AD-A090 832 FISH AND WILDLIFE SERVICE FAYETTEVILLE AR NATIONAL RE--ETC F/G 12/1
SIMULATION MODELING OF ZOOPLANKTON AND BENTHOS IN RESERVOIRS: D--ETC(U)
MAR 80 G R LEIDY, G R PLOSKEY

UNCLASSIFIED WES-TR-E-80-4 NL

1 OF 4
AD
A090832

(18) WES (14) TR-E-80-4

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE

READ INSTRUCTIONS BEFORE COMPLETING FORM

1. REPORT NUMBER
Technical Report E -80-4

2. GOVT ACCESSION NO.
AD-A090832

3. RECIPIENT'S CATALOG NUMBER

4. TITLE (and Subtitle)
(6) SIMULATION MODELING OF ZOOPLANKTON AND BENTHOS IN RESERVOIRS: DOCUMENTATION AND DEVELOPMENT OF MODEL CONSTRUCTS

5. TYPE OF REPORT & PERIOD COVERED
(9) Final rep[redacted]t

6. PERFORMING ORG. REPORT NUMBER

7. AUTHOR(s)
(10) George
G[redacted] R. Leidy
G. R. Ploskey

(12) 311

8. CONTRACT OR GRANT NUMBER(s)
Interagency Agreement
WES-77-3

9. PERFORMING ORGANIZATION NAME AND ADDRESS
USDI Fish and Wildlife Service
National Reservoir Research Program
Fayetteville, Arkansas 72701

10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS
EWQOS Task IB.1

11. CONTROLLING OFFICE NAME AND ADDRESS
Office, Chief of Engineers, U. S. Army
Washington, D. C. 20314

12. REPORT DATE
(11) Mar[redacted]980

13. NUMBER OF PAGES
308

14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)
U. S. Army Engineer Waterways Experiment Station
Environmental Laboratory
P. O. Box 631, Vicksburg, Mississippi 39180

15. SECURITY CLASS. (of this report)
Unclassified

15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)
Approved for public release; distribution unlimited.

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

Benthos	Simulation
Environmental effects	Stochastic models
Mathematical models	Zooplankton
Reservoirs	

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

A literature review and analysis of published data on zooplankton and benthos bioenergetics form the basis used in this report for the development of stochastic model constructs for the simulation of zooplankton and benthos dynamics in reservoirs. Parameters reviewed and modeled were selected from the mass balance equation:

$$\frac{db}{dt} = b\left[G\left(\frac{A}{G}\right) - R - NPM - PM\right] \qquad (1)$$

(Continued)

DD FORM 1 JAN 73 1473 EDITION OF 1 NOV 65 IS OBSOLETE

Unclassified

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

20. ABSTRACT (Continued).

where b = biomass (mg carbon), t = time (days), G = consumption or grazing rate (mg carbon·mg carbon^{-1}·day^{-1}), A = assimilation (mg carbon·mg carbon^{-1}·day^{-1}), R = respiration (mg carbon·mg carbon^{-1}·day^{-1}), NPM = nonpredatory mortality (mg carbon·mg carbon^{-1}·day^{-1}, and PM = predatory mortality (mg carbon·mg carbon^{-1}·day^{-1}).

Mathematical constructs, where appropriate or justified by the available literature, were developed to describe the effects of environmental components (for example, food, temperature, and oxygen concentration) on rate terms in Equation 1. Frequency distributions of rate coefficients were formed for as many taxonomic or functional categories of aquatic invertebrates as possible. By using carbon units and providing frequency histograms of carbon-nitrogen and carbon-phosphorus ratios, the model can trace the cycling of nitrogen and phosphorus through zooplankton and benthos compartments. An evaluation is presented of strengths and weaknesses in the literature on zooplankton and benthos consumption, assimilation, respiration, and nonpredatory mortality.

PREFACE

This report was prepared by the U. S. Department of the Interior, U. S. Fish and Wildlife Service, National Reservoir Research Program (NRRP), Fayetteville, Arkansas, for the U. S. Army Engineer Waterways Experiment Station (WES) under Interagency Agreement WES-77-3 dated 3 February 1977. The study forms part of the Environmental and Water Quality Operational Studies (EWQOS), Task IB.1, Improved Description of Reservoir Ecological and Water Quality Processes. The EWQOS Program is sponsored by the Office, Chief of Engineers, and is assigned to the WES under the purview of the Environmental Laboratory (EL).

The research, documentation, and development of model constructs for reservoir zooplankton and benthos were conducted by Messrs. George R. Leidy and Gene R. Ploskey for the NRRP; Mr. Robert M. Jenkins is the Director of NRRP.

The study was under the direct WES supervision of Dr. Kent Thornton and Mr. Joseph Norton and the general supervision of Mr. Donald L. Robey, Chief, Water Quality Modeling Group; Dr. Rex L. Eley, Chief, Ecosystem Research and Simulation Division; Dr. Jerry Mahloch, Program Manager, EWQOS; and Dr. John Harrison, Chief, EL.

The Directors of WES during this study were COL John L. Cannon, CE, and COL Nelson P. Conover, CE. The Technical Director was Mr. F. R. Brown.

CONTENTS

LIST OF FIGURES

LIST OF FIGURES

LIST OF FIGURES

LIST OF FIGURES

LIST OF TABLES

LIST OF TABLES

SIMULATION MODELING OF ZOOPLANKTON AND BENTHOS IN RESERVOIRS: DOCUMENTATION AND DEVELOPMENT OF MODEL CONSTRUCTS

PART I: INTRODUCTION

Modeling Concepts

1. Modeling, as an approach to understanding biotic communities, has achieved considerable attention in recent years. With the inception of the International Biological Program in 1966, modeling has attracted a growing number of researchers who have applied modeling techniques to almost all areas of biological investigation. Today, modeling is considered the solution for many problems, especially in decision making for resource management.

2. Populations and communities of organisms can be considered as complicated, dynamic systems of regularly interacting and interdependent components forming a unified whole. Environmental factors influence these systems through inputs and the systems, in turn, influence the environment through outputs. Systems analysts have attempted to provide a quantitative description of the relationships within these systems and their functions. However, because most biological communities are intractable to detailed analysis even by direct observation, the most common, efficient, and, in certain instances, the only method of investigating these systems is through modeling (Menshutkin 1971).

3. In developing a mathematical model of a population, community, or ecosystem, the first and most difficult step is to define the objectives of the analysis. A model constructed without clearly stated objectives would in all likelihood result in the description of extraneous components and functional relationships, the effect of which would be to waste time, money, and effort in the collection of data and development of concepts. Furthermore, critical components that are necessary for the model may be omitted, seriously affecting model performance and leading to erroneous conclusions.

4. The second step in model development is to determine which components are necessary to meet the objectives. Third, the functional relationships among ecosystem components must be determined and quantified. Often the development of these relationships is difficult because it requires a thorough knowledge of the population dynamics of the organisms modeled (e.g., population size, growth rate, and mortality rates). Step four involves the construction of the mathematical model itself, a step many biologists are poorly prepared to deal with. Finally, the model is applied and the results compared to field data. Refinements are made until the model achieves the desired objectives.

Objectives

5. Following consultation with personnel at the Environmental Laboratory (EL) of the U. S. Army Engineer Waterways Experiment Station (WES), several objectives were developed:

- a. To review and evaluate the literature on zooplankton and benthos community dynamics and to select information suitable for developing and documenting various model constructs.
- b. To summarize, in frequency distributions, the literature values for various model parameters. These frequency distributions will later be converted to probability distributions and incorporated into the model for a stochastic capability.
- c. To propose, where appropriate, suitable model constructs that describe the dynamics of zooplankton and benthos communities.

6. We did not propose a definitive compartmental scheme for modeling zooplankton and benthos. Based on objective b above, we have provided frequency distributions of model parameters for potential compartments. Compartment selection is relegated to the modeler. They should not create model compartments for which frequency distributions of parameter values are unavailable. The documentation provided in this report should allow the modeler to critically evaluate the existing data base and understand its limitations. Stockmayer (1978) succinctly summarized the data evaluation dilemma:

> Uncritical acceptance of bad scientific information can lead to social penalties....A particularly pernicious aspect of this problem involves numerical data, which are essential in all branches of science and technology and are often needed to arrive at valid operational decisions. Unfortunately, the scientific literature contains many erroneous values. Few scientists or engineers seem to have given much thought to the magnitude of the problem, and some probably regard every numerical entry in a handbook as revealed truth. Yet anyone who has had to seek a particular number in the literature and searched out a dozen or more reports, only to end up with a set of widely disparate values, comes to realize that a substantial intellectual effort and a considerable background in the field are needed to arrive at reliable figures.

7. Recent review papers that compare and contrast existing aquatic ecosystem models include those of Swartzman (1977), Swartzman and Bentley (1978), and Scavia and Robertson (1979).

Scope

Model framework

8. In conducting the literature review and analyses, it was necessary to organize our work so that it could be integrated with the existing ecological model being developed at the WES. The model was originally constructed by Water Resource Engineers, Inc., of Walnut Creek, California. Various versions of the model have been applied to field situations (see Chen and Orlob (1975) for a description of the model and a summary of applications). Our analyses were formulated to include various structural considerations of the model. The first structural consideration was that the model use differential equations to describe transfer rates, and, second, that the model have compartments. Third, it is a mass balance model that tracks carbon, nitrogen, and phosphorus to account for material flow in the system. Fourth, the recommended minimum time frame for model simulation is 1 day.

Subject areas covered by the literature review

9. A vast literature exists dealing with the population dynamics of zooplankton and benthos. Many subjects are of direct relevance to

simulation modeling. The overall objective of modeling zooplankton and benthos populations is hopefully to duplicate biomass changes in these populations as they respond to changes in their environment. These changes are reflected in a series of inputs to the population and outputs to the environment. We assume that zooplankton and benthos population (i.e., model compartments) respond as if they were individual organisms faced with a changing environment. To keep track of this response we utilized the following mass-balance, differential equation for all model compartments:

$$\frac{db}{dt} = b\left[G\left(\frac{A}{G}\right) - R - NPM - PM\right] \tag{1}$$

where b = biomass (mg carbon), t = time (days), G = consumption (mg carbon·mg carbon^{-1}·day^{-1}), A = assimilation (mg carbon·mg carbon^{-1}·day^{-1}), A/G = assimilation efficiency (%), R = respiration (mg carbon·mg carbon^{-1}·day^{-1}), NPM = nonpredatory mortality (mg carbon·mg carbon^{-1}·day^{-1}), and PM = predatory mortality (mg carbon·mg carbon^{-1}·day^{-1}).

10. Equation 1 also defined the subject areas that had to be reviewed in order to define the equation. Each of the remaining sections of this report describes our efforts to review and evaluate each of the subjects on the right-hand side of the equation, with the exception of predatory mortality. Predatory mortality is defined as the grazing function of a consumer compartment, i.e., one compartment's consumption is another compartment's predatory mortality.

Extent of the literature review

11. Our review of the subject areas relevant to the simulation modeling of zooplankton and benthos was comprehensive and worldwide in scope but selective for relevant publications for some subjects. Processes most critical to defining zooplankton and benthos population dynamics (e.g., grazing) were given the greatest attention.

12. Many papers that appeared highly relevant were unavailable in English translation and were not reviewed. Most papers in this category were from Eastern Europe, particularly the USSR (Union of Soviet

Socialist Republics). When translations were unavailable, English abstracts such as those found in various abstracting periodicals or comments by other authors were used. Papers in German and French were translated by the authors when unavailable in translation elsewhere.

PART II: ELEMENTAL CARBON, NITROGEN, AND PHOSPHORUS COMPOSITION OF ZOOPLANKTON AND BENTHOS

Introduction

13. The study of elemental chemical composition has become increasingly important to our understanding of bioenergetics, production, and biochemical cycling of elements in aquatic systems (Omori 1969). For modeling purposes, it is necessary to know the elemental carbon (C), nitrogen (N), and phosphorus (P) composition of the various species that compose zooplankton and benthos. This knowledge is used to trace the cycling of nutrients through the ecosystem by application of the mass balance equation previously described (Equation 1).

14. In most models of aquatic ecosystems, ratios of carbon to nitrogen and of carbon to phosphorus are very useful. Estimates of zooplankton and benthos carbon losses (e.g., egestion, excretion, respiration, and nonpredatory and predatory mortality) can readily be used to estimate losses of nitrogen and phosphorus. Nitrogen and phosphorus compounds released from aquatic animals serve as important nutrients for phytoplankton, periphyton, and macrophytes. In short, the use of C:N and C:P ratios allows the modeler to trace the transfer of chemical substances through various trophic levels (Chen and Orlob 1975). Scavia et al. (1976) stoichiometrically determined the incorporation and excretion of P by using a C:P ratio. Twelve models reviewed by Swartzman and Bentley (1978) had phosphorus and nitrogen flow parallel to carbon in zooplankton and detritus. Baca et al. (1974) used a range of ratios (i.e., C:N = 5.9-20.0; and C:P = 33.3-200.0) to derive the quantities of N and P excreted, or the quantities lost after nonpredatory mortality. Steele (1974) used a C:N ratio of 5.4 to estimate N assimilated and excreted by zooplankton. Carbon, nitrogen, and phosphorus also were released in accordance with their concentration in zooplankton in the models of Umnov (1972) and Menshutkin and Umnov (1970).

15. Ratios of C:N and C:P are not constant but vary significantly among taxonomic groups of animals, as well as within single species,

depending on sex, age, and nutritional state. Nutritional state is influenced by season of the year and geographical distribution. Methods of determining elemental C, N, and P undoubtedly produce some variation among ratios, but we do not believe that this effect is significant enough, considering the variability due to other factors, to warrant detailed discussion. The handling of marine zooplankton samples immediately after collection (e.g., rinsing and preservation) may greatly alter C:N and C:P ratios. Since many of the values we collected were for marine zooplankton (Appendix A), this problem requires further comment.

16. The determination of single C:N and C:P ratios probably is inaccurate for broad categories of animals such as zooplankton and benthos. The relative abundance of the various groups composing the total biomass differs geographically and seasonally. Variations in percent C, N, and P (i.e., percent of dry weight) exist among taxa and are compounded when percentages are estimated for total zooplankton--an ever changing assemblage of taxa (Beers 1966).

17. We have collected percent C, N, and P data from both the freshwater and marine literature. With the exception of one or two groups of animals, percent C, N, and P in marine and freshwater organisms do not differ significantly. This fact probably is a function of the variability of percent C, N, and P in marine and freshwater animals (Appendix A). Percent P of marine copepods was consistently 50 to 75 percent of the values for other crustacea (Beers 1966). Corner (1973) noted that P in marine zooplankton varied from 0.14 percent in forms such as hydromedusae and ctenophores to a range of 0.55 to 1.16 percent in copepods. Beers (1966) also found that percent C was similar in most marine zooplankton, except hydromedusae which typically have low percent C contents. With the notable exception of the freshwater jellyfish (Craspedacusta sowerbyi), which is extremely sporadic in occurrence, fresh waters generally lack animals comparable to marine medusae and ctenophores. Consequently, we did not consider percent C, N, and P data for these forms of marine zooplankton.

18. If samples are collected from saltwater, they should be washed

to remove adhering inorganic salts that may contain C, N, or P. Platt et al. (1969) found that significant weights of inorganic salts were removed by a 2-min rinse in distilled water. Contrary to the observation of Omori (1978), rinses in distilled water for periods of 2 to 60 min did not result in the osmotic rupture of cells and subsequent loss of organic matter from specimens. Omori (1978) estimated 6 and 7 percent reductions in the C and N contents, respectively, of zooplankters rinsed in distilled water. However, these losses were calculated as C and N lost per individual and not in a form comparable for animals of a different size (e.g., percent C and N). The losses of C and N as a percent of dry weight (recalculated from Omori (1978)) were not significant.

19. Preservation of samples in formalin, alcohol, or other leaching chemicals may alter percent C, N, and P or the ratios of C:N and C:P. Omori (1970) found that _Calanus cristatus_ preserved for 1 month in formalin lost 59 and 48 percent of their original carbon and nitrogen, respectively. In addition, the rates of loss of C and N were different and resulted in a decreased C:N ratio. Apparently the rate of loss depends upon the original quantity of matter present. The euphausid _Nematocelis difficilis_ lost 17 percent C and 19 percent N after 15 weeks in a buffered Hexamine solution (Hopkins 1968). Hopkins believed that most of the leached material was protein. Similar findings were presented for _Sagitta nagae_ and _Calanus sinicus_ (Omori 1978).

Nitrogen

20. Variations of percent N primarily result from differences in gross body components (i.e., protein, lipid, and carbohydrate). Percent N varies among taxa and within a single taxon, due to differences in age, sex, or nutritional state. Most body nitrogen is included in the amino acids of protein (Table 1).

21. Percent N usually is greater in young than in old _Dreissena polymorpha_, Mollusca (Stanczykowska and Lawacz 1976); _Temora stylifera_ and _Centropages typicus_, Copepoda (Razouls 1977); _Pareuchaeta novegica_,

Table 1

Percent Composition of C, N, and P in Proteins, Lipids, and Carbohydrates

	Carbon*	Nitrogen*	Phosphorus**
Protein	50-55	13-17	ca 0.10
Lipid	79	ca 0	ca 0.17
Carbohydrate	37.2	ca 0	ca 0

* Carbon and nitrogen data of Schottelius and Schottelius (1973).
** Phosphorus data of Head and Livingston (unpublished) as cited by Corner (1973).

Copepoda (Nemoto et al. 1976); and Daphnia hyalina, Cladocera (Baudoin and Ravera 1972). Greater percent N content in young individuals probably stems from the fact that young organisms typically have more protein relative to dry weight than older individuals. High protein content results from rapid growth associated with protein anabolism and insignificant lipid accumulation in young animals (e.g., Daphnia magna, Ceriodaphnia reticulata, and Moina macrocopa (Cladocera) and Brachionus calyciflorus (Rotajoria) (Bogatova et al. 1971)). Under the same trophic conditions, adult female "oceanic Copepoda" (Itoh 1973) and Calanus cristatus (Omori 1970) often had less percent N than adult males. This may have been due to the greater lipid content in females. The fact that percent C was greater in females seems to support this hypothesis. Postspawning females of Pareuchaeta novegica had less pecent N than prespawned females (Nemoto et al. 1976). This finding suggests that catabolism of body protein, due to the great energy demand for reproduction, resulted in a decreased N content per unit dry weight. Several authors have also observed differences in the percent N of single species as a result of season of the year and geographical distribution (Omori 1970, Itoh 1973, Boucher et al. 1976). Omori (1970) found that seasonal and geographical changes in trophic conditions were principally responsible for percent N changes in Calanus cristatus (Copepoda). During times of (or in areas of) poor food availability, copepods exhibited an initial fat loss that resulted in an increase of percent N. Later, starving copepods began to metabolize protein which decreased percent N.

Carbon

22. Percent carbon also varies among taxa and within a single taxon due to age (Omori 1970, Baudoin and Ravera 1972, Itoh 1973, Razouls 1977, Omori 1978), season (Beers 1966, Platt et al. 1969, Omori 1970, Stanczykowska and Lawacz 1976), geographical distribution (Boucher et al. 1976), and reproductive condition (Nemoto et al. 1976). Percent carbon did not vary with age in *Dreissena polymorpha* (Stanczykowska and Lawacz 1976) or with season in *Daphnia hyalina* (Baudoin and Ravera 1972). Omori (1970) showed that changes in trophic conditions that affect nutritional state actually underlie the dependence of percent C on geographical distribution and season of the year.

23. In ecological models, either carbon transfer or energy flow is used to link trophic levels. Since carbon and energy units are highly correlated (Salonen et al. 1976), the choice apparently is arbitrary. The use of carbon units does have the added advantage of providing an index to the flux of matter through trophic levels. For this reason, we prefer carbon transfer data and have employed the following factors: zooplankton = 10.98 cal/mg C (Salonen et al. 1976) and phytoplankton = 11.4 cal/mg C (Platt and Irwin 1973) to convert from energy to carbon units.

Carbon:Nitrogen Ratios

24. The distribution of carbon and nitrogen among the major body components, i.e., protein, lipid, and carbohydrates (Table 1), and the relative abundance of these major components determine the percentages of C and N present in an organism. Although percent C and N are influenced by the same environmental elements, they do not always fluctuate in the same manner. In general, C:N ratios should vary directly with carbohydrate and lipid content and inversely with protein content.

Omori (1970) found a negative correlation between changes in percent C and percent N in _Calanus cristatus_. Elements affecting the C and N composition in the copepods were trophic conditions and sex. Since lipids contain primarily carbon and essentially no nitrogen (Table 1), the seasonal loss or gain of lipids, as influenced by trophic conditions, would result in a concomitant decrease or increase, respectively, of the C:N ratio. If females of a species contain a greater proportion of fat than males, they also would exhibit higher C:N ratios than males.

25. Using the data on percent C and N (Appendix A), we prepared frequency distributions of C:N ratios for various categories (taxonomic or other) of aquatic invertebrates. A frequency distribution of C:N ratios for benthic macroinvertebrates (Figure 1) appeared to have two potential peaks (i.e., at 3.5 to 4.0 and 5.0 to 5.5), so we attempted to separate the distribution on the basis of feeding type. Unfortunately, insufficient data exist on carnivore C:N ratios. When more experimental data on these ratios are available, this potential refinement could be used in model formulation. The basic form of the frequency distributions of C:N ratios for zooplankton, Cladocera, and Copepoda (Figures 2, 3, and 4, respectively) is essentially the same. Apparently most C:N ratios of zooplankton and benthos are within the range of 3.5 to 5.5.

Phosphorus

26. The total P in zooplankton is normally low, often accounting for less than 1 percent of dry weight (Corner 1973). The distribution of phosphorus among body protein, lipid, and carbohydrate is shown in Table 1. Phosphorus is important in the structure of nucleic acids, which contain approximately 21 percent of the total P. Of total P, 53 percent is inorganic (unpublished data of Head and Kilvington as cited in Corner 1973).

27. Phosphorus uptake and release by zooplankton is very important to the cycling of P in aquatic ecosystems. Conover (1966a) recognized two pools in _Calanus finmarchicus_, 6 percent as labile compounds which have a half-life of a few hours. The remaining 94 percent has a

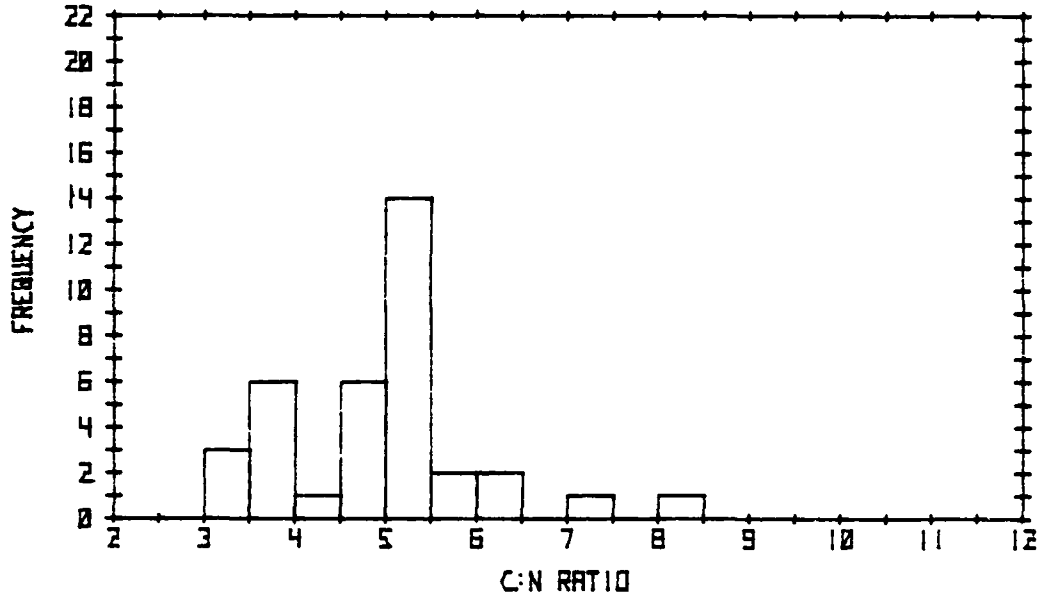

Figure 1. Frequency distribution of macrobenthos C:N ratios

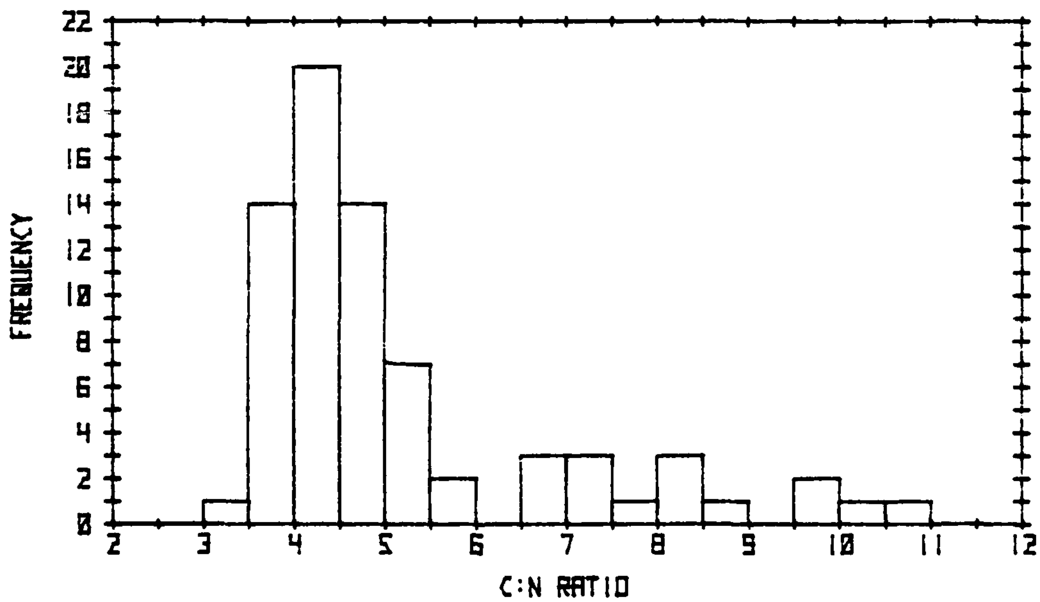

Figure 2. Frequency distribution of zooplanton C:N ratios

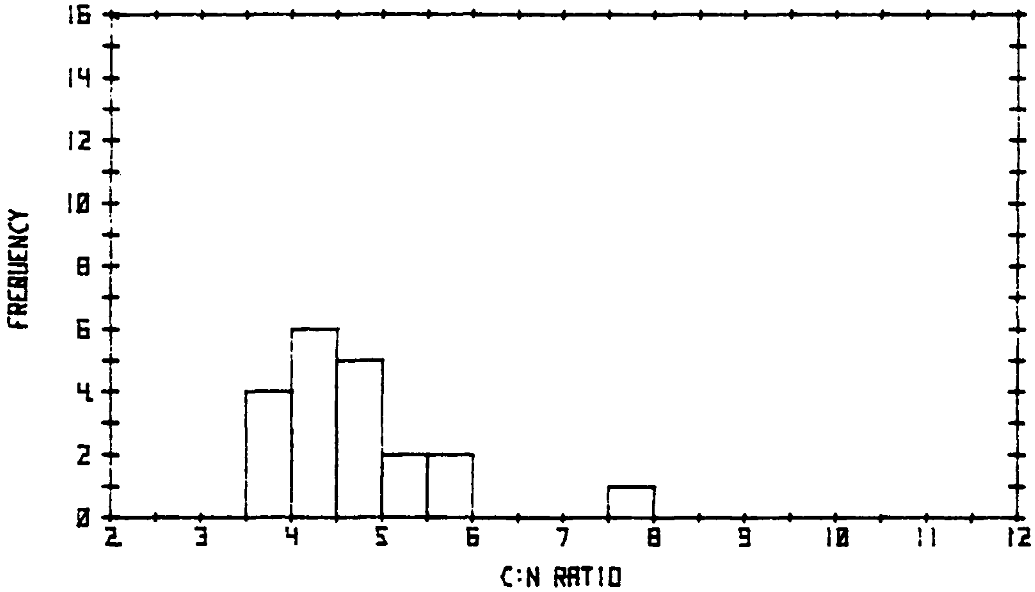

Figure 3. Frequency distribution of cladoceran C:N ratios

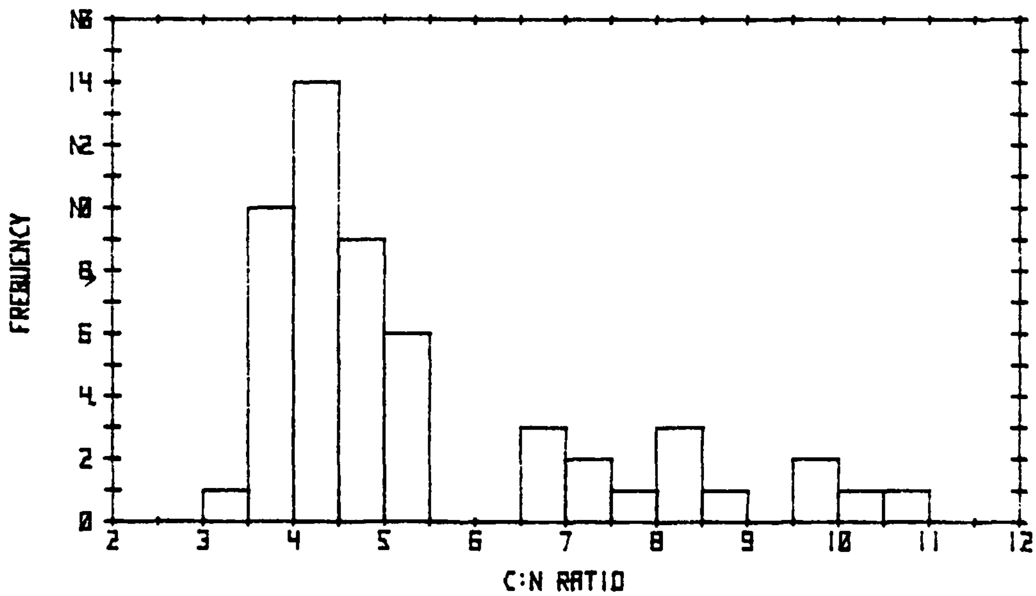

Figure 4. Frequency distribution of copepod C:N ratios

half-life of roughly 13 days. Although several studies have been conducted on P excretion (Pomeroy et al. 1963, Johannes 1964, Satomi and Pomeroy 1965, Butler et al. 1970), we still do not know precisely how, or in what form, P compounds are released (Corner 1973).

28. Age, sex, and season of the year may influence the P content of aquatic invertebrates. Percent P increased during the development of Daphnia hyalina eggs but, thereafter, decreased with age (Baudoin and Ravera 1972). Butler et al. (1970) found differences in the percent P between male and female Calanus finmarchicus and also between adult and stage V copepodids. Calanus finmarchicus contained about 50 percent more P during a spring diatom increase than at other times of the year. This large increase may have been the result of uptake beyond that required by the body. The percent composition of P in marine copepods, euphausids, mysids, polychaetes, and chaetognaths changes significantly during the year (Beers 1966). Changes in the percent composition in any of these groups probably depends on differences in species or age groups taken in collections or an adjustment of the P composition of individual organisms.

29. Figures 5 and 6 are frequency distributions of C:P ratios for benthos and zooplankton, respectively. In Figures 7 and 8, the zooplankton distribution is split into two taxonomic categories, i.e., Cladocera and Copepoda. Copepods tend to have greater percentages of C than other zooplankton (Appendix A), and this fact may account for higher C:P ratios in Copepoda.

Summary of Constructs

30. By using frequency histograms of C:N and C:P, modelers can calculate a range of probable nitrogen and phosphorus transfer rates for compartment processes. The procedure involves the following: (a) convert histograms (Figures 1-8) to probability distributions, (b) select a series of C:N or C:P ratios from the appropriate probability distributions, and (c) divide weight-specific rates (mg C·mg $C^{-1}\cdot day^{-1}$) of consumption (Part III), assimilation (Part IV), egestion + excretion

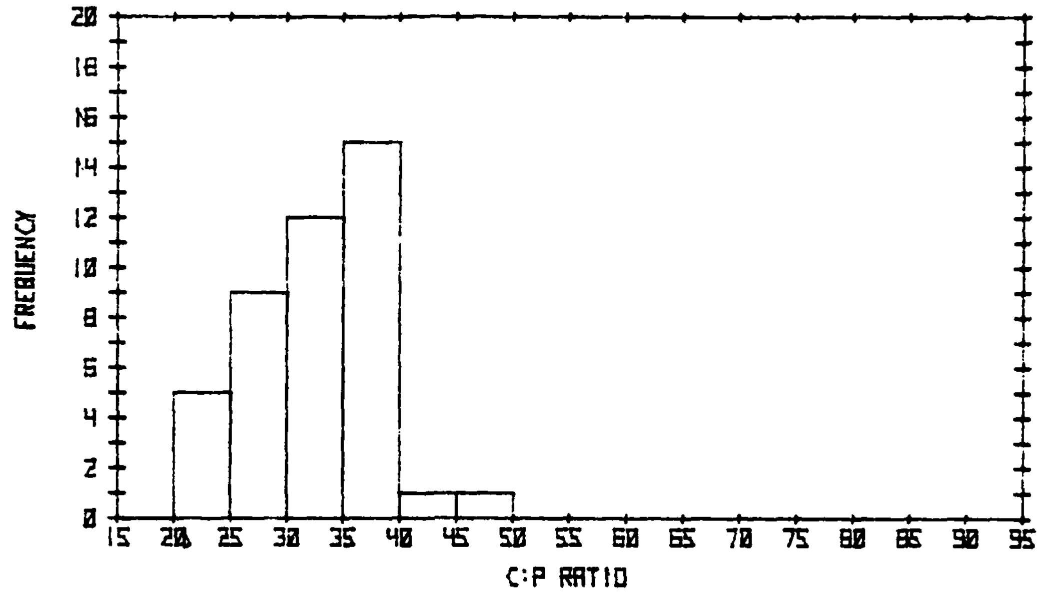

Figure 5. Frequency distribution of macrobenthos C:P ratios

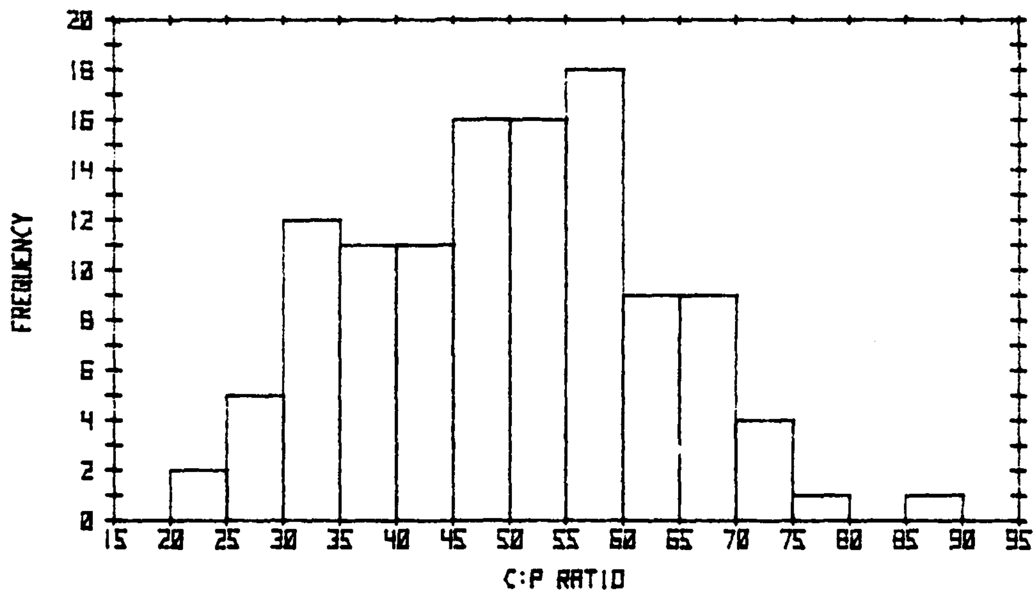

Figure 6. Frequency distribution of zooplankton C:P ratios

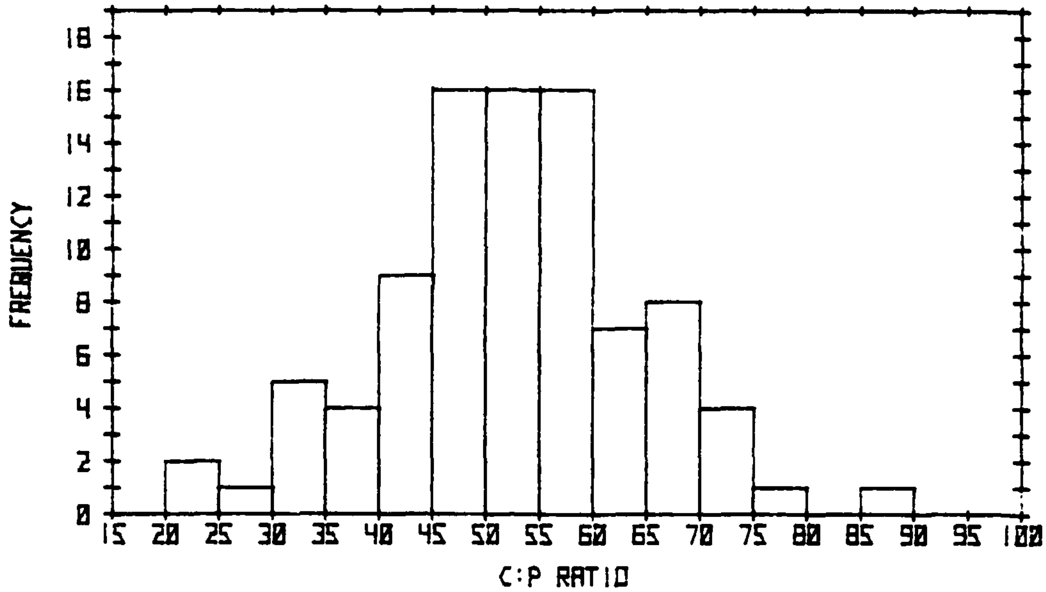

Figure 7. Frequency distribution of copepod C:P ratios

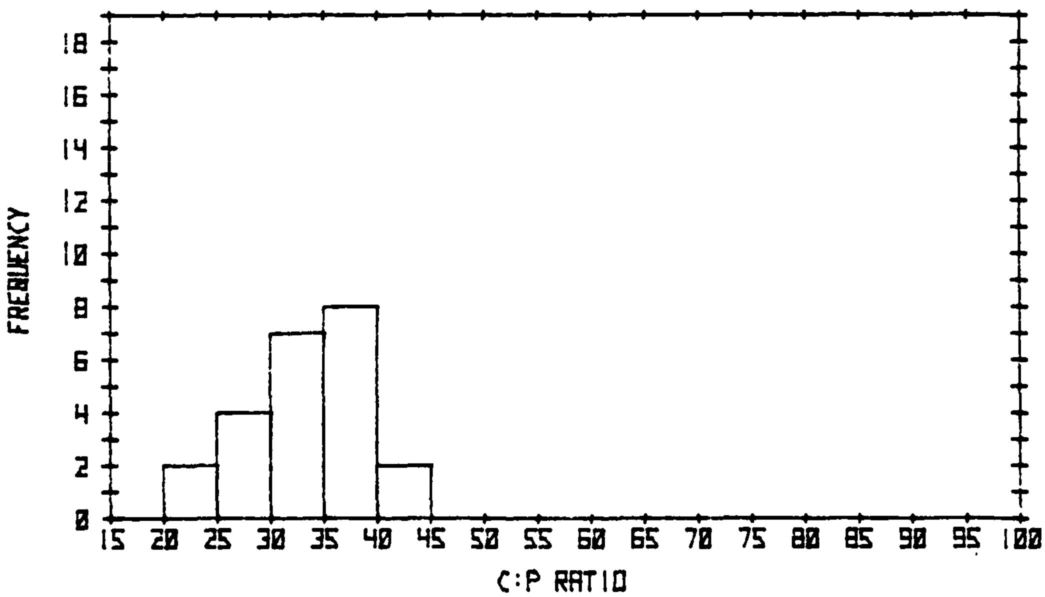

Figure 8. Frequency distribution of cladoceran C:P ratios

(Part IV), respiration (Part V), and nonpredatory mortality (Part VI) by the selected C:N and C:P ratios. The results are the weight-specific rates of N and P transfer (mg N or mg P·mg C^{-1}·day^{-1}) in the above processes. Gains and losses of N and P from a compartment may be determined by multiplying the weight-specific rates of N and P transfer, for each of the transfer processes mentioned above, by the biomass (mg C) of the model compartment.

31. Frequency histograms of macrobenthos C:N and C:P ratios (Figures 1 and 5, respectively) should be used to estimate N and P movements through the benthos compartment. When no better data on the present composition of Cladocera and Copepoda biomass in zooplankton are available, we recommend that users assign 60 percent to caldocerans and 40 percent to copepods and use Figures 8 and 7, respectively, to determine their appropriate C:N or C:P ratios. The net flux of P through Cladocera, for example, may be estimated as $0.60\ b\ \left[G(A/G) - R - NPM - PM\right] \div (C{:}P)$, where b = total zooplankton biomass, (C:P) = carbon-phosphorus ratio of cladocera (Figure 8), and the items in brackets are as described in Equation 1. A similar calculation may be performed for copepods and summed to the results for cladocera to yield the flux of P through the zooplankton compartment.

Conclusions

32. Ratios of C:N and C:P are used to trace the movement of nutrients through major energy pathways of zooplankton and benthos. Elemental carbon, nitrogen, and phosphorus are not constant but vary with gross body composition (relative proportions of lipid, carbohydrate, and protein). Gross body composition varies among species and within a single species due to differences in nutrition (which varies seasonally) and in sex or age. Although C:N ratios of zooplankton and benthos are usually within the range from 3.5 to 5.5, most C:P ratios vary greatly in both groups (20 to 40 in benthos and 30 to 70 in zooplankton).

PART III: CONSUMPTION BY ZOOPLANKTON AND BENTHOS

33. In studies of the flow of any substance through an ecosystem, be it energy, biomass, or nutrients, it is critical to know the transfer pathways from one ecosystem component to another. This transfer occurs in animal communities through a series of predator-prey interactions which we call consumption. For example, a simple food chain in which phytoplankton is consumed by zooplankton which in turn is eaten by fish is one pathway. Modeling such a simple flow of material would be relatively easy, but, unfortunately, it would probably have little relation to the real world. The aquatic communities of temperate lakes and reservoirs are highly complex, and trophic relations can best be described as interacting food webs. Modeling of all these feeding relationships is beyond the present state of the art. As a result, most modelers attempt to portray only the major energy flow pathways of which we have some knowledge. Other feeding relations are recognized but presently cannot be adequately quantified. In this section of the report we review what is currently known about the feeding relations of zooplankton and benthos and attempt to place this information in a modeling perspective.

34. In conducting this review, we stressed the quantitative aspects of feeding. Food habits, although often interesting, have generally been ignored because they tell nothing of the rate and control of consumption. We have also stressed those areas most amenable to modeling and have related our analyses to previous modeling efforts. In addition, we have reviewed several subjects of current topical interest to modelers, including the role of organic detritus as a food supply, zooplankton grazing on blue-green algae, and the comparability of field and laboratory data.

35. More information is available on the dynamics of zooplankton feeding than is available for benthos. The rather functionally homogeneous nature of zooplankton, the relative ease in culturing and experimenting with zooplankton as compared to benthos, and its importance in phytoplankton dynamics have led to a better documented literature.

Benthic communities of reservoirs are not as homogeneous a unit as zooplankton, taxonomically or functionally, and they are often difficult to culture in the lab or study in the field.

Section A: Zooplankton Grazing

36. The zooplankton community of freshwater lakes and reservoirs consists of widely divergent taxonomic groups of organisms. Crustaceans of the subclass Copepoda and order Cladocera make up the bulk of the community biomass in most lakes. Rotifers are also an important part of the zooplankton community in many lakes.

37. The mathematical formulation of zooplankton feeding is a critical element in the equation describing zooplankton population dynamics. Most of the products of primary production pass through zooplankton in the aquatic ecosystem model as a direct result of grazing; zooplankton feeding, therefore, serves as a resource pathway to other model compartments, i.e., benthos and fish.

38. The primary zooplankton groups, Cladocera, Copepoda, and Rotatoria, generally can be classified as either herbivorous filter feeders or as carnivores, based on their feeding mechanisms and food habits. In reality, many zooplankters are omnivores and do not fit into neatly defined trophic groups. Nevertheless, some groupings and distinctions must be made in deference to our limited knowledge of individual taxa and the logistics of describing all possible interactions. Filter-feeding zooplankton make up a greater proportion of the zooplankton community, both numerically and as biomass, than do the carnivores. They are also more important to our understanding of the dynamics of phytoplankton populations, and phytoplankton dynamics are especially important to water quality modeling. Consequently, the feeding relations of filter feeders have been more heavily emphasized in this report.

39. The quantitative feeding relations of zooplankters have been studied in some detail for only a few major taxonomic groups. Feeding relations of copepods and cladocerans were documented for the more

common forms, but little quantitative information was available on feeding by rotifers and protozoans. Of the 127 species of Cladocera listed by Brooks (1959) as occurring in North America, filtering or grazing rates have been examined to some degree for only 18 species, or 14 percent of the total. Within the Cladocera, the genus Daphnia has been most intensively studied. Brooks (1957) listed 30 species in this genus occurring worldwide. Our review indicates that feeding of only 12 Daphnia species, or 40 percent of the total, has been studied. Of the 15 North American species of Daphnia, 9 (60 percent of the total) have been studied. Because Daphnia represents the most intensively studied genus within the Cladocera, and because data are available for many United States species, our analysis is biased toward this genus.

40. Calanoid copepods constitute a major group of filter-feeding zooplankton. Wilson (1959) listed 92 species for North America and our review revealed that the feeding for only 7 species (8 percent of the total) has been studied. Six of the seven species are in the genus Diaptomus (= Eudiaptomus), which includes 78 North American species.

41. Rotifers constitute the third major group of filter-feeding zooplankters. The literature on the number of North American species is contradictory, but easily exceeds 200. Feeding rate values are available for only six species.

42. This brief statistical summary illustrates that the feeding relations of most filter-feeding zooplankters are unknown and indicates that caution must be used in extrapolating grazing results to all species.

Consumption by Filter-Feeding Zooplankton

43. Factors that influence food consumption by filter-feeding zooplankton include animal density, size, sex, reproductive state, nutritional or physiological state, as well as the type, quality, concentration, and particle size of food. Other factors include water quality and temperature. Some of these variables are more important

than others in controlling feeding. The effects of many are poorly understood and synergistic effects among variables do occur.

44. The purpose of this section of the report is to examine in detail those variables of primary importance in regulating zooplankton feeding and which are considered suitable for mathematical description. Table 2 summarizes factors influencing feeding and lists information sources. Concerning the difficulties of comparing feeding data, Geller (1975) stated:

> It is difficult or impossible to compare the results obtained by these authors, because they used different methods of investigation. The size of the animals is not specified precisely or is omitted; the habitation and acclimation periods cited in many publications are obviously insufficient, and the food particles used range from clay particles, yeasts, algae, and bacteria to synthetic particles and 'artificial detritus.' The measuring units employed for determining food biomass also differ, and may be either the number of cells, wet weight, dry weight, carbon content, or energy content, and conversion from one unit to another is possible only in exceptional cases.

45. We found Geller's comments to be wholly justified. Appendix B presents a comparison of zooplankton filtering rates found in the literature.

46. The objectives of this section are as follows: (a) to describe the effect of food concentration, type of food, and temperature on feeding rates, including a review of field versus laboratory results, as well as synergistic effects; (b) to examine the role of diel and annual variations in feeding rates; and (c) to discuss possible model formulations for grazing by filter-feeding zooplankton. Further information on the biology of filter feeding was presented by Jorgensen (1966), and a critique of experimental methods employed to measure filtering and feeding rates was given by Rigler (1971).

Effect of food concentration

47. Literature synopsis. The question of how zooplankton grazing rates are influenced by changes in food concentration is central to the development of a model describing zooplankton biomass dynamics. The first workers to examine the effects of food concentration on feeding

Table 2

Factors Reported to Influence the Feeding of Filter-Feeding Zooplankton and a List of References

Factor	References
Food concentration	Ryther (1954), Richman (1958), Monakov and Sorokin (1960), Rigler (1961a), Galkovskaya (1963), McMahon and Rigler (1963), Richman (1964), McMahon (1965), McMahon and Rigler (1965), Richman (1966), Burns and Rigler (1967), Kryutchkova and Sladecek (1969), Ivanova (1970), Tezuka (1971), Ivanova and Klekowski (1972), Crowley (1973), O'Brien and DeNoyelles (1974), Chisholm et al. (1975), Green (1975), Geller (1975), Kersting and Leeuw-Leegwater (1976), Hayward and Gallup (1976), Pilarska (1977a), Pourriot (1977).
Size of food	Ryther (1954), McMahon and Rigler (1965), Gliwicz (1969), McQueen (1970), Berman and Richman (1974), Kryutchkova (1974), Bogdan & McNaught (1975), Geller (1975), Hayward and Gallup (1976), Pilarska (1977a), Pourriot (1977).
Age of food	Ryther (1954), McMahon and Rigler (1965), Stross et al. (1965).
Type of food	Ryther (1954), Comita (1964), Burns (1968b), Schindler (1968), Burns (1969a), Gliwicz (1970), McQueen (1970), Kersting and Holterman (1973), Haney (1973), O'Brien and DeNoyelles (1974), Geller (1975), Hayward and Gallup (1976), Pilarska (1977a), Pourriot (1977), Webster and Peters (1978).
Temperature	McMahon (1965), Burns and Rigler (1967), McMahon (1968), Schindler (1968), Burns (1969b), Kibby (1971a), Chisholm et al. (1975), Green (1975), Geller (1975), Gophen (1976), Hayward and Gallup (1976).
Light intensity	McMahon (1965), Schindler (1968), Buikema (1973), Hayward and Gallup (1976).

(Continued)

Table 2 (Concluded)

Factor	References
Water quality	McMahon (1968), Schindler (1968), Tezuka (1971), Ivanova and Klekowski (1972), Kring and O'Brien (1976).
Size of animal	Ryther (1954), Richman (1958), McMahon (1965), Burns and Rigler (1967), Schindler (1968), Kryutchkova and Sladecek (1969), Burns (1969b), Ivanova and Klekowski (1972), Buikema (1973), Kibby and Rigler (1973), Bogdan and McNaught (1975), Chisholm et al. (1975), Haney and Hall (1975), Green (1975), Geller (1975), Hayward and Gallup (1976), Pilarska (1977a), Webster and Peters (1978).
Sex of animal	Haney and Hall (1975), Green (1975), Hayward and Gallup (1976).
Nutritional state of animal	Ryther (1954), McMahon and Rigler (1965), Geller (1975).
Reproductive state of animal	Schindler (1968), Hayward and Gallup (1976).
Circadian rhythms and behavior	Nauwerck (1959), Burns and Rigler (1967), McMahon (1968), Burns (1968a), Haney (1973), Starkweather (1975), Chisholm et al. (1975), Haney and Hall (1975), Hayward and Gallup (1976), Duval and Green (1976), Gulati (1978), Andronikova (1978).
Animal density	Schindler (1968), Buikema (1973), Hayward and Gallup (1976).
Acclimation period	McMahon (1965), Schindler (1968), Buikema (1973), Geller (1975), Hayward and Gallup (1976).

investigated the marine copepod Calanus finmarchicus (Fuller and Clarke 1936, Fuller 1937, Harvey 1937). They and their contemporaries concluded that the filtering rates (volume of water filtered per unit of time) of marine filter-feeding zooplankton were independent of food concentration. The corollary to this hypothesis was that grazing rates (weight of food eaten per unit body weight per unit of time) were directly proportional to food concentration (Figure 9). These results suggested that a species-specific filtering rate could be established.

48. It was not until Ryther's 1954 paper on the filtering response of Daphnia magna that attention was directed to freshwater zooplankters. The most significant result of Ryther's work was that he demonstrated that filtering rate per animal decreased as food concentration increased. This relation was found to hold for all three algal species tested and was the first evidence to suggest that zooplankton did not filter at a constant rate at all food concentrations. Ryther's results suggested that filtering rate may be reasonably constant and high at very low food densities (less than ca 700 mg C/m^3 for Chlorella), decline sharply at

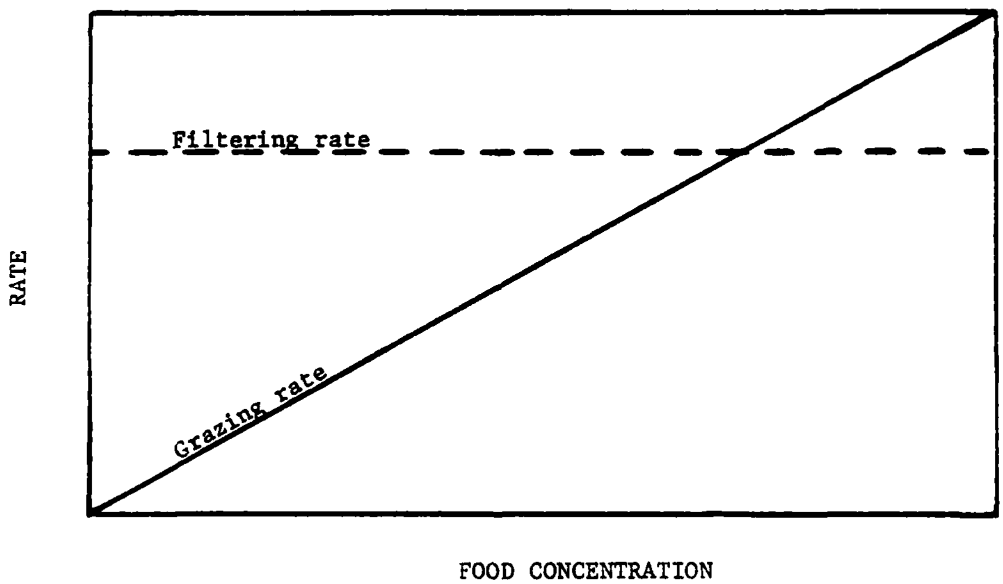

Figure 9. Relation among food concentration, filtering rate, and grazing rate, based upon early studies of filter-feeding marine zooplankton

intermediate densities, and possibly reach a minimum filtering level at high food densities (greater than ca 2000 mg C/m^3).

49. With all three species of algae introduced as food by Ryther, grazing rate increased with increased food density (the one exception was *Daphnia* fed senescent *Chlorella*). In examining Ryther's data where *Daphnia* were fed growing algal cultures (Figure 10), it is clear that grazing increased with food density in a linear or near linear fashion.

50. The results of Ryther's work stimulated other workers to examine zooplankton feeding relationships over a wide range of food concentrations. Rigler (1961a) demonstrated that the grazing rate of the zooplankter *Daphnia magna* may approach a maximum as food concentration is increased. The grazing response changed markedly at a food concentration of approximately 600 mg C/m^3. The grazing rate was nearly constant above this concentration, but too few data points prevent firm conclusions. Similar results were obtained by McMahon and Rigler (1965) (Figure 11).

51. Rigler (1961a) offered this hypothesis:

> ...when a filter-feeding Crustacean encounters low concentrations of food, the feeding rate is limited by the ability of the animal to filter water and hence feeding rate is proportional to concentrations of food. But above a critical concentration of food, which will vary with the species of Crustacean and food organisms, feeding rate is constant and limited by the ability of the animals to ingest or digest the food....

52. Subsequent studies by Rigler and his associates (McMahon and Rigler 1963, 1965; McMahon 1965, 1968; Burns and Rigler 1967; Burns 1968a, 1969a, b) have validated the above hypothesis and clearly support the earlier conclusion that "above a critical concentration of food, the feeding rate is independent of concentration of food" (Rigler 1961a). The concentration of food at which feeding becomes constant, called the "critical concentration" by Rigler, is now usually termed the "incipient limiting level" after Fry (1947). This relationship is illustrated in Figure 12.

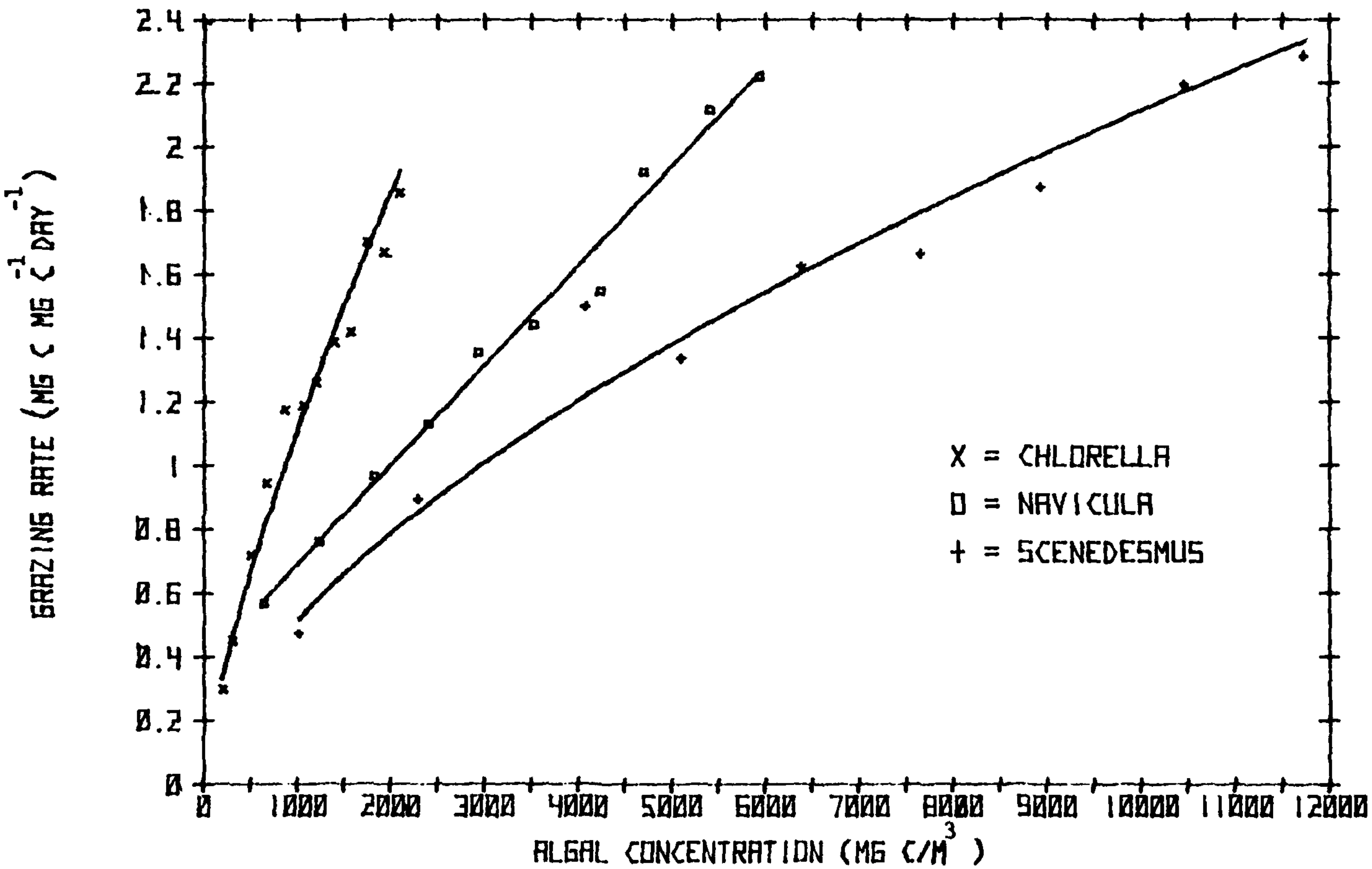

Figure 10. Grazing rate of Daphnia magna at various concentrations of three algal species bease on the data of Ryther (1954)

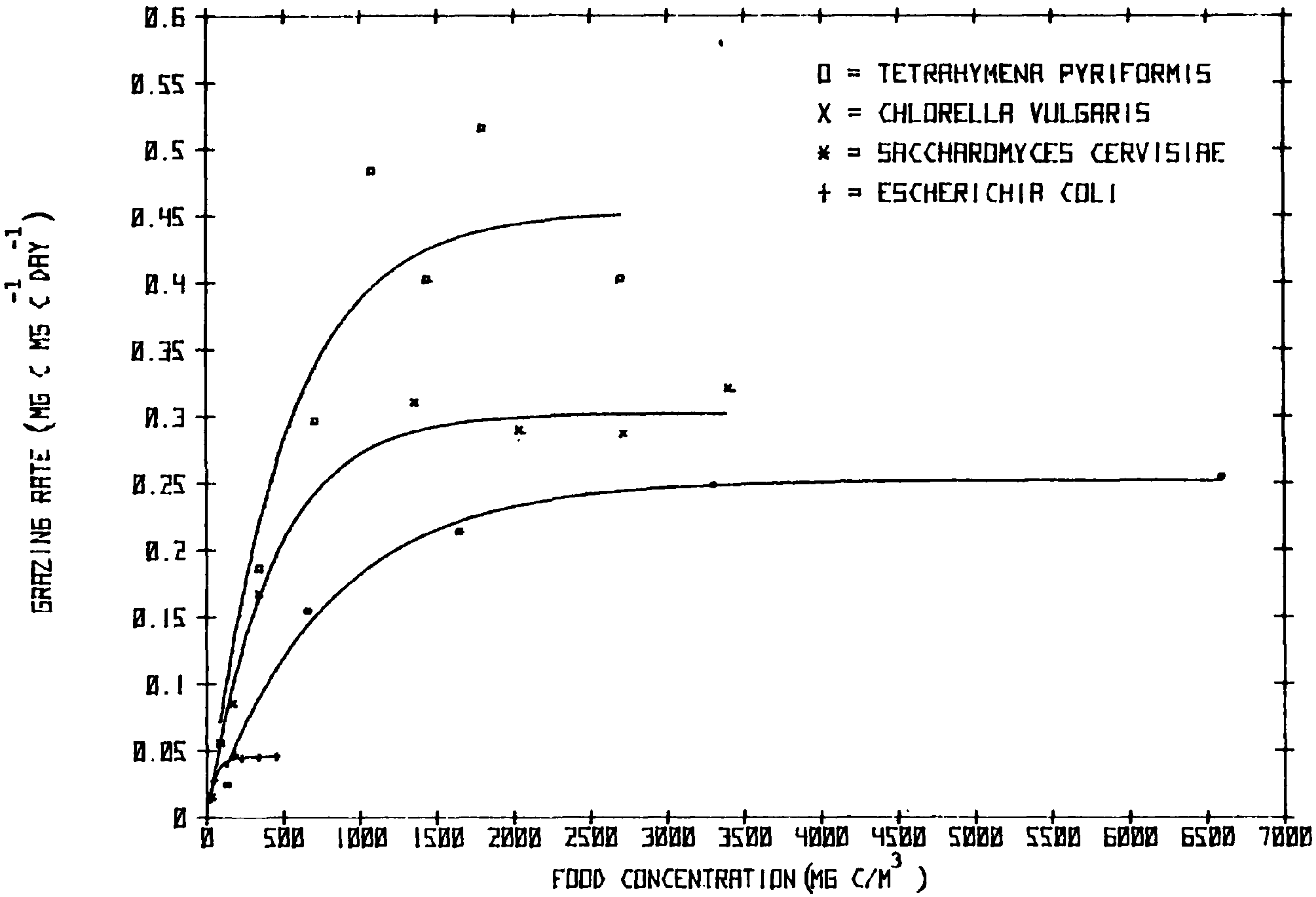

Figure 11. Grazing rates of Daphnia magna at various concentrations of four food sources based on the data of McMahon and Rigler (1965). An Ivlev function was fitted to the values (see Saturation Response Models)

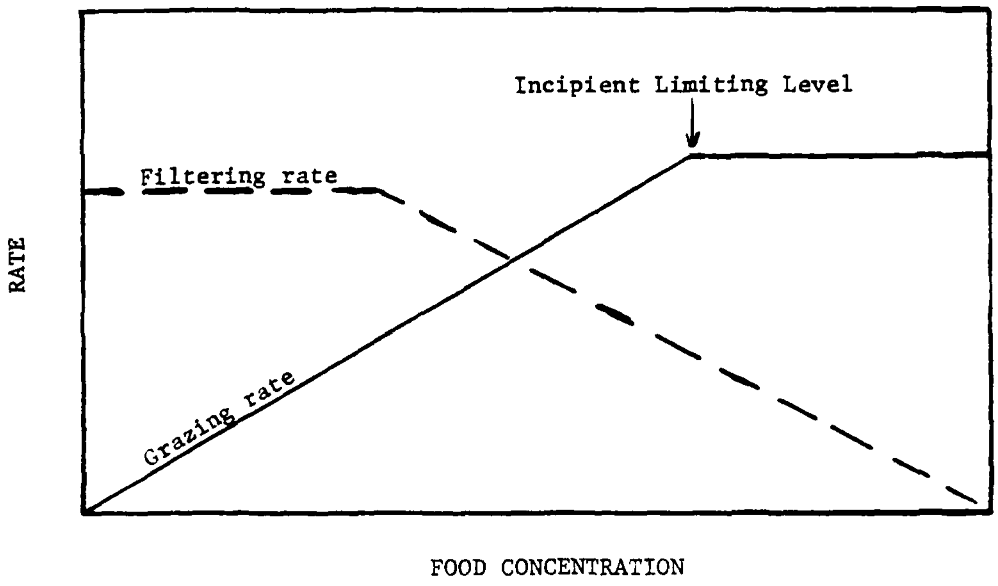

Figure 12. Relation among food concentration, filtering rate, and grazing rate first proposed by Rigler (1961a)

53. Work by Mayzaud and Poulet (1978) on marine zooplankters suggested that the earlier conclusions (that filtering rate was independent of high food concentrations) were not incompatible with results showing a declining filtering rate with increasing food concentration. In a 1-year field study they found a linear relationship between feeding rates and food supply for five copepod species. However, they also found that if the marine zooplankter Pseudocalanus minutus was fed a range of food concentrations over an 18- to 20-hr period, a saturation-type curve, showing a maximum feeding rate, was obtained. Their experimental work indicated that the levels of digestive enzymes of the copepod population also varied linearly with food concentration on a seasonal basis. These results suggest that both ingestion and digestion by copepods were seasonally acclimated to the concentration of food particles. The authors noted:

> From our results and those published earlier it becomes evident that saturation curves have been obtained in experiments where time and season are eliminated as influential parameters. The feeding saturation level found by so many workers is very likely partially a function of the time needed by the copepods to acclimate their ingestion and digestion to the qualitative and quantitative variations of their food.

54. Thus, it may be that zooplankton grazing rates are proportional to food concentration, if the animals have had time to acclimate, and that a maximum grazing rate of the saturation type only is approached in the field under very high food concentrations, as might occur during a phytoplankton bloom.

55. Model constructs. Scavia (1979) reviewed various mathematical constructs for describing consumption by filter-feeding zooplankton. Our purpose is to synthesize existing information and to present a mathematical expression describing the relation between feeding rate and food concentration. The terms feeding rate and grazing rate are used interchangeably.

56. Based on the work of Mayzaud and Poulet (1978) in the preceding section, we noted that the two divergent viewpoints on the relation between food concentration and feeding rate may not necessarily be incompatible. The first viewpoint held that a linear relationship exists between feeding rate and food concentration (Figure 9). Evidence by Mayzaud and Poulet (1978) indicated that if the time is sufficiently long (probably more than 24 hr but less than 6 days), zooplankters can adjust their ingestion rates, through changes in digestive enzyme activity, to acclimate to varying food concentrations. Over the range of naturally occurring food densities, the relation is essentially linear. The second viewpoint held that as food concentration increases, feeding rate also increases but reaches a maximum rate at the incipient limiting food concentration. At higher food densities, feeding is constant and maximal (Figure 12). Many workers have demonstrated the second viewpoint to be generally true in short-term feeding experiments. Mayzaud and Poulet (1978) also found the same result for *Pseudocalanus minutus* when it was exposed to varying food concentrations after short-term incubation periods of 18 to 20 hr.

57. Research results suggest two conclusions. First, for short-term incubation periods, zooplankters respond to increasing food concentrations in a curvilinear manner, often described as a "saturation curve," where feeding rate attains a constant maximum value. Second, if zooplankton are allowed to incubate at the test concentrations for longer periods (>24 hr but <6 days), then digestive enzyme acclimation may occur and the feeding rate response is linear. These conclusions emphasize the importance of specifying duration when comparing laboratory and field studies. Of the papers that examined the effects of food concentration on feeding rate, we found none that involved food incubation periods exceeding 24 hr. Thus, the results of laboratory experiments conducted to date must be interpreted as short-term feeding responses of incompletely acclimated zooplankters.

58. The above hypothesis concerning the functional response of field populations of zooplankton to varying food concentrations was first outlined by Mayzaud and Poulet (1978). Because little experimental work has been conducted to support or refute this proposal, it must be tentatively accepted. It is our opinion that this hypothesis will be verified, and we have accepted the conclusions and proposals of the above authors in presenting a model construct for zooplankton consumption.

59. Saturation response models. The currently accepted saturation response models are easily verified by existing laboratory data, and because of the limited verification of the Mayzaud-Poulet model to follow, the reader may wish to use one of these constructs instead. Because the Mayzaud-Poulet model is an elaboration of saturation response models, a basic understanding of these functions is needed.

60. Scavia (1979) described three expressions normally used to describe the saturation type of response of zooplankton feeding on varying food concentrations. The first is a rectilinear form presented by Rigler (1961a), which consists of two straight lines with different slopes above and below the incipient limiting food concentration (Figure 12). The remaining two forms are curvilinear and have been represented by Michaelis and Menten (1913) and Ivlev (1966) formulations:

Michaelis-Menten

$$G = G_{max}\left(\frac{B}{k + B}\right) \tag{2}$$

where, G = observed grazing rate

G_{max} = maximum grazing rate

B = food concentration

k = half-saturation constant

Ivlev

$$G = G_{max}\left(1 - e^{-kB}\right) \tag{3}$$

where the parameters G, G_{max}, and B are the same as described for the Michaelis-Menten equation and k is a proportionality constant. According to Mullin et al. (1975), using the results of Frost (1972), none of these three model formulations differ significantly in representing the filtering rate response of *Calanus pacificus*. At food concentrations below the half-saturation constant, the Ivlev equation produces relative feeding rates that are slightly less than those determined by the Michaelis-Menten relationship. The opposite is true of feeding rates at food concentrations above the half-saturation constant (Swartzman and Bentley 1977) (Figure 13).

61. We have selected the Ivlev formulation for use in our model constructs for two reasons. First, the determination of the proportionality constant, k, is straightforward. Second, the Ivlev formulation is used in the model of Mayzaud and Poulet (1978) thus eliminating conversions to the Michaelis-Menten expression.

62. Both the Michaelis-Menten and Ivlev equations have been modified in some models to include a lower threshold food concentration below which zooplankton do not feed. The Ivlev equation then becomes,

$$G = G_{max}\ (1-e^{-k(B-B_o)}) \tag{4}$$

where B_o is a threshold food concentration at which grazing commences. Experimental evidence for such a threshold came from work on marine species (Parsons et al. 1967, McAllister 1970). However, Frost (1975), also studying a marine zooplankter, found no clear threshold at low food concentrations but rather greatly reduced feeding. We have found no evidence to support the concept of a threshold food concentration for feeding in freshwater zooplankton. McMahon and Rigler (1963) reported that, in the absence of food, both the collecting and ingesting mechanisms function in Daphnia magna, and Crowley (1973) noted that, in Daphnia pulex, the movement of the thoracic appendages serves respiration as well as feeding. He concluded that it was essential for

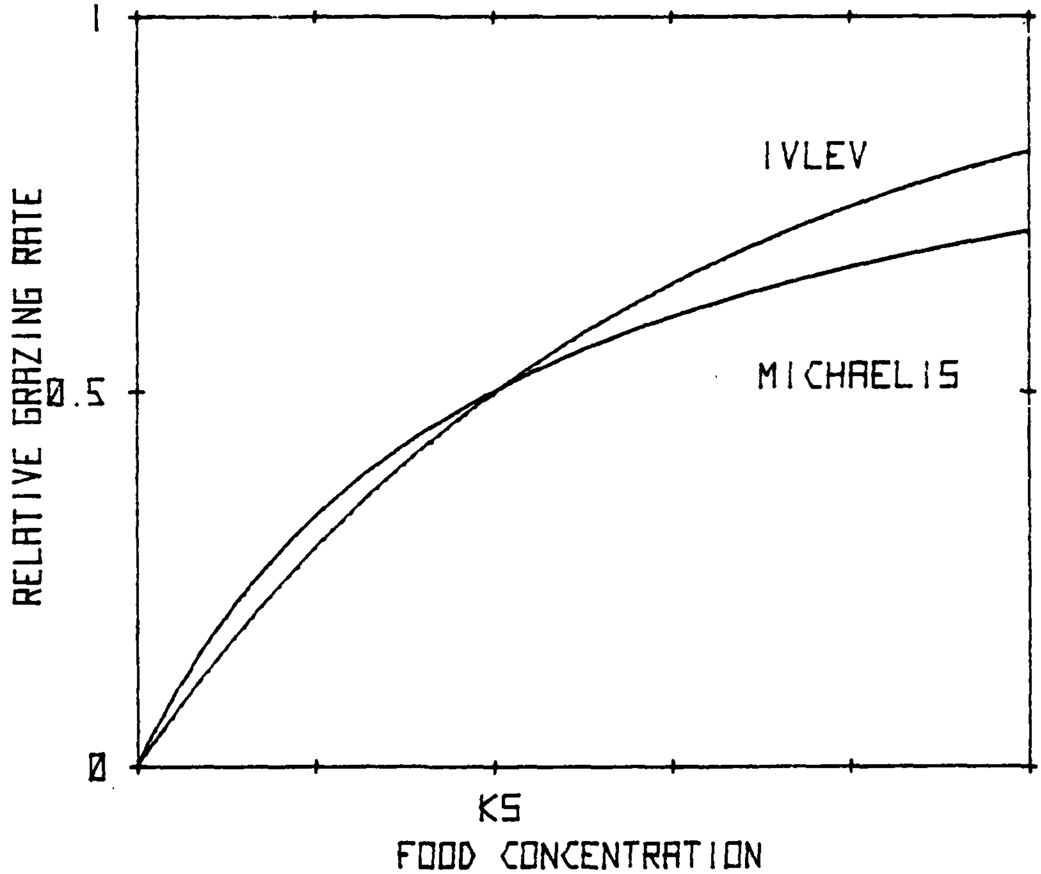

Figure 13. Comparison of the Ivlev and Michaelis-Menten functions with the same half-saturation value, k_s (based on Swartzman and Bentley 1977)

filtering to continue, even when food was absent. It has been suggested that threshold levels are needed to prevent the zooplankton from grazing algal foods to extinction. This simulation phenomenon appears to be the primary reason for including threshold levels in most models. It is likely that extinction is an artifact of the simulation process and results from inappropriate assumptions or our ignorance of zooplankton grazing dynamics. Wroblewski and O'Brien (1976) showed that the addition of zooplankton vertical migration to their model made threshold levels unnecessary. Grazing pressure was not sufficient to drive food supplies to extinction. In light of these results and because threshold food concentrations have not been demonstrated for freshwater zooplankters, threshold levels are not included in our model construct.

63. Parameters of the Ivlev equation. Filtering and feeding rates are seldom presented in biomass units, particularly as carbon. The results of a few papers were deemed to be suitable for conversion to carbon units. Our analysis method was to convert the raw data to carbon units and then to find the best fit to the data using the Ivlev function (Table 3). Variability of values for the grazing rate parameters can be attributed to variations in animal size, species, and physiological state, as well as to differences in food source, temperature, and assumptions made in our conversion of the literature data. The results presented in Table 3 are only for studies that made it reasonably clear that a maximum grazing rate existed.

64. Values for the maximum grazing rates ranged from 0.045 to 3.44 $mg\ C \cdot mg\ C^{-1} \cdot day^{-1}$. Several investigators found a linear or nearly linear increase in the grazing rate with increasing food concentration but did not state the maximum grazing rate. Because these studies only allowed for short-term acclimation, we assumed that the ranges of food concentrations tested were below the incipient limiting level. The variability among values (Table 4) was high.

65. Many studies reported grazing as a percentage of the organism's body weight consumed daily (Table 5). These results are not directly comparable to carbon grazing rates but probably are reasonably close approximations.

Table 3

Grazing Rate Parameters of the Ivlev Equation Calculated From Experimental Studies That Demonstrated the Existence of a Maximum Grazing Rate

Taxon	Food	Approximate Range of Food Concentrations, B (mg C/m^3)	Food Concentration When Observed Grazing Rate Reaches 95% of the Maximum Grazing Rate, 0.95 B_{lim} (mg C/m^3)	Maximum Grazing Rate, G_{max} (mg C mg C^{-1} Day^{-1})	Value of Empirical Constant, k	Reference
Class: Crustacea						
Order: Cladocera						
Family: Daphnidae						
Daphnia magna	*Saccharomyces cervisiae*	132-6,600	2,346	0.251	0.001277	McMahon and Rigler (1965)
Daphnia magna	*Tetrahymena pyriformis*	90-2,700	1,559	0.452	0.001922	McMahon and Rigler (1965)
Daphnia magna	*Chlorella vulgaris*	34-3,400	1,302	0.301	0.002300	McMahon and Rigler (1965)
Daphnia magna	*Escherichia coli*	22-450	155	0.045	0.01936	McMahon and Rigler (1965)
Daphnia magna	*Chlorella vulgaris*	64-2,157	2,140	0.760	0.0014	Kersting and Leeuw-Leegwater (1976)
Daphnia magna	*Saccharomyces cerivisiae*	33-6,336	1,275	0.350	0.00235	Rigler (1961a)
Daphnia pulex	*Chlorococcum* sp.	150-7,150	1,362	1.200	0.0022	Monokov and Sorokin (1961) as reported by Ivanova (1970)
Daphnia rosea	*Rhodotorula glutinis*	250-5,000	1,664	0.900	0.0018	Burns and Rigler (1967) as reported by Ivanova (1970)
PHYLUM: ROTATORIA						
Family: Brachionidea						
Brachionus rubens	*Chlorella vulgaris*	160-134,000	10,699	3.438	0.00028	Pilarska (1977a)

Table 4

Range of Grazing Rates Calculated From Experimental Studies in Which A Maximum Grazing Rate Could Not be Demonstrated

Taxon	Food	Approximate Range of Food Concentrations, B (mg C/m^3)	Range of Calculated Grazing Rates, G (mg C mg C^{-1} day^{-1})	Reference
Class: Crustacea				
Order: Cladocera				
Family: Daphnidae				
Daphnia longispina	*Chlorococcum* sp.	347-5,805	0.935-2.697	Monakov and Sorokin (1960) and Monakov (1972)
Daphnia longispina	Bacteria	961-31,636	0.837-1.736	Monakov and Sorokin (1960 and Monakov (1972)
Daphnia magna	*Chlorella vulgaris**	174-2,100	0.106-1.857	Ryther (1954)
Daphnia magna	*Navicula pelliculosa**	588-5,935	0.460-2.219	Ryther (1954)
Daphnia magna	*Scenedesmus quadricauda**	1,020-11,730	0.474-2.286	Ryther (1954)
*Daphnia pulex***	*Chlamydomonas reinhardti*	4,975-19,900	1.332-13.764	Richman (1958)

* Results combined for scenescent and growing cell cultures. Also includes prefeeding study for *Chlorella vulgaris*.
** The results are combined for the three sizes of *Daphnia* tested.

Table 5

Literature Values for the Daily Ration of Filter-Feeding Zooplankters

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Cladocera			
Family: Holopedium			
Holopedium gibberum	Phytoplankton	12.1	Gutel'mackher (1973)
	Bacteria	7.5	
Family: Chydoridae			
Acroperus harpae	Detritus	253	Smirnov (1969)
Family: Bosmidae			
Bosmina coregoni	*Chlorella* sp.	32.9-177.8	Semenova (1974)
	Bacteria	13.5-125.0	
Bosmina longirostris	*Chlorella* sp.	96	Sorokin (1966b)
Bosmina longirostris	Phytoplankton	42.2	Gutel'mackher (1973)
	Bacteria	16.4	
Family: Daphnidae			
Daphnia longispina	*Chlorella* sp.	93	Sorokin (1966b)
Daphnia magna		56	Duncan et al. (1974)
Simocephalus espinosus	*Chlorella* sp.	59	Sorokin (1966b)
Simocephalus vetulus	*Chlorella* sp.	108	Sorokin (1966b)

(Continued)

Table 5 (Concluded)

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Eucopepoda			
Family: Diaptomidae			
Diaptomus graciloides	Phytoplankton	40.0	Gutel'mackher (1973)
	Bacteria	17.3	
Diaptomus graciloides	*Chlamydomonas eugamentos*	23-700	Kryutchkova and Rybak (1974)
	Chlorella vulgaris	20-366	
PHYLUM: ROTATORIA			
Family: Brachionidae			
Brachionus plicatilis	*Dunaliella salina*	1000	Doohan (1973)
Brachionus rubens	*Chlorella vulgaris*	58-250	Pilarska (1977a)

66. Because only nine maximum grazing rates could be estimated from literature data, and because of the variability of those values, a frequency distribution of maximum grazing rates could not be established. Therefore, we attempted to develop several empirical formulations to estimate the maximum grazing rate, G_{max}, the constant, k, and the incipient limiting food concentration, B_{lim}.

67. When the Ivlev equation is solved for k at any given incipient limiting food concentration, B_{lim}, the value of k decreases as B_{lim} increases for <u>any</u> maximum grazing rate (Figure 14). If G_{max} is plotted against k, based on literature data (Table 3), a similar relationship is apparent (Figure 15). As G_{max} increases, k decreases. G_{max} appears to be linearly related to B_{lim}, as shown in Figure 16. Even though only a limited number of data points are available to plot Figures 15 and 16, we believe that the data are of good quality and the apparent relations among G_{max}, k, and B_{lim} are valid. These relationships are true <u>only</u> if zooplankton foods are edible and of a size range suitable for filtering. In general, these two requirements would be met under field conditions. The three equations based on literature data relating G_{max}, k, and B_{lim} can be written as follows (Note: For calculation, we have arbitrarily let B_{lim} equal the food concentration at which the observed grazing rate, G, is within 5 percent of the maximum grazing rate, G_{max}. Equations 6 and 7 are based on a temperature of 20°C):

$$k = 10^{(0.4773 - 1.0002 * \log (B_{lim}))} \quad ; R^2 = 1.00 \qquad (5)$$

$$k = 10^{(-2.9664-0.9787 * \log (G_{max}))} \quad ; R^2 = 0.77 \qquad (6)$$

$$G_{max} = 0.0788 + 0.0003105 * B_{lim} \quad ; R^2 \;\; 0.89 \qquad (7)$$

68. If any one parameter is known, the above equations, although tentative, allow the calculation of any other grazing parameter. The following hypothetical argument supports Equation 7 as potentially the most useful relationship.

69. As we previously stated, Mayzaud and Poulet (1978) found a

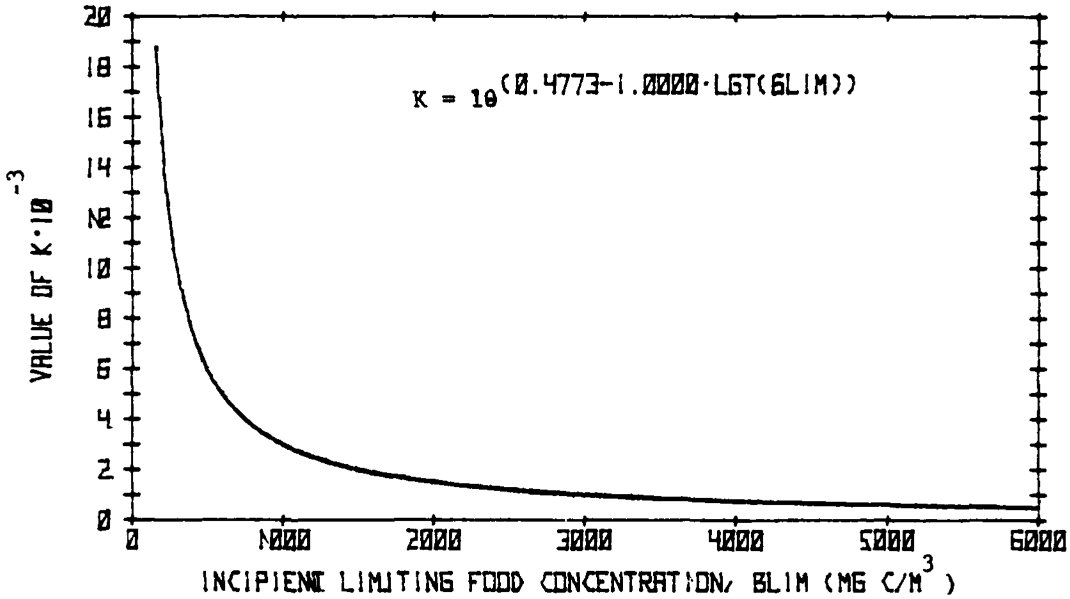

Figure 14. The relation of the constant, k, to the incipient limiting food concentration, B_{lim}. This relation is true for any value of G_{max}

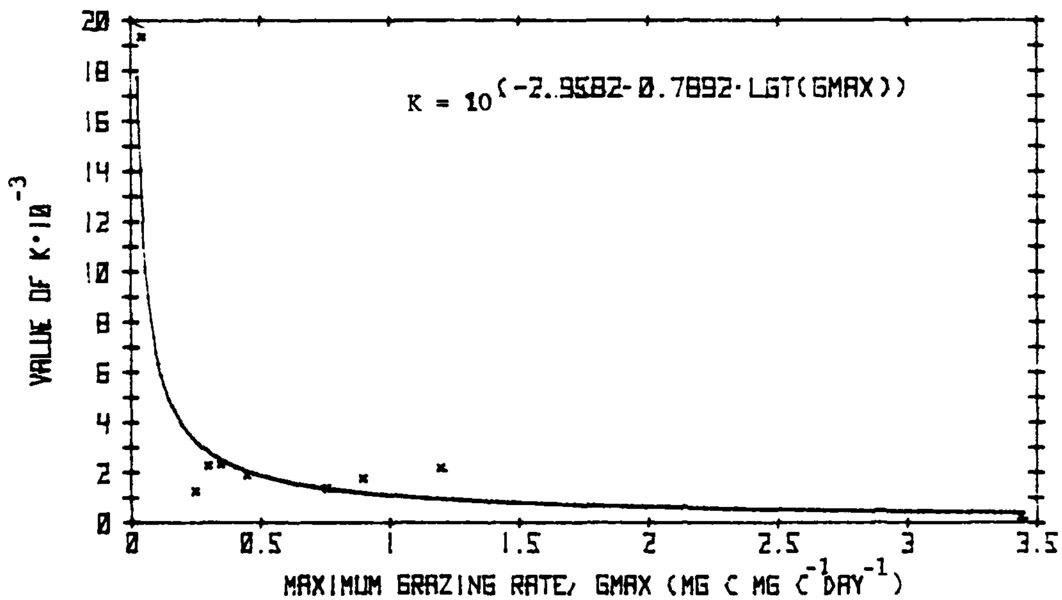

Figure 15. The relation of the constant, k, to the maximum grazing rate, G_{max}. The curve was fitted to values of k and G_{max} from Table 3

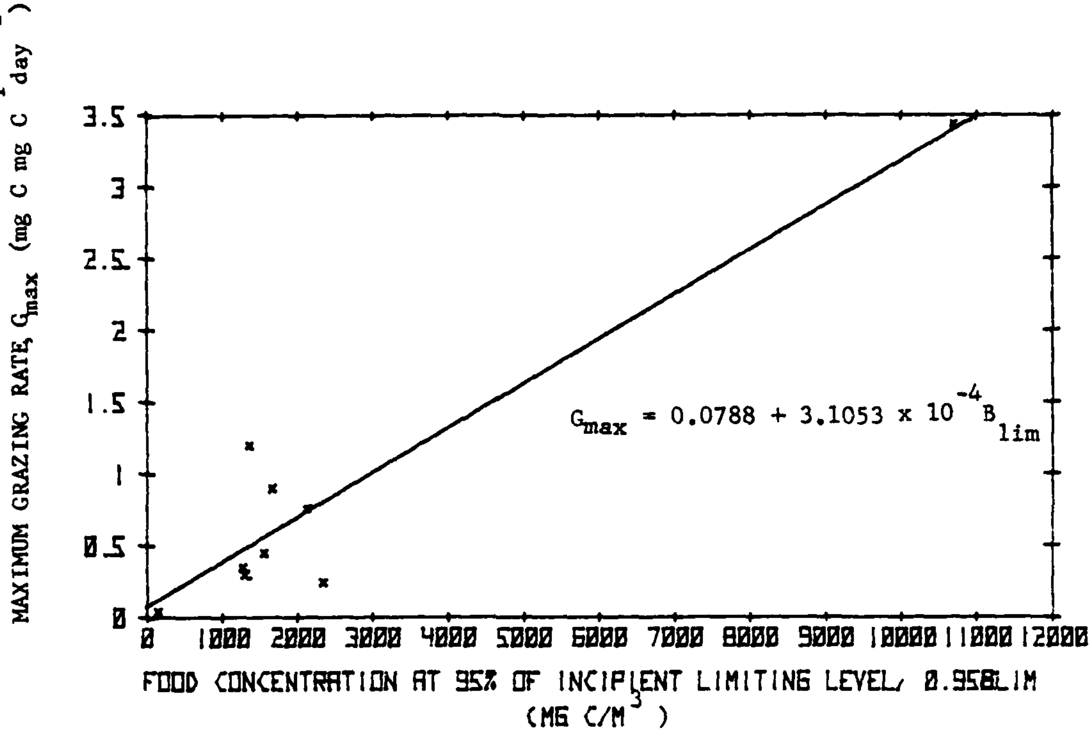

Figure 16. The relation of the maximum grazing rate, G_{max}, to the incipient limiting food concentration, Blim (values for 0.95 B_{lim} have actually been plotted because the Ivlev equation can not be directly solved for B_{lim}). The line was fitted from values in Table 3

linear relationship between food concentration and ingestion for five marine copepods. They also found that ingestion was linear up to the ambient concentrations, when copepods were feeding in a range of food concentrations that were below and above the ambient level. This result suggests that under most field conditions, when the zooplankters are acclimated to the ambient food concentration, they feed maximally at the ambient level. For all practical purposes, then, the ambient food concentration is equivalent to the incipient limiting concentration of laboratory studies. At higher food concentrations, grazing rate approaches an asymptote at G_{max}. If this argument is valid, it becomes clear that the observed grazing rate at the ambient food concentration is equivalent to, or closely approximates, the maximum grazing rate. If true, Equation 7 can be used to estimate the grazing rate for any ambient food concentration. The benefit of such a relationship is obvious. Zooplankton grazing could be described by a linear relationship for any food concentration. Only the biomass of zooplankton and the biomass of available food would need to be measured in the field.

70. The above argument, although supported by the results of Mayzaud and Poulet (1978), is not sufficiently documented in the literature to be generally accepted. Our analysis of the available data provides additional support. Perhaps Equation 7 could be incorporated into some preliminary simulations and these compared to simulations based on the more generally accepted zooplankton feeding constructs. Further experimental work should clarify these relationships.

71. In concluding this analysis, we describe the feeding construct of Mayzaud and Poulet (1978). Although problems are presented in applying the grazing relationship, we believe that it is more realistic than alternative formulations and should be used in the simulation of zooplankton feeding.

72. Mayzaud and Poulet proposed the following feeding construct, which we have changed to our terminology. The acclimation time for a significant increase in food supply, B, occurring over a period t is defined as Γ. Acclimation time corresponds to the maximum ingestion and digestion rates reached at a given food concentration. For $t \leq \Gamma$ the physiological response will follow a saturation-type curve. For $t > \Gamma$ the maximum grazing rate is shifted upward according to a linear relationship. For $t \leq \Gamma$ the grazing rate can be defined by Equation 3. If $0 < t < \Gamma$, the maximum grazing rate remains constant and independent of time. If $\Gamma < t < \infty$, and B is within natural limits, G_{max} can be defined as

$$G_{max} = ZB_t \tag{8}$$

where Z is a constant and B_t is the food concentration at time t. By substitution Equation 3 becomes

$$G = ZB_t \left(1-e^{-kB_t}\right) \tag{9}$$

This equation becomes linear when B_t is increasing. Values for Z for different G_{max} and B_t are presented in Table 6.

Table 6

Relationship Among G_{max}, B_t, and Z as Defined by Equation 8 and Based on the Data in Table 3

G_{max} (mg C mg C^{-1} Day^{-1})	B_t (mg C/m^3)	Z
0.5	1,356.5	3.68×10^{4}
1.0	2,966.8	3.37×10^{-4}
1.5	4,577.1	3.28×10^{-4}
2.0	6,187.4	3.23×10^{-4}
2.5	7,797.7	3.21×10^{-4}
3.0	9,408.0	3.19×10^{-4}
3.5	11,018.4	3.18×10^{-4}

The constant, k, can be determined by using either Equation 5 or Equation 6. The relationship between B_t and Z can be described mathematically by

$$Z = 10^{(-3.2295 - 0.06787 * \log (B_t))} \tag{10}$$

$$R^2 = 0.93$$

Mayzaud and Poulet (1978) report:

> Equation [9] can account for three ecological situations found in various data: a sudden large increase in phytoplankton results in saturation of the feeding system until acclimation has had sufficient time to take place; over a long time such as a yearly cycle, ingestion is directly proportional to food supply, and because the...environment has a highly variable energy supply the feeding system of herbivorous zooplankters is in a more or less continuous state of being acclimated. Hence we could sample a copepod population in a state of equilibrium with a saturation level at or close to the environmental particle concentration. If the sampling takes place during acclimation to an increase in particle

concentration, the saturation will be obtained for values significantly smaller than the environmental concentration. If sampling occurs during an acclimation to a decrease in particulate concentration, a linear relationship with no apparent saturation will be observed.

Mayzaud and Poulet concluded by stating,

> At the moment we do not have experimental values for Γ but from the results of Mayzaud and Conover (1976) it should be <6 days and probably >24 h. Whether all copepods have such an acclimation ability remains to be seen. In the neritic environment off Nova Scotia it appears that both adult copepods and copepodites have it (Poulet 1977).

73. Brandl and Fernando (1975) found that, for three species of cyclopoid copepods, the predation rate was different among groups differing in their previous diet up to the fourth day after the transfer to the same diet. This suggests that Γ may be equal to or greater than 4 days. The acclimation time Γ can be empirically determined by varying its value within the above noted limits during simulation runs.

Food Selectivity by Zooplankton

74. All zooplankters are selective feeders resulting from a combination of (a) an organism's mechanical limitations in capturing and processing food items of varying size and configuration, (b) the chemical nature of the food, and (c) feeding behavior. Herbivorous filter feeders predominate in freshwater zooplankton communities. For purposes of describing a general zooplankton model, species in this group can all be regarded as passive, indiscriminate filter feeders subject to the mechanical and chemical restraints mentioned above. Scavia (1979) discussed selective feeding in a modeling context and commented on aspects needing further research.

75. Zooplankters have a wide variety of potential food sources available to them. Two questions are of central concern to any modeling effort: "What is the size range of food items eaten by zooplankton?" and "Is preference shown to one type of food over another?".

76. Size range of food particles consumed. The size of food

particles that are suitable for consumption vary by species. Generally, the larger the animal, the larger the size of food that can be eaten (Burns 1968b). For discussion we treat all zooplankton as a single community and hence are interested in the range of usable food sizes. Edmondson (1957), Jorgensen (1962), and Kryutchkova (1974) have reviewed literature on this subject and our conclusions draw heavily on these summaries.

77. No absolute size range can be established for a zooplankton community. We have defined size to mean the length in microns of the long axis of a food particle. Clearly, width and volume are also important factors. Reported literature values for the size of ingested particles range from approximately 0.2 to 100 μm in diameter, but most values are less than 20 μm. The preferred or most efficiently consumed particles are generally between 1 and 10 μm. Rotifers clearly feed on smaller particles, with the exception of Asplanchna, a predaceous genus. Ascertaining the maximum size of food consumed by predators is difficult because many species are raptorial feeders capable of tearing prey items into smaller particles before consumption. The range of sizes consumed (0.2 to 100 μm) potentially covers organisms from bacteria to large algae or algal colonies. We suggest that the grazing construct only allow the zooplankton community to feed on particles of 100 μm or less. Further division of the zooplankton community into smaller groups, i.e., rotifers, copepods, predators, etc., would necessitate establishing a maximum and minimum food size for each group. Although division of the zooplankton community may be highly desirable for some model applications, data needed to establish particle-size preference for subcategories of zooplankton are too few and variable within the major taxa.

78. Preference among food sources. Food preference is demonstrated if an organism consumes a food item in a proportion greater than the food item's relative contribution to the total of all available foods in the environment. Preferences among variable food sources have been incorporated into recent models (e.g., Scavia 1979). Most of these models use a food preference term or electivity index for each food source. Seldom are more than two types of food available to the grazing

community in simulation models, i.e., phytoplankton or detritus. Often values for the food preference terms are the modeler's best guess because little sound documentation exists.

a. Detritus and microflora as food

79. Detritus, or unidentifiable, particulate organic and inorganic material, is a significant food source for zooplankton in some models. Although ample evidence exists to show that detritus is consumed by zooplankton, no evidence exists to show that detritus is consumed preferentially. Several studies have shown that detritus is ingested in proportion to its composition in the environment. When detritus is included as a food source in a grazing formulation, it should be given equal ranking with other suitable foods.

80. Since Odum and de la Cruz (1963) first described organic detritus, a fairly extensive body of literature has developed that is concerned with the functional role of detritus in trophic webs of aquatic ecosystems. Detritus consists of organic carbon that is lost from any trophic level by nonpredatory means (e.g., nonpredatory mortality, egestion, excretion) or that is derived from allocthonous sources. The detritus food chain is any route by which chemical energy from detritus is made available to biota (Wetzel 1975). These definitions recognize bacterial action on detrital substrates as trophic transfer (Wetzel 1975). Goldman and Kimmel (1978) reviewed much of the previous work conducted on energy flow and matter cycling through detrital pathways and emphasized the importance of detritus in reservoirs.

81. The upper reaches of reservoirs typically act as sediment traps for tremendous loads of clay, silt, and detritus. As a result, river impoundments may receive a significant portion of their driving energy from inflowing allocthonous detritus. In Tuttle Creek Reservoir, Kansas, Marzolf (1978) found that 1200 mg $C \cdot m^{-2} \cdot day^{-1}$ came from allocthonous sources and only 70 mg $C \cdot m^{-2} \cdot day^{-1}$ from autochthonous origins. Sorokin (1972) suggested that 25 percent of the driving energy in Rybinsk Reservoir, USSR, was derived from allocthonous organic substances. Twenty-three percent of the organic matter in a Texas reservoir came from upstream areas (Lind 1971). In addition to the detritus flowing

into reservoirs, a substantial quantity may enter impoundments when new areas are inundated by high water levels (Romanenko 1966, Winberg 1972).

82. Diets of nonpredatory zooplankton often include significant quantities of detritus or bacteria (Smirnov 1962, Conover 1964, Petipa 1967, Andronikova et al. 1972, Poulet 1976). Edmondson (1957) discussed the potential importance of detritus in zooplankton diets and cited previous observations of zooplankton consuming detritus and bacteria. Bacteria made up 58 percent of the nonpredatory zooplankton diet during the freezing period in Red Lake, USSR (Andronikova et al. 1972). Marzolf (1978) observed zooplankton gorged with clay particles and detritus. Gutel'mackher (1973) determined that dispersed bacteria composed 28 to 38 percent of the diets of *Bosmina longirostris*, *Holopedium gibberum*, and *Diaptomus graciloides*.

83. Bacteria probably make indigestible detritus available to nonpredatory zooplankton (Edmondson 1957, Sorokin 1972). In some cases, microflora on the detritus may represent the primary source of energy (Overbeck 1972). That bacteria colonize detrital particles is well established (Rodina 1963; Paerl 1973, 1974). According to Rodina (1963), the mass of bacteria on detritus is often enormous, and an aggregate often consists of a small organic core with an overgrowth of bacteria and bacterial filaments.

84. Bacteria also may appear as free-living plankton (Azam and Hodson 1977, Kimmel 1978, Sieburth and Smetacek 1978). In fact, Sieburth and Smetacek (1978) found that the bacteria attached to the seston which passed through a 20-μm screen consisted of only about 0.1 percent of the total cells they concentrated on 0.2-μm nucleopore membranes. Although most dispersed bacteria probably are not filterable by zooplankton (Monakov and Sorokin 1972), colonization of detritus may increase the availability of dispersed bacteria for zooplankton consumption (Goldman and Kimmel 1978). Haney (1973), however, considered particles within the size range of 0.45 to 30 μm to be available for zooplankton consumption. Some dispersed bacteria probably are at the lower end of this size range.

85. Few data exist on the assimilation of detritus and bacteria

by zooplankton (Appendix C). Assimilation efficiencies of Cladocera feeding on phytoplankton (8 to 99 percent; $\bar{X} = 47.4$) tend to be higher than that of Cladocera fed detritus and bacteria (8 to 55 percent; $\bar{X} = 23.3$; Appendix C). Similarly, Copepoda assimilate algae (10 to 99 percent; $\bar{X} = 59.5$) somewhat more efficiently than they do yeast and bacteria (21 to 67 percent; $\bar{X} = 44.2$; Appendix C) (Gutel'mackher 1973; Green 1975).

86. Nonpredatory zooplankton fed detritus and bacteria apparently can survive, even though assimilation of these foods is relatively low. Baylor and Sutcliffe (1963) observed that *Artemia* sp. fed particulate, organic detritus grew as well as those shrimp fed yeast, through the fourth day of their experiment. Thereafter, *Artemia* continued to grow but at a slower rate than yeast-fed specimens. Cladocera fed sterile, crushed plant and animal detritus survived 38 days but did not reproduce effectively (Rodina 1963). When fed detritus that was colonized by bacteria, the Cladocera survived and reproduced through several generations. Apparently the bacteria provided certain vitamins needed by the Cladocera for reproduction and development. Other zooplankters also have been observed to survive, mature, and reproduce on diets of detritus and/or bacteria (Gellis and Clarke 1935, Rodina 1963, Yesipova 1969, Monakov 1972, Winberg et al. 1973).

87. Zooplankters apparently must feed on detritus and bacteria to balance their energy budgets when phytoplankton production is insufficient to support the biomass of zooplankton present. In the tropical Atlantic, food needs for zooplankton were 1.5 to 4 times greater than chlorophyll *a* primary production (Finenko and Zaika 1970). Nauwerck (1963) calculated that the July growth rates of *Diaptomus* sp. could not have been maintained with the available phytoplankton production. Like inefficient benthic herbivores that feed on detritus and bacteria (e.g., Hargrave 1971), zooplankters may have high tissue growth efficiencies and simply process large quantities of poorly assimilated food. Welch (1968) demonstrated an inverse relation between assimilability and growth efficiency.

88. In field studies, large temporal discrepancies have been observed between peaks in phytoplankton and the abundance of herbivorous

zooplankton. In fact, zooplankton dynamics occasionally correlate better with the production of bacteria than with that of phytoplankton (Moskalenko and Votinsev 1972, Jassby 1975). Colonization and partial decomposition of senescent algae by bacteria and fungi may make them secondarily available for zooplankton consumption (Edmondson 1957). Jassby and Goldman (1974) concluded that a majority of the phytoplankton losses in Castle Lake, California, were the result of natural senescence and not grazing.

89. A tremendous quantity of chemical energy in the form of bacteria has been largely ignored by limnologists. While bacterial biomass typically is low in most waters throughout the year (1 g wet weight per m^3 was a common estimate by Rodina (1963) and Sieburth and Semtacek (1978)), turnover time is rapid (e.g., 3 to 48 hr). As a result, bacterial production can exceed primary production under certain conditions (Winberg 1972, Jassby 1975). On a yearly basis, bacterial production is usually less than primary production, but of the same magnitude (Kuznetsov et al. 1966, Overbeck 1972, Pechlander et al. 1972, Tilzer 1972). Such a potential source of energy in reservoirs is of too great a magnitude to be ignored, even if inefficiently utilized.

90. If detritus is considered a second food source for zooplankton, then a term indicating preference for detritus or phytoplankton should be incorporated into a model's grazing construct. Four zooplankton models include detritus as a source of food for zooplankton (i.e., Menshutkin and Umnov 1970, Umnov 1972, MacCormick et al. 1974, Patten et al. 1975). The Wingra Model (MacCormick et al. 1974) includes a preference term for detrital and algal foods that usually was set at unity (i.e., indicating no preference), or that was empirically derived. Patten et al. (1975) assumed that small zooplankton feed 20 percent on phytoplankton and 80 percent on particulate organic matter. These values are similar to the percent composition (by weight) of these components in net seston. Menshutkin and Umnov (1970) and Umnov (1972) assigned zooplankton preferences for detritus or phytoplankton on the basis of the percent composition (by weight) of these components in the ecosystem. Data of Ryther (1954) and Lampert (1974) suggested that the

use of a preference term, based on the concentration of food particles of a filterable size, may be reasonable. Particle selection by Cladocera in these studies depended on the concentration of filterable-sized particles and not on the type of particles present. Particles are not rejected simply because they have limited food value. Copepods ingest and form fecal pellets of particles of India ink (Marshall and Orr 1952) or polystyrene pellets (Paffenhofer and Strickland 1970).

91. The seasonal abundance of phytoplankton, bacteria, and detritus may be the main factor determining the percent composition of these components in the diets of many zooplankton. For example, Poulet (1976) determined that the balance between living and nonliving particle consumption in _Pseudocalanus minutus_ was related to the relative concentrations of these components within each particle peak (i.e., the size range of particles which are filtered at a maximum rate). Riley (1970) stated that such nonselective feeding, based on available particle size, should not distinguish between living and nonliving particles. Detrital carbon constituted 71 percent of the food ration of _Pseudocalanus minutus_ (Poulet 1976). This figure is about the same as the percent composition of detritus in the seston of the sea (78 to 95 percent, Finenko and Zaika 1970; 76 percent, Beers and Steward 1969; 70 to 93 percent, Poulet 1976).

92. In some models, animals are limited to one food source. DiToro et al. (1971) and Steele (1974) developed models in which zooplankton fed exclusively on phytoplankton. Food of benthic organisms was limited to detritus in a model by Zahorcak (1974). Other models primarily have been concerned with particle size selection (e.g., Scavia et al. 1976, Taghon et al. 1978). Elaborate constructs dealing with food selection based on prey availability, catchability, and desirability (e.g., Park et al. 1974, Zahorcak 1974, Scavia et al. 1976) may not represent substantial improvements over single-food models if they cannot be effectively evaluated. While such interactions and behavior probably exist, they have not yet been adequately quantified.

93. Clesceri et al. (1977) presented a model simulating free and attached microflora, particulate and dissolved organic matter, and nitrogen and phosphate in limnetic areas. Feeding terms for bacteria were

the same as those used for zooplankton and benthos feeding in the Lake George model (Park et al. 1974). Insofar as we know, the effort of Clesceri et al. (1977) represented the first attempt to model bacteria dynamics.

94. In reviewing the literature on assimilation and feeding, we became aware of several gaps in the knowledge needed to effectively model zooplankton. We urgently need accurate methods for determining the percent composition and turnover of detritus, bacteria, and phytoplankton in seston. With these methods, we could better elucidate the seasonal dynamics of these components and determine their relationship to zooplankton feeding. In addition, more studies are needed of assimilation and survival when zooplankton are fed protozoa, detritus and/or bacteria, or various combinations for several generations. Until these data are available and incorporated into models of reservoir zooplankton, simulations of the real environment may be inaccurate.

95. Dissolved organic matter (DOM) is another potential source of food for benthos and zooplankton of which we know little. We do know that DOM is about 10 times more abundant than particulate organic matter (POM) in marine and freshwater ecosystems (Jorgensen 1962, Wetzel 1975). Data on the use of DOM by aquatic invertebrates are rare. *Peloscolex multisetosus*, an oligochaete, actively took up glycine from solution (Brinkhurst and Chua 1969). Epidermal tissues of soft-bodied marine invertebrates have been shown to actively transport dissolved, free amino acids. Larval forms with large surface-area-to-volume ratios, especially, may benefit from such uptake (West et al. 1977). Southward and Southward (1971) believed that some marine polychaetes can meet all of their nutritional requirements by absorbing DOM. Gellis and Clarke (1935) found that *Daphnia magna* could not survive in a glucose solution but could effectively use unfilterable, colloidal organic matter as food. The osmotic assimilation efficiency of DOM by *Daphnia pulex* in sterile water is about 2 percent (Monakov and Sorokin 1972). More research is necessary to determine what types of animals in reservoirs, if any, can directly (by uptake) or indirectly (via a bacterial trophic link) utilize the energy in DOM.

b. Selectivity among algae

96. Conflicting evidence on the nutritional value and grazability of blue-green algae has appeared for many years. Our review of assimilation, in a later section, clearly shows that blue-green algae are generally not as assimilable as are other algal species. This does not mean, however, that blue-green algae are ignored as a food source by zooplankton. Birge (1898) may have been the first worker to speculate on the ability of zooplankton to graze filamentous blue-green algae. He suggested, on the basis of qualitative observations, that Chydorus could utilize Anabaena but not Lyngbya.

97. Lefevre (1942) compared the suitability of many algal species as food for Daphnia magna and Daphnia pulex. Blue-green algae were not included in the analysis, but his results showed that species differences within the same genus could produce widely divergent suitability ratings. Because Lefevre did not measure actual consumption of the algal species he examined, his results are not directly comparable to more recent work. However, they do illustrate the contention that it is not necessarily the taxonomic position of the algae that makes it suitable or unsuitable as food but rather the attributes of each algal species such as size, shape, and toxicity.

98. Lefevre (1950) found that the filamentous blue-green Aphanizomenon gracile was unsuitable as food for Daphnia magna and D. pulex. Both species of Daphnia could filter the algae but rejected it because they could not ingest the filaments.

99. Ryther (1954) considered the possibility that Daphnia magna filtered large algal cells less efficiently than small cells. In a group of experiments in which Daphnia was fed mixed cultures containing equal numbers of the large Scenedesmus and the smaller Chlorella, each prey species was eaten in equal numbers suggesting no difference in filtering efficiency.

100. Ryther also suggested, then experimentally demonstrated, that the age of the algal culture was important in determining filtering rate. For all species investigated, Daphnia magna filtered senescent cells at a much lower rate than it filtered growing cells. Ryther

hypothesized that antibiotics produced by the senescent cultures inhibited Daphnia feeding. His results were supported by McMahon and Rigler (1965) and Stross et al. (1965).

101. Blazke (1966) found that Daphnia pulicaria was able to grow and reproduce when feeding on a bloom of blue-green algae. However, Arnold (1971) noted that bacteria may have been consumed along with the blue-green algae in Blazka's study.

102. In her study of Daphnia feeding in Heart Lake, Canada, Burns (1968a) found that the filamentous blue-green algae Anabaena, Oscillatoria, and Lyngbya were numerically dominant during the summer. Also present were colonies of Gomphosphaeria and Microptis. Daphnia filtering rate declined as the concentration of Anabaena colonies in the water increased. Burns noted,

> When Daphnia were feeding in lakewater, many of the colonies were drawn into the thoracic chamber. Most of the colonies were cast out by movements of the postabdomen alone, but many of the filaments came to lie in the food groove parallel to the long axis of the body. In D. rosea, an immediate and vigorous labral rejection occurred whenever an Anabaena filament, or cell from a filament, reached the region of the maxillules. Several rejections were sometimes necessary to dislodge a filament.

Burns suggested that the decline in Daphnia filtering rate could be due to the presence of the filamentous blue-green algae which interrupted the filtering process. Her results supported the conclusion that Daphnia rosea was not utilizing the predominant phytoplankton of Heart Lake for 5 months of the year.

103. Burns found, in contrast, that Daphnia galeata ingested single cells or small fragments of Anabaena at times when the food level in Heart Lake was low. Her hypothesis was that perhaps Daphnia galeata could use less desirable food sources in times of inadequate food supply.

104. Although Daphnia rosea and D. galeata showed similar filtering rates and feeding behavior in Heart Lake water, Burns noted,

> ...that during June, D. galeata adults ingested small colonies of a chrysophycean alga whereas D. rosea adults did not. This implies not only that an active selection of food particles in lakewater might occur in nature, as

has been suggested by other authors (Smith, 1936; Gajevskaya, 1961), but also that two species of Daphnia might differ in an ability to select food.

105. Schindler (1968) fed Daphnia magna three algal species separately (Chlorella sp., Chlamydomonas sp., and Anabaena sp.) and found no significant difference in the feeding rate. The assimilation rates of Daphnia fed Chlorella sp. and Chlamydomonas sp. were not significantly different, but the assimilation rate for Anabaena sp. was significantly lower. Food energy content (2 to 5 calories/mg) had a significant effect on feeding and assimilation.

106. Schindler noted that planktonic Copepoda and Cladocera from a turbid Minnesota lake, when observed in the laboratory, ate particles of different origin nonselectively, although there was some selection for size and shape of particles.

107. Experiments conducted by Gliwicz (1969) on eight zooplankton species fed various sizes of mineral grains and diatom frustules support the hypothesis that filtering may be primarily passive and mechanical. Gliwicz found that as the proportion of mineral particles in the food suspension increased, the amount consumed also increased. He concluded that when large amounts of valueless food which cladocerans cannot avoid or reject are present, filtering rates did not decrease. He also examined the contents of alimentary canals of various zooplankton species from Lakes Mikolajskie and Taltoursko, Poland. This quantitative study revealed that the following species consumed blue-green algae along with other foods: Daphnia cucullata, D. longispina, Bosmina coregoni, B. longirostris, Brachionus angularis, and Asplanchna priodonta.

108. McQueen (1970) found that Diaptomus oregonensis did not feed on the platelike colonies of the blue-green Merismopedia in Marion Lake, British Columbia (although this species was of a filterable size), nor on two species of the diatom Cyclotella that were within the size range normally eaten by Diaptomus. McQueen concluded that cell type, rather than size and concentration alone, is important in determining filtering rates.

109. Schindler (1971) fed Daphnia longispina, Diaptomus gracilis,

and *Cyclops strenuus* 11 algal species, three of which were blue-green algae. The zooplankters ate each of the 11 species, although the assimilation efficiencies were highly variable.

110. Arnold (1971), who examined the effects of seven species of blue-green algae on *Daphnia pulex*, found that ingestion, assimilation, survival, and reproduction were lower in specimens fed blue-green algae than in those fed green algae. The degree to which the different blue-green algae affected the *Daphnia* was variable. Arnold concluded that the blue-green algae tested did not supply sufficient nutrition to support the *Daphnia pulex* population unless additional food sources were available.

111. Porter (1973), who examined in situ the selective grazing of algae by a zooplankton community in Fuller Pond, Connecticut, reported that artificial increases in grazing pressure resulted in a decline of the phytoplankton community as a whole. The most heavily grazed groups were ciliates, small algal species, large diatoms, flagellates, and nanoplankton. Unaffected groups were large algal species, small blue-green algae, small diatoms, large desmids, large dinoflagellates, and large chrysophytes. Large blue-green algae showed a variable response and large green algae increased.

112. *Anabaena affinis* and *A. flos-aquae* were rarely consumed by the zooplankton and were unaffected by increased grazing pressure. The green algae that were enhanced by grazing were encased in gelatinous sheaths and passed through the gut intact. *Sphaerocystis schroeteri* and *Elakatothrix gelatinosa* reproduced after gut passage.

113. Porter suggested that gelatinous green algae must be included with blue-green algae and other very large species as being poorly utilized as food by zooplankton. She concluded,

> By their responses to grazing, algae can be divided into three major groupings that cut across taxonomic lines. One contains species that are large, rare, or filamentous and seldom found in the guts of the zooplankton, either because they are not eaten or are actively rejected. They are unaffected by manipulations of grazing pressure. The second contains small, edible species that are eaten, digested and suppressed by grazers. The third contains species encased in thick gelatinous sheaths that pass through the grazers, frequently intact and in viable condition. These are

increased by an increase in grazers. Grazing pressure, like physical and chemical factors, may determine the relative proportions of algal species and drive seasonal succession from a spring association dominated by edible flagellates and diatoms to gelatinous greens and filamentous blue-greens in autumn. The impact of grazing on the phytoplankton community is determined by the proportions of suppressed, increased and unaffected algae present.

114. In a continuation of her study, Porter (1975) found blue-green algae to be consumed in limited quantities by three zooplankters in Fuller Pond, Connecticut. *Cyclops scutifer* fed to a very small extent on *Aphanothece* sp. (4.3 percent of gut volume) and *Chroococcus limneticus* (3.5 percent). Only *Daphnia galeata* consumed *Anabaena flos-Aquae* (0.2 percent), along with seven other species of blue-green algae. She presented evidence to show that some species of blue-green and green algae with gelatinous sheaths can be consumed and pass through the digestive tract of zooplankters intact and viable.

115. Haney (1973) contrasted his work with that of Burns (1968a). Contrary to Burn's conclusions, he found that it was unlikely that *Anabaena* filaments were the direct cause of the rapid decline in zooplankton filtering rates in the spring in Heart Lake, Canada.

116. O'Brien and DeNoyelles (1974), who fed *Ceriodaphnia reticulata* on a natural assemblage of phytoplankton, with and without the colonial blue-green algae *Microcystis aeruginosa* added to the culture, found that the presence or absence of *M. aeruginosa* had no significant effect on the filtering rate. The authors did not state whether or not *Ceriodaphnia* consumed any of the blue-green algae.

117. Geller (1975), after examining the filtering rate of *Daphnia pulex* on eight algal species in pure culture, showed that *Scenedesmus*, *Nitzchia*, and *Asterionella* were all filtered at about the same rate. *Staurastrum* and the blue-green *Microcystis* were filtered at a much lower rate, which Geller attributed to cell size and shape and the cells gelatinous sheath. *Anabaena* was filtered very little if at all. The green alga *Stichococcus* was filtered at a reduced rate that was explained by the small cell size and reduced filtering efficiency of *Daphnia*. Geller stated,

> The ingestion rates measured during feeding with blue-green algae permit the assumption that they are accepted if they are individual cells in suspension, though the ingestion rates do not reach those for green algae and diatoms, which are taken up quite readily. Filamentous forms, e.g., colonies of *Anabaena*, which in the present investigation were short filaments of 50-200 cells, are taken up to a very small extent.

118. Hayward and Gallup (1976) examined the filtering and feeding rates of *Daphnia schodleri* fed seven species of algae. Feeding occurred for all species except the filamentous *Anabaena* and *Aphanizomenon*, both blue-green species. Both species were rejected by *Daphnia*, and high mortality rates occurred. *Daphnia schodleri* did not eat single cells of *Anabaena* when the filamentous chains were broken up. The authors suggested that *Daphnia* may be able to recognize *Anabaena* by chemical and physical detection.

119. Pourriot (1977), who reviewed the food habits of rotifers, stated, "The polyphagous *Keratella* species (*quadrata* group) feed on many kinds of food including detritus and small living cells (Flagellates, green algae) but none ingested the cyanophycean *Synechocystis* which is of suitable size."

120. Pourriot also listed 28 species of filter-feeding rotifers and their foods. Of the 18 species of freshwater rotifers listed, 17 did not ingest Cyanophyceae. One species, *Brachionus diversicornis*, ingested blue-green algae (species unspecified) and exhibited moderate reproduction. None of the seven raptorial feeding species of rotifers listed fed on blue-green algae, but rather on large Cryptomonadales, Chyrsomonadales, and some diatoms and Centrales. Two of the three brackish or alkaline water species listed fed on blue-green algae and reproduced successfully. Both of these species were in the genus *Brachionus*. It appears that *Brachionus* is the only rotifer genus utilizing blue-green algae. Many of the 28 species did not feed on other algal groups or on detritus and bacteria. Most species except the raptorial feeders maintained themselves reasonably well on detritus.

121. Webster and Peters (1978), who performed experiments to see if large zooplankters were differentially affected by blue-green algal

filaments over small zooplankters, indicated that in large zooplankters (Daphnia pulex, D. ambigua, Simocephalus vetulus) the filtering rate declined and the rejection rate increased as the filament concentration increased. The filtering rates for Bosmina longirostris, the smallest animal, showed little change with variations in filament concentrations. Results for Ceriodaphnia quadrangula were variable. These results show that filtering of large zooplankters is impeded by the presence of filamentous blue-green algae.

122. Published data generally indicate that the zooplankton community, as a whole, is capable of filtering and consuming all major algal groups, including the blue-green Myxophyceae. The size, shape, and chemical nature of the algae available as food appear to be of primary importance in controlling the rate of consumption. Senescent cells have been shown to inhibit feeding, and this chemical inhibition is not limited to blue-green algae. Large species with gelatinous sheaths are consumed by zooplankton but may pass through the digestive tract undamaged and perhaps enhanced in terms of increased growth rates. Rejection and reduced feeding may occur in the presence of large quantities of filamentous algae.

123. With respect to water quality problems resulting from eutrophication, the blue-green algae pose the most serious problem. The blue-green "bloom" species, such as Anabaena and Aphanizomenon, are filamentous forms that are unlikely to be consumed by the zooplankters. Even under unperturbed conditions, such as might be found in natural lakes, filamentous blue-green algae may predominate in the lake phytoplankton during the summer and early fall. In any situation where filamentous algal forms become a significant proportion of the phytoplankton community, grazing rates are affected. Grazing on these species should not be modeled at the same rate as that on other nonfilamentous forms.

124. Model construct. In view of the water quality orientation of the model which this report is intended to supplement, we propose the following construct based on our literature evaluation. First, food preference is equal among all potential food sources except filamentous algae.

Filamentous noncyanophyte species are normally not water quality problems, nor do they predominate phytoplankton of reservoirs. We do not believe sufficient justification exists to separate these species from the bulk of the phytoplankton community. Filamentous blue-green algae should be distinguished from other algal groups and should be grazed at a lower rate. To reduce the grazing rate on filamentous blue-green algae, the modeler should introduce a preference term into the grazing equation. The magnitude of the term is not supportable quantitatively by literature data but probably should be allowed to range from 0 (no grazing) to 0.3. The greater the concentration of filamentous blue-green algae in the total algal concentration, the lower the total grazing rate. This construct can be written as:

$$G_i = ZB_t \left[1 - e^{-kB_i \left(\frac{W_i B_i}{\Sigma W_i B_i} \right)} \right] \tag{11}$$

where

G_i = observed grazing rate on food type i

Z = proportionality constant defined by Equation 10

B_t = concentration of food at time t

B_i = concentration of food type i

W_i = preference coefficient for food type i

k = proportionality constant

Effect of Temperature on Consumption

125. Temperature is known to influence many types of biological functions, including the filtering rates and hence the grazing rates of filter-feeding aquatic organisms. We next review information on the effects of temperature on zooplankton grazing rates, analyze these results critically, and, finally, propose a model construct incorporating temperature into the grazing function. Although alluded to here, lethal temperature limits are discussed in the section "Nonpredatory Mortality," page 166.

126. Literature synopsis. The earliest reference to temperature effects on the grazing rates of freshwater zooplankters is that of Cohn (1958). His study of *Daphnia pulex* and *D. schodleri* showed no change in the grazing rates over the limited temperature range of 17° to 21°C. Nauwerck (1959), who conducted in situ experiments at Lake Erken, Sweden, with *Daphnia longispina* and *Diaptomus* sp., found that over a temperature range of 8° to 18°C, they both filtered most rapidly between 16° and 18°C.

127. The first comprehensive examination of the influence of water temperature on feeding behavior was conducted by McMahon (1965) on *Daphnia magna*. The feeding response was recorded at temperatures ranging from 5° to 35°C. At food concentrations above the incipient limiting level, the grazing rate reached a maximum at 24°C. McMahon found that at food concentrations below the incipient limiting level, the maximum grazing rate was reached at 28°C, but it was not clear whether this rate was significantly different from the rate at 24°C. Kryutchkova and Kondratyuk (1966) found that *Daphnia pulex* achieved a maximum filtering rate at 24°C, over the temperature range of 18° to 26°C.

128. Burns and Rigler (1967) found the optimum temperature for *Daphnia rosea* to be 20°C. McMahon (1968) studied the rate of movement of the thoracic appendages in *Daphnia magna*, as a reflection of filtering rate, and found that *Daphnia* cultured in the laboratory at 24°C had a slightly higher rate of thoracic appendage movement than those cultured in open field tanks of natural lake water at 16° ± 4°C. Schindler (1968) found no significant difference in the grazing rate of *Daphnia magna* at 10° and 20°C.

129. Burns (1969b) examined the filtering rates of immature and adult instars of four species of *Daphnia* at three temperatures: 15°, 20°, and 25°C. Adult and immature *D. magna* showed increasing filtering rates with increasing temperature. Adult *D. schodleri* showed a peak at 20°C, while the immatures reached a maximum filtering rate at 15°C with declining rates as temperatures increased. Adult *D. pulex* and *D. galeata* reached a maximum filtering rate at 20°C, while the immatures of these species showed increasing filtering rates at temperatures up to 25°C. These results indicate that there are species differences as well as age

differences in the filtering response to temperature.

130. Daphnia rosea raised at 12°C were used in a study of the effects of temperature on feeding behavior by Kibby (1971a). The maximum filtering rate was at 14°C but was not significantly different from the rate at 12°C. These results differ from those reported earlier by Burns and Rigler (1967) and illustrate the importance of acclimation temperature in determining optimum temperatures for grazing.

131. Chisholm et al. (1975) studied the effects of temperature on the filtering rate of Daphnia middendorffiana, a species of primarily Arctic and alpine distribution. The maximum filtering rate was at temperatures near 12°C for ages of Daphnia tested and decreased at higher and lower temperatures.

132. Perhaps the most comprehensive examination of the influence of temperature on the grazing rate of a zooplankter was conducted by Geller (1975) on Daphnia pulex. He showed that the previous temperature exposure of the animals is very important in determining grazing rate. Geller made a distinction between short-term acclimation of hours to days and long-term acclimation from weeks to months. Animals acclimated to 15°C and then tested at 10°, 15°, 20°, and 25°C had higher grazing rates at temperatures other than their acclimation temperature. At an acclimation temperature of 15°C the grazing rate reached a maximum at 20°C. Temperature responses were similar for animals acclimated to the other test temperatures. In another set of experiments, in which Geller examined the grazing rate of Daphnia that had been acclimated to the test temperatures for periods up to 3 years, grazing rate increased in a linear manner with temperature. Such a linear relation might be expected under field conditions, provided ambient temperature did not change too rapidly (i.e., on the order of 1° to 2°C per week over a seasonal period).

133. In support of Geller's results, Zankai and Ponyi (1976) found the filtering rate of Eudiaptomus gracilis (= Diaptomus gracilis) to be linearly related to temperature over the temperature range of 0° to 27°C. Gophen (1976) found that the grazing rate of Ceriodaphnia reticulata increased linearly over the range of 15° to 27°C. Hayward and

Gallup (1976), who studied the grazing rate of Daphnia schodleri at temperatures of from 5° to 30°C, found an increase in grazing rate with temperature up to a maximum at 20°C. At higher temperatures grazing declined.

134. Calamoecia lucasi, a freshwater copepod of a primarily tropical marine genus, was studied by Green (1975). He examined the filtering rate of adults and immature instars of this species from 10° to 25°C. Results indicate that filtering rates increased with temperature up to 20°C. At higher temperatures filtering declined for adult females and copepodite stages III, IV, and V. Filtering remained relatively constant between 20° and 25°C for nauplii, and filtering increased slightly for copepodites I and II and for adult males.

135. No information is available on the effects of temperature on the grazing rates of rotifers. Table 7 summarizes the results of the papers cited in this review.

136. Analysis. With the exception of Nauwerck (1959), all information on the effects of temperature on grazing rates was derived in controlled laboratory studies. Consequently, it is imperative that the previous thermal history of the test animals be known. In attempting to model temperature effects, a data base that closely reflects the natural environmental conditions is needed. With respect to temperature, zooplankton in a natural environment are acclimated at any period of time to a specific thermal regime, usually diel in character. Changes in the thermal regime over days to months normally occur gradually and allow zooplankton to acclimate physiologically and behaviorly to meet these changes. Seldom are zooplankters faced with sudden temperature changes such as might be experienced upon entrainment in a thermal plume from a power plant. Laboratory studies in which test animals are allowed to fully acclimate to the test temperatures can be expected to best reflect field conditions.

137. Work by Geller (1975) on Daphnia pulex represents the most comprehensive examination of the role of temperature acclimation yet undertaken. Geller concluded that the maximum time required for temperature acclimation for newly established cultures was proportional to the

Table 7

Summary of Literature Data on the Effects of Temperature on the Grazing Rates of Filter-Feeding Zooplankton

Taxa	Temperature (°C) to Which the Animals Were Assumed to be Acclimated	Period Allowed for Animals to Adjust to the Test Temperature	Grazing Rates of Adult Zooplankters Expressed as a Percentage of the Maximum Observed Rate (100% - Maximum Observed Rate) Temperature (°C)																				Reference
			5	7	8	10	12	14	15	16	17	18	20	22	24	25	26	27	28	30	33	35	
ORDER: Cladocera																							
Family: Daphnidae																							
Ceriodaphnia reticulata	Variable	24 hr							39					94				100					Gophen (1976)
Daphnia galeata	15,20, or 25	Several weeks							26				100			91							Burns (1969b)
Daphnia longispina	Variable	Na								100	100	100											Nauwerck (1959)
Daphnia magna	20	1 hr	8			16			25				41		100				49		45	5	McMahon (1965)
Daphnia magna	15,20, or 25	Several weeks							54				88			100							Burns (1969b)
Daphnia middendorffiana	Variable	1 hr	21				100				66												Chisholm et al. (1975)
Daphnia pulex	Variable	24 hr**										52	58		100		61						Kryutchkova and Kondratyuk (1966) as reported by Geller (1975)
Daphnia pulex	15,20, or 25	Several weeks							81				100			59							Burns (1969b)
Daphnia pulex	15	None				60			45				100			91							Geller (1975)
Daphnia pulex	7,10,15,20, or 25	Up to 3 years		24		35			54				74			100							Geller (1975)
Daphnia rosea	20	48 hr	48			63			87				100			90							Burns and Rigler (1967)
Daphnia rosea	12	48 hr	67		82	90	98	100		94		89	85			31							Kibby (1971a)
Daphnia schedleri	15,20, or 25	Several weeks							53				100			68							Burns (1969b)
Daphnia schedleri	20	12 hr?	26			60			87				100			91					71		Hayward and Gallup (1976)
ORDER: Eucopenpoda																							
Family: Centropagidae																							
Calamoecia lucasi	Variable	48 hr				29			51				100			86							Green (1975)
Family: Diaptomidae																							
Diaptomus sp.	Variable	Na*								100	100	100											Nauwerck (1959)
ORDER: Eucopepoda																							
Family: Centropagidae																							
Calamoegia lucasi	Variable	48 hr				29			51				100			86							Green (1975)
Family: Diaptomidae																							
Diaptomus sp.	Variable	Na*								100	100	100											Nauwerck (1959)

* Not applicable; experiment was conducted in situ in a natural lake.
** Test temperatures ranged from 18° to 30° C.

growth rate. He estimated this time period to be about 6 weeks at temperatures near 7° to 10°C, and about 4 weeks at temperatures of 15°C or higher. Geller noted, "The physiological adaptability of Daphnia to environmental temperature can be fully realized only if they are reared from eggs at a constant temperature."

138. A comparison of literature values of the time periods allowed for animals to acclimate to test temperatures (Table 7) clearly indicates that most experimental results are based on insufficient acclimation periods to reflect the gradual adjustments made to thermal change by field populations. Only the work by Geller (1975), and possibly Burns (1969b), allowed sufficient time for acclimation. The fact that the results of different authors do not agree led Geller (1975) to the conclusion that it was impossible to calculate the temperature effect for even a single species of Daphnia (Figure 17).

139. Early workers recognized the importance of thermal history on the feeding behavior of zooplankton (Cohn 1958, Nauwerck 1959), but for many years information was unavailable on the period of time necessary to fully acclimate animals to test temperatures. Kibby (1971a) was first to examine acclimation temperature as a factor influencing filtering rates. His results for Daphnia rosea acclimated to 12°C, when compared with results for this species acclimated to 20°C (Burns and Rigler 1967), indicated that filtering rates may be higher at lower temperatures than previously demonstrated (Figure 18). Since the acclimation period of Burns and Rigler was 48 hr, it is evident that this time period is insufficient to allow for complete acclimation.

140. Burns (1969b) allowed four species of Daphnia to acclimate for "several weeks" before conducting her tests. By the standards for acclimation time presented by Geller (1975), a period of about 4 weeks would be needed for Daphnia pulex at temperatures above 15°C. Therefore, it is not clear whether Burns allowed sufficient acclimation time. Her results show that the filtering rate of Daphnia magna increased over the range of temperatures tested, while rates for D. pulex, D. schodleri, and D. galeata reached a maximum at 20°C and declined at higher temperatures. Geller (1975) found that acclimated Daphnia pulex showed

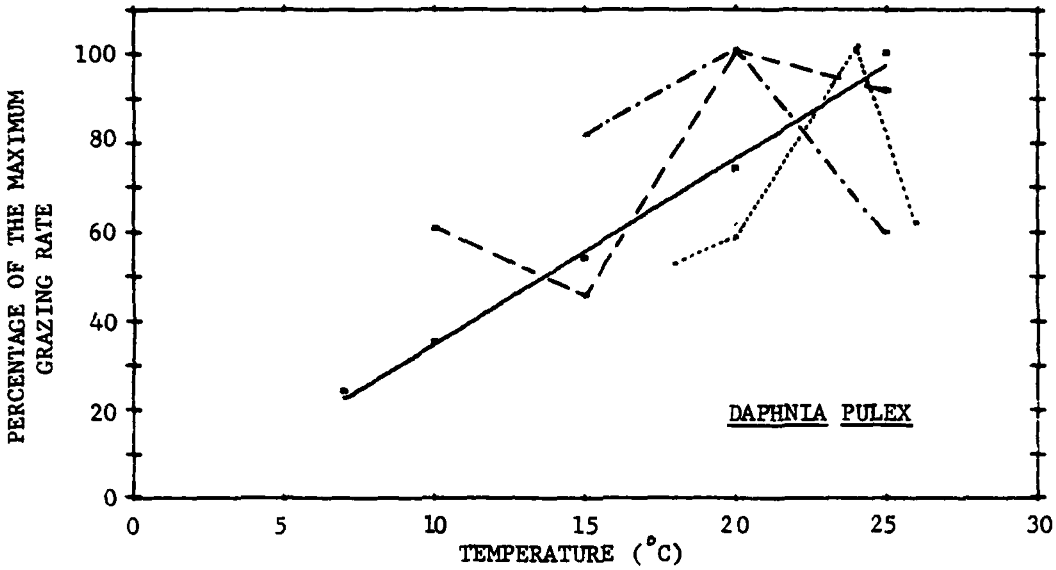

Figure 17. Grazing rate as a function of temperature for Daphnia pulex. Based on the data of Kryutchkova and Knodratyuk (1966) (••••••), Burns (1969b) (-•-•-•), Geller (1975) (———— for long-term acclimation), and Geller (1975) (— — — for short-term acclimation)

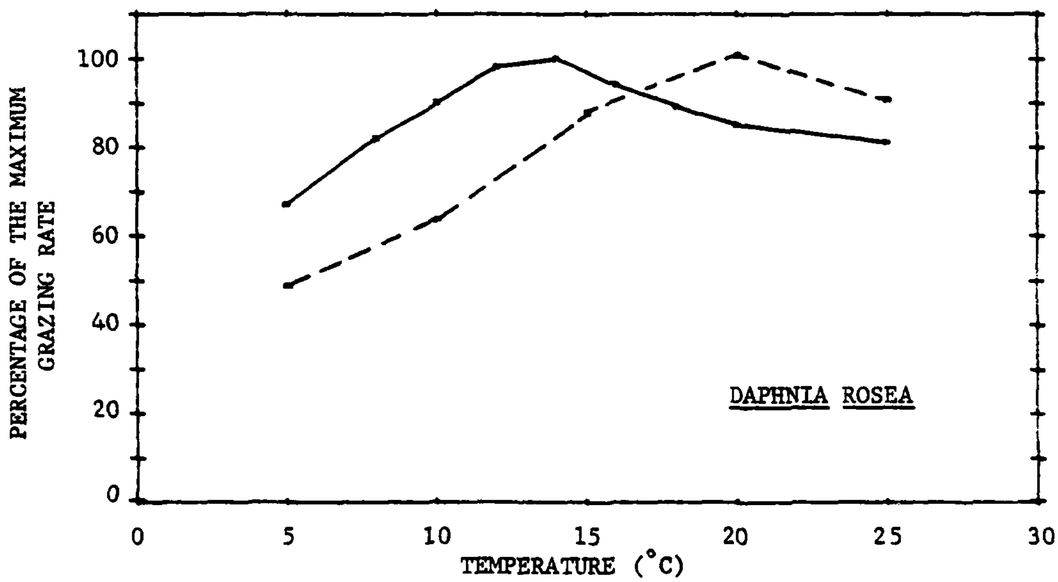

Figure 18. Grazing rate as a function of temperature for Daphnia rosea. Based on the data of Kibby (1971a) (————) and Burns and Rigler (1967) (— — —)

linearly increasing filtering rates with increasing temperature over the range of temperatures tested. Most reported temperature "optima" for grazing must, therefore, be considered to be responses of incompletely acclimated animals to temperature stress. Such results do not reflect the normal physiological response of acclimated animals. These results are, however, valuable when one is considering short-term responses of zooplankters to abrupt changes in temperature, such as might occur upon entrainment in the thermal plumes of power plants.

141. Temperatures of 20° or 25°C are the optimum temperatures for grazing (Table 7). It is clear that these optima are to a great extent artifacts of experimental design. Most authors measure grazing rates at fairly wide intervals, for example 5°, 10°, 20°, 25°, and 30°C. Because these experimental designs did not allow for a continuum of temperatures, it could not be ascertained whether the optimum grazing rate occurred at the cited temperature. Referring to Table 7, one can determine that 20° and 25°C are almost the most frequently measured temperatures.

142. Model construct. The form of the relationship between temperature and grazing rate is unclear for reasons previously discussed. Based on a theoretical argument, a maximum (or optimum) grazing rate must exist at some temperature, for a given food concentration, near the upper lethal limit of the organism. Beyond this temperature one would expect grazing to decline or cease completely as physiological processes become impaired. For field populations not under stress from thermal pollution, it is unlikely that lethal or near-lethal temperatures would occur for long periods (1 day or more in the model).

143. Based on this argument and on the assumption that field populations gradually acclimate to temperature changes, we propose a linear model to describe the relationship between grazing rate and temperature (Figure 19). The equation for Figure 19 can be written,

$$y = 0.67T - 0.33 \qquad (12)$$

where y = scalar of the grazing rate and T = temperature (°C). Such a relationship, although lacking some biological reality, is in

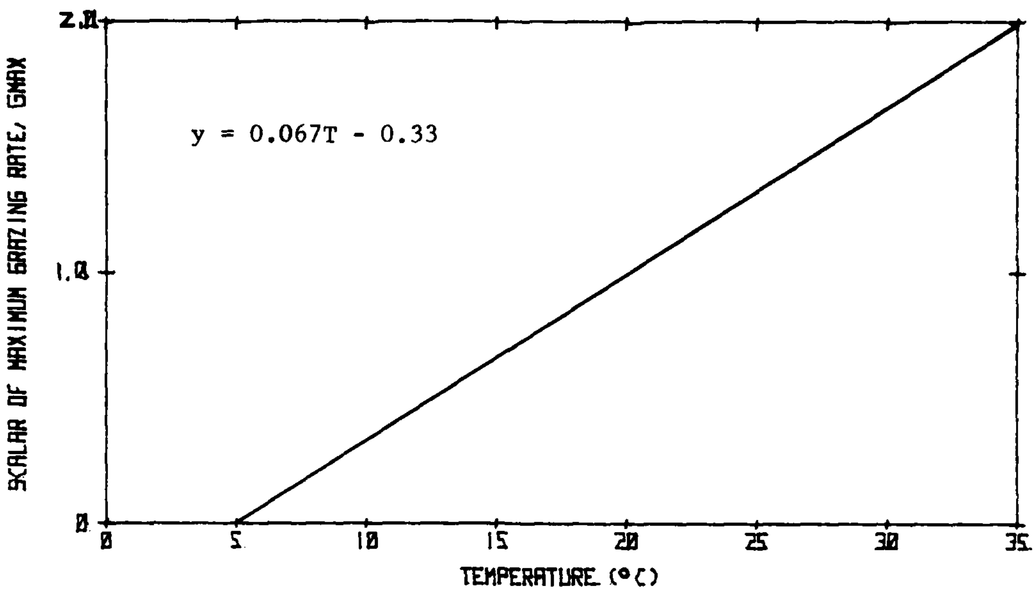

Figure 19. The relation of temperature to the relative increase in grazing rates for animals fully acclimated to test temperatures. The maximum grazing rate is equal to one on the ordinate

accordance with the results of Geller (1975). The bounds of the model are the lower and upper lethal temperatures for the species, approximately 0° to 34°C. This model is predicated on zooplankton populations from temperate lakes and does not consider the synergistic effects of temperature with metabolic processes and food concentration, although these factors are recognized as influencing variables (Chisholm et al. 1975, Hayward and Gallup 1976).

144. Clearly, a second construct is needed if abrupt thermal changes need to be incorporated into the modeling framework. Again, thermal pollution effects serve as an example. The grazing response increases with temperature to a maximum value and then declines at higher temperatures, with a cessation of grazing at the upper lethal limit (Figure 20).

145. Most laboratory studies support a function of this form. The optimum grazing rate usually occurs at or only slightly above the acclimation temperature of the animal. Therefore, the temperature at which the maximum grazing rate occurs differs for an animal acclimated

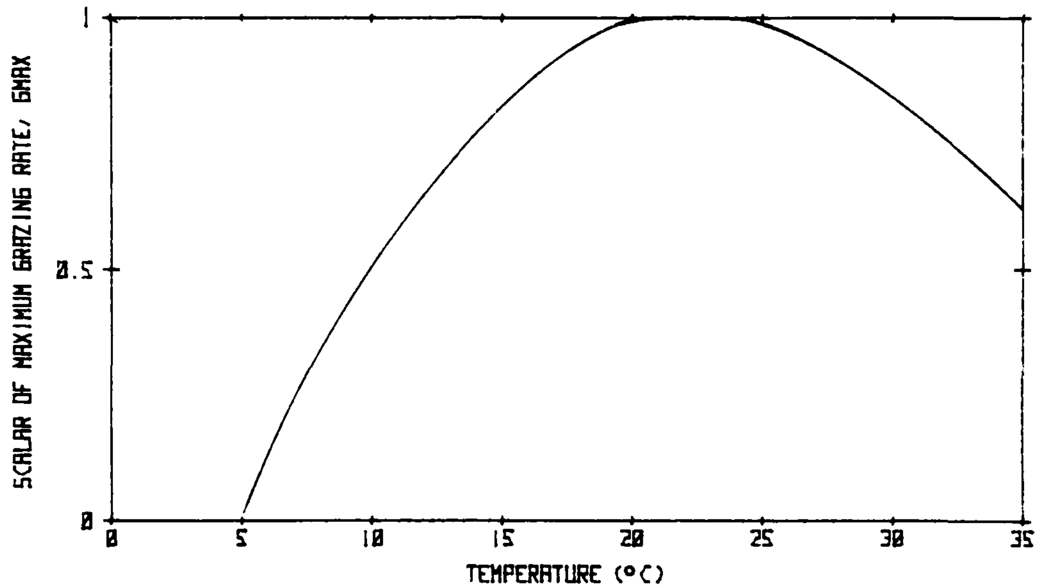

Figure 20. The relation of temperature to the relative increase in grazing rate for animals incompletely acclimated to test temperatures. In this example, the animal is fully acclimated to 20°C. The maximum grazing rate is equal to one on the ordinate

to 10°C, and subjected to a sudden heat stress, than it will be for an animal acclimated to 20°C and subjected to the same relative stress. Furthermore, upper and lower lethal temperature limits will vary.

146. Because no data are available on the maximum grazing rates of animals fully acclimated to various temperatures, the following construct is proposed. For animals acclimated to temperatures between 0° and 30°C, the maximum grazing rate is assumed to occur at the acclimation temperature and to remain constant with increasing temperature until the acclimation temperature plus 20 percent is reached. If the acclimation temperature is 30° to 34°C, the maximum grazing rate is assumed to be constant up to 34°C. Temperatures above 34°C are considered lethal. Temperatures at 30°C and above are not likely to normally occur in the field for periods long enough for acclimation to occur. Indeed, Geller (1975) stated that *Daphnia pulex* could not be successfully raised for any length of time at temperatures above 27°C. Burns (1969b) noted that temperatures above 25°C rarely occur in temperate lakes inhabited by *Daphnia pulex* or *D. galeata*, two widely distributed zooplankters.

147. To complete this construct we must define the form of the function above and below the temperatures at which maximum grazing occurs. Experimental results indicate that grazing tapers off less rapidly as temperatures decline from the maximum grazing temperature than occurs as temperatures increase above the maximum grazing temperature. Furthermore, filter-feeding zooplankters tend to graze at a greater rate at temperatures closer to their upper lethal limit than to their lower lethal limit (Figure 20). A generalized biological reaction rate curve similar to that described by Thornton and Lessem (1978) would adequately define this function. The reader is referred to this paper for details. The upper and lower lethal temperature limits must be known for each acclimation temperature. These data are unavailable for all temperatures for even one zooplankton species. In light of this, we have proposed such limits based on qualitative judgment (Table 8).

Diel Variations in Filtering and Feeding Rates

148. Most modelers of zooplankton grazing assume that the grazing rate remains constant on a diel basis, the rate being determined only by food concentration and temperature. In recent years it has become increasingly clear that grazing is a complex interaction among food supply and its distribution, zooplankton food habits, feeding behavior, and environmental variables. The role of zooplankton migratory behavior and endogenous rhythms is now recognized as a major influence on phytoplankton dynamics. A number of models now include diel vertical migrations of zooplankton. Bowers (1979) reviewed the role of vertical migration of zooplankton and its incorporation into simulation models of zooplankton grazing. The objective of the present section is to review the experimental evidence for diel variations in the grazing of freshwater zooplankton and to propose a simplified construct for including these changes in the grazing function.

149. Literature synopsis. Nauwerck (1959) in his study of the plankton of Lake Erken was the first worker to comment on diel changes in zooplankton grazing. He found that *Eudiaptomus graciloides* fed more

Table 8

Acclimation Temperature, Upper and Lower Lethal Temperatures, and the Temperature Range for a Constant Maximum Grazing Rate for Zooplankters Exposed to Rapid Temperature Stress

Acclimation Temperature, °C	Lower Lethal Temperature Limit, °C	Upper Lethal Temperature Limit, °C	Temperature (°C) Range Over Which the Maximum Grazing Rate Remains Constant (Ta to 1.2 Ta)
0	--	--	Lethal
5	0	25	5-6
10	0	30	10-12
15	2	33	15-18
20	5	34	20-24
25	7	34	25-30
29	10	34	29-34
30	10	34	30-34
31	12	34	31-34
34	15	34	34
35			Lethal - No Grazing

actively during the day than at night. However, he found the opposite to be true for Daphnia longispina. Haney (1973) reported on unpublished data of Gliwicz, who found that zooplankton feeding declined at night by 7 to 20 percent in two Polish lakes. Haney (1973) found contradictory evidence in Heart Lake, Canada. He found that zooplankton migrated toward the surface at night, but found no difference between the grazing rate at noon and midnight. Repeating the experiment later in the year, he again found vertical migration by some species and a nearly twofold increase in grazing from noon to midnight. Haney noted that the results may reflect differences in environmental conditions and changes in the species composition of zooplankton between the two sampling dates. Starkweather (1975), who subjected laboratory populations of Daphnia pulex to a light:dark cycle of 16:8 hr (16L:8D), found that the maximum filtering rate occurred during the dark phase and that the filtering rate increased significantly with the onset of darkness (Figure 21). The maximum filtering rate, which occurred during the dark phase, was two to three times greater than the minimum rate. Based on additional experiments, Starkweather concluded that his results provided circumstantial evidence that diel changes in filtering rate may be endogenous in nature.

150. Chisholm et al. (1975) observed diel changes in the grazing rate of Daphnia middendorffiana and that feeding peaks occurred consistently at 2400 hr and 1400 hr, times when the water temperature passed through 11°C, the optimum temperature for this species. The authors suggested that Daphnia may maximize their activity when the temperature is optimum. The maximum grazing rate was approximately double the minimum rate.

151. In a series of detailed studies at Lawrence Lake and Little Mill Lake, Michigan, Haney and Hall (1975) found that the filtering rates of Daphnia pulex and D. galeata were significantly higher at midnight than at noon. The filtering rate of medium-sized Daphnia was five to ten times higher at night than during the day. Furthermore, the magnitude of change in filtering rate between noon and midnight was not influenced by water temperature in species of Daphnia, but only by body

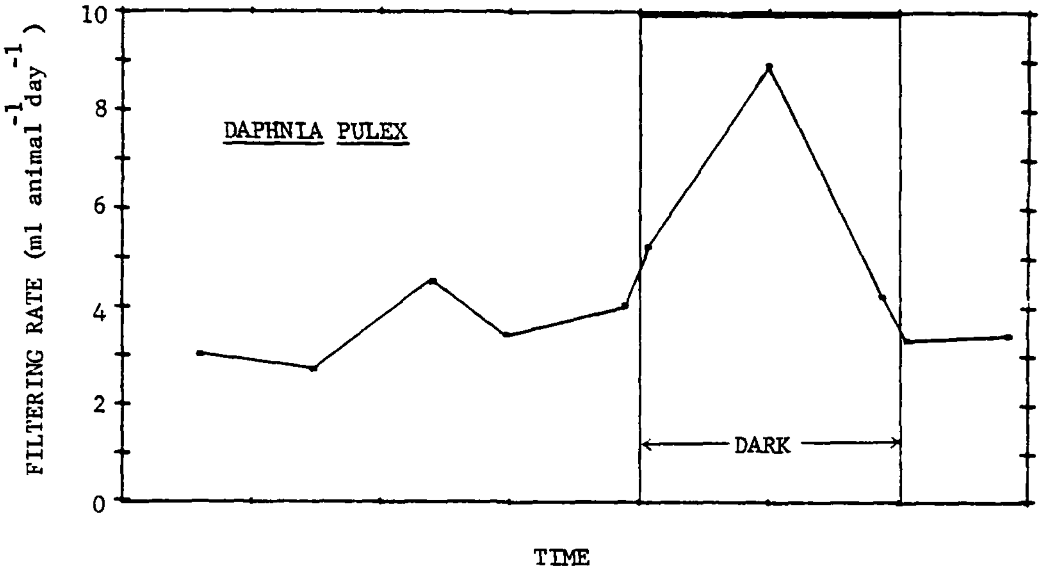

Figure 21. The diel pattern of filtering rate change at 18°C in a light:dark 16:8 photocycle. Based on data from Starkweather (1975)

size. Large animals had a greater increase in filtering rate. Both migrating and nonmigrating populations of Daphnia showed the change in filtering rate between day and night, and the authors concluded that vertical migration was not a necessary prelude to high night filtering. In contrast to these results, Diaptomus pallidus showed no significant difference between the noon and midnight filtering rates, even though some vertical migration toward the surface at night was detected.

152. Haney and Hall (1975) examined the role of light intensity and vertical migration on filtering in Daphnia. Daphnia galeata in Wintergreen Lake, Michigan, and D. pulex in Three Lakes, Michigan, increased filtering rates during the night. The filtering rates of both species were clearly related to photoperiod and showed a bimodal peak (Figure 22). The maximum filtering rate was approximately six times the minimum rate for Daphnia galeata and from 5 to 27 times the minimum, depending on animal size, for D. pulex. Differences in temperature and quantity of filterable particles showed no clear relationship to the daily filtering rate changes. Two species of Diaptomus were also studied

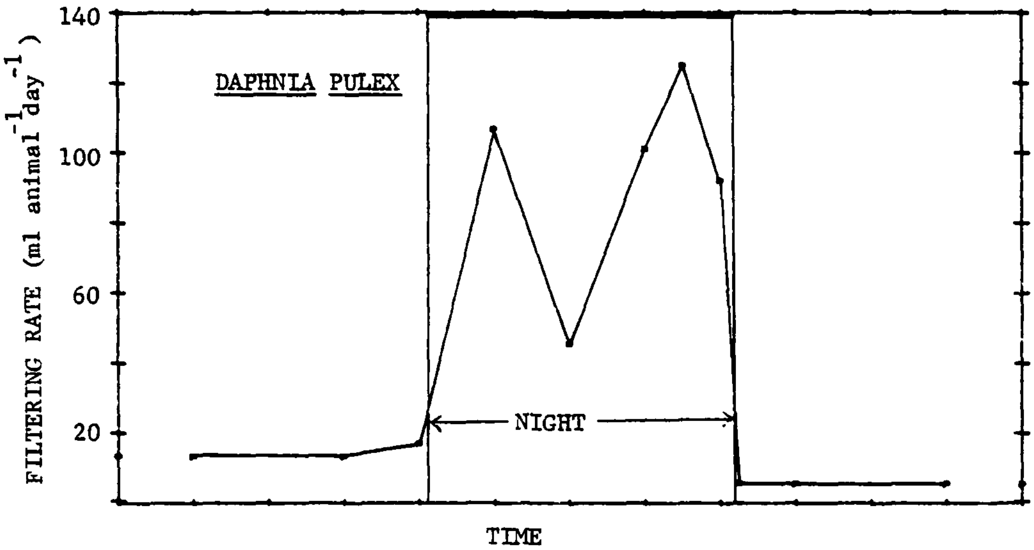

Figure 22. The diel pattern of filtering rate change of *Daphnia pulex* in Three Lakes, Michigan. Based on data from Haney and Hall (1975)

in Three Lakes. No clear increase in the filtering rate could be demonstrated during the night, although the evidence suggested that it may have increased slightly between 2100 and 0200 hr.

153. Haney and Hall noted that *Daphnia* in Wintergreen Lake and Three Lakes should be considered nocturnal grazers because 85 percent of the filter feeding in both lakes occurred during the night period. The authors calculated the error that would result if only the daytime value for grazing rate were used in the estimate of grazing pressure. For Three Lakes, the daytime calculations underestimated *Daphnia* grazing by a factor of 4.2.

154. Haney and Hall concluded that the diel activity patterns of vertical migration and change in filtering rate in *Daphnia* are strongly correlated with light intensity. They suggested that these are endogenous cycles synchronized to a 24-hr time period by relative light changes.

155. Duval and Geen (1976), who examined diel feeding of the zooplankton community of Eunice Lake, British Columbia, also found bimodal grazing during the night period, with maxima occurring at 0200

and 1800 hr or times just prior to sunrise and sunset. Similar results were obtained for populations of Daphnia pulex and Cyclops scutifer from Deer Lake, British Columbia. The maximum feeding rate varied by a factor of 8 over the minimum rate for the Eunice Lake population, and by 5 and 14 for the winter and summer populations, respectively, from Deer Lake. Extrapolation of the diurnal values of feeding to a diel basis resulted in an underestimate of grazing pressure ranging from 37 to 72 percent.

156. Similar diel grazing rhythms have been described by Mackas and Bohrer (1976) for marine filter feeders.

157. Model construct. Although the preceding results are by no means definitive, they do suggest the potential importance of diel grazing cycles for some species of zooplankton. Many models currently employing data based on diurnal grazing values may considerably underestimate the impact of zooplankton populations on their food supply. Diel cycles have been demonstrated for several species of Daphnia. These cladocerans often compose a significant, if not overwhelming, part of the zooplankton biomass of temperate lakes. Therefore, it may be reasonable to treat zooplankters of the entire community as if they behaved like Daphnia.

158. For discussion, we adopted this treatment. The data base developed in this report is designed to function in a model that simulates zooplankton and benthos dynamics, normally on a daily basis. Such a design presents problems in incorporating diel grazing rhythms which ideally must be simulated at a time interval less than 1 day. Additionally, diel cycles in vertical migration could potentially improve model performance by more realistically portraying zooplankton grazing behavior. Bowers (1979) discussed the simulation of vertical migration.

159. Four approaches to including diel changes in grazing rate are presented. Whether one method is better than another cannot be determined until test simulations are conducted against field data. Numerical simulation results may indicate that a diel grazing cycle is unnecessary for certain applications. Because the magnitude of increases in grazing from daytime to nighttime is highly variable and

dependent on species, size, temperature, and possible other factors, we have elected to increase daytime grazing by a factor of five to represent the night value in our examples. The factor five was selected based on the mean of literature values.

a. Method No. 1

160. The most straightforward approach to adjusting the grazing rate to reflect average diel grazing is to correct the maximum grazing rate by either increasing its value, if you assume that the maximum rate is representative of daytime conditions, or by decreasing its value, if you assume that it better reflects nocturnal grazing. There is no evidence to support one of these alternatives as superior to the other. In our opinion the maximum grazing rate better reflects nocturnal conditions, but only simulation with a range of values will clarify this hypothesis. Nighttime grazing rates have been shown to range from 2 to 27 times the daytime rate, depending on such factors as species, food, and water temperature.

b. Method No. 2

161. A second approach to including diel grazing involves these points: (a) set the maximum nighttime grazing rate equal to the maximum grazing rate; (b) calculate the diurnal grazing rate, i.e., $G_{night}/5 = G_{day}$; and (c) assume that zooplankton grazes at the nocturnal rate for the entire period between sunset and sunrise, or some other threshold light concentration (Table 9). For a 16-hr day and 8-hr night (16L:8D), this grazing construct could be written as follows:

$$G_{diel} = \left(G_{day}/24\right) 16 + \left(G_{night}/24\right) 8 \qquad (13)$$

Substituting $G_{night} = 5\ G_{day}$ (14)

$$G_{diel} = \left(G_{day}/24\right) 16 + 5 \left(G_{day}/24\right) 8 \qquad (15)$$

$$= 2.33\ G_{day}$$

The appropriate Ivlev function or linear relationship can be substituted for G_{day}.

Table 9

Values for Relative Change in Light Intensity, as Cited by Haney and Hall (1975), that Represent Threshold Light Intensity for Positive Phototaxis

Species	Rate of Light Change When Vertical Migration Began, sec^{-1}	Reference
Daphnia magna	-0.0013 to 0.0024	Ringelberg (1964)
Daphnia galeata	-0.0007	Haney and Hall (1975)
Daphnia pulex	-0.0021	Haney and Hall (1975)
Daphnia longispina	-0.011	Siebeck (1960)
Bosmina longispina	-0.011	
Cyclops tatricus	-0.011	

c. Method No. 3

162. With the same assumptions presented in Method No. 2, we assumed that a unimodel peak occurs during the night. This peak is the maximum grazing rate. The temporal bounds are set as above, and Figure 23 illustrates this construct for a 16L:8D period. The curve in Figure 23 is one of many possible functions that could be used to describe a unimodal peak. Integrating this curve and simplifying the result indicates that the average diel grazing rate can be written,

$$G_{diel} = 1.48\ G_{day} \tag{16}$$

d. Method No. 4

163. This method is identical to Method No. 3 except that a bimodal peak occurs during the night (Figure 24). Bimodal peaks have been observed in several studies. We have simplified the experimental results by making the two maxima equal in value (they may not be according to some studies) and have set the minimum grazing value between the maxima at 70 percent of the maximum (literature values range from 35 to 89 percent of the maximum). The bimodal curve can be integrated and simplified to show that:

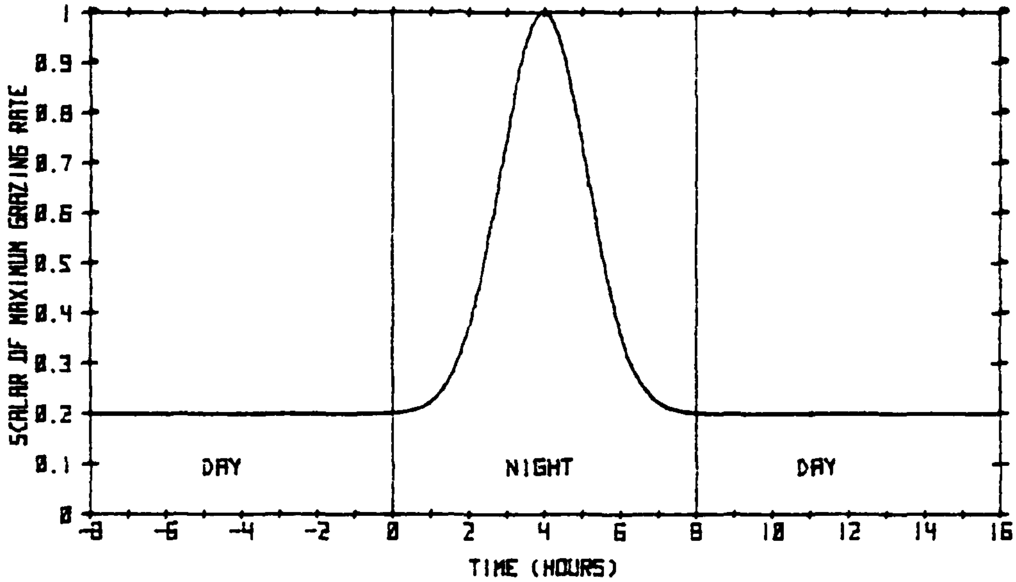

Figure 23. The diel grazing function of filter-feeding zooplankton exhibiting a unimodal peak in grazing during the night. Hour 0 represents the time at which increased grazing begins and hour 8 the time when increased grazing ceases

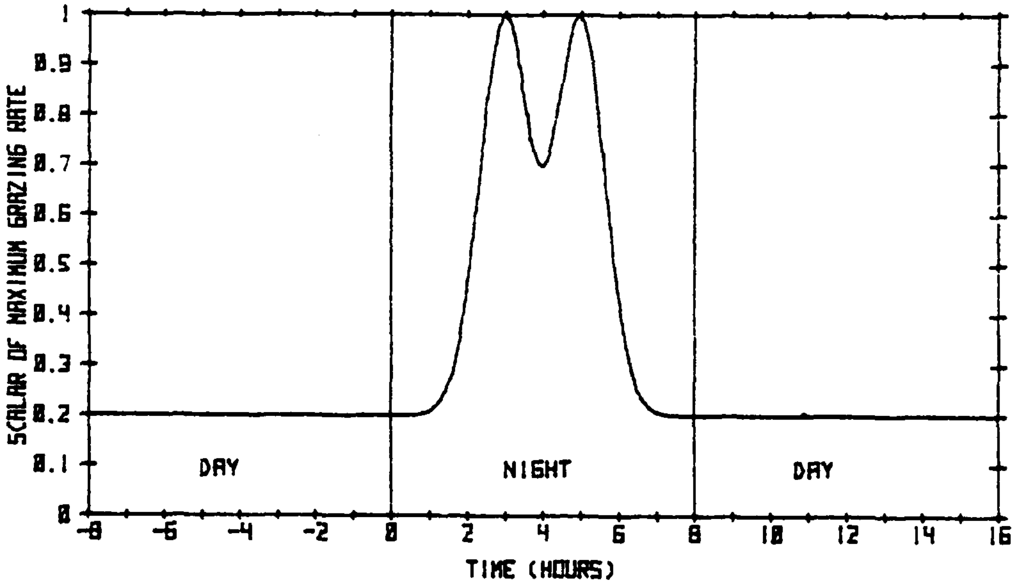

Figure 24. The diel grazing function of filter-feeding zooplankton exhibiting a biomodal peak in grazing during the night. Hour 0 represents the time at which increased grazing begins and hour 8 the time when increased grazing ceases

$$G_{diel} = 1.54\ G_{day} \tag{17}$$

Other solutions are possible.

164. We suggest using Method No. 3 for initial simulation runs.

Consumption by Predatory Zooplankton

165. A predatory zooplankter is difficult to define. In temperate fresh waters, cyclopoid copepods, the cladocerans *Leptodora kindtii* and *Polyphemus pediculus*, and several rotifers, particularly *Asplanchna*, are usually considered predators. However, as Fryer (1957) has pointed out, many of the so-called predatory zooplankters should more appropriately be classed as omnivores. The problem in definition partly arises from the mode of feeding employed by most of the "predatory" species. Almost without exception these species are raptorial feeders; that is, they grasp or seize their prey, whether it be animal or plant material. In the past, most raptorial feeders have been automatically considered predators, the assumption being that raptorial feeding is characteristic of carnivority. The few carefully executed food studies that are available have revealed that this assumption is not always warranted.

166. The central question relevant to this review is whether or not the form of the feeding response by predatory zooplankton species differs from that of herbivorous filter feeders. Quantitative information on the feeding of predatory zooplankters is scarce. The scarcity is partly due to problems in designing experiments to measure food consumption by raptorial feeders. For example, when a carnivorous copepod such as *Cyclops* captures a prey item, possibly *Ceriodaphnia*, not all of the prey is consumed. The process of raptorial feeding often leaves prey dismembered, with a resultant loss in biomass. Brandl and Fernando (1975) estimated that the three species of cyclopoid copepods they studied ingested only about one third of the prey biomass that they attacked. Similar results have been found for the carnivorous marine amphipod *Calliopius laeviusculus* (Dagg 1974).

167. Because data are poorly detailed for predatory feeding, we

have included a summary of reported values for daily ration for both omnivores and predators (Table 10). Daily ration, when expressed as a percentage of body weight, is a good approximation of grazing rate. A synopsis of the literature for freshwater predatory zooplankters follows.

Literature synopsis

168. Shushkina and Klekowski (1968) examined how the daily ration of *Macrocyclops albidus* varied with food concentration. Although their results are not directly convertible to carbon units, they do show that under conditions of short-term food acclimation, consumption increased with increasing food concentration until a maximum rate was reached; thereafter, consumption remained constant with further increases in food concentration (Figure 25). This relation appeared to be true for all developmental stages when fed *Paramecium aurelia* at concentrations from

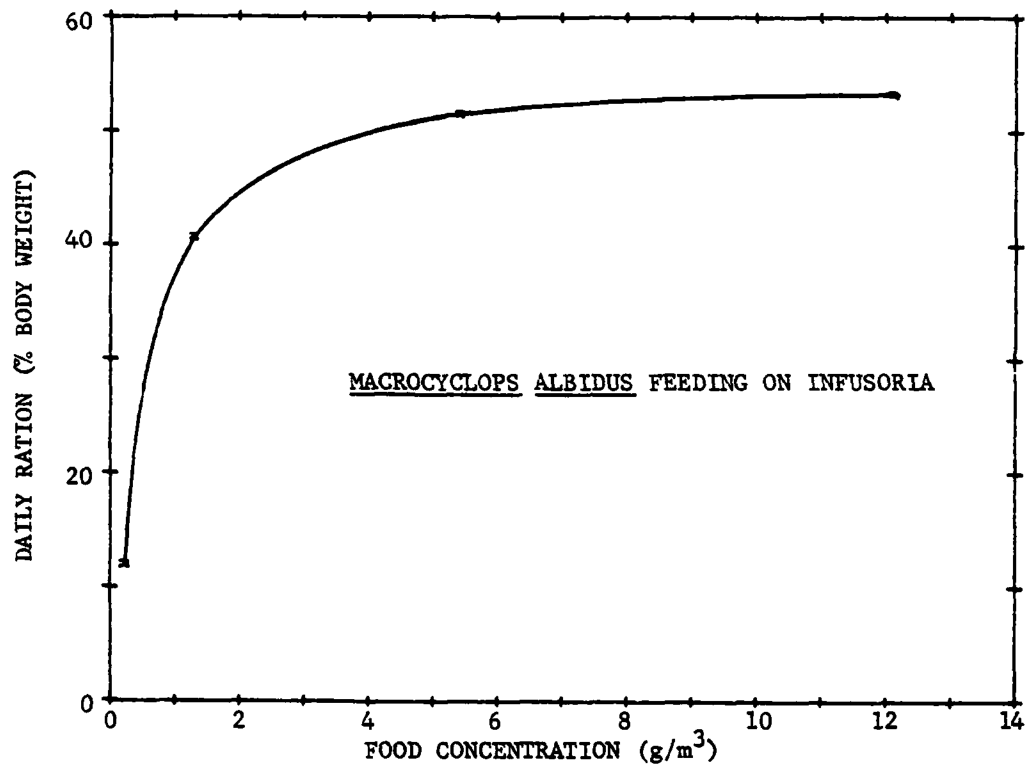

Figure 25. The daily ration of *Macrocyclops albidus* females as a function of food concentration. Based on the data of Shushkina and Klekowski (1968)

Table 10

Published Values for the Daily Ration of the Planktonic Omnivores and Predators

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Cladocera Family: Leptodoridae			
Leptodora kindtii	Natural assemblage of zooplankton	30-48	Hillbricht-Ilkowska and Karabin (1970)
Leptodora kindtii	Zooplankton	5-20	Stepanova (1972)
Order: Eucopepoda Family: Cyclopidae			
Cyclops vicinus	*Chilodonella* sp. *Stylonychia pustulata* *Paramecium caudatum* *Askenasia* sp.	9.6-79.2($\bar{X}$=29.3)	Korniyenko (1976)
Macrocyclops albidus	*Paramecium aurelia*	12-240	Klekowski and Shushkina (1966a)
Mesocyclops leuckarti	Zooplankton	10-34	Stepanova (1972)
Mesocyclops leuckarti	*Ceriodaphnia reticulata* *Artemia salina*	63-113 30-200	Gophen (1977)
Acanthocyclops vernalis	*Stylonychia pustulata* *Paramecium caudatum* *Askenasia* sp.	27.4-64.8($\bar{X}$=41.2)	Korniyenko (1976)
Family: Tortanidae			
Tortanus discaudatus	*Calanus pacificus*	ca 4-98*	Ambler and Frost (1974)

* Marine species. These values are probably overestimates because the authors assumed that any *Calanus* attacked was ingested.

0.1 to 10 g/m^3 wet weight. Their results clearly showed that the grazing rate of this predatory zooplankter can be defined by an Ivlev function identical to the construct used to describe herbivorous zooplankton grazing. Data presented showed that daily grazing rates for Macrocyclops albidus may be as high as 240 percent of body weight, depending on zooplankter age and food concentration (Klekowski and Shushkina 1966a, 1966b).

169. McQueen (1969) found that the predator Cyclops bicuspidatus thomasi fed most extensively on copepod nauplii, both its own and those of Diaptomus, and on rotifers. Few cladocerans and diaptomid copepodids were eaten. Laboratory results showed that as prey density increased, predation rate also increased, usually linearly or with a maximum feeding rate being reached at high prey densities. Field measurements of predation rates on nauplii of Diaptomus oregonensis, D. hesperus, and Cyclops bicuspidatus thomasi, in Marion Lake, British Columbia, agreed well with laboratory results. The predation rate increased linearly with increasing prey density. The rotifer Keratella cochlearis was readily eaten in laboratory studies but was seldom preyed upon in the field, suggesting selective grazing by Cyclops.

170. Confer (1971) examined predation rates of Mesocyclops edax on natural densities of the prey Diaptomus floridanus. When fed Diaptomus copepodite stages V and VI, Mesocyclops showed an increasing predation rate with increasing prey density. This relationship was linear.

171. Stepanova (1972), who discussed the daily rations of Mesocyclops leukarti and Leptodora kindtii, showed (although poorly) that Mesocyclops approached a maximum grazing rate of about 34 percent of body weight per day as food concentration increased. Leptodora, on the other hand, reached a peak grazing rate of 20 percent of wet weight per day as food concentration increased; the rate then declined at higher food densities. No explantion was offered for this occurrence.

172. Fedorenko (1975) found that predation rates of the larval phantom midges Chaoborus americanus and C. trivittatus on the copepod Diaptomus tyrelli increased as prey density increased. The relation of

predation to prey density followed a saturation curve. When Chaoborus was fed Diaptomus kenai and Diaphanosoma, the results were similar. In one experiment, Chaoborus showed a linear feeding response to increasing density of Diaphanosoma.

173. Korniyenko (1976) found in laboratory studies that Acanthocyclops vernalis, when fed various concentrations of four species of infusorians, consumed between 27.4 and 64.8 percent (mean = 41.2 percent) of its body weight per day. Cyclops vicinus ate between 9.6 and 79.2 percent (mean 29.3 percent) of its wet weight per day. The authors noted that their results were in agreement with daily ration values given by Bogatova (1951) for Cyclops strenuus and C. viridis.

174. When adult female Mesocyclops leuckarti were fed Ceriodaphnia reticulata, the daily ration ranged from 63 to 113 percent of the wet body weight per day, depending on temperature (Gophen 1977). As temperature increased from 15° to 27°C, so did the daily ration. Similarly, the rations of adult male and female Mesocyclops also increased when they were fed Artemia salina nauplii at various temperatures. Male daily rations (30 to 200 percent of their body weight) were greater than those of females (30 to 130 percent). These results are generally higher than values reported by Stepanova (1972) under similar temperature regimes.

175. Similar feeding responses to those outlined above have been found for predaceous marine zooplankton (Ambler and Frost 1974, Landry 1978).

Model construct

176. Little quantitative work on feeding by predatory zooplankton has been undertaken. No data are available for freshwater predators to allow the calculation of grazing in carbon units. We have therefore based our proposed model construct for predatory zooplankton grazing on three assumptions:

a. For short-term feeding experiments, the available evidence indicates that grazing follows a linear or saturation curve response to increases in prey density. We assume the saturation curve response to be characteristic and that this response can be described by an Ivlev function (Equation 3). This type of response has been previously demonstrated for herbivorous filter feeders.

b. Under field conditions, wherein zooplankton populations are acclimated to ambient conditions, we assume that grazing by predatory species is linearly related to food concentration (Equation 9). There is currently no literature documentation to support this assumption.

c. Daily rations (Table 10) of predatory zooplankters are an approximation of grazing rates and are within the range of daily grazing rates reported previously for filter-feeding zooplankton. We assume that the entire range of grazing rates is similar for herbivorous and carnivorous zooplankters. Metabolic similarities among herbivores, omnivores, and carvivores support this assumption.

177. We believe the assumptions outlined above are reasonable and will be documented as additional information becomes available. The acceptance of these assumptions will allow the modeler to design a predatory zooplankton grazing function, if desired. Predators could be assigned about 20 percent of zooplankton biomass in the event that herbivorous and predatory zooplankton are divided. This figure was based on ecological growth efficiencies tabulated by Welch (1968).

Seasonal Changes in Grazing

178. Seasonal changes in grazing are highly variable and dependent on the species composition of the zooplankton community, available food supply, temperature, and many other environmental variables. Generally, in temperate lakes minimum grazing rates occur during the winter, followed by increased grazing in the spring and peak rates in early summer. A gradual decline may follow through late summer to fall. Often another minor fall peak in grazing is observed. Major pulses in grazing activity are usually well correlated with peaks in the population density of the predominate zooplankters. A summary of several field studies is presented in Table 11.

Synergistic Effects of Environmental Variables

179. With many model processes, such as grazing, the understanding

Table 11

Seasonal Changes in the Grazing Rate of Zooplankton Communities

Lake	Season	Year	Mean Grazing Rate (% of Wet Weight Per Day)	Percent of Total Annual Grazing	Reference
Heart Lake, Canada	Jan-May	1969	19.2	17.4	Haney (1973)
	Jun-Sep		80.1	61.7	
	Oct-Jan		35.2	20.9	
Lake Vechten, The Netherlands	Mar-Apr	1976-77	9.8	22.0	Gulati (1978)
	May-Sep		24.0	69.0	
	Oct-Nov		5.5	4.5	
	Dec-Feb		2.1	4.5	
Lake Krasnoye, USSR Littoral zone	May	1973	4	1	Andronikova (1978)
	Jun		32	11	
	Jul		120	43	
	Aug		80	28	
	Sep		32	11	
	Oct		16	6	
Pelagic zone	May	1973	0.6	0.6	
	Jun		12	12	
	Jul		37	36	
	Aug		35	34	
	Sep		14	14	
	Oct		4	4	
Lake Balaton, Hungary	Spring	1974-75		30	Zankai and Ponyi (1976)
	Summer			46	
	Fall			20	
	Winter			4	

of system dynamics results from the interpretation of studies that are often designed to examine single variable effects (e.g., the effects of food concentration or temperature on grazing). As a result, we end up mathematically describing model processes by a series of variables that we assume are independent. In many situations this is not a valid assumption. Most modelers realize the inherent problems in attempting to combine experimental results for variables that may not be independent. Unfortunately, few data are available on synergistic effects to clarify these relationships.

180. Hayward and Gallup (1976) are the only workers who have examined potential synergistic effects on zooplankton feeding. Their objective was to identify how feeding would be affected when two or three parameters were altered simultaneously in one experiment. A partial abstract of their work follows.

> Feeding and filtering rates of Daphnia schoedleri were measured at different temperatures, light intensities, food concentrations, crowding conditions, and with different diet species. The rates were compared as well for different sizes, sexes, and reproductive states of the experimental animals. All of the above factors were found to affect feeding rates in a significant fashion in single variate experiments. However, when two or more environmental parameters were varied simultaneously, the previously defined relationships did not hold, and indeed were obscured as extremes of temperatures or cell concentrations were approached. The effects of these parameters which most dramatically altered feeding rates were then determined for assimilation rates and digestive efficiency estimates ... .
>
> Results showed that a change in one environmental parameter can significantly alter Daphnia schoedleri's response to a change in a second parameter. The incipient limiting food concentration was found to be significantly different at different temperatures. Similarly, different shaped temperature curves were obtained as food concentrations were changed, the most dramatic alterations being evident in the extremes. When comparable experiments were performed with ^{14}C-labeled algae, no incipient limiting level was observed for assimilation rates, but rather, peaked curves became evident. Three environmental parameters: temperature, food concentration, and diet species, were found to alter responses to other parameters in a measurable manner. This would seem to indicate that feeding behavior of the zooplankton must be thoroughly understood before results from

AD-A090 832 FISH AND WILDLIFE SERVICE FAYETTEVILLE AR NATIONAL RE--ETC F/G 12/1
SIMULATION MODELING OF ZOOPLANKTON AND BENTHOS IN RESERVOIRS: D--ETC(U)
MAR 80 G R LEIDY, G R PLOSKEY

UNCLASSIFIED WES-TR-E-80-4 NL

2 OF 4
AD
A090832

laboratory or field studies can be applied to even approximate estimates of secondary production in natural conditions.

Model constructs to handle synergistic effects are generally unavailable. Clearly, further research on this subject is needed.

Section B: Benthic Grazing

181. The benthos of freshwater lakes and reservoirs is highly diverse, both taxonomically and functionally, complicating the modeling process. Current understanding of the role of the benthic community in the energy and nutrient dynamics of lentic ecosystems is poor. Indeed, little information is available on the basic life history of most species.

182. Little quantitative information exists on food consumption by benthos. We were unable to find a single reference that documented, in units convertible to carbon, the change in benthic grazing as food concentration increased.

183. The functional diversity of benthic organisms contributed to the problem of defining feeding relationships. Filter feeders, predators, deposit feeders, and surface grazers are all represented in most benthic communities.

184. Because of the lack of quantitative feeding data, it is our opinion that benthic communities are better treated as a whole in any modeling effort. Daily rations (an approximation of the daily grazing rate) of some benthic species are listed in Table 12. Unfortunately, the values listed in this table include most of what is quantitatively known of consumption by benthic organisms.

Effect of Food Concentration

185. Sorokin (1966b), who reviewed data on the filtering rate of *Dreissena polymorpha* on bacteria, showed that the relative feeding intensity increased nearly linearly with increasing bacterial concentration.

Table 12

Daily Ration of Benthic Organisms

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
PHYLUM: NEMATODA			
Plectus palustris	*Acinetobacter* sp.	650	Duncan et al. (1974)
Aphelenchus avenae	fungal mycelia	26	Soyza (1973)
PHYLUM: MOLLUSCA			
Dreissena polymorpha	bacteria	1-12*	Sorokin (1966b)
Goniobasis clavaeformis	aufwuchs	1-24**	Malone and Nelson (1969)
PHYLUM: ARTHROPODA Class: Crustacea Order: Amphipoda			
Hyalella azteca	surface sediments	17-103	Hargrave (1970)
Pontogammarus robustoides	*Cladophora* sp. *Tubifex* sp.	7.4-98.0 18.7-163.0	Kititsyna (1975)
Order: Isopoda			
Asellus aquaticus	*Alnus glutinosa*	25†	Prus (1972)

(Continued)

* It is unclear whether these values are for live weight, shell-free weight, or dry weight.
** Shell-free, ash-free dry weight based on a shell-free weight of 68.5 mg/snail.
† Based on energy units of food and organism.

(Sheet 1 of 3)

Table 12 (Continued)

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Podocopa			
Herpetocypris reptans	*Spirogyra* sp.	128	Yakovleva (1969)
	Zygnema sp.	93	
	Mougeotia sp.	93	
	Chironomus plumosus	66	
	Asellus aquaticus	66	
	fish fry	109	
Heterocyris incongruens	*Spirogyra* sp.	240	Liperovskaya (1948) as cited by Yakovleva (1969)
Class: Insecta††			
Order: Diptera			
Chaoborus flavicans	Natural plankton assemblage	3.6-11.4	Kajak and Dusoge (1970)
Procladius choreus	Chironomidae and Crustacea	7-11	Kajak and Dusoge (1970)
Chironomidae	Variable	100-300	Results of several Russian studies reported by Olah (1976)
Order: Ephemeroptera			
Stenonema pulchellum	*Navicula minima*	23.4-21.4‡	Trama (1972)

(Continued)

†† Larval forms only
‡ Based on dry weights of food and organism.

(Sheet 2 of 3)

Table 12 (Concluded)

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Plecoptera			
Acroneuria californica	*Hydropsyche* sp.	0.2-8.7‡	Heiman and Knight (1975)
	Simulium sp.	1.1-9.0‡	

‡ Based on dry weights of food and organism.

Morton (1971) studied the filtering rate of *D. polymorpha* on various concentrations of several algal and infusorian species. We converted his results to feeding rates and compared the number of cells per animal per day to cell concentration. For all of the six food species offered, the number of cells consumed increased linearly or almost linearly as cell concentration increased. These results (Table 13) suggest that filter-feeding benthic mollusks may have the same functional relationship to changes in food concentration as do filter-feeding zooplankton. At extremely low food concentration levels, filtering continued with no threshold food concentration apparent. Morton's experiments allowed for short-term acclimation to the varying food concentrations. Because the results indicated nearly linear responses to increasing food concentration, it may be reasonable to assume that the food densities tested were below the incipient limiting food concentrations.

Effect of Temperature

186. Although data are limited, it may be reasonable to assume that benthic organisms show the same grazing response to temperature as that shown by zooplankton. Kititsyna (1975) found that the amphipod *Pontogammarus robastoides* increased its daily ration linearly as temperature was increased from 9° to 29°C. Elwood and Goldstein (1975) acclimated the snail *Goniobasis clavaeformis* for 1 week to 13.8°C before testing the snail's grazing response over the temperature range of 10° to 19.3°C. The temperature at which the maximum grazing rate occurred was 14°C. These results indicate a short-term grazing response to temperature similar to that demonstrated for zooplankton (see "Effects of Temperature on Consumption," page 66).

Effect of Diel Variations

187. Although quantitative documentation of diel changes in grazing rate is virtually nonexistent, other evidence (primarily for

Table 13

Filtering Rates of Molluscs Reported in the Literature

Mollusca Taxon	Length (mm)	Tempera-ture (°C)	Type of Food	Range of Food Concentrations Tested (cell/ml)	Range of Measured Filtering Rates (ml/animal/day)	Reference
Sphaerium rivisola	19	?	?	?	up to 2400	Alimov (1965) as reported by Mitropol'skii (1966)
Sphaerium corneum	7	13-15	*Chlorella* sp.	$7.35x10^3$-$3x10^6$	0.23-4976	Mitropol'skii (1966)
Dreissena polymorpha	2-30	20-22	*Chlorella* sp.	?	24-1536	Mikheev (1966)
			bacteria	?	72-1080	
			detritus-*Chlorella* sp.	$5x10^4$-$1.5x10^6$ particles	72-1584	
			reservoir seston	?	3-1200	
Dreissena polymorpha	1.6-3.5	?	colloidal graphite	?	ca 115-1800	Morton (1971)
			colloidal graphite and *Chlamydomonas globosa*	ca $1x10^4$ to $80x10^4$	ca 460 3530	
			colloidal graphite and *Pedinomonas minar*	ca $1.6x10^3$ to $1.4x10^5$	ca 450-1060	
			colloidal graphite and *Pediastrum boryanum*	ca 4 to 160	ca 265-720	
			colloidal graphite and *Euglena spirogyra*	ca 3 to 430	ca 185-1120	
			Colloidal graphite and *Cosmarium botrytis*	ca 56 to 2820	ca 670-1700	
			Colloidal graphite and *Pleodorina illinoiensis*	ca 6 to 640	ca 300-1300	

stream macrobenthos) indicates that some benthic invertebrates feed more at night. Kroger (1974) suggested that nocturnal activity may have evolved, in some aquatic insects, as a protective mechanism against trout predation. Elliott (1968) documented a significant diel foraging pattern for the mayfly *Baetis rhodani*. Nymphs moved to the upper surfaces of stones to feed at night, and foraging apparently peaked right after sunset. *Baetis flavistriga*, collected 2 hr after sunset, contained significantly more food biomass than those nymphs collected 4 hr earlier (Ploskey 1978). Although we realize that some species are day active (e.g., some caddisflies), for modeling purposes we recommend that diel grazing constructs for zooplankton be tested in benthos simulations to determine whether such a construct improves results. Only future work on diel grazing of reservoir benthos will unequivocally justify such a formulation.

Section C: Model Constructs

188. A sound data base does not exist on which to establish firm model constructs for benthic grazing, and much more research is needed. Consequently, we propose to model benthic grazing in the same manner as described for zooplankton. The only major change is that food concentration should be expressed on a square meter basis, and a diel grazing correction should not be employed unless its use improves simulations. We again recommend the use of Equation 9, which corrects for the effects of food concentration in acclimated animals, and Equation 12, which corrects for the effects of temperature in acclimated animals. We base this grazing proposal on the same assumptions outlined under the model construct of consumption by predatory zooplankton. Most modelers have used this approach when simulating the benthic community.

Summary of Constructs

189. The constructs described below are equally applicable to zooplankton and benthos except as noted. Consult the text for analyses and details.

Definitions

b = zooplankton or benthos biomass

$B = B_t$ = concentration of food at time t (mg $C \cdot m^{-3}$ - zooplankton; mg $C \cdot m^{-2}$ - benthos)

B_i = concentration of food of type i (mg $C \cdot m^{-3}$ - zooplankton; mg $C \cdot m^{-2}$ - benthos)

G = observed grazing rate (mg C·mg $C^{-1} \cdot day^{-1}$)

G_{max} = maximum grazing rate (mg C·mg $C^{-1} \cdot day^{-1}$)

G_{diel} = diel grazing rate (mg C·mg $C^{-1} \cdot day^{-1}$)

G_{day} = diurnal grazing rate (mg C·mg $C^{-1} \cdot day^{-1}$)

G_{night} = nocturnal grazing rate (mg C·mg $C^{-1} \cdot day^{-1}$)

W_i = preference factor for food of type i (unitless; ranging from 0 to 1)

k and Z = proportionality constants

y = scalar of the maximum grazing rate, G_{max} (unitless; ranging from 0 to 2)

T = temperature (°C)

Step 1 - Food Concentration

190. To obtain a baseline grazing rate that is corrected for the effects of food concentration, solve for G in the equation:

$$G = ZB_t \left[1 - e^{-kB_t}\right] \qquad (9)$$

where B_t is measured in the field, Z is defined by:

$$Z = 10^{(-3.2295 - 0.0678 \log B_t)} \qquad (10)$$

k is defined by:

$$k = 10^{(-2.9664 - 0.9787 \log G_{max})} \qquad (6)$$

G_{max} is defined by:

$$G_{max} = ZB_t \qquad (8)$$

We assume that most natural populations are fully acclimated to food concentrations and therefore recommend the use of the above construct (Equation 9). However, occasionally populations may be incompletely acclimated and, in such cases, solve for G in the equation:

$$G = G_{max}\left(1 - e^{-kB}\right) \tag{3}$$

where B is measured in the field, k is defined by:

$$k = 10^{(-2.9664 - 0.9787 \log G_{max})} \tag{6}$$

and G_{max} is defined by:

$$G_{max} = 0.0788 + 0.0003105B \tag{7}$$

The rate of consumption obtained above (G) may also be obtained for zooplankton and benthos communities that have more than one food source. This procedure is given in Step 2. If only one food type is available, proceed to Step 3.

Step 2 - Food Selectivity

191. The grazing rate of zooplankton or benthos on a particular food item (i) is given by the equation:

$$G_i = ZB_t\left[1 - e^{-kB_i \cdot \left(\frac{W_iB_i}{\Sigma W_iB_i}\right)}\right] \tag{11}$$

where Bi measured in the field, k is defined by Equation 6 (Step 1), Bt = concentration of food at time t (measured in the field), Z is defined by Equation 10 (Step 1), and W_i is the same for all potential food sources, except for filamentous blue-green algae (where $W_i = 0 - 0.3$). When data are available on the fractional composition of foods in the environment, W_i should be set equal to the fraction that a particular food contributes to the total. The baseline grazing rate G, corrected for food concentration, is given by the sum of the grazing rates on all individual food items obtained from Equation 11. Proceed to Step 3.

Step 3 - Temperature

192. After obtaining a grazing rate G that has been corrected for the effects of food concentration (from Equation 9, Step 1) or for the effects of food concentration and selection (Equation 11, Step 2), the rate must also be corrected for the effects of temperature. This correction may be accomplished by multiplying G by a scalar (y) that is defined by:

$$y = 0.67T - 0.33 \tag{12}$$

where y is a scalar and T = temperature (°C). Equation 12 is based on the assumption that most natural populations are fully acclimated to temperature. For incompletely acclimated animals, refer to Figure 20 in the text and to Thornton and Lessem (1978). Proceed to Step 4.

Step 4 - Diel Variations

193. To correct zooplankton grazing rates for the effects of diel variations in consumption, we recommend Method 3. This method assumed that the grazing rates obtained from Equation 9 (Step 1) and Equation 11 (Step 2) represent mean daytime rates and as such should be multiplied by a correction factor to account for increased nighttime grazing (G_{diel} = Factor × G_{day} = Factor × G). G_{diel} is the average diel rate, and the correction factor is obtained from Method 3 (paragraph 162).

Step 5

194. Grazing rates obtained from Steps 1-4 above must be multiplied by the biomass of the model compartment to yield the weight of

carbon consumed daily [i.e., b (mg carbon) times G (mg carbon·mg carbon^{-1} ·day^{-1}) = biomass of food consumed daily (mg carbon·day^{-1})]. For use in Equation 1, consumption should be left as a weight-specific rate G.

Section D: Conclusions

195. The mathematical formulation for feeding is one of the most critical elements in the equation describing zooplankton and benthos population dynamics. Filter-feeding zooplankton make up a greater proportion of the zooplankton community, both numerically and as biomass, than do the carnivores. Consequently, the feeding relations of filter feeders have been more heavily emphasized. More information is available on the dynamics of zooplankton feeding than is available for benthos. Even so, the feeding relations of most filter-feeding zooplankters are unknown and caution must be used in extrapolating grazing results to all species.

196. Factors which influence food consumption by filter-feeding zooplankton include animal density, size, sex, reproductive state, nutritional or physiological state, as well as the type, quality, concentration, and particle size of food. Other factors include water quality and temperature.

197. Papers that examined the effects of food concentration on feeding rate must be interpreted as short-term feeding responses of incompletely acclimated zooplankters. We believe the following hypothesis to be true. For short-term incubation periods, zooplankters respond to increasing food concentrations by increasing their grazing rate in a curvilinear manner, where feeding rate attains a constant maximum value. If zooplankton are allowed to acclimate at the test concentrations for longer periods (possible 1 to 6 days), then digestive enzyme acclimation may occur and the feeding rate response is linear.

198. Threshold food concentrations for feeding have not been demonstrated for freshwater zooplankters. Further, most zooplankton feed on particles of 100 μm or less. Little quantitative data exist on the feeding of predatory zooplankton and virtually nothing suitable for

modeling purposes could be found for the benthic community.

199. When detritus is included as a food source in a grazing formulation, it should be given equal preference, according to availability, with other suitable foods. Published data generally indicate that the zooplankton community, as a whole, is capable of filtering and consuming all major algal groups, including the blue-green Cyanophyta. Filamentous algal forms are difficult for most zooplankters to consume. Rejection and reduced feeding may occur in the presence of large quantities of filamentous algae.

200. There are species differences as well as age differences in the filtering response of zooplankton to temperature. In addition, the previous thermal history of the animal is extremely important in determining the grazing rate. Most reported temperature "optima" for grazing must be considered to be responses of incompletely acclimated animals to temperature stress. These results are valuable when one is considering short-term responses of zooplankters to abrupt changes in temperature. Fully acclimated animals, such as might be found in a field population, show a linear increase in grazing with temperature over the temperature range normally experienced in temperate lakes and reservoirs.

201. Not all zooplankters or benthos show diel variations in grazing rate. For those that do, diel patterns of foraging often are correlated with light intensity and can result in significant changes in the grazing rate. Grazing rates often are highest during the dark period.

202. Synergistic effects of environmental variables on grazing are poorly understood and model constructs to handle synergistic effects are currently unavailable.

PART IV: ASSIMILATION EFFICIENCY, EGESTION, AND EXCRETION OF ZOOPLANKTON AND BENTHOS

Introduction

203. Assimilation (A) is the food absorbed from an individual's digestive system. Assimilation efficiency (A/G) is the proportion of consumption (G) actually absorbed (Sushchenya 1969, Odum 1971, Wetzel 1975). Although the term A/G is usually used in reference to individual organisms, it also can be applied to populations. Egestion is food that is not assimilated by the gut and which is eliminated as feces (Pennak 1964). By contrast, excretion is a waste product formed from assimilated food and generally is eliminated in a dissolved form.

204. Energy flow refers to the assimilation of a population and is designated as the sum of production (P) and respiration (R), i.e., $A = P + R$ (Sushchenya 1969; Odum 1971). The efficiency of energy flow in a population, $\frac{P + R}{G}$, may be approximately equal to the assimilation efficiency of an individual in that population (Sushchenya 1969). However, since A/G often depends on age (Schindler 1968, Waldbauer 1968, Winberg et al. 1973, McDiffett 1970, Lawton 1970, Fischer 1972, Pilarska 1977b), the A/G of an individual may differ significantly from that of the population. Population A/G is essentially the mean A/G of the individuals composing the population and therefore depends on the age-class structure of the population. At the community level, the efficiency of energy flow through trophic webs ultimately influences the rates of fish production and eutrophication, both of which are important to man.

205. The importance of assimilation efficiencies in the modeling of zooplankton and benthos is paramount, particularly when models approach trophic dynamics by way of feeding equations. Assimilation efficiencies may be used in feeding equations to modify consumption and to yield the quantity of energy entering an individual or population. In most models, a constant A/G value is used to modify consumption (e.g. 0.70, Menshutkin and Umnov 1970; 0.70, Umnov 1972;

0.57, MacCormick et al. 1972; 0.80, Male 1973; 0.70, Steele 1974; 0.20, Thomann et al. 1975; 0.20 and 0.50, Scavia et al. 1976), but in other models A/G ratios were varied (e.g., 0.50 to 0.76, DiToro et al. 1971; 0.50 to 0.70, Baca et al. 1974; 0.64 to 0.90, Ross and Nival 1976). Assimilation was determined by the difference in consumption and the quantity: excretion (E) plus egestion (F), in models by Zahorcak (1974) and MacCormick et al. (1974). A potential drawback to this method is that literature data on E and F are relatively scarce. However, if assimilation efficiency and consumption data are used to estimate E and F, a fairly large data base is available in the literature. Assimilation efficiencies have been used to determine the quantity of matter or energy entering a detrital pool from egestion or excretion (Menshutkin and Umnov 1970, Patten et al. 1975, Swartzman and Bentley 1978). The difference in consumption (i.e., when G = 1) and A/G represents the fraction of consumption that is egested and excreted. We have used this method to estimate E and F losses from zooplankton and benthos.

206. Our approach to assimilation, egestion, and excretion was to tabulate A/G (Appendix C) and to set up frequency distributions of A/G and $\frac{F + E}{G}$ for potential model compartments (Figures 26-35). In doing so, we hoped to attain the largest possible data base and determine the degree of variation among values within potential model compartments. The following discussion primarily concerns assimilation efficiencies and factors influencing A/G. Because A/G and $\frac{F + E}{G}$ are additive inverse functions (i.e., $\frac{A}{G} + \frac{(F + E)}{G} = 1$), the discussion also indirectly applies to egestion and excretion (i.e., as A/G changes in response to environmental conditions, $\frac{F + E}{G}$ also must exhibit changes that are of equal magnitude but opposite in direction). Thus, Figures 26 and 27 are mirror images of Figures 34 and 35, respectively. Both A/G and $\frac{F + E}{G}$, from frequency distributions, are to be used as multiplicative modifiers of consumption to yield the quantities of carbon assimilated and lost, respectively.

207. Energy equations of individuals or populations are essential to a thorough understanding of assimilation efficiency. A complete energy equation may be expressed as:

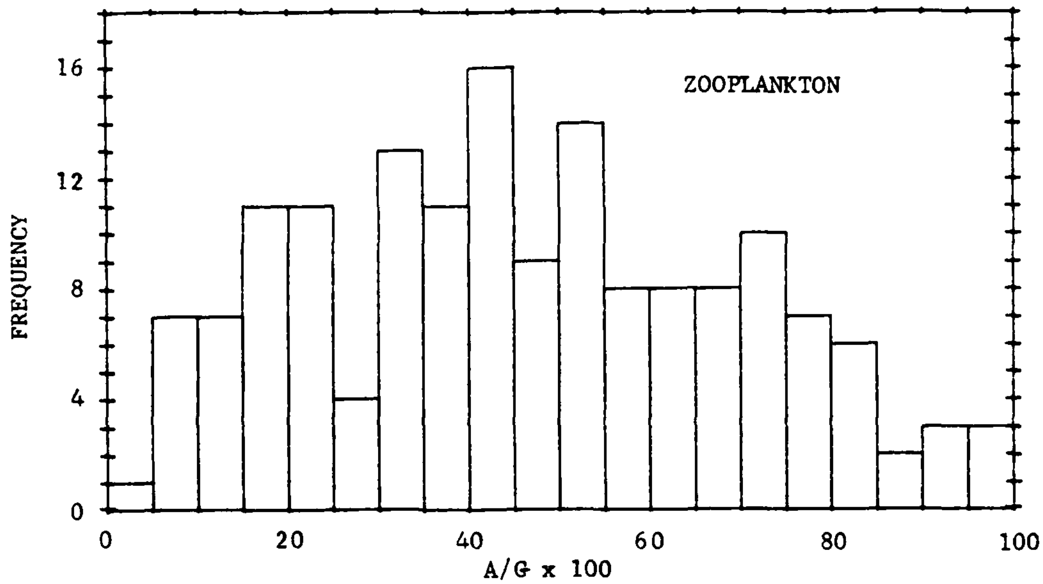

Figure 26. Frequency histogram of zooplankton assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

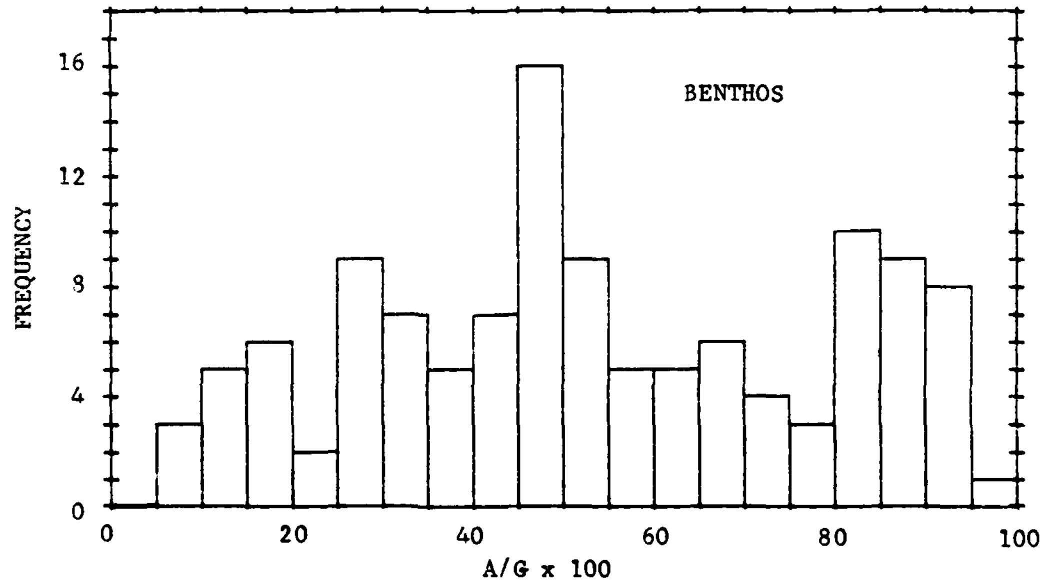

Figure 27. Frequency histogram of benthos assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

$$G = P_{(g + r + ev + s)} + R + F + E \tag{18}$$

where G = consumption; P = production, elements of which are growth (g) reproduction (r), exuvia (ev), and secretion (s); R = respiration; F = egestion; E = excretion. Assimilation efficiencies can be estimated in two ways from the basic energy equation, i.e., $\frac{A}{G} = \frac{P + R}{G}$, and $\frac{A}{G} = \frac{G - F - E}{G}$.

208. In the last two decades, radioactive-isotope methods that directly measure uptake have been applied (see Appendix C for a tabulation of methods). These methods use radioisotope movements to evaluate energy parameters in Equation 18. Conover (1966a) developed an ash-ratio method that did not require quantitative measurements of G and F. All methods have technical problems, and results produced by the various methods are often far from similar (Conover 1966a, Streit 1976, Pechen'-Finenko 1977). To better understand why the assimilation efficiencies cited in the literature are so variable (ca 2 to 99 percent, Figures 26 and 27), we have examined the methods and environmental factors which influence them.

Methodology

209. One of the earliest methods was to evaluate:

$$\frac{A}{G} = \frac{P + R}{G} \tag{19}$$

Production (P) in Equation 19, often is measured in terms of growth (Pg) (Czeczuga and Bobiatynska-Ksok 1972, Fischer 1972, Trama 1972) or perhaps as growth and exuvial production (Pg + Pev) (Lasker 1966) or as growth and reproduction (Pg + Pr) (Richman 1958, Kryutchkova and Rybak 1974, Duncan et al. 1974). However, rarely are all components of production, including estimates of secretion (Ps), determined.

210. Secretions lost to the environment during feeding and upon egestion may constitute a significant portion of production (McDiffett 1970). Otto (1975) estimated Pg, Pev, and Ps in larval *Potamophylax*

cingulatus (Trichoptera) and found that Pev and Ps constituted 16.3 percent (4.1 and 12.2 percent, respectively) of total production. Had he neglected these parameters, A/G would have been significantly underestimated.

211. Potential errors in the estimation of respiration or consumption are discussed under their respective headings. It is sufficient to conclude that potential errors are numerous, and they all decrease the accuracy of A/G estimates.

212. When A/G is calculated with three independently determined parameters (i.e., P, R, and G), researchers may encounter fairly high variation among results. This variability often results because independent determinations of P, R, and G are conducted under different experimental conditions. For example, Comita (1964) estimated the consumption of *Diaptomus siciloides* by measuring changes in the concentration of one food item (*Pandorina* or *Chlamydomonas*) before and after feeding, in 50 ml of pond water. Respiration was determined in small, 2-ml vials which contained no algae. Production was estimated by evaluating reproduction (Pr) exclusively. This estimation was made by computing the daily egg production of females that were collected from the field 8 years earlier.

213. The equation used to calculate assimilation efficiency (Zimmerman et al. 1975) is:

$$\frac{A}{G} = \frac{G - F - E}{G} \qquad (20)$$

However, most authors omit the excretion term (E) because it is difficult to quantify and is sometimes considered negligible (Lawton 1970, McDiffett 1970, Daborn 1975, Sweeney and Schnack 1977). Technically, the following equation measures absorption efficiency (Ricker 1968) or incorporation (Lasker 1960, Bell and Ward 1970) and not assimilation efficiency:

$$\frac{A}{G} = \left(\frac{G - F}{G} \right) \qquad (21)$$

214. The excretion component (E) sometimes appears to be insignificant and probably could be eliminated from assimilation estimates. When Daphnia pulex swallowed algae whole, it lost only 4 percent of its ingested carbon as dissolved organic carbon (DOC) (Lampert 1978). Excretion by Hexagenia limbata was generally less than 1 percent of consumption (Zimmerman et al. 1975).

215. In contrast, Johannes and Satomi (1967) found that Palaemonetes pugio (an estuarine decapod) lost DOC one third as fast as it consumed particulate organic carbon (POC). This estimate is probably high, because some of the DOC measured undoubtedly was derived from food items ruptured during ingestion (Conover 1966a). Up to 17 percent of the algal carbon filtered by Daphnia pulex was lost as DOC from ruptured cells (Lampert 1978). Perhaps the best quantitative approach is to combine F and E and simply measure all losses (Johannes and Satomi 1967). Until more research is conducted, researchers cannot be certain of the magnitude of error involved when E is not evaluated. Apparently it varies among taxa. For the purpose of this model, this potential overestimation of A/G is considered as part of the random error affecting all values.

216. Quantitative collection of feces, especially from small zooplankton, is perhaps the most serious problem with the $\frac{G - F - E}{G}$ method. In macrobenthos, however, the quantitative collection of feces is not always a problem (Lawton 1970, McDiffett 1970). Torn fecal pellets and the subsequent loss of feces, as DOC or POC, usually results in an overestimation of A/G (Conover 1964, 1966a). The situation is complicated by the suspension and reconsumption of zooplankton feces. Coprophagy results in underestimates of F and G and overestimates of A/G (Conover 1966a, Schindler 1968). Unless precautions are taken (e.g., short feeding periods), these errors can be very significant. Though the loss of feces is the most common source of error, the collection of foreign matter such as algae, exuvia, bacteria, fungi, or detritus with the feces, especially in prolonged experiments, may result in an underestimation of A/G (Conover 1962, 1966b). Lawton (1970) discussed

in some detail the potential sources of error in determinations of A/G by Equation 21. He concluded as did Conover (1964) that most of the potential errors tend to overestimate A/G.

217. Since previous methods failed to yield comparable results, Conover (1966a) developed an ash-ratio method. His method does not require quantitative collection of feces nor measurements of consumption. The method is based on the assumption that the inorganic fraction (ash) of ingested foods is unaffected during gut passage. Assimilation efficiency is defined as

$$\frac{A}{G} = \frac{F' - E'}{(1-E')\ (F')} \times 100 \tag{22}$$

where F' and E' are the fractions of organic matter (i.e., ash-free dry wt:dry wt ratio) in the ingested food and feces, respectively.

218. Prus (1971), who calculated the A/G of *Asellus aquaticus* (Isopoda) by the ash-ratio and $\frac{G - F}{G}$ methods, found that *Asellus aquaticus* excreted minerals in excess during the winter and absorbed them during the summer. The differential use of minerals by this species thus rendered the ash-ratio method unreliable (Prus 1971).

219. At one time, the most promising methods appeared to be those in which foods were labeled with radioisotopes of phosphorus (Marshall and Orr 1955a, 1956; Cohn 1958) or carbon (Monakov and Sorokin 1960, Schindler 1968, Vannote 1969). Using these methods, investigators can directly measure the accumulation of isotopes in the body, excreta, and feces of an animal, as well as provide an estimate of consumption. Though many variations exist, the basic steps of the method are as follows: (a) label food items and correlate the radioactivity, in counts per minute (cpm), to the caloric value of the food; (b) feed animals labeled food (preferably for a short period of time so that defecation and excretion of isotopes are minimal); and (c) feed animals unlabeled food until all radioisotopes in the gut have been eliminated. By measuring the difference in radioactivity accumulated in the body of the animal before and after the elimination of radioisotopes, a researcher can estimate consumption and assimilation, respectively. Radioactivity of

the respired CO_2 and feces provides estimates of E and F, respectively. Thus, A/G can be calculated by using the terms A = (cpm in the body and CO_2) or (cpm consumed minus cpm in F and CO_2) in the numerator, and G = (cpm consumed) or (cpm in the body, F, and CO_2) in the denominator.

220. Radioisotope methods often are considered to be significantly more accurate than the other methods of determining A/G (Marshall and Orr 1955b, Sorokin 1966a, Pechen'-Finenko 1977). The basis for this belief is that radioisotope movements into an animal constitute the only direct measurements of consumption and assimilation. By contrast, a number of researchers seriously question the value of most tracer studies conducted to date.

221. Johannes and Satomi (1967) stated that most A/G values determined by radiocarbon methods are overestimates. Overestimates result from losses of unlabeled materials from the gut wall to the gut lumen. Unless the worker is absolutely sure that no ^{14}C is excreted, respired, or lost to the environment, the experiment is uninterpretable without detailed information on reaction kinetics (Conover and Francis 1973). Lampert (1975) demonstrated that ^{14}C losses (i.e., as $^{14}CO_2$) can be accurately measured only during feeding experiments. Carbon losses as $^{14}CO_2$ usually are negligible when measured at the end of feeding periods (Schindler 1968, Kibby 1971b); however, in _Daphnia pulex_ monitored during feeding, ^{14}C losses were about 10, 20, and 30 percent of assimilated carbon in 10-, 60-, and 300-min experiments, respectively (Lampert 1975). Unmonitored losses of this magnitude result in significant overestimates of A/G. Lampert (1975) developed a model of ^{14}C loss for _Daphnia pulex_.

222. Some of the assumptions on which the isotope methods are based apparently are invalid. For example, the specimen is assumed to be a single compartment system in which there is instantaneous and complete mixing of labeled and unlabeled compounds. In addition, labeled compounds are supposedly evenly distributed and do not recycle. Unfortunately, several pools of carbon and phosphorus with different turnover rates have been demonstrated and tracer recycling does occur (Conover 1964, Conover and Francis 1973, Lampert 1975). Conover (1961)

recognized two phosphorus pools in Calanus finmarchicus, and Lampert (1975) stated that Daphnia pulex was not a single compartment system. Conover and Francis (1973), who developed a multicompartment model to account for tracer recycling among compartments, stated,

> Unless it is known that no recycling of isotope has occurred, the assumption of linear uptake, when in fact the system is not linear, even for short periods, can lead to significant errors in the estimation of ingestion or feeding.

223. In summary, none of the methods of assessing assimilation, egestion, and excretion are invariably foolproof, but one method may be significantly more accurate than another for a particular species or under specific experimental conditions. Although assimilation efficiencies have been calculated for many animals (Appendix C), many of the estimates are probably of limited value. Variation in experimental results is a function of a multitude of factors, but major discrepancies probably result from variable experimental conditions (Marshall 1973). Apart from variation among species, age groups, and sex, factors such as temperature, light, container size, animal density, animal size, and quality of food all exert a marked influence on experimental results (Marshall 1973). Thus, methodology is not the only cause of variability in A/G estimates.

Factors Affecting Assimilation Efficiency

Food type

224. Undoubtedly the most significant factor affecting assimilation efficiency is food type. The effect is not very apparent in carnivores, like the odonate Pyrrhosoma nymphula (Lawton 1970), the plecopteran Acroneuria californica (Heiman and Knight 1975), and the amphipod Calliopius laeviusculus (Dagg 1976; Appendix C), because the food type, energy content, and digestibility of animal foods do not vary greatly. For example, most benthic carnivores have A/G ratios between 0.80 and 0.95 (Figure 28). By contrast, ranges in A/G are wide in herbivore-detritivores (Figure 29) because these animals often consume foods of varying energy content and digestibility--e.g., the

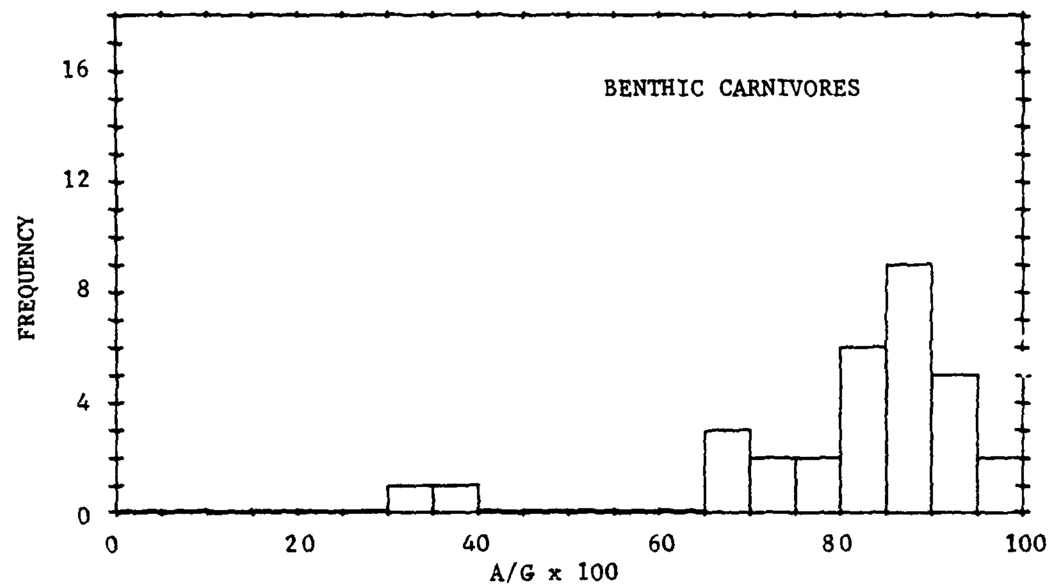

Figure 28. Frequency histogram of benthic carnivore assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

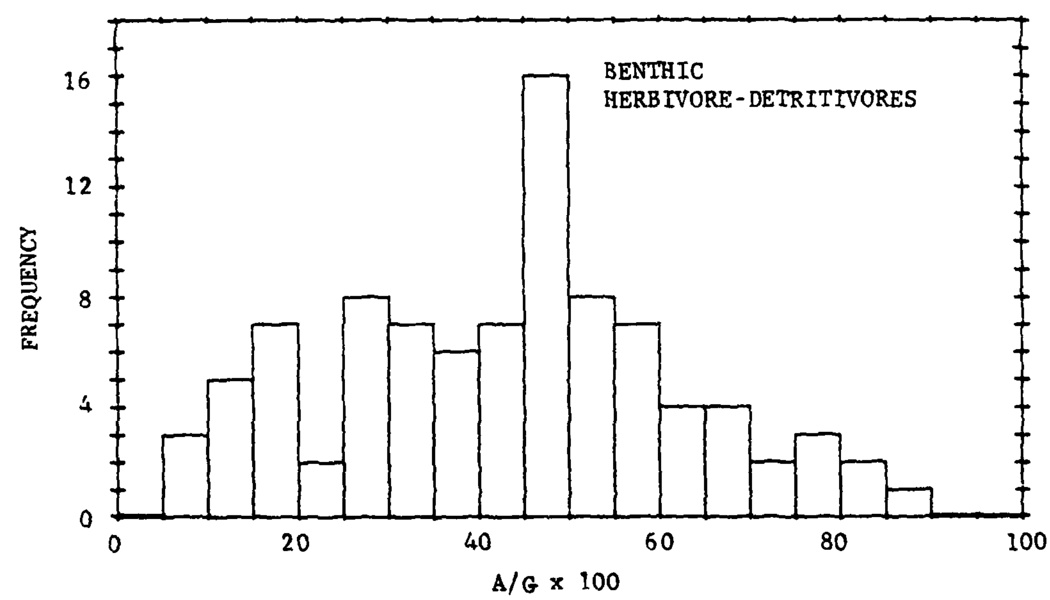

Figure 29. Frequency histogram of benthic herbivore-detritivore assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

cladocerans Daphnia longispina (Schindler 1971) and Sida crystallina (Monakov and Sorokin 1972) and the amphipod Gammarus pseudolimnaeus (Barlocher and Kendrick 1975).

225. Many workers have correlated A/G with the caloric value of foods (Odum 1971, Wetzel 1975). Schindler (1968) found that the assimilation efficiency of Daphnia magna increased from about 10 to 99 percent as the caloric content of its diet increased from 1.3 to 5.3 calories/mg dry weight. Thereafter, further increases in caloric value resulted in decreasing A/G--perhaps due to decreased digestibility of these foods. Similar correlations have been cited for planktonic crustaceans (Pechen'-Finenko 1971) and suggested for Asellus sp. and Gammarus sp. (Swiss and Johnston 1976).

226. Assimilation efficiencies also depend directly upon the quality and digestibility of foods (McDiffett 1970, Fischer 1970, Odum 1971, Wetzel 1975) and apparently are inversely related to the ash content (Conover 1966a, Schindler 1968). By contrast, Lawton (1970) found that the A/G of Pyrrhosoma nymphula was not correlated to ash content nor to caloric content.

227. In general, the A/G of animals fed living or senescent plant matter is less than that of animals fed living or dead animal tissue (Sushchenya 1969, Monakov 1972, Monakov and Sorokin 1972). This observation was substantiated by most of the literature values for benthic carnivores and herbivore-detritivores (cf Figures 28 and 29). Certain phytoplankters, however, may be assimilated very efficiently by zooplankton (e.g., see Schindler 1971, Monakov and Sorokin 1972, Hayward and Gallup 1976). Digestibility is probably more related to the high caloric and low cellulose contents of some phytoplankters than to increased efficiency of digestion by zooplankton. We separated zooplankton assimilation efficiencies on the basis of diet. Blue-green algae and detritus are apparently assimilated less efficiently than are green algae (Figures 36 and 37, respectively). The data for the assimilation of green algae are highly variable, perhaps reflecting the tremendous diversity of structure within the Chlorophyta.

228. Though the use of detritus and/or microflora as food by

benthos is widely accepted (Cummins et al. 1966, Hynes 1970, Fisher and Likens 1972, Marzolf 1964, Barlocher and Kendrick 1975, Rodina 1966), the use of these items by zooplankton is not generally acknowledged. In most models, zooplankton and benthos depend primarily upon phytoplankton as a food source. This basic premise probably is inaccurate for reservoir benthos and zooplankton. A detailed discussion of this topic was given in the section "Detritus and Microflora as Food" in Part III of this report, page 53.

Food concentration and feeding rate

229. Assimilation efficiencies have been observed to decrease significantly with increasing food concentration or ration in filter-feeding zooplankton, e.g., *Daphnia magna* (Ryther 1954, Schindler 1968), *Daphnia pulex* (Richman 1958), *Brachionus pilcatilis* (Doohan 1973), *Diaptomus graciloides* (Kryutchkova and Rybak 1974), and seven species of Entomostraca (Winberg et al. 1973). The same trend also has been observed in other animals such as the nematode *Plectus palustris* (Duncan et al. 1974), the gastropod *Goniobasis clavaeformis* (Elwood and Goldstein 1975), and various Crustacea (Sushchenya 1969). The above findings seem to support the theory of superfluous feeding (Harvey et al. 1935, Beklemishev 1962), which holds that animals assimilate food most efficiently when it is present in small quantities. When food is abundant and consumption exceeds the animal's food requirement, the efficiency of digestion decreases because of the animal's inability to efficiently process the large quantities of food. In filter-feeding Cladocera, Copepoda, and perhaps Rotatoria, filtration rates cannot be reduced enough to limit the intake of food, when the food is present at very high concentrations. Under these conditions extra or superfluous feeding can occur (Monakov and Sorokin 1961, as cited by Monakov 1972). Field observations also seem to substantiate superfluous feeding. King (1967) noted that undigested algae appeared in the feces of the rotifer *Euchlanus dilitata* only when the algae were present at very high concentrations. A similar observation also was made for *Daphnia magna* (Ryther 1954).

230. Some authors have observed constant A/G with increasing food concentration and therefore disagree with the theory of superfluous feeding. Pechen'-Finenko (1973) noted that in raptorial zooplankters (mostly predators), A/G remains constant over a wide range in food concentration. Presumably, these types of animals can regulate consumption and therefore optimize A/G. *Pyrrhosoma nymphula*, a carnivorous odonate (Lawton 1970), and *Neanthes virens*, a carnivorous polychaete (Kay and Brafield 1972), also exhibit fairly uniform A/G regardless of the quantity of food consumed. Even the filter-feeding copepods *Diaptomus gracilis* (Kibby 1971b) and *Calanus hyperboreus* (Conover 1964, 1966a) exhibit fairly uniform assimilation efficiencies (64.2 to 68.4 percent and 39.6 to 71.1 percent, respectively) when food concentrations are varied significantly.

231. Pechen'-Finenko (1973) argued that the concentration at which superfluous feeding occurs exceeds the concentrations of food found in nature. In addition, he suggested that automatic filter feeders can regulate assimilation by altering their filtration rate and A/G. Pechen'-Finenko (1977) expressed the belief that the apparent discrepancies in previous results of experiments on food concentration were entirely due to variations in methodology. For example, he viewed the downward trend in the A/G of *Daphnia pulex* (Richman 1958) as an artifact generated by Richman's use of the $\frac{P + R}{G}$ method. However, Schindler (1968) and Hayward and Gallup (1976), using radiocarbon techniques, also observed decreasing A/G as food concentrations were increased. Schindler (1971) believed that superfluous feeding may become evident only when zooplankton are feeding on certain types of food. He concluded that assimilation efficiency varies inversely with the ingestion rate, when different foods are consumed.

232. Firm conclusions cannot be made regarding the relation of assimilation efficiency to food concentration. Lawton (1970) noted that the A/G of *Pyrrhosoma nymphula* may increase, decrease, or remain constant as feeding rates increase. He suggested that all three responses are possible in nature. Hayward and Gallup (1976) pointed out that the situation is even more complicated than most people believe. According

to their work, A/G is a function of food concentration, but this function varies with temperature. They stressed the need for multivariate information on assimilation and suggested that great care be exercised in the interpretation of results.

233. Practically all models we reviewed used grazing constructs that were dependent on food density. In other words, these authors believed that assimilation efficiency remains constant at all food concentrations, whereas consumption changes at low to moderate food concentrations. This premise may or may not be correct, but it is practical in that the effects of concentration on grazing are easier to examine and simulate than are those same effects on assimilation efficiency. DiToro et al. (1971) used a density independent (i.e., linear) grazing relationship based on the idea of superfluous feeding and made assimilation efficiencies vary with food concentration. The relation of feeding rate to food concentration is essentially linear over most food concentrations and though a linear function may be appropriate in most cases, difficulties in determining the exact effect of food concentration on assimilation efficiencies render this approach less appealing.

Temperature

234. Changes in A/G have been positively correlated with water temperature for Cladocera (Webb and Johannes 1967, Schindler 1968, Hayward and Gallup 1976), Copepods (Conover 1962), various Crustacea (Sushchenya 1969, Pechen'-Finenko 1971), Insecta (Heiman and Knight 1975, Otto 1975), and Gastropoda (Elwood and Goldstein 1975). Effects of temperature on metabolism have been described by the Q_{10} law (Prosser and Brown 1961), which states that ectotherm metabolism increases two to three times with a 10° increase in temperature. Under ideal conditions, A/G should be low at low temperatures, increase to a maximum as temperature increases to a species-specific optimum, and gradually decline as temperature approaches the upper tolerance limit for the species.

235. Unfortunately, the ideal relationship of A/G to temperature is not always observed. The A/G of Calanus hyperboreus (Conover 1962), between 2° and 11°C, did not vary significantly (64.5 to 68.0 percent). In the gastropod Goniobasis clavaeformis A/G remained constant between

10° and 20°C (Elwood and Goldstein 1975). Assimilation efficiency also was unaffected by temperature in a number of other animals (Lawton 1971, Kibby 1971b, Dagg 1976).

236. A possible explanation for these discrepancies in published data is that temperature not only affects P and R but also consumption (G) through the effects of food concentration and temperature on filtration rates (Hayward and Gallup 1976). There is a good possibility that increased temperature, within a certain range, may not increase the A/G of an organism. This response could occur if the increase in assimilation (P + R) was matched by a concomitant increase in consumption (G also increases with temperature; see "Effects of Temperature on Consumption" in Part III of this report, page 66). In short, several variables are interrelated and the final result may have emergent properties (i.e., properties that cannot be predicted by separately examining the effects of the individual variables).

Animal development

237. Assimilation efficiencies have been observed to change significantly as animals develop. Whether this result is a function of age or weight is not certain, but, in some organisms at least, the change is clearly related to life history events such as metamorphosis (Fischer 1966). Many organisms change their diet during development (e.g., nauplii of predaceous copepods often are herbivorous until they reach a certain size). Because food type probably is the most significant factor influencing assimilation efficiency, changes in diet during the course of development may significantly alter A/G ratios (Schindler 1968, Waldbauer 1968).

238. Assimilation efficiencies have been observed to decrease, remain constant, or even increase during the development of various aquatic invertebrates. Decreasing A/G ratios during development were noted in the zooplankters *Daphnia magna* (Schindler 1968) and *Macrocyclops albidus* (Shushkina et al. 1968), and in the insects *Pyrrhosoma nymphula* (Lawton 1970), *Pteronarcys scotti* (McDiffett 1970), *Hedriodiscus truquii* (Stockner 1971), and *Lestes sponsa* (Fischer 1972). However, assimilation efficiencies remained constant during the development of the copepod

Macrocyclops albidus (Klekowski and Shushkina 1966b), the mollusc Dreissena polymorpha (Monakov 1972), the amphipods Gammarus pulex (Nilsson 1974), and Calliopius laeviusculus (Dagg 1976). Brachionus rubens (Rotatoria) exhibited increased A/G during development (Pilarska 1977b), and Lawton (1970) believed that the A/G of Pyrrhosoma nymphula (Odonata) could increase, decrease, or remain constant under a given set of environmental conditions.

Reproductive state

239. Few data are available that describe the effects of an animal's reproductive state on assimilation efficiency. Daphnia magna and D. schodleri bearing eggs or embryos assimilate at a higher rate than nonovigerous females (Schindler 1968, Hayward and Gallup 1976). The assimilation efficiency of Asellus aquaticus varied from 26 to 44 percent depending on reproductive condition, sex, and population density (Prus 1976).

Summary of Constructs

240. First, users should select the frequency histogram (Figures 26-33, 36, and 37) that best describes the model compartment they are considering. Second, the frequency histogram should be transformed into a probability distribution of A/G ratios (restricted by the confidence limits placed on the probability distribution by the user), and a range of A/G ratios should be selected. Third, consumption (mg carbon$\cdot$mg carbon$^{-1}\cdot$day^{-1})--generated by grazing constructs in Part III--should be multiplied by the selected A/G ratios, according to Equation 1. The resulting products describe the range of weight-specific assimilation (mg carbon$\cdot$mg carbon$^{-1}\cdot$day^{-1}) by the compartment. To determine the range of weight-specific loss (egestion + excretion--mg carbon$\cdot$mg carbon^{-1} $\cdot$day^{-1}), users should subtract A/G ratios from one and multiply weight-specific consumption by the resulting difference. The product of the weight-specific rates of assimilation or egestion + excretion (as determined above) and the biomass of the model compartment (mg carbon) yields the weight of carbon assimilated or lost, respectively.

241. Because the distribution of A/G values for cladocerans (Figure 32) was essentially uniform, we recommend that zooplankton be considered as a single compartment (Figure 26). However, when greater resolution is required, the frequency histograms of rotifer and copepod A/G (Figures 30 and 31, respectively) may be used, but cladoceran A/G ratios should be randomly selected from a range of 0.05 to 0.55. Biomass of zooplankton should be arbitrarily assigned as follows: Cladocera = 60 percent, Copepoda = 35 percent, Rotatoria = 5 percent, unless more accurate data are available. Rotatoria assimilation, for example, may be calculated as 0.05b [G(A/G)], where b = total zooplankton biomass (mg carbon), G = zooplankton consumption (mg carbon·mg carbon^{-1}·day^{-1}), and A/G = Rotatoria assimilation efficiency (from Figure 30).

242. Benthos should be compartmentalized into carnivores and herbivores-detritivores on the basis of their respective assimilation efficiencies (Figures 28 and 29). Based on the ecological growth efficiencies of a nematode (Duncan et al. 1974), a chironomid (Kajak and Dusoge 1970), and an oligochaete (Ivlev 1939), we believe that carnivores should constitute 20 ± 10 percent of total benthic biomass, when the benthos compartment is divided. Assimilation by benthic herbivores-detritivores may be calculated as 0.80b $[G(A/G)_1]$ and that of benthic carnivores as 0.20b $[G(A/G)_2]$, where b = total benthic biomass (mg carbon), G = benthos consumption (mg carbon·mg carbon^{-1}·day^{-1}), $(A/G)_1$ = A/G ratio for herbivore-detritivores (Figure 29), and $(A/G)_2$ = A/G ratio for carnivores (Figure 28).

Conclusions

243. Assimilation efficiencies are important in biological models because they can be used to modify consumption and thereby yield the rate of energy flow into model compartments. Egestion (F) and excretion (E), which technically differ, are defined as a single loss in the model--the additive inverse of assimilation efficiency $\left(A/G + \frac{(F + E)}{G} = 1\right)$.

244. Because methods employed to estimate A/G are inaccurate, we

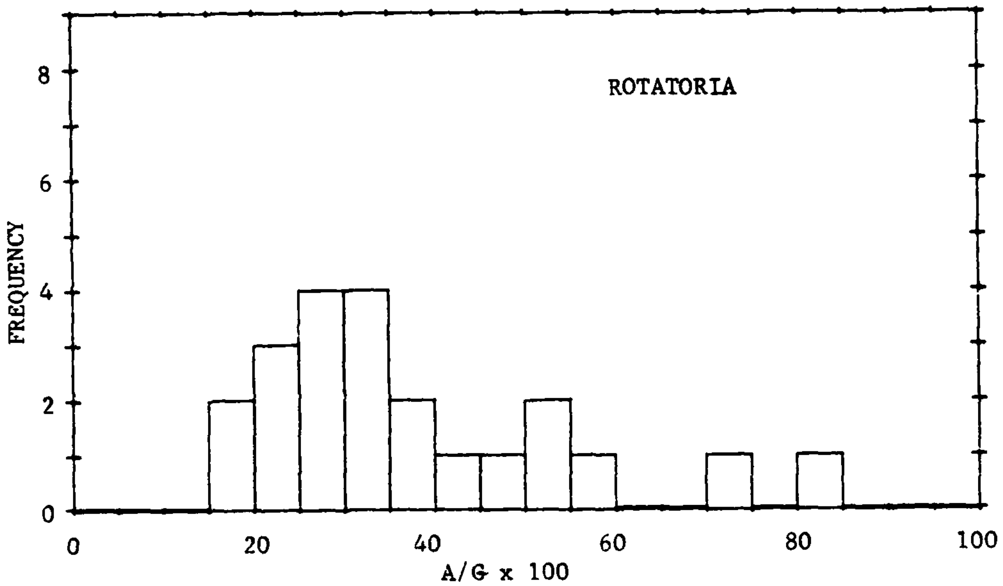

Figure 30. Frequency histogram of Rotatoria assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

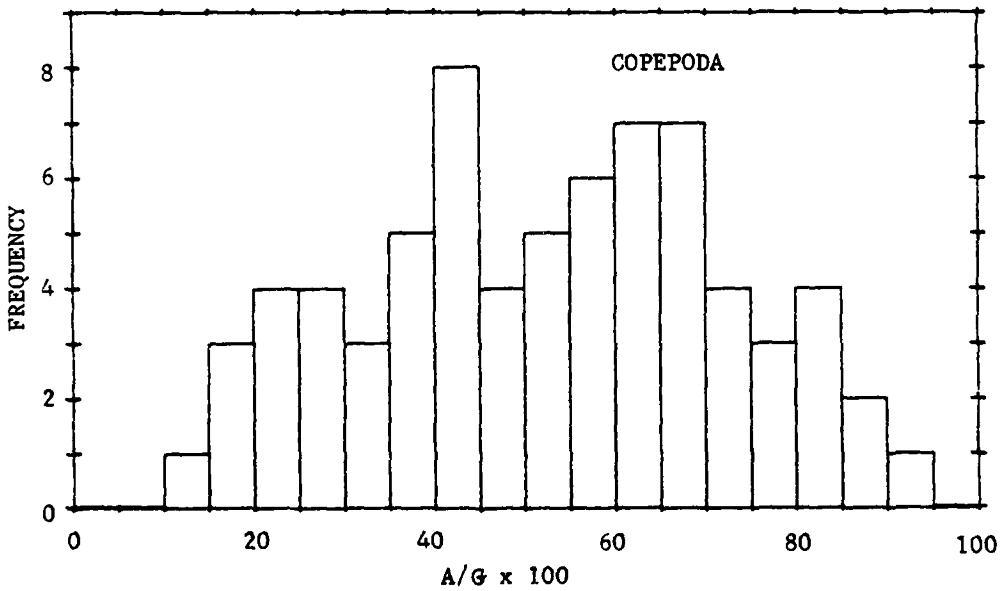

Figure 31. Frequency histogram of Copepoda assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

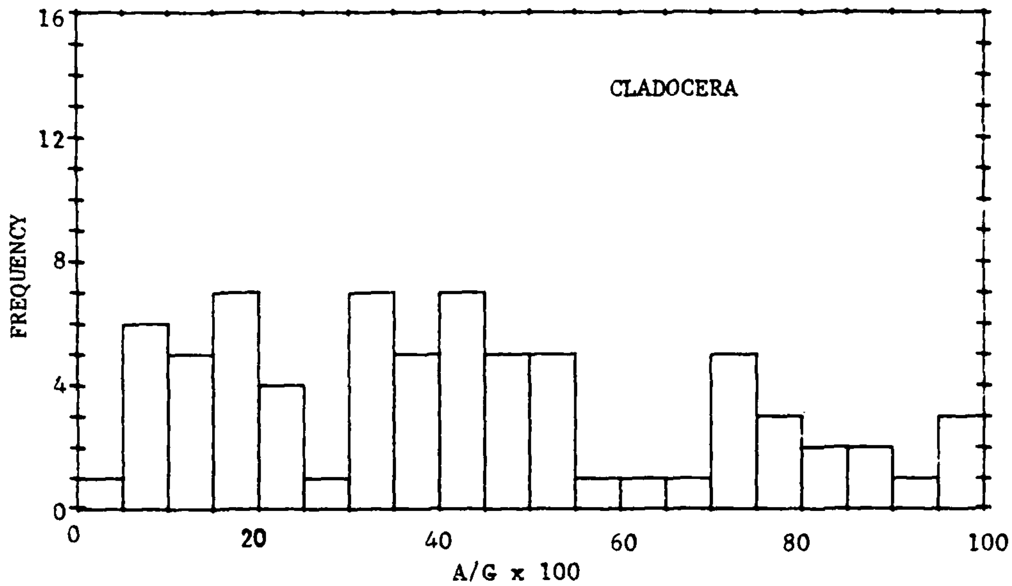

Figure 32. Frequency histogram of Cladocera assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

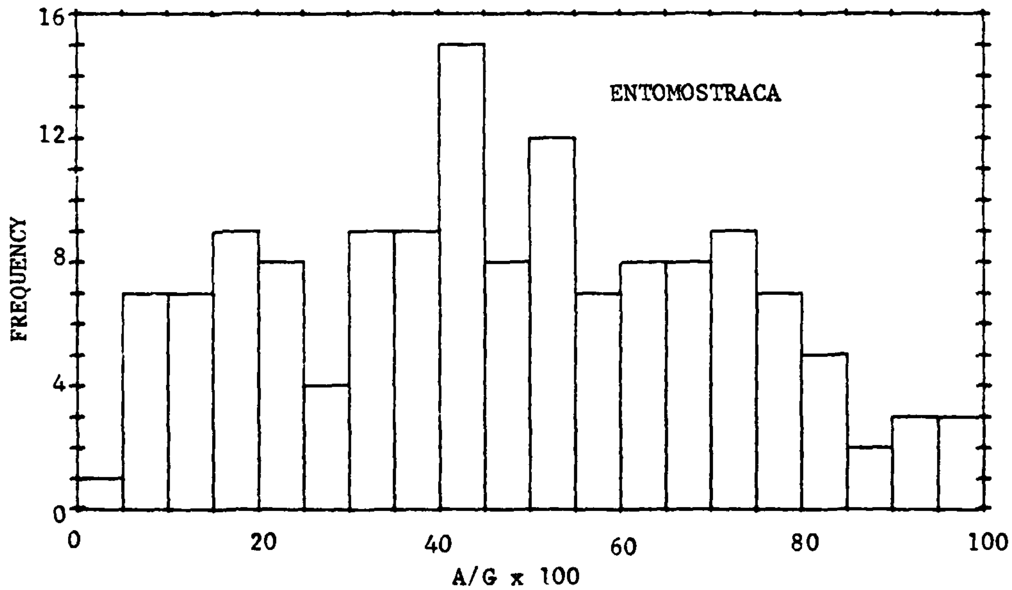

Figure 33. Frequency histogram of Entomostraca assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

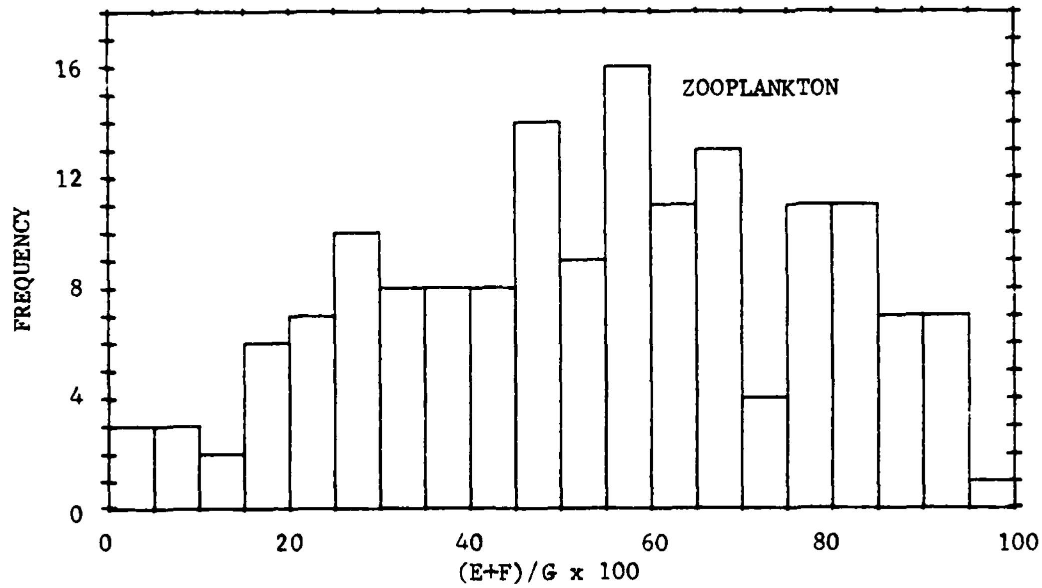

Figure 34. Frequency histogram of zooplankton egestion (F) and excretion (E) values as a percentage of consumption (G). Based on data in Appendix C

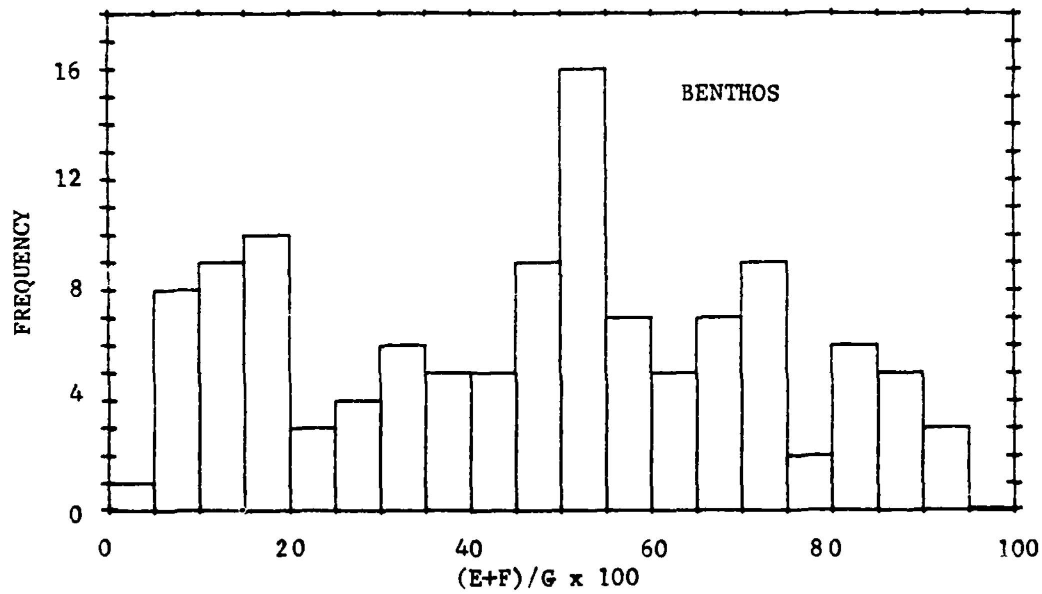

Figure 35. Frequency histogram of benthos egestion (F) and excretion (E) values as a percentage of consumption (G). Based on data in Appendix C

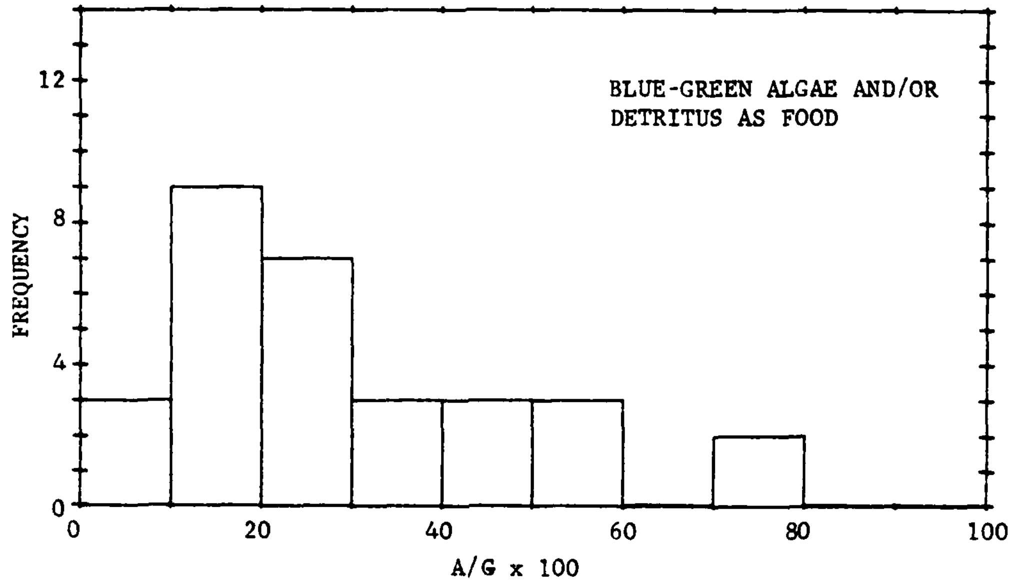

Figure 36. Frequency histogram of assimilation values (A) as a percentage of consumption (G) when zooplankton were fed blue-green algae and/or detritus

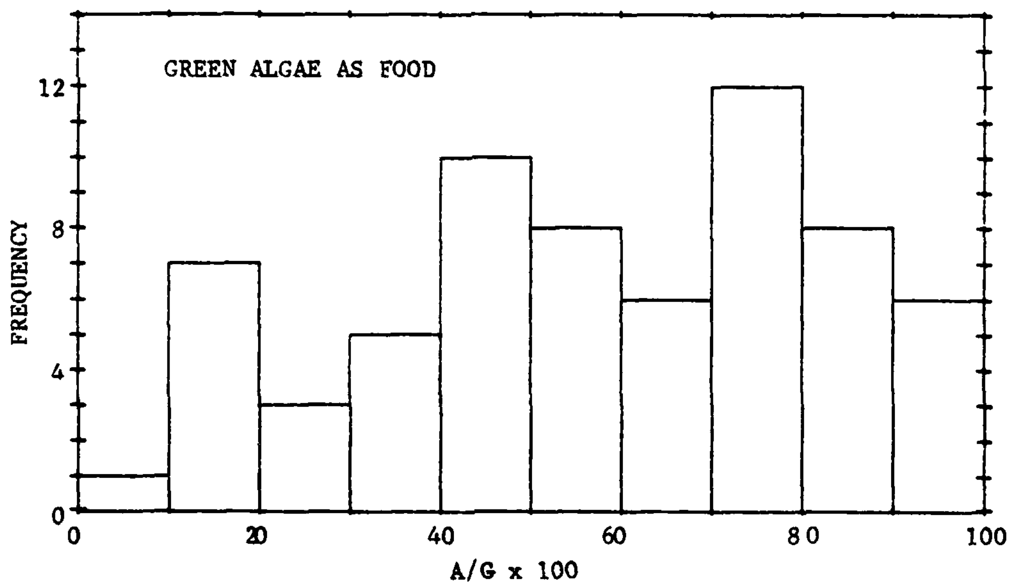

Figure 37. Frequency histogram of assimilation values (A) as a percentage of consumption (G) when zooplankton were fed green algae

did not develop constructs to predict cause-effect relations between A/G and factors such as food concentration, temperature, animal development, or reproductive state. When similar methods were used, food type generally was the most important factor affecting A/G (cf Figures 28-29 and 36-37), but food concentration and temperature effects were inconsistent. Few data that illustrate the effects of reproductive state or animal development have been published.

PART V: RESPIRATION OF ZOOPLANKTON AND BENTHOS

Introduction

245. Respiration is the sum of all physical and chemical processes by which organisms oxidize organic matter to produce energy. During aerobic respiration, oxygen and organic matter are consumed and carbon dioxide and water produced (Pennak 1964). Components of respiration include specific-dynamic action (SDA), basal-respiratory rate (BRR), standard-respiratory rate (SRR), and a respiratory component for activity. Specific-dynamic action refers to the energetics of digestion and is the smallest component of respiration--e.g., 15.4 percent of the total in the plecopteran *Acroneuria californica* (Heiman and Knight 1975). Basal-respiratory rate is the minimum energy expenditure required to sustain life. Standard-respiratory rate (SRR) is equal to the sum SDA + BRR. The activity component is highly variable and accounts for most of the variation in total respiration (Calow 1975).

246. Respiration is a very important parameter in energy budgets. Maintenance energy constitutes a major portion of energy expenditures by populations of aquatic invertebrates (80 to 90 percent) and therefore can be used as a first approximation of total assimilation (Moshiri et al. 1969). Respiration was 92.7 percent of assimilation in the cladoceran *Leptodora kindtii* (Moshiri et al. 1969) and 81.8 percent in the isopod *Asellus aquaticus* (Klekowski 1970). Since maintenance costs must be met for survival, respiration may exceed assimilation under unfavorable environmental conditions. Under such conditions, biomass may be catabolized to meet the increased demand for energy.

Methodology

247. Respiration rates of aquatic invertebrates usually are estimated directly by monitoring oxygen consumption, since the estimation of heat loss from ectotherms is impractical by direct calorimetry (Hughes 1970). By multiplying O_2 consumed by an oxycaloric coefficient,

e.g., 4.83 cal/ml O_2 (Winberg et al. 1934), respiratory rate can be estimated. Some degree of error is inherent to the application of an oxycaloric coefficient because the coefficient varies with the type of body component oxidized. Winberg et al. (1934) found different oxycaloric coefficients for oxidation of carbohydrate (4.686 cal/ml O_2), protein (4.721 cal/ml O_2), and fat (5.043 cal/ml O_2). Without measuring nitrogen excretion and CO_2 production during experiments, one has no way of determining what type of material is being oxidized and therefore is unable to appropriately adjust the oxycaloric coefficient. As a result, the oxycaloric coefficients for the three body components usually are averaged (i.e., it is assumed that specimens burn protein, fat, and carbohydrates equally). Hughes (1970) stated that the error involved in applying a mean coefficient was small--certainly smaller than the error inherent to an extrapolation of lab results to a field situation.

248. Manometric methods (e.g., the use of Warburg, Gilson, and Cartesian diver respirometers) require a manometer to measure decreases in gas pressure within a closed chamber. In the respiratory chamber, specimens consume O_2 and produce CO_2. Because the experimental medium is alkaline and absorbs CO_2, the gas pressure in the chamber decreases in proportion to the rate of O_2 consumption (Umbreit et al. 1964). There are two disadvantages to manometric techniques: (a) alkaline solutions may affect respiration in some species (Sushchenya 1969) and (b) shaking (often employed to ensure absorption of CO_2) may excite specimens and elucidate artificially high rates of respiration (Rueger et al. 1969). In contrast to Warburg and Gilson respirometers, Cartesian divers have extremely small chambers for specimens and, consequently, are the only respirometers suited to measure respiration rates of individual zooplankters. Differences in the respiratory rates of individuals of the same species often become apparent in Cartesian divers (Ivanova and Klekowski 1972). Such differences are usually masked in other methods where many specimens are enclosed concomitantly in one chamber.

249. Chemical methods, usually Winkler titration (American Public Health Association 1971), Modified-Winkler titration, or Micro-Winkler titration, measure O_2 concentrations in a closed system before and after

a suitable experimental period. The period must be long enough for a detectable difference in O_2 concentration to develop but short enough to preclude significant development of bacterial populations or starvation of experimental specimens (Marshall 1973). The difference between the initial and final O_2 concentration is taken to represent oxygen consumption by the enclosed specimens. The combined use of a closed bottle and Winkler titration has been the most popular means of determining respiration in aquatic invertebrates (Appendix D, Parts I and II). Part of the popularity is due to the fact that the system is simple and can be used in the field or laboratory.

250. Polarographic methods require the measurement of current flowing in the external circuit of a polarographic cell (Lingane 1961). These methods are advantageous in that they provide continuous monitoring of O_2 tensions (Rueger et al. 1969). Electrodes are most often employed in a flow-through chamber (e.g., Jonasson 1964, Berg and Jonasson 1965, Rueger et al. 1969, Calow 1975), but they may be used in a closed bottle (e.g., Brinkhurst et al. 1972, Roff 1973, Foulds and Roff 1976, Swiss and Johnston 1976, Welch 1976) when a stirring mechanism is present. Flow-through systems remove animal wastes which may affect results in long-term experiments (Rueger et al. 1969).

251. No previous investigations found significant differences among respiration methods. Lawton and Richards (1970) found no significant difference between results produced by Cartesian diver and Winkler methods, nor between Cartesian diver and Gilson methods. Richman (1958) obtained similar results when he compared rates for *Daphnia pulex* determined from Winkler and Warburg methods. Polarographic and manometric methods were deemed suitable for measuring the O_2 consumption of aquatic invertebrates (Rueger et al. 1969). Results produced by a Scholander respirometer (manometric) and Micro-Winkler for *Leptodora kindtii* were not significantly different. Calow (1972) demonstrated that chemical, manometric, and polarographic techniques all measured similar rates of respiration in the mollusc *Planorbis contortus* and *Ancylus fluviatilis*.

Variation Due to Experimental Conditions

252. Laboratory conditions under which measurements of O_2 consumption are taken seldom approximate conditions in the field. Nonetheless, over 95 percent of the respiration studies have been conducted in laboratories (Appendix D). This fact results from the technical difficulties of isolating and determining the respiration of an individual or population in a natural community.

253. Laboratory specimens often are starved 24 to 96 hr prior to experiments, e.g., 24 hr for the mollusc *Helisoma trivolvis* (Sheanon and Trama 1972), 96 hr for the plecopteran *Tarniopteryx nebulosa* (Nagell 1973), 24 hr for the cladoceran *Daphnia pulex* (Richman 1958). When fed during experiments, *Diaptomus siciloides* (Comita 1968) and *Calanus hyperboreus* (Conover 1962) exhibited higher rates of respiration than when starved. According to Satomi and Pomeroy (1965), small benthos and most zooplankton are subjected to starvation if held without food for a few hours, and after 24 hr of starvation, small specimens apparently exhibit a significant depression in respiratory rate. In contrast, Ikeda (1971) found that *Calanus cristatus* exhibited increased rates of respiration during the first few days of starvation. In general, most researchers probably would approve of the recommendation by Cummins (1975) that specimens be fed during or immediately before experiments.

254. Research of Conover (1962), Marshall (1973), and Sushchenya (1969) indicated that increased food concentrations increased rates of respiration in Crustacea. Pilarska (1977c), however, observed increased respiration in the rotifer *Brachionus rubens* when food concentrations were below or above an optimum. When exposed to changes in food concentration, aquatic invertebrates exhibit respiratory rates that may depend on their present level of feeding and on the degree of previous starvation (Marshall 1973). Obviously, more research is needed. Estimates should be made over a broad range of food concentrations and taxa.

255. Another major cause of variation in respiration rates is inadequate acclimation to test temperature. Unacclimated specimens may be exposed to temperature changes that exceed any in their native

habitat. In many studies, collected specimens were acclimated to test temperatures for 24 to 28 hr (Appendix D, Parts I and II). These specimens may have been acclimated in the sense that they overcame the initial shock of capture and handling (Marshall et al. 1935, Bishop 1968, Roff 1973), but they were far from acclimated to temperature in terms of respiratory rate. According to Geller (1975), the rate of temperature acclimation in Daphnia pulex was proportional to its growth rate, and acclimation required 6 weeks at temperatures of 7° to 10°C and 4 weeks at temperatures above 15°C. Blazka (1966) observed that Daphnia hyalina, acclimated to 20°C in the laboratory, exhibited higher respiratory rates than did field populations at various ambient temperatures. This difference probably resulted from sufficient acclimation to temperature by field populations. To avoid acclimation problems, Cummins (1975) suggested that specimens be studied at the ambient temperature of their native habitat. Some rates in Appendix D, Part I, are for specimens studied at 5° to 10°C above or below their acclimation temperature in the field. These data undoubtedly increase the variance of our data base, but since we have no way to consistently correct aberrant rates, we must consider the error as part of the random variability affecting all estimates.

256. Many of the existing data are conflicting. For example, Roff (1973) and Siefken and Armitage (1968) found no effect of light on the metabolic rates of the copepods Limnocalanus macrurus and Diaptomus sp., respectively. In contrast, Marshall (1973) found that bright light stimulated respiration rates in the copepod Calanus finmarchicus, and Buikema (1972) found that light inhibited respiration in the cladoceran Daphnia pulex. Bishop (1968) observed depressed respiration rates in zooplankton as pressure increased, but Roff (1973) observed no significant effect of pressure on the respiration of Limnocalanus macrurus. Crustaceans exhibited three potential responses to increased salinity: (a) no effect, (b) increased respiratory rates at hypertonia and decreased rates at hypotonia, and (c) increased rates at both hypertonia and hypotonia (Sushchenya 1969). When pH was shifted beyond the compensation limits for a crustacean species, metabolism was either

depressed or disrupted completely (Sushchenya 1969). The problem is that compensation limits vary significantly among freshwater animals. In contrast to the results of Satomi and Pomeroy (1965) for estuarine zooplankton, research on oligochaetes (Brinkhurst et al. 1972) and copepods (Marshall and Orr 1958, Conover and Corner 1968, Siefken and Armitage 1968, Roff 1973) failed to demonstrate any effect of crowding on rates of respiration. Although it is known that a significant correlation exists between respiratory rates and activity, few investigators have effectively quantified activity and certainly not in a manner comparable for a wide variety of aquatic animals.

257. Seasonal trends in metabolic rates are difficult to explain in terms of any one environmental characteristic. Sweeney (1978) pointed out that diel and seasonal shifts in metabolism, as a result of temperature changes, may increase efficiency of resource allocations and energy partitioning. Siefken and Armitage (1968) suggested that seasonal trends were the result of seasonal changes in weight and previous thermal history. Some authors have noted seasonal trends in metabolism and correlated these trends with food concentration (e.g., Conover 1962, Blazka 1966, Marshall 1973, Larow et al. 1975). By contrast, Roff (1973) failed to observe any seasonal trends in the metabolism of Limnocalanus macrurus. Seasonal trends probably emerge as a cumulative effect of several variables on respiration (e.g., temperature, body weight, and oxygen concentration).

258. Experimental conditions that affect respiration rates often differ in laboratory and field experiments--for example, temperature (Moshiri et al. 1969, Hughes 1970, Pourriot 1973), pressure (Bishop 1968, Roff 1973), light (Buikema 1972, Marshall 1973, Sigmon et al. 1978), oxygen concentration (Jonasson 1964, Palmer 1968, Nagell 1973), salinity (Lance 1965, Sushchenya 1969), pH (Sushchenya 1969), size composition (Appendix D, Part II), crowding (Satomi and Pomeroy 1965), interspecific interactions (Brinkhurst et al. 1972), and reproductive condition (Berg and Jonasson 1965, Moshiri et al. 1969, Burky 1971). These variables also may affect activity, an extremely important factor directly influencing respiration rate (Moshiri et al. 1969, Sushchenya

1969, Ulanoski and McDiffett 1972, Trama 1972, Foulds and Roff 1976, Wycliffe and Job 1977). Absence of substrate in laboratory experiments increased the respiration rates of the ephemeropterans *Hexagenia limbata* and *Ephemera simulans* (Eriksen 1964). The respiratory rate of the chironomid *Lauterbornia* sp. decreased 31 percent when a substrate was provided (Welch 1976).

259. The above list of factors that influence rates of respiration is not exhaustive, nor are the effects of all of the factors similar for different species. Of the factors listed, only the effects of temperature, body size, and oxygen concentration are sufficiently documented to allow us to develop constructs. Fortunately, these factors probably are the most important, and model constructs for these factors should greatly reduce the variance of predicted rates.

Variation Due to Conversion of Units

260. Since respiratory rates of aquatic invertebrates have been expressed in a multitude of incomparable units (see "Original Units" in Appendix D, Part II), we converted all literature rates to a standard, weight-specific unit (mg carbon·mg $carbon^{-1}\cdot day^{-1}$).

261. Factors for the conversion of wet weight to dry weight and for dry weight to carbon are given in a table at the front of Appendix D. Most of the conversions used were obtained from the percent - H_2O Column in Table 2 of Cummins and Wuycheck (1971). Conversion factors for dry weight to carbon were obtained from various sources (Appendix A). When percent - H_2O data were lacking for a taxon, we used data for a closely allied group or that of the next higher taxon for which percentages were available. Since water content undoubtedly varies significantly among species, we introduced an error by using mean factors to convert wet to dry weight for broad taxonomic categories. Fortunately, authors who listed O_2 consumption per unit wet weight were in the minority. A disturbing number of papers from international journals gave no indication of whether their data were in terms of wet, dry, or ash-free weight. Had researchers who used wet weights included data on percent -

H_2O for each species, the magnitude of errors associated with wet to dry weight conversions could have been greatly reduced. Though some error exists in the conversion of dry weight to carbon (Part II), it is insignificant compared to that involved in conversions of wet to dry weight.

262. To convert oxygen consumed to carbon metabolized, we applied an oxy-carbon coefficient derived by combining the mean oxycaloric coefficient of Winberg et al. (1934) (4.83 cal/ml O_2) with the energy to carbon relation for aquatic invertebrates (10.98 cal/mg carbon) derived by Salonen et al. (1976). The result is $\frac{4.83 \text{ cal}}{\text{ml } O2} \cdot \frac{\text{mg carbon}}{10.98 \text{ cal}} = 0.44$ mg carbon/ml O_2. Sources of error due to the use of oxycaloric coefficients are discussed in the section "Methodology," page 127. The variation of energy per unit organic carbon is insignificant (i.e., ca one third less variable than energy per unit ash-free dry weight (Salonen et al. 1976)). The conversion of oxygen consumed to carbon respired probably represents an insignificant error, in proportion to the total error present in laboratory experimentation and extrapolation to real aquatic systems.

263. The worst potential error in our conversions was the extrapolation of respiration per hour to respiration per day. To make this extrapolation we assumed that aquatic invertebrates respire at a constant rate throughout a 24-hr period. Some aquatic invertebrates may behave in this fashion. For example, no diel cycles of metabolism have been observed in the plecopteran *Acroneuria californica* (Heiman and Knight 1975), the ephemeropteran *Stenonema fuscus* (Ulansoki and McDiffett 1972), the odonate *Anax junius* (Petitpren and Knight 1970), the mysid *Mysis relicta* (Foulds and Roff 1976), the dipteran *Chaoborus punctipennis* (Sigmon et al. 1978), or the cladoceran *Leptodora kindtii* (Moshiri et al. 1969). On the other hand, diel cycles in metabolism have been observed in the ephemeropterans *Isonychia bicolor* (Sweeney 1978) and *Isonychia* sp. (Ulanoski and McDiffett 1972). There is no way to quantify the error involved, but when we extrapolated from an hourly to a daily rate for species exhibiting a diel cycle of metabolism, we may have significantly underestimated or overestimated daily respiration.

Overestimates would result when experiments were conducted during periods of maximum diel respiration and underestimates when experiments were conducted during periods of low respiration.

Model Constructs

Literature synopsis

264. Previous respiration constructs range from unmodified constants to constants modified by several factors. In all models, respiration terms represent energy loss and either are linear functions of compartment biomass or a percentage of compartment consumption. Ross and Nival (1976) included respiration in a term for death rate (a_2 = 0.42 mg carbon·mg carbon^{-1}·day^{-1}) that was determined from batch experiments on the respiratory rates of starved zooplankton. In the zooplankton models by Scavia et al. (1976) and Chen and Orlob (1975) and in the zooplankton and benthos models by MacCormick et al. (1974), respiration rates were modified exclusively by temperature. Respiration rates were modified solely by the body size of zooplankton in a model by Menshutkin and Umnov (1970). Constructs of respiration rates as functions of temperature and body size have been developed (DiToro et al. 1971, Umnov 1972, Baca et al. 1974, Kremer 1975, Patten et al. 1975). Waters and Efford (1972) developed constructs with respiration rates as functions of temperature, body size, and food intake. Steele (1974) considered body size and food intake effects but omitted a function for temperature effects, since temperature was essentially constant in the North Sea. The most elaborate respiration constructs were those for zooplankton and benthos in a model by Park et al. (1974) and those for benthos by Zahorcak (1974). Park et al. (1974) modeled the effects of temperature, body size, and behavior on rates of respiration. Zahorcak (1974) considered the same factors as Park et al. (1974) but, in addition, developed constructs for the effects of crowding and oxygen concentration.

265. The importance of food consumption as a factor affecting rates of respiration is controversial. Waters and Efford (1972) and

Steele (1974) considered consumption effects important enough to warrant model constructs. We do not believe that sufficient data are yet available to permit us to accurately model the effects of consumption on respiration. Steele (1974) made respiration of copepods a linear function of consumption. However, other data for copepods (Ikeda 1971) and for rotifers (Pilarska 1977c) indicated that the relationship may not be linear. In fact, Swartzman and Bentley (1978) noted that rates predicted by Steele (1974), for copepods at high concentrations of food, were 2.7 times higher than those observed in laboratory populations of Mullin and Brooks (1970). Mayfly and stonefly nymphs (Nagell 1973) did not exhibit significant decreases in metabolism during brief periods of starvation.

266. Our first approach to modeling respiration was to consider it as a proportion of consumption (R/G, Table 14). Figure 38 shows the frequency histogram of R/G ratios for a wide range of taxa. Unfortunately, only a limited number of studies have determined both respiration and consumption, and, therefore, little is known about how the ratio R/G responds to changes in the environment. Because respiration and consumption generally are affected similarly by temperature, oxygen concentration, and body size, the ratio R/G should be less variable than other expressions of respiration. More research is required before the potential of R/G ratios in ecosystem models can be fully realized. Figure 38 provides some insight into the range of potential values for aquatic invertebrates. The product of consumption (mg C·mg C^{-1}·day^{-1}, Part III) and R/G (Figure 38) yields weight-specific respiration for a community. As more data are collated, frequency distributions for major taxa such as Cladocera, Copepoda, Rotatoria, and Diptera could be formed.

267. Our second approach to respiration involved the conversion of literature data on oxygen consumption to rates of weight-specific respiration (mg carbon·mg $carbon^{-1}$·day^{-1}). Respiration rates were tabulated for taxa (Appendix D, Part I), and frequency distributions of rates were constructed for various taxonomic categories and weight classes. Respiration losses are proportional to the biomass of the

Table 14

Respiration as a Percentage of Consumption for Aquatic Invertebrates

Taxon	Trophic Condition	$\frac{\text{Respiration}}{\text{Consumption}} \times 100$	Reference
Mollusca			
Scrobicularia plana	Fed	47.9	Hughes (1970)
Plecoptera			
Acroneuria californica	Starved	51.0	Heiman and Knight (1975)
Pteronarcys scotti	?	6.9	McDiffett (1970)
Ephemeroptera			
Stenonema pulchellum	Fed	37.6, 37.0, 41.2, 38.6	Trama (1972)
Odonata			
Pyrrhosoma nymphula	?	43.5, 41.6, 42.9	Lawton (1971)
Megaloptera			
Corydalus cornutus	Starved	25.7	Brown (1978)
Isopoda			
Asellus aquaticus	?	25.0	Prus (1972)
Mysidacea			
Mysis relicata	Fed	69.3, 63.7, 70.6, 70.5, 70.6, 73.7, 70.2	Lasenby and Langford (1972)
Copepoda			
Macrocyclops albidus	?	ca 20	Klekowski and Shushkina (1966a)
Diaptomus siciloides	?	53.7, 76.3, 53.0, 38.8	Comita (1964)

(Continued)

Table 14 (Concluded)

Taxon	Trophic Condition	$\frac{\text{Respiration}}{\text{Consumption}} \times 100$	Reference
Rotatoria			
Brachionus rubens	Starved	45	Pilarska (1977c)
Brachionus calyciflorus	Fed	7-13	Galkovskaya (1963)
Brachionus plicatilis	Fed	8	Doohan (1973)
Cladocera			
Daphnia pulex	Starved	4-14	Richman (1958)
Simocephalus vetulus	?	11.5-19.5	Klekowski (1970)

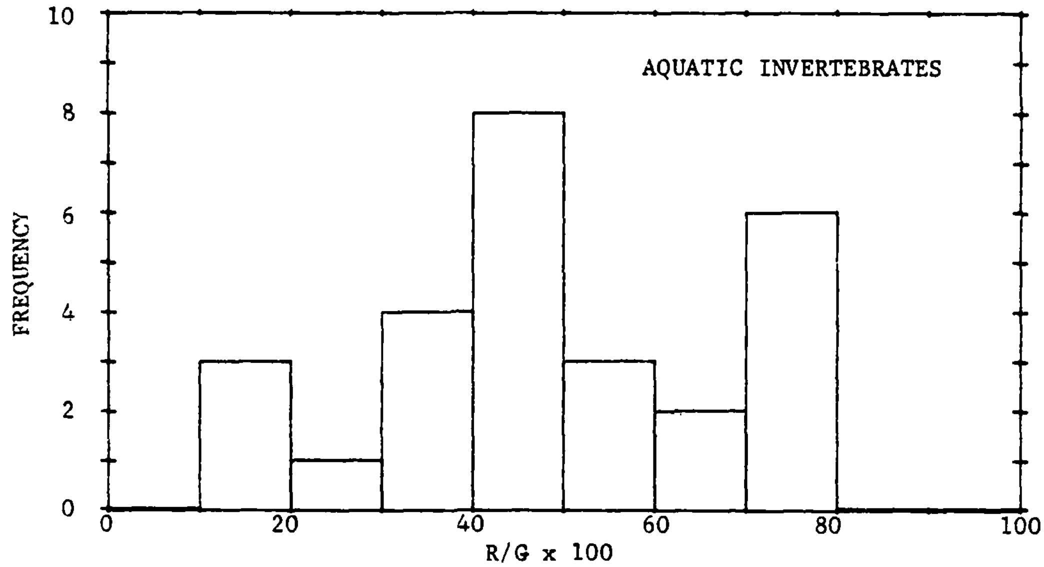

Figure 38. Frequency histogram of respiration (R), as a percentage of consumption (G), for aquatic invertebrates. Based on the data in Table 14

donor compartment. In other words, the product of compartment biomass (mg carbon) and respiration (mg carbon·mg carbon^{-1}·day^{-1}) is the weight of carbon respired daily by that compartment.

268. Frequency histograms were constructed from respiration rates in Appendix D (Part I) for major taxa of zooplankton, i.e., Cladocera (Figure 39), Copepoda (Figure 40), and Rotatoria (Figure 41). All rates in the frequency histograms were corrected to 20°C. Rotifers generally exhibit higher rates ($\bar{x}$ = 0.430; range = 0.20 - 1.10 mg carbon·mg carbon^{-1}·day^{-1}) than entomostracans (Figures 39 and 40; $\bar{x}$ = 0.240; range = 0.050 - 0.800 units). Cladocera exhibit slightly higher rates ($\bar{x}$ = 0.250; range = 0.050 - 0.800 units) than Copepoda ($\bar{x}$ = 0.232; range = 0.050 - 0.800 units). These data are generally within the range of weight-specific rates used in other phytoplankton and zooplankton models (e.g., 0.096 - MacCormick et al. 1972; 0.16 - Bierman et al. 1973; 0.20 - Thomann et al. 1975; 0.23 - Kremer 1975; 0.50 - Steele 1974).

269. Frequency histograms of respiration rates also were constructed for the major taxa of benthos. Rates of benthic Crustacea,

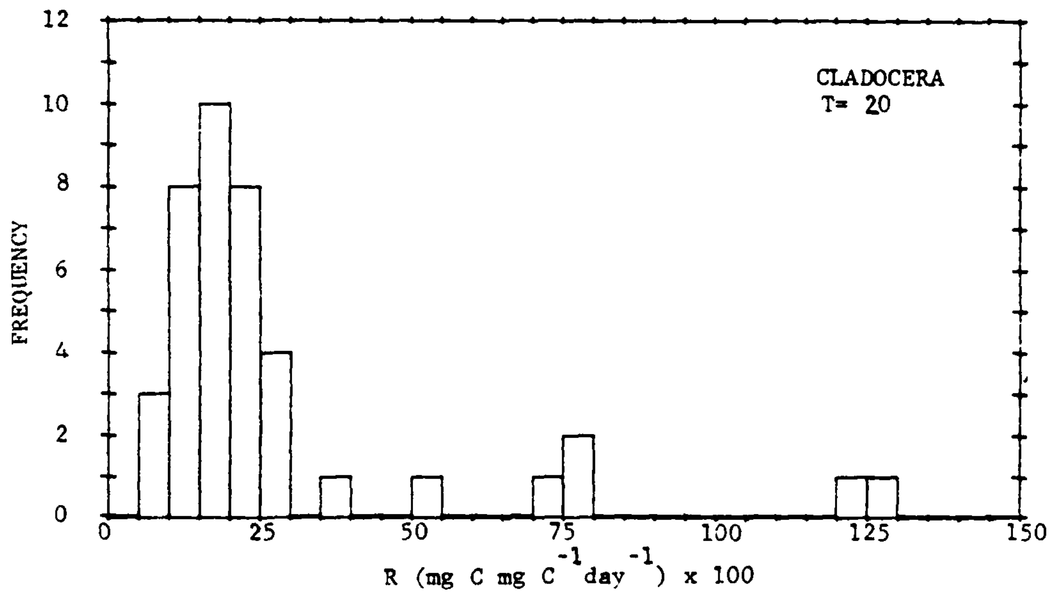

Figure 39. Frequency histogram of respiration rates for Cladocera. Based on data in Appendix D, Part I. T = temperature (°C)

Insecta, Oligochaeta, and Mollusca (Figures 42-45, respectively) are all of equal magnitude but considerably lower than those of zooplankton (Figures 39-41). We anticipated these results, however, based on the relation of weight-specific respiration to body weight.

Effects of Body Weight

270. The fact that rotifers exhibit higher metabolic rates than entomostracans exemplifies the well-documented observation that weight-specific respiration is a negative exponential function of body weight (Appendix D, Part II). For example, Figure 46 illustrates the relationship of respiration to body weight for aquatic invertebrates. The fitted line is log R = log 1.472 - 0.285 log W, where W = weight (carbon units) and R = respiration rate (mg carbon·mg carbon^{-1}·day^{-1}) × 100. This equation has an R^2 of 0.96 and was fitted to data collected at 20°C (Appendix D, Part I).

271. Respiration as a function of body weight is described by the general equation:

$$Y = aW^b \tag{23}$$

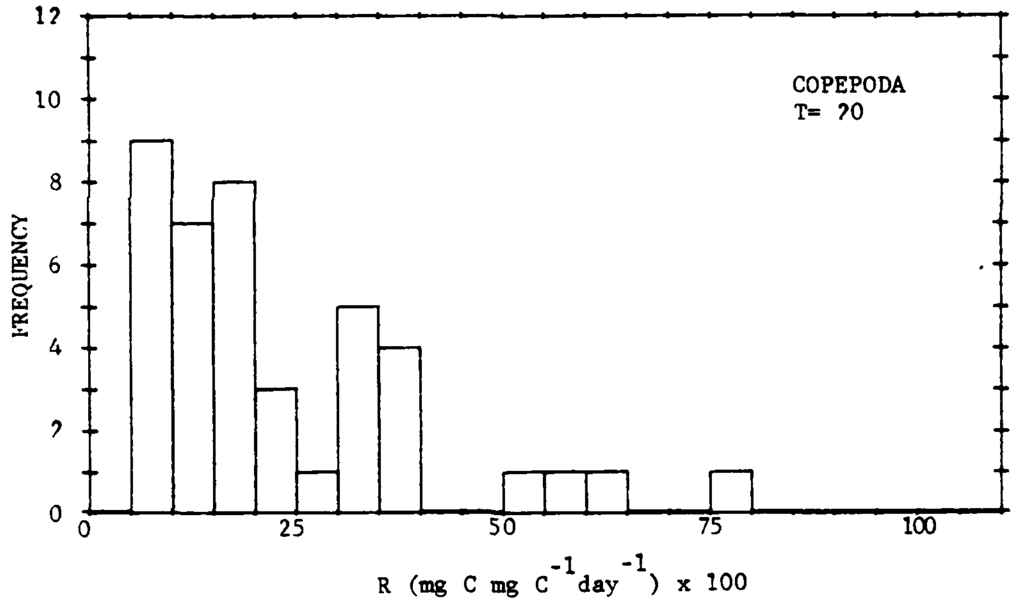

Figure 40. Frequency histogram of respiration rates for Copepoda. Based on data in Appendix D, Part I. T = tempertature (°C)

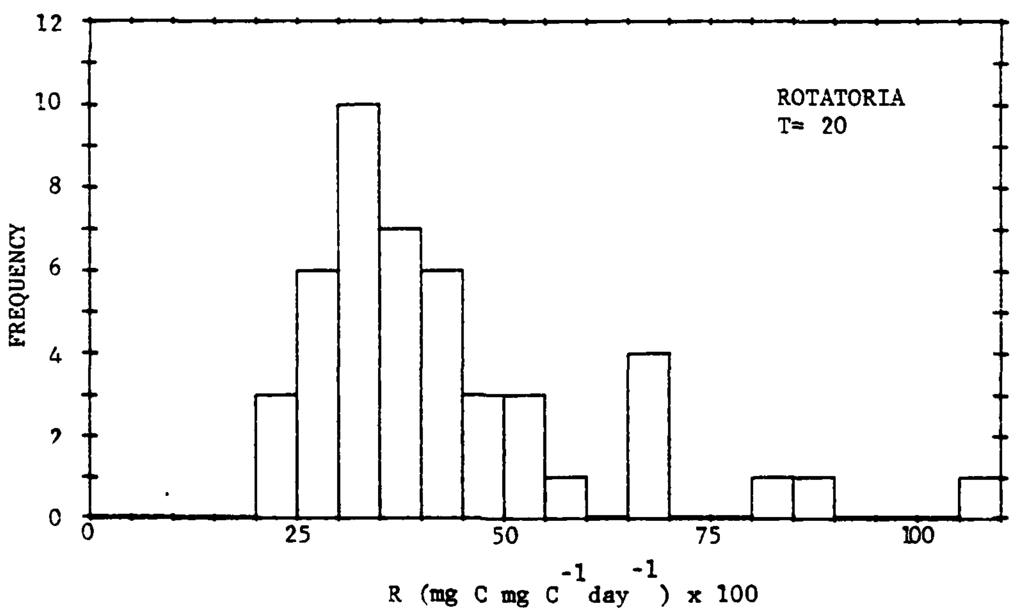

Figure 41. Frequency histogram of respiration rates for Rotatoria. Based on data in Appendix D, Part I. T = temperture (°C)

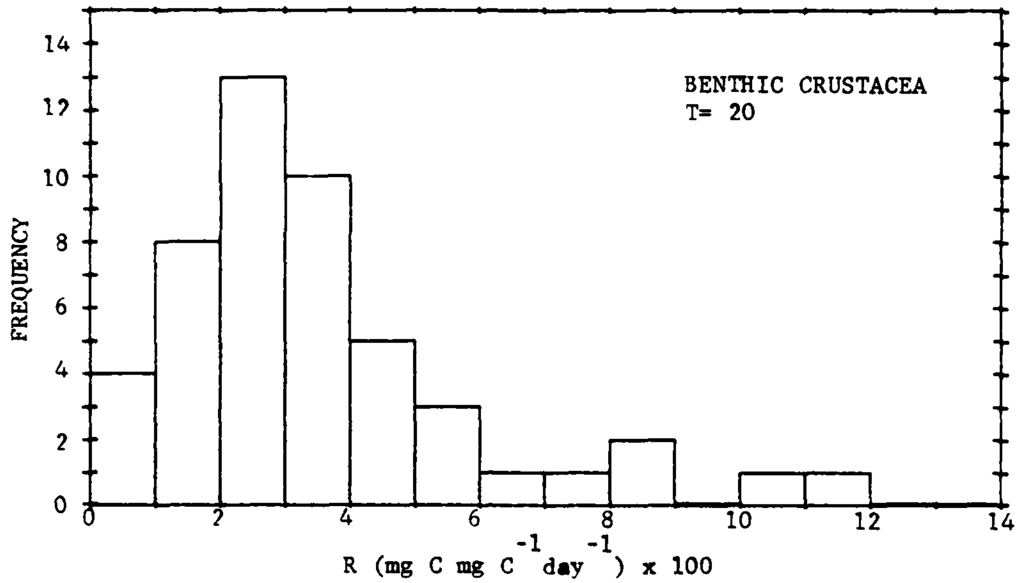

Figure 42. Frequency histogram of respiration rates for benthic Crustacea. Based on data in Appendix D, Part I. T = temperature (°C)

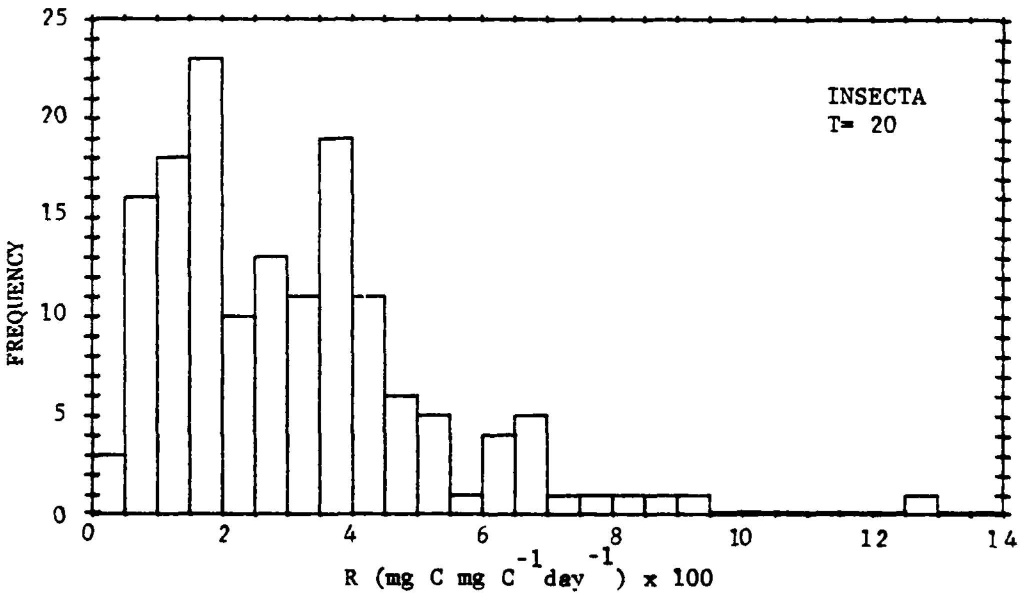

Figure 43. Frequency histogram of respiration rates for aquatic Insecta. Based on data in Appendix D, Part I. T = temperature (°C)

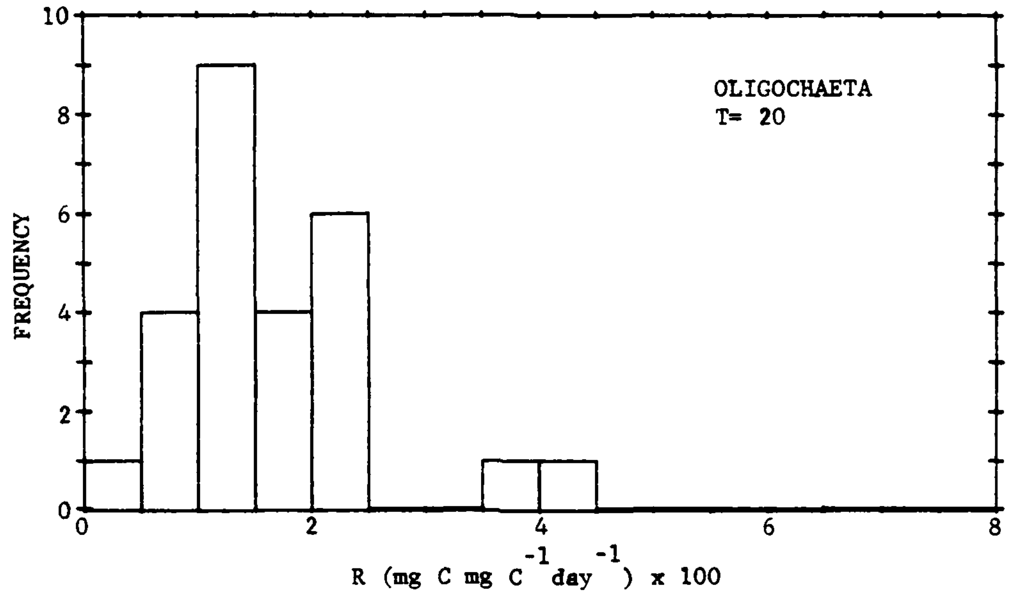

Figure 44. Frequency histogram of respiration rates for Oligochaeta. Based on data in Appendix D, Part I. T = temperature (°C)

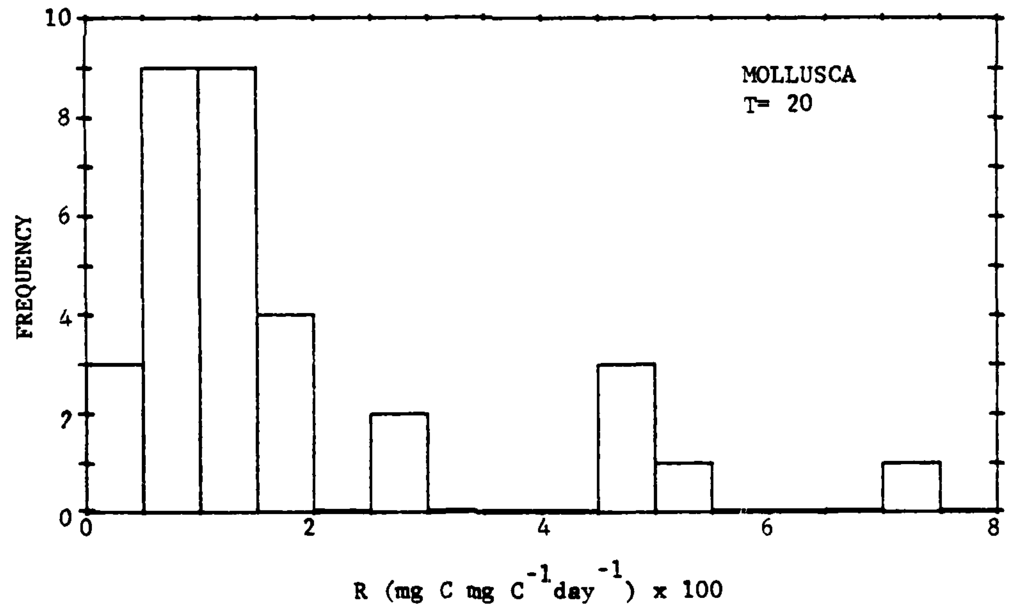

Figure 45. Frequency histogram of respiration rates for Mollusca. Based on data in Appendix D, Part I. T = temperature (°C)

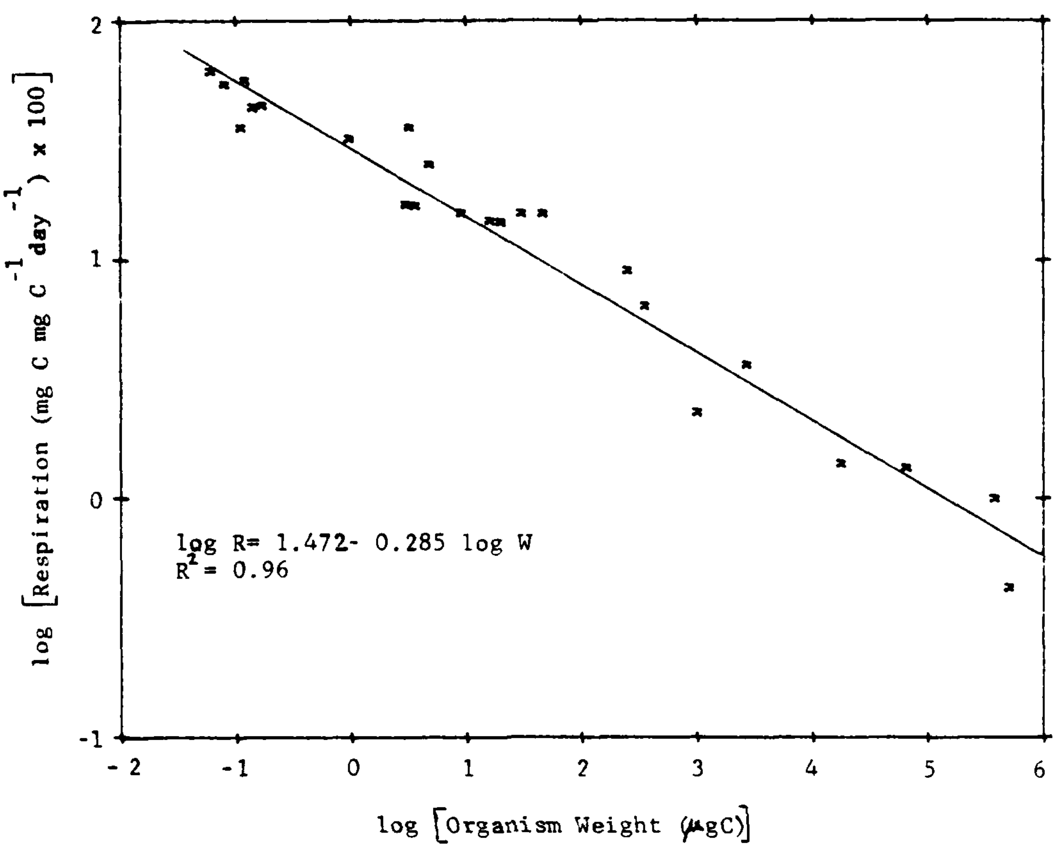

Figure 46. Respiration (R) as a function of organism weight (W) for aquatic invertebrates at 20°C. Based on data in Appendix D, Part I

where Y = respiration rate (mg C/day), W = weight (mg C), and a and b are constants. To obtain weight-specific respiration (R), both sides of Equation 23 must be divided by the specimen's weight:

$$Y/W = aW^b/W \text{ to yield:}$$

$$Y/W = R = aW^{b-1} \tag{24}$$

where R = weight-specific respiration (mg carbon·mg carbon^{-1}·day^{-1}). Appendix D, Part II, is a tabulation of equations relating weight-specific respiration to body weight for various taxa of aquatic invertebrates. Weight distributions for various aquatic taxa could be used in these respiration equations to stochastically describe the effects of body size on respiration. Unfortunately, weight distributions for aquatic invertebrates are virtually nonexistent, owing to the dynamic nature of such distributions and to technical difficulties associated with measuring the dry weights of small individuals.

272. Since young animals of large species overlap in size with adults of smaller species, the use of taxonomic categories may be unjustified to separate animals into groups according to their rates of respiration. To justify using taxonomic categories, one must perceive each taxon as a group of a static mean weight, rather than as a continuum of weights. Perhaps a more realistic approach is to classify all species according to weight, without regard to their phylogenetic affinities. We originally formed six weight classes of aquatic invertebrates but later reduced the number to three, since the mean rates of the three heaviest groups were essentially identical. The weight range of each class is: $0 <$ Class I < 0.1 mg dry wt (Figure 47); $0.1 \leq$ Class II < 1.0 mg dry wt (Figure 48); $1.0 \leq$ Class III (Figure 49). Class I consisted exclusively of zooplankton and Classes II and III exclusively of benthos.

273. Bertalanffy (1951) classified aquatic invertebrates into three categories based on the value of b exponents (Equation 23). Accordingly, Type 1 animals have metabolic rates proportional to the 2/3 power of their body weight ($b = 0.67$; $b-1 = 0.33$). Since surface area generally is related to the 2/3 power of body weight, Type 1 specimens supposedly have metabolic rates that are directly porportional to surface area. Bertalanffy cited isopod crustaceans as an example of Type 1 organisms. Type 2 animals (mostly insects) have metabolic rates proportional to their body weight (i.e., $b = 1$; $b-1 = 0$). Type 3 organisms, pond snails for example, have b values between 0.67 and 1 ($b-1$ values between -0.33 and 0). The $b-1$ exponents in Appendix D (Part II) illustrate the arbitrary nature of Bertalanffy's classification. Many specimens have $b-1$ exponents between -0.33 and 0 (Figure 50), but there is no significant correlation between taxa and the magnitude of the $b-1$ exponent in Equation 24.

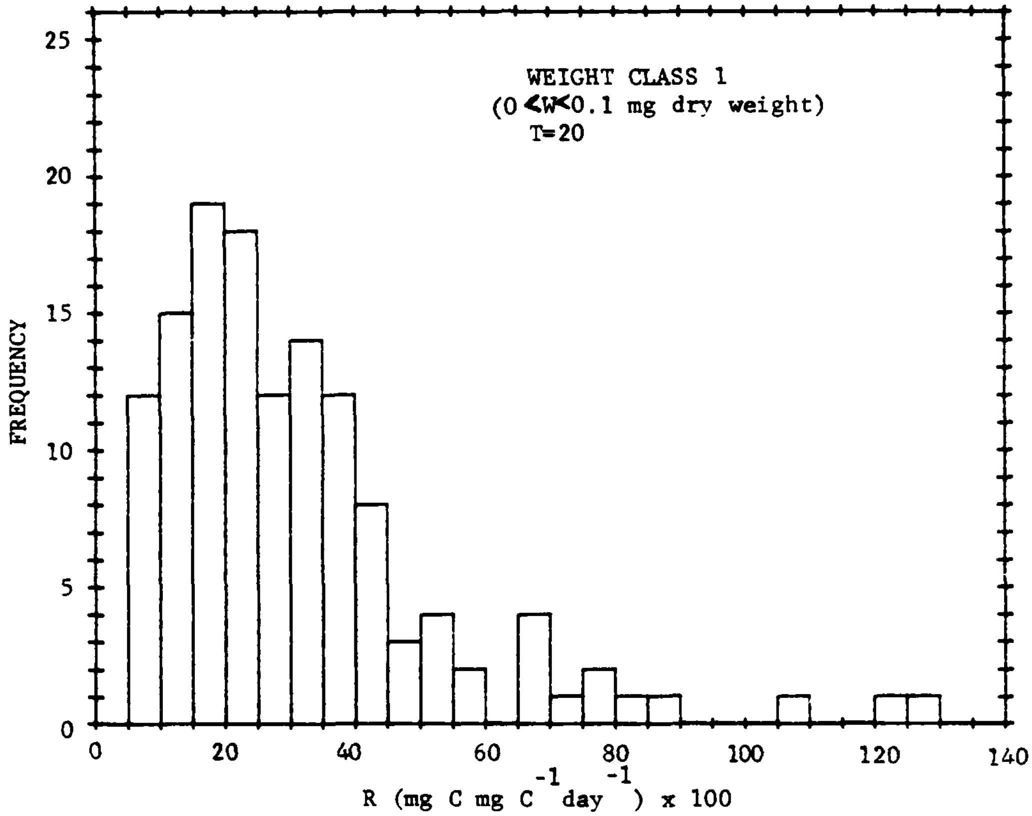

Figure 47. Frequency histogram of respiration rates for aquatic invertebrates of weight class I. Based on data in Appendix D, Part I. T = temperature (°C)

274. The exponent b or b-1 illustrates the effects of body size on oxygen consumption (Bishop 1968) and probably is unrelated to phylogenetic position. Zeuthen (1970) stated that he had always observed invertebrate respiration to be a function of body size, regardless of whether the variation of rates was due to phylogenetic or ontogenetic increases in size. Alimov (Winberg et al. 1973) found similar rates of respiration among molluscs of the same size, although they were of different taxa.

275. Values of b or b-1 (Equations 23 and 24, respectively) are influenced by several factors besides surface area Knight and Gaufin (1966) found that body shape affected b even when respiration was

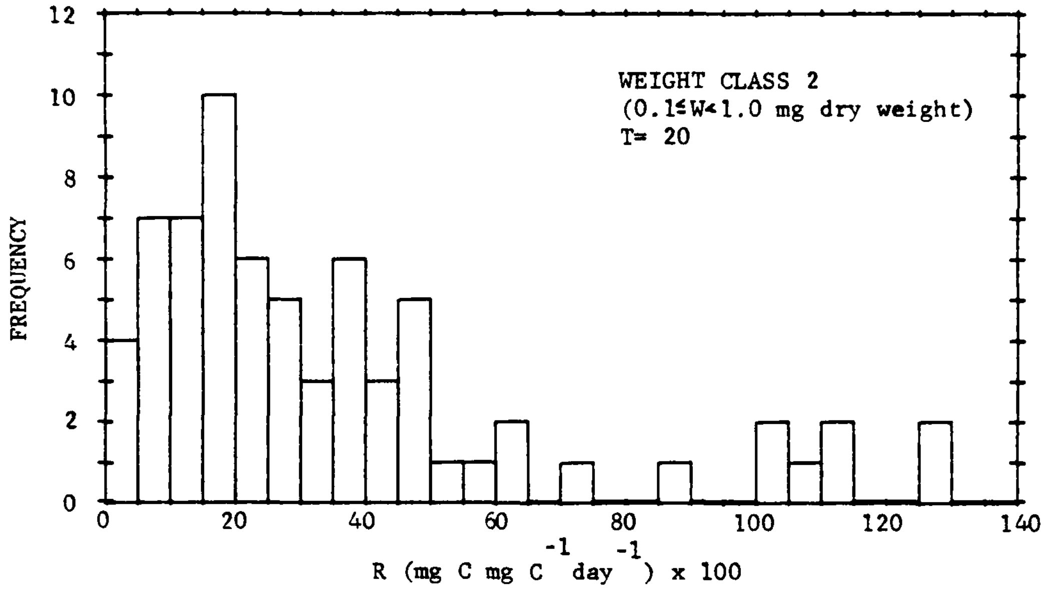

Figure 48. Frequency histogram of respiration rates for aquatic invertebrates of weight class II. Based on data in Appendix D, Part I. T = temperature (^{0}C)

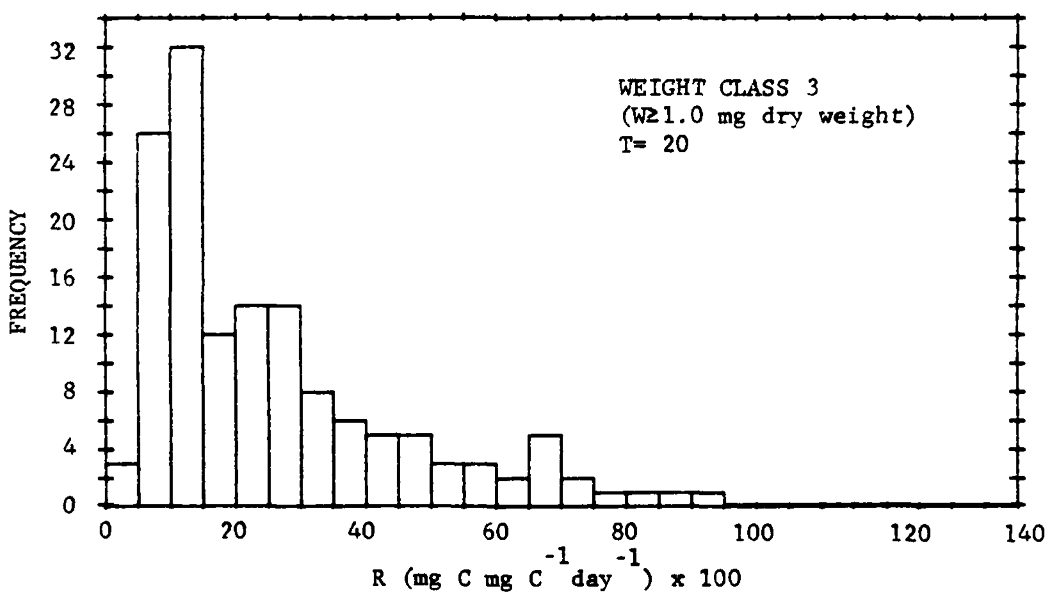

Figure 49. Frequency histogram of respiration rates for aquatic invertebrates of weight class III. Based on data in Appendix D, Part I. T = temperature (^{0}C)

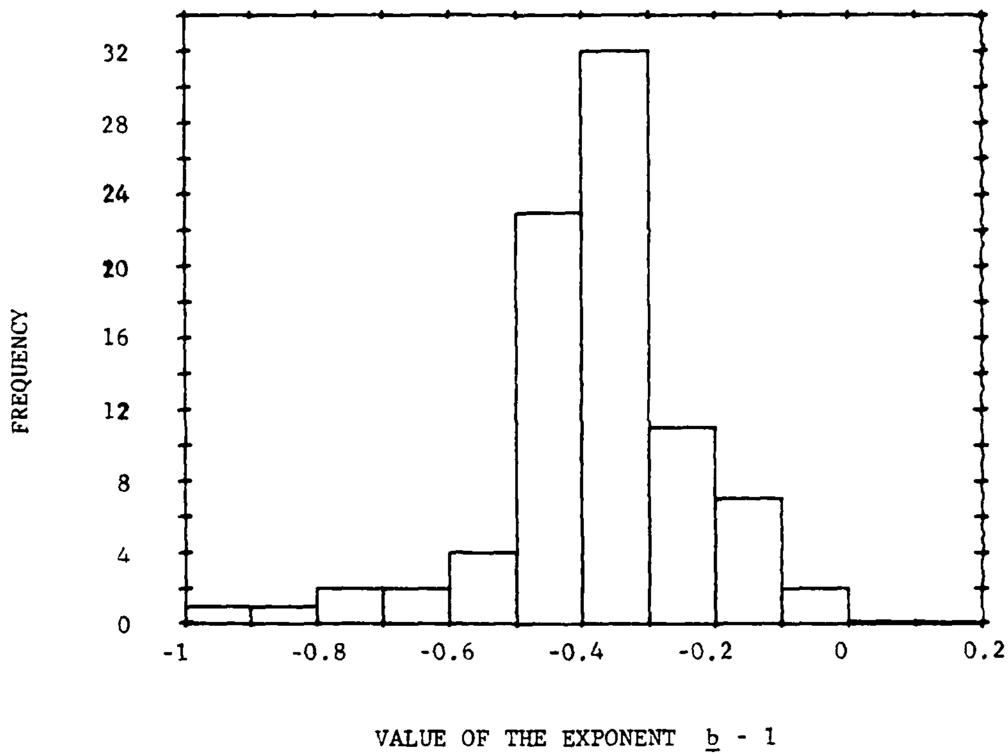

Figure 50. Frequency histogram of the exponent b-1 from the equation: $R = aw^{b-1}$, where R = respiration (mg C·mg C^{-1}·day^{-1}) × 100 and w = weight (mg C)

proportional to surface area. This finding suggested that surface area/volume ratios influence the value of b. The ratio of living to inert protoplasm may affect b exponents (Knight and Gaufin 1966). Calow (1975) found that the b exponents of pond snails were influenced by the type of weight measured (i.e., wet, dry, or ash-free dry weight). Edwards (1957) observed that b had no constant value when wet weight was used as a measure of body size for *Chironomus riparius*. On the other hand, he found that log transformations of dry weight data suggested that b values were constant. His results further suggested that O_2 consumption was not proportional to surface area, although it varied with dry weight to the 0.7 power. Buikema (1972) determined that b exponents were higher in unacclimated than in acclimated zooplankton.

276. The relative rates of respiration by animals of equal size is given by the coefficient a in Equations 23 and 24 (Bishop 1968). Several authors (e.g., Comita 1968, Hughes 1970, Calow 1975, Green 1975, Sweeney and Schnack 1977) have correlated a coefficients with temperature. Figure 51 is a frequency histogram of a values for various aquatic invertebrates as tabulated in Appendix D (Part II). Our regression of a coefficients on temperature (Figure 52) was significant ($r^2 = 0.45$; $t_{(0.01,\ 38)} = 5.48$).

277. Frequency distributions of "b-1" and "a" values are of limited utility unless the mean weight of each model compartment is known (e.g., Steele 1974). Nevertheless, we have provided this information with the hope that it will be more useful in the future. Hopefully, when biomass and separation techniques improve for subcategories of zooplankton and benthos, mean biomass will be easier to quantify. Once a mean weight is quantified for a model compartment, the weight can be substituted for W in Equation 24. Randomly selected b-1 and a values, from their respective frequency distributions (Figures 50 and 51), modify W to yield a weight-specific rate of respiration (R). This respiration rate is that of an average individual within the compartment. The product of R and total biomass yields daily respiration for the entire model compartment.

Effects of Dissolved Oxygen Concentration

278. Dissolved oxygen concentrations may significantly affect the rate of respiration of aquatic invertebrates. Two types of animals have been recognized, according to their response to changes in oxygen concentrations (Prosser and Brown 1961). Regulators are able to maintain their metabolic rates at fixed levels, relatively independent of oxygen concentrations. The range over which an animal can regulate varies among species and within species, depending on their physical condition and history of acclimation. Conformers are animals that faithfully track concentrations of dissolved oxygen (i.e., metabolic rates are directly proportional to oxygen concentration).

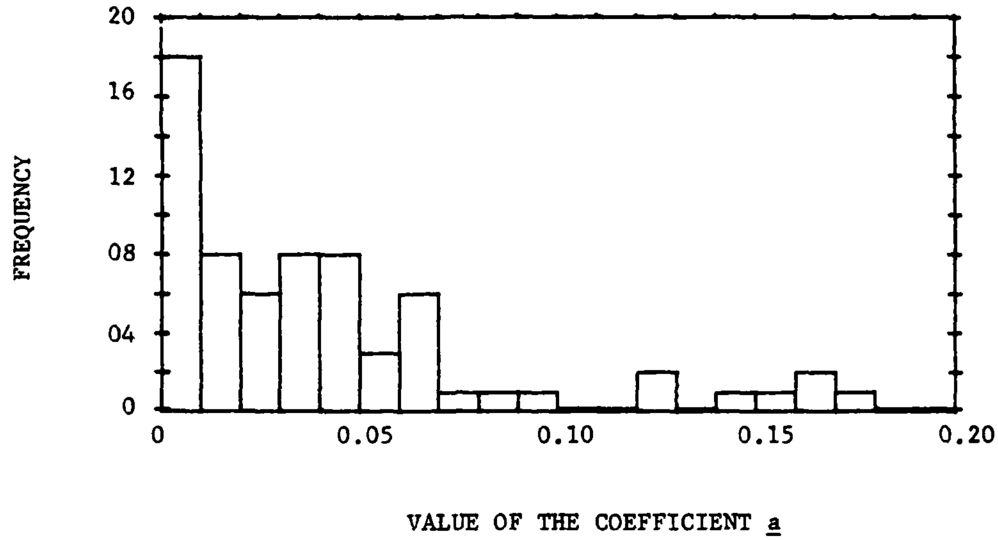

Figure 51. Frequency histogram of the coefficient a from the equation: $R = aw^{b-1}$, where R = respiration (mg C mg $C^{-1}day^{-1}$) × 100 and w = weight (mg C)

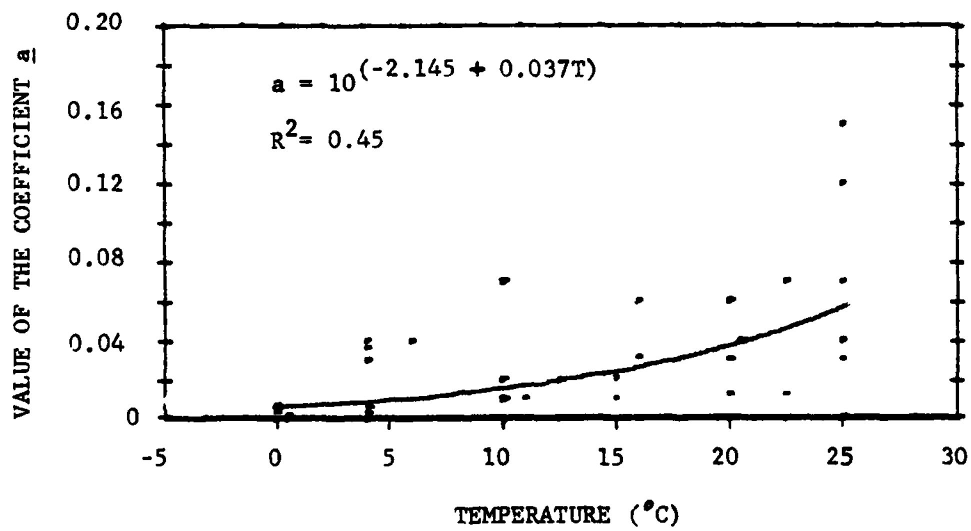

Figure 52. Values of the coefficient a as a function of temperature (T) for aquatic invertebrates. Based on data in Appendix D, Part II

279. Whether a species is a conformer or regulator may depend on its history of acclimation to dissolved O_2. In contrast to most conformers that exhibit some degree of regulation at high or low O_2 tensions, the decapod *Pacifastacus leniusculus* was a conformer over all concentrations of O_2 (Moshiri et al. 1971). Apparently the metabolic response of this species was characteristic of animals living in waters with continually high levels of oxygen. Such organisms would gain little selective advantage by having respiratory systems capable of regulation (Moshiri et al. 1971).

280. Generally, all poikilotherms must conform when concentrations of oxygen fall below a critical level for that species (i.e., the incipient-limiting level of Calow (1975). The gastropods *Ancylus fluviatilis* and *Planorbis contortus* were able to regulate down to O_2 concentrations of 4.7 mg/ℓ and 2.7 mg/ℓ, respectively (Calow 1975). Palmer (1968) found that the oligochaete *Tubifex tubifex* was a regulator down to ca 1.5 percent of saturation. Below this concentration metabolic rates declined sharply. Even diffusion of O_2 into worms at this concentration was insufficient to meet oxygen demands for respiration. Critical concentrations also have been recognized in the ephemeropterans *Hexagenia limbata* and *Ephemera simulans*, i.e., 1.2 and 0.80 ml O_2/ℓ (Eriksen 1964). Interestingly, these species regulate when a substrate is provided but conform when none is present. The decapod *Caridina fernandoi* maintained rates of respiration independent of O_2 concentrations down to approximately 1.4 mg/ℓ (Wycliffe and Job 1977). The oxygen content of water affected the metabolic rate of the copepod *Calanus finmarchicus* only when it was low (Marshall 1973). Below 3 mg O_2/ℓ, respiration decreased very rapidly (Marshall et al. 1935). Sushchenya (1969) found that the respiration of most Crustacea decreased linearly at O_2 tensions below 20 to 60 percent of saturation.

281. Some aquatic invertebrates are extremely tolerant of low O_2 tensions and exhibit little change in metabolism as O_2 tensions decrease. Chaston (1969) found that *Cyclops varicans* could withstand deoxygenated water for up to 36 hr by building a lactic acid debt. Respiration rate doubled, however, after specimens were returned to water of normal O_2

tensions. The O_2 consumption of Glyptotendipes polytomus larvae (Chironomidae) was several hundred times lower at low than at high concentrations of oxygen. Tissues of specimens collected from anoxic mud contained traces of lactic acid which indicated that the chironomids had met their metabolic requirements by anaerobic pathways (Kamler and Srokosz 1973).

282. Few models have constructs for the effects of oxygen concentration on respiration, although oxygen often may be limiting to organisms in aquatic ecosystems. Zahorcak (1974) developed the stepwise construct "BEHAVE" which reduced respiration as O_2 concentrations decreased. The function finally reduced respiration to zero when the field concentrations of O_2 fell below the critical level for the compartment.

283. Our oxygen construct decreases the respiration of all invertebrates logarithmically as O_2 tensions decrease. We assumed that most aquatic invertebrates in reservoirs are capable of some degree of regulation over O_2 concentrations in the range of 4 to 14 mg/ℓ. At low concentrations (< ca 4 mg/ℓ), we assumed that most aquatic animals must conform, i.e., exhibit decreased metabolism which is proportional to concomitant decreases in O_2 concentration. When R = 0, the term $\frac{db}{dt}$ in Equation 1: $\frac{db}{dt} = [G(A/G) - R - NPM - PM]$, should not increase significantly because another oxygen construct increases nonpredatory mortality (NPM) when O_2 tensions decrease (see "Oxygen Concentration," page 170, Part VI). Table 15 lists logarithmic equations which describe the relation of respiration to O_2 concentration for several benthic macroinvertebrates. Unfortunately, similar data for zooplankton were few. Data from Appendix D (Part I) for each of the species in Table 15 were corrected to 20°C before regression analysis.

284. Based on the equations in Table 15, we calculated an oxygen-correction factor (F_o) for respiration as a function of ambient concentrations of O_2. We let respiration (R) equal one at 14.6 mg O_2/ℓ (saturation at 0°C and 760 mm Hg) and calculated F_o, according to the last equation in Table 15, for O_2 tensions ranging from 0 to 14.6 mg/ℓ. A curve fitted to these points is described by the equation:

$$F_o = 0.426 + 0.482 \log O_2 \quad (25)$$

where O_2 = O_2 tension (mg/ℓ) and F_o = oxygen correction. Equation 25 is graphically depicted in Figure 53. We assume that R = 0 when O_2 tensions are less than 0.13 mg/ℓ for 24 hr. The product of F_o and weight-specific respiration (from frequency histograms) yields a rate corrected for oxygen effects.

Table 15

Respiration Rates (R) (mg carbon·mg carbon^{-1}·day^{-1}), as a Function of O_2 Concentration (mg/ℓ), for Several Aquatic Invertebrates

Taxon	Equation*	N	R^2
Oligochaeta			
Tubifex tubifex	$R = 0.124 + 0.0062 \log O_2$	5	0.78
Plecoptera			
Tarniopteryx nubulosa	$R = 0.010 + 0.0400 \log O_2$	5	0.98
Nemoura cinerea	$R = 0.023 + 0.0380 \log O_2$	5	0.93
Dirua nanseni	$R = 0.002 + 0.0410 \log O_2$	5	0.83
Ephemeroptera			
Cloeon dipterum	$R = 0.025 + 0.0230 \log O_2$	4	0.95
Crustacea			
Pacifastacus leniusculus	$R = -0.002 + 0.023 \log O_2$	8	0.83
Mean of constants	R = 0.030 + 0.0370 log O2	6	
SE of means	±0.092; ±0.016		

* Equations were calculated from data of Palmer (1968), Nagell (1973), and Moshiri et al. (1970).

285. Due to insufficient data for zooplankton, we were unable to calculate another O_2 correction. Inasmuch as the data of Marshall et al. (1935) and Sushchenya (1969) show that the relation of zooplankton respiration to O_2 concentration is similar to that for benthos (Table 15), we decided to use Equation 25 for all aquatic invertebrates.

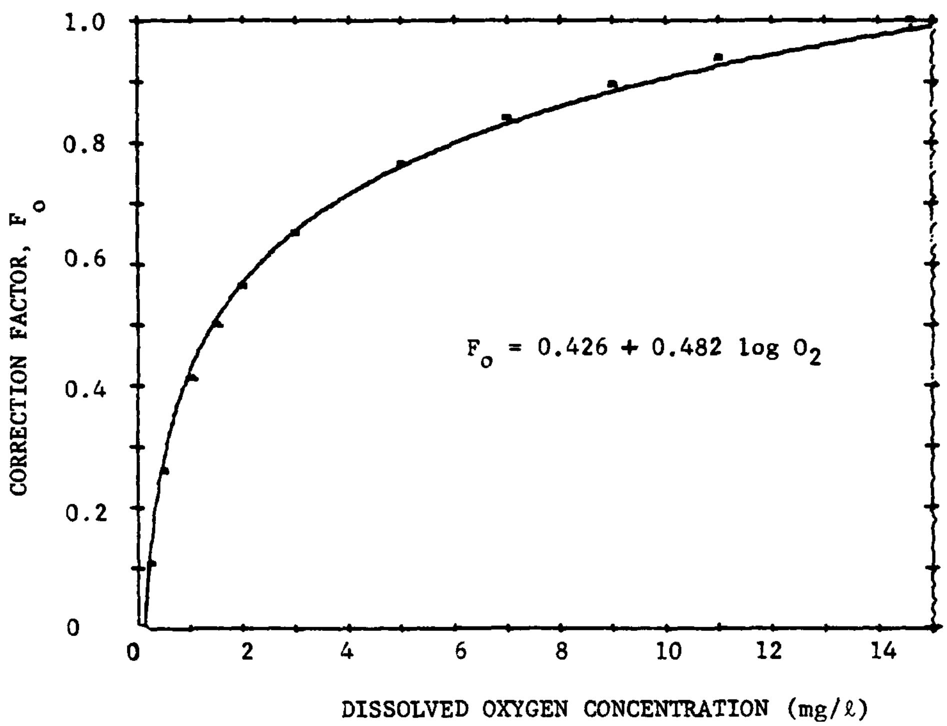

Figure 53. Respiration correction factor (F_o) as a function of dissolved oxygen concentration. Based on equations in Table 15

286. The oxygen correction (F_o) was derived from very limited information and should be treated with caution. Until further research is conducted, especially on the effects of O_2 tensions on zooplankton respiration, constructs like ours and that of Zahorcak (1974) are state of the art. Although such constructs greatly simplify known effects, we believed that some effort should be made to approximate this important relation.

Effects of Temperature

287. Temperature probably affects the respiration of aquatic ectotherms more than any other single factor. Temperature explained 56 percent of the variation in the respiration of the mayfly Isonychia

bicolor (Sweeney 1978). The amounts of variation in respiration explained by temperature ranged from 49 to 79 percent for the copepod Diaptomus sp. (Comita 1968) and from 46.2 to 98.8 percent for the stonefly Acroneuria californica (Heiman and Knight 1975). Larow et al. (1975) found that roughly 34 percent of the variance in zooplankton rates was explained by temperature.

288. Respiration rates usually increase exponentially with increases in temperature until upper lethal temperatures are reached. For example, the metabolism of the coleopteran Dineutes indicus was slow at low temperatures, increased rapidly with increasing temperature, and then suddenly decreased as upper lethal temperatures were approached (Tonapi and Rao 1977). Ivanova (1972) noted similar temperature effects on all instars of the amphipod Gammaracanthus lacustris. Ivanova also noted a sharp decline in rates at upper lethal temperatures (15° to 18°C). Blazka (1966), Comita (1968), Moshiri et al. (1971), Gophen (1976), and others (Appendix D, Part II) noted similar relationships of metabolism to temperature.

289. Equations that predict rates of respiration at different temperatures, e. g., Q_{10} functions (Prosser and Brown 1961) and Krogh's normal curve (Krogh 1914), are reasonably accurate for many aquatic ectotherms. Better still are the predictive equations derived specifically for one species (See Appendix D, Part II). Nevertheless, deviations from predicted rates do occur (Conover 1962, Sushchenya 1969, Hughes 1970, Marshall 1973, Roff 1973). Most often, deviations result from acclimation or compensation.

290. Acclimation was defined by Prosser and Brown (1961) as the ability of ectotherms to maintain respiration rates independent of temperature within narrow ranges. Buffington (1969) defined acclimation as a shift in metabolic rate from that which would be predicted on the basis of purely physical and chemical processes. Acclimation has been observed in many aquatic invertebrates, for example, Mollusca (Calow 1975, Burkey 1971), Decapoda (Moshiri et al. 1971), Diptera (Buffington 1969), Copepoda (Conover 1962, Suschenya 1969, Ostapenya et al. 1969, Marshall 1973), and Cladocera (Blazka 1966, Moshiri et al. 1969).

Although the capability of temperature acclimation apparently is common among aquatic invertebrates, it is not universal and varies with sex (Moshiri et al. 1969) and among species based on genetic differences.

291. Because temperature greatly influences respiration, constructs are imperative for models of aquatic systems where temperature fluctuates seasonally. Respiration was considered to be a linear function of temperature in models by DiToro et al. (1971) and Baca et al. (1974). More often, an exponential function is used to describe the relation of respiration to temperature (Umnov 1972, Patten et al. 1975, Chen and Orlob 1975, Scavia et al. 1976). An exponential form that is widely used for ecological work is the Q_{10} function (Prosser and Brown 1961). This function is the ratio of two rate constants for respiration at temperatures 10°C apart. A typical equation is $k_2 = k_1 \, Q_{10}^{(T_2 - T_1)/10}$, where k_2 is a rate constant at T_2 (2nd temperature) and k_1 is a rate constant at T_1 (1st temperature). By knowing T_1, k_1, and the Q_{10} for the temperature range T_1 to T_2, k_2 may be calculated for the second temperature (Lassiter 1975). Krogh's normal curve (Krogh 1914) has been used to describe respiration-temperature relations for many aquatic ectotherms and may be approximated by a set of Q_{10} coefficients (Winberg 1956). MacCormick et al. (1974), Park et al. (1974), and Zahorcak (1974) in the Eastern Deciduous Forest Biome models (International Biological Program) used a respiration-temperature function in which respiration increased exponentially with temperature to an optimum and then decreased as temperatures approached upper tolerance limits. They also used Q_{10} values.

292. Our construct for the relation of respiration to temperature is bascially exponential, with the added assumption that respiration rate drops to zero when the upper lethal temperature (34°C) is reached. The construct is essentially a Krogh curve (Krogh 1914, Winberg 1956), but was calculated from the data tabulated in Appendix D (Part I). Rates of respiration for aquatic invertebrates, regardless of taxon or size, were selected from Appendix D, Part I. The criterion for selection was the availability of estimates of metabolic rates at a minimum of three experimental temperatures. Rates of these specimens were averaged for each temperature and plotted (Figure 54). The curve fitted to these points

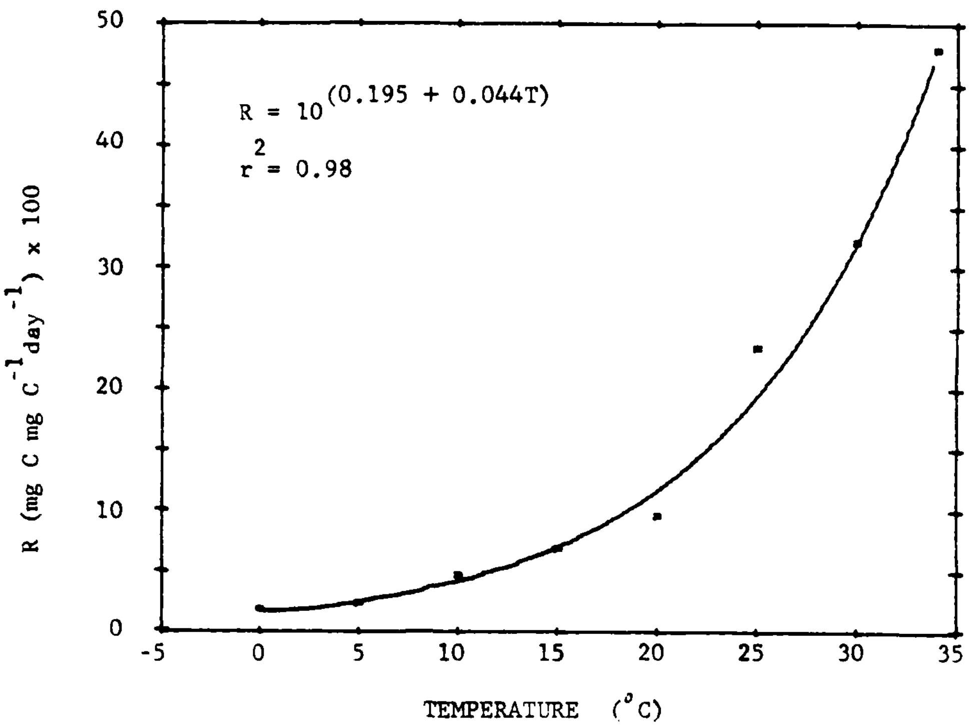

Figure 54. Mean rates of respiration (R) as a function of temperature (T) for aquatic invertebrates. Based on data in Appendix D, Part I

has the form $R = 10^{(0.195 + 0.044T)}$ ($r^2 = 0.98$), where T is temperature (°C) and R is respiration rate [(mg carbon·mg carbon^{-1}·day^{-1}) × 100].

293. The variance of mean rates of respiration at different temperatures (Figure 54) was high. Most of the variation resulted from size differences among selected taxa. For example, Brachionus rubens Rotatoria ($\bar{x}$ - dry weight = 7.6×10^{-5} - 1.4×10^{-4} mg, Pilarska (1977c)) had weight-specific rates that were ca 60 times those of Ferrissia rivularis Mollusca ($\bar{x}$ - dry weight = 1.38 - 1.62 mg, Burky (1971)). For this reason, we were interested in the shape of the curve and not the predicted rates themselves.

294. To obtain coefficients that would permit the conversion of rates in Appendix D (Part I) to rates at 20°C, we assigned the value of one to the respiration rate at 20° (Figure 54) and calculated the appropriate temperature correction ($F_{to\ 20}$), to convert rates at 0°, 5°,

10°, 15°, 30°, and 34°C to rates to 20°C. The resulting factors ($F_{to\ 20}$) were plotted, and the curve was calculated:

$$F_{to\ 20} = 0.887 - 0.045T \tag{26}$$

where T = temperature (°C) and $F_{to\ 20}$ = coefficient for correction of rates to 20°C (Figure 55).

295. Using Equation 26, we adjusted all respiration rates (Appendix D, Part I) to 20°C before forming frequency histograms (Figures 39-41 and 43-49). Thus, rates from any frequency histogram are at 20°C and must be corrected to ambient temperatures before they can be used in the model. Figure 56 illustrates the rate of change of $F_{from\ 20}$ (a correction factor to convert rates at 20°C to rates at ambient temperatures) with temperature. The equation for calculating $F_{from\ 20}$ is:

$$F_{from\ 20} = 10(-0.887 + 0.045T) \tag{27}$$

where T = ambient temperature and $F_{from\ 20}$ = correction factor for temperatures at 20°C. At the same temperature, the factor $F_{from\ 20}$ is the reciprocal of $F_{to\ 20}$. The product of weight-specific rates of respiration (from frequency histograms) and $F_{from\ 20}$ yields a weight-specific rate which is corrected for temperature effects.

Summary of Constructs

296. Weight-specific rates of respiration (R) at 20°C may be obtained from frequency distributions of rates for major taxa of zooplankton and benthos (Figures 39-41 and 42-45, respectively) or from similar distributions for three weight classes of aquatic invertebrates (Figures 47-49). Selected rates must be modified to rates at ambient temperatures and oxygen concentrations. Modification is accomplished by multiplying R by $F_{from\ 20}$ (temperature correction from Equation 27) and by F_o (oxygen correction from Equation 25). Respiration is set to zero when temperatures are below zero or above 34°C for 24 hr. Similarly, R = 0 when oxygen concentrations fall below 0.13 mg/ℓ for 24 hr. When R

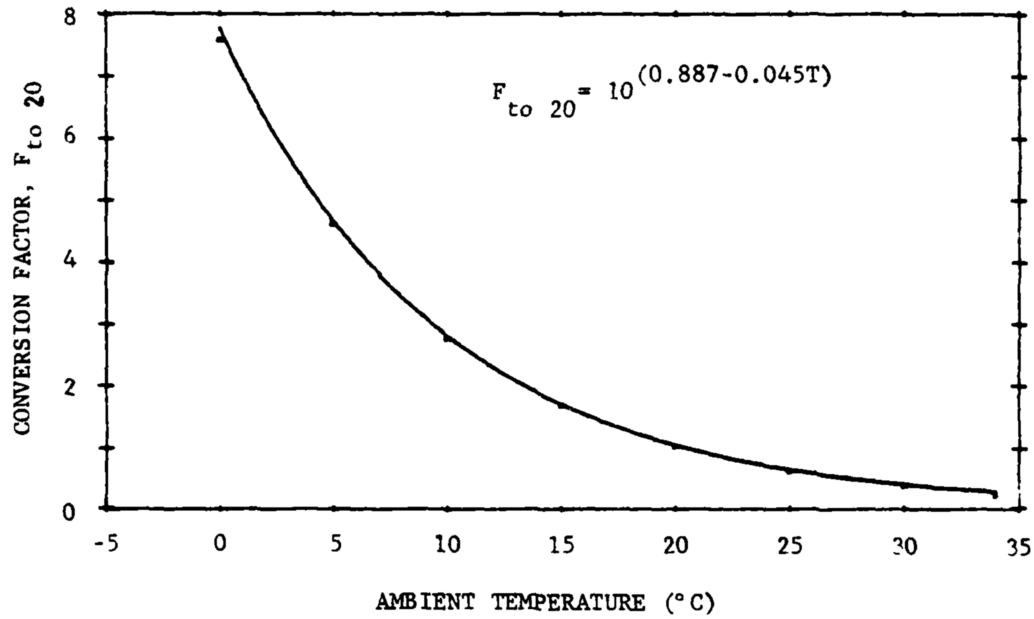

Figure 55. The conversion function, $F_{to\ 20}$, for adjusting respiration rates (R) at ambient temperatures to rates at 20°C

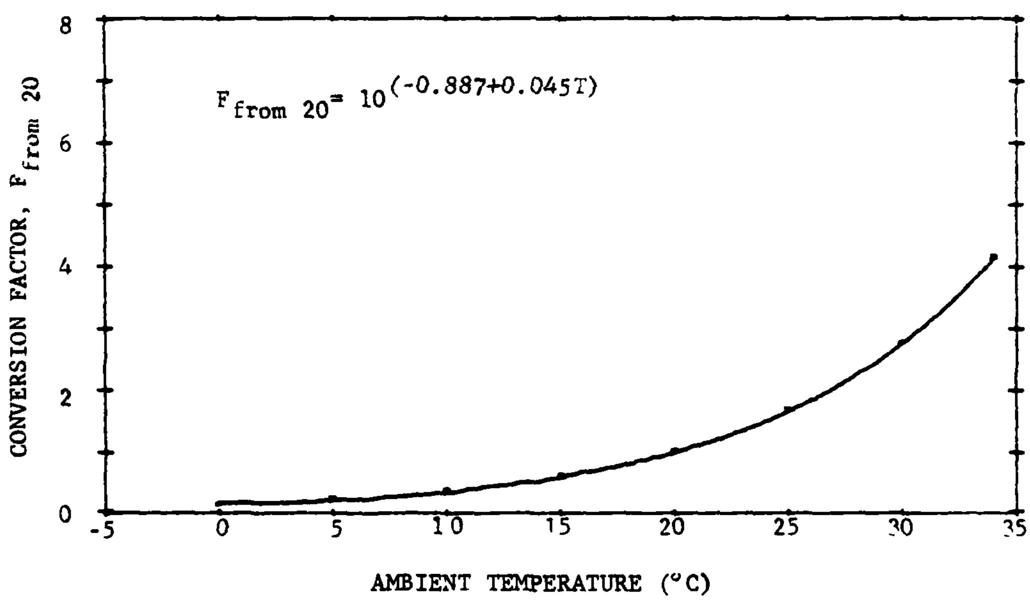

Figure 56. The conversion function, $F_{from\ 20}$, for adjusting respiration rates (R) at 20°C (i.e., respiration histograms) to rates at ambient temperature

(mg carbon·mg carbon^{-1}·day^{-1}), corrected for the effects of temperature and oxygen concentration, is multiplied by the initial biomass of the model compartment, the result is the total carbon respired by the compartment daily. According to Equation 1, respiration rates should be subtracted from assimilated carbon: $\frac{db}{dt} = b\ [G(A/G) - R - NPM - PM]$.

297. Because we had no realistic way to apportion total benthic biomass among smaller taxonomic compartments, respiration rates should be selected from a probability distribution formed from Figures 48 and 49. Rates for zooplankton may be obtained from Figure 47, which was formed exclusively from zooplankton data, or from Figures 39-41 if the users wish to divide the zooplankton compartment. When the compartment is divided, zooplankton biomass should be assigned as follows: Cladocera = 60 percent, Copepoda = 35 percent, Rotatoria = 5 percent (when no better data are available). Copepod respiration rates at 20°C, for example, may be calculated as 0.35b(R), where b = total zooplankton biomass (mg carbon) and R = weight-specific respiration at 20°C (Figure 40). The sum of this result and similar results for Cladocera and Rotatoria represents total zooplankton respiration at 20°C.

Conclusions

298. Because respiration constitutes a major portion of energy expenditures, it is a very important parameter in the energy budgets of aquatic invertebrates. Methods employed to determine rates of respiration (i.e., Warburg, Gilson, Cartesian diver, chemical, and polarographic) yield similar results, but differences in experimental conditions (e.g., whether specimens are fed or acclimated) increase variability among rates. Though factors potentially affecting rates are numerous, only body size, O_2 concentration, and temperature effects were well documented by published data. Apparently, these effects account for most of the variability among respiration rates in field populations.

PART VI: NONPREDATORY MORTALITY OF ZOOPLANKTON AND BENTHOS

Introduction

299. The mortality rate of a population may be expressed as a ratio of total deaths to total population per unit of time (Pennak 1964). In aquatic models, mortality is often subdivided into predatory and nonpredatory categories. This approach separates two processes which differ significantly in their effects on aquatic ecosystems. Predation primarily results in a flow of energy to higher trophic levels and may act to control population size. Nonpredatory mortality (NPM) may also act to control a population but primarily results in the addition of organic matter and nutrients to the detrital pool. The two categories are indirectly related. Environmental conditions that increase NPM also weaken organisms and may increase their susceptibility to predation. Natural mortality is a term occasionally used to refer to NPM (e.g., Otto 1975). We prefer the usage NPM because predatory mortality (PM) may also be considered natural.

300. When acquiring NPM data, we limited our review to literature data that were obtained under typical environmental conditions, i.e., conditions which would normally prevail in temperate reservoirs. Similarly, we discuss those factors most likely to influence NPM in temperate reservoirs, although many factors (physical, chemical, and biological) potentially affect NPM.

Previous Models

301. The differential equations for biomass in most aquatic models treat NPM as a loss from zooplankton or benthos compartments. Nonpredatory mortality may be treated as a single negative term (Chen and Orlob 1975, DiToro et al. 1971, Scavia et al. 1976), as a constant proportion of the biomass in the donor group (MacCormick et al. 1974, Zahorcak 1974, Waters and Efford 1972, Menshutkin and Umnov 1970, Umnov 1972), or in combination with other losses. Ross and Nival (1976)

combined NPM with metabolic losses. Nonpredatory mortality was included with egestion and molting losses by Patten et al. (1975) and with respiration and sinking by Parker (1973). Baca et al. (1974) and Steele (1974) discussed the inadequacy of this approach for most environmental situations. Steele also proposed the alternative assumption that mortality tends primarily to occur during certain critical periods, i.e., NPM is a function of age.

302. Although the magnitude of NPM is variable and a function of a multitude of chemical, physical, and biological factors, NPM often is an empirical constant in aquatic models (e.g., 1.5 percent/day, DiToro et al. 1971; 0.5 percent/day, MacCormick et al. 1974; 0.14 to 0.34 percent/day, Ross and Nival 1976; 0.1 percent/day, Umnov 1972). Attempts have been made to make NPM a function of season (Umnov 1972), temperature (Scavia et al. 1974, Zahorcak 1974, Park et al. 1974), dissolved oxygen concentration (Zahorcak 1974, Menshutkin and Umnov 1970), and density (Scavia et al. 1974, Zahorcak 1974, Park et al. 1974).

Experimental Estimates

303. The constant NPM values cited above are within the range of values we tabulated in Appendix E, Part I. Though values potentially range from 0 to 100 percent of biomass per day, given ideal and catastrophic conditions, respectively, NPM normally is less than 1 percent/day in both zooplankton and benthos (Figures 57 and 58, Appendix E: Part I). Welch (1976) could not demonstrate chironomid mortality until their last year of larval life, when fish predation began. However, Thornton and Wilhm (1975) observed two critical periods of increased NPM in larval *Chironomus attenuatus*. *Daphnia* exhibited an estimated 0.12 and 0.17 percent/day NPM during April-June and July-August, respectively, in Canyon Ferry Reservoir, Montana (Wright 1965). Nonpredatory mortality was probably underestimated in most field studies because of initial assumptions. For example, Wright (1965) assumed that *Leptodora kindtii* was the sole predator and that predation was negligible when *Leptodora* populations were low. Hall (1964) suggested that the

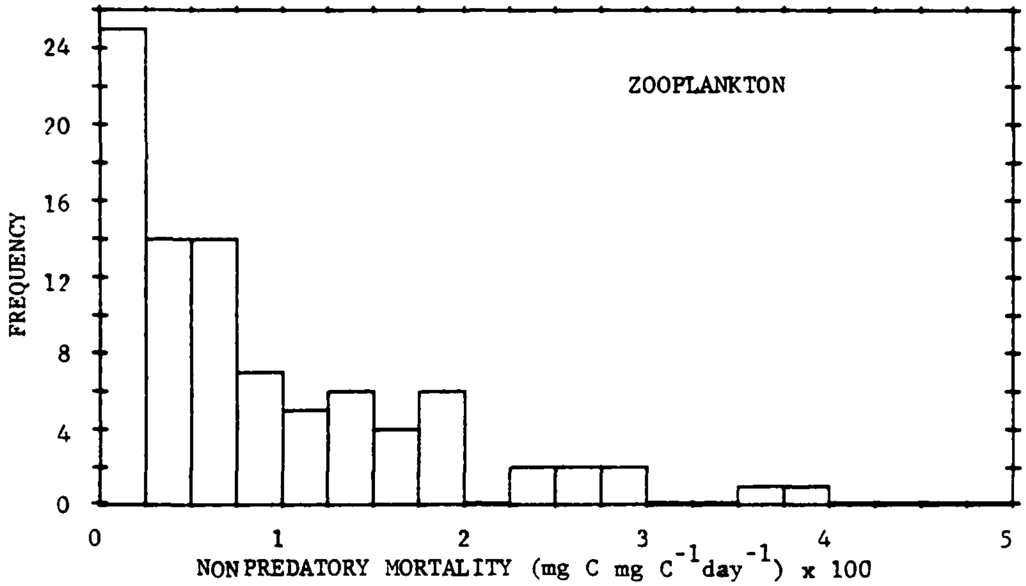

Figure 57. Frequency histogram of nonpredatory mortality rates (NPM) for zooplankton. Based on data in Appendix E, Part I

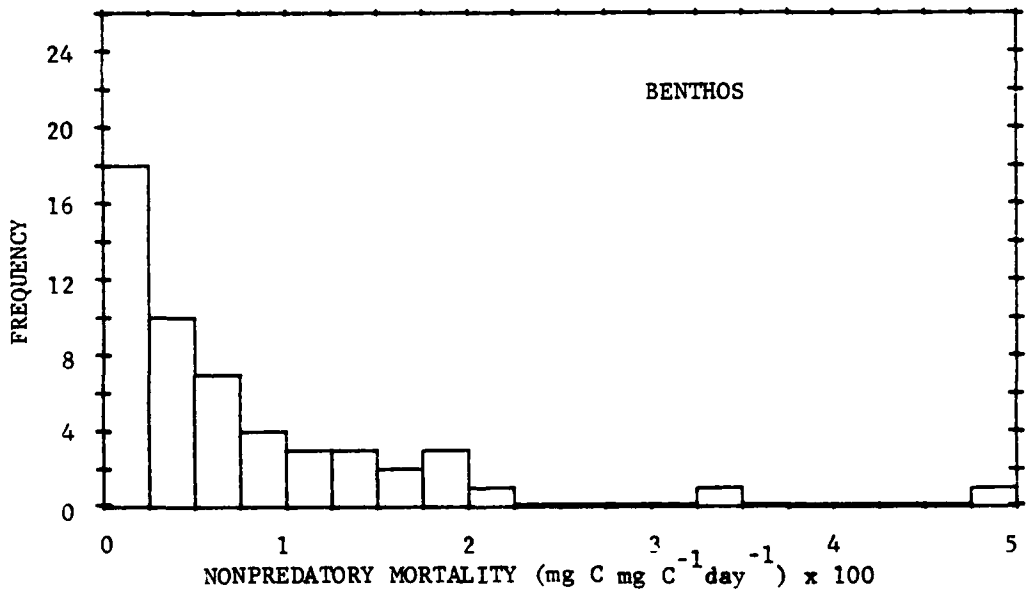

Figure 58. Frequency histogram of nonpredatory mortality rates (NPM) for benthos. Based on data in Appendix E, Part I

physiological mortality rate of Daphnia galeata was probably less than 3 percent per day throughout the year. His suggestion was based on observations of the laboratory survival of this species.

304. Estimates of NPM are difficult to obtain in the field and when obtained usually involve questionable assumptions or uncertain correlations of population phenomena (Hall 1964). For example, Dodson (1972) assumed that Chaoborus spp. and salamanders were the only predators of Daphnia rosea. After estimating PM he obtained NPM by difference, i.e., NPM = total mortality - PM. Clark and Carter (1974) considered predation on cladocerans in Sunfish Lake, Ontario, to be insignificant because the lake lacked planktonic predators, and fish supposedly were restricted to the littoral zone. A direct approach is to cage animals and eliminate predators altogether (e.g., Otto 1974). Still, researchers must assume that conditions within field cages closely approximate the conditions outside the cages with respect to factors such as food, density, light. Given the problems inherent in accurately sampling zooplankton (Bottrell et al. 1977) and benthos (Brinkhurst 1974), and the broad assumptions required in most field estimates of NPM, one must consider field data to be crude approximations at best. By contrast, laboratory studies produce analyses that often yield accurate knowledge of fundamental population growth. Unfortunately, laboratory work is often limited to conditions that are not found in nature (Hall 1964). Furthermore, study specimens are seldom given sufficient time to acclimate to experimental conditions (e.g., temperature, food concentration, and density). In short, investigators often are torn between potentially inaccurate estimates of NPM from field studies and accurate estimates of NPM from unnatural laboratory experiments. Nevertheless, some NPM data from laboratory and field experiments are surprisingly close (Appendix E, Part I). Hall et al. (1970), who constructed life tables for Ceriodaphnia reticulata and Simocephalus serrlatus from both laboratory and field data, found that although temperatures fluctuated from 20° to 26°C in the field and were constant at 23°C in the lab, rate functions produced by laboratory and field experiments were similar.

Factors Affecting Nonpredatory Mortality

Chemicals

305. The concentrations of many chemicals in natural waters influence the NPM of aquatic invertebrates, and, though in most cases we lack sufficient published data to accuratelv model these effects, some are worth mentioning. Toxicity models must be highly specific (as to animal and chemical species considered) and therefore are beyond the scope of this general ecosystem model. For example, the fairy shrimp *Parartemia zietziana* exhibited tremendous NPM as a result of mild increases in salinity (Marchant and Williams 1977). By contrast, Thornton and Sauer (1972) found a high optimum salinity near 68.4 millimoles per litre in *Chironomus attenuatus*. Willoughby and Sutcliffe (1976) found that a combination of low pH, low cation concentration (especially K^+), and unsuitable food supply prohibited *Gammarus pulex* from colonizing a stream. Apparently, osmoregulatory mechanisms were insufficient to maintain homeostasis at extreme ion concentrations. High concentrations of organic chemicals may indirectly affect NPM by way of low dissolved oxygen concentrations that result from increased biological oxygen demand (Lieberman 1970). High concentrations of some chemical may be directly toxic to biota (e.g., copper sulfate, pesticides, herbicides). Heavy sedimentation of tripton (Willoughby and Sutcliffe 1976) may result in increased mortality, especially in the headwaters of some reservoirs.

Diet

306. Seasonal fluctuations in the quantity and quality of foods may produce seasonal variations in the NPM of *Gammarus pulex* (Willoughby and Sutcliffe 1976). Paffenhofer (1971, 1976) found that the quality or digestibility of foods, as well as its concentration, influence the NPM of *Calanus helgolandicus*. Similar observations were made for *Rhincalanus nasutus* (Mullin and Brooks 1970). The diversity of food types in natural waters and the diversity in invertebrate diets combine to make impossible any realistic attempt at modeling the effects of diet.

Age and density

307. Nonpredatory mortality depends on the age structure of a population but does not affect all species in the same manner. For example, 85.9 percent of total NPM occurred in the naupliar stages of Calanus helgolandicus (Paffenhofer 1976) and Diaptomus clavipes (Gehrs and Robertson 1975). By contrast, young Daphnia pulex survived the effects of high temperature better than did mature specimens (Craddock 1976), and, in the bivalve mollusc Sphaerium striatinum, the oldest generation exhibited the highest NPM (Avolizi 1976). Similar results were obtained for the trichopteran Potamophylax cingulatus (Otto 1975), the mollusc Anodonta anatina (Negus 1966), and the cladoceran Daphnia pulex (Frank et al. 1957). Because the effect of age on NPM varies among species, we made no attempt to model this parameter.

308. Denisty is another population parameter which may influence the magnitude of NPM. Though data are limited, Frank et al. (1957) found that increased density of Daphnia pulex increased its survival. Because population density modifies such important variables as metabolic rates, intraspecific competition, and food availability, density may eventually (i.e., after further research) be acknowledged as a principal factor affecting NPM. Presently, however, scientific data to substantiate hypotheses of density dependent or independent mortality for zooplankton and benthos are lacking.

Temperature

309. Mechanisms. There are several mechanisms by which temperature can affect the survival of aquatic ectotherms (Goss and Bunting 1976). First, animals have upper and lower temperature tolerances, above and below which mortality occurs. Second, within tolerance limits, high rates of temperature change can produce shock and increase NPM. Third, the first two mechanisms can function together, producing an emergent effect.

310. Upper limits of thermal tolerance have been examined to a greater extent than other aspects of temperature response, probably due to a general concern for the effects of thermal pollution on aquatic biota. Upper lethal temperatures (ULT's) and lower lethal temperatures

(LLT's) are tabulated in Appendix E, Part II. Unfortunately, we found few data on the LLT's of aquatic invertebrates.

311. The ULT's and LLT's both depend on the acclimation temperature of study specimens. For example, the LLT of Corbicula manilensis was 12°C when the clams were acclimated to 30°C, and only 2°C when they were acclimated to 15°C. Clams acclimated to 5°C and 30°C exhibited ULT's of 24° and 34°C, respectively (Mattice and Dye 1976). Figure 59 is a graphical representation of these results. Comparable results were obtained by

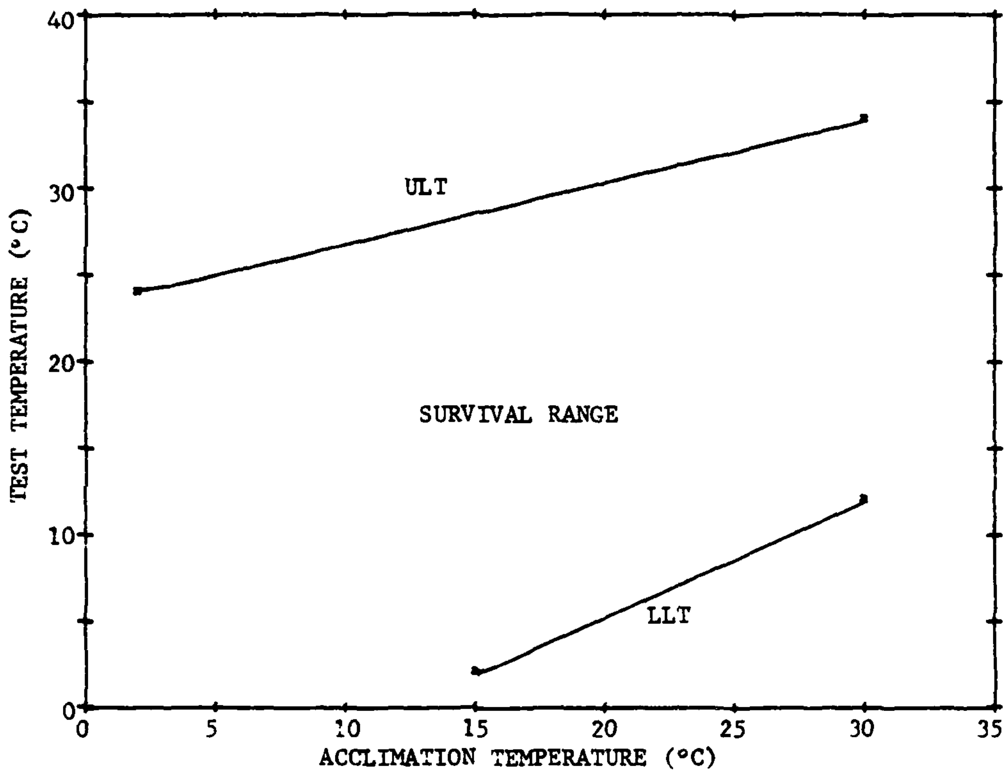

Figure 59. Upper lethal temperatures (ULT) and lower lethal temperatures (LLT) for the clam Corbicula manilensis acclimated to different temperatures. After Mattice and Dye (1976)

Becker et al. (1977), Sprague (1963), and Goss and Bunting (1976), as shown in Appendix E, Part II. Surprisingly, the range of ULT's, even for such a diverse group of animals as aquatic invertebrates in various states of acclimation, is fairly narrow (Figure 60).

312. In a reservoir, animals normally have enough time to acclimate to slowly changing temperatures. Rapid changes in temperature such as those produced by entrainment in the effluent of a power plant, however, may exceed the rate at which a species can acclimate and therefore result in high NPM. Goss and Bunting (1976) found that the NPM of Daphnia pulex increased significantly with an increasing rate of change in temperature between 20° and 35°C. Unfortunately, their experiment did not demonstrate the exact cause of the high NPM. The increased rates of temperature change (ΔT) may have been the cause, but a better hypothesis is that increased NPM resulted from longer exposure to lethal temperatures after water reached the ULT. There was not sufficient information available to accurately model NPM as a function of ΔT. Because rapid temperature changes on the order of 3°C per hour are rare in nature, the lack of such a construct probably will not affect the performance of the model, unless it is applied to a thermally polluted reservoir.

313. Model construct. We formed a construct for temperature effects (Figure 61) by using data that related NPM to temperature (Appendix E, Part I) and data for upper and lower lethal temperatures (Appendix E, Part II). According to Figure 61, NPM increases exponentially toward asymptotes located at about 0° and 35°C. However, between 5° and 25°C inclusive, NPM is very low ($\leq$2 percent/day). Previous research corroborates this relationship (see Cooper 1965, Mattice 1976, Ginn et al. 1976). Hall (1964) found that the median life span of Daphnia galeata was 30 days at 25°C, 60 to 80 days at 20°C, and 150 days at 11°C. At 5°C no mortality was observed in 2 months.

314. When ambient temperatures are less than 5°C or greater than 25°C, ambient temperature should be substituted for T in,

$$\mathrm{NPM} = \left[10^{(1.121 - 0.261T)} + 10^{(0.145T - 2.978)}\right] \div 100 \qquad (28)$$

where NPM = nonpredatory mortality ($\mathrm{mg\ C \cdot mg\ C^{-1} \cdot day^{-1}}$) and T = temperature (°C). The equation should be solved for NPM.

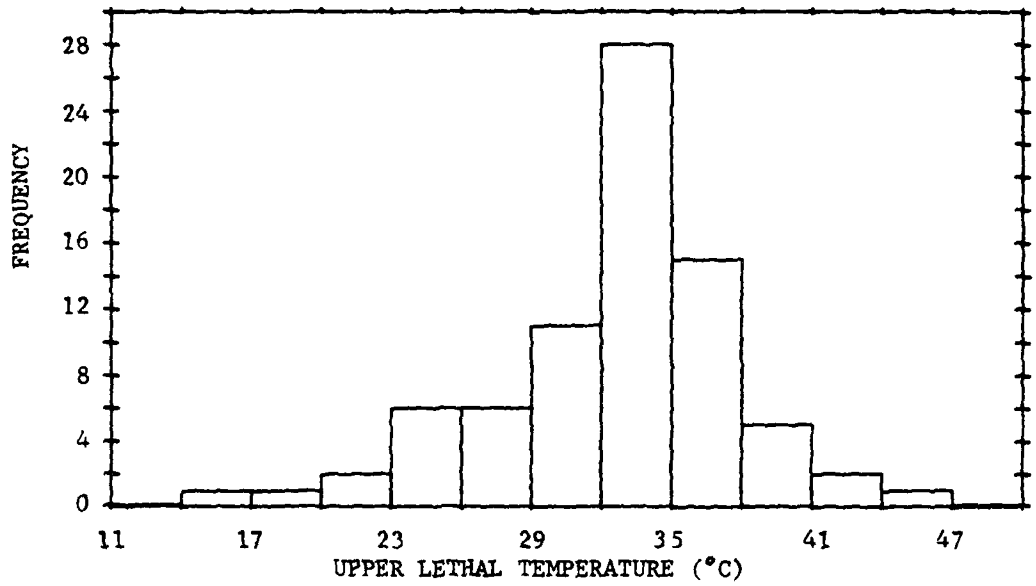

Figure 60. Frequency histogram of upper lethal temperature (ULT) for aquatic organisms. Based on data in Appendix E, Part II

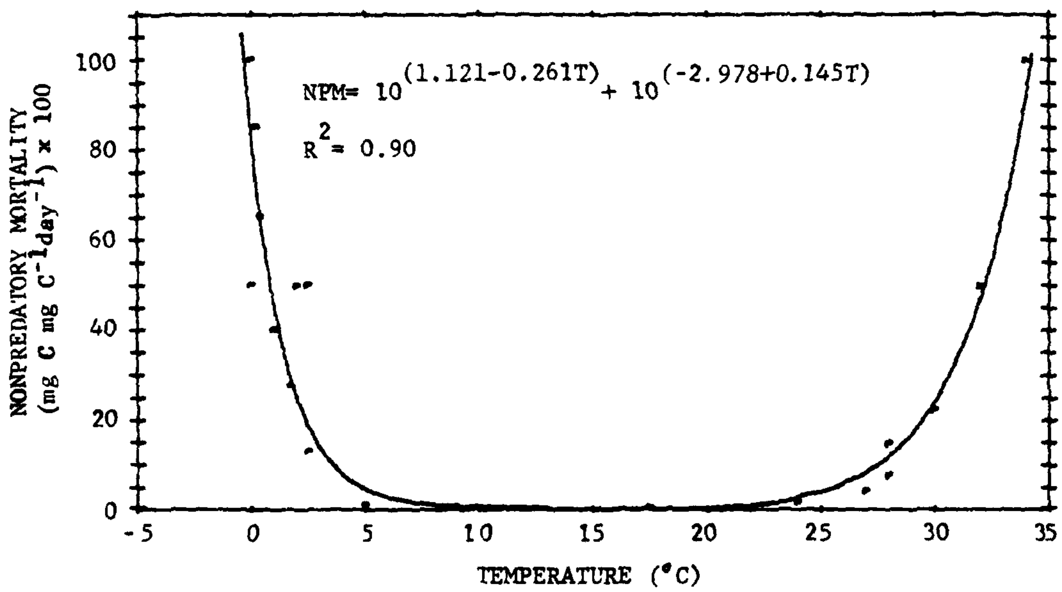

Figure 61. Nonpredatory mortality (NPM) as a function of temperature (T) for aquatic organisms. Based on data in Appendix E, Parts I and II

Oxygen concentration

315. Effects. Low dissolved oxygen (DO) concentrations have a profound effect on the survival of aquatic invertebrates. Above a critical concentration, however, NPM is unaffected (Berg and Jonasson 1965). The effects of low DO concentrations have been modeled in two ways. Menshutkin and Umnov (1970) increased NPM when DO concentrations were less than those needed to meet the respiration of the total community. NPM was increased to a point where the remaining animals could meet their respiratory demand. In the Lake George model (Zahorcak 1974), a construct "BEHAVE" stepped mortality above a base level, when DO fell below some critical concentration for several days. With the data currently available, these constructs probably are the most sophisticated yet applied.

316. Critical concentrations of DO may vary among individuals of the same species. This is especially true when the duration of exposure is varied (Berg and Jonasson 1965). Table 16 shows the concentrations of DO at which 50 percent mortality of insects occurred in 96-hr and 30-day experiments. All species listed, with the exception of *Tanytarsus dissimilis*, which exhibited no detectable mortality in either case, show more tolerance for short-term than for long-term exposure to critically low levels of DO.

317. Animals may be able to acclimate or behaviorally adjust to low DO tensions. Evidence presented in the section on "Respiration of Zooplankton and Benthos," page 127, showed that animals limit their metabolic rates during periods of low O_2 concentration. These types of adjustments alter the rate of NPM when oxygen becomes limiting. To date, there is no method of accurately modeling these phenomena.

318. Model constructs. Using data for various insects (Nebeker 1972), especially for the burrowing mayfly *Ephemera simulans* and for the limnetic copepod *Limnocalanus macrurus* (Roff 1973), we developed a model construct (Figure 62) that exponentially increases NPM above a normal rate, as O_2 falls below a critical concentration. A base rate of NPM (4 percent per day) was chosen from Appendix E, Part I, because it represents maximum NPM under optimal environmental conditions. We let NPM_{DO} equal

Table 16

Comparison of Critical Concentrations (mg/ℓ) of DO (i.e., Those Producing 50 Percent Mortality) for Insects Exposed to These Conditions for 96 hr and 30 days (Berg and Jonasson 1965)

Insect	Concentrations Exposure Time 96 hr	30 days
Pteronarcys dorsata	2.2	4.6
Baetisca laurentina	3.5	5.0
Tanytarsus dissimilis	<0.6	<0.6
Ephemerella spp.	3.9	4.5

four and solved the following exponential equation for O_2:

$$NPM_{DO} = 10^{(1.04 - 0.15O_2)} \tag{29}$$

$$r^2 = 0.80$$

where NPM_{DO} = oxygen correction and O_2 = ambient O_2 concentration. The result, 2.9 mg/ℓ, is the critical concentration. When DO concentrations fall below 2.9 mg/ℓ, NPM should be increased above the selected rate (i.e., the rate obtained from frequency histograms; Figures 57 or 58) by $(NPM_{DO} - 4) \div 100$ mg C·mg C^{-1}·day^{-1}. Rates of NPM may be obtained by substituting the ambient oxygen concentration for O_2 in Equation 29. After tensions drop to zero for 24 hr, we assumed that NPM = 1·mg C·mg C^{-1} ·day^{-1}.

319. Data in Figure 62 are from aquatic organisms that are fairly intolerant of low DO concentrations. Therefore, this figure is taken to represent zooplankton and littoral benthos. Though the critical concentration (2.9 mg/ℓ) seems low, evidence suggests that it is reasonable. For example *Hexagenia limbata* had a 96-hr LC50 of 1.4 mg/ℓ (Nebeker 1972). Roff (1973) observed that *Limnocalanus macrurus* began to settle

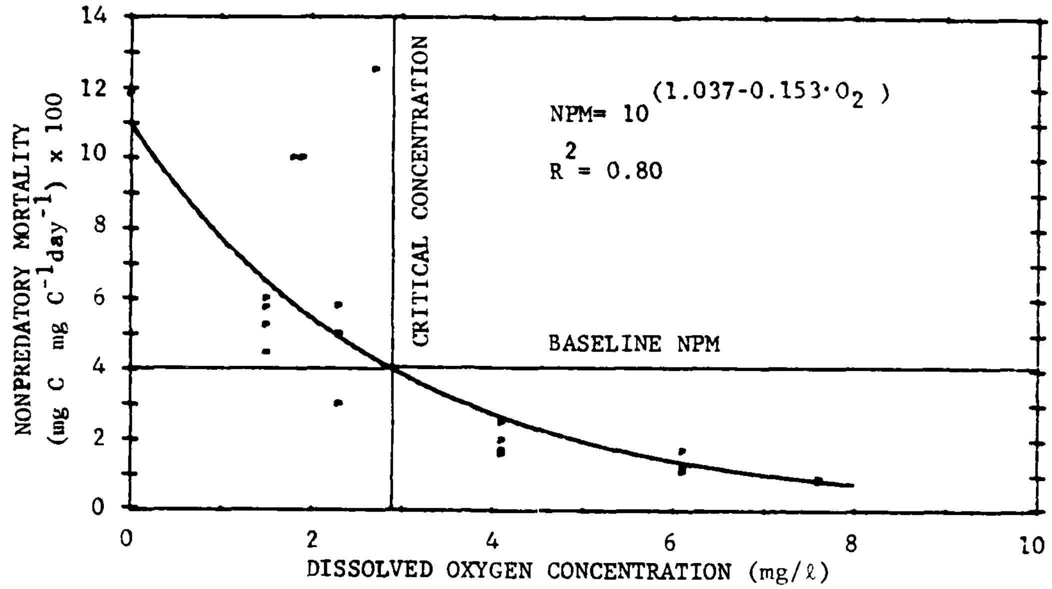

Figure 62. Nonpredatory mortality (NPM) as a function of dissolved oxygen concentration (O_2) for zooplankton and littoral benthos. Based on data from Nebeker (1972) and Roff (1973)

out and die at 2 mg O_2/ℓ. Moina brachiata survived DO concentrations approaching zero for extended periods of time (Lieberman 1970). Some zooplankton undoubtedly will exhibit high NPM at concentrations above our critical O_2 concentration of 2.9 mg/ℓ. On the other hand, some species probably will be more tolerant to low concentrations than our hypothetical average species.

320. Figure 63 depicts the NPM of profundal benthos as a function of DO concentration. Figure 63 is similar to Figure 62 in that it still contains data points for Ephemera simulans. The retention of these data points was essential to provide sufficient data on NPM at nonlethal concentrations. Figure 63 differs from Figure 62 to the extent that we added data points for Chaoborus flavicans (Berg and Jonasson 1965), Tanytarsus dissimilis (Nebeker 1972), and Planorbis contortus (Calow 1975) and deleted data points for the intolerant species in Figure 62. By manipulating the data in this fashion, we obtained:

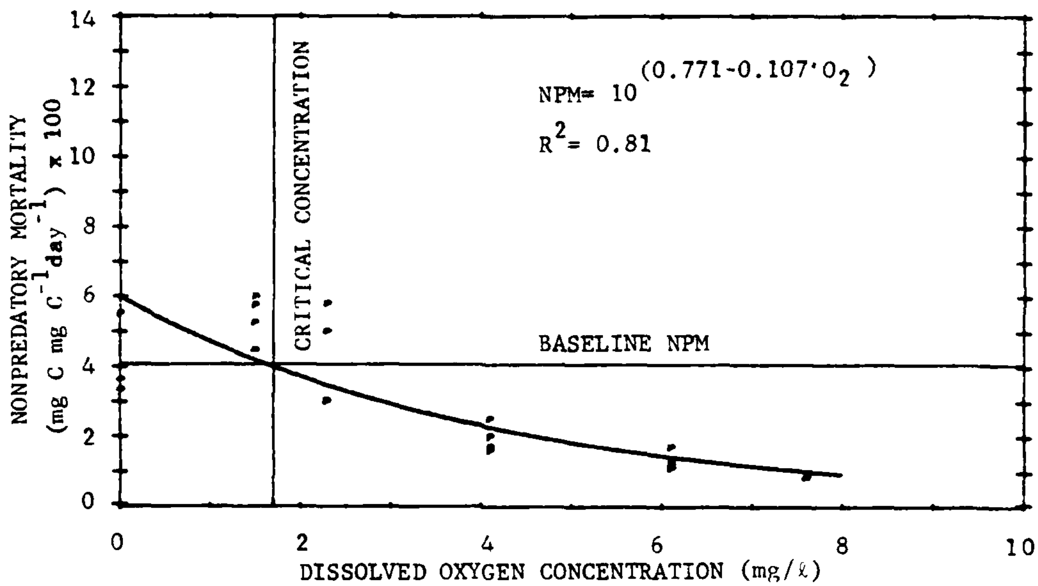

Figure 63. Nonpredatory mortality (NPM) as a function of dissolved oxygen concentration (O_2) for profundal benthos. Based on data from Berg and Jonasson (1965), Calow (1975), and Nebeker (1972)

$$NPM_{DO} = 10^{(0.77 - 0.11O_2)} \tag{30}$$

$$r^2 = 0.81$$

We again let NPM_{DO} = 4 percent/day (maximum NPM under optimal environmental conditions) and solved for O_2. We obtained a critical concentration of 1.7 mg O_2/ℓ. When O_2 concentrations drop below 1.7 mg/ℓ, NPM should be increased by $[(NPM_{DO} - 4) \div 100]$.

321. Observations indicate that many species of profundal benthos are extremely tolerant of low DO concentrations. Curry (1965) indicated that some midges (Chironomidae) can tolerate concentrations as low as 1.0 mg/ℓ for indefinite periods. Tanytarsus dissimilis exhibited no NPM in 30 days at concentrations less than 0.6 mg/ℓ (Nebeker 1972). Tubifex tubifex and Ilyodrilus hammoniensis were able to live in anoxic water for 1 month, and Chironomus anthracinus and Procladius pectinatus lived for 3 weeks at zero mg/ℓ (Berg and Jonasson 1965). Chaoborus flavicans

survived for a few days without oxygen but then exhibited 50 percent NPM in 2 weeks (Berg and Jonasson 1965). Similar observations were made for chironomids by Cole (1921). Calow (1975) found that *Planorbis contortus* and *Ancylus fluviatilis* exhibited 50 percent NPM only after 9 and 4.5 days, respectively, in anoxic water. To make our construct consistent with these data, we assumed that NPM = $1 \cdot mg\ C \cdot mg\ C^{-1} \cdot day^{-1}$, after 24 days of anoxia.

Summary of Constructs

322. Nonpredatory mortality represents loss of biomass from a model compartment. Zooplankton and benthos NPM, corrected for the effects of temperature and oxygen concentration, are readily obtained from the following steps.

Step 1

323. Convert frequency histograms of zooplankton and benthos NPM (Figures 57 and 58, respectively) to probability distributions.

Step 2

324. Select a series of rates from the appropriate probability distribution (zooplankton or benthos). Users may set confidence limits on the distribution to restrict the selection range to the more probable rates.

Step 3

325. Based on ambient temperatures in the reservoir, determine whether a temperature correction is required.

a. Not required - Ambient temperatures are between 5° and 25°C, inclusive. Proceed to Step 4.

b. Required - Ambient temperatures are below 5° or above 25°C. Substitute ambient temperature for T in:

$$NPM = \left[10^{(1.121 - 0.261T)} + 10^{(0.145T - 2.978)}\right] \div 100 \qquad (28)$$

where T = temperature (°C) and NPM = nonpredatory mortality ($mg\ C \cdot mg\ C^{-1} \cdot day^{-1}$), and solve for NPM. Proceed to Step 4.

Step 4

326. Based on the concentration of O_2 in the pelagic or profundal zone of the reservoir, determine whether an O_2 correction is required for zooplankton or benthos, respectively.

a. Not required.

(1) Zooplankton - O_2 tensions in the pelagic zone exceed 2.9 mg/ℓ.

(2) Benthos - O_2 tensions in the profundal zone exceed 1.7 mg/ℓ.

Use rates obtained from Step 3a or 3b above and proceed to Step 7.

b. Required.

(1) Zooplankton - O_2 tensions in the pelagic zone are less than or equal to 2.9 mg/ℓ. Proceed to Step 5.

(2) Benthos - O_2 tensions in the profundal zone are less than or equal to 1.7 mg/ℓ. Proceed to Step 6.

Step 5

327. Substitute O_2 in the pelagic zone for O_2 in:

$$NPM_{DO} = 10^{(1.04 - 0.15\, O_2)} \tag{29}$$

where NPM_{DO} = O_2 correction and O_2 = ambient concentration and solve for NPM_{DO}. Add $[(NPM_{DO} - 4)] \div 100$ to NPM rates obtained from Step 3a or 3b above. If O_2 tensions = 0 mg/ℓ for 24 hr, NPM = 1 mg C·mg C^{-1}·day^{-1}. Proceed to Step 7.

Step 6

328. Substitute O_2 concentration in the profundal zone for O_2 in:

$$NPM_{DO} = 10^{(0.77 - 0.11\, O_2)} \tag{30}$$

where NPM_{DO} = O_2 correction and O_2 = ambient oxygen concentration. Solve for NPM_{DO}. Add $[(NPM_{DO} - 4) \div 100]$ to NPM rates obtained from Step 3a or 3b above. If O_2 tensions = 0 mg/ℓ for 24 days, NPM = 1 mg C mg C^{-1}·day^{-1}. Proceed to Step 7.

[illegible] compartment biomass (mg C) and NPM (mg C·mg

$C^{-1} \cdot day^{-1}$) to obtain the biomass of carbon lost to nonpredatory mortality daily. According to Equation 1, the NPM rate (mg C·mg $C^{-1} \cdot day^{-1}$) should be subtracted from assimilated carbon: $\frac{db}{dt} = b[G(A/G) - NPM - R - PM]$.

Conclusions

330. Nonpredatory mortality is important because it represents the loss of biomass from model compartments to a detrital pool. In previous models NPM often has been designated as an empirical constant, although it may vary significantly in response to environmental factors such as oxygen concentration, temperature, and chemicals or to biological factors such as diet, age, and density. Attempts have been made to express NPM as a function of season, temperature, oxygen concentration, and density. Investigators are often torn between accurate estimates of NPM under potentially unrealistic conditions in the laboratory and potentially inaccurate estimates from field experiments.

331. Though many factors influence NPM, we only found sufficient data to model the effects of dissolved oxygen concentration and temperature. Oxygen corrections must be made when O_2 is less than or equal to 2.9 mg/ℓ in the pelagic or 1.7 mg/ℓ in the profundal zone of a reservoir. Temperature corrections must be made when ambient temperatures are less than 5° or greater than 25°C.

PART VII: RECOMMENDATIONS

General

332. The present model represents a framework that should be tested, refined, and calibrated prior to use as a predictive tool. New data should be added when appropriate, and old constructs should be modified or new ones developed. Modelers should use new data from research to improve the model, and the improved model should in turn be used to direct research - thereby completing a cycle that efficiently advances the science.

333. We strongly recommend that published literature on zooplankton and benthos production be reviewed to provide a check for this model.

334. Literature and data on the skewed-horizontal distribution of aquatic animals in reservoirs should be examined in detail. Greater numbers, biomass, and diversity of animals in headwater areas may be related to significantly greater energy flow through detrital pathways.

Chemical Composition

335. Carbon, nitrogen, and phosphorus data, as determined for broad taxonomic categories of aquatic invertebrates (e.g., zooplankton) or for preserved specimens, should not be used in the data base.

336. Carbon, nitrogen, and phosphorus data as determined for marine plankton (except for medusoid forms) should be used in the data base.

337. Frequency histograms of C:N and C:P ratios for macrobenthos (Figures 1 and 5, respectively) and similar ratios for zooplankton (Figures 2 and 6, respectively) should be used to estimate N and P movements through model compartments. When greater resolution is desired, zooplankton biomass should be divided as follows: 60 percent Cladocera and 40 percent Copepoda, with Figures 7 and 8 used to determine appropriate ratios.

Consumption by Zooplankton and Benthos

338. We recommend the use of the Ivlev function (Equation 3 for acclimated specimens or Equation 9 for unacclimated specimens) to describe the relation between zooplankton and benthos grazing rates and food concentration.

339. We suggest that a threshold food concentration not be included in the grazing construct.

340. Equation 7 should be tested as an estimate of the grazing rate for any ambient food concentration. Results should be compared to simulations based on Equations 3 and 9.

341. The grazing construct should only allow the zooplankton community to feed on particles of 100 μm or less.

342. We recommend that food preference be considered equal among all potential foods except filamentous blue-green algae. A preference factor (Equation 11) should be introduced to modify the grazing equation when zooplankton are feeding on these species.

343. We believe that a linear model should be used to describe the relation between grazing rate and temperature for fully acclimated animals (Figure 19). We recommend that the reaction rate function of Thornton and Lessem (1978) be used to define the relation between grazing rate and temperature for incompletely acclimated animals.

344. We recommend that a correction factor for diel variations in grazing be tested in initial simulations to see whether such a term improves model performance. We suggest using Method No. 3.

345. The same model constructs used to describe grazing by filter-feeding zooplankton should be used to describe grazing by predatory zooplankton and benthos. When zooplankton are to be split into herbivores and predators, we recommend that predators be assigned 20 percent of total zooplankton biomass, based on the ecological growth efficiencies cited by Welch (1968).

346. We need accurate methods for determining the percent composition and turnover of detritus, bacteria, and phytoplankton in seston. In addition, more studies are needed of assimilation and survival when

zooplankton are fed protozoa, detritus or bacteria, or various combinations, for several generations.

347. More research is necessary to determine what types of animals in reservoirs, if any, can directly (by uptake) or indirectly (through a bacterial trophic link) utilize the energy available in dissolved organic matter (DOM).

348. Further research is needed to describe synergistic effects among variables influencing grazing rates.

349. Considerably more research needs to be done to describe the feeding relationships of zooplankton and benthos in a quantitative manner (i.e., as carbon or energy consumed). Special attention must be directed toward studying the responses of acclimated animals to fluctuations in food concentration and temperature.

Assimilation Efficiency (A/G), Egestion (F), and Excretion (E)

350. Although physiologically incorrect, F and E should be considered as a single loss in the model and calculated as 1 - A/G. Research that accurately quantifies excretion by aquatic invertebrates is needed to fill a tremendous void in published data.

351. Methods used to determine A/G have not produced similar results and therefore should be experimentally compared so that results can be standardized. When accurate methods are perfected, researchers should investigate how A/G is affected by factors such as temperature, food concentration, food type, development, consumption, and reproductive condition.

352. Because the distribution of A/G values for cladocerans (Figure 32) was essentially uniform, we recommend that zooplankton be considered as a single compartment (Figure 26). When greater resolution is required, the frequency histograms of rotifer and copepod A/G (Figures 30 and 31, respectively) should be used, but cladoceran A/G values should be randomly selected from a range of 5 to 55 percent. Biomass of zooplankton should be arbitrarily assigned as follows: 60 percent

Cladocera, 35 percent Copepoda, and 5 percent Rotatoria, unless more accurate data are available.

353. Benthos should be compartmentalized into carnivores and herbivores-detritivores on the basis of their respective assimilation efficiencies (Figures 28 and 29). Based on the ecological growth efficiencies of a nematode (Duncan et al. 1974), a chironomid (Kajak and Dusoge 1970), and an oligochaete (Ivlev 1939), we believe carnivores should constitute 20 ± 10 percent of total benthic biomass when the compartment is divided.

Respiration

354. Oxygen consumption should only be considered as an index to respiration and should be converted to carbon or energy equivalents by the original investigators. Because these investigators can measure CO_2 evolution and N excretion from respiring specimens, they can accurately adjust oxycaloric and oxy-carbon coefficients to account for the proportions of fat, carbohydrate, and protein oxidized.

355. Experimental specimens (especially small individuals) should be adequately fed and acclimated prior to respiration experiments.

356. Effects of environmental and biological factors (e.g., temperature, salinity, pH, O_2 concentration, density, consumption, and reproductive state) on rates of respiration should be examined for more species of benthos and zooplankton.

357. The ratio of respiration to consumption (R/G) should be experimentally explored to determine its variability due to biological and environmental perturbations and thereby evaluate its potential as a modifier of consumption.

358. During calibration of the model, special attention should be directed at achieving a balance between decreased respiration (R) and increased nonpredatory mortality (NPM) at critically low concentrations of dissolved oxygen.

359. Because data that relate zooplankton respiration to oxygen

concentrations are few, research specifically designed to describe these effects should be conducted.

360. Although many equations that relate R to individual body weight have been developed, they cannot be used to correct for body weight effects in models unless the mean weight of the individuals in a compartment is known. Seasonal changes in length frequency and the regressions of body weight on length for zooplankton should be explored as a method of estimating mean weight.

361. Because we found no realistic way to apportion total benthic biomass among smaller taxonomic compartments, respiration rates should presently be selected from a probability distribution formed from Figures 48 and 49. Weight-specific rates of respiration for zooplankton can be obtained from Figure 47, or from Figures 39-41 provided that zooplankton biomass is apportioned among groups. We suggested 60 percent Cladocera, 35 percent Copepoda, and 5 percent Rotatoria (unless better data are available).

362. Rates of respiration for selected zooplankton and benthos should be corrected for the effects of temperature and oxygen concentration, as described in "Summary of Constructs" (Part IV, page 120).

Nonpredatory Mortality (NPM)

363. Published data that relate NPM to concentrations of natural chemicals are few. Future bioassay research should examine the effects of single chemicals over a full range of O_2 concentrations, temperatures, specimen ages, or any other factors that have potential synergistic effects.

364. More research is needed to determine the effects of age and density on the NPM of a wide variety of zooplankton and benthos species.

365. Information on the NPM of zooplankton as a result of decreased O_2 concentrations and lower lethal temperatures is minimal and represents another area for additional research.

366. Rates of NPM for zooplankton and benthos should be selected from Figures 57 and 58, respectively, and selected rates should be corrected for the effects of temperature and oxygen concentration, as described in "Summary of Constructs" (Part V, page 158).

REFERENCES

ADAMS, S. M. and J. W. ANGELOVIC. 1970. Assimilation of detritus and its associated bacteria by three species of estuarine animals. Chesapeake Science, 11: 249-259.

ALIMOV, A. F. 1965. Filtration rate of mollusks of the genus Sphaerium. In: Voprosy Theoreticheskoi i Prikladnoi Malakologii (Tezisy Doklada), Sbornik II, Izd. Nauka, Moscow and Leningrad (in Russian).

ALTMAN, P. L. and D. S. DITTMER (eds.). 1966. Environmental Biology, Federation of American Societies for Experimental Biology, Bethesda, Maryland, 694 p.

AMBLER, J. W. and B. W. FROST. 1974. The feeding behavior of a predatory copepod, Tortanus discaudatus. Limnology and Oceanography, 19: 446-451.

AMERICAN PUBLIC HEALTH ASSOCIATION. 1971. Standard Methods for the Examination of Water and Wastewater. 13th edition, American Public Health Association, Inc., New York, New York, 874 p.

ANDRONIKOVA, I. N. 1978. Estimation of the role of zooplankton in the processes of selfpurification. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 20: 1022-1025.

ANDRONIKOVA, I. N., V. G. DRABKOVA, K. N. KUZMENKO, N. F. MICHAILOVA, and E. A. STRAVINSKAYA. 1972. Biological productivity of the main communities of the Red Lake. In: Productivity Problems of Freshwaters, Z. Kajak and A. Hillbricht-Ilkowsha (eds.), Polish Scientific Publishers, Warszawa and Krakow, p. 57-71.

ARNOLD, D. E. 1971. Ingestion, assimilation, survival, and reproduction by Daphnia pulex fed seven species of blue-green algae. Limnology and Oceanography, 16: 906-920.

AVOLIZI, R. J. 1976. Biomass turnover in populations of viviparous sphaeriid clams: Comparisons of growth, fecundity, mortality. Hydrogiologia, 51: 163-180.

AZAM, F. and R. E. HODSON. 1977. Size distribution and activity of marine microheterotrophs. Limnology and Oceanography, 22: 492-501.

BACA, R. G., M. W. LORENZEN, R. D. MUDD, and L. V. KINNEL. 1974. A generalized water quality model for eutrophic lakes and reservoirs. Battelle Pacific Northwest Laboratories, Richland, Washington, 150 p.

BARLOCHER, F. and B. KENDRICK. 1975. Assimilation efficiency of Gammarus pseudolimnaeus (Amphipoda) feeding on fungal mycelium or autumn-shed leaves. Oikos, 26: 55-59.

BAUDOIN, M. F. and O. RAVERA. 1972. Weight, size, and chemical composition of some freshwater zooplankters: Daphnia hyalina (Levdig). Limnology and Oceanography, 17: 645-649.

BAYLOR, E. R. and W. H. SUTCLIFFE. 1963. Dissolved organic matter as a source of particulate food. Limnology and Oceanography, 8: 369-371.

BECKER, C. D., R. G. GENOWAY, and M. J. SCHNEIDER. 1977. Comparative cold resistance of three Columbia River organisms. Transactions of the American Fisheries Society, 106: 178-184.

BEERS, J. R. 1966. Studies in the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. Limnology and Oceanography, 11: 520-528.

BEERS, J. R. and G. L. STEWART. 1969. Microzooplankton and its abundance relative to the larger zooplankton and other seston components. Marine Biology (Berlin), 4: 182-189.

BEKLEMISHEV, T. T. 1962. Superfluous feeding of marine herbivorous zooplankton. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer, 153: 108-113.

BELJACKAJA-POTAENKO, Y. S. 1964. Quantitative data on the feeding of zooplankton on bacteria. In: Trudy 10 Nauk Konf. po Vnutrennvh Vodoemah Pribaltiki, Minsk, p. 277-282 (in Russian).

BELL, R. K. and F. J. WARD. 1970. Incorporation of organic carbon by Daphnia pulex. Limnology and Oceanography, 15: 713-726.

BERG, K. and P. M. JONASSON. 1965. Oxygen consumption of profundal lake animals at low oxygen contents of the water. Hydrobiologia, 26: 131-143.

BERMAN, M. S. and S. RICHMAN. 1974. The feeding behavior of Daphnia pulex from Lake Winnebago, Wisconsin. Limnology and Oceanography, 19: 105-109.

BERTALANFFY, L. VON. 1951. Metabolic types and growth types. American Naturalist, 85: 111-117.

BIERMAN, Z. J., JR., F. H. VERHOFF, T. L. POULSON, and M. W. TENNEY. 1973. Multi-nutrient dynamic models of algal growth and species completion in eutrophic lakes." pp. 89-109. E. J. Middlebrooks et al. (eds). Modeling the Eutrophication Process, Ann Arbor Science Publishers, Ann Arbor, Michigan.

BIRGE, E. A. 1898. Plankton studies on Lake Mendota. II. The Crustacea of the plankton from July 1894, to December 1896. Transactions of the Wisconsin Academy of Sciences Arts and Letters, 11: 274-451.

BIRGE, E. and C. JUDAY. 1922. The inland lakes of Wisconsin. The plankton. Part I. Its quantity and chemical composition. Wisconsin Geological and Natural History Survey Bulletin, 64: 1-222.

BISHOP, J. W. 1968. Respiratory rates of migrating zooplankton in the natural habitat. Limnology and Oceanography, 13: 58-62.

BLAZKA, P. 1966. Metabolism of natural and cultured populations of Daphnia related to secondary production. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 16: 380-385.

BOGATOVA, I. B. 1951. Quantitative data on the feeding of Cyclops strenuus Fischer and Cyclops viridis Jurine. Trudy Saratov otd. Kasp. fil. VNIRO, 1 (in Russian).

BAGATOVA, I. B., M. A. SHCHERBINA, V. V. OVINNIKOVA, and N. A. TAGIROVA. 1971. The chemical composition of certain plaktonic animals under different growing conditions. Hydrobiological Journal, 7: 39-43.

BOGDAN, K. G. and D. C. McNAUGHT. 1975. Selective feeding by Diaptomus and Daphnia. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 19: 2935-2942.

BOTTRELL, H. H., A. DUNCAN, Z. M. GLIWICA, E. GRYGIEREK, A. HERZIG, A. HILLBRICHT-ILKOWSKA, H. KURASAWA, P. LARSSON, and T. WEGLENSKA. 1977. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology, 24: 419-456.

BOUCHER, J., C. RAZOULS, AND S. RAZOULS. 1976. Composition chemique elementaire en carbone et azote de Centropages typicus et Temora stylifera. Analyze des variations en fonction de la physiologie et des conditions ecologiques. Cahiers de Biologie Marine, 17: 37-43.

BOVEE, E. C. 1949. Studies on the thermal death rate of Hyallela azteca, Saussure. Biological Bulletin (Woods Hole), 96: 123-128.

BOWERS, J. A. 1979. Zooplankton grazing in simulation models; The role of vertical migration. In: Perspectives on Lake Ecosystem Modeling, D. Scavia and A. Robertson (eds.), Ann Arbor Science Publishers, Inc., Ann Arbor, p. 53-73.

BRAND, T. F. VON. 1927. Stoffbestand und Ernahrung einiger Polychaten und anderer mariner Wurmer. Zeitschrift fuer Vergeichende Physiologie, 5: 643.

BRANDL, Z. and C. H. FERNANDO. 1975. Investigations on the feeding of carnivorous cyclopoids. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 19: 2959-2965.

BRANDT, K. and E. RABEN. 1919-1922. Zur Kenntnis der chemischen zusammensetzung des planktons und einiger bodenorganismen. Wissenschaftliche Meeresuntersuchungen, 19: 175.

BRINKHURST, R. O. 1974. The Benthos of Lakes, St. Martins Press, Inc., New York, 190 p.

BRINKHURST, R. O. and K. E. CHUA. 1969. Preliminary investigation of the exploitation of some potential nutritional resources by three sympatric tubificid oligochaetes. Journal of the Fisheries Research Board of Canada, 26: 2659-2668.

BRINKHURST, R. O., L. E. CHUA, and N. K. KAUSHIK. 1972. Interspecific interactions and selective feeding by tubificid oligochaetes. Limnology and Oceanography, 17: 122-133.

BROOKS, J. L. 1957. The systematics of North American Daphnia. Memoirs of the Connecticut Academy of Arts and Sciences, 13: 1-180.

BROOKS, J. L. 1959. Cladocera. In: Freshwater Biology, 2nd edition, W. T. Edmonson (ed.), John Wiley & Sons, Inc., New York, p. 587-656.

BROWN, A. V. 1978. Life history and population energetics of the dobson fly, Corydalus cornutus. Ecology, 59: 1091-1108.

BROWN, L. A. 1928. Comparison of the rates of killing of the parthenogenetic and sexual forms of Daphnia magna at high temperatures. Proceedings of the Society for Experimental Biology and Medicine, 25: 732-734.

BROWN, L. A. and W. J. CROZIER. 1927. The rate of killing of cladocerans at higher temperatures. Journal of General Physiology, 11: 25-36.

BUFFINGTON, J. D. 1969. Temperature acclimation of respiration in Culex pipiens (Diptera: Culicidae) and the influences of seasonal selection. Comparative Biochemistry and Physiology, 30: 565-578.

BUIKEMA, A. L., Jr. 1972. Oxygen consumption of the cladoceran, Daphnia pulex as a function of body size, light and light acclimation. Comparative Biochemistry and Physiology, 42: 877-888.

BUIKEMA, A. L., Jr. 1973. Filtering rate of the cladoceran, Daphnia pulex as a function of body size, light and light acclimation. Hydrobiologia, 41: 515-527.

BURKY, A. J. 1971. Biomass turnover, respiration, and inter-population variation in the stream limpet, Ferrissia rivularis (Say.). Ecological Monographs, 41: 235-251.

BURNS, C. W. 1968a. Direct observations of mechanisms regulating feeding behavior of Daphnia, in lakewater. Internationale Revue der Gesamten Hydrobiologie, 53: 83-100.

BURNS, C. W. 1968b. The relationship between body size of filter-feeding Cladocera and the maximum size of particle ingested. Limnology and Oceanography, 13: 675-678.

BURNS, C. W. 1969a. Particle size and sedimentation in the feeding behavior of two species of Daphnia. Limnology and Oceanography, 14: 392-402.

BURNS, C. W. 1969b. Relation between filtering rate, temperature, and body size in four species of Daphnia. Limnology and Oceanography, 14: 693-700.

BURNS, C. W. and F. H. RIGLER. 1967. Comparison of filtering rates of Daphnia rosea in lake water and in suspensions of yeast. Limnology and Oceanography, 12: 492-502.

BUTLER, E. I., E. D. S. CORNER, and S. M. MARSHALL. 1970. On the nutrition and metabolism of zooplankton. VII. Seasonal survey of nitrogen and phosphorus excretion by Calanus in the Clyde Sea-Area. Journal of the Marine Biological Association of the United Kingdom, 50: 525-560.

CALOW, P. 1972. The structural and functional dynamics of selected species populations of freshwater snails: Towards a systems approach. Ph.D. thesis, Leeds University, United Kingdom.

CALOW, P. 1975. The respiratory strategies of two species of fresh-water gastropods Ancylus fluviatilus (Mull) and Planorbis contortus (Linn) in relation to temperature, oxygen concentration, body size, and season. Physiological Zoology, 48: 114-129.

CHASTON, I. 1969. Anaerobiosis in Cyclops varicans. Limnology and Oceanography, 14: 298-301.

CHEN, C. W. and G. T. ORLOB. 1975. Ecologic simulation for aquatic environments. In: Systems Analysis and Simulation in Ecology, Vol III, B. C. Patten (ed.), Academic Press, Inc., New York, p. 475-588.

CHISHOLM, S. W., R. G. STROSS, and P. A. NOBBS. 1975. Environmental and intrinsic control of filtering and feeding rates in Arctic Daphnia. Journal of the Fisheries Research Board of Canada, 32: 219-226.

CLARK, A. S. and J. C. H. CARTER. 1974. Population dynamics of cladocerans in Sunfish Lake, Ontario. Canadian Journal of Zoology, 52: 1235-1242.

CLESCERI, L. S., R. A. PARK and J. A. BLOOMFIELD. 1977. General model of microbial growth and decomposition in aquatic ecosystems. Applied and Environmental Microbiology, 33: 1047-1058.

COHN, M. F. 1958. Experimental study of ingestion and assimilation in Daphnia (Cladocera). Ph.D. Thesis, Yale University, New Haven, Connecticut, 56 p.

COKER, R. E. 1934. Reaction of some freshwater copepods to high temperatures. Journal of the Elisha Mitchell Scientific Society, 50: 143-159.

COLE, A. E. 1921. Oxygen supply of certain animals living in water containing no dissolved oxygen. Journal of Experimental Zoology, 33: 293-316.

COMITA, G. W. 1964. The energy budget of Diaptomus siciloides, Lilljeborg. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 15: 646-653.

COMITA, G. W. 1968. Oxygen consumption in Diaptomus. Limnology and Oceanography, 13: 51-57.

COMITA, G. W. 1972. The seasonal zooplankton cycles, production and transformation of energy in Severson Lake, Minnesota. Archiv fuer Hydrogiologie, 70: 14-66.

CONFER, J. L. 1971. Intrazooplankton predation by Mesocyclops edax at natural prey densities. Limnology and Oceanography, 16: 663-666.

CONOVER, R. J. 1961. The turnover of phosphorus by Calanus finmarchicus. Journal of the Marine Biological Association of the United Kingdom, 41: 484-488.

CONOVER, R. J. 1962. Metabolism and growth in Calanus hyperboreus in relation to its life cycle. Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mar, 153: 190-197.

CONOVER, R. J. 1964. Food relations and nutrition of zooplankton. University of Rhode Island Graduate School of Oceanography, Occasional Publication No. 2: 81-91.

CONOVER, R. J. 1966a. Assimilation of organic matter by zooplankton. Limnology and Oceanography, 11: 338-345.

AD-A090 832 FISH AND WILDLIFE SERVICE FAYETTEVILLE AR NATIONAL RE--ETC F/G 12/1
SIMULATION MODELING OF ZOOPLANKTON AND BENTHOS IN RESERVOIRS: D--ETC(U)
MAR 80 G R LEIDY, G R PLOSKEY

UNCLASSIFIED WES-TR-E-80-4 NL

3 OF 4
AD
A090832

CONOVER, R. J. 1966b. Factors affecting the assimilation of organic matter by zooplankton and the question or superfluous feeding. Limnology and Oceanography, 11: 346-354.

CONOVER, R. J. and E. D. S. CORNER. 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. Journal of the Marine Biological Association of the United Kingdom, 48: 49-75.

CONOVER, R. J. and V. FRANCIS. 1973. The use of radioactive isotopes to measure the transfer of materials in aquatic food chains. Marine Biology (Berlin), 18: 272-283.

COOPER, W. E. 1965. Dynamics and production of a natural population of fresh-water amphipod, Hyalella azteca. Ecological Monographs, 35: 377-394.

CORNER, E. D. S. 1973. Phosphorus in marine zooplankton. Water Research, 7: 93-110.

COWGILL, U. M. and C. W. BURNS. 1975. Differences in chemical composition between two species of Daphnia and some freshwater algae cultured in the laboratory. Limnology and Oceanography, 20: 1005-1011.

CRADDOCK, D. R. 1976. Effects of increased water temperatures on Daphnia pulex. U. S. Fish and Wildlife Service Fishery Bulletin, 74: 403-408.

CROWLEY, P. H. 1973. Filtering rate inhibition of Daphnia pulex in Wintergreen Lake water. Limnology and Oceanography, 18: 394-402.

CUMMINS, K. W. 1975. Macroinvertebrates. In: River Ecology, B. A. Whitton (ed.), University of California Press, Berkeley, p. 170-198.

CUMMINS, K. W., W. P. COFFMAN, and P. A. ROFF. 1966. Trophic relations in a small woodland stream. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 18: 1-158.

CUMMINS, K. W., R. R. COSTA, R. E. ROWE, G. A. MOSHIRI, R. M. SCANLON, and R. K. ZAJDEL. 1969. Ecological energetics of a natural population of the predaceous zooplankter Leptodora kindtii Focke (Cladocera). Oikos, 20: 189-223.

CUMMINS, K. W. and J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Mitteilungen, 18: 1-158.

CURL, H., Jr. 1962. Analysis of carbon in marine plankton organisms. Journal of Marine Research, 20: 181-188.

CURRY, L. L. 1965. A survey of environmental requirements for the midge (Diptera: Tendipedidae). In: Biological Problems in Water Pollution, C. M. Tarzwell (ed.), U. S. Public Health Service Publication No. 999-WP25, Cincinnati, p. 127-141.

CZECZUGA, B. and E. BOBIATYNSKA-KSOK. 1972. The extent of consumption of the energy contained in the food suspension by *Ceridaphnia reticulata* (Jurine). In: Productivity Problems of Freshwaters, Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, p. 740-748.

DABORN, G. R. 1975. Life history and energy relations of the giant fairy shrimp *Brachinecta gigas* Lynch 1937 (Crustacea: Anostraca). Ecology, 56: 1025-1039.

DAGG, M. J. 1974. Loss of prey body contents during feeding by an aquatic predator. Ecology, 55: 903-906.

DAGG, M. J. 1976. Complete carbon and nitrogen budgets for the carnivorous amphipod, *Calliopius laeviusculus* (Kroyer). Internationale Revue der Gesamten Hydrogiologie, 61: 297-357.

DELFF, C. 1912. Bietrage zur kenntnis des chemischen zusammensetzung wirbelloser meerestiere. Wissenschaftliche Meeresuntersuchungen, 14: 53.

DiTORO, D. M., D. J. O'CONNOR, and R. V. THOMANN. 1971. A dynamic model of the phytoplankton populations in the Sacramento-San Joaquin delta. In: Nonequilibrium Systems in Natural Water Chemistry, Advances in Chemistry Series No. 106, American Chemical Society, p. 131-150.

DODSON, S. I. 1972. Mortality in a population of *Daphnia rosea*. Ecology, 53: 1011-1023.

DOOHAN, M. 1973. An energy budget for adult *Brachionus plicatilis* Muller (Rotatoria). Oecologia (Berlin), 13: 351-362.

DUNCAN, A., F. SCHIEMER, and R. A. KLEKOWSKI. 1974. A preliminary study of feeding rates on bacterial food by adult females of a benthic nematode, *Plectus palustris* de Man 1880. Polskie Archiwum Hydrobiologii, 21: 249-258.

DUVAL, W. S. and G. H. GEEN. 1976. Diel feeding and respiration rhythms in zooplankton. Liminology and Oceanography, 21: 823-829.

EDMONDSON, W. T. 1957. Trophic relations of the zooplankton. Transactions of the American Microscopical Society, 76: 225-245.

EDWARDS, R. W. 1957. The relation of oxygen consumption to body size and to temperature in the larvae of *Chironomus riparius* Meigen. Journal of Experimental Biology, 35: 383-395.

ELLIOTT, J. M. 1968. The daily activity patterns of mayfly nymphs (Ephemeroptera). Journal of Zoology, 155: 201-221.

ELWOOD, J. W. and R. A. GOLDSTEIN. 1975. Effects of temperature on food ingestion rate and adsorption, retention, and equilibrium burden of phosphorus in an aqautic snail, *Goniobasis clavaeformis* Lea. Freshwater Biology, 5: 397-406.

ERIKSEN, C. H. 1964. The influence of respiration and substrate upon the distribution of burrowing mayfly naiads. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Werhandlungen, 15: 903-911.

ERMAN, L. A. 1956. Feeding habits of Rotifera from the quantitative aspect. Zoologicheskii Zhurnal, 35: 965-971 (in Russian with English summary).

ERMAN, L. A. 1962. On the quantitative aspect of feeding and selectivity of food in the plankton rotifer *Brachionus calyciflorus* Pall. Zoologicheskii Zhurnal, 41: 34-48 (in Russian).

FEDORENKO, A. Y. 1975. Feeding characteristics and predation impact of *Chaoborus* (Diptera, Chaoboridae) larvae in a small lake. Limnology and Oceanography, 20: 250-258.

FINENKO, Z. Z. and V. E. ZAIKA. 1970. Particulate organic matter and its role in the productivity of the sea. In: *Marine Food Chains*, J. H. Steele (ed.), University of California Press, Berkeley, p. 32-45.

FISCHER, Z. 1966. Food selection and energy transformation in larvae of *Lestes sponsa* (Odonata) in astatic waters. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 16: 600-603.

FISCHER, Z. 1970. Some remarks about the food ration. Polski Archiwum Hydrobiologii, 17: 177-182.

FISCHER, Z. 1972. The energy budget of *Lestes sponsa* (Hans.) during its larval development. Polskie Archiwum Hydrobiologii, 19: 215-322.

FISHER, S. G. and G. E. LIKENS. 1972. Stream ecosystems: Organic energy budget. Bioscience, 22: 33-35.

FOULDS, J. B. and K. H. MANN. 1978. Cellulose digestion in *Mysis stenolepis* and its ecological implications. Limnology and Oceanography, 23: 760-766.

FOULDS, J. B. and J. C. ROFF. 1976. Oxygen consumption during simulated vertical migration in Mysis relicta (Crustacea, Mysidacea). Canadian Journal of Zoology, 54: 377-385.

FRANK, P. W., C. D. BOLL, and R. W. KELLY. 1957. Vital statistics of laboratory cultures of Daphnia pulex DeGeer as related to density. Physiological Zoology, 30: 287-305.

FROST, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod Calanus pacificus. Limnology and Oceanography, 17: 805-815.

FROST, B. W. 1975. A threshold feeding behavior in Calanus pacificus. Limnology and Oceanography, 20: 263-266.

FRY, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Studies, Biological Series. No. 55. Publications of the Ontario Fisheries Research Laboratory, 68: 62 p.

FRYER, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. Journal of Animal Ecology, 26: 263-286.

FULLER, J. L. 1937. Feeding rate of Calanus finmarchicus in relation to environmental conditions. Biological Bulletin (Woods Hole), 72: 233-246.

FULLER, J. L. and G. L. CLARKE. 1936. Further experiments on the feeding of Calanus finmarchicus. Biological Bulletin (Woods Hole), 70: 233-246.

GAJEVSKAJA, N. S. 1961. Nouvelles methodes pour l'etude de l'alimentation des animaux aquatiques et quelques resultats de leur application. International Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 14: 999-1008.

GALKOVSKAYA, G. A. 1963. Utilization of food for growth and conditions for maximum production of the rotifer Brachionus calyciflorus Pallas. Zoologicheskii Zhurnal, 42: 506-512. (English translation available as Fisheries Research Board of Canada Translation Series No. 997, 1968, 13 p.)

GALKOVSKAYA, G. A. 1965. Planktonic rotifers and their role in productivity of water bodies. Ph.D. thesis, Belorusski gosud. Univ. im. V. I. Lenina, Minsk (in Russian).

GALKOVSKAYA, G. A. 1970. The utilization of food by pond zooplankton. Hydrobiological Journal, 6: 42-47.

GEHRS, C. W. and A. ROBERTSON. 1975. Use of life tables in analyzing the dynamics of copepod populations. Ecology, 56: 665-671.

GELLER, W. 1975. Die Nahrungsaufnahme von Daphnia pulex in Abhangigkeit von der Futterhonzentration, der Temperatur, der Korpergroesse und dem Hungerzustand der Tiere (The food uptake of Daphnia pulex as a function of food concentration, temperature, animals' body length, and starvation). Archiv fuer Hydrobiologie Supplementband, 48: 47-107. (Fisheries and Marine Service of Canada Translation Series No. 4017, 1977, 96 p.)

GELLIS, S. S. and G. L. CLARKE. 1935. Organic matter in dissolved and in colloidal form as food for Daphnia magna. Physiological Zoology, 8: 127-137.

GENG, H. 1925. Der futterwert der naturlichen fischnahrung. Zeitschrift fuer Fischerei und deren Hilfswissenschaften, 23: 137.

GINN, T. C., W. T. WALLER and G. J. LAUER. 1976. Survival and reproduction of Gammarus spp. (Amphipoda) following short-term exposure to elevated temperatures. Chesapeake Science, 17: 8-14.

GLIWICZ, Z. M. 1969. Studies on the feeding of pelagic zooplankton in lakes with varying trophy. Ekologia Polska Seria A, 17: 1-44.

GLIWICZ, Z. M. 1970. Calculation of food ration of zooplankton community as an example of using laboratory data for field conditions. Polskie Archiwum Hydrobiologii, 17: 169-175.

GOLDMAN, C. R. and B. L. KIMMEL. 1978. Biological processes associated with suspended sediment and detritus in lakes and reservoirs. In: Current Perspectives on River-Reservoir Ecosystems, North American Benthological Society, p. 19-44.

GOPHEN, M. 1976. Temperature dependence of food intake, ammonia excretion and respiration in Ceriodaphnia reticulata (Jurine) (Lake Kinneret, Israel). Freshwater Biology, 6: 451-455.

GOPHEN, M. 1977. Food and feeding habits of Mesocyclops leuckarti (Claus) in Lake Kinneret (Israel). Freshwater Biology, 7: 613-618.

GOSS, L. B. and D. L. BUNTING. 1976. Thermal tolerance in zooplankton. Water Research, 10: 387-398.

GREEN, J. D. 1975. Feeding and respiration in the New Zealand copepod Calamoecia lucasi Brady. Oecologia (Berlin), 21: 345-358.

GREEN, J. D. 1976. Population dynamics and production of the calanoid copepod Calomaecia lucasi in a northern New Zealand lake. Archiv fuer Hydrobiologie Supplementband, 50: 313-400.

GULATI, R. D. 1978. Vertical changes in filtering, feeding and assimilation rates of dominant zooplankters in a stratified lake. International Vereinigung fuer Theoretische und Angewandt Limnologie Verhandlungen, 20: 950-956.

GUTEL'MACKHER, B. L. 1973. Relative importance of phyto- and bacterio-plankton in the feed ration of planktonic crustaceans. Hydro-biological Journal, 9: 15-20.

GUTEL'MACKHER, B. L. 1977. Quantitative evaluation of the role of zooplankton in the phosphorus cycle in water bodies. Zhurnal Obshchei Biologii, 38: 914-921 (in Russian).

HABEL, M. L. 1970. Oxygen consumption, temperature tolerance and filtration rate of the introduced Asiatic clam, Corbicula manilensis from the Tennessee River. M.S. thesis, Auburn University, Auburn, Alabama.

HALBACK, U. and G. HALBACK-KEUP. 1974. Quantitative Beziehungen swischen Phytoplankton und der Populationsdynamik des Rotators Brachionus calyciflorus Pallas. Befunde aus Laboratoriumsexperimenten und Freilanduntersuchungen. Archiv fuer Hydrobiologie, 73: 273-309.

HALL, D. J. 1964. An experimental approach to the dynamics of a natural population of Daphnia galeata mendotae. Ecology, 45: 94-112.

HALL, D. J., W. E. COOPER, and E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography, 15: 839-928.

HANEY, J. F. 1973. An in situ examination of the grazing activities of natural zooplankton communities. Archiv fuer Hydrobiologie, 72: 87-132.

HANEY, J. F. and D. J. HALL. 1975. Diel vertical migration and filter-feeding activities of Daphnia. Archiv fuer Hydrologie, 75: 413-441.

HARGRAVE, B. T. 1970. The utilization of benthic microflora by Hyalella azteca (Amphipoda). Journal of Animal Ecology, 39: 427-437.

HARGRAVE, B. T. 1971. An energy budget for a deposit-feeding amphipod. Limnology and Oceanography, 16: 99-103.

HARIS, E. and G. A. RILEY. 1956. Chemical composition of the plankton. Bulletin of the Bingham Oceanographic Collection, Yale University, 15: 315-325.

HARVEY, H. W. 1937. Note on selective feeding by Calanus. Journal of the Marine Biological Association of the United Kingdom, 22: 97-100.

HARVEY, H. w., L. H. N. COOPER, M. V. LEBOUR, and F. S. RUSSELL. 1935. Plankton production and its control. Journal of the Marine Biological Association of the United Kingdom, 15: 407-441.

HAYWARD, R. S. and D. N. GALLUP. 1976. Feeding, filtering and assimilation in Daphnia schoedleri Sars as affected by environmental conditions. Archiv fuer Hydrobiologie, 77: 139-163.

HEIMAN, D. R. and A. W. KNIGHT. 1975. The influence of temperature on the bioenergetics of the carnivorous stonefly nymph, Acroneuria californica Banks (Plecoptera: Perlidae). Ecology, 56: 105-116.

HEINLE, D. R. 1969. Temperature and zooplankton. Chesapeake Science, 10: 186-209.

HILLBRICHT-ILKOWSKA, A. and A. KARABIN. 1970. An attempt to estimate consumption, respiration and production of Leptodora kindtii (Focke) in field and laboratory experiments. Polskie Archiwum Hydrobiologii, 17: 81-86.

HILLYARD, S. D. and A. VINIGAR. 1972. Respiration and thermal tolerance of the phyllopod crustacea Triops longcaudatus and Thamnocephalus platyurus inhabiting desert ephemeral ponds. Physiological Zoology, 45: 189-195.

HOPKINS, T. L. 1968. Carbon and nitrogen content of fresh and preserved Nematocelis difficilis, a euphausiid crustacean. Journal du Conseil International pour l'Exploration de la Mer, 31: 300-304.

HUGHES, R. N. 1970. An energy budget for a tidal-flat population of the bivalve Scrobicularia plana (Da Costa). Journal of Animal Ecology, 39: 357-381.

HUNTER, R. D. 1975. Growth, fecundity, and bioenergetics in three populations of Lymnaea palustris in upstate New York. Ecology, 56: 50-63.

HYNES, H. B. N. 1970. The ecology of stream insects. Annual Review of Entomology, 15: 25-42.

IKEDA, T. 1971. Changes in respiration rate and in composition of organic matter in Calanus cristatus (Crustacea: Copepoda) under starvation. Bulletin of the Faculty of Fisheries, Hokkaido University (Hokkaido Daigaku Suisan Gakubu Kenkyu Iho), 21: 280-298.

ISOM, B. 1971. Evaluation and control of macroinvertegrate nuisance organisms in freshwater industrial supply sustems. Paper presented at the 19th Annual Meeting of the Midwest Benthological Society, March 24-26, 1971.

ITO, T. 1955. Studies on Mizukawari in eel-culture ponds. 1. Feeding activity of Brachionus plicatilis on phytonannoplankton. Report of the Faculty of Fisheries Prefectural, University of Mie (Mie Kenritsu Daigaku Suisamgakubu Hokoku), 2: 162-276 (in Japanese).

ITOH, K. 1973. Food requirements of copepods estimated from their metabolic rates. Bulletin of the plankton Society of Japan (Nippu Kai Ho), 20: 78-83. (English translation available as Fisheries and Marine Service of Canada Translation Series No. 3354, 1975, 12 p.)

IVANOVA, M. B. 1970. Relations between the food concentration, filtration rate and effectiveness of oxygen utilization by Cladocera. Polski Archiwum Hydrobiologii, 17: 161-168.

IVANOVA, M. B. 1972. The influence of temperature on the oxygen consumption by Gammaracanthus lacustris Sars (Amphipoda). Polskie Archiwum Hydrobiologii, 19: 319-324.

IVANOVA, M. B. and R. Z. KLEKOWSKI. 1972. Respiratory and filtration rates in Simocephalus vetulus (O. F. Muller) (Cladocera) at different pH. Polskie Archiwum Hydrobiologii, 19: 303-318.

IVLEV, V. S. 1939. Transformation of energy by aquatic animals: Coefficient of energy consumption by Tubifex tubifex (Oligochaeta). Internationale Revue der Gesamten Hydrobiologie, 38: 449-458.

IVLEV, V. S. 1966. The biological productivity of waters. Journal of the Fisheries Research Board of Canada, 23: 1727-1759.

JASSBY, A. D. 1975. Dark sulfate uptake and bacterial productivity in a subalpine lake. Ecology, 56: 627-636.

JASSBY, A. D. and C. R. GOLDMAN. 1974. Loss rates from a lake phytoplankton community. Limnology and Oceanography, 19: 618-627.

JAWED, M. 1969. Body nitrogen and nitrogenous excretion in Neomysis rayii Murdock and Euphausia pacifica Hansen. Limnology and Oceanography, 14: 748-754.

JENSEN, L. D., R. M. DAVIES, A. S. BROOKS, and C. D. MEYERS. 1969. The effect of elevated temperature upon aquatic invertebrates. Edison Electric Institute Publication No. 69-900, 232 p.

JOHANNES, R. E. 1964. Uptake and release of phosphorus by a benthic marine amphipod. Limnology and Oceanography, 9: 235-242.

JOHANNES, R. E. and M. SATOMI. 1967. Measuring organic matter retained by aquatic invertebrates. Journal of the Fisheries Research Board of Canada, 24: 2467-2471.

JONASSON, P. M. 1964. The relationship between primary production and production of profundal bottom invertebrates in a Danish eutrophic lake. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 15: 471-479.

JORGENSEN, C. B. 1962. The food of filter feeding organisms. Rapports et proces-Verbaux des Reunions Conseil International pour l'Exploration de lar Mer, 153: 99-107.

JORGENSEN, C. B. 1966. Biology of Suspension Feeding, Pergamon Press, Inc., New York, 357 p.

KAJAK, Z. and K. DUSOGE. 1970. Production efficiency of Procladius choreus Mg (Chironomidae, Diptera) and its dependence on the trophic conditions. Polskie Archiwum Hydrobiologii, 17: 217-224.

KAMLER, E. and K. SROKOSZ. 1973. Calorific values and metabolism of Glyptotendipes polytomus Kieff (Chironomidae) in early spring. Polskie Archiwum Hydrobiologii, 20: 489-506.

KAY, D. G. and A. E. BRAFIELD. 1972. The energy relations of the polychaete Neanthes(Nereis) virens (Sars). Journal of Animal Ecology, 42: 673-692.

KERSTING, K. and W. HOLTERMAN. 1973. The feeding behavior of Daphnia magna, studied with the Coulter counter. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 18: 1434-1440.

KERSTING, K. and C. VAN DE LEEUW-LEEGWATER. 1976. Effect of food concentration on the respiration of Daphnia magna. Hydrobiologia, 49: 137-142.

KIBBY, H. V. 1971a. Effect of temperature on the feeding behavior of Daphnia rosea. Limnology and Oceanography, 16: 580-581.

KIBBY, H. V. 1971b. Energetics and population dynamics of Diaptomus gracilis. Ecological Monographs, 41: 311-327.

KIBBY, H. V. and F. H. RIGLER. 1973. Filtering rates of Limnocalanus. International Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 18: 1457-1461.

KIMMEL, B. L. 1978. Size distribution of autotrophic and heterotrophic microorganism activities in Lake Texoma (Oklahoma-Texas). Paper presented at the 5th Annual Great Plains Limnology Meeting, 1978, Lincoln, Nebraska.

KING, C. E. 1967. Food, age and the dynamics of a laboratory population of rotifers. Ecology, 48: 111-128.

KITITSYNA, L. A. 1975. Feeding rates of Pontogammarus robustoides at different temperatures. Hydrobiological Journal, 11: 35-40.

KLEKOWSKI, R. Z. 1970. Bioenergetic budgets and their application for estimation of production efficiency. Polskie Archiwum Hydrobiologii, 17: 55-80.

KLEKOWSKI, R. Z. and E. A. SHUSHKINA. 1966a. The energetic balance of Macrocyclops albidus (Jurine) during the period of its development. In: Ekologiya Vodnykh Organizmov. Akademiya Nauk SSSR. Izdatel'stvo "Nauka", Moskva, p. 125-136. (The Ecology of Aquatic Organisms. Published by "Science," Moscow.) (English translation available as Fisheries Research Board of Canada Translation Series No. 1031, 1968, 20 p.)

KLEKOWSKI, R. A. and E. A. SHUSHKINA. 1966b. Ernahrung, Atmung, Wachstum und Energie-Umformung in Macrocyclops albidus (Jurine). International Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 16: 399-418. (English translation available as Fisheries Research Board of Canada Translation Series No. 1034, 1968, 26 p.)

KLEKOWSKI, R. Z., E. FISCHER, Z. FISCHER, M. IVANOVA, T. PRUS, A. SHUSHKINA, T. STACHURSKA, Z. STEPIEN, and H. ZYROMSKI-RUDZKA. 1972. Energy budgets and energy transformation efficiencies of several animal species of different feeding types. In: Productivity Problems of Freshwaters, Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, P. 749-763.

KNAUTHE, K. 1907. Dass Susswasser, chemische, biologische, und bakteriologische Untersuchungsmethoden unter besonderer Berucksichtigung der Biologie und der Fischereiwietschaftlichen Praxis. J. Neumann, Neudamm, 663 p.

KNIGHT, A. W. and A. R. GAUFIN. 1966. Oxygen consumption of several species of stoneflies (Plecoptera). Journal of Insect Physiology, 12: 347-355.

KORNIYENKO, G. S. 1976. Contribution of infusoria to the nutrition of Acanthocyclops vernalis and Cyclops vicinus. Hydrobiological Journal, 12: 62-65.

KREMER, J. N. 1975. Analysis of a plankton-based temperate ecosystem: An ecological simulation model of Narragansett Bay. Ph.D. thesis, University of Rhode Island.

KREY, J. 1958. Chemical determination of net plankton, with special reference to equivalent albumin content. Journal of Marine Research, 17: 312-324.

KRING, R. L. and W. J. O'BRIEN. 1976. Accommodation of *Daphnia pulex* to altered pH conditions as measured by feeding rate. Limnology and Oceanography, 21: 313-315.

KRISHNAMURTHY, K. 1962. Phosphorus in plankton. Journal of the Zoological Society of India, 14: 161-164.

KROGER, R. L. 1974. Invertebrate drift in the Snake River, Wyoming. Hydrobiologia, 44: 369-380.

KROGH, A. 1914. The quantitative relation between temperature and standard metabolism in animals. Internationale Zeitschrift fuer Physiologie-Chemie Biologie, 1: 491-508.

KRYUTCHKOVA, N. M. 1974. The content and size of food particles consumed by filter-feeding planktonic animals. Hydrobiological Journal, 10: 89-94.

KRYUTCHKOVA, N. M. and V. G. KONDRATYUK. 1966. The dependence of the feeding filtration rate of some types of Cladocera on temperature. Doklady Akademii Nauk Belorusskii SSR, 10: 120-123 (in Russian).

KRYUTCHKOVA, N. M. and V. K. RYBAK. 1974. Growth of *Eudiaptomus graciloides* (Lill.) under different feeding conditions. Hydrobiological Journal, 10: 30-36.

KRYUTCHKOVA, N. M. and V. SLADECEK. 1969. Quantitative relations of the feeding and growth of *Daphnia pulex obtusa* (Kurz) Scourfield. Hydrobiologia, 33: 47-64.

KUZNETSOV, S. I., V. I. ROMANENKO, and N. S. KARPOVA. 1966. Bacterial population and production of organic matter in the Rybinsk Reservoir in 1963 and 1964. Trudy Instituta Biologii Vnutrennikh Vod Akademii Nauk SSSR, 13(16). English translation in: *Production and Circulation of Organic Matter in Inland Waters*, B. K. Shtegman (ed.), Israel Program for Scientific Translations, Jerusalem, 1969, p. 121-126.

LACKEY, R. T. 1975. Recreational fisheries management and ecosystem modeling. Virginia Polytechnic Institute and State University, Division of Forestry and Wildlife, Blacksburg, Virginia, FWS-4-75, 44 p.

LAMPERT, W. 1974. A method for determining food selection by zooplankton. Limnology and Oceanography, 19: 995-998.

LAMPERT, W. 1975. A tracer study on the carbon turnover of Daphnia pulex. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 19: 2913-2921.

LAMPERT, W. 1978. Release of dissolved organic carbon by grazing zooplankton. Limnology and Oceanography, 23: 831-834.

LANCE, J. 1965. Respiration and osmotic behavior of the copepod Acartia tonsa in diluted sea water. Comparative Biochemistry and Physiology, 14: 155-165.

LANDRY, M. R. 1978. Predatory feeding behavior of a marine copepod, Labidocera trispinosa. Limnology and Oceanography, 23: 1102-1113.

LAROW, E. J., J. W. WILKINSON, and K. D. KUMAR. 1975. The effect of food concentration and temperature on respiration and excretion of herbivorous zooplankton. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 19: 966-973.

LASENBY, D. C. and R. R. LANGFORD. 1972. Growth, life history, and respiration of Mysis relicta in an arctic and temperate lake. Journal of the Fisheries Research Board of Canada, 29: 1701-1708.

LASKER, R. 1960. Utilization of organic carbon by a marine curstacean: Analysis with C-14. Science (Washington, D. C.), 131: 1098-1100.

LASKER, R. 1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. Journal of the Fisheries Research Board of Canada, 23: 1291-1317.

LASSITER, R. R. 1975. Modeling dynamics of biological and chemical components of aquatic ecosystems. U. S. Environmental Protection Agency, Office of Research and Development, National Environmental Research Center, Corvallis, Oregon, EPA-660/3-75-012, 54 p.

LAWTON, J. H. 1970. Feeding and food energy assimilation in larvae of the damselfly Pyrrhosoma nymphula (Sulz.) (Odonata: Zygoptera). Journal of Animal Ecology, 39: 669-689.

LAWTON, J. H. 1971. Ecological energetics studies on larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). Journal of Animal Ecology, 40: 385-423.

LAWTON, J. H. and J. RICHARDS. 1970. Comparability of Cartesian diver, Gilson, Warburg, and Winkler methods of measuring the respiratory rates of aquatic invertebrates in ecological studies. Oecologia (Berlin), 4: 319-324.

LEFEVRE, M. 1942. L'utilization des algues d'eau douce par les Cladoceres. Bulletin Biologique de la France et de la Belgique, 76: 250-276.

LEFEVRE, M. 1950. Aphanizamenon gracile Lem. Cyanophyte defavorable au zooplankton. Annales de la Station Centrale de Hydrobiologie Appliquee, 3: 205-208.

LEVINS, R. 1966. The strategy of model building in population biology. American Scientist, 54: 421-431.

LEVENS, R. 1968. Ecological engineering: Theory and practice. Quarterly Revue of Biology, 43: 301-305.

LIEBERMAN, M. E. 1970. The response of Miona brachiata (Jurine) 1820 to biological oxygen demand, oxygen and light. Hydrobiologia, 36: 9-16.

LIND, O. T. 1971. The organic matter budget of a central Texas reservoir. In: Reservoir Fisheries and Limnology, G. E. Hall (ed.) Special Publication No. 8, American Fisheries Society, p. 193-202.

LINGANE, J. J. 1961. Chromopotentionmetric study of oxygen reduction at a platinum wire cathode. Journal of Electroanalytical Chemistry, 2:296-309.

LIPEROVSKAYA, Y. S. 1948. The nutrition of freshwater Ostracoda. Zoologicheskii Zhurnal, 27: ? (in Russian).

LUFEROVA, L. A. and Y. I. SOROKIN. 1970. The role of Ostracoda in food chains of Rybinsk Reservoir. Cited by Monakov (1972) as in press.

MacCORMICK, A. J. A., O. L. LOUCKS, J. F. KOONCE, J. F. KITCHELL, and P. R. WEILER. 1972. An ecosystem model for the pelagic zone of Lake Wingra. Eastern Deciduous Forest Biome IBP Memo Report 72-122, 103 p.

MacCORMICK, A. J. A., O. L. LOUCKS, J. F. KOONCE, J. F. KITCHELL, and P. R. WEILER. 1974. An ecosystem model for the pelagic zone of Lake Wingra. Oak Ridge National Laboratory, Eastern Deciduous Forest Biome, EDFB-IBP 74-7, 93 p.

MACKAS, D. and R. BOHRER. 1976. Flourescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. Journal of Experimental Marine Biology and Ecology, 25: 77-85.

MALE, L. M. 1973. A temporal-spatial model for studying nutrient cycling dynamics of a phytoplankton production system. Part 1. Development of model. University of Washington, Seattle, Center for Quantitative Science. Paper 35, 29 p.

MALONE, C. R. and D. J. NELSON. 1969. Feeding rates of freshwater snails (Goniobasis clavaeformis) determined with cobalt 60. Ecology, 50: 728-730.

MALOVITSKAYA, L. M. and Y. I. SOROKIN. 1961. Experimental investigation of nutrition in Diaptomus (Crustacea, Copepoda) with carbon-14. Trudy Instituta Biologii Vodokhranilishcha Akademii Nauk SSSR, 4: 262-272 (in Russian).

MANUILOVA, E. F. 1958. The question of the role of bacterial numbers in the development of Cladocera in natural conditions. Doklady Akademii Nauk SSSR Biological Science Section, 120: 438-441.

MARCHANT, R. and W. D. WILLIAMS. 1977. Population dynamics and production of a brine shrimp, Parartemia zietziana Sayce (Crustacea: Anostraca), in two salt lakes in Western Victoria, Australia. Austrailian Journal of Marine and Freshwater Research, 28: 417-438.

MARSHALL, S. M. 1973. Respiration and feeding in copepods. In: Advances in Marine Biology, Vol 11, F. S. Russell and M. Yonge (eds.), Academic Press, Inc., New York, p. 57-120.

MARSHALL, S. M., A. D. NICHOLLS, and A. P. ORR. 1935. On the biology of Calanus finmarchicus. VI. Oxygen consumption in relation to environmental conditions. Journal of the Marine Biological Association of the United Kingdom, 20: 1-28.

MARSHALL, S. M. and A. P. ORR. 1952. On the biology of Calanus finmarchicus. VII. Factors affecting egg production. Journal of the Marine Biological Association of the United Kingdom, 30: 527-537.

MARSHALL, S. M. and A. P. ORR. 1955a. On the biology of Calanus finmarchicus. VIII. Food uptake, assimilation and excretion in adult and Stage V Calanus. Journal of the Marine Biological Association of the United Kingdom, 34: 495-529.

MARSHALL, S. M. and A. P. ORR. 1955b. The Biology of a Marine Copepod, Calanus finmarchicus (Gunnerus), Oliver and Boyd, Edinburgy, 188 p.

MARSHALL, S. M. and A. P. ORR. 1956. On the biology of Calanus finmarchicus. IX. Feeding and digestion in the young stages. Journal of the Marine Biological Association of the United Kingdom, 35: 587-603.

MARSHALL, S. M. and A. P. ORR. 1958. On the biology of Calanus finmarchicus. XII. Seasonal changes in oxygen consumption. Journal of the Marine Biological Association of the United Kingdom, 37: 459-472.

MARZOLF, G. R. 1964. The trophic position of bacteria and their relation to the distribution of invertebrates. University of Pittsburg, Pymatuning Laboratory of Ecology, Special Publication No. 4: 131-135.

MARZOLF, G. R. 1978. Zooplankton resource gradients resulting from export of materials from rivers into reservoirs. Paper presented at the 5th Annual Great Plains Limnology Meeting, 1978, Lincoln, Nebraska.

MASON, C. F. 1977. Populations and production of benthic animals in two contrasting shallow lakes in Norfolk. Journal of Animal Ecology, 46: 147-172.

MATTICE, J. S. 1976. The effects of temperature on growth, mortality, reproduction and production of adult snails. In: Thermal Ecology II, G. W. Esch and R. W. McFarlane (eds.), U. S. Energy Research and Development Administration Technical Information Center CONF-750425, p. 73-80.

MATTICE, J. S. and L. L. DYE. 1976. Thermal tolerance of the adult Asiatic clam. In: Thermal Ecology II, G. W. Esch and R. W. McFarlane (eds.), U. S. Energy Research and Development Administration Technical Information Center CONF-750425, p. 130-135.

MAY, R. M. 1973. Stability and Complexity in Model Ecosystems, Monographs in Population Biology No. 6, Princeton University Press, Princeton, 235 p.

MAYZAUD, P. 1976. Respiration and nitrogen excretion of zooplankton. 4. The influence of starvation on the metabolism and the biochemical composition of some species. Marine Biology (Berlin) 37: 47-58.

MAYZAUD, P. and R. J. CONOVER. 1976. Influence of potential food supply on the activity of digestive exzymes of neritic zooplankton. In: Proceedings of the 10th European Symposium on Marine Biology, Vol 2, Universa, Wetteren, Belgium, p. 415-427.

MAYZAUD, P. and S. A. POULET. 1978. The importance of the time factor in the response of zooplankton to varying concentrations of naturally occurring particulate matter. Limnology and Oceanography, 23: 1144-1154.

McALLISTER, D. C. 1970. Zooplankton rations, phytoplankton mortality and estimation of marine production. In: Marine Food Chains, J. H. Steele (ed.), University fo California Press, Berkeley, p. 419-457.

McCULLOUGH, D. A. 1975. The bioenergetics of three aquatic insects determined by radioisotope analysis. Battelle Pacific Northwest Laboratories, Richland, Washington, Report BNWL-1928, 219 p.

McDIFFETT, W. F. 1970. The transformation of energy by a stream detritivore Pteronarcys scotti (Plecoptera). Ecology, 51: 975-988.

McMAHON, J. W. 1965. Some physical factors influencing the feeding behavior of Daphnia magna Straus. Canadian Journal of Zoology, 43: 603-611.

McMAHON, J. W. 1968. Environmental factors influencing the feeding behavior of Daphnia magna Straus. Canadian Journal of Zoology, 46: 759-762.

McMAHON, J. W. and F. H. RIGLER. 1963. Mechanisms regulating the feeding rate of Daphnia magna Straus. Canadian Journal of Zoology, 41: 321-332.

McMAHON, J. W. and F. H. RIGLER. 1965. Feeding rate of Daphnia magna Straus in different foods labelled with radioactive phosphorus. Limnology and Oceanography, 10: 105-113.

McQUEEN, D. J. 1969. Reduction of zooplankton standing stocks by predaceous Cyclops bicuspidatus thomasi in Marion Lake, British Columbia. Journal of the Fisheries Research Board of Canada, 26: 1605-1618.

McQUEEN, D. J. 1970. Grazing rates and food selection of Diaptomus oregonensis (Copepoda) from Marion Lake, British Columbia. Journal of the Fisheries Research Board of Canada, 27: 13-20.

MENSHUTKIN, V. V. 1971. Development trends in methods used to model populations and communities. In: Communities, Nauka, Leningrad (English translation available from U. S. Department of Commerce, National Technical Information Service, as TT-73-55111, 1975, 306 p.).

MENSHUTKIN, V. V. and A. A. UMNOV. 1970. A mathematical model of a very simple aquatic ecosystem. Hydrobiological Journal, 6: 18-23.

MEYER, J. A. 1914. Beitrage zur Kenntnis der chemischen Zusammensetzung wirbellosen Tiere. Wissenschaftliche Meeresuntersuchungen, 16: 233.

MICHAELIS, L. and M. L. MENTEN. 1913. Biochemische Zeitschrift, 49: 333.

MIKHEEV, V. P. 1966. Rate of filtration of water by Dreissena. Trudy Instituta Biologii Vntrennikh Vod Akademii Nauk SSR, 12(15). English translation in: Plankton and Benthos of Inland Waters, B. K. Shtegman (ed.), Israel Program for Scientific Translations, Jerusalem, 1969, p. 150-155.

MITROPOL'SKII, V. I. 1966. Mechanism of filtration and feeding of sphaeriids (Mollusca, Lamellibranchia). Trudy Instituta Biologii Vntrennikh Vod Akademii Nauk SSSR, English translation in: Plankton and Benthos of Inland Waters, B. K. Shtegman (ed.), Israel Program for Scientific Translations, Jerusalem, 1969, p. 143-149.

MONAKOV, A. V. 1972. Review of studies on feeding of aquatic invertebrates conducted at the Institute of Inland Waters, Academy of Science, USSR. Journal of the Fisheries Research Board of Canada, 29: 363-383.

MONAKOV, A. V. and Y. I. SOROKIN. 1960. An experimental investigation of Daphnia nutrition using C^{14}. Doklady Akademii Nauk SSSR, 135: 1516-1518 (English translation in Doklady Adademii Nauk SSSR Biological Science Section, 135: 925-926, 1961).

MONAKOV, A. V. and Y. I. SOROKIN. 1961. Quantitative data on the feeding of daphnids. Trudy Instituta Biologii Vodokhranilishcha Akademii Nauk SSSR, 4: 251-261 (in Russian).

MONAKOV, A. V. and Y. I. SOROKIN. 1972. Some results on investigations on nutrition of water animals. In: Productivity Problems of Freshwaters, Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, p. 767-773.

MORTON, B. 1971. Studies on the biology of Dreissena polymorpha Pall. V. Some aspects of filter-feeding and the effect of microorganisms upon the rate of filtration. Proceedings of the Malacological Society of London, 39: 289-301.

MOSHIRI, G. A., K. W. CUMMINS, and R. R. COSTA. 1969. Respiratory energy expenditures by the predaceous zooplankter Leptodora kindtii (Focke) (Crustacea: Cladocera). Limnology and Oceanography, 14: 475-484.

MOSHIRI, G. A., C. R. GOLDMAN, G. L. GODSHALK, and D. R. MULL. 1970. The effects of variations in oxygen tension on certain aspects of respiratory metabolism in Pacifastacus leniusculus (Dana) (Crustacea: Decapoda). Physiological Zoology, 43: 23-29.

MOSHIRI, G. A., C. R. GOLDMAN, D. R. MULL, G. L. GODSHALK, and J. A. COIL. 1971. Respiratory metabolism in Pacifactacus leniusculus (Dana) (Crustacea: Decapoda) as related to its ecology. Hydrobiologia, 37: 183-195.

MOSKALENKO, B. K. and K. K. VOTINSEV. 1972. Biological productivity and balance of organic substance and energy in Lake Baikal. In: Productivity Problems of Freshwaters, Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, p. 206-226

MULLIN, M. M. 1963. Some factors affecting the feeding of marine copepods of the genus Calanus. Limnology and Oceanography, 8: 239-250.

MULLIN, M. M. and E. R. BROOKS. 1970. Growth and metabolism of two planktonic marine copepods as influenced by temperature and type of food. In: Marine Food Chains, J. H. Steele (ed.), University of California Press, Berkeley, p. 74-95.

MULLIN, M. M., E. F. STEWART, and F. J. FOGLISTER. 1975. Ingestion by planktonic grazers as a function of concentration of food. Limnology and Oceanography, 20: 259-262.

NAGELL, B. 1973. The oxygen consumption of mayfly (Ephemeroptera) and stonefly (Plecoptera)larvae at different oxygen concentrations. Hydrobiologia, 42: 461-489.

NAUWERCK, A. 1959. Zur Bestimmung der Filtrierrate limnischer Planktontiere. Archiv fuer Hydrobiologie Supplementband, 25: 83-101.

NAUWERCK, A. 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. Symbolae Botanicae Upsalienses, 17: 1-163.

NEBEKER, A. V. 1972. Effect of low oxygen concentration on survival and emergence of aquatic insects. Translations of the American Fisheries Society, 101: 625-679.

NEGUS, C. 1966. A quantitative study of growth and production of unionid mussels in the River Thames at Reading. Journal of Animal Ecology, 35; 513-532.

NEMOTO, T., J. MAUCHLINE, and K. KAMADA. 1976. Brood size and chemical composition of Pareuchaeta nowegica (Crustacea: Copepoda) in Loch Etuie, Scotland. Marine Biology (Berlin), 36: 151-157.

NILSSON, L. M. 1974. Energy budget of a laboratory population of Gammarus pulex (Amphipoda). Oikos, 25: 35-42.

O'BRIEN, W. J. and F. DeNOYELLES, Jr. 1974. Filtering rate of Ceriodaphnia reticulata in pond waters of varying phytoplankton concentrations. American Midland Naturalist, 91: 508-512.

ODUM, E. P. 1971. Fundamentals of Ecology, W. B. Saunders Co., Philadelphia, 574 p.

ODUM, E. P. and A. A. DE LA CRUZ. 1963. Detritus as a major component of ecosystems. Bulletin of the American Institute of Biological Sciences, 13: 39-40.

ODUM, E. P. and A. E. SMALLEY. 1959. Comparison of population energy flow of a herbivorous and a deposit feeding invertebrate in a salt marsh ecosystem. Proceedings of the National Academy of Sciences of the United States of America, 45: 617-622.

OLAH, J. 1976. Energy transformation by Tanypus punctipennis (Meig.) (Chironomidea) in Lake Balaton. Annales Instituti Biologici (Tihany) Hungaricae Academiae Scientiarum, 43: 83-92.

OMORI, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. Marine Biology (Berlin), 3: 4-10.

OMORI, M. 1970. Variations of length, weight, respiratory rate, and chemical composition of Calanus cristatus in relation to its food and feeding. In: Marine Food Chains, J. H. Steele (ed.), University of California Press, Berkeley, p. 113-126.

OMORI, M. 1978. Some factors affecting on dry weight, organic weight and concentrations of carbon and nitrogen in freshly prepared and in preserved zooplankton. Internationale Revue der Gesamten Hydrobiologie, 63: 261-269.

OSTAPENYA, A. P., G. A. PECHEN', V. A. BIBITSKII, and A. P. PAVLYUTIN. 1969. Metabolism intensity of Diaptomus graciloides (Lill.) at a low temperature. Hydrobiological Journal, 5: 88-91.

OTTO, C. 1975. Energetic relationships of the larval population of Potamophylax cingulatus (Trichoptera) in a south Swedish stream. Oikos, 26: 159-169.

OTTO, R. G. 1974. The effects of acclimation to cyclic thermal regions on heat tolerance of the western mosquitofish. Transactions of the American Fisheries Society, 103: 331-335.

OVERBECK. J. 1972. Distribution pattern of phytoplankton and bacteria, microbial decomposition of organic matter and bacterial production in a eutrophic, stratified lake. In: Productivity Problems of Freshwaters, Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, P. 227-237.

PAERL, H. W. 1973. Detritus in Lake Tahoe: Structural modification by attached microflora. Science (Washington, DC), 180: 496-498.

PAERL, H. W. 1974. Bacterial uptake of dissolved organic matter in relation to detrital aggregation in marine and freshwater systems. Limnology and Oceanography, 19: 966-972.

PAFFENHOFER, G. A. 1971. Grazing and ingestion rates of nauplii, copepods and adults of the marine planktonic copepod Calanus helgolandicus. Marine Biology (Berlin), 11: 286-298.

PAFFENHOFER, G. A. 1976. Feeding, growth, and food conversion of the marine planktonic copepod Calanus helgolandicus. Limnology and Oceanography, 21: 39-50.

PAFFENHOFER, G. A. and J. D. H. STRICKLAND. 1970. A note on the feeding of Calanus helgolandicus on detritus. Marine Biology (Berlin), 5: 97-99.

PALMER, M. F. 1968. Aspects of the respiratory physiology of Tubifex tubifex in relation to its ecology. Journal of the Linnean Society of London Zoology, 154: 463-473.

PARK, R. A., D. SCAVIA, and N. L. CLESCERI. 1974. Cleaner, the Lake George model. Rensselaer Fresh Water Institute at Lake George, Eastern Deciduous Forest Biome IBP Contribution No. 186, 32 p.

PARKER, R. A. 1973. Some problems associated with computer simulation of an ecological system. In: The Mathematical Theory of the Dynamics of Biological Populations, M. S. Bartlett and R. W. Hiorns (eds.), Academic Press, Inc., New York, p. 269-288.

PARSONS, T. R., R. J. LeBRASSEUR, and J. D. FULTON. 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. Journal of the Oceanographical Society of Japan (Nippon Kaiyo Gakkaishi), 23, 10-17.

PATTEN, B. C., D. A. EGLOFF, T. H. RICHARDSON et al. 1975. Total ecosystem model for a cove in Lake Texoma. In: Systems Analysis and Simulation in Ecology, B. C. Patten (ed.), Academic Press, Inc., New York, p. 205-421.

PECHEN'-FINENKO, G. A. 1971. Efficiency of assimilation of food by plankton crustaceans. Ekologiya, 3: 64-72 (in Russian).

PECHEN'-FINENKO, G. A. 1973. Effect of food concentration on the efficiency of its assimilation by planktonic crustaceans with different feeding habits. Hydrobiological Journal, 9: 265-271.

PECHEN'-FINENKO, G. A. 1977. Efficiency of food assimilation by planktonic crustaceans in different trophic conditions. Zoologicheskii Zhurnal, 56: 1458-1465 (English translation available as Fisheries and Marine Service of Cannada Translation Series No. 4188, 1978, 13 p.).

PECHLANDER, R., G. BRETSCHKO, P. GOLLMANN, H. PFEIFER, M. TILZER, and H. P. WEISSENBACH. 1972. The production processes in two high-mountain lakes (Vorderer and Hinterer Finstertaler See, Kuhtai, Austria). In: Productivity Problems of Freshwaters, Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, p. 239-269.

PENNAK, R. W. 1964. Collegiate Dictionary of Zoology, Ronald Press Co., New York, 583 p.

PENNAK, R. W. and W. N. ROSINE. 1976. Distribution and ecology of Amphipoda (Crustacea) in Colorado. American Naturalist, 96: 324-331.

PETIPA, T. S. 1967. On the efficiency of utilization of energy in pelagic ecosystems of the Black Sea. In: Struktura i dinamika vodnykh soobshchestv i populyatsii, Respublikanskii Mezhvedomstvennyi Sbornik, Seriya "Biologiya Morya," Akademii Nauk Ukrainskoi SSR, p. 44-64 (English translation available as Fisheries Research Board of Canada Translation Series No. 973, 1967, 34 p.).

PETIPA, T. S., E. V. PAVLOVA, and G. N. MIRONOV. 1970. The food structure, utilization and transport of energy by trophic levels in the planktonic communities. In: Marine Food Chains, J. H. Steele (ed.), University of California, Berkeley, p. 142-167.

PETITPREN, M. F. and A. W. KNIGHT. 1970. Oxygen consumption of the dragonfly, *Anax junius*. Journal of Insect Physiology, 16: 449-459.

PHILLIPSON, J. 1970. The "best estimate" of respiratory metabolism: Its applicability to field situations. Polskie Archiwum Hydrobiologii, 17: 31-41.

PILARSKA, J. 1977a. Eco-physiological studies on *Brachionus rubens* Ehrbg (Rotatoria). I. Food selectivity and feeding rate. Polskie Archiwum Hydrobiologii, 24: 319-328.

PILARSKA, J. 1977b. Eco-physiological studies on *Brachionus rubens* Ehrbg (Rotatoria). III. Energy balances. Polskie Archiwum Hydrobiologii, 24: 343-354.

PILARSKA, J. 1977c. Eco-physiological studies of *Brachionus rubens* Ehrbg. (Rotatoria). II. Production and respiration. Polskie Archiwum Hydrobiologii, 24: 329-341.

PLATT, T., V. M. BRAWN, and B. IRWIN. 1969. Caloric and carbon equivalents of zooplankton biomass. Journal of the Fisheries Research Board of Canada, 26: 2345-2349.

PLATT, T. and B. IRWIN. 1973. Caloric content of phytoplankton. Limnology and Oceanography, 18: 306-310.

PLOSKEY, G. R. 1978. Drift of Baetis flavistriga as a result of feeding activity and in relation to larval density. University of Arkansas, Fayetteville, Arkansas. M.S. Thesis, 46 pp.

POMEROY, L. R., H. M. MATHEWS, and H. S. MIN. 1963. Excretion of phosphate and soluble organic phosphorus compounds by zooplankton. Limnology and Oceanography, 8: 50-55.

PORTER, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature (London), 224: 179-180.

PORTER, K. G. 1975. Viable gut passage of gelatinous green algae ingested by Daphnia. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 19: 2840-2850.

POULET, S. A. 1976. Feeding of Pseudocalanus minutus on living and non-living particles. Marine Biology (Berlin), 34: 117-125.

POULET, S. A. 1977. Grazing of marine copepod developmental stages on naturally occurring particles. Journal of the Fisheries Research Board of Canada, 34: 2381-2387.

POURRIOT, R. 1973. Effect of protein content, temperature and fasting on the respiration of leleoplanktonic Rotifera. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 18: 1429-1433.

POURRIOT, R. 1977. Food and feeding habits of Rotifera. Archiv fuer Hydrobiologie Beihefte, Ergebnisse der Limnologie, 8: 243-260.

PROSSER, C. L. and F. A. BROWN. 1961. Comparative Animal Physiology, Saunders, Philadelphia, Pennsylvania, 688 p.

PRUS, T. 1971. The assimilation efficiency of Asellus aquaticus L. (Crustacea, Isopoda). Freshwater Biology, 1: 287-305.

PRUS, T. 1972. Energy requirement, expenditure, and transformation efficiency during development of Asellus aquaticus L. (Crustacea, Isopoda). Polskie Archiwum Hydrobiologii, 19: 97-112.

PRUS, T. 1976. Experimental and field studies on ecological energetics of Asellus aquaticus L. (Isopoda). I. Assimilability of lipids, proteins and carbohydrates. Ekologia Polska Seria A, 24: 461-472.

RANSOM, J. D., F. L. RAINWATER, and C. G. BEAMES, Jr. 1971. A note on the metabolism of two Diptera larvae, Chaoborus punctipennis and Chironomus plumosus. Proceedings of the Oklahoma Academy of Sciences, 49; 215-217.

RAZOULS, S. 1977. Analysis of weight, chemical composition and calorific values in juvenile stages of pelagic copepods over a one year period. Journal of Experimental Marine Biology and Ecology, 26: 265-273.

REEVE, M. R., J. E. G. RAYMONT, and J. K. B. RAYMONT. 1970. Seasonal biochemical composition and energy sources of Sagitta hispida. Marine Biology (Berlin), 6: 357-364.

RICHMAN, S. 1958. The transformation of energy by Daphnia pulex. Ecological Monographs, 28: 273-291.

RICHMAN, S. 1964. Energy transformation studies on Diaptomus oregonensis. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 15: 654-659.

RICHMAN, S. 1966. The effect of phytoplankton concentration on the feeding rate of Diaptomus oregonensis. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 16: 392-398.

RICKER, W. F. (ed.) 1968. Methods for Assessment of Fish Production in Fresh Waters, IBP Handbook No. 3, Blackwell Scientific Publishers, Oxford and Edinburge, 313 p.

RIGLER, F. H. 1961a. The relation between concentration of food and feeding rate of Daphnia magna Straus. Canadian Journal of Zoology, 39: 857-868.

RIGLER, F. H. 1961b. The uptake and release of inorganic phosphorus by Daphnia magna Straus. Limnology and Oceanography, 6: 165-174.

RIGLER, F. H. 1971. Zooplankton. In: A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters, W. T. Edmondson and G. G. Winberg (eds.), Blackwell Scientific Publications, Oxford, p. 228-255.

RILEY, G. A. 1970. Particulate organic matter in seawater. In: Advances in Marine Biology Vol. 8, Academic Press, Inc., New York, p. 1-118.

RINGELBERG, J. 1964. The positively phototactic reaction of Daphnia magna Straus, a contribution to the understanding of diurnal vertical migration. Netherlands Journal of Sea Research, 2: 319-406.

RODINA, A. G. 1963. Micorbiology of detritus of lakes. Limnology and Oceanography, 8: 388-393.

RODINA, A. G. 1966. Nutritive importance and structure of detritus. In: Biologicheskie Resursy Vodoemov, Puti Ikh Rekonstruktsii i Ispol'Zovaniya, Izdatel'Stvo "Nauka," Moscow, p. 35-42 (English translation available as National Research Council of Canada Technical Translation 1625, 1972, 11 p.

ROFF, J. C. 1973. Oxygen consumption of Limnocalanus macrurus Sars (Calanoida, Copepoda) in relation to environmental conditions. Canadian Journal of Zoology, 51: 877-885.

ROMANENKO, V. I. 1966. Microbiological processes in the formation and breakdown of organic matter in the Rybinsk Reservoir. Trudy Instituta Biologii Vntrennikh Vod Akademii Nauk SSSR, 13(16). English translation in: Production and Circulation of Organic Matter in Inland Waters, B. K. Shtegman (ed.), Israel Program for Scientific Translations, Jerusalem, 1969, p. 137-158.

ROSS, G. C. and P. NIVAL. 1976. Plankton modeling in the Bay of Villefranche. Journal of Theoretical Biology, 56; 381-399.

RUEGER, M. E., T. A. OLSON, and J. I. SCOFIELD. 1969. Oxygen requirements of benthic insects as determined by manometric and polarographic techniques. Water Research, 3: 99-120.

RYTHER, J. H. 1954. Inhibitory effects of phytoplankton upon the feeding of Daphnia magna with reference to growth, reproduction, and survival. Ecology, 35: 522-533.

SALONEN, K. and J. SARVALA. 1978. Estimation of the inorganic fraction of total carbon in aquatic invertebrates. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 20: 1221-1225.

SALONEN, K., J. SARVALA, I. HAKALA, and M. VILJANEN. 1976. The relation of energy and organic carbon in aquatic invertebrates. Limnology and Oceanography, 21: 724-730.

SATOMI, M. and L. R. POMEROY. 1965. Respiration and phosphorus excretion in some marine populations. Ecology, 46: 877-881.

SCAVIA, D. 1979. The use of ecological models of lakes in synthesizing available information and identifying research needs. In: Perspectives on Lake Ecosystem Modeling, D. Scavia and A. Robertson (eds.), Ann Arbor Science Publishers, Inc., Ann Arbor, p. 109-168.

SCAVIA, D., J. A. BLOOMFIELD, J. S. FISHER, J. NAGY, and R. A. PARK. 1974. Documentation of CLEANX: A generalized model for simulating the open-water ecosystems of lakes. Simulation, 24: 51-56.

SCAVIA, D., B. J. EADIE, and A. ROBERTSON. 1976. An ecological model for Lake Ontario. Model formulation, calibration, and preliminary evaluation. U. S. National Oceanic and Atmospheric Administration, Environmental Research Laboratories, Boulder, Colorado, NOAA-TR-ERL 371-GLERL 12, 64 p.

SCAVIA, D. and A. ROBERTSON (eds.). 1979. Perspectives on Lake Ecosystem Modeling, Ann Arbor Science Publishers, Inc., Ann Arbor, 326 p.

SCHINDLER, D. W. 1968. Feeding, assimilation and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. Journal of Animal Ecology, 37: 369-385.

SCHINDLER, J. E. 1971. Food quality and zooplankton nutrition. Journal of Animal Ecology, 40: 589-595.

SCHINDLER, J. E. and G. W. COMITA. 1966. The feeding rate of *Diaptomus leptopus*. Proceedings of the North Dakota Academy of Science, 20: 125-130.

SCHOTTELIUS, B. A. and D. D. SCHOTTELIUS. 1973. Textbook of Physiology, Mosby Co., St. Louis, 590 p.

SEDELL, J. R. 1971. The trophic ecology and natural history of *Neophylax concinnus* and *N. oligius* (Trichoptera: Limnophilidae). Ph.D. Thesis, University of Pittsburg, Pittsburg, Pennsylvania, 154 p.

SEMENOVA, L. M. 1974. The feeding habits of *Bosmina coregoni* Baird (Cladocera). Hydrobiological Journal, 10: 28-34.

SHEANON, M. J. and F. B. TRAMA. 1972. Influence of phenol and temperature on the respiration of a freshwater snail: *Helisoma trivolvis*. Hydrobiologia, 40: 321-328.

SHERBERGER, F. F., E. F. BENFIELD, L. L. DICKSON, and J. CAIRNS, Jr. 1977. Effects of thermal shocks on drifting aquatic insects: A laboratory simulation. Journal of the Fisheries Research Board of Canada, 34: 529-536.

SHUSHKINA, E. A., S. I. ANISIMOV, and R. Z. KLEKOWSKI. 1968. Calculation of production efficiency in plankton copepods. Polskie Archiwum Hydrobiologii, 15: 251-261.

SHUSHKINA, E. A. and R. Z. KLEKOWSKI. 1968. The relation between the feeding, growth and metabolism of Macrocyclops albidus Jur. (Copepoda) and food conditions and actual zooplankton production in lakes of various types. Zoologicheskii Zhurnal, 47: 525-533. (English translation available as Fisheries Research Board of Canada Translation Series No. 1197, 1968, 23 p.

SHUSHKINA, E. A. and G. A. PECEN'. 1964. Food rations and its assimilation by carnivorous Cyclops and Daphnia longispina; determination with the radiocarbon method. In: Trudy 10 Nauk Konf. po Vnutrennyh Vodoemah Pribaltiki, Minsk, p. 312-322. (in Russian)

SIEBECK, O. 1960. Untersuchungen uber die Vertikalwanderung planktischer Crustacean unter Berucksichtigung der Strahlungsverhaltnisse. International Revue der Gesamten Hydrobiologie, 45: 381-454.

SIEBURTH, J. and V. SMETACEK. 1978. Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnology and Oceanography, 23: 1256-1263.

SIEFKEN, M. and K. B. ARMITAGE. 1968. Seasonal variation in metabolism and organic nutrients in three Diaptomus (Crustacea: Copepoda). Comparative Biochemistry and Physiology, 24: 591-609.

SIGMON, C. F., A. S. TOMBES, and L. TILLY. 1978. Diel oxygen uptake in Chaoborus punctipennis (Diptera: Chaoboridae). Hydrobiologia, 61: 69-73.

SKOOG, G. 1976. Effects of acclimation and physiological state on the tolerance to high temperatures and reactions to desiccation of Theodoxus fluviatilis and Lymnea peregra. Oikos, 27: 50-56.

SMIRNOV, N. N. 1962. Eurycercus lamellatus (O. F. Muller) (Chydoridae, Cladocera): Field observations and nutrition. Hydrobiologia, 20: 280-295.

SMIRNOV, N. N. 1969. Morphological and functional bases for the mode of life of cladoceran crustaceans. II. The functional complex in chydorids (Chydoridae, Cladocera) ensuring the digestion of food. Hydrobiological Journal, 5: 32-36.

SMITH, M. W. 1936. Notes on the food of Daphnia pulex De Geer in fertilized water. Transactions of the American Fisheries Society, 66: 287-290.

SMITH, W. E. 1970. Tolerance of Mysis relicta to thermal shock and light. Transactions of the American Fisheries Society, 99: 418-422.

SMITH, W. E. 1972. Culture, reproduction, and temperature tolerance of Pontoporeia affinis in the laboratory. Transactions of the American Fisheries Society, 101: 253-256.

SMITH, W. E. 1973. Thermal tolerance of two species of Gammarus. Transactions of the American Fisheries Society, 102: 431-433.

SOROKIN, Y. I. 1966a. Carbon-14 method in the study of nutrition of aquatic animals. International Revue der Gesamten Hydrobiologie, 51: 209-224.

SOROKIN, Y. I. 1966b. Use of radioactive carbon for the study of the nutrition and food relationships of aquatic animals. Trudy Instituta Biologii Vntrennikh Vod Akademii Nauk SSSR, 12(15). Gnglish translation in: Plankton and Benthos of Inland Waters, B. K. Shtegman (ed.), Israel Program for Scientific Translations, Jerusalem, 1969, p. 83-132.

SOROKIN, Y. I. 1969. The seasonal dynamics of the productivity of the plankton of the shore area and the open part of the Volga arm of the Rybinsk Reservoir. Biologiya Vnutrennykh Vod Informatsionii Byulleten', 3: 7-10. (in Russian)

SOROKIN, Y. I. 1972. Biological productivity of the Rybinsk Reservoir. In: Productivity Problems of Freshwaters Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, p. 494-503.

SOROKIN, Y. I. and E. D. MORDUKHAI-BOLTOVSKAYA. 1962. The study of the nutrition of the rotifer Asplanchna using C-14. Byulleten' Instituta Biologii Vodokhranilischa Akademii Nauk SSSR, 12: 17. (in Russian)

SOUTHWARD, A. J. and E. C. SOUTHWARD. 1971. Observations on the role of dissolved organic compounds in the nutrition of benthic invertebrates. Sarsia, 50: 29-46.

SOYZA, K. 1973. Energetics of Aphelenchus avenae in mono-azenic culture. Proceedings of the Helminthological Society of Washington, 40: 1-10.

SPRAGUE, J. B. 1963. Resistance of four freshwater crustaceans to lethal high temperature and low oxygen. Journal of the Fisheries Research Board of Canada, 20: 387-415.

STANCZYKOWSKA, A. and W. LAWACZ. 1976. Caloric value of the Dreissena polymorpha (Pall.) dry body weight in some Mazurian lakes. Polskie Archiwum Hydrobiologii, 23: 271-275.

STARKWEATHER, P. L. 1975. Diel patterns of grazing in Daphnia pulex Leydig. International Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 19: 2851-2857.

STARKWEATHER P. L. and J. J. GILBERT. 1977. Radiotracer determination of feeding in Brachionus calyciflorus: The importance of gut passage times. Archiv fuer Hydrobiologie Beihefte, Ergebnisse der Limnologie, 8: 261-263.

STEELE, J. H. 1974. The Structure of Marine Ecosystems, Harvard University Press, Cambridge, 128 p.

STEPANOVA, L. A. 1972. Rations of Mesocyclops leuckarti (Claus) and Leptodora kindtii (Focke) populations in Lake Ilmen. Hydrobiological Journal, 8: 70-72.

STOCKMAYER, W. H. 1978. Data evaluation: A critical activity. Science (Washington, DC), 201: 1.

STOCKNER, J. G. 1971. Ecological energetics and natural history of Hedriodiscus truquii (diptera) in two thermal spring communities. Journal of the Fisheries Research Board of Canada, 28: 73-94.

STREIT, B. 1976. Energy flow in four different field populations of Ancylus fluviatilis (Gastropoda-Basommatophora). Oecologia (Berlin), 22: 261-273.

STROSS, R. G., F. M. UNGER, J. C. JONES, and J. M. VAIL. 1965. Utilization of algae by Daphnia as influenced by cell senescence and UV irradiation. Purdue University Engineering Bulletin No. 118: 706-714.

SUSHCHENYA, L. M. 1958a. Quantitative data on the filtration feeding of planktonic Curstacea. Doklady Wish. Shkoli Biol. Sci., 1: 16-20. (in Russian)

SUSHCHENYA, L. M. 1958b. Dependence of filtration rate in planktonic Crustacea on the concentration of food particles. Trans. Biol. Sta. Lake Naroch, 1: 241-260. (in Russian)

SUSHCHENYA, L. M. 1969. Quantitative relations of metabolism and transformation of matter and energy in Crustacea. Avtoreferat dissertatsii na soiskanie uchenoi stepeni doktora biologicheskikh nauk, Akademii Nauk SSSR. Inst. Okeanol. im P. P. Shirshov, 105: 3-42 (Author's abstract of doctorial thesis, published by the P. P. Shirshov Institute of Oceanology, USSR Academy of Sciences) English translation available as Fisheries Research Board of Canada Translation Series No. 1374, 1970, 78 p.).

SUTCLIFFE, D. W., T. R. CARRICK, and W. H. MOORE. 1975. An automatic respirometer for determining oxygen uptake in crayfish (Austropotamobius pallipes (Lereboullet)) over periods of 3-4 days. Journal of Experimental Biology, 63; 673-688.

SWARTZMAN, G. L. 1977. A comparison of plankton simulation models emphasizing their applicability to impact assessment. Center for Quantitative Science, College of Fisheries, University of Washington, Seattle, 38 p.

SWARTZMAN, G. L. and R. BENTLEY. 1977. A comparison of plankton models with emphasis on application to assessing non-radiological nuclear plant impacts on plankton in natural ecosystems. Center for Quantitative Science, College of Fisheries, University of Washington, Seattle, 127 p.

SWARTZMAN, G. L. and R. BENTLEY. 1978. A review and comparison of plankton simulation models. Center for Quantitative Science, College of Fisheries, University of Washington, Seattle, 69 p.

SWEENEY, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. Limnology and Oceanography, 23: 461-477.

SWEENEY B. W. and J. A. SCHNACK. 1977. Egg development, growth, and metabolism of Sigara alternata (Say) (Hemiptera: Corixidae) in fluctuating thermal environments. Ecology, 58: 265-277.

SWISS, J. J. and M. G. JOHNSTON. 1976. Energy dynamics of two benthic crustaceans in relation to diet. Journal of the Fisheries Research Board of Canada, 33: 2544-2550.

TAGHON, G. L., R. F. L. SELF, and P. A JUMARS. 1978. Predicting particle selection by deposit feeders: A model and its implications. Limnology and Oceanography, 23: 752-759.

TEZUKA, Y. 1971. Feeding of Daphnia on planktonic bacteria. Japanese Journal of Ecology (Nippon Seitai Gakkaishi), 21: 127-134.

THOMANN, R. V., D. M. DiTORO, R. P. WINFIELD, and D. J. O'CONNOR. 1975. Mathematical modeling of phytoplankton in Lake Ontario, Part 1. Model development and verification. U. S. Environmental Protection Agency, Corvallis, Oregon, EPA-660/3-75-005.

THORNTON, K. W. AND J. R. SAUER. 1972. Physiological effects of NaCl on Chironomus attenuatus (Diptera: Chironomidae). Annals of the Entomological Society of America, 65: 872-875.

THORNTON, K. W., and J. L. WILHM. 1975. The use of life tables in demonstrating the effects of pH, phenol, and NaCl on Chironomus attenuatus populations. Environmental Entomology, 4: 325-328.

THORNTON, K. W. and A. S. LESSEM. 1978. A temperature algorithm for modifying biological rates. Transactions of the American Fisheries Society, 107: 284-287.

TILZER, M. 1972. Bacterial productivity of a high mountain lake. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 18: 188-196.

TONAPI, G. T. and H. N. MOHAN RAO. 1977. Effect of temperature on the oxygen consumption in the larvae of Dineutes indicus Aube (Gyrinidae, Coleoptera). Hydrobiologia, 53: 113-116.

TRAMA, F. B. 1972. Transformation of energy by an aquatic herbivore (Stenonema pulchellum) Ephemeroptera. Polskie Archiwum Hydrobiologii, 19: 113-121.

TULLY, J. P. 1936. The nutritive value of marine procucts. XIV. Proximate analyses of fresh British Columbia oysters. Journal of the Biological Board of Canada, 2: 477.

ULANOSKI, J. T. and W. F. McDIFFETT. 1972. Diurnal variations in respiration of mayfly nymphs (Ephemeroptera). Physiological Zoology, 45: 97-105.

UMBREIT, W. W., R. H. BURRIS, and J. F. STAUFFER. 1964. Manometric Techniques, 4th edition, Burgis Publ. Co., Minneapolis, Minnesota, 357 p.

UMNOV, A. A. 1972. Mathematical model of the biotic cycle in a lake ecosystem. Hydrobiological Journal, 8: 1-8.

VANNOTE, R. L. 1969. Detrital consumers in natural systems. In: The Stream Ecosystem, K. W. Cummins (ed.), Michigan State University Institute of Water Research Technical Report No. 7: 20-23.

VINOGRADOV, A. P. 1933. La composition chemique elementaire des organismes vivants et le systeme periodique des elements chimiques. Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, 197: 1673.

VINOGRADOV, A. P. 1953. The Elementary Chemical Composition of Marine Organisms, Sears Foundation for Marine Research, Yale University Press, New Haven, 647 p.

WALDBAUER, G. P. 1968. The consumption and utilization of food by insects. In: Advances in Insect Physiology, J. W. L. Beament, J. E. Treherne, and V. B. Wigglesworth (eds.), Academic Press, Inc., New York, p. 229-288.

WALTERS, C. J. and I. E. EFFORD. 1972. Systems analysis in the Marion Lake IBP Project. Oecologia (Berlin), 11: 33-44.

WATT, K. E. F. 1975. Critique and comparison of Biome ecosystem modeling. In: *Systems Analysis and Simulation in Ecology* Vol. III, B. C. Patton (ed.), Academic Press, Inc., New York, p. 139-152.

WEBB, K. L. and R. E. JOHANNES. 1967. Studies of the release of dissolved free amino acids by marine zooplankton. Limnology and Oceanography, 12: 376-382.

WEBSTER, K. E. and R. H. PETERS. 1978. Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. Limnology and Oceanography, 23: 1238-1245.

WEIGELT, C. 1891. *Die Abfaller der Seefischerei; experimentelle Untersuchungen uber deren Natur, Menge, Verarbeitung und Verwertung*, Sonderbeilage zu den Mitteilungen der Sektionen fuer Kusten und Hochseefischerei, Moeser, Berlin, 111 pp.

WELCH, H. E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology, 49: 755-759.

WELCH, H. E. 1976. Ecology of Chironomidae (Diptera) in a polar lake. Journal of the Fisheries Research Board of Canada, 33: 227-247.

WEST, B., M. deBURGH, and F. JEAL. 1977. Dissolved organics in the nutrition of benthic invertebrates. In: *Biology of Benthic Organisms*, B. F. Keegan, P. O. Ceidegh, and P. J. S. Boaden (eds.), Pergamon Press, Oxford, p. 587-593.

WETZEL, R. G. 1975. *Limnology*, W. B. Saunders Co., Philadelphia, 743 p.

WILLOUGHBY, L. G. and D. W. SUTCLIFFE. 1976. Experiments on feeding and growth of the amphipod *Gammarus pulex* (L.) related to its distribution in the River Dudden. Freshwater Biology, 6: 577-586.

WILSON, M. S. 1959. Free-living Copepoda: Calanoida. In: *Freshwater Biology*, 2nd edition, W. T. Edmondson (ed.), John Wiley and Sons, Inc., New York, P. 738-794.

WINBERG, G. G. 1956. Rate of metabolism and food requirements of fishes. In: *Nauchnye Trudy Belorusskovo Gosudarstvennovo*, Universiteta imeni V. I. Lenina, Minsk, 253 p. (English translation available as Fisheries Research Board of Canada Translation Series No. 194, 1960, 239 p.)

WINBERG, G. G. 1972. Some interim results of Soviet IBP investigations on lakes. In: *Productivity Problems of Freshwaters*, Z. Kajak and A. Hillbricht-Ilkowska (eds.), Polish Scientific Publishers, Warszawa and Krakow, p. 368-381.

WINBERG, G. G., A. F. ALIMOV, G. A. GALKOVSKAYA, M. B. IVANOVA, L. A. KITITSYNA, N. M. KRYUTCHKOVA, A. V. MONAKOV, A. P. OSTAPENYA, G. A. PECHEN'-FINENKO, N. Y. SOKOLOVA, and T. V. KHLEVOVICH. 1973. The progress and state of research on the metabolism, growth, nutrition, and production of fresh-water invertebrate animals. Hydrobiological Journal, 9: 77-84.

WINBERG, G. G., V. S. IVLEV, T. P. PLATOVA, and L. L. ROSSOLIMNO. 1934. Procedures for determining organic matter. Experiment on a calorific evaluation of food supplies in a body of water. Trudy Limnologicheskogo Sta. Kosino, 18: 25-40. (in Russian)

WRIGHT, J. C. 1958. The limnology of Canyon Ferry Reservoir, I. Phytoplankton-zooplankton relationships in the euphotic zone during September and October, 1956. Limnology and Oceanography, 3: 150-159.

WRIGHT, J. C. 1965. The population dynamics and production of Daphnia in Canyon Ferry Reservoir, Montana. Limnology and Oceanography, 10: 583-591.

WROBLEWSKI, J. S. and J. J. O'BRIEN. 1976. A spatial model of phytoplankton patchiness. Marine Biology (Berlin), 35: 161-175.

WYCLIFFE, M. J. and S. V. JOB. 1977. Standard, routine and active oxygen consumption of a freshwater shrimp. Hydrobiologia, 54: 33-40.

YAKOVLEVA, N. A. 1969. The nutrition of the ostracod Herpetocypris reptans (Baird) (Fam. Cypridae). Hydrobiological Journal, 5: 15-18.

YAMAMURA, Y. 1934. Chemical study of food organisms for fish. Bulletin of the Japanese Society of Scientific Fisheries (Nihon Suisan Gakkai-Shi), 3: 357.

YESIPOVA, M. A. 1969. Growth and reproduction of Daphnia magna (Straus) and D. longispina (O. F. Muller) fed on detritus. Hydrobiological Journal, 5: 9-15.

ZAHORCAK, C. L. 1974. Formulation of a numbers-biomass model for simulating the dynamics of aquatic insect populations. Rensselaer Fresh Water Institute at Lake George, Eastern Deciduous Forest Biome IBP Memo Report 74-5, 42 p.

ZANKAI, N. P. and J. E. PONYI. 1976. Seasonal changes in the filtering rate of Eudiaptomus gracilis (G. O. Sars) in Lake Balaton. Annales Instituti Biologici (Tihany) Hungaricae Academiae Scientiarum, 43: 105-116.

ZEUTHEN, E. 1970. Rate of living as related to body size in organisms. Polskie Archiwum Hydrobiologii, 17: 21-30.

ZIMMERMAN, M. C., T. E. WISSING, and R. P. RUTTER. 1975. Bioenergetics of the burrowing mayfly *Hexagenia limbata* in a pond ecosystem. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen, 19: 3039-3049.

APPENDIX A: ELEMENTAL CARBON, NITROGEN, AND PHOSPHORUS COMPOSITION OF ZOOPLANKTON AND BENTHOS

1. Elemental carbon, nitrogen, and phosphorus composition (expressed as a percentage of the organism's dry weight) of various taxa of zooplankton and benthos is presented herein. The appendix abbreviations are defined as follows:

AFDW = ash-free dry weight

N = nitrogen

$\bar{X}$ = mean

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCE
PHYLUM: MOLLUSCA						
Mollusca	Marine	Range and $\bar{X}$ of 12 spp.		7.3-12.5; 9.9		Twelve references cited by Vinogradov (1953)
Mollusca	Marine	Range and $\bar{X}$ of 6 spp.			0.6-1.1; 0.8	Six references cited by Vinogradov (1953)
Mytilus sp.	Marine	January		5.7		Delff (1912) cited by Vinogradov (1953)
		April		10.1		
		July		8.2		
		October		9.3		
		December		8.2		
Crassostrea virginica	Marine			7.2		Tully (1936) cited by Vinogradov (1953)
Crassostrea gigas	Marine			7.9		
Ostrea lurida	Marine			7.9		
Physa fontinalis	Freshwater	$\bar{X}$ of specimens including shells	32.2			Salonen and Sarvala (1978)
Radix peregra	Freshwater		30.5			
Pisidium amnicum	Freshwater		22.5			
Lymnea stagnalis	Freshwater		25.6			
Anodonta piscinalis	Freshwater		27.5			
Sphaerium corneum	Freshwater		23.7			
Dreissena polymorpha	Freshwater	July (Early)	37.9	11.6		Stanczykowska and Lawacz (1976)
		July (Middle)	45.1	11.7		
		July (Late)	42.6	11.9		
		August	44.0	11.8		
		September	42.2	11.3		
PHYLUM: ANNELIDA						
Class: Polychaeta						
Polychaeta	Marine	Yearly range and $\bar{X}$	15.9-43.9; 29.9	4.4-11.2; 8.9	0.4-1.8; 1.0	Beers (1966)

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCE
Polychaeta	Marine	Range and $\bar{X}$ of 20 spp.		7.5-15.4; 11.1		Brand (1927) cited by Vinogradov (1953)
Nereis japonicus	Marine				0.4	Yamamura (1934) cited by Vinogradov (1953)
Nereis diversicolor	Marine			10.1		Delff (1912) cited by Vinogradov (1953)
Arenicola marina	Marine			9.7		
Arenicola marina	Marine			5.2		Weigelt (1891) cited by Vinogradov (1953)
Class: Hirudinea						
Erpobdella octoculata	Freshwater	N values converted from % AFDW (Table 1)	48.3	9.0		Salonen et al. (1976)
Class: Oligochaeta						
Limnodrilus sp.	Freshwater				0.4	Yamamura (1934) cited by Vinogradov (1953)
PHYLUM: ARTHROPODA Class: Insecta Order: Diptera						
Chironomus plumosus	Freshwater	N values converted from % AFDW (Table 1)	45.1	8.3		Salonen et al. (1976)
Chaoborus flavicans	Freshwater		47.3	8.8		
Order: Hemiptera						
Halobates sericeus	Marine		52.6			Omori (1969)
Notonecta glauca	Freshwater	N values converted from % AFDW (Table 1)	50.0	9.9		Salonen et al. (1976)
Order: Ephemeroptera						
Leptophlebia vespertina	Freshwater	N values converted from % AFDW (Table 1)	49.3	9.5		Salonen et al. (1976)

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCE
<u>Centroptilium luteolum</u>	Freshwater	N values converted from % AFDW (Table 1)	49.7	9.1		Salonen et al. (1976)
<u>Heptagenia fuscogrisea</u>	Freshwater		52.2	8.3		
Order: Odonata						
<u>Cordulia aenea</u>	Freshwater	N values converted from % AFDW (Table 1)	47.4	8.6		Salonen et al. (1976)
Order: Megaloptera						
<u>Sialis</u> sp.	Freshwater	N values converted from % AFDW (Table 1)	49.2	8.9		Salonen et al. (1976)
Order: Trichoptera						
Limnephilidae	Freshwater	N values converted from % AFDW (Table 1)	46.4	5.6		Salonen et al. (1976)
<u>Agrypnia obsoleta</u>	Freshwater		47.3	7.6		
<u>Stenopsychae griseipennis</u>	Freshwater		51.1	10.0	1.3	
Class: Crustacea						
Crustacea	Freshwater	Range and $\overline{X}$		3.6-12.7; 8.6		Seven references cited by Vinogradov (1953)
Crustacea	Marine	Hearly range and $\overline{X}$	32.9-41.7; 36.9	7.0-8.9; 7.8		Beers (1966)
Subclass: Malacostraca Order: Mysidacea						
Euphausids - mysids	Marine	Yearly range and $\overline{X}$	35.4-43.4; 40.7	9.4-10.5; 10-0	1.4-1.6; 1.5	Beers (1966)
<u>Siriella aequiremis</u>	Marine		42.4	11.0		Omori (1969)
<u>Mysis flexuosa</u>	Marine			11.9		Delff (1912) cited by Vinogradov (1953)
<u>Mysis relicta</u>	Marine	N values converted from % AFDW (Table 1)	50.0	9.1		Salonen et al. (1976)
<u>Neomysis rayii</u>	Marine			8.7-11.4		Jawed (1969)

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCES
Order: Isopoda						
Asellus aquaticus	Freshwater	N values converted from % AFDW (Table 1)	34.3	6.9		Salonen et al. (1976)
Asellus aquaticus	Freshwater		30.4	7.9		Meyer (1914) cited by Vinogradov (19[illegible])
Order: Amphipoda						
Parathemisto japonica	Marine		48.4	8.2		Omori (1969)
Platyscelus serratulus	Marine		25.9	4.4		
Cyphocaris challengeri	Marine		45.9	6.1		
Gammarus locusta	Freshwater	Table 234	38.1	7.8		Vinogradov (1953)
Gammarus locusta				9.7		Delff (1912) cited by Vinogradov (1953)
Gammarus pulex locusta	Freshwater			9.2		Geng (1925) cited by Vinogradov (1953)
Gammarus pulex	Freshwater		40.3	8.1		Meyer (1914) cited by Vinogradov (1953)
Pallasea quadrispinosa	Freshwater	N values converted from % AFDW (Table 1)	35.4	6.6		Salenon et al. (1976)
Gammaracanthus lacustris	Freshwater		41.7	7.6		
Gammaracanthus lacustris	Freshwater		44.9-49.5			Salonen and Sarvala (1978)
Order: Euphausiacea						
Euphausia krohnii	Marine		35.8			Curl (1962)
Euphausia pacifica	Marine	Calculated from author's regression equation of total N on dry weight		11.6-11.7		Jawed (1969)
Euphausia pacifica	Marine		38.7	10.7		Omori (1969)
Euphausia pacifica	Marine		39.6	10.1		
Tessarabrachion occulatus	Marine		47.2	10.0		

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCE
Order: Decapoda						
Lucifer reynaudii	Marine		41.1	9.3		Omori (1969)
Subclass: Brachiopoda Order: Cladocera						
Daphnia hyalina	Freshwater	Eggs	53.6	9.3	1.2	Baudoin and Ravera (1972)
		New born	42.8	9.7	1.6	
		Young 1	42.7	9.8	1.5	
		Young 2	43.5	10.7	1.3	
		Adult 1	44.2	9.6	1.2	
		Adult 2	44.5	9.6	1.1	
		Adult 3	42.8	9.1	1.0	
		Adult 4	42.0	8.8	1.2	
Daphnia pulex	Freshwater			10.3		Geng (1925) cited by Vinogradov (1953)
Daphnia pulex	Freshwater		37.9	8.0		Meyer (1914) cited by Vinogradov (1953)
Daphnia pulex	Freshwater			7.5		Birge and Juday (1922) cited by Vinogradov (1953)
Daphnia pulex	Freshwater		43.1	10.1		Vinogradov (1933) cited by Vinogradov (1953)
Daphnia pulex	Freshwater				1.3	Cowgill and Burns (1975)
Daphnia pulex	Freshwater			8.0		Knauthe (1907) cited by Vinogradov (1953)
Daphnia pulex	Freshwater				1.3-1.9	Rigler (1961b)
Daphnia magna	Freshwater				1.6	Cowgill and Burns (1975)

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCES
Daphnia magna	Freshwater	Calculated from Table 5			0.2	Rigler (1961b)
Daphnia magna	Freshwater	Juveniles	48.0			Bogatova et al. (1971)
		Adults	47.7			
Daphnia cristata	Freshwater	N values converted from % AFDW (Table 1)	50.7	6.8		Salonen et al. (1976)
Moina rectirostris	Freshwater				1.3-1.9	Gutel'mackher (1977)
Moina macrocopa	Freshwater	Calculated assuming 1 mg organic carbon = 10.98 calories	49.4			Bogatova et al. (1971)
Ceriodaphnia reticulata	Freshwater		48.8			
Holopedium gibberum	Freshwater			8.4		Birge and Juday (1922) cited by Vinogradov (1953)
Leptodora kindti	Freshwater			8.9		
Bosmina sp.	Freshwater			10.3		Knauthe (1907) cited by Vinogradov (1953)
Subclass: Copepoda						
Copepoda	Marine			9.2		Brandt cited by Vinogradov (1953)
Copepoda	Marine			9.2		Krey (1958)
Copepoda	Marine		35.6			Curl (1962)
Copepoda	Marine	January	43.2	10.1	0.9	Beers (1966)
		February	43.5	10.6	0.9	
		March	42.9	10.0	0.8	
		April	47.6	10.1	0.8	
		May	44.2	8.8	0.9	
		June	41.6	9.5	0.8	
		July	39.8	8.3	0.7	
		August	35.8	8.7	0.7	
		September	35.2	8.8	0.7	
		October	39.2	9.0	0.8	
		November	42.5	11.1	0.8	
		December	44.1	11.2	0.9	

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN			PHOSPHORUS			REFERENCES
Copepoda	Marine	Coastal Copepoda	47.0	12.6						Itoh (1973)
		Oceanic males and stage IV females	57.0	10.9						
		Oceanic females	57.0	7.5						
Calanus finmarchicus	Marine	Table 236	45.9	10.2						Vinogradov (1933) cited by Vinogradov (1953)
Calanus finmarchicus	Marine		47.7	10.1						Brandt and Raben (1919-1922) cited by Vinogradov (1953)
Calanus finmarchicus	Marine		39.8-41.7							Curl (1962)
Calanus finmarchicus	Marine			Female	Male	Juv. V	Female	Male	Juv. V	Butler et al. (1970)
		January		11.2	9.7	8.8	0.8	0.9	0.7	
		February		12.4	11.1					
		March		13.9			1.1			
		April		11.0	8.6		1.2		0.8	
		May		11.1					1.3	
		June		9.3	7.6		1.5	1.0	0.5	
		July		12.9	10.6		0.9	0.7	1.1	
		August		10.9	9.5		1.2	0.7		
		September		9.0			0.7	0.8	0.6	
		December		11.9			0.9		0.6	
		Seasonal $\bar{X}$		11.4	9.5		1.0	0.8	0.8	
Calanus finmarchicus	Marine		67.5	9.3			0.7			Reeve et al. (1970)
Calanus finmarchicus	Marine		67.2-67.5	8.4-10						Mayzaud (1976)
Calanus cristatus	Marine		60.9	6.3						Omori (1969)
Calanus cristatus	Marine		39.0	7.6						
Calanus cristatus	Marine		59.0	5.9						

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCES
Calanus cristatus	Marine	Female geographical variations (north to south)	60.9, 60.0, 61.8, 62.6, 62.7	7.5, 8.2, 6.8, 7.4, 8.6		Omori (1970)
		Male geographical variations (north to south)	55.9, 56.0, 56.1, 52.4, 54.1	10.5, 10.8, 11.2, 11.5, 11.9		
		Copepodite V geographical variations (north to south)	58.9, 58.3, 56.8 53.9, 50.3	8.3, 9.5, 10.3, 10.7, 10.6		
		Preservation methods:				
		Freezing	59.9	6.7		
		Drying	57.3	7.1		
		Formalin	55.5	7.5		
Calanus sinicus	Marine	Rinse Type / Volume				Omori (1978)
		Salt water 0.3 ml/mg	59.4	7.0		
		Distilled water 0.3 ml/mg	60.8	7.2		
		Ammonium formate 0.3 ml/mg	59.5	7.1		
		Salt water 3.3 ml/mg	56.5	5.5		
		Distilled water 3.3 ml/mg	58.2	6.1		
		Ammonium formate 3.3 ml/mg	56.7	6.0		
		Calculated from Table 1				
Calanus plumchrus	Marine		61.8	7.0		Omori (1969)
Calanus pacificus	Marine		46.1	11.2		
Calanus pacificus	Marine		58.4	7.8		
Calanus lighti	Marine		48.0	12.7		
Eucalanus bungii bungii	Marine		49.9	7.6		
Rhincalanus nasutus	Marine		52.2	9.9		
Limnocalanus sp.	Freshwater			7.2		Birge and Juday (1922) cited by Vinogradov (1953)
Limnocalanus macrurus	Freshwater	N values converted from % AFDW (Table 1)	62.1	6.0		Salonen et al. (1976)
Pareuchaeta norvegica	Marine	Eggs	63.6	5.8		Nemoto et al. (1976)
		Prespawning females	53.0	10.3		
		Spent females	50.6	10.0		

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCES
Pareuchaeta birostrata	Marine		58.4	7.0		Omori (1969)
Pareuchaeta sarsi	Marine		66.6	5.1		
Pleuromamma xiphias	Marine		47.5	13.1		
Pleuromamma xiphias	Marine	Rinse Type — Volume				Omori (1978)
		Salt water — 0.24 ml/mg	39.9	12.6		
		Distilled water — 0.24 ml/mg	40.6	12.7		
		Ammonium formate — 0.24 ml/mg	41.7	12.9		
		Calculated from Table 1				
Centropages sp.	Marine		38.5-38.7			Curl (1962)
Centropages hamatus	Marine		36.3			
Centropages typicus	Marine	$\bar{X}$ of 5 ages; Spring	37.2	9.1		Razouls (1977)
		Summer	42.3	9.3		
Centropages typicus	Marine	Male	28.0	7.1		Boucher et al. (1976)
		Female	26.3	6.3		
Lophogaster sp.	Marine		46.8			Curl (1962)
Temora stylifera	Marine	Fall	50.3			Razouls (1977)
		Winter	31.4			
		Copepodids II	42.3			
		III	39.3			
		IV	35.1			
		V	40.7			
Temora stylifera	Marine	Male	28.7	6.4		Boucher et al. (1976)
		Female	28.2	6.1		
Meganyctiphanes norvegicus	Marine		42.0			Curl (1962)
Metridea okhotensis	Marine		63.5	5.8		Omori (1969)
Disseta palumboi	Marine		51.0	10.7		
Candacia aetiopica	Marine		46.6	12.6		

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCE
Candacia columbiae	Marine		46.6	11.2		Omori (1969)
Pontellina plumata	Marine		44.3	12.2		
Labidocera actifrons	Marine		45.8	12.9		
Labidocera acuta	Marine				0.1	Krishnamurthy (1962)
Sapphirina nigromaculata	Marine				0.1	
Anomalocera patersoni	Marine			11.6		Delff (1912) cited by Vinogradov (1953)
Anomalocera patersoni	Marine		43.0	10.6		Brandt and Raben (1919-1922) cited by Vinogradov (1953)
Calamoecia lucasi	Freshwater	Seasonal range and $\bar{X}$ N value = protein/7.3	30.5-56.4; 43.6	6.5		Green (1976)
Eudiaptomus gracilis	Freshwater	N value calculated from % AFDW (Table 1)	49.8	9.6		Salonen et al. (1976)
Eudiaptomus gracilis	Freshwater				2.3	Cowgill and Burns (1975)
Diaptomus sp.	Freshwater			10.4		Birge and Juday (1922) cited by Vinogradov (1953)
Cyclops sp.	Freshwater			9.6		
Macropcyclops albidus	Freshwater	N value calculated from % AFDW (Table 1)	48.2	9.7		Salonen et al. (1976)
PHYLUM: ROTATORIA						
Branchionus calyciflorus	Freshwater	Calculated assuming 1 mg organic carbon = 10.98 calories	52.5			Bogatova et al. (1971)
PHYLUM: CHAETOGNATHA						
Chaetognatha	Marine	Yearly range and $\bar{X}$	21.0-34.3; 28.3	6.3-9.4; 7.8	0.5-0.7; 0.6	Beers (1966)

APPENDIX A (Continued)

TAXON	MARINE OR FRESHWATER	COMMENTS	CARBON	NITROGEN	PHOSPHORUS	REFERENCES
Sagitta elegans			38.2	10.9		Mayzaud (1976)
			40.7	12.8		
			42.7	14.0		
Sagitta elegans	Marine		39.0	15.1	0.8	Reeve et al. (1970)
Sagitta hispida	Marine	April		11.7		
		May		13.8-15.3		
		June		14.0		
		September		15.0-15.5		
		October		13.5		
		X		14.1		
Sagitta nagae	Marine	Rinse Type — Volume				Omori (1978)
		Salt water — 0.14 ml/mg	39.9	12.2		
		Distilled water — 0.14 ml/mg	41.0	12.6		
		Ammonium formate — 0.14 ml/mg	41.3	13.0		
		Salt water — 1.35 ml/mg	43.4	11.4		
		Distilled water — 1.35 ml/mg	46.5	11.6		
		Ammonium formate — 1.35 ml/mg	43.8	11.5		
		Data calculated from Table 1				
Zooplankton	Marine	Many medusae and ctenophora present Range and X	6-30; 14.3			Platt et al. (1969)
Zooplankton	Marine	Few medusae and other watery forms present	33.7			
Zooplankton	Marine	January		10.8	1.0	Haris and Riley (1956)
		January		10.0	0.9	
		April		9.3	0.7	
		April		8.4	0.7	
		July		9.8	1.1	
		November		5.6	0.6	
		X		8.9	0.8	

APPENDIX B: FILTERING RATES REPORTED FOR FRESHWATER ZOOPLANKTERS

1. Literature data are presented on the filtering rates of freshwater filter-feeding zooplankton herein. Columnar headings of the appendix are described as follows.

TAXON. The arrangement is by family then by species. Within a family, entries are in alphabetical order with general results listed at the end of the appropriate taxon. Some taxonomic corrections have been made to the original data.

LENGTH AND WEIGHT. Organism length in millimetres (mm) and weight in milligrams (mg) are presented, if known. Weights are expressed as either dry weight (mg dry) or as wet weight (mg wet). In some cases estimates of these values were made.

LIFE STAGE. The developmental stage of the organism is presented. For Copepods, development proceeds from nauplius to copepodie to adult stages.

TEST LOCALITY. Laboratory studies are indicated by "Lab." Field studies give the field locality by water body and state abbreviation if it is in the U. S., otherwise by water body and country.

TEST METHOD. The basic experimental method used to determine filtering or feeding rates is listed.

TEMPERATURE. The experimental temperature in degrees Celsius is given.

TYPE OF FOOD. The food type used during the experiments is given. Field studies using the entire available food spectrum are designated "natural assemblage."

RANGE OF FOOD CONCENTRATIONS TESTED. Values are presented as cells per millilitre (cells/ml) unless otherwise indicated. Field studies in which the food concentration was not actually measured have been designated as "in situ." Many values were approximated from figures presented by the author.

RANGE OF MEASURED FILTERING RATES. All values are expressed as millilitres per animal per day (ml/animal/day). We have converted values presented in other time frames to a daily basis. Many values were approximated from figures presented by the author. Mean filtering values are also indicated when known.

REFERENCE. The sources of the data are presented.

2. In addition to the definitions described above, the following abbreviations and symbols with their definitions have been used in the appendix.

a. The following abbreviations have been used to describe Life Stage:

A = Adult
AS = All sizes
AF = Adult female
F = Female, age not stated
AM = Adult male
M = Male, age not stated
CI-CVI = Copepodid stages 1 through VI

b. The following abbreviations have been used to describe the Test Method used:

32P = Radioactive tracer technique using phosphorus 32
14C = Radioactive tracer technique using carbon 14
CC = Cell count
CCC = Coulter counter
PL = Phytoplankton loss
OD = Oxygen depletion

c. The following abbreviations have been used to describe Temperature:

RT = Room temperature
AB = Ambient temperature
V = Variable temperature

d. Other abbreviations used include:

? = Unknown
$\bar{X}$ = Mean value
Ca. = Approximately
avg. max. = Average maximum value
C = Carbon
μ = Micron = 10^{-6} metres
μ^3 = Cubic microns
< = Less than
> = Greater than
NA = No significant filtering occurred

3. Appendix footnotes a through n are described below:

a. Filaments of Anabaena supp., Aphanizomenon flos-aquae, and Oscillatoria tenuis and/or Gleatilia sp.

b. Based on Ivanova (1970).

c. Based on Monakov and Sorokin (1960).

d. Ivanova (1970) says the temperature was 20°C, Monakov (1972) says it was 15°C.

e. Includes Diaptomus graciloides.

f. Includes Diaptomus gracilis.

g. Ivanova (1970).

h. It was assumed that the experiments were conducted at the same temperature that the algal cultures were incubated, but this is not stated by the authors.

i. Includes *Diaptomus oregonensis*.

j. Includes *Diaptomus*

k. Based on a summary of data from other authors.

l. *Daphnia cucullata* and *Daphnia hyalina*.

m. This entry may be based on the same data from Erman (1956) and reported by Pilarska (1977a) under the name *B. uriceolaris* although the measured filtering rates are slightly different.

n. Kryutchkova and Rybak (1974) say the food was *Scenedesmus* sp. at a concentration of 13.6×10^3 cells/ml.

TAXON	LENGTH (mm) and/or Weight (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
ORDER: CLADOCERA									
Family: Sididae									
Diaphanosoma brachyurum	0.0053 mg dry	?	?	?	?	Chlorella pyrenoidosa	6×10^{-5} mg dry wt/ml	10	Sushchenya (1958a,b) as reported by Jorgensen (1966)
Diaphanosoma brachyurum	?	?	L. Erken, Sweden	?	?	Nanoplankton	In situ	1	Nauwerck (1959) as reported by Jorgensen (1966)
Diaphanosoma brachyurum	?	A	Lab	?	?	?	?	15.6	Beljackaja-Potaenko (1964) as reported by Gliwicz (1970)
Diaphanosoma brachyurum	0.9-1.4 mm	AS	Heart L., Canada	^{32}P	AB	Natural assemblage plus yeast tracer	In situ	0-5.7 ($\bar{X}$=1.6)	Haney (1973)
Diaphanosoma brachyurum	?	AS	Drowned Bog L., Canada	^{32}P	AB	Natural assemblage plus yeast tracer	In situ	0.98-1.4 ($\bar{X}$=1.2)	Haney (1973)
Diaphanosoma brachyurum	?	?	Lab	^{14}C	V	Nanoplankton 33	Variable	ca. 0.45-2.73($\bar{X}$=1.33)	Gulati (1978)
Family: Holopedidae									
Holopedium gibberum	?	AS	Drowned Bog L., Canada	^{32}P	AB	Natural assemblage plus yeast tracer	In situ	7.5-12.4($\bar{X}$=9.4)	Haney (1973)
Holopedium gibberum	1.00 mm 0.074 mg wet	?	Lab	^{14}C	17.9-21.1	Natural assemblage from L. Krivove, USSR	Natural concentration	6.33-22.87	Gutel'mackher (1973)
Family: Chydoridae									
Chydorus sphaericus	?	A	Lab	?	?	?	?	9.8	Beljackaja-Potaenko (1964) as reported by Gliwicz (1970)
Chydorus sphaericus	0.1-0.2	AS	Heart L., Canada	^{32}P	AB	Natural assemblage plus yeast tracer	In situ	0.03-0.42($\bar{X}$=0.18)	Haney (1973)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Family: Bosmidae									
Bosmina longirostris	0.002 mg dry	?	?	?	?	Chlorella pyrenoidosa	$1.5x10^{-4}$ mg dry wt/ml	2.6	Sushchenya (1958a,b) as reported by Jorgensen (1966)
Bosmina longirostris	0.44 mm 0.013 mg wet	?	Lab	^{14}C	17.9-21.1	Natural assemblage from L. Krivoye, USSR	Natural concentration	1.61-4.93	Gutel'macher (1973)
Bosmina longirostris	0.4-0.6 mm	AS	Heart L., Canada	^{32}P	AB	Natural assemblage plus yeast tracer	In situ	0.009-0.9($\bar{X}$=0.44)	Haney (1973)
Bosmina longirostris	?	AS	Drowned Bog L., Canada	^{32}P	AB	Natural assemblage plus yeast tracer	In situ	0.45-0.46($\bar{X}$=0.46)	Haney (1973)
Bosmina longirostris	?	?	Lab	^{14}C	V	Nanoplankton 33	Variable	ca. 0.3-7.2($\bar{X}$=2.0)	Gulati (1978)
Bosmina longirostris	0.4 mm	A	Lab	^{32}P	RT	Natural assemblage[a] Lyngbya sp. mixed w/ Scenedesmus sp.	? Variable	0.6-1.0($\bar{X}$=0.8) 0.4	Webster and Peters (1978)
Bosmina coregoni	0.01 mg dry	?	?	?	?	Bacteria	$2x10^{-4}$ mg dry wt/ml	10	Manuilova (1958) as reported by Jorgensen (1966)
Bosmina coregoni	?	?	L. Erken, Sweden	?	?	Nanoplankton	In situ	1	Nauwerck (1959) as reported by Jorgensen (1966)
Bosmina coregoni	?	A	Lab	?	?	?	?	40.1	Beliackaja-Potaenko (1964) as reported by Gliwicz (1970)
Family: Daphnidae									
Simocephalus vetulus	0.09 mg dry	?	?	?	?	Chlorella pyrenoidosa	$5x10^{-5}$ mg dry wt/ml	133	Sushchenya (1958a,b) as reported by Jorgensen (1966)
Simocephalus vetulus	0.012 mg dry	?	?	?	?	Bacteria	$2x10^{-4}$ mg dry wt/ml	26	Manuilova (1958) as reported Jorgensen (1966)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Simocephalus vetulus	0.7-2.5 mm 0.007-0.127 mg dry	?	Lab	?	22	Chlorella sp.	$1.8x10^6$-$4.5x10^6$	0.13-18.0	Ivanova and Klekowski (1972)
Simocephalus vetulus	1.8 mm	A	Lab	^{32}P	RT	Natural assemblage[a] Lyngbya sp. mixed w/ Scenedesmus sp.	? Variable	21-48($\bar{X}$-33) 3.9	Webster and Peters (1978)
Ceriodaphnia pulchella	?	?	Lab	^{14}C	V	Nanoplankton 33	Variable	ca. 0.6-3.0 ($\bar{X}$=1.82)	Gulati (1978)
Ceriodaphnia quadrangula	0.7-0.9 mm	AS	Heart L., Canada	^{32}P	AB	Natural assemblage	In situ	0.4-7.7($\bar{X}$=4.6)	Haney (1973)
Ceriodaphnia quadrangula	0.7 mm	A	Lab	^{32}P	RT	Natural assemblage[a] Lyngbya sp. mixed w/ Scenedesmus sp.	? Variable	4.8($\bar{X}$=5.7) 1.1	Webster and Peters (1978)
Ceriodaphnia reticulata	0.8 mm	?	Pond water taken to lab, Michigan	^{14}C	25	Natural assemblage	$1.4x10^3$-$5.9x10^5$ particles/ml	0.38-5.95	O'Brien and DeNovelles (1974)
Ceriodaphnia reticulata	0.00003 mg	?	Lab	^{14}C	15-27	Chlorella vulgaris	$1.0x10^5$	0.79-2.06	Gophen (1976)
Daphnia ambigua	1.2 mm	A	Lab	^{32}P	RT	Natural assemblage[a] Lyngbya sp. mixed w/ Scenedesmus sp.	? Variable	4-13($\bar{X}$=8.2) 2.2	Webster and Peters (1978)
Daphnia carinata	0.070 mg dry	A	Lab	CC	27	Escherichia coli and Flavobacterium sp.	$2.6x10^4$-$3.1x10^8$	6.2-21.6	Tezuka (1971)
Daphnia cucullata	0.0055 mg dry	?	?	?	?	Bacteria	$2x10^{-4}$ mg dry wt/ml	14	Manuilova (1958) as reported by Jorgensen (1966)
Daphnia cucullata	?	A	Lab	?	?	?	?	43	Beljackaja-Potaenko (1964) as reported by Gilwicz (1970)
Daphnia galeata mendotae	1.30-1.53 mm	?	Heart L., Canada water taken to lab	^{32}P	AB	Natural assemblage	In situ	3.7	Burns and Rigler (1967)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Daphnia galeata mendotae	ca. 0.8-2.2 mm ca. 0.006-0.095 mg dry	AS	Lab	^{32}P	15-25	Rhodotorula glutinus	$2.5x10^4$	ca. 2.3-45.4	Burns (1969b)
Daphnia galeata	1.5-1.7 mm	AS	Heart L., Canada	^{32}P	AB	Natural assemblage	*In situ*	1.9-20.8($\bar{X}$=6.4)	Haney (1973)
Daphnia galeata	0.91-1.29 mm	?	L. George, NY *water taken to lab*	^{14}C	19-24	Natural assemblage	In situ	2.6-11.0	Bogdan and McNaught (1975)
Daphnia galeata	1.4 mm	AS	Wintergreen L., MI	^{32}P	AB	Natural assemblage	In situ	0.8-5.4	Haney and Hall (1975)
Daphnia galeata	1.1-2.1 mm	AS	Lawrence L., MI	^{32}P	AB	Natural assemblage	In situ	6.2-20.3	Haney and Hall (1975)
Daphnia galeata	?	AS	Little Mill L., MI	^{32}P	AB	Natural assemblage	In situ	2.5-16.2	Haney and Hall (1975)
Daphnia galeata	1.3-1.7 mm	A	Three Lakes, MI	^{32}P	AB	Natural assemblage	In situ	47 avg. max.	Haney and Hall (1975)
Daphnia longispina	0.0083 mg dry	?	?	.	?	Bacteria	$2x10^{-4}$ mg dry wt/ml	23	Manuilova (1958) *as reported* by Jorgensen (1966)
Daphnia longispina hyalina	?	?	L. Erken, Sweden water taken to lab	^{14}C	?	Nanoplankton	In situ	0.5-4.6($\bar{X}$=2.3)	Nauwerck (1963) *as reported* by Burns and Rigler (1967)
Daphnia longispina	0.12 mg wet[b]	?	Lab[c]	^{14}C[c]	15[d]	Chlorococcum sp. Bacteria	$5.5x10^3$-$92x10^3$ $2.4x10^6$-$79x10^6$	2.9-17.2 0.2-5.4	Monakov and *Sorokin* (1961) *as* reported by Monakov (1972)
Daphnia longispina	0.0116 mg dry	?	?	^{14}C	?	?	$2.2x10^{-3}$ mg dry wt/ml	4.8	Shushkina and Pecen' (1964) as reported by Ivanova (1970)
Daphnia longispina	0.011 mg dry	A	Lab	CC	20	Mixed bacteria	$3.3x10^4$-$4.4x10^4$	1.7.19	Tezuka (1971)
Daphnia magna	?	?	?	?	?	Chlorella pyrenoidosa	$7x10^{-2}$ mg dry wt/ml	8	Lefevre (1942) as reported by Jorgensen (1966)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Daphnia magna	2.5-2.9 mm 0.095-0.135 mg dry	AF	Lab	CC	18-20	Chlorella vulgaris Navicula pelliculosa Scenedesmus quadricauda	$5x10^4$-$6x10^5$ $5x10^4$-$5x10^5$ $4x10^4$-$4.6x10^5$	4.4-79.6 10.6-48.5 8.3-25.7	Ryther (1954)
Daphnia magna	0.13 mg dry	A	?	?	?	Chlorella pyrenoidosa	$2x10^{-3}$ mg dry wt/ml	7	Sushchenya (1958a,b) as reported by Jorgensen (1966)
Daphnia magna	0.23-0.27 mg dry	AF	Lab	^{32}P	?	Saccharomyces cerevisiae	ca. $5x10^3$-$9.6x10^5$	ca. 7-96	Rigler (1961a)
Daphnia magna	1.25-3.54 mm 0.01-0.44 mg dry	AF	Lab	^{32}P	20	Chlorella vulgaris	$1x10^4$-$2x10^5$	ca. 10.8-104.4	McMahon (1965)
	2.8-3.3 mm 0.22-0.34 mg dry				5-35	Saccharomyces cerevisiae	$1x10^4$-$6x10^5$	ca. 0.9-143.3	
Daphnia magna	2.8-3.3 mm 0.22-0.34 mg dry	AF	Lab	^{32}P	20	Escherichia coli Chlorella vulgaris Saccharomyces cerevisiae Tetrahymena pyriformis	$5x10^5$-$1x10^7$ $1x10^4$-$1x10^6$ ca. $2x10^4$-$1x10^6$ ca. $1x10^2$-$3x10^3$	ca. 13.4-81.6 ca. 12.6-67.2 ca. 5.2-24.0 ca. 20-84	McMahon and Rigler (1965)
Daphnia magna	ca. 1.3-3.3 ca. 0.023-0.28 mg dry	AS	Lab	^{32}P	15-25	Rhodotorula glutinus	$2.5x10^4$	ca. 6.5-141.3	Burns (1969b)
Daphnia magna	0.112-0.164 mg dry	?	Lab	CLC	18	Chlorella vulgaris	ca. $0.6x10^3$ 3- $22x10^3$ 3/ml	ca. 36-98	Kersting and Leeuw-Leegwater (1976)
Daphnia middendorffiana	1.3-2.6 mm	A	Lab	^{14}C	5.2-11.5	Natural assemblage w/ Chlamydomonas reinhardti added as a tracer	ca. $2.6x10^3$-$83x10^3$	ca. 3-177	Chisholm, Stross, and Nobbs (1975)
Daphnia parvula	0.7-1.2	AS	Heart L., Canada	^{32}P	AB	Natural assemblage	In situ	2.5-5.2($\bar{X}$-3.8)	Haney (1973)
Daphnia parvula	?	AS	Drowned Bog L., Canada	^{32}P	AB	Natural assemblage	In situ	1.6	Haney (1973)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (^oC)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Daphnia pulex	0.68-1.86 mm 0.003-0.03 mg dry	F	Lab	CC	20	Chlamydomanas reinhardti	$25x10^3$-$100x10^3$	0.8-5.5	Richman (1958)
Daphnia pulex	0.32 mg wet	?	Lab	?	15[d]	Chlorococcum sp.	$3x10^{-7}$-$1.4x10^{-5}$ mg dry wt/ml[e]	3-64[g]	Monakov and Sorkin (1961) as reported by Monakov (1972)
Daphnia pulex	Variable	A	Lab	CC	21[h]	Chlamydomonas reinhardti	$2x10^5$-$5x10^5$	0.5-6.2	Stross, et. al. (1965)
Daphnia pulex	ca. 0.6-1.5 mm ca. 0.003-0.034 mg dry	AS	Lab	^{32}P	15-25	Rhodotorula glutinus	$2.5x10^4$	ca. 1.2-15.5	Burns (1969b)
Daphnia pulex obtusa	ca. 0.8-3.0 mm ca. 0.027-1.40 mg dry	AS	Lab	CC	22.2	Scenedesmus abandans	$6.8x10^5$-$20.4x10^5$	32.3-45.5	Kryutchkova and Sladecek (1969)
Daphnia pulex	0.036 mg dry	A	Lab	CC	25	Bacteria mixed w/ Microcystis aeruginosa Escherichi coli	$3.1x10^4$-$2.6x10^5$ 40-$1.3x10^4$	4.8-6.2 5.5-14.2	Tezuka (1971)
Daphnia pulex	0.7-2.8 mm 0.003-0.056 mg dry	AF	Lab	CC	22	Chlamydomonas reinhardti	$3x10^4$	ca. 1-200	Buikema (1973)
Daphnia pulex	2.0 mm	AF	Lab	^{32}P	20	Rhodotorula sp. with and without seston	Variable	ca. 6-37	Crowley (1973)
Daphnia pulex	0.7-3.5 mm	F	Lab	^{14}C	15	Scenedesmus cutus	ca. $1x10^{-4}$-$3.3x10^{-3}$ C/ml	ca. 2.2-52.3	Geller (1975)
Daphnia pulex	0.8-2.4 mm	AS	Little Mill L., MI	^{32}P	AB	Natural assemblage	In situ	2.8-25.6	Haney and Hall (1975)
Daphnia pulex	1.5-2.7 mm	AS	Three Lakes, MI	^{32}P	AB	Natural assemblage	In situ	2.5-125.0	Haney and Hall (1975)
Daphnia pulex	?	A	Lab	^{32}P	12-18	Chlamydomonas reinhardti	$5x10^5$	3.1-9.1	Starkweather (1975)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Daphnia pulex	1.8 mm	AF	Lab	CC	20	Ankistrodesmus sp.	ca. 1 x 10^4	1.3	Hayward and Gallup (1976)
Daphnia pulex	1.9 mm	A	Lab	^{32}P	RT	Natural assemblage[a] Lyngbya sp. mixed w/ Scenedesmus sp.	? Variable	20.45($\bar{X}$=35) 9.6	Webster and Peters (1978)
Daphnia rosea	0.64-1.85 mm	AS	Lab	^{32}P	20	Rhodotorula glutinis	2.5x10^4-5x10^5	1.9-42.0	Burns and Rigler (1967)
Daphnia rosea	1.15-1.38 mm	?	Heart L., Canada water taken to lab	^{32}P	AB	Natural assemblage	In situ	7.6	Burns and Rigler (1967)
Daphnia rosea	1.65-1.85 mm	A	Lab	^{32}P	5-25	Chlamydomonas sp.	2.5x10^4	ca. 0.9-1.4	Kibby (1971a)
Daphnia rosea	1.3-1.6 mm	AS	Heart L., Canada	^{32}P	AB	Natural assemblage	In situ	1.7-20.8($\bar{X}$=5.5)	Haney (1973)
Daphnia schodleri	ca. 0.8-2.5 mm ca. 0.006-0.13 mg dry	AS	Lab	^{32}P	15-25	Rhodotorula glutinis	2.5x10^4	ca. 2.3-64.9	Burns (1969b)
Daphnia schodleri	1.2-2.4 mm 1.5-2.0 mm	AF, AM AF	Lab	CC	5-30	Ankistrodesmus sp. Chlamydomonas sp. Frustulia sp. Anabaena sp. Aphanizomenon sp.	ca. 1.7x10^3-1.2x10^4 ca. 3 x 10^4 ca. 8.9x10^3 ? ?	ca. 3.6-49.2 ca. 24 max. ca. 26 max. NS NS	Hayward and Gallup (1976)
Daphnia spp.[l]	?	?	Lab	^{14}C	V	Nanoplankton 33	Variable	ca. 1.3-9.1($\bar{X}$=3.8)	Gulati (1978)
Mixed community but primarily Daphnia spp.	0.037 mg dry	AS	Canyon Ferry Reservoir, MT	PL	AB	Natural assemblage	3.8x10^{-4}-9.0x10^{-4} mg dry wt/ml	ca. 39	Wright (1958)
Generalized cladoceran[k]	0.001-0.01 mg dry	?	?	OD	?	Variable	2x10^{-4}-4x10^{-2} mg dry wt/ml	0.1-11.5	Ivanova (1970)
ORDER: COPEPODA Family: Diaptomidae									
Diaptomus gracilis[e]	0.011 mg dry	?	?	?	?	Chlorococcus sp.	?	4.1	Malovitskaya and Sorokin (1961) as reported by Jorgensen (1966)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Diaptomus gracilis	?	?	?	?	?	Melosira sp. and Asterionella sp.	$24.2x10^3$-$198.0x10^3$	0.68-1.96	Malovitskaya and Sorokin (1961) as reported by Kryutchkova and Ryback (1974)
Diaptomus gracilis	?	F, M	Queen Elizabeth II Reservoir, G. B., water taken to lab	^{14}C	4-14.5	Natural assemblage	$2x10^2$-$7.3x10^3$	0.83-2.40	Kibby (1971b)
Diaptomus gracilis	?	F, M	King George IV Reservoir, G.B., water taken to lab	^{14}C	7-15	Natural assemblage	$9.7x10^2$-$8.2x10^3$	1.09-1.97	Kibby (1971b)
Diaptomus gracilis	?	F, M	Lab	^{14}C	5-20 12-20 20	Chlorella sp. Scenedesmus sp. Diplosphaeria sp. Ankistrodesmus sp. Carteria sp. Nitzchia sp. Pediastrum sp. Haematococcus sp. Bacteria	$3x10^4$	0.61.2.40 0.94-1.32 1.76-2.54 1.61-2.45 0.87 1.96 0.02 2.16 0.19	Kibby (1971b)
Diaptomus gracilis	?	AM, AF	L. Balaton, Hungary	^{14}C	AB	Natural assemblage	0.42-1.90 gC/ml	0.01-3.27	Zankai and Ponyi (1976)
Diaptomus gracilis	?	?	Lab	^{14}C	V	Nanoplankton 33	Variable	ca. 1.8-20.0($\bar{x}$-5.6)	Gulati (1978)
Diaptomus graciloides	0.01 mg dry	?	L. Erken, Sweden	?	AB	Natural assemblage	?	0.3-3	Nauwerck (1959 as reported by Jorgensen (1966) and Kryutchkova and Ryback (1974)
Diaptomus graciloides[f]	0.011 mg dry	?	?	?	?	Chlorococcus sp.[n]	$13.6x10^3$ [n]	4.1	Malovitskaya and Sorokin (1961) as reported by Jorgensen (1966)
Diaptomus graciloides	?	A	Lab	?	?	?	?	35.0	Beljackaja-Potaenko (1964) as reported by Gliwicz (1970)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCES
Diaptomus graciloides	1.04 mm 0.010 mg wet	?	Lab	^{14}C	17.9-21.1	Natural assemblage from L. Krivoye, USSR	In situ	0.41-1.00	Gutel'mackher (1973)
Diaptomus graciloides	0.253-0.959 mm	AS	Lab	?	17.5-24.5	Chlamydomonas eugametos	$1x10^3$ - $12x10^3$	2.4-3.4	Kryutchkova and Ryback (1974)
Diaptomus leptopus	?	?	?	?	?	Chlamydomonas sp.	$50x10^3$	1.0-1.8	Schindler and Comita (1966) as reported by Kryutchkova and Ryback (1974)
Diaptomus minutus	0.87-0.97 mm $\bar{X}$=0.003 mg dry	?	?	?	?	Plankton	?	0.5-2.9	Bogdan and McNaught (1975)
Diaptomus pallidus	?	AF, AM	Little Mill L.,MI	^{32}P	AB	Natural assemblage	In situ	0.60-1.54	Haney and Hall (1975)
Diaptomus pallidus[i]	?	A	Three Lakes, MI	^{32}P	AB	Natural assemblage	In situ	0.26-1.66($\bar{X}$=0.83)	Haney and Hall (1975)
Diaptomus oregonensis	0.011 mg dry	AF	L. Winnebago, WI	^{14}C	22-23	Nanoplankton (90% Chlorella sp.)	In situ (30-$1x10^5$)	0.058-0.074	Richman (1964)
Diaptomus oregonensis	0.011 mg dry	AF	Lab	^{14}C	22-23	Nanoplankton	30-$1x10^5$	0.097-0.139	Richman (1964)
Diaptomus oregonensis	?	?	Lab	^{14}C	20?	Chlamydomonas reinhardti Chlorella vulgaris	$1.5x10^3$-$5x10^5$ $2.5x10^3$-$4.1x10^5$	ca. 0.1-3.5 ca. 0.1-3.0	Richman (1966)
Diaptomus oregonensis	?	CV, AF	Marion L., B. C., water taken to lab	CLC	18	Natural assemblage 70	175-7,461	1.49-12.90	McQueen (1970)
Diaptomus oregonensis	?	CV, AF	Lab	CLC	18	Chromulina scherfellii Chlorella pyrenoidosa Ochronomas sp. Chlamydomonas sp. Chryptomonas sp. Navicula spp.	2,100 20,700 20,000 23,000 19,700 247-22,675	1.50 1.33 1.68 1.43 1.07 0 2.07	McQueen (1970)
Diaptomus oregonensis	1.0-1.4 mm	AS	Heart L. Canada	^{32}P	A	Natural assemblage	In situ	0-1.4($\bar{X}$=0.48)	Haney (1973)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (°C)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCE
Diaptomus oregonensis	?	AS	Drowned Bog L., Canada	^{32}P	A	Natural assemblage	In situ	2.1-2.2	Haney (1973)
Diaptomus oregonensis[j]	?	AS	Three Lakes, MI	^{32}P	A	Natural assemblage	In situ	0.26-1.66($\bar{X}$-0.83)	Haney and Hall (1975)
Diaptomus siciloides	?	F	Lab	CLC	10-20	Pandorina morum or Chlamydomonas sp.	?	1-2	Comita (1964)
Family: Centropagidae									
Boeckella delicata	0.0101 mg dry for AF, AM	AS	L. Koutu, New Zealand, water taken to lab	^{14}C	20?	Natural assemblage w/ yeast tracer	$1.2x10^5$	0.043-0.419	Green (1975)
Calamoecia lucasi	ca. 0.00015-0.00123 mg dry	AS	Lab	^{14}C	20	Saccharomyces cerivisae	$1x10^3$-$6x10^4$	ca. 0.01-1.43	Green (1975)
Calamoecia lucasi	?	AS	Campus Pond, New Zealand, water taken to lab	^{14}C	20?	Natural assemblage w/ yeast tracer	?	0.006-0.753	Green (1975)
Calamoecia lucasi	?	F, M	L. Koutu, New Zealand, water taken to lab	^{14}C	20?	Natural assemblage w/ yeast tracer	$1.2x10^6$	0.506-0.549	Green (1975)
Limnocalanus macrurus	?	CI-CVI, A	Lab	^{32}P?	0.2	Scenedesmus sp. or Chlamydomonas sp.	Natural range found in Char and Resolute Lakes, Canada	0.42-3.05	Kibby and Rigler (1973)
PHYLUM: ROTATORIA Family: Branchionidae									
Brachionus calyciflorus	?	?	?	?	20	Variable	?	0.0312-0.319	Erman (1962) as reported by Doohan (1973) and Pourriot (1977)

APPENDIX B (Continued)

TAXON	LENGTH (mm) and/or WEIGHT (mg)	LIFE STAGE	TEST LOCALITY	TEST METHOD	TEMP. (^oC)	TYPE OF FOOD	RANGE OF FOOD CONCENTRATIONS TESTED (cells/ml)	RANGE OF MEASURED FILTERING RATES (ml/animal/day)	REFERENCE
Brachionus calyciflorus	?	?	?	CC	19-20	Scenedesmus obliguus	$5x10^5$	ca. 0.024	Galkovskaya (1963)
Brachionus calyciflorus	?	?	?	?	?	?	?	0.576	Galkovskaya (1965) as reported by Pilarska (1977a)
Brachionus calyciflorus	?	?	?	?	?	Chlorella pyrenoidosa	$5x10^5$	0.0142-0.087	Halbach and Halbach-Keup (1974) as reported by Pilarska (1977a)
Brachionus calyciflorus	?	A	Lab	^{32}P	?	Euglena gracilis	$5x10^4$	0.024-0.025	Starkweather and Gilbert (1977)
Brachionus pilcatilis	?	?	?	?	?	Synechococcus sp.	$8x10^6$	0.073	Ito (1955) as reported by Doohan (1973)
Brachionus pilcatilis	0.000158 mg for adults	?	Lab	^{14}C	20	Dunaliella salina	$5.9x10^5$-$1.44x10^6$	0.015-0.036	Doohan (1973)
Brachionus rubens	?	?	?	?	?	?	$5x10^5$	ca. 0.024	Erman (1956) as reported by Doohan (1973)
Brachionus rubens[m]	?	?	?	?	20	Scenedesmus acuminatus	$1x10^4$ coenobia	0.106 maximum	Erman (1956) as reported by Pourriot (1977)
Brachionus rubens	0.00013 mg dry	AF	Lab	^{14}C	20	Chlorella vulgaris	$1.2x10^4$-$1.0x10^7$	ca. 0.002-0.270	Pilarska (1977a)
Brachionus arceolaris	?	?	?	?	?	Scenedesmus acuminatus	$1x10^4$ coenobia	0.015-0.120	Erman (1956) as reported by Pilarska (1977a)
Keratella cochlearis	?	A	Lab	?	?	?	?	0.168	Erman (1956) as reported by Gliwicz (1970)
Kellicottia sp.	?	?	Drowned Bog L., Canada	^{32}P	AB	Natural assemblage	In situ	0.007	Haney (1973)
Family: Philodinavidae									
Philodina roseola	?	?	?	?	?	?	?	0.024	Erman (1956) as reported by Pourriot (1977)

APPENDIX C: ZOOPLANKTON AND BENTHOS ASSIMILATION EFFICIENCIES

Definitions of Abbreviations and Symbols Used in Appendix C

A	assimilation
G	consumption
A/G	assimilation efficiency (mg C/mg C/day) x 100
E	excretion
F	egestion
R	respiration
P	total production
Pg	production as growth
Pev	production as exuvia
Pr	production as reproduction
Ps	production as secretion
^{14}C	carbon 14 radioisotope
$^{14}CO_2$	labeled carbon dioxide respired (may be used to represent excretion)
cpm	counts per minute (radioactivity)
VS	varied seasonally
°C	degrees Centigrade
ca	approximately
ml	millilitre
mg	milligram
cm^2	square centimeter
ℓ	litre
@	at
?	unknown or could not be determined from data
$\bar{X}$	mean value
%	percent
<	less than
AFDW	ash-free dry weight

Definitions of Experimental Methods Listed in Appendix C

Method 1. A/G - (G -F)/G

Method 2. A/G = (^{14}HC in body + $^{14}CO_2$)/(^{14}C in body + $^{14}CO_2$ + F)

Method 3. A/G = $^{14}CO_2$/($^{14}CO_2$ + F)

Method 4. A/G = (PG + Pr + R)/G

Method 5. Radiosotope (type not specified)

Method 6. A/G = (G - F - E)/G

Method 7. A.G = (PG + R)/G

Method 8. A/G = (Pg + Pev + Ps + R)/G

Method 9. A/G = (^{14}C ingested - F)/^{14}C ingested

Method 10. A/G = (Pg + Pev + R)/G

Method 11. A/G = ^{14}C in body/(^{14}C in body + F + E)

Method 12. A/G = ((calories/cpm ^{14}C)(^{14}C/individual))/((^{14}C consumed) (calories/cpm ^{14}C))

Method 13. A/G = ^{14}C in body/^{14}C consumed

Method 14. A/G = ^{32}P in body/^{32}P consumed

Method 15. A/G = (^{14}C in body + $^{14}CO_2$)/^{14}C consumed

Method 16. Ash-ratio (see text for details)

Method 17. A.G = (^{32}P in body and eggs)/(^{32}P in body + F)

Method 18. A.G = (Pr + R)/G

Method 19. A/G = (^{14}C consumed - F - $^{14}CO_2$)/^{14}C consumed

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation efficiency (%)	Reference
PHYLUM: MOLLUSCA Class: Pelecypoda						
Scrobiculari plana	0.5-22.5	organic sediment	1	Based on field population energy budget	60.6	Hughes (1970)
Dreissena polymorpha	?	bacteria @ 5×10^6 cells/ml	2	Based on a carbon budget for an individual; A/G is inversely proportional to age	44.1-57.8($\bar{X}$=49.4)	Sorokin (1969)
Class: Gastropoda						
Ancylus fluviatilis	7-25	algae	1	Based on a field population carbon budget	49.4-54.6	Streit (1976)
Bittium varium	?	sterilized detritus unsterilized detritus	3	Based on a carbon budget for an individual; three-day experimental period	46.3 48.6	Adams and Angelovic (1970)
Littorina irrorata	?	detritus	?		45.0	Odum and Smalley (1959) as cited by Hughes (1970)
Lymnaea palustris	14.9-15.2	aufwuchs	1	Based on a carbon budget for an individual	44.0-71.9($\bar{X}$=59.9)	Hunter (1975)
Valvata pulchella	?	dead *Scenedesmus* sp.	2	Based on a carbon budget for an individual	14	Monakov and Sorokin (1972)
PHYLUM: NEMATODA Class: Adenophorea						
Plectus palustris	20	bacteria @ 6.7-13.5 calories/ml	4	Based on an energy budget for an individual; ^{14}C used to determine C	12	Duncan et al. (1974)
PHYLUM: ANNELIDA Class: Oligochaeta						
Tubifex tubifex	16-18	sediment	1	Based on an energy budget for an individual	47.1-60.0($\bar{X}$=50.4)	Ivlev (1939)

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Class: Polychaeta						
Neanthes virens	13-17	*Nephtys hombergii*	1	Based on an energy budget for an individual	82.1-88.9	Kay and Brafield (1972)
PHYLUM: ARTHROPODA Class: Insecta Order: Diptera						
Hedriodiscus truquii	35-41	algae	1	Based on an energy budget for an individual; instars I-III	56.0-67.5	Sweeney and Schnack (1977)
Simulium sp.	?	?	5		9.4-65.7	McCullough (1975) as cited by Sweeney and Schnack (1977)
Tipula abdominalis	?	?	5		33	Vannote (1969) as cited by Sweeney and Schnack (1977)
Order: Ephemeroptera						
Hexagenia limbata	19.5-26.5	surface sediment	6	Based on an energy budget for an individual	62-72 ($\bar{X}$=68)	Zimmerman et al. (1975)
Stenonema pulchellum	20	*Navicula minima*	7	Based on an energy budget for an individual	46.4-56.9($\bar{X}$=53.1)	Trama (1972)
Tricorythodes minutes	?	?	5		6.4-55.2	McCullough (1975) as cited by Sweeney and Schnack (1977)
Order: Tricoptera						
Neophylax concinnus	?	?	?		20.6-54.7	Sedell (1971) as cited by Sweeney and Schnack (1977)
Cheumatopsyche sp.	?	?	5		45.9-49.1	McCullough (1975) as cited by Sweeney and Schnack (1977)

APPENDIX C (Continued)

Taxon	Temperature (^{o}C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Glossoma nigrior	VS	algae	7	Based on a field population energy		Cummins (1975)
				budget; winter	13.6-20.6	
				summer	31.5-32.3	
Potamophylax cingulatus	VS	leaf litter detritus	8	Based on a field population energy		Otto (1975)
				budget; October	29	
				November	28	
				December	27	
				January	17	
				February	10	
				March	10	
				April	11	
				May	19	
				June	25	
				July	26	
Order: Megaloptera						
Corydalus cornutus		chironomids		Mean of 5 acclimation groups	85.8	Brown (1978)
Order: Odonata						
Pyrrhosoma nymphula	4	Daphnia sp.	1	Based on a dry weight biomass budget	85.2	Lawton (1970)
	10	Daphnia sp.		for an individual	86.2	
	15	Daphnia sp.			81.2-87.2	
	15	Chironomidae			84.0	
	15	Asellus sp.			76.9	
	15	Cloeon sp.			90.6	
	15	Daphnia sp.	1	Based on an energy budget for an	86.2-86.8	Lawton (1970)
	15	Chironomidae		individual	86.8	
	15	Asellus sp.			82.8	
	15	Cloeon sp.			91.3	
Lestes sponsa	20	Daphnia magna and Tubifex tubifex	7	Based on an energy budget for an individual	35-46	Fischer (1972)
Order: Plecoptera						
Acroneuria californica	17	Hydropsyche and Simulium sp.	1	Based on an energy budget for an	80.8	Heiman and Knight (1975)
	18	Simulium sp.		individual; A/G miscalculated in	89.2-94.6	
	18	Hydropsyche sp.		Table 2 of reference	86.8	

APPENDIX C (Continued)

Taxon	Temperature (^{o}C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Pteronarcys scotti	5-10	leaves	1	Based on an energy budget for an individual	8.5-15.9($\bar{X}$=10.6)	McDiffett (1970)
Class: Crustacea Subclass: Malacostraca Order: Mysidacea						
Mysis stenolepsis	?	hay-detritus cellulose	9	Based on a carbon budget for an individual	20-35 35-50	Foulds and Mann (1978)
Neomysis mirabilis	19.9-21.1	algae @ 0.01-0.1 mg dry weight/l	2	Based on a carbon budget for an individual	85	Pechen'-Finenko (1977)
Order: Euphausiacea						
Euphausia pacifica	ca. 10	Three marine algal species and nauplii of Artemia sp.	5 and 10	Based on a carbon budget for an individual	66-95 ($\bar{X}$ = 84)	Lasker (1966)
Order: Decapoda						
Palaemonetes pugio	26	Nitzschia closterium	1	Based on a carbon budget for an individual	78-79	Johannes and Satomi (1967)
Palaemonetes pugio	?	detritus detritus and bacteria	3	Based on a carbon budget for an individual; three-day experimental period	28.3-72.7 82.0-90.9	Adams and Angelovic (1970)
Order: Isopoda						
Asellus aquaticus	10	slightly decayed alder leaves	1	Based on an energy budget for an individual:		Prus (1971)
				nonovigerous females	40.8	
				ovigerous females	43.6	
				male	33.2	
				density: 1/12.6 cm^2	30.3	
				5/33.2 cm^2	35.2	
				10/33.2 cm^2	40.2	
				20/33.2 cm^2	40.2	
				annual mean	30.0	
			16		55.8	

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Order: Amphipoda						
Calliopius laeviusculus	12	Calanus sp.	1	Based on a carbon budget for an individual	87-95	Dagg (1976)
	12	Cosinodiscus angstii			92-96	
	8	Calanus sp.			83-95	
	15	Calanus sp.			90	
Gammarus pseudolimnaeus	17	elm leaves	1	Based on an energy budget for an individual	18.6	Barlocher and Kendrick (1975)
		maple leaves			17.2	
		fungi			67.9-83.2 ($\bar{X}$=76.9)	
Gammarus pulex	2-15	alder leaves	1	Based on an energy budget for an individual	30-40	Nilsson (1974)
		beech leaves			0-35	
Hyalella azteca	15	surface sediment and microflora	11	Based on an energy budget for an individual	15	Hargrave (1971)
Subclass: Brachiopoda Order: Anostraca						
Artemia salina	17.9-21.1	algae @ 0.11-27.9 calories/l	2	Based on a carbon budget for an individual; A/G constant over wide range of food concentrations	73	Pechen'-Finenko (1977)
Branchinecta gigas	15-20	Diaptomus nevadensis and Brachinecta mackini	1	Based on an energy budget for an individual; male	67.2	Daborn (1975)
				female	93.9	
Order: Cladocera						
Polyphemus pediculus	?	juvenile Polyphemus pediculus	2	Based on a carbon budget for an individual	42	Monakov and Sorokin (197[illegible])
Leptodora kindtii	VS	natural prey	estimate	Only P and yield were directly measured	40	Cummins et al. (1969)
Leptodora kindtii	16-17	primarily Cladocera	4	Based on an energy budget for an individual	87	Hillbricht-Ilkowska and Karabin (1970)

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Daphnia longispina	15	Microcystis sp. @ 0.01 mg/ml	12		17.9	Schindler, J. E. (1971)
		Oocystis sp. @ 0.01 mg/ml			10.5	
		Elakatothrix sp. @ 0.01 mg/ml			ca. 100	
		Gloeocystis sp. @ 0.01 mg/ml			13.6	
		Anabaena sp. @ 0.01 mg/ml			50.8	
		Tribonema sp. @ 0.01 mg/ml			68.6	
		Coelastrum sp. @ 0.01 mg/ml			20.8	
		Oscillatoria sp. @ 0.01 mg/ml			25.6	
		Asterionella sp. @ 0.01 mg/ml			38.4	
		Ankistrodesmus sp. @ 0.01 mg/ml			ca. 100	
		Cryptomonas sp. @ 0.01 mg/ml			91.6	
Daphnia longispina	?	Chlorococcus sp. and bacteria	2		10-25	Monakov and Sorokin (1960) as cited by Conover (1964)
Daphnia longispina	?	Chlorella sp.	2		42	Monakov and Sorokin (1972)
		bacteria			50	
Daphnia longispina	15	Chlorella sp.	?		42.5	Sorokin (1966a) as cited by Monakov (1972)
Daphnia pulex	?	sterile dissolved organic matter	2	A/G is inversely related to food concentration	2	Monakov and Sorokin (1972)
		dissolved organic matter and microflora			24	
Daphnia pulex	20	Chlamydomonas sp. @ 25,000 cells/ml	4	Based on a field population energy budget	31.7	Richman (1958)
		@ 50,000 cells/ml			20.2	
		@ 75,000 cells/ml			16.8	
		@ 100,000 cells/ml			14.2	
Daphnia magna	20	Chorella sp. @ 1 mg/l @ 2.5 mg/l @ 5 mg/l @ 10 mg/l	12	Based on an energy budget for an individual; estimated from Figure 9 of reference	60-84	Schindler, D. W. (1968)
Daphnia schodleri	10	Ankistrodesmus sp. @ 10,000 cells/ml	13	Based on an energy budget for an individual; A/C is inversely related to food concentration	90	Hayward and Gallup (1976)
		@ 20,000 cells/ml			88	
		@ 30,000 cells/ml			73	
		@ 40,000 cells/ml			60	

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Daphnia schodleri (Cont.)	20	Ankistrodesmus sp. @ 10,000 cells/ml			70	
		@ 20,000 cells/ml			77	
		@ 30,000 cells/ml			99	
		@ 40,000 cells/ml			76	
Daphnia sp.	?	algae	14	C was estimated from cell counts	8-25	Cohn (1958) as cited by Conover (1964)
Bosmina longirostris	17.9-21.1	phytoplankton	15	Based on a carbon budget for an individual	22.5-31.9	Gutel'mackher (1973)
		bacteria			8.7-10.2	
Bosmina longirostris	15	Chlorella sp.	2		43	Sorokin (1966a) as cited by Monakov (1972)
Bosmina coregoni	19-21	Stephanodiscus sp.	2		47.1	Semenova (1974)
		Chlorella sp.			45.3	
		bacteria			35.3-55.0	
		detritus			24.2	
		Diatoma sp.			51.2	
		Scenedesmus sp.			52.7	
		Staurastrum sp.			34.2	
		Anabaena sp.			10.4	
		Oscillatoria sp.			77.4	
		Microcystis sp.			9.5	
		Ankistrodesmus sp.			10.7	
Holopedium gibberrum	17.9-21.1	phytoplankton	15		32.8-47.3	Gutel'mackher (1973)
		bacteria			10.3-10.8	
Simocephalus vetulus	22	Chlorella sp.	7	Based on an energy budget for an individual; 1 day old	44.0	Ivanova and Klekowski (1972) as cited by Klekowski et al. (1972)
				4 days old	74.3	
				7 days old	72.4	
				9 days old	54.1	
				12 days old	41.0	
				16 days old	34.8	
				20 days old	31.7	
Simocephalus espinosus	15	Chlorella sp. up to 10 mg/l	15	Based on a carbon budget for an individual	46.1	Sorokin (1969)

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Ceriodaphnia reticulata	?	Chlorella sp. Scenedesmus obliguus Chlamydomonas nivalis Ankistrodesmus falcatus	7	Based on an energy budget for an individual	75.5-91.2 ($\bar{X}$= 85.7) 47.0-71.4 ($\bar{X}$=62.6) 6.2-13.1 ($\bar{X}$=9.6) 66.3-88.8 (X=80.6)	Czeczuga and Bobiatynska-Ksok (1972)
Sida crystallina	?	Chlorella sp. Aphanizomenon sp. Anabaena sp. Microcystis sp.	2	Based on a carbon budget for an individual; estimated from Figure 4 of reference	99 75 20 17	Monakov and Sorokin (1972)
Eurycercus lamellatis	17	detritus	1	Based on an energy budget for an individual; 1-7 days old 8-12 days old	7.7 32.2	Smirnov (1962)
Subclass: Copepoda						
Calanus hyperboreus	2 5 8	Thalassiosira flaviatilis @ $1.2x10^9$-$3.0x10^9$ cells/animal	1	Based on a dry weight biomass budget for an individual	13.0-38.9 ($\bar{X}$=27.6) 19.0-49.7 ($\bar{X}$=32.7) 13.4-29.9 (X=21.7)	Conover (1962)
Calanus hyperboreus	4	Exuviella sp. @ 1.8 mg/ml	1	Based on a dry weight biomass budget for an individual	72.1	Conover (1966a)
			16		69.0	
Calanus hyperboreus	2	Thalassiosira fluviatilis @ 6.4 mg dry weight/l;	?	Copepodid IV	44.0	Conover (1964)
				Copepodid V	47.6	
		@ 1.7 mg dry weight/l		Copepodid V	71.1	
		Ditylum brightwellii @ 0.6 mg dry weight/l		Copepodid V	53.0	
	5	Thalassiosira fluviatilis @ 6.7 mg dry weight/l;		Copepodid IV	52.7	
				Copepodid V	50.9	
		@ 1.7 mg dry weight/l		Copepodid V	64.1	
		Thalassiosira nordenskioldii @ 2.6 mg dry weight/l		Copepodid V	39.6	
		Rhizoselenia setigera @ 1.4 mg dry weight/l		Copepodid V	63.1	
	4	Thalassiosira fluviatilis @ 0.3 mg dry weight/l;		Copepodid V	57.2	
		@ 1.8 mg dry weight/l		Copepodid V	56.2	

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Calanus finmarchicus	14.5	Skeletonema sp. @ 2.6×10^5 cells/ml	17	Based on biomass balance for an individual;		Marshall and Orr (1956)
				copepodid I	48.0-91.5 ($\bar{X}$=68.9)	
				copepodid II	77.8-82.6 ($\bar{X}$=80.8)	
		Ditylum sp. @ 57 cells/ml		nauplius VI	93.3-95.9 ($\bar{X}$=94.7)	
Calanus finmarchicus	10-20	Skeletonema costatum @ 14 cells/ml	17	Based on a biomass balance for an individual; adults	51.4-66.2 ($\bar{X}$=61.5)	Marshall and Orr (1955b)
		@ 72 cells/ml			49.9-68.1 ($\bar{X}$=57.3)	
		@ 288 cells/ml			40.1-67.9 ($\bar{X}$=54.5)	
		Syracosphaera sp. @ 720 cells/ml			96.9-99.1 ($\bar{X}$=98.1)	
		Bacillus globigii spores @ 9520 cpm/ml			4.0-12.8 ($\bar{X}$=8.7)	
		Chaetoceros sp. @ 11,500 cells/ml			72.1-94.5 ($\bar{X}$=80.2)	
		diatoms @ 10,500 cells/ml			96.7-99.0 ($\bar{X}$=97.5)	
		@ 343 cells/ml			96.8-98.2 ($\bar{X}$=97.5)	
		Ditylum sp. @ 122 cells/ml			67.0	
		Lauderia borealis @ 6-1,590 cells/ml			49.0-95.0 ($\bar{X}$=78.1)	
		flagellates @ $20\text{-}2.4 \times 10^6$ cells/ml			15.0-98.7 ($\bar{X}$=77.0)	
		dinoflagellates @ $5\text{-}2.0 \times 10^4$ cells/ml			43.0-99.0 ($\bar{X}$=84.3)	
Calanus sp.	?	diatoms, flagellates, Artemia sp. nauplii	1	Based on a carbon budget for an individual	10-99	Mullin (1963) as cited by Conover (1964)
Acartia clausi	17.9-21.1	algae @ 0.04-30.0 mg dry weight/l	2	Based on a carbon budget for an individual	66-73	Pechen'-Finenko (1977)
Calamoecia lucasi	20	yeast	?	Males	63.5	Green (1975)
				Females	67.4	
Diaptomus siciloides	20	Pandorina morum or Chlamydomonas sp.	18	Based on a field population energy budget; the experimental period was 24 hours	40.0-82.9 ($\bar{X}$=60.0)	Comita (1964)
Diaptomus gracilis	15	Microcystis sp.	12	Based on an energy budget for an individual	45.3	Schindler, J. E. (1971)
		Oocystis sp.			13.7	
		Elakatothrix sp.			31.3	
		Gloeocystis sp.			44.2	
		Anabaena sp.			73.5	
		Ankistrodesmus sp.			49.4	
		Tribonema sp.			19.9	
		Coelastrum sp.			29.1	
		Oscillatoria sp.			29.7	
		Asterionella sp.			20.1	
		Cryptomonas sp.			ca. 100	

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Diaptomus gracilis	20	Chlorella sp. @ < 30,000 cells/ml	19		68.4	Kibby (1971b)
	12				67.3	
	5				64.2	
	20	Scenedesmus sp.			39.7	
	12				41.3	
	20	Diplosphaeria sp.			78.0	
	12				69.2	
	20	Ankistrodesmus sp.			74.3	
	12				69.1	
	ca. 5	mixed algae @ 213 cells/ml		March	38.3	
	ca. 7	@ 4336 cells/ml		April	44.2	
	ca. 12	@ 636 cells/ml		May	63.3	
	ca. 14	@ 1233 cells/ml		June	58.4	
	ca. 17	@ 7313 cells/ml		July	60.7	
	ca. 17	@ 689 cells/ml		August	39.0	
	ca. 16	@ 513 cells/ml		September	44.5	
	ca. 15	@ 204 cells/ml		October	44.7	
Diaptomus oregonensis	22-23	?	estimate	Only filtering rate and R were measured	77	Richman (1964)
Diaptomus graciloides	20	Chlamydomonas sp. @ 0.5-10 mg wet weight/l and Chlorella vulgaris @ 0.5-5 mg wet weight/l	4	Based on an energy budget for an individual; nauplius	14-33 ($\bar{X}$=23.7)	Kryutchkova and Ryback (1974)
				copepodid	16-64 ($\bar{X}$=34.0)	
				adult	8-28 ($\bar{X}$=18.3)	
				mean	13-52 ($\bar{X}$=29.0)	
Diaptomus gracioloides	17.9-21.1	algae @ 0.04-30.0 mg dry weight/l	2	Based on a carbon budget for an individual; A/G is constant over wide range of food concentrations	81	Pechen'-Finenko (1977)
Diaptomus graciloides	17.9-21.1	phytoplankton	14	Based on a carbon budget for an individual	81.5-93.6	Gutel'makher (1973)
		bacteria			21.7-24.4	
Macrocyclops albidus	21	Paramecium sp. @ 100/l	7	Based on a field population energy budget	45-50	Klekowski and Shushkina (1966a)
Cyclops vicinus	?	infusoria	2	Based on a carbon budget for an individual	80	Monakov and Sorokin (1972)

Taxon	Temperature (^{o}C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Cyclops strenuus	15	Daphnia sp.	12	Based on an energy budget for an individual	50	Schindler, J. E. (1971)
Subclass: Ostracoda						
Cypridopsis vidua	15	Chlorella sp.	2	Based on a carbon budget for an individual	69.2	Luferova and Sorokin (1970) as cited by Monakov (1972)
		Potamogeton sp.			88.1	
		fungi			63.1	
		Potamogeton sp. as detritus			84.6	
		Potamogeton sp. as sterile detritus			61.5	
Dolerocypris fasciata	15	Chlorella sp.	2	Based on a carbon budget for an individual	44.2	Luferova and Sorokin (1970) as cited by Monakov (1972)
		Potamogeton sp.			72.7	
		fungi			62.7	
		yeast			66.9	
Dolerocypris fasciata	15	bacteria	2	Based on a carbon budget for an individual; A/G is inversely related to age	43-57 ($\bar{X}$=48.8)	Monakov and Sorokin (1972)
Entomostraca	?	?	?		58.4	Sushchenya (1969)
Entomostraca	VS	bacteria and phytoplankton	2	Based on a carbon budget for an individual	51.7	Sorokin (1972)
PHYLUM: ROTATORIA						
Rotatoria	VS	bacteria and phytoplankton	2	Based on a carbon budget for an individual; average of several species	53	Sorokin (1972)
Asplanchna sp.	?	variable	2	Based on a carbon budget for an individual; A/G is inversely related to food concentration	16-22	Sorokin and Mordukhai-Boltovskaya (1962)
Brachionus plicatilis	20	Dunaliella salina @ 4.4 calories/ml	13	Based on a carbon budget for an individual	19.4	Doohan (1973)

APPENDIX C (Continued)

Taxon	Temperature (°C)	Food and concentration	Experimental method	Comments	Assimilation Efficiency (%)	Reference
Brachionus rubens	20	Chlorella vulgaris @ $1.2x10^4$-$1x10^7$ cells/ml	4	Based on an energy budget for an individual;		Pilarska (1977a)
				age I	12.2-52.0	
				age II	12.2-55.8	
				age III	13.2-57.8	
				ovigerous females	15.1-68.8	
				Based on a carbon budget for an individual; age I - III	23.0-23.8	
				ovigerous females	30.8-32.3	
Brachionus calyciflorus	19-20	Scenedesmus obliguus and Lagerheimia ciliata	7	Based on a field population energy budget; A/G was inversely related to food concentration	21-52	Galkovskaya (1963)
Brachionus sp.	VS	natural assemblage	6	Based on a field population energy budget; calculations based on 2 species	52.6	Comita (1972)
Kerratella quadrata	VS	natural assemblage	6	Based on a field population energy budget	73.4	Comita (1972)
Keratella cochlearis	VS	natural assemblage	6	Based on a field population energy budget	38.3	Comita (1972)
Polyarthra vulgaris	VS	natural assemblage	6	Based on a field population energy budget	81.8	Comita (1972)
Filina longiseta	VS	natural assemblage	6	Based on a field population energy budget	56.9	Comita (1972)

APPENDIX D: RESPIRATION OF ZOOPLANKTON AND BENTHOS

PART I: RESPIRATION RATES OF AQUATIC INVERTEBRATES FOR VARIOUS TAXONOMIC AND FUNCTIONAL GROUPS

PART II: RESPIRATION RATES OF AQUATIC INVERTEBRATES AS A FUNCTION OF BODY WEIGHT AND TEMPERATURE FOR VARIOUS TAXONOMIC AND FUNCTIONAL GROUPS

1. The definitions of abbreviations and symbols used in Appendix D, Parts I and II, are listed below:

L	laboratory study
F	field study
T	temperature
W	weight
R	respiration
BOD	biological oxygen demand
AFDW	ash-free dry weight
h	hour
mg	milligram
μg	microgram
ℓ	litre
μℓ	microlitre
wt	weight
g	gram
m	metre
mm	millimetre
ca.	approximately
fc	foot-candle
ind	individual
cal	calorie
cm/sec	centimetre per second
O_2	dissolved oxygen concentration
?	unknown or could not be determined from data
$\bar{X}$	mean value
%	percent
>	greater than

PART I: RESPIRATION RATES OF AQUATIC INVERTEBRATES FOR VARIOUS TAXONOMIC AND FUNCTIONAL GROUPS

APPENDIX D: PART I - RESPIRATION RATES OF AQUATIC INVERTEBRATES FOR VARIOUS TAXONOMIC AND FUNCTIONAL GROUPS

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
PHYLUM: MOLLUSCA						
Class: Gastropoda						
Helisoma trivolvis	L	Manometric (Gilson respirometer)	5	1.00	Control data; acclimated to 15°C and starved 24h; 86.3 mg dry tissue weight	Sheanon and Trama (1972)
			15	3.30		
			20	4.60		
Planorbis contortus	L	Polarographic (flow through chamber)	10	2.60	Acclimated to 10°C (4 days); fed native food; free movement; dry wt.= 1 mg	Calow (1975)
Planorbis albus	L	Manometric (Warburg respirometer)	8	0.84	Calculated from Tables 3 and 4; Dry weight = 1.0 mg (without shell)	Mason (1977)
Bithynia tentaculata	L		8	0.59		
			20	0.58		
Valvata piscinalis	L		8	0.14		
			20	0.67		
Ancylus fluviatilus	L	Polarographic (flow through chamber)	18	4.00	Acclimated to 18°C (4 days); fed native food; free movement; dry wt. = 1 mg	Calow (1975)
Ferrissia rivularis	L	Polarographic (?)			Calculated from Figure 4; Specimens were collected at night and immediately tested	Burky (1971)
			10	0.26-0.25	January - February	
				0.26-0.48	March - April	
				0.53-0.51	May - June	
				0.48-0.40	July - August	
				0.40-0.32	September - October	
				0.26-0.24	November - December	
				0.37	$\bar{X}$ monthly rate	
			20	0.56-0.48	January - February	
				0.56-0.96	March - April	
				1.17-1.28	May - June	
				1.28-1.28	July - August	
				1.12-0.88	September - October	
				0.77-0.64	November - December	
				0.91	$\bar{X}$ monthly rate	

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Ferrissia rivularis (cont.)	L	Polarographic (?)	0 4.5 6 11 15 18	0.13 0.16 0.22 0.33 0.96 0.99	Calculated from Figure 2; acclimated to test temperature dry wt. = 1.38-1.62 mg	Burky (1971)
Class: Pelecypoda						
Pisidium casertanum	L	Polarographic (flow through chamber)	11	0.13 0.43	O_2 = 1%; specimens active = 19%; dry wt = ?	Jonasson (1964)
Pisidium casertanum	L	Polarographic (flow through chamber)	8 16	0.78 0.38	Dry wt. = 0.20 mg = O_2 = 1.8% = 0.27 mg = = 2.2%	Berg and Jonasson (1965)
Pisidium casertanum	L	Manometric (Warburg respirometer)	8 20	0.58 0.42	Calculated from Tables 3 and 4, dry wt. = 1 mg (without shell)	Mason (1977)
Scrobicularia plana	L	Polarographic (flow through chamber)	0.5 4.0 9.5 13.5 17.5 22.5	0.20 0.30 0.40 0.64 1.02 1.42	Calculated for a standard snail (dry wt. = 0.5 g, without shell); acclimated to ambient field temperature in lab	Hughes (1970)
PHYLUM: ANNELIDA						
Class: Hirudinea						
Helobdella stagnalis	L	Manometric (Warburg respirometer)	8 20	0.67 1.78	Calculated from Tables 3 and 4; dry weight = 1 mg at each temperature	Mason (1977)
Class: Oligochaeta						
Potamothrix hammoniensis	L	Manometric (Warburg respirometer)	8 20	1.29 1.55	Calculated from Tables 3 and 4; dry weight = 1 mg	Mason (1977)
Enchytraeidae	L	Manometric (Warburg respirometer)	8 20	0.60 2.19		Mason (1977)

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Tubifex tubifex	L	Polarographic (closed bottle)	5	0.53	$\bar{X}$ Dry weight = 72.2 mg; $O_2 > 85\%$; Fed Sediment	Brinkhurst et al. (1972)
			10	0.46	= 55.8	
			15	0.87	= 56.6	
			20	1.15	= 58.7	
Tubifex tubifex	L	Manometric (Warburg respirometer)	20	2.19	O_2 = 0.5%; acclimated at test temperature	Palmer (1968)
				5.66	= 1.0% for 3 days; Dry Wt. = 2.5 mg	
				12.89	= 3.0%	
				11.15	= 10.0%	
				12.88	= 21.0%	
Tubifex baratus	L	Polarographic (flow through chamber)	8	0.42	Dry weight = 1.09 mg; O_2 = very low (1.7-2.4%)	Berg and Jonasson (1965)
				0.15	= 4.30 mg;	
				0.55	= 1.78 mg;	
					specimens were active	
Tubifex baratus	L	Polarographic (flow through chamber)	11	0.05	O_2 = 1%; specimens were active	Jonasson (1964)
				0.51	= 19%; Dry weight = ?	
Ilyodrilus hammoniensis	L			0.10		
				0.31		
Ilyodrilus hammoniensis	L	Polarographic (flow through chamber)	8	0.20	Dry weight = 0.35 mg; O_2 = very low (1.8-2.2%)	Berg and Jonasson (1965)
			16	0.53	Dry weight = 0.23 mg	
					Specimens were active	
Limnodrilus hoffmeisteri	L	Polarographic (closed bottle + BOD probe)	5	0.39	$\bar{X}$ Dry weight = 72.2 mg; $O_2 > 85\%$; Fed sediment	Brinkhurst et al. (1972)
			10	0.46	= 66.8	
			15	0.68	= 59.9	
			20	1.05	= 55.2	
Peloscolex multisetosus	L	Polarographic (closed bottle + BOD probe)	5	0.85	$\bar{X}$ Dry weight = 17.4 mg;	Brinkhurst et al. (1972)
			10	0.77	= 18.8	
			15	0.92	= 15.8	
			20	1.22	= 15.6	

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments		Reference
ARTHROPODA							
Insecta							
Plecoptera							
Taeniopteryx nebulosa	L	Polarographic (flow through chamber)	8	0.25	O_2 = 1 mg/l	Calculated from Figure 2 (Curve B); acclimated 6 days and starved 96 h; Dry weight = ?	Nagell (1973)
				0.90	= 3		
				1.26	= 5		
				1.32	= 7		
				1.26	= 9		
Nemoura cinerea	L	Polarographic (flow through chamber)	8	0.63	= 1 mg/l	Calculated from Figure 3 (Curve B); acclimated for 1 day and starved 96 h; Dry Weight = ?	Nagell (1973)
				1.26	= 3		
				1.61	= 5		
				1.68	= 7		
				1.61	= 9		
Nemoura californica	L	Manometric	10	2.39	Dry weight = 1-2 mg; Acclimated 48 h		Knight and Gaufin (1966)
Diura nanseni	L			0.42	= 2 mg/l	Calculated from Figure 4 (Curve B); acclimated 6 days and starved 96 h; Dry weight = ?	Nagell (1973)
				0.84	= 3		
				1.38	= 5		
				1.34	= 7		
				1.32	= 9		
Acroneuria californica	L	Manometric (Gilson respirometer)	15	1.01	July - August; Dry weight = 5.4-11.3 mg		Heiman and Knight (1975)
			24	4.20			
			30	1.20			
			16	0.88	September; Dry weight = 11.3 mg		
			25	2.10			
			30	2.51			
			12	0.84	November; Dry weight = 18.28 mg		
			20	1.26			
			23	1.68	All specimens were acclimated 5-15 days and starved 48 h.		

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
<u>Acroneuria pacifica</u>	L	Manometric (Gilson-Warburg apparatus)	10	2.72	Dry weight = 10-40 mg Acclimated [illegible]	[illegible]
				1.56	= 50-80	
				0.99	= 100-200	
				3.92	= 10-40	
				1.81	= 40-80	
				1.32	= 100-200	
<u>Pteronarcys californica</u>	L	Manometric (Gilson-Warburg apparatus)	10	1.99	= 10-30 Acclimated [illegible]	[illegible]
				0.93	= 100-200	
				0.58	= 150-250	
				0.43	= 300-450	
				2.96	= 10-30	
				1.09	= 100-200	
				0.96	= 150-250	
				0.99	= 300-450	
<u>Classenia sabulosa</u>	L	Manometric (Gilson-Warburg apparatus)	10	2.54	= 10-40 Acclimated [illegible]	[illegible]
				1.53	= 50-80	
				0.98	= 100-200	
			20	3.55	= 10-40	
				2.14	= 50-80	
				1.46	= 100-200	
<u>Pteronarcella badia</u>			10	1.25	= 50	
<u>Arcynopteryx signata</u>	L	Manometric (Gilson-Warburg apparatus)	10	2.43	Dry weight = 10-30 mg; Acclimated for 48 h	Knight and Gaufin (1966)
			20	4.15	= 10-30	
<u>Arcynopteryx parallela</u>	L	Manometric (Gilson-Warburg apparatus)	10	1.39	= 10-50	Knight and Gaufin (1966)
<u>Isoperla fulva</u>	L	Manometric (Gilson-Warburg apparatus)	10	3.29	= 10-40	Knight and Gaufin (1966)
<u>Brachyptera</u> spp.	L	Manometric (Gilson-Warburg apparatus)	10	4.62	= 2	Knight and Gaufin (1966)
Order: Ephemeroptera						
<u>Isonychia</u> sp.	L	Winkler titration (closed bottle)	6.5	1.69	$\bar{X}$ Dry weight = 6.2 mg. Acclimated for 72 h; artificial substrate provided. O_2 = 95% of initial	Ulanoski and McDiffett (1972)

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Isonychia bicolor	L	Manometric (Gilson respirometer)	2- 7 3- 8 5-10 5-11 6-11 10-15	1.44 1.78 1.91 2.14 2.88 2.27	$\bar{X}$ Dry weight = 4.0 mg; Values are means of 8-hour = 2.7 rates during pulses; = 4.6 Specimens collected and = 3.0 immediately tested; = 2.8 substrate provided = 2.3	Sweeney (1978)
Stenonema fuscum	L	Winkler titration (closed bottle)	6.5	1.40	$\bar{X}$ Dry weight = 5.2 mg; Acclimated for 72 h; artificial substrate provided, O_2 = 95% of initial	Ulanoski and McDiffett (1972)
Stenonema pulchellum	L	Modified Winkler titration (closed bottle)	15 20 25	2.64 3.64 5.51	$\bar{X}$ Dry weight = 1.19 mg; Fed diatoms (Range = 1-2.01 mg)	Trama (1972)
Stenonema bicpunctatum	L	Polarographic (flow through chamber) Manometric (Gilson-Warburg apparatus)	20	2.20 2.21	From Table 2. Dry weight range = 1.2-12 mg	Rueger et al. (1969)
Stenonema canadensis	L	Polarographic Manometric		0.79 0.85		Rueger et al. (1969)
Stenonema nepotellum	L	Polarographic Manometric		2.66 1.91		Rueger et al. (1969)
Potamanthus rufous	L	Manometric (Warburg respirometer)	20	0.61	From Figure 12. Dry weight range = 1.2-10.8 mg	Rueger et al. (1969)
Baetisca laurentina	L	?		0.66	From Figure 12. Dry weight range = ?	Rueger et al. (1969)
Leptophlebia sp.	L	?		0.84	From Figure 12. Dry weight range = ?	Rueger et al. (1969)
Ephemera simulans	L	?		0.50	From Figure 12. Dry weight range = ?	Rueger et al. (1969)
Ephemera simulans	L	Winkler tritration (closed bottle)	13	1.88 0.86 0.55 0.87 1.79 1.76	Substrate size = none; Dry weight = ? = -4 (length = 20-22 mm) = -2 = 0 = 2 = 4	Eriksen (1964)

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Ephemera simulans	L	Winkler titration (closed bottle)	13	0.29	O_2 = 0.6 mg/l; Substrate size = 2;	Eriksen (1964)
				0.57	= 1.0 Dry weight = ? (Length =	
				0.57	= 3.0 20-22 mm)	
				0.87	= 5.0	
Hexagenia limbata	L	Winkler titration (closed bottle)		2.30	Substrate size: none; Dry weight = ?	Eriksen (1964)
				1.67	-4 (length = 20-22 mm)	
				1.42	-2	
				1.71	0	
				1.99	2	
				1.99	4	
				1.60	O_2 = 0.45 mg/l; Glass burrows provided	
				0.78	= 1.00	
				0.79	= 3.00	
				0.84	= 5.00	
Cloeon dipterum	L	Polarographic (flow through chamber)	8	0.63	O_2 = 1.0 mg/l; Calculated from Table 5	Nagell (1973)
				0.84	= 1.5 (curve B); starved for 3 days	
				1.05	= 2.0= Dry weight = ?	
				1.11	= 3.0	
				1.17	= 5.0	
				1.19	= 7.0	
				1.21	= 9.0	
				1.23	= 11.0	
Cloeon dipterum	L	Manometric (Warburg respirometer)	8	1.91	Calculated from Tables 3 and 4, Dry weight = 1 mg	Mason (1977)
			20	1.59		
Caenis boraria	L	Manometric (Warburg respirometer)	8	2.98		Mason (1977)
			20	1.49		
Order: Megaloptera						
Corydalus cornutus	L	Winkler titration (Closed bottle)	20	4.6	Dry weight = 16.4 mg	Brown (19[illegible]8)
				1.1	= 121.0 mg	
				1.6	= 129.0 mg	
Order: Odonata						
Anax junius	L	Manometric (Gilson respirometer)	13	2.03-1.30	Dry weight = 10.0-40.0 mg; Acclimated to test	Petitpren and Knight (1970)
				1.02-0.85	= 85.0-150.0 temperature; substrate	
				0.75-0.69	= 225.0-275.0 provided; activity	
				2.66-0.95	range moderate	
			20	3.61-2.41	= 10.0-40.0	
				1.94-1.64	= 85.0-150.0	
				1.46-1.38	= 225.0-275.0	
				2.34-1.81	range	

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Anax junius (Cont.)	L	Manometric (Gilson respirometer)	27	3.49-3.34 3.27-3.24 3.17-3.16 3.31-3.24	Dry weight = 10.0-40.0 mg; = 85.0-150.0; = 225.0-275.0 range; Acclimated to test temperature; substrate provided; activity moderate	Petitpren and Knight (1970)
			20	1.36-1.77 0.90-1.89	Summer males Summer females	
Pyrrhosoma nymphula	L	?	Measured at 10 corrected to 8.5		"Best Estimate"; Table 1; $\bar{X}$ Dry weight = 20.74 mg	Phillipson (1970)
Erythromma najas	L	Manometric (Warburg respirometer)	8	0.95	Calculated from Tables 3 and 4; Dry weight = 1 mg	Mason (1977)
Order: Diptera						
Arthocladinae	L	Manometric (Warburg respirometer)	8 20	0.7 1.7	Calculated from Tables 3 and 4; Dry weight = 1 mg	Mason (1977)
Chaoborus flavicans	L	Polarographic (flow through chamber)	8 16	0.29 1.00	Dry weight = 0.95 mg; O_2 = 1.8-2.2% = 1.00 mg; = 2.0-2.2% Specimens active	Berg and Jonasson (1965)
Chaoborus flavicans	L	Polarographic (flow through chamber)	11	0.31	O_2 = 19%; specimens active (profundal) Dry = ca. 1 mg	Jonasson (1964)
Chaoborus punctipennis	L	Manometric (Gilson respirometer)	20	2.95 13.30	Winter; Dry weight = ? (4th instar) Summer and Fall	Sigmon et al. (1978)
Chironomus anthracinus	L	Polarographic (flow through chamber)	8 16	0.12 0.80	Dry weight = 2.7 mg; O_2 = 1.8-2.1% = 2.6 mg = 1.9-2.8%	Berg and Jonasson (1965)
Chironomus anthracinus	L	Polarographic (flow through chamber)	11	0.20 0.34 0.58	O_2 = 1% - profundal Dry weight = ? = 19% - sublittoral = 19% - sublittoral	Jonasson (1964)
Chironomus punctipennis	L	Manometric (Warburg respirometer)	30	17.40	Note high test temperature; Dry weight = 0.15 mg	Ransom et al. (1971)
Chironomus plumosus	L	Manometric (Warburg respirometer)	8	1.4	Calculated from Tables 3 and 4; Dry weight = 1 mg	Mason (1977)
Chironomus plumosus	L	Manometric (Warburg respirometer)	30	9.62	Note high test temperature; Dry weight = 1.05 mg	Ransom et al. (1971)

Appendix D, Part I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 10C	Comments	Reference
Chironomus piparius	L	Manometric (Warburg respirometer)	20	4.81 4.96	Normal shaking; $\bar{X}$ Dry weight = ca. 1 mg Normal shaking x 2; (Acclimated 24 h)	Edwards (1957)
Chironomus tentans	L	Manometric (Warburg respirometer)	8 20	1.1 3.5	Calculated from Tables 3 and 4; Dry weight=1 mg	Mason (1977)
Glyptotendipes polytomus	L	Volume respirometer (pressure constant)	8	2.54 3.96 3.63 0.01 0.002	March Dry weight = ca. 2.02 mg April (early) (late) O_2 = 1.6% - 3.1% O_2 O_2 = 1.3% - 0.6% O_2	Kamler and Srokosz (1973)
Tanytarsus holochoris	L	Manometric (Warburg respirometer)	8 20	0.9 2.4	Calculated from Tables 3 and 4; Dry weight = 1 mg	Mason (1977)
Procladius pectinatus	L	Polarographic (flow through chamber)	8	0.27 0.19	Spring dry wt. = 0.66 mg; O_2 = 1.8-2.2% Winter dry wt. = 0.48 mg	Berg and Jonasson (1965)
Pseudodiamesa arctica	L	Polarographic (closed bottle)	0	0.69 0.48	Calculated from Table 10 ($\bar{X}$ per day for 305 days); $\bar{X}$ Dry weight = 0.338 mg	Welch (1976)
Lauterbornia sp.	L	Polarographic (closed bottle)		1.10 1.18	$\bar{X}$ Dry weight = 0.069 mg	Welch (1976)
Heterotrissocladius oliveri	L	Polarographic (closed bottle)		0.49	$\bar{X}$ Dry weight = 0.104 mg	Welch (1976)
Trissocladius sp.	L	Polarographic (closed bottle)		1.0-1.2	$\bar{X}$ Dry weight = 0.048 mg	Welch (1976)
Orthocladius sp.	L	Polarographic (closed bottle)		0.8-1.5	$\bar{X}$ Dry weight = 0.051 mg	Welch (1976)
Class: Crustacea Subclass: Malacostraca Order: Isopoda						
Asellus aquaticus	L	(Volumetric respirometer)	23	6.3 5.7 5.0 4.9 4.5 4.5 5.2	Dry weight = 0.43 mg = 0.85 = 2.55 = 2.98 = 5.10 = 5.53 $\bar{X}$ Dry weight = 2.81	Prus (1972)

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Asellus aquaticus	L	Manometric (Warburg respirometer)	8	1.13	Calculated from Tables 3 and 4; Dry weight = 1 mg	Mason (1977)
			20	4.91		
Asellus racovitzai	L	Polarographic (closed BOD bottle)	18	1.76	Unfed; no substrate provided; Dry weight = ?	Swiss and Johnston (1976)
				1.99	Fed *Scenedesmus*	
				2.05	*Anabaena*	
				2.43	*Oscillatoria*	
				2.72		
Order: Amphipoda						
Gammaracanthus lacustris	L	Winkler titration (closed bottle)	4-5	0.48	Dry weight = 149.31 mg	Ivanova (1972)
				0.52	= 106.70	
				0.58	= 63.99	
				0.75	= 21.33	
				0.89	= 10.66	
				1.02	= 5.33	
				1.77	= 2.13	
				1.94	= 0.85	
Gammarus pulex	L	Manometric (Warburg respirometer)	8	1.14	Calculated from Tables 3 and 4; Dry weight = 1 mg	Mason (1977)
			20	2.09		
Order: Mysidacea						
Mysis relicta	L	Modified Winkler titration (closed bottle)	0.9	2.4	$\overline{X}$ annual temperature in Char Lake	Lasenby and Langford (1972)
			5.3	3.3	in Stony Lake	
					Dry weight = 1 mg (Acclimated 24 h at each temperature)	
Mysis relicta	L	Polarographic (closed bottle)	4	1.8	Dry weight = 5 mg	Foulds and Roff (1976)
Order: Decapoda						
Caridina fernandoi	L	Winkler titration (flow through chamber)	28	2.7	Dry weight = 3.5 mg; Standard metabolism	Wycliffe and Job (1977)
				2.6	= 52.5	
				4.6	= 3.5; Routine metabolism	
				3.7	= 52.5	
				11.2	= 3.5; Active metabolism	
				7.6	= 52.5	

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Repiration rate mg C/mg C/day x 100	Comments	Reference
Austropotamobius pallipes	L	Polarographic (closed, mixing respirometer)	10	0.3	Dry weight = 1.2-2.2 mg; standard metabolism	Sutcliffe et al. (1975)
				0.7	= 0.11 active metabolism	
				0.6	= 0.11	
				0.7	= 0.18	
				1.0	= 0.30	
				0.3	= 0.41	
				1.0	= 0.41	
Pacifastacus leniusculus	L	Winkler titration (closed bottle)	20	0.7	O_2 = 1.67 mg/l; Dry weight = 2.4 g	Moshiri et al. (1970)
				0.8	= 2.29	
				1.4	= 5.02	
				2.2	= 7.00	
Pacifastacus leniusculus	L	Modified Winkler titration (closed bottle)	15	light dark	Experimental conditions; males only; acclimated 1 - 2 h, starved 48 h	Moshiri et al. (1971)
				5.1 6.5	Dry weight = ca. 0.371 g (assuming ash - 10% of dry weight)	
				5.3 6.9	= ca. 0.733	
				1.1 1.3	= ca. 6.071	
				0.6 0.7	= ca. 12.987	
				3.0 3.9	= ca. 5.041	
			2.5	0.9 1.0	$\bar{X}$ Dry weight = ca. 1.832	
			5.0	1.2 1.7		
			10.0	1.3 1.8		
			15.0	2.6 3.3		
			20.0	2.0 2.3		
				1.7 2.0	$\bar{X}$ for all temperatures	
Subclass: Branchiopoda Order: Cladocera						
Daphnia galeata	L	Winkler titration (closed bottle)	10	13.0	Algae concentration = $5x10^5$ cell/l; Dry weight = ? (probably 0.001-0.03 mg)	Larow et al. (1975)
				44.1	= $5x10^6$	
				46.2	= $10x10^6$	
				27.7	= $5x10^5$	
				62.1	= $5x10^6$	
				77.2	= $10x10^6$	
Daphnia pulex	L	?	?	15.5	Light intensity: 0 f.c.; Dry weight=0.003-0.056 mg	Buikema (1972)
				23.7	14	
				58.2	110	

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Daphnia pulex	L	Winkler titration (closed bottle)	20	18.2-19.2	Range in light; Dry weight = 0.0036 mg	Tezuka (1971)
Daphnia pulex	L	Manometric and Winkler Warburg and closed bottle	20	21.6	Dry weight = 0.003 mg; starved 24 h	Richman (1958)
				15.6	= 0.009	
				13.8	= 0.016	
				18.8	= 0.020	
				19.8	= 0.026	
				15.5	= 0.046	
Daphnia magna	L	Polarographic BOD probe (closed, circulating chamber)	18	14.6	Food concentration = $5.3x10^5$ μ^3/ml, Dry weight = 0.138 mg	Kersting and Leeuw-Leegwater (1976)
				17.5	= $4.2x10^6$	
				11.8	= $8.4x10^6$	
				8.5	= $17.7x10^6$	
Daphnia magna	?	?	?	14.8		Sushchenya (1958b) as cited by Ivanova (1970)
Daphnia longispina	L	Winkler titration (closed bottle)	16-18	12.1-13.5	Range (in dark); Dry weight = 0.0011 mg	Tezuka (1971
Daphnia longispina	?	?	?	16.02		Manuilova (1958) as cited by Ivanova (1970)
Daphnia longispina	?	?	?	14.6		Shushkina and Pecen' (1964) as cited by Ivanova (1970)
Daphnia cuculata	?	?	?	16.1		Manuilova (1958) as cited by Ivanova (1970)
Daphnia hyalina	F	?	3	0.9	Seston concentration: 0.8 cal/l; Dry weight = ?	Blazka (1966)
				1.4	1.4	
				2.5	2.5	
	L	?	5	5.0		
			10	8.4		
			20	17.9		
	F	?	5	4.2		
			10	4.6		
			20	9.0		
Diaphanosoma brachyurum	?	?	?	27.2		Sushchenya (1958b) as cited by Ivanova (1970)

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Bosmina longirostris	?	?	?	18.5		Sushchenya (1958b) as cited by Ivanova (1970)
Bosmina coregoni	?	?	?	17.0		Manuilova (1958) as cited by Ivanova (1970)
Simocephalus vetulus	?	?	?	13.1		Sushchenya (1958b) as cited by Ivanova (1970)
Simocephalus vetulus	?	?	?	15.4		Manuilova (1958) as cited by Ivanova (1970)
Simocephalus vetulus	L	Manometric (Cartesian diver)	?	5.7	pH= 4; Dry weight = 0.0629 mg; Resting rate	Ivanova and Klekowski (1972)
				9.6	4.8	
				9.6	5.8	
				9.6	6.9	
				9.8	8.7 = 0.053	
		Winkler titration (closed bottle)		23.6	4.0 = 0.063; ordinary rate	
				19.5	4.8	
				16.1	5.8	
				13.5	6.9	
				20.1	8.7 = 0.053	
Ceriodaphnia reticulata	L	?	15	18.0	Food consumption = 1.12 cal/cal/day, Dry	Gophen (1976)
		(closed bottle)	22	20.0	= 2.72 weight = 0.0021-0.0041mg	
			27	50.0	= 2.91	
Leptodora kindtii	L	Manometric (Scholander respirometer)		light / dark	Illumination condition; Dry weight = ? (length = 6.7 mm); (Acclimated 1 h at each temperature)	Moshiri et al. (1969)
			5	10.6 / 3.8	female	
				7.8 / 4.0	(ovigerous)	
				9.4 / 4.0	male	
			15	90.3 / 43.6	female	
				51.9 / 30.4	(ovigerous)	
				261.9 / 162.2	female	
				160.0 / 81.6	(ovigerous)	
				84.5 / 47.1	$\bar{X}$	
Leptodora kindtii	L	?	Measured at 16 and corrected to 20	12.5	Dry weight = 0.051 mg	Hillbricht-Ilkowska and Karabin (1970)

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Subclass: Copepoda						
Copepoda	F	Modified Winkler titration (closed bottle)	18-20	17.8 20.4 14.5 15.1 10.8 9.1 7.5	Light; dry weight = 0.003 mg; Depth 6 m; ambient pressure Dark Light Dark	Bishop (1968)
Diaptomus kenai	L	Modified Winkler titration (closed bottle)	22	27.2 44.8	$\bar{X}$ for 1900-1500 h; Dry weight = ? (Probably ca. 0.005 mg) $\bar{X}$ for 1500-1900 h	Duval and Green (1976)
Diaptomus ashlandii	L	Modified Winkler titration (closed bottle)		44.7 73.8	$\bar{X}$ for 1900-1500 h; $\bar{X}$ Dry weight ~ 0.0056 mg $\bar{X}$ for 1500-1900 h	Duval and Green (1976)
Diaptomus oregonensis	L	Modified Winkler titration	22-23	19.4	Adult female; Dry weight = 0.011 mg	Richman (1964)
Diaptomus oregonensis	L	Micro-Winkler titration (closed bottle)	 10 15 20	Fed Starved 14.5 10.8 19.3 13.2 30.1 19.8	Food condition; Dry weight = 0.0048 mg	Comita (1968)
Diaptomus siciloides	L	Micro-Winkler titration (closed bottle)	10 15 20	11.9 5.6 34.3 30.0 52.4 44.8	Food condition; Dry weight = 0.0032 mg	Comita (1968)
Diaptomus septopus	L	Micro-Winkler titration (closed bottle)	15 20	11.2 8.0 17.9 14.9	Food condition; Dry weight = 0.022 mg	Comita (1968)
Diaptomus clavipes	L	Micro-Winkler titration (closed bottle)	15 20	11.7 11.6 16.5 15.7	Food condition; Dry weight = 0.028 mg	Comita (1968)
Diaptomus arcticus	L	Micro-Winkler titration (closed bottle)	10 15 20	3.6 4.4 6.4	Food condition; Dry weight = 0.300 mg	Comita (1968)
Diaptomus graciloides	L	Winkler titration (closed bottle)	0.5 2.5 3.9	0.9 1.2 1.3	$\bar{X}$ Dry weight = 0.006 mg; Note low temperatures	Ostapenya et al. (1969)

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Cyclops varicans	L	Polarographic electrode (closed respirometer)	16	25.7	$\bar{X}$ normal rate; Dry weight = 0.020-0.031 mg	Chaston (1969)
				52.6	$\bar{X}$ after 9 h of anaerobiosis	
Macrocyclops albidus	L	Manometric (Cartesian diver)	21	25.0-46.0	Nauplii; Dry weight = $6x10^{-5}$-$4x10^{-4}$ mg	Klekowski and Shushkina (1966b)
				10.0-20.0	Copepodids; = $4x10^{-4}$-0.010	
				10.0	Adults and Stage V Copepodids; = ca. 0.032	
Limnocalanus macrurus	F, L	Polarographic electrode (closed bottle)	0.2	10.7	Dry weight = 0.0003 mg; Calculated from Figure 1	Roff (1973)
				6.7	= 0.0006	
				6.4	= 0.0016	
				4.3	= 0.0060	
				3.4	= 0.0100	
				2.7	= 0.0300; Calculated from Figure 2	
				3.0		
			2	3.2		
			4	4.1		
			10	8.3		
			15	9.6		
Calamoecia lucasi	L	Micro-Winkler titration (closed bottle)	25	13.3	Food concentration = $1x10^4$ yeast cells/ml; Dry	Green (1975)
				28.5	= $2x10^4$ weight = 0.0023 mg	
				33.3	= $4x10^4$	
				52.3	= $6x10^4$	
					Acclimated to experimental temperature 36-48 h	
PHYLUM: ROTATORIA						
Brachionus calyciflorus	L	Micro-Winkler titration (closed bottle)	20	Fed / Starved	Food condition; Estimated Dry weight =	Galkovskaya (1963)
				181.5 / 30.3	from (Pilarska 1977c) = $6x10^{-5}$ mg	
				141.8 / 22.7	= $8x10^{-5}$	
				113.4 / 18.2	= $1x10^{-4}$	
				94.4 / 15.1	= $1.2x10^{-4}$	
				81.0 / 12.9	= $1.4x10^{-4}$	
				66.7 / 10.7	= $1.7x10^{-4}$	
				113.2 / 18.3	$\bar{X}$	
				65.7	Grand $\bar{X}$	
Brachionus calyciflorus	L	Micro-Winkler titration (closed bottle)	10	20.6	Dry weight = $1.69x10^{-4}$ mg	Pourriot (1973)
			15	31.4		
			20	50.5		
			23	64.6		

APPENDIX D, PART I (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Brachionus rubens	L	Manometric (Cartesian diver)	20	41.4	Food concentration: $1x10^7$ algal cells/l; Dry weight	Pilarska (1977c)
				24.1	$1x10^6$ = $7.6x10^{-5}$ mg; Age 12 h	
				29.0	$1.2x10^3$	
				49.1	$1x10^7$ = $9.3x10^{-5}$ mg; 13-24 h	
				24.5	$1x10^6$	
				32.4	$1.2x10^3$	
				40.8	$1x10^7$ = $1.1x10^{-4}$ mg; 24 h	
				28.0	$1x10^6$	
				37.6	$1x10^3$	
				41.8	$1x10^7$ = $1.4x10^{-4}$ mg; 24 h	
				29.0	$1x10^6$ (ovigerous female)	
				37.6	$1x10^3$	
Brachionus plicatilis	L	Manometric (Cartesian diver)	20	16.3	Senile adult; Dry weight = $1.58x10^{-4}$ mg	Doohan (1973)
				67.7	Postovigerous adult	
				35.0	Ovigerous female (2 eggs); = $3.42x10^{-4}$	
				38.1	(1 egg); = $2.52x10^{-4}$	
				26.0	Adult = $1.58x10^{-4}$	
				37.1		
				40.1		
				30.0		
				26.1		
				27.6		
				30.3		
				31.4		
				35		
				32		
				30		
				33.9	$\bar{X}$ adult rate	
Rhinoglena frontalis	L	Micro-Winkler titration (closed bottle)	5	19.1	$\bar{X}$ Dry weight = $1.27x10^{-4}$ mg; Acclimated 15 min	Pourriot (1973)
			10	24.0		
			15	26.6		
			20	31.6		
			23	42.4		
Zooplankton (Diaptomus kenai, Diaptomus tyrelli, Holopedium gibberrum, Daphnia rosea)	L	Modified Winkler titration (closed bottle)	10	91.8	Dry weight (Biomass) = 0.050 mg/ml; Acclimated 24 h	Duval and Green (1976)
			16	23.0	to each temperature, $\bar{X}$ Daily rates (Figure 1)	
			20	21.0		

APPENDIX D, PART I, (Continued)

Taxon	Lab or field	Method	Temperature (°C)	Respiration rate mg C/mg C/day x 100	Comments	Reference
Zooplankton (primarily copepods)	F	Modified Winkler titration (closed bottle)	18-20	32.1	Dry weight/individual = 0.00096 mg; Captured at 5M-Tested at 5M	Bishop (1968)
			4	6.2	= 0.00101 5M- 45M	
				28.0	= 0.00302 45M- 5M	
				8.7	= 0.00336 45M- 45M	
			4	7.5	= 0.0030-0.0034 mg	
			8	9.2		
			12	10.7		
			16	15.0		
			20	20.4		

AD-A090 832 FISH AND WILDLIFE SERVICE FAYETTEVILLE AR NATIONAL RE--ETC F/G 12/1
SIMULATION MODELING OF ZOOPLANKTON AND BENTHOS IN RESERVOIRS: D--ETC(U)
MAR 80 G R LEIDY, G R PLOSKEY

UNCLASSIFIED WES-TR-E-80-4 NL

4 OF 4

END
DATE FILMED
12-80
DTIC

PART II: RESPIRATION RATES OF AQUATIC INVERTEBRATES AS A FUNCTION OF BODY WEIGHT AND TEMPERATURE FOR VARIOUS TAXONOMIC AND FUNCTIONAL GROUPS

APPENDIX D: PART II - RESPIRATION RATES OF AQUATIC INVERTEBRATES AS A FUNCTION OF BODY WEIGHT AND TEMPERATURE FOR VARIOUS TAXONOMIC AND FUNCTIONAL GROUPS

Taxon	Temperature (°C)	Method	Respiration (mg C/mg C/day)	Original equation and comments	Reference
PHYLUM: MOLLUSCA					
Class: Gastropoda					
Planorbis contortus	4	Polarographic (flow through chamber)	$R= 0.04W^{-0.325}$	log R=0.20+0.68 log W (R in μl O_2/ind/h) W in mg AFDW (ca. 0.3-1 mg)	Calow (1975)
	10		$R=0.07W^{-0.342}$	log R=0.45+0.66 log W	
	15		$R=0.12W^{-0.340}$	log R=0.67+0.664 log W	
Potamopygus jenkinsi	10	Manometric (Cartesian diver)	$R=0.009W^{-0.176}$	log 1000 R=0.194+0.824 log 100 W (R in μl/ind/h) W in mg wet wt. (0.02-10 mg Dry weight)	Lawton and Richards (1970)
		(Gilson respirometer)	$R=0.010W^{-0.21}$	log 1000 R=0.234+0.795 log 100 W	
Ancylus fluviatilis	4	Polarographic (flow through chamber)	$R=0.036W^{-0.34}$	log R=0.147+0.659 log W (R in μl O_2/ind/h) W in mg AFDW (ca. 1-9 mg)	Lawton and Richards (1970)
	10		$R=0.066W^{-0.31}$	log R=0.415+0.693 log W	
	18		$R=0.177W^{-0.323}$	log R=0.841+0.677 log W	
Class: Plecypoda					
Pelecypoda	20	?	$R=0.012W^{-0.28}$	$R=0.094W^{0.721}$ (R in mg O_2/ind/h) W in mg AFDW; calculated from data on freshwater species	Winberg et al. (1973)
Scrobicularia plana	0.5	Polarographic electrode (flow through chamber)	$R=0.0018W^{-0.224}$	$R=71.78W^{0.7757}$ (R in μl O_2/ind/h) W in g dry wt. (20-1000 mg dry weight - tissue)	Hughes (1970)
	4.0		$R=0.0026W^{-0.242}$	$R=102.22W^{-0.7580}$	
	9.5		$R=0.0035W^{-0.233}$	$R=138.84W^{0.7580}$	
	13.5		$R=0.0054W^{-0.249}$	$R=212.18W^{0.7673}$	
	17.5		$R=0.0071W^{-0.440}$	$R=279.76W^{0.7507}$	
	22.5		$R=0.0120W^{-0.236}$	$R=479.82W^{0.5596}$	
	30.75		$R=0.0042W^{-1.034}$	$R=164.25W^{0.7636}$	
				a=0.0362T+1.851 (a value in $R=aW^b$)	

APPENDIX D, PART II (Continued)

Taxon	Temperature (°C)	Method	Respiration (mg C/mg C/day)	Original equation and comments	Reference
PHYLUM: ARTHROPODA					
Class: Insecta					
Order: Plecoptera					
Acroneuria californica	12-30	Manometric (Gilson respirometer)	$R=2.1x10^{-5}$ $6278.3+680.6(T)-144.8(T^2)$	$R=-6278.3-680.6(T)-14.88(T^2)$ (R in µl/g dry wt/h) T in °C (July-August); acclimated 5-15 days at 24°C	Heiman and Knight (1975)
	16-30		$R=2.1x10^{-5}$ $-613.3+88.5(T)-0.916(T^2)$	$R=-613.3+88.5(T)-0.916(T^2)$; (September)	
	6-24		$R=2.1x10^{-5}$ $772.1-83.4(T)-3.74(T^2)$	$R=772-83.4(T)-3.74(T^2)$; (November); all specimens were acclimated to 24°C	
Order: Ephemeroptera					
Isonychia bicolor	12.5-28.5	Manometric (Gilson respirometer)	$R=0.0134W^{-0.225}(T^{0.031})$	log R=-0.225 log W + 0.31 log T-0.193 (R in µl O_2/mg dry wt/h); W in mg dry wt (T in °C); 0.01-2 mg dry wt	Sweeney (1978)
Order: Odonata					
Anax junius	13	Manometric (Gilson respirometer)	$R=0.0422W^{-0.3153}$	log R=3.268-0.3153 log W (R in µl O_2/g dry wt/day) W in g dry wt; (0.02-400 dry wt)	Petitpren and Knight (1970)
	20		$R=0.058W^{-0.2410}$	log R=3.402-0.2410 log W (0.004-30 g dry wt)	
	27		$R=0.038W^{-0.0300}$	log R=3.227-0.0300 log W (0.002-30g dry wt)	
Pyrrhosoma nymphula	16	Manometric (Cartesian diver)	$R=0.057W^{-0.316}$	log 100 R=0.684 log 100 W-0.320 (R in µl O_2/ind/h); W in mg wet wt. (0.05-60 mg dry wt)	Lawton and Richards (1970)
		Winkler titration (closed bottle)	$R=0.048W^{-0.12}$	log 100 R=0.822 log 100 W-0.397 (acclimated to 10°C for 4 months)	
Order: Hemiptera					
Sigara alternata	12.5	Manometric (Gilson respirometer)	$P=0.017W^{-0.101}$	$R=0.825W^{-0.101}$ (R in µl O_2 mg dry wt/h); W in mg dry wt.; calculated from Table 4 (Dry weight = ?)	Sweeney and Schnack (1977)
	16.5		$R=0.031W^{-0.194}$	$R=1.49W^{-0.194}$	

APPENDIX D, PART II (Continued)

Taxon	Temperature (°C)	Method	Respiration (mg C/mg C/day)	Original equation and comments	Reference
Sigara alternata (Cont.)	20.5	Manometric (Gilson respirometer)	$R=0.041W^{-0.30}$	$R=2.00\ W^{-0.30}$	Sweeney and Schnack (1977)
	25.0		$R=0.069W^{-0.399}$	$R=3.326W^{-0.399}$	
Order: Diptera					
Culex pipiens	25	Manometric (Gilson respirometer)	$R=0.017W^{-0.814}$	None (estimated from Figures 1-3); 0.018-0.32 mg dry wt	Buffington (1969)
			$R=0.121W^{-0.293}$		
			$R=0.151W^{-0.254}$		
Pseudodiamesa arctica	0	Polarographic (closed bottle)	$R=0.0048W^{-0.38}$	ln R=-1.227+0.620 ln XV (R in μg O_2/ind/h); W in mg dry wt (calculated from Table 7); dry wt = ?	Welch (1976)
Lauterbornia sp.	0	Polarographic (closed bottle)	$R=0.0071W^{0.028}$	ln R=-0.8431+1.028 ln XV	Welch (1976)
Heterotrissocladius oliveri	0	Polarographic (closed bottle)	$R=0.0025W^{-0.264}$	ln R=-1.902+0.7360 ln XV	Welch (1976)
Trissocladius sp.	0	Polarographic (closed bottle)	$R=0.0047W^{-0.235}$	ln R=-1.242+0.7652 ln XV	Welch (1976)
Orthocladius sp.	0	Polarographic (closed bottle)	$R=0.042W^{-0.207}$	ln R=0.932+0.794 ln W	Welch (1976)
Tanypus punctipennis	5-30	Winkler titration (closed bottle)	$R=0.0042T^{0.825}$	None; 0.392 mg dry wt	Olah (1976)
			$R=0.0062T^{0.825}$	0.064 mg dry wt	
			$R=0.0026T^{0.413}$	0.020 mg dry wt calculated from Figure 5	
Glytotendipes polytomus	8	Manometric (volumetric respirometer)	$R=0.0348W^{-0.33}$	$R=0.3W^{0.67}$ (R in μl O_2/ind/h); W= mg wet wt (0.202-4.04 mg dry wt)	Kamler and Srokosz (1973)
Chironomus riparius	10	Manometric (volumetric respirometer)	$R=0.023W^{-0.29}$	$R=1W^{-0.29}$(R in μl/mg dry wt/h); W in mg dry wt (0.1-2.0 mg dry wt); calculated from Figure 4	Edwards (1957)
	20		$R=0.061W^{-0.30}$	$R=2.61W^{-0.30}$	

APPENDIX D, PART II (Continued)

Taxon	Temperature (°C)	Method	Respiration (mg C/mg C/day)	Original equation and comments	Reference
Class: Crustacea					
Freshwater Crustacea	20	?	$R=0.0028W^{-0.213}$	$R=0.14W^{0.787}$ (R in µl O_2/ind/h); W in g wet wt (0.0086-0.173 mg dry wt)	Suschenya (1969)
			$R=0.0056W^{-0.213}$		
			$R=0.056W^{-0.213}$		
Subclass: Malacostraca Order: Isopoda					
Asellus aquaticus	23	Manometric (volumetric respirometer)	$R=0.069W^{-0.133}$	$R=0.45W^{0.8675}$ (R in µl O_2/ind/h); W in mg dry wt (1.06-6.4 mg dry wt)	Prus (1972)
Order: Amphipoda					
Gammaracanthus lacustris	4-5	Winkler titration (closed bottle)	$R=0.0064\ W^{-0.201}$	$R=0.0778W^{0.799}$ (R in mg O_2/ind/h); W in g dry wt (2.3-213.3 dry wt)	Ivanova (1972)
	11		$R=0.0124W^{-0.228}$	$R=0.147W^{0.772}$	
	15-18		$R=0.008W^{-0.23}$	$R=0.093W^{0.77}$	
Order: Mysidacea					
Mysis relicta	6	Modified Winkler titration (closed bottle)	$R=0.041W^{0.221}$	$R=0.0024W^{0.779}$ (R in mg O_2/ind/h); W in mg dry wt (0.098-1 mg dry wt); acclimated 24 h	Lasenby and Langford (1972)
Mysis relicta	4	Polarographic electrode (closed bottle)	$R=0.0255W^{-0.222}$	log R=0.1789+0.778 log W (R in µg O_2/ind/h); W in mg dry wt (0.5-20 mg dry wt); resting	Foulds and Roff (1976)
			$R=1.390W^{-0.297}$	log R=1.917+0.703 log W (1.6 cm/sec - swimming speed)	
			$R=2.790W^{-0.285}$	log R=2.218+0.714 log W (2.1 cm/sec)	

Taxon	Temperature (°C)	Method	Respiration (mg C/mg C/day)	Original equation and comments	Reference
Order: Decapoda					
Caridina fernadoi	28	Winkler titration (flow through chamber)	$R=0.032W^{-0.045}$	$R=0.283W^{1.050}$ (R in mg O_2/ind/h); W in mg wet wt (0.35-52.5 mg dry wt); standard metabolism	Wycliffe and Job (1977)
			$R=0.043W^{-0.004}$	$R=0.384W^{1.004}$ (Routine metabolism)	
			$R=0.081W^{-0.075}$	$R=0.713W^{0.925}$ (Active metabolism)	
Austropotamobius pallipes	10	Mackereth O_2 electrode (mixing respirometer)	$R=0.003W^{-0.002}$	$R=27.21W^{1.002}$ (R in µg O_2/ind/h); W in g wet wt standard metabolism (1.25-2.1 g dry wt)	Sutcliffe et al. (1975)
			$R=0.009W^{-0.139}$	$R=84.88\ W^{0.861}$; active metabolism	
Subclass: Branchiopoda Order: Cladocera					
Daphnia pulex	?	?	$R=aW^{-0.23}$	light spectrum: violet (0.003-0.056 mg dry wt)	Buikema (1972)
			$R=aW^{-0.367}$	blue	
			$R=aW^{-0.620}$	green	
			$R=aW^{-0.172}$	red	
			$R=aW^{-0.161}$	light intensity: 110 fc	
			$R=aW^{-0.358}$	55	
			$R=aW^{-0.56}$	28	
			$R=aW^{-0.012}$	7	
			$R=aW^{-0.201}$	35	
			$R=aW^{-0.63}$	1.7	
			$R=aW^{-0.070}$	0	
			$R=aW^{-0.274}$	$\bar{X}$	

APPENDIX D, PART II (Continued)

Taxon	Temperature (°C)	Method	Respiration (mg C/mg C/day)	Original equation and comments	Reference
Daphnia pulex	20	Manometric and Winkler (Warburg and closed bottle, respectively)	$R=0.00003W^{-0.119}$	$R=0.0014W^{0.881}$ (R in μl O_2/ind/h); W in mg dry wt (0.0031-0.046 mg dry wt)	Richman (1958)
Daphnia magna	18	Polarographic probe (closed circulating respirometer)	$R=0.098W^{-0.184}$	$R=4.15W^{0.816}$ (R in μl O_2/ind/h); W in mg dry wt (0.001-0.18 mg dry wt)	Kersting and Leeuw-Leegwater (1976)
Daphnia magna	20	Winkler titration (closed bottle)	R=0.023(0.293T-4.28W±0.882)	R=0.293T-4.375W+0.882 (R in μl O_2/mg/h); W in mg dry wt (ca. 0.005-0.165 mg dry wt)	Schindler (1968,
Subclass: Copepoda					
Diaptomus spp.	?	Modified Winkler titration (closed bottle)	$R=0.595W^{-0.483}$	long R=1.425-0.483 long W (R in μl O_2/mg/h); W in mg dry wt (0.0013-0.13 mg dry wt)	Siefken and Armitage (1968)
Diaptomus spp.	5	Micro-Winkler titration	$R=0.145W^{-0.391}$	$R=6.50W^{0.669}$ (R in μl O_2/ind/h); W in mg dry wt ($\bar{X}$ of 5 species = 0.003-0.3 mg dry wt)	Comita (1968)
	10		$R=0.163W^{-0.279}$	$R=7.27W^{0.721}$	
	15		$R=0.332W^{-0.346}$	$R=14.87W^{0.654}$	
	20		$R=0.554W^{-0.374}$	$R=24.76W^{0.626}$	
	25		$R=0.846W^{-0.378}$	$R-37.80W^{0.622}$	
Diaptomus siciloides	5-25	Micro-Winkler titration	log R=6.99 0.057(T)-2.389	log R=0.0574(T)-2.389 (R in μl O_2/ind/h); T in °C (0.0032 mg dry wt)	Comita (1968)
Diaptomus oregonensis	5-25	Micro-Winkler titration	log R=4.71 0.034(T)-1.1914	log R-0.0342(T)-1.1914 (R in μl O_2/ind/h); T in °C (0.0048 mg dry wt)	Comita (1968)
Diaptomus leptopus	5-25	Micro-Winkler titration	log R=1.01 0.0398(T)-1.573	log R=0.0398 (T)-1.578 (R in μl O_2/ind/h); T in °C (0.022 mg dry wt)	Comita (1968)
Diaptomus clavipes	5-25	Micro-Winkler titration	log R=0.779 0.0431(T)-1.545	log R=0.0431(T)-1.545 (R in μl O_2/ind/h); T in °C (0.028 mg dry wt)	Comita (1968)

APPENDIX D, PART II (Continued)

Taxon	Temperature (^oC)	Method	Respiration (mg C/mg C/day)	Original equation and comments	Reference
<u>Diaptomus arcticus</u>	5-25	Micro-Winkler titration	log R=0.075 0.029 (T)-0.647	log R=0.0288 (T)-0.647 (R in μl O_2/ind/h); T in ^oC (0.300 mg dry weight)	Comita (1968)
<u>Limnocalanus macrurus</u>	0.2	Polarographic electrode (closed bottle)	$R=0.0743W^{-0.287}$	$R/W=4.615W^{-0.287}$ (R/W in μg O_2/μg dry wt/h) W= g dry wt (0.003-0.030 mg dry wt)	Roff (1973)
	0-15		log R=0.016 0.0317(T)-1.271	log R=0.0317(T)-1.2711 (R in μg O_2/ind/h); T in ^oC	
<u>Calamoecia lucasi</u>	10	Micro-Winkler titration (closed bottle)	$R=0.021W^{-0.404}$	log R=0.8933-0.404 log W (R in μl O_2/mg dry wt/h); W in mg dry wt. (0.00015-0.0012 mg dry wt)	Green (1975)
	15		$R=0.021W^{-0.3439}$	log R=0.9510-0.3439 log W	
	20		$R=0.028W^{-0.4000}$	log R=1.2063-0.40000 log W	
	25	$R=0.032W^{-0.3806}$	$R=0.032W^{-0.3806}$	log R-1.398-0.3806 log W	
	variable		log R=0.023 0.035(T)-0.38(log W)+ 0.49	log R=0.0356(T)-0.3823(log W)+0.4892	
<u>Macrocyclops albidus</u> (Nauplii)	21	Manometric (Cartesian diver)	$R=0.327W^{-0.55}$	$R=2.27W^{0.45}$ (R in μl O_2/μg/h); W in μg wet wt (0.001-0.003 mg dry wt.)	Klekowski and Shushkina (1966b)
Zooplankton	18-20	Modified Winkler titration	$R=0.355W^{-0.44}$	$R=12.0W^{-0.44}$ (R in μl O_2/mg dry wt/h); W in mg dry	Klekowski and Shushkina (1966a)
	4		$R=0.308W^{-0.99}$	$R=10.4W^{-0.99}$	

APPENDIX E: NONPREDATORY MORTALITY OF ZOOPLANKTON AND BENTHOS

PART I: NONPREDATORY MORTALITY RATES OF ZOOPLANKTON AND BENTHOS

PART II: UPPER AND LOWER LETHAL TEMPERATURES OF ZOOPLANKTON AND BENTHOS

1. The definitions of abbreviations and symbols used in Appendix E, Parts I and II, are given below:

@	at
ca.	approximately
CI-CV	copepodids I - V of Copepoda
C	carbon
°C	degrees Centigrade
F	field study
K	constant
L	laboratory study
μg	microgram
NI-NVI	nauplii I - VI of Copepoda
NPM	nonpredatory mortality
?	unknown or could not be determined from data
ULT	upper lethal temperature
VS	varied seasonally
$\bar{X}$	mean

PART I: NONPREDATORY MORTALITY RATES OF ZOOPLANKTON AND BENTHOS

APPENDIX E: PART I (Continued)

Taxon	Field or lab	Temperature (°C)	Food	Comments	Nonpredatory mortality (mg C/mg C/day) x 100	Reference
PHYLUM: MOLLUSCA						
Class: Pelecypoda						
Anodonta anatina	F	VS	natural assemblage	$\bar{X}$ daily NPM = annual NPM/365; predatory mortality assumed to = 0		Negus (1966)
				5-6 years old	0.05	
				6-7 years old	0.07	
				7-8 years old	0.10	
				8-9 years old	0.23	
Class: Gastropoda						
Lymnea obruusa	L	10	*Elodea* sp. and *Ludwigia* sp.	NPM was significantly correlated with temperature	0.59	Mattice (1976)
		15			0.29	
		17			0.36	
		20			0.50	
		25			1.80	
		26			1.71	
PHYLUM: ARTHROPODA						
Class: Insecta						
Order: Trichoptera						
Potamophylax cingulatus	F	VS	detritus	Cages in the stream excluded predators;		Otto (1975)
				November	0.22	
				December	0.38	
				January	0.38	
				February	0.11	
				March	0.07	
				April	0.17	
				May	0.10	
				June	0.85	
				July	1.95	
				August	8.98	
				Annual $\bar{X}$	1.32	

APPENDIX E: PART I (Continued)

Taxon	Field or lab	Temperature (°C)	Food	Comments	Nonpredatory mortality (mg C/mg C/day) x 100	Reference
Class: Crustacea						
Subclass: Malacostraca						
Order: Amphipoda						
Hyalella azteca	L	10	?	No 1st instar survival	——	Cooper (1965)
		15	?		0.20	
		20	?		0.55	
		25	?		0.61	
Gammarus spp.	L	7.1-11.2	Cabomba sp., Myriophyllum sp., and green algae	NPM estimates are based on control data	0.78-1.23	Ginn et al. (1976)
		11.7			0.49-0.63	
		25.5			0.60-1.00	
		26.5			0.40-1.10	
		27.7			4.00-5.80	
Gammarus pulex	L	15		$\bar{X}$ % NPM is given at 21, 42, and 70 days for each food type	21 42 70	Willoughby and Sutcliffe (1976)
			decayed elm and oak leaves		0 0 0	
			undecayed elm and oak leaves		0 0 0	
			green grass		0.68 0.48 0.36	
			Clavariopsis sp.		0 0.60 0.48	
			Zygogonium sp.		0.81 1.43 1.43	
			brown grass		0 0 1.14	
			no food		1.78 3.03*	
			Tricladium sp.		1.19 1.52	
					1.09 2.16	
					0.30 0.30	
Subclass: Brachiopoda						
Order: Cladocera					IF MF	
Daphnia pulex	L	15	Chlamydomonas sp. Chlorella sp.	IF = immature females; MF = mature females	1.19 0.98	Craddock (1976)
		18			1.35 0.98	
		21			5.55 1.04	
		24			6.25 1.85	
		27			4.55 2.38	
		30			63.28 57.14	
		33			400.00 400.00	

* Percent NPM for 33 days.

APPENDIX E: PART I (Continued)

Taxon	Field or lab	Temperature (°C)	Food	Comments	Nonpredatory mortality (mg C/mg C/day) x 100	Reference
Daphnia pulex	L	X	*Chlamydomonas mocurusi*	Density in 25 ml of media: 1	2.32	Frank et al. (1957)
				2	2.70	
				4	1.88	
				8	1.82	
				16	1.82	
				24	1.96	
				32	1.96	
Daphnia galeata	L	5	*Chlorella* sp.	Median % mortality/day	0	Hall (1964)
		11	*Ankistrodesmus* sp.		0.33	
		20	and other green algae		0.71	
		25			1.66	
Daphnia rosea	F	VS	VS	6-14 July	0.35	Dodson (1972)
				14-20 July	0.70	
				20-25 July	0.71	
				25 July - 1 August	0.36	
				1-8 August	0.40	
				8-15 August	0.59	
				15-22 August	0.37	
				22-29 August	0.18	
				8 August - 4 September	0.63	
				$\bar{X}$	0.57	
Daphnia rosea	F	VS	VS	Predation was considered negligible;		Clark and Carter (1974)
				May	0.05	
				June	0.15	
				July	0.12	
				August	0	
				September	0.04	
				October	0.05	
Daphnia spp.	F	VS	VS	% NPM/day was estimated assuming that *Leptodora kindtii* was the only predator;		Wright (1965)
				April-June	0.12	
				July-August	0.17	

APPENDIX E: PART I (Continued)

Taxon	Field or lab	Temperature (°C)	Food	Comments	Nonpredatory mortality (mg C/mg C/day) x 100			Reference
					Egg-CI	CI-CIII	CIII-Adult	
Daphnia retrocurva	F	VS	VS	Predation was considered negligible;				Clark and Carter (1974)
				May	0.14			
				June	0.10			
				July	0.15			
				August	0			
				September	0.02			
				October	0.03			
Diaphanosoma leuchtenbergiana	F	?	?	May	0			Clark and Carter (1974)
				June	0			
				July	0			
				August	0.02			
				September	0.09			
				October	0.1			
Ceriodaphnia reticulata	L, F	23 in lab 20-26 in field	?	Lab and field experiments yield the same results	1.62			Hall et al. (1970)
Simocephalus serrulatus	L, F	23 in lab 20-26 in field	?	Lab and field experiments yield the same results	2.5-2.7			Hall et al. (1970)
Subclass: Copepoda								
Calanus helgolandicus	L	14.7-15.3	Prococentrum micans @	Data are presented for 3 life periods				Paffenhofer (1976)
			70.9 μg C/l		0.54	0	0	
			41.8 μg C/l		0.40	0.25	0	
			Gymnodinium polyedra @					
			41.0 μg C/l		0	0	0	
			Gymnodinium splendens @					
			95 μg C/l		3.35	0.49	0	
			Lauderina borealis @					
			48.3 μg C/l		4.80	0.33	0	
			49.9 μg C/l		3.97	0.30	0.38	
			102.3 μg C/l		1.01	0		
			100.6 μg C/l		0.89	0.26		
Calanus helgolandicus	?	15	Thalassiosira sp. @					Mullin and Brooks (1970)
			177 μg C/l		2.35			
			266 μg C/l		1.50			

APPENDIX E: PART I (Continued)

Taxon	Field or lab	Temperature (°C)	Food	Comments	Nonpredatory mortality (mg C/mg C/day) x 100	Reference
Calanus helgolandicus	L	15	Gymnodinium splendens @ 95 μg C/l	Data was calculated assuming a mean life of 36 days	0.33	Paffenhofer (1971)
			Lauderica borealis @ 49 μg C/l		0.72-0.81	
			101 μg C/l		0.05-0.15	
			36 μg C/l		1.38-1.53	
Rhincalanus nasutus	L	15	Ditylum sp. @ 145 μg C/l		0.64	Mullin and Brooks (1970)
		15	Thalassiosira sp. @ 196 μg C/l		1.47	
		10	Thalassiosira sp. @ 352 μg C/l		1.50	
		10	Ditylum sp. @ 200 μg C/l		1.15	
Copepod nauplii	F	17-18	natural assemblage		0.60-1.74	Petipa et al. (1970)
Paracalanus sp.	F	17-18	natural assemblage	Copepodite I - III	0.27-0.62	Petipa et al. (1970)
				Copepodite IV - VI	0.41-0.44	
Diaptomus clavipes	L	20-25	?	Egg-NII	15.55	Gehrs and Robertson (1975)
				NIV-NVI	4.26	
				CI	0.70	
				CII	1.09	
				CIII	0.67	
				CIV	0.38	
				CV	0.91	
				X	1.47-2.5	
Omnivorous zooplankton	F	17-18	natural assemblage		0.98-1.31	Petipa et al. (1970)
Carnivorous zooplankton	F	17-18	natural assemblage	Primary carnivores	0.74-1.33	Petipa et al. (1970)
				Secondary carnivores	0.94-0.96	
				Tertiary carnivores	0 -.24	

PART II: UPPER AND LOWER LETHAL TEMPERATURES OF ZOOPLANKTON AND BENTHOS

APPENDIX E: PART II (Continued)

Taxon	Comments	Acclimation temperature (°C)	Exposure time	Lower lethal temperature (°C)	Upper lethal temperature (°C)	Reference
PHYLUM: MOLLUSCA						
Class: Pelecypoda						
Corbicula manilensis		5 30 15	long term	 12 2	24 34	Mattice and Dye (1976)
Corbicula manilensis		10	several minutes		43	Isom (1971)
Corbicula manilensis		23	4 days		34	Habel (1970)
Class: Gastropoda						
Theodoxus fluviatilis	Acclimatization increased tolerance		variable		36-38	Skoog (1976)
Lymnea peregra			variable		36-38	Skoog (1976)
PHYLUM: ARTHROPODA						
Class: Crustacea						
Subclass: Branchiopoda						
Order: Anostraca						
Triops longicaudatus		?	20 minutes		40	Hillyard and Vinigar (1972)
Thamnocephalus platyurus		?	1 hour		42	Hillyard and Vinigar (1972)
Branchipus serratus	Adults	?	?		28	Altman and Dittmer (1966) as cited by Goss and Bunting (1976)
Streptocephalus seali	Temperature was increased 1°C /6-10 minutes in the 1st hour and then 1°C /12-20 minutes thereafter	28-31	?		44.5	Altman and Dittmer (1966) as cited by Goss and Bunting (1976)
Order: Conchostraca						
Caenestheriella synecia	Adults	?	?		38	Jensen et al. (1969) as cited Goss and Bunting (1976)

APPENDIX E: PART II (Continued)

Taxon	Comments	Acclimation temperature (°C)	Exposure time	Lower lethal temperature (°C)	Upper lethal temperature (°C)	Reference
Order: Cladocera						
<u>Daphnia pulex</u>	Reproduction ceased after 27°C	15 or 20	192 hours 0.5 hours		27 30	Craddock (1976)
<u>Daphnia pulex</u>		15,10,15,20,25,30	48 hours		32-35	Goss and Bunting (1976)
<u>Daphnia pulex</u>	Adults	ambient	variable		32	Brown and Crozier (1927) as cited by Goss and Bunting (1976)
<u>Daphnia pulex</u>	Adults	?	?		30	Altman and Dittmer (1966) as cited by Goss and Bunting (1976)
<u>Daphnia pulex</u>		?	?		35-41	Brown (1928) as cited by Bovee (1949)
<u>Daphnia magna</u>		5,10,15,20,25,30	48 hours		30	Goss and Bunting (1976)
<u>Daphnia schodleri</u>	Lethal at high food concentrations Lethal at low food concentrations	? ?	? ?		30 35	Hayward and Gallup (1976)
<u>Daphnia atkinsoni</u>		?	?		26.8-30+	Jensen et al. (1969) as cited by Goss and Bunting (1976)
<u>Daphnia</u> sp.	Highest temperature for successful culture	?	One life cycle		27	Geller (1975)
<u>Alona affinis</u>	Adults	?	?		40.5	Jensen et al. (1969) as cited by Goss and Bunting (1976)
<u>Chydorus globosus</u>		?	?		35.0-35.5	Jensen et al. (1969) as cited by Goss and Bunting (1976)
<u>Eurycercus lamellatus</u>	Adults	?	?		35.0-35.5	Jensen et al. (1969) as cited by Goss and Bunting (1976)
Subclass: Copepoda						
<u>Limnocalanus macrurus</u>	Arctic species; temperature was increased 10°C /hour	3	ca. 2 hours		18-21	Roff (1973)

APPENDIX E: PART II (Continued)

Taxon	Comments	Acclimation temperature (°C)	Exposure time	Lower lethal temperature (°C)	Upper lethal temperature (°C)	References
Cyclops serrulatus	Adults; stepped from 26° C to death point	ambient	—		34-35	Coker (1934) as cited by Goss and Bunting (1976)
Cyclops vernalis		9 15 29	?		32.6-33.0 32+ 37.0-39.6	Coker (1934) as cited by Goss and Bunting (1976)
Cyclops viridus		9 12 15 29	?		31.0 32.5 32.5-34.0 35-37	Coker (1934) as cited by Goss and Bunting (1976)
Eucyclops agilis	Stepped from 26°C to death point	ambient	—		34-35	Coker (1934) as cited by Goss and Bunting (1976)
Thermocyclops neglectus		35	One life cycle		35	Goss and Bunting (1976)
Eurytemora affinis	Adults	5,10,15,20,25	48 hours		25-30	Heinle (1969) as cited by Goss and Bunting (1976)
Subclass: Malacostraca Order: Mysidacea						
Mysis relicta		7.5 4.5	5 hours 16 days; 1.0°C /day 6 days; 2.5° C /day 4 days; 5.0°C /day		16.0-16.5 16 18 16	Smith (1970) as cited by Goss and Bunting (1976)
Order: Isopoda						
Asellus intermedius		10 20 25 30	100 minutes		33.4 35.3 35.9 36.7	Sprague (1963)
Order: Amphipoda						
Pontoporeia affinis		6	24 hours 96 hours 30 days		12.0 10.8 10.4	Smith (1972) as cited by Goss and Bunting (1976)

APPENDIX E: PART II (Continued)

Taxon	Comments	Acclimation temperature (°C)	Exposure time	Lower lethal temperature (°C)	Upper lethal temperature (°C)	Reference
Hyalella azteca		10	?		34.4	Sprague (1963)
Hyalella azteca	Temperature raised $10^{\circ}C$/5 days	?	?		35-37	Pennak and Rosine (1976)
Hyalella azteca	Temperature raised $0.2^{\circ}C$/day	22-23	?		33-35	Bovee (1949)
Gammarus fasciatus		10 20	100 minutes		32 34	Sprague (1963)
Gammarus pseudolimnaeus		10 20	100 minutes		32 34	Sprague (1963)
Gammarus pseudolimnaeus	The acclimation temperature is the optimum for growth	18	96 hours 30 days		26 22-24	Smith (1973)
Gammarus lacustris		18	96 hours 30 days		26 25	Smith (1973)
Gammarus lacustris	Temperature raised $10^{\circ}C$/5days	?	?		26-28	Pennak and Rosine (1976)
Gammarus spp.	97% mortality in 5 days 87% mortality in 5 days	26.5 27.7	1 hour 2 hours		38.2 36.0	Ginn et al. (1976)
Order: Decapoda						
Pacifastacus leniusculus	The lower median tolerance limits depended on the acclimation temperature	25 20 15	96 hours	2.5 0.4 0.0		Becker et al. (1977)
Class: Insecta Order: Ephemeroptera						
Isonychia sp.	Neither acclimation temperature nor the magnitude of thermal shock were consequential until a combination of the two approached the ULT	4-24	1-40 minutes		33.5-35.0	Sherberger et al. (1977)

APPENDIX E: PART II (Continued)

Taxon	Comments	Acclimation temperature (°C)	Exposure time	Lower lethal temperature (°C)	Upper lethal temperature (°C)	Reference
Order: Trichoptera						
Hydropsyche sp.	Neither acclimation temperature nor the magnitude of thermal shock were consequential until a combination of the two approached the ULT	4-24	1-40 minutes		36-38	Sherberger et al. (1977)

In accordance with letter from DAEN-RDC, DAEN-ASI dated 22 July 1977, Subject: Facsimile Catalog Cards for Laboratory Technical Publications, a facsimile catalog card in Library of Congress MARC format is reproduced below.

Leidy, George R
Simulation modeling of zooplankton and benthos in reservoirs: documentation and development of model constructs / by G. R. Leidy, G. R. Ploskey, USDI Fish and Wildlife Service, National Reservoir Research Program, Fayetteville, Arkansas. Vicksburg, Miss. : *U. S. Waterways Experiment Station ; Springfield, Va.* : available from National Technical Information Service, 1980.
221, [86] p. : ill. ; 27 cm. (Technical report - U. S. Army Engineer Waterways Experiment Station ; E-80-4)
Prepared for Office, Chief of Engineers, U. S. Army, Washington, D. C., under EWQOS Task IB.1.
References: p. 183-221.

1. Benthos. 2. Environmental effects. 3. Mathematical models. 4. Reservoirs. 5. Simulation. 6. Stochastic models. 7. Zooplankton. I. Ploskey, G. R., joint author. II. United States. Fish and Wildlife Service. National Reservoir Research Program. III. United States. Army. Corps of Engineers. IV. Series: United States. Waterways Experiment Station, Vicksburg, Miss. Technical report ; E-80-4.
TA7.W34 no.E-80-4


2