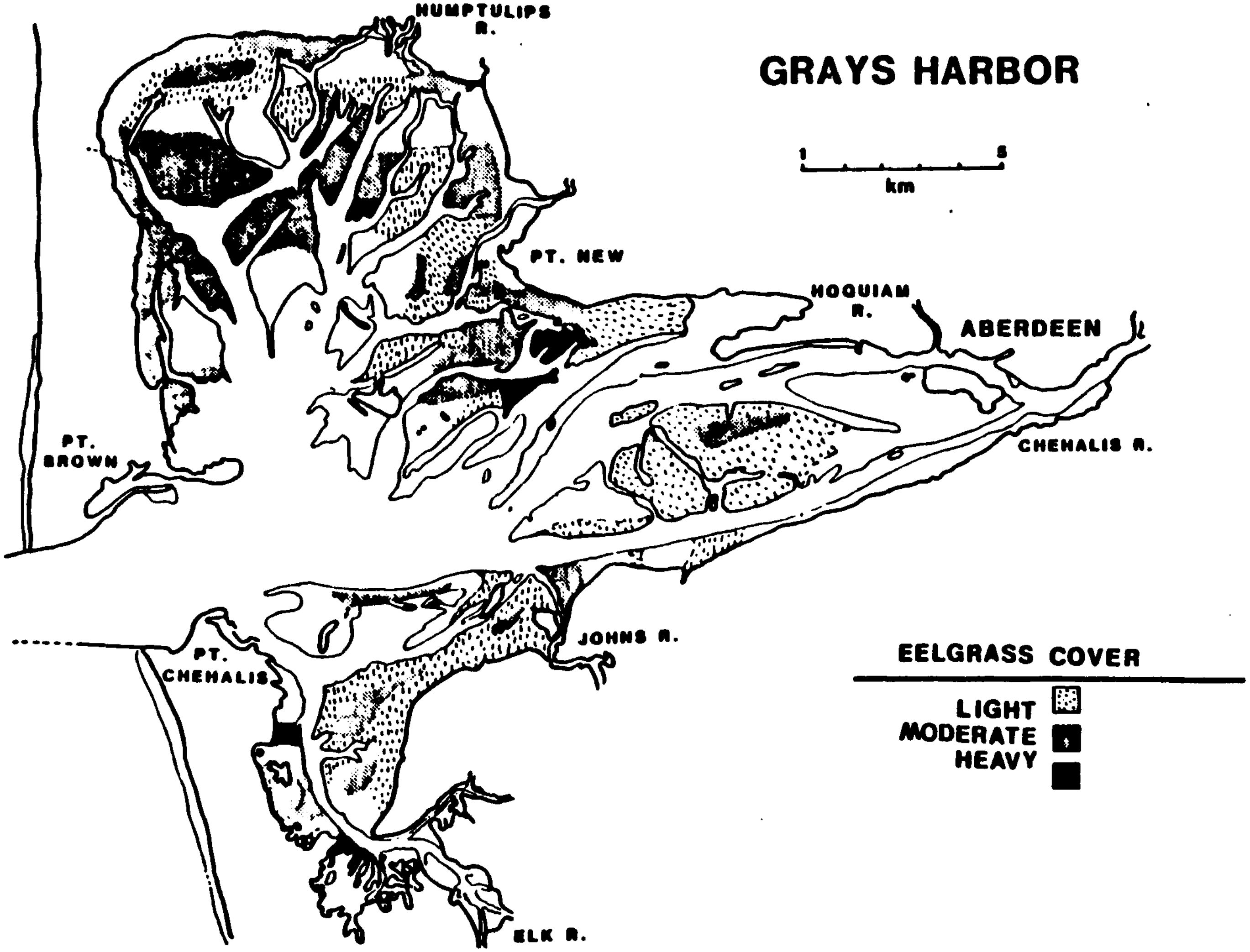


Figure 4.3. Map of eelgrass cover in Grays Harbor as determined from helicopter overflights in August 1984, hovercraft survey in May 1985, and ground truthing in 1985 (from Dumbauld and Armstrong 1987).

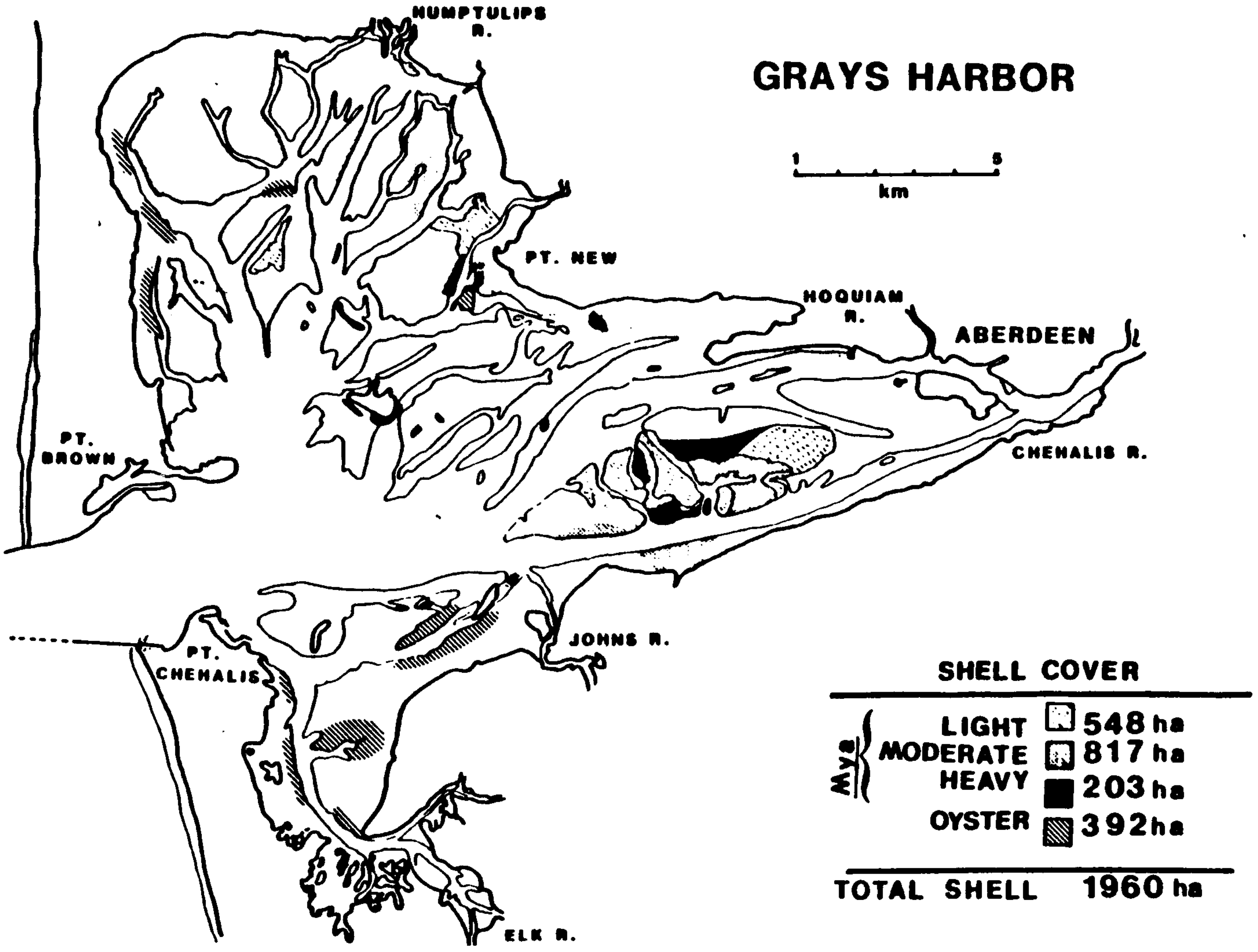


Figure 4.4. Map of shell substrate cover in Grays Harbor determined from helicopter overflights in August 1984, hovercraft survey in May 1985, and ground truthing in 1985. Area estimates were derived from digitizing this map. Shells of the eastern sotshell clam, <u>Mya arenaria</u>, composed the major fraction of shell cover (1,568 ha) and were split into 3 categories of relative thickness. Oyster culture also contributed a significant amount of shell habitat (392 ha) (from Dumbauld and Armstrong 1987).

collected in Boundary Bay (U.S. - Canadian border) under inverted cockle shells; an indication of the protection afforded by shell which is viewed as critical habitat of 0+ *C. magister* in Grays Harbor.

4.2 LARVAE

Fluctuations in population abundance (see Section 5.0) have been seen most dramatically in fishery landings, and the implications relative to the W&D project were noted in Section 3.0 where it was observed that the strength of a year class and, in turn the future fishery, may be set in the first year of life for Dungeness crab and other decapod species as well (Botsford 1986; McKelvey et al. 1980). The absolute and even relative impact of W&D construction will vary substantially in different years as population abundance and age class composition change. Some researchers argue that events which affect larval survival and transport largely influence year class strength. This section is a review of larval biology, habitat and appropriate oceanography that might affect larval stages.

4.2.1 Larval Decapods and Fisheries Oceanography

Over the last 10 years, interpretations of decapod crustacean life history characteristics and population dynamics have been increasingly cast in light of oceanographic processes that affect year class strength and eventual fisheries (Bakun et al. 1982; Wooster 1983). Although direct experiments to elucidate causal relationships between decapod year class strength and physical oceanographic features are few, authors have been increasingly tempted to interpret any body of ecological or life history data in this context because of the meroplanktonic life history strategy of this group. The notion is that to the extent that early life history stages of commercial decapods are planktonic, oceanographic features and processes must in some way affect production, survival and distribution. The impetus of such interpretation goes back many decades to the pioneering work of Hjort (1914) who suggested that survival of early life history stages was important in establishing year class strength, and that survival was most affected by the vagaries of food and the suitability of currents to transport larvae to habitat that maximizes survival of benthic juvenile stages after settlement. Hardy (1935) elaborated the view that larvae are affected by current regimes by stating that they are capable of directed movement (e.g. vertical migration) as a means to select water masses that provide advantages in terms of either food or current direction.

The perception that meroplanktonic life history strategies pose risks to species has more frequently influenced the purpose and design of field studies and laboratory experiments that seek to explain cause-and-effect behind year class strength and eventual fisheries. It is often stated explicitly, or assumed implicitly, that larvae are a critical stage of the life history cycle and the point

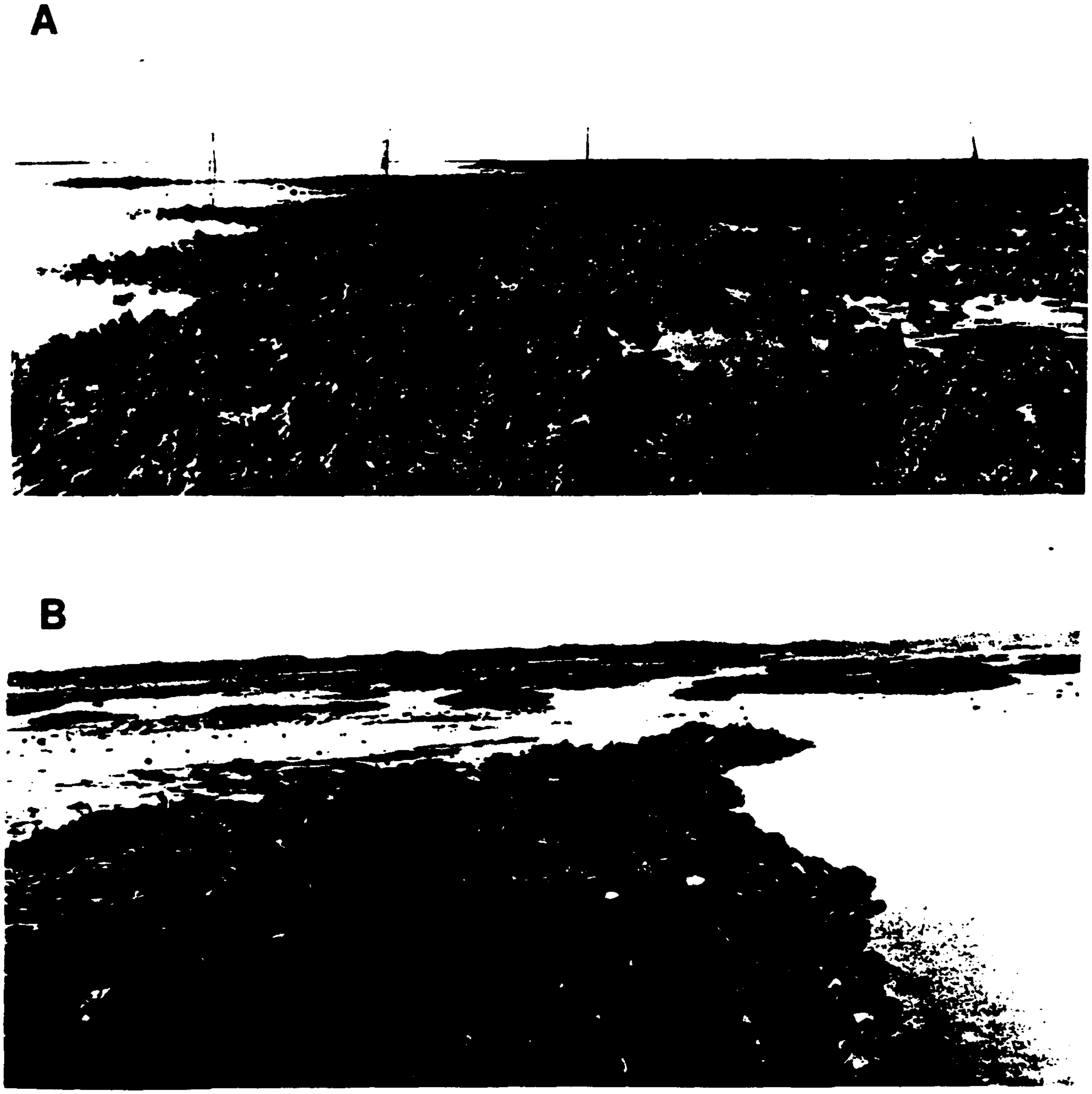


Figure 4.5. Intertidal shell substrate cover found in Grays Harbor consisted primarily of (A) commercial live oyster (Crassostrea gigas) beds, and (B) shell deposits from the eastern softshell clam, Mya arenaria.

at which year class strength is fixed (e.g. Bakun et al. 1982; McKelvey et al. 1980; Johnson et al. 1984) but survival of early juvenile stages is also a likely determinant of year class strength (e.g. Botsford and Wickham 1978; Armstrong and Gunderson 1985a; Armstrong et al. 1985; Incze et al. 1987; Morgan et al. 1982).

Much literature dealing with population dynamics of commercial Decapoda takes an oceanographic perspective of factors that affect larval survival, transport and juvenile settlement. Apart from generalized mortality due to predators, larval survival is viewed as dependent on food production that is consistent in time and space with larval hatch and quality and quantity of food necessary for survival and growth. Starvation of commercial decapod larvae is seen as a viable hypothesis to explain interannual variability of larval numbers of Tanner crab (*Chionoecetes opilio* and *C. bairdi*; Incze et al. 1987), red king crab (*Paralithodes camctshatica*; Paul and Paul 1980), Dungeness crab (Lough 1976) and a variety of other decapod Crustacea as well (see review by Dawirs 1984). More commonly though, decapod larvae and oceanography are considered together in the context of current regimes, transport to or away from areas optimal for settlement and survival, and distances traversed during periods of development typical of planktonic larvae (e.g. penaeid shrimp a few days; Dungeness and king crab several months; spiny lobster up to a year).

Zoeal stages of penaeid shrimp in the Gulf of Carpentaria, Australia, are transported distances of over 150 km from adult spawning grounds to estuaries where they metamorphose and develop as postlarvae (Rothlisberg 1982; Rothlisberg et al. 1983). Dynamics of larval drift and production as it affects future fisheries of the edible crab, Cancer pagurus, off the east coast of England have been described by Nichols et al. (1982). Larvae of pandalid shrimp along the western coast of the United States are eventually transported back offshore to settle on adult spawning grounds by currents created by summer upwelling and resultant Ekman transport (Rothlisberg and Miller 1983). Larvae of the blue crab (Callinectes sapidus) are spawned in Chesapeake Bay on the eastern U.S. coast, and transported to the Middle Atlantic Bight on the Continental Shelf where they are retained by seasonal wind-driven reversals of nearshore currents. They then reinvade estuaries by either surface transport during such reversals or via residual drift in shoreward directed bottom waters which they occupy near metamorphosis (see reviews by Epifanio et al. 1984; Johnson et al. 1984; Sulkin and Epifanio 1986).

Importance of larval transport in the context of fisheries oceanography is primarily the need that larvae arrive or return to areas where metamorphosis to benthic juvenile stages will enhance survival, usually by virtue of refuge habitat, or conditions such as temperature and food that optimize growth rate. Penaeid shrimp in both the Gulf of Carpentaria (Rothlisberg 1982; Staples and Vance 1985) and along the Gulf Coast of the United States (Turner 1977; Zimmerman et al. 1984) are critically dependent on the vegetation (as refuge), temperatures and food of coastal estuaries for rapid growth and enhanced survival. *Homarus* spp. lobster are dependent on rock and cobble substrate for survival of juveniles and, in turn, size of the fishery (Howard 1980; Pottle and Elner 1982) and have the capacity to select such substrate in transition from late larval to benthic juvenile stages (Cobb 1968). Larvae of commercial blue king crab (*Paralithodes platypus*) must settle nearshore around islands in the southeastern Bering Sea so that juvenile survival is enhanced in the shell debris substrate that characterizes those systems (Armstrong et al. 1985b), and a similar dependence of juvenile Dungeness crab on shell and other refuge material nearshore and in coastal estuaries has been shown by Armstrong and Gunderson (1985) and Stevens and Armstrong (1984).

Whether survival of larval or early juvenile stages of decapod Crustacea is most responsible for future fisheries is an intractable question at this time. Bakun et al. (1982) in a review article concerning ocean sciences and living resources noted that physical effects on larvae are most critical to eventual recruitment, and that survival of juveniles represents a point of "fine tuning" of future recruitment numbers. Both stages are apparently highly susceptible to the vagaries of oceanographic events and processes, and Dungeness crab is a particularly good example of such susceptibility along the California to Washington coast.

4.2.2 Dungeness Larvae: Timing of Occurrence

Dungeness crab larvae are planktonic and pass through five zoeal stages and one megalopal stage before settling to the benthos. A prezoeal stage of 10-15 min duration has been observed in laboratory culture (Buchanan and Milleman 1969). Studies of larvae prior to the 1970s were primarily descriptions of larval morphology (Mir 1961; Poole 1966) and it was not until Reed (1969) developed laboratory culture methods that larval environmental requirements were first described (Reed 1969). Optimal ranges of temperature and salinity for laboratory-cultured zoeae are 10.0° to 13.9°C and 25 to 30 ppt, respectively, but their survival not significantly affected by temperatures and salinities approximating ranges of these factors at the time of year when larvae are commonly found in the waters off Oregon where the study was conducted. Later studies (Lough 1976; Fig. 4.6) suggest higher salinities favor survival over the long-term but basically support Reed's (1969) observations.

The temporal occurrence of larvae in outer coast oceanic waters varies somewhat according to latitude, with larvae being present earliest in the season in the southern part of the species' range of distribution (Table 4.1). In California the Dungeness crab larval season extends from December to June (Wild and Tasto 1983), whereas in waters off the west coast of Vancouver Island, British Columbia, the season extends from about January to August (G. Jamieson, Pacific Biological Station, pers. com.). Off San Francisco, California, ovigerous female Dungeness crab can be found as early as mid-September in the Gulf of Farallones and most eggs hatch by late January (Reilly 1983a). At Tofino on the west coast of Vancouver Island, ovigerous females are first observed in abundance in mid-October, with most egg hatching completed by March (G. Jamieson, pers. com.). Ovigerous females have been observed at Tofino, B.C. from September to June.

Within waters of Georgia Strait, Puget Sound and Juan de Fuca Strait the temporal occurrence of larvae appears to differ significantly from that in nearshore coastal waters. Both larval hatching and settlement either extend over a longer time period or are delayed in the season. In northern Puget Sound, there is often an initial larval settlement in late June-July, followed by a larger settlement in August-early September (Dinnel et al. 1986, 1987). Early settlement may largely consist of open coast larvae transported inshore through Juan de Fuca Strait whereas later settlement may consist of larvae retained within the inshore system throughout their developmental period. Implicit in this scenario is that females of inland waters hatch larvae later than do females along the coast. However, extensive work on ovigerous female crab at Ship Harbor near Anacortes, Washington, showed that eggs were carried December through February and most hatching was completed by March (Armstrong et al. 1987b).

The seasonal range and dates of first occurrence of Dungeness crab larval stages in central and northern California (Reilly 1983a) indicate that megalopae are present there from early March to mid-April. This suggests a relatively narrow time window exists in the southern part of the species' range during which settlement can occur, compared to more northerly areas where megalopae can be collected in abundance in open coast waters off British Columbia from mid-April to August (G. Jamieson, pers. com., Fig. 4.7). This phenomenon may partially result from the influence of environmental factors on larval spatial distribution (especially transport) that results in a mixture of megalopae from different adult stocks whose eggs hatch at different times.

Temporal duration of larval stages has been estimated both by laboratory rearing (Ebert et al. 1983; Gaumer 1973; Poole 1966; Reed 1969) and the first appearances of larval stages in field studies (Lough 1976; Poole 1966; Reilly 1983a). The length of the total larval period has been reported as 130 days (range: 89-143 days) by Lough (1976), 45-108 days at 17.8° and 10.0°C, respectively, by Reed (1969), and 128-158 days under natural conditions by Poole (1966). In laboratory studies, Poole (1966) found the total time required was 111 days at 10.5°C. The megalopal stage has been estimated to take 25 to 30 days of development by Reilly (1983a) from field data and 31 days by Poole (1966) from laboratory rearing. Hatfield (1983) described intermolt stages of megalopae caught off San Francisco, based on laboratory culture at 14.7°C and reported that about 28 days were required for development.

4.2.3 Habitat and Transport

As a planktonic stage, geographical location at settlement is very dependent on oceanographic and meterological features during development. Adult Dungeness crab are usually found in

Table 4.1. Temporal range of occurrence of larval Dungeness crab stages in outer coastal waters from California to British Columbia.

	Range of Occurrence			
Stage	**California**[1]	**Oregon**[2]	**Washington**[3]	**British**[4] **Columbia**
Eggs	mid Sept late Jun	Oct-Mar	Oct - ?	Sept-June
Zoea I	mid Dec- early Jan	mid Jan- early Mar	- -	- -
Zoea II	early Jan- late Jan	Mid Jan- mid Feb	- -	- -
Zoea III	early Jan- mid Feb	mid Feb -	- -	- -
Zoea IV	late Jan- late Feb	- -	- -	- -
Zoea V	mid Feb- mid Mar	- -	- -	- -
Megalops	early Mar- mid Apr	mid Apr- mid July	mid Apr- Aug	mid Apr- Aug

Sources:

[1] Reilly 1983a.
[2] Lough 1976.
[3] Cleaver 1949; Stevens and Armstrong 1984; Armstrong et al. 1987.
[4] McKay 1942; Butler 1956, Jamieson, unpub. data.

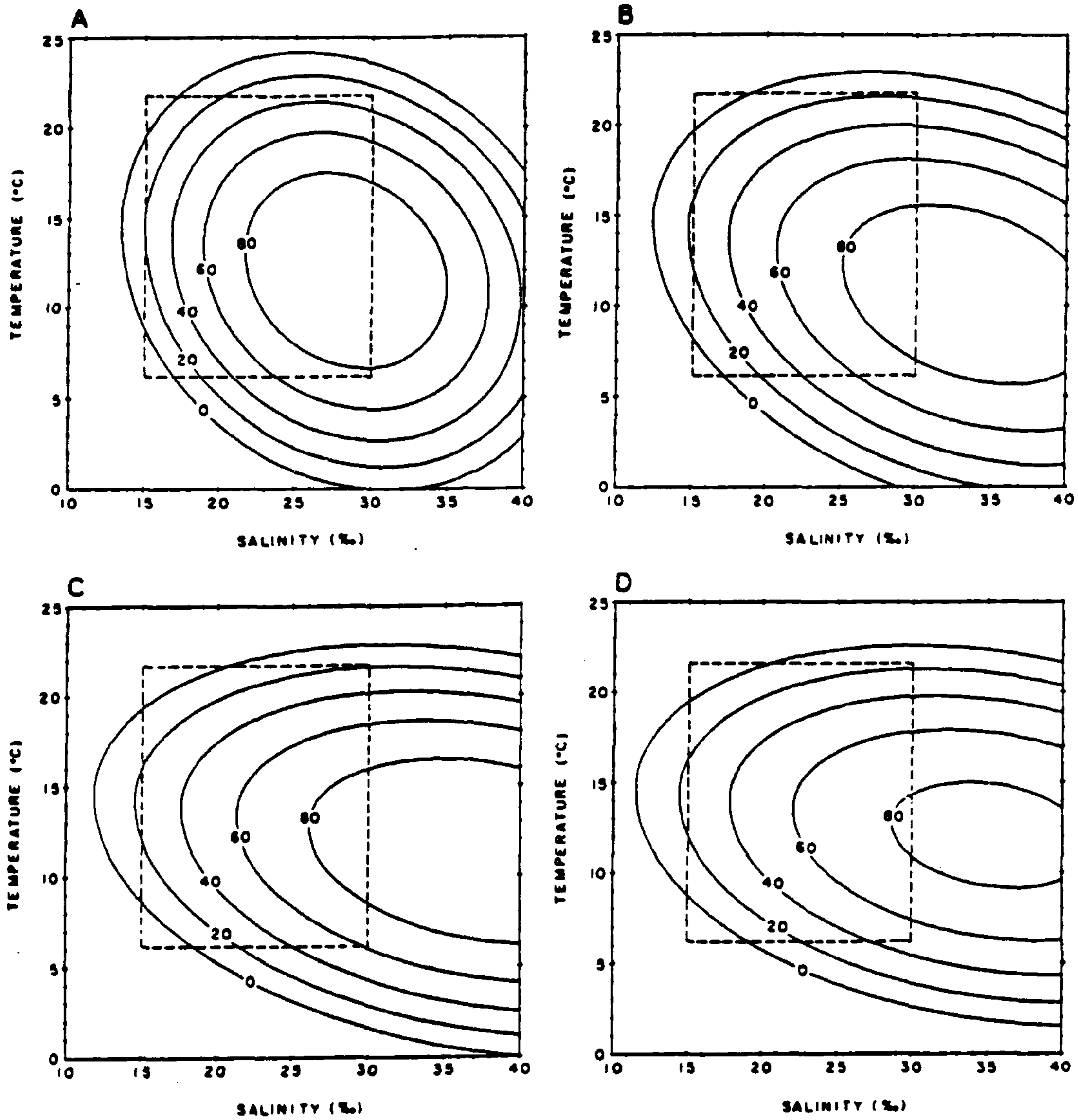


Figure 4.6. Response surface estimation of percent survival of Cancer magister larvae after (A) 20 days, (B) 30 days, (C) 40 days, and (D) 50 days of development at 20 different temperature and salinity combinations (from Lough 1976).

Swimming speeds of larvae measured in directional light

Instar	*n*	Mean ± standard deviation swimming speed (cm s^{-1})	Pairwise comparisons[a]	Fastest swimming speed (cm s^{-1})
Zoea 1	8	0.95 ± 0.59	1 = 2 < 3 =	2.6
Zoea 2	12	0.95 ± 0.68	4 = 5 < Meg	2.6
Zoea 3	26	1.5 ± 0.77		4.2
Zoea 4	26	1.3 ± 0.013		3.6
Zoea 5	9	1.5 ± 1.02		4.2
Megalopa	22	4.2 ± 2.46		10.0

[a] Significant ($p \leq 0.05$) inequalities determined by Kruskal–Wallis analysis of variance by ranks and Dunn's multiple comparison procedure.

Table 4.2. Swimming speeds of larvae measured in directional light, in cm/sec (Jacoby 1982).

nearshore, shallow-water habitats, and such environments are apparently both the origin of larvae at hatch and preferred destination at metamorphosis and settlement. Along the open coast, larvae are known to settle in both estuarine and nearshore areas (Armstrong and Gunderson 1985a and b; Stevens and Armstrong 1984; Wild and Tasto 1983). Relative survival rates of YOY juvenile crabs in these two habitats is currently under investigation in Washington (D. Armstrong, University of Washington, unpublished data; Armstrong et al. 1987a), and preliminary studies indicate that major estuaries such as Grays Harbor are important nursery habitats, although larvae also settle and survive nearshore along the open coast. In more inland waters such as Puget Sound, Straits of Georgia and Queen Charlotte Straits and to a lesser extent, Hecate Strait, Dixon Entrance and southeastern Alaska, larval crab may remain nearshore throughout their developmental period. However, along the outer coast larvae may be hatched nearshore but, according to prevailing hypotheses, are subsequently moved longshore and perhaps offshore and then inshore, often over considerable distances (Johnson et al. 1986). Larvae hatched off California and Oregon in late winter move northward with the Davidson Current before its reversal in March-April, and offshore as a result of upwelling, Ekman transport, estuarine runoff and geostrophic flow, depending on location and season (Lough 1976; Reilly 1983a). Later stage zoeae are typically found progressively farther offshore and it seems to be the megalopal stage which returns inshore as it develops (Lough 1976; Reilly 1983a; G. Jamieson, pers. com.; Fig. 4.8). The megalopal stage is the strongest swimming stage (Table 2, Jacoby 1982), and in currents has sustained speeds up to 20 cm/s for 7 hr (J. Booth, Pacific Biological Station, pers. com.). However, there is no evidence to date that swimming is directional in a horizontal plane and, although it does presumably facilitate larval return to nearshore locations, how this is achieved remains unknown.

Off the west coast of Vancouver Island, Jamieson (unpublished data) found that megalopae appeared to be concentrated in areas of convergence (Fig. 4.9) between surface currents flowing in opposite directions 22 to 54 NM (40 to 100km) from shore. In 1985, larvae were concentrated about 27 NM (50km) from shore (Figs. 4.7 and 4.10) whereas in 1986, larvae were concentrated about 54 NM (100km) from shore (Fig. 4.10). In 1986 there was no major crab settlement observed on the outer coast between Bodega Bay, California and Tofino, B.C. From May to July, sustained northerly winds may be required to drive the surface water containing the megalopae sufficiently onshore to permit significant survival of a year class after settlement (Botsford 1986; Johnson et al. 1986). Jamieson (pers. comm.) suggests that with the strong currents off the west coast of Vancouver Island, storms may be required to transport larvae across nearshore current boundaries before they are carried out of the area and back offshore (Fig. 4.11). General wind direction off the B.C.-Washington coast (Fig. 4.12; Thomson 1981) will tend to drive megalopae offshore during the spring and summer. Water depths off British Columbia where megalopae

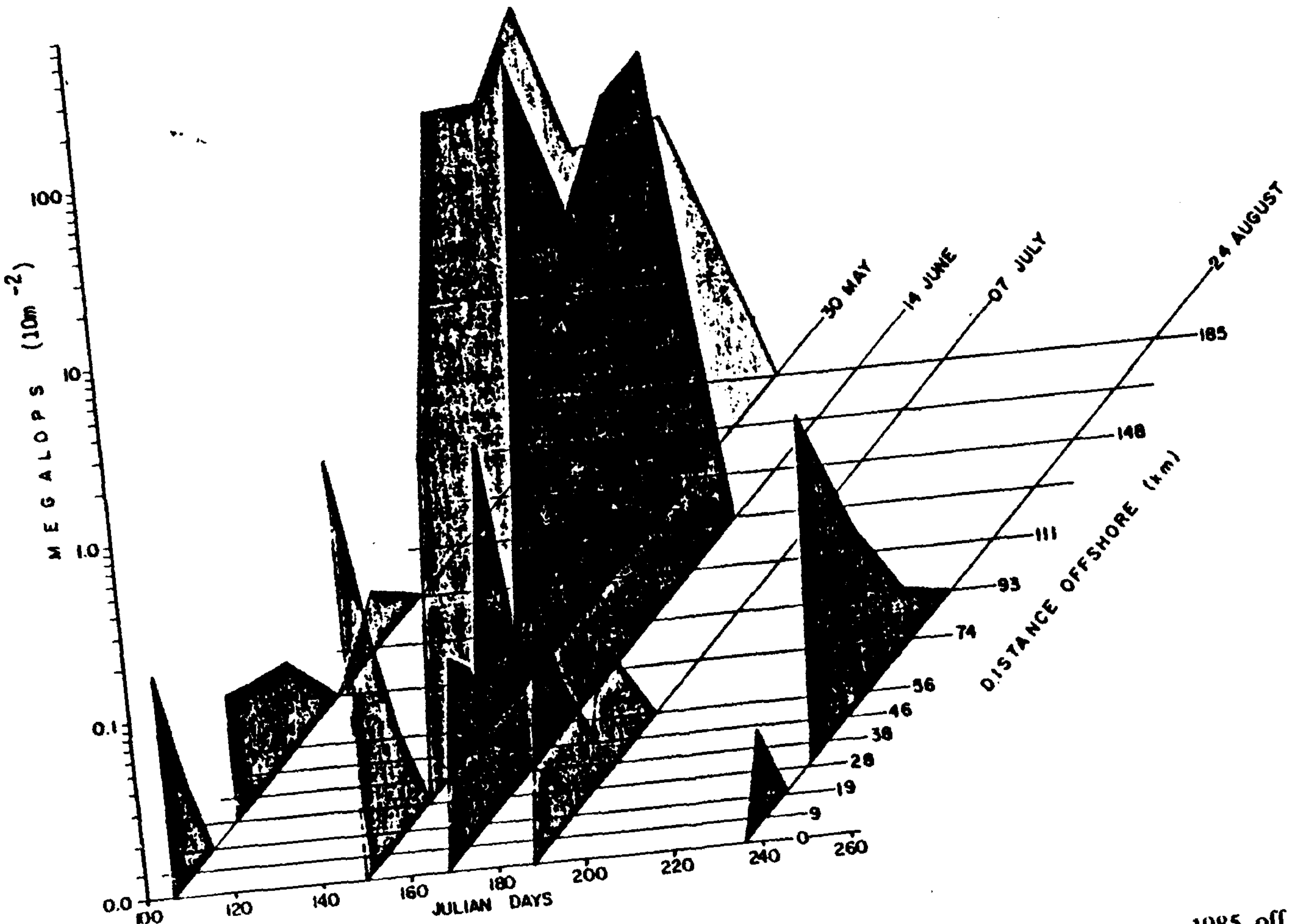


Figure 4.7. Megalopal abundance in nocturnal neuston tows (not weighted by time) over the season, 1985, off west coast of Vancouver Island (G. Jamieson, unpublished data).

were most abundant in 1985 and 1986 were 200-1500 m. Larval survival after settlement at these depths is considered negligible, and there was no significant occurrence of young juveniles in nearshore waters near Tofino, B.C., in either of these years. Nearshore of Grays Harbor, juvenile settlement was very strong in 1985 (Armstrong et al. 1986) but the weakest in four consecutive years in 1986 (see Section 5.3.1). Somewhat consistent with this pattern, megalopal abundance along transect lines extending from Vancouver Island southwest to Washington was highest about 38 NM offshore in 1985 but almost 60 NM in 1985 during June of both years (Fig. 4.13). High juvenile abundance in 1985 may reflect closer inshore distribution of megalopae that year near or within current regimes that favor onshore transport.

In the water column, larvae appear to show a diel vertical migration (Fig. 4.14), although this has only been well documented in the field with the megalopal stage (J. Shenker and G. Jamieson, pers. com.; Booth et al. 1985). Jacoby (1982) has conducted laboratory studies involving all larval stages to investigate larval responses to light, pressure and gravity. He predicted that during both day and night, early zoeal stages should be at about 20 m depth and later zoeal stages in the upper 2 m. His observations of megalopae were limited, but he suggested they should be near 20 m both day and night. Field observations do not support this latter observation and indicate that while megalopae may be at depths of about 10-60 m during the day, they are in surface waters at night (Booth et al. 1985). Recent studies (Jamieson, pers. com., Fig. 4.14) indicate that megalopae are probably in the top meter of the water column at nautical twilight (sun 12 degrees below horizon) in the evening but that their abundance subsequently declines during the night (larvae are presumably moving deeper), with a smaller peak around nautical twilight in the morning. Virtually no megalopae can be found in surface waters during the day, although on a few occasions, they have been observed to be in association with the hydroid *Velella* (Wickham 1979); 14 megalopae were collected in 1986 from 11 Velella at midday 32 NM offshore by Jamieson (pers. com.). In 1983 and 1984, megalopae were common in the neuston of Grays Harbor within long parallel drift lines during flood tide that indicate small convergence zones or features of internal waves. Shanks (1985, 1986) has shown that crab larvae are transported onshore in such waves which, in addition to directed swimming during flood tide, may facilitate megalopal arrival into estuaries.

Understanding the horizontal and vertical distributions of crab larvae in the water column is essential if transport mechanisms of larvae are to be understood and predictions made as to larval destinations after hatching. Water currents frequently move at different velocities and in different directions at different depths and it is important to establish the time durations in which larvae are in each water mass. Jacoby (1982) has suggested that because they are at depth, first and second zoeal stages off northern California would be transported northward and offshore in a subsurface counter current whereas later zoeal stages would be transported southward and onshore in the

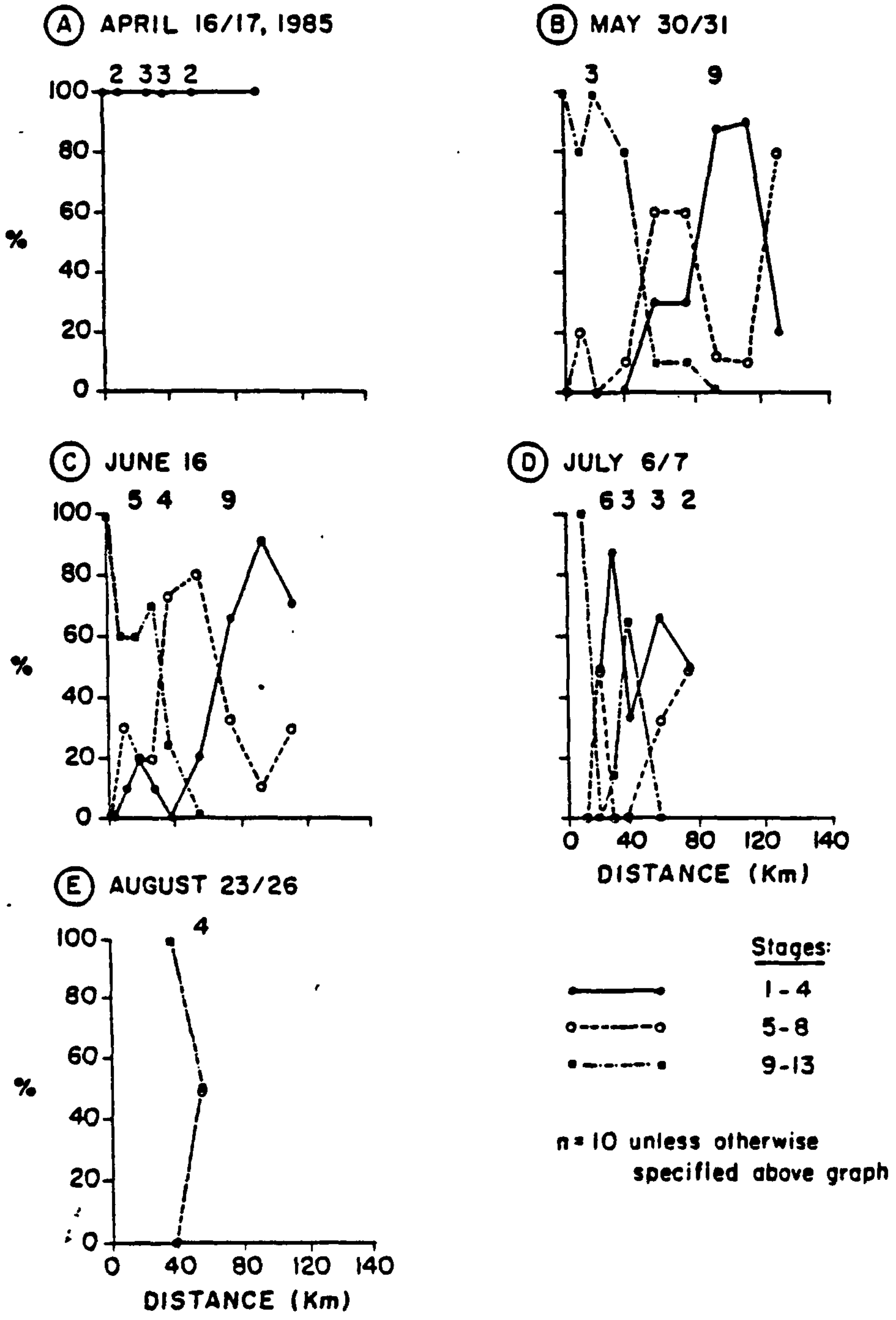


Figure 4.8. Proportion of megalopal intermoult stages (Hatfield, 1983) found at different distances offshore off Tofino, British Columbia, in 1985 (G.S.Jamieson, unpublished data). The higher the stage number, the older and more advanced the megalopae. Numbers along the top are sample size as indicated (otherwise n=10).

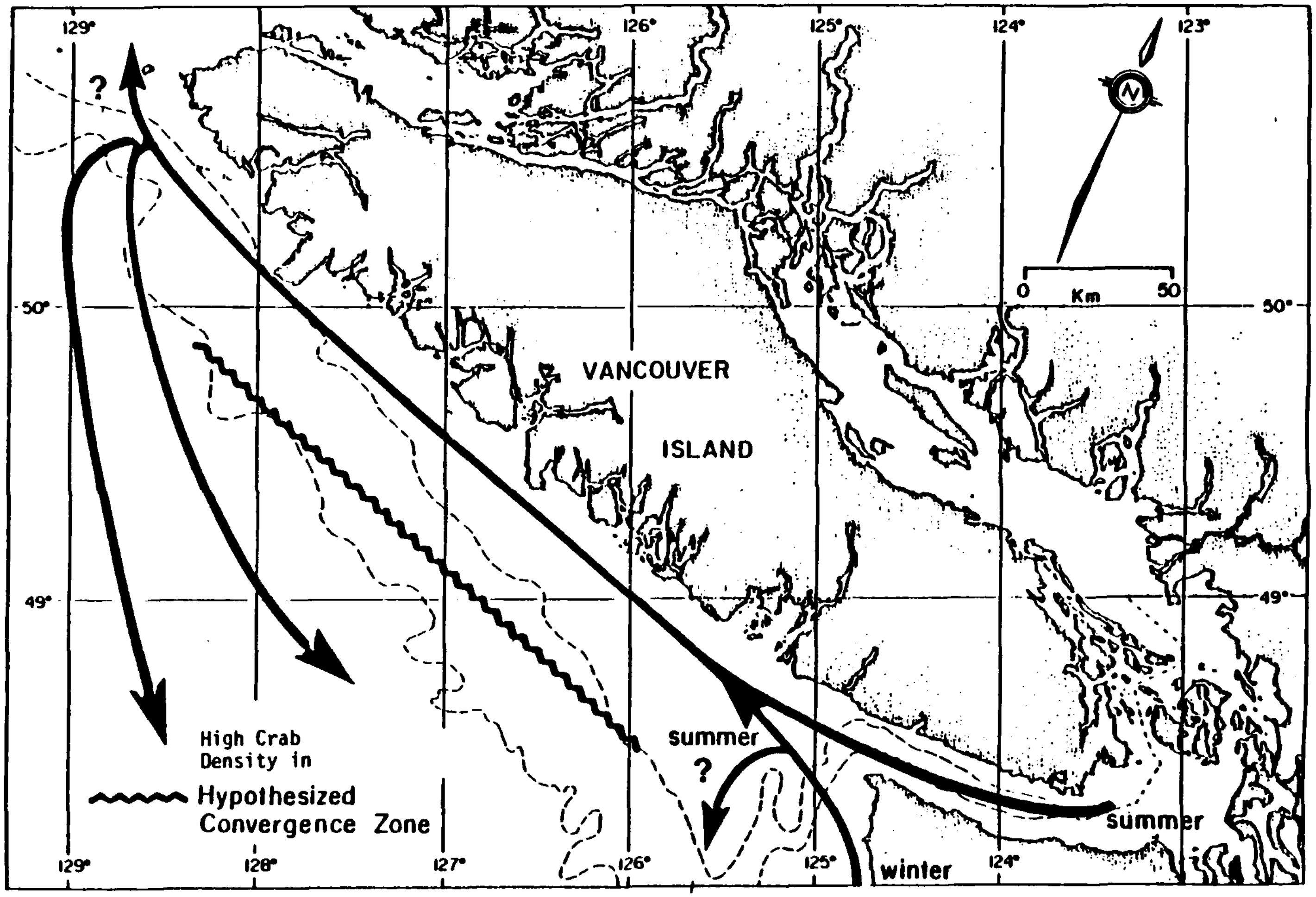


Figure 4.9. Location of high densities of crab megalopae in 1985 in a hypothetical convergence zone off Vancouver Island, British Columbia (G.Jamieson, unpublished data).

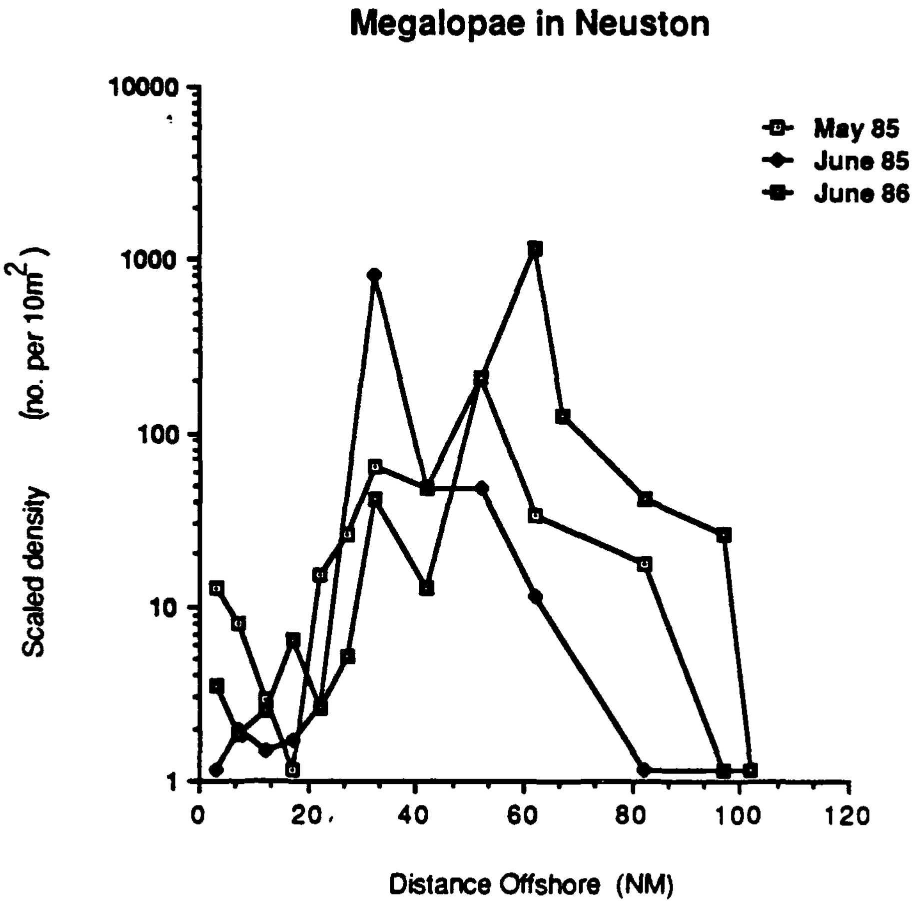


Figure 4.10. Abundance of Cancer magister megalopae in neuston (scaled by nocturnal abundance cycle, Figure 4.14) off Tofino, British Columbia, in 1985 and 1986 (G.Jamieson, unpublished data).

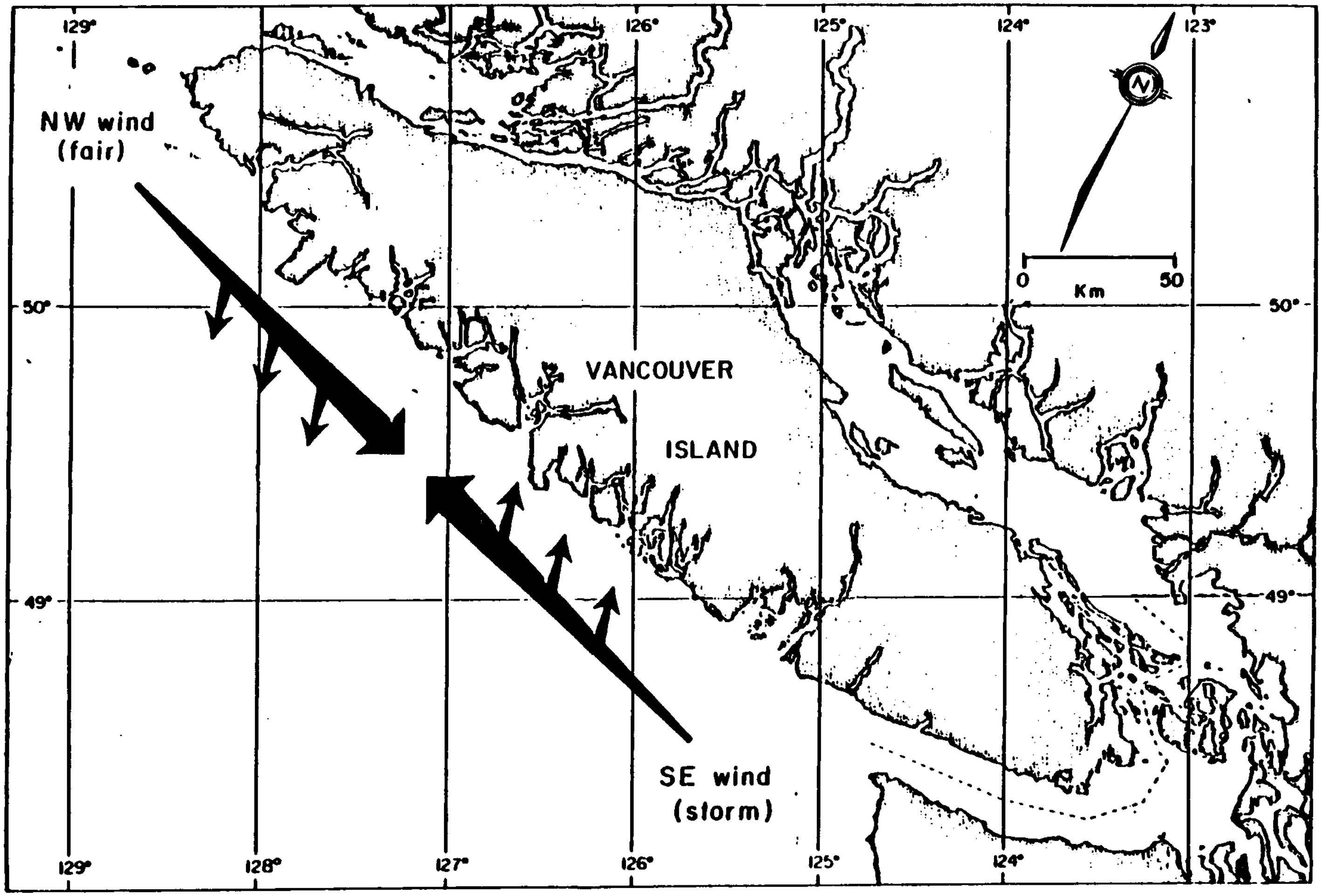


Figure 4.11. The general movement of larvae in surface waters (small arrows) with the two main wind vectors (large arrows) observed off Vancouver Island.

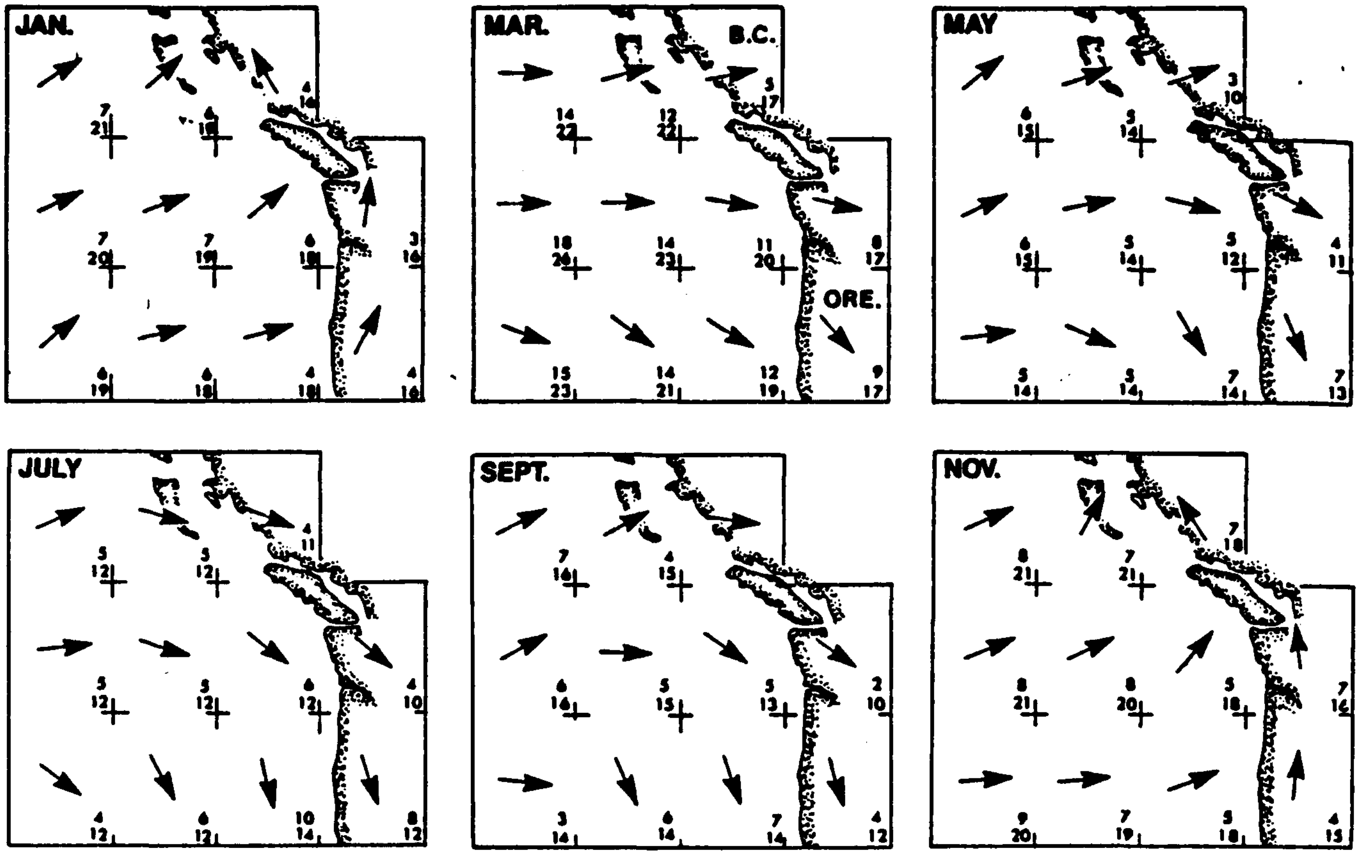


Figure 4.12. Wind directions and speeds off British Columbia-Washington coast. Arrows show net (resultant) direction of wind for month, averaged over a 5 x 5° oceanic region. Upper number in each region gives speed (kn) of resultant wind, lower number gives wind speed regardless of direction (kn) (Adapted from National Marine Fisheries Service). (Thomson 1981).

surface-flowing California current. However, conventional Ekman theory (Thomson 1981) indicates that movement is to the right, making shoreward movement opposite to that suggested by Jacoby (1982). Regardless, Jacoby's predictions would only occur after the northward, surface-flowing Davidson Current disappeared in late March since prior to this date, the entire water column is largely moving northward. This demonstrates the need to acquire more detailed information on larval behavior in relation to oceanographic events, and until this is accomplished, larval dispersion and settlement locations for larvae hatched in a specified general area will remain largely speculative.

Finally, although limited in latitudinal range, recent work (Crawford pers. com.) off the west coast of Vancouver Island indicates that on an annual basis, current regimes can differ significantly on a relatively large geographical scale. In 1985, ocean drifters, which indicate the movement of specified water masses, were set at 5-10 m depth and deployed in June off the entrance to Juan de Fuca Strait. They moved in a general southward, onshore manner and would probably have gone ashore somewhere south of Cape Flattery. In 1986, drifters deployed in a similar manner moved northwards. The observation of megalopae further offshore of Vancouver Island in 1986 and the correlating lack of any major settlement of Dungeness crab along the Washington coast in 1986 (there was major settlement in 1985) may be related. This supports the argument that Dungeness crab larval dispersion is very dependent on ocean events and that our understanding of them remains too limited to allow accurate prediction of crab settlement patterns at the present. Even on a small local scale, effects of currents, eddies and related mechanisms can cause highly patchy distribution of newly settled first instar crab (as an indication of megalopal dispersion just prior to metamorphosis). Samples of juvenile crab collected by W. Pearson of Pacific Northwest Laboratories and analyzed by Armstrong and Armstrong (1985a) show changes in density of first instars of up to two orders of magnitude over less than 100 m (see Section 4.3.1). Video footage taken by W. Pearson over proposed nearshore disposal sites verifies abrupt demarcation of megalopal settlement and resultant juvenile distribution (Pearson et al. 1987).

4.3 JUVENILES

The most important life history stage in regards to potential impact of W&D on Dungeness crab resources and fisheries are several age classes of juveniles from 0+ (settlement) through 2+ (subadult at or near maturity). Primarily because juveniles use estuaries extensively (Armstrong and Gunderson 1985a; Gotshall 1978; Gunderson et al. 1989; Stevens and Armstrong 1984; Tasto 1983), several scenarios of W&D projects have been considered in the DIM, and all predict impact on one (1+) and two (2+) year old crab populations due to the high proportions that occur in Grays Harbor compared to nearshore along the coast, especially in spring to early fall. Most reports over

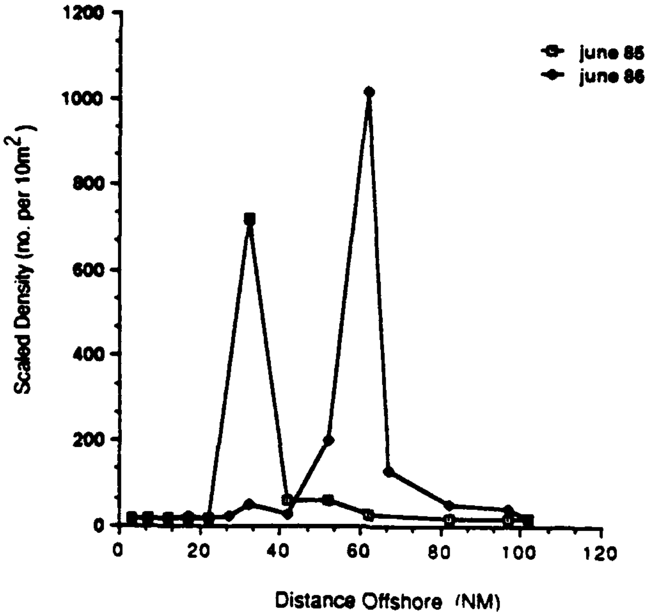


Figure 4.13. Cancer magister megalopal abundance in the neuston off west Vancouver Island, June 1985 and 1986. Note shoreward location in 1985 compared to 1986 (G. Jamieson, unpublished data).

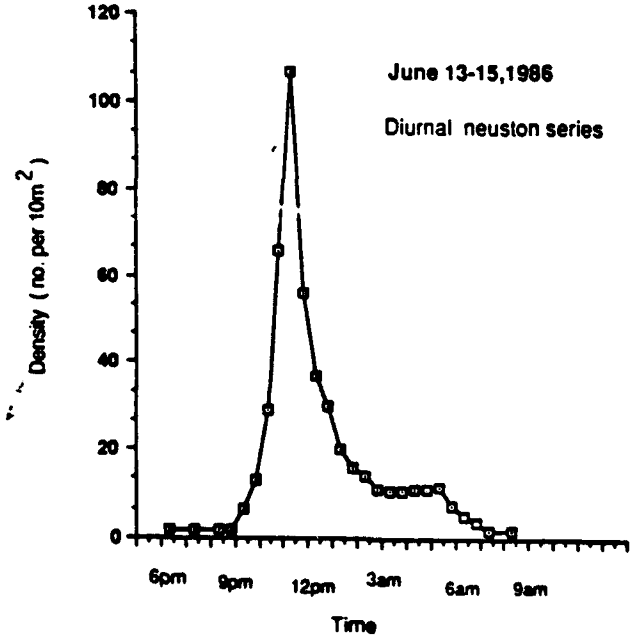


Figure 4.14. Megalopal abundance over a 24 h neuston time series sampled in the same water mass tracked with drogues (G.Jamieson, unpublished data).

Bay	Season	Year	Transect		No. crabs/ha
			Method	Area (m^2)	
San Francisco-San Pablo, Calif.	Summer	1975-77	Trawl	[1]1,500	90-340
	September	1977-78	Trawl	1,500	13-170
Humboldt Bay, Calif.	January	1967	Trawl	2,400	4,910
	August	1967	Trawl	2,400	300
	April	1968	Trawl	2,400	140
	August	1968	Trawl	2,400	1,280
	October	1968	Trawl	2,400	930
		(Mean of trawl samples, 1967-68 = 890)			
	August	1967	Scuba	140	520
	April	1968	Scuba	140	0
	August	1968	Scuba	140	4,480
	October	1968	Scuba	140	280
		(Mean of scuba samples, 1967-68 = 1,080)			
Pacific Ocean, near Humboldt Bay, Calif.	October	1968	Trawl	[2]6,667	0-9,400
	November	1968	Trawl	6,667	0-36,000 ($\bar{x}$ = 800)
Grays Harbor, Wash. Outer Harbor	June	1980	Trawl	variable	200-1,000
	December	1980	Trawl	1,400	310
	May	1981	Trawl	2,000	1,320

[1] Distance estimated as 50 m/min.

[2] Area estimated as distance (given) × ⅔ (headrope length).

Table 4.3. Comparison of Cancer magister densities in Grays Harbor, Wash. (Stevens and Armstrong 1984); Humboldt Bay, Calif. (Gotshall, 1978a), and San Francisco Bay-San Pablo Bay, Calif. (Wild and Tasto 1983). Data are not corrected for gear efficiency.

the last 40 years of high numbers of juvenile crab in estuaries have been observational and unquantified. Stevens and Armstrong (1984) reviewed work on crab density in San Francisco Bay (Tasto 1983) and Humbolt Bay (Gotshall 1978) and compared it to data from Grays Harbor collected in 1980/81 (Table 4.3). The present review includes systematic data on crab density in Grays Harbor as well as nearshore from 1983 through 1986, which allows a comparison between the two systems for impact calculations in the DIM (Armstrong et al. 1987a).

Much of the species ecology of *C. magister* within the estuary is concerned with timing of arrival and movement to and from nearshore and estuarine habitats. A summary is presented (Fig. 4.15) of immigration and emigration by two age classes that occur in high density within Grays Harbor. Briefly, YOY 0+ crab enter Grays Harbor about May as megalopae, settle to the benthos and metamorphose to first instar juveniles (Fig. 2.1). Although settlement occurs throughout the estuary, 0+ are most abundant within intertidal shellhash throughout most of the summer and survival in the subtidal is low. Movement of 0+ from the inter- to the subtidal probably occurs in mid to late summer as individuals become too large for the shell cover and are beyond the size range taken by most predators. 0+ juveniles overwinter in subtidal channels (avoid exposure intertidally to very cold winter temperatures) and become active the following spring as 1+ estuarine juveniles (EJ; Fig. 4.15). A second source of 1+ crab in the estuary comes via immigration from nearshore of members of the same year class that settled as megalopae the previous year directly along the coast (nearshore juveniles, NJ), which can be distinguished by smaller size from EJ (see Section 6.1). Both groups of 1+ crab occur subtidally within Grays Harbor for a second (EJ) or first (NJ) summer of estuarine growth, and finally emigrate from the estuary in late summer through fall as relatively large juveniles (generally >100 mm CW) approaching sexual maturity (Fig. 4.15).

4.3.1 Nearshore

The life history cycle of Dungeness crab begins along the open coast nearshore where reproduction, egg incubation and larval development occur (Section 1.0). Arrival of the megalops stage nearshore (Section 4.2) and metamorphosis to first instar crab mark the beginning of benthic existence on a substrate that is relatively homogeneous sand and gravel (Section 4.1) and offers little refuge for small crab (Fig. 4.1). The Sea Grant design used to quantify distribution and abundance of crab nearshore between 1983 through 1986 is shown in Fig. 4.16, and is based on stations grouped within three geographical areas (strata) by depth that, together, total about 174,000 ha. This and several other coastal surveys nearshore of Grays Harbor are the only quantified studies of juvenile *C. magister* along the open coast, but several others in the literature provide useful data on timing of arrival and movement elsewhere within the species range.

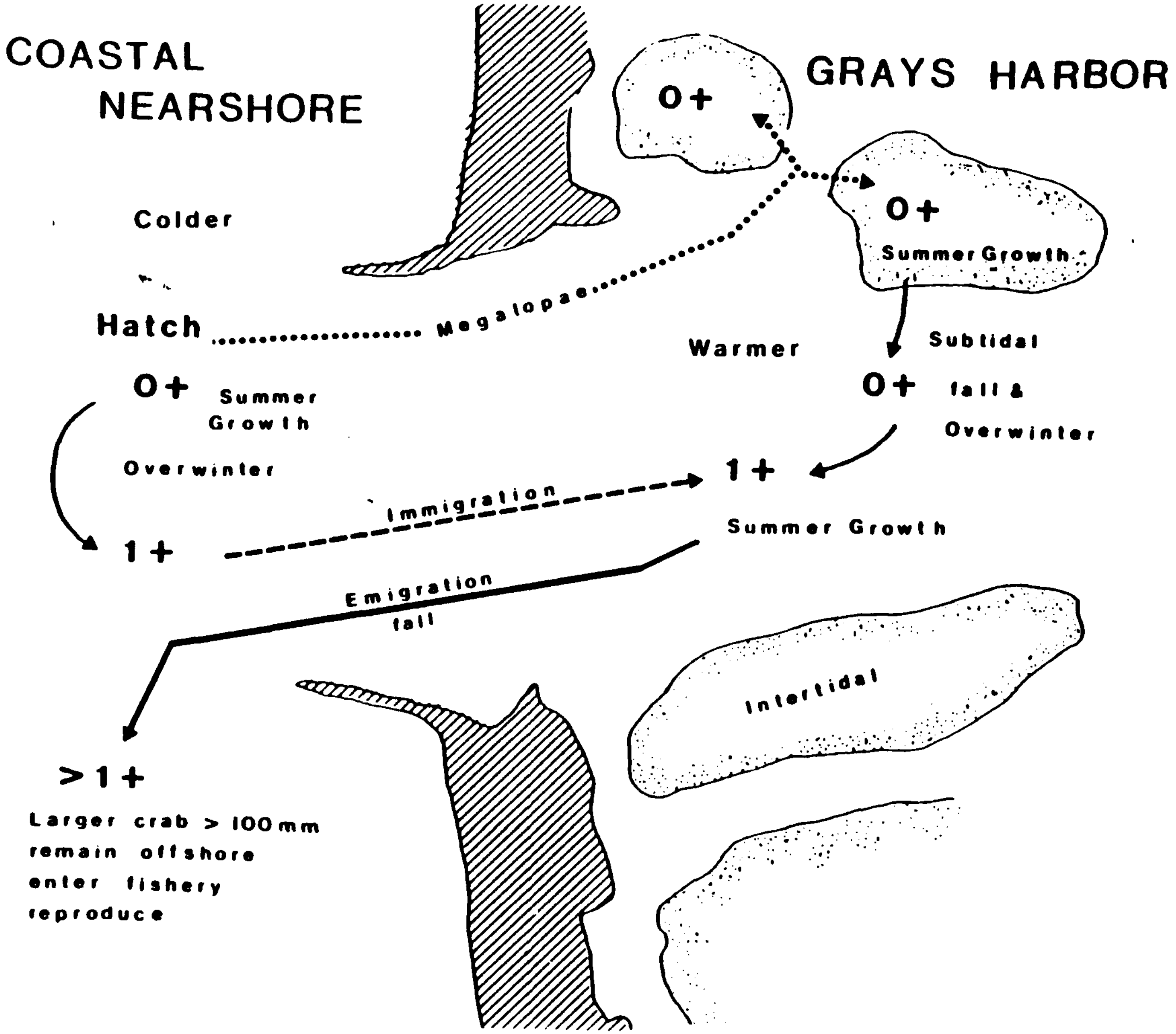


Figure 4.15. Refined schematic (see Fig. 4.16) showing generalized movements of juvenile Dungeness crab to and from Grays Harobr and the nearshore environment.

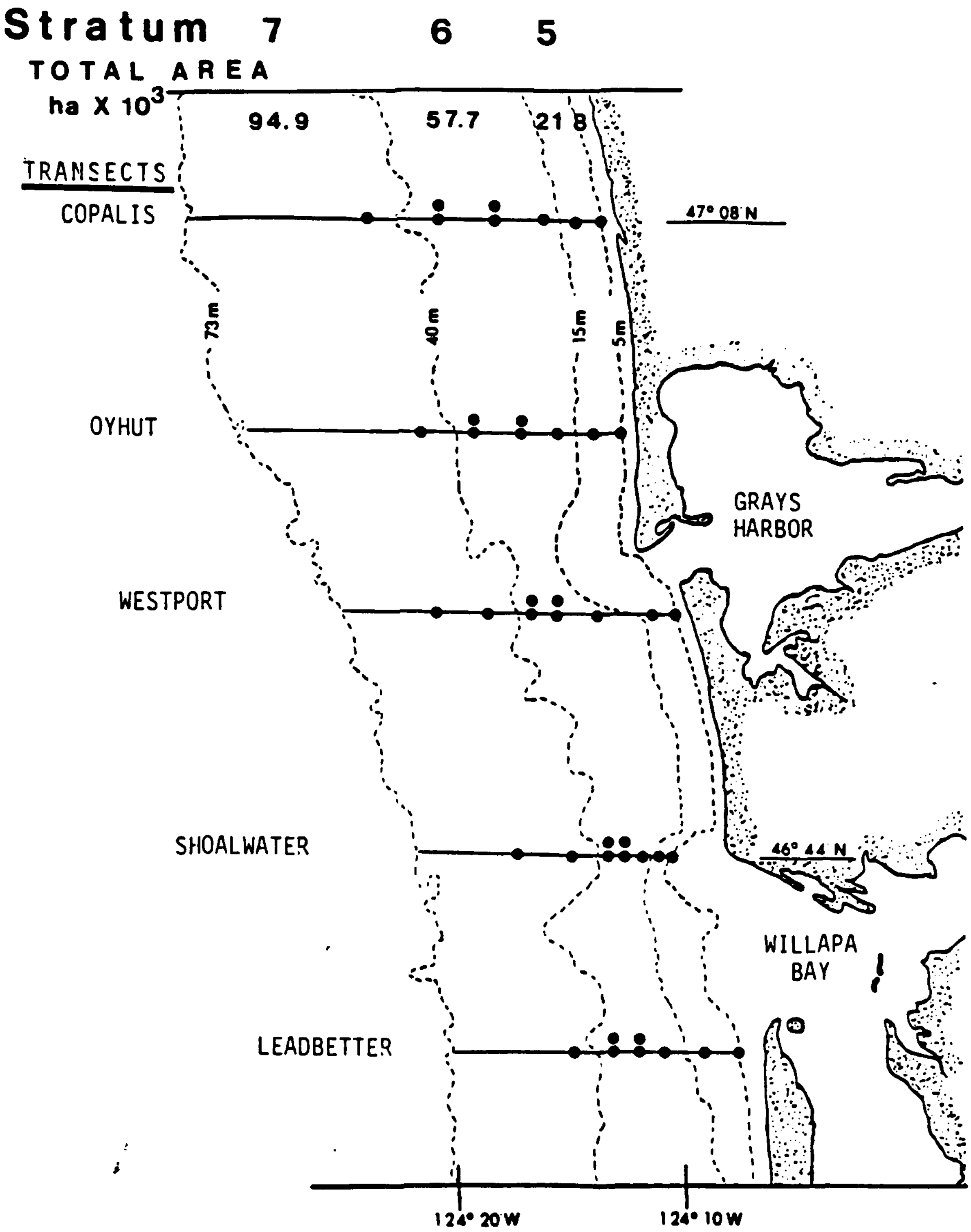
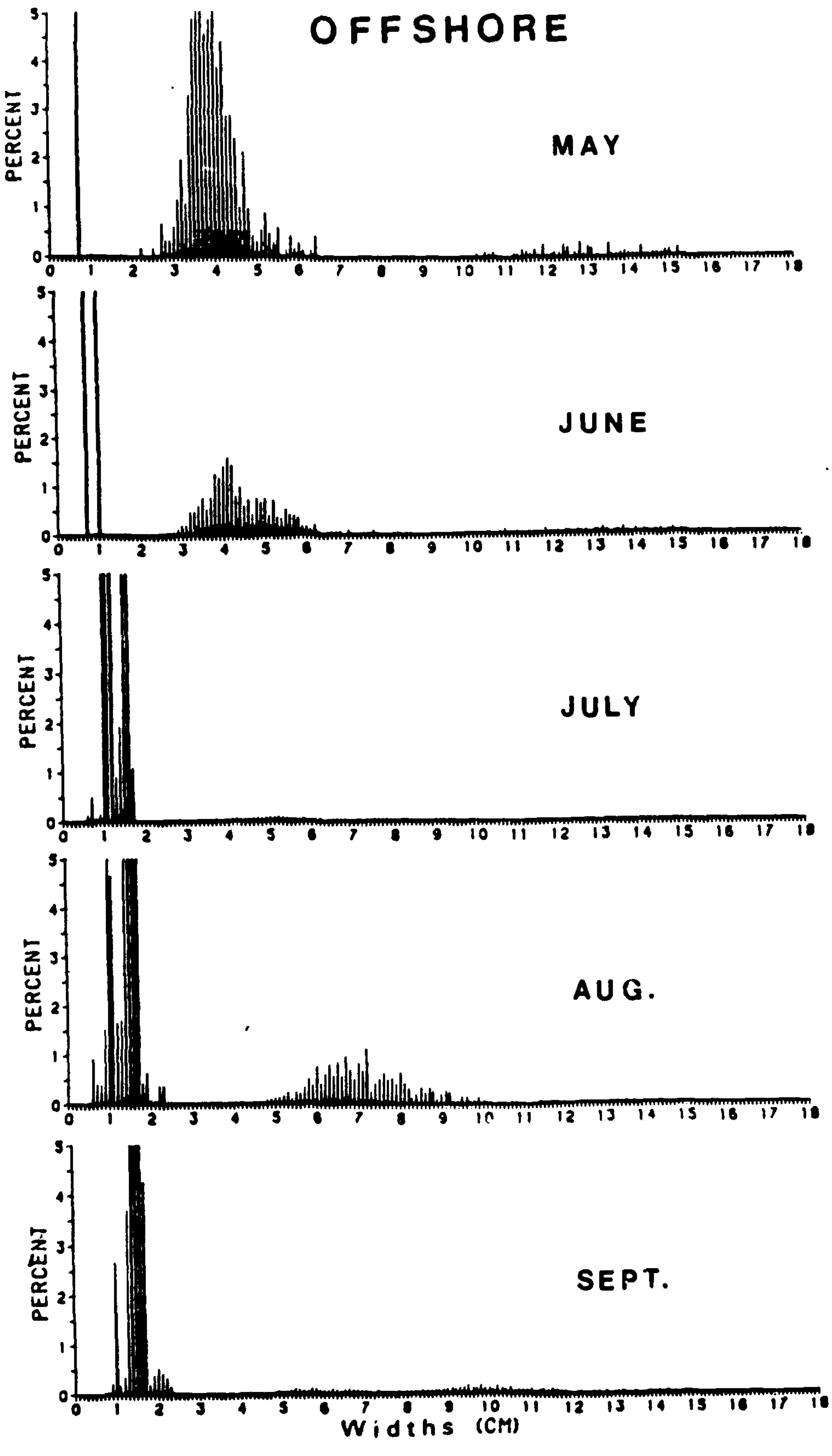


Figure 4.16. Nearshore survey area and station array (dark circles) used to estimate populations of Dungeness crab. Shown are three strata (# 5, 6, 7) that include stations in common depth intervals from 5 m to 73 m (3 fm to 40 fm). The total nearshore area of 174,440 ha is over 20 times greater than the subtidal area of Grays Harbor used to estimate population size in the estuary. In 1985 two new transects were added at Oyhut and Leadbetter; the other three have been sampled since 1983.

0+ Juveniles: Along the open coast from central California through Washington, 0+ crab first recruit to the benthos in late April but the majority of settlement occurs in May through mid June, which is consistent with timing of megalopae nearshore and in estuaries (Lough 1976; Poole 1967; Reilly 1983; Stevens and Armstrong 1984; Wickham 1979). Tasto (1983) reported that early instar Dungeness crab occur nearshore of San Francisco Bay and north to Bodega Bay in early May in accord with evidence of timing of occurrence in the same area based on fish stomach analyses (Reilly 1983b). The majority of young NJ in Tasto's study were inside 18m (10 fm) depth at densities of 10 to 300/ha (otter trawl samples). Nearshore of Humbolt Bay, California, Gotshall (1978) found high but variable densities of newly settled 0+ first and second instar crab at a typical density of 1000/ha with a range from 0 to 36,000/ha (Table 4.3).

The most extensive research on nearshore ecology of 0+ juveniles has been conducted along the southern Washington coast, most of it with support from Washington Sea Grant and COE. A relatively strong cohort of 0+ crab recruited to the benthos by May of each spring in 1983 through 1986 as evidenced by a size mode of 7 mm CW in size frequency distributions (SFD; e.g. 1985, Fig. 4.17). Based on the size-at-instar schedule given in Section 6.0, modes at 7, 10 and 15 mm CW approximately correspond to juvenile instar stages 1, 2 and 3 (J1, J2 and J3) respectively, which are most common May through July. Protracted settlement of a year class may occur, and in August of 1983, 1984 and 1986, modes at a size typical of J1 were still seen in size frequency data (Fig. 4.18). Even as late as September, J2 around 10 mm CW comprised about 2 to 6% of total 0+ nearshore in each survey year. Development of 0+ nearshore is significantly slower than of those in the estuary (see Section 6.1.2 for details), probably due to much colder coastal bottom water temperatures which average 5° to 6°C less during spring-summer when resultant Ekman transport from northwesterly winds causes frequent upwelling episodes. About five months after settlement, the average CW of nearshore juveniles is less than half that of estuarine counterparts (Fig. 4.19).

The spatial distribution by depth of 0+ crab at settlement is strongly nearshore, primarily in Str 6 (Figs. 1.3, 4.18) at stations between 15 to 40 m (during the first two years of the Sea Grant study in 1983 and 1984, so few 0+ crab were caught at the 76m, 35 fm, stations on all transect lines that those stations were dropped in 1985 and 1986). Initial densities following settlement of 0+ crab are usually highest in Str 6 (e.g. 1983, Fig. 4.20) but through the summer comparable densities may occur at both slightly shallower (Str 5) and deeper (Str 7) stations. Within a single year, density of 0+ crab can range from exceedingly low values of just a few/ha in deeper water of Str 7 to several thousand per ha at mid depths of Str 6 (e.g. 1984, Table 4.4). In 1984, a year of strong 0+ recruitment, mean density exceeded 8,000/ha nearshore and in 1985 (the strongest of the four years), surpassed 21,000/ha. Virtually no 0+ crab were found nearshore in 1986 until August when a fairly strong cohort was found in Str 7, but by September was gone (see Section 5.0).



Figu-e 4.17. Size composition of Dungeness crab population nearshore (strata comined) by trip in May to September, 1985. Note strong 0+ age group and small size by September.

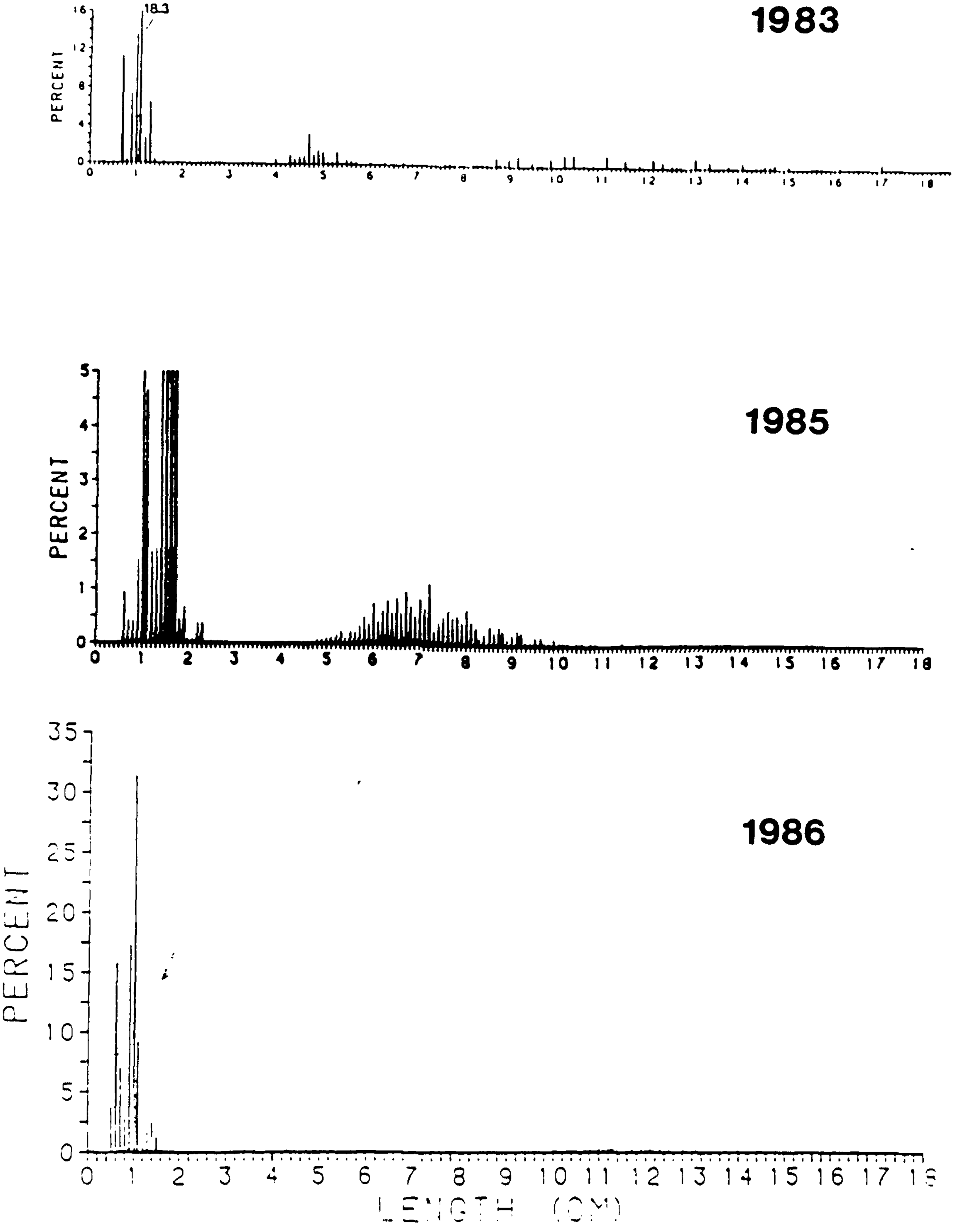


Figure 4.18. Composite of nearshore Dungeness crab population size frequency plots for August 1983, 1985, and 1986. Note the small size of 0+ juveniles (including first instar at about 7 mm CW) this late in the summer.

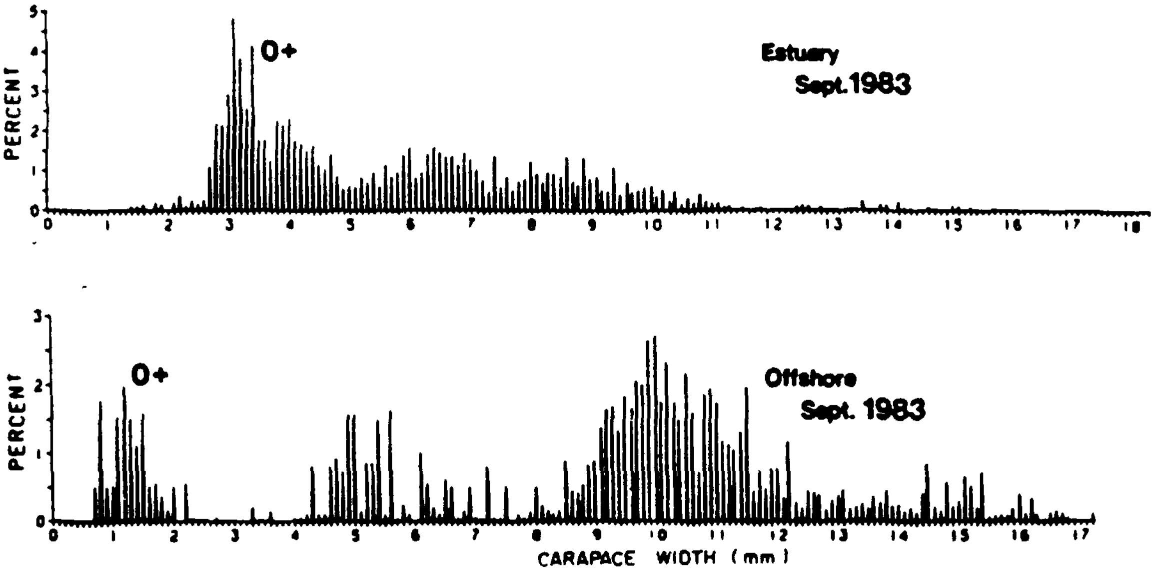


Figure 4.19. Size frequency data for the entire, weighted population estimate offshore and in Grays Harbor in September, 1983. Notice the 0+ mode offshore around 15 mm which contains a mixture of 2nd, 3rd and 4th instars. The 0+ mode in the estuary represents 5th and 6th instars.

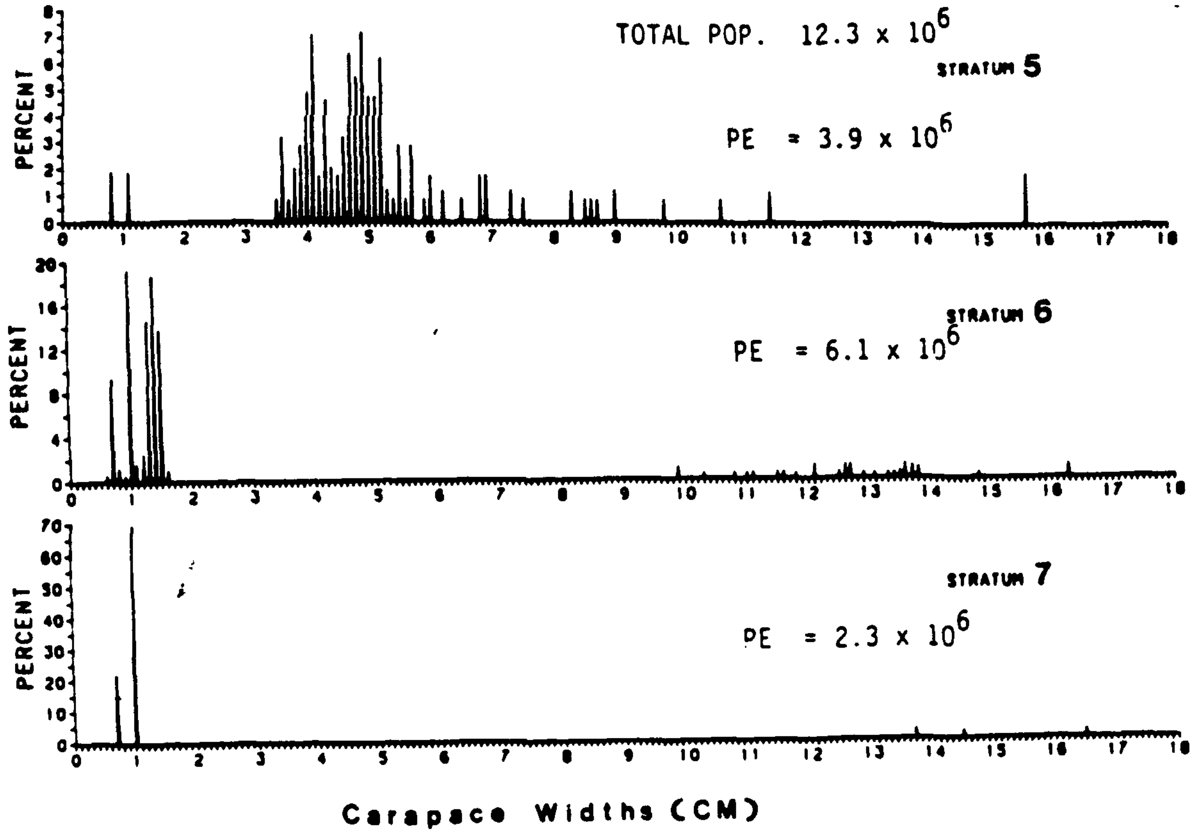


Figure 4.20. Size frequency histograms for Dungeness crab offshore, July 1983, by stratum. Total offshore population and strata populations estimates (PE) are noted to the right. Most 1+ occur in the shallowest Stratum 5.

Table 4.4. Crab density and population estimates nearshore along the southern Washington coast (Figure 1.4) in 1983 and 1984. Given are data for each geographical/depth stratum and strata combined.

1983

	STRATUM DEPTH (M)	DENSITY NO/HA (2SE)	POPULATION MILLIONS (2SE)	STRAT PROP	MONTH /YEAR	OFFSHORE TOTAL MILLIONS (2SE)
5	5-15	328(158)	6.226(3.000)	.09	5/83	68.995(53.702)
6	15-40	1249(1095)	61.146(53.582)	.89		*RE = 78%
7	40-75	20(24)	1.623(1.984)	.02		
5	5-15	203(145)	3.855(2.749)	.31	7/83	12.264(9.298)
6	15-40	124(163)	6.074(7.994)	.50		RE = 76%
7	40-75	28(47)	2.335(3.872)	.19		
5	5-15	135(80)	2.569(1.524)	.21	8/83	11.959(8.313)
6	15-40	115(142)	5.619(6.933)	.47		RE = 70%
7	40-75	46(53)	3.771(4.327)	.32		
5	5-15	206(215)	3.906(4.074)	.34	9/83	11.591(4.650)
6	15-40	145(44)	7.083(2.131)	.61		RE = 40%
7	40-75	7(8)	0.602(0.696)	.05		

1984

5	5-15	247(127)	4.683(2.402)	.35	4/84	13.273(15.133)
6	15-40	171(305)	8.385(14.940)	.63		RE = 114%
7	40-75	3(2)	0.206(0.176)	.02		
5	5-15	273(164)	5.188(3.119)	.02	5/84	334.216(364.750)
6	15-40	6700(7451)	327.969(364.735)	.98		RE = 109%
7	40-75	13(12)	1.059(1.018)	.00		
5	5-15	262(349)	4.976(6.622)	.01	6/84	404.730(438.501)
6	15-40	8066(8955)	394.815(438.346)	.98		RE = 108%
7	40-75	60(117)	4.939(9.576)	.01		
5	5-15	3795(6754)	72.038(128.195)	.26	8/84	273.424(320.509)
6	15-40	1038(694)	50.832(33.947)	.19		RE = 117%
7	40-75	1837(3559)	150.555(291.787)	.55		
5	5-15	642(652)	12.190(12.383)	.09	9/84	134.313(163.851)
6	15-40	749(600)	36.658(29.386)	.27		RE = 122%
7	40-75	1043(1961)	85.465(160.718)	.64		

STRATA AREAS:

5 = 18981 HECTARES
6 = 48950 HECTARES
7 = 81975 HECTARES

*RE = relative error: percent of the mean covered by ± 2SE.

Although such density is very high and exceeds values reported from other studies (Table 4.3), patterns of settlement and initial distribution are patchy and high density very transitory. Samples of 0+ juveniles collected by the Pacific Northwest Laboratory in June 1985 (Pearson et al. 1987), and analyzed by Armstrong and Armstrong (1985a,b) showed very high density of 0+ at settlement southwest of the Grays Harbor jetties in a pattern consistent with depth zonation seen along standard Sea Grant transects (Fig. 4.16). Mean crab density was 1,330 (±726=1SEM), 78,670 (±46,770) and 5,600 (±2,050)/ha in depth intervals of 41-49m (19-23 fm), 31-40 m (14-18 fm), and 24-30 m (11-17 fm), respectively (Fig. 4.21). Although some of the highest densities of 0+ crab recorded over the four summers 1983-1986 were measured in June 1985 (in excess of 400,000 crab/ha), most striking aspects of the data were the patchy array of settlement where densities of 100 to 100,000/ha were separated by a couple of hundred meters, and the abrupt decline in numbers seaward of about 42m depth (Fig. 4.21). Despite such high density at settlement, mortality of small instars is very high (Section 6.2.1) and two months later in September 1985 when the same station array was sampled, mean density of 0+ juvenile instar stages J3 and J4 (15 to 20 mm CW) was about 300/ha (Fig. 4.22).

Movement of 0+ crab does not seem to occur on a broad scale when very small, especially over extensive sand beds nearshore that afford little protection. Our impression from distribution of this age class in habitats within the estuary is that small instars require refuge for good survival and without it mortality is high. As mentioned, eelgrass and wood debris are important nearshore habitat for 0+ in years that such materials occur (e.g. 1983, 1984). Nearshore of San Francisco Bay, fish predation on small *C. magister* was primarily on J1, J2, J3 and J4 from 7 to about 20 mm CW (Reilly 1983b; Fig. 4.23) suggesting that refuge habitat is of primary importance to small crab that eventually reach a size that constitutes refuge from many predators.

The most important interpretation to give data on 0+ distribution is that year classes usually settle by May/June nearshore but interannual variability in mean density is high and distribution very patchy. Even in a year of apparently strong settlement (e.g. 1985), initial mortality can be so severe that density of survivors in September is a better estimate of relative year class strength within the year than are members in early summer.

1+ Juveniles: Crab in their second year of life (1+) have usually not been abundant nearshore during summer of the four survey years (1983-1986) with the exception of 1985 (strong 1984 year class; Gunderson et al. 1989). Beginning with samples in spring, there is sometimes a SFD mode around 20 to 30 mm CW (Fig. 4.24) which is the size range of 1+ crab that settled directly nearshore the previous spring. In SFDs, the mode for 1+ usually disappears in the summer because of: 1) the strength of 0+ settlement that numerically dominates the SFDs (e.g. 1986;Fig. 4.25) and; 2) immigration of a large portion of coastal 1+ NJ crab into the estuary. Those 1+ that remain nearshore through a second summer after metamorphosis grow very slowly (about 30 to 40

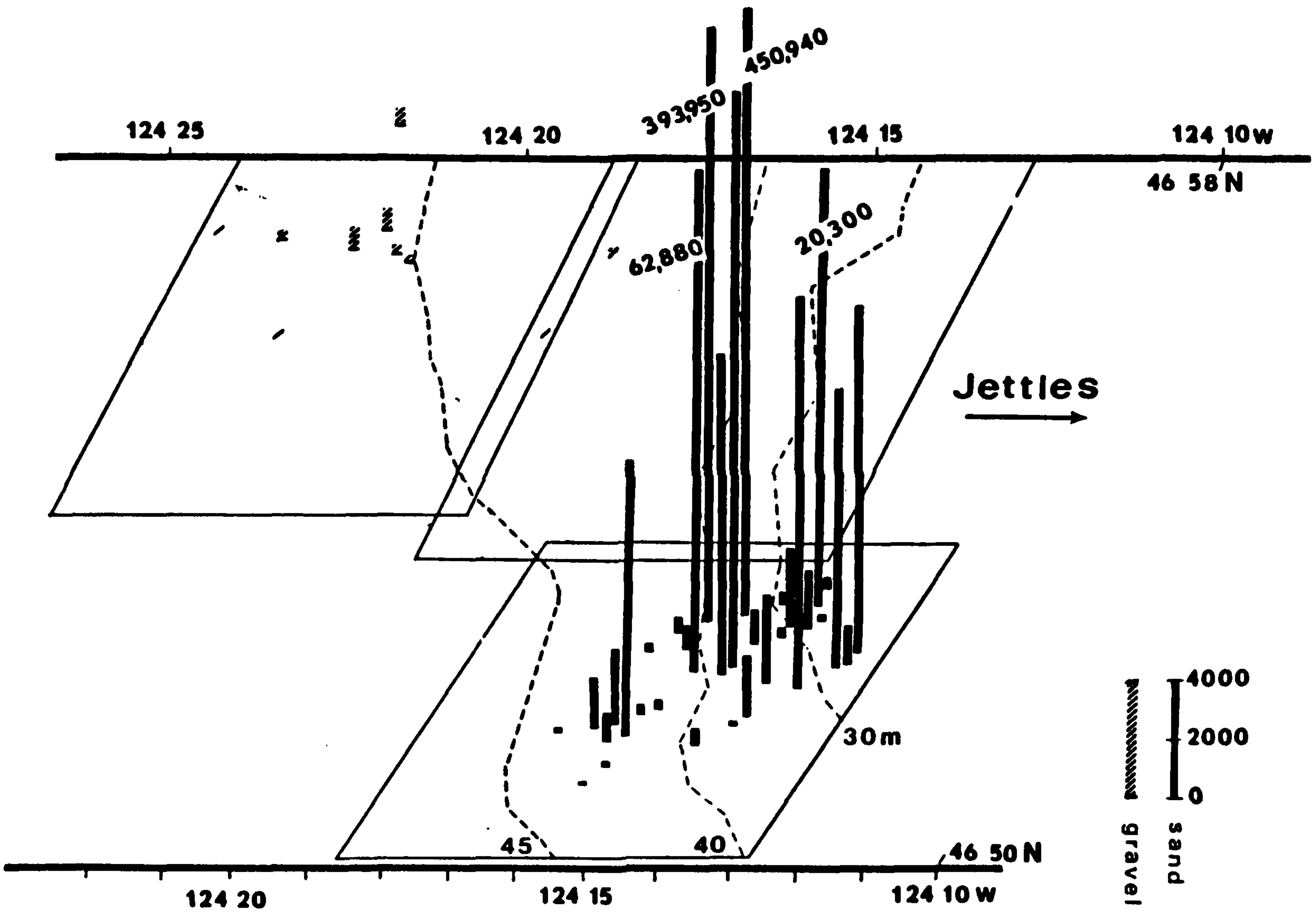


Figure 4.21. Dungeness crab density (no./ha) offshore of Grays Harbor, June 1985. Station location and substrate type are similar to the depiction in Figure 4.1 (from Armstrong and Armstrong, 1985b).

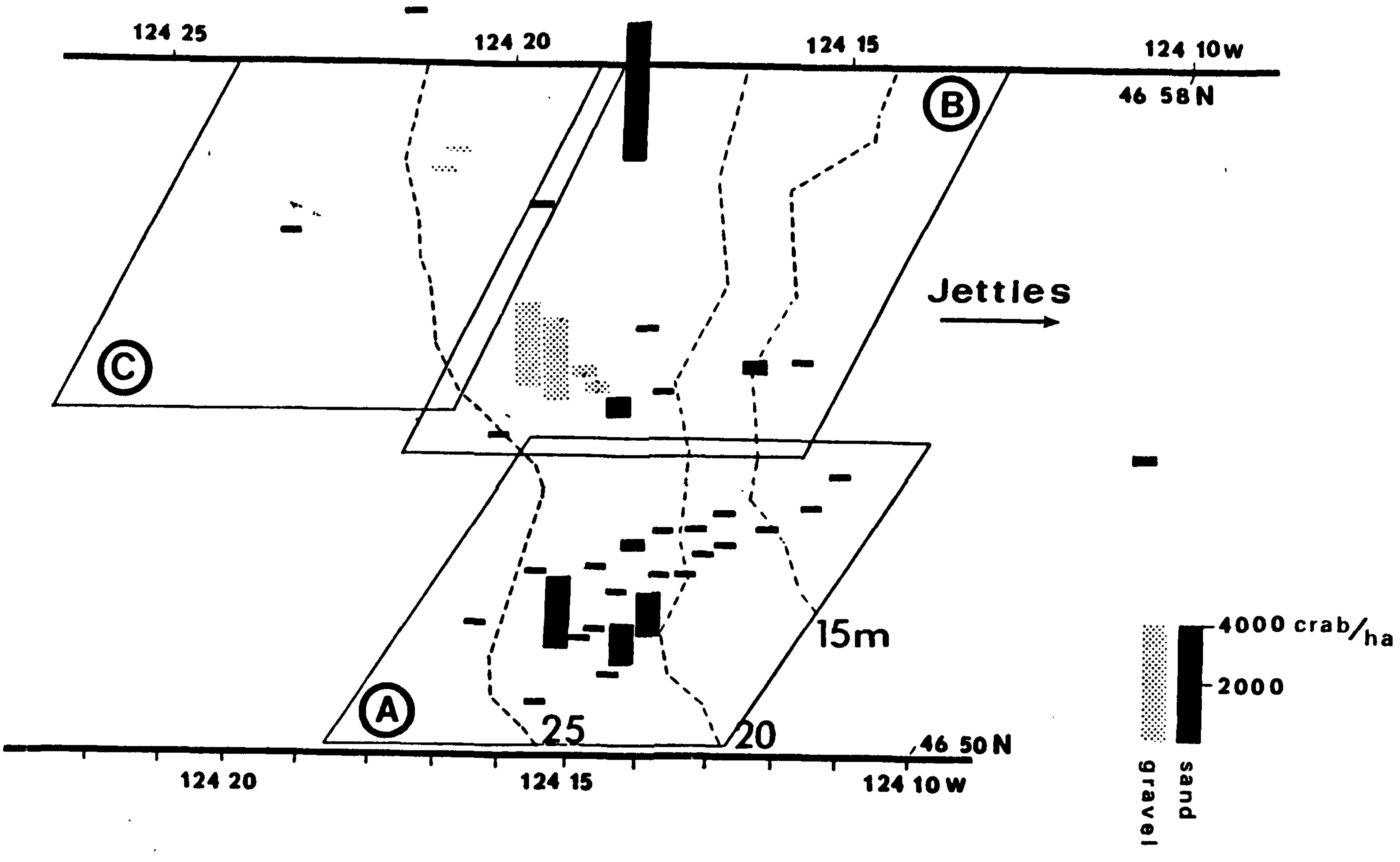


Figure 4.22. Dungeness crab density (no./ha) offshore of Grays Harbor, September 1985. Station locations and substrate type are the same as depicted in Figure 4.1. Note the substantial decrease since June, Figure 4.21.

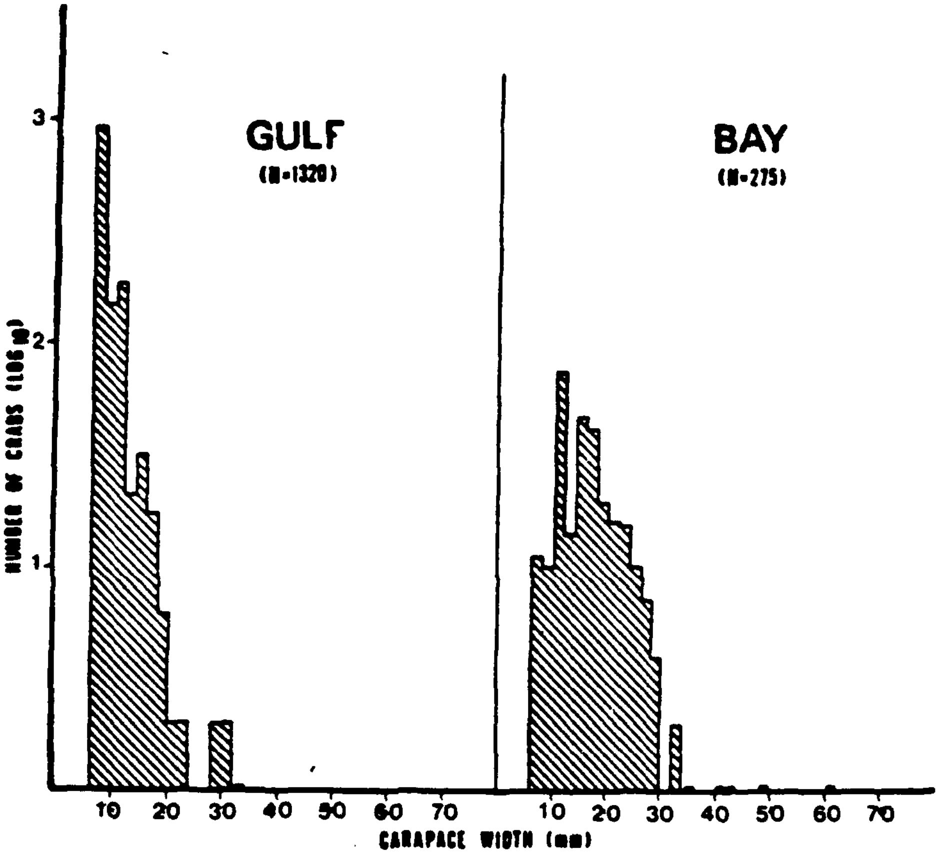


Figure 4.23. Carapace width frequency distributions (2 mm intervals) of post-larval young-of-the-year Dungeness crabs found in demersal fish stomachs, 1975-79, in the San Francisco area (from Reilly 1983b).

mm CW in July 1986; Fig. 4.25), and may be only about 40 to 60 mm CW by September of their second summer (Fig. 4.26).

Those 1+ crab that do occur nearshore in spring and early summer are found primarily at shallower stations of Str 5 (5 to 15 m depth) or just inside Str 6, but are virtually absent at the deeper stations of Str 7 (e.g. 1985, Table 4.5; refer to Fig 4.16 for nearshore strata). Distribution at shallow stations in spring is consistent with evidence of immigration of coastal 1+ crab into estuaries in that season (Fig. 4.27) to grow faster in warmer estuarine waters. In both 1983 and 1984, 1+ crab populations nearshore declined as abundance in the estuary increased and the pulse of these immigrants (that join the resident 1+ EJ as shown in Fig. 4.15) can be seen in estuarine SFDs (see Section 4.3.2). Only one year (1985) in four did a large population of 1+ NJ reside a second summer along the coast. Otherwise the density of coastal 1+ is usually very low (only a few/ha), compared to high summer densities in the estuary (Gunderson et al. 1989).

4.3.2 Estuary Subtidal

The original hypothesis constructed for the University of Washington Sea Grant program in Grays Harbor was that estuaries provide critical nursery habitat for YOY 0+ crab and contain a significant portion of any 0+ year class during the summer. Through the four years of the program thus far (1983-1986) this view has been modified in the sense that: 1) 0+ reside in higher abundance in the inter- rather than subtidal as originally assumed and; 2) 1+ crab also use the estuary in their second summer and occur in the subtidal at much higher densities than nearshore.

0+ Juveniles: Although meglopal stage larvae may move throughout the estuary in high abundance (Figure 4.15) and settle both in the sub- and intertidal regions of the estuary, long-term density and abundance tends to be relatively low in the subtidal compared to the intertidal. In some years apparently strong recruitment of 0+ juveniles can decline quickly through various form of predation (Fig. 4.28) in certain subtidal regions of Grays Harbor, such as the North Bay, South Channel and South Bay (Fig. 1.3). In some areas, subtidal habitat undoubtedly offers certain refuge to small 0+ crab, but the high density of older 1+ crab and a variety of other potential predators leads to rapid decline of a newly settled year class. Evidence presented by Stevens et al. (1982) indicate that substantial cannibalism can occur and thus relative density and total abundance of 0+ is, in most years, usually not high compared to other regions.

1+ Juveniles: Older juvenile age classes of Dungeness crab are extremely abundant throughout the subtidal of estuaries such as Grays Harbor and Willapa Bay and typically range in density from 500-1000/ha (Armstrong et al., 1986) and in certain years such as 1983 may range from 1500 to over 2000/ha throughout the estuary (Fig. 4.29). Particularly the shallow, narrow channels of regions such as the North Bay of Grays Harbor and north and east central areas of Willapa Bay are preferred habitat of 1+ Dungeness crab. In trawls conducted during the Washington Sea Grant

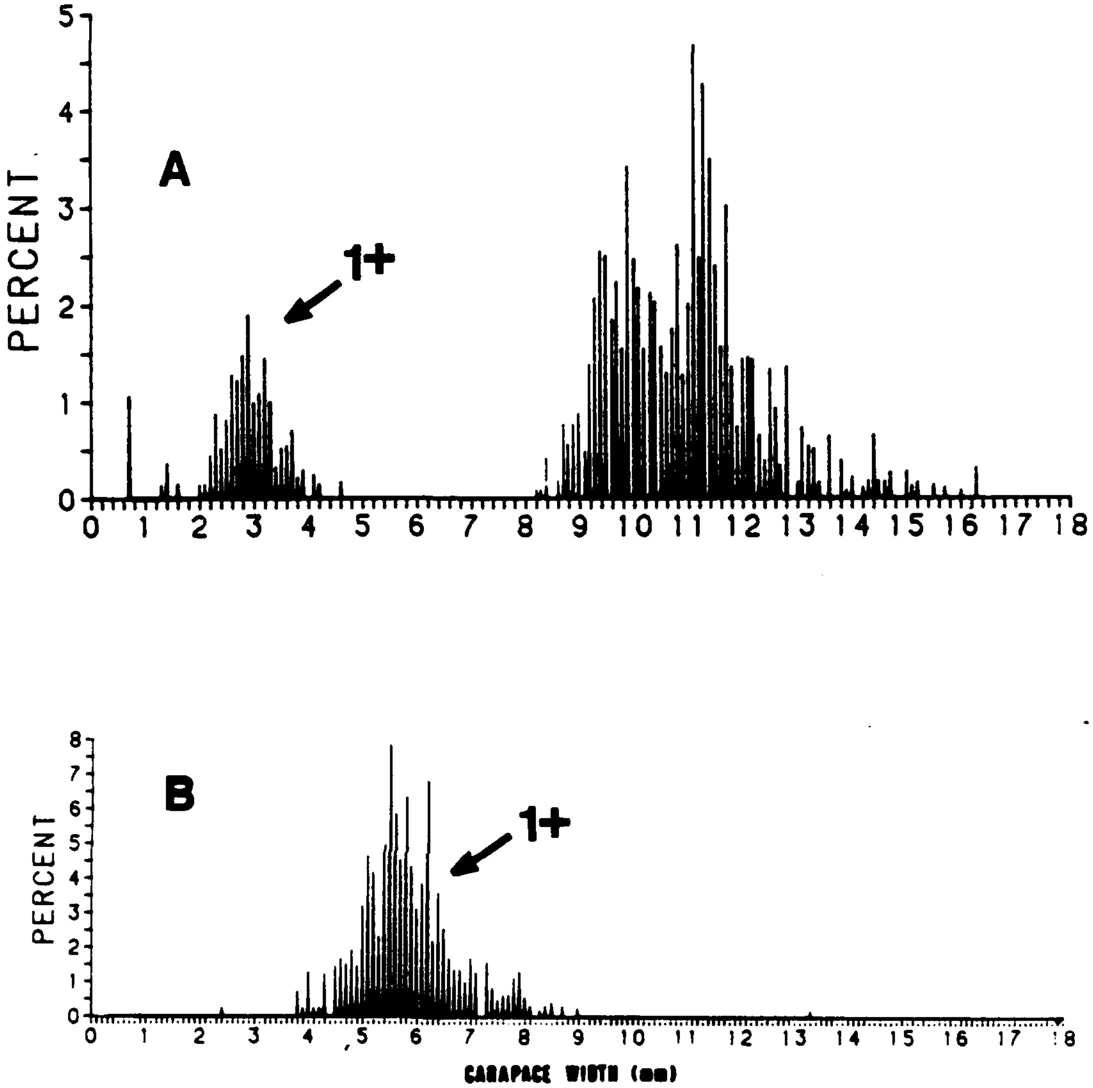


Figure 4.24. Size frequency plots for nearshore Dungeness crab in May 1986 (A) and Grays Harbor crab in May 1985 (B). Note the substantial difference in size of the 1+ age class in spring, one year after settlement, of cohorts that settled either along the coast or in the estuary as 0+.

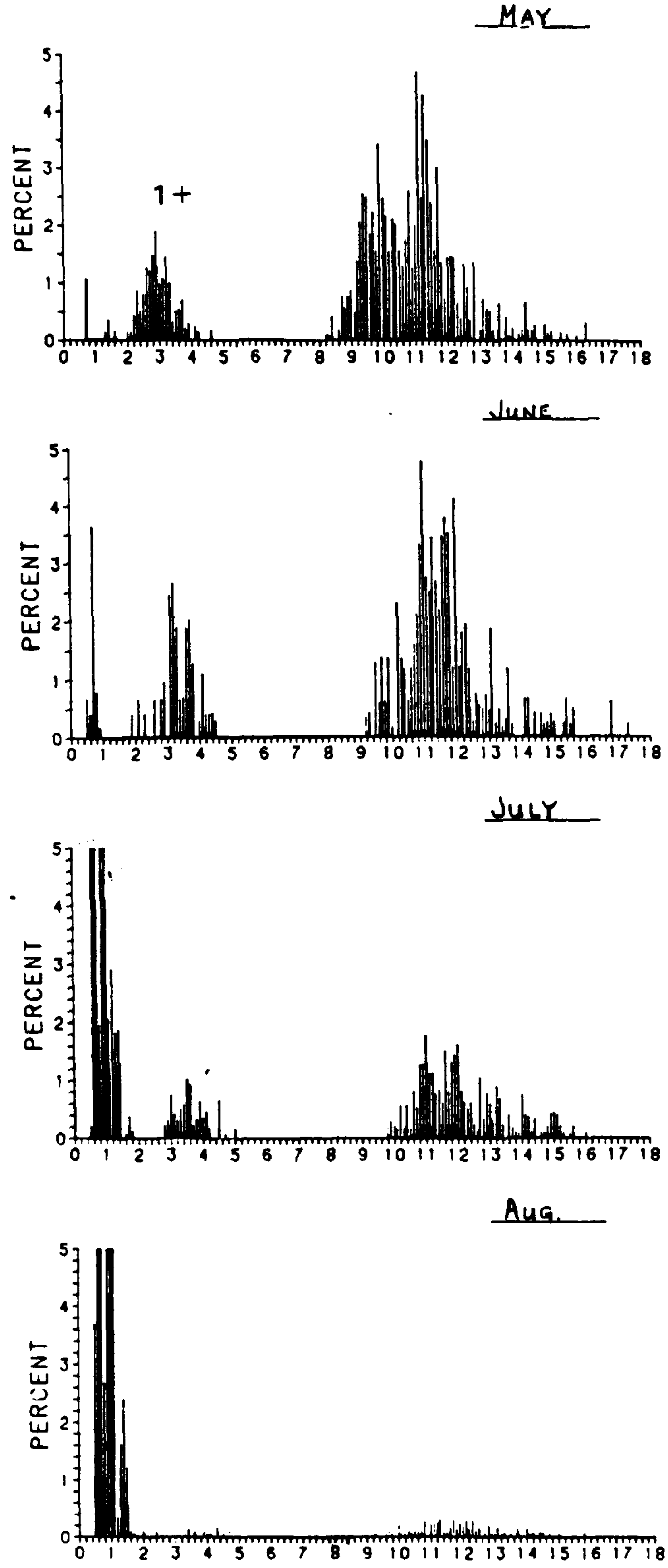


Figure 4.25. Nearshore Dungeness crab size frequency plots, May through August 1986. Note the decline of the 1+ population as it immigrates into estuaries (see Figure 5.7 for population estimates).

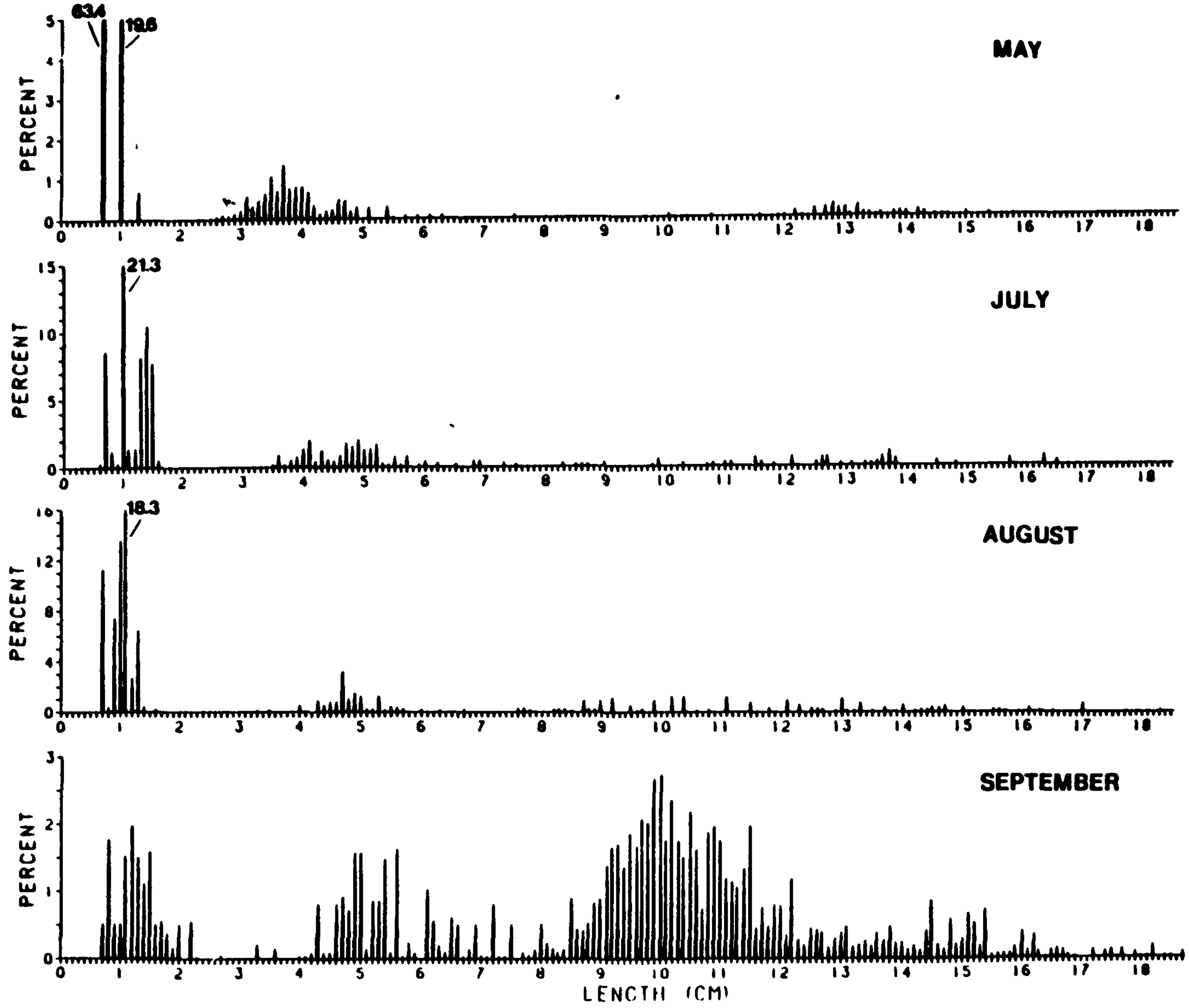


Figure 4.26. Size composition of the Dungeness crab population in the nearshore survey area (all depths combined), by month, 1983. Note little growth by 0+ from May to September.

Table 4.5. Population estimates of Dungeness crab nearshore of Grays Harbor, May-September 1985, by age class and stratum expressed as millions of crab.

Month of Trip	Age group	Stratum # 5	Stratum # 6	Stratum # 7	All strata Combined
May	0+	0.86	10.41	0.53	11.30
	1+	10.31	15.72	--	26.03
	>1+	0.30	1.48	0.11	1.89
	All ages	11.47	27.61	0.64	39.72
June	0+	1.16	75.45	1.04	77.65
	1+	12.14	9.69	0.09	21.92
	>1+	0.47	2.11	--	2.58
	All ages	13.77	87.25	1.13	102.15
July	0+	1.42	1235.56	27.73	1264.71
	1+	6.78	19.50	0.07	26.35
	>1+	0.52	3.12	--	3.64
	All ages	8.72	1258.18	27.80	1294.70
August	0+	2.94	287.46	138.94	429.34
	1+	95.21	10.30	--	105.51
	>1+	3.07	0.48	0.42	3.97
	All ages	101.22	298.24	139.36	538.82
Sept.	0+	2.21	54.97	346.49	403.67
	1+	6.50	14.63	0.09	21.22
	>1+	0.08	6.42	0.06	7.10
	All ages	8.79	76.02	347.18	431.99

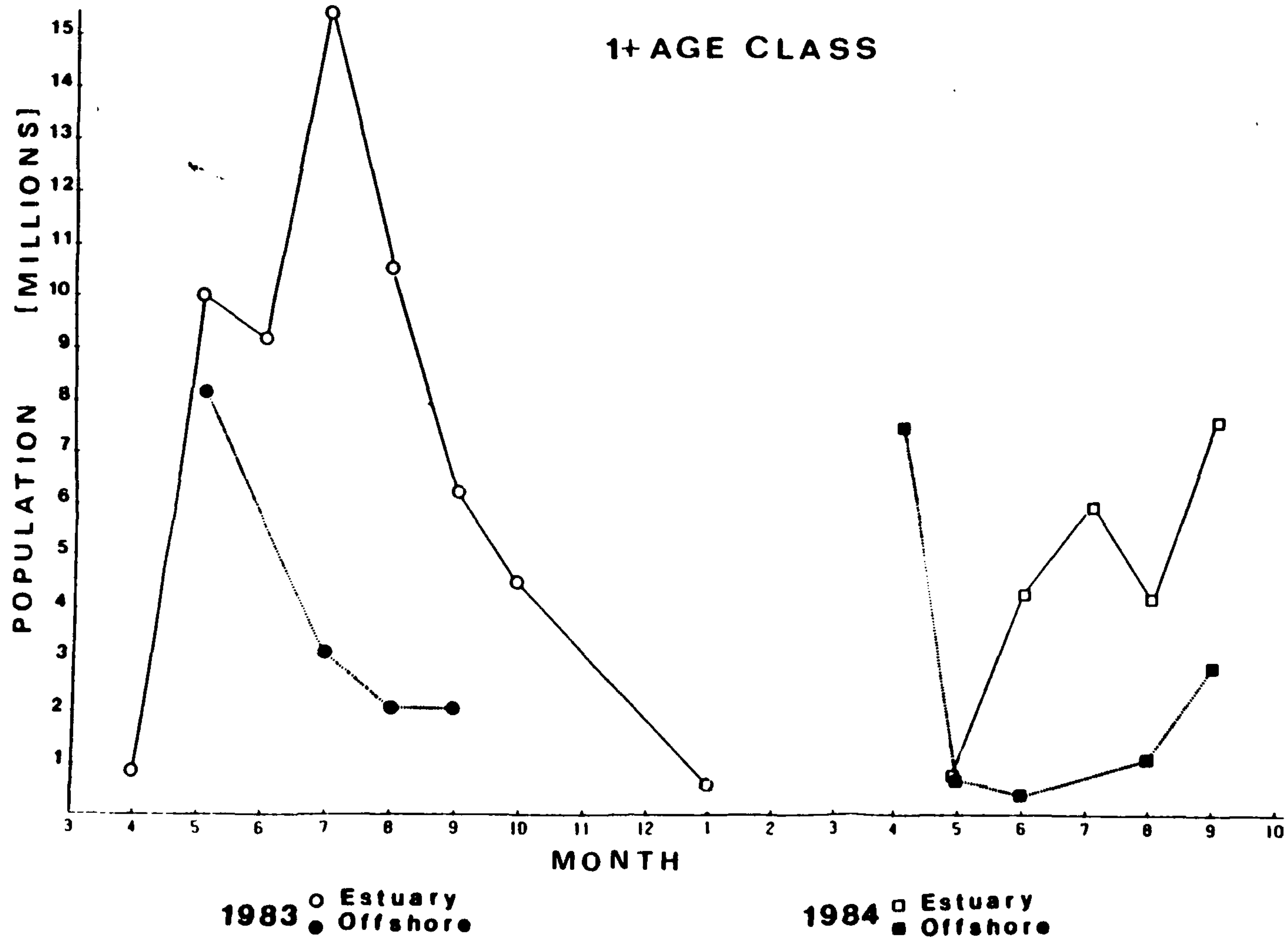


Figure 4.27. Comparison of population estimates for Dungeness crab 1+ age class from April 1983 to September 1984 both within the estuary and offshore of Grays Harbor.

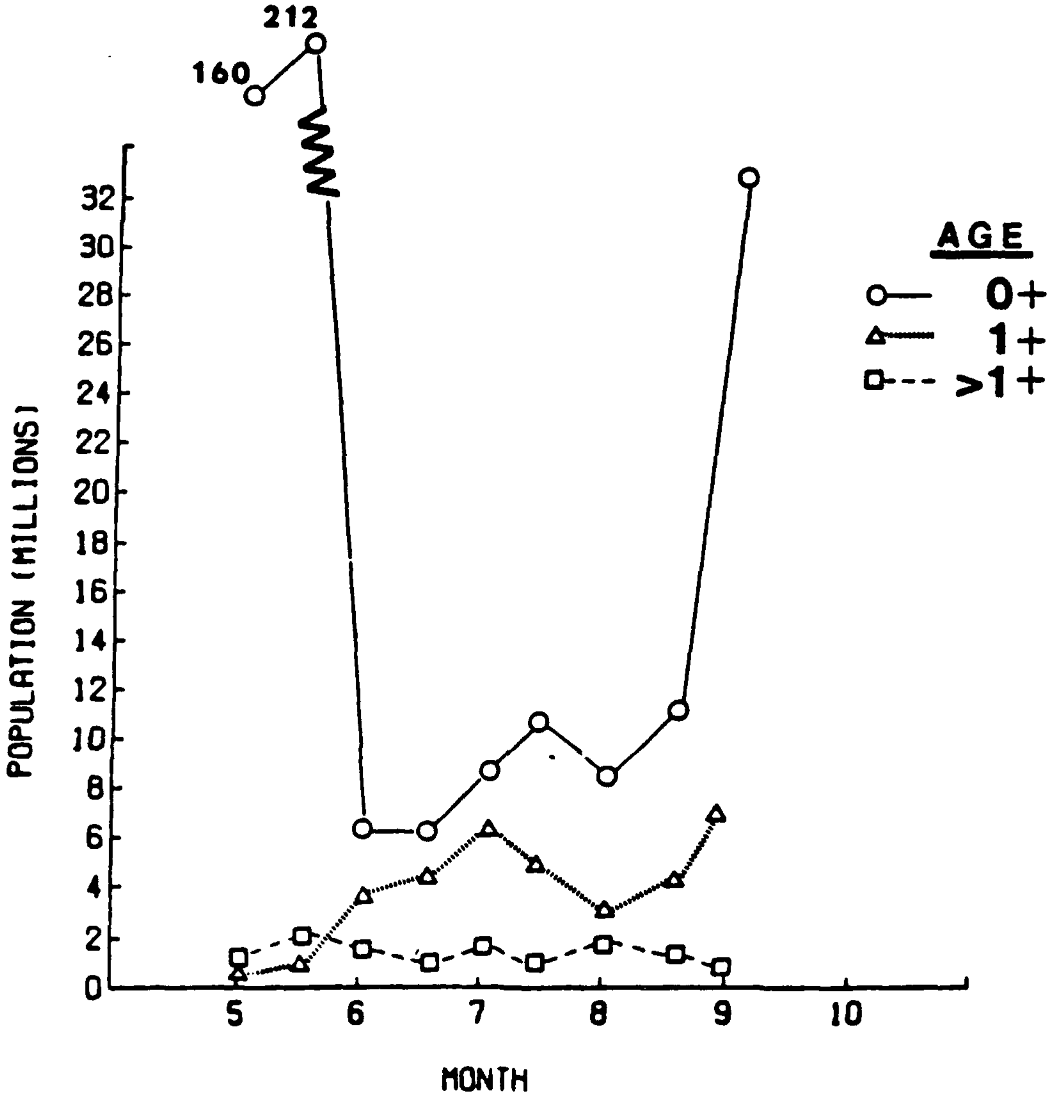


Figure 4.28. Population estimates of Dungeness crab by age classes in Grays Harbor estuary from May to September 1984. Note the abrupt increase in 0+ caused by movement from the intertidal in September.
Figure 4.29. Summer 1983 Dungeness crab mean density by age class in Grays Harbor. Vertical bars are ± 1 SEM.

Program it was not uncommon to measure densities of 3000-4000 juveniles/ha in areas where summer bottom water temperature is 15 to 17°C and the substrate is mixed shell, stick and leaf debris.

4.3.3 Estuary Intertidal

0+ Juveniles: As described by Dumbauld and Armstrong (1987) densities of YOY juvenile crab are orders of magnitude greater in many intertidal habitats that afford refuge from predation compared to subtidal locations. Particularly in shell and eelgrass described in section 4.1.3, densities in May through September may range as high as several hundred per square meter immediately following settlement in June and decline to more typical summertime density of 5-10/m^2 through September (Fig. 4.30; Dumbauld and Armstrong 1987). In units of hectares, these densities are from 50,000 to 100,000, substantially greater than occurs in the subtidal. Intertidal distribution and abundance of 0+ crab varies in accord with substrate, and small instars are virtually nonexistent in open exposed tide flats. Throughout the summer 0+ densities are low in eelgrass, moderately high in oyster shell and highest in naturally occurring deposits of *Mya arenaria*. The distribution of these materials throughout the intertidal of Grays Harbor has been mapped by Dumbauld and Armstrong (1987; Figs. 4.3, 4.4). Extensive utilization of such habitat by 0+ crab may permit habitat enhancement as one means to mitigate for mortality of older 1+ crab killed during subtidal dredging operations by COE (Armstrong et al. 1987a).

1+ Juveniles: Older juvenile crab make use of intertidal locations on a diel basis when they occupy such regions during flood tide but move off as the tide ebbs and flats are exposed (Stevens et al. 1984). For the most part there is not adequate refuge and means to avoid desiccation and prolonged exposure on tide flats during ebb tide and so larger crab move back into adjacent channels for portions of the day. Stevens et al. (1984) showed directed movement of older crab onto the flats with flood tide apparently to feed on such pray as crangonid shrimp (Stevens et al., 1982). Another indication of movement of 1+ crab onto tide flats during flood tide has been in the context of the annual Sevin (carbaryl) pesticide spray. After intertidal mudflats are sprayed with the insecticide at low tide, older juvenile crab move onto the flats at high tide to forage on prey organisms killed by the insecticide. Washington Department of Fisheries typically counts and estimates mortality of 1+ juveniles on the tide flats 24 h following intertidal application of carbaryl (Buchanan et al. 1985).

4.4 ADULTS

Both adult male and females aggregate nearshore along the coast, which tends to accentuate the nursery features of estuaries where juveniles are in proportionately greater abundance. As

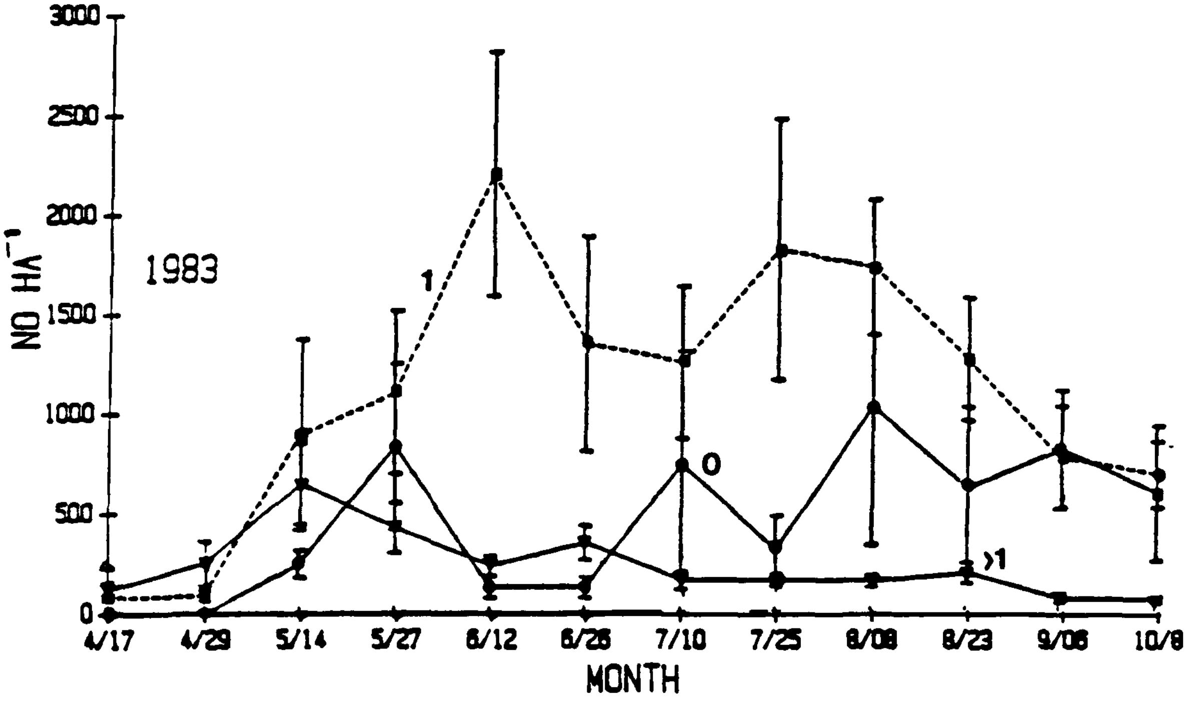


Figure 4.29. Summer 1983 Dungeness crab density in Grays Harbor by age class (0+, 1+, >1+); vertical bars are ± 1 SEM (from Gutermuth 1987).

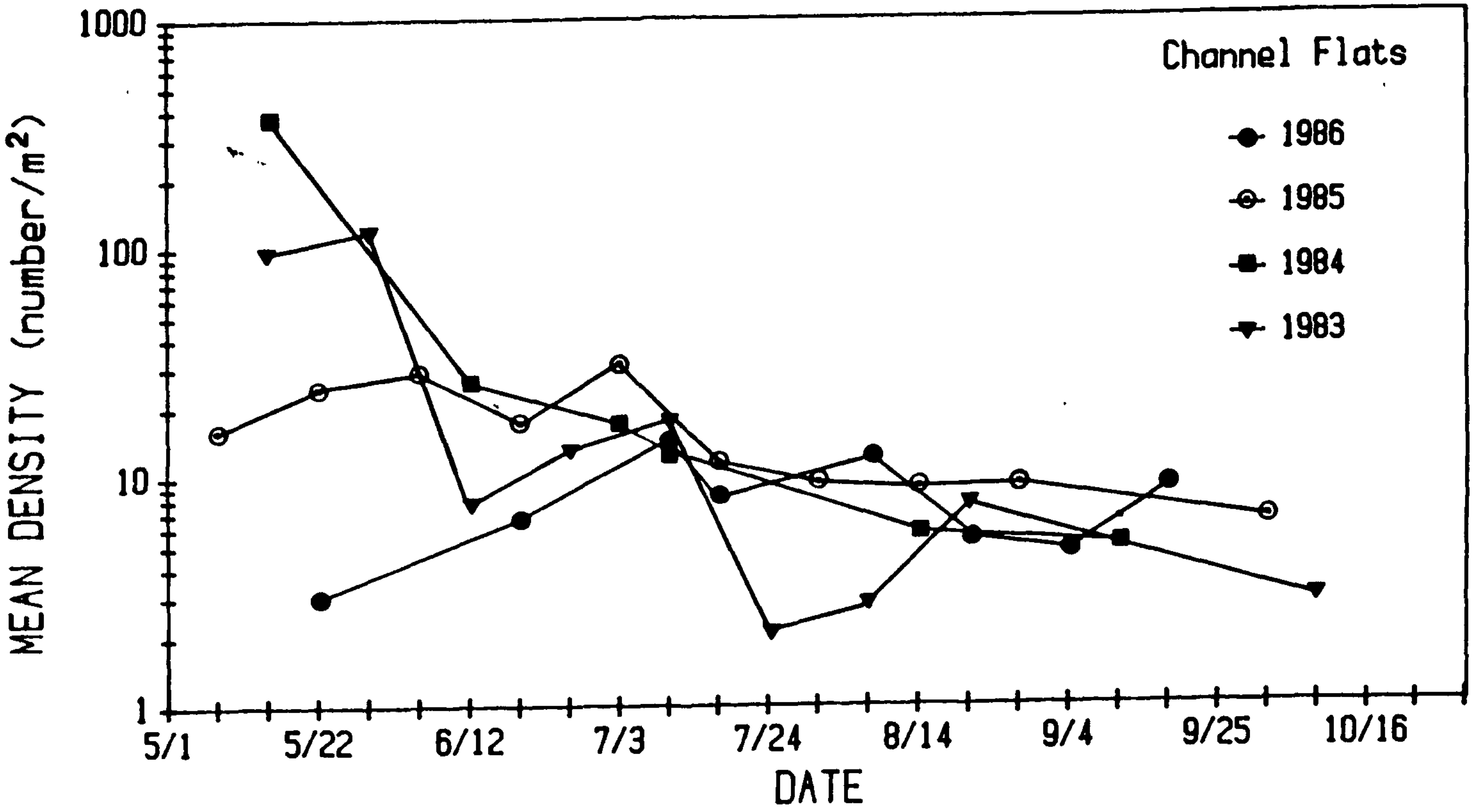


Figure 4.30. Comparison of mean density estimates (number/m2) for juvenile Dungeness crab found at Station 1 along the South Channel in 1985 and 1986 (this study) and similar estimates from a nearby station sampled by Sea Grant researchers in 1983 and 1984. Note the log scale and therefore order of magnitude differences in density levels at initial settlement in May and June, but consistent values of 8 to 10 crab/m2 by August and September (from Dumbauld and Armstrong 1987).

summarized in Section 3.0, the adult male fishery occurs along the open coast and only about 10% of the seasonal catch is taken in estuaries (Barry 1985; Demory 1985). Adults of the species occur primarily over broad homogeneous sand substrates and virtually never in areas of heavy rock outcrop or cobble/gravel. All reproductive events occur along the open coast as well, including molt of mature females, copulation, extrusion and incubation of the eggs until hatch. While females of theoretically mature size are sometimes found within estuaries, occurrence of ovigerous stages has never been reported in estuarine systems. Thus, apart from the limited fishery, there is relatively little use of estuaries by adult stages except in a transitory manner within the outer portions during spring and summer.

5.0 POPULATION DYNAMICS AND MOVEMENT

It was pointed out that the relative impact of COE widening and deepening might vary substantially based on the population size of juveniles at the time of construction (Section 3.0), and such variability in density and abundance was taken into account by Armstrong et al. (1987a) when they calculated different dredge impacts in areas based on a range of population densities. The most prevalent issue considered during deliberations of the Crab Study Panel was estimation of absolute number of crab killed at various life history stages and the loss posed to future commercial fisheries. Another perspective of such impacts is whether the loss of crab resources at any life history stage could be detected in light of population fluctuations, and whether high or low abundance at the time of construction exacerbates relative impact of the project on later fisheries. Population dynamics play an important role in addressing these perspectives of impacts but such data have been provided on juvenile stages only in limited investigations, and for adult stages comes only as an index of relative abundance derived from the commercial fisheries.

5.1 FISHERIES CYCLES AND POPULATION DYNAMICS

Quite apart from activities of the COE that might impact juvenile stages, Dungeness crab populations as measured by the commercial fishery vary over a seven-fold range (PMFC 1985; Washington Landings 1984-85 = 2.9 million lbs, 1969-70 = 17.7 million lbs 1988-89 = 20.6 million lbs; S. Barry, WDF, pers. comm.). Further, as noted in Section 3.0, populations seem to cycle in abundance over some regular interval of approximately 9 - 10 years (Botsford and Wickham 1978; Botsford 1986). Mechanisms other than human impacts (e.g. insecticides, dredging, landfill, etc.) which have been hypothesized to affect crab recruitment and abundance are broadly divided into biotic and abiotic (environmental) mechanisms which have been investigated through correlation studies or models of environmental and density-dependent recruitment.

5.1.1 Correlation studies

Analyses in this category have generally used trends in fishery data lagged back in time varied numbers of years to the point (the year) of egg development, larval hatch, and settlement to the juvenile stage for a given year class. To the extent that the size of the crab fishery in a given year can be linked to plausible biological and abiotic processes operative in the year of hatch, it is most important that the age of crab in the fishery be determined with some accuracy. Characterization of growth rate and determination of size-at-age of crab has been addressed through the years (Mackay and Weymouth 1935; Butler 1961) and the fishery is, in fact, usually composed of several age classes of crab between 3.5 to 6 years old, which potentially confounds the attempt to take annual fishery landings as an index of the relative strength of a given larval/juvenile year class (Botsford 1984).

Still, lag correlations have been used widely with some interesting results. Peterson (1973) found a correlation between crab landings in a given year and strong upwelling indices 1.5 years earlier in California and Oregon and only 0.5 years earlier in Washington. He ascribes some sort of nutrient-enhanced survivorship in strong upwelling years that somehow benefits the fishery. This finding is not biologically satisfying since it says that the benefit of high water column production comes to older juvenile and subadult crab only 0.5 to 1.5 years from the fishery. More intuitively appealing would have been a lag relationship back to the year of hatch where the effect of upwelling on larvae would relate either to food production or current regimes and transport. Botsford and Wickham (1975) challenged Peterson's hypothesis by showing through autocorrelation that while crab landings are definitely cyclical, upwelling is not (Fig. 5.1).

Mean annual sunspot number was correlated to west coast crab landings by Love and Westphal (1981; Fig. 5.2) although the suspect nature of their use of sunspot information and lack of any apparent biological meaning to the correlation have given little credence to the hypothesis (Hankin 1985; Botsford 1986). Regular cycles of crab landings in northern California as well as a trend of long term decrease in central California were correlated to a three year lag of sea surface temperatures by Wild (1980) who observed that troughs in the crab catch record corresponded to peaks in local winter sea surface temperatures that annually impacted eggs and/or larvae three years earlier (Fig. 5.2). The biological explanation for this came from laboratory studies that showed a decrease in egg survival with increasing water temperatures during incubation on the abdomen of the female. The average number of larvae hatched per crab egg mass declined from 685,000 at 10°C to only 14,000 at 16.7°C. Thus, any long term or annual warming trend that would elevate bottom water temperatures above approximately 14°C was viewed as potentially deleterious to the reproductive effort of the population that year. Such occurrences might correspond to El Nino events or long term ocean warming trends as hypothesized for central California.

A final correlation model between crab landings and environmental forces operative during the year of hatch and larval development was proposed by Johnson et al. (1986) who found some correlation between the strength of spring wind stress and crab landings along the coast 4 to 5 years later (Fig. 5.3). They speculated that this positive correlation reflects a process by which pelagic larvae at the megalops stages are returned onshore in the neuston layer driven by prevailing northwesterly winds.

Most of the correlative analyses done with physical data such as upwelling, wind speed and direction, and ocean temperatures have contemplated an effect on larval stages in terms of survival and/or transport. Transport is viewed as critical for return of larvae onshore (although larval

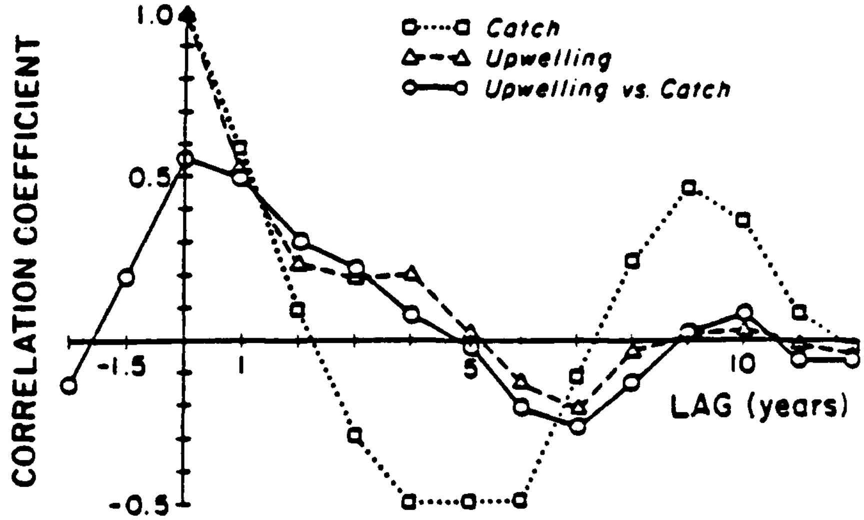


Figure 5.1. The cross-correlation between upwelling index and crab catch, the autocorrelation of upwelling index, and the autocorrelation of crab catch for northern California (redrawn from Botsford and Wickham, 1975).

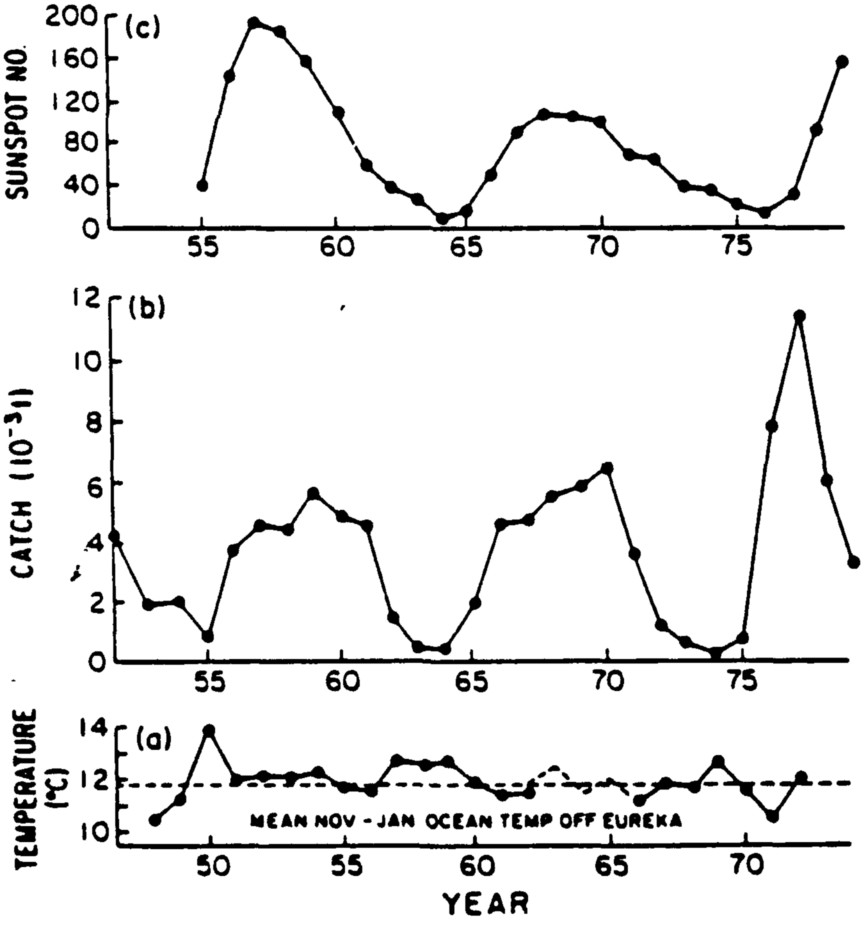


Figure 5.2. A comparison of crab catch in northern California (b) and sea surface temperature 4 yr earlier (a) (redrawn from Wild 1980), along with sunspot numbers (c) (redrawn from Love and Westphal 1981).

behavior may facilitate retention in locale areas; Sulkin 1984) and into estuaries where it assumed survival is higher or at least growth rates faster (Stevens and Armstrong 1984; Armstrong and Gunderson 1985a; Gutermuth and Armstrong 1989).

5.1.2 Models of environmental and density-dependent recruitment

Another approach taken to interpret the evidence of cycles seen in the crab fishery data has been to study possible biological interaction between crab, their food and predators as responsible for population levels. A density-dependent crab egg-predator model based on nemertean worms (*Carcinonemertes errans*) was proposed by Wickham (1979) in which worm predation on crab eggs increases or relaxes depending on number of crab larvae produced and resultant number of females relative to densities of predatory worms. Although this mechanism might at times exacerbate population levels, its influence on the cycles seen in the fishery was discounted in a review by Botsford (1986). Along similar lines of predator impact, Botsford et al. (1982) discounted the possible impact of salmon predation as a cause of cyclic landings of crab in the California fishery, but Thomas (1985) argued for a link between salmon abundance and predation on crab megalopae and a long term decline in abundance off central California.

Cannibalism by large mature crab on very small YOY 0+ crab was suggested by Botsford and Wickham (1978) to be evidence of a density-dependent cause of cycles in the fishery. They hypothesized that progeny of an exceptionally strong adult year class settle to the benthos and are so heavily cannibalized by large parental crab that the resultant low survival of that year class is manifested about four years later as a weak fishery. There is evidence, however, that virtually any crab larger in size will eat smaller crab, and indeed Stevens et al. (1982) showed that a substantial component of the diet of 1+ crab in the Grays Harbor estuary was comprised of small (approximately 7-20 mm CW) newly settled 0+ crab. Although cannibalism is not a compelling hypothesis at this time, Botsford (1986) argues that it is still tenable but complex and in need of more data.

In a further attempt to model fluctuations in the commercial landings against a number of hypotheses, McKelvey et al. (1980) concluded that the best explanation for abundance cycles (in terms of fit of crab landing data against various life history stages and processes) was density-dependent survival of eggs/larvae. Hankin (1985) elaborated on this issue by pointing out the tremendous increase in survival to reproductive age when there is only a slight change in overall mortality rates from larvae to adults. The biological underpenning or explanation of why egg/larval survival is density-dependent was not satisfactorily addressed in the paper by McKelvey et al. (1980), but Hankin (1985) suggests that food supply, as affected by upwelling, and time of larval hatch (issue of starvation) might be the cause. Lough (1976) reported a substantial difference in

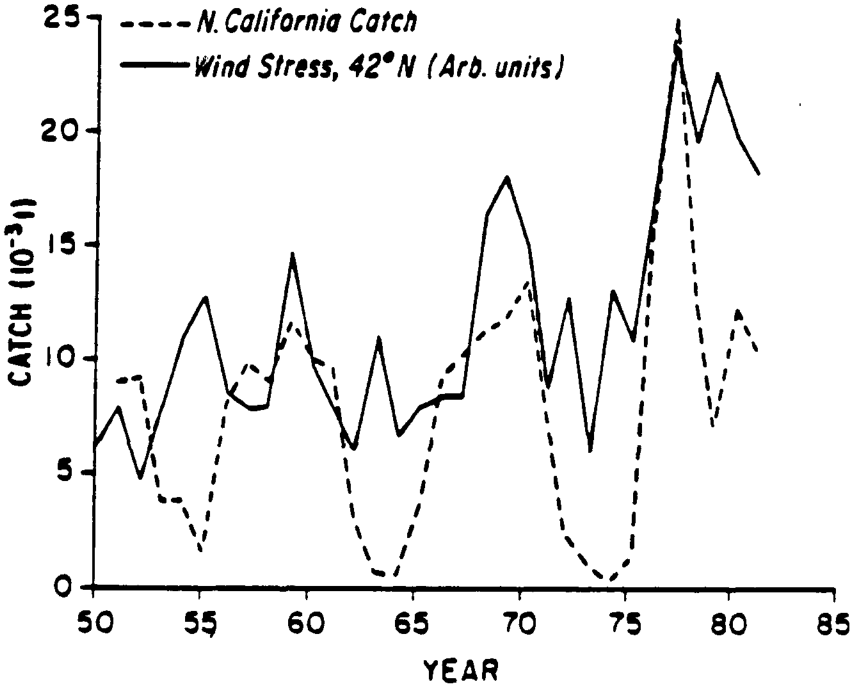


Figure 5.3. A comparison of the Dungeness crab catch record from northern California with wind stress at 42° four years earlier (from Johnson et al. 1986).

survival of two consecutive years of Dungeness crab larvae off the Oregon coast, possibly attributable to decreased feeding success in the year of lower abundance.

Which of these hypothesized mechanisms, singularly or together, actually affect crab year class strength is not known. To the extent that fluctuations in abundance are real, however, they must be considered when assessing the impact of COE W&D on crab resources.

5.2 OTHER POPULATION STUDIES

Apart from records derived from the commercial fisheries, very few studies of population density and abundance have been conducted throughout the range of the species despite its high economic importance. Qualitative studies by Cleaver (1949) in Grays Harbor and Butler (1956) in British Columbia documented occurrence of juveniles in estuaries and, at times, large scale movement of some adults into these systems from the open coast. The relative abundance of juvenile Dungeness crab in Humbolt Bay, northern California was studied over a four year period by Gotshall (1978) who found that density ranged from several hundred to about 5,000/ha, comparable to Grays Harbor. Studies in and offshore San Francisco Bay in the mid 1970s showed that 0+ recruit to the estuary in late spring and estimated abundance ranged from as little as 0.4 million in 1978 to 9.3 million in 1975 (Tasto 1983). In a comparison between the estuary and nearshore coast, Tasto estimated that as high as 80% of a particular Dungeness year class used the San Francisco estuary during early juvenile stages.

Research in the Columbia River estuary was reported by Emmett and Durkin (1985) and McCabe et al. (1986) who found particularly heavy use of the estuary in late spring and early summer during settlement of the 1985 year class when densities were measured in excess of 10,000/ha. Population abundance was estimated somewhat in accord with Stevens and Armstrong (1984) and was as high as 57 million in early summer of 1985 (McCabe et al. 1986). Older crab in the 1+ and 2+ age groups, were much less abundant, however, and estimates for the years 1983 to 1985 ranged from as low as several hundred thousand to 3 million over the extensive area of the Columbia River estuary included in abundance estimates.

Quantified studies of Dungeness crab recruitment and population dynamics in Grays Harbor estuary was first reported by Armstrong et al. (1982) and Stevens and Armstrong (1984) based on work supported by COE. They showed patterns from time series of density estimates that corresponded to spring settlement of the 0+ age class, occurrence of 1+ crab at high densities during summer, and a substantial decline of larger crab in fall and early winter. These seasonal patterns of density corresponded to estimates of total abundance throughout the estuary which were as low as 3.3 million crabs in winter but increased to 39 million crab in summer during the years 1980-81 (Stevens and Armstrong 1984).

5.3 NEARSHORE POPULATIONS, WASHINGTON COAST

Following from the work of Stevens and Armstrong, a comprehensive study of juvenile crab recruitment and population dynamics began in 1983 under Sea Grant sponsorship (see Section 1.5). For the first time, systematic measures of juvenile crab distribution and abundance were made along an open coast in order to test the hypothesis that estuaries serve as major nursery habitat for juveniles of the species.

5.3.1 0+ Juveniles

YOY crab begin recruiting along the nearshore as early as April-May, but may not peak in abundance until late June or early July (Fig. 5.4). In all years between 1983-86 this age class dominates the total estimated nearshore population (Figs. 5.4, 5.5). Although 0+ crab settle at all depths sampled during the Sea Grant survey (Fig. 1.4), in most years and months their densities are greatest at mid depths between 15-40 m. Throughout the nearshore survey area (Fig. 1.4) total estimated abundance has varied tremendously between the four years 1983-86 (Fig. 5.6) from about 60 million crab in 1983 and 1986 to 1.3 billion in 1985. However, mortality is extensive and by the end of summer populations have decreased 4 to 8 fold from peak estimates (Fig. 5.6). Such declines were particularly striking in 1985 during an intensive Pacific NW Labs/University of Washington survey program nearshore of Grays Harbor. In June, density estimates at some stations were in excess of 400,000/ha, but by September 0+ juveniles could virtually not be found in the area (Figs. 4.21, 4.22).

Growth nearshore along the coast is particularly slow compared to that of siblings in the estuary (see Section 6.0) and by the end of summer crab only range between 10-20 mm CW (Fig. 5.5). This may in part contribute to extensive mortality in fall and winter since animals remain relatively small and thus vulnerable to predation in a size range typically consumed by fish (Fig. 4.23; Reilly 1983b). Crab at this small size probably do not move great distances and there is very little indication in size frequency distributions that animals which settle nearshore immigrate into the estuary in that first summer, although such movement has been proposed for San Francisco Bay (see reviews in Wild and Tasto 1983).

5.3.2 1+ Juveniles

Beginning the second spring after settlement, 1+ juveniles can be found nearshore along the southern Washington coast in April and May, but their abundance is substantially lower than estimated the previous September for the same year class (Fig. 5.6; e.g. compare September abundance estimates for 1984 and 1985 to spring estimates the next year). Mortality of small 0+

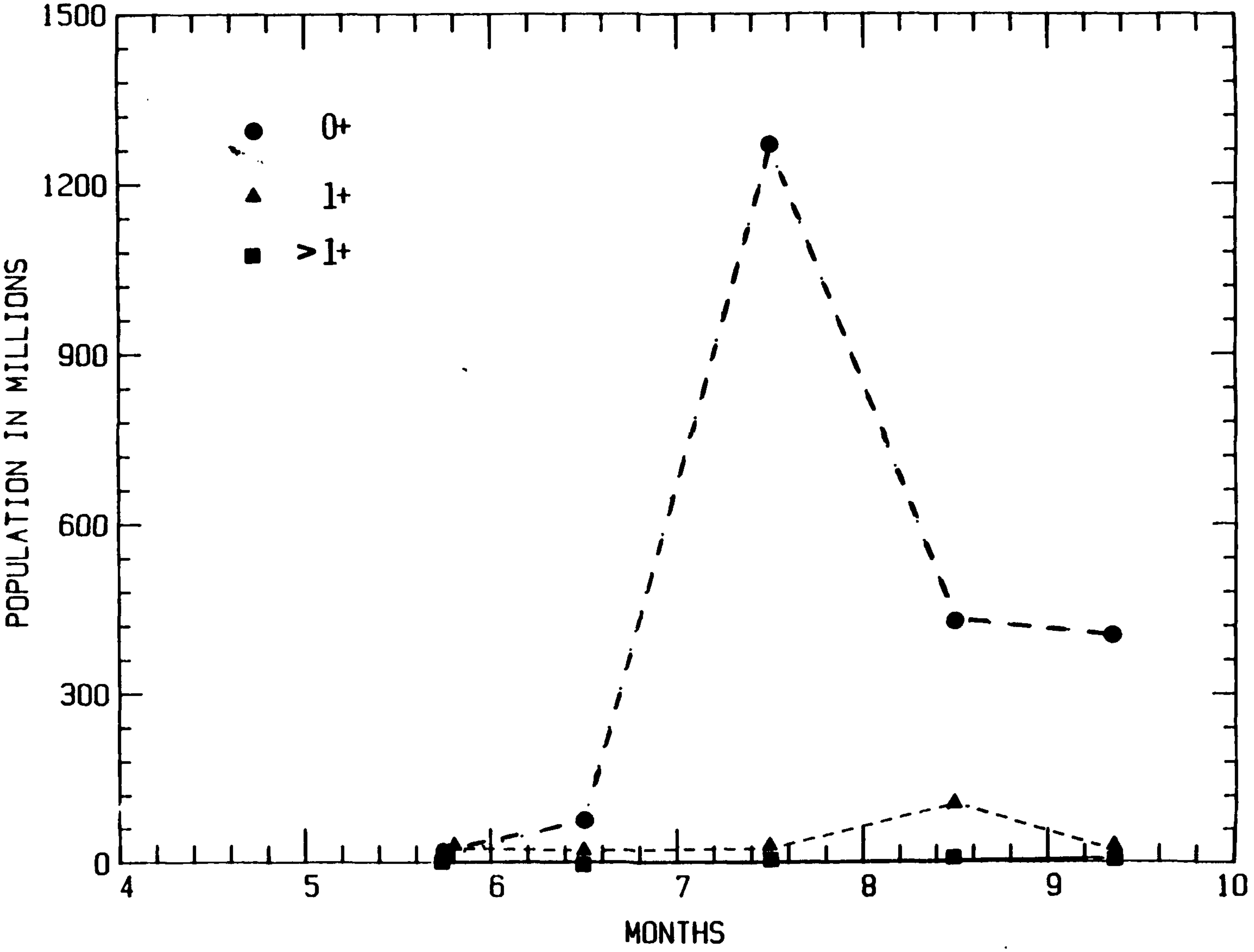


Figure 5.4. Population estimates of Dungeness crab by age classes nearshore of Grays Harbor from May to September 1985.

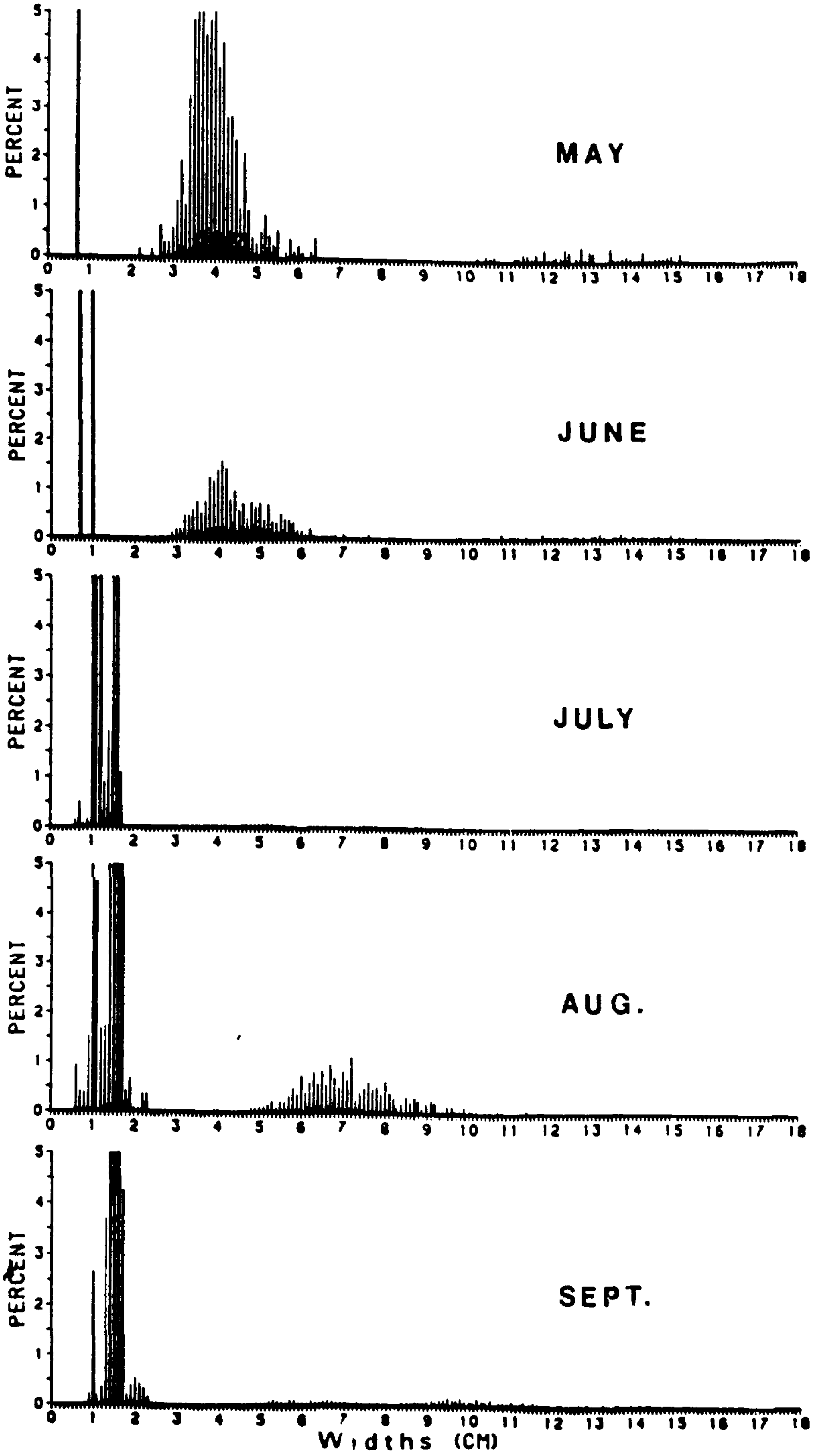


Figure 5.5. Size composition of Dungeness crab population nearshore (strata combined) by trip in May to September 1985. Note the relatively large size of 1+ (30-50 mm CW) from the fast-growing 1984 year class.

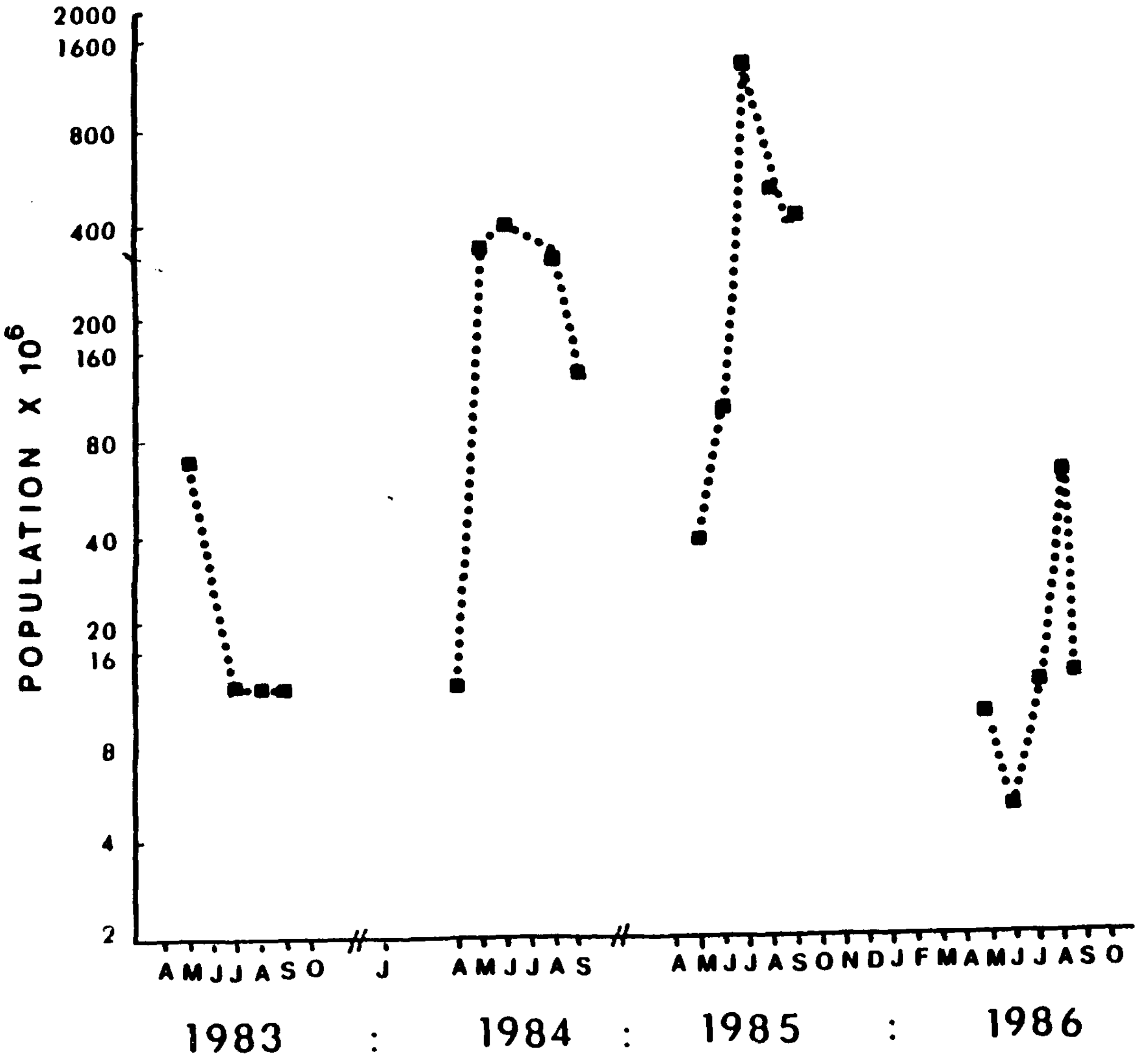


Figure 5.6. Trend in estimated population abundance nearshore over four years. More than 99 % crab are 0+.

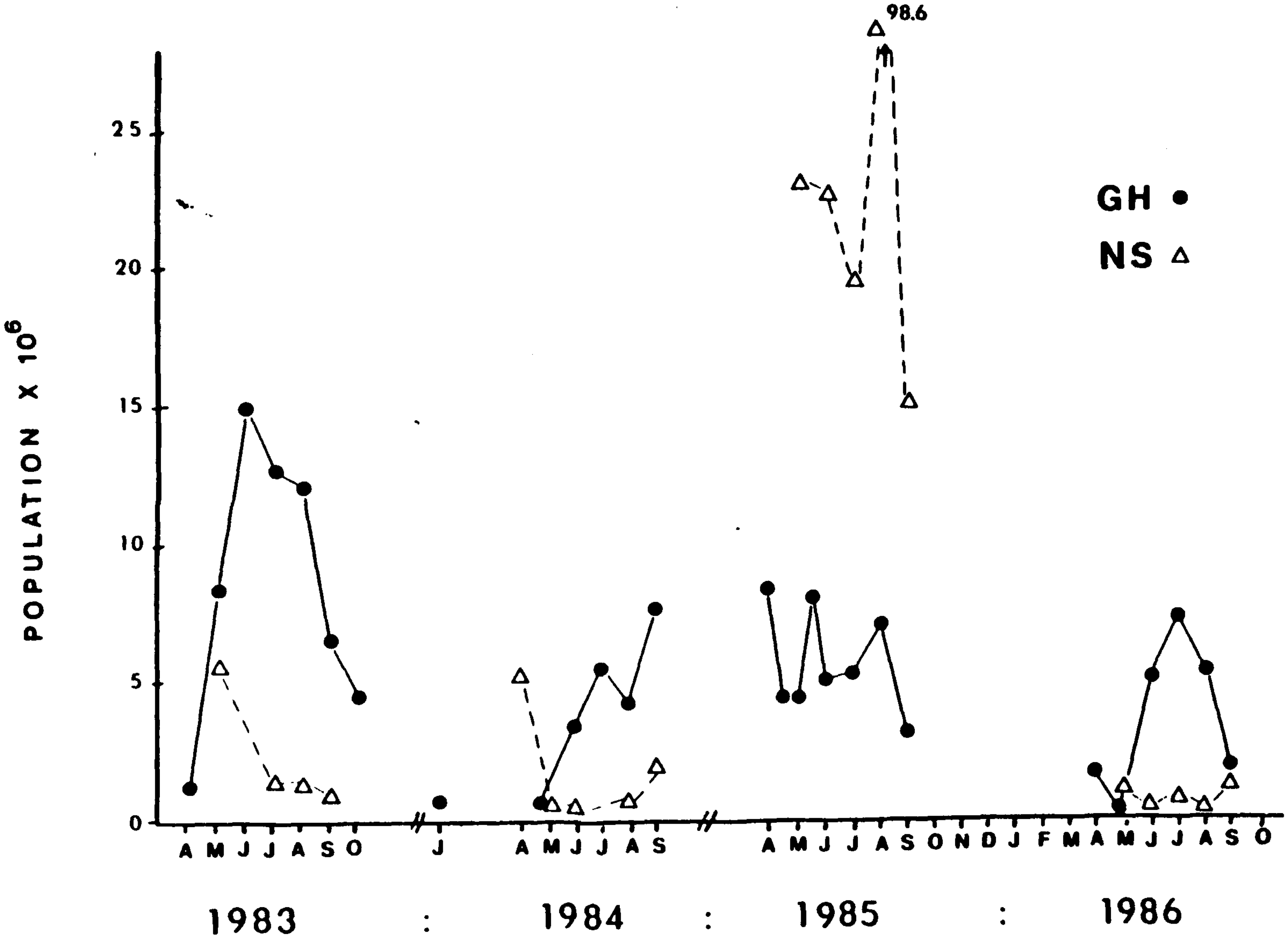


Figure 5.7. Estimated population abundance of 1+ Dungeness crab in Grays Harbor estuary (GH) and nearshore (NS). Note that in three of the four years abundance was greater inside Grays Harbor.

crab probably continues at a high rate in fall through winter so that the year class is even further reduced by the following spring as 1+ juveniles.

Movement: In most years of the Sea Grant survey there is evidence for immigration of 1+ juveniles from the nearshore into coastal estuaries such as Grays Harbor (Fig 5.7). From April to June, abundance of 1+ crab declines substantially resulting in estimates of only a couple million crab throughout the entire survey area depicted in Figure 1.4. The numerical decline nearshore coincides with an increase in Grays Harbor as further evidence of immigration into the estuary where 1+ crab of nearshore and estuarine origin (NJ, EJ) mix and grow through the summer. This entry into the estuary of NJ can be detected in some years as an abrupt decline in mean size of the age class that occurs in mid May (Fig. 5.8). Essentially, the larger size distribution of EJ is "diluted" by the arrival of smaller NJ which mix to give the appearance of reduction in size of the 1+ age class.

Most of the 1+ crab that remain along the coast occur at relatively shallow depths between 10-20 m, somewhat in proximity to the mouths of estuaries. A notable exception to this pattern of spring immigration occurred in 1985 when the very large nearshore 1+ population (1984 year class) remained in that location and did not appear to move into the estuary (Fig. 5.7). However the tendency for 1+ juveniles to immigrate to estuaries in other years underscores the importance of such systems to older juveniles as well as to young-of-the-year 0+.

5.4 GRAYS HARBOR POPULATIONS

In many respects the issue at hand concerning potential impact of the COE W&D program on juvenile Dungeness crab focuses attention on population dynamics in the estuary. It is there that large populations of juvenile crab occur on a seasonal basis and yet vary spatially in their distribution and abundance according to age class. Estimates of potential entrainment and mortality have been calculated in accord with COE dredge operation scenarios and reported elsewhere by Armstrong et al. (1987a). What is particularly relevant to the issues of potential impact is how it changes in magnitude according to life history stage, variable distribution within the estuary and inter-annual differences in estimated abundance.

5.4.1 Intertidal 0+ Populations

When YOY 0+ crab recruit to the estuary, their population density and abundance is often very high but transitory throughout most habitats (Section 4.3). Even in optimal intertidal shellhash habitats such as oyster and *Mya* shellhash, initial density and settlement may often be greater than apparently can be supported within the three dimensional matrix composed by shell, and so populations rapidly decline from over 100 to perhaps 10 to 20 crab/m^2 within several weeks

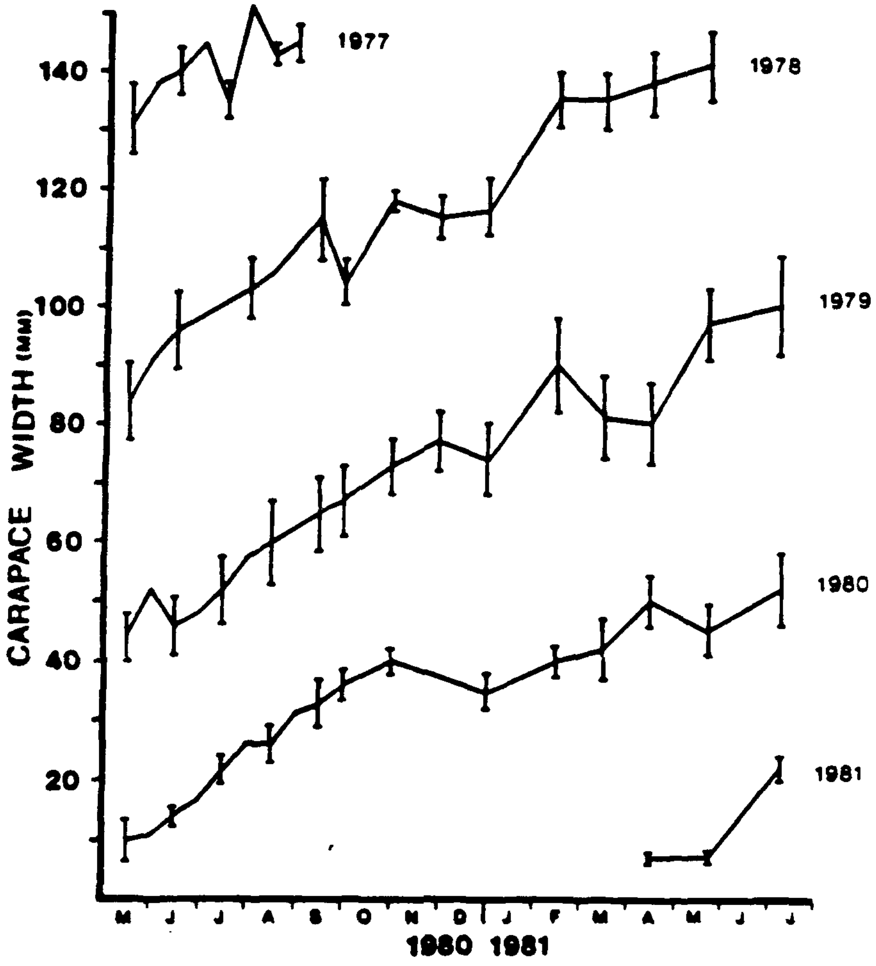


Figure 5.8. Mean carapace widths (± 1 SD) of three dominant age-classes (0+, 1+, 2+) in Grays Harbor 1980-1981 (from Stevens and Armstrong, 1984).

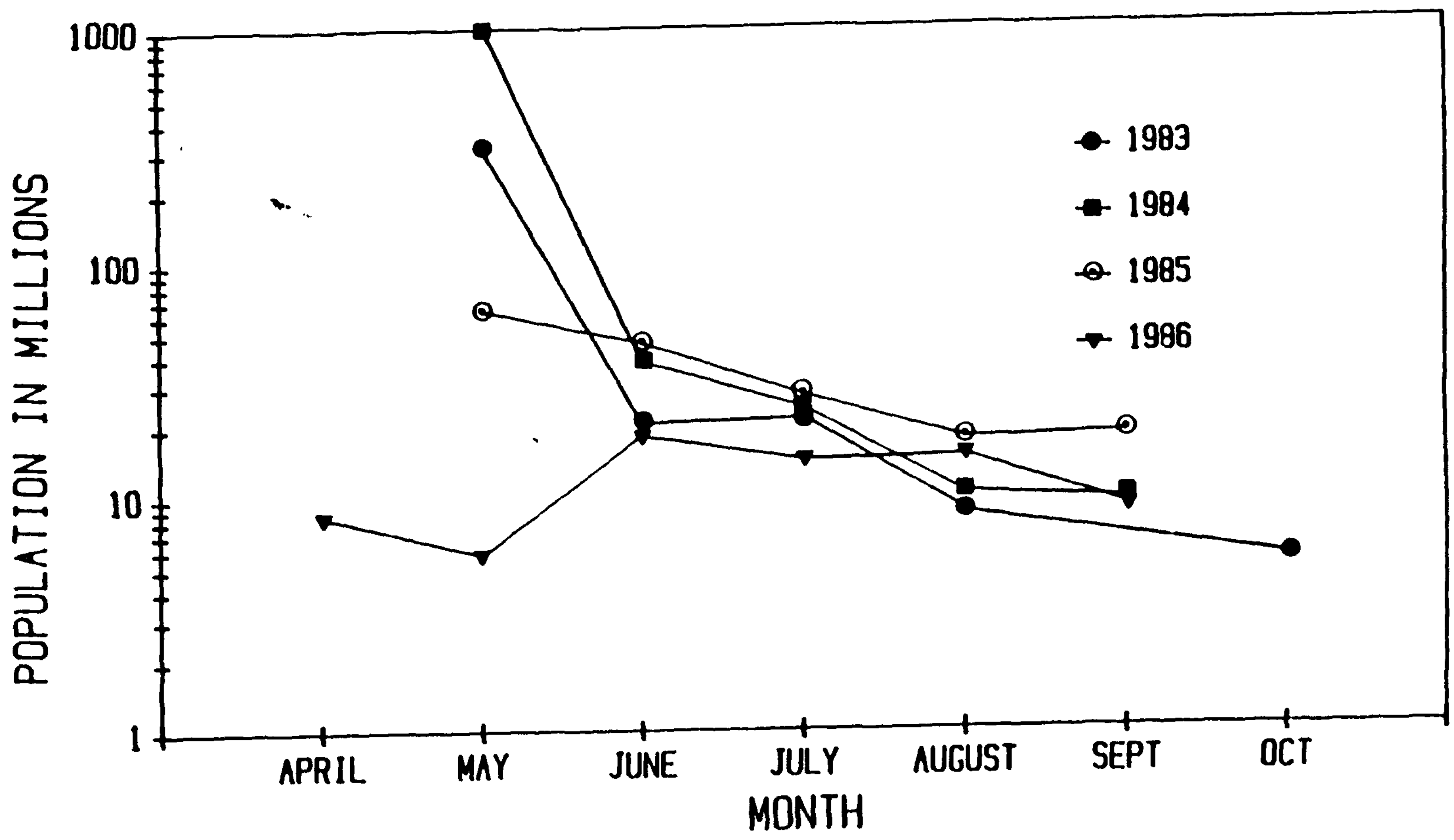


Figure 5.9. Estimated seasonal population abundance of 0+ crab in intertidal areas of Grays Harbor extrapolated to areas shown in Figure 4.4 (note logarithmic scale).

(Figure 4.30). Nonetheless, the relatively high density of 0+ crab that occupy shell habitat throughout the intertidal of Grays Harbor represents a substantial population when extrapolated to larger regions of shell distribution, as mapped by Dumbauld & Armstrong (1987, Fig. 4.4). Throughout Grays Harbor they estimated there is approximately 1,000 ha of Mya shell useful as habitat and approximately 400 ha of commercial oyster grounds. Even when corrected for actual percentage cover, based on ground truthing, population estimates for 0+ crab in the intertidal are quite high. From sampling data collected in May of the years 1983 - 1986, estimates of initial abundance have ranged from <10 million throughout the intertidal of Grays Harbor in 1986, to over a billion in 1984 (Fig. 5.9). Yet in all years population estimates rapidly decline and range between 15 to 30 million by July and about 10 to 25 million by September (Fig. 5.9). This indicates that long term population abundance through the first summer after settlement is relatively constant although interannual variability and initial recruitment may vary by almost two orders of magnitude at intertidal locations. This information has been used by Dumbauld and Armstrong (1987) to help the extent of shellhash mitigation (directed toward recruitment of 0+ crab) that would be required to offset loss of subtidal 1 and 2 year old crab during W&D.

Intertidal 0+ crab grow rapidly in individual size and appear to move from the intertidal to subtidal as they attain sizes greater than 25 - 30 mm CW. This has the effect of stabilizing (and even slightly increasing) the subtidal population which may be decimated after initial settlement (Fig. 4.28). In fact, broad scale immigration from the intertidal to subtidal, sometimes in late summer may significantly increase 0+ abundance in the subtidal (Fig. 4.28). Of the total 0+ estuarine population, a much greater percentage occurs in the intertidal through most of the summer than is found subtidally (Fig. 5.10). Based on a four year mean of monthly population estimates, abundance in the intertidal is 30x greater than in the subtidal during June, is only about two times higher in August and abundance is virtually equal between the two locations in September; a trend which likely reflects the movement of 0+ crab off the intertidal as they grow larger.

Two other studies of 0+ distribution in the intertidal failed to locate populations of any significance in San Francisco Bay (Tasto 1983) or in the Columbia River Estuary (McCabe et al. 1986). In both situations the intertidal areas surveyed seemed to be open sand and mud flats with little protection of the sort described for Grays Harbor. Other studies of intertidal juvenile crab distribution in Puget Sound have reported very high densities and estimated abundance of crab in areas such as Padilla Bay (Dinnel, et al. 1987) and Lummi Bay (Dinnel, et al. 1986). Rather than shell, other substrates such as macroalgae eelgrass, and cobble seem to be important habitat that support high 0+ abundance in Puget Sound (Armstrong et al. 1987).

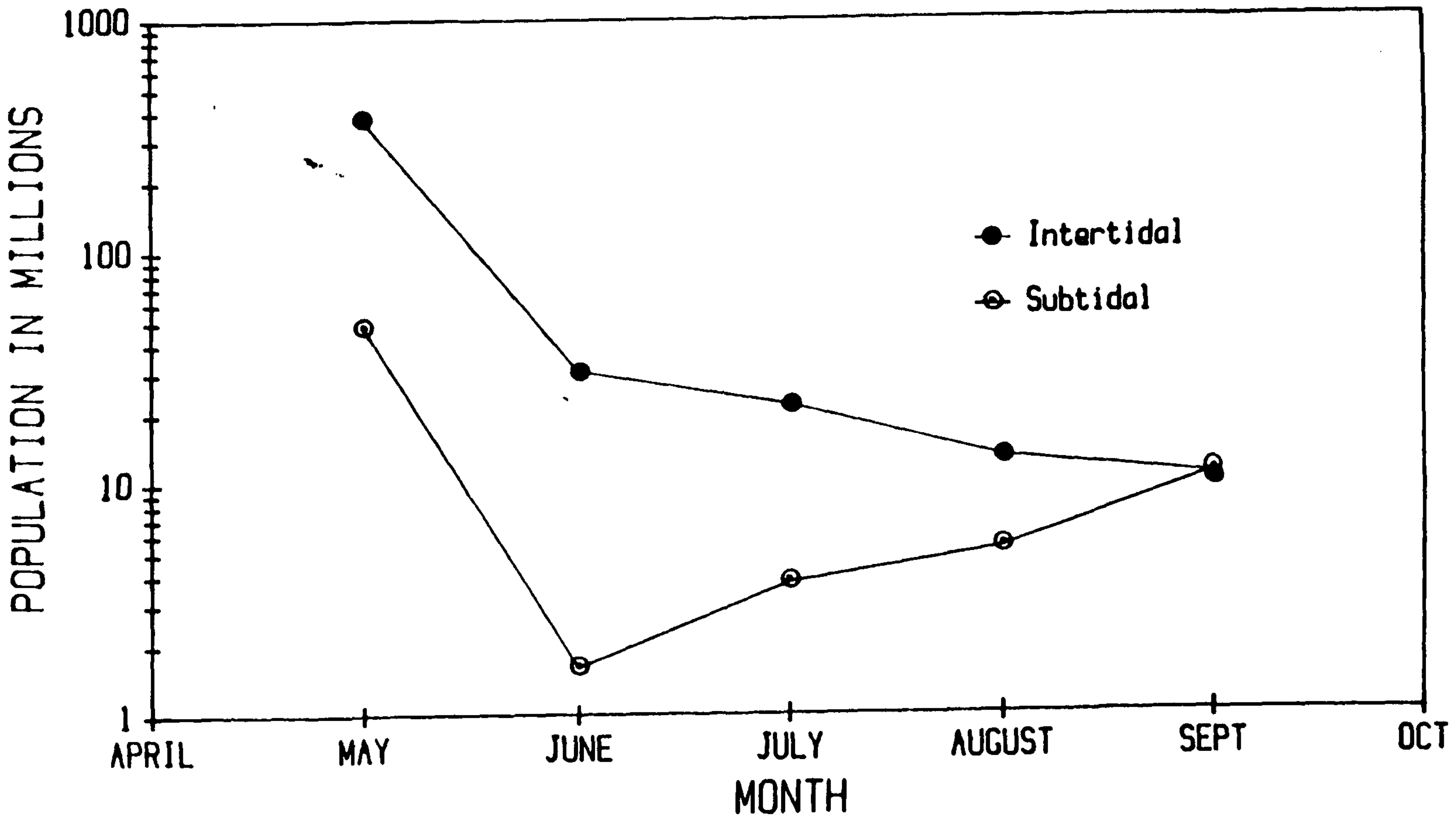


Figure 5.10. Comparison of four-year monthly estimated mean population of 0+ crab in the subtidal and intertidal areas of Grays Harbor (note logarithmic scale).

5.4.2 Subtidal 1+ Populations

Despite the high variability in interannual recruitment of 0+ juvenile crab, population abundance of 1+ crab in the subtidal of Grays Harbor has remained relatively constant between the years 1983 - 1986, although there is a seasonal component to the estimates (Fig. 5.7). In most years, abundance of 1+ crab is relatively low in the spring and increases by June for two reasons: 1) resumption of activity after torpor in cold winter months thus becoming more accessible to the gear; 2) immigration of siblings from the nearshore into the estuary (Fig. 5.7; see decrease in mean size of 1+ May to June, Fig. 5.8). Abundance usually peaks in July and in some years decreases between August and September possibly due to emigration from the estuary. Population abundance through the summer has been relatively constant throughout Grays Harbor and has varied by a factor of about three (Fig. 5.7). Highest resident populations were estimated to be about 15 million 1+ crab in 1983 but more typically, 4-7 million in the other years. As pointed out in section 5.3.2, population levels of 4 to 8 million inside Grays Harbor estuary are much higher than the estimates of about one to two million nearshore in all years except 1985 (Fig. 5.7).

By the end of summer, or perhaps as a function of size at any point during summer, larger 1+ juveniles emigrate from the estuary to the nearshore region. Evidence for this is not only a decrease in the numerical abundance as in the years 1983, 1985, and 1986 (Fig. 5.7), but also can be seen in time series plots of mean size for the age class. Both in 1985 and 1986 there was a rapid increase in mean carapace width of 1+ crab nearshore between July and September in 1985 (Fig. 11), and in August through September in 1986. It is not possible that the growth rate of these animals was suddenly much higher than the rate of estuarine juveniles, particularly given the colder bottom water temperatures nearshore. Rather, emigration of larger estuarine juveniles caused an abrupt and significant increase in apparent size of the coastal population as large estuarine crabs mixed nearshore.

5.5 WILLAPA BAY POPULATIONS

Although widening and deepening will obviously affect crab in the Grays Harbor estuary, analysis of this impact to a given year class should also consider a braoder extent of such populations including those in Willapa Bay where abundance of juvenile crab was measured since 1985. Estimates of 1+ abundance in 1985 were as high as 11.3 million in July, about twice the estimated abundance in Grays Harbor, but by September, total abundance of 1+ in both estuaries was nearly equal (Fig. 5.12). In 1987, total juvenile abundance ranged from 5.6 million crab in June to over 10 million crab in July and September. Without further analysis, it is reasonably accurate to say that total crab abundance in Willapa Bay is comparable to that of Grays Harbor, and that together, both estuaries account for a major fraction of the 1+ age group, and perhaps 10-20

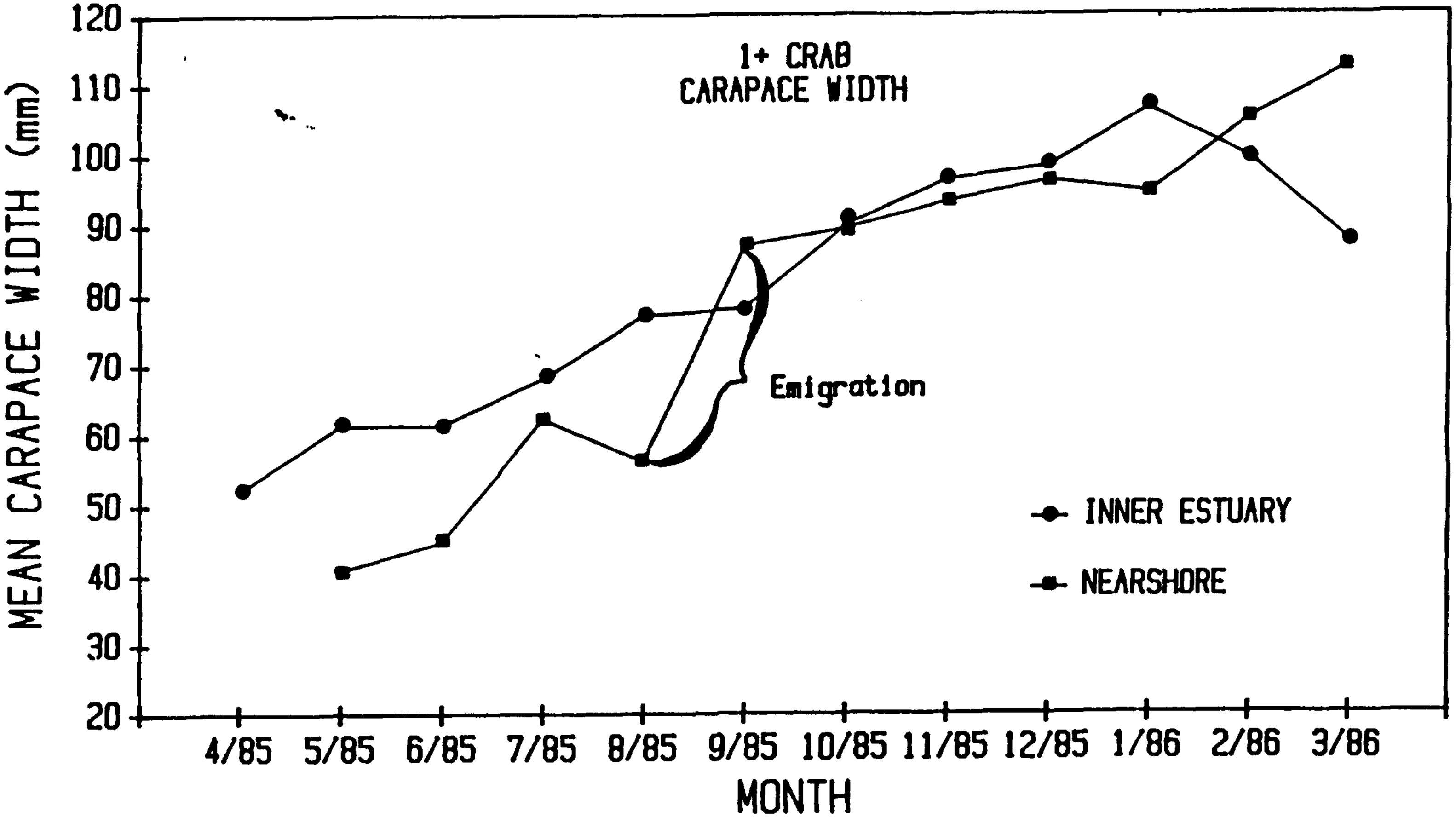


Figure 5.11. Change in mean size of 1+ Dungeness crab in the inner Grays Harbor estuary (Stratum 3; Figure 1.3) and intermediate depths (15-40 m) nearshore, April 1985 to March 1986. The sudden increase in size of nearshore 1+ crab between August and September is assumed to be caused by emigration of larger estuarine crab to the nearshore coastal area.

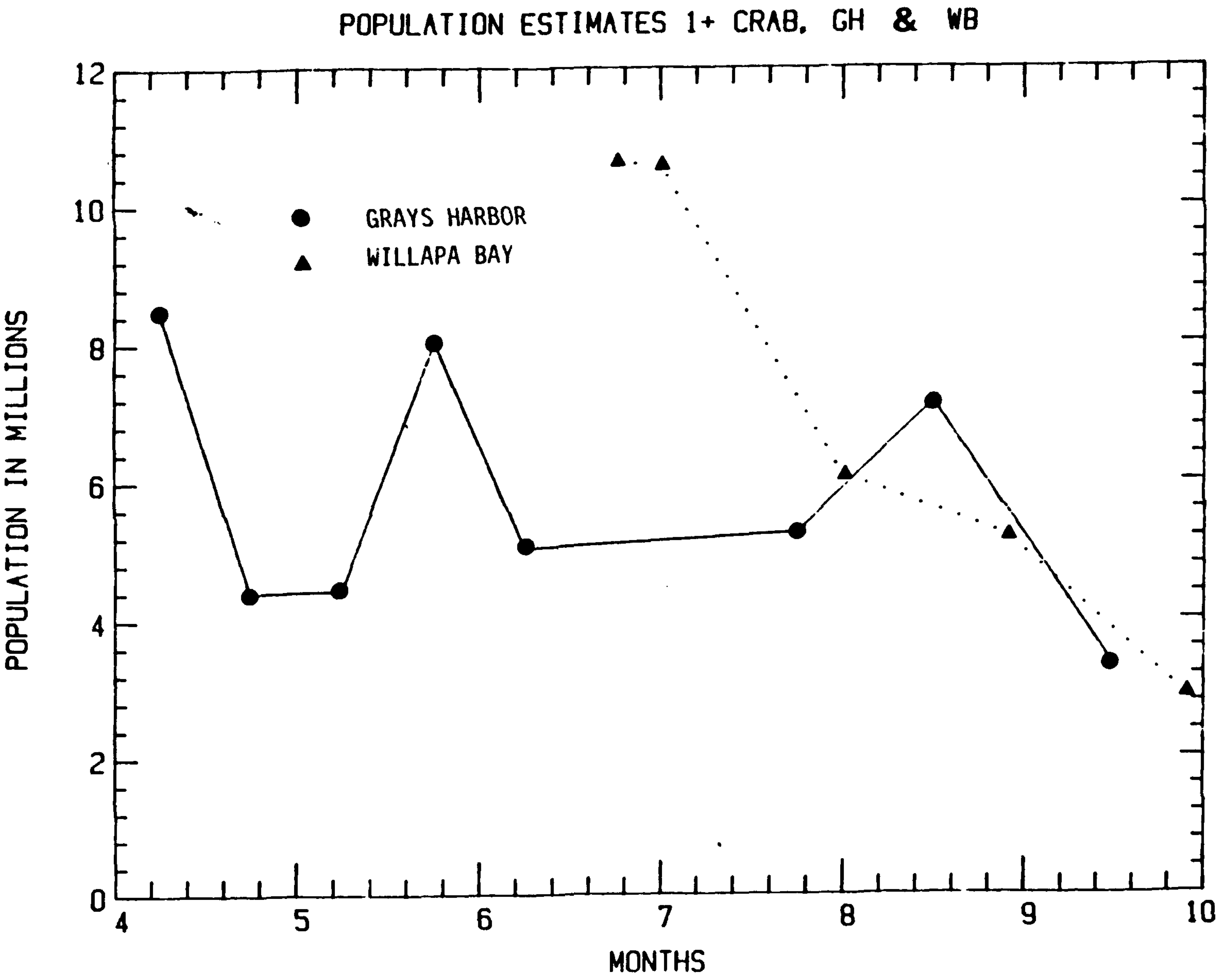


Figure 5.12. Comparison of population estimates of 1+ Dungeness crab from April through September, 1985; Grays Harbor and Willapa Bay.

times more are estimated to occur nearshore. Like Grays Harbor, Willapa Bay has an extensive intertidal system that supports the state's major oyster production and simultaneously creates extensive shell habitat for newly settled 0+ crab. The total juvenile production of both estuaries combines to support the coastal fishery but the relative contribution of each has not been calculated at this time.

5.6 ESTUARINE CRAB PRODUCTION

5.6.1 Energy Requirements

Another perspective of population dynamics within the estuary is that of production and respiration as a means to contrast the relative energy requirements of age classes through spring and summer. Eriksson and Edlund (1977) calculated a population energy budget for 0+ crab, *Carcinus maenas*, in a Swedish fjord. Through the course of a year in 1975/76, the year class consumed a total of about 13,000 kcals, half of which went to respiration and about 24% of which went to production of tissues.

A population scale energy budget and production estimates were calculated by Gutermuth (1987) for juvenile Dungeness crab in Grays Harbor during the spring and summer of 1983 and 1984. Based on estimates of population abundance by age and size class, biomass values were converted to measures of ash-free dry weight (AFDW). In May and early June of 1983, population biomass was dominated by older juvenile crab greater than 1+ (2+ age group for the most part) which reached a peak of about 90,000 kg AFDW in May and declined to about 40,000 kg by September (Fig. 5.13a). As both the abundance and growth rate of 1+ crab increased, their biomass increased from about 27,000 kg in mid-May to about 90,000 kg by mid-August. Compared to the other age groups, 0+ crab comprised only a small fraction of the total estuarine biomass through most of the summer and there were only about 9,000 kg in September. In stark contrast to the pattern in 1983, older juvenile crab (>1+) comprised the largest fraction of total biomass through most of the summer in 1984 (Fig. 5.13b) and ranged from about 20,000 to 40,000 kg AFDW. Biomass of 0+ crab was again small until September when it rapidly increased to over 80,000 kg and was the largest fraction by age class at the end of summer.

Production of dry weight organic matter was distinctly different between the three age classes through the summer of 1983, with highest values generally produced by 1+ crab until the end of summer (Figs. 5.14a b). Monthly production values range from as low as 2 million kcals for 0+ crab to about 50 million kcals for 1+ crab until September (Fig. 5.14a). Production by age class in 1984 was fairly equal at about 20 million kcals/month but increased to almost 180 million kcals by the 0+ age group in September (Fig. 5.14b). A similar trend was seen in respiration as measured by caloric expenditure (Gutermuth and Armstrong 1989) and was greatest for the 1+ age class

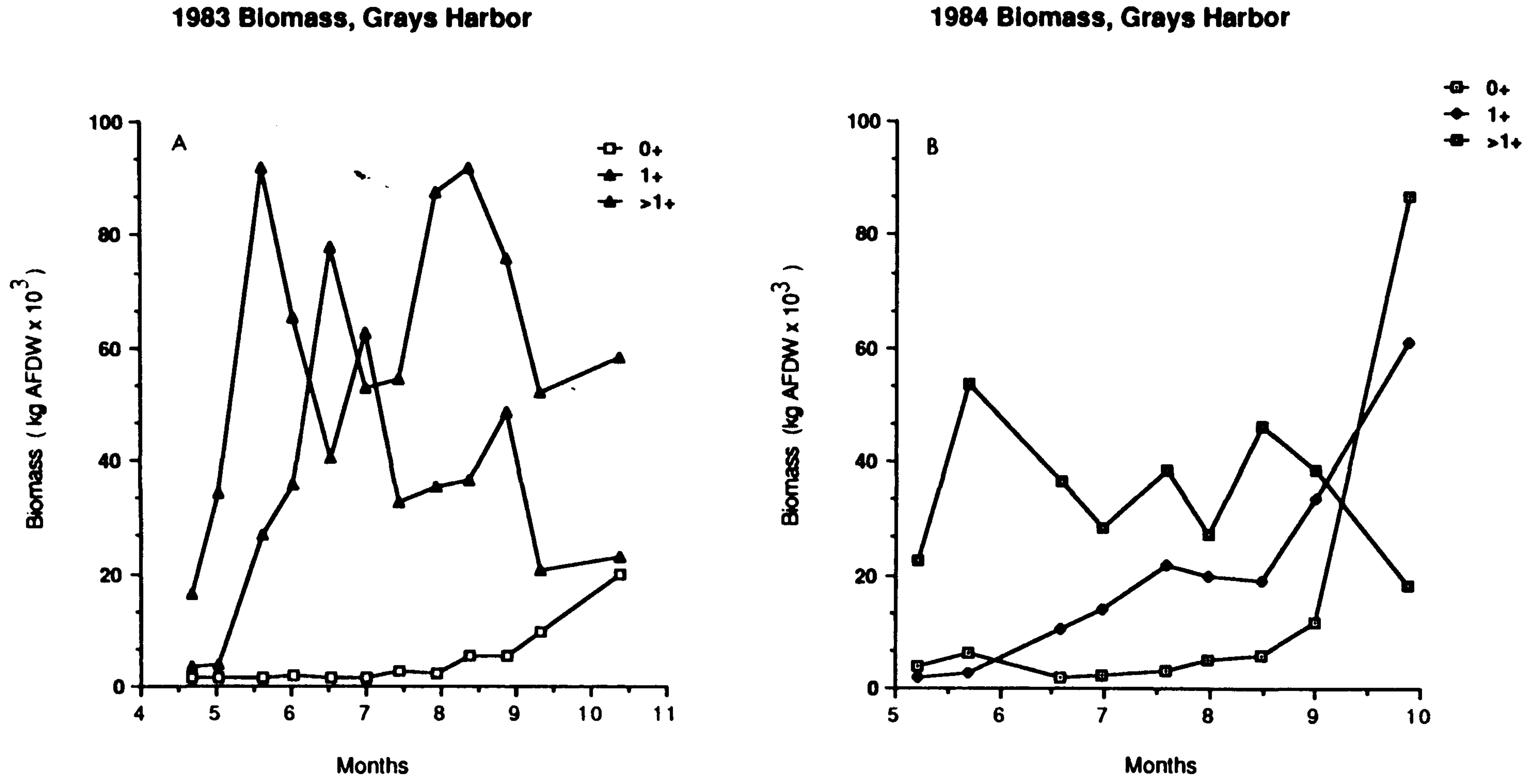


Figure 5.13. Dungeness crab population biomass by age class in Grays Harbor, 1983 (A) and 1984 (B). Estimates are equivalent to standing stock measured during bimonthly trips April through September (after Gutermuth 1987).

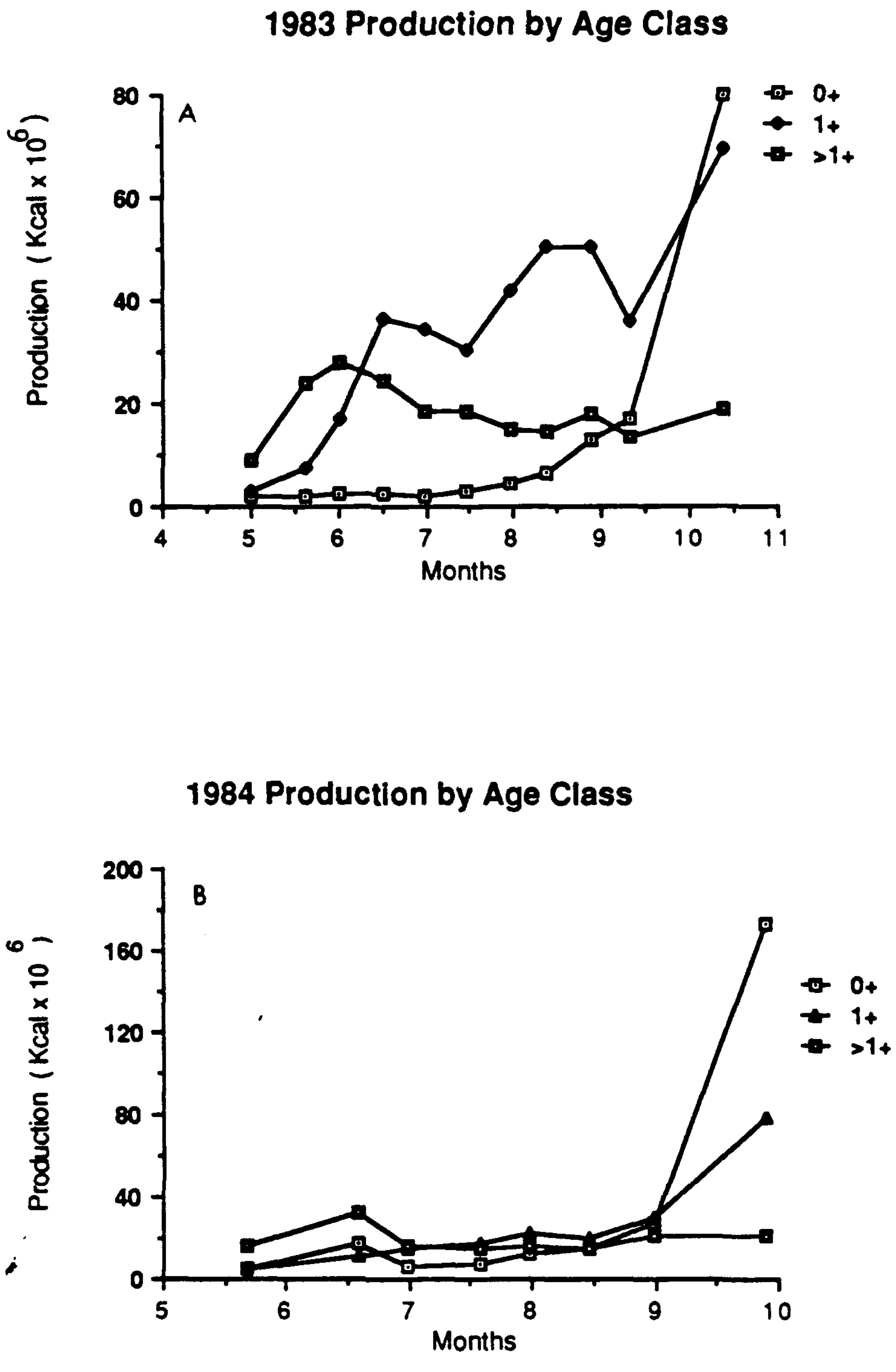


Figure 5.14. Dungeness crab population production (tissue and exoskeleton) by age class in Grays Harbor in 1983 (A) and 1984 (B) (after Gutermuth 1987).

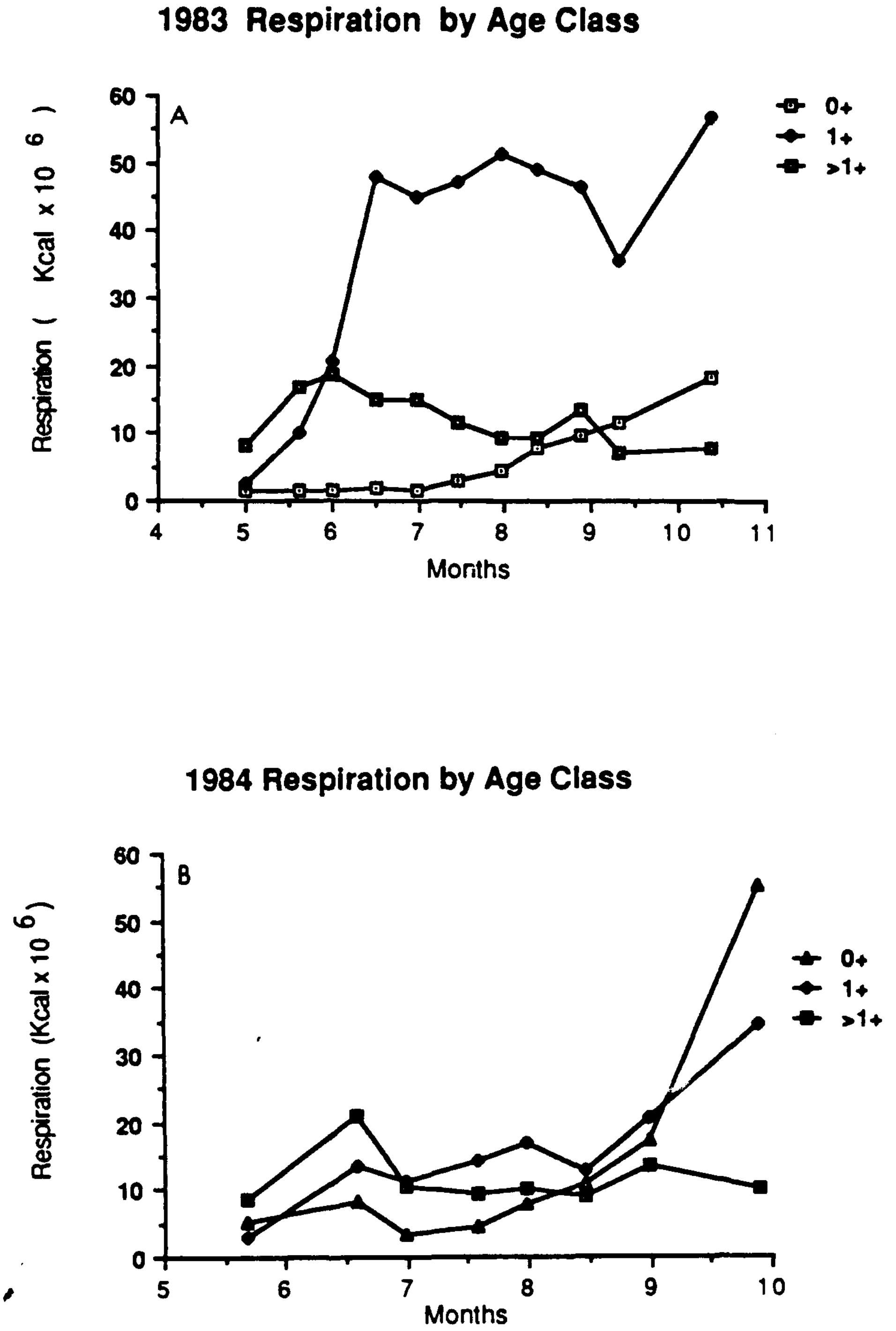


Figure 5.15. Dungeness crab population respiration (corrected for temperature) by age class in Grays Harbor in 1983 (A) and 1984 (B) (after Gutermuth 1987).

throughout the summer of 1983 (Fig. 5.15a). Monthly respiration expenditure was as high as 50 million kcals for this age group, but at least five times less for older juveniles and 0+ crab. The pattern for respiratory expenditure by age class in 1984 was very similar (Fig. 5.15b) to the production pattern seen in that year as well.

The total energy expended through the summer was generally higher for production than for respiration (Fig. 5.16). In 1983 the 1+ age class throughout the Grays Harbor estuary required more than 700 million kcals for the population (sum of production and respiration). In contrast, 0+ crab energetics accounted for only about 100 million kcals total (Fig. 5.16), but in 1984 0+ juveniles expended more than 300 million kcals on the combined energy requirements for respiration and production. Figured another way, the entire energy requirement for the resident juvenile crab population in 1983 was about 1 billion kcals. On average, there are approximately 4.5 kcals/gm AFDW organic matter (this value fluctuates depending upon the relative proportions of carbohydrates, proteins, and lipids). Using this figure to convert kcal of energy into grams, the 1 billion kcals equates to about 222,000kg ash free dry weight; ie. about 222 metric tons (MT) AFDW. Since many potential food items are about 25% dry weight, the wet weight equivalent of 222 MT AFDW is 888 MT. In 1985, the Washington Dungeness crab fishery was about 1360 MT (3 million lbs) along the coast (PMFC 1985). Thus the energy need of the resident Grays Harbor juvenile crab population in summer, 1983, was about 65% of the 1984-85 crab fishery itself (by weight). However figured and compared, food and energy needs of juvenile crab in Grays Harbor are high and attest to the production and standing stocks of prey organisms that support crab and many other species as well.

5.6.2 Food Habits

Qualitative estimates derived from the Sea Grant coastal crab project indicate that *Cancer magister* is usually the dominant (by biomass) epibentic species present in the estuary and its energy needs are high. Food habits of Dungeness crab have been studied a number of times and were reviewed by Stevens et al.(1982) who studied food habits of Dungeness crab in Grays Harbor. A summary of their information was presented as relative proportions of the total IRI (Index of Relative Importance) of food in different prey categories within the diet. Food habits varied substantially by age class and also location within the estuary. Among larger 0+ age class animals, small bivalves comprised 60% of the diet in the Outer harbor (similar to Str 1; Fig. 1.3), but were only 30% of the diet in the Inner Harbor (Str 3). Instead, 0+ crab farther into the estuary consumed a large fraction of *Cancer magister* (cannibalism) and *Crangon* shrimp and other Crustacea. The diet of 1+ and 2+ crab was composed mostly of fish and *Crangon* shrimp, and 2+ crab consumed virtually no bivalves (Fig. 5.17). In general, Dungeness crab seem to forage opportunistically and many select prey items over a broad size range that corresponds to relative

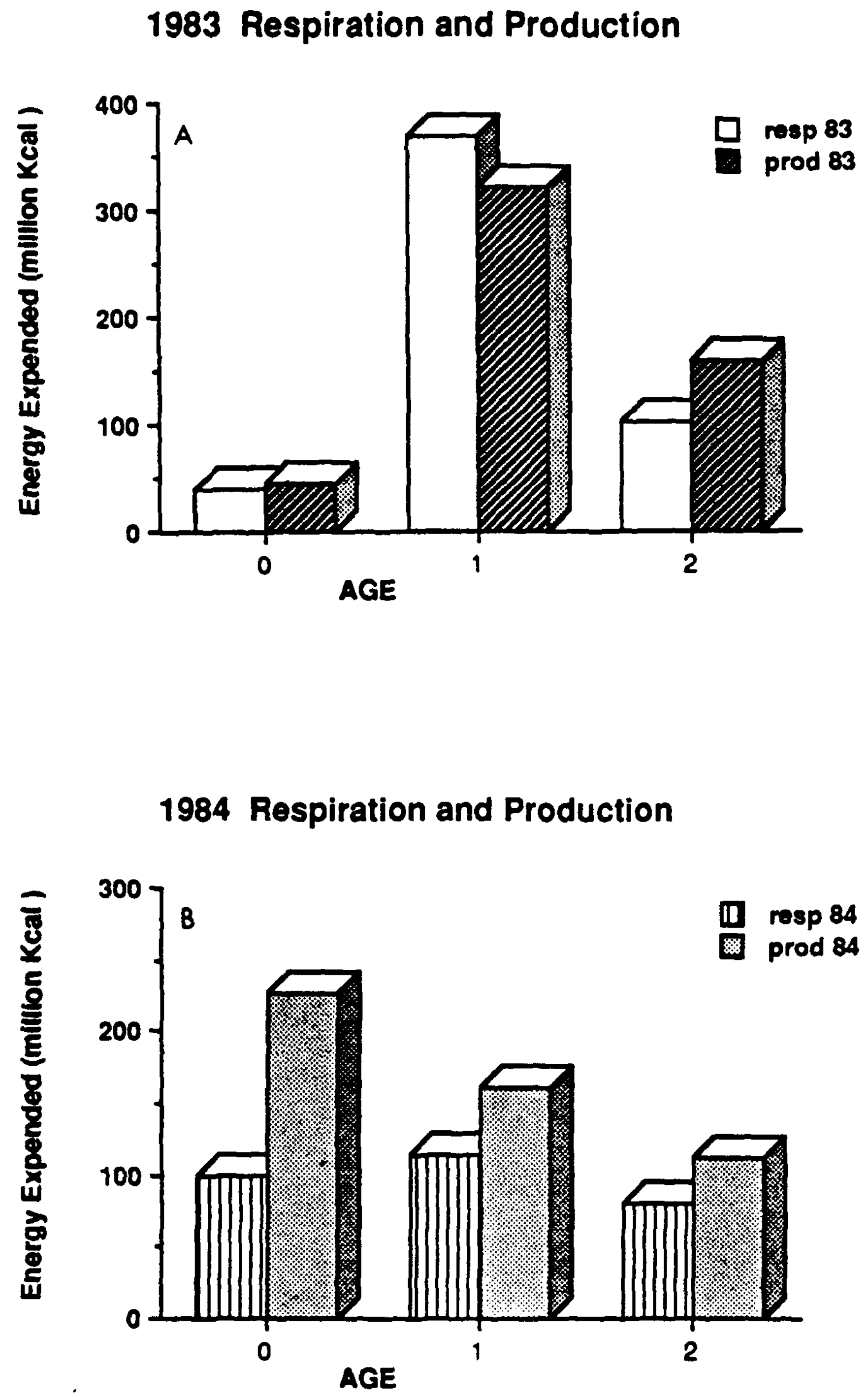


Figure 5.16. Cummulative energy expended by three age classes of Dungeness crab in Grays Harbor for respiration and production in summer, 1983 (A) and 1984 (B) (after Gutermuth 1987).

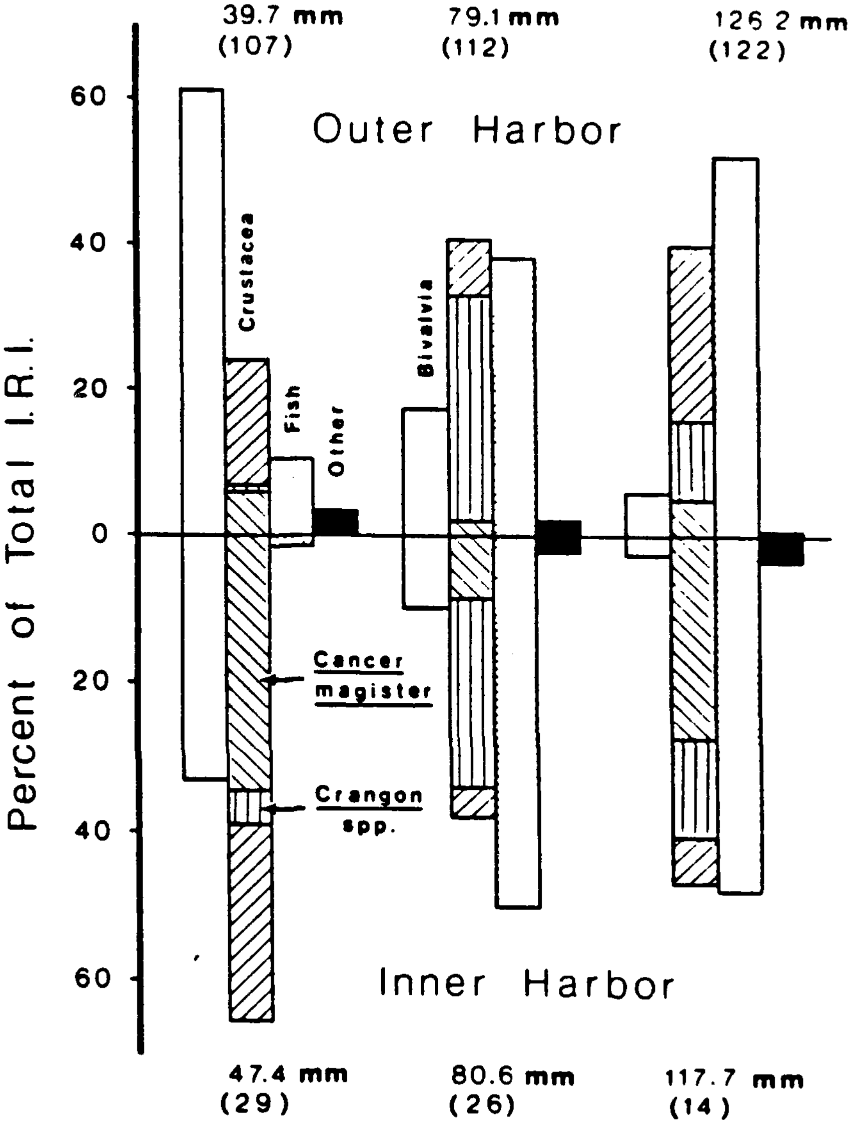


Figure 5.17. Cancer magister. Relative composition of diet of 3 size classes of crabs collected in the Outer Harbor and Inner Harbor. Mean carapace width (in mm) and number of crabs are shown above or below each bar. All prey items were grouped into 4 major categories: bivalves (open bars), crustaceans (hatched bars), fish (stripped bars), or "others" (filled bars). Bar lengths are equivalent to percent of total IRI for each prey category.

differences in body size by age class. The energy requirements of an entire estuarine population are extremely high and vary between years and between areas in the estuary. Changes in food supply and production might effect crab survival and growth but limits to crab population size and production based on over consumption of resources has not been shown.

6.0 GROWTH AND MORTALITY

The impact of W&D on crab resources and future fisheries can be most easily calculated as immediate, absolute loss but such numbers are not adequate to portray the relative loss in the context of future population abundance years later. The DIM (Armstrong et al. 1987a) relies on data concerning the rate of natural mortality to predict how many of crab killed at several ages (0+, 1+, 2+) would have reached maturity and, in the case of males, the fishery. Estimates of natural mortality also provide a perspective of crab loss during W&D in the much broader context of population decrease due to myriad forms of mortality from other causes.

Information on growth rate and size-at-age is essential to divide an estimate of a "total population" into component age/year classes. If under a given scenario the COE W&D project is estimated to kill 100,000 crab, it makes a tremendous difference in estimated loss to the fishery whether they are mostly 0+ or 2+, for example. Older crab have less time to grow before entering the fishery and will suffer less natural mortality (lower rates for fewer years) than younger crab. In this example, older crab are "more important" as a future fishery resource and their loss is more critical than is loss of younger small crab whose numbers will decline at a greater exponential rate over more intervening years between impact and a future fishery.

But how old is a crab of a given size killed during W&D? How fast would it have grown, how long until it reached legal size? What portion of any age class would have lived to enter the fishery? More subtly, if growth rates of juveniles are different between estuary and nearshore, will crab of the same age enter the fishery in different years? If so, can loss due to W&D of crab equal in age be proportioned over two or more years of a future fishery rather than just one? Can the resident population of 1+ and 2+ crab in the estuary during a specific year of W&D construction be divided into "slow" and "fast" growers (nearshore and estuarine juveniles, NJ and EJ, respectively) as a further refinement of estimates of relative loss due to dredging?

All these questions asked by agencies and fishermen concerning W&D impacts on crab are addressed in the DIM. Answers depend on good information concerning growth and mortality rates of Dungeness crab.

6.1 GROWTH

Modeling the dynamics of a population involves the estimation of growth and survival rates, assessing recruitment, identifying patterns of year class strength (YCS) and understanding migrations. The usual data include information on size, abundance, and patterns of geographic distribution at given ages. Ages are obtained from either age readings in hard structures (e.g.

otoliths), or modal analyses of size-frequency distributions (SFDs). The rate at which individual crab increase in size has important implications for population dynamics, the fishery, and the impact of induced mortality in early life. Unfortunately, growth of Dungeness crab is not well understood, but we can put some bounds on growth rate by reviewing the various studies of growth.

Growth rate is difficult to determine in the case of crab and other crustaceans since these organisms grow by "molts" and all hard parts are shed in each molting episode. The analyses of SFDs, while feasible, is difficult and has rarely been attempted. What complicates the procedure is the fact that each age group is normally composed of several "modal groups", one corresponding to each instar that represents each molting episode. This contrasts with the usual case in fishes which are affected by seasonal environments and where each age group is composed of a single "modal group" (Fig. 6.1). Thus, modal analyses for crab does not lead to the dissection of the basic SFD into year classes, but rather into instars. In order to pool instars by age groups, it is necessary to have additional information on molting frequency, which can be obtained from field samples of molted exoskeletons, from laboratory experiments or, as in the case of the Grays Harbor study, from periodic sampling of the population.

Thus, growth rate of crab depends on two quantities: 1) molt increment (growth per molt) and 2) intermolt interval (time between molts), estimation of which usually requires tagging individuals. Because of this discrete growth process, growth is usually estimated in one of two ways. The first is by following a size mode of a cohort of crab through SFDs from samples taken at different sequential times. This is usually only possible when the animals are young, because as the individuals grow, variability in the growth processes "blur" the size mode enough that it is eventually undetectable in the size distribution. Growth patterns can be affected by the genetic makeup of the individuals and by the environment (e.g. temperature, salinity, food availability), and for that reason they are expected to show geographic and seasonal variation. All these sources of variation, together with a mixing of populations due to migratory displacements, tend to blur patterns in the SFDs which has often discouraged their analyses. The second way of estimating growth rate is to determine the frequency of molting (e.g. number of molts per year) and the molt increment, then project growth on that basis. Many decapod crustaceans molt a variable number of times per year when young, then slow to a constant once per year at maturity and beyond. Thus, this technique is more successful with older crab.

6.1.1 Review of Dungeness Crab Growth Studies

The studies relevant to Dungeness crab growth are a series of collections along the coast over the past fifty years. In most of these, size modes are followed for young crab and size increment and interval data are used for older crab.

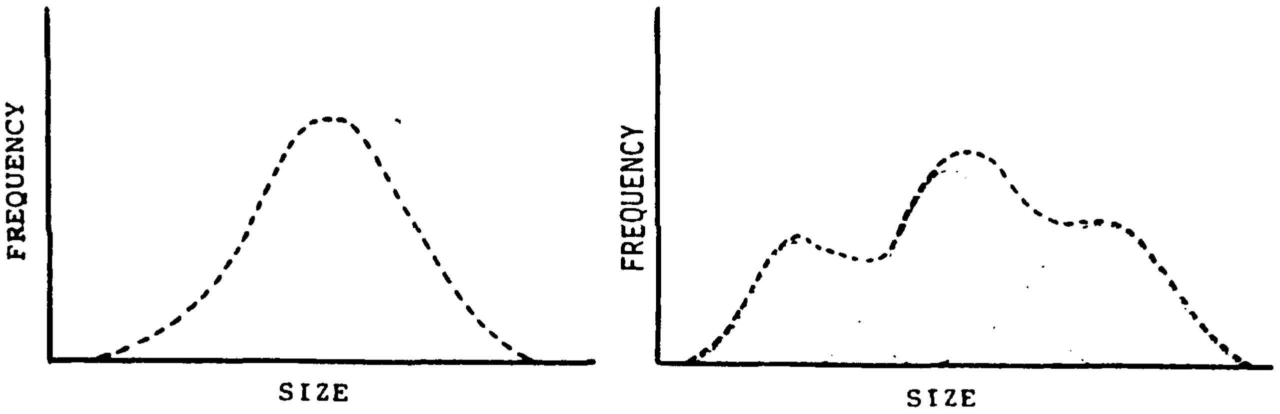


Figure Schematic representation of the size-frequency distribution of a single year class of a fish (left) and a crab (right).

MacKay and Weymouth (1935) recorded molt increments from crab molting in captivity and under natural conditions in Boundary Bay, British Columbia, and near San Francisco, California. The average molt increment in males decreased from 40% at 50 mm CW to 15% at 135 mm CW. Of the more than 1000 crab tagged by them, there was only one case of a crab having gone more than 1 year without molting. From this they concluded that a single annual molt was likely. From their observations of size distribution in the first 3 years (10-20, 40-70 and 100-120 mm for shortly after metamorphosis 1, 2, and 3 years later, respectively) and from molting data they constructed a model of crab growth. From this model the average male crab becomes 150 mm in his 6th year after metamorphosis and reaches legal size the next year.

Cleaver (1949) determined molt increments for crab taken in the state of Washington and held in aquaria. Male crab increased by 3 mm at 10 mm CW (30%) and by 24.0 mm at 155.0 mm CW (16%). Size distributions from trawls inside Grays Harbor showed individuals between 30 and 70 mm 1 year after metamorphosis and between 80 and 120 mm the next year. The size 1 year later was identified by Cleaver to be between 140 and 160 mm but the transition from the previous year is not very clear in the intermediate distributions. He then assumed that 3-yr-old crab are the same size in the ocean that they are in Grays Harbor and followed a year class through the commercial traps. He supported this assumption by comparing frequency distributions of cast exoskeletons inside and outside of the harbor. The distributions shown in support of this assumption do not appear to be similar. Based on this procedure of connecting the growth pattern of younger crab in Grays Harbor to that of older crab outside the harbor, Cleaver (1949) concluded that crab are 30, 95, 150, and 175 mm CW at 1, 2, 3, and 4 yr of age, respectively.

Butler (1961) collected molt increment data on crab from the Queen Charlotte Islands, British Columbia, that had molted in live wells, in traps, and while tagged. The molt increment declined from approximately 28% at 80.0 mm CW to approximately 18% at 160.0 mm CW. Using these data he derived the size at each molt stage (Fig. 6.2) and used that relationship to interpret size distributions from the field. His size distributions show a peak that moves from 20 mm to 30-80 mm almost 1 yr after metamorphosis. Size distributions from which sizes at later ages are determined are from different locations. These generally show crab distributed from 100 to 200 mm with no clearly defined modes between these sizes. Based on comparisons of these plots with sizes expected at each molt (from the molt increment data), Butler (1961) concluded that males are approximately 120 mm at 2 yr, 148 mm at 3 yr, and 175 mm at 4 yr (from metamorphosis).

Poole (1967) collected molt increment data on crab from Bodega Bay that had molted in traps, in tanks shortly after capture, and while tagged in the ocean. Size increments declined from approximately 30% at 20 mm CW to approximately 15% at 160 mm CW (Fig. 6.3). Poole (1967) was successful in following a good year class through several years of development. He followed the 1961 year class for several years after June 1961 at which time it ranged from 5 to 18 mm CW.

One year after metamorphosis the year class ranged from 70 to 110 mm. Although the size distribution of the single age class eventually became difficult to identify he concluded that some crab enter the fishery at 2.5 yr after metamorphosis, most enter at 3.5 yr, and the remainder at 4.5 and possible 5.5 yr after settlement. Poole (1967) noted that growth of this year class was faster than growth of crab in Washington and Oregon, appeared to be faster than the 1962 year class, and was faster than projected by molt increment data.

Growth data on crab size distributions from trawl samples were taken by the California Department of Fish and Game in Northern California each November (before the fishing season) from 1958 to 1975. In two instances these show a large year class of young crab that can be followed through several years. As shown in Fig. 6.4, samples taken in 1966-69 clearly show the 1966 year class. They indicate a small contribution to the fishery at age 2.5 (age from metamorphosis) and slightly less than one half of the cohort in the fishery at age 3.5. There were no trawl samples the following year but it appears that the second half would have entered the fishery in that year.

Also shown in Fig. 6.4 is the 1972 year class in samples taken with a trawl and commercial traps with closed escape ports each November through 1975 and sampled only with commercial traps with closed escape ports for 2 yr thereafter. Traps are ineffective for small crab, and trawls may be less effective for larger crab, but traps and trawls appear to have similar size distributions for crab larger than about 150 mm. From these data, the 1972 year class appears to contribute a minor amount to the fishery at age 2.5 (note that the catch for that year is only 1.38×10^6kg) and then contributes to the catch over the next 2 yr and possibly the third. Interpretation of these data is complicated by the fact that the 1973 year class cannot be differentiated from the 1972 year class in later years.

In a study of population dynamics of *C. magister* , Botsford (1984) formulated a model of crab growth that attempted to resolve SFDs of year classes later in life when size ranges "smear" into adjacent year classes of younger and older crab. Using the 1972 year class which could not be clearly distinguished beyond age 4.5 yr, he adopted a baseline growth pattern that approximated that of the 1966 and 1972 year class without crab entering the fishery beyond 4.5 years (Table 6.1; unfortunately, he used age from hatching [November] rather than age from metamorphosis/settlement [May off Grays Harbor]; settlement age is used by other authors, e.g. Butler, 1961 and Stevens and Armstrong, 1984, to equate size and years of age). The resultant model predicted a small number of the 1972 year class would enter the fishery at age 2.5 years in winter 1974 (Fig. 6.5), but most at ages 3.5 and 4.5. Female growth rates were taken from the modes in Poole (1967) and the California Fish and Game data for the first 3 yr of growth with a constant increment of 16 mm/yr for the following 2 yr. To evaluate the effect of crab entering the fishery at age 5.5 yr, he also examined model behavior for a growth pattern that included crab

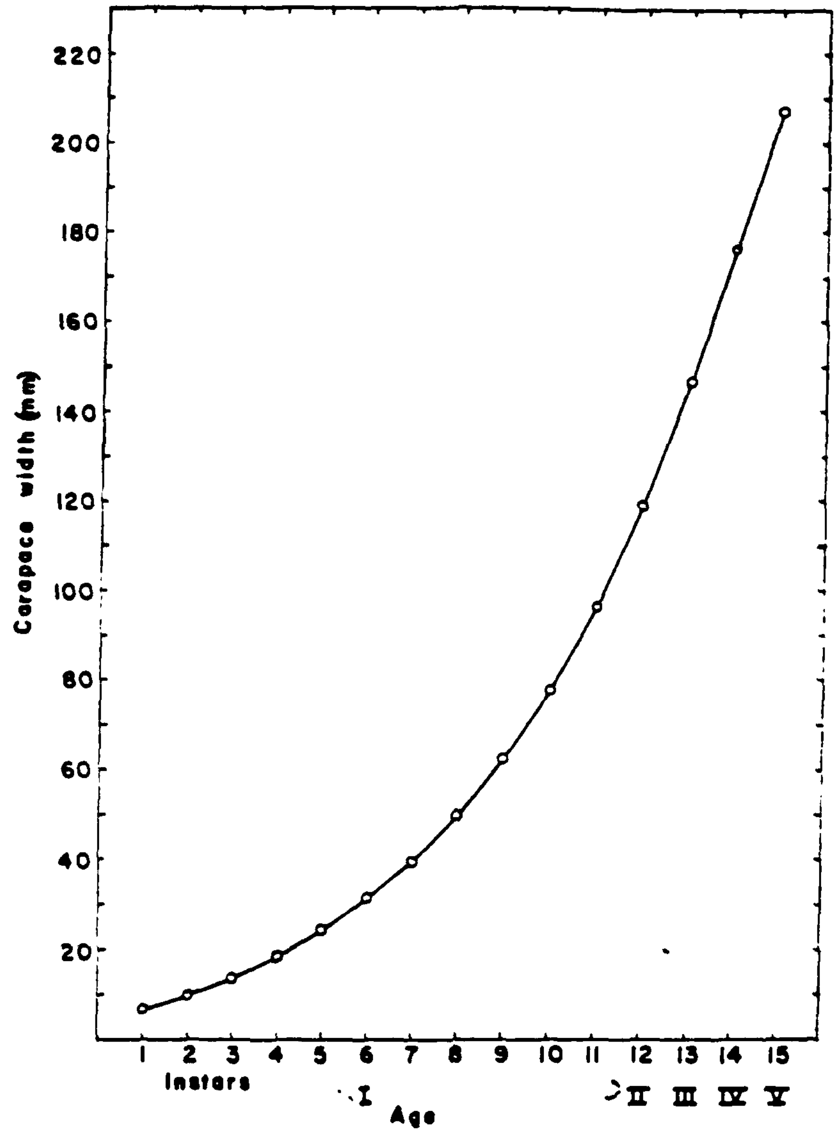


Figure 6.2. Size at age and instar number of male Dungeness crab in British Columbia (from Butler 1961).

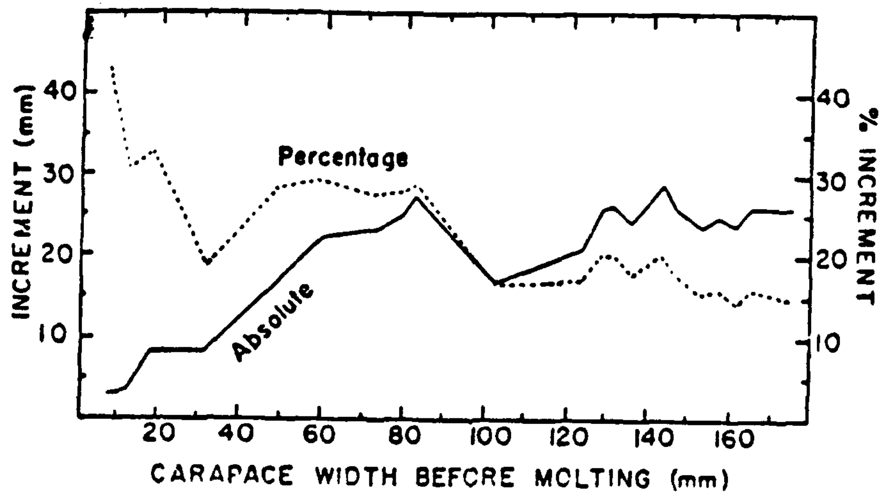


Figure 6.3. Absolute and percentage increments at molting of male Dungeness crabs in northern California (from Poole 1967).

Age (yr)	Carapace width (mm)			
	Males		Females	
	Mean	SD	Mean	SD
1	25	3.0	25	3.0
2	90	10.8	90	10.8
3	130	15.6	120	14.4
4	158	19.0	136	16.3
5	186	22.3	152	18.2
6	214	25.7	152	18.2
≥7	214	25.7	152	18.2

Table 6.1. Description of growth of Dungeness crabs used in the model of number of years over which a year class enters the fishery. The effect of fishing is not included. One year of age is taken to be the November after hatching the previous winter. All are sizes in November (from Botsford 1984).

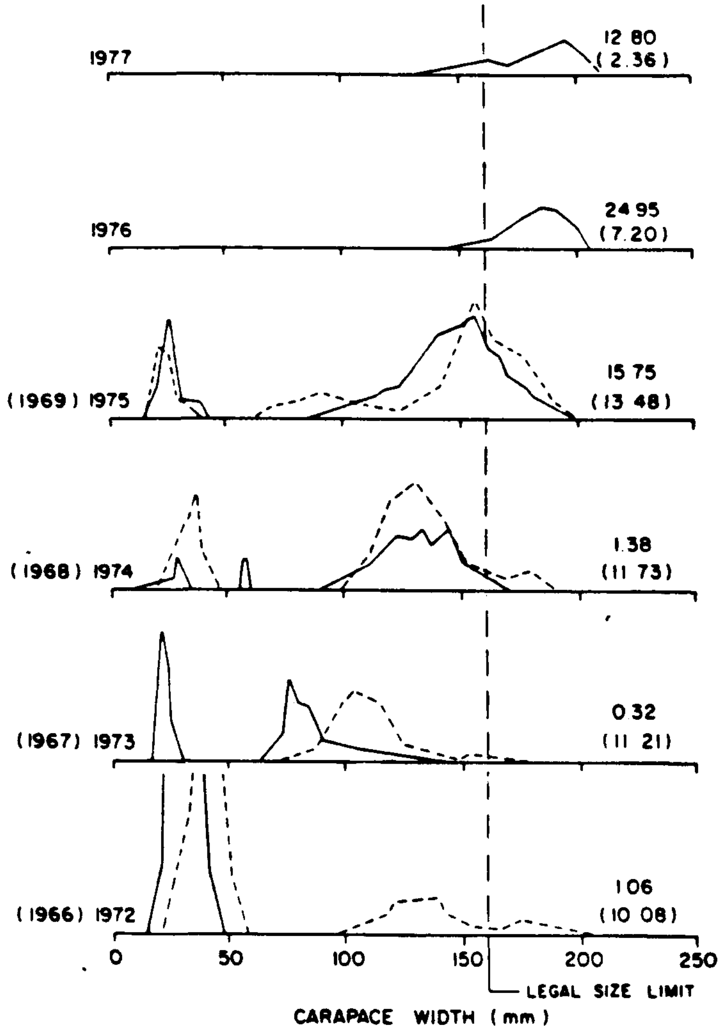


Figure 6.4. Size distribution from November cruises by the California Department of Fish and Game for 1972-77 (solid curve) and 1966-69 (broken curve). Total catch in the commercial fishery for the fishing season following the sample (December-June) is listed to the right of each plot (1966-69 in parentheses). Data for 1976 and 1977 were collected using commercial traps, hence are biased to sizes greater than 150 mm. Data for earlier years were collected by trawl. Because of changes in sampling procedures, vertical scales are not necessarily the same for each year.

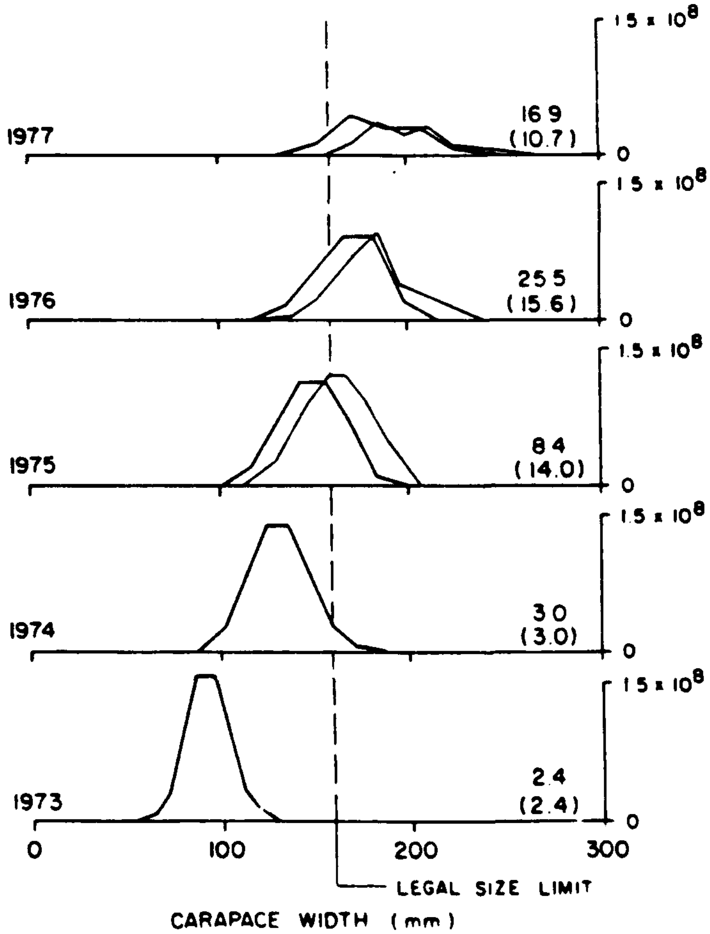


Figure 6.5. Size distribution from simulation show both the baseline interpretation of growth (i.e. faster growth) and the alternative interpretation. Catch for each year (assuming a harvest rate of 0.6) is listed to the right of each plot (baseline in parentheses) (from Botsford 1984).

entering the fishery at ages 3.5, 4.5, and 5.5 in the approximate ratio of 1:2:1 (with a small amount entering at age 2.5). For comparison with Fig. 6.4, the size distributions that resulted from these two assumed growth patterns are shown in Fig. 6.5. For this example, recruitment rate was set to a low, constant level for all years except 1972 when a large recruitment pulse was introduced. The harvest rate was set constant at 0.6.

The resultant growth rates are somewhat slower than those determined by Cleaver (1949). His result was based on following size modes in Grays Harbor through the 3rd year of age and then assuming that growth rate in the harbor was the same as that outside. His conclusion that the major contribution to the fishery would occur at 3.5 yr of age (years from metamorphosis) depends critically on that assumption.

There is now clear evidence that juvenile Dungeness crab grow more rapidly in bays and estuaries than in the open ocean. Tasto (1983) reported that 0+ crab of the 1977 year class were much larger in San Francisco Bay than offshore in November, six months after settlement (Fig. 6.6). Substantial differences in growth rates of coastal versus estuarine crab have been reported by Armstrong and Gunderson (1985a,b) and Carrasco et al. (1985) and are discussed in the next section (6.1.2). Gotshall's (1978) size distribution mode is approximately 80 mm in November in Humboldt Bay and does not change much in the following 6 months. These values are in contrast with the mode in Fig. 6.4 at approximately 30 mm in November 6 months after settlement along the open coast of northern California.

This cursory review of the growth studies of Dungeness crab reveals little agreement although this is partially caused by problems such as differences in month of metamorphosis, month of sampling, and whether reared in estuaries or nearshore. Typically, size modes can be followed through the first couple of years, but sizes at later ages have not been confidently identified. Studies in which young crab of known age are tagged and followed through the next several years are required for better definition of crab growth.

An illuminating means of summarizing the two types of available data (i.e. size modes in early life and increment per molt in later life) is to plot known size distributions of known ages for the early years of life and project their entry into the fishery assuming a single molt each year at a specified increment (Fig. 6.7). This representation allows one to project the age at which a crab of a certain size would enter the fishery. Based on the studies referenced above, growth increment of 28 mm/molt for carapace widths approaching legal size (i.e. used only for those size distributions in early life that can be clearly followed from year to year) are plotted. Although this plot requires some care in interpretation (e.g. the California Department of Fish and Game 1972 data may actually be two year classes as noted earlier) it implies that few crab enter the fishery at ages 3 and 6 and most enter at ages 4 and 5 (years from hatch; 3.5 and 4.5 years from metamorphosis).

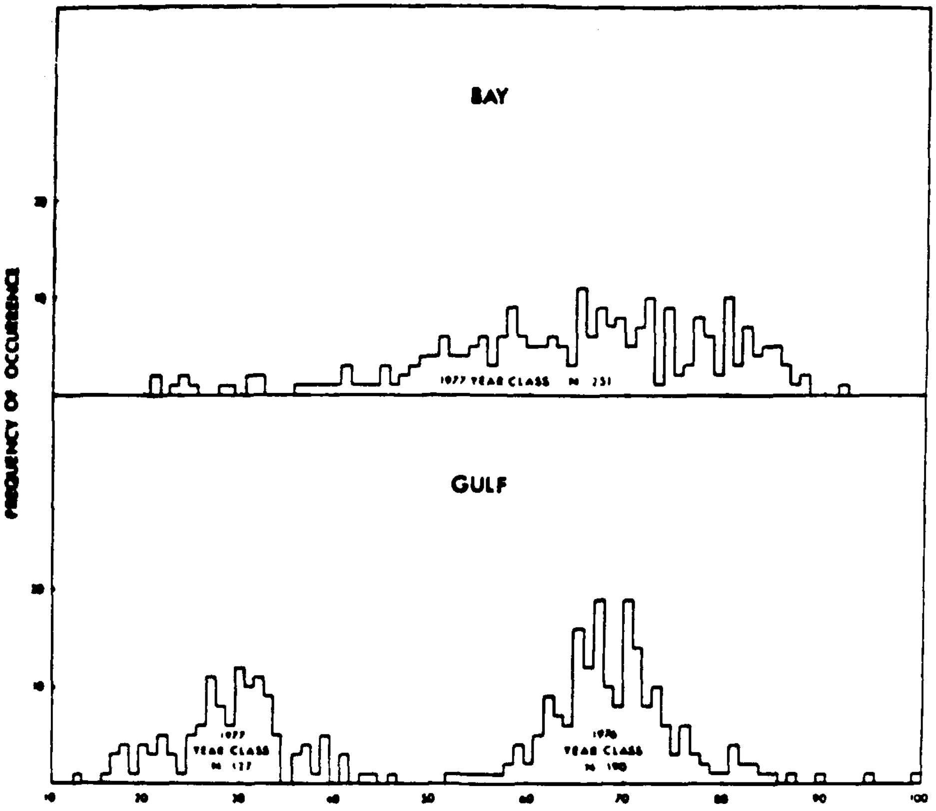


Figure 6.6. A comparison of 0+ crab population size structure in the San Francisco estuary versus offshore (from Tasto, 1983).

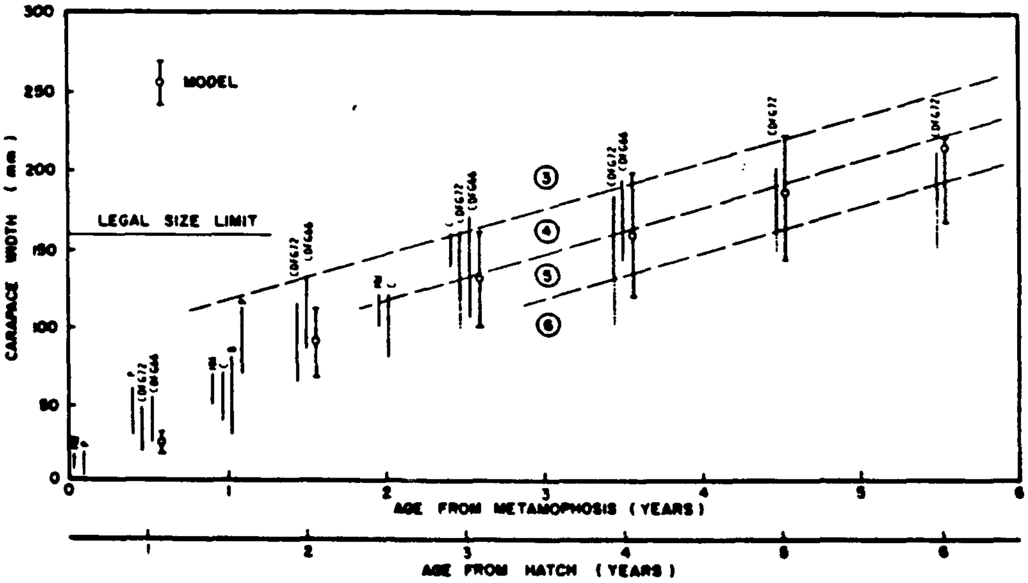


Figure 6.7. Summary of male Dungeness crab data. Vertical lines are size distributions of known age from specific references (B= Butler 1961; C= Cleaver 1949; MW= Mackay and Weymouth 1935; P= Poole 1965; CDFG72= California Department of Fish and Game samples (1972-77); CDFG66= California Department of Fish and Game samples (1966-69). Circles with error bats are the mean size and twice the standard deviations used he- in the baseline growth interpretation (with the effects of the fishery included in later years). Circled numbers indicate the age (from hatching) at which a crab between the two increasing lines will enter the California fishery it he grows at 28 mm/yr. Dotted parts of the CDFG72 line indicate possible involvement of a second age-class (from Botsford 1984).

The results obtained here have significant implications for the interpretation of research on the cause of cycles in the northern California Dungeness crab fishery and those of other states as well. With slower growth rate the expected period of cycles produced by any specific mechanism is greater than previously thought. This results from the use of a description of growth in which an age class enters the fishery at 3.5 and 4.5 yr from metamorphosis rather than being completely recruited at age 3.5 as in previous models (Botsford and Wickham 1978; McKelvey et al. 1980).

Dungeness crab growth rate also has implications for hypotheses involving environmental variables as the cause of these cycles. Since most evaluation of these hypotheses is based on statistical comparison of time series of environmental variables with crab catch or abundance, accurate knowledge of the length of time from the larval phase (the stage at which the environment is most likely to affect crab survival) is necessary to interpret mechanisms. From the results obtained here one would expect a correlation between the catch record and environmental variable at a lag of 4 and 5 yr if it were directly influencing larval survival. If such an environmental variable were affecting growth rate, it could increase the number of individuals entering the fishery at age 3 yr. This growth pattern also has several implications for the impact of dredging mortality on the fishery. The average growth rate will determine the time lag between juvenile mortality and the impact on the fishery. For Dungeness crab, this time lag will be about 3.5 or 4.5 years for mortality of 0+ first year crab. The variability in growth will determine whether the impact of a single year's mortality is spread over several years when that cohort reaches the fishery. For Dungeness crab the major impact of dredging will be over two years (Armstrong et al. 1987a).

A unique study of growth rate and molt increments of adult female Dungeness crab (greater than 90 mm CW) was done by Hankin et al. (1985), and is the only other study of coastal female crab since Butler's work in the late 1950s (Butler 1960, 1961). Based on tagging studies, Hankin et al. (1985) determined molting increments for females that decreased from about 22% at a premolt size of 95 mm CW to 11% at 150 mm CW. Most significant among their data was the substantial decrease in annual molting probability of females >135 mm CW (Fig. 6.8) that was 50% and 0% for females greater than 145 and 155 mm CW, respectively. Further, females that did not molt annually still extruded fertilized egg masses in many cases which implies either the ability to carry viable sperm for 1.5 years or more, or copulation with males may occur even though a female does not molt in a year. The data of Hankin et al. (1985) suggests that the growth models of Botsford (1984) and others may be highly inaccurate for females beyond age 2+.

6.1.2 Growth In and Nearshore of Grays Harbor

Cleaver's (1949) study of crab growth in Grays Harbor was discussed in the previous section, but in general could be improved since his collection gear was biased against 0+ crab. Stevens and Armstrong (1984) studied growth of 0+ and 1+ juveniles in Grays Harbor and found that six

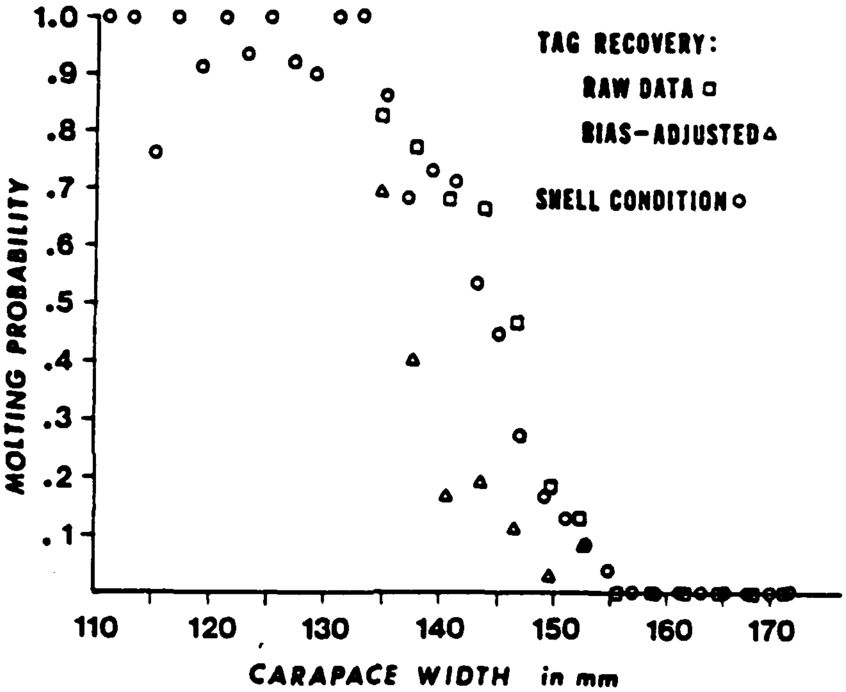


Figure 6.8. Estimated annual molting probabilities for female Dungeness crabs plotted against female carapace width (from Hankin et al. 1985).

months after metamorphosis (May to October) 0+ crab averaged 40 mm CW and by one year were 50 mm (Fig. 6.9). This indicates that 0+ in Washington estuaries may molt 6 to 8 times in the first summer growing season after which the frequency apparently declines with the onset of winter (Fig. 6.9) and larger size. A more dramatic indication of seasonal growth is based on change in dry weight over time (Fig. 6.10). First instar crab at 7 mm CW weigh 0.2 g dry weight while sixth instars (33-35 mm) are 5.7 g, an increase of 280 fold. The monthly percent weight increase for 0+ crab in summer of 1980 was 206% dry weight per month which declined to 15.8% in winter. Armstrong and Gunderson (1985a) showed with data collected in 1983 (first year of the Sea Grant program) that populations of 0+ crab which settle directly nearshore grow significantly slower than those in the estuary (Fig. 6.11). YOY in Grays Harbor grew from a first instar size of 7 mm in May to a mean carapace width of 38 mm. (sixth instar) by October, 1983. Mean estuarine bottom water temperatures were 15°-16°C during this time while those nearshore were 8.5°-10°C. Perhaps as a consequence of this, 0+ crab nearshore in November had only reached a mean width of 18.9 mm, a mixture of third and fourth instars.

Advantages to more rapid growth in estuaries include decreased time to reproduction and greater avoidance of predators. The second point may be critical to population survival (see Section 5.4), since mortality of young, small instars is apparently very high. Stomach analyses of fish offshore of San Francisco Bay showed that the size frequency composition of Dungeness crab taken by predators was skewed toward first through fourth instars but decreased rapidly approaching 30 mm CW (Reilly 1983b; Fig. 4.23).

These previous studies of Dungeness crab populations made use of "fixed size boundaries" to separate age classes (e.g. Stevens and Armstrong 1984). The method works well to segregate the first age group (0+) but has obvious limitations for older animals (as discussed in Section 6.1.1). Figure 6.12 illustrates some of these: 1) the overlap between adjacent year classes is disregarded; 2) year-to-year variation in the spread of a given year class (see the 1+ group, for example) is not accounted for and; 3) the information contained in the intra-year class SFD is not utilized.

To overcome all these difficulties, and in order to make full use of the information available, the application of numerical methods to analyze SFD data were used to better calculate growth rate and size-at-instar (see the DIM, Armstrong et al. 1987a, for details). Analyses of SFDs were done with 1983 through 1986 data from the Grays Harbor estuary and nearshore after substantial compaction of data based on sex, stations and sampling trips. The problem is to identify components (for *C. magister*, the number of instars) in a mixture of distributions. To identify size-at-instar with computer programs similar to that used by MacDonald and Pitcher (1979), two assumptions were made: 1) the SFD for each individual instar is approximately normal and; 2) for a given cohort of animals, the standard deviations (SD) of the component distributions are linearly related to the respective means. In reporting results, juvenile instars whose average size is below a

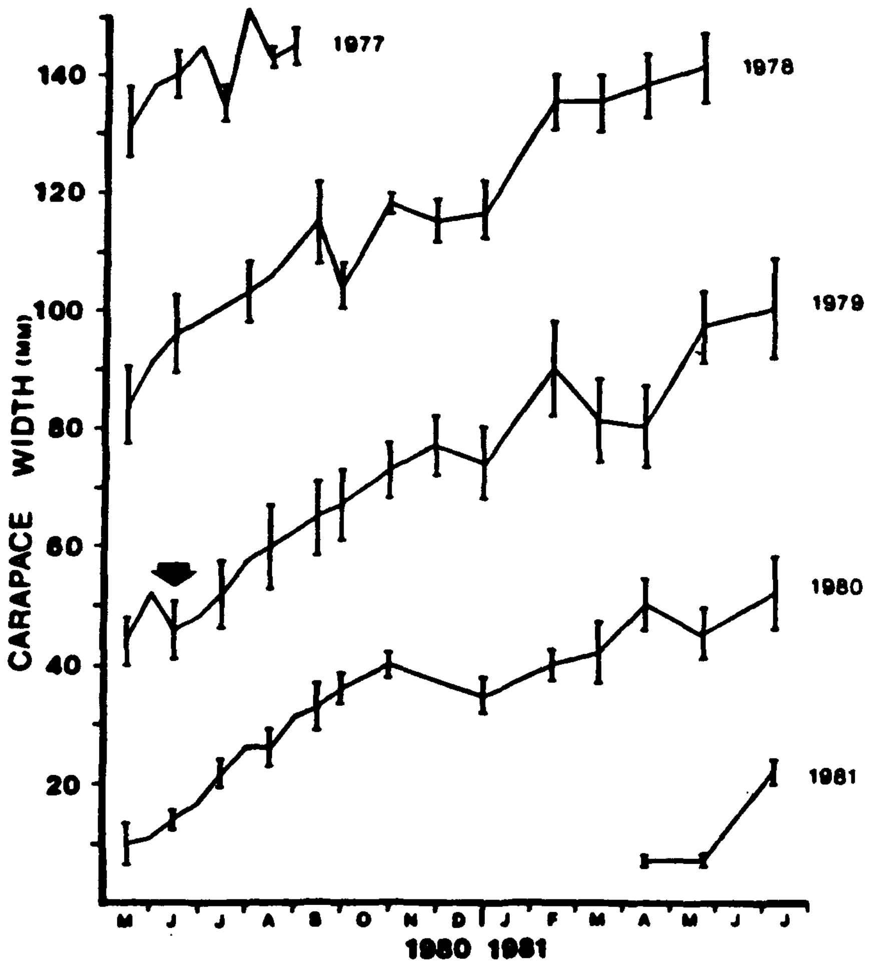


Figure 6.9. Mean carapace widths (± 1 SD) of three dominant age-classes (0+, 1+, 2+) in Grays Harbor, 1980-81 (from Stevens and Armstrong, 1984). Arrow shows decline in size of 1+ crab caused by immigration of smaller nearshore crab into the estuary.

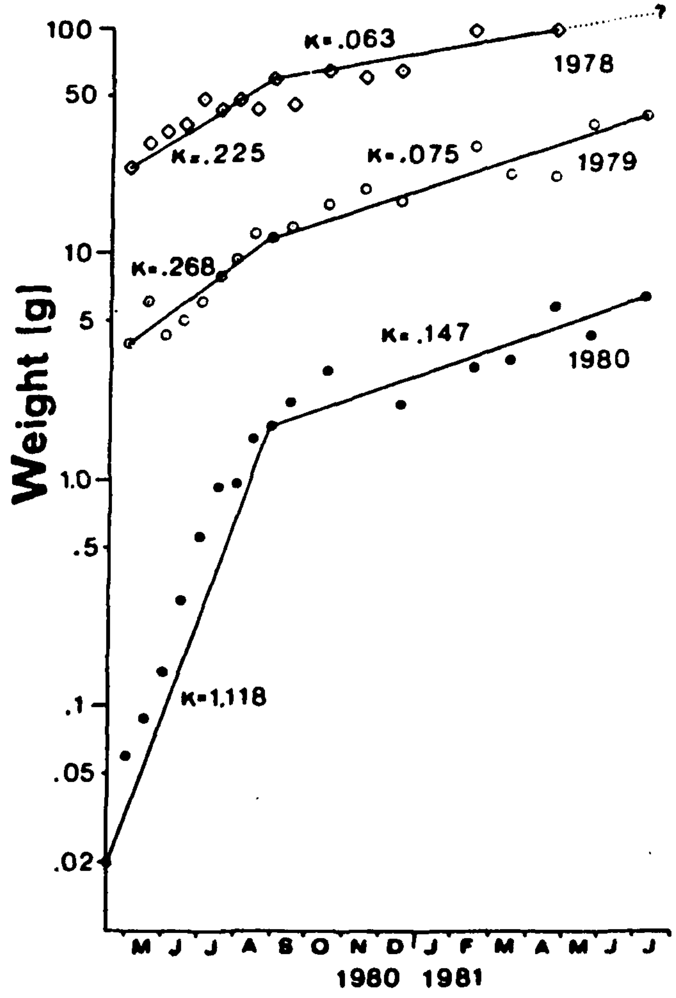


Figure 6.10. Change in dry weight over time of three age classes of Dungeness crab in Grays Harbor. Growth rates = k as g/g dry weight per unit time. Note the rapid growth of 0+ in summer and decline of all age-classes in winter (from Stevens and Armstrong 1984).

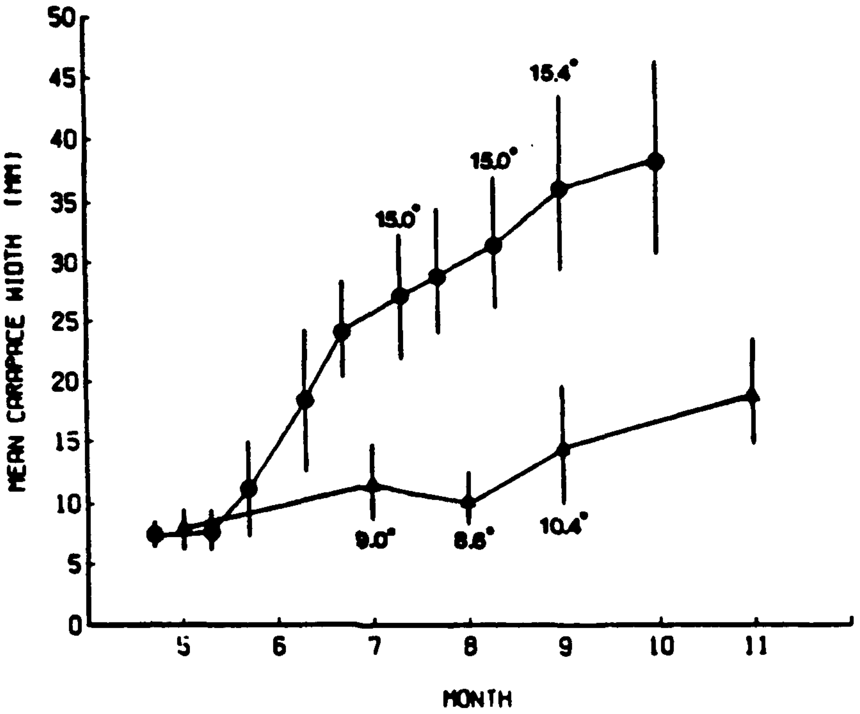


Figure 6.11. Mean carapace width of 0+ crab, from settlement as 7 mm first instars in May into early fall. Grays Harbor population = solid circles; nearshore crab = triangles. Shown are mean bottom water temperatures during several summer cruises. Bar = ± 1 SD.

100 mm CW (theoretical size of 50% sexual maturity; Butler 1960, 1961) are labelled "J1, J2...J+" (J+ is the largest juvenile instar), and adult instars above 100 mm CW are labelled "A1, A1...".

Crab from the estuary molt more often than those nearshore, but size-increments per molt are larger for the nearshore crab. As a result, nearshore crab pass through 10 (as opposed to 11) J-instars to size = 100 mm CW. The contrast in size of estuary versus nearshore juveniles was best seen in the 1984 year class (Fig. 6.14) which was well represented in both locales. Interestingly Cleaver's data on mean size-at-instar indicates smaller animals in the estuary (about 2.5mm) than calculated from the Sea Grant data (Table 6.2). The growth pattern of the 1984 year class in the estuary and nearshore shows that inter-molt periods are longer during the winter ("winter anecdysis") and that the number of molts per year decreases with age (Fig. 6.13). The pattern is very similar to that of the 1945 year class, implicit in Cleaver's Fig. 4 (1949).

Relative growth-per-molt increments on the average, decrease with size and there is some seasonal variation. Increments tend to be lower than expected when temperature is low. Figure 6.14 illustrates relative size increments for both the estuary and nearshore.

<u>Adult Size-at-Instar</u>: Crab above 90 mm CW that originated both nearshore and in the estuary are well mixed and converge in size (Fig. 6.13). Size-at-instar for J^+ and A1 through A3 were estimated for each year 1983-1986 from a pool of data and results are given in Table 6.3 and compared with Cleaver's estimates for crab in Grays Harbor.

The small discrepancies between our 4-year averages and Cleaver's values are within the range of year-to-year variation observed by us. The average size of instar A3, however, is consistently lower than expected given the observed average size at instar A2, and growth schedules that result from other studies (see for example Table 20 in Cleaver, 1949). A size of about 160 mm (17% size increase from A2 to A3) is probably closer to reality and two alternative hypotheses can be formulated to account for the smaller size estimated from the Sea Grant data: 1) The gear utilized in our study may not efficiently catch large crab which biases the estimate downward; 2) At least part of the A3 crab in every year class are of legal (commercial) size and taken by the winter fishery before the start of sampling in spring. The bulk of males molt from A2 to A3 during the fall, the largest among them becoming available to the fishery during the winter. Fishing pressure tends to concentrate at the beginning of the fishing season which opens in December. Since the surveys were always conducted between April and September, the SFD of the A3 males sampled may reflect the selective (size-dependent) effect of the fishery. Elucidation of this question is of great importance. Hypothesis (1) should be critically examined and if substantiated, then the survey

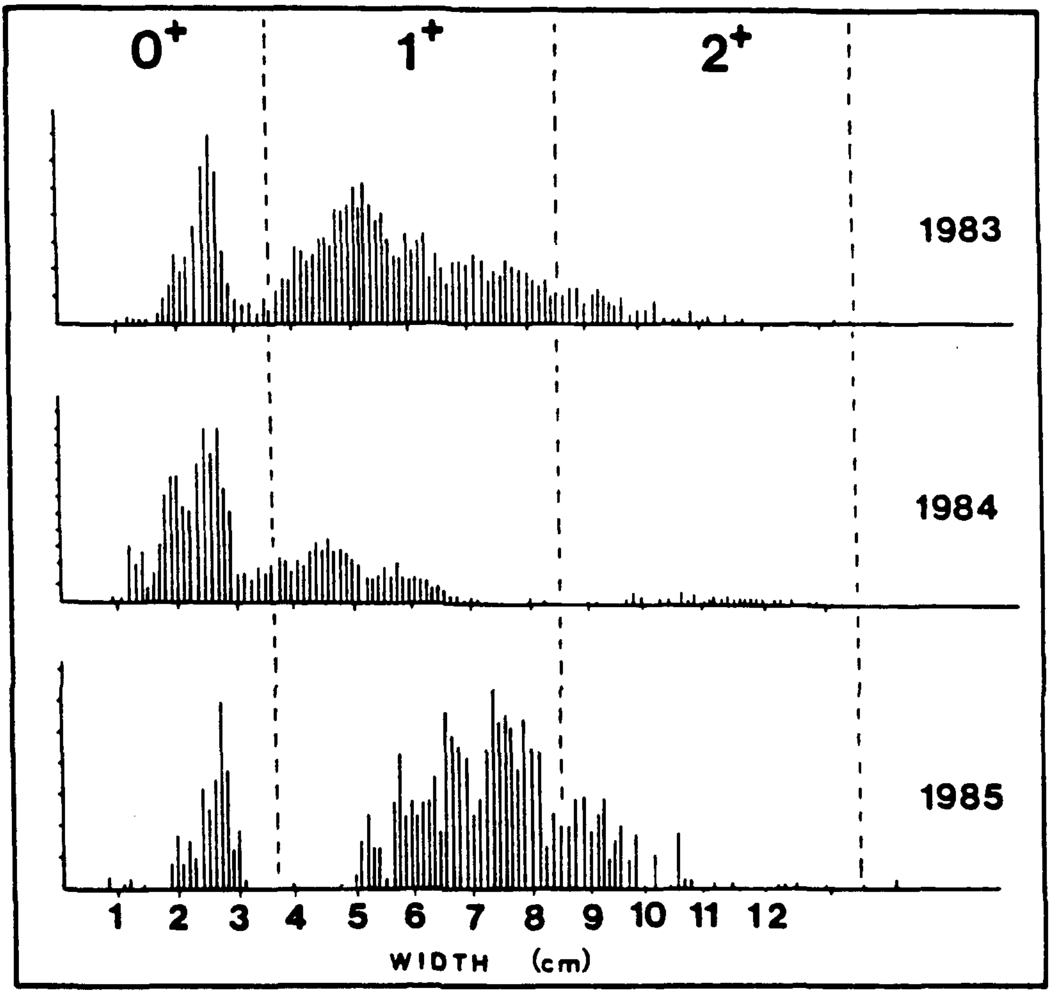


Figure 6.12. Size-frequency distributions of Dungeness crab from Grays Harbor in the month of July, 1983-1985. Notice year-to-year variation in mean size and spread of the 1+ group, as compared with visually determined fixed boundaries (vertical bars) (from Armstrong et al. 1987a).

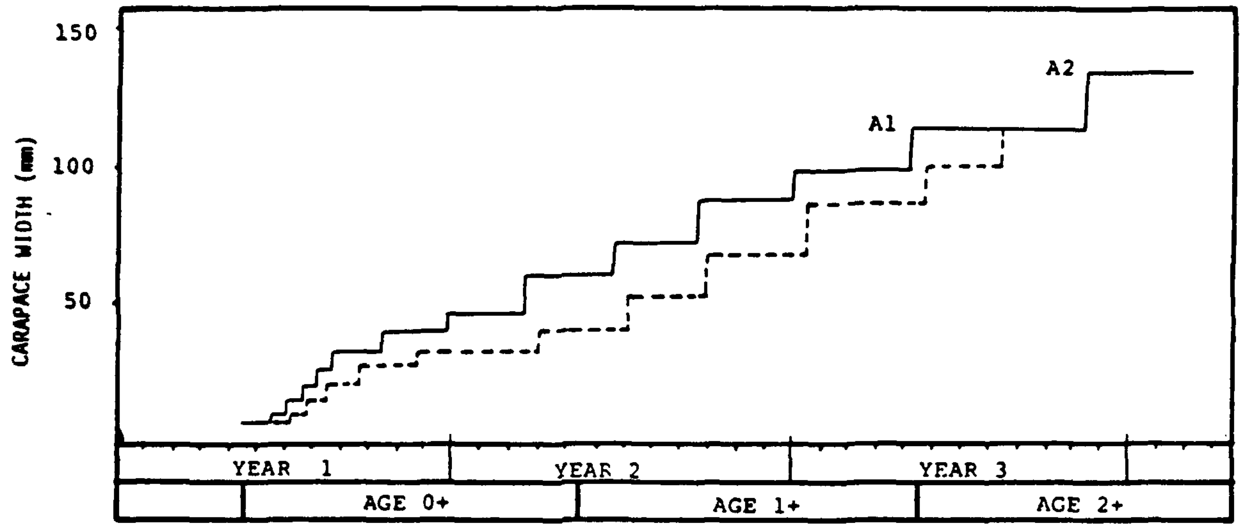


Figure 6.13. Schematic representation (based on growth of the 1984 year class) of size over ages 0+ to 2+. Solid line, estuary; dashed line, nearshore (from Armstrong et al. 1987a).

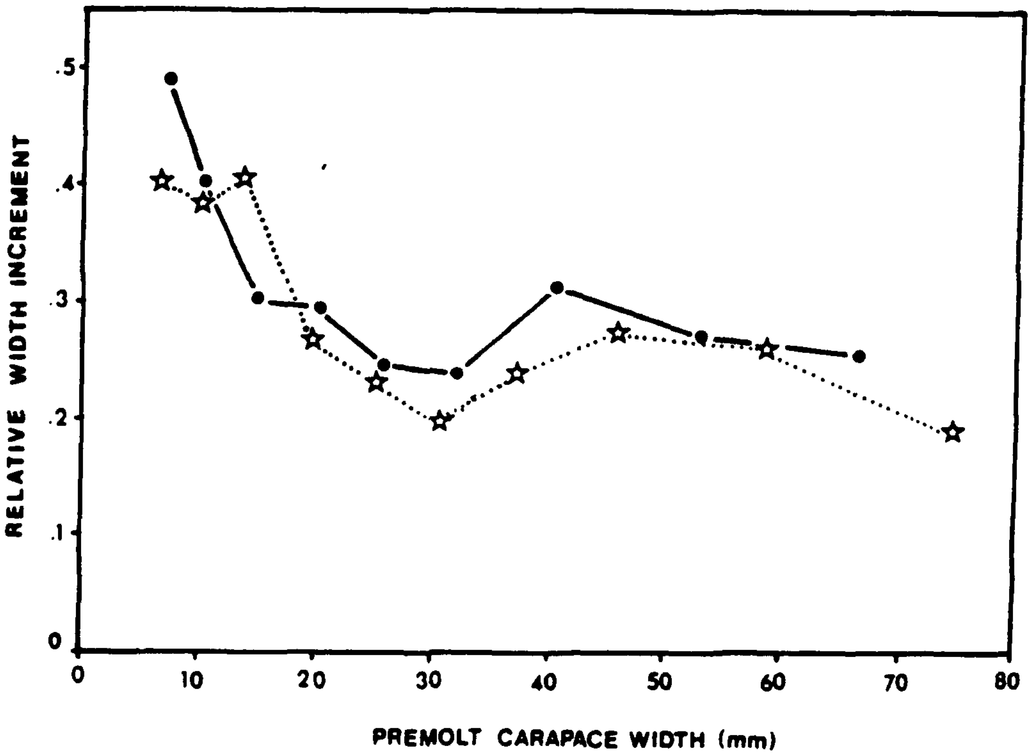


Figure 6.14. Size dependence of relative size increments per molt (expressed as a fraction of premolt size), as obtained from the numerical analysis of size-at-instar schedules. Stars, estuary; dots, nearshore (from Armstrong et al. 1987a).

Table 6.2. Estimated mean size-at-instar of Dungeness crab in Grays Harbor estuary and nearshore along the coast. Mean carapace width (mm) for juvenile stages 1 through 11 are given along with comparative data from Cleaver (1949).

	J1	J2	J3	J4	J5	J6	J7	J8	J9	J10	J11
Nearshore	7.3	10.9	15.3	20.0	25.9	32.3	40.0	52.5	55.8	84.2	
Estuary	7.2	10.1	14.0	19.8	25.1	30.9	37.1	46.0	58.6	73.7	87.8
Cleaver	5-7	9.0	12.0	16.0	22.4	28.8	35.2	44.6	56.4	68.4	84.9

Table 6.3. Mean size-at-instar of Dungeness crab in Grays Harbor estuary and nearshore along the coast for the largest juvenile stage (J+) and adult instar stages A1 through A3 (size transition taken to be 100 mm CW). Data based on the four-year Sea Grant series 1983-1986. Comparative size-at-instar data from Cleaver (1949) are also given.

	Males				Females		
	J+	A1	A2	A3	J+	A1	A2
Nearshore	96.7	115.9	137.7	154.6	96.5	113.3	133.7
Estuary	92.2	110.7	137.4	151.7	90.1	103.8	125.8
Cleaver	84.9	106.4	129.1	154.4	84.9	106.4	-

Table 6.4. Correspondence between age and instar number over the first five years of life for a male Dungeness crab that settles to the Grays Harbor estuary. The number of juvenile and adult instars per age class category correspond to data presented in Figure 6.13.

Calendar year of life	Age during survey season (Apr.-Oct.)	Instars
1	0+	J1-J7
2	1+	J7-J10/11(J+)
3	2+	J1 & A1
4	3+	A2
5	4+	A3

estimates of abundance should be corrected. If it is rejected, the depression of average size at instar A3 following the fishing season could be of great value to estimate fishing mortality.

The small size-at-instar of the females from the estuary, as compared to those from nearshore, may be explained by one of the following alternative hypotheses: (1) Females emigrate when they reach sexual maturity (see Sections 4.3, 5.4 Fig. 4.15). This and other migratory movements seem to be size-dependent, larger animals within a group migrate ahead of smaller ones. (2) The difference reflects actual smaller size-at-instar of estuarine females. The difference between estuarine and nearshore males is blurred by movements in and out of the estuary, but females do not re-enter the estuary once they emigrate after reaching maturity.

Growth Patterns: Growth of Grays Harbor (estuarine) crab was portrayed by Cleaver (1949, his Table 21) and depicted by Stevens and Armstrong (1984; Fig. 6.10) and Armstrong and Gunderson (1985) for 0+ crab. Their conclusions are schematically compared in Fig. 6.15. Inferred growth patterns are similar for the first two years of life. Cleaver s values were derived from visual inspection of modes for samples from 1946 and early 1947. His estimated size of 150 mm at age 3 years after hatching is based on the assumption that two modal groups in February 1947 (instars A2 and A3) correspond to a single age class. This is inconsistent with other pieces of evidence, including the growth pattern of the 1945 year class (implicit in Cleaver's Fig. 4).

Stevens and Armstrong's depiction was derived from the dissection of periodic SFDs by use of fixed size boundaries between age classes 0+ to 3+ corresponding to the 1980 through 1977 year classes. Their results (Fig. 6.9) agree rather well with the schematic representation introduced above (Fig. 6.15), which follows from the application of more elaborate techniques to data gathered in 1983-1986.

Crab tend to molt less frequently as they grow larger. Following settlement, an estuarine crab will go through, on the average, 6 molts during the first year, and through 3 or 4 during the second year. As crab approach maturity, molting tends to become seasonal and crab generally molt only once per year (older crab may even skip molting; see Hankin et al. 1985), and male and female molting seasons tend to diverge. Males molt during the fall (this being the reason for the fall fishing closure), and females during the spring which marks the reproductive season. The analyses given here and those of Stevens and Armstrong (1984) show that the bulk of a cohort will reach instar A1 by the end of the third calendar year of life after hatching (roughly 2.5 years after settlement). From this size (110-115mm CW) on, males seem to molt once per year, at least until they reach instar A3 (average size just below 160 mm CW for the study period). Table 6.4 summarizes the average instar/age relationship for male crab that settles in an estuary during its first 5 years of life.

Recruitment to the Fishery: Although there is much intra-year class variation in growth, the bulk of a cohort seems to be rather synchronic in reaching instar A3 during the fall of the 4th calendar year of life (3.5 years after settlement). The amount of interannual variation in size-at-instar schedules is such that recruitment to the fishery of the bulk of a year class can be apportioned in a number of different ways between ages 3.5 and 4.5 years after settlement. If the average size of instar A3 is very small, one can expect: a) delayed recruitment to the fishery (at 4.5 years of age for most crab), and b) large size of crab in the commercial catch. Conversely, a large size at instar A3 can be expected to result in: a) early recruitment to the fishery (about 3.5 years of age), and b) a commercial harvest composed of relatively small crab. The last seems to have been the case for the Grays Harbor area in recent years (e.g. 1986/87 season; Steve Barry, WDF, pers. comm.). There are well substantiated anecdotal reports of occurrence of the first scenario for Washington and Oregon.

6.2 MORTALITY ESTIMATES

Despite the long years of study on Dungeness crab little work has been done on natural mortality rates, primarily because of the acute lack of quantified data on population dynamics. From the data on population abundance and structure derived from the four year (1983-1986) Sea Grant program, mortality estimates are possible and have been calculated for use in the DIM (Armstrong et al. 1987).

6.2.1 Natural Mortality

For years the only published estimate of natural mortality rate derived from field data was an annual rate of 0.15 (Jow 1965), which was based on tagging studies of larger male crab. A value of 0.2, approximating that of Jow's, was used in models of population fluctuations based on fisheries data by Botsford and Wickham (1978) and McKelvey et al. (1980). Stevens and Armstrong (1984) estimated survival to the commercial fishery of 0+ and 1+ crab populations in Grays Harbor during 1980 and 1981. They used annual rates of mortality from metamorphosis of 0.8 (first half year), 0.5 (second half) and 0.2 each year thereafter, but there was no direct calculation of these values.

In their study of adult female growth and movement along the northern California coast, Hankin et al. (1[illegible]85) used extensive tagging data to estimate annual mortality (survival) of "large" (>155 mm CW) and "small" (>125 but <140 mm CW) females. Interestingly, the larger crab had much higher annual mortality rates of about 0.87 and 0.92 (in the first and second year of release after tagging), compared to a rate of 0.5 for smaller females. This observation is consistent with the notion of "senescence" of older, larger females noted by Botsford and Wickham (1978) who

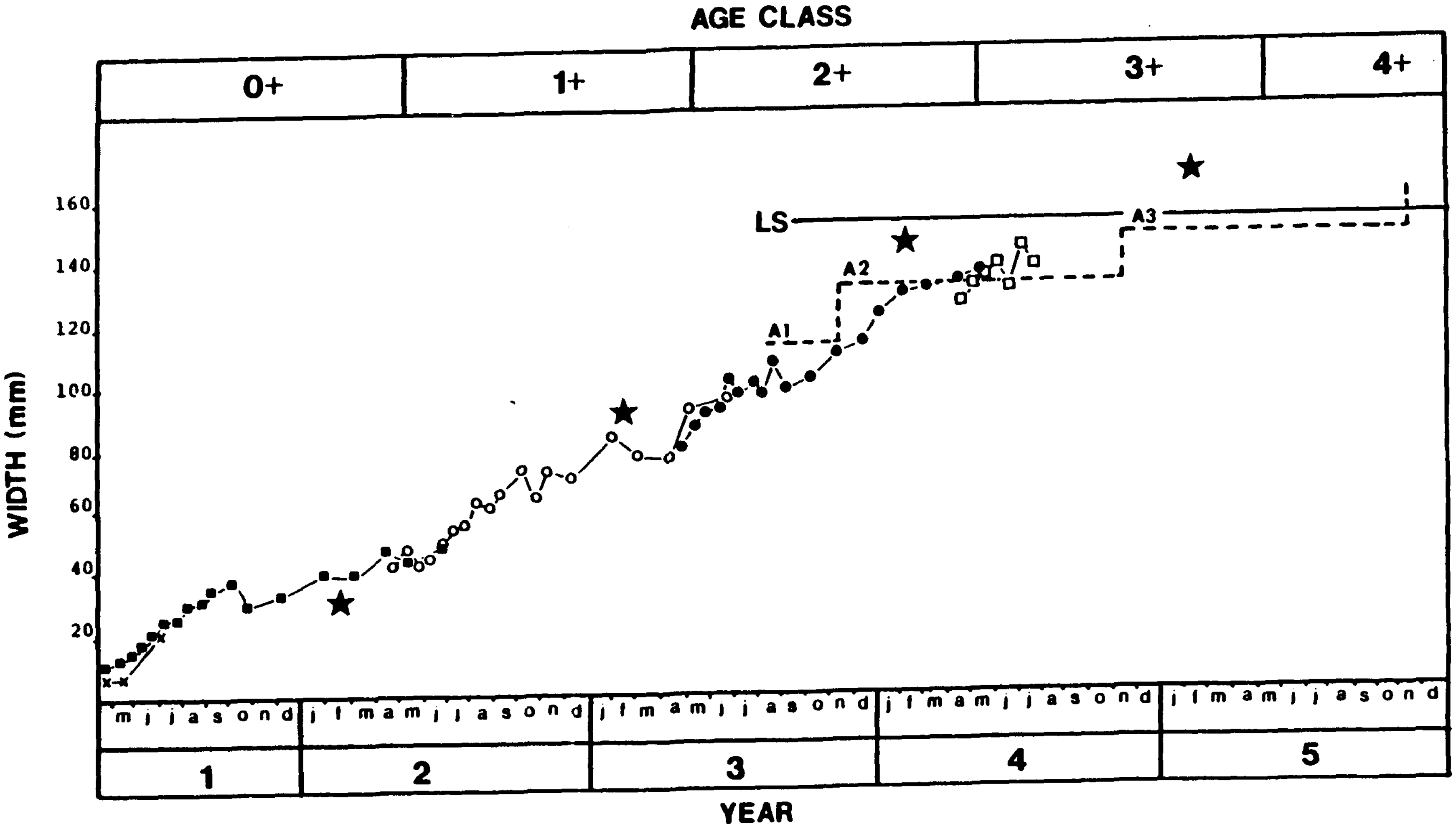


Figure 6.15. Schematic representation of growth results from different studies. Symbols connected by solid lines correspond to the 5 year classes present in the estuary in 1980-1981 (Stevens and Armstrong 1984). The dashed line tracks male growth under the assumption that the bulk of a year class molts from instar A1 to A2 at about 2.5 years of age, and from A2 to A3 at about 3.5 years of age, based on the 1983-1986 Sea Grant Surveys. Stars correspond to the size-at-age schedule proposed by Cleaver (1949). LS, legal size limit.

used a mortality value of 0.9 for this stage crab. In accord with results of tagging by Hankin et al. (1985), Stevens and Armstrong (1981) reported a mass mortality along the southern Washington coast of adult female Dungeness crab whose average size was 147 mm CW. They too speculated that senescence (i.e. general weakening of physiological functions) and attendant susceptibility to disease might increase mortality of very old crab.

Grays Harbor Populations: Based on initial data from 1983, Armstrong et al. (1984) calculated a three month (May through July) mortality rate of 0.84 for 0+ crab nearshore of Grays Harbor which would be in excess of 0.99 annually. Nominal estimates of mortality of 1+ were 0.63 and about 0.55 for coastal and estuarine populations, respectively, between July through September.

A more extensive analysis of population data collected between 1983-1986 to derive natural mortality rates (Z) is given by Armstrong et al. (1987a) in the DIM. Data used to estimate survival include: 1) monthly assessments of crab abundance and, 2) estimation of the proportion contributed by each instar in the total sample from each month or cruise. The instars were grouped by age classes according to the growth patterns described in Section 6.1.2 and abundances per age class were subsequently obtained for each month. The values assembled in this way have a number of acknowledged limitations: 1) the confidence intervals for the monthly abundance estimates are wide (±2SE, about 40-50% of mean in estuary; up to 80-100% nearshore) so that values should be seen only as indices of abundance; 2) the gear utilized in the surveys is not 100% efficient and there is good evidence that efficiency depends on the size of the crabs and may be less efficient for large crab; 3) there may be a seasonal component in the catchability of crab of all sizes. Catchability seems to be at a minimum in winter and early spring and at a maximum in late summer.

Mortality of 0+ Crab Within the Estuary: YOY estuarine crab include both subtidal and intertidal populations from settlement through July of the second calendar year of life. The data indicate two very different phases of mortality (survival) in this part of the life history: 1) the first month of post-settlement life (Instar J1) and, 2) the rest of the first year of life.

During the first month of life it seems that the estuarine population (intertidal areas included) is reduced from over 400 million (on average) to 20-40 million crab depending on the number that settled in spring (see Section 5.0). This was apparent for two years (1983-1984) in which there was high intertidal settlement followed by severe post-settlement mortality of 93 to 96% in one month. For these reasons the data from May 1983 and May 1984 were excluded from the analyses. Early survival of very large estuarine cohorts requires *ad hoc* treatment.

The rest of the data fit rather well a negative exponential model (constant mortality coefficient),

$$dN/dt = -Zt$$

where N is population size, t is time (in years), and Z (with dimensions l/time) is the total mortality coefficient.

Z was estimated in two ways:

1) each monthly N-value was divided by the N_0 of the respective year class. N_0 was taken as the abundance of 0+ crab in the month when settlement peaked in 1985 and 1986, or one month following peak settlement in 1983 and 1984 (for the reasons explained above). In this way all the data [log (N/N_0), for 4 year classes] could be regressed on age. Results were as follows:

$$Z = 3.407/\text{yr}, \text{ significance} = 0.00001$$
$$r2 = 77.8\%, n=24$$
$$\text{Mortality } (Z) = 0.97 \text{ for the first year.}$$

2) N per month were calculated using the data of the four year classes (N values of May 1983 and May 1984 excluded as above). The N values are plotted vs time in Fig. 6.16. Regression of log (N) on t gave a value of Z=2.85/yr (mortality of 0.94 for the first year); a survival rate of 3-6% for the first year of life seems reasonable.

Survival Throughout the Whole Region, All Ages: Given the limitations of the data outlined above, the estimation procedure is inevitably coarse at this stage and is intended to give a broad idea of the pattern contained in the data. No attempt was made to guess the shape of the following two functions: a) seasonal variation in catchability and, b) size-dependence of the gear's efficiency. A better knowledge of these two components will be indispensable to make full use of the data base.

Only the nearshore and subtidal estuary data were utilized to estimate Z through several age classes. Thus, the survival estimates pertain only to crabs that have emigrated from the intertidal flats. Data from the estuary and nearshore were combined for the months where both were available and N values for each month were partitioned into instars, and instars were subsequently grouped in age classes. All monthly values for each age class were averaged across year classes, and then all the monthly averages corresponding to each age class were averaged for the four years of the survey to give an overall average N for each age class (all year classes combined) during the survey season April to October. The resulting N-values were utilized to calculate summer-to-summer age-specific S (survival) and Z values (Table 6.5).

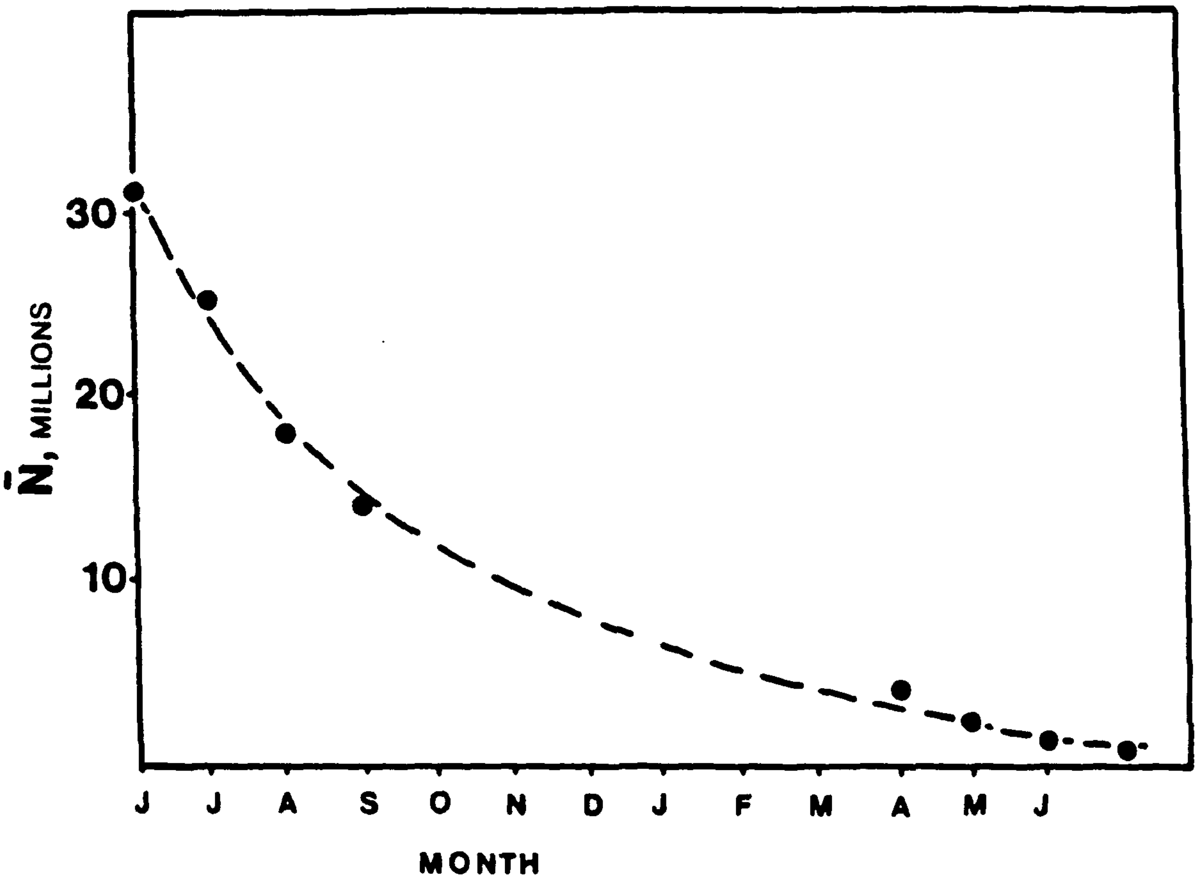


Figure 6.16. Survival of the 0+ crabs within the estuary based on an average population size from the four years of survey, 1983-1986.

Figure 6.17 illustrates the decay of the N values and of their logs over time, and Z as a function of age. The four Z values are linearly related to age; regression of Z on age gives the following result:

$$Z = 2.49 - 0.43\ (\text{age})$$

This age-dependent Z implies the survival model:

$$dN/dt = -(a + b\ x\ \text{age})\ t$$

which integrated gives:

$$N(t) = N_0\ x\ e\ -(a + b/2\ x\ \text{age})\ t$$

There is implicit agreement among specialists that Z must decrease monotonically as a function of age. The function obtained here happens to coincide with a linear interpolation between two "educated guesses" that have made their way into the literature: 1) a survival below 10% for the early life history (initial survival is 8% in the line fitted) and; 2) a natural mortality rate of 0.2/yr for large crab around 5 years old (Botsford and Wickham 1978; McKelvey et al. 1980).

Leaving aside all the statistical problems implicit in the estimation procedure, the data base presents the following difficulties: 1) The efficiency of the trawl gear for crab of different sizes is unknown. The trawl may be inefficient for large crab near legal size; although since the spring/summer survey follows the winter fishery, there could be very few large males left to catch. The average estimated number of instar A3 males (more than half of them "sublegal") seems smaller than the average commercial catch of legal crab from the area. 2) Pooling year classes may distort the pattern if a strong year class is well represented for a part of the life history. Although the strength of the year classes pooled is rather variable, the strong 1984 year class may change the picture of age-specific survival over the following two years.

Given that the 1984 year class has, so far, been followed for three years (1984-1986), its inclusion in the overall averages might be expected to depress the estimation of survival from age 2+ and 3+. This might happen if inclusion of the 1984 year class causes the estimated annual mean abundance of 0+ 1+ and 2+ to be high relative to abundance of 3+ and 4+ that come from other year classes which do not include the 1984 group. For that reason the analyses were also done excluding the 1984 year class from the data base. Table 6.6 contains results that show higher estimates of mortality in the first year but lower in the second and third year (compare Tables 6.5 and 6.6). It is important to note that Z from age 2.5 to 3.5 yr may reflect the fact that at least part of the males are recruited to the fishery at 3.5 yr. The mortality coefficient (Z) from age 3+ to 4+ would include both natural (M) and fishing (F) mortality if true.

6.2.2 Fishing Mortality

Tagging studies and analyses of catch-per-unit-of-effort (CPUE) indicate that about 85% of available legal males are harvested each year (see review in Methot and Botsford 1982). A Leslie

Table 6.5. Estimated mean population for five year classes of Dungeness crab based on the combined nearshore and estuarine population information from the four year Sea Grant survey, 1983-1986. Annual survival rate (S) and instantaneous per capita mortality rate (Z) are shown and correspond to results depicted in Figure 6.17.

AGE	$\bar{N}$ (millions)	S (% per year)	Z (per year)
0	186.167		
		10.2	2.28
1	19.074		
		16.2	1.82
2	3.089		
		23.4	1.45
3	0.724		
		38.0	0.97
4	0.275		

Table 6.6. Same as Table 6.5, but excluding the exceptionally strong 1984 year class.

Age	N(millions)	S(% per year)	Z/yr
0	179.859		
		4.6	3.08
1	8.259		
		19.5	1.63
2	1.609		
		45.0	0.79
3	0.724		
		38.0	0.97
4	0.275		

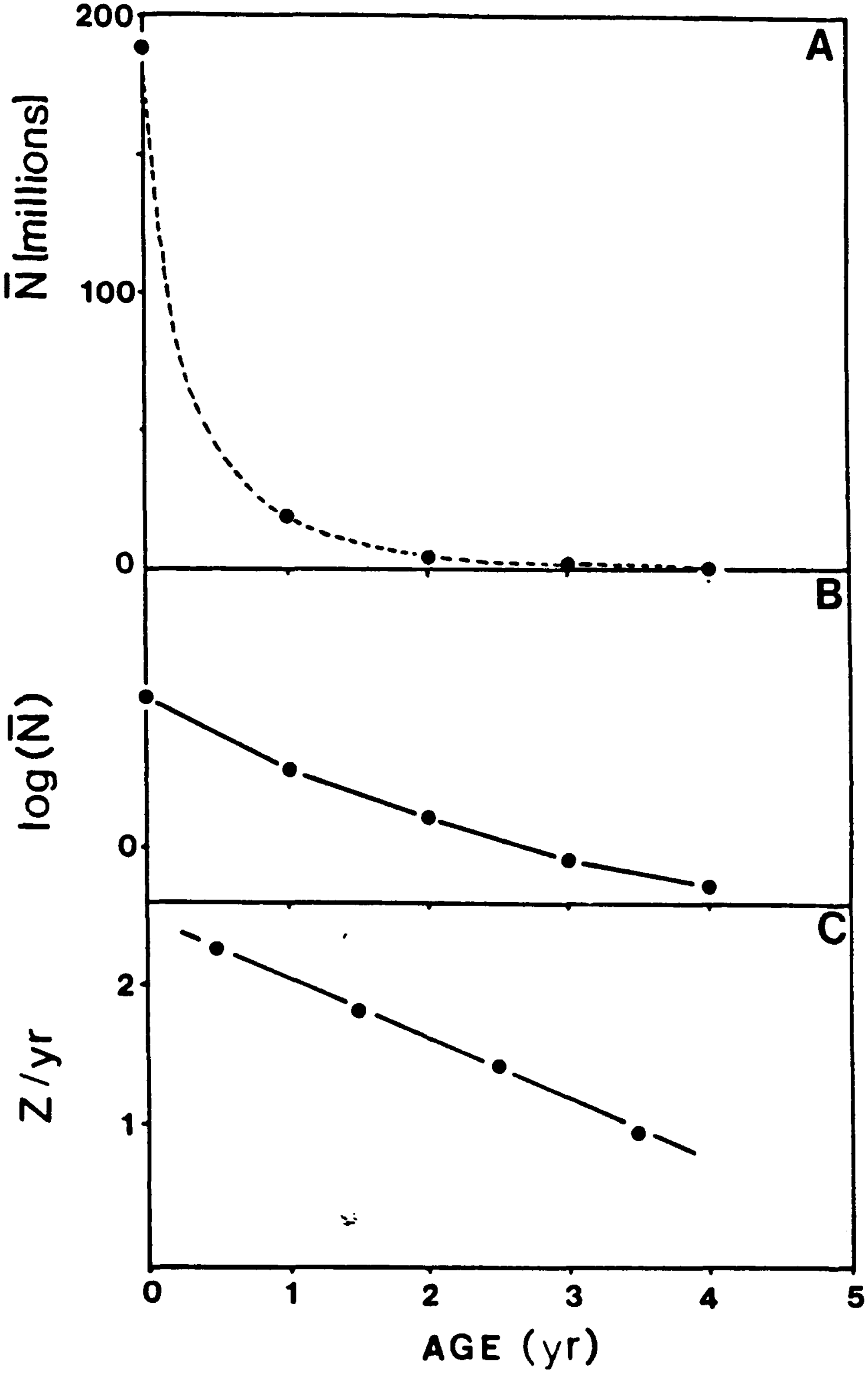


Figure 6.17. Survival for the whole study area, Grays Harbor (intertidal excluded) plus nearshore. A: average survival curve. B: same, with logarithmic scale (notice that points do not fall on a straight line). C: age-dependence of the mortality coefficient (Z).

analysis of declining CPUE in the northern California fishery by Methot and Botsford (1982) show that exploitation rate is not at all constant nor as high as previously assumed. Particularly, exploitation (F) is high as abundance cycles increase but low when abundance decreases. In most years between 1951 through 1977, exploitation rate (fishing mortality) ranged from 0.52 to 0.65. Only when abundance and landings were decreasing in 1961-1962 and again in 1969-1972 was F between 0.7 and 0.9 (Methot and Botsford 1982). These variable exploitation rates were used to correct estimates of preseason abundance of crab which, based on fishery landings, were cycling with apparently increasing amplitude. Their interpretation of the cycles is that amplitude has not varied substantially over three periods of cycles, but recruitment is not as smooth as implied by the catch record (Fig. 3.2).

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