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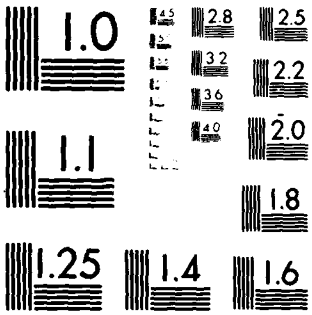

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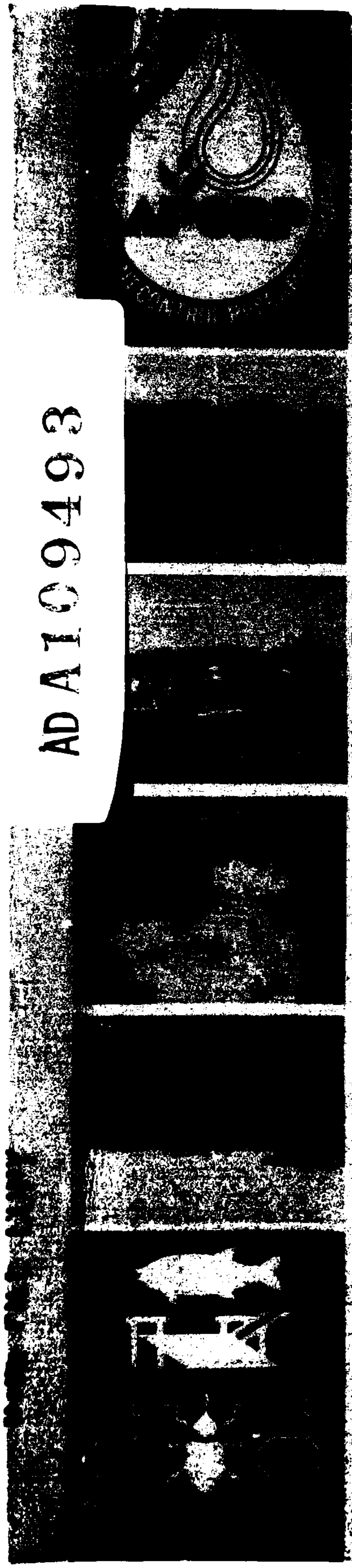

TECHNICAL REPORT A-78-2

LARGE-SCALE OPERATIONS MANAGEMENT TEST OF USE OF THE WHITE AMUR FOR CONTROL OF PROBLEM AQUATIC PLANTS

Report 2

FIRST YEAR POSTSTOCKING RESULTS

162

Volume VII

A Model for Evaluation of the Response of the Lake Conway, Florida, Ecosystem to Introduction of the White Amur

By Katherine C. Ewel and Thomas D. Fontaine III

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November 1981

Report 2 of a Series

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P. O. Box 631, Vicksburg, Miss. 39180

LARGE-SCALE OPERATIONS MANAGEMENT TEST OF USE OF THE WHITE AMUR FOR CONTROL OF PROBLEM AQUATIC PLANTS

Report 1: Baseline Studies

- Volume I: The Aquatic Macrophytes of Lake Conway, Florida
- Volume II: The Fish, Mammals, and Waterfowl of Lake Conway, Florida
- Volume III: The Plankton and Benthos of Lake Conway, Florida
- Volume IV: Interim Report on the Nitrogen and Phosphorus Loading Characteristics of the Lake Conway, Florida, Ecosystem
- Volume V: The Herpetofauna of Lake Conway, Florida
- Volume VI: The Water and Sediment Quality of Lake Conway, Florida
- Volume VII: A Model for Evaluation of the Response of the Lake Conway, Florida, Ecosystem to Introduction of the White Amur
- Volume VIII: Summary of Baseline Studies and Data

Report 2: First Year Poststocking Results

Report 3: Second Year Poststocking Results

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Simulation of a model summarizing relationships between major biotic and abiotic components in Lake Conway, Florida, indicated that the establishment of significant growths of submersed plants had enabled nutrients in sediments, previously removed from the mainstream of nutrient cycling, to be reintroduced into the water column where stimulation of phytoplankton production can occur. Internal recycling of phosphorus by submersed plants was estimated to represent

(Continued)

20. ABSTRACT (Continued).

nearly half of the annual phosphorus input to the lake. Apparently, nutrient loading from outside sources has declined over the last few years, and the simulations showed slowly declining submersed plant biomass and productivity after six years as nutrients were washed out. Phytoplankton biomass and productivity also began to decline after six years.

In the simulation, the addition of white amur accelerated the decline of submersed plant biomass. As a result, the transfer of phosphorus into the water column also decreased, which in turn accelerated the reduction in phytoplankton biomass and productivity. Consumers that depended most heavily on the pelagic-grazing food chain decreased while consumers that depended most heavily on the benthic-detrital food chain showed little change. Ecosystem gross production and respiration decreased at a fairly constant rate over a ten-year period but net ecosystem production (community gross production minus community respiration) remained essentially the same as in baseline simulations. Hence, the percent of gross production that became net production increased and the ecosystem was set back to an earlier stage of succession.

PREFACE

The work described in this volume was performed under Contract No. DACW39-76-C-0019 between the U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Miss., and the University of Florida, Gainesville. The work was sponsored by the U. S. Army Engineer District, Jacksonville, and by the Office, Chief of Engineers, U. S. Army. Information contained in this report has also been published as a Ph.D Dissertation by Thomas D. Fontaine III: "Community Metabolism Patterns and a Simulation Model of a Lake in Central Florida" (Univ. of Fla., Dept. of Environmental Engineering Sciences, 1978). This report is the second in a series of three reports that documents the development of a model for evaluating the response of Lake Conway to the introduction of white amur. Therefore, the model described herein is a preliminary one.

This study was conducted as a part of a general project funded by the U. S. Corps of Engineers to study the effects of white amur on a lake in central Florida having aquatic weed problems. Additional research was conducted on zooplankton populations by E. Blancher of the Department of Environmental Engineering Sciences, at the University of Florida; hydrologic and nutrient budgets were also prepared by E. Blancher; C. Fellows measured seepage of water between the lake and aquifer; D. Sompongse studied nitrogen cycling; and F. Kooijman studied benthic invertebrate populations. These studies were done under the supervision of J. Fox and T. Crisman. Aquatic macrophytes were sampled by L. Nall and J. Schardt of the Florida Department of Natural Resources (DNR); water chemistry measurements were conducted by the Orange County Pollution Control agency; and fish population dynamics were studied by the Florida Fresh Water Fish and Game Commission. Computer facilities were provided by the Northeast Regional Data Center of the University System of Florida.

The work was monitored at WES by the Environmental Laboratory (EL) under the general supervision of Dr. John Harrison, Chief, EL, and Mr. B. O. Benn, Chief, Environmental Systems Division, and under the direct supervision of Mr. J. L. Decell, Manager, Aquatic Plant Control Research Program.

Commanders and Directors of WES during the period of the contract were COL J. L. Cannon, CE, and COL N. P. Conover, CE. Technical Director was Mr. F. R. Brown.

This report should be cited as follows:

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CONTENTS

LARGE-SCALE OPERATIONS MANAGEMENT TEST OF USE OF THE WHITE AMUR FOR CONTROL OF PROBLEM AQUATIC PLANTS

A MODEL FOR EVALUATION OF THE RESPONSE
OF THE LAKE CONWAY, FLORIDA, ECOSYSTEM
TO INTRODUCTION OF THE WHITE AMUR

PART I: INTRODUCTION

Purpose of Study

1. An understanding of how lakes work is required for sensible management and conservation of freshwater resources. Cultural eutrophication of lakes has, in most cases, included undesirable effects on fisheries, water supplies, and recreation because of rapid growth and changes in composition of plankton and submersed plant communities. Successful invasion of the exotic aquatic plants hydrilla (*Hydrilla verticillata*) and waterhyacinth (*Eichhornia crassipes*) has been documented in many parts of the world, but is particularly noticeable in regions such as the southeastern United States where growing seasons are lengthy. The kind of control that exotic as well as native submersed plants exert over nutrient cycling and productivity in aquatic systems, and the effects that introduction of white amur (*Ctenopharyngodon idella*), an exotic fish proposed as an aquatic weed control agent, can have upon lake systems are of interest in determining the effects that aquatic weeds and their control practices have on lake ecosystems.

2. In this report, results of a lake simulation model are presented. By integrating results of earlier metabolism studies with results of a simulation model, insight is offered into the dynamics of a warm temperate lake, how it compares with dynamics of northern temperate lakes, and how introduction of an herbivorous fish, white amur, may alter storages and flows in an aquatic system.

Previous Metabolism Study

3. Ewel and Fontaine[48] reported that average annual community gross production in 1976 was 1150 g C/m^2 and average annual community 24-hour respiration was 1193 g C/m^2. Community gross production and community respiration followed the same trends during the year, implying rapid use of newly synthesized organic matter. Mid-winter and spring peaks of community metabolism occurred during or immediately following periods of rapid change in water temperature. A fall peak of community production and respiration occurred one month prior to fall turnover. Community metabolism was significantly depressed during the summer months, and it appeared that submersed plant metabolism was greatly reduced during this time, possibly as a result of temperature effects. Annual plankton gross production was 426 g C/m^2 (37 percent of community production) and annual plankton 24-hour respiration was 585 g C/m^2 (49 percent of community respiration).

4. The use of models has been suggested as a method of studying the seasonal dynamics of metabolism in ecosystems when time and financial constraints limit the extent of experimental work that can be done.[122] If the standing crops of components in an ecosystem are known, interactions among components can be simulated using general information on material transfer rates between trophic levels.

Aquatic Ecosystem Models

5. Numerous conceptual and simulation models of aquatic systems have been published (Table 1). Many models are theoretical and use causal relationships between variables and measured rate constants.[165] Some models are empirical,[149] and use multiple regression techniques without attempting definition of causal relationships. Many large ecosystem models, including several listed in Table 1, now incorporate both approaches, using empirical relationships where causal relations are unknown or unimportant.

6. Simulation models provide a means for testing hypotheses

concerning ecosystem function that usually cannot be tested experimentally. Hence, Sell[148] investigated the effects of herbicides on mangroves in Vietnam; Grocki[57] investigated the effects of drawdown on a Florida lake; and Boynton[15] projected the effects that damming a river would have on Florida oyster reefs.

7. The way in which a model is constructed, condensed or expanded, and simulated is very much a function of the questions to be answered by the model. The problems and approaches of setting up and simulating an ecosystem model, as well as the various philosophies regarding organization, are reviewed by Wiegert.[174] Elaboration can be found in articles by Moreau,[114] Patten,[131,132] and Odum.[119]

8. Few lake models are so detailed that compartments represent actual species. Instead, organisms sharing some common trait are normally grouped under a functional heading such as filter-feeding fishes, carnivorous vertebrate harvesters, etc. Although all theoretical lake models include producer components, the number of trophic levels included thereafter varies from author to author. Data limitations may prevent detailed expansion of the food chain; some modelers account for the presence of consumers without explicitly modeling them by assuming that, as a unit, they account for a constant percentage of ecosystem respiration. This approach is supported by energy evaluations of food chains, which show that consumer compartments often process a small percentage of the incoming energy.[34,74,96,120,160,170] Others,[91,121] however, believe that, despite the low energy processing rate of consumers, feedbacks that may control the rest of the system are significant and increase as a function of the number of trophic levels between them and the producers. Some models therefore include a detailed consumer food web.

9. Studies done on consumer populations in Lake Wingra, Wisc., support feedback control theories and have shown that size selective predation of fish on zooplankton is important in regulating phosphorus concentrations, which in turn affect primary production.[100] Similar support for feedback control theories comes from studies of the relationship between aphids and plants,[125] the effects of predation by

mosquitofish,[70] and the effects of fish and fertilization on macrophytes and epiphytic algae.[116] A simulation model was used to show that consumer response time to fluctuations in food resources is a more important factor than either the size of the consumer compartment or the actual amount of material transferred to it.[91] Thus, it seems that, if data are available, inclusion of consumer compartments in models is desirable.

Submersed Plants and Lake Dynamics

10. Submersed macrophytes play a number of physical, chemical, and biotic roles in lake systems. Macrophytes produce oxygen for use in community respiration, serve as substrate for epiphytes,[4] provide cover for young fish and benthic invertebrates, and contribute dissolved and particulate matter to the water column where it can be utilized by plankton and bacteria.[172] In some areas, submersed macrophytes are an important source of food for waterfowl. In addition, submersed macrophytes promote faster sinking rates of water column particulate matter because of decreased turbulence in their vicinity.[26] Increased sedimentation in submersed macrophyte beds provides detritus for colonization by microbes and consumption by benthic invertebrates. Thus, both benthic and grazing food chains are affected by the presence or absence of submersed plants.

11. Submersed macrophytes have also been implicated as a major factor in lake nutrient dynamics. Recent work has shown, for instance, that after 10 days up to 60 percent of labeled phosphorus in sediments was taken up by submersed plants and excreted into the water column where it was then utilized by plankton.[177] *Elodea* sp. was shown to release three times as much phosphorus every day as there was present in the plant at any instant in time.[95] *Zostera marina* excreted 60 percent of the phosphorus it took up into the water column.[105] Only 1 percent of radiophosphorus in an experimental medium surrounding foliage was transported to the roots, whereas 54 percent of the radiophosphorus added to the medium surrounding roots was transported to the foliage.[146]

It appears then that the major direction of nutrient movement in plants is from the roots into the shoots and leaves and then into the water column.

Potential Effects on Lake Systems Through Perturbation of Submersed Macrophyte Communities

12. Much effort is directed towards eliminating aquatic weed problems in lakes. Commonly employed control measures include lake drawdown, chemical poisoning, mechanical harvesting, and biological control. Herbicides are usually applied when aquatic plant biomass exceeds some threshold level. Therefore, they do not exert continual, even pressure unless the herbicide used is a slow-release type or is unusually persistent. If the herbicide is persistent, undesirable effects may be incurred by nontarget organisms in the food web. Often, the most severe effects of herbicide application are associated with the decomposition of plants[18] which may produce high biological oxygen demand deleterious to fish and invertebrates, in addition to the rapid release of nutrients[158,72] which can trigger algal blooms.[43]

13. Mechanical harvesting, on the other hand, removes plants and associated nutrients from the system. Since the removed plants do not decay in the water column, the high biological oxygen demand and nutrient release which occur after herbicide application are avoided. Exudation of nutrients through cut stumps of macrophytes may occur, however.[27] Removal of plant biomass makes light available to other producers such as phytoplankton or benthic algae, which may then increase their productivity rates.

14. Mechanical harvesting also is usually instigated when plant levels reach a threshold. The costs and effectiveness of eliminating macrophytes are similar for herbicides and mechanical harvesting.[118]

15. Biological control of aquatic plants differs in several interesting ways from chemical and harvest methods of control. For instance, biological control agents such as herbivorous fish, pathogenic fungi, and phytophagous insects should exert a more steady, even pressure on macrophyte growth. If the biological control agent is a large

herbivore, it may act as another storage unit in the food chain and thereby serve as a time delay in recycle pathways. In support of this view, Lembi et al.[93] have shown that up to 54 percent of the phosphorus and 42 percent of the nitrogen associated with plants consumed by white amur were incorporated into new fish tissue. Stanley[155] also showed that phosphorus was retained in new fish tissue. By storing nutrients, the rate of nutrient cycling may be slowed and a decrease in primary production could occur. On the other hand, grazing by herbivores and the subsequent excretion of nutrients and egestion of partially digested plant parts which are easily remineralized may stimulate primary production.[33,53] Excretion by herbivorous fish may also contribute to the nutrient loading of freshwater ecosystems.[85] A more detailed discussion of herbivore effects in ecosystems is given by Lomolino.[97]

16. This project was intended to determine the metabolic rates of a nutrient-enriched lake that has significant growth of native and exotic weed species, to conceptualize and simulate a model describing the lake, and to thereby determine what the prevailing concepts of lake dynamics predict about the effect of an added herbivore and how these results compare with observed data.

17. Field work in this study included measurements of photosynthesis and respiration of the whole lake community, as well as the plankton community, in the East Pool of Lake Conway. In addition, laboratory studies of phosphorus release from Lake Conway sediments were made. The model shown in Figure 1 was simulated, and, when integrated with results of field work, allowed the authors to address the following questions:

a. How do components of the model interact with each other and with forcing functions to produce observed patterns of storages and flows?

b. Do submersed plants "pump" nutrients from the sediments into the water column where they can be used by other producers? How significant is this internal loading pathway relative to loading from sediments and external sources?

c. How do final values of rates and turnover times arrived at through modeling compare with those found in the literature?

d. How will the proposed weed control agent, the white amur, affect the pattern and magnitude or community metabolism? Will the new arrangement capture more, less, or the same amount of energy per unit time, and will energy capture occur with the same temporal pattern as in the pre-white amur system?

e. Will changes in trophic level interaction occur as a result of introduction of the white amur? More specifically, if a change in the composition and/or productivity of the producer community occurs, will alterations in the benthic-detrital or pelagic-grazing food chains be observed?

Objectives of Study

18. The model of the Lake Conway ecosystem showing major flows and storages of carbon and phosphorus is shown in Figure 1; explanation of the abbreviations is given in Table 2. The current model summarizes knowledge and hypotheses of warm temperate lake structure and function. Relationships among the organisms and storages are summarized in two models that abstract the major features of this detailed model.

19. Included in a food web model (Figure 2) are the following state variables: phytoplankton, submersed plants (with attached epiphytes) and associated tubers, epipelic algae, zooplankton, benthos, forage fish (primary level fish), numbers and biomass of two types of adult and juvenile fish (secondary and tertiary level fish), the white amur, and detritus. Phosphorus components (Figure 3) include phosphorus contained in the organisms and the detritus, and two inorganic phosphorus compartments. Although standing stocks of bacteria in the sediment and water column are not explicitly modeled, their presence is accounted for in respiration pathways. Forcing functions are solar insolation, heat (temperature), and inflow of phosphorus.

20. In the overall model (Figure 1) and the food web (Figure 2), sunlight enters at the left-hand side of the diagram and interacts with nutrients and other factors to produce biomass of phytoplankton, submersed plants and attached epiphytes, and epipelic algae. Photosynthesis is controlled by the amount of light available: some is reflected from

the lake surface and some is absorbed and scattered by particulate matter, submersed plant biomass, and physical properties of the lake water. Zooplankton graze on all three producers as well as detritus. Benthic invertebrates consume detritus, epipelic algae, and epiphytes on submersed plants. A fish food web includes three classes of fish, all of which are dependent to some extent on both the pelagic-grazing food chain and the benthic-detrital food chain.

21. Each producer component has a distinct source of nutrients (Figures 1 and 3). Phytoplankton obtain their orthophosphate from the water column; submersed plants obtain nutrients from the sediments; and epipelic algae obtain their phosphorus from the interstitial waters. Phosphorus taken up by all plant forms is leached directly into the water column, settles out as a constituent of sloughed plant parts, or is passed on to herbivores and then carnivores through consumption. Animals release phosphorus into the water column through excretion, passing the remaining phosphorus to higher trophic levels in proportion to carbon flow. Phosphorus is returned to the sediments in egestions, or is remineralized from dead organic matter before settling out. Some phosphorus leaves the lake through hydrologic outflow.

PART II: DEVELOPMENT OF A MODEL OF LAKE CONWAY

Description of Study Site

22. Lake Conway comprises five connected bodies of water and is located directly southeast of Orlando, Fla., in a heavily urbanized area. Little original shoreline vegetation remains; most has been removed for the establishment of private beaches.

23. Historically, the lake was clear and sandy bottomed. In the last 20 years, however, the lake has become nutrient enriched and exotic and native submersed plants have proliferated. Surficial sediments now found in the lake vary from predominantly sandy to predominantly organic in composition; organic sediments often are found in lake bottom depressions. In general, the compactness of the sediments decreases with the increasing depth. Deep areas, however, often have a 1-m-deep zone of black, fine particles that grade vertically into a more compacted organic ooze.

24. The lake has a surface area of 7.6 km^2. Maximum depth varies from 8 to 12 m among the pools, and the mean depth of the five pools is approximately 5 m. Hydrologic inputs to the lake are from rain and runoff; the only surface outflow from the lake is located in the South Pool. Seepage into and out of the lake was estimated to be 17 percent.[50]

25. Temperatures measured in 1976 showed that deeper areas of the lake were moderately stratified from late April until late September. A much shorter period of stratification began in mid-February and lasted until late March. Coinciding with the longer period of stratification was depletion of dissolved oxygen in hypolimnetic waters at three sites greater than 6.5 m in depth. The anoxic period lasted from late March to late August.

26. The lake is typical of the many limestone solution lakes that are found in Florida. Hardness and total alkalinity show little variation around mean values of 60 and 35 mg/ℓ (as $CaCO_3$), respectively. The range of pH values is between 6.0 and 8.6, and highest values occur during the summer. Total phosphorus concentration is generally low

($\bar{x}$ = 0.02 mg P/ℓ), and, during half of the year, orthophosphate concentration is undetectable (<0.001 mg PO_4-P/ℓ). Concentrations of total phosphorus and orthophosphate are highest during the winter and lowest during the summer. Total nitrogen is almost completely organic in form and the average concentration found in the lake is 0.5 mg/ℓ.

27. Shallow areas (1 to 2 m) of the lake characteristically have substantial growths of pondweed (*Potamogeton illinoensis*) and eelgrass (*Vallisneria americana*). Hydrilla and *Nitella flexis* were characteristically found at medium depth areas (4 m). At depths greater than 6 m little rooted vegetation occurs. Presently, growths of pondweed and *Nitella* represent the major aquatic weed problem. Hydrilla has been a major problem in the past, but it has never completely recovered from chemical treatment in 1975.

Model Quantification

28. The method by which pathways in the model (Figure 1) were defined numerically was an evolutionary process in which model results were compared with available real data, and the information gained from such comparisons was fed back to the model development process. Initial estimates of pathway values, then, often changed as pathway coefficients were varied within a realistic range, and new mathematical configurations of the same pathway were tested in order to obtain the most meaningful results.

29. Initial estimates of standing stocks and material transfers in the model were based upon several sources of information: community and planktonic metabolism data obtained in this study; data collected by other researchers working on Lake Conway; and information obtained during an extensive literature search. Values of amounts or biomass of components in Lake Conway were averages of samples reported from all five pools. Productivity, however, was measured only in the East Pool. Early measurements showed that productivity levels in the other large pools were similar. Tables were prepared from the literature sources and were used to delineate the possible ranges of pathway values and,

hence, of pathway coefficients. Most components were assumed to be neither growing nor declining from year to year. The major exceptions were the fish, which field data suggested were not recruiting young (Roy Land, personal communication).

30. Appendix A summarizes producer and heterotroph process rates used in this model as compared with surveyed literature.

Forcing Functions

31. The values of solar radiation used in the model had been measured at Disney World near Orlando, Fla., for all months of 1976 except January and February (Figure 4). Daily insolation at Orlando in January was estimated from Gainesville January data to be:

$$\text{Orlando (cal/m}^2\text{-day)} = 0.7272 \text{ (Gainesville cal/m}^2\text{-day)} + 91.1 \quad (r^2 = 0.61) \tag{1}$$

Daily insolation at Orlando in February was estimated from Gainesville February data to be:

$$\text{Orlando (cal/m}^2\text{-day)} = 0.6522 \text{ (Gainesville cal/m}^2\text{-day)} + 379.3 \quad (r^2 = 0.79) \tag{2}$$

32. An estimate of total external phosphorus loading to Lake Conway during 1976 was determined by Blancher (personal communication) (Figure 5).

33. In the model, temperature affected rates of production and respiration of producers, and feeding and respiration rates of all heterotrophs. Ambient temperatures differed for many organisms because of their location in the water column. The temperatures used for different components are given in Figure 6.

Plant Communities

Primary production equations

34. The equations used to predict gross photosynthesis by each plant compartment had the general form

$$K \times f(\text{BIOMASS}) \times f(\text{NUTRIENTS}) \times f(\text{TEMPERATURE}) \times \begin{matrix}\text{PREDICTED}\\ \text{AVAILABLE}\\ \text{LIGHT}\end{matrix} \times \begin{matrix}\text{PHOTOSYNTHETIC}\\ \text{EFFICIENCY AT}\\ \text{THE PREDICTED}\\ \text{LIGHT LEVEL}\end{matrix} \qquad (3)$$

where K is a proportionality coefficient. For phytoplankton, predicted available light was determined by the equation:

$$L_{Q_1} = S \times (1 - R) \times f_1(Q_2) \times e\left\{-\left[K_{12}(Q_1 + Q_5 + Q_6) + K_{13}(\text{LEVEL})\right]\right\}$$

where

L_{Q_1} = predicted amount of solar radiation available for phytoplankton photosynthesis, kcal/m^2-month

S = incident solar radiation on the lake surface, kcal/m^2-month

R = proportion of the solar radiation reflected at the lake surface

$f_1(Q_2)$ = a function describing shading of phytoplankton by vascular plants (Figure 7). In this function, at maximum biomass, light penetration to the hydrosoil is reduced by 48 percent

$K_{12}(Q_1 + Q_5 + Q_6)$ = term which accounts for shading of phytoplankton by itself and other planktonic organisms, in addition to shading from nonliving suspended matter

$K_{13}(\text{LEVEL})$ = a function which specifies the amount of light available for phytoplankton photosynthesis at the observed depth-location of maximal photosynthesis (Figure 8). (This term accounts for photo-inhibition near the lake surface.)

This equation is similar to those used by DiToro et al.[42] and Canale et al.[23] but differs in that it includes shading effects by vascular plants.

35. An equation predicting the amount of light available to submersed plants, which accounted for changes in light availability as a function of seasonally changing submersed plant canopy levels, was developed:

$$L_{Q_2} = S \times (1 - R) \times K_{28} \times e^{-\left[K_{13}Z' + K_{29} \times Z'(Q_1+Q_5+Q_6)/Z\right]} \qquad (4)$$

where

L_{Q_2} = predicted amount of light available to the submersed plants, kcal/m^2-month

K_{28}, K_{13} = constants in the light extinction equation for clear Lake Conway water:

$$I_z = I_o \times K_{28} \times e^{-K_{13}Z}$$

where

I_z = solar radiation at depth Z, kcal/m^2-month

I_o = net incident solar radiation at the lake surface, kcal/m^2-month

Z = depth, m

Z' = distance (metres) from the water surface to the plant canopy. This varies as a function of cumulative plant biomass (Figure 7)

$K_{29} \times Z'(Q_1+Q_5+Q_6)/Z$ = effects of the average amount of nonliving suspended organic matter Q_5, phytoplankton biomass Q_1, and zooplankton biomass Q_6 per cubic metre, and the depth of plant canopy Z' on reduction of light available to the submersed plants. At high levels of the quantity $(Q_1+Q_5+Q_6)$, the light available to submersed plants can be reduced significantly.[170] For instance, maximum levels of suspended organic matter Q_5 reduced light transmission by half in the model

36. The amount of light available for epipelic algae was predicted by the equation:

$$L_{Q_3} = S(1 - R) \times f_3(Q_2) \times e^{-\left[K_{13}\times Z+K_{12}(Q_1+Q_5+Q_6)\right]} \qquad (5)$$

where

L_{Q_3} = predicted amount of solar radiation available for epipelic algal photosynthesis, kcal/m^2-month

$f_3(Q_2)$ = a function describing shading of epipelic algae by vascular plants (Figure 7)

$e^{-\left[K_{13}\times Z+K_{12}(Q_1+Q_5+Q_6)\right]}$ = light extinction, determined by the optical properties of the water as well as shading by nonliving suspended matter, phytoplankton biomass, and zooplankton biomass

37. Photosynthetic efficiencies for the plant compartments were predicted by the general equation:

$$E = \frac{E_{Q_i}}{1 + L_{Q_i}/L_{Q_{i-50}}} \qquad (6)$$

where

E = predicted efficiency for plant Q_i (expressed as a decimal)

E_{Q_i} = maximum efficiency of plant Q_i at naturally occurring light levels, percent

L_{Q_i} = predicted amount of solar radiation for plant Q_i

$L_{Q_{i-50}}$ = light level at which plant Q_i is at half its maximum efficiency, cal/m^2-month

Values of E_{Q_i} and $L_{Q_{i-50}}$ are given in Table 3 for phytoplankton, submersed plants, and epipelic algae.

Plant group
photosynthetic characteristics

38. Phytoplankton. The phytoplankton component of the model is shown in Figure 9. Equations describing the module are shown in Table 4. Biomass of phytoplankton in January was calculated to be 0.1 g C/m^2 based on chlorophyll-*a* data provided by the Orange County Pollution Control Board and E. Blancher (personal communication). Chlorophyll-*a* values were converted to carbon by assuming that 1 mg of chlorophyll-*a* is equivalent to 25 mg of carbon. Ranges of possible carbon to chlorophyll-*a* ratios have been reported as 3.7:1 to 50:1[126] and 20:1 to 66:1.[170]

39. The initial gross primary productivity value used was 10.0 g C/m^2-month and was estimated from field data reported earlier. Constraints imposed on those pathway values of this compartment that were not measured in the field were determined from the literature (Table 5). These values acted as boundaries within which the magnitude of certain flows could be varied. Since estimates of the initial standing crop and gross production of the phytoplankton were available, initial estimates of the other pathways were calculated as a percent of the gross production. Turnover time of phytoplankton biomass was calculated from the initial flows and biomass to make sure that the overall formulation of the model was correct. Approximate values of turnover times were estimated to range from less than 1 day to 60 days.[170]

40. The response of phytoplankton gross production to phosphorus concentration was modeled with the limiting-factor configuration:

$$\frac{Q}{K + Q} \qquad (7)$$

where

Q = nutrient concentration

K = nutrient concentration at which gross productivity reaches half its maximum value for a given level of other variables interacting in the photosynthesis equation

The value of this half-saturation constant in the model was set at 0.0125 and was then doubled to a value of 0.025 to account for the 2 m of depth over which the phytoplankton were found. The value of the half-saturation constant was based on work summarized in Table 6. The effect of temperature on planktonic metabolism was assumed to be a parabolic response curve (Figure 10).[6]

41. Annual losses due to grazing, sinking, leakage, and respiration represented 6, 7, 12, and 75 percent, respectively, of phytoplankton respiration. Annual efficiency of direct solar energy utilization was 0.84 percent. Efficiency was calculated by assuming 10 kcal/g of carbon fixed.[119]

42. Submersed plants. A diagram of the submersed plant-epiphyte complex is given in Figure 11. Equations describing the model are given in Table 7. All submersed plant species were combined into one population unit since differences in productivity and functional roles are not well defined for individual species. Moreover, the diet of the white amur depends almost entirely on what is available in the habitat in which it is found, and it will eat anything in the absence of preferred food.[151,106,51] This constitutes further justification for not distinguishing among species.

43. Dry weight values of submersed plants were converted to grams of carbon using the proportion reported by DNR: 0.35 g C/g dry weight. The standing stock of submersed macrophytes cleaned of epiphytes was found to be 31.5 g C/m^2 in January. Because 30 percent of the plant biomass in Silver Springs, Fla., was estimated to be attributable to epiphytic algae,[120] the total biomass of the submersed plant-epiphyte complex at Lake Conway was increased to 45 g C/m^2.

44. Gross primary productivity was initialized at 50 g C/m^2-month. This value was determined by subtracting known phytoplankton production and an estimate of epipelic algae production (1.3 percent of available light) from the January community production value measured by the diurnal curve method.

45. Possible relationships between photosynthesis and respiration of the submersed plants and temperature are given in Figure 12 and were derived from data collected at Lake Conway. These relationships were

determined by plotting normalized values of estimated submersed plant photosynthesis and respiration against ambient water temperature (Figure 13). Estimates of submersed plant photosynthesis were determined by subtracting measured phytoplankton gross production values and an estimate of photosynthesis due to epipelic algae from the measured total community gross production values and then dividing by the largest difference to obtain a normalized scale. In a similar fashion, estimates of normalized submersed plant respiration were determined by subtracting planktonic community respiration from total community respiration and then dividing the resulting figures by the largest difference. This assumes that submersed plants are responsible for the major part of the nonplanktonic respiration, as has been reported for several systems (87 percent in Lake Mendota,[74] 84 percent in Silver Springs,[118] 79 percent in Cedar Bog Lake,[96] and 93 percent in Severson Lake.[34] This assumes that sediment and benthos respiration are low.

46. The Q_{10} for respiration in aquatic macrophytes probably varies from 1.32 to 3.48.[147] For temperature, between 15° and 28°C, the proposed Q_{10} is 2.33.

47. Study of the mechanisms by which submersed plants obtain nutrients (that is, via the roots or shoots) has recently been a focal point in aquatic ecology. Uptake of phosphorus through the root system has been shown to be an important process in many rooted submersed plants.[17,40,96,146] Moreover, although *Myriophyllum spicatum* can take up nitrogen through its leaves, it can satisfy all its nitrogen requirements through root uptake from the sediments.[117] While most studies agree that the most important nutrient uptake pathway is through the roots, evidence of foliar uptake of nutrients caused some problems with regard to formulating the correct mechanistic relationship in the model. During the evolution of the model, several configurations were tested: foliar uptake only, a combination of foliar and root uptake, and root uptake only. Best results were obtained using root uptake only. The response of submersed plant production to sediment phosphorus concentration was modeled with the same limiting factor configuration used for phytoplankton nutrient uptake. The half-saturation constant was set at 1.2×10^{-4} mg/ℓ.[55]

48. Most species of submersed plants have an underground organ that may initiate vegetative growth. Hydrilla forms tubers, while plants such as *Vallisneria* or *Potamogeton* have rhizomelike structures. The underground storage organs of the generalized plant in the model received 11 percent of the carbon fixed annually by the above-soil parts. Vegetative growth from these organs, however, was programmed to occur during a discrete time period (late March to late September). Tuber biomass of more than 273 g fresh weight/m^2 has been reported in a reservoir in Florida,[111] or approximately 11 g C/m^2.

49. By knowing the initial biomass and gross productivity of the submersed plants, values of the other pathways were determined using the data shown in Table 8. Over an annual cycle, respiration accounted for a major portion (94 percent) of total submersed plant-epiphyte losses. Herbivory losses were greatest during the summer months and represented 3 percent of total plant losses. Wetzel[170] emphasizes that dissolved organic carbon leachate is newly synthesized material, and that its release is not related to photorespiration or glycolate metabolism. He[171] also notes that highest release rates occur in the fall during senescence. Based on this information, leaching of dissolved organic carbon was made proportional to the photosynthetic rate and the plant biomass, and accounted for 7 percent of total plant losses.

50. Senescence and death during an annual period of active growth has been reported to be 2 to 10 percent of the maximum biomass.[170] In the model, it was assumed that a small but constant percentage of biomass was sloughed each month and that in the fall a much higher percentage was sloughed. Total annual losses of plant parts due to sloughing represented 1 percent of annual plant losses.

51. Annual efficiency of direct solar energy conversion was 1.3 percent.

52. Epipelic algae. Data on epipelic algae were not available for Lake Conway. However, field observations indicate that it can be an important seasonal component of the community. The relationships that were derived for this component are shown in Figure 14. Equations are given in Table 9. Gross primary productivity of this component in

January was estimated to be 7.8 g C/m^2-month based on measurements of total community metabolism and estimates of the productivities of other producers. January standing crop was estimated to be 1.0 g C/m^2, based on an arbitrary turnover time of 5.5 days. Turnover times of 9 to 30 days have been measured for epipelic algae in Marion Lake, British Columbia,[60] which is considerably further north.

53. Nutrient relationships for these algae are not clear, but they are assumed to depend on dissolved orthophosphate in the interstitial waters. Phosphorus uptake by epipelic algae was assumed to fit the same limiting factor configuration used for phytoplankton; the half-saturation coefficient was set at 0.025 g P/m^3.

54. Loss of epipelic algal biomass due to leaching has been reported to equal 3.8 percent annually.[80] Losses resulting from leaching, respiration, herbivory, and cell decay accounted for 7, 27, 32, and 34 percent, respectively, of annual gross production. Annual efficiency of direct solar energy conversion was 0.54 percent.

Animal Populations

55. The hypothesized feeding relationships of zooplankton, benthos, and three trophic levels of fish in Lake Conway are shown in Figure 15. Data used to generate these values came from various sources, notably Carlander[24,25] and Calhoun[21] for information on fish feeding. Some of the values were derived from the model itself. Percentages shown represent annual averages that emerged from the modeling process. The type of plant eaten most universally is the macrophyte-epiphyte complex. The macrophytes themselves are probably only lightly grazed, considerably heavier pressure being directed toward the epiphytic algae. This group is grazed by every consumer except the tertiary level fish and is utilized most heavily by zooplankton and benthic invertebrates. In most cases, predation by one trophic level upon another is influenced by the amount of cover provided by submersed plant biomass. Hence, the chance of encountering a prey item is greatly diminished by increases in vegetation. The relationships between temperature and consumer

population feeding and respiration rates that were used in the model are shown in Figure 16.

Zooplankton

56. The zooplankton component of the model is shown in Figure 17. Equations are given in Table 10. The initial standing crop (0.1 g C/m^2) was calculated by multiplying numbers of zooplankton per square metre (E. Blancher, personal communication) by the species-specific dry weight of each individual.[16] Total dry weight was then multiplied by 0.5 to convert the value to grams of carbon.[168]

57. Input and output rates for zooplankton were established according to the range of values of turnover times (biomass/net production), assimilation rates, and respiration rates reported in Table 11. Turnover times of zooplankton in temperate lakes may range between 9 and 29 days,[170] although turnover times in subtropical Lake Sibaya are faster ($\bar{X}$ = 5.5 days).[61] By knowing the initial biomass and assuming a turnover time within the range of values reported (13.5 days), an initial estimate of net production was obtained.

58. Respiration of zooplankton has been estimated to be 20 percent of the body weight per day.[58] However, values may range between 20 and 43.4 percent of the body weight per day.[86] By adding the initial estimate of net production to an assumed rate of respiration, the amount of assimilated food was determined. The proportion of nonassimilated material has been estimated to be 59 to 73 percent of total food ingested.[58] Other values range from 10.6 to 75.0 percent.[34,38,39,81,82,115,137,170] A value of 56.9 percent was used in the model. Since assimilated material represents 43.1 percent of the total food ingested, total food ingested was calculated to equal assimilated food multiplied by (100/43.1). Total food ingested was then divided up among the food components of zooplankton (Figure 15). Losses due to respiration, nonpredation mortality, and predation represented 76, 19, and 5 percent, respectively, of the annual assimilation rate.

59. The relationship that was derived for temperature and rates of zooplankton feeding and respiration is shown in Figure 16.[19] The

Q_{10} of this relationship is 1.2 and is comparable to the value of 1.5 determined by LaRow et al.[88]

Benthic invertebrates

60. The benthic invertebrate component of the model is shown in Figure 18, and the equations are listed in Table 12. Standing stock of benthic invertebrates was initialized at 1.73 g C/m^2. This was determined by multiplying numbers of a species by an average of species-specific dry weights (Table 13). Dry weight values were converted to grams of carbon assuming that 50 percent of dry weight is carbon. Data later made available by Kooijman (personal communication) substantiate the estimate (1.5 g C/m^2).

61. Input and output rates for benthic invertebrates were calculated from the known standing crop and literature values of net production, respiration rates, and assimilation rates (Table 14). Estimated turnover rates of benthic invertebrates include 1.23/yr,[2] 2 to 4/yr,[13] 4 to 8/yr,[5] and 14/yr.[75] Initial calculation of net production was based upon a turnover rate of eight times per year. It was hypothesized that turnover rates would be faster at this latitude than at the latitudes from which the literature data were obtained. The value used was 2/yr, but was based on predation losses. If nonpredation losses had been separated from respiration losses and included with predation, this value would have been higher.

62. Literature values of benthic invertebrate respiration were often reported with other metabolism data such as assimilation, excretion, and mortality rates. Rarely, however, was the initial weight of the organism reported, thus making direct calculation of respiration per unit biomass difficult. Wetzel,[170] however, summarized data reported for the scud *Hyalella azteca*,[61] for which respiration was found to be 3.4 percent of the body weight per day. This value was used and then checked against ratios of respiration to excretion, net production, etc., which could be calculated from other authors' data (Table 14) to make sure that it fell within the proper range.

63. Addition of calculated net productivity and respiration yielded an estimate of assimilated food. Estimates of the proportion of

total food ingested that becomes assimilated food include 18,[61] 40,[73] and 70 percent.[178] The intermediate value was used; total food ingested was thus calculated to be assimilated food multiplied by (100/40). Ingestion rates for aquatic insects may range from 2-23 percent of the body weight per day.[37] Of the total food assimilated by the benthos, 94 percent was respired, and 6 percent was utilized by higher trophic levels.

64. In a review of feeding studies of aquatic insects, Cummins[37] stresses the heavy dependence of this group on detritus. Grocki[57] estimated, after reviewing several reports, that algae comprised 30 percent and detritus 70 percent of the diet of benthic invertebrates in Lake Kissimmee. It was assumed in the model that all the invertebrates were detritivorous except *Chaoborus*, which preys on zooplankton,[130] and snails, which graze the epiphytes on macrophytic plants.[78] Proportions of the overall diet comparable to the food requirements of these organisms were specified in the model. The effect of temperature on benthos feeding and respiration is shown in Figure 16.

Fish populations

65. Blocknet samples of Lake Conway fish populations were taken by a team from the Florida Game and Fresh Water Fish Commission during 1976 and 1977. Biomass and numbers from the October 1977 data were assumed to be representative of values which would be obtained on January 1 and were used as the initial conditions for the fish populations in the model. Fresh weight values of fish were converted to carbon by multiplying by 0.1.[138]

66. The fish found in Lake Conway and their major food items are listed in Tables 15, 16, and 17. The percent of the total biomass of each trophic level that an individual species contributed in the October 1977 sample is shown in Table 18.

67. Effects of temperature on feeding and respiration were assumed to be the same for primary and secondary level fish (Figure 16). A normalized relationship was derived using the following equation:[133]

$$\frac{Z}{1 + e^{-0.13(T-18)}} \tag{8}$$

Other data[25] support this relationship and show that food consumption by bluegills is optimum between 25° and 27°C, while the optimum temperature respiration is 30°C.

68. Effects of temperature on feeding by the tertiary fish are shown in Figure 16. The same relationship between respiration and temperature that was used for the primary and secondary level fish was used for the tertiary level fish.

69. Weight values and specific rates of consumption, respiration, and growth from a bioenergetic model for yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*)[79] were used as guidelines in modeling and monitoring Lake Conway fish bioenergetics during simulation (Table 19). Since this work had been carried out on fish acclimated to a 2° to 27°C temperature range (north temperate lakes), the values reported were not viewed as strict constraints.

70. The primary level compartment (Figure 19 and Table 20) is composed of fish that eat algae, zooplankton, benthos, detritus, and epiphytes. The following average percent occurrence of major food items in the diet of threadfin shad have been reported:[20] 25.3 percent phytoplankton, 22.1 percent zooplankton, 24.2 percent benthos, and 28.5 percent detritus. However, 47.6 percent of the total diet of the golden shiner is attributable to consumption of plants (plankton and sessile algae), 16.4 percent to zooplankton, and 37.3 percent to benthos.[102] Values used in the model are shown in Figure 15. Since the young of the species comprising the primary level fish group have essentially the same food preferences, no distinction between adults and young was made.

71. The percentages of annually assimilated food that were allocated to respiration and predation were 78 and 22 percent, respectively.

72. The seconday level fish component (Figure 20) is more detailed than primary level fish since the young and adults of this compartment do not have similar food habits. Equations used in the model are given in Tables 21 and 22. The model includes biomass and numbers of both the adults and young, and seasonal breeding and recruitment pathways. Breeding was programmed to occur during the entire growing season (February to October) as suggested by Carlander[24,25] citing data reported for brown

bullhead,[112] redear sunfish,[32,176] bluegill,[32,113] and warmouth.[87] Recruitment was programmed to occur when the average weight of an individual in a normally distributed population reached 0.6 g C (6.0 g wet weight; 100 mm in length).

73. Additional characteristics of fish populations found in the secondary trophic level that were used as constraints during modeling are listed in Table 23.

74. The total biomass shunted into gamete production was calculated to be 1 percent of the body weight per year, or 2000 eggs, according to ratios of gravid fish weight to number of eggs produced, reported in Carlander[25] citing Estes,[47] and Emig[44] citing Mayhew.[101]

75. Adult secondary level fish respired 72 percent of their total assimilated food; young fish respired 83 percent. Relationships of the tertiary level fish are shown in Figure 21. The equations used for tertiary level fish are given in Tables 24 and 25. Constraints imposed upon this section of the model are listed in Tables 19 and 26. Adult tertiary fish respired 77 percent of their total assimilated food; 1 percent was used in gamete production. Young fish respired 95 percent of their assimilated food.

Suspended and Sedimented Detrital Matter

76. The majority of the organic matter produced in the lake will either settle out to the bottom sediments or be decomposed in the water column. A small fraction will be lost through insect emergence, fish harvest, and outflow. In the model, it was assumed that, during periods of stratification, decaying phytoplankton, zooplankton, and zooplankton fecal pellets entered the suspended, nonliving particulate carbon compartment (Figure 22), where they decomposed or were reingested by zooplankton. A small percentage, however, was allowed to rain through the thermocline down to the sediments. During isothermal periods, the model allows free mixing to take place between the epilimnion and interstitial water. Decomposition of nonliving particulate carbon is accomplished by water column microorganisms whose metabolic responses to temperature were shown

in Figure 16. A listing of equations governing the dead particulate carbon storage is given in Table 27.

77. Initial condition of the nonliving particulate carbon variable was calculated in the following way. The percentage of total particulate organic matter represented by phytoplankton weight varies between 5 and 25 percent.[140,170] Based upon this percentage and a January standing crop of phytoplankton of 0.1 g C/m^2, the initial condition could be between 0.4 and 2.0 g C/m^2. A turnover time of 40.7 days has been reported for particulate organic carbon in Lawrence Lake.[110,170] From estimates of the inputs to the particulate organic carbon storage in Lake Conway (6.23 g C/month) and an assumed turnover time (0.66 month) of half the value above, a standing stock value of 4.11 g C/m^2 was determined. An average of these two possible values (2.4 g C/m^2) was used initially.

78. Over an annual cycle, inputs to the dead particulate carbon storage from phytoplankton sinking and zooplankton egestion were approximately equal. Together they constituted 94 percent of the total input. The remaining inputs were from dead zooplankton and resuspended detritus. More than half the yearly input to the simulated dead particulate carbon storage became sediment. The remainder was either respired in the water column or consumed by zooplankton and planktivorous fish.

79. The dynamics of the sediment detrital pool are shown in Figure 23 and the equations describing them are given in Table 28. Its inputs include all egestion from consumers, including the white amur, as well as dead macroconsumers and seasonal inputs from the nonliving particulate matter storage in the water column and from sloughing of submersed plant parts. Major losses from this storage include both aerobic and anaerobic respiration (54 and 32 percent of total carbon loss, respectively), and detritivory by benthos (12 percent).

Phosphorus Dynamics

80. Levels of dissolved orthophosphate in the water column and

interstitial waters are included in the model as state variables. Other phosphorus forms that make up the remainder of the total phosphorus in unfiltered water are accounted for in the biomass of phytoplankton and zooplankton, and in dead particulate carbon. Initial conditions of the two orthophosphate storages were set at 0.005 mg/ℓ since data reported by the Orange County Pollution Control were below detectable limits (0.01 mg/ℓ). All flows of phosphorus in the model are of phosphorus as orthophosphate. In order to retain a mass balance of phosphorus in the model without modeling the phosphorus content of each component, phosphorus was assumed to maintain a constant 100:1 molar ratio with all carbon storages and flows. However, an exception to this ratio was allowed for submersed plants, whose average molar ratio in Lake Conway was determined to be 738.7:1 as determined by DNR. This prevented overestimation of the amount of phosphorus internally loaded by submersed plant leaching.

81. Dynamics of phosphorus flow in the water column are shown in Figure 24 and equations are given in Table 29. This component is affected by the input of phosphorus from rainfall and runoff, by mixing with interstitial waters during periods of turnover, by uptake and excretion of phosphorus by plants and animals, and by remineralization of nonliving particulate matter in the water column. In the simulation, the amount of phosphorus contributed annually to the water column by internal sources was approximately seven times greater than phosphorus loading from external sources. Only 69 percent of the total input is accounted for in the losses, so internal loading by plants may have been overestimated. An outflow representing phosphorus leaving the lake via outlets accounted for 44 percent of the loss of phosphorus from the water column.

82. Simulated release of phosphorus by the plant compartments occurred in two ways: passive release as a normal accompaniment to plant respiration, and active secretion by plants associated with secretion of organic carbon and associated compounds. Both of these pathways can be viewed as pumps from the sediments to the water since it was assumed that phosphorus uptake by the sumbersed plants was through the roots only. Simulated release of phosphorus by animal activity occurred through

excretory losses, which were set proportional to their respective respiration pathways. Both phosphorus excretion by zooplankton and remineralization of dead particulate organic matter were much less significant than leaching and release by phytoplankton.

83. Phosphorus associated with egestion was shunted to the sediment detrital pool for remineralization (Figure 25, Table 30), comprising slightly more than half of the yearly input to the sediment phosphorus storage. Phosphorus released from dead materials such as sloughed submerged plant parts contributed most of the other half. The initial condition of the sediment phosphorus compartment was determined from the average carbon to phosphorus weight ratio of the sediments: 91.9:1 (Orange County Pollution Control, unpubl. data).

84. Leaching of phosphorus from dead macrophytes results in a loss of between 20 and 50 percent of the plants' total phosphorus content in a few hours and 65 to 85 percent over longer periods.[154,170] Hence, it was assumed that 60 percent of the phosphorus in dead plant parts was released to the interstitial water phosphorus compartment (Figure 26, Table 31) immediately after entering the sediment detrital pool. This constituted 21 percent of the total input to this compartment. Phosphorus is also released to the interstitial compartment from the sediments. Sediment phosphorus release was modeled such that release rates under anaerobic conditions were up to 50 times greater than for aerobic conditions.[10] Microcosm studies of phosphorus release from Lake Conway sediments suggest that release rates can range from 0.2 to 30.0 mg PO_4-P-m^2-day at 23°C, with highest values found in the shallow water, low oxygen sediments that support moderate growth of *Vallisneria*. Using these data, phosphorus release from sediments was modeled by fitting the data to a curve showing temperature dependence of phosphorus release (Figure 27).[79] Anaerobic release rates were assumed to be twice aerobic release rates.

Dynamics of White Amur

85. Many of the studies that have been done on basic biological

features of the white amur have been translated and summarized from the Russian literature by Fischer and Lyakhnovich.[51] They suggest that three distinct growth phases are discernible: during the first two years, highest growth efficiency occurs; from the second to fifth year, growth efficiency is 3 percent per year; and after the fifth or sixth year, when sexual maturity has been reached, only about 1 percent of the food intake is used for body growth (Table 32).

86. Weight-specific consumption rates of white amur are variable and show similar ranges for fish weighing 1 and 2 kg (Table 33). Information on weight-specific consumption rates of fish heavier than 2 kg was not found. Assimilation efficiencies of white amur were reported to range between 31.2 and 90.1 percent of ingested food.[51] An estimated 85.5 percent of assimilated food is lost as respiration and death.

87. Age-varying growth rates were incorporated into the model by adjusting respiratory losses from 85.5 percent for a young fish to 100 percent for a 5- to 6-yr-old fish, or one that weighs 10 kg. Fish can reach a size of 32 kg, but leveling off generally occurs closer to 10 kg.[51]

88. Feces and dead white amur were assumed to sink to the sediments, while excretion of phosphorus from white amur was shunted into the epilimnetic phosphorus compartment.

89. The model of white amur used in simulations is shown in Figure 28, and equations are given in Table 34.

PART III: RESULTS OF MODEL SIMULATION

Baseline Computer Simulations

90. Stable baseline simulations were obtained for a period of 6 yr. After this time, nonsteady-state conditions developed that were directly attributable to decreasing sediment phosphorus availability for submersed plants. Calculations by Blancher (personal communication) show a decrease in total lake phosphorus over the last 3 yr. Provided that the submersed plant-sediment nutrient pumping hypothesis is correct and significant, and that the lake continues to have an outflow, the hypothesis that sediment nutrient content is decreasing may be valid. It is to be expected, then, that the model would develop nonsteady-state behavior when sediment phosphorus becomes limiting for submersed plants.

Ecosystem carbon dynamics

91. Simulated carbon flows in the baseline model are summarized in Figure 29. Simulated gross production totaled 1837 g C/m^2-yr and represented a 1.4 percent efficiency of solar energy utilization. Submersed plants accounted for 56 percent of the total gross production in the simulation, while phytoplankton and epipelic algae accounted for 31 and 13 percent, respectively. Total simulated respiration was 1776 g C/m^2-yr, 81 percent of which was attributable to the producer compartments. Respiration of detritus, dead particulate matter, and carbon leachates from plants accounted for an additional 15 percent of the total, while the remainder resulted from respiration of zooplankton, benthic invertebrates, and fishes. Simulated net ecosystem production was 61 g C/m^2-yr, which is within the range of the measured value. Simulated net production of the plankton community was -96 g C/m^2-yr, which was slightly greater than the measured value.

92. Carbon flows through the grazing and benthic food chains were nearly equal (Figure 30). In addition, the contributions of benthic heterotrophs to water column heterotrophs and of water column heterotrophs to benthic heterotrophs were nearly identical.

93. The simulated pattern of total community production followed

the same pattern as the field data, but, after the April production peak, started to lag behind the measured response by approximately 1 month (Figure 31). Similarly, simulated total respiration lagged behind measured respiration, but after July the patterns became synchronous again (Figure 32). Observed mid-March depressions of gross production and respiration did not appear in the simulation.

94. The simulated annual pattern of net community production was similar to measured net production (Figure 33). Closest agreement with observed data occurred between April and Septmeber; simulated values during the early winter months were higher than measured values.

95. The contributions of the three producer compartments to the simulated gross production curve showed that submersed plants were responsible for the majority of the annual gross production, but that during the summer decline their relative contribution was much diminished (Figure 34).

Plant populations

96. The pattern and magnitude of simulated submersed plant-epiphyte biomass coincided with available 1976 data (Figure 35). No measurements of biomass were available for the period April through September. Simulated biomass of underground organs decreased from the period March through August and increased during the remainder of the year.

97. The pattern of simulated phytoplankton biomass coincided with available 1976 data (April through December) (Figure 36). Since no data for the period January through April 1976 were available, data from 1977 for this period are plotted for comparison. Simulation results showed the same pattern as these data but were higher in magnitude.

98. Simulated gross planktonic production showed more variability than field measurements indicated was present (Figure 37). Discrepancy between simulated and field values was greatest during spring and fall months. The pattern of simulated planktonic respiration for the first 11 months was similar to the observed pattern except for the magnitude of the April peak (Figure 37). The model did not explain the high respiration observed during December.

99. Simulated epipelic algae biomass varied between approximately 1 and 2.5 g C/m^2 (Figure 38). Peaks occurred during the periods March-April and August. Interestingly, a green algae (*Oedogonium*) bloom was observed in April of 1976. Highest simulated gross production metabolic losses and herbivory coincided with periods of greatest biomass.

Invertebrates

100. Simulated zooplankton biomass followed a bimodal pattern during all simulation years except the first (Figure 39). The pattern of zooplankton biomass during the second year is similar to that measured by E. Blancher (personal communication); simulated peak values of biomass were higher than reported, however. Highest assimilation rates, as well as highest rates of respiration and predatory and nonpredatory losses, occurred during the May-June peak of zooplankton biomass. At least half of the zooplankton predation losses were due to secondary level adult fish.

101. Simulated benthic invertebrate biomass followed a bimodal pattern with the higher peak occurring in the spring (Figure 40). The simulation predicted biomass levels within the observed range of data but showed greater variation. Observed patterns of decline during the periods November-December and January-February were predicted by the model.

Fish populations

102. Highest simulated primary level fish biomass occurred during the summer, and lowest biomass occurred during the winter (Figure 41). Predicted levels fell within the range of observed data, but few data points were available.

103. Peak biomass values of secondary level adult fish occurred during late summer in the simulation (Figure 42a). After reaching maximum biomass at this time, biomass levels decreased for the rest of the year and reached a minimum value in April. Predicted biomass levels fell within the range of observed data; seasonal biomass trends were difficult to determine from the available data, but the simulated decline occurring after August was similar in slope to the decline shown by the data at approximately the same time.

104. Simulated biomass of young secondary level fish showed peak values during the late summer and lowest values during the winter and spring months (Figure 42b). Predicted biomass levels fell below all of the three available estimates.

105. Simulation of numbers of adult secondary fish suggested that no recruitment of young into the adult population could occur given the conditions used in the model (Figure 43a). Hence, numbers of adult fish declined as a result of predation. Simulated numbers of young secondary level fish increased to their maximum in August and then declined throughout the remainder of the year to their lowest levels during the winter and early spring (Figure 43b). Simulated values of peak numbers agreed closely with the data.

106. Simulated biomass of adult tertiary level fish peaked during October, coinciding with data reported for that month (Figure 44a). Field data suggest highest biomass levels occur during the summer, however, when the simulation predicted lowest values.

107. Simulations showed that peak biomass levels of young tertiary level fish could be expected to occur during the summer (Figure 44b). The magnitude of the predicted biomass peak fell within the lower boundary of the observed data range.

108. Simulation of numbers of adult tertiary fish suggested that no recruitment of young into the adult population could occur, given the conditions used in the model (Figure 45a). Therefore, numbers of adult tertiary level fish declined at an average rate of 20 percent annually as a result of natural mortality. Simulated numbers of young tertiary level fish increased to their maximum in June and then declined throughout the remainder of the year to their lowest level during February (Figure 45b). Field data show a similar trend, although the highest numbers recorded were approximately three times higher than in the simulation.

Phosphorus

109. Simulated concentration of orthophosphate in the water column remained less than 0.005 g/m^3 for most of the year except during the period between May and July when concentrations as high as 0.013 g/m^3 were reached (Figure 46a). A similar pattern of orthophosphate

concentration in the interstitial waters occurred in the simulations but the range in concentration was not so great as that found in the water column (Figure 46b). Measurements of the orthophosphate concentration in the water column by the Orange County Pollution Control Board were consistently below the limits of detection of their instruments. Their measurements showed, however, a decrease during the months that the simulation predicted highest concentrations. Measurements by Blancher (personal communication) show the opposite: highest values during June and, in addition, another peak during October. Winter and spring values reported by Blancher (personal communication) were lower than those reported by the Orange County Pollution Control Board. Concentration of orthophosphate in interstitial waters was not reported.

110. Total phosphorus concentration in the water column was calculated by summing orthophosphate and the phosphorus in dead organic matter, zooplankton, and phytoplankton. Total phosphorus had a bimodal pattern in the simulation, the first peak occurring in May and the second in October (Figure 46c). Measured total phosphorus had a pattern similar to the simulated pattern but did not show a May peak. The magnitudes of the observed peaks were not nearly so high as those in the simulation. Total phosphorus concentration in the sediments decreased during the simulation (Figure 46d).

Dead particulate carbon and detritus

111. A large peak of dead particulate carbon occurred in June in the simulation, and a smaller peak occurred in November (Figure 47). The pattern of suspended volatile solids measured by the Orange County Pollution Control Board did not show the late summer decline, but rather a single peak intermediate between the two. The rates of spring increase and fall decrease in simulated levels of dead particulate matter were, however, similar to those characterizing the observed data.

112. In the simulation, detritus accumulated at an average rate of 100 g C/m^2-yr (Figure 48). This represents 10 percent of the annual gross production.

Simulated Effects of White Amur on the Lake Conway Ecosystem

113. Approximately 5 years after the September 1977 stocking of five 1-lb white amur per acre (0.45 kg white amur per 4046.9 sq m), maximum levels of submersed plants were reduced in the simulation to less than half the level simulated when no white amur were present (Figure 49a). After ten years, maximum levels were less than 20 percent of original levels. Underground storage organs of submersed plants showed a similar decrease (Figure 49b).

114. During the first year after their introduction, the average white amur showed extremely rapid growth and leveled off at an average biomass of 6000 g wet weight (13.3 lb) after 1 year (Figure 50a). Roy Land (personal communication) reports catches of 12-lb (5.4-kg) white amur from Lake Conway 1 year after introduction. During the first year, the average white amur consumed as much as 120 percent of its body weight per day (Figure 50b). In the following years, the percent of body weight eaten per day decreased. Total white amur biomass also began to decrease after the first year of introduction (Figure 50c) due to a diminishing food resource and to natural mortality (Figure 50d).

115. During the first year after introduction, phytoplankton biomass remained essentially the same as it was before addition of white amur (Figure 51a). During the second year after introduction, however, peak biomass levels were markedly diminished and continued to decline over the next 8 years. Average epipelic algae biomass showed a small but sustained increase after introduction of white amur (Figure 51b).

116. The response of zooplankton was dramatic. Although their biomass levels decreased only slightly during the first year after introduction, drastic reductions occurred in the following years (Figure 52a). Benthic invertebrates were not significantly affected by introduction of white amur (Figure 52b). Primary level fish biomass, on the other hand, diminished rapidly during the first year of stocking and remained low for the rest of the simulation (Figure 52c). Biomass of the adult secondary level fish, which increased during the second year of

simulation without white amur, decreased instead in the simulation with white amur (Figure 53a). After this initial decrease, however, biomass levels rose to higher peaks than they had in the baseline simulation. Despite increases in the adult secondary level fish, young secondary level fish declined during the first year of stocking, much as the primary fish did (Figure 53b).

117. Adult tertiary level fish declined rapidly during the first year after introduction of white amur (Figure 54a). Biomass levels, while beginning to recover 3 years later, remained lower than in steady-state, baseline simulations until the seventh year after introduction. Biomass of the young tertiary level fish also declined after introduction of white amur, but showed some recovery during the next 10 years (Figure 54b).

118. Concentration of orthophosphate in the epilimnion decreased slightly after introduction of white amur, but more noticeable were changes in the seasonal pattern of orthophosphate (Figure 55a). Baseline simulations showed one peak of epilimnetic phosphorus during the year; during the second and sixth through ninth years after introduction of white amur, two peaks of orthophosphate instead of one occurred. During the period between the second and sixth year after introduction of white amur, the seasonal pattern of orthophosphate in the epilimnion was more erratic. The pattern of orthophosphate concentrations in the interstitial waters remained unchanged (Figure 55b).

119. Sediment phosphorus concentration continued to decline as it had in the baseline simulation (Figure 56a). Concentration of total phosphorus in the epilimnion decreased shortly after introduction of white amur (Figure 56b). In addition, peaks of the bimodal pattern observed in baseline simulations were shifted slightly and magnitude of the peaks became more similar to each other than before.

120. Concentration of dead particulate carbon in the water column declined the second year following introduction of white amur (Figure 57a). Concentrations became stable for the ensuing years at less than one half the level observed in baseline simulations. In addition, the biomodal pattern of dead particulate carbon observed in the baseline

simulations disappeared. After introduction of white amur, the rate of detrital accumulation remained similar to the rate observed in baseline simulations (Figure 57b).

121. Ecosystem gross production and respiration declined after introduction of white amur (Figure 58a,b). Two measurements of community metabolism made during the first year after stocking white amur showed depressed ecosystem metabolism also. Seasonal variability in net ecosystem production diminished (Figure 58c). Gross production of phytoplankton declined during the first year after introduction and continued to do so for the remainder of the simulation (Figure 59a). One measurement of phytoplankton gross production during the year after stocking white amur was lower than predicted values. The measurement did not, however, vary significantly from measurements taken in the previous year. Six years after introduction of white amur the fall production peak observed in baseline simulations was completely eliminated. Planktonic respiration also declined (Figure 59b). Little effect of white amur on net planktonic production occurred, however (Figure 59c).

PART IV: INTERPRETATION OF MODEL RESULTS

Submersed Plants, Phosphorus Dynamics, and Lake System Evolution

122. Invasion of the exotic plant *Hydrilla* has been successful, possibly because it has been able to tap the sediment resources that native species have not been able to utilize. *Hydrilla* is well adapted to do this because it has a low light compensation point which enables it to survive at the depths of the sediments.[59] Simulation of the model suggests that the ability to utilize sediment nutrients not only resulted in significant growths of submersed plants, but, in addition, enabled nutrients to be reintroduced into the water column by submersed plant "pumping" allowing stimulation of plankton production to occur. Model results suggested that nearly half of the phosphorus input to the water column in Lake Conway came from submersed plant nutrient cycling. Without submersed macrophytes as a source of internal phosphorus recycling in the model, reasonable agreement of simulated and observed parameters could not be achieved.

123. Corroboration of this finding comes from Blancher (personal communication) who simulated an input-output model of Lake Conway seasonal phosphorus dynamics. He found that phosphorus levels in the lake declined precipitously during the first year of simulation if the only sources of loading were from external sources or sediment release. Addition to his model of 20 percent of the estimated maximum phosphorus loading from submersed plants (derived from the authors' model) resulted in close agreement of simulated and observed phosphorus levels in Lake Conway. He determined that inputs from submersed plants were equal to 36 percent of the total annual phosphorus loading to Lake Conway. In the authors' model, a higher percentage (33 percent) of the estimated maximum phosphorus loading from submersed plants was used. Plants, therefore, provided a higher percentage (43 percent) of the total annual loading.

124. Another instance in which freshwater macrophytes were suspected of contributing significant amounts of phosphorus to a lake was

reported for Shagawa Lake, Minn., where aquatic plant communities were as important a source of phosphorus loading as were sediments, and where macrophytes released significant amounts of phosphorus to the epilimnion during times when the lake was phosphorus limited.[95] Phosphorus release from aquatic macrophytes explained much of the observed rise of total phosphorus levels in the lake.

125. For lakes whose external sources of nutrient input are declining, prolific submersed plant biomass is possibly temporary if the lakes have hydrologic outflows that can gradually remove the phosphorus that submersed plants and other sources contribute to the water column. As sediment phosphorus decreases, exotic submersed plants should decline and plankton populations adapted to the plants nutrient cycling should also decrease. Simulations indicated that this trend toward oligotrophy could occur in Lake Conway. This type of succession towards lower metabolism does not fit the traditional model[119] of increases in organic matter and flows of energy. Rather, the predicted pattern of succession follows a pattern not unlike that proposed for historically steady-state systems that receive a pulse of previously unavailable energy.[119] In such situations, new structure is built in order to utilize the new energy source, and more energy is needed to support it. Energy flow increases to some maximum rate. Because no energy source is inexhaustible, however, systems that have developed structure in excess of the future rates of energy flow available for its support have to decrease structure to prevent total collapse. Thus, energy flow will decrease. In the case of Lake Conway, the new energy source was probably increased nutrient input from fertilizer runoff and septic tank drainage resulting from increased urbanization of the area. Higher plankton production contributed to increased deposition of organic sediments in what was originally a clear, sand-bottomed lake. Since these sediments represented a rich source of nutrients that phytoplankton could not directly use, selection processes favored the success of new structure in the form of submersed plants that were able to tap the stored energy of the sediments. The model predicted a decline in submersed plant structure, however, because nutrients in the sediment became less available with time. Hence,

simulations suggested that the amount of submersed plant structure established when sediment nutrient concentration was high cannot be supported in the future. Ecosystem gross production may decline not only because of declining submersed plant photosynthesis, but also because phytoplankton photosynthesis, dependent on nutrients pumped from the sediments by submersed plants, would decline.

Evaluation of Simulated Effects of White Amur in the Lake Conway Ecosystem

Ecosystem properties

126. Simulations suggested that herbivory by the white amur will accelerate the present trend of lake processes (as suggested by baseline simulations) toward oligotrophy. Decreases in gross production and community respiration to levels below those simulated in the baseline conditions model should occur. The simulations did not suggest, however, that net production levels of the total and plankton community will change appreciably. Hence, the percent of gross production which becomes net production may increase. Progression towards this state resembles an earlier state of succession, except that nutrient levels are declining.

127. In the model, the rate of sediment detritus accumulation remained unchanged after introduction of white amur. Because detrital respiration rates and consumption of detritus by benthic invertebrates remained essentially unchanged, the model results suggest that a larger percentage of gross production will go into sediments instead of food chains. The pelagic-grazing food chain was affected most significantly and those organisms most heavily dependent upon it showed significant decreases.

Primary producers

128. The submersed plant-epiphyte community was reduced by white amur herbivory but not with the rapidity that has been observed in some studies of the white amur in small ponds (W. Miley, personal communication). However, the stocking density of white amur in many of these small ponds was several times greater than the stocking density used in

Lake Conway; this difference could account for differences in removal of rates of vegetation.

129. The decline in simulated phytoplankton biomass was caused by slowly decreasing phosphorus levels. Changes in seasonal patterns of water column orthophosphate concentration, caused by changed patterns of phosphorus leaching from submersed plants, were responsible for the altered pattern of simulated phytoplankton biomass after stocking of white amur.

130. It has been suggested that nutrients associated with excretions and egestions of white amur might stimulate the growth of phytoplankton.[64] One instance of stimulated phytoplankton growth was observed, but in a very small pond in which a high stocking rate of white amur was used.[135] In other studies of white amur in small ponds, no change in phytoplankton biomass or chlorophyll concentration was noticed.[93,139,9,161,150] In a large impoundment stocked with white amur, a decrease in phytoplankton biomass was documented.[112]

131. The slight increase in epipelic algae that was simulated to occur after stocking of white amur was caused by small decreases in herbivory by zooplankton and fish. Heavy growths of *Spirogyra* sp. on the bottoms of ponds in which submersed plants had been eliminated by white amur were reported.[93] Whether this heavy growth represented a real increase in biomass or merely appeared to be due to the elimination of a visual obstruction (submersed plants) was not determined.

Invertebrates

132. A pronounced reduction in simulated zooplankton biomass occurred 2 yr after introduction of white amur because all food resources of zooplankton (except epipelic algae) decreased markedly in the simulation during the second year. In addition, losses due to fish predation increased significantly at this time. Signficant decreases in numbers of calanoid copepods and the cladoceran *Diaphanosoma brachyurm* were recorded during a 3-yr period after introduction of white amur into Lake Wales, Fla.[150] In addition, a shift in dominance to the smaller cladoceran, *Bosmina pulchella*, was recorded. The decline in the calanoid copepods was attributed to size-selection predation effects. The decline

of *Diaphanosoma* was attributed to habitat alteration since it is mainly associated with littoral zone plants. Recorded increases in numbers of zooplanktivorous *Chaoborus* larvae, a benthic community inhabitant, also could have influenced the decline in zooplankton.

133. In the simulation, benthic invertebrates showed little change after introduction of white amur. During the 3 yr after introduction of white amur into Lake Wales, increases in numbers of Oligochaetes and *Chaoborus* larve were recorded, but there were no changes in numbers of chironomid larvae.[150] Changes in total biomass were not reported.

Native fish populations

134. The total standing crop of native fish populations in 31 Arkansas lakes fluctuated markedly after stocking with white amur; control populations of native fish did not.[7] In the majority of cases, standing crops of native fish in lakes containing white amur returned to their prestocking levels within 5 yr. During the transition period after stocking, some natural fish populations appeared to be adversely affected while others appeared to be enhanced. In half of the eight most vegetated lakes, standing crops of shad populations increased to levels higher than had been recorded before addition of white amur. Changes in the standing crop of largemouth bass and bluegill redear sunfish populations were not reported separately. The condition factor of "catchable size" redear sunfish was reported to show significant improvement but no clear trend in condition factors of bass and bluegill was discernible.

135. The model simulating the effects of white amur on Lake Conway showed marked fluctuations in native fish standing crop after introduction of white amur. In the model, primary level fish (mainly planktivores) and the young of the secondary and tertiary level fish were deleteriously affected and showed little recovery. On the other hand, adult secondary and tertiary level fish, which showed decreases soon after introduction of white amur, recovered to their original levels within approximately 1.5 and 6.5 yr, respectively. After their recovery to previous levels, both fish populations showed further increases. Approximately 3.5 yr after introduction of white amur, however, the

adult secondary level fish standing crop began a decline to prestocking levels. Adult tertiary level fish standing crop remained higher than prestocking levels after 10 yr of simulation.

136. The simulated decline in biomass of primary level fish and young secondary and tertiary level fish was caused by a decline in their food sources: zooplankton, dead particulate carbon, phytoplankton, and submersed plants-epiphytes. The initial decrease in biomass of adult secondary level fish was also caused by a decrease in food sources: primary level and young fish, as well as zooplankton. Because a major portion of the secondary level fish diet included benthic invertebrates (which were not significantly affected by white amur), the adult secondary level fish were able to recover. The recovery was enhanced by decreased predation pressure from adult tertiary level fish since their biomass was significantly diminished at this time. Biomass of adult tertiary level fish declined because their preferred food source, the primary level fish, declined. The adult tertiary level fish were, however, able to recover by preying upon newly increased levels of adult secondary level fish.

137. Shireman et al.[150] noted that condition factors of the two largest size classes of bluegill and redear sunfish were significantly improved after introduction of white amur to Lake Wales, Fla. Improvement in the condition factor of largemouth bass was also reported, but was confined to bass measuring less than 350 mm in length.

138. In a joint study by the Florida Game and Fresh Water Fish Commission and the Florida DNR, the effects of white amur on native fish populations in two ponds were investigated. Correct interpretation of the data from this study was a major point of contention because some felt that the intensity of fish sampling carried out in the small ponds removed a significant quantity of fish biomass; hence, sampling effects could have obscured the true effects of white amur. Ware and Gasaway[167] assumed that sampling did not seriously affect the fish populations and concluded that the decrease in standing crop of largemouth bass in Pasco Pond from 27 to 2 lb/acre (3 to 0.224 g/sq m) resulted from the presence of white amur. A substantial decrease in young bass was noted. In the

same pond, bluegill standing crop remained essentially the same and biomass of warmouth sunfish declined.

139. In Suwanee Pond, Ware and Gasaway[167] concluded that native fish populations were not as adversely affected as in Pasco Pond. They reported that the standing crop of young bass increased but that total biomass of harvestable size bass decreased. Total biomass of young and harvestable size bluegill showed similar trends. Coarse species (mainly brown bullhead and lake chubsucker), the authors noted, were a small part of the total fish population biomass prior to white amur introduction but dominated the fish biomass at the end of the study.

140. From the studies and simulations discussed above, it is evident that the effects of white amur on biomass and numbers of individual native fish species will vary from lake to lake. Trends of total native fish biomass after introduction of white amur are unclear but do suggest that greater yearly fluctuations in biomass may occur. In the specific case of Lake Conway, simulations suggest that the biomass of native fish which feed most heavily on plankton and epiphytes will be significantly reduced.

Phosphorus

141. Of all the phosphorus compartments modeled, total phosphorus concentration in the water column changed most significantly when white amur were stocked in the lake. The decrease in total phosphorus was primarily due to decreases in dead particulate carbon, but also to decreases in phytoplankton and zooplankton biomass. Lower levels of orthophosphate in Lake Conway were recorded by the Orange County Pollution Control during the first year after introduction of white amur. Lembi et al.[93] reported increased levels of total phosphorus during the first 3 months after white amur were introduced into small Indiana ponds. Since the study lasted only 1 yr, however, long-term trends of total phosphorus in the ponds were not determined. The model did not predict noticeable changes in sediment phosphorus levels. Terrell,[161] however, recorded increased sediment phosphorus levels in Georgia ponds stocked with white amur. Changed seasonal patterns of phosphorus release from macrophytes was the major reason that seasonal patterns of epilimnetic

orthophosphate changed several years after simulated introduction of white amur. Additional factors that contributed to the new pattern of epilimnetic orthophosphate concentrations were decreased mineralization rates of dead particulate matter and differences in patterns of phytoplankton biomass and related leaching of phosphorus.

Detrital carbon

142. Simulated material transfers among phytoplankton, zooplankton, dead particulate carbon, and epilimnetic phosphorus were very sensitive to changes in each other's storages. Hence, the decline in epilimnetic orthophosphate levels caused by introduction of white amur was the initial change that eventually led to the simulated decrease in dead particulate carbon levels.

Summary

143. Simulation of an ecosystem-level model has demonstrated that high levels of sedimentary phosphorus from previous cultural eutrophication can favor the establishment and proliferation of submersed plants such as the exotic weed hydrilla. Submersed plants that tap sediment phosphorus storages were shown in simulations to increase ecosystem metabolism by their role in recycling phosphorus. Submersed plants, therefore, apparently help to flush phosphorus from the lake, but, in doing so, erode their own nutrient base. The addition of white amur may accelerate the decline of submersed plant biomass and productivity, although the rate of sediment phosphorus decrease may not change. Organisms that are heavily dependent on the pelagic-grazing food chain may decline because of decreased phytoplankton productivity. However, the detritus-based food chain does not seem to be affected.

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Table 1

Models Describing Lake Ecosystems or Processes

Lake	Emphasis of Model
Lake Dalnee, USSR [83]	Whole ecosystem model with emphasis on fisheries (not simulated)
Marion Lake, B. C., Canada [166]	Biological food web model
Kootenay Lake, B. C., Canada [129]	Model of algal growth and nutrients
Lake Ontario, Canada [143]	Model of phosphorus cycling and control mechanisms of phytoplankton productivity
Lake Ontario, Canada [144]	Comparison of an ecological model with a phosphorus-loading model
Lake Washington, Washington [29]	Entire biological, chemical, and hydrodynamic system
Lake Washington, Washington [98]	Input-output phosphorus model
Great Lakes, U. S. [104]	Model of zooplankton production and species composition as influenced by fish predation
Lake Michigan, U. S. [23]	Model of plankton-based food web
Saginaw Bay, Wisconsin [12]	Model of plankton-nutrient dynamics
Shagawa Lake, Michigan [89]	Model of algal growth dynamics
Stone Lake, Michigan [41]	Model of phytoplankton succession and nutrient dynamics
Lake Wingra, Wisconsin [67]	Model of Lake Wingra response to urban runoff and nutrient loading
Lake Wingra, Wisconsin [163]	Productivity model (WEED) of *Myriophyllum spicatum*

(Continued)

Table 1 (Concluded)

Lake	Emphasis of Model
Lake Wingra, Wisconsin [79]	Bioenergetics model of yellow perch and walleye
Lake Wingra, Wisconsin [99]	Biological and chemical model of Lake Wingra
Lake George, New York, and Lake Wingra, Wisconsin [13, 127]	Generalized model simulating lake ecosystems (CLEAN)
Lake George, New York, and Lake Wingra, Wisconsin [128]	Model of Lake George and Lake Wingra (CLEANER)
Lake George, New York, and Lake Wingra, Wisconsin [145]	Documentation of aquatic model: CLEANER
Beaver Reservoir, Arkansas [162]	Generalized whole ecosystem model including biological, chemical, and hydrodynamic properties
Lake Texoma Cove, Texas [133]	Linear model of complex food web
Lake Alice, Florida [110]	Model of waterhyacinth management
Hypothetical lake [142]	Generalized International Biological Programme model for simulating pelagic zones
Unspecified [90]	Model of phytoplankton changes and nutrient fluctuations
Unspecified [12]	Model of algal growth and species competition

Table 2

Components of Model Shown in Figure 1

Designations	Component
Q_1	Phytoplankton, g C/m^2
Q_2	Submersed plants-epiphytes, g C/m^2
Q_3	Epipelic algae, g C/m^2
Q_4	Epilimnetic orthophosphate, g $P\text{-}PO_4/m^2$
Q_5	Dead particulate matter, g C/m^2
Q_6	Zooplankton, g C/m^2
Q_7	Benthic invertebrates, g C/m^2
Q_8	Primary level fish, g C/m^2
Q_9,Q_{10}	Biomass, number of adult secondary level fish, g C/m^2, number/m^2
Q_{11},Q_{12}	Biomass, number of young secondary level fish, g C/m^2, number/m^2
Q_{13},Q_{15}	Biomass, number of adult tertiary level fish, g C/m^2, number/m^2
Q_{16},Q_{17}	Biomass, number of young tertiary level fish, g C/m^2, number/m^2
Q_{18}	Detritus, g C/m^2
Q_{19}	Interstitial orthophosphate, g $P\text{-}PO_4/m^2$
Q_{21},Q_{22}	Biomass, number of white amur, g wet weight/m^2, number/m^2
Q_{23}	Orthophosphate in sediments, g $P\text{-}PO_4/m^2$
R, B, C	Recruitment, breeding, cover (time- and biomass-dependent functions)
T	Turnover (time-dependent function)
F, S	Fall, spring (time-dependent function)

Table 3

Photosynthetic Characteristics of Selected Plants

Plant Group	E_{Q_i} * percent	$L_{Q_{i-50}}$ ** cal/m^2-month
Phytoplankton		
Tropical Lakes [170]	2-3	12667
Lake Leven, Scotland [170]	1.76	
Lake Titicaca [175]	0.293	
Lake Tahoe [170]	0.035	
Submersed Plants [59]		
Hydrilla verticillata		1290
Ceratophyllum demersum		4831
Myriophyllum spicatum		2097
Cabomba carolina		2688
Epipelic Algae [60]	3.1	3402

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* E_{Q_i} = maximum measured photosynthetic efficiency.

** $L_{Q_{i-50}}$ = light level at which one half of the maximum measured photosynthetic efficiency occurs.

Table 4

Rate Equations of Phytoplankton Biomass

Description	Equation
Gross production	$K_1 \cdot L_{Q_1} \cdot [E_{Q_1}/(1 + L_{Q_1}/L_{Q_{1-50}})] \cdot [Q_2/(K_2 + Q_2)] \cdot T_1(T) \cdot K_3 \cdot Q_1$
	where:
Available light	$L_{Q_1} = S \cdot (1-R) \cdot e^{-[K_{12}(Q_1 + Q_5 + Q_6) + K_{13} \cdot \text{level}]} \cdot f_1(Q_1)$
Respiration	$K_4 \cdot Q_1 \cdot f_2(T)$
Sinking	$K_5 \cdot Q_1$
Leaching	$K_6 \cdot Q_1$ (gross production equation)
Consumption by:	
Zooplankton	$K_7 \cdot [Q_1/(K_8 + Q_1)] \cdot Q_6 \cdot f_3(T)$
Primary level fish	$K_9 \cdot Q_1 \cdot Q_8 \cdot f_4(T)$
Secondary level fish (young)	$K_{10} \cdot Q_1 \cdot Q_{11} \cdot f_4(T)$
Tertiary level fish (young)	$K_{11} \cdot Q_1 \cdot Q_{16} \cdot f_4(T)$

Table 5

Estimated Losses From Phytoplankton

Pathway	Gross Photosynthesis percent	Net Production percent	Ecosystem
Respiration	25.0	33.3	Lake Mendota, Wis.[74]
	25.0	33.0	Cedar Bog Lake, Minn.[96]
	53.0	113.0	Severson Lake, Minn.[34]
Leaching	20	--	Unspecified[170]
	--	5.7	Lawrence Lake, Mich., annual average[170]
	4.0	--	Unspecified[156]
	5.8	--	Annual average[171]
Sinking	10	--	Unspecified[60]
Herbivory	11.0	15.0	Lake Mendota, Wis.[74]
	16.0	22.0	Cedar Bog Lake, Minn.[96]
	10.0	21.0	Severson Lake, Minn.[34]

Table 6

Half-Saturation Constants for Phosphorus-Limited Algal Growth

Value of Phosphorus Half-Saturation Coefficient, g/m^3	Species of Algae
0.0025	All Species[23]
0.025 and 0.05	Two hypothetical[30] species
0.2	*Euglena*[31]
0.51	*Euglena*[92]
0.128 - 0.160	*Chlorella*[92]
0.055	*Thalassiosira*[92]
0.035	*Pediastrum*[92]
0.032	*Nitzschia*[92]
0.019	*Scenedesmus*[92]
0.019	*Cyclotella*[92]

Table 7

Rate Equations of Submersed Plant-Epiphyte Biomass

Description	Equation
Gross production	$K_{14} \cdot L_{Q_2} \cdot [E_{Q_2}/1 \;+\; (L_{Q_2}/L_{Q_{2-50}})] \cdot f_5(T) \cdot K_3 \cdot Q_2 \cdot f_2(Q_2) \cdot$ $[(Q_{23}/Q_{18})/(K + Q_{23}/Q_{18})]$
	where:
Available light	$L_{Q_2} = S \cdot (1-R) K_{28} \cdot e^{-[K_{13} Z' + K_{29} Z' (Q_1 + Q_5 + Q_6)/Z]}$
Respiration	$K_{17} \cdot Q_2 \cdot f_6(T)$
Leaching	$K_{18} \cdot Q_2 \cdot$(gross production equation)
Sloughing	$K_{15} \cdot Q_2 \cdot \mathrm{DIE} + K_{16} \cdot Q_2$
Tuber formation	$K_{19} \cdot K_{15} \cdot Q_2$
Tuber germination	$K_{20} \cdot Q_{16} \cdot \mathrm{TUGERM}$
Consumption by:	
Benthic invertebrates	$K_{21} \cdot Q_7 \cdot Q_2 \cdot f_7(T)$
1° level fish	$K_{22} \cdot Q_2 \cdot Q_8 \cdot f_4(T)$
2° level fish	$K_{23} \cdot Q_2 \cdot Q_{11} \cdot f_4(T)$
Zooplankton	$K_{24} \cdot Q_2 \cdot Q_6 \cdot f_3(T)$
2° level fish (adult)	$K_{25} \cdot Q_9 \cdot Q_2 \cdot f_4(T)$
3° level fish (young)	$K_{26} \cdot Q_{16} \cdot Q_2 \cdot f_4(T)$

Table 8

Estimated Losses From Submersed Plant-Epiphyte Complex

Pathway	Gross Photosynthesis percent	Net Productivity percent	Standing Crop percent	Source
Respiration	58.0	135.0	---	*Sagittaria* - epiphyte community in Silver Springs, Fla. [120]
	79.0 - 189.0	---	---	Daily values for *Vallisneria asiatica* and *Potamogeton crispus* [71]
Secretion	4.0	---	---	Annual value, highest rates in fall [169]
	2.0	---	---	Unspecified [65]
	---	5.0	---	Unspecified [1]
	7.0	---	---	Unspecified [4]
	4.0	---	---	Annual value [171]
	0.05 - 25.3	---	---	Daily value [171]
	1.5	---	---	*Zostera marina* [134]
Herbivory	---	0.5 - 8.0	---	Unspecified [170]
Sloughing	---	---	2 - 10	Annual value for actively growing plants [147, 168]

Table 9

Rate Equations of Epipelic Algae Biomass

Description	Equation
Gross production	$K_{31} \cdot L_{Q_3} \cdot [E_{Q_3}/1 + (L_{Q_3}/L_{Q_{3-50}})][Q_{15}/(K_{30} + Q_5)] \cdot$ $f_1(T) \cdot K_3 \cdot Q_3$
	where:
Available light	$L_{Q_3} = S \cdot (1-R) \cdot e^{-[K_{13} \cdot Z + K_{12} \cdot (Q_1 + Q_5 + Q_6)]} \cdot f_3(Q_2)$
Respiration	$K_{32} \cdot Q_3 \cdot f_1(T)$
Death	$K_{33} \cdot Q_3$
Leaching	$K_{34} \cdot Q_3 \cdot$(gross production equation)
Consumption by:	
Zooplankton	$K_{35} \cdot Q_3 \cdot Q_6 \cdot f_3(T)$
1° level fish	$K_{36} \cdot Q_3 \cdot Q_8 \cdot f_4(T)$
2° level fish (adults)	$K_{37} \cdot Q_3 \cdot Q_9 \cdot f_4(T)$
2° level fish (young)	$K_{38} \cdot Q_3 \cdot Q_{11} \cdot f_4(T)$
3° level fish (young)	$K_{39} \cdot Q_{16} \cdot Q_3 \cdot f_4(T)$
Benthic invertebrates	$K_{40} \cdot Q_3 \cdot Q_7 \cdot f_7(T)$

Table 10

Rate Equations of Zooplankton Biomass

Flow	Equation
Consumption of:	
Phytoplankton	$K_7 \cdot [Q_1/(K_8 + Q_1)] \cdot Q_6 \cdot f_3(T)$
Dead particulate organic carbon	$K_{45} \cdot [Q_5/(K_{46} + Q_5)] \cdot Q_6 \cdot f_3(T)$
Epipelic algae	$K_{35} \cdot Q_3 \cdot Q_6 \cdot f_3(T)$
Submersed plant-epiphytes	$K_{24} \cdot Q_2 \cdot Q_6 \cdot f_3(T)$
Assimilation	$K_{41} \cdot$(consumption equations)
Egestion	$(1.-K_{41}) \cdot$(consumption equations)
Respiration	$K_{48} \cdot Q_6 \cdot f_3(T)$
Natural mortality	$K_{49} \cdot Q_6$
Predation by:	
Benthic invertebrates	$K_{50} \cdot Q_6 \cdot Q_7 \cdot f_7(T) \cdot f_7(T)/f_3(T)$
2° level fish (adults)	$K_{51} \cdot Q_6 \cdot Q_9 \cdot f_4(T) \cdot f_4(T)/f_3(T)$
1° level fish	$K_{52} \cdot Q_6 \cdot Q_8 \cdot f_4(T) \cdot f_4(T)/f_3(T)$
2° level fish (young)	$K_{53} \cdot Q_6 \cdot Q_{11} \cdot f_4(T) \cdot f_4(T)/f_3(T)$
3° level fish (young)	$K_{54} \cdot Q_6 \cdot Q_{16} \cdot f_4(T) \cdot f_4(T)/f_3(T)$

Table 11

Metabolic Characteristics of Zooplankton Populations

Parameter	Value	Reference
Turnover time, days	2-10	Lake Sibaya [62]
	17.4	Average value for 10; temperate lakes [170]
Assimilation rate, percent of ingested	52.63	Average for adult and juvenile zooplankton [170]
	41.0	Unspecified [58]
	27.0	Unspecified [58]
Respiration	33.0% of assimilated	Average for adult and juvenile zooplankton [170]
	46.2% of assimilated	Average for adults only [170]
	71.0% of assimilated (15.9% of body wt/day)	Unspecified [58]
	69.0% of assimilated (19.35% of body wt/day)	Unspecified [58]
	38.8-43.4% of body wt/day	Unspecified [86]
Net production,* percent of assimilated	67	Average of adult and juvenile population [170]
	54	Average for adult zooplankton only [170]
	71	Unspecified [58]
	70	Unspecified [58]

---

* Growth increments, plus losses due to mortality and predation, plus production.

Table 12

Rate Equations of Benthic Invertebrate Biomass

Flow	Equation
Consumption of:	
Zooplankton	$K_{58} \cdot Q_6 \cdot Q_7 \cdot f_7(T) \cdot f_7(T)/f_3(T)$
Submersed plants-epiphytes	$K_{57} \cdot Q_2 \cdot Q_7 \cdot f_7(T)$
Epipelic algae	$K_{56} \cdot Q_3 \cdot Q_7 \cdot f_7(T)$
Detritus	$K_{59} \cdot K_{55}$ [(other consumption)$\cdot$2.5 - (other consumption equations)]
Assimilation	$K_{59} \cdot K_{55} \cdot$ (first three consumption equations)
Egestion	$(1-K_{55}) \cdot$ (consumption equations)
Respiration	$K_{60} \cdot Q_7 \cdot f_7(T)$
Natural mortality	$K_{68} \cdot Q_7$
Predation by:	
1° level fish	$K_{62} \cdot Q_7 \cdot Q_8 \cdot f_4(T) \cdot \mathrm{COVER} \cdot f_4(T)/f_7(T)$
2° level fish (adults)	$K_{63} \cdot Q_7 \cdot Q_9 \cdot \mathrm{COVER} \cdot f_4(T) \cdot f_4(T)/f_7(T)$
2° level fish (young)	$K_{64} \cdot Q_7 \cdot Q_{11} \cdot \mathrm{COVER} \cdot f_4(T) \cdot f_4(T)/f_7(T)$
3° level fish (young)	$K_{65} \cdot Q_7 \cdot Q_{16} \cdot \mathrm{COVER} \cdot f_4(T) \cdot f_4(T)/f_7(T)$
3° level fish (adult)	$K_{67} \cdot Q_7 \cdot Q_{13} \cdot \mathrm{COVER} \cdot f_{12}(T) \cdot f_{12}(T)/f_7(T)$

Table 13

Weight Estimates of Benthic Invertebrates

(g dry wt/individual)

	Calculated From Wetzel[170] Summarizing Data from Okland[124]	Junk[75]	Sapkarev and Tocko[140]	Value Used in Model
Oligochaeta	5.83×10^{-4}	0.19×10^{-4}	24.3×10^{-4}	10.11×10^{-4}
Hirudinea	---	---	392.7×10^{-4}	---
Ephemeroptera	4.45×10^{-4}	62.6×10^{-4}	---	35.53×10^{-4}
Trichoptera	7.18×10^{-4}	19.9×10^{-4}	---	13.54×10^{-4}
Chaoborus	4.18×10^{-4}	---	---	4.18×10^{-4}
Chironomidae	4.88×10^{-4}	0.22×10^{-4}	3.04×10^{-4}	2.71×10^{-4}
Gastropoda	21.8×10^{-4}	---	---	21.8×10^{-4}
Ostracoda	---	0.03×10^{-4}	---	0.03×10^{-4}
Isopoda	---	---	5.96×10^{-4}	5.96×10^{-4}
Amphipoda	---	---	8.4×10^{-4}	8.4×10^{-4}

Table 14

Metabolic Characteristics of Benthic Invertebrates

Characteristic	Value	Organism
Percent of body weight eaten per day	10	*Chaoborus* larvae [37, 77]
	2-23	---
Assimilation rate, percent of ingested	40	Carnivorous benthic fauna [73, 170]
	70	Dragon fly nymph [178]
	18	*Hyallela azteca* [61]
Respiration	3.4% of body weight per day	*Hyallela azteca* [61]
	41% of assimilated food	*Hyallela azteca* [61]
	77% of assimilated food	Carnivorous benthic fauna [73, 168]
Net production, percent of assimilated food	23	Carnivorous benthic fauna [73, 168]
	59	*Hyallela azteca* [61]

Table 15

Food Preferences of Primary Level Fish Found in Lake Conway

Fish	Major Food Items
Dorosoma petenense (threadfin shad)	Plankton, benthic invertebrates, detritus [20, 24, 159]
D. cepedianum (gizzard shad)	Zooplankton, phytoplankton [25, 35]
Ictalurus catus (white catfish)	Benthic invertebrates, macrophytes, snails, filamentous algae, detritus [103, 107]
Notemigonus crysoleucas (golden shiner)	Phytoplankton, zooplankton, benthic invertebrates [25, 102]
Notropis petersoni (coastal shiner)	Filamentous algae and other plants, insect larvae, nymphs [103]
Jordanella floridae (flagfish)	Algae and other vegetation [103]
Erimyzon sucetta (lake chubsucker)	Filamentous algae, other plant matter, detritus, benthic invertebrates [103]

Table 16

Food Preferences of Adult Secondary Level Fish Found in Lake Conway

Fish	Major Food Items
Fundulus seminolis (seminole killifish)	Benthic invertebrates, seeds of aquatic plants [103]
F. chrysotus (golden topminnow)	Benthic invertebrates, zooplankton [103]
Lucania goodei (bluefin killifish)	Benthic invertebrates [103]
Labidesthes sicculus (brook silverside)	Insects and crustacea [49, 103]
Enneacanthus gloriosus (bluespotted sunfish)	Insect larvae, small crustaceans [28, 103]
Lepomis gulosus (warmouth sunfish)	Benthic invertebrates, small fish [66]
L. macrochirus (bluegill)	Zooplankton, benthic invertebrates, crustaceans, aquatic plants [28, 44, 52, 68]
L. microlophus (redear sunfish)	Benthic invertebrates [44, 68]
L. marginatus (dollar sunfish)	Zooplankton, bethic invertebrates [28, 103]
L. punctatus (spotted sunfish)	Insects, crustaceans [28]
Etheostoma fusiforme (swamp darter)	Benthic invertebrates, zooplankton [103]
Notarus gyrinus (tadpole madtom)	Zooplankton, benthic invertebrates [24, 103]
Heterandria formosa (least killifish)	Benthic invertebrates, zooplankton, filamentous algae [103]
Gambusia affinis (mosquitofish)	Insects, zooplankton, filamentous algae [103]
Ictalurus natalis (yellow bullhead)	Benthic invertebrates, zooplankton, aquatic plants [103]
I. nebulosus (brown bullhead)	Benthic invertebrates, detritus algae, plants, insects, fish, fish eggs [25, 45]
Aphredoderus sayannus (pirate perch)	Benthic invertebrates, zooplankton, aquatic plants [103]

Table 17

Food Preferences of Tertiary Level Fish Found in Lake Conway

Fish	Major Food Items
Lepisosteus platyrhyncus (Florida gar)	Fish, crustacea, insects [25, 36]
Micropterus salmoides (largemouth bass)	Fish, crustaceans, benthic invertebrates [46, 103]
Pomoxis nigromaculatus (black crappie)	Fish, benthic invertebrates [56, 68]
Lepisosteus osseus (longnose gar)	Fish, benthic invertebrates [36, 84]
Amia calva (bowfin)	Fish, benthic invertebrates [103]
Esox niger (chain pickerel)	Fish [21, 25]
Esox americanus (redfin pickerel)	Benthic invertebrates, fish [103]

Table 18

Distribution in October 1977 Sample of Biomass Among Species in Three Trophic Levels*

Trophic Level	Species	Percent of Biomass		
		Adult		Young
1	*Dorosoma petenense*	---	79.42	---
	Erimyzon sucetta	---	0.35	---
	Notemigonus crysoleucas	---	20.22	---
2	*Ictalurus nebulosus*	1.39		0.43
	Lepomis microlophus	46.04		16.19
	L. macrochirus	48.52		34.00
	Enneacanthus gloriosus	0.00		40.11
	Lepomis gulosus	4.05		5.42
	Fundulus chrysotus	0.00		3.09
	Others	0.00		0.76
3	*Micropterus salmoides*	81.83		100.00
	Esox niger	17.18		0.00
	Pomoxis nigromaculatus	0.99		0.00
	Others			

---

* Calculated from data supplied by the Florida Game and Fresh Water Fish Commission, Orlando, Fla.

Table 19

Bioenergetics of Fish[79]

Parameter	Value
Specific rate of consumption	0.02 to 0.14 g/g-day over a temperature range of 2° to 22°C
Specific rate of respiration	0.004 to 0.02 g/g-day over a temperature range of 2° to 22°C
Specific rate of growth	Less than -0.01 to 0.06 g/g-day over a temperature range of 2° to 27°C
Percent of consumed food egested	30 to 15 percent over a temperature range of 2° to 27°C

Table 20

Rate Equations of Primary Level Fish Biomass

Flow	Equations
Consumption of:	
Phytoplankton	$K_9 \cdot Q_1 \cdot Q_8 \cdot f_4(T)$
Zooplankton	$K_{52} \cdot Q_6 \cdot Q_8 \cdot f_4(T) \cdot f_4(T)/f_3(T)$
Dead particulate organic matter	$K_{85} \cdot Q_8 \cdot Q_5 \cdot f_4(T)$
Submersed plants-epiphytes	$K_{22} \cdot Q_2 \cdot Q_8 \cdot f_4(T)$
Benthic invertebrates	$K_{62} \cdot Q_7 \cdot Q_8 \cdot \mathrm{COVER} \cdot f_4(T) \cdot f_4(T)/f_7(T)$
Assimilation	$K_{69} \cdot$ (consumption equations)
Egestion	$(1.-K_{69}) \cdot$ (consumption equations)
Respiration	$K_{71} \cdot Q_8 \cdot f_4(T)$
Natural mortality	$K_{75} \cdot Q_8$
Predation by:	
2° level fish (adults)	$K_{74} \cdot Q_8 \cdot Q_9 \cdot f_4(T) \cdot \mathrm{COVER}$
3° level fish (adults)	$K_{73} \cdot Q_8 \cdot Q_{13} \cdot f_{12}(T) \cdot f_{12}(T)/f_4(T) \cdot \mathrm{COVER}$

Table 21

Rate Equations of Secondary Level Adult Fish Biomass and Numbers

Flow	Equations
Biomass	
Consumption of:	
Zooplankton	$K_{51} \cdot Q_6 \cdot Q_9 \cdot f_4(T) \cdot f_4(T)/f_3(T)$
Benthic invertebrates	$K_{64} \cdot Q_7 \cdot Q_9 \cdot f_4(T) \cdot f_4(T)/f_7(T) \cdot \mathrm{COVER}$
Primary level fish	$K_{74} \cdot Q_8 \cdot Q_9 f_4(T) \cdot \mathrm{COVER}$
Submersed plants-epiphytes	$K_{25} \cdot Q_9 \cdot Q_2 \cdot f_4(T)$
Assimilation	$K_{76} \cdot$(consumption equations)
Egestion	$(1.-K_{76}) \cdot$(consumption equations)
Respiration	$K_{77} \cdot Q_9 \cdot f_4(T)$
Natural mortality	$K_{78} \cdot Q_{10} \cdot Q_9 \cdot 3./Q_{10}$
Predation by:	
3° level fish	$K_{82} \cdot Q_9 \cdot Q_{13} \cdot f_{12}(T) \cdot f_{12}(T)/f_4(T) \cdot \mathrm{COVER}$
Gamete production	$K_{80} \cdot Q_9 \cdot \mathrm{BRTH1}$
Recruitment	$\cdot \mathrm{READY} \cdot \frac{Q_{11}}{Q_{12}} \cdot \frac{1}{4047}$
Numbers	
Recruitment	$\mathrm{READY1} \cdot 1./4047$
Nonpredatory mortality	$K_{78} \cdot Q_{10}$
Predation	$[Q_{10}/(Q_9 \cdot 3.][K_{81} \cdot Q_9 \cdot Q_{14} \cdot f_8(T)\ f_8 \cdot (T)/f_4(T) \cdot \mathrm{COVER} +$ $K_{82} \cdot Q_9 \cdot Q_{13} \cdot f_{12} \cdot (T)/f_4 \cdot T \cdot \mathrm{COVER}]$

Table 22

Rate Equations of Secondary Level Young Fish Biomass and Numbers

Flow	Equation
Biomass	
Consumption of:	
Zooplankton	$K_{53} \cdot Q_6 \cdot Q_{11} \cdot f_4(T) \cdot f_4(T)/f_3(T)$
Benthic invertebrates	$K_{64} \cdot Q_7 \cdot Q_{11} \cdot \mathrm{COVER} \cdot f_4(T) \cdot f_4(T)/f_7(T)$
Phytoplankton	$K_{10} \cdot Q_1 \cdot Q_{11} \cdot f_4(T)$
Submersed plants-epiphytes	$K_{23} \cdot Q_2 \cdot Q_{11} \cdot f_4(T)$
Epipelic algae	$K_{38} \cdot Q_3 \cdot Q_{11} \cdot f_4(T)$
Assimilation	$K_{81} \cdot$ (consumption equations)
Egestion	$(1.-K_{81}) \cdot$ (consumption equations)
Respiration	$K_{86} \cdot Q_{11} \cdot f_4(T)$
Nonpredatory mortality	$K_{87} \cdot Q_{12} \cdot Q_{11}/Q_{12}$
Predation by:	
3° level fish	$K_{89} \cdot Q_{11} \cdot Q_{13} \cdot f_{12}(T) \cdot f_{12}(T)/f_4(T) \cdot \mathrm{COVER}$
Recruitment	$\mathrm{READY} \cdot 1 \cdot \dfrac{Q_{11}}{Q_{12}} \cdot \dfrac{1}{4047}$
Numbers	
Birth	$K_{90} \cdot K_{80} \cdot Q_9 \cdot \mathrm{BIRTH}$
Recruitment	$\mathrm{READY1} \cdot 1./4047$
Nonpredatory mortality	$K_{87} \cdot Q_{12}$
Predation	$Q_{12}/Q_{11} \cdot K_{88} \cdot Q_{11} \cdot Q_{14} \cdot f_8(T) \cdot f_8(T)/f_4(T) \cdot \mathrm{COVER} + K_{89} \cdot$ $Q_{11} \cdot Q_{13} f_{12}(T) \cdot f_{12}(T)/f_4(T) \cdot \mathrm{COVER}$

Table 23

Dynamics of Secondary Level Fish Populations

Parameter	Value
Turnover time	Approximately 1 yr for adult bluegills in northern Indiana [54]
	Approximately 2 yr for bluegills in Oklahoma [173]
Consumption	4.7-6.2% of body weight per day [63]
Gamete production	
Mortality	0-25% per year for fry if food is abundant [153]
	30% per year for bluegill if ponds stocked with bass [136]
Specific growth rates	0.08-1.78 g/g-day (highest values measured for smallest fish) [54]

Table 24

Rate Equations of Tertiary Level Adult Fish Biomass and Numbers

Flow	Equation
Biomass	
Consumption of:	
1° level fish	$K_{73} \cdot Q_8 / f_4(T)$
2° level fish (adults)	$K_{82} \cdot Q_9 / f_4(T)$
2° level fish (young)	$K_{89} \cdot Q_{11} / f_4(T)$
3° level fish (young)	$K_{113} \cdot Q_{16} / f_4(T)$
Benthic invertebrates	$K_{67} \cdot Q_7 / f_7(T)$
Assimilation	$K_{112} \cdot$ (consumption equations)
Egestion	$(1. - K_{112}) \cdot$(consumption equations)
Respiration	$K_{97} \cdot Q_{13} \cdot f_4(T)$
Mortality	$K_{10\,5} \cdot Q_{13}$
Gamete production	$K_{114} \cdot Q_{13} \cdot \mathrm{BRTH3}$
Recruitment	$\mathrm{READY2} \cdot (Q_{16}/Q_{17}) \cdot (1./4057) \cdot [Q_{13}/(Q_{13} + Q_{14})]$
Numbers	
Recruitment	$\mathrm{READY2} \cdot 1./4047$
Mortality	$K_{10\,5} \cdot Q_{15}$

Table 25

Rate Equations for Tertiary Level Young Fish Biomass and Numbers

Flow	Equation
Biomass	
Consumption of:	
Zooplankton	$K_{54} \cdot Q_6 \cdot Q_{16} \cdot f_4(T) \cdot f_4(T)/f_3(T)$
Benthic invertebrates	$K_{65} \cdot Q_7 \cdot Q_{16} \cdot \mathrm{COVER} \cdot f_4(T) \cdot f_4(T)/f_7(T)$
Phytoplankton	$K_{11} \cdot Q_1 \cdot Q_{16} \cdot f_4(T)$
Submersed plants-epiphytes	$K_{26} \cdot Q_{16} \cdot Q_2 \cdot f_4(T)$
Epipetic algae	$K_{39} \cdot Q_{16} \cdot Q_3 \cdot f_4(T)$
Assimilation	$K_{117} \cdot$ (consumption equations)
Egestion	$(1.-K_{117}) \cdot$ (consumption equations)
Respiration	
Nonpredatory mortality	$K_{108} \cdot Q_{17} \cdot Q_{16}/Q_{17}$
Predation by:	
3° level fish (warm)	$K_{113} \cdot Q_{16} \cdot Q_{13} \cdot f_{12}(T) \cdot f_{12}(T)/f_4(T) \cdot \mathrm{COVER}$
Recruitment	$\mathrm{READY2} \cdot (Q_{16}/Q_{17}) \cdot (1./4047)$
Birth	$K_{114} \cdot Q_{13} \cdot \mathrm{BRTH3}$
Numbers	
Birth	$K_{111} \cdot K_{114} \cdot Q_{13} \cdot \mathrm{BRTH3} + K_{116} \cdot Q_{14} \cdot \mathrm{BRTH2} \cdot \mathrm{SBSTRA}$
Recruitment	$\mathrm{READY2} \cdot 1./4047$
Mortality	$K_{108} \cdot Q_{17}$
Predation	$[Q_{17}/Q_{16}] \cdot K_{115} \cdot Q_{16} \cdot Q_{14} \cdot f_8(T)/f_4(T) \cdot \mathrm{COVER} + K_{113} \cdot Q_{16} \cdot Q_{13} \cdot f_{12}(T) \cdot f_{12}(T)/f_4(T) \cdot \mathrm{COVER}$

Table 26

Some Characteristics of Tertiary Level Fish Populations

Parameter	Value
Percent of body weight eaten per day	9.5% by small adult bass [63] 6.7% by adult bass [69] 5.2% by adult bass [94]
Mortality	Between 19.5 and 92% per year ($\overline{X}$ = 58%); most data reported for north temperate lakes where overwinter mortality can be high; highest mortality among young [25]
Specific growth rates	-0.015 - 0.080 g/g-day for Florida bass and -0.002 - 0.101 g/g-day for northern largemouth bass in Florida. Values varied with season and initial weight of fish [32]

Table 27

Rate Equations for Suspended, Dead Particulate Carbon

Flow	Equation
Inflow from:	
Phytoplankton death	$K_5 \cdot Q_1$
Zooplankton egestion	$(1.-K_{41}) \cdot$ (zooplankton consumption)
Zooplankton death	$K_{49} \cdot Q_6$
Suspension of detritus	TRNOVR $(K_{101} \cdot Q_{18} - Q_5)$
Outflows due to:	
Settling	$K_{100} \cdot Q_5$
Zooplankton detritivory	$K_{45} \cdot Q_5 \cdot Q_6 \cdot f_3(T) \cdot Q_5/(K_{46} + Q_5)$
1° level fish detritivory	$K_{85} \cdot Q_5 \cdot Q_8 \cdot f_4(T)$
Respiration	$K_{94} \cdot Q_5 \cdot f_{10}(T)$

Table 28

Rate Equations for Detritus

Flows	Equation
Inflows from:	
Sloughed submersed plant parts	$K_{15} \cdot Q_2 \cdot DIE + K_{16} \cdot Q_2$
Benthic invertebrate egestion	$(1.-K_{55})$ (consumption equation)
1° level fish egestion	$(1.-K_{69})$ (consumption equation)
2° level fish (adult) egestion	$(1.-K_{78})$ (consumption equation)
2° level fish (young) egestion	$(1.-K_{84})$ (consumption equation)
3° level fish (adult) egestion	$(1.-K_{112})$ (consumption equation)
3° level fish (young) egestion	$(1.-K_{117})$ (consumption equation)
White amur egestion	K_{122} $(1.-K_{118})$ (consumption equation)
Benthic invertebrate mortality	$K_{68} \cdot Q_7$
1° level fish mortality	$K_{75} \cdot Q_8$
2° level fish (adult) mortality	$K_{78} \cdot Q_{10} \cdot Q_9 \cdot 3./Q_{10}$
2° level fish (young) mortality	$K_{87} \cdot Q_{12} \cdot Q_{11}/Q_{12}$
3° level fish (adult) mortality	$K_{105} \cdot Q_{15} \cdot (Q_{13} + Q_{14})/Q_{15}$
3° level fish (young) mortality	$K_{108} \cdot Q_{17} \cdot Q_{16}/Q_{17}$
White amur mortality	
Outflows from:	
Benthic invertebrate consumption	$K_{59} \cdot K_{55}$ [(other consumption)$\cdot$2.5 - (other consumption equations)]
Detrital respiration	f_9 (T)
Detrital suspension	$TRNOVR \cdot (K_{101} \cdot Q_{18} - Q_5)$

Table 29

Rate Equations for Epilimnetic Phosphorus

Flow	Equation
Inflow from:	
External sources	Table function (Figure 2-10)
Phytoplankton leaching & respiration	$K_{91} \cdot [K_6 \cdot Q_1 \cdot (\text{gross production equation}) + K_4 \cdot Q_1 \cdot f_2(T)]$
Submersed plant-epiphyte leaching and respiration	$K_{92} \cdot [K_{18} \cdot Q_2 \cdot (\text{gross production equation}) + K_{17} \cdot Q_2 \cdot f_6(T)] \cdot \text{KFIXIT}$
Remineralization of suspended organic matter	$K_{93} \cdot K_{94} \cdot Q_5 \cdot f_{10}(T)$
Exchange with interstitial water phosphorus	$\text{TRNOVR} \cdot (Q_4 - Q_{19})$
Zooplankton excretion	$K_{91} \cdot K_{48} \cdot Q_6 \cdot f_3(T)$
1° level fish excretion	$K_{91} \cdot K_{71} Q_8 \cdot f_4(T)$
2° level fish (adults) excretion	$K_{91} \cdot K_{77} \cdot Q_9 \cdot f_4(T)$
2° level fish (young) excretion	$K_{91} \cdot K_{86} \cdot Q_{11} \cdot f_4(T)$
3° level fish excretion	$K_{91} \cdot K_{97} \cdot Q_{13} \cdot f_4(T)$
3° level fish (young) excretion	$K_{91} \cdot K_{45} \cdot Q_{16} \cdot f_4(T)$
White amur excretion	$K_{122} \cdot K_{123} \cdot K_{120} \cdot Q_{21} \cdot f_4(T)$
Outflows due to:	
Phytoplankton uptake	$K_{91} \cdot (\text{gross production equations})$
Unaccountable hydrologic outflows	$K_{99} \cdot Q_4$

Table 30

Rate Equations for Sediment Phosphorus

Description	Equation
Inflows from:	
Benthic invertebrate egestion	$K_{91} \cdot (1.-K_{55}) \cdot$ (consumption equation)
1° level fish egestion	$K_{91} \cdot (1.-K_{69}) \cdot$ (consumption equation)
2° level fish (adult) egestion	$K_{91} \cdot (1.-K_{78}) \cdot$ (consumption equation)
2° level fish (young) egestion	$K_{91} \cdot (1.-K_{84}) \cdot$ (consumption equation)
3° level fish (adult) egestion	$K_{91} \cdot (1.-K_{112}) \cdot$ (consumption equation)
3° level fish (young) egestion	$K_{91} \cdot (1.-K_{117}) \cdot$ (consumption equation)
Benthic invertebrate mortality	$K_{91} \cdot K_{68} \cdot Q_7$
1° level fish mortality	$K_{91} \cdot K_{75} \cdot Q_8$
2° level fish (adult) mortality	$K_{91} \cdot K_{78} \cdot Q_{10} \cdot Q_9 \cdot 3./Q_{10}$
2° level fish (young) mortality	$K_{91} \cdot K_{87} \cdot Q_{12} \cdot Q_{11}/Q_{12}$
3° level fish (adult) mortality	$K_{91} \cdot K_{105} \cdot Q_{15} \cdot Q_{13}/Q_{15}$
3° level fish (young) mortality	$K_{91} \cdot K_{108} \cdot Q_{17} \cdot Q_{16}/Q_{17}$
Settling suspended particulate matter	$K_{91} \cdot (K_{100} \cdot Q_5 + TRNOVR \cdot K_{101} Q_{18} - Q_5)$
Sloughed submersed plant parts	$K_{92} \cdot 0.4 \cdot (K_{15} \cdot Q_2 \cdot DIE + K_{16} \cdot Q_2)$
White amur egestion	$K_{92} \cdot K_{122} \cdot (1.-K_{118}) \cdot$ (consumption equation)
White amur mortality	$K_{92} \cdot K_{123} \cdot Q_{22} \cdot Q_{21}/Q_{22}$
Outflows due to:	
Consumption of detritus by benthos	$K_{91} \cdot K_{59} \cdot K_{55} \cdot$ (consumption of detritus)
Aerobic phosphorus release	$AEROBC \cdot f_{11} \cdot (T) \cdot K102$
Anaerobic phosphorus release	$ANOXIC \cdot f_{11} \cdot (T) \cdot K103$
Net uptake by submersed plants	$K_{92} \cdot$ (Gross production) $\cdot (1 - K_{fixit})$

Table 31

Rate Equations for Interstitial Phosphorus

Flow	Equation
Inflow from:	
Aerobic sediment release	$\mathrm{AEROBC} \cdot f_{11}(T) \cdot K_{10\,2}$
Anaerobic sediment release	$\mathrm{ANOXIC} \cdot f_{11}(T) \cdot K_{10\,3}$
Exchange with epilimnetic phosphorus	$\mathrm{TRNOVER} \cdot (Q_4 - Q_{19})$
Epipelic algae leaching and respiration	$K_{91} \cdot (K_{32} \cdot f_2(T) \cdot Q_3 + K_{34} \cdot Q_3$
	(gross production equation)
Decay of dying epipelic algae	$K_{91} \cdot K_{33} \cdot Q_3$
Decay of sloughed submersed plant parts	$K_{92} \cdot (0.6) \cdot [K_{15} \cdot Q_2 \cdot \mathrm{DIE} + K_{16} \cdot Q_2]$
Outflows due to:	
Epipelic algae uptake	$K_{91} \cdot$(gross production equation)
Unaccounted for outflows	$K_{10\,6} \cdot Q_{119}$

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LARGE-SCALE OPERATIONS MANAGEMENT TEST OF USE OF THE WHITE AMUR--ETC(U)
NOV 81   K C EWEL, T D FONTAINE   DACW39-76-C-0019
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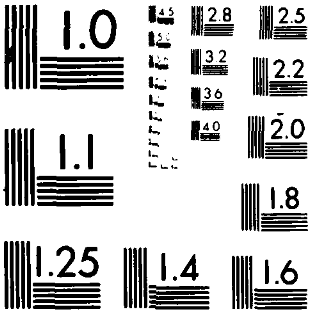

MICROCOPY RESOLUTION TEST CHART
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Table 32

Growth Efficiencies of White Amur of Different Ages and Sizes

Age, years	Size, g	Growth Food Intake, %*
0-2		10**
2-5		3**
5-6		1**
1†	80-90	3.4-4.3††
1	100-199	1.2-2.8††
2	200-299	2.6-3.8††
2	479	0.7††
3	680	0.1††
3	700-799	1.0-2.1††
3	955	1.0††

---

* Percentages calculated from wet weights of both food and fish.

** Data summarized in Fischer and Lyakhnovich.[51]

† Ages estimated from data summarized by Fischer and Lyakhnovich.[51]

†† Data from Singh et al.[152] Variability is due primarily to different weeds that were fed the fish to determine weed-specific growth efficiencies.

Table 33

Daily Weight-Specific Consumption Rates of White Amur

Initial Wet Weight, kg	Daily Food Intake, kg	Intake Biomass, %
1	0.115-1.350	12-135*
2	0.500-2.300	25-115*
---	---	30*
---	---	30-130**

---

* From Fischer and Lyakhnovich (1973).[51]

** From Stanley (1974).[155]

Table 34

Rate Equations for White Amur Biomass and Numbers

Description	Equation
Consumption	$K_{111} \cdot Q_{21} \cdot Q_{2} \cdot f_{4}(T) \cdot \mathrm{ENUF} \cdot \mathrm{STOCK}$
Assimilation	$K_{118} \cdot$ (consumption equation)
Egestion	$K_{27} \cdot$ (consumption - assimilation)
Respiration	$K_{120} \cdot Q_{21} \cdot f_{4}(T) \cdot \mathrm{STOCK}$
Mortality (biomass)	$K_{121} \cdot Q_{22} \cdot (Q_{21}/Q_{22}) \cdot \mathrm{STOCK}$
Mortality (numbers)	$K_{121} \cdot Q_{22} \cdot \mathrm{STOCK}$

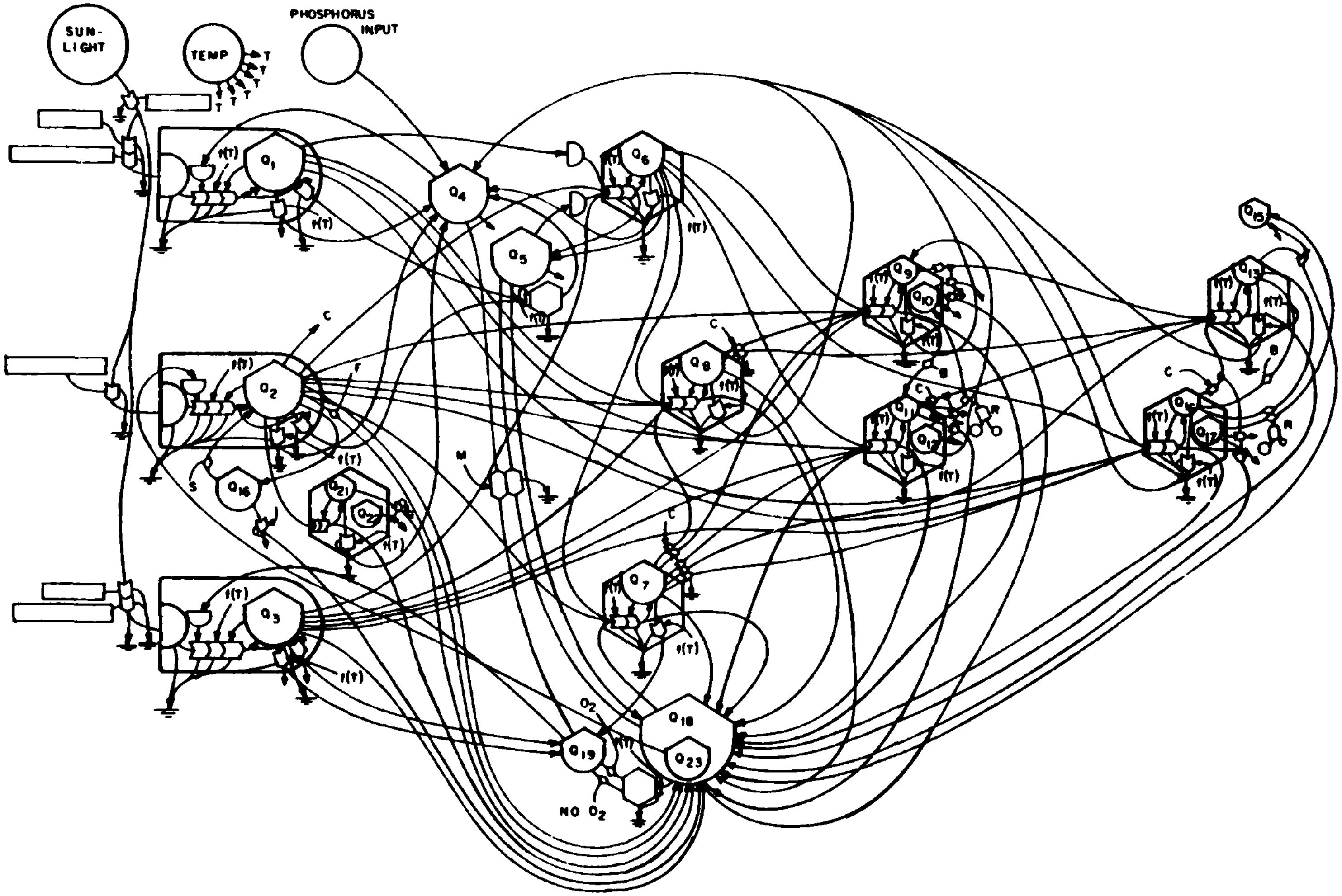

Figure 1. Model of Lake Conway (see Table 2 for explanation of symbols)

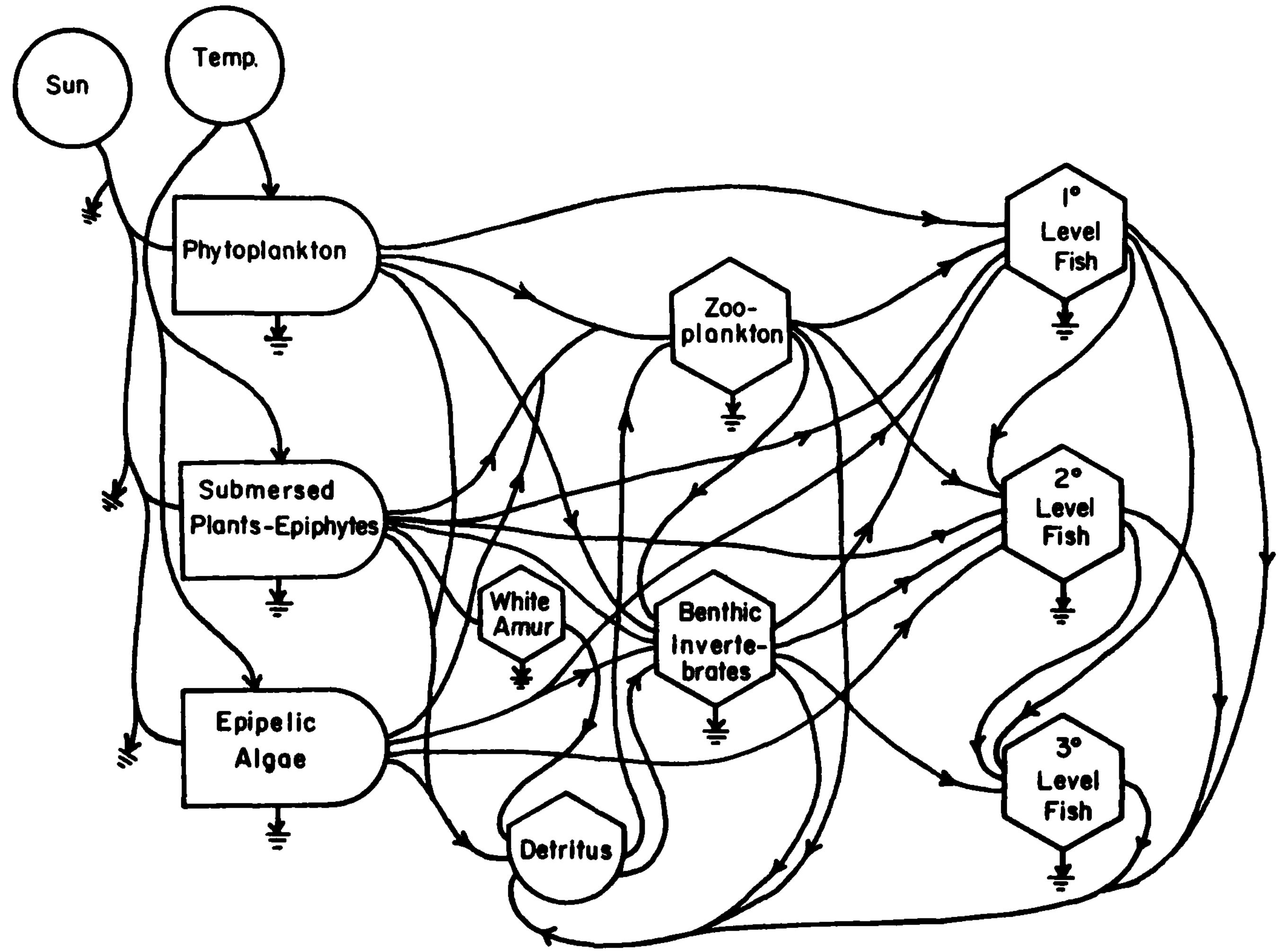

Figure 2. General model of food web in Lake Conway

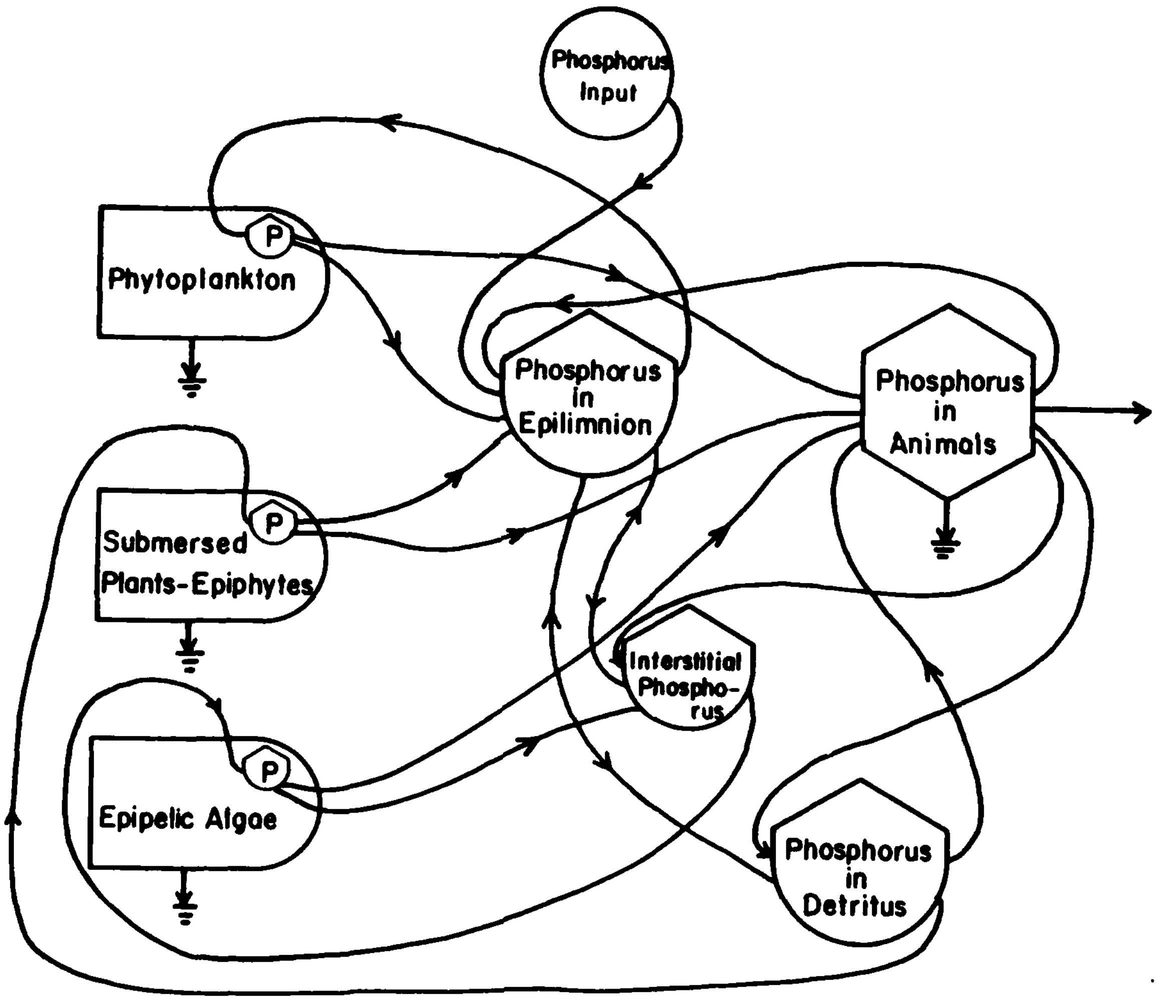

Figure 3. General model of phosphorus transfers in Lake Conway

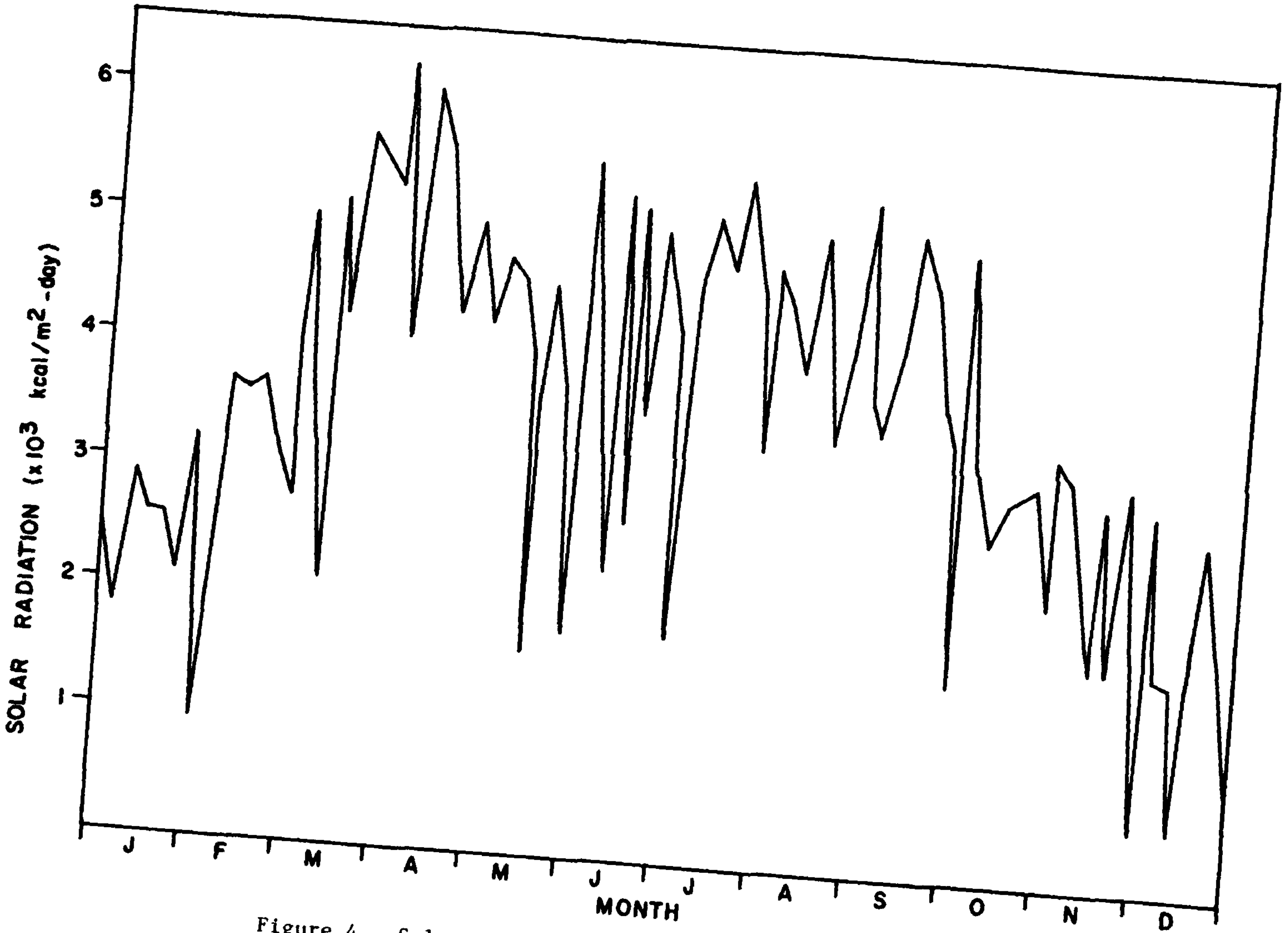

Figure 4. Solar radiation at Lake Conway during 1976

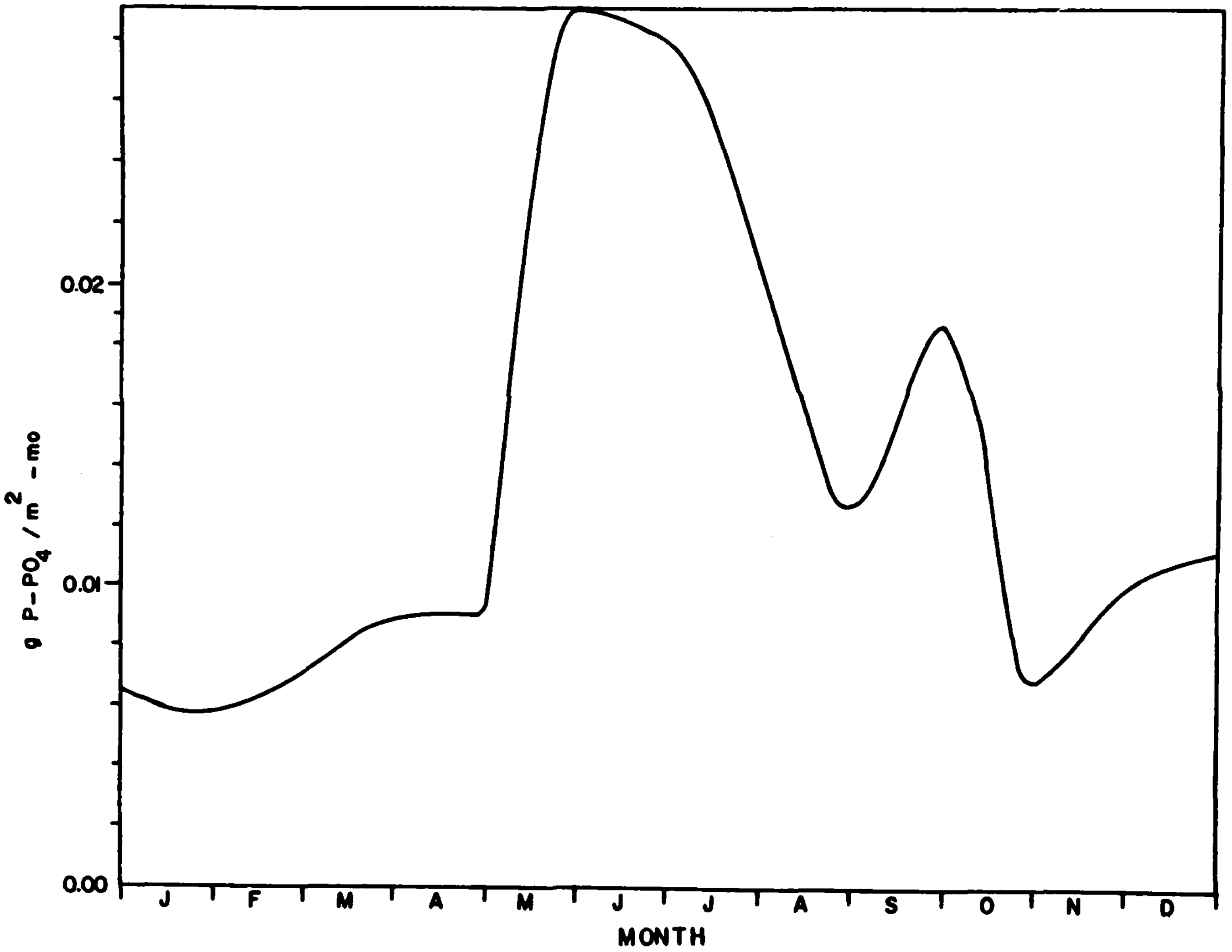

Figure 5. External phosphorus loading to Lake Conway during 1976

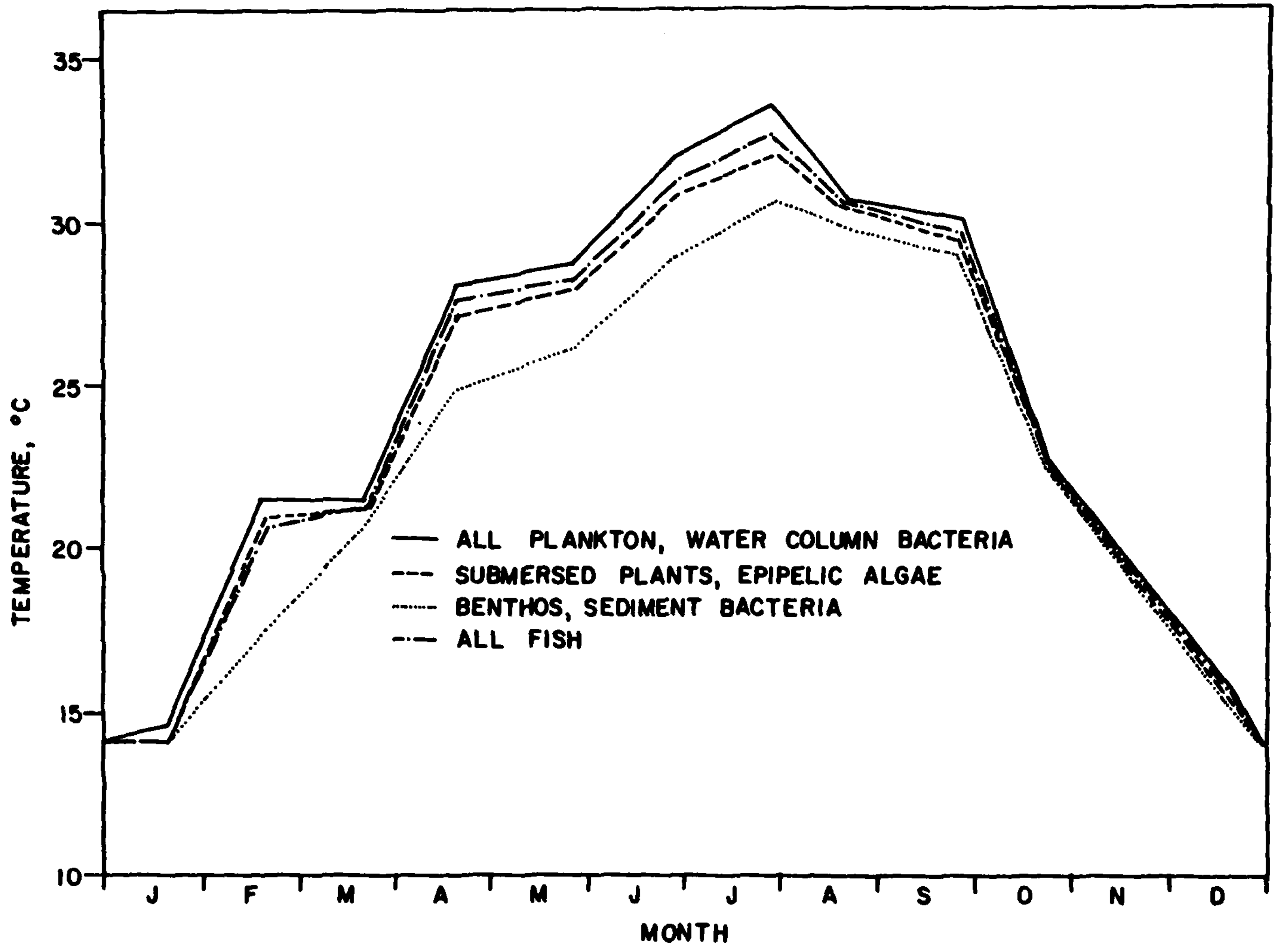

Figure 6. Ambient temperatures affecting Lake Conway organisms

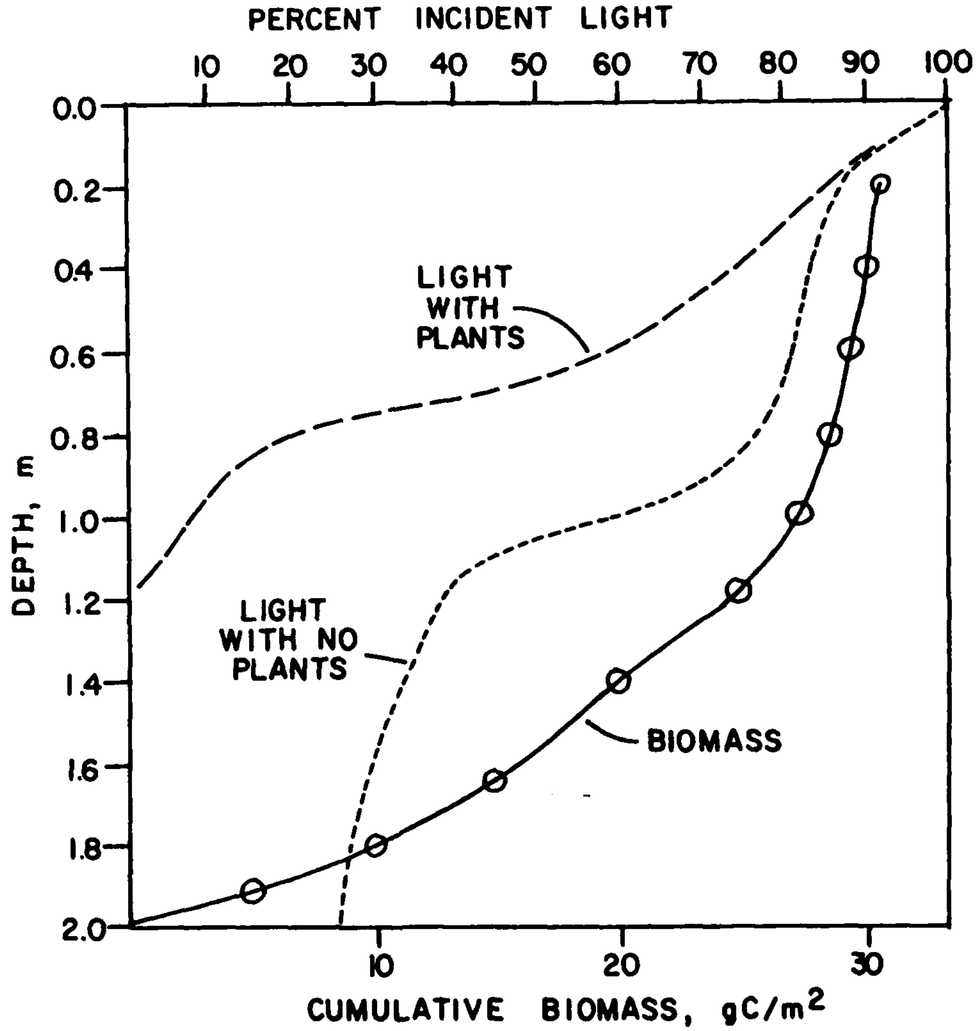

Figure 7. Measured relationship between light penetration and submersed plant (*Potamogeton illinoensis*) biomass

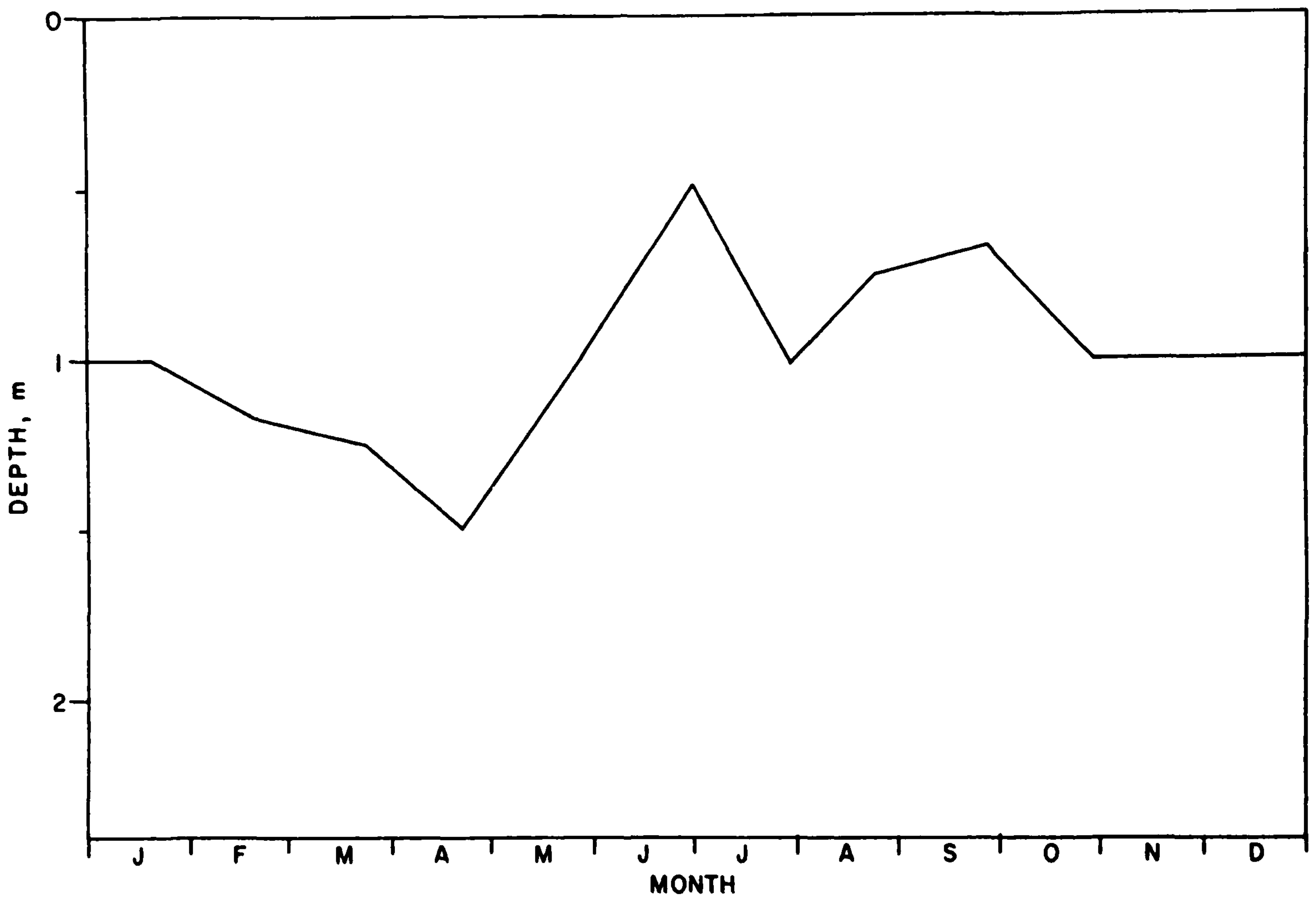

Figure 8. Average monthly location of phytoplankton photosynthetic maxima

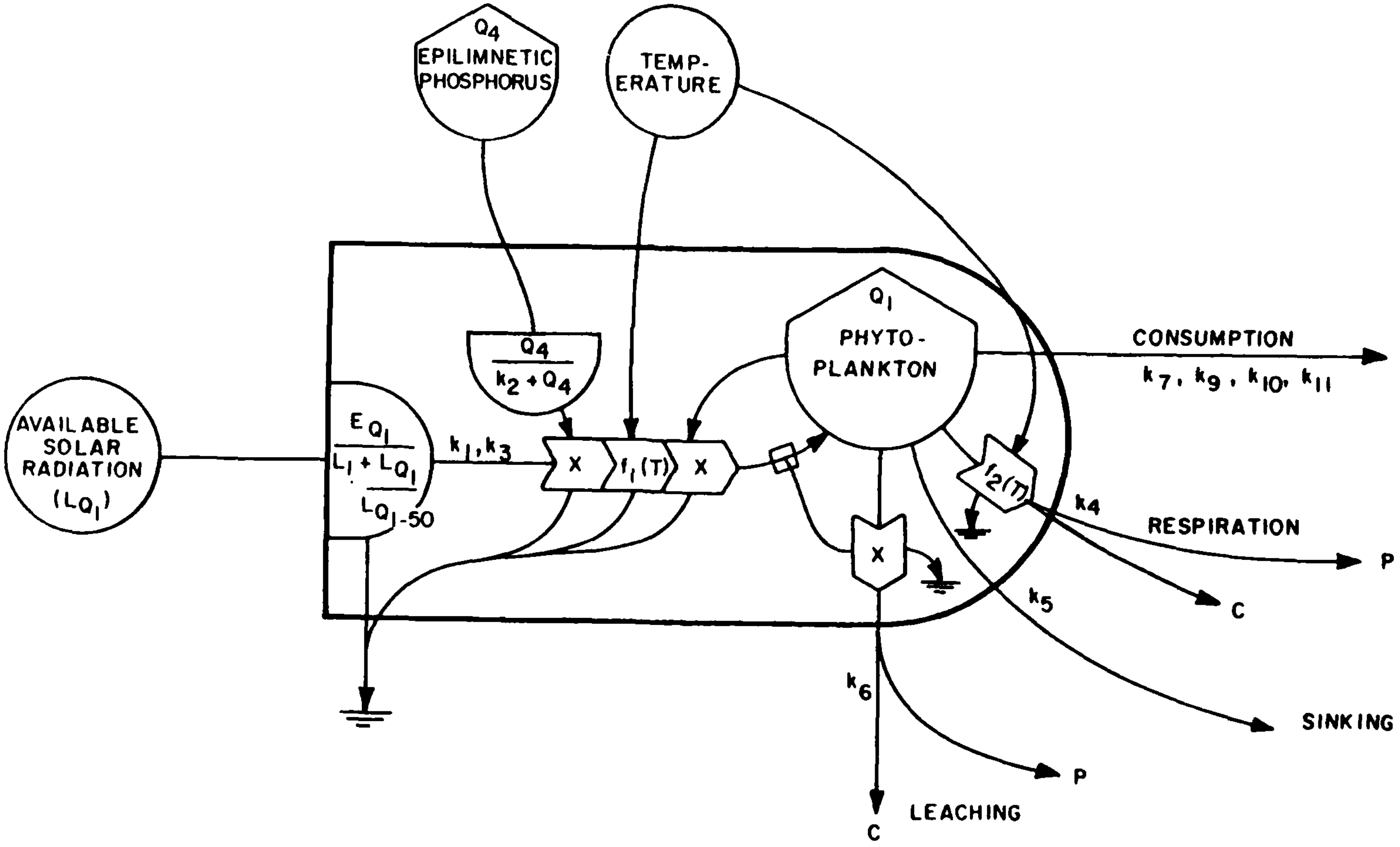

Figure 9. Phytoplankton module showing simulated annual fluxes of carbon (g C/m^2). Solar radiation expressed as cal/m^2-yr

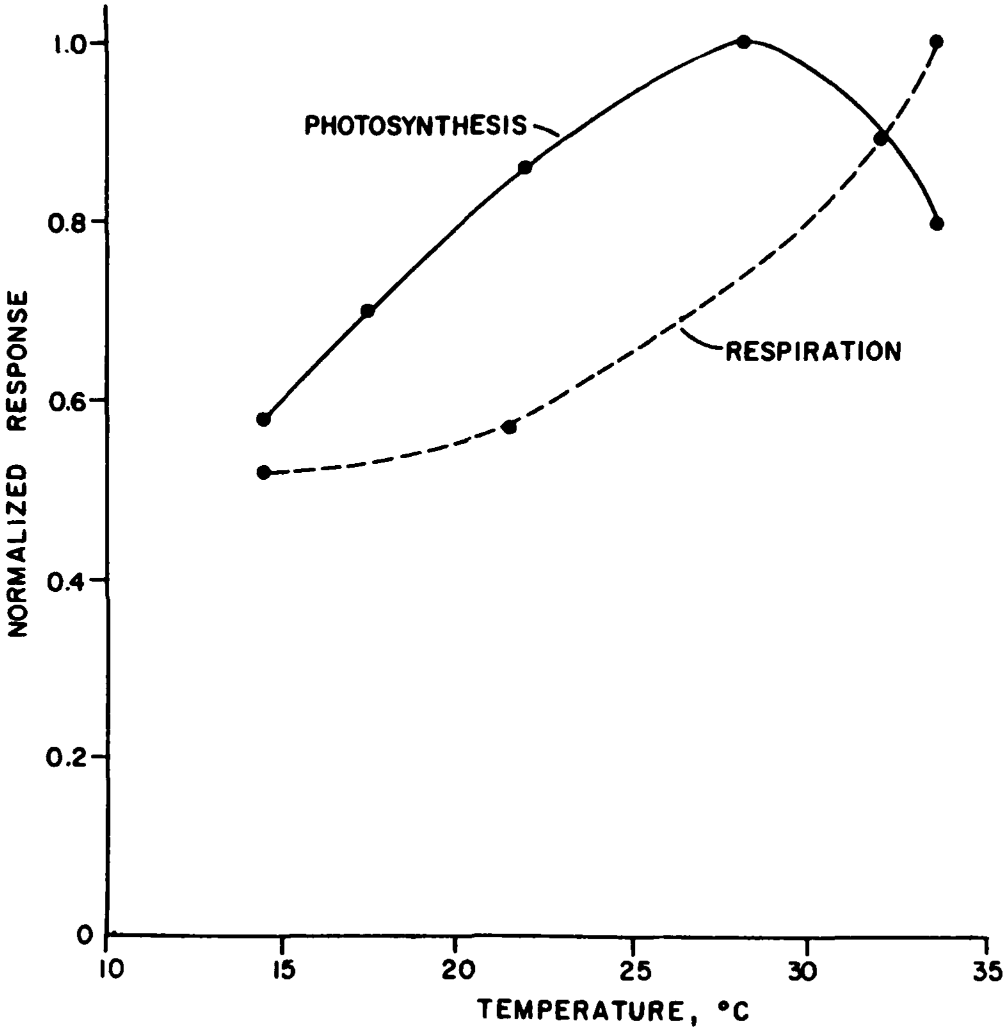

Figure 10. Relationship between algal photosynthesis and respiration with temperature

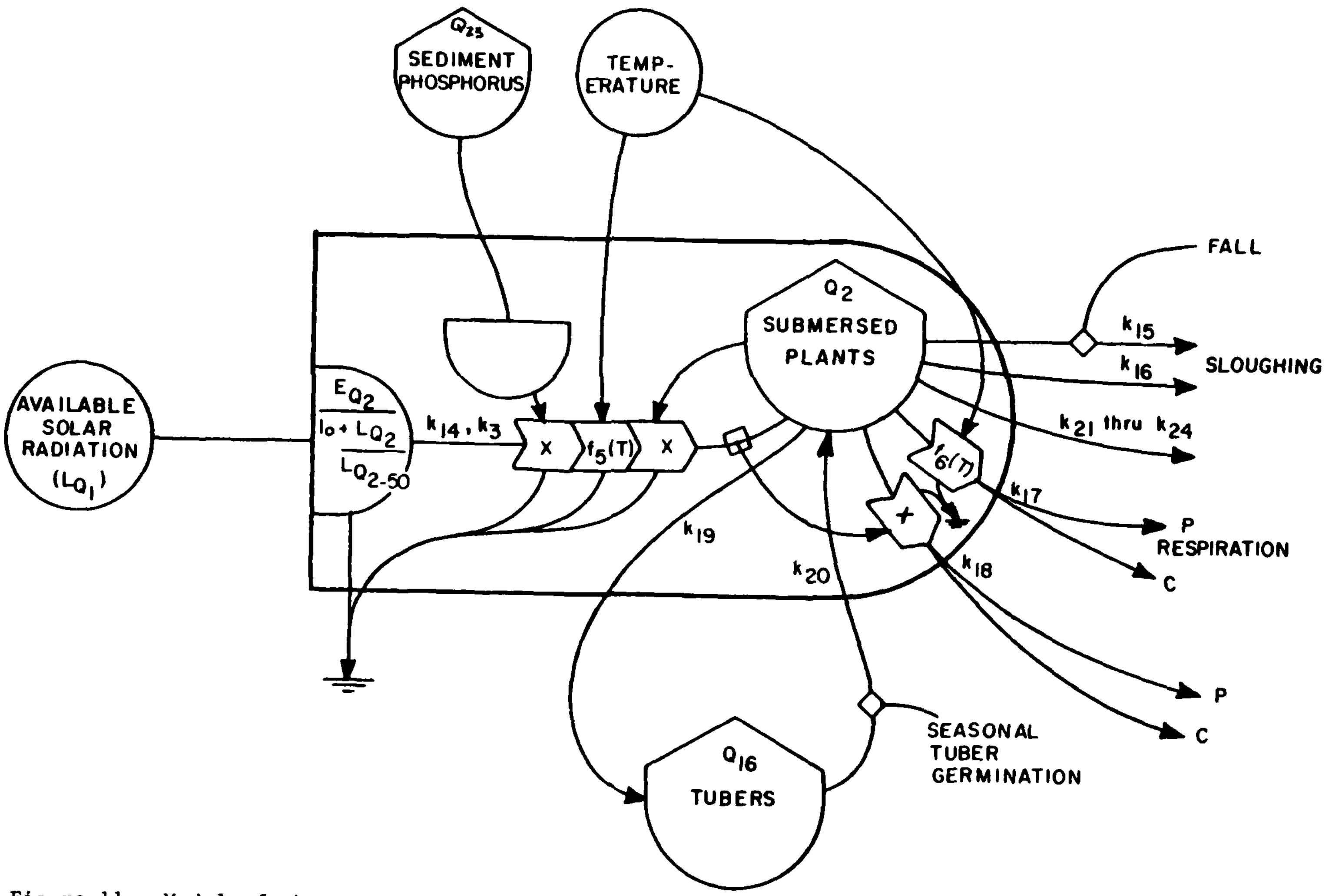

Figure 11. Model of the submersed plant-epiphyte complex showing simulated annual fluxes of carbon ($g\ C/m^2$). Solar radiation expressed as ca/m^2-yr

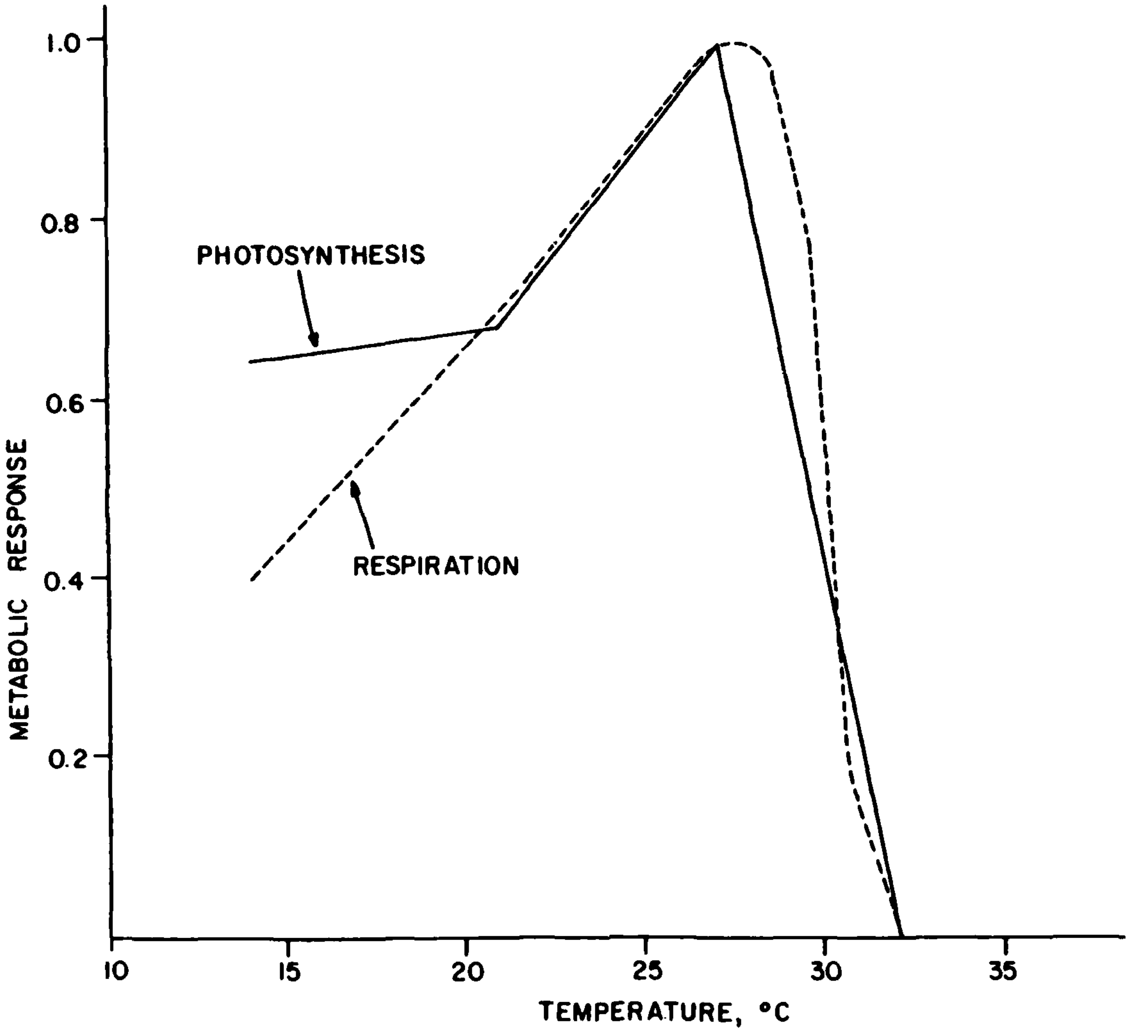

Figure 12. Hypothesized relationship of submersed plant metabolisms and temperature

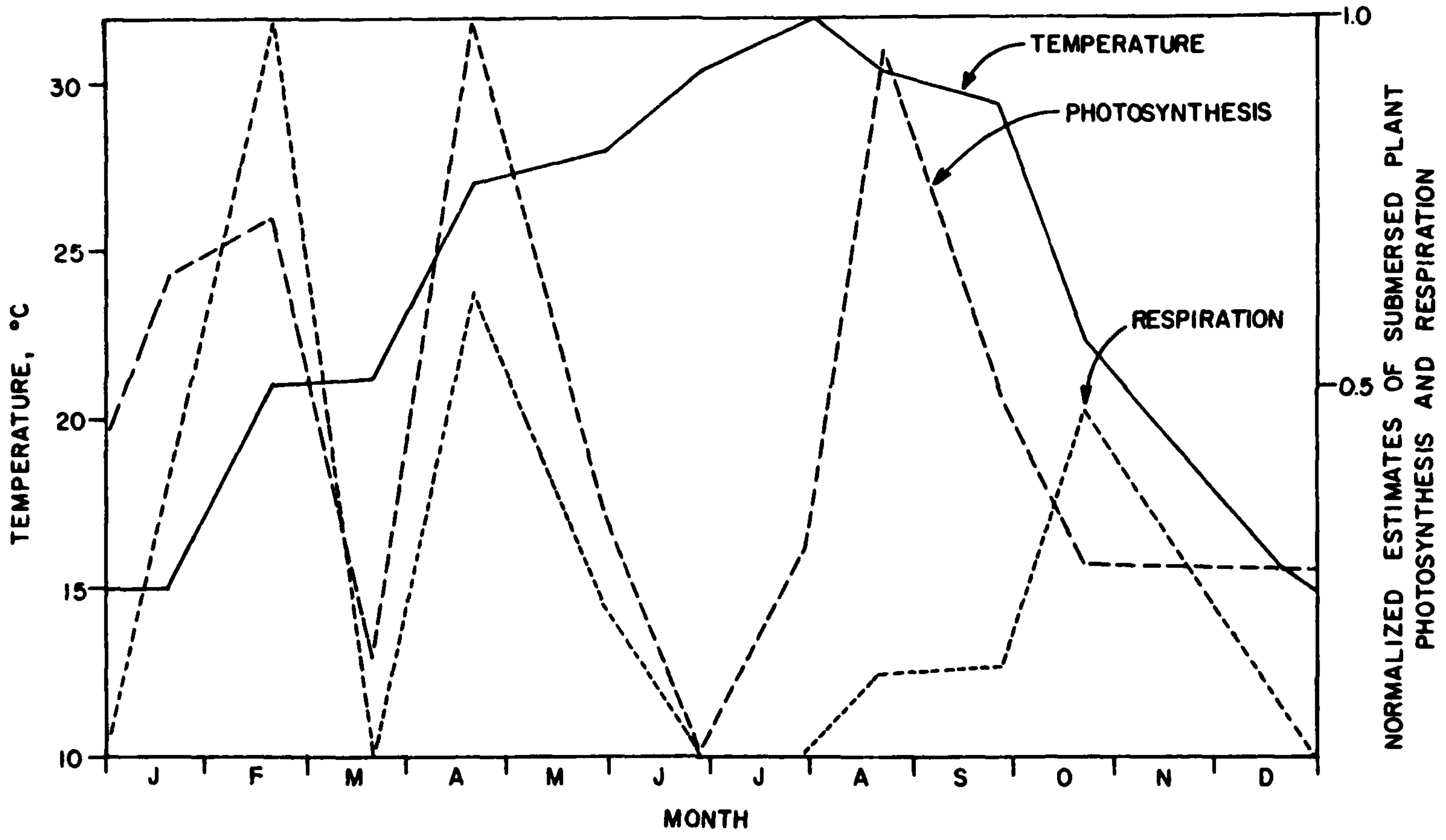

Figure 13. Plot of average Lake Conway temperature and normalized values of estimated submersed plant photosynthesis and respiration

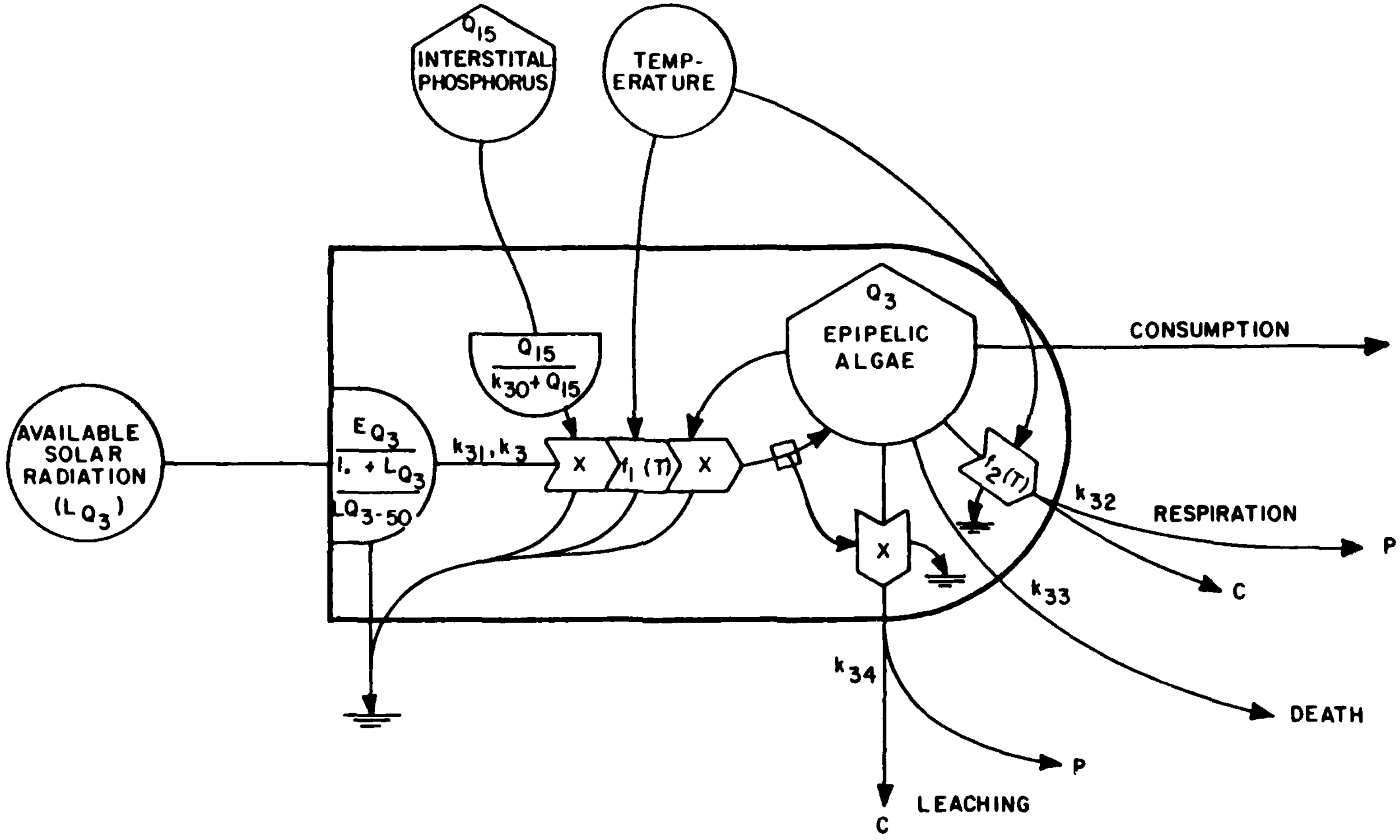

Figure 14. Model of epipelic algae showing annual fluxes of carbon (g C/m^2). Solar radiation expressed as cal/m^2-yr

	PHYTO-PLANKTON	MACRO-PHYTES & EPIPHYTIC ALGAE	EPIPELIC ALGAE	ZOO-PLANKTON	BENTHIC INVERTE-BRATES	PRIMARY LEVEL FISH	ADULT SECONDARY LEVEL FISH	YOUNG SECONDARY LEVEL FISH	ADULT TERTIARY LEVEL FISH	YOUNG TERTIARY LEVEL FISH	SUSPENDED DEAD PARTICULATE CARBON	DETRITUS	
ZOOPLANKTON	98.6 50.4	48.7 21.6	11.9 14.6								90.7 13.5		100.1
BENTHIC INVERTEBRATES		45.7 13.2	87.4 70.1	3.1 <0.1				PERCENT OF AMOUNT CONSUMED ↓ PERCENT OF DIET →				100.0 16.7	100.0
PRIMARY LEVEL FISH	1.0 13.8	5.0 58.3		12.4 5.0	8.1 8.3						3.7 14.6		100.0
ADULT SECONDARY LEVEL FISH		0.1 2.2		48.5 25.8	49.6 67.6	23.5 4.4							100.0
YOUNG SECONDARY LEVEL FISH	0.3 3.5	0.5 5.6	0.7 24.1	28.9 12.1	29.8 31.9						5.6 22.8		100.0
ADULT TERTIARY LEVEL FISH					10.1 27.5	76.5 29.6	100.0 40.7	100.0 2.2		100.0 <1.1			100.1
YOUNG TERTIARY LEVEL FISH	0.1 3.8	0.1 4.8	<0.1 43.2	7.2 39.1	2.5 34.1								100.0
TOTAL	100.0	100.1	100.0	100.1	100.1	100.0	100.0	100.0		100.0	100.0	100.0	

Figure 15. Feeding relationships among plants, animals, and detritus in the Lake Conway ecosystem model. Numbers are percentages of yearly diet

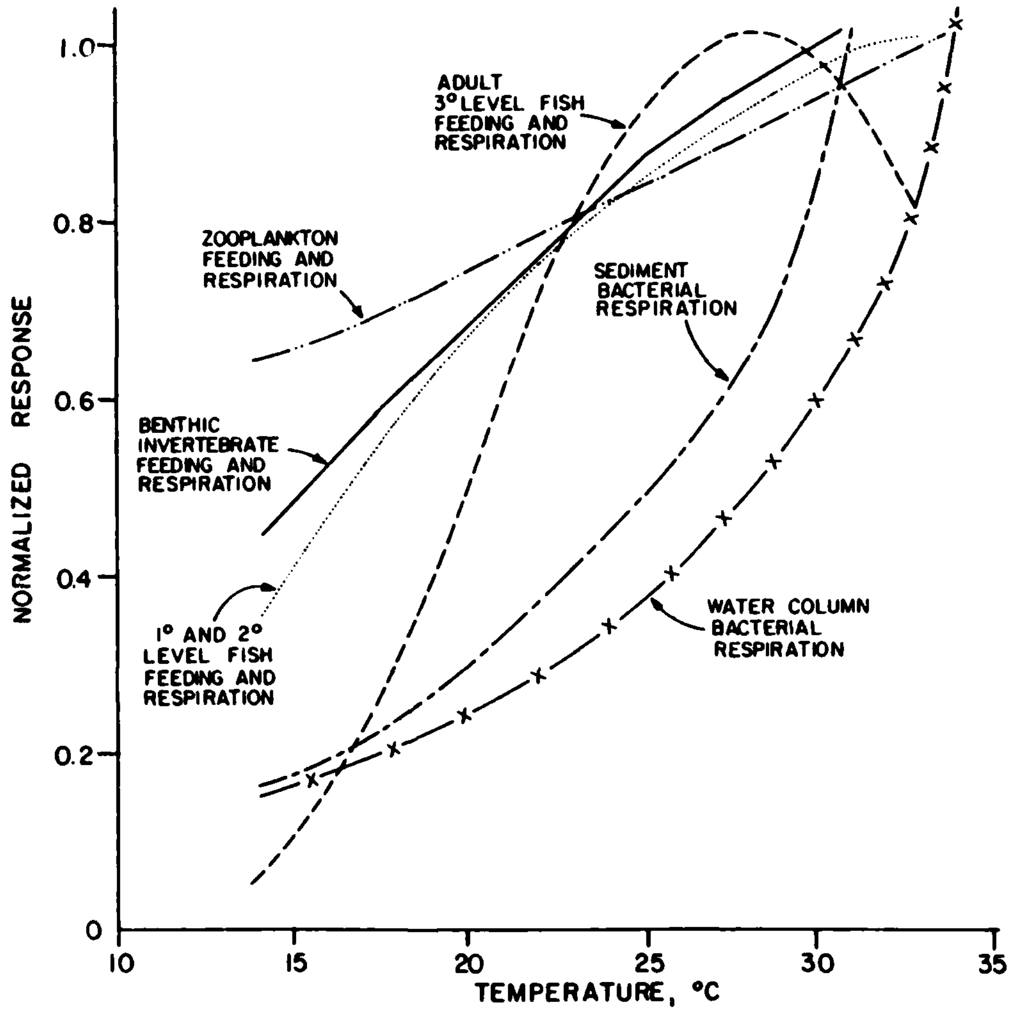

Figure 16. Relationships used in the model to account for temperature heterotroph feeding and respiration rates [3, 19, 25, 60, 61, 133]

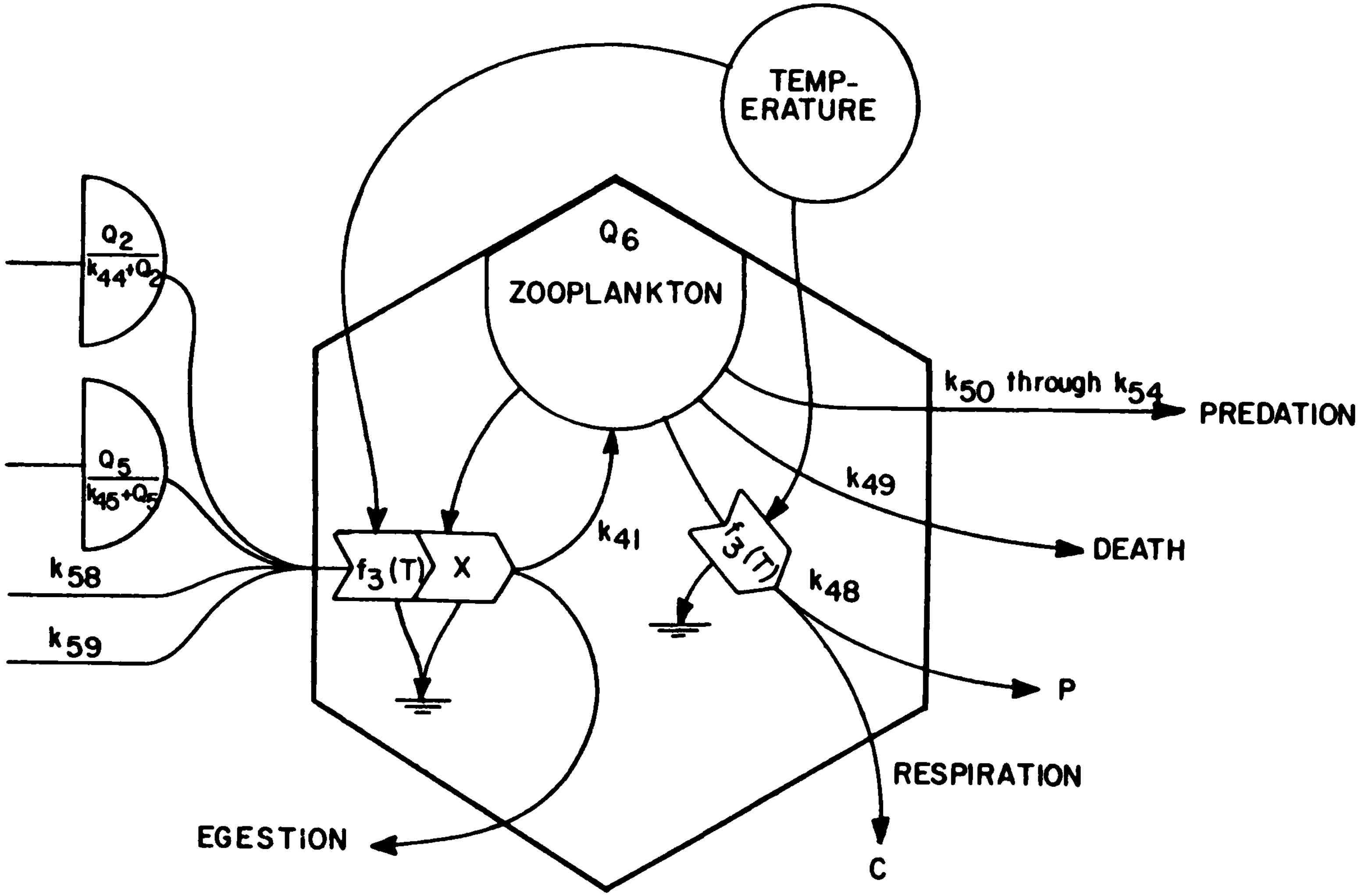

Figure 17. Model of zooplankton showing simulated annual fluxes of carbon (g C/m^2)

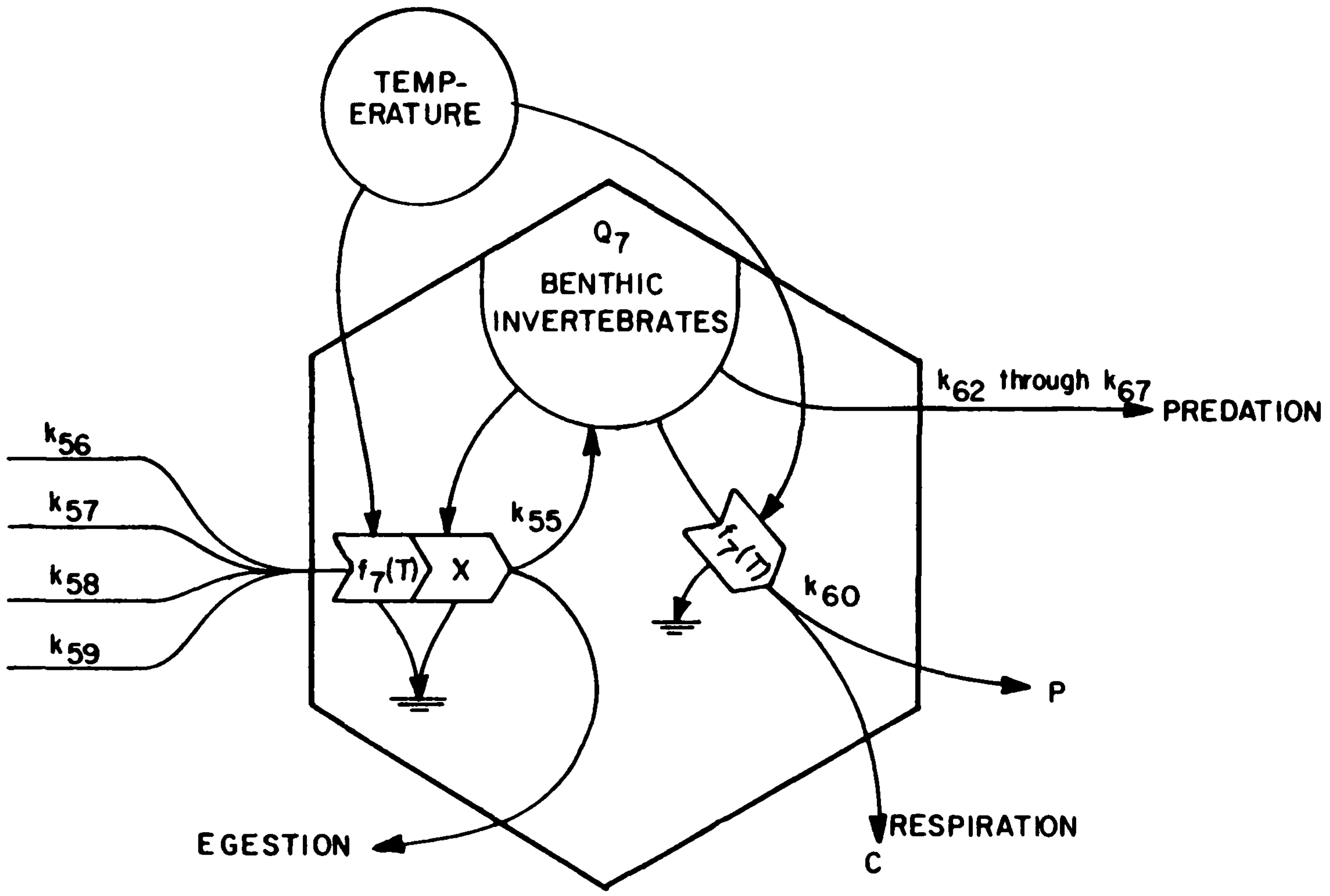

Figure 18. Model of benthic invertebrates showing simulated annual fluxes of carbon (g C/m^2)

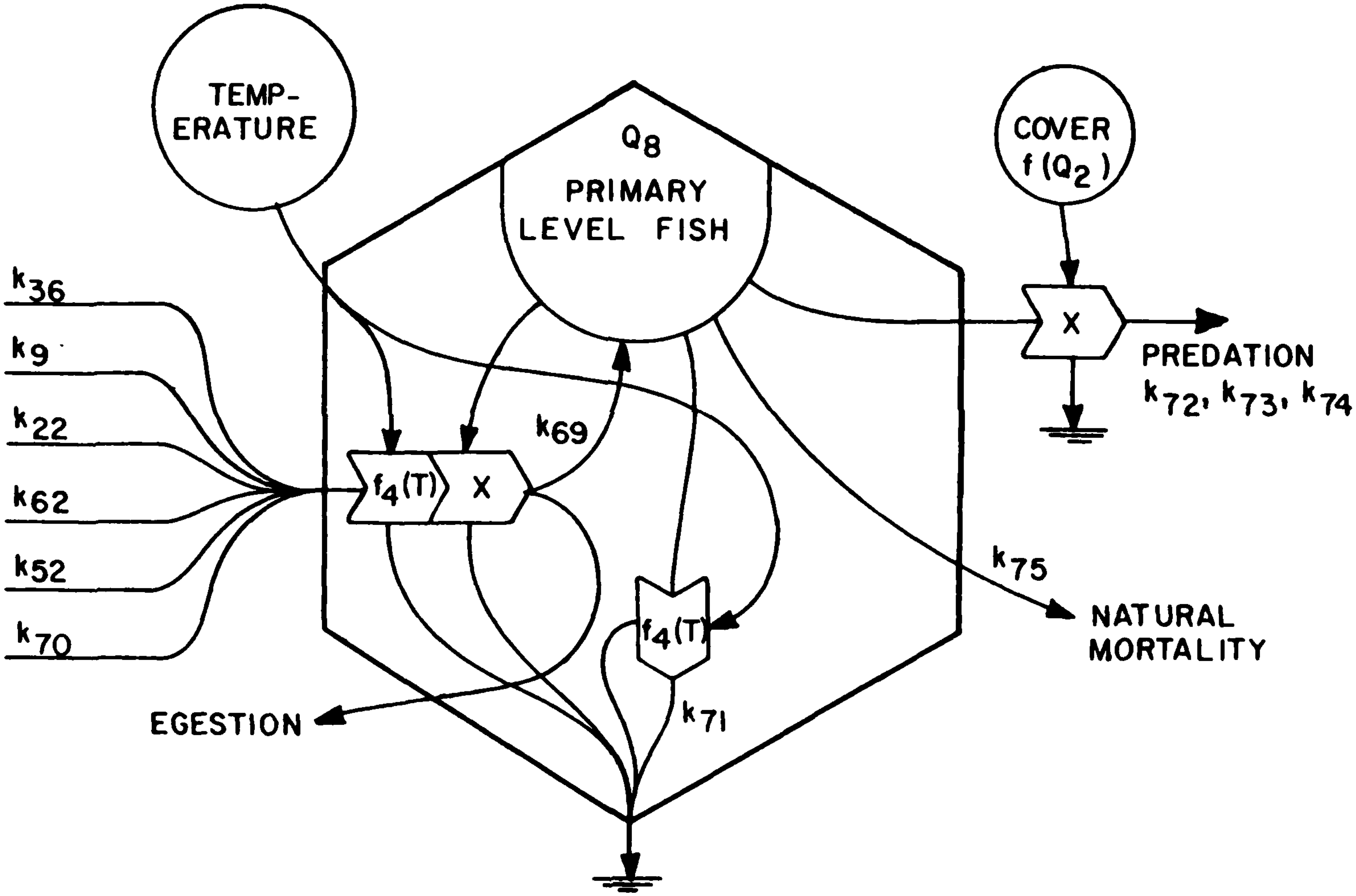

Figure 19. Model of primary level fish showing simulated annual fluxes of carbon (g C/m^2)

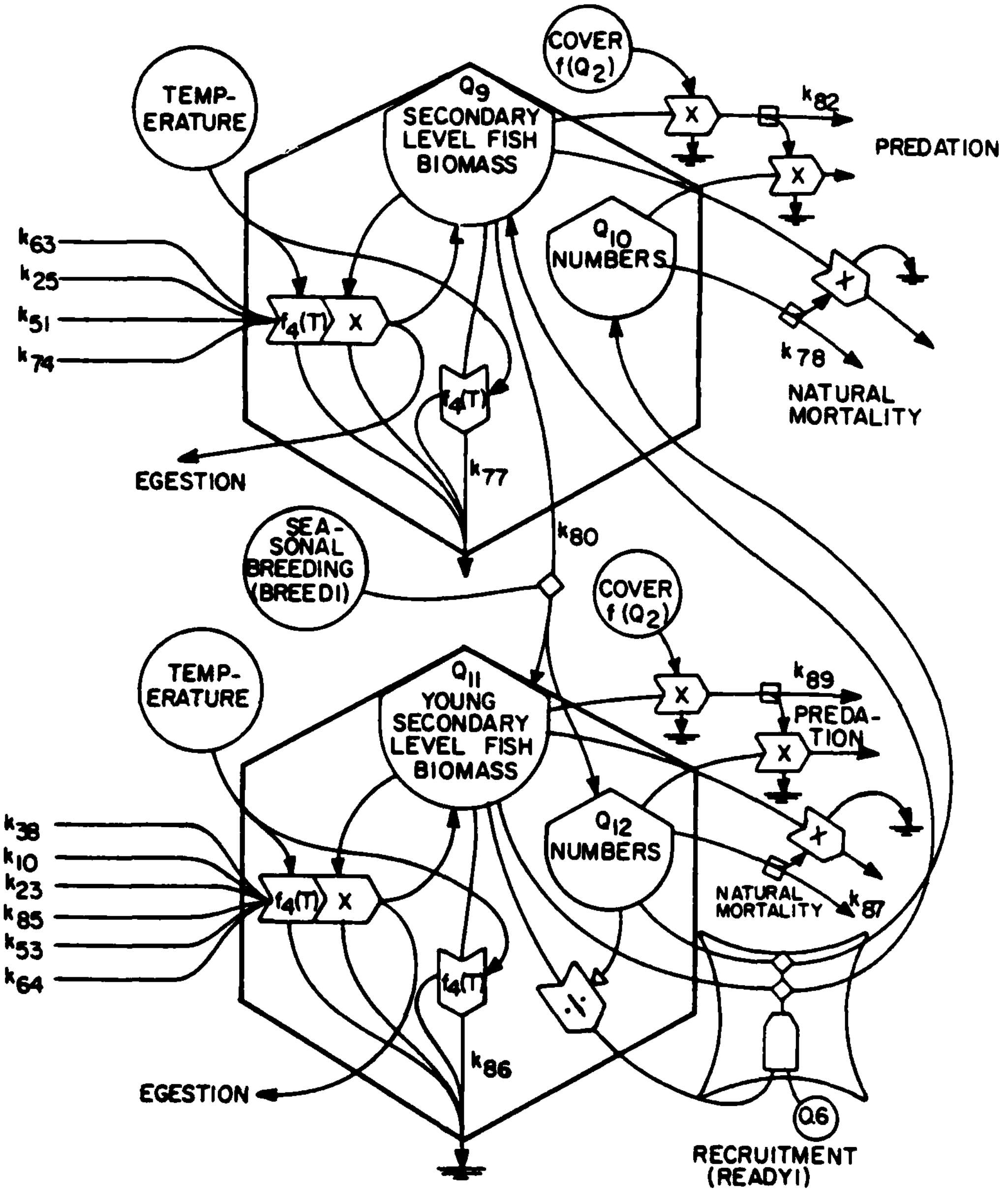

Figure 20. Model of numbers and biomass of young and adult secondary level fish (Biomass fluxes are g C/m^2-yr. Numerical flows are individuals/m^2-yr.)

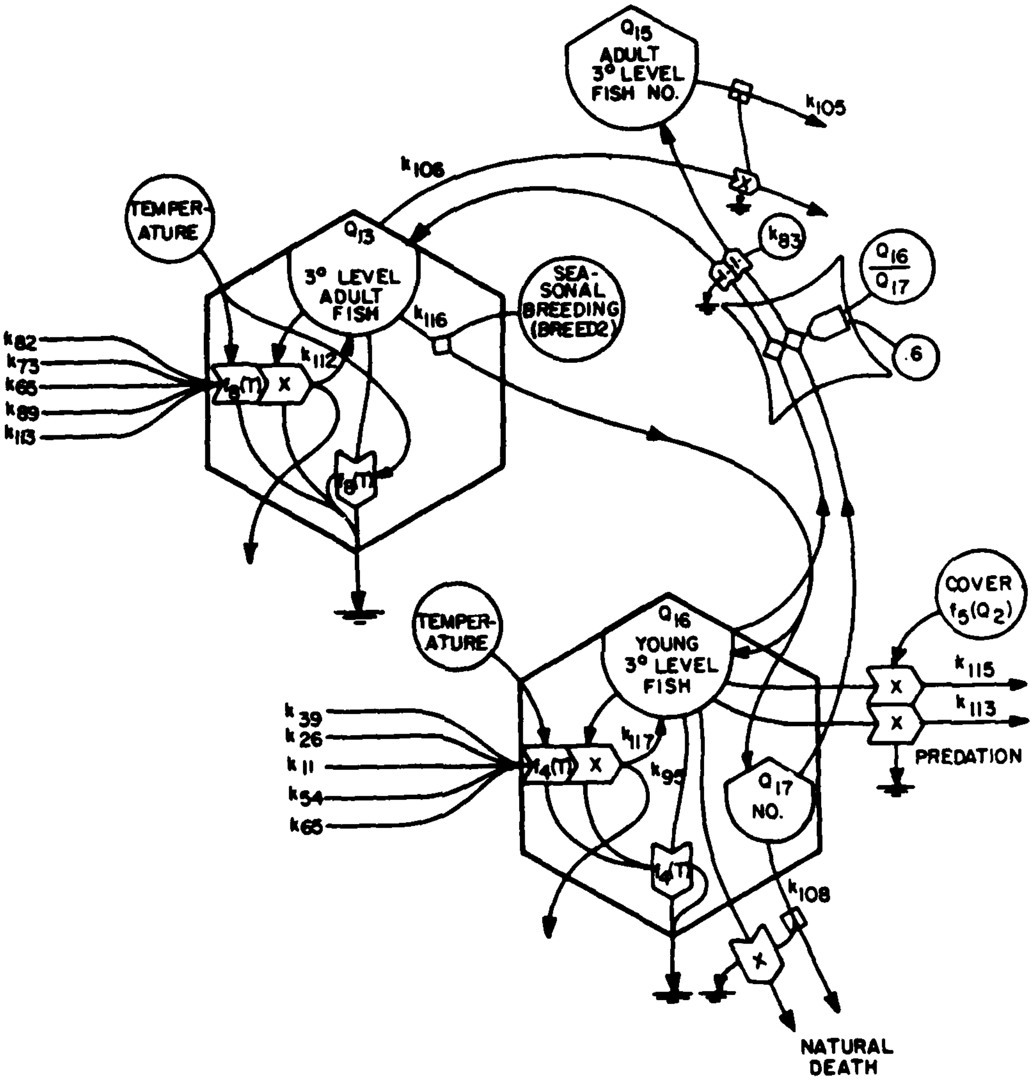

Figure 21. Model of numbers and biomass of young and adult tertiary level fish (Biomass fluxes in g C/m^2-yr. Numerical flows are individuals/m^2-yr.)

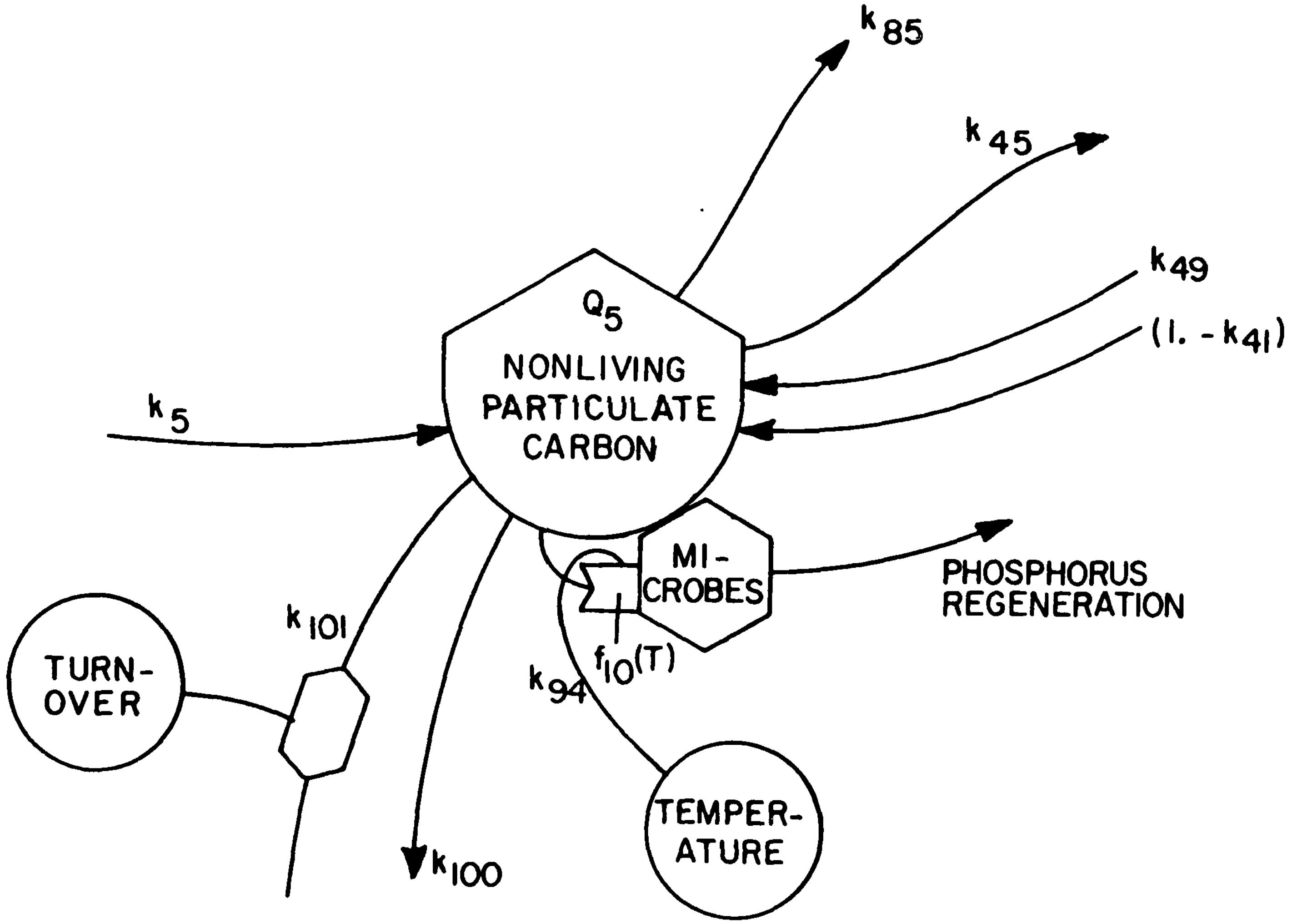

Figure 22. Model of dead particulate organic carbon showing annual carbon fluxes (g C/m^2)

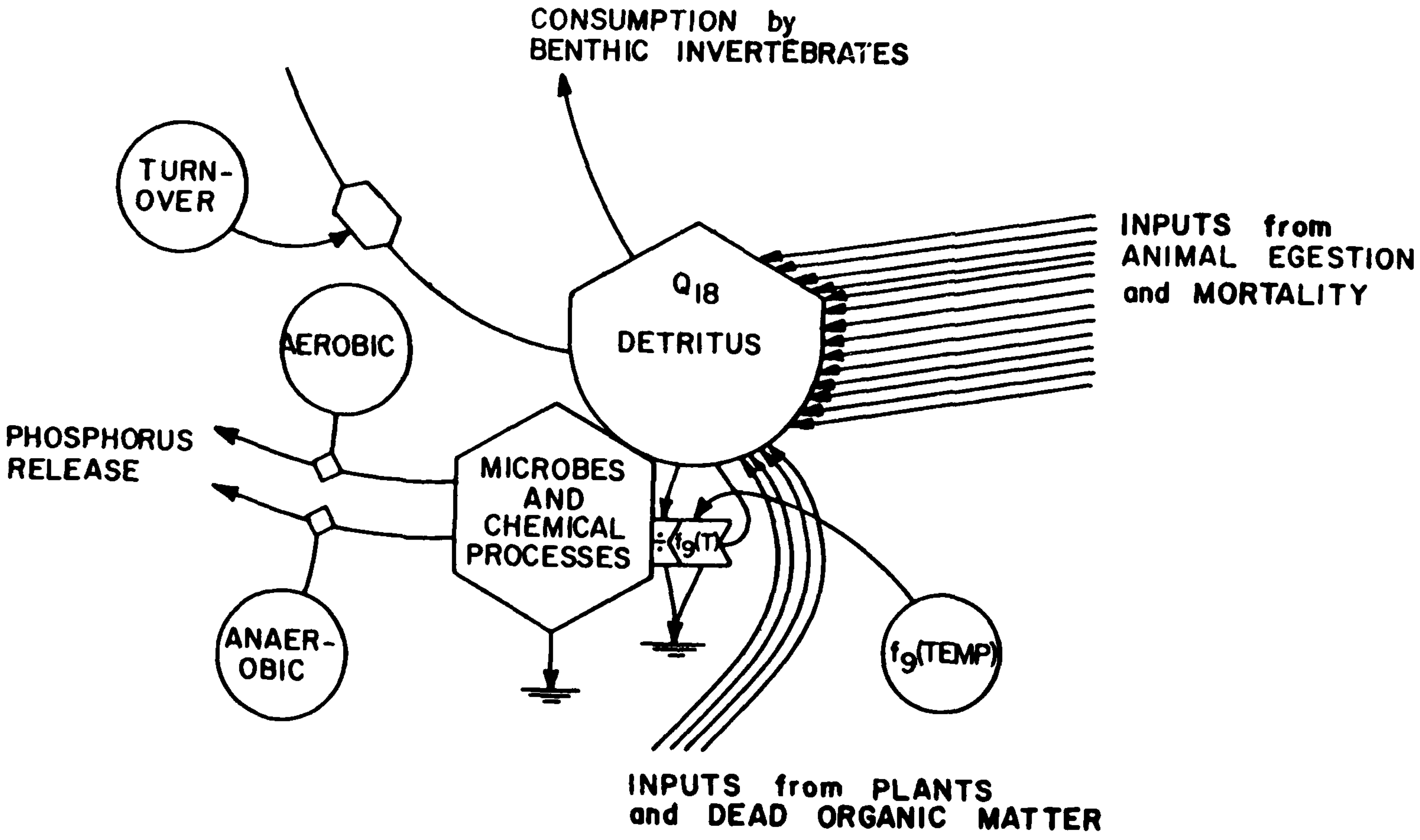

Figure 23. Model of sediment detritus showing annual carbon fluxes (g C/m^2)

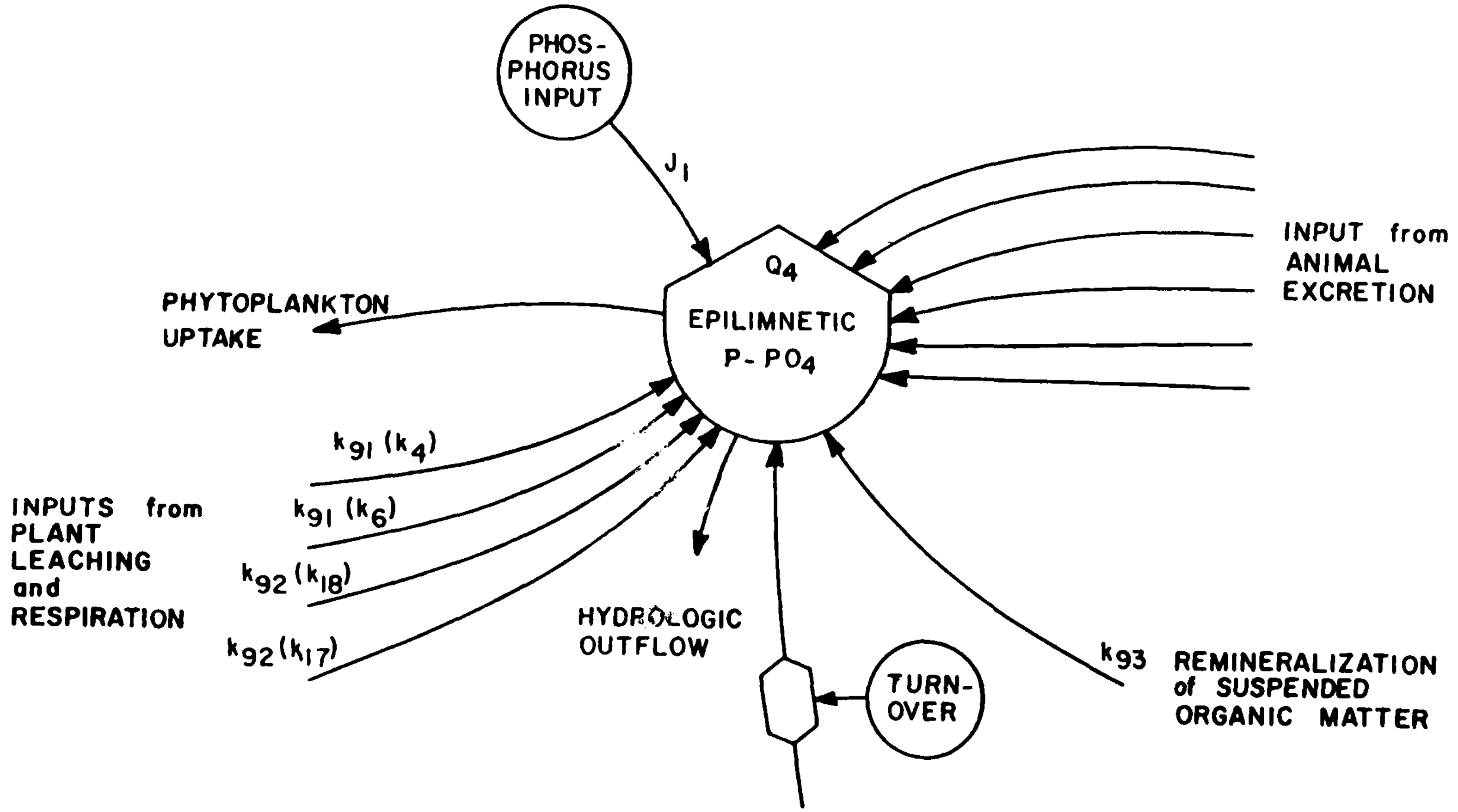

Figure 24. Model of epilimnetic orthophosphate showing annual fluxes of phosphorus (g PO_4-P/m^2)

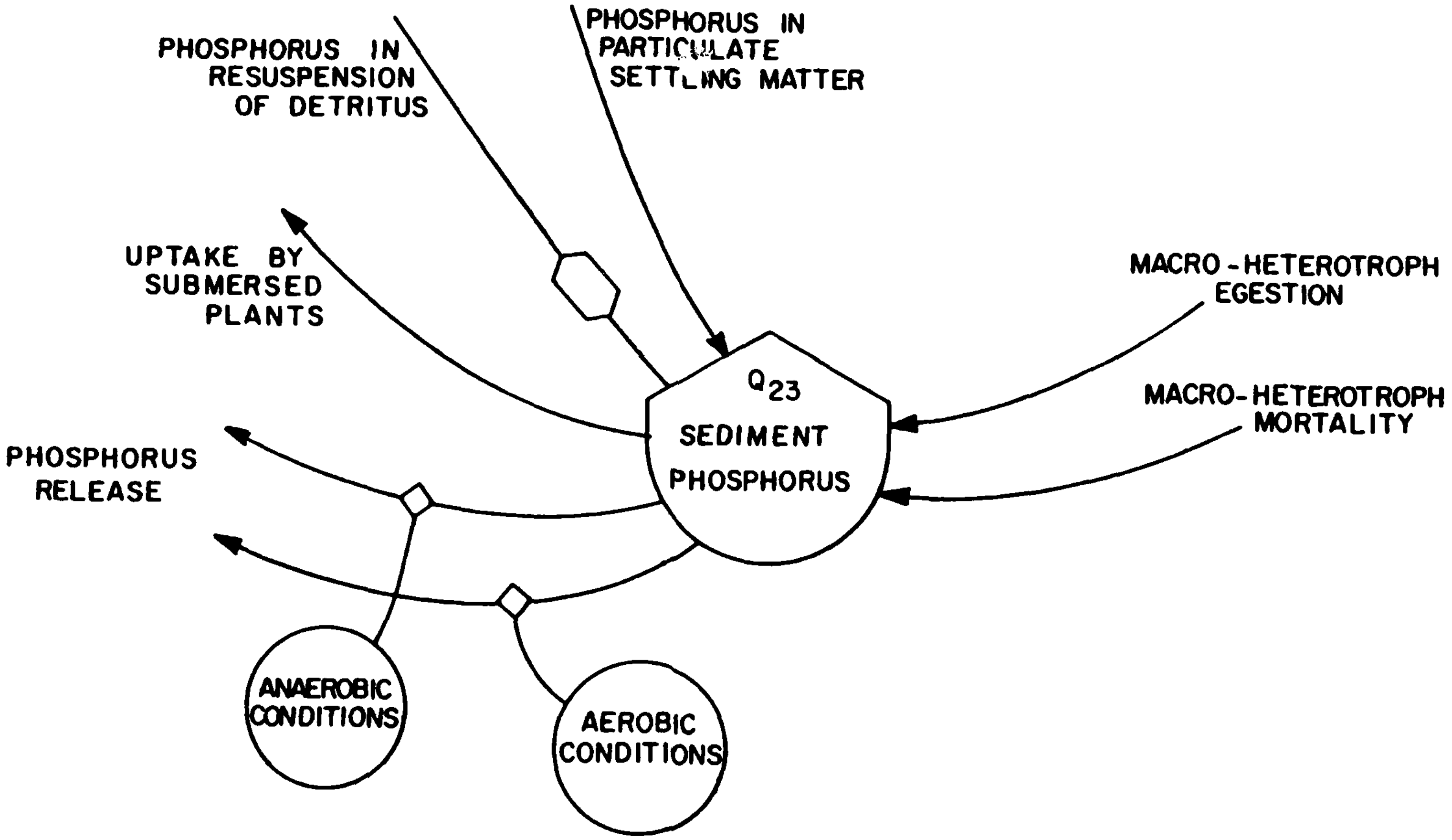

Figure 25. Model of sediment phosphorus showing annual fluxes (g P/m^2)

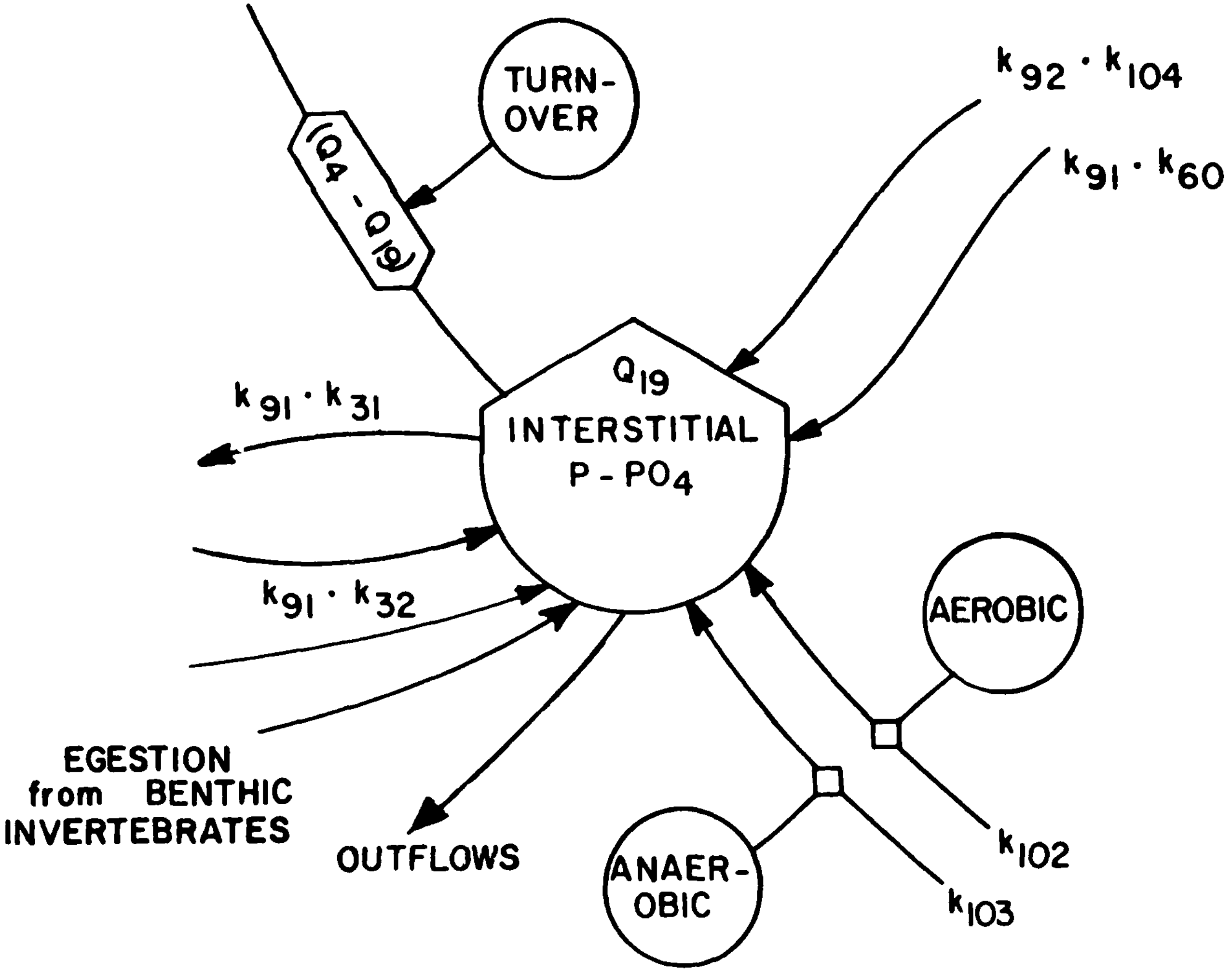

Figure 26. Model of interstitial orthophosphate showing annual fluxes of phosphorus ($g\ PO_4$-P/m^2)

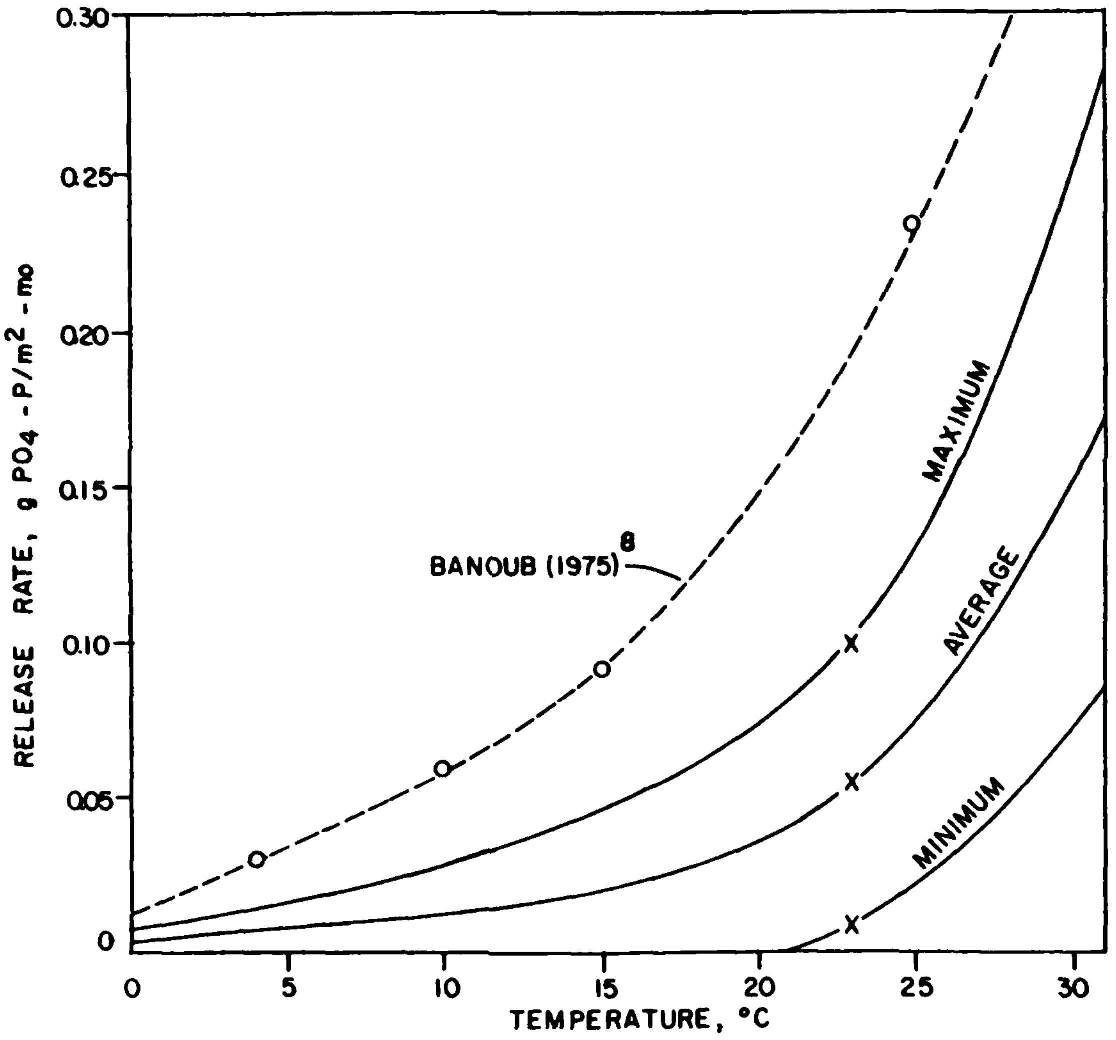

Figure 27. Effect of temperature on phosphorus release from sediments

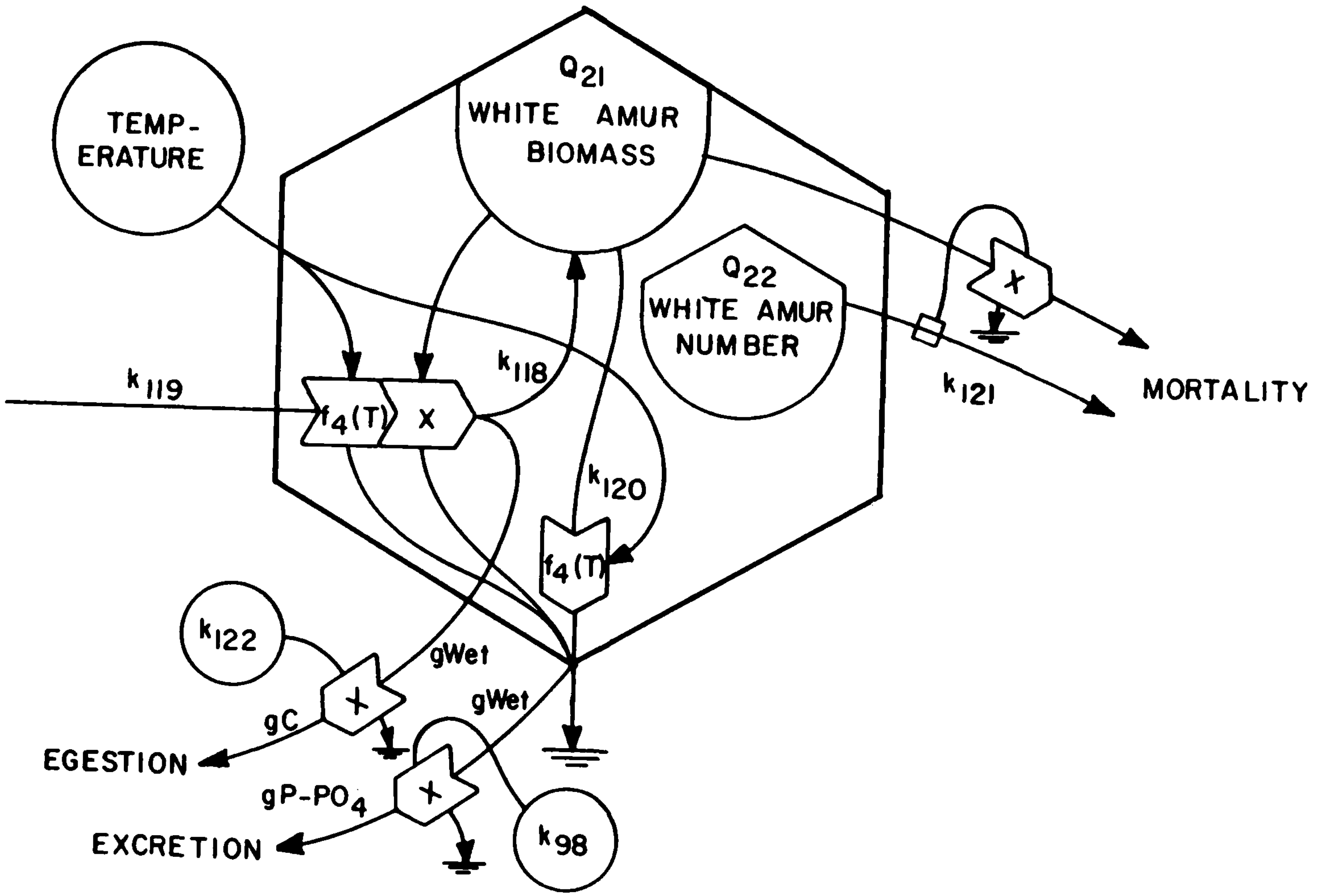

Figure 28. White amur model

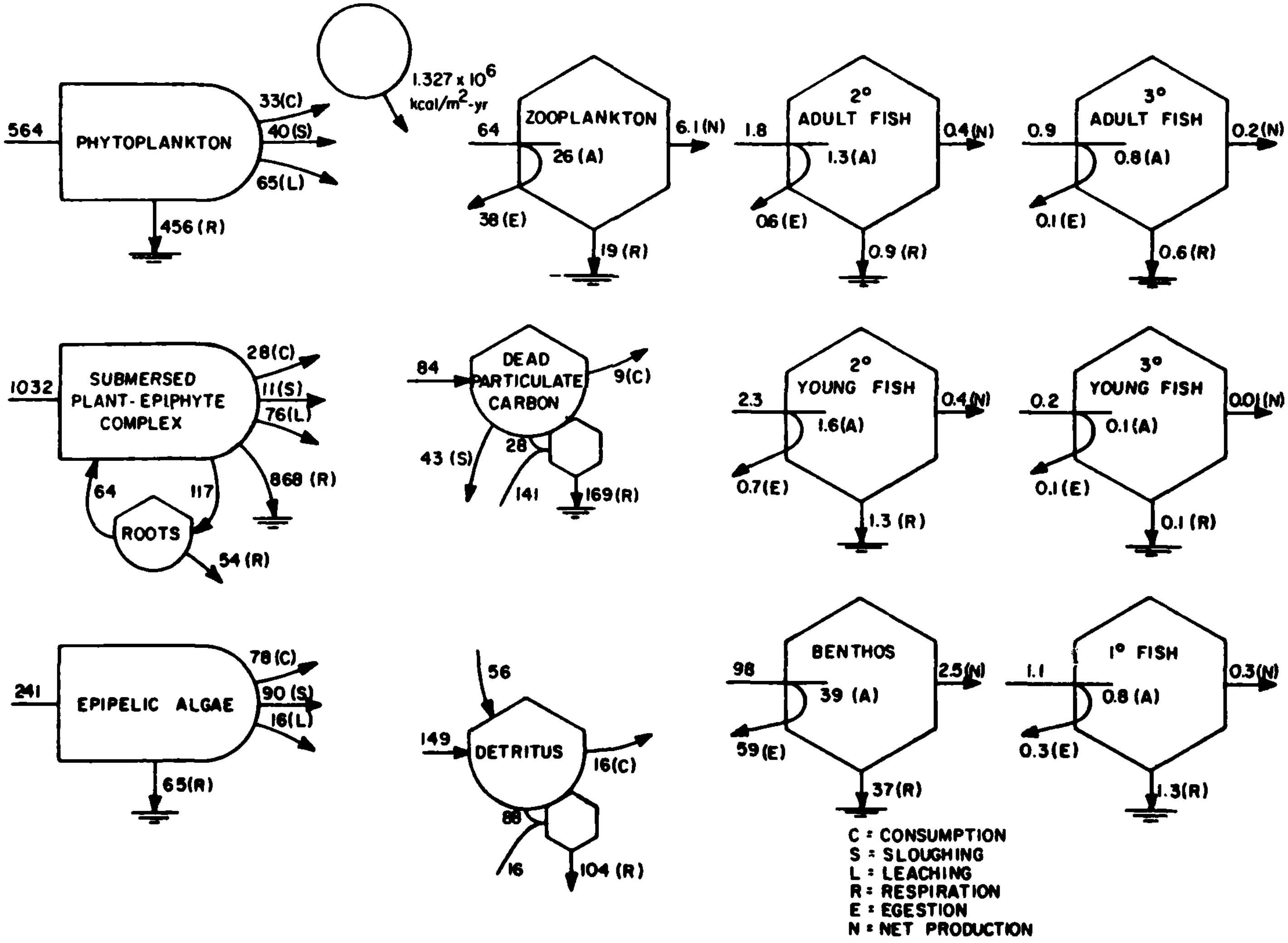

Figure 29. Simulated carbon flows (numbers represent g C/m^2-yr unless ortherwise indicated)

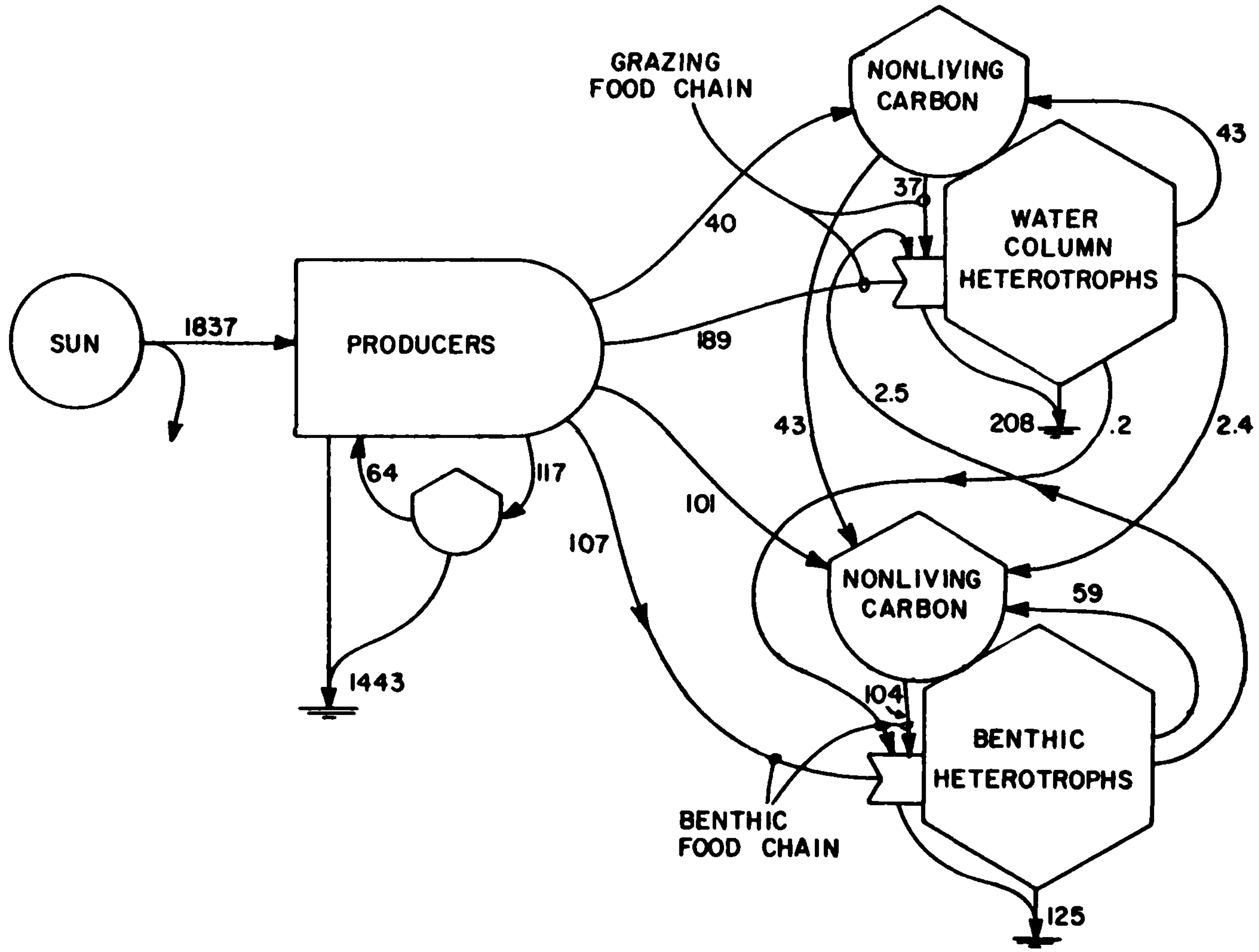

Figure 30. Aggregated model of simulated carbon dynamics in Lake Conway

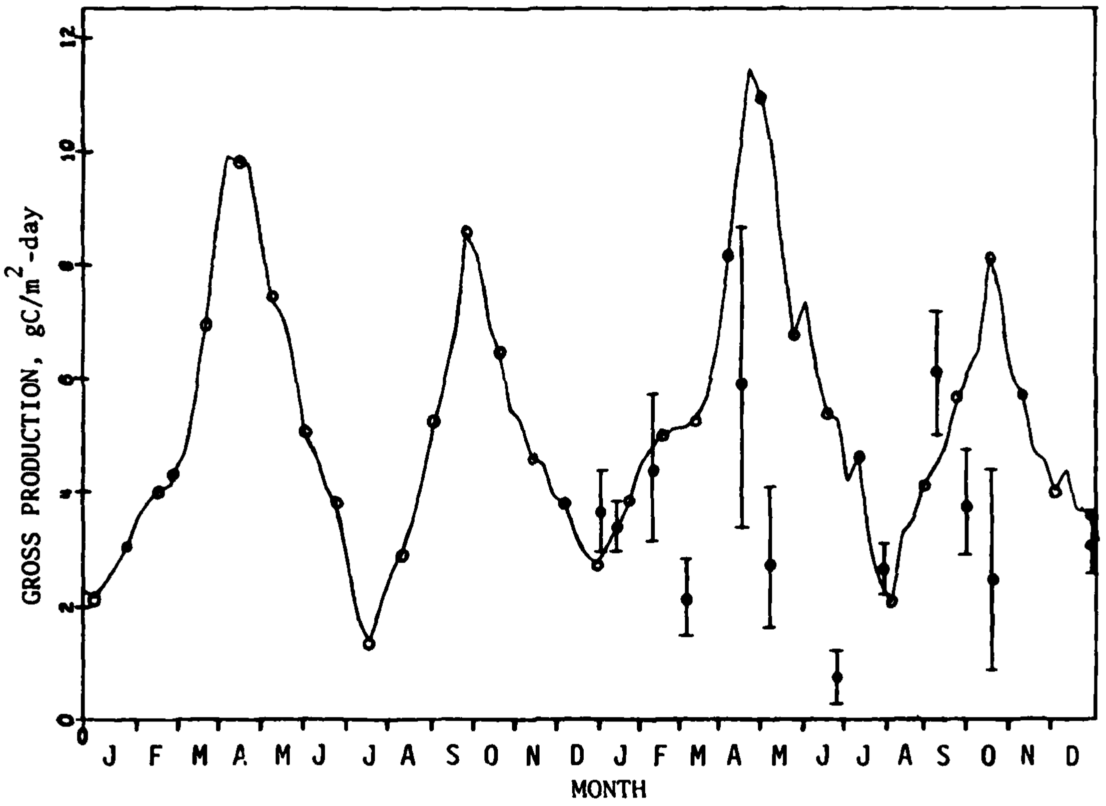

Figure 31. Simulated and observed pattern of gross production in Lake Conway (bars represent ± one standard error of the mean of measurements made in 1976)

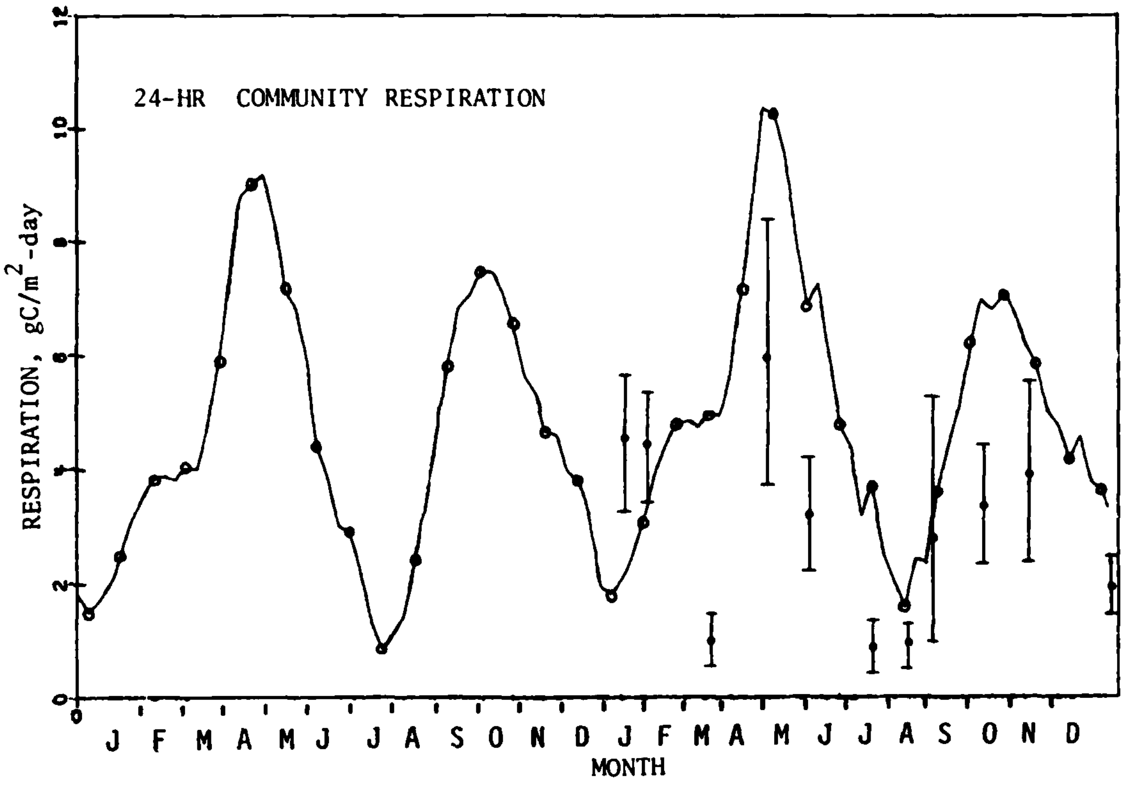

Figure 32. Simulated and observed pattern of community respiration in Lake Conway (bars represent ± one standard error of the mean of measurements made in 1976)

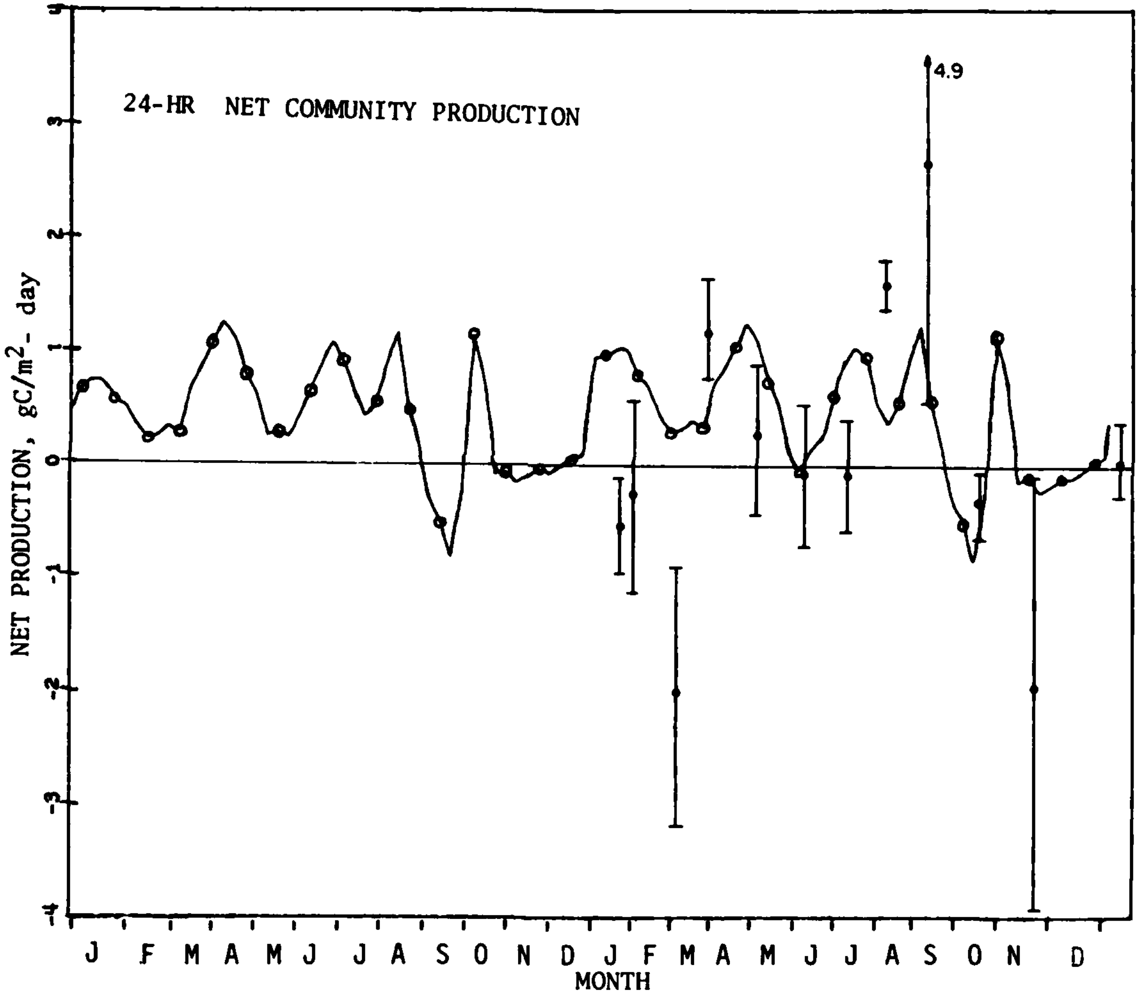

Figure 33. Simulated and observed pattern of net community production in Lake Conway (bars represent $\pm$ one standard error of the mean around measurements made in 1976)

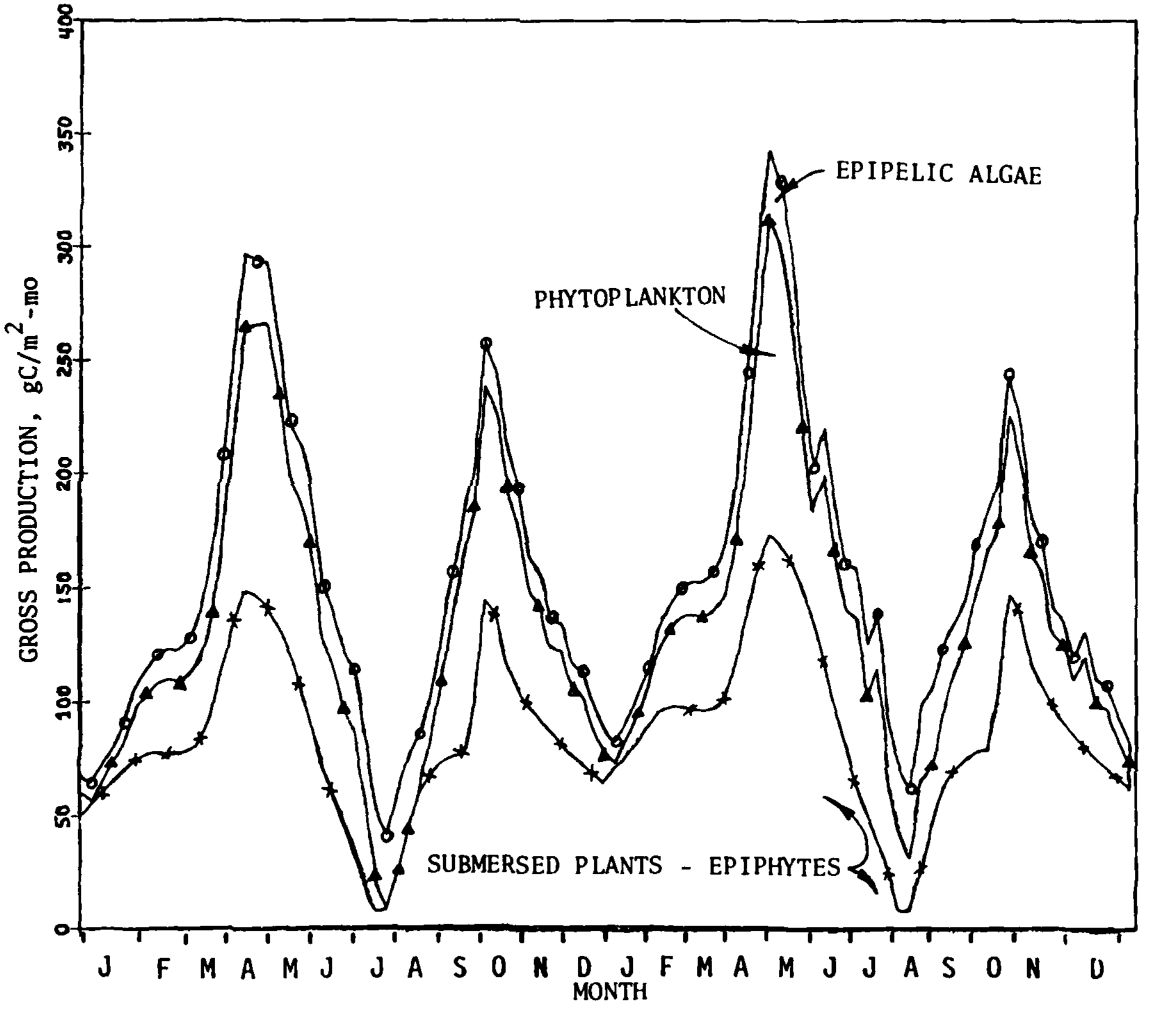

Figure 34. Contributions of phytoplankton, submersed plants, and epipelic algae to simulated gross production. (Area between the curves represents the magnitude of contribution.)

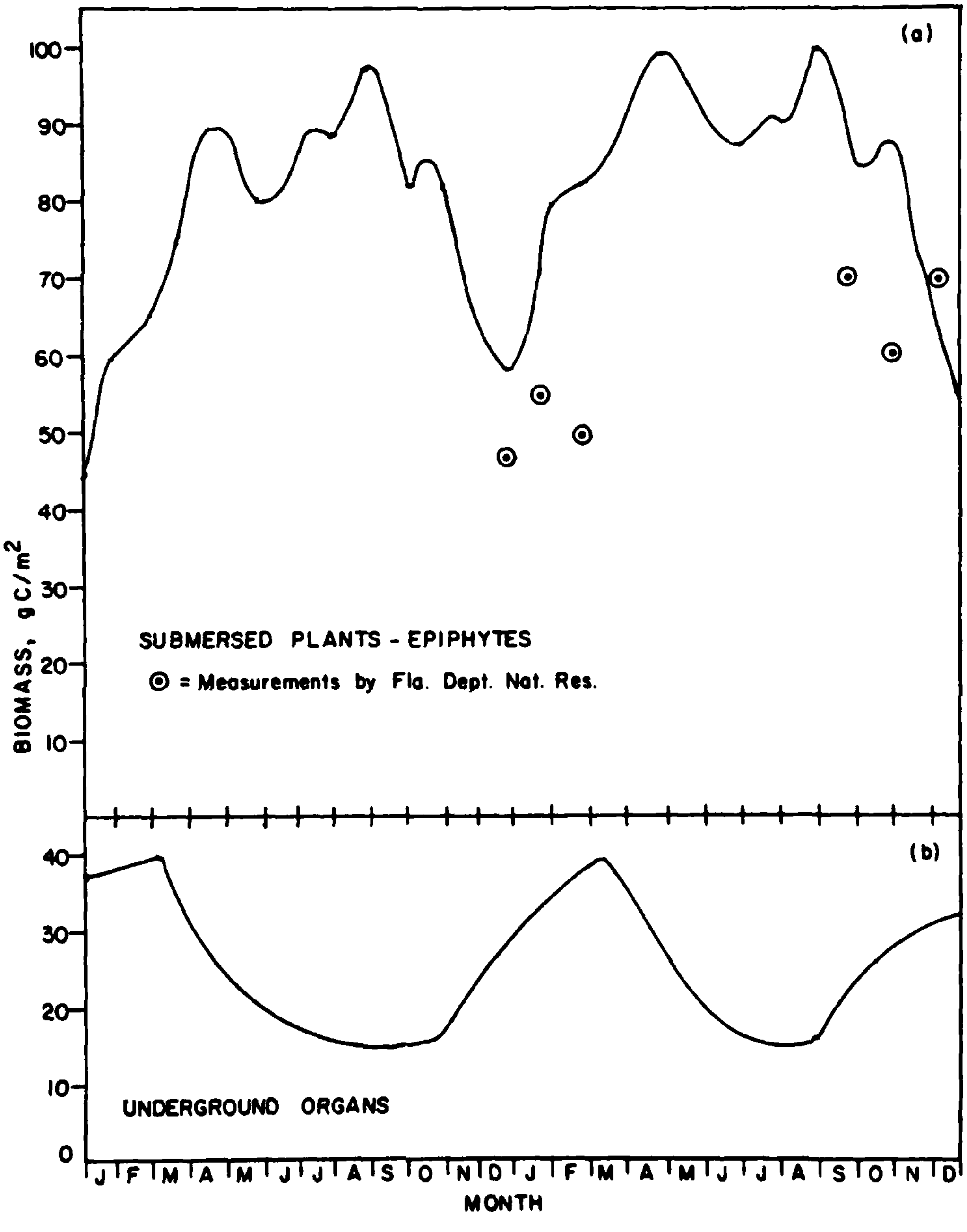

Figure 35. Simulation of submersed plant-epiphyte biomass: (a) simulated and observed aboveground biomass; (b) simulation of underground biomass

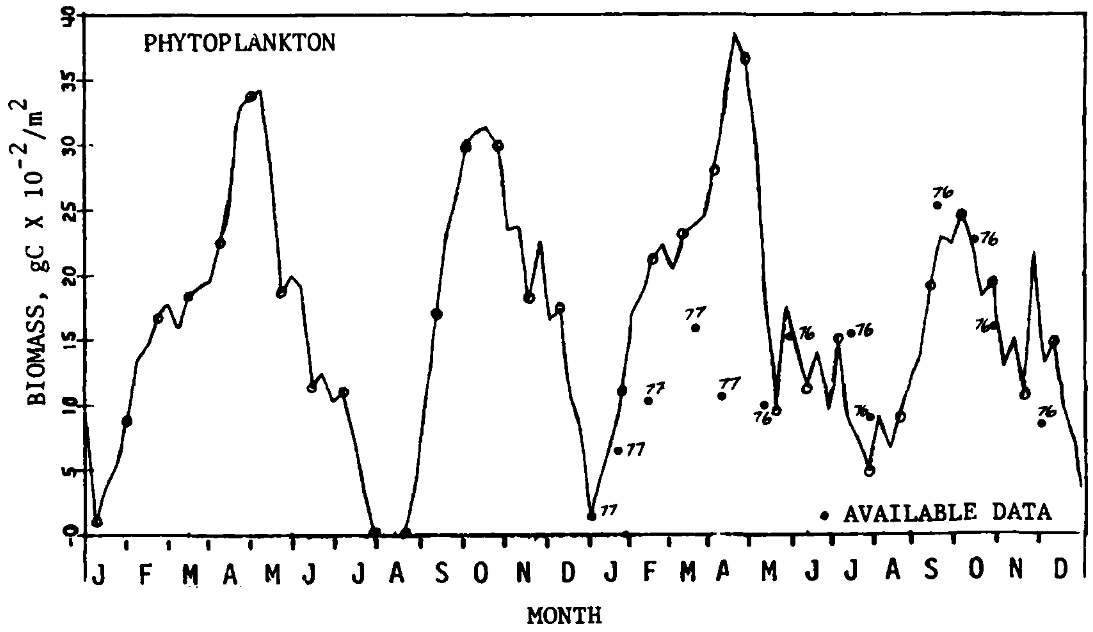

Figure 36. Simulated and observed phytoplankton biomass

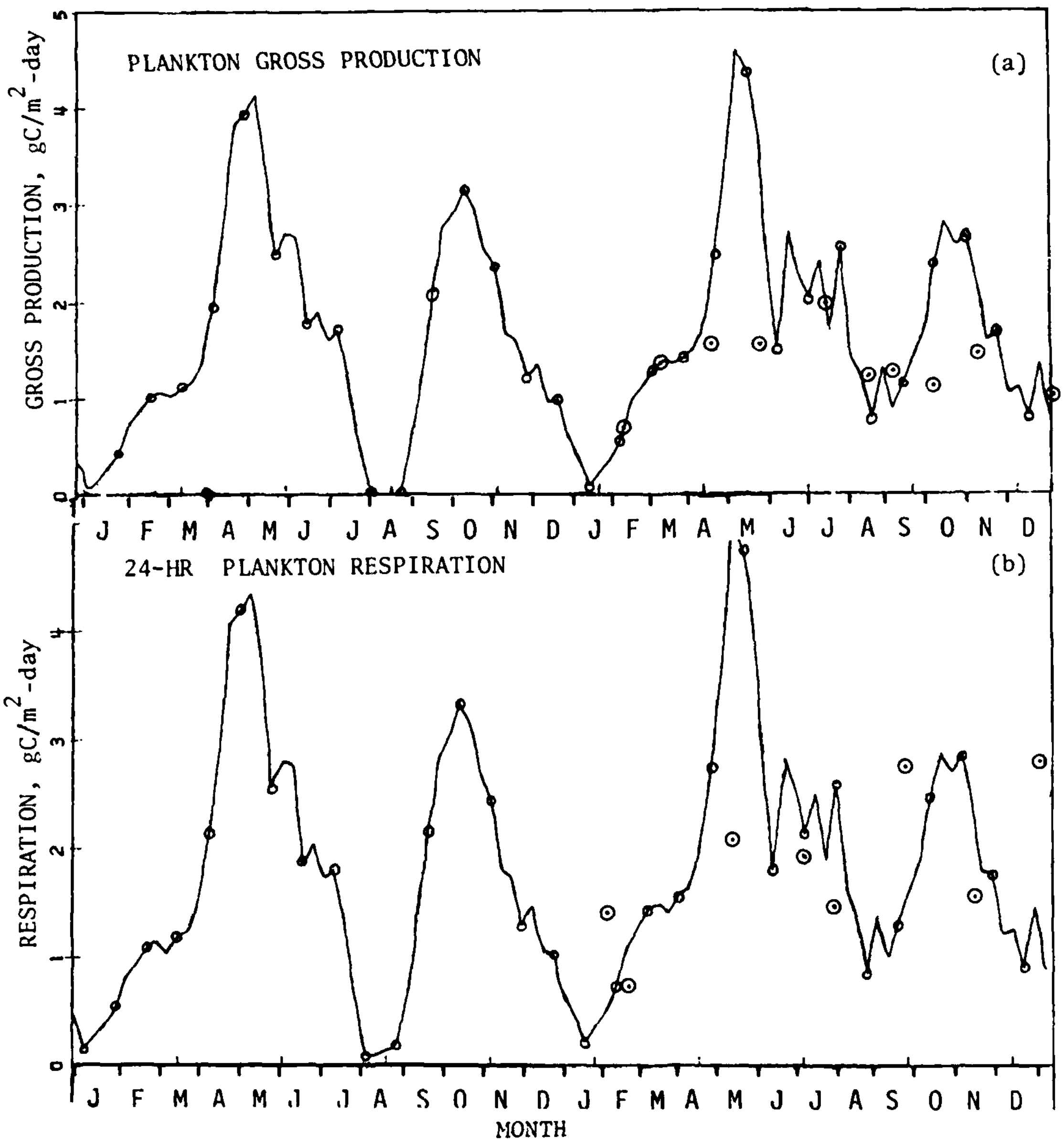

Figure 37. Simulated and observed plankton metabolism

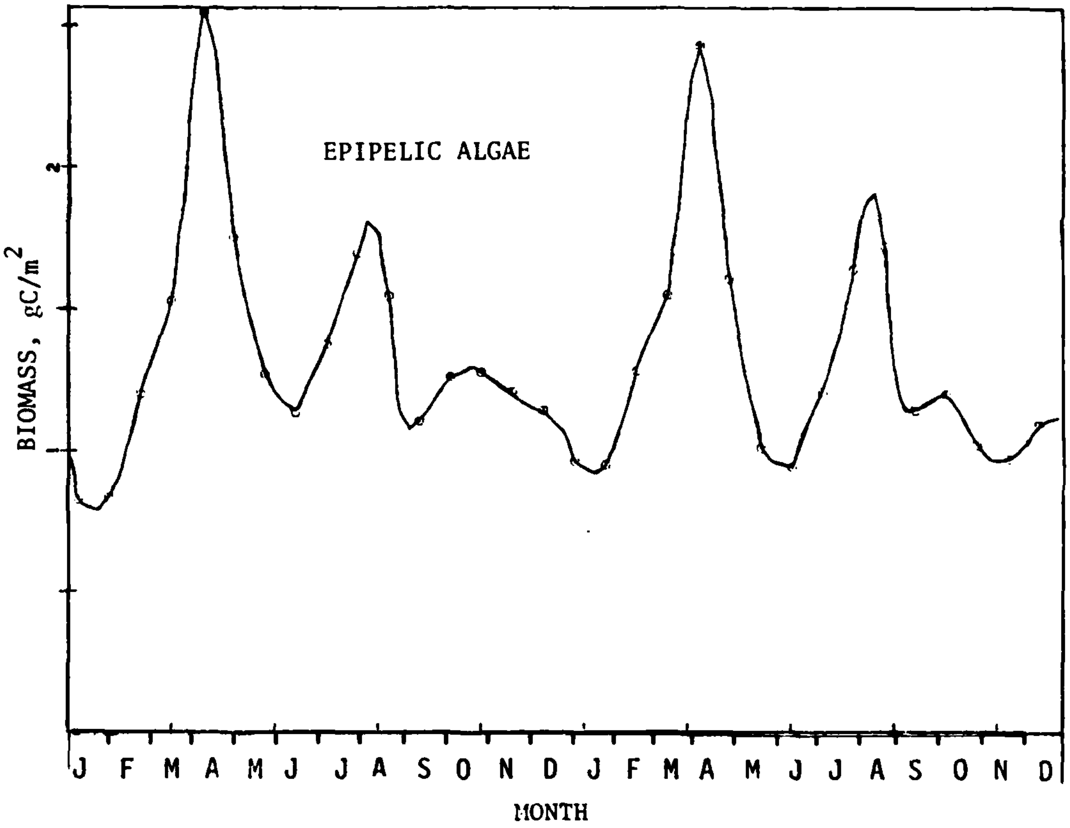

Figure 38. Simulated biomass of epipelic algae

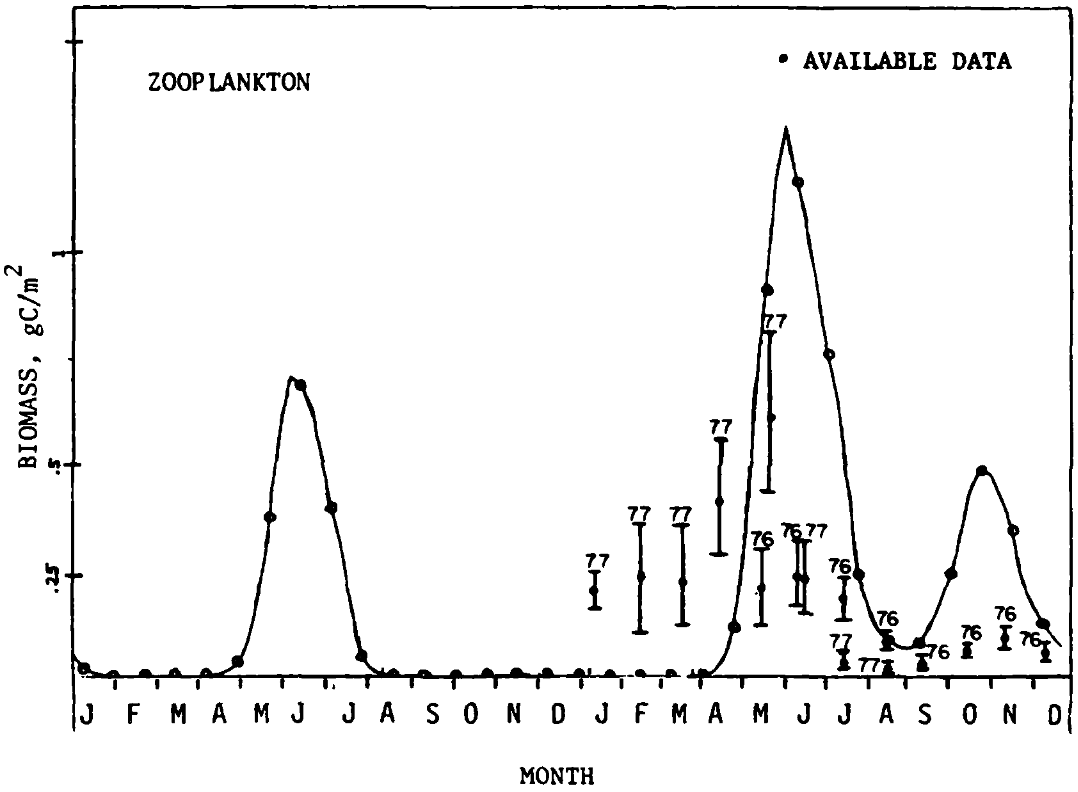

Figure 39. Simulated and observed zooplankton biomass

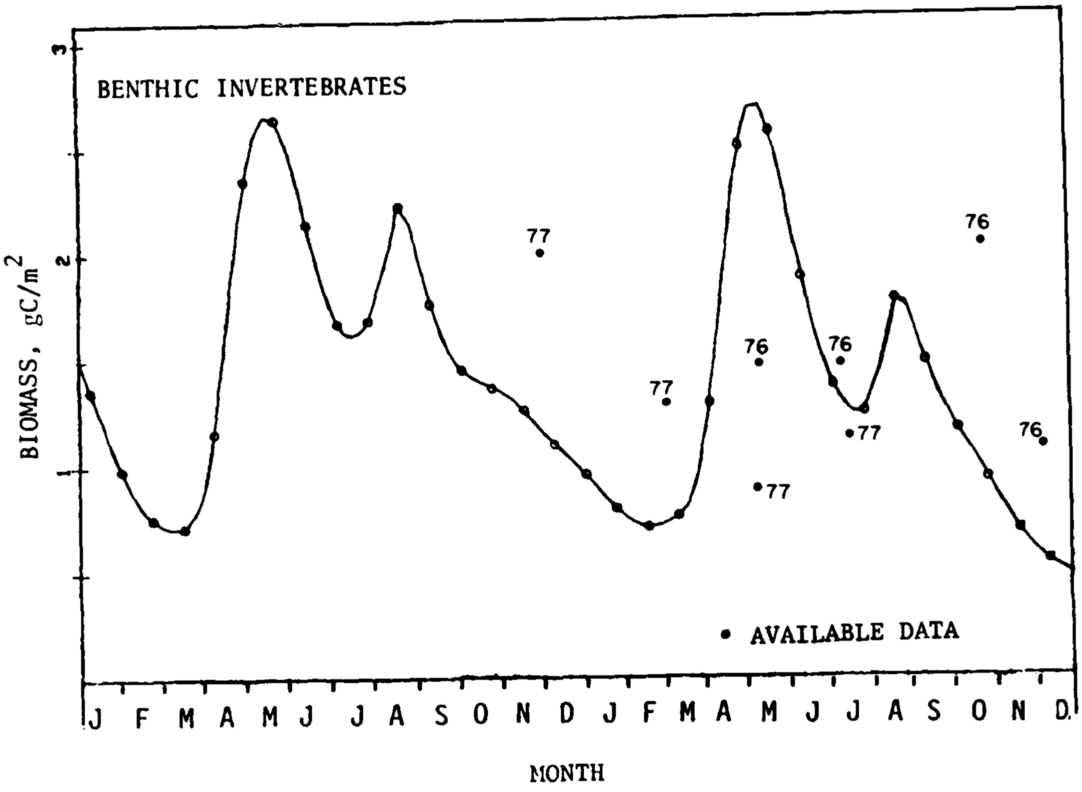

Figure 40. Simulated and observed benthic invertebrate biomass

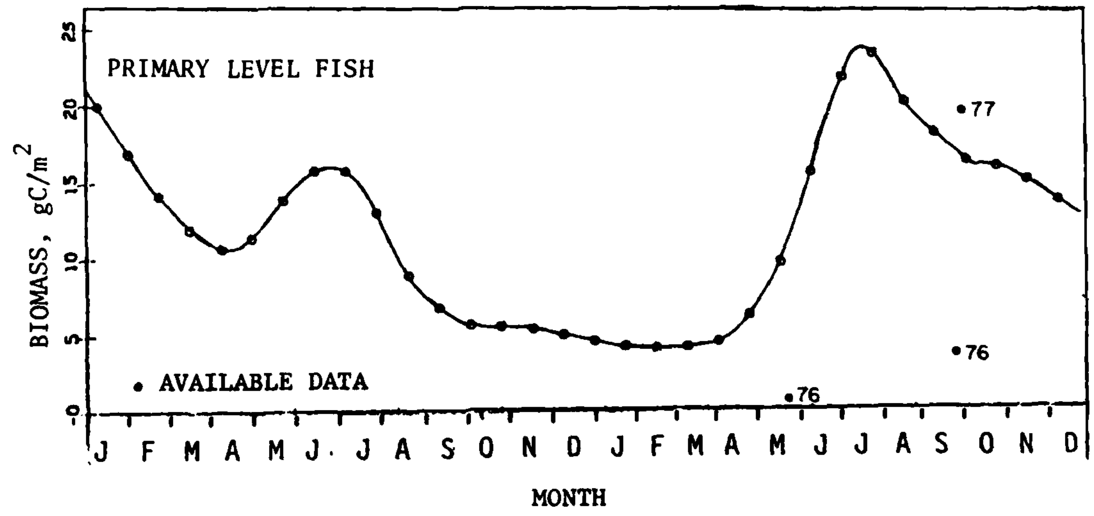

Figure 41. Simulated and observed biomass of pimary level fish

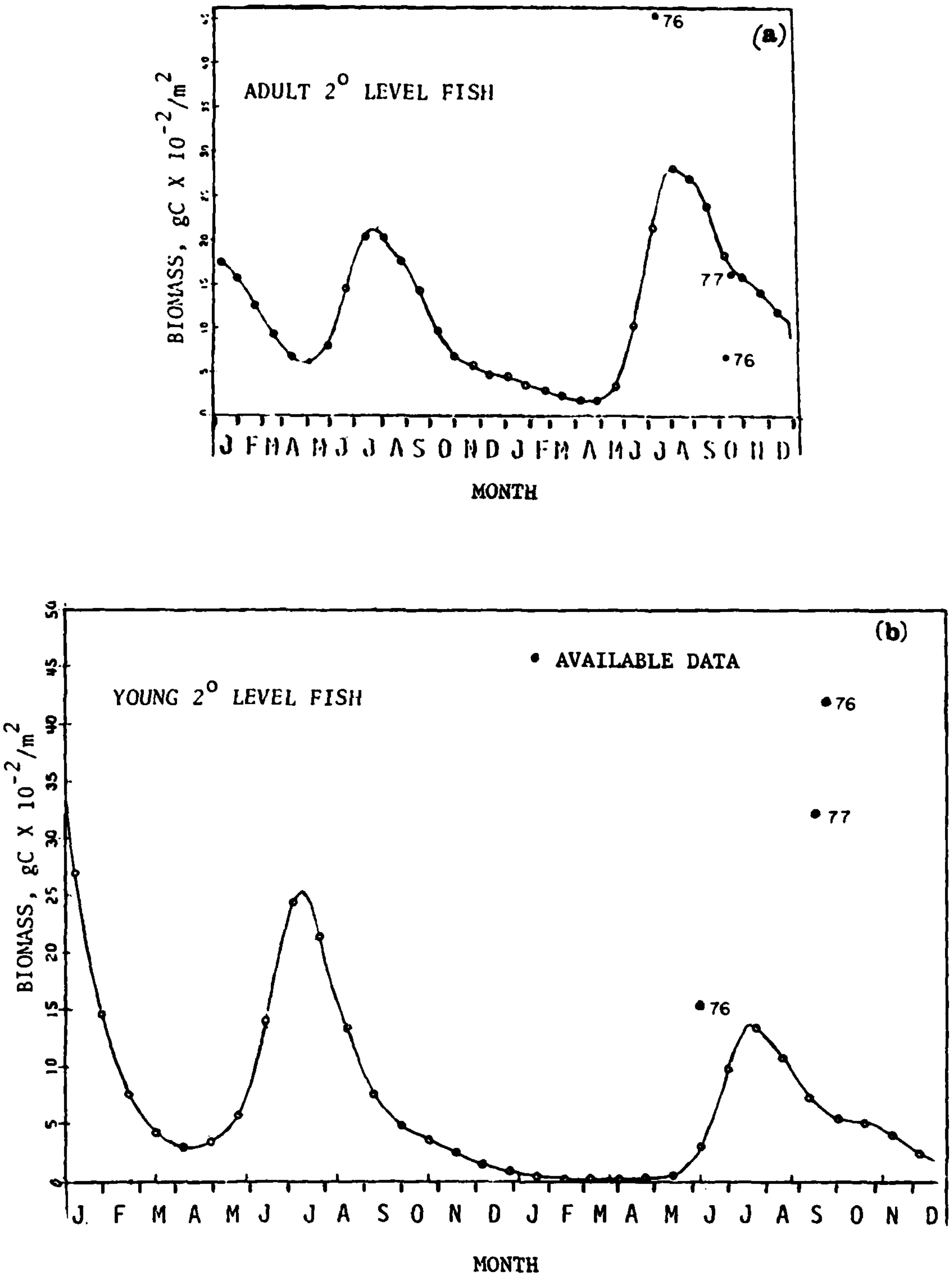

Figure 42. Simulated and observed biomass of secondary level fish

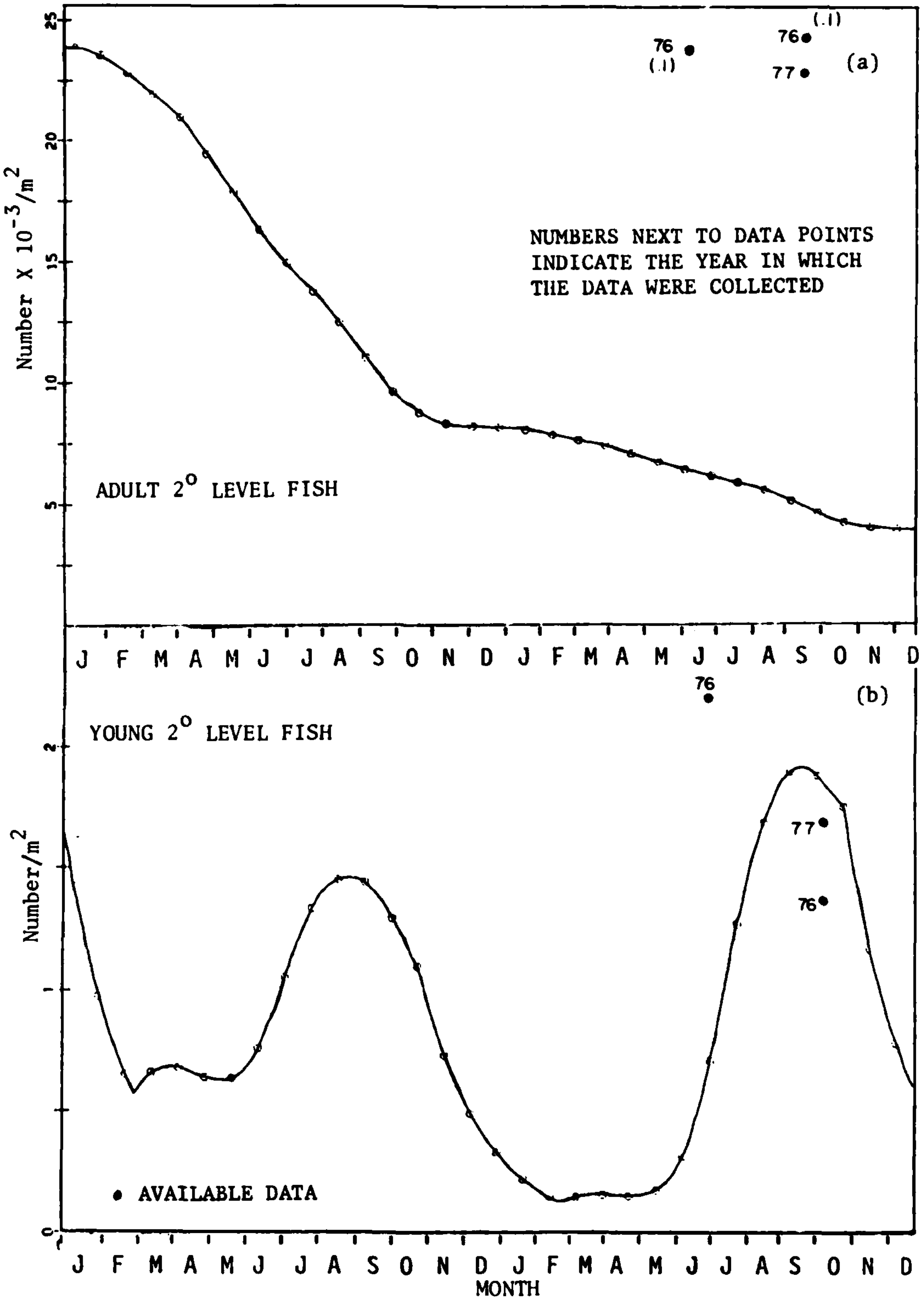

Figure 43. Simulated and observed numbers of secondary level fish

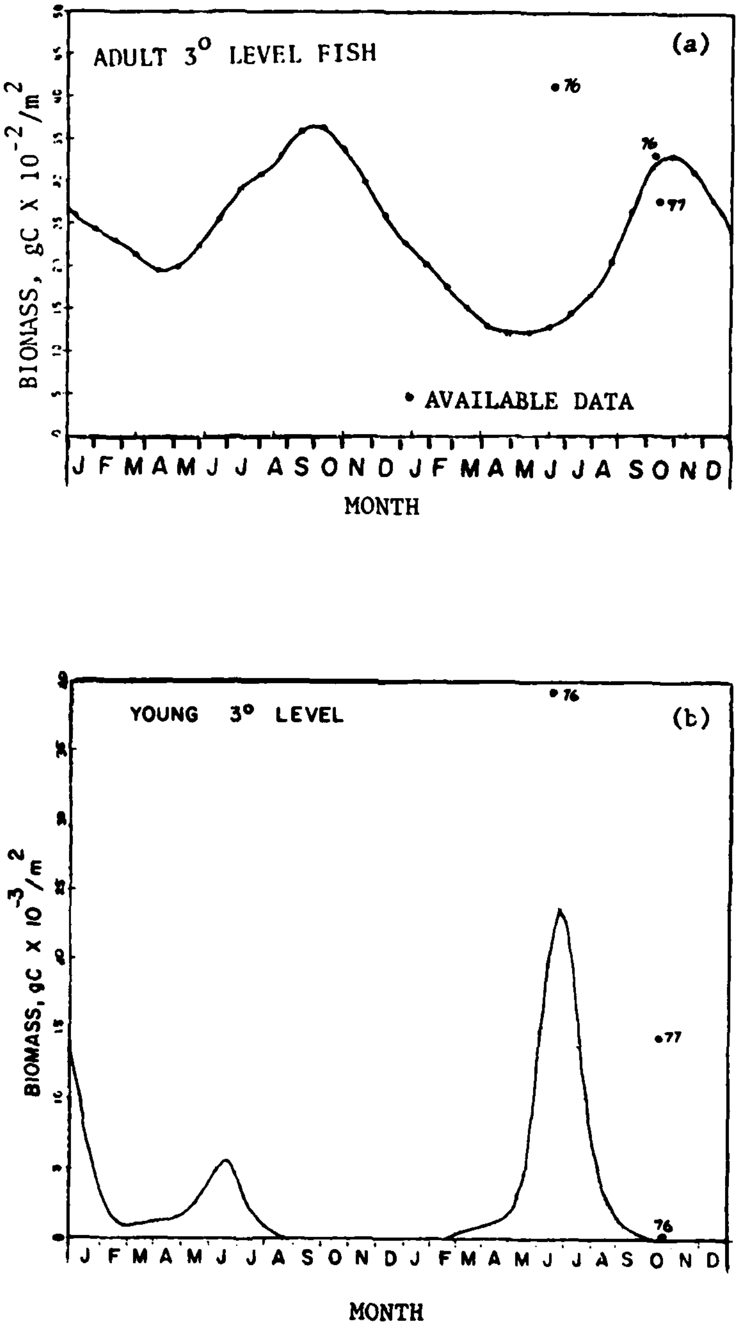

Figure 44. Simulated and observed biomass of tertiary level fish

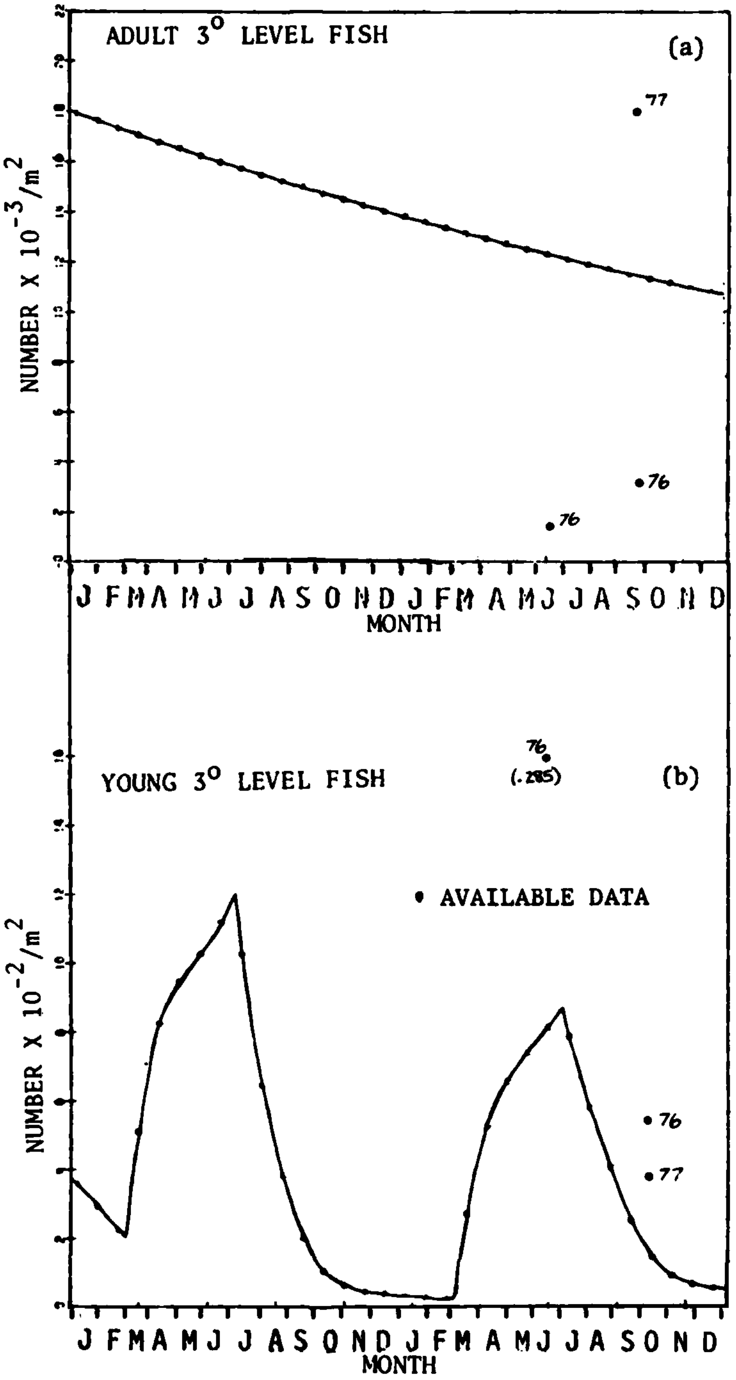

Figure 45. Simulated and observed numbers of tertiary level fish

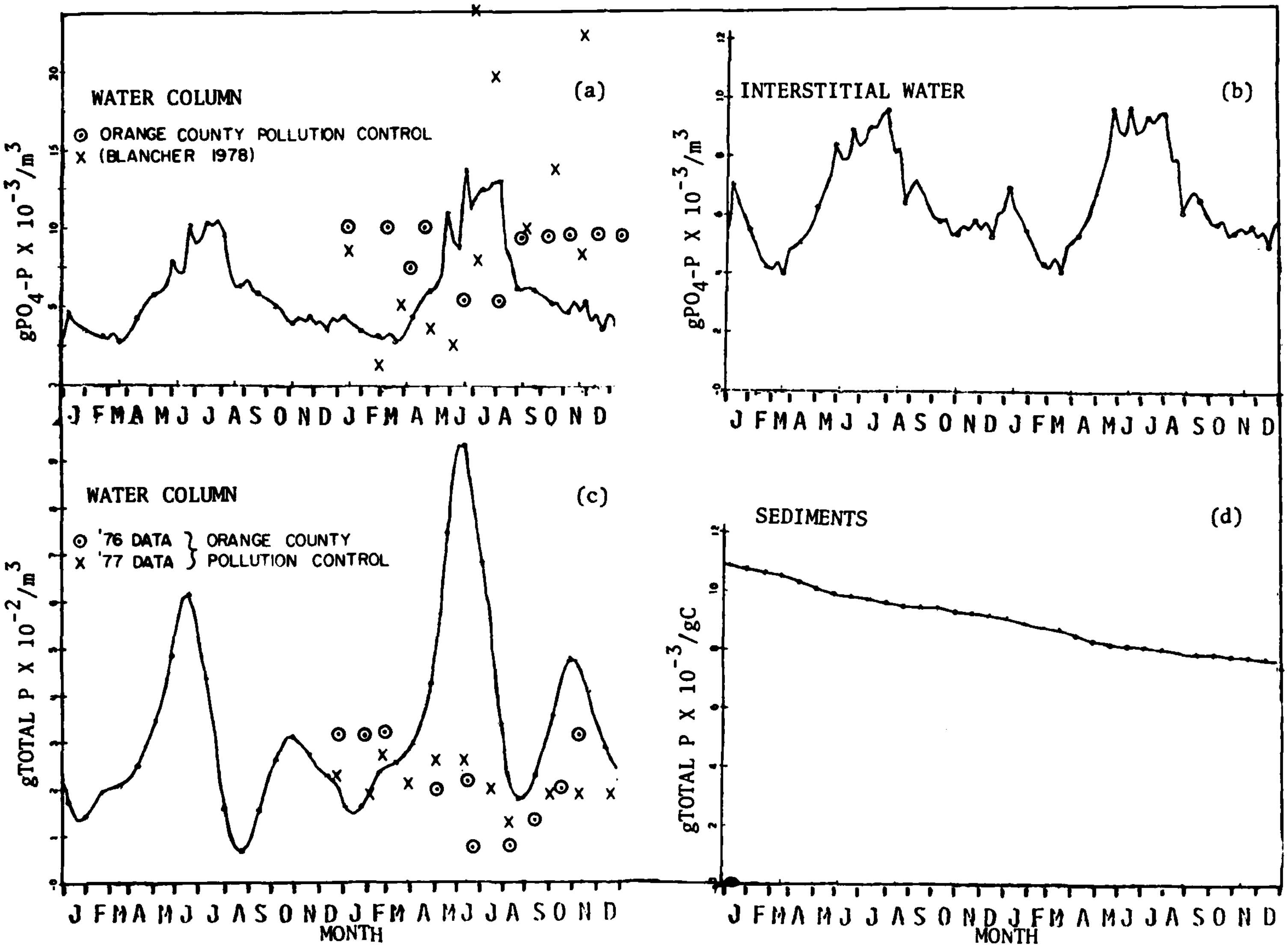

Figure 46. Simulated and observed phosphorus levels: (a) Orthophosphate in water column; (b) Orthophosphate in interstitial waters; (c) Total phosphorus in water column; (d) Total phosphorus in sediments

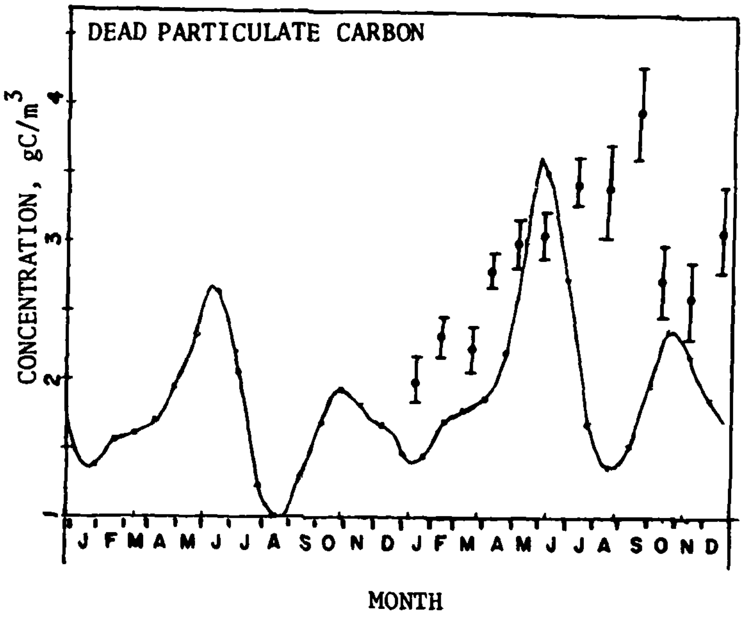

Figure 47. Simulated concentration of dead particulate carbon and observed concentrations (1977) of volatile suspended solids in water column (Curve represents simulated concentrations; range bars with dots represent observed concentrations.)

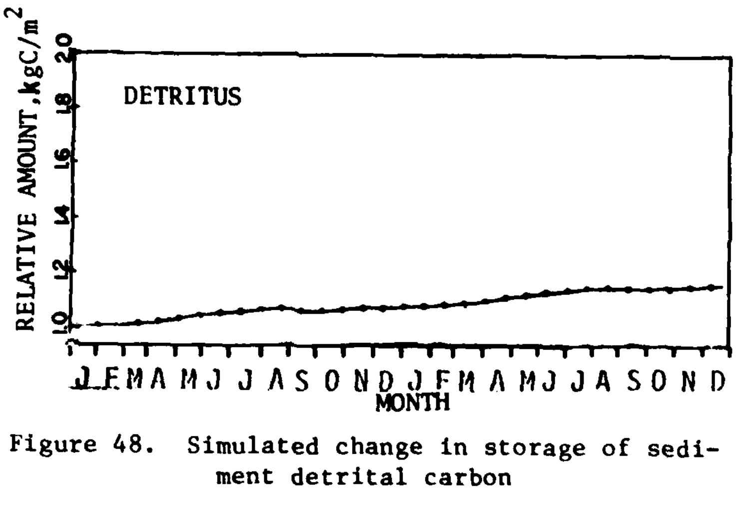

Figure 48. Simulated change in storage of sediment detrital carbon

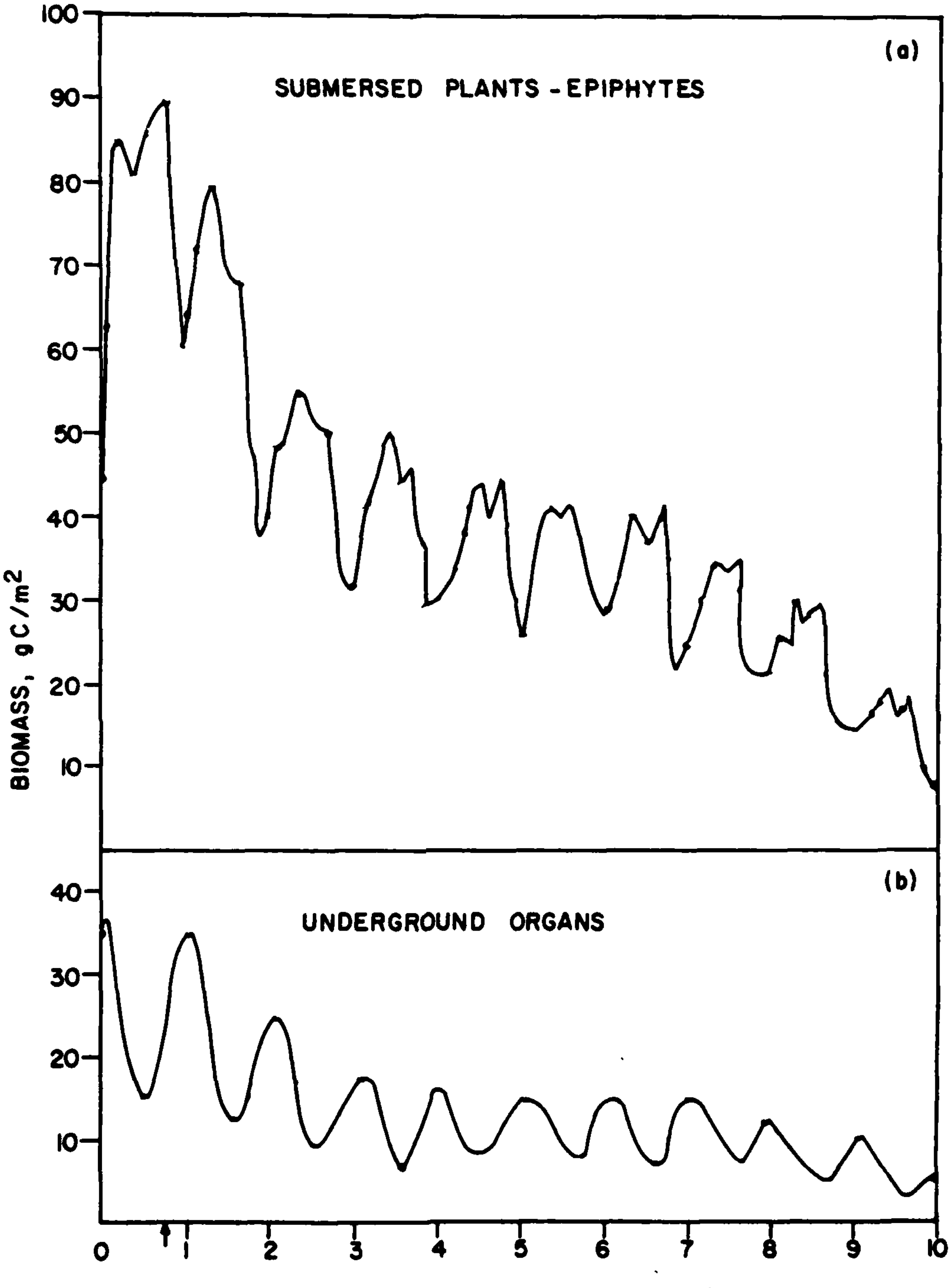

Figure 49. Simulated effects of white amur on: (a) submersed plants and (b) underground organs (arrow denotes time of stocking)

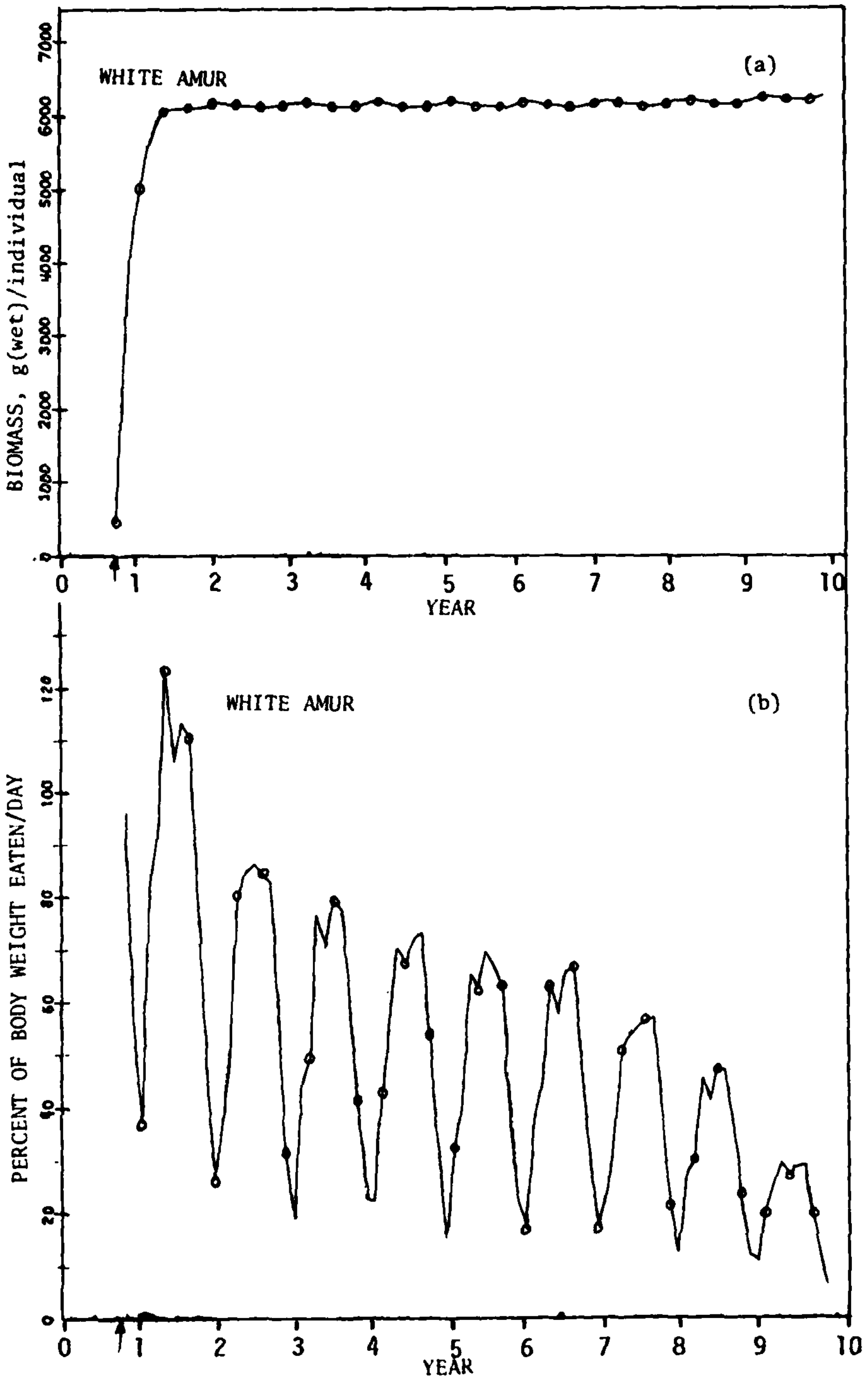

Figure 50. Simulation of white amur (Continued): (a) average biomass; (b) percent of body weight eaten daily

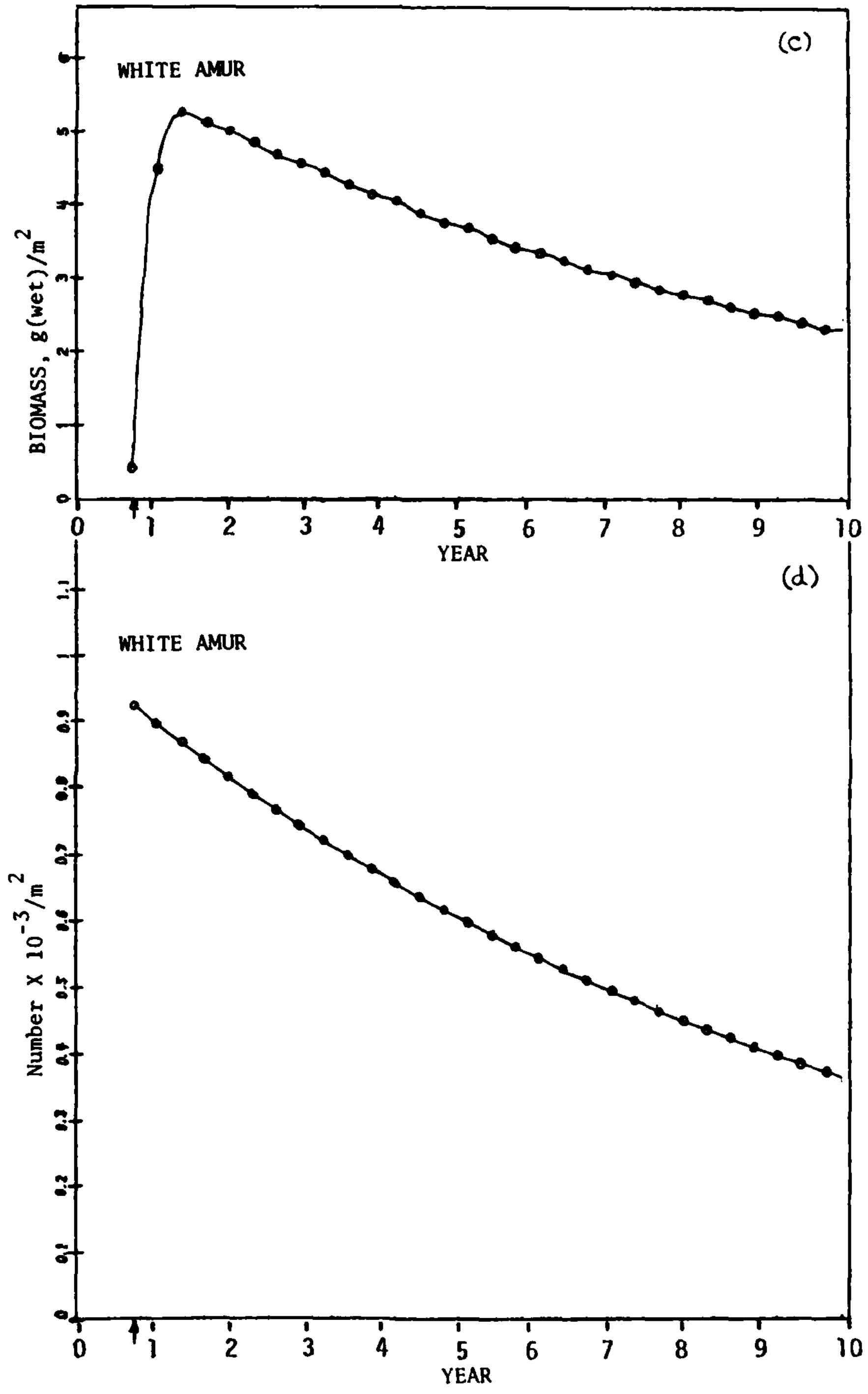

Figure 50 (Concluded): (c) total white amur biomass; (d) number of white amur

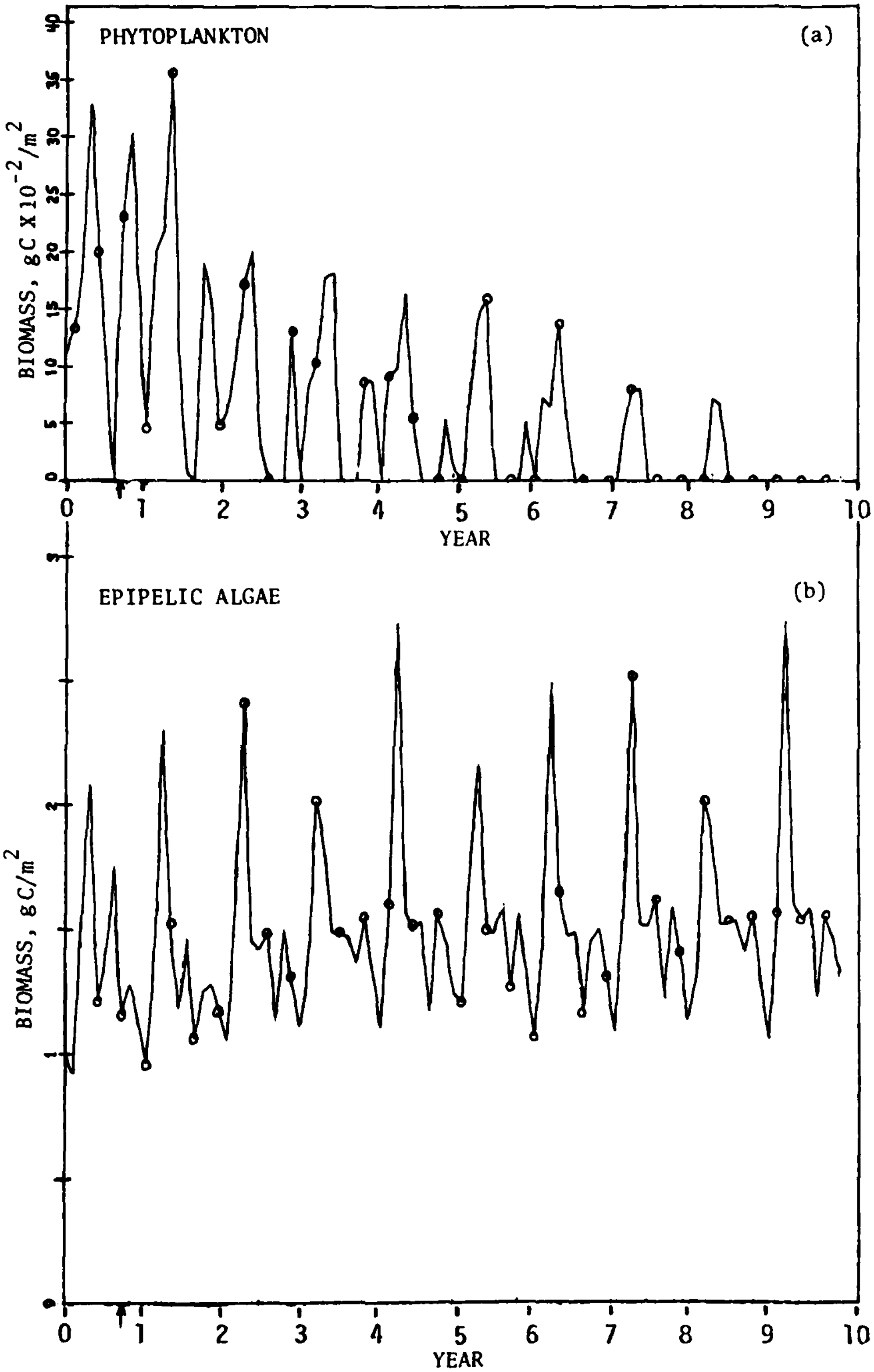

Figure 51. Simulated effects of white amur on algal biomass (arrow denotes time of stocking)

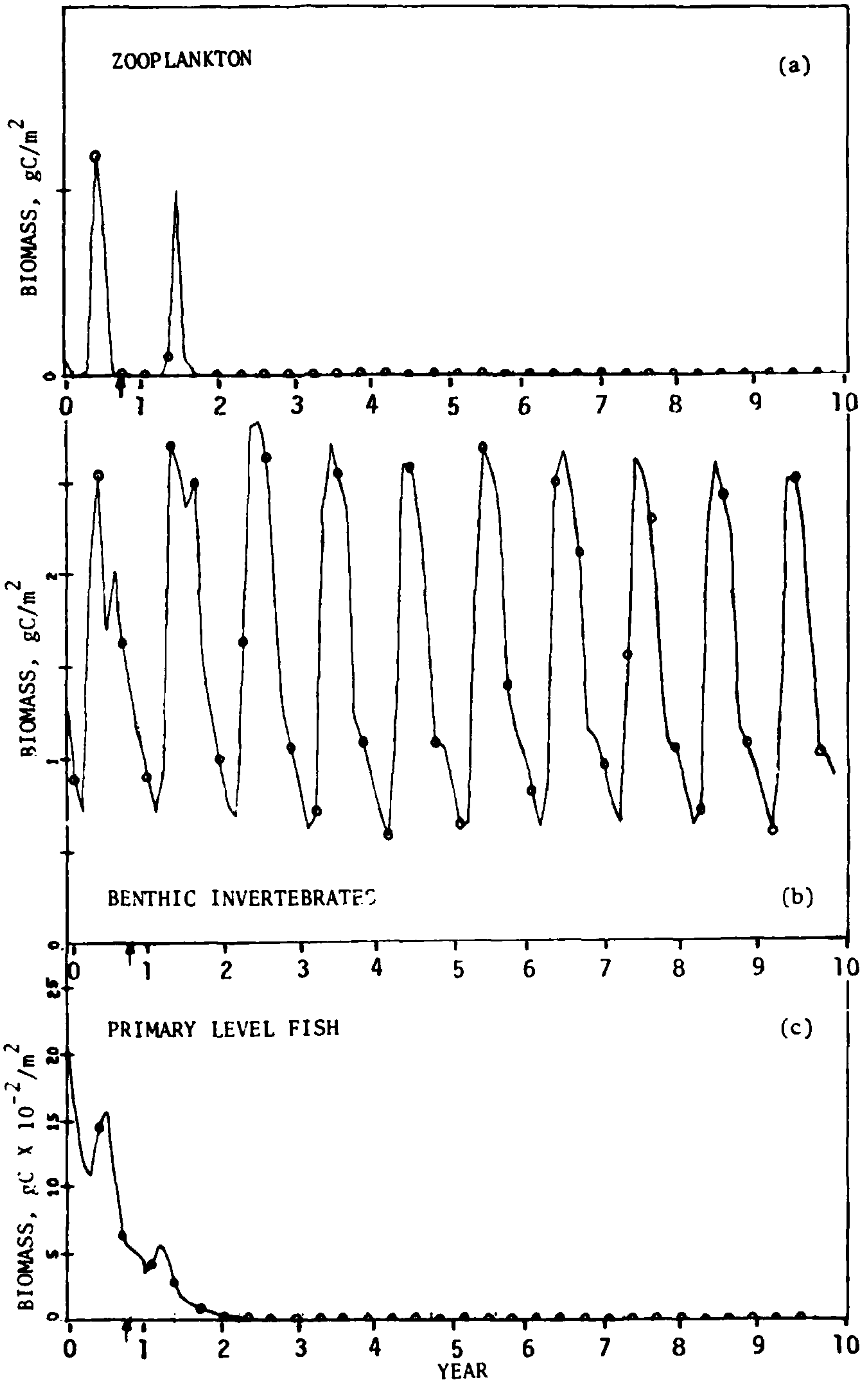

Figure 52. Simulated effects of white amur on animal populations (arrow denotes time of stocking)

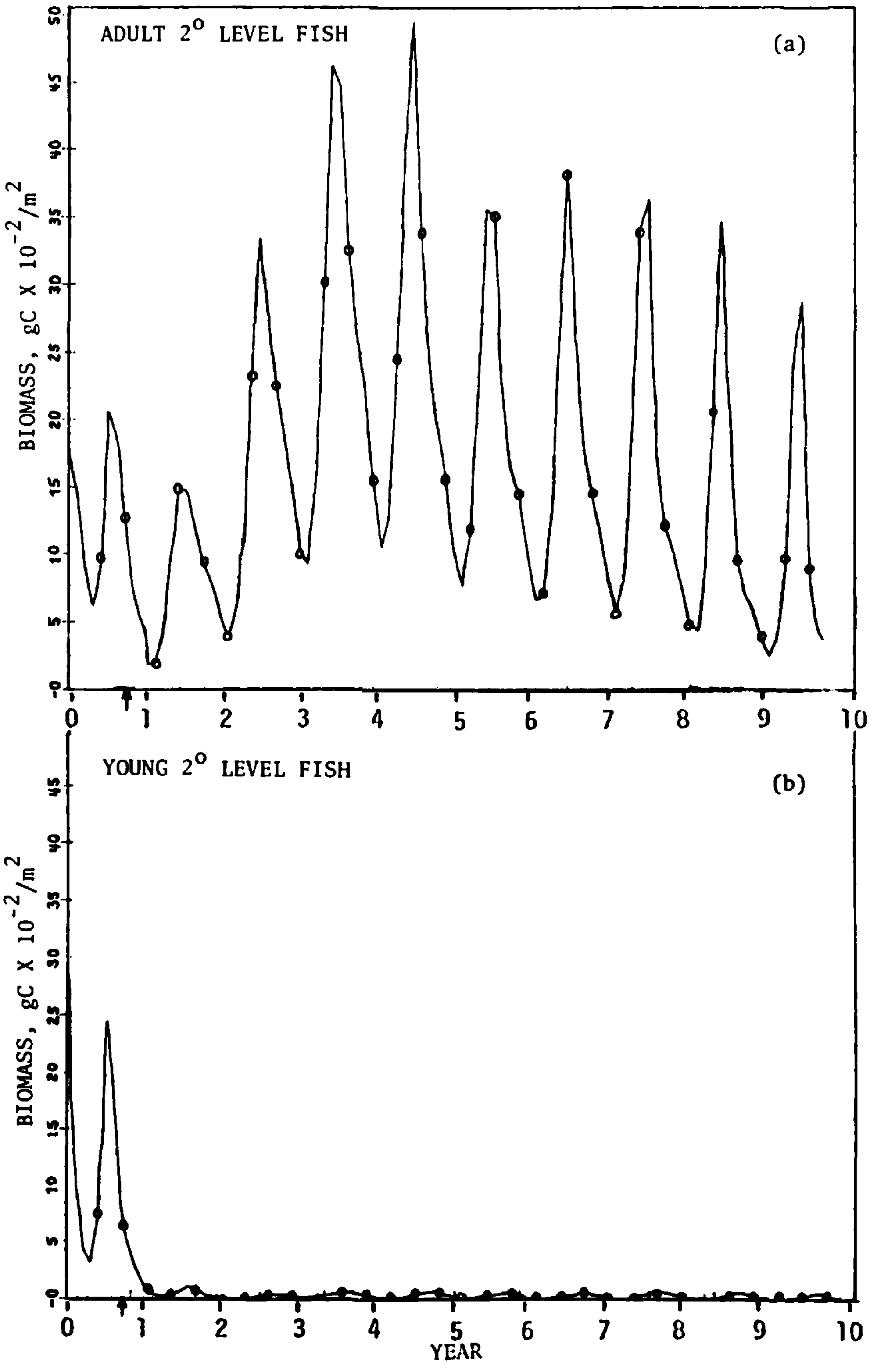

Figure 53. Simulated effects of white amur on secondary level fish (arrow denotes time of stocking)

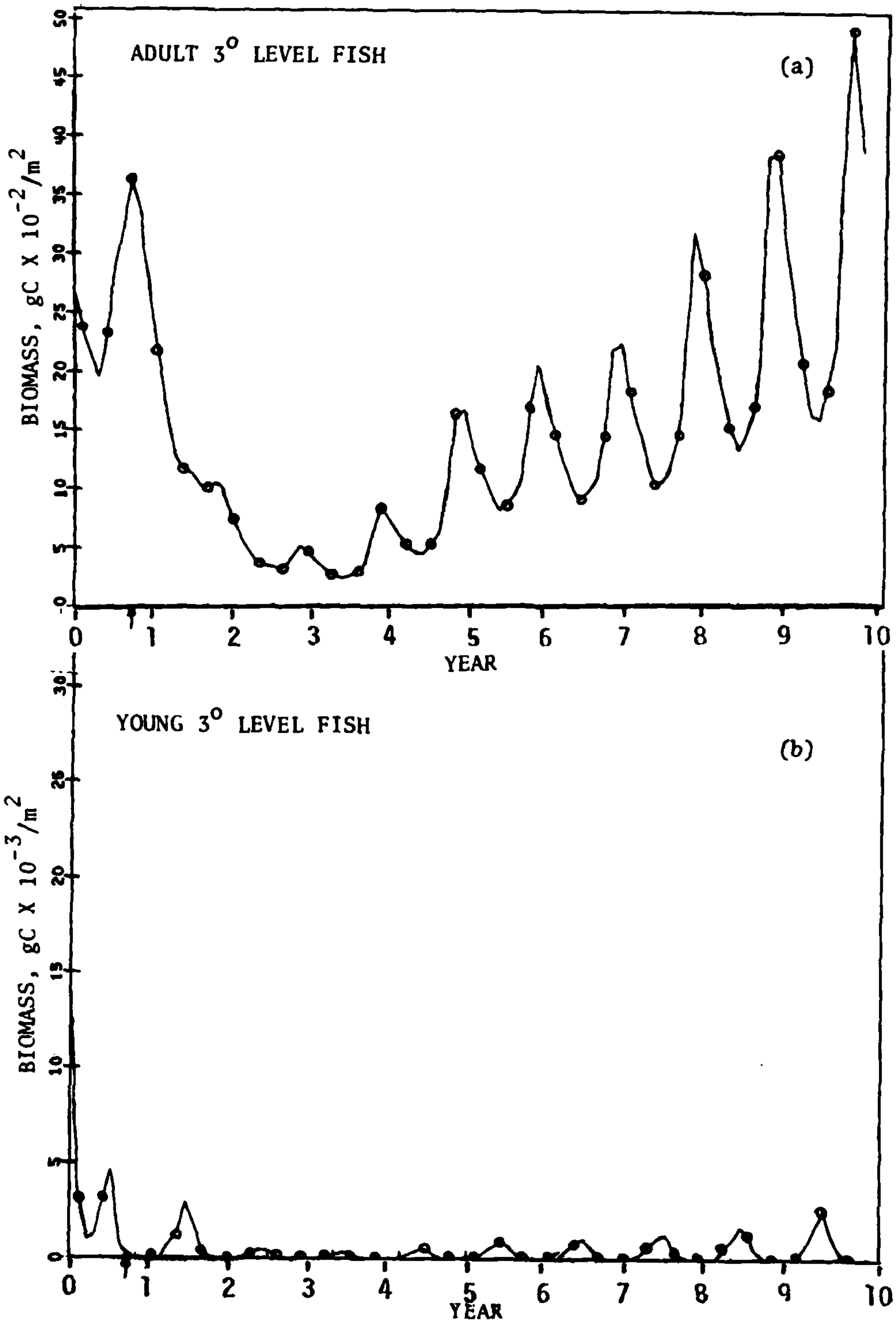

Figure 54. Simulated effects of white amur on tertiary level fish (arrow denotes time of stocking)

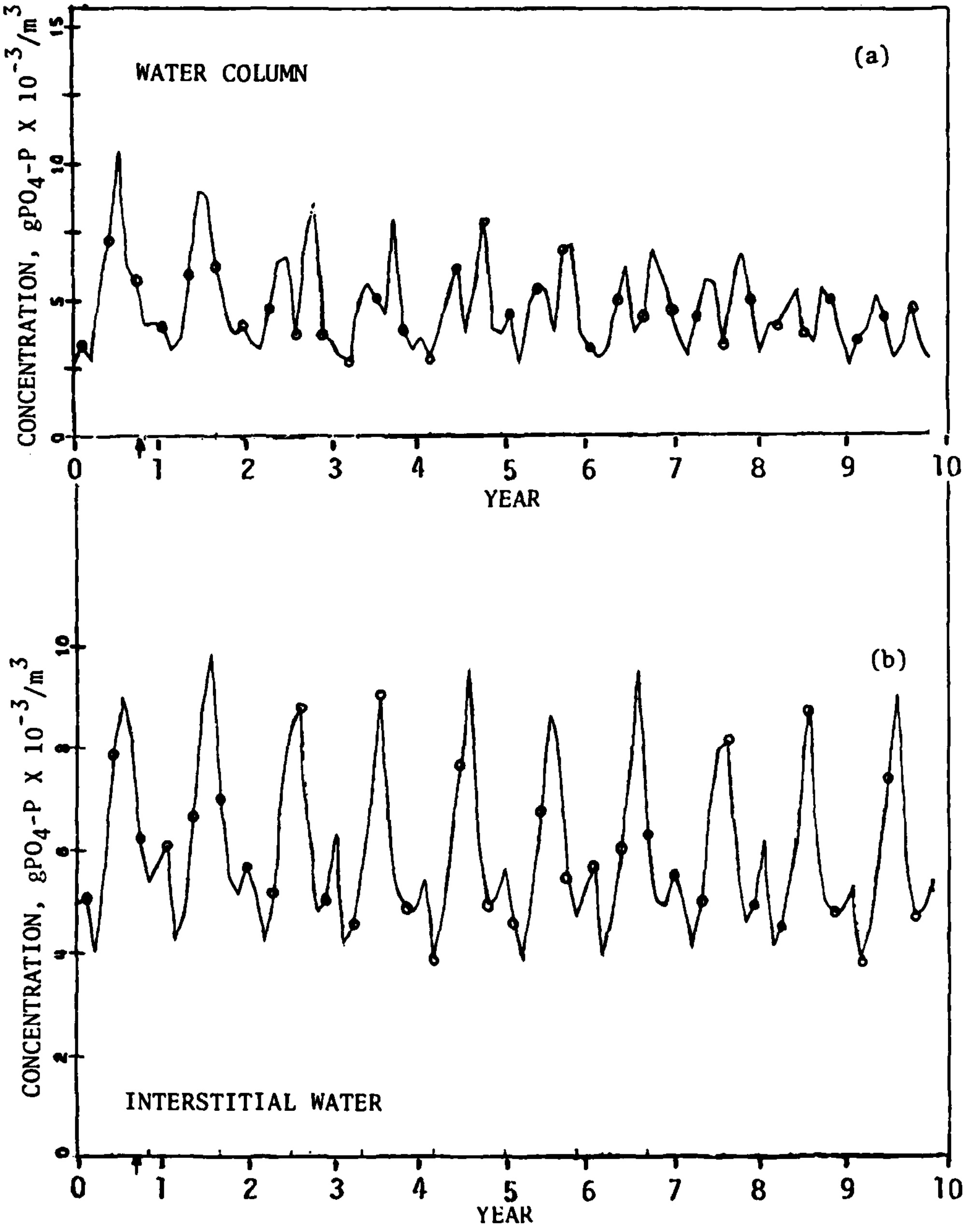

Figure 55. Simulated effects of white amur on orthophosphate concentrations (arrow denotes time of stocking)

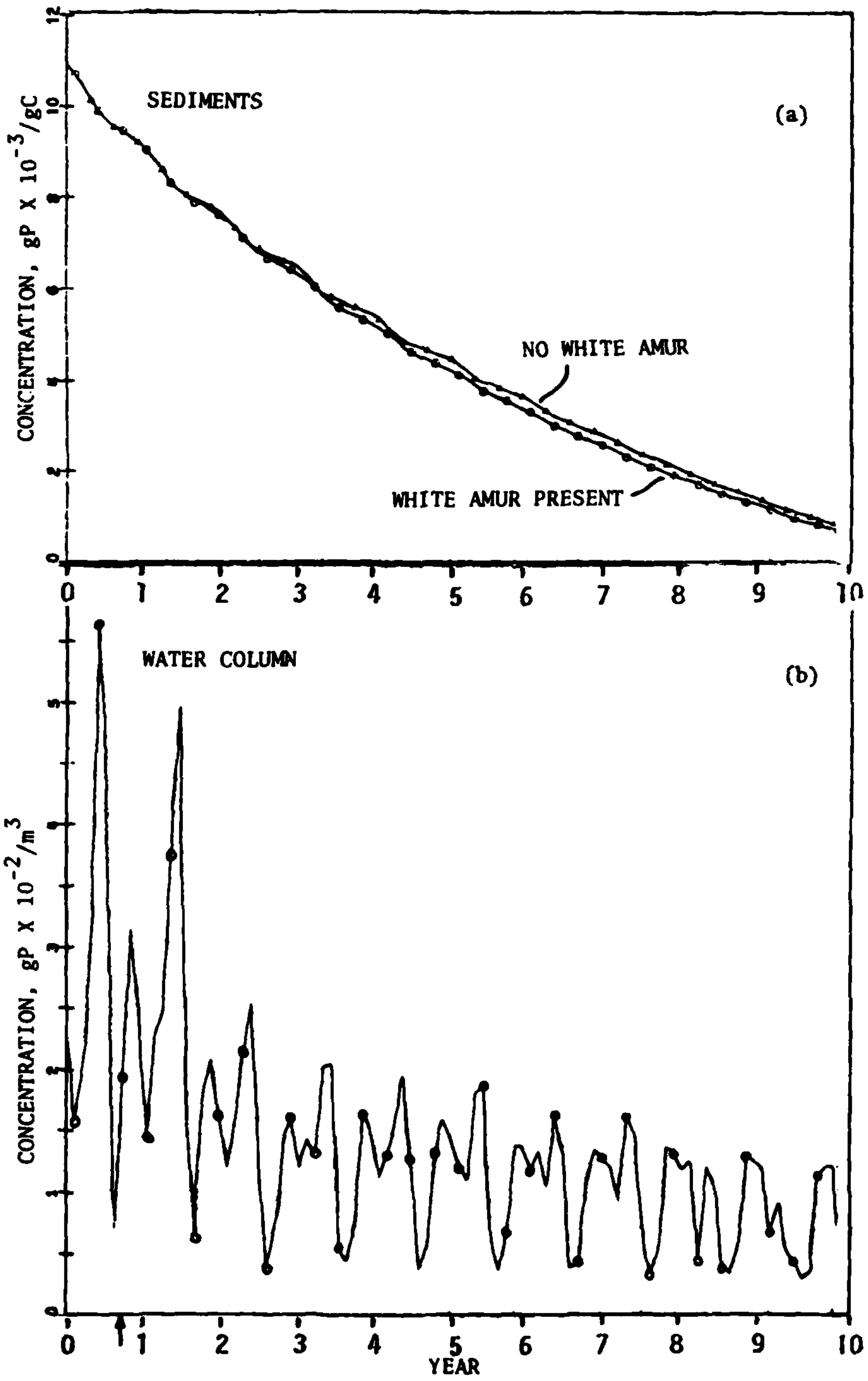

Figure 56. Simulated effects of white amur on total phosphorus concentrations (arrow denotes time of stocking)

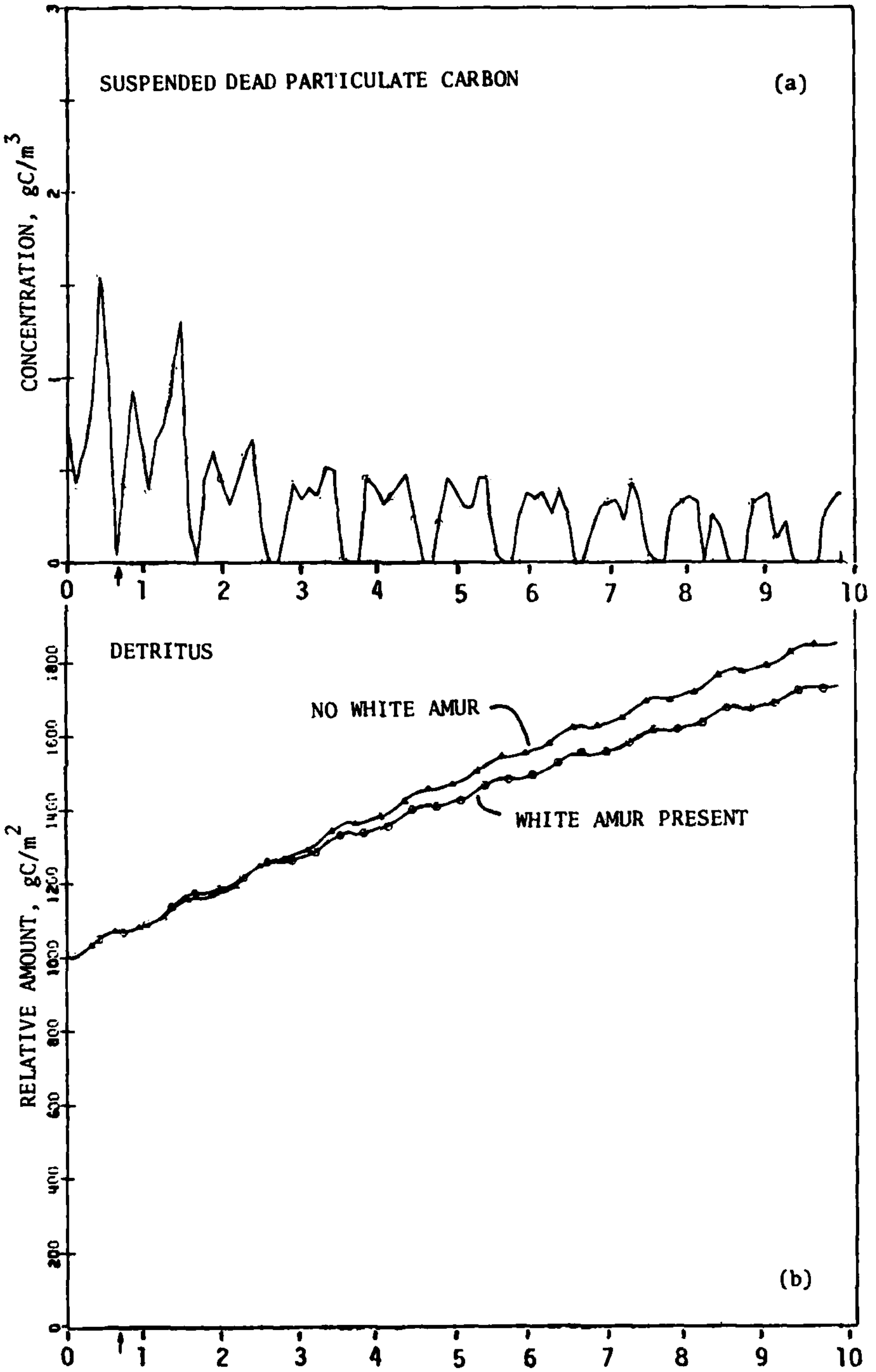

Figure 57. Simulated effects of white amur on detrital carbon levels (arrows denote time of stocking)

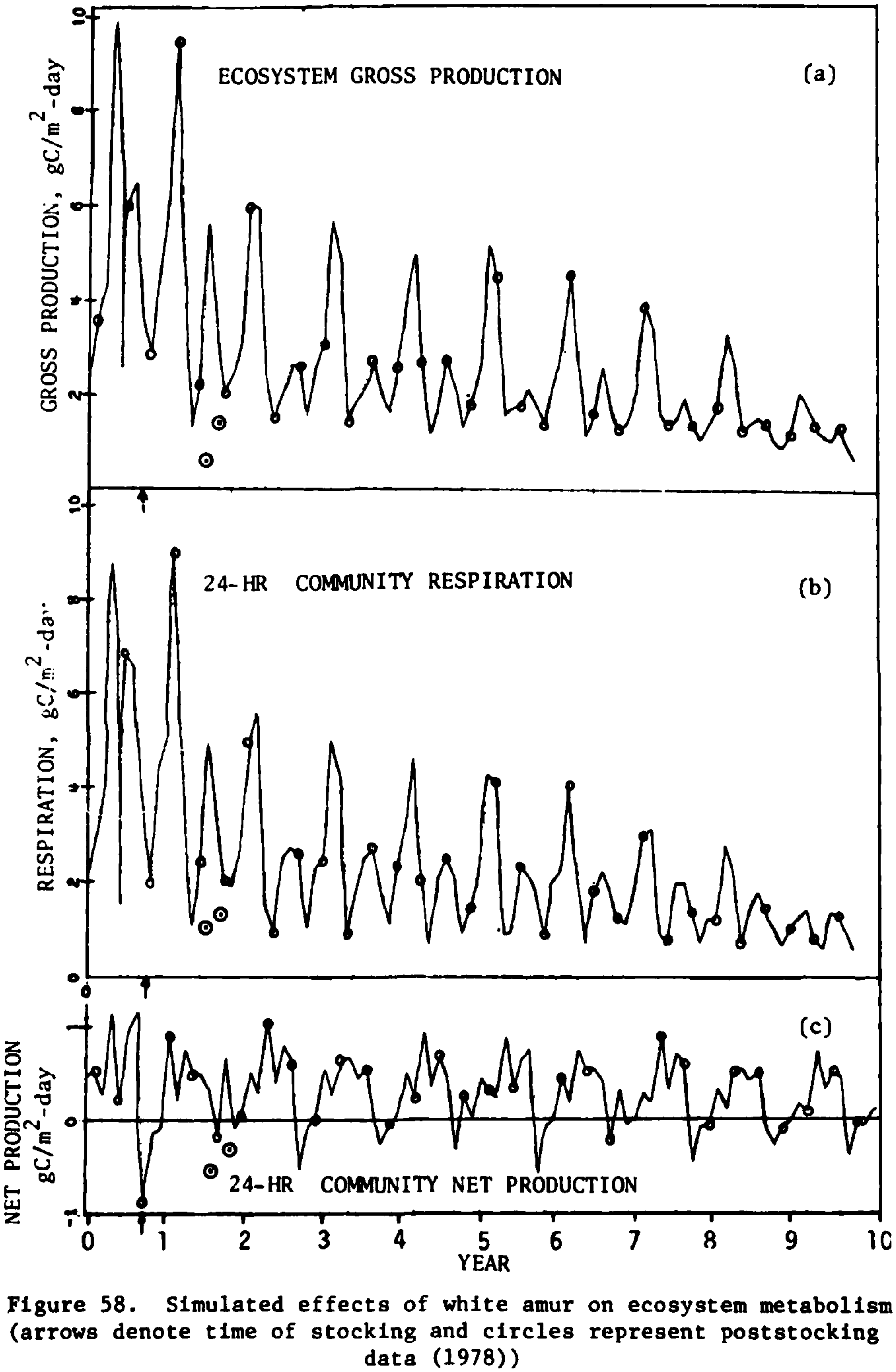

Figure 58. Simulated effects of white amur on ecosystem metabolism (arrows denote time of stocking and circles represent poststocking data (1978))

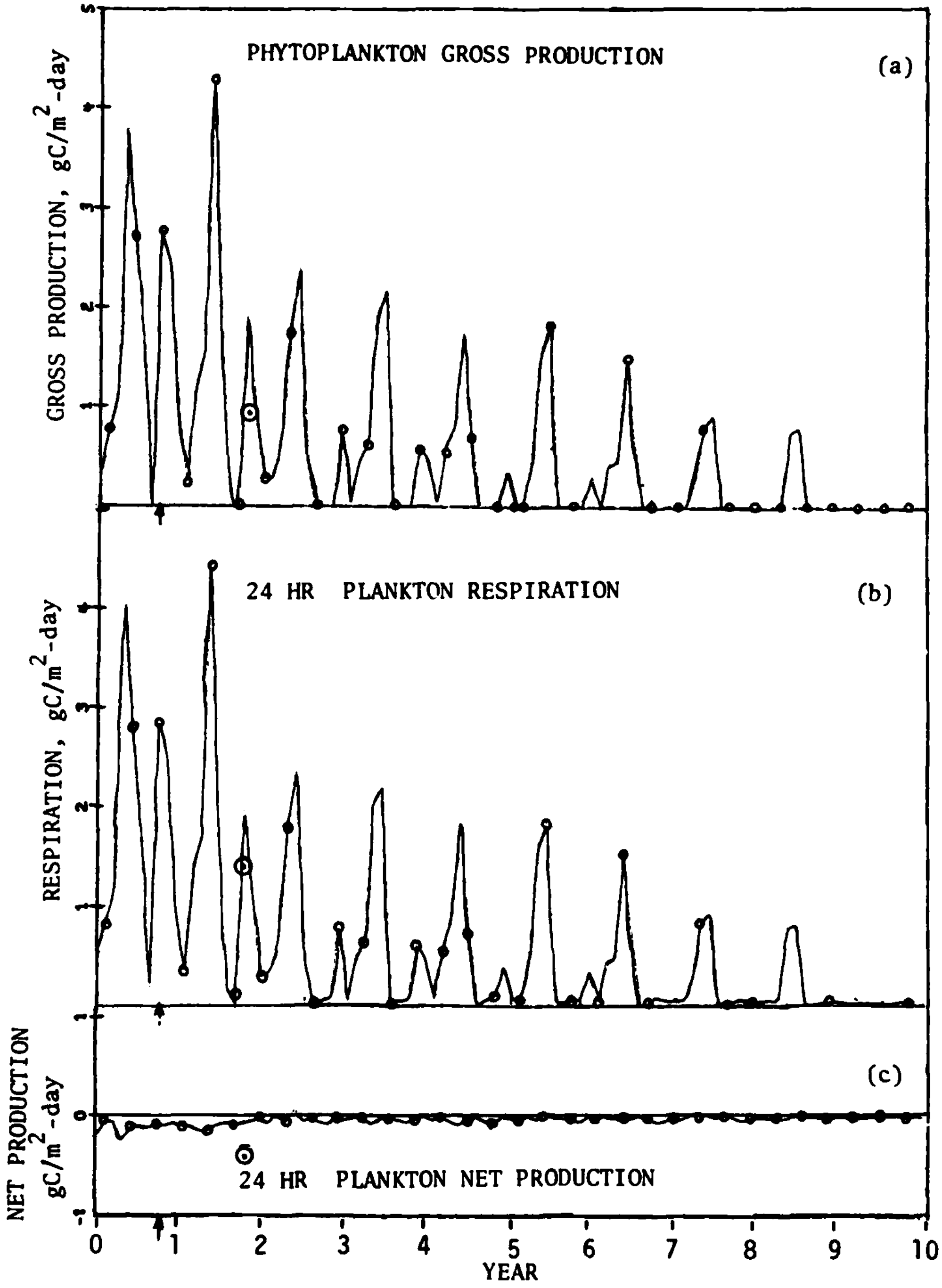

Figure 59. Simulated effects of white amur on plankton metabolism (arrows denote time of stocking and circles represent poststocking data (1978))

APPENDIX A: COMPARISON OF SIMULATED AND REPORTED VALUES OF LAKE COMPONENT PROCESS RATES

Table A1

Comparison of Simulated Characteristics of Producer Process Rates with Literature Values

Component and Major Processes	Simulated Percentage of Total Energy Flow*	Range of Observed Values**
Phytoplankton		
Respiration	81	25 - 53
Herbivory	6	10 - 16
Sinking	7	10
Leaching	12	4 - 20
Submersed Plants		
Respiration	84	58 - 189†
Herbivory (percent of net production)	3 (16)	ND†† (0.3 - 8)
Sloughing (percent of average standing crop)	1 (16)	ND (2 - 10)
Leaching	7	0.5 - 7
Translocation to underground organs	11	
Epipelic algae		
Respiration	27	ND
Herbivory	32	ND
Sloughing	38	ND
Leaching	7	3.8

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* Percentages do not add up exactly to 100 because of slight variations from steady-state and round off errors.

** References listed in methods section.

† High value is for a single day; low value represents annual percentage.

†† ND = No data found in the literature that adequately described this pathway.

Table A2

Comparison of Simulated Characteristics of Heterotroph Process Rates with Literature Values

Component and Characteristics of Process Rates	Simulated Value	Range of Observed Values*
Zooplankton		
Turnover time, days	14	2-29
Percent of assimilated food respired	76	33-71
Percent of body weight respired daily	23	16-43
Percent of assimilated food which becomes net production	24	54-71
Benthic invertebrates		
Turnovers per year	2	1-8
Percent of body weight eaten per day	18	2-23
Percent of assimilated food respired	94	41-77
Percent of body weight respired daily	7	3.4
Percent of assimilated food which becomes net production	6	23-59
Primary level fish		
Specific growth rate, g/g-day	-0.56-1.60	-0.01-0.06
Specific consumption rate, g/g-day	0.01-0.11	0.02-0.14
Specific respiration rate, g/g-day	0.014-0.04	0.004-0.02
Turnover time, yr	0.44	ND**
Adult secondary level fish		
Specific growth rate, g/g-day	-0.56-1.60	-0.01-1.78
Specific consumption rate, g/g-day	0.005-0.12	0.02-0.17

(Continued)

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* References listed in methods section.

** ND = no data found in the literature that adequately described this pathway.

Table A2 (Concluded)

Component and Characteristics of Process Rates	Simulated Value	Range of Observed Values
Specific respiration rate, g/g-day	0.09-0.027	0.004-0.02
Mortality rate, percent of numbers		0-30
Turnover time, yr	0.35	1.0
Young secondary level fish		
Specific growth rate, g/g-day	-0.92-2.50	-0.01-1.78
Specific consumption rate, g/g-day	0.02-0.23	0.02-0.14
Specific respiration rate, g/g-day	0.023-0.067	0.004-0.02
Mortality rate, percent of numbers		0-30
Turnover time, yr	0.17	ND
Adult tertiary level fish		
Specific growth rate, g/g-day	-0.22-0.35	-0.01-0.06
Specific consumption rate, g/g-day	0.00-0.03	0.02-0.14
Specific respiration rate, g/g-day	0.004-0.01	0.004-0.02
Mortality rate, percent of numbers		
Turnover time, yr	1.46	ND
Young tertiary level fish		
Specific growth rate, g/g-day	-1.56-4.44	-0.01-0.06
Specific consumption rate, g/g-day	0.03-0.30	0.02-0.14
Specific respiration rate, g/g-day	0.05-0.13	0.004-0.02
Mortality rate, percent of numbers		
Turnover time, yr	0.10	ND

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.

Ewel, Katherine C.
Large-scale operations management test of use of the white amur for control of problem aquatic plants : Report 2 : First year poststocking results : Volume VII : A model for evaluation of the response of the Lake Conway, Florida, ecosystem to introduction of the white amur / by Katherine C. Ewel and Thomas D. Fontaine III (School of Forest Resources and Conservation, University of Florida). -- Vicksburg, Miss. : U.S. Army Engineer Waterways Experiment Station ; Springfield, Va. : available from NTIS, 1981.
60, [97] p. : ill. ; 27 cm. -- (Technical report / U.S. Army Engineer Waterways Experiment Station ; A-78-2, Report 2, Volume 7)
Cover title.
"November 1981."
"Prepared for U.S. Army Engineer District, Jacksonville and Office, Chief of Engineers, U.S. Army under Contract No. DACW39-76-C-0019."

Ewel, Katherine C.
Large-scale operations management test of use : ... 1981.
(Card 2)

"Monitored by Environmental Laboratory, U.S. Army Engineer Waterways Experiment Station."
Bibliography: p. 48-60.

1. Aquatic weeds. 2. Lake Conway (Fla.) 3. Fishes. 4. Mathematical models. I. Fontaine, Thomas D., III. II. University of Florida. School of Forest Resources and Conservation. III. United States. Army. Corps of Engineers. Jacksonville District. IV. United States. Army. Corps of Engineers. Office of the Chief of Engineers. V. U.S. Army Engineer Waterways Experiment Station. Environmental Laboratory. VI. Title VII. Series: Technical report (U.S. Army Engineer Waterways Experiment Station) ; A-78-2, Report 2, Volume 7.
TA7.W34 no.A-78-2 Report 2 Volume 7

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