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

FISH AND WILDLIFE SERVICE, FAYETTEVILLE,
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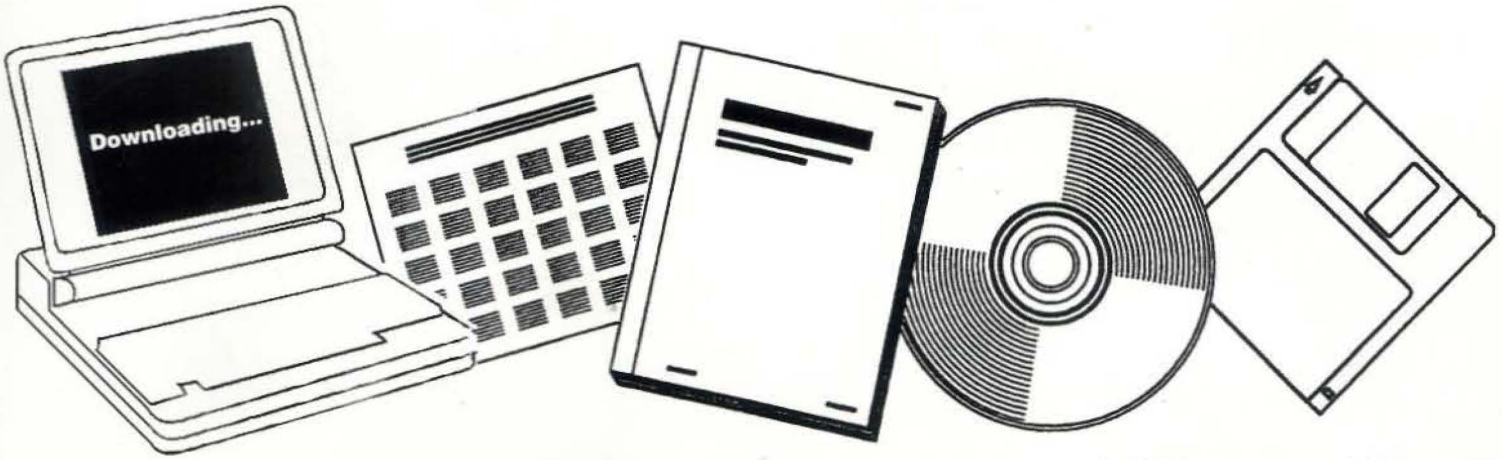

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A literature review and analysis of published data on zooplankton and benthos bioenergetics form the basis used in this report for the development of stochastic model constructs for the simulation of zooplankton and benthos dynamics in reservoirs. 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)

20. ABSTRACT (Continued).

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

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.

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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

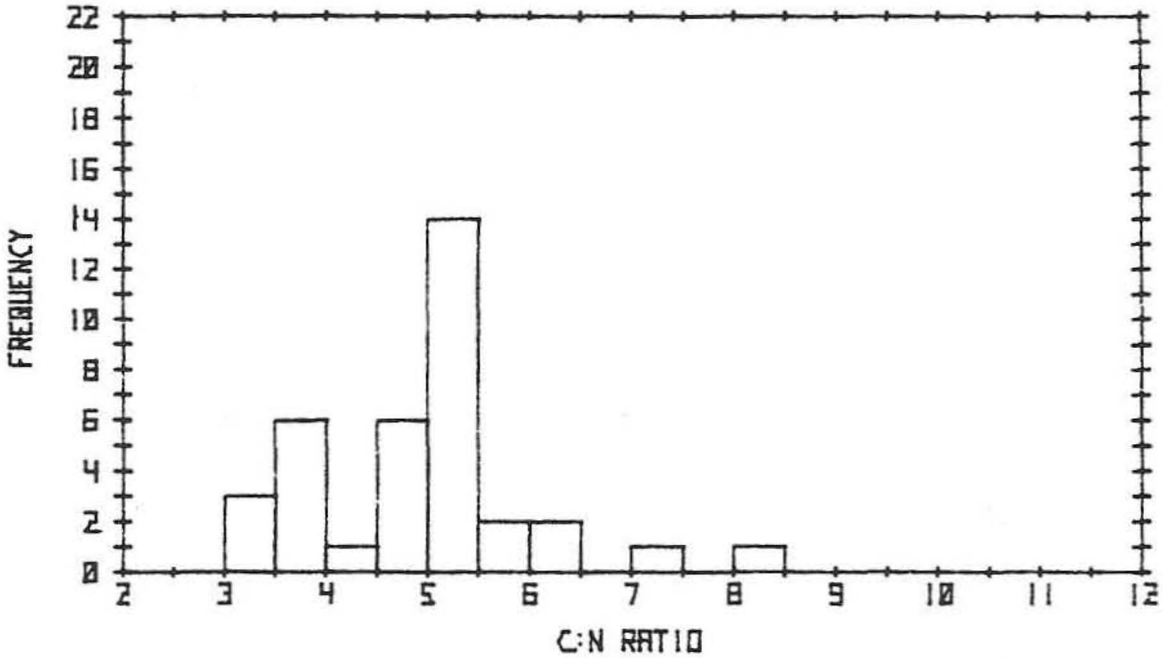

Figure 1. Frequency distribution of macrobenthos C:N ratios

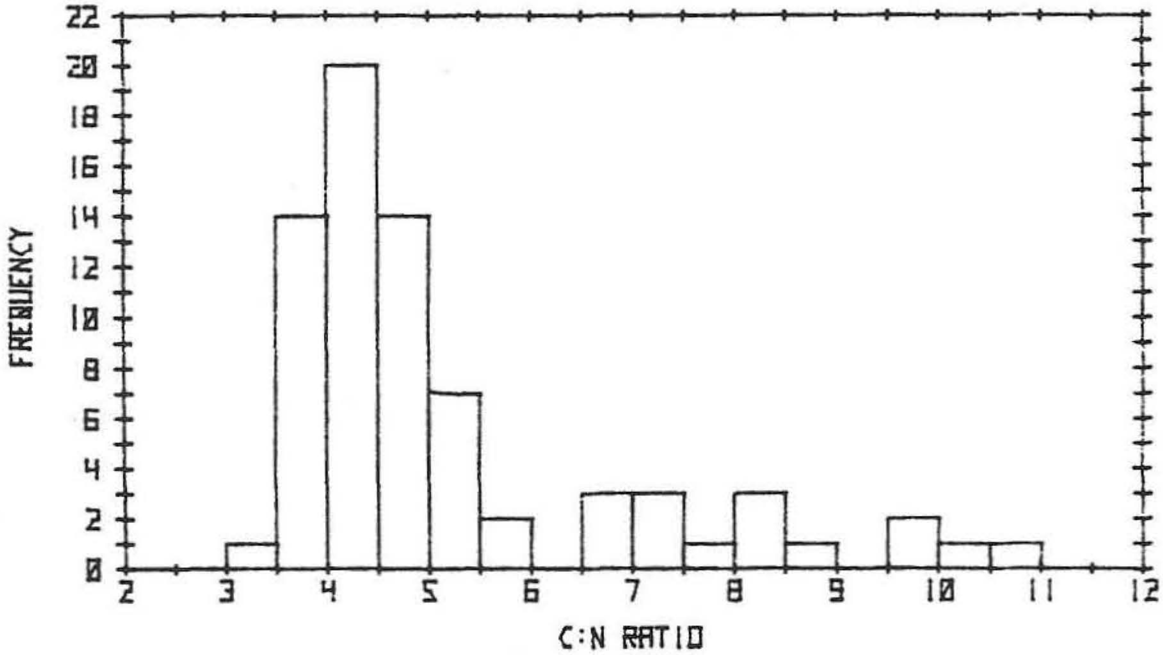

Figure 2. Frequency distribution of zooplanton C:N ratios

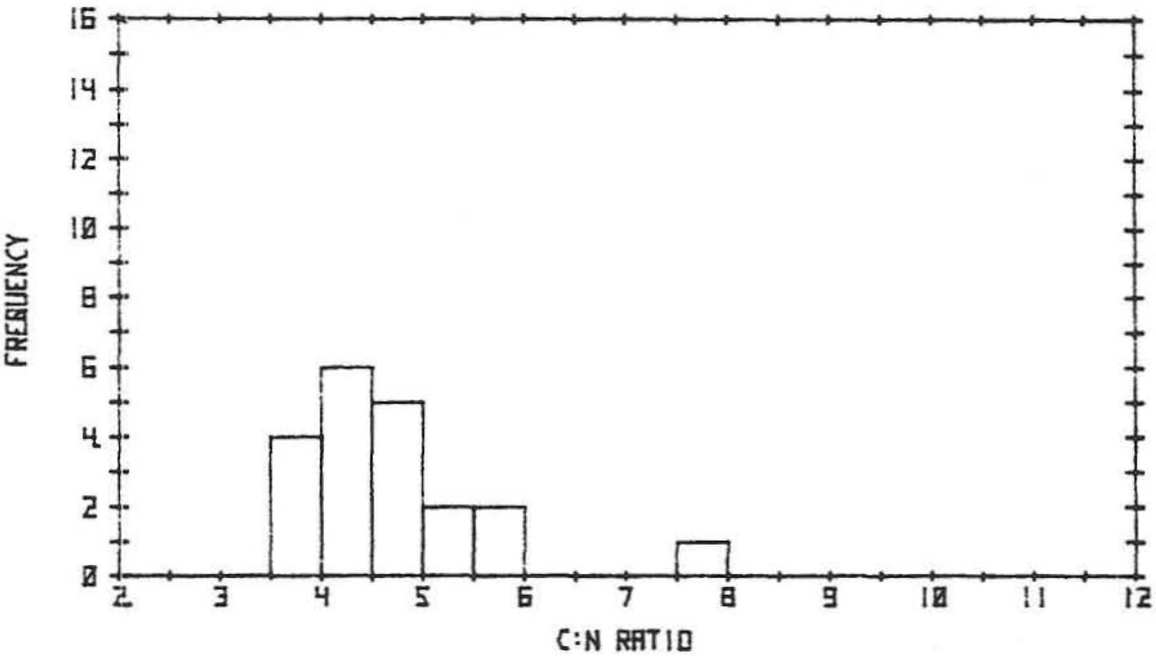

Figure 3. Frequency distribution of cladoceran C:N ratios

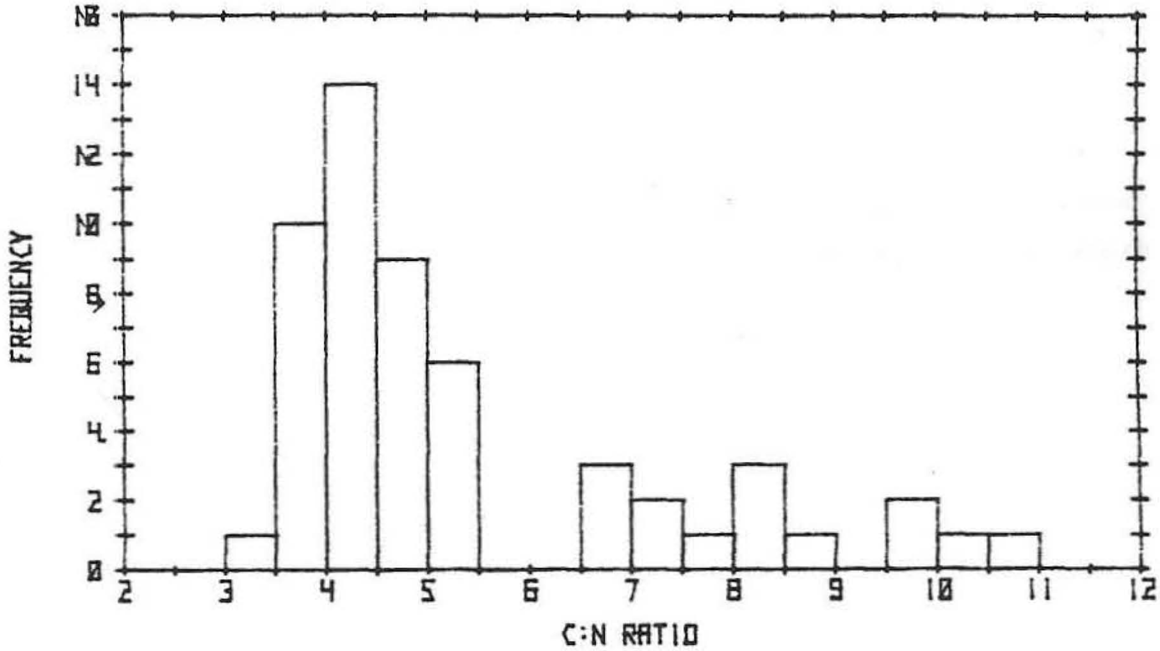

Figure 4. Frequency distribution of copepod C:N ratios

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 ($\text{mg C} \cdot \text{mg C}^{-1} \cdot \text{day}^{-1}$) of consumption (Part III), assimilation (Part IV), egestion + excretion

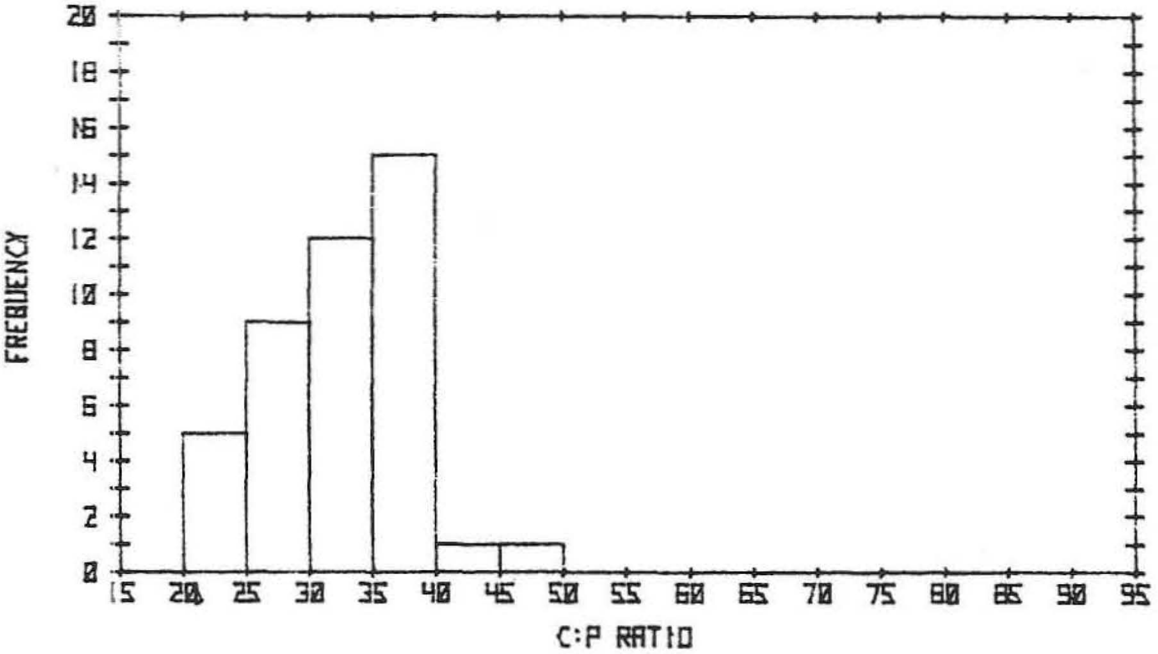

Figure 5. Frequency distribution of macrobenthos C:P ratios

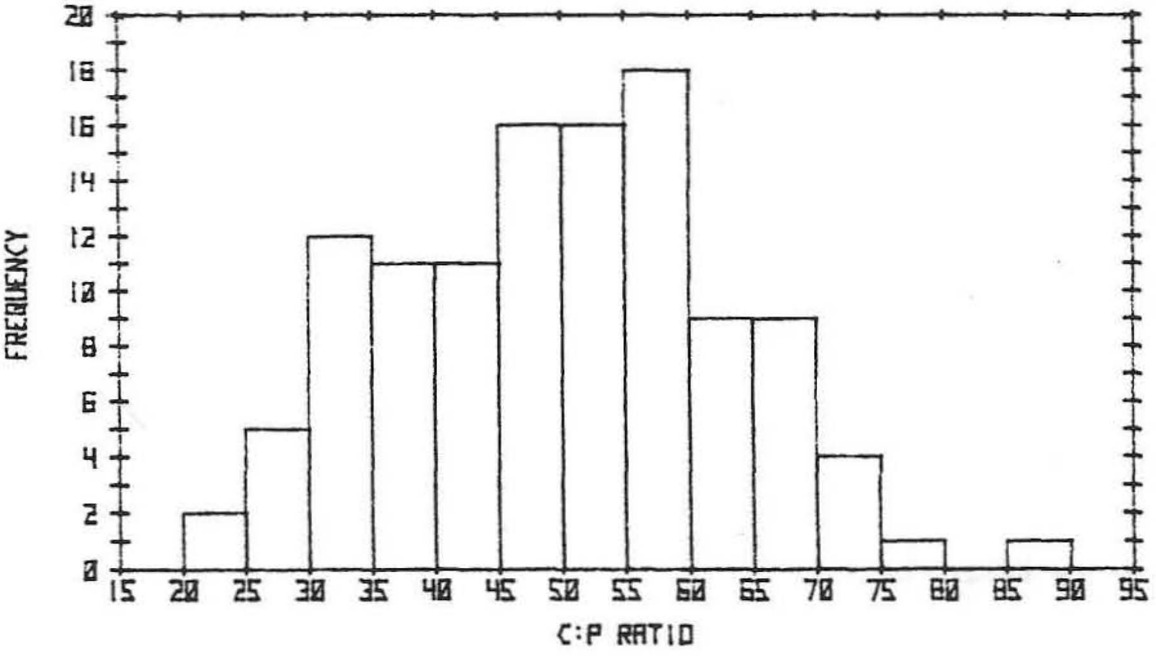

Figure 6. Frequency distribution of zooplankton C:P ratios

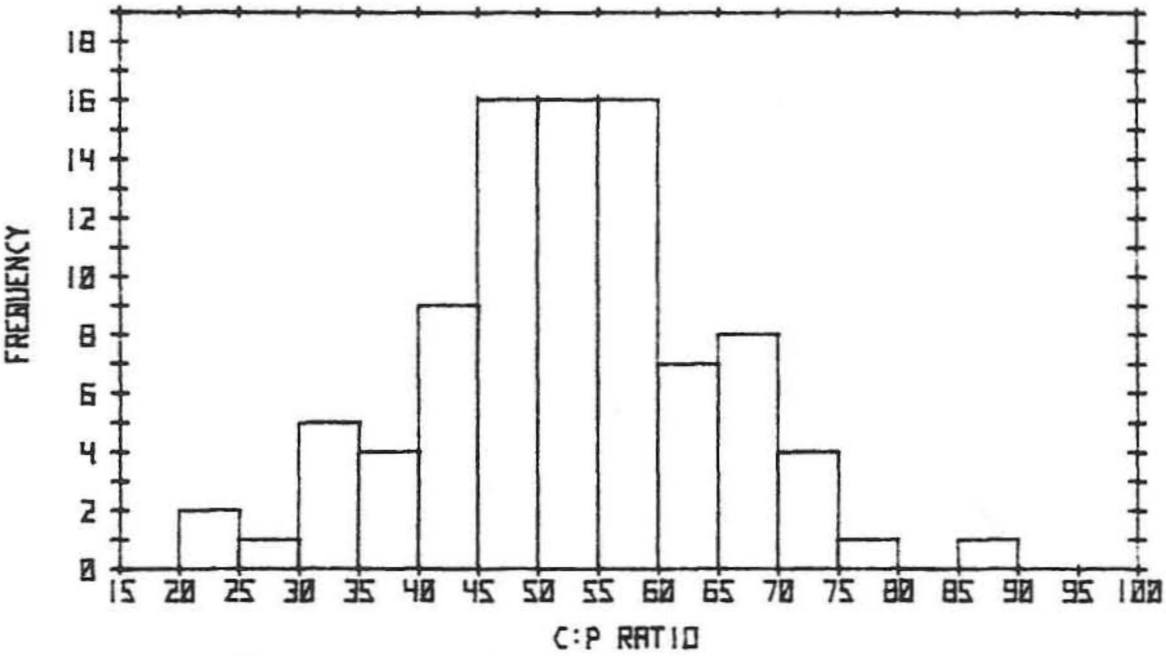

Figure 7. Frequency distribution of copepod C:P ratios

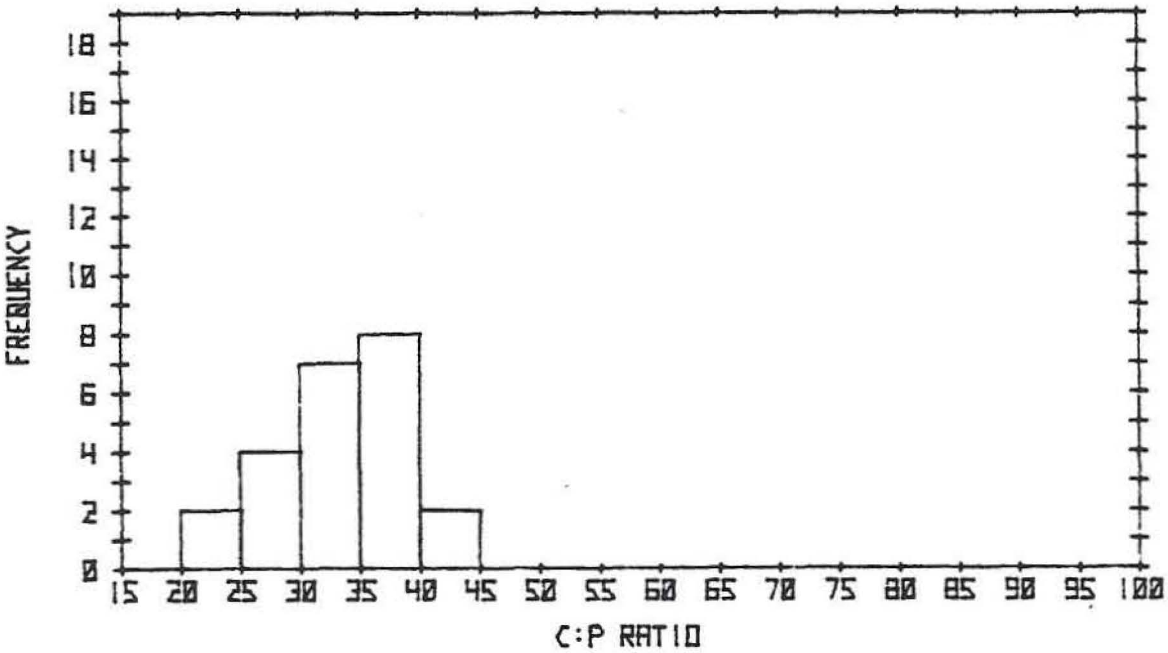

Figure 8. Frequency distribution of cladoceran C:P ratios

(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 ($\text{mg N or mg P} \cdot \text{mg C}^{-1} \cdot \text{day}^{-1}$) 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).