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

FISH AND WILDLIFE SERVICE, FAYETTEVILLE, AR. NATIONAL RESERVOIR RESEARCH PROGRAM

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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:

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

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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.

The findings in this report are not to be construed as an official Department of the Army position unless so designated by other authorized documents

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

	Page
PREFACE	1
PART I: INTRODUCTION	9
Modeling Concepts	9
Objectives	10
Scope	11
PART II: ELEMENTAL CARBON, NITROGEN, AND PHOSPHORUS COMPOSITION OF ZOOPLANKTON AND BENTHOS	14
Introduction	14
Nitrogen	16
Carbon	18
Carbon:Nitrogen Ratios	18
Phosphorus	19
Summary of Constructs	22
Conclusions	25
PART III: CONSUMPTION BY ZOOPLANKTON AND BENTHOS	26
Section A: Zooplankton Grazing	27
Consumption by Filter-Feeding Zooplankton	28
Food Selectivity by Zooplankton	51
Effect of Temperature on Consumption	66
Diel Variations in Filtering and Feeding Rates	76
Consumption by Predatory Zooplankton	85
Seasonal Changes in Grazing	90
Synergistic Effects of Environmental Variables	90
Section B: Benthic Grazing	93
Effect of Food Concentration	93
Effect of Temperature	97
Effect of Diel Variations	97
Section C: Model Constructs	99
Summary of Constructs	99
Definitions	100
Step 1 - Food Concentrations	100
Step 2 - Food Selectivity	101
Step 3 - Temperature	102
Step 4 - Diel Variations	102
Step 5.	102
Section D: Conclusions	103
PART IV: ASSIMILATION EFFICIENCY, EGESTION, AND EXCRETION OF ZOOPLANKTON AND BENTHOS	105
Introduction	105
Methodology	108
Factors Affecting Assimilation Efficiency	113
Summary of Constructs	120
Conclusions	121
PART V: RESPIRATION OF ZOOPLANKTON AND BENTHOS	127

Introduction 127
Methodology 127
Variation Due to Experimental Conditions 130
Variation Due to Conversion of Units 133
Model Constructs 135
Effects of Body Weight 140
Effects of Dissolved Oxygen Concentration 149
Effects of Temperature 154
Summary of Constructs 158
Conclusions 160

PART IV: NONPREDATORY MORTALITY OF ZOOPLANKTON AND BENTHOS . . . 161

Introduction 161
Previous Models 161
Experimental Estimates 162
Factors Affecting Nonpredatory Mortality 165
Summary of Constructs 174
Conclusions 176

PART VII: RECOMMENDATIONS 177

General 177
Chemical Composition 177
Consumption by Zooplankton and Benthos 178
Assimilation Efficiency (A/G), Egestion (F), and Excretion (E) 179
Respiration 180
Nonpredatory Mortality (NPM) 181

REFERENCES 183

APPENDIX A: ELEMENTAL CARBON, NITROGEN, AND PHOSPHORUS COMPOSITION OF ZOOPLANKTON AND BENTHOS A1

APPENDIX B: FILTERING RATES REPORTED FOR FRESHWATER ZOOPLANKTERS ZOOPLANKTERS B1

APPENDIX C: ZOOPLANKTON AND BENTHOS ASSIMILATION EFFICIENCIES . C1

Definitions of Abbreviations and Symbols Used in Appendix C C2
Definitions of Experimental Methods Listed in Appendix C . C3

APPENDIX D: RESPIRATION OF ZOOPLANKTON AND BENTHOS D1

Part I: Respiration Rates of Aquatic Invertebrates for Various Taxomonic and Functional Groups . . . D4
Part II: Respiration Rates of Aquatic Invertebrates as a Function of Body Weight and Temperature for Various Taxonomic and Functional Groups . . . D22

APPENDIX E: NONPREDATORY MORTALITY OF ZOOPLANKTON AND BENTHOS . E1

Part I: Nonpredatory Mortality Rates of Zooplankton and Benthos E3
Part II: Upper and Lower Lethal Temperatures of Zooplankton and Benthos E9

LIST OF FIGURES

No.		Page
1	Frequency distribution of macrobenthos C:N ratios	20
2	Frequency distribution of zooplankton C:N ratios	20
3	Frequency distribution of cladoceran C:N ratios	21
4	Frequency distribution of copepod C:N ratios	21
5	Frequency distribution of macrobenthos C:P ratios	23
6	Frequency distribution of zooplankton C:P ratios	23
7	Frequency distribution of copepod C:P ratios	24
8	Frequency distribution of cladoceran C:P ratios	24
9	Relation among food concentration, filtering rate, and grazing rate, based upon early studies of filter-feeding marine zooplankton	32
10	Grazing rate of Daphnia magna at various concentrations of three algal species based on the data of Ryther (1954)	34
11	Grazing rates of Daphnia magna at various concentrations of four food sources based on the data of McMahon and Rigler (1965)	35
12	Relation among food concentration, filtering rate, and grazing rate first proposed by Rigler (1961a)	36
13	Comparison of the Ivlev and Michaelis-Menten functions with the same half-saturation value, k_s	40
14	The relation of the constant, k , to the incipient limiting food concentration, B_{lim}	47
15	The relation of the constant, k , to the maximum grazing rate, G_{max}	47
16	The relation of the maximum grazing rate, G_{max}, to the incipient limiting food concentration, B_{lim}	48
17	Grazing rate as a function of temperature for Daphnia pulex	72
18	Grazing rate as a function of temperature for Daphnia rosea	72
19	The relation of temperature to the relative increase in grazing rates for animals fully acclimated to test temperatures	74
20	The relation of temperature to the relative increase in grazing rate for animals incompletely acclimated to test temperatures	75

LIST OF FIGURES

No.		Page
21	The diel pattern of filtering rate change at 18°C in a light:dark 16:8 photocycle	79
22	The diel pattern of filtering rate change of Daphnia pulex in Three Lakes, Michigan	80
23	The diel grazing function of filter-feeding zooplankton exhibiting a unimodal peak in grazing during the night . .	84
24	The diel grazing function of filter-feeding zooplankton exhibiting a biomodal peak in grazing during the night . .	84
25	The daily ration of Macrocyclops albidus females as a function of food concentration	86
26	Frequency histogram of zooplankton assimilation values (A) as a percentage of consumption (G)	107
27	Frequency histogram of benthos assimilation values (A) as a percentage of consumption (G)	107
28	Frequency histogram of benthic carnivore assimilation values (A) as a percentage of consumption (G)	114
29	Frequency histogram of benthic herbivore-detritivore assimilation values (A) as a percentage of consumption (G)	114
30	Frequency histogram of Rotatoria assimilation values (A) as a percentage of consumption (G)	122
31	Frequency histogram of Copepoda assimilation values (A) as a percentage of consumption (G)	122
32	Frequency histogram of Cladocera assimilation values (A) as a percentage of consumption (G)	123
33	Frequency histogram of Entomostraca assimilation values (A) as a percentage of consumption (G)	123
34	Frequency histogram of zooplankton egestion (F) and excretion (E) values as a percentage of consumption (G)	124
35	Frequency histogram of benthos egestion (F) and excretion (E) values as a percentage of consumption (G) . .	124
36	Frequency histogram of assimilation values (A) as a percentage of consumption (G) when zooplankton were fed blue-green algae and/or detritus	125
37	Frequency histogram of assimilation values (A) as a percentage of consumption (G) when zooplankton were fed green algae	125

LIST OF FIGURES

No.		Page
38	Frequency histogram of respiration (R), as a percentage of consumption (G), for aquatic invertebrates	139
39	Frequency histogram of respiration rates for Cladocera	140
40	Frequency histogram of respiration rates for Copepoda	141
41	Frequency histogram of respiration rates for Rotatoria	141
42	Frequency histogram of respiration rates for benthic Crustacea	142
43	Frequency histogram of respiration rates for aquatic Insecta	142
44	Frequency histogram of respiration rates for Oligochaeta	143
45	Frequency histogram of respiration rates for Mollusca	143
46	Respiration (R) as a function of organism weight (W) for aquatic invertebrates at 20°C	144
47	Frequency histogram of respiration rates for aquatic invertebrates of weight class I	146
48	Frequency histogram of respiration rates for aquatic invertebrates of weight class II	147
49	Frequency histogram of respiration rates for aquatic invertebrates of weight class III	147
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)	148
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)	150
52	Values of the coefficient a as a function of temperature (T) for aquatic invertebrates	150
53	Respiration correction factor (F_o) as a function of dissolved oxygen concentration.	154
54	Mean rates of respiration (R) as a function of temperature (T) for aquatic invertebrates	157
55	The conversion function, $F_{\text{to } 20}$, for adjusting respiration rates (R) at ambient temperatures to rates at 20°C	159
56	The conversion function, $F_{\text{from } 20}$, for adjusting respiration rates (R) at 20°C to rates at ambient temperature	159
57	Frequency histogram of nonpredatory mortality rates (NPM) for zooplankton	163

LIST OF FIGURES

No.		Page
58	Frequency histogram of nonpredatory mortality rates (NPM) for benthos	163
59	Upper lethal temperatures (ULT) and lower lethal temperatures (LLT) for the clam Corbicula manilensis acclimated to different temperatures	167
60	Frequency histogram of upper lethal temperatures (ULT) for aquatic organisms	169
61	Nonpredatory mortality (NPM) as a function of temperature (T) for aquatic organisms	169
62	Nonpredatory mortality (NPM) as a function of dissolved oxygen concentration (O_2) for zooplankton and littoral benthos	172
63	Nonpredatory mortality (NPM) as a function of dissolved oxygen concentration (O_2) for profundal benthos	173

LIST OF TABLES

1	Percent Composition of C, N, and P in Proteins, Lipids, and Carbohydrates	17
2	Factors Reported to Influence the Feeding of Filter-Feeding Zooplankton and a List of References	30
3	Grazing Rate Parameters of the Ivlev Equation Calculated from Experimental Studies that Demonstrated the Existence of a Maximum Grazing Rate	42
4	Range of Grazing Rates Calculated from Experimental Studies in which a Maximum Grazing Rate Could Not be Demonstrated	43
5	Literature Values for the Daily Ration of Filter-Feeding Zooplanktons	44
6	Relationship Among G_{max}, B_t, and Z as Defined by Equation 8 and Based on the Data in Table 3	50
7	Summary of Literature Data on the Effects of Temperature on the Grazing Rates of Filter-Feeding Zooplankton	70
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	77

LIST OF TABLES

No.		Page
9	Values for Relative Change in Light Intensity, as Cited by Haney and Hall (1975), that Represent Threshold Light Intensity for Positive Phototaxis	83
10	Published Values for the Daily Ration of the Planktonic Omnivores and Predators	87
11	Seasonal Changes in the Grazing Rate of Zooplankton Communities	91
12	Daily Ration of Benthic Organisms	94
13	Filtering Rates of Molluscs Reported in the Literature	98
14	Respiration as a Percentage of Consumption for Aquatic Invertebrates	137
15	Respiration Rates (R) (mg carbon·mg carbon^{-1}·day^{-1}), as a Function of O_2 Concentration (mg/ℓ), for Several Aquatic Invertebrates	153
16	Comparison of Critical Concentrations (mg/ℓ) of Dissolved Oxygen for Insects Exposed to These Conditions for 96 hr and 30 Days	171

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:

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

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

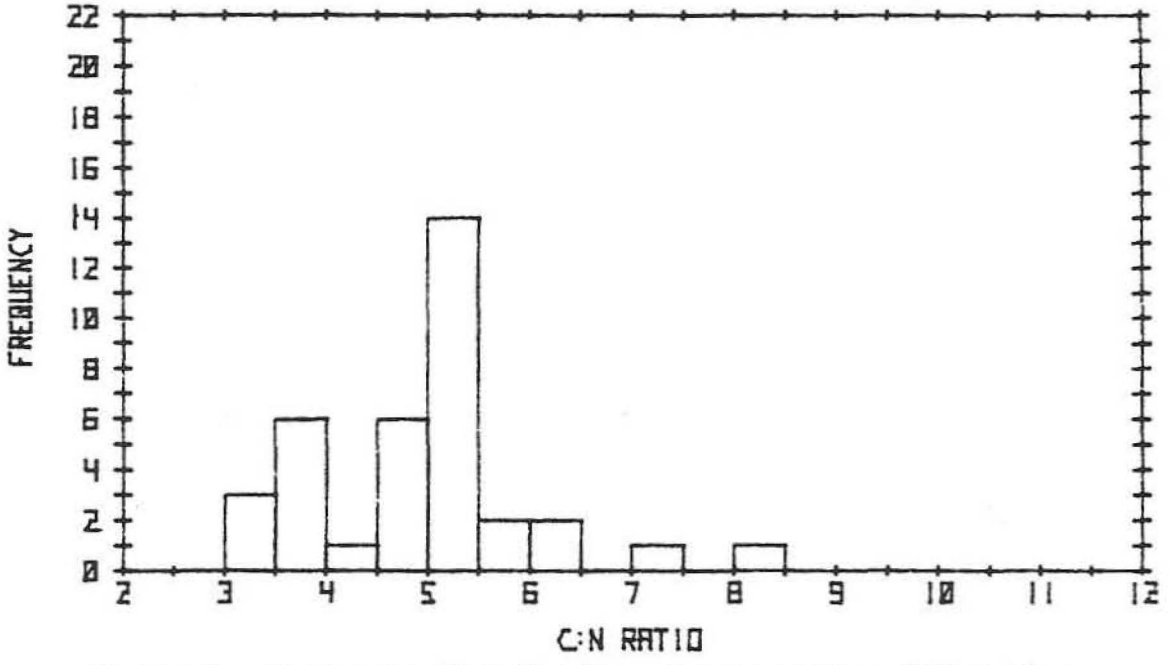

Figure 1. Frequency distribution of macrobenthos C:N ratios

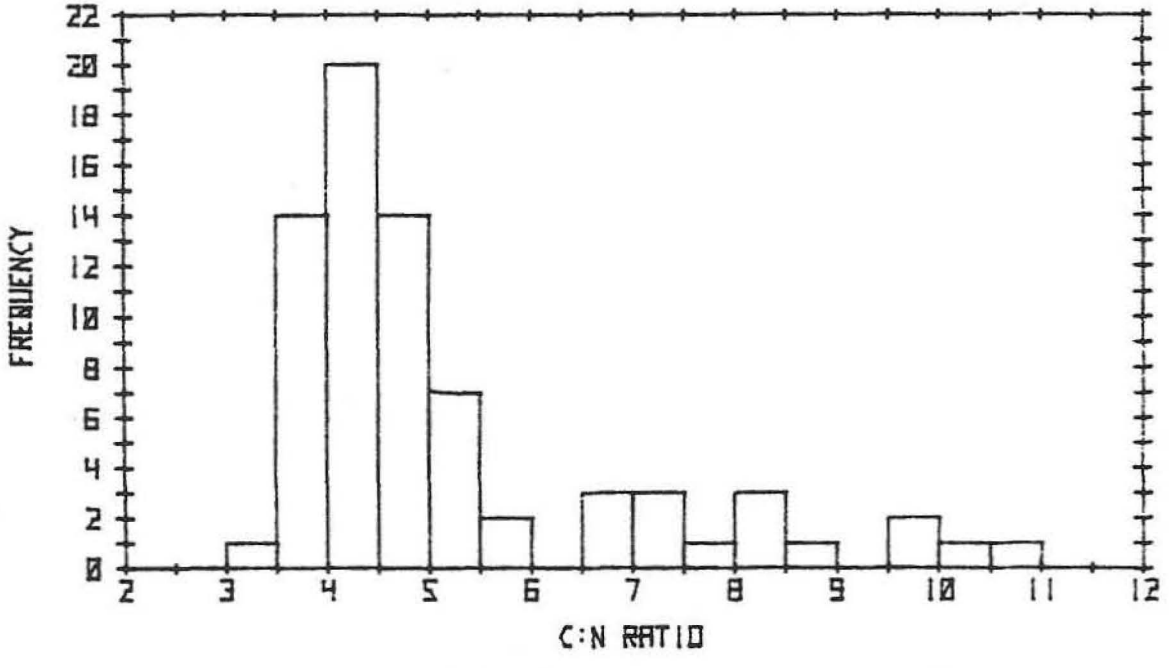

Figure 2. Frequency distribution of zooplanton C:N ratios

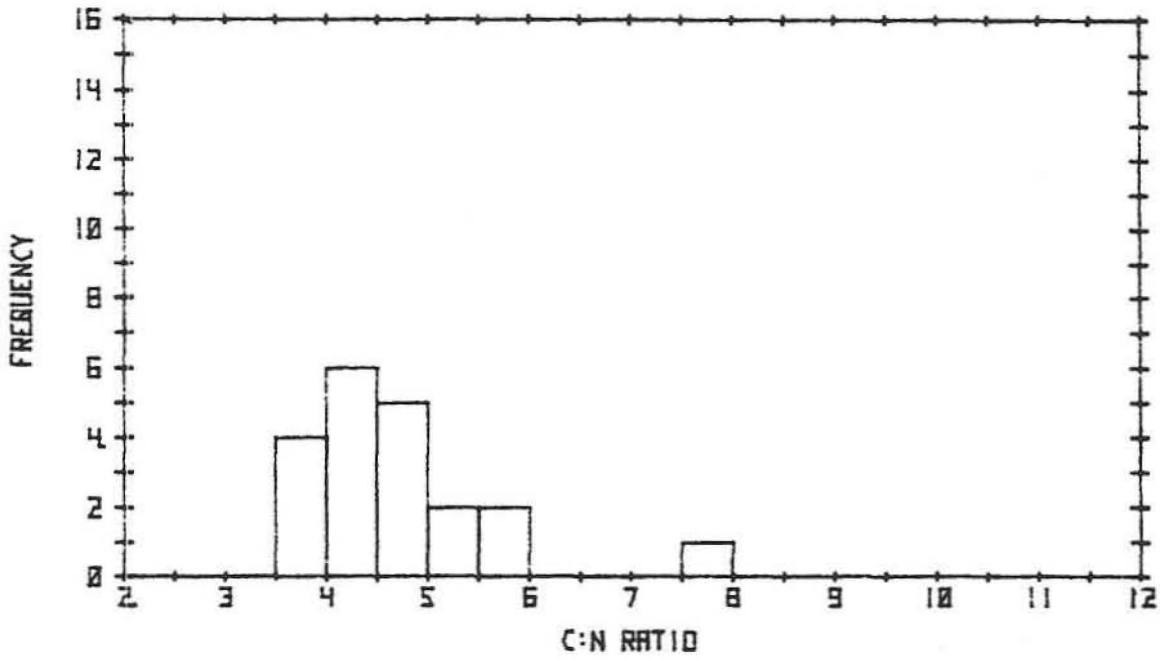

Figure 3. Frequency distribution of cladoceran C:N ratios

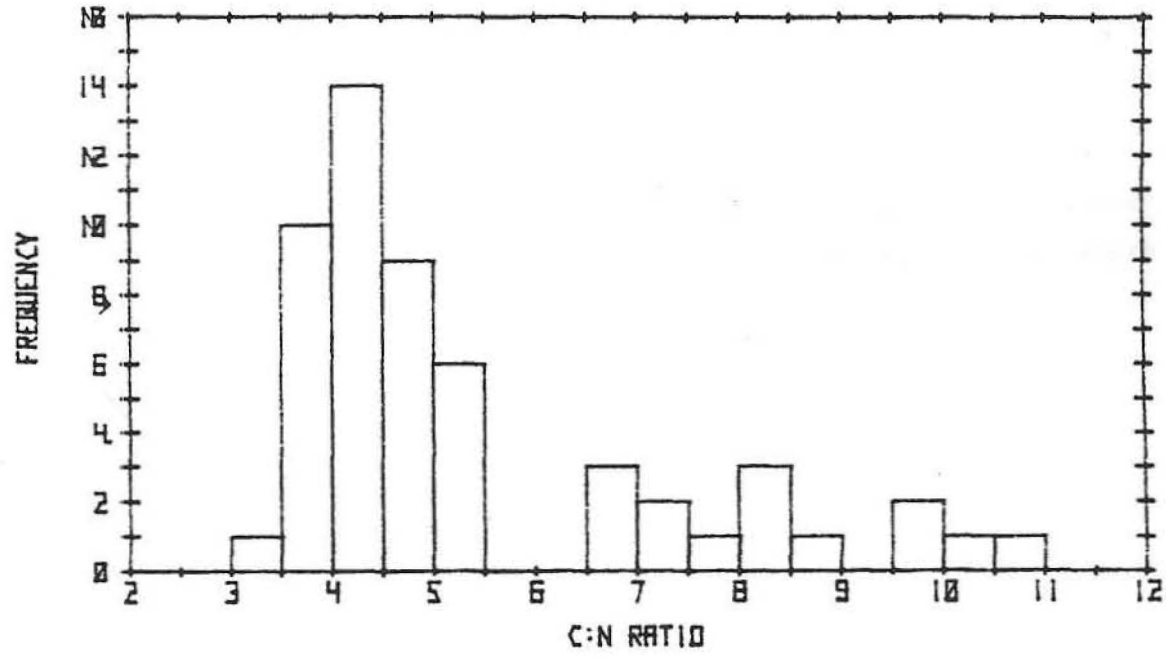

Figure 4. Frequency distribution of copepod C:N ratios

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}·day^{-1}) of consumption (Part III), assimilation (Part IV), egestion + excretion

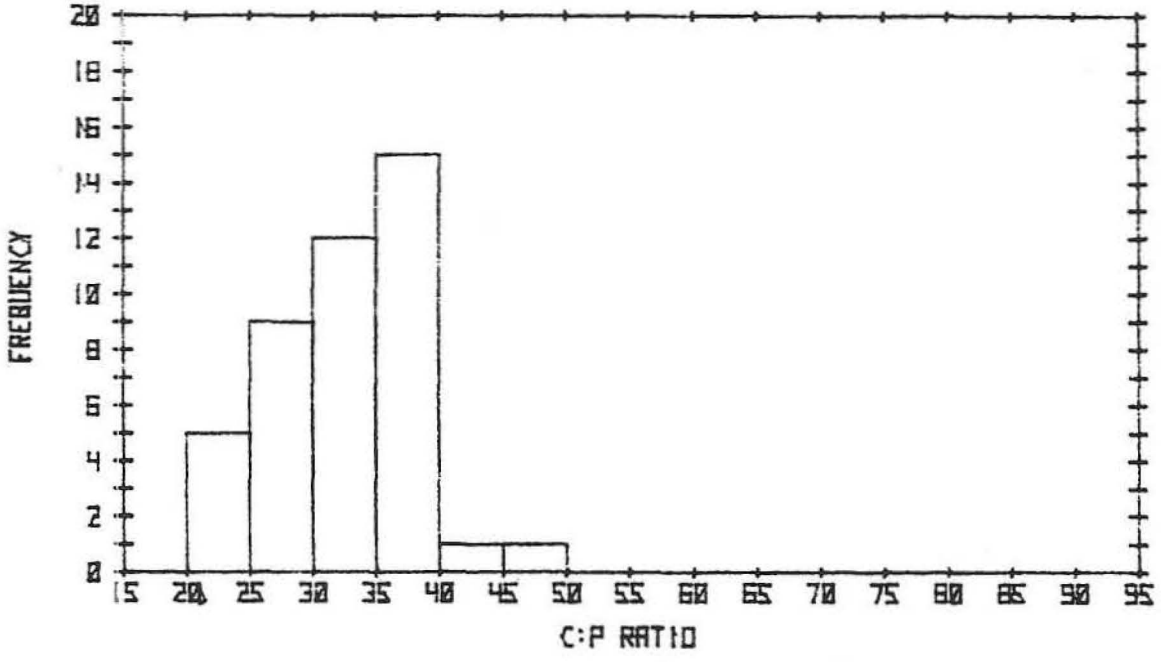

Figure 5. Frequency distribution of macrobenthos C:P ratios

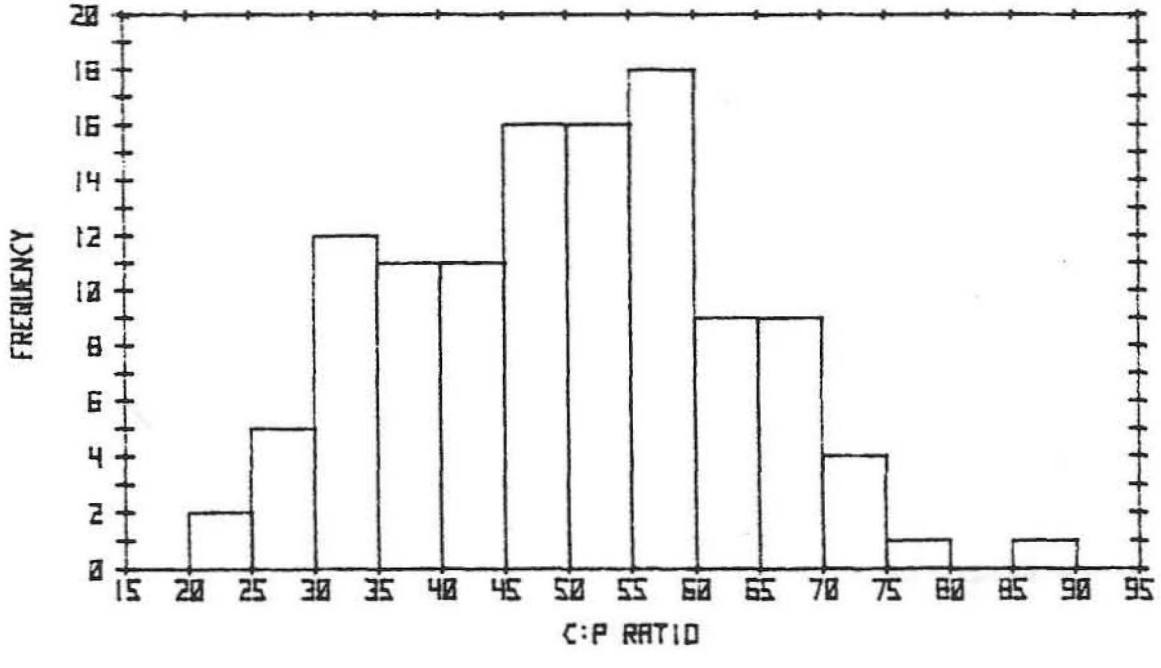

Figure 6. Frequency distribution of zooplankton C:P ratios

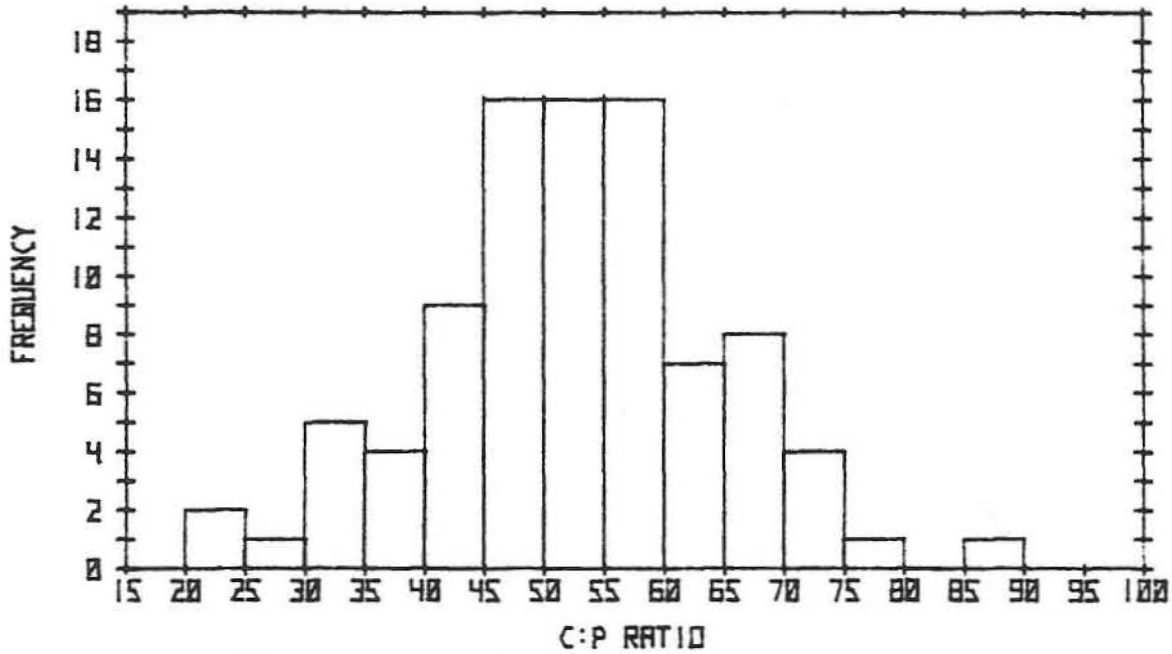

Figure 7. Frequency distribution of copepod C:P ratios

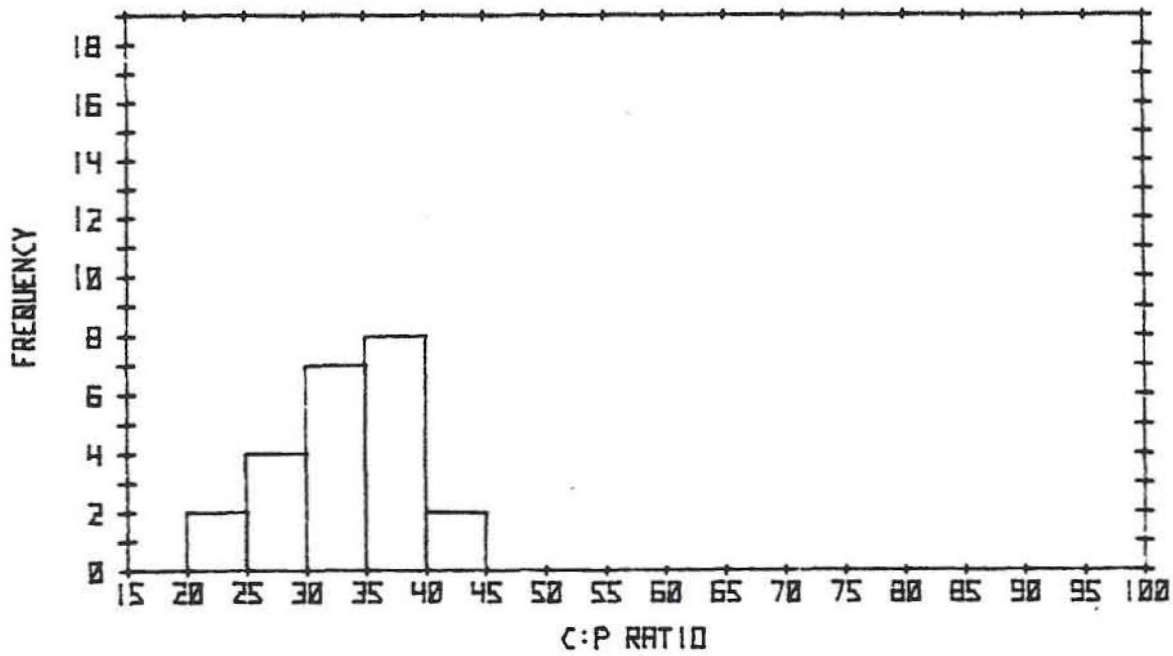

Figure 8. Frequency distribution of cladoceran C:P ratios

(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 $0.60\ b\ [G(A/G) - R - NPM - PM] \div (C:P)$, 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).