
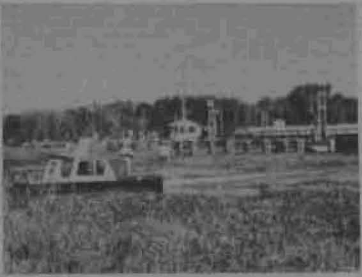

TECHNICAL REPORT A-78-2

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

Report 1

BASELINE STUDIES

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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Report 1 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

REPORT DOCUMENTATION PAGE

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A model has been formulated which, when completed, will represent the main components and interactions believed to be important in the ecosystem of Lake Conway and other southeastern lakes as well. Information from both field work and literature surveys was used in formulating the model. The model as currently formulated requires better definition of nutrient-productivity relationships and of zooplankton population dynamics. Given simulated introduction of

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20. ABSTRACT (Continued).

white amur, the model predicts decreases in phytoplankton, zooplankton, and herbivorous fish and increases in epipelic algae (i.e. that living upon the sediment), benthic invertebrates, and secondary predator fish, all for a 10-year period. The model also predicts a decrease in the quantity of sediments, which suggests a possible reversal of trend in the trophic state of the lake. However, these results may change with further refinement of the model.

SUMMARY

A model has been formulated which, when completed, will represent the main components and interactions that are believed to be important in the ecosystem of Lake Conway and other southeastern lakes as well. The model includes phytoplankton, epipelic algae (i.e. that living upon the sediment), and macrophytic plants with their associated epiphytic algae, as well as zooplankton, benthic invertebrates, herbivorous fish, young and adult primary predator fish, and secondary predator fish. In the model, the lake is divided into epilimnion and hypolimnion, and the sediments comprise a third physical unit.

Information from both field work and literature surveys was used in formulating the model. Productivity studies on the lake provided an estimate of gross primary productivity of 898 g C/m^2 per year, and community respiration was nearly equal to it. Changes in biomass of components were used that were reported by other researchers. Temperature measurements made during the study year were used in modeling the feeding and respiration functions of various components. Shading effects of the phytoplankton and macrophytic plants on each other and on epipelic algae were taken into account in programming seasonal changes in photosynthesis. Macrophytic plants were assumed to obtain nutrients from the sediments and to release nutrients into the surrounding water at a rate proportional to their rate of respiration. The model as currently formulated requires better definition of nutrient-productivity relationships and of zooplankton population dynamics.

Given simulated introduction of white amur, the model predicts decreases in phytoplankton, zooplankton, and herbivorous fish and increases in epipelic algae, benthic invertebrates, and secondary predator fish, all for a 10-year period. The model also predicts a decrease in the quantity of sediments, which suggests a possible reversal of trend in the trophic state of the lake. However, these results may change with further refinement of the model.

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.

This is the seventh of eight volumes that constitute the first of a series of reports documenting a large-scale operations management test of use of the white amur for control of problem aquatic plants in Lake Conway, Fla. Report 1 presents the results of the baseline studies of Lake Conway; subsequent reports will present the annual poststocking results.

The work was performed and this volume was written by Dr. Katherine C. Ewel and Mr. Thomas D. Fontaine of the School of Forest Resources and Conservation of the University of Florida. Mr. Ronald L. Myers and Mr. James Sampson assisted at several stages of the project. Mr. Glenn Smerage and Dr. Jerome Shireman made useful comments on an earlier version of the model, and Dr. H. T. Odom made several helpful suggestions on model development and productivity data interpretation. The Shenandoah Park Residents' Association at Lake Conway generously allowed the authors use of their dock and launching ramp for the productivity study.

The work was monitored at WES in the Mobility and Environmental Systems Laboratory (MESL) under the general supervision of Mr. W. G. Shockley, Chief of MESL, and Mr. B. O. Benn, Chief of the Environmental Systems Division, and under the direct supervision of Mr. J. L. Decell, Chief of the Aquatic Plant Research Branch (APRB). The APRB is now part of the recently organized Environmental Laboratory of which Dr. John Harrison is Chief.

Director of WES during the period of the contract was COL J. L. Cannon, CE. Technical Director was Mr. F. R. Brown.

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PART I: INTRODUCTION

Background

1. The U. S. Army Corps of Engineers is currently conducting a large-scale field test of the ability of the white amur (*Ctenopharyngodon idella*) to control excessive growths of hydrilla (*Hydrilla verticillata*) in Lake Conway, near Orlando, Fla. Lake Conway comprises a chain of five bodies of water and has a surface area of 7.6 km^2 (Figure 1). Maximum depth varies from 8 to 12 m among the five pools,* but the mean depth of all pools is approximately 5 m. As a result of the lake's lobed morphology, it has 2.6 times the shoreline that it would have if it were circular but had the same area. Because of this, it has considerable potential for littoral zone plant proliferation. Since the lakeshore has been developed for residential use, however, only small areas of emergent macrophytes still remain. Nevertheless, submersed plants are common in depths of up to 4 m. Considerable stands of pondweed (*Potamogeton illinoensis*) are found in shallow areas, and mats of hydrilla have covered large areas of open water in the past. During the study year, 1976-1977, *Nitella megacarpa* was the main submerged aquatic plant found in Lake Conway.

Scope

2. This report describes the development and summarizes the

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* E. Blancher, personal communications.

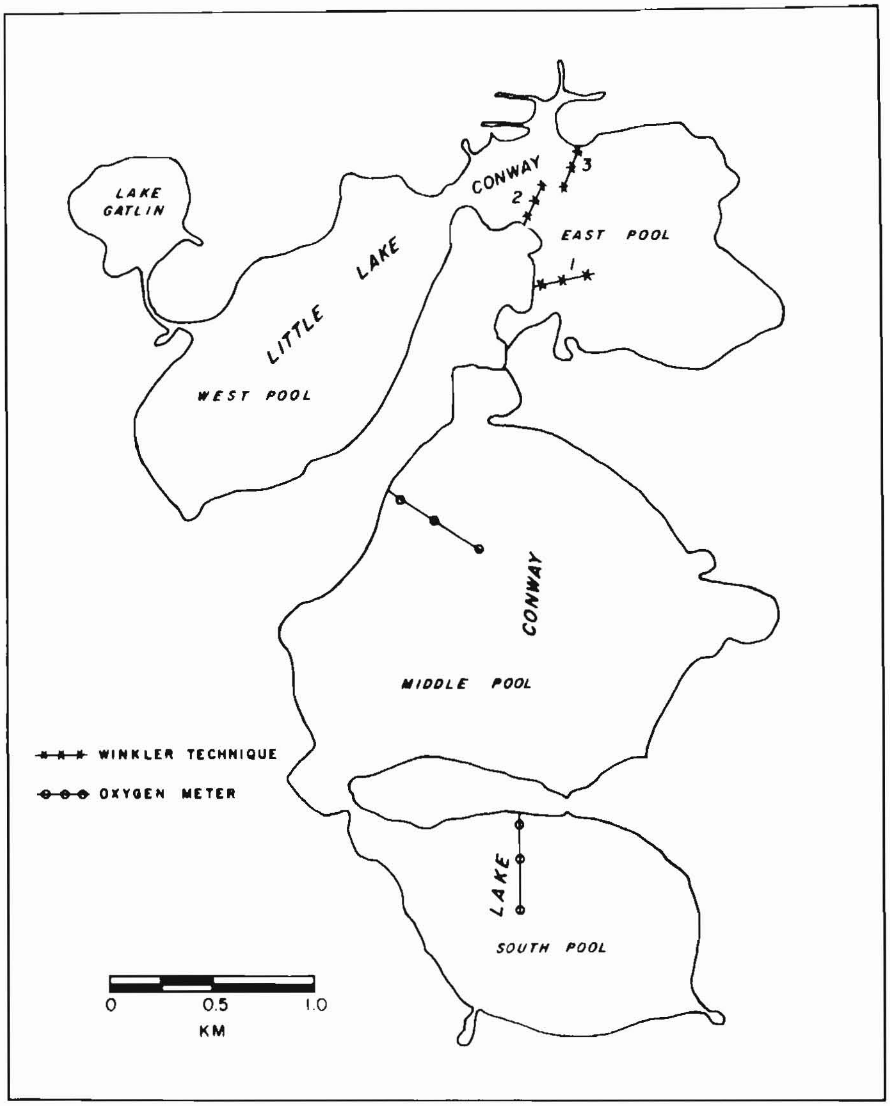


Figure 1. Map of Lake Conway, Fla., showing locations of transects used for productivity measurements

content of a mathematical model that has been formulated in order to predict the long-term effects of introduction of the white amur not only on the population of hydrilla but on the entire Lake Conway ecosystem as well. In addition to the modeling effort, community and planktonic metabolism data were collected on Lake Conway for 1 year, 1976-1977. These data indicate the relative importance of different producer populations in the lake. Data on levels of producer and consumer populations as well as water chemistry, which were collected by researchers working on other segments of the baseline studies, are included in the model.

PART II: METABOLISM MEASUREMENTS

Methods

Temperature and dissolved oxygen

3. Measurements of temperature and dissolved oxygen were made monthly at three stations on each of three transects in the East Pool of Little Lake Conway (Figure 1). The three transects are each about 100 m long and extend from shorelines having different degrees of development. Transect 1 extends from a forested area but runs parallel to a residential shoreline. Transect 2, located near the joining of the two pools comprising Little Lake Conway, is influenced primarily by a forested shoreline and cattail marsh. Transect 3, which is most heavily influenced by urban development, is across the lake from Transect 2. It starts at a lawn and is underlain by sand for part of its length.

4. The three stations at each transect were characterized by different vegetational communities. Pondweed and eelgrass (*Vallisneria americana*) were found at the most shallow stations (2 m); hydrilla and nitella were characteristic of the medium-depth stations (4 m); and phytoplankton were dominant at the pelagic, deepwater stations (6 to 8 m).

5. Water samples for dissolved oxygen determination were collected with a Van Dorn bottle and analyzed by the Winkler method. Samples were taken at the surface, at 0.5 m, from 1 to 6 m at 1-m intervals at the two deepest stations, and at 0.5-m intervals at the marsh. Samples were collected as close to dawn and dusk as possible, with an additional sample in the middle of the night and from one to five additional daytime samples.

6. Light and dark bottles were also incubated each month in the photic zone at each station on one of the transects in order to differentiate between planktonic and macrophytic contributions to the production and respiration rates of the entire community. Incubation time was generally from 4 to 6 hours during the day.

7. On three occasions, under conditions ranging from smooth to

choppy water, measurements of the rate of diffusion of oxygen from the water to the air were made. A plastic diffusion dome painted gray (to stop internal heat buildup) was used. The internal volume of the dome was 5.7 ℓ and the surface area was 0.1225 m^2. The dome was purged with nitrogen gas until an oxygen probe inside the dome (previously calibrated to 100 percent saturation in the air) registered zero percent saturation. The rate of change of percent oxygen saturation was then monitored.

8. In addition to the three transects described above, two other transects were established--one in each of the other two large pools of Lake Conway (Figure 1). Dissolved oxygen was measured with an oxygen meter at stations along these transects. Results after several months indicated that the differences between these stations and the ones in the East Pool were not significant enough to warrant continuing these additional measurements.

Calculations of diurnal curves

9. To calculate productivity on an areal basis from the dissolved oxygen measurements, it was necessary to assess dissolved oxygen changes in 1-m-deep layers of water. Dissolved oxygen levels at the surface, at 0.5 m, and at 1 m were averaged to obtain a representative value for the first metre-deep layer. Measurements at 1 and 2 m were then averaged to obtain a value for the second layer, and so on.

10. An example of a diurnal oxygen curve is given for Station 1B in Figure 2. In this case, the oxygen concentration in the water column reached its highest value approximately 2 hours before sundown and then declined to its lowest value at dawn. Surface temperature and percent oxygen saturation are also plotted so that diffusion of oxygen into and out of the water can be calculated. Diffusion was negligible in all cases. The rate of oxygen change in the water column is shown in the lower part of the figure. The area under the segment of the rate curve which is bounded by the solar insolation curve (dashed line) represents daytime net photosynthesis. The area under the other rate curve represents nighttime respiration. All values above the zero line indicate

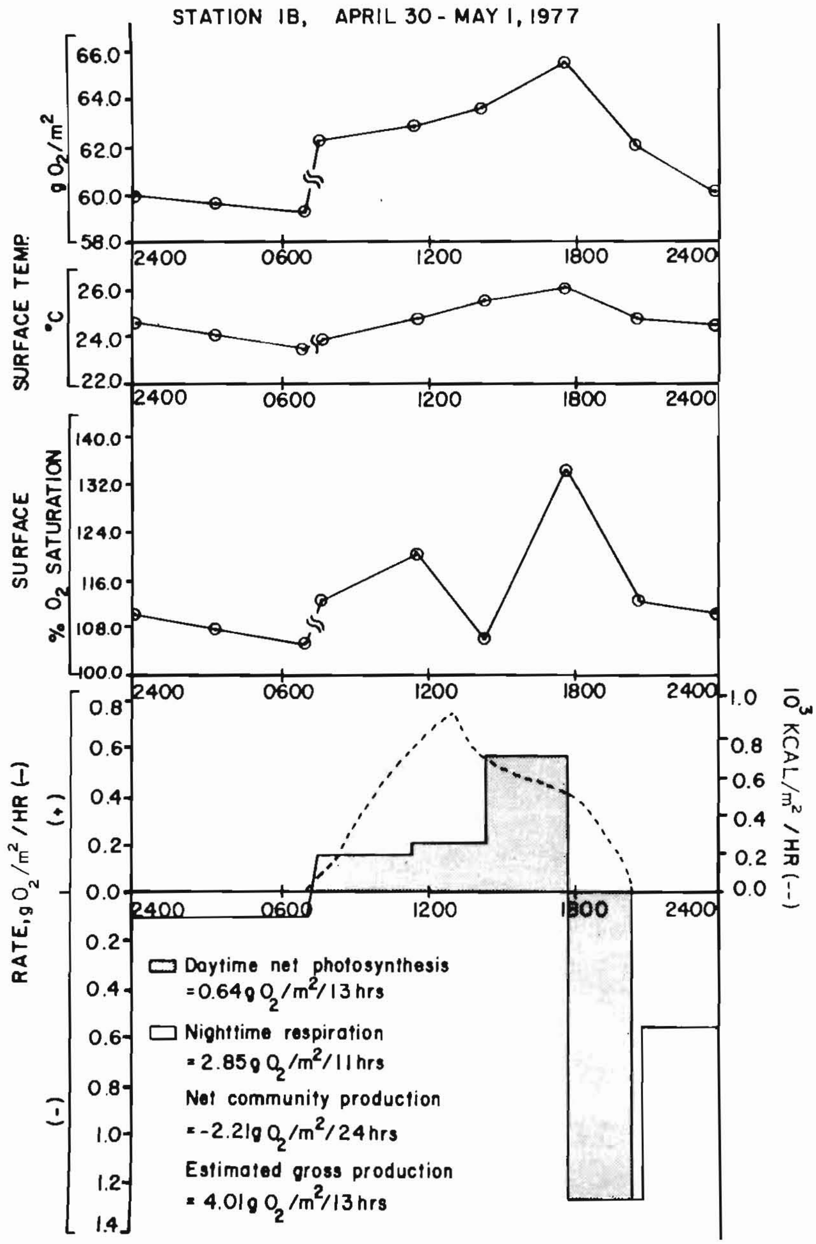


Figure 2. Sample set of curves calculated from measurements of diurnal changes in oxygen concentration

a net production of oxygen; values below the line indicate that utilization of oxygen was greater than production.

11. The following formula was used to estimate gross primary productivity:

$$\text{gross primary productivity} = \text{daytime net photosynthesis} + \left(\text{night respiration} \times \frac{\text{daylight hours}}{\text{nighttime hours}}\right)$$

12. Wetzel[1] indicates that the relationship between day and night respiration has not been evaluated satisfactorily and that current methods of estimating photosynthesis, or gross primary productivity, at best allow only general comparisons to be made.

13. The amount of carbon fixed was determined by assuming a ratio of 2.67 to 1 for oxygen to carbon produced. Light and dark bottles provided estimates of planktonic productivity and respiration in the photic zone at each station. These values were subtracted from the values obtained in the diurnal measurements to estimate productivity of the macrophyte-epiphyte complex and respiration of macrophytes, epiphytes, and benthos. During the study year, Nitella was the major species of macrophyte in the lake. Since this macroalga does not have a vascular system, the use of diurnal dissolved oxygen measurements for estimating its productivity is valid. Hartman and Brown[2] have pointed out that vascular plants store much of the oxygen they produce within their lacunar system, preventing detection by the diurnal technique.

Results

14. The annual metabolic pattern shown in Figure 3 for an average square metre of lake surface includes three peaks of gross production: spring, fall, and midwinter. The peaks of community respiration followed the same general pattern, but rarely did the rates of gross production and respiration equal each other. Net community production (calculated by subtracting community respiration from gross production) was positive during the spring and late summer but was negative at all other times. Greatest accumulation of organic matter occurred in the late summer, coinciding with the large pulse of gross primary productivity at that time. A major midsummer decline in gross primary productivity as well as in respiration also occurred.

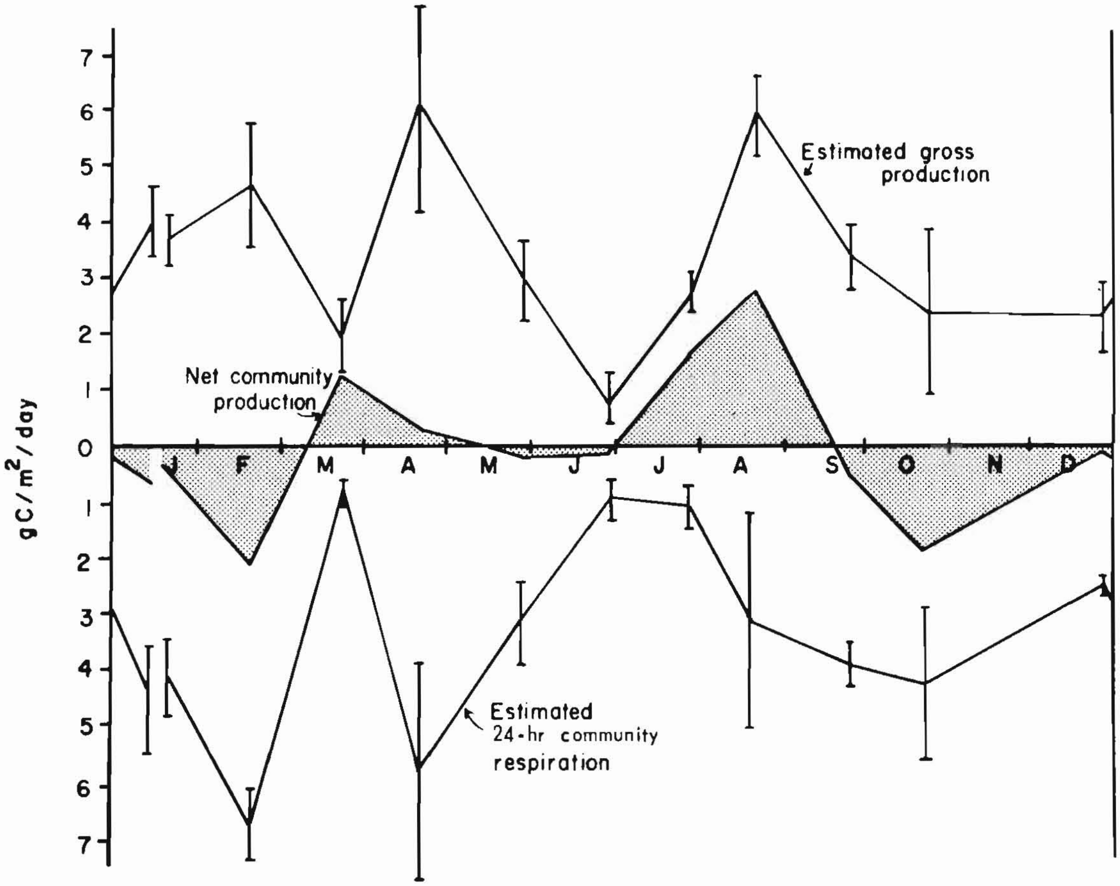
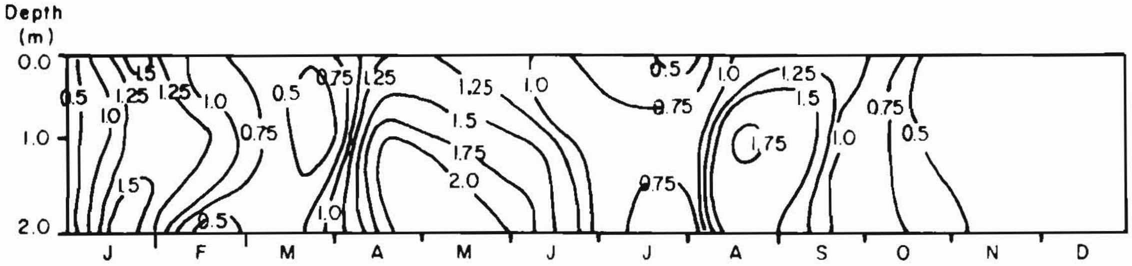


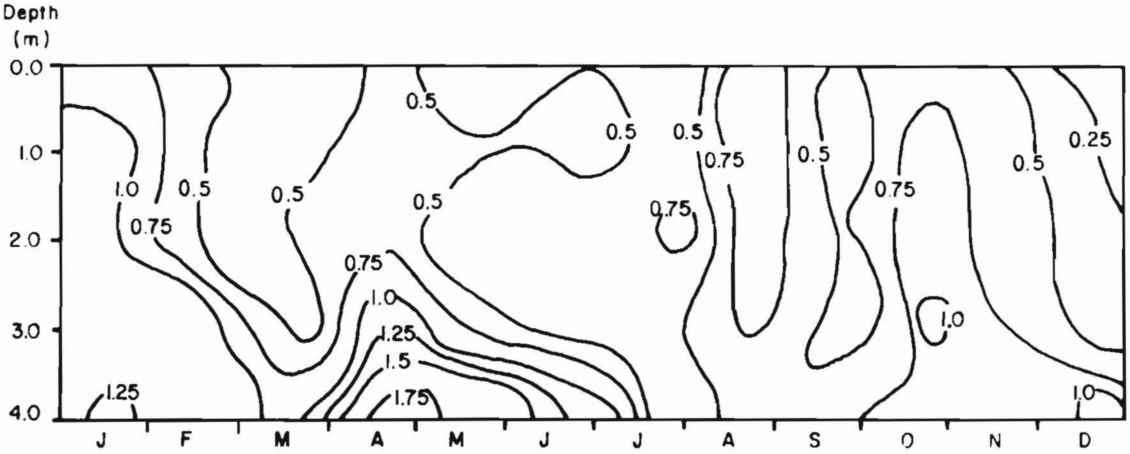
Figure 3. Annual pattern of production and respiration calculated for Lake Conway. (Measurements were made monthly at nine stations. Vertical bars represent standard errors of the mean)

15. The distribution of gross productivity for different depths and times is shown in Figure 4. At the shallow stations (Figure 4a), peaks of gross productivity occurred in the spring and late summer. The larger peak was in the spring and lasted nearly twice as long as the late summer peak. The maximum spring value of gross productivity at the shallow depths was slightly greater than 2.0 g C/m^2 per day.

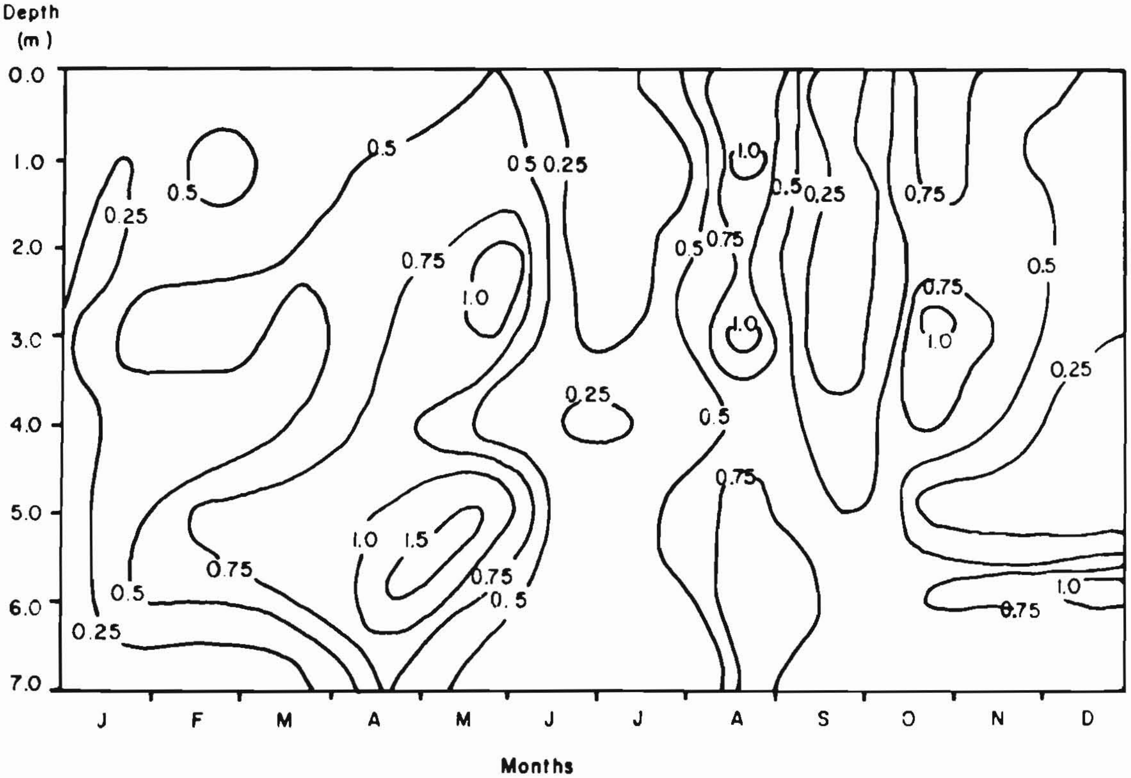
16. At the medium-depth stations (Figure 4b), a spring peak of productivity occurred, but there was no late summer peak. Highest productivity at these stations occurred near the bottom, and maximum values were slightly greater than 1.75 g C/m^2 per day. The duration of the spring productivity pulse was about the same as that for the shallow stations.



a. Shallow stations



b. Medium-depth stations



c. Deep stations

Figure 4. Changes in distribution of productivity ($g\ C/m^2$ per day) with depth

17. The deep stations also showed a spring pulse of productivity near the bottom, but it was smaller in magnitude and shorter in duration than the others (Figure 4c). Values of 1.0 g C/m^2 per day were observed several times throughout the year at depths of 1 and 3 m.

18. Comparison of the annual metabolic rates of the three community types shows that, on an areal basis, the pelagic zone had the highest gross productivity and the Vallisneria-Potamogeton (shallow) zone had the lowest (Figure 5). Communities in both of these zones exhibited positive net community respiration in excess of gross production. The weighted mean metabolic rates for the entire lake show a nearly perfect balance between gross production and community respiration. The gross productivity value of 898 g C/m^2 per year is in the eutrophic range as classified by Wetzel.[1]

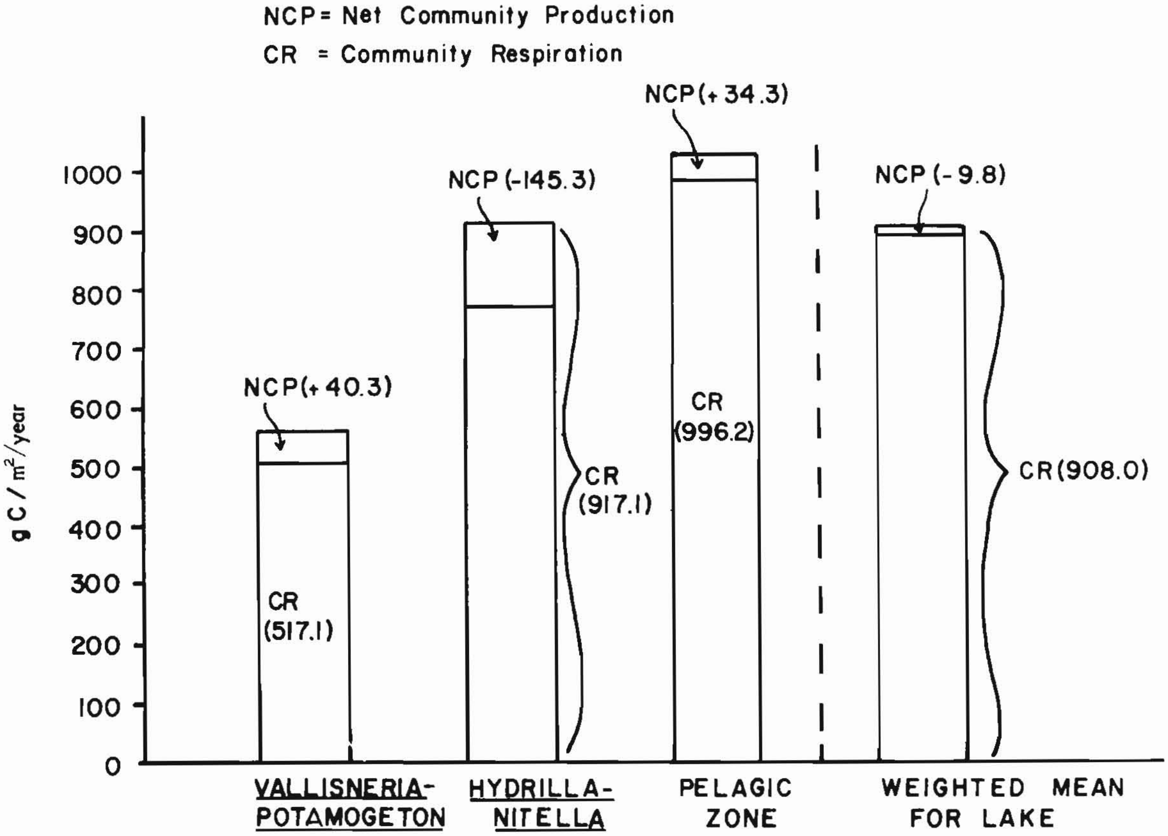


Figure 5. Total productivity and respiration for shallow, medium-depth, and deep zones in Lake Conway and weighted mean for entire lake

19. If the areal metabolism values are divided by their respective depths, an estimate of the metabolism for an average cubic metre in the water column is obtained (Figure 6). It is now clear that productivity on a volumetric basis was highest in the shallow zone and lowest in the pelagic zone.

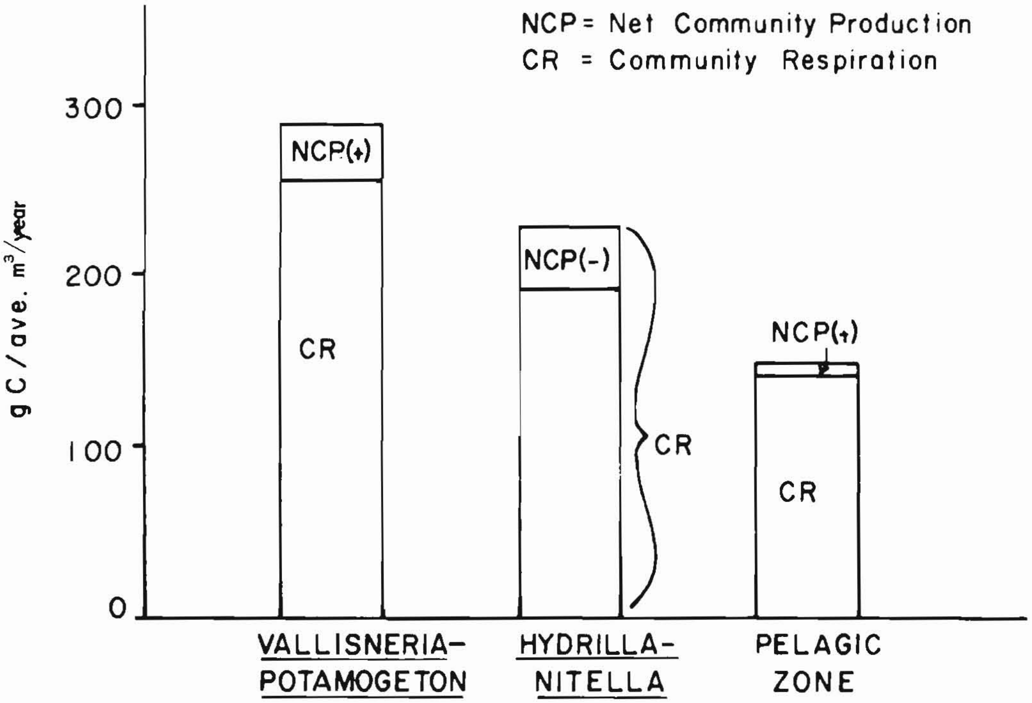
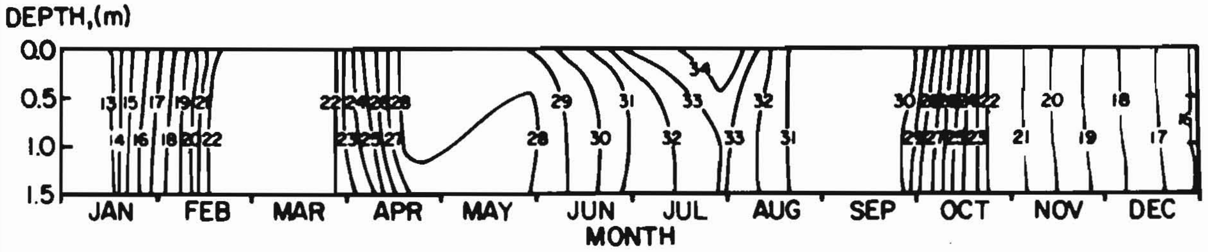


Figure 6. Productivity and respiration per cubic metre for shallow, medium-depth, and deep zones in Lake Conway

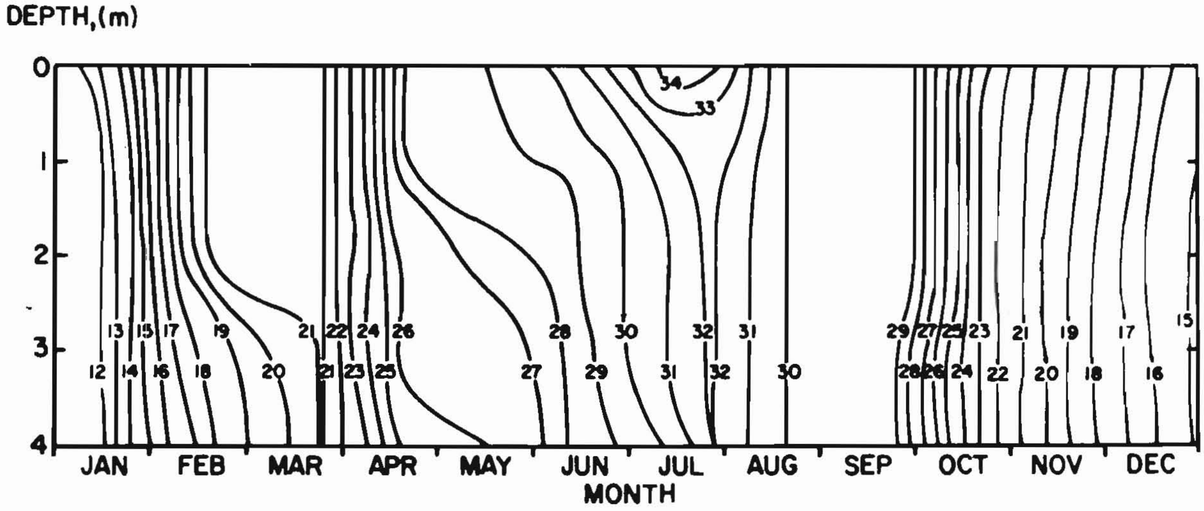
20. Temperature measurements during 1976 showed that deeper areas of the lake exhibited a moderately strong stratification which began in late April and lasted until late September (Figure 7). A much shorter stratification period began in mid-February and lasted until late March. Coinciding with the longer period of stratification was depletion of dissolved oxygen in hypolimnetic waters at three sites which were deeper than 6.5 m. This anoxic period lasted from late March to late August.

Discussion

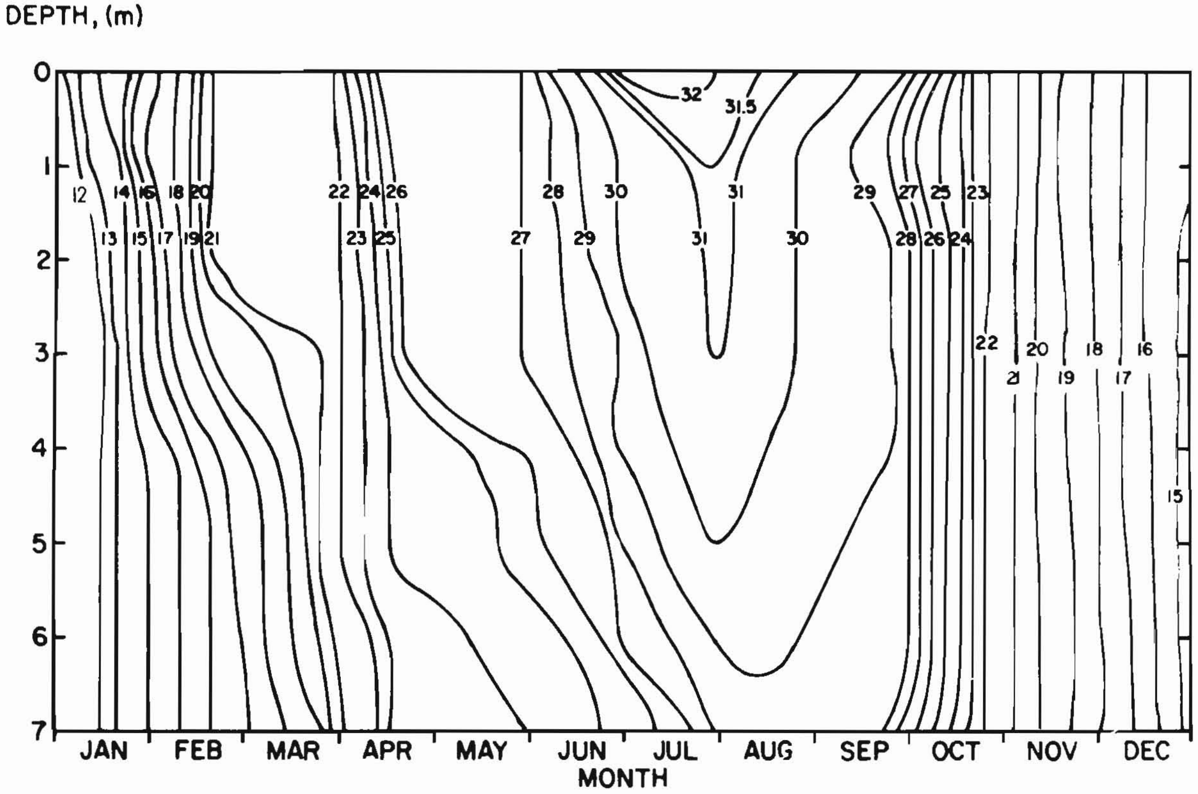
21. Many factors may be interacting to produce peaks and troughs



a. Shallow stations



b. Medium-depth stations



c. Deep stations

Figure 7. Changes in temperature (°C) over time and depth

of productivity and respiration. The pattern of solar radiation on Lake Conway is shown in Figure 8. A notable feature in this pattern is the midsummer dip in sunlight caused by the daily accumulation of thunderheads which bring late afternoon rains. Estimated inputs of total phosphorus from rainfall and runoff are shown in Figure 9. Inputs were highest in September, when 20 percent of the year's rainfall occurred, and lowest in October and November, when only 3 percent occurred.

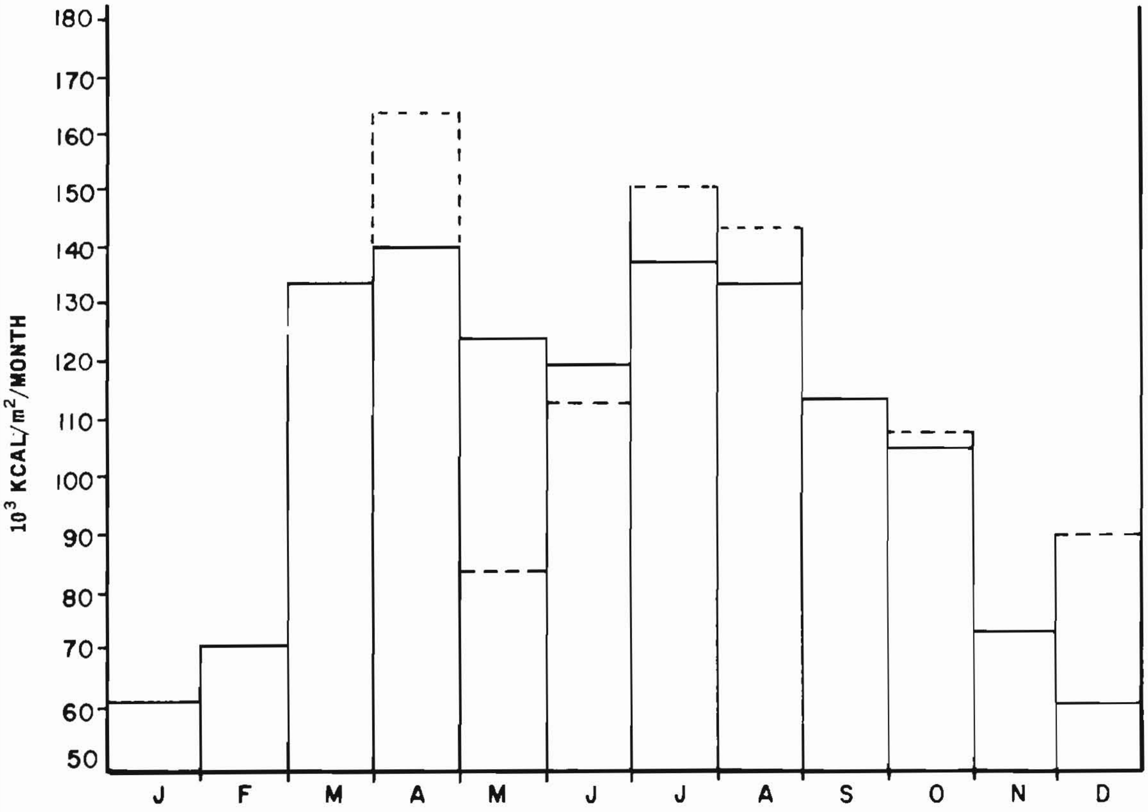


Figure 8. Solar radiation of Lake Conway. Solid lines represent monthly averages, and dashed lines represent what the monthly averages would have been had the values on the days that measurements were made been typical. (Data provided by P. Nawrocki, Florida Solar Energy Center)

22. The midwinter peaks of gross productivity and respiration do not appear to be related to any one variable. However, minimum shading by vascular plants and lack of sufficient sunlight to cause photoinhibition near the surface may have brought about the evenly distributed, moderate pulse of phytoplankton productivity seen at this time. Cold

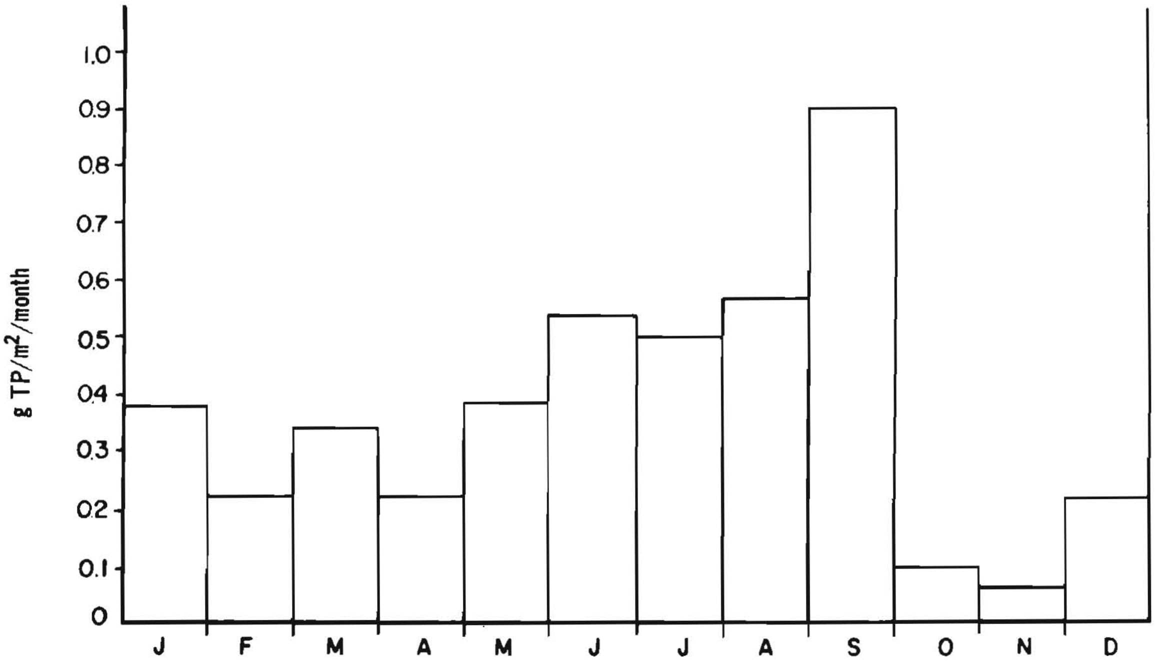


Figure 9. Estimated inputs of total phosphorus to Lake Conway. (See Table 6 for assumptions)

water temperatures in February probably prevented higher levels of productivity and respiration from developing.

23. The trough which follows this midwinter peak may have been a result of the temperature distribution at that time. As the lake became slightly stratified, nutrients in the photic zone may have been depleted. It is also possible that photoinhibition of phytoplankton may have occurred as the levels of solar radiation doubled over those of the previous month.

24. The spring peak was probably due to increased levels of light as well as isothermal conditions. As shown previously, gross productivity was higher near the bottom for all depths in the lake. This suggests that the major portion of the productivity is due to vascular plants and associated epiphytic algae, especially since the vascular plants had not grown to the surface at any station.

25. The midsummer decline in the lake's metabolism was probably due to epilimnetic nutrient depletion resulting from an absence of free mixing in the water column. The slight drop in sunlight intensity

during this period may also have contributed to the depressed metabolism. It should be noted that, since the hypolimnetic waters were anoxic during this period, the diurnal oxygen technique, which measures only changes in oxygen, would tend to underestimate the actual respiration. This problem is compensated for later on, however, as the by-products of anaerobic metabolism exert a chemical and biological oxygen demand as the oxygen is replenished to the hypolimnion during late summer turnover. Therefore, part of the community respiration values seen after late summer turnover may represent a metabolic time lag.

26. The late summer peak of productivity can also be related to the turnover at this time when limiting nutrients such as phosphorus that accumulate in the anaerobic hypolimnion are freely mixed within the water column. The depths for which productivity peaks were found during this time suggest that the phytoplankton were responsible for the majority of the productivity.

27. A comparison of the average metabolic rates of Lake Conway with those of other lakes of varying latitude shows no clear trend (Table 1). Lake morphology, age, and basin characteristics are of sufficient importance to prevent the expression of a simple latitudinal cline.

PART III: THE LAKE CONWAY ECOSYSTEM MODEL

28. The Lake Conway model presented in this report is based on three major sources of information: (a) productivity rates, respiration rates, and relationships among submersed plants summarized earlier in this report; (b) data collected by other researchers participating in the Lake Conway baseline studies; and (c) estimates and assumptions obtained from an extensive literature search. Two simulations of the ecosystem are presented. The first is a simulation of Lake Conway under "undisturbed" conditions, analyzing conditions that were measured in the lake during the study year 1976-1977 with respect to the variation seen in a 10-year simulation. The second is a simulation which predicts the effect of the addition of white amur on the ecosystem of the lake over a 10-year period. The model itself is nonlinear and has been programmed in CSMP (Continuous System Modeling Program), a language which permits the solution of difference equations on a digital computer. The program is listed in Appendix A.

Data and Assumptions Used in the Model

Plant populations in Lake Conway

29. Three major plant components are included in the model: phytoplankton, epipelic algae (i.e. that living upon the sediment), and a component which includes both submersed macrophytes and their attached epiphytic algae. Allen[6] has shown that dissolved organic matter released by mcarophytes can be utilized and transformed by epiphytic algal communities, which were responsible for over 20 percent of the total annual production in a northern lake. The macrophytes and their associated epiphytic algae therefore appear to act as a complex rather than separately and have been considered as such in the model.

30. All macrophytic plants are combined into one population unit in the model. Since productivity data were not obtainable for individual species, and, at present, only general morphological characteristics can be used to separate the species by function, it was felt that

separation by species in the model would be too arbitrary to be defensible. Moreover, several studies on the white amur suggest that feeding preferences of the fish will not lead to the exclusion of any species. Sills,[7] Michewicz, Sutton, and Blackburn,[8] and Fischer and Lyakhnovich,[9] in reviewing studies of feeding preferences, conclude that the diet of the white amur depends almost entirely on the habitat in which it is found and that it will eat virtually anything in the absence of preferred food. Prowse[10] points out that succulent plants with low fiber content are selected preferentially. During the study year at Lake Conway, *Nitella* was more abundant than *Hydrilla*. The white amur is known to readily eat *Chara*, a closely related macroalga.[11,12] This lack of specificity in the organism of interest to the study was further justification for not distinguishing between plants by species in the model.

31. Light availability for photosynthesis is an important part of the equations used for calculating gross primary productivity for plant populations. These equations focus on two important functions. First, they must determine the amount of photosynthetically active radiation which is available to the plant; second, they must predict the plant's photosynthetic response to that amount of light. Several authors have derived detailed photosynthesis equations describing still or mixed phytoplankton systems.[13-15] Few photosynthesis equations for systems containing both plankton and submersed vascular plants have been published. One such equation, in the model proposed by Titus et al.,[16] is unsatisfactory for use in this case because it assumes a constant height for the submersed vascular plant canopy. In Lake Conway, the canopy height changes seasonally and so, therefore, does the amount of light available to it.

32. To calculate the amount of light available to the vascular plants, the following expression is used:

$$L_{Q_2} = S \cdot (1 - R) \cdot \left[K_1 \cdot e^{-(K_2 Z' + K_3 Z' \cdot Q_1/Z)} \right]$$

where

S = solar radiation on a horizontal surface

R = decimal percentage of the solar radiation reflected

K_1, K_2 = constants in the light extinction equation for Lake Conway (which is

$$I_Z = I_0 \cdot K_1 \cdot e^{K_2 Z}$$

where

I_Z = radiation at depth Z

I_0 = net incident radiation)

Z' = distance from the water surface to the plant canopy. This varies as a function of cumulative plant biomass. The function was determined for harvests of two species of plants from several depths at five stations. The results are shown in Figure 10; data for Potamogeton are used in the model

$K_3 Z' \cdot Q_1/Z$ = empirical relationship which reduces the light available to the submersed plants by a function of the average amount of phytoplankton biomass per cubic metre Q_1/Z and the depth of the plant canopy Z'. At maximum phytoplankton levels, the light available for the vascular plants is reduced by half

33. The plant's photosynthetic response to the available light is determined by the plant's efficiency of light utilization at various light levels. The predictive efficiency term used for aquatic macrophytes is

$$\frac{E_{Q_2}}{1 + L_{Q_2}/L_{Q_{2-50}}}$$

where

E_{Q_2} = maximum efficiency for naturally occurring light conditions

L_{Q_2} = predicted amount of light available to the submersed plants

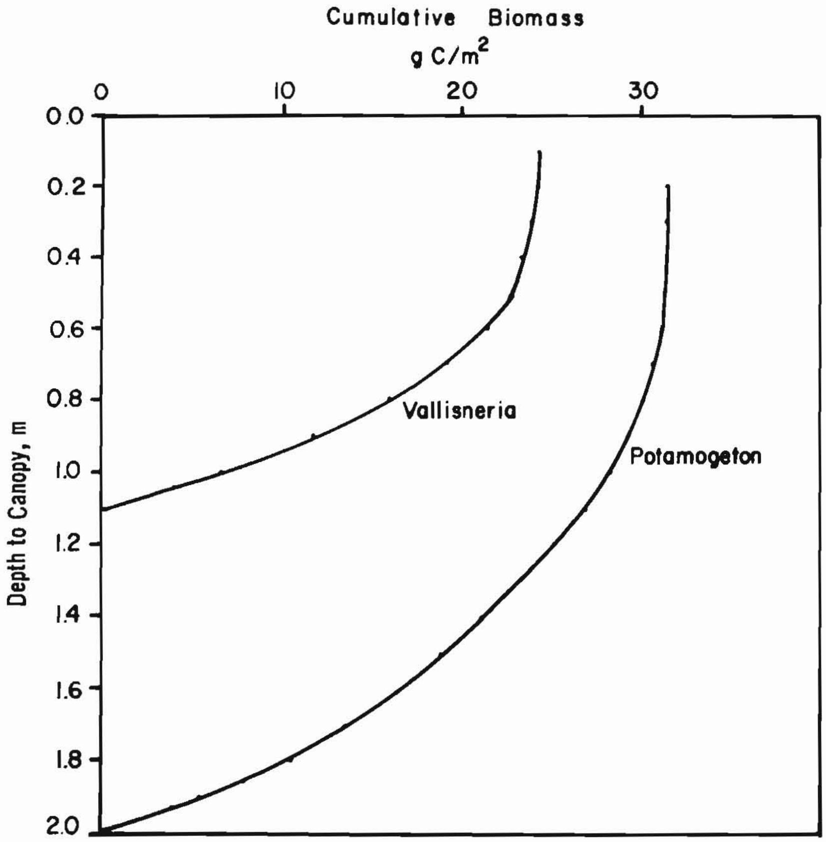


Figure 10. Cumulative biomass of two species of aquatic plants found at different depths

$L_{Q_{2-50}}$ = light level at which the plant is at half its maximum efficiency. The value for this in the model was calculated from photosynthesis and light data for four submersed plant species[17]

34. The efficiency term is multiplied by the available light to give production in kilocalories, which is converted to grams of carbon by a conversion factor of 9.3 kcal/g C.

35. The light available for phytoplankton is predicted by

$$L_{Q_1} = S \cdot (1 - R) \cdot \left(K_{12} \cdot e^{-K_{13}Q_1} \right) \cdot f_2 Q_2$$

where

K_{12} = constant

$e^{-K_{13}Q_1}$ = self-shading term which reduces the amount of available light by one half at maximum phytoplankton biomass levels

f_2Q_2 = function describing shading of phytoplankton by vascular plants. At maximum vascular plant levels, half of the light available to phytoplankton will be blocked

36. The photosynthetic response of phytoplankton is then determined by solving for the efficiency of light use with

$$\frac{E_{Q_1}}{1 + L_{Q_1}/L_{Q_{1-50}}}$$

and then multiplying by available light to give productivity in kilocalories and converting to grams of carbon by a factor of 9.3 kcal/g C. E_{Q_1} and $L_{Q_{1-50}}$ were calculated using data from Aruga.[18]

37. The amount of light available for epipelic algae is predicted using the expression

$$L_{Q_3} = S \cdot (1 - R) \cdot f_3Q_2 \cdot e^{-(K_2Z + K_7 \cdot Q_1)}$$

where

f_3Q_2 = function describing shading of epipelic algae by vascular plants

$e^{-(K_2Z + K_7 \cdot Q_1)}$ = light extinction according to the optical properties of the water as well as shading by phytoplankton

38. The predictive efficiency term for epipelic algae is

$$\frac{E_{Q_3}}{1 + L_{Q_3}/L_{Q_{3-50}}}$$

The same factor for conversion to grams of carbon is used.

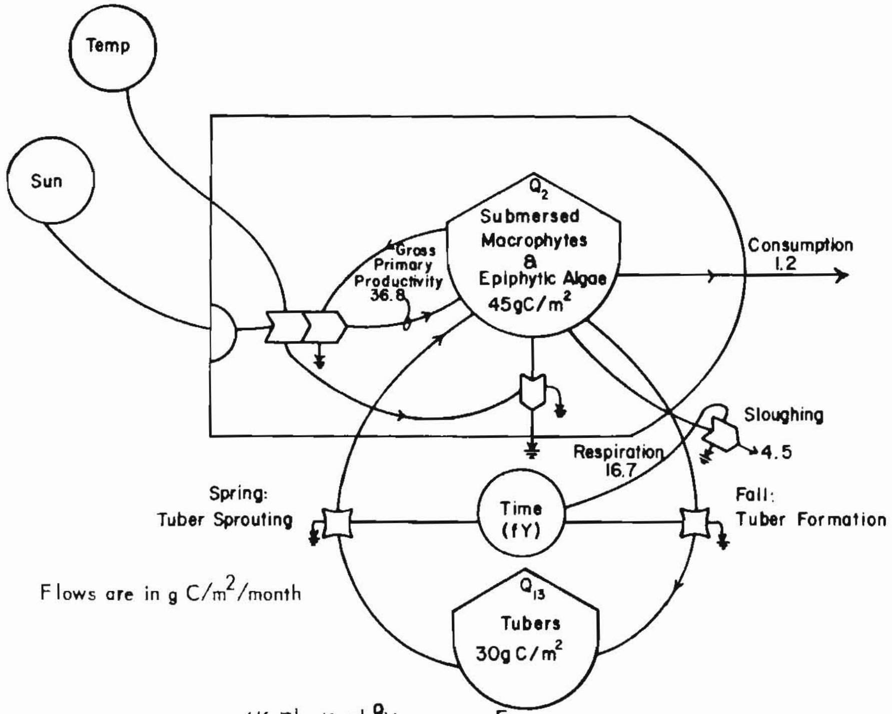
39. The average relationship between net photosynthesis and temperature in three species of aquatic vascular plants is shown in Table 2. The original values were converted to a relative scale in which the highest value for the three reference temperatures became one

and the other two values were fractions of that. Data summarized in Sculthorpe[20] suggest that Q_{10} (see paragraph 63) for respiration in aquatic macrophytes varies from 1.32 to 3.48, but data from Ikusima[21] suggest that Q_{10} for hydrilla may be at the lower end of the scale. Without sufficient data for all species of plants found in Lake Conway, a value of 1.4 was selected. The values calculated from this relationship were also normalized, and the normalized values are the ones listed in Table 2. In order to combine temperature relationships for net productivity and respiration into a factor that could be used to express temperature dependence of gross primary productivity, the relative values for net productivity and respiration were summed, and the resulting value for gross primary productivity was in turn converted to a relative scale (Table 2).

40. Temperature relationships for phytoplankton were taken from Wetzel's interpretation[1] of Aruga's data.[18] The same relationships were assumed to hold for epipelic algae.

41. The inputs and outputs to the macrophyte complex are outlined in Figure 11. Biomass data were collected by researchers from the Florida Department of Natural Resources. Dry weight values were converted to grams of carbon by assuming 0.40 g C per gram of dry weight.[20] Total biomass of submersed aquatic macrophytes was actually about 34 g C/m^2 in Lake Conway in January. Odum[22] estimated that 30 percent of the plant biomass in Silver Springs, Fla., was attributable to epiphytic algae; in the model, it is assumed that they represent 25 percent of the biomass of the complex. The biomass of the macrophyte-epiphyte component is therefore estimated to be 45 g C/m^2. Gross primary productivity values were obtained from the productivity study.

42. Nutrients were not considered to be limiting to this group of organisms since most of the macrophytes have root systems. Bristow and Whitcombe,[23] Schults and Malueg,[24] and Denny[25] have shown that uptake of phosphorus through the root system is an important process in many rooted submersed plants. Moreover, Nichols and Keeney[26] have shown that, although *Myriophyllum spicatum* L. can take up nitrogen through its



$$\mathring{Q}_2 = (K_{21}\cdot S\cdot(1-R)\cdot(K_1\cdot e^{-(K_2 Z^1 + K_3 Z^1\cdot\frac{Q_1}{Z})})\cdot Q_2\cdot\frac{E_{Q_2}}{1+L_{Q_2}/L_{Q_{2-50}}}\cdot T_{10}\cdot K_{27}\cdot Q_{11}) + fY\cdot K_{132}\cdot Q_{13} - K_{24}\cdot Q_2\cdot T_{11}$$

$$-(K_{25}\cdot Q_2 - fY\cdot K_{26}\cdot Q_2) - K_{131}\cdot Q_2\cdot fY - Q_2((K_{53}\cdot T_6\cdot Q_5) + (K_{64}\cdot T_1\cdot Q_6) + (K_{84}\cdot T_1\cdot Q_8))$$

$$\mathring{Q}_{13} = K_{131}\cdot Q_2\cdot \overline{fY} - fY\cdot K_{132}\cdot Q_{13}$$

Figure 11. Inputs and outputs affecting biomass of aquatic macrophytes and associated epiphytic algae. (Explanations of terms in equations are listed in Appendix B)

leaves, it can satisfy all its requirements through root uptake from sediment.

43. Wetzel[1] indicates that secretion of organic carbon by macrophytes may vary from 0.05 percent to over 100 percent of the photosynthate but that most values lie between 1 and 10 percent. However, he also points out that exchanges of inorganic and organic matter occur between macrophytes and their associated epiphytic algae. In the model, it is assumed that no organic carbon is leached into the surrounding water.

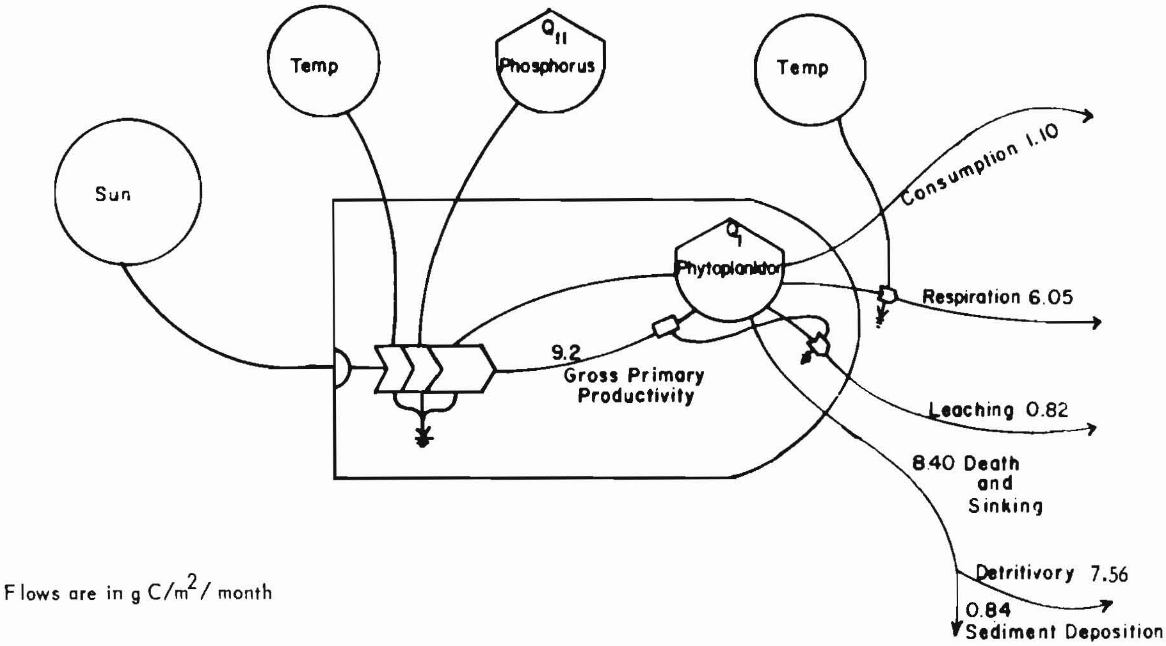
44. Herbivory is estimated to constitute only 5 percent of net primary productivity (8 percent is the maximum amount estimated by

Wetzel[1]) and much of this is presumed to be concentrated on the epiphytic algae. Thus, much of the biomass that appears as net primary productivity becomes dead organic matter, i.e., leaves and other plant parts that die in situ. In the model, 10 percent of the biomass each month is sloughed off as dead organic matter, and an additional pulse occurs in early September.

45. Several species of plants in Lake Conway, including hydrilla, form tubers. These are included as a separate state variable in Figure 11. In the model, these tubers are assumed to start forming in October and to begin germination in late April. Haller, Miller, and Garrard[27] have found that tubers of hydrilla form in the bottom sediment in the fall, winter, and early spring months and germinate in the late spring, summer, and early fall. Miller, Garrard, and Haller[28] report tuber biomass of more than 273 g/m^2 (fresh weight) in a reservoir in Florida or approximately 11 g C/m^2. A value of 30 g C/m^2 per month was chosen for the model to compensate for the presence of tubers of other species as well.

46. The phytoplankton component of the model is shown in Figure 12. Biomass of phytoplankton in January was calculated to be 0.84 g C/m^2 for Lake Conway. A team from the Orange County Pollution Control Department provided estimates of chlorophyll a, which were converted to carbon by assuming that 1 mg of chlorophyll a is equivalent to 50 mg of carbon. Gross primary productivity values were obtained from the productivity study.

47. Zooplankton and fish consume phytoplankton at 35 percent of net primary productivity. Wetzel et al.[29] found that up to 18 percent of gross primary productivity was released as organic carbon; the annual mean percentage was 7 percent. Several factors affect this release, but, in their study, rates seemed to be highest in early spring when productivity was increasing and in late summer when it began decreasing. A function is incorporated in the model to allow secretion of 18 percent of the photosynthate under intermediate gross primary productivity levels. This decreases gradually to 1 percent at higher and lower levels. Golterman[30] estimates that 20 percent of the total net

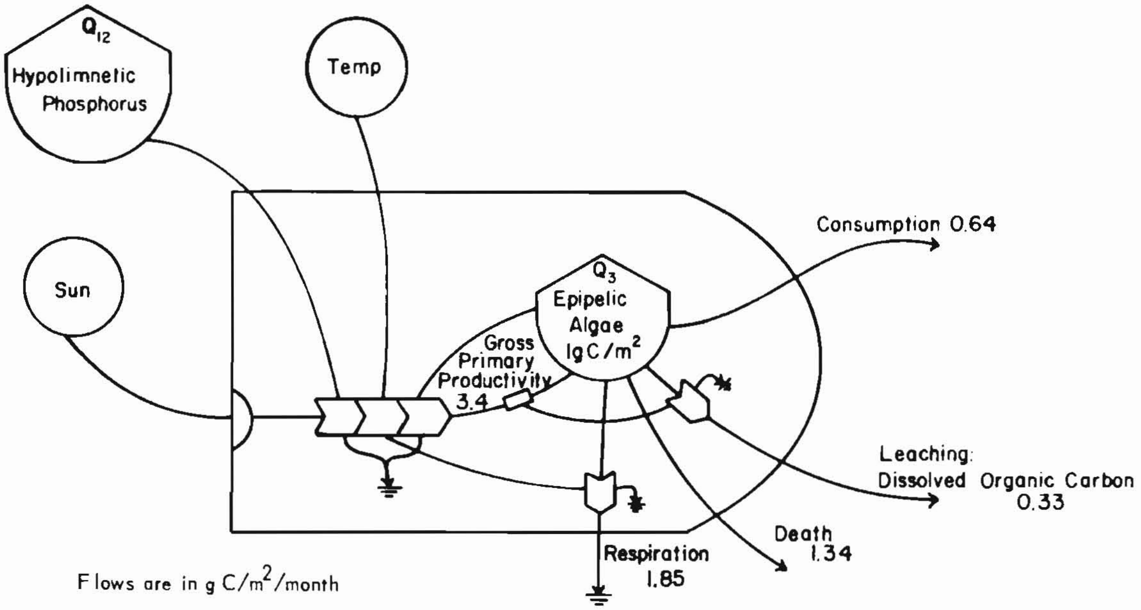


$$\mathring{Q}_1 = K_{11} \cdot S \cdot (1-R) \cdot K_{12} \cdot e^{-K_{13} \cdot Q_1} \cdot f_2 Q_2 \cdot \frac{K_{14}}{1+S \cdot (1-R) \cdot K_{12} \cdot e^{-K_{13} \cdot Q_1} \cdot f_2 Q_2 \cdot K_{15}} \cdot Q_{11} \cdot T_8 \cdot K_{27} \cdot Q_1 \cdot (1-fY)$$
$$-K_{17} \cdot T_9 \cdot Q_1 - Q_1 \cdot ((K_{63} \cdot Q_6 \cdot T_1) + (K_{43} \cdot Q_4 \cdot T_5) + (K_{83} \cdot Q_8 \cdot T_1)) - K_{18} \cdot Q_1$$

Figure 12. Inputs and outputs affecting biomass of phytoplankton. (Explanations of terms in equations are listed in Appendix B)

productivity may reach the sediment; sediment deposition accounts for 27 percent in the model.

48. Data on epipelic algae were not available for Lake Conway. However, observations during the study indicate that this is an important component of the community. The relationships that were derived for this component are shown in Figure 13. Hargrave[31] and Gruendling[32] reported gross primary productivity levels of 40 to 45 g C/m^2 per year for epipelic algae in Marion Lake, British Columbia. Gross primary productivity for January in Lake Conway was estimated to be 3.3 g C/m^2. The January standing crop was estimated to be 1.0 g C/m^2 based on an arbitrary turnover time of 10 days. Nutrient relationships for these algae are not clear, but they are assumed to depend on dissolved orthophosphate in the hypolimnion because of the depth at which they grow. Leaching of organic carbon was assumed to follow the relationship



$$\overset{\circ}{Q}_3 = (K_{31} \cdot S \cdot (1-R) \cdot e^{-(K_2 Z + K_7 \cdot Q_1)} \cdot f_3 Q_2 \cdot \frac{E_{Q_3}}{1 + L_{Q_3}/L_{Q_{3-50}}} \cdot Q_{12} \cdot T_8 \cdot K_{27} \cdot Q_3)(1-fY)$$

$$-K_{33} \cdot T_8 \cdot Q_3 - K_{34} \cdot Q_3 - Q_3 \cdot ((K_{42} \cdot T_5 \cdot Q_4) + (K_{62} \cdot T_1 \cdot Q_6) + (K_{75} \cdot T_1 \cdot Q_7) + (K_{82} \cdot T_1 \cdot Q_8))$$

Figure 13. Inputs and outputs affecting biomass of epipelic algae. (Explanations of terms in equations are listed in Appendix B)

described for phytoplankton. Consumption is 41 percent of net primary productivity.

Animal populations in Lake Conway

49. Dynamics of zooplankton, benthic invertebrates, and four divisions of fish (herbivorous, young and adult primary predator, and secondary predator fish) are included in the model. The rates of respiration, consumption, and predation of these organisms are temperature-dependent. These relationships are incorporated into the model by using terms reported by Patten, Egloff, and Richardson[33] for organisms in an Oklahoma reservoir. Although the effects of temperature on consumption and digestion are treated separately, the average of the two values is used in the model. The relationship for zooplankton is Q_{10} equals 1.25; the following terms are used for the other organisms:

Benthic invertebrates: $\frac{2}{1 + e^{-0.13(T-18)}}$

Fish: $\frac{2}{1 + e^{-0.19(T-18)}}$

50. The values calculated with these terms are normalized so that full activity predicted by a term in an equation occurs at the highest temperature. The fractions of full activity for a year's span are shown for zooplankton, benthic invertebrates, and fish in Figure 14. The temperatures used were recorded during the diurnal measurements in 1976-1977 and reflect the depths most commonly occupied by the organisms. Thus, benthic invertebrates are affected only by temperatures at the bottom of the lake, while the zooplankton and fish are affected by the

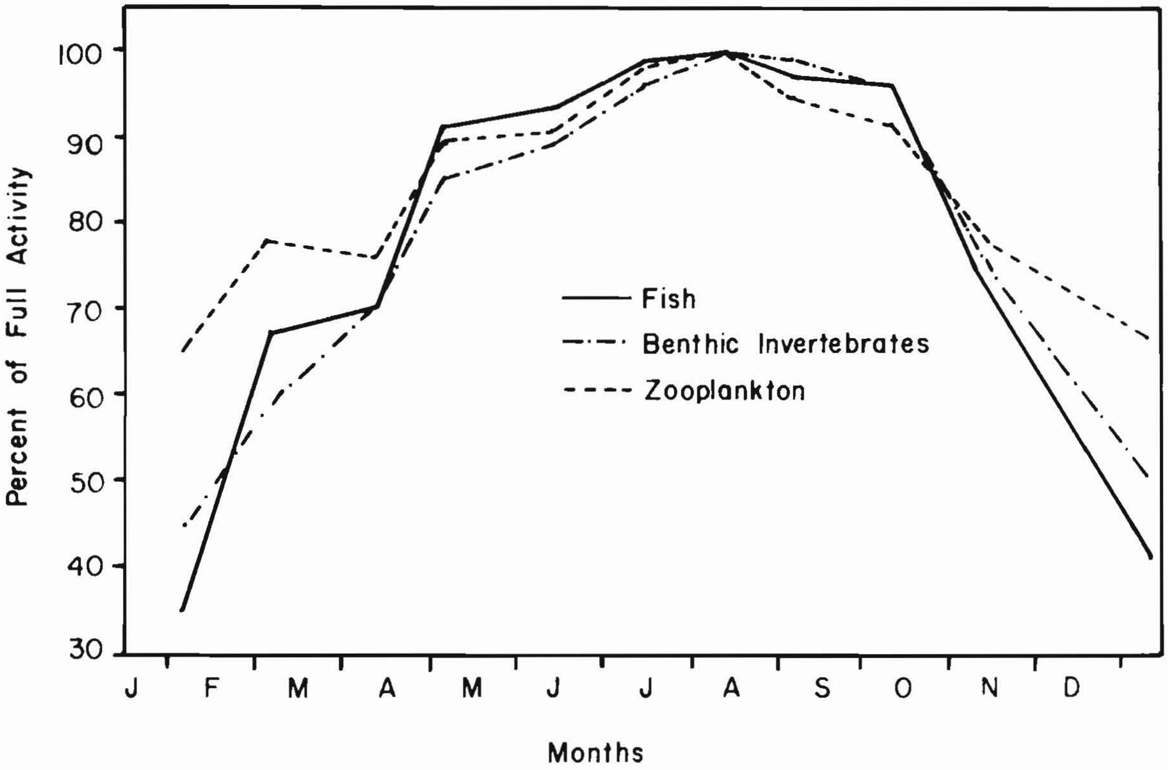
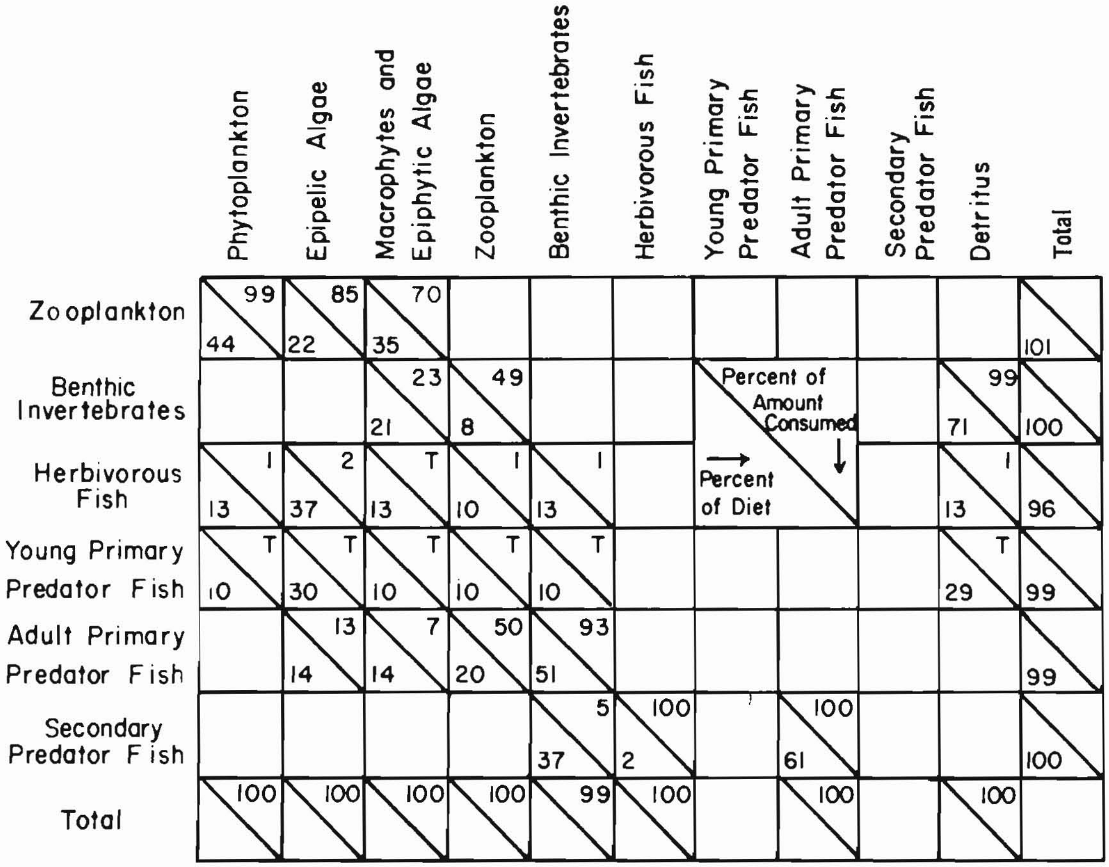


Figure 14. Annual variation in feeding and respiration rates of aquatic organisms. (Relationships used to calculate activity are given in text. Monthly temperatures used in these relationships were actual measurements from different depths at Lake Conway)

average temperature of the lake. In the model, the rates of predation of fish and benthic invertebrates are programmed as functions of temperature-dependent percentages of activity of both predators and prey. Zooplankton, for instance, might be at an advantage over both benthic invertebrates and fish in the late fall and early spring when they enjoy a higher percentage of their potential activity. Fish are dominant over the others in late spring through midsummer but are relatively less active by midfall.

51. The hypothesized feeding relationships in the Lake Conway ecosystem are shown in a matrix in Figure 15. Initial amounts were

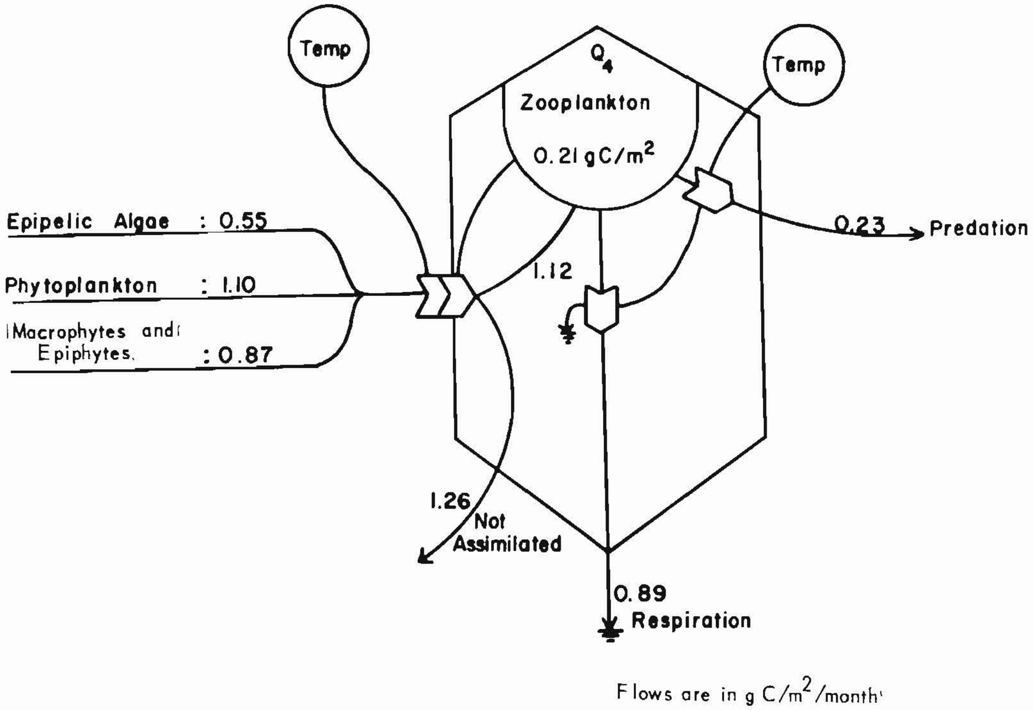


	Phytoplankton	Epipelic Algae	Macrophytes and Epiphytic Algae	Zooplankton	Benthic Invertebrates	Herbivorous Fish	Young Primary Predator Fish	Adult Primary Predator Fish	Secondary Predator Fish	Detritus	Total
Zooplankton	99 44	85 22	70 35								101
Benthic Invertebrates			23 21	49 8			Percent of Amount Consumed ↓ → Percent of Diet			99 71	100
Herbivorous Fish	1 13	2 37	T 13	1 10	1 13					1 13	96
Young Primary Predator Fish	T 10	T 30	T 10	T 10	T 10					T 29	99
Adult Primary Predator Fish		13 14	7 14	50 20	93 51						99
Secondary Predator Fish					5 37	100 2		100 61			100
Total	100	100	100	100	99	100		100		100	

Figure 15. Feeding relationships among plants, animals, and detritus in the Lake Conway ecosystem model. Numbers are percentages. The percent composition of an item listed along the top in the diet of an animal listed on the left side is given in the lower left half of each square; the percent of each item listed along the top that is consumed by the animal on the left is listed in the upper right half of each square

determined arbitrarily, and many of these were readjusted during the initial simulation of the ecosystem. The type of plant eaten most universally is of 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 secondary predator fish and is utilized most heavily by zooplankton and benthic invertebrates. These two organisms are the most universally grazed of the animals. The herbivorous fish have the widest food spectrum of any of the consumers, with a preference toward epipelic algae.

52. The zooplankton component of the model is shown in Figure 16. Biomass values for zooplankton were calculated by multiplying numbers of zooplankton per square metre by the dry weight of each individual as reported in Brezonik, Morgan, and Shannon.[34] Total dry weight for each



$$\overset{\circ}{Q}_4 = K_{41} \cdot Q_4 \cdot T_5 \; (K_{42} \cdot Q_3) + (K_{43} \cdot Q_1) + (K_{44} \cdot Q_2) - K_{45} \cdot Q_4 \cdot T_5 - Q_4 \cdot \; (K_{52} \cdot Q_5 \cdot T_3 \cdot T_6)$$
$$+ (K_{74} \cdot Q_7 \cdot T_1 \cdot T_4) + (K_{67} \cdot Q_6 \cdot T_1 \cdot T_4) + (K_{87} \cdot Q_8 \cdot T_1 \cdot T_4)$$

Figure 16. Inputs and outputs affecting biomass of zooplankton. (Explanations of terms in equations are given in Appendix B)

month's sample was then multiplied by 0.5 to convert the value to grams of carbon. Values for 1976-1977 varied from 0.15 to 0.44 g C/m^2 per month. This is lower than the value of 1.29 g C/m^2 reported by Nordlie to Grocki[35] for Newman's Lake in Alachua County, Fla. Annual variation in standing crop (expressed as a percentage of the maximum monthly standing crop) is shown in Figure 17.

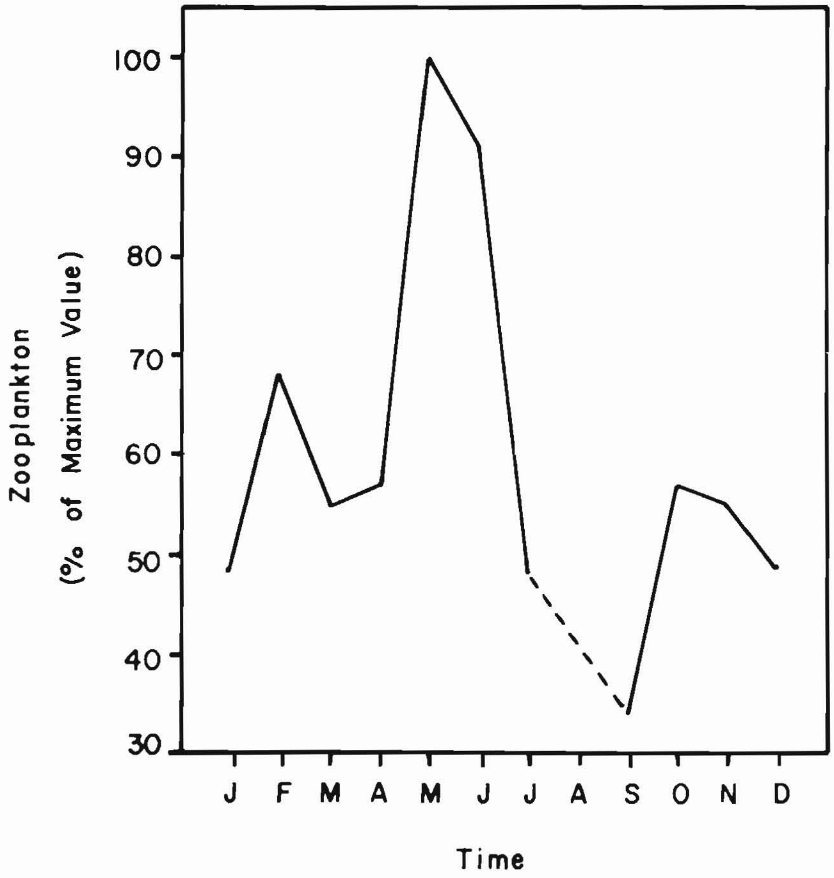


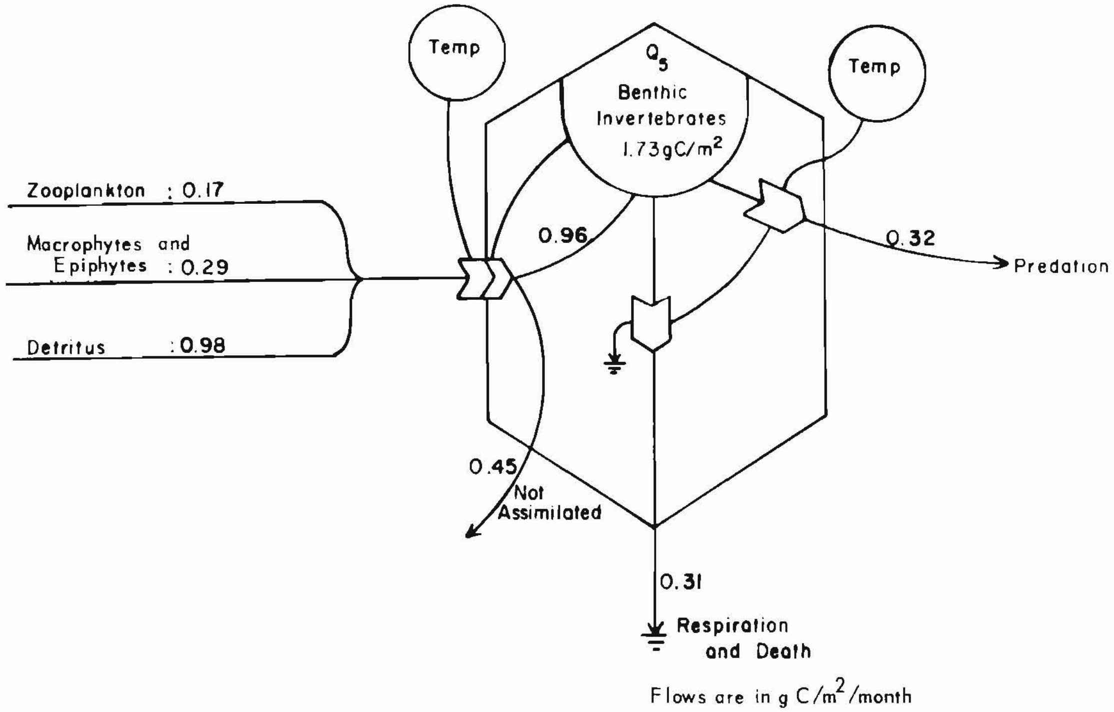
Figure 17. Relative variations in standing crop of zooplankton. (Values were calculated from data provided by a research team from the University of Florida's Department of Environmental Engineering Sciences. Possible trend of values within data gap are represented by the dashed line)

53. Several studies summarized by Wetzel[1] show that, in general, 10 to 75 percent of the energy ingested by zooplankton is assimilated. Gulati[36] estimated 36 percent efficiency for herbivorous zooplankton in Dutch lakes. Assimilation in the Lake Conway model is estimated to be

47 percent of ingestion. Gulati also estimated that respiration is 20 to 30 percent of the amount of energy ingested, although Wetzel listed values varying from 27 to 93 percent. McAllister[37] estimated that respiration is roughly 10 percent of the standing crop per day. If respiration is assumed to account for two thirds of the energy assimilated (or 31 percent of energy ingested), the respiration rate in the model is 12 percent of the standing crop per day. The general distribution of energy resources is therefore in agreement with those from these previous studies. Wetzel[1] summarized several zooplankton studies which showed turnover (net annual productivity divided by biomass) varying between 9 and 25 per year in eutrophic Polish lakes, with values of 14 and 15 per year for other studies. Turnover in the Lake Conway population, using the assumptions given and the January biomass estimate, is 21 per year, which is reasonable when climatic differences are taken into account.

54. The benthic invertebrate component of the model is shown in Figure 18. Four months of data (April, May, July, and September) were available for calculation of benthic invertebrate biomass. Biomass estimates summarized in Wetzel[1] from Junk[38] and Sapkarev and Tocko[39] were used to convert numbers of organisms to dry weights of sample. Dry weights were then converted to grams of carbon by multiplying by 0.5. Biomass varied from 1.35 to 2.27 g C/m^2. Grocki[35] estimated 1.45 g C/m^2 for Lake Kissimmee, while citing data from other authors which varied between 1.07 and 3.00 for different parts of the lake. Since no seasonal trends were apparent from the Lake Conway data (the lowest value was for September and the highest for April), an intermediate value of 1.73 g C/m^2 was selected to represent initial conditions in January.

55. In a review of feeding studies of aquatic insects, Cummins[40] stresses the heavy dependence of this group on detritus. Grocki[35] estimated, after reviewing several reports, that algae comprised 30 percent and detritus 70 percent of the diet of benthic invertebrates in Lake Kissimmee. It is assumed in the Lake Conway model that all the invertebrates are detrivorous except Chaoborus, which preys on zooplankton,[41] and snails, which graze the epiphytes on macrophytic plants.[42]



$$\dot{Q}_5 = K_{51} \cdot Q_5 \cdot T_6 \cdot (K_{52} \cdot Q_4 \cdot T_7) + (K_{53} \cdot Q_2) + (K_{54}) - K_{54} \cdot Q_5 \cdot T_6 - Q_5 \cdot (K_{66} \cdot Q_6 \cdot T_1 \cdot T_3)$$
$$+ (K_{72} \cdot Q_7 \cdot T_1 \cdot T_3) + (K_{86} \cdot Q_8 \cdot T_1 \cdot T_3) + (K_{95} \cdot Q_9 \cdot T_1 \cdot T_3 \cdot FQ_2)$$

Figure 18. Inputs and outputs affecting biomass of benthic invertebrates. (Explanations of terms in equations are given in Appendix B)

Proportions of the overall diet comparable to the biomass of these organisms are specified in the model. Detritus comprises 68 percent of the diet.

56. Ingestion rates summarized by Cummins[40] indicate that 2 to 23 percent of the body weight of aquatic insects is ingested per day. The rate used in the model is 2 percent. Assimilation efficiency is 69 percent, a value determined by Zimmerman, Wissing, and Rutter[43] for mayfly larvae.

57. Fish were collected by researchers from the Florida Game and Freshwater Fish Commission. Data from block net samples taken in Lake Conway in June were used in the model. The fish found in Lake Conway are listed in Tables 3-5. Assignment to trophic group (herbivore, primary predator, or secondary predator) was based on the information given

in these tables. Since young primary predator fish eat a substantially different diet from the adults, they are separated as another state variable and assumed to eat the same diet items as the herbivorous fish. Relative proportions of the diet items in each group were assigned before simulations, but many were changed during simulation.

58. Total fish biomass in Lake Conway is estimated to be 1.39 g C/m^2 by assuming 1 g C per 10 g of dry weight.[65] This biomass value is approximately half of what Patten, Egloff, and Richardson[33] estimated for an Oklahoma reservoir. However, Grocki[35] estimated only 16 g C/m^2 for the littoral zone of Lake Kissimmee and 2 g C/m^2 for the limnetic zone using data from Wegener, Williams, and Holcomb.[66] Horrel* estimated 0.7 to 3.5 g C/m^2 for Lake Trafford, Fla. Assimilation efficiencies for these groups of fish were determined by the following procedure. Winberg[68] estimates that 80 percent of the food consumed by wild fish is metabolizable, and Balogh[69] has pointed out that nonselective feeders have lower assimilation efficiencies than more highly selective consumers. In the Lake Conway model, assimilation efficiency has been set at 0.69 for the least selective group, the herbivorous fish, at 0.80 for the primary predator fish, and at 1.0 for the secondary predator fish.

59. The dynamics of the herbivorous fish component are shown in Figure 19. Biomass is estimated to be 0.07 g C/m^2 or 5 percent of the total biomass of fish. Using an arbitrary turnover time of 4 years, net productivity of this group of fish is estimated at 0.0015 g C/m^2 per month. For all fish, removal by fishing is ignored, and predation is considered to be the only significant cause of death in herbivorous and primary predator fish.[70] In the model, the herbivorous fish depends most heavily on epipelic algae but equally on all other food items. The feeding rate is 1 percent of body weight per day in January; Patten, Egloff, and Richardson[33] estimated no more than 10 percent per day.

60. Primary predator fish are divided into two groups, as shown in Figure 20. The young fish are born in April, and most have advanced

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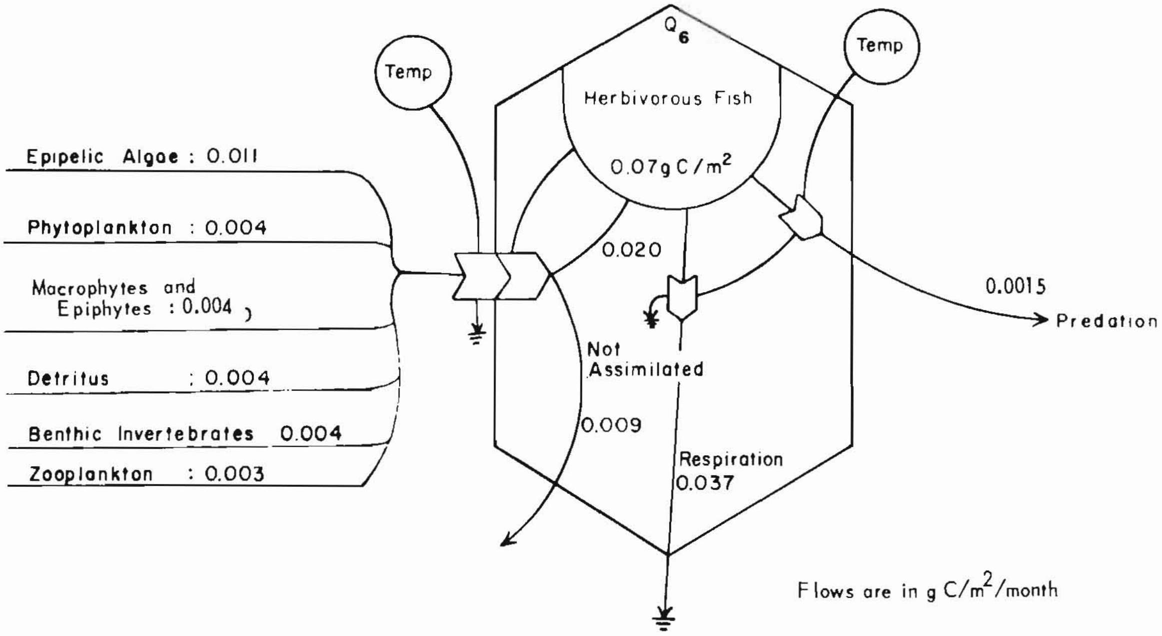
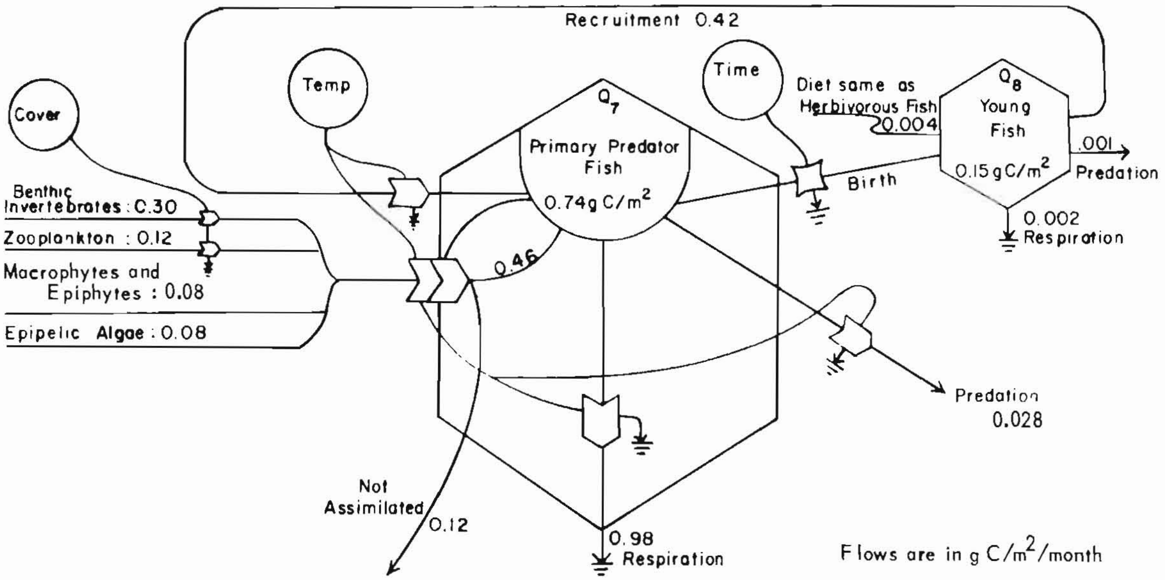
* Unpublished report cited by Carlson and Duever.[67]



$$\mathring{Q}_6 = K_{61} \cdot T_1 \cdot Q_6 \left((K_{62} \cdot Q_3) + (K_{63} \cdot Q_1) + (K_{64} \cdot Q_2) + K_{65} + (K_{66} \cdot Q_5 \cdot T_2) + (K_{67} \cdot Q_4 \cdot T_3) \right)$$
$$- K_{68} \cdot Q_6 \cdot T_1 - K_{93} \cdot Q_6 \cdot Q_9 \cdot T_1 \cdot fQ_2$$

Figure 19. Inputs and outputs affecting biomss of herbivorous fish. (Explanations of terms in equations are given in Appendix B)



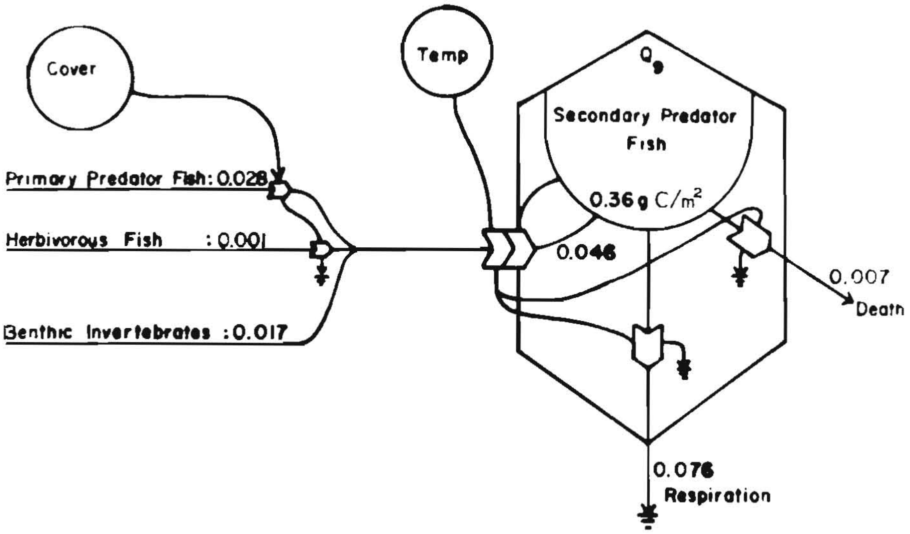
$$\mathring{Q}_7 = K_{71} \cdot Q_7 \cdot T_1 \left((K_{72} \cdot Q_5 \cdot T_2) + (K_{73} \cdot Q_2) + (K_{74} \cdot Q_4 \cdot T_4) + (K_{75} \cdot Q_3) \right) + K_{88} \cdot Q_8 \cdot T_1$$
$$- K_{76} \cdot Q_7 \cdot fY - K_{92} \cdot Q_9 \cdot Q_7 \cdot T_1 \cdot fQ_2 - K_{77} \cdot Q_7 \cdot T_1$$
$$\mathring{Q}_8 = K_{81} \cdot Q_8 \cdot T_1 \left((K_{82} \cdot Q_3) + (K_{83} \cdot Q_1) + (K_{84} \cdot Q_2) + (K_{85} \cdot Q_{10}) + (K_{86} \cdot Q_5 \cdot T_2) + (K_{87} \cdot Q_4 \cdot T_3) \right)$$
$$- K_{88} \cdot Q_8 \cdot T_1 - K_{89} \cdot Q_8 \cdot T_1 - K_{94} \cdot Q_8 \cdot Q_9 \cdot T_1 \cdot fQ_2$$

Figure 20. Inputs and outputs affecting biomass of young and adult primary predator fish. (Explanations of terms in equations are given in Appendix B)

into adult age classes by the end of the year. As young, they eat the same food items as the herbivorous fish. LeCren[71] observed that perch stop feeding on plankton after they have grown to 100 mm in length, so biomass of young fish in Lake Conway was determined by adding the weights of all fish less than 100 mm except the minnows, killifish, and silverside. Seventeen percent of the primary predator fish fell into this category.

61. Primary predator fish comprise 64 percent of the total fish population. Turnover time for bluegills in northern Indiana is slightly more than 1 year.[72] Turnover time of the adult primary predator fish in the model is estimated to be about 2 years. Primary predator fish feed most heavily on the macrophyte-epiphyte complex, moderately on benthic invertebrates, and less on epipelic algae and zooplankton.

62. Secondary predator fish (Figure 21) comprise 31 percent of the total fish biomass. Turnover time is estimated to be 4 years. These fish depend most heavily on primary predator fish and moderately



Flows are in g C/m^2/month

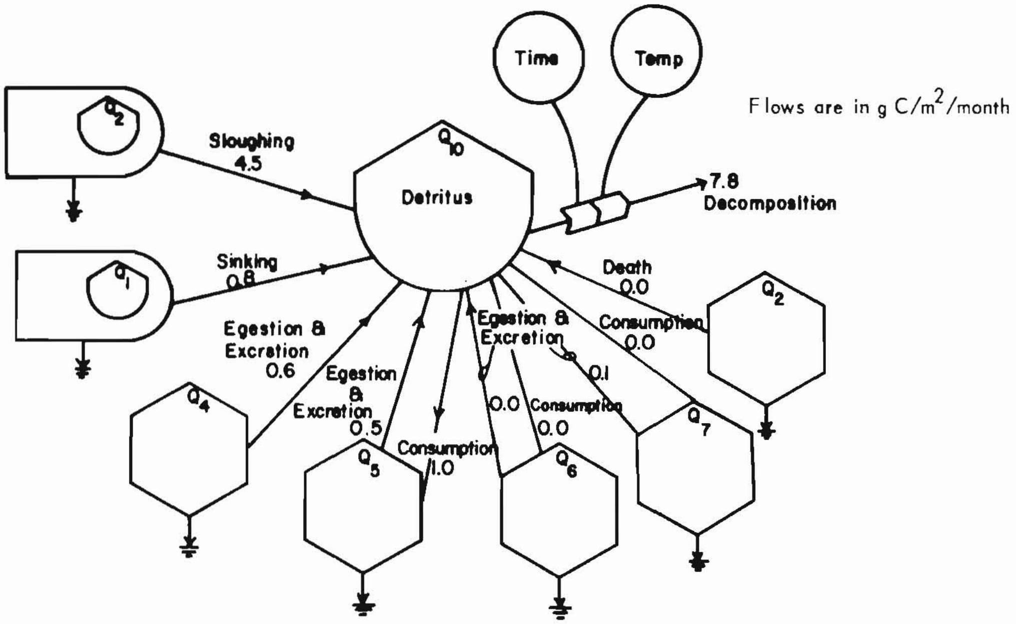
$$\dot{Q}_9 = K_{91} \cdot T_1 \cdot (K_{92} \cdot Q_9 \cdot Q_7) + (K_{93} \cdot Q_6 \cdot Q_9 \cdot T_1 \cdot fQ_2) + (K_{94} \cdot Q_8 \cdot Q_9 \cdot T_1 \cdot fQ_2) + (K_{95} \cdot Q_5 \cdot Q_9 \cdot T_1 \cdot T_3 \cdot fQ_2)) - K_{96} \cdot Q_9 \cdot T_1 - K_{97} \cdot Q_9 \cdot T_1$$

Figure 21. Inputs and outputs affecting biomass of secondary predator fish. (Explanations of terms in equations are given in Appendix B)

on benthic invertebrates; only 2 percent of their diet is derived from the herbivorous fish.

Detritus

63. All dead material sinks into the detritus, from which respiration and consumption by benthic invertebrates, herbivorous fish, and young primary predator fish are the only outflows. The dynamics of detritus flows are shown in Figure 22. The variable rates of loss of respiratory products are discussed in the following section.



$$\begin{aligned}\dot{Q}_{10} = {} & 0.10 \cdot K_{18} \cdot Q_1 + 0.9 \cdot (K_{25} \cdot Q_2 + fY \cdot K_{26} \cdot Q_2) + 0.5 \cdot 0.53 \cdot (K_{41} \cdot Q_4 \cdot T_5 \cdot ((K_{42} \cdot Q_3 + K_{43} \cdot Q_1 + K_{44} \cdot Q_2)) + 0.53 \cdot (K_{51} \cdot Q_5 \cdot T_6 \cdot \\ & ((K_{52} \cdot Q_4 \cdot T_7) + (K_{53} \cdot Q_2) + K_{54})) + 0.31 \cdot (K_{61} \cdot T_1 \cdot Q_6 ((K_{62} \cdot Q_3) + (K_{63} \cdot Q_1) + (K_{64} \cdot Q_2) + K_{26} + (K_{66} \cdot Q_5 \cdot T_2))) \\ & + 0.8 \cdot ((K_{71} \cdot Q_7 \cdot T_1 \cdot (K_{72} \cdot Q_5 \cdot T_2) + K_{74} \cdot Q_4 \cdot T_4) + (K_{75} \cdot Q_3)) + (K_{81} \cdot Q_8 \cdot T_1 ((K_{82} \cdot Q_3) + (K_{83} \cdot Q_1) + (K_{84} \cdot Q_2) + K_{85} \\ & + (K_{86} \cdot Q_5 \cdot T_2) + (K_{87} \cdot Q_4 \cdot T_3)))) + K_{101} \cdot (K_{54} \cdot Q_5 \cdot T_6) + K_{102} \cdot (K_{68} \cdot Q_6 \cdot T_1) + K_{103} \cdot (K_{77} \cdot Q_7 \cdot T_1) + K_{66} \cdot Q_8 \cdot T_1 \\ & + K_{97} \cdot Q_9 \cdot T_1 - K_{54} \cdot K_{51} \cdot Q_5 \cdot T_6 - K_{65} \cdot K_{61} \cdot T_1 \cdot Q_6 - K_{85} \cdot K_{81} \cdot Q_8 \cdot T_1 - K_{121} \cdot T_1 \cdot fY - K_{122} \cdot T_1 \cdot fY\end{aligned}$$

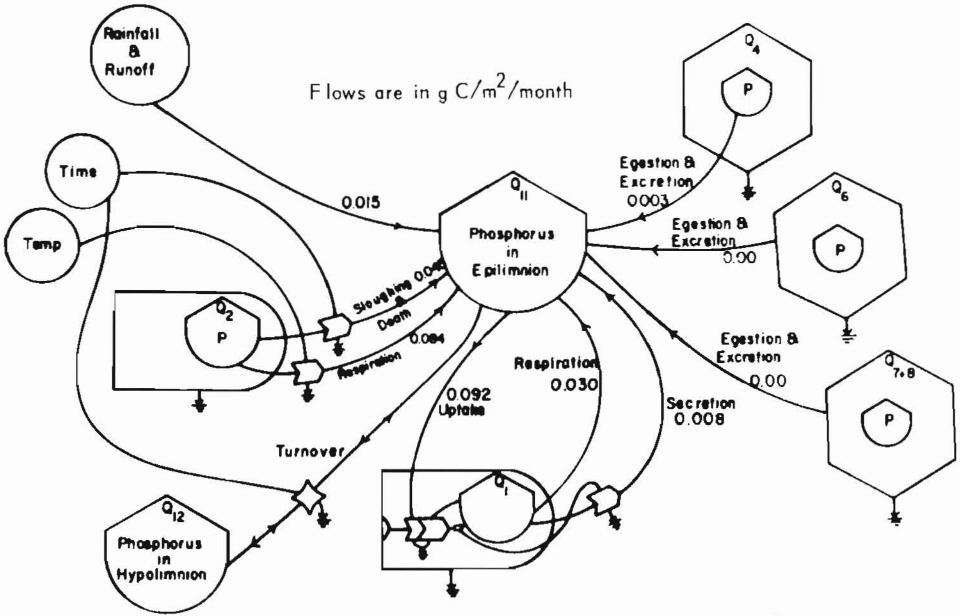
Figure 22. Inputs and outputs affecting amount of detritus. (Explanations of terms in equations are given in Appendix B)

Phosphorus dynamics in Lake Conway

64. Levels of dissolved orthophosphate in the epilimnion and the hypolimnion are included in the model as state variables. Data on phosphorus levels in Lake Conway were monitored by researchers from the

Orange County Pollution Control Department. The phosphorus inputs to Lake Conway through rainfall and runoff are shown in Table 6. Orthophosphate is estimated to be 39 percent of total phosphorus, based on actual measurements.* Hendry and Brezonik[75] reported 36 percent for an Alachua County site during 1976. All flows of phosphorus in this model are of phosphorus as orthophosphate.

65. Dynamics of phosphorus flow in the epilimnion are shown in Figure 23. This component is affected by the input of phosphorus from rainfall and runoff, by mixture with the hypolimnion in the late summer or fall and spring during turnover, and by uptake and excretion of phosphorus by plants and animals. However, few data could be found on the



$$\dot{Q}_{11} = fY \cdot K_R + K_P \cdot ((0.5 \cdot K_{24} \cdot Q_2 \cdot T_{11} + 0.05 \cdot (K_{25}\, Q_2 + fY \cdot K_{26} \cdot Q_2) + (fY-1) \cdot K_{11} \cdot S \cdot (1-R) \cdot L_{Q_1} \cdot \frac{E_{Q_1}}{1 + L_{Q_1} / L_{Q_{1-5C}}})$$

$$+ K_{1} \cdot T_9 \cdot Q_1 + 0.25 \cdot 0.53 \cdot K_{41} \cdot Q_4 \cdot T_5\ ((K_{42} \cdot Q_3) + (K_{43} \cdot Q_1) + (K_{44} \cdot Q_2)) + 0.024 \cdot 0.31 \cdot K_{6} \cdot T_1 \cdot Q_6((K_{62} \cdot Q_3)$$

$$+ (K_{63} \cdot Q_1) + (K_{64} \cdot Q_2) + K_{26} + (K_{66} \cdot Q_5 \cdot T_2) + (K_{67} \cdot Q_4 \cdot T_3)) + K_{81} \cdot Q_8 \cdot T_1\ ((K_{82} \cdot Q_3) + (K_{83} \cdot Q_1) + (K_{84} \cdot Q_2) + K_{85}$$

$$+ (K_{86} \cdot Q_5 \cdot T_2) + (K_{87} \cdot Q_4 \cdot T_3)) + K_{71} \cdot Q_7 \cdot T_1\ ((K_{72} \cdot Q_5 \cdot T_2) + (K_{74} \cdot Q_4 \cdot T_4) + (K_{75} \cdot Q_3)) + (Q_{12} - Q_{11}) \cdot fY)$$

Figure 23. Inputs and outputs affecting level of orthophosphate in epilimnion. (Explanations of terms in equations are given in Appendix B)

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* E. Blancher, personal communication.

magnitudes and controls of these amounts. Consequently, the flow of orthophosphate was at first assumed to be proportional to the flow of carbon, with the C:P ratio of roughly 100:1 used for conversion. In many cases, this had to be altered in order to derive a balanced phosphorus budget. These cases are noted below.

66. Release of phosphorus may occur in three ways: passive release as a normal accompaniment to plant respiration and to egestion and excretion in animals, active secretion by plants along with organic carbon and associated compounds; and leaching from dead materials.

67. The pumping of phosphorus from the sediment to the water by macrophytes has been documented in several instances.[76-78] As mentioned earlier, the secretion of organic compounds is not believed to be detectable when a community of epiphytic algae is present on the plants. Losses with respiration are considered to release only half the proportional levels of phosphorus in plants. Mineralization from dead leaves is probably a relatively slow process, although there are few data to document this. Pieczynska[79] indicates that two species of Potamogeton required 7 to 14 days to lose 6 to 92 or 95 percent of their biomass. In the model, it is assumed that only 5 percent of the phosphorus in dead material leaches into the epilimnion before the material sinks to the bottom.

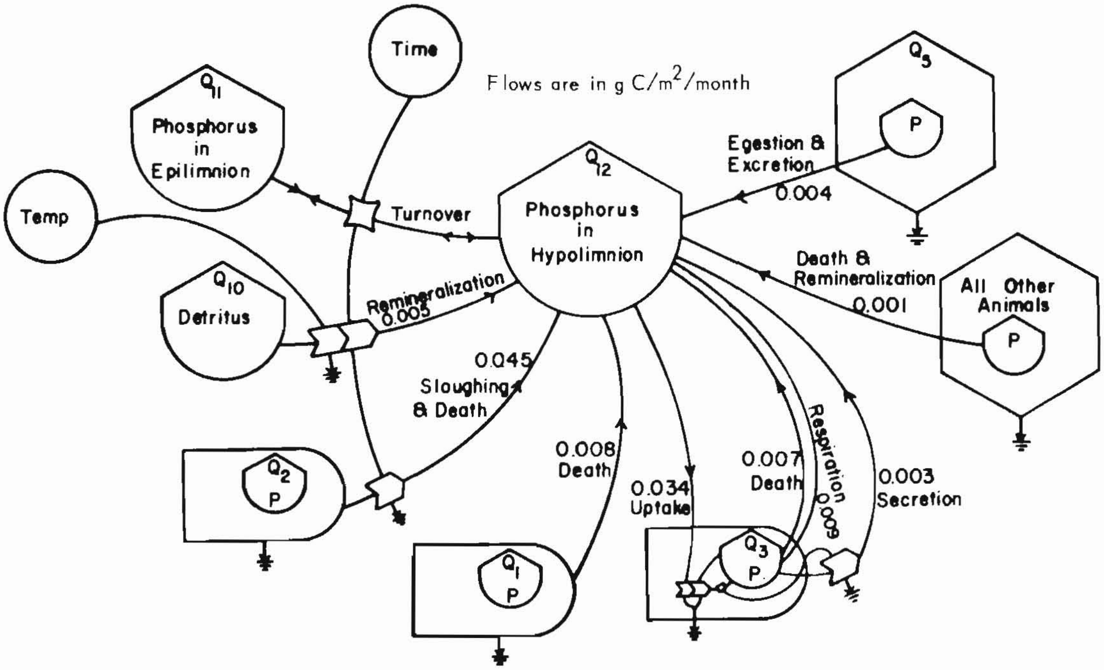
68. Phosphorus is released from phytoplankton through both respiration and secretion of organic matter. Only half the normal complement of phosphorus is judged to be released through respiration. Phosphorus uptake is considered to be proportional to gross primary productivity and phosphorus secretion to the active release of organic compounds.

69, For zooplankton, 25 percent of the proportional amount of phosphorus is accounted for in egestion and excretion. Kitchell, Koonce, and Tennis[80] report that bluegill remineralize less than 1 percent. The value was therefore set at 0.5 percent of egested and excreted materials for all fish. The contribution of zooplankton is substantially more than this.

70. It is assumed that complete turnover between epilimnion and

hypolimnion will be achieved in 1 month. The two compartments are begun at the same value, since measurements by the Orange County Pollution Control Department showed no consistent differences.

71. Phosphorus flows in the hypolimnion are shown in Figure 24.



$$\overset{\circ}{Q}_{12} = K_P \cdot (K_{121} \cdot T_1 \cdot fY + K_{122} \cdot T_1 \cdot fY + 0.05 \cdot (K_{25} \cdot Q_2 + fY \cdot K_{26} \cdot Q_2) + 0.81 \cdot (K_{18} \cdot Q_1) \cdot 0.50 - \frac{L_{Q_3} \cdot E_{Q_3}}{1 + L_{Q_3}/L_{Q_{3\text{-}50}}} \cdot (1 - fY)$$

$$+ 0.50 \cdot (K_{33} \cdot T_8 \cdot Q_3 + K_{34} \cdot Q_3) + 0.53 \cdot K_{51} \cdot Q_5 \cdot T_6 \{((K_{52} \cdot Q_4 \cdot T_7) + (K_{53} \cdot Q_2) + K_{54}) + 0.50\{((K_{97} \cdot Q_9 \cdot T_1)$$

$$+ 0.10 \cdot (K_{68} \cdot Q_6 \cdot T_1) + (K_{77} \cdot Q_7 \cdot T_1))) + (Q_{11} - Q_{12}) \cdot fY$$

Figure 24. Inputs and outputs affecting level of orthophosphate in hypolimnion. (Explanations of terms in equations are given in Appendix B)

Release of phosphorus from the sediments involves two pathways. It is believed to be fastest when the lake is anaerobic during the summer. This assumption is based on studies in the Great Lakes[81] where most of the phosphorus is commonly adsorbed onto clays and ferric hydroxides. If the lake is well-oxygenated, the top few millimetres of the sediments are oxidized, and iron, manganese, and phosphate are trapped. The phosphorus adsorbs onto and complexes with ferric oxides and hydroxide. If this zone remains oxidized, nothing escapes from the sediments. However, when oxygen levels at the interface between water and sediments fall below 1 mg/ℓ, orthophosphate ions are transferred from the sediment to the water. Release during aerobic periods will be much lower, but activity by benthic invertebrates will allow some phosphorus to be released. Stumm and Leckie[82] estimated the release rate for undisturbed sediment in the summer to be 1 g/m^2 per year. The rate in the model is assumed to be 150 percent of this, because of higher temperatures, and the release rate in aerobic waters is arbitrarily assumed to be one third of the anaerobic rate.

72. Half of the phosphorus leaching from dead phytoplankton sinking from the epilimnion is released into the hypolimnion; 5 percent of the phosphorus in dead organic material sloughed from macrophytes is also released. The phosphorus flows involving epipelic algae in the hypolimnion derive from the same assumptions that governed the phytoplankton in the epilimnion. Like the phytoplankton, half the phosphorus in the dead material leaches into the hypolimnion before becoming detritus.

73. The phosphorus from egested and excreted products by the benthic invertebrates is released into the hypolimnion. Fish bones and scales mineralize very slowly; 50 percent of the phosphorus in fish biomass is in this form.[80,83] Secondary predator fish are the only group making a substantial contribution to this pathway.

Simulation of the Ecosystem

74. The Lake Conway ecosystem was simulated for a 10-year period using January measurements for initial conditions. Although it is unlikely that Lake Conway is currently in steady state, the goal of the modeling effort is the achievement of a steady state simulation for a 10-year period. Without knowing the histories of each component, it must be assumed that the correlations observed among components during the study year can represent a stable condition.

75. Simulated changes in biomass of the macrophyte-epiphyte complex are shown in Figure 25. Summer biomass in the tenth year is

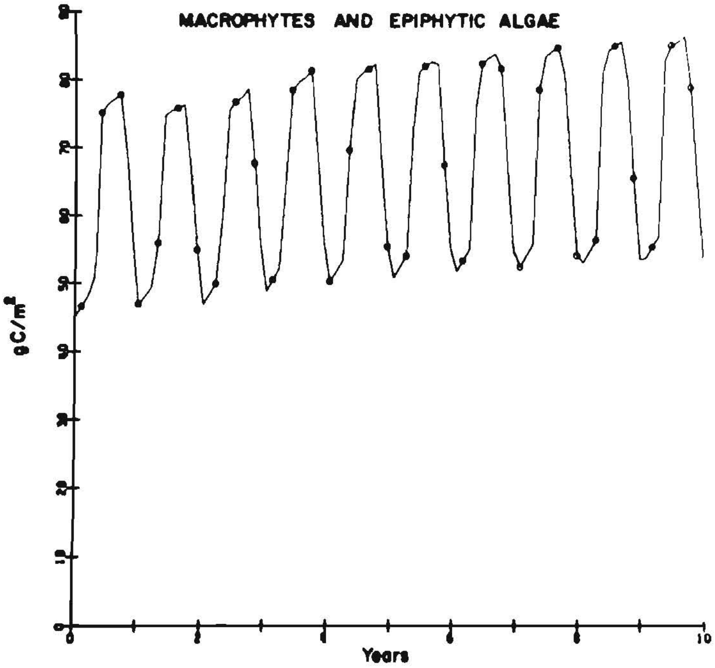


Figure 25. Simulated pattern of change in macrophyte-epiphyte complex biomass under undisturbed conditions for 10 years

12 percent greater than in the first year, but the annual pattern of growth and decline is stable. The simulated changes in the second year are shown in Figure 26, along with seven measurements reported by researchers from the Florida Department of Natural Resources. The simulation does not show biomass in the summer to reach nearly the extreme suggested by the September data point. Nor does the simulation show the secondary biomass increase in December. The significance of the higher September biomass will be evaluated when the summer data are available; the small peak in December is probably not significantly different from the other fall and winter points. Further information on rates of biomass sloughing by the macrophytes, nutrient uptake mechanisms, and photosynthetic responses to variable light conditions might provide clues to discrepancies between assumptions and reality.

76. The simulated changes in phytoplankton biomass are shown in Figure 27. One year's data from the Orange County Pollution Control Department and a partial set of data from researchers from the University of Florida's Department of Environmental Engineering

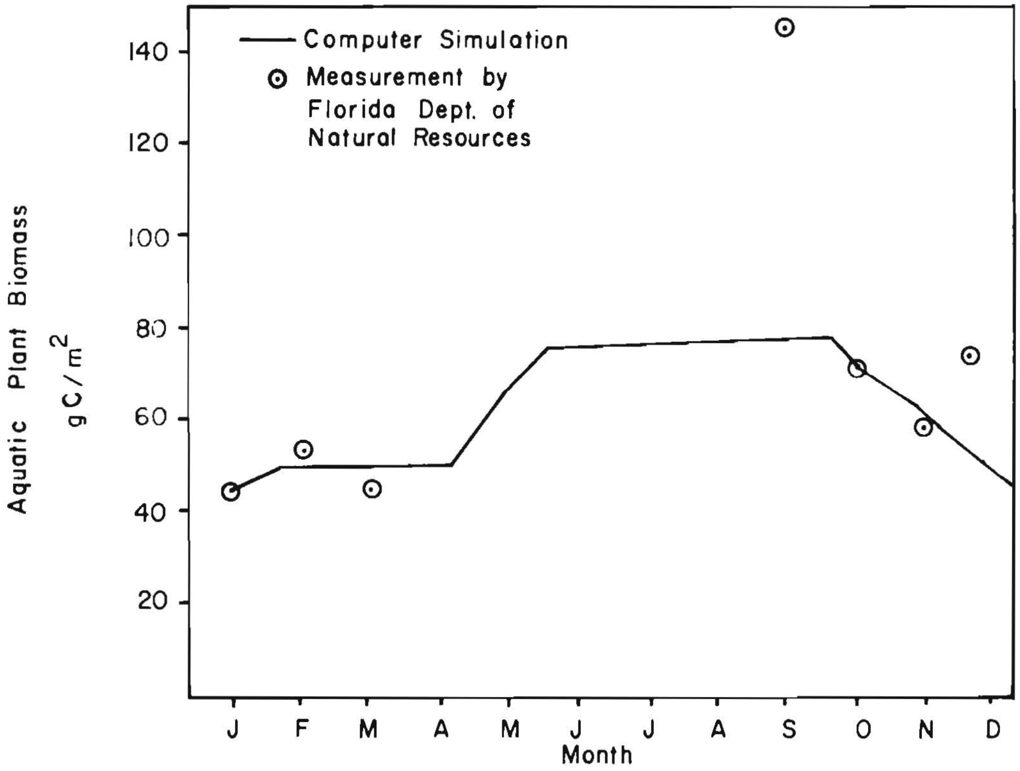


Figure 26. Simulated changes in macrophyte (and epiphyte) biomass for 1 year and seven biomass measurements made by a research team from the Florida Department of Natural Resources

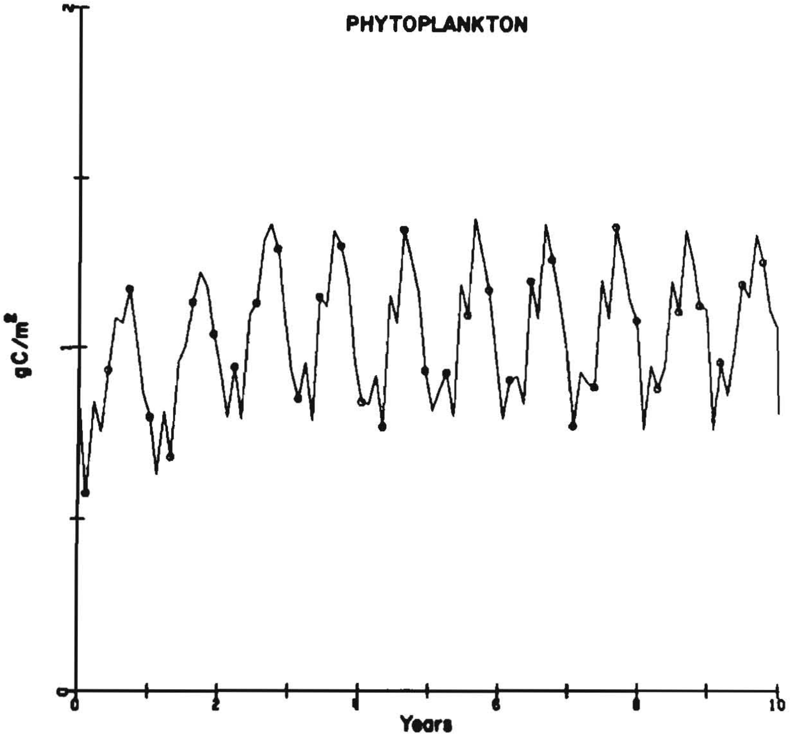


Figure 27. Simulated changes in phytoplankton biomass under undisturbed conditions for 10 years

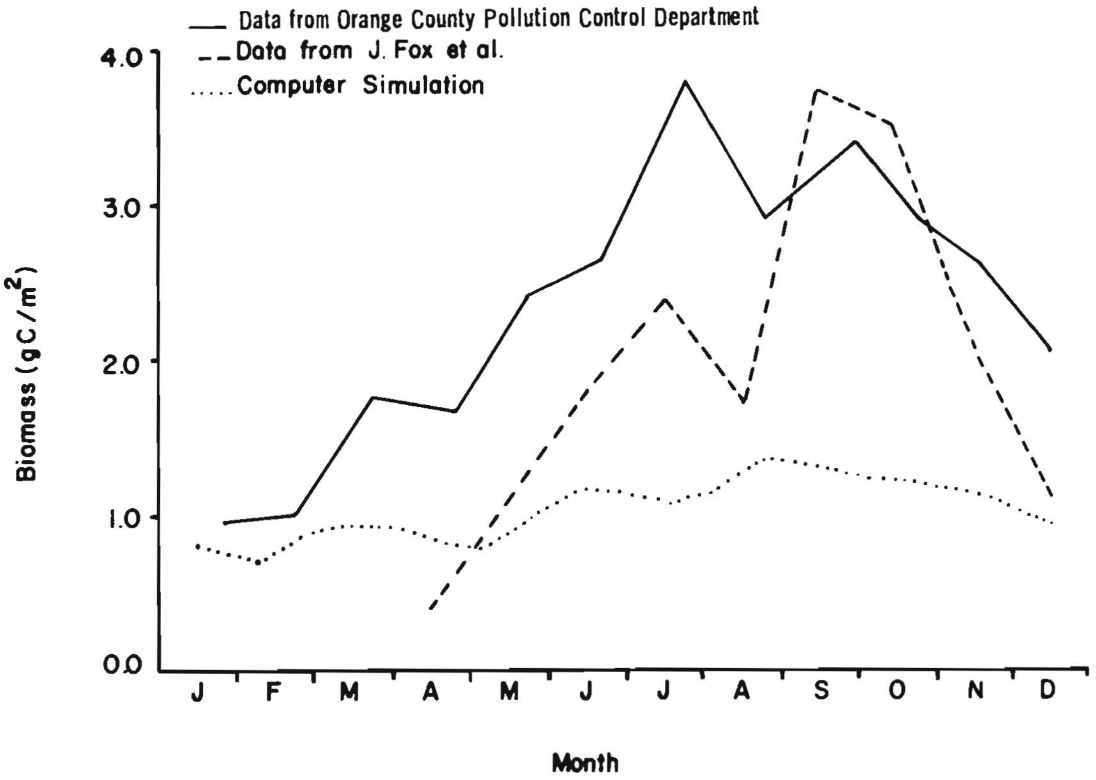


Figure 28. Simulated changes in phytoplankton biomass for 1 year. (Biomass estimates made from data reported by teams from the Orange County Pollution Control Department and from the University of Florida's Department of Environmental Engineering Sciences are also shown)

Sciences* are shown in Figure 28. The latter set of data was collected under a more restricted sampling scheme. Plotted with these curves are biomass values from the fourth year of the simulation. The simulation underestimates summer biomass predicted by both sets of data, although it follows the pattern of increase shown in the data from the Orange County Pollution Control Department.

77. Nutrient relationships between the phytoplankton and the surrounding water are a sensitive area in the model, and the factors controlling rates of uptake and loss are not clearly defined in the literature. In further simulations, the effect of nutrients will be modeled as a limiting factor; in the model at present, only availability

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* J. Fox et al., personal communications.

of phosphorus controls phytoplankton growth. There is little basis, however, for accurately determining the dynamics of this relationship. Seasonal changes that have not been accounted for in the relationship between chlorophyll a and biomass may also affect the biomass estimate itself.

78. Winter biomass of epipelic algae evolves to be about 50 percent higher than predicted in the initial conditions (Figure 29).

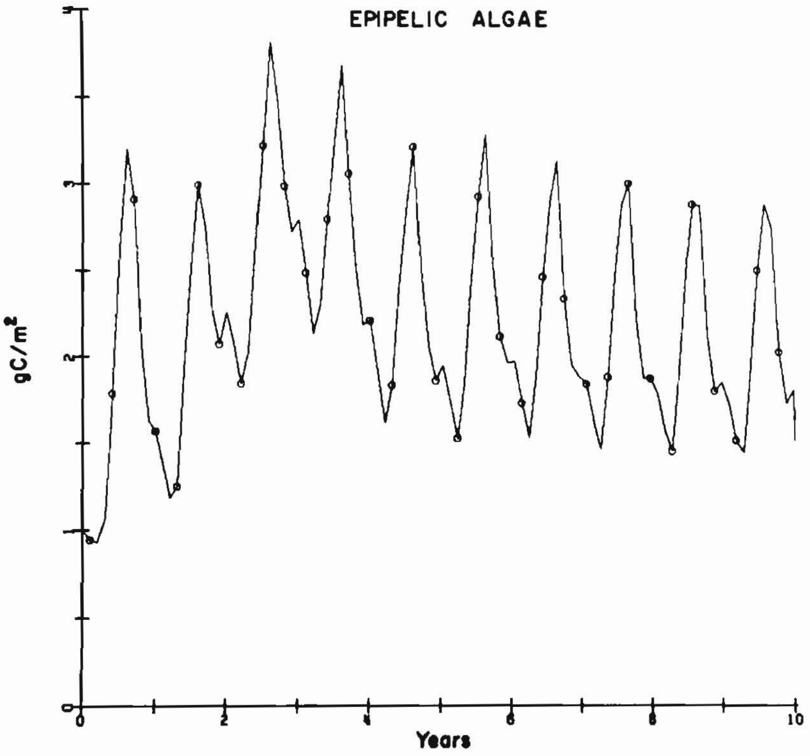


Figure 29. Simulated changes in biomass of epipelic algae under undisturbed conditions for 10 years

Interrelationships between this component and nutrients in the bottom sediment, water, and macrophytic plants (epipelic algae frequently grow thickly around the plants) need better definition. However, little work has been published on epipelic algae, and measurements of its biomass in Lake Conway are not available.

79. Neither zooplankton nor benthic invertebrates display a stable simulation pattern until the fifth year of simulation. Zooplankton (Figure 30) do not show the midsummer decrease in biomass recorded

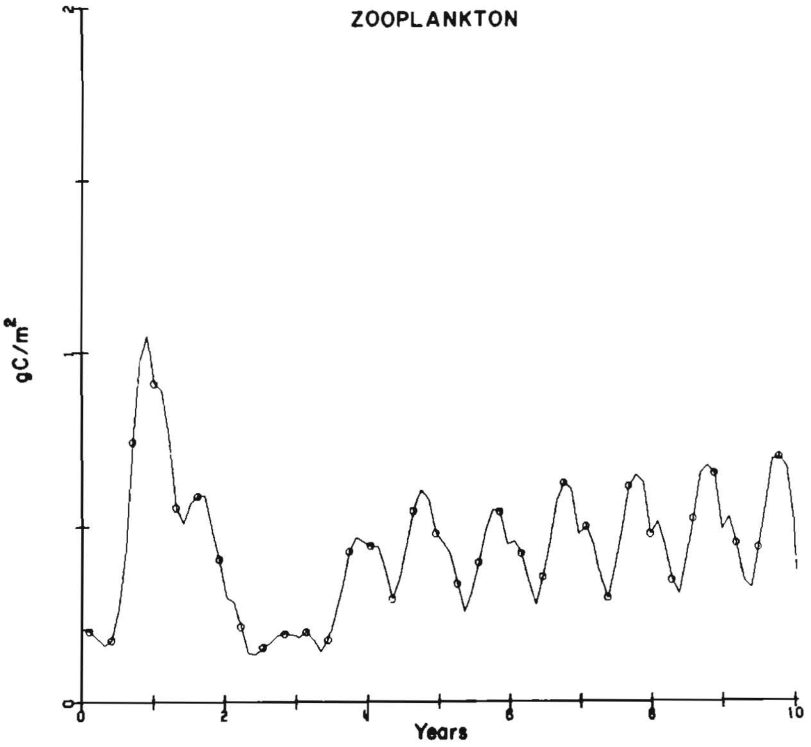


Figure 30. Simulated changes in biomass of the zooplankton population under undisturbed conditions for 10 years

in Lake Conway (Figure 17). A biomodal pattern such as apparently occurs in Lake Conway is common in northern temperate lakes, where many of the smaller species are subject to predation by larger zooplankton in the summer while other species aestivate.[84-86] The importance of fish predation may be underestimated in the model; several studies cited by Wetzel[1] stress the importance of fish predation on size distribution among zooplankton.

80. The small seasonal changes in biomass shown by the simulation of benthic invertebrates (Figure 31) are probably reasonable. Cummins[40] points out that temperature is the primary control over feeding and respiration rates when food sources are both abundant and consistent all year. Four measurements of biomass of benthic invertebrates in Lake Conway (taken by researchers from the University of Florida's Department of Environmental Engineering Sciences) varied from 1.35 g C/m^2 in September to 2.27 g C/m^2 in April, with intermediate values of 1.53 in

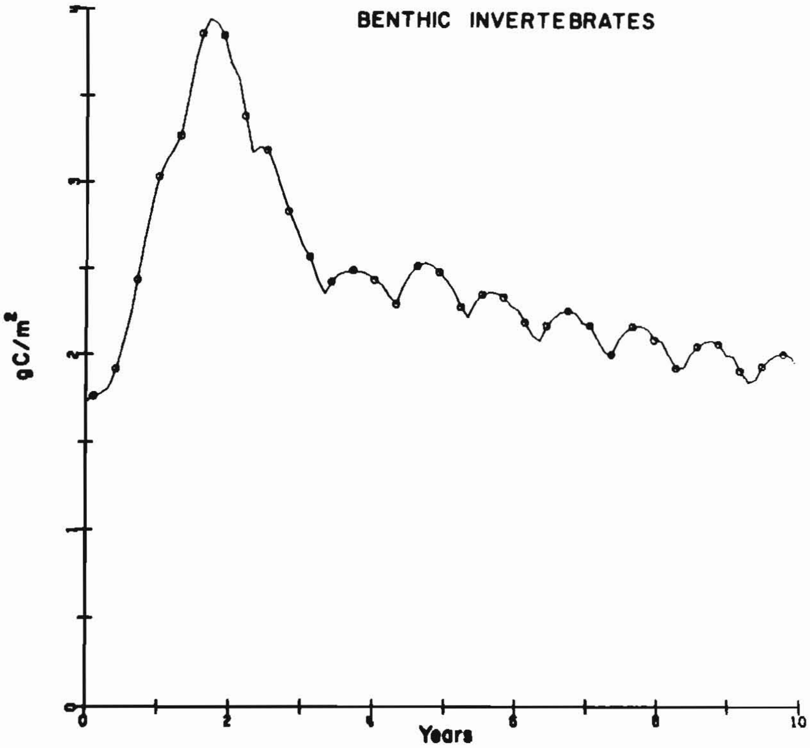


Figure 31. Simulated changes in biomass of the benthic invertebrate population under undisturbed conditions for 10 years

May and 1.76 in July. One sample was taken in each of these months, and the number of individuals in the samples ranged from 8 to 234. The variation is therefore probably not significant. This simulated pattern is not satisfactory, however, and seems to be a product of the instability that occurs early in the simulation of the zooplankton component. Assumptions of productivity and respiration rates for this group need to be reexamined also since the turnover rate does not fall within the range determined by Waters[87] in a review of several studies.

81. Data on fish populations were available for only 1 month, so it is difficult to assess the results of the simulations. Changes in biomass of all fish are shown in Figure 32. Simulations of herbivorous, primary predator, and secondary predator fish are shown in Figures 33-35, respectively. Levels of both primary predator fish and herbivorous fish vary seasonally and rise above the initial levels used in the model. Irregularities in the simulations of these fish appear to be related to

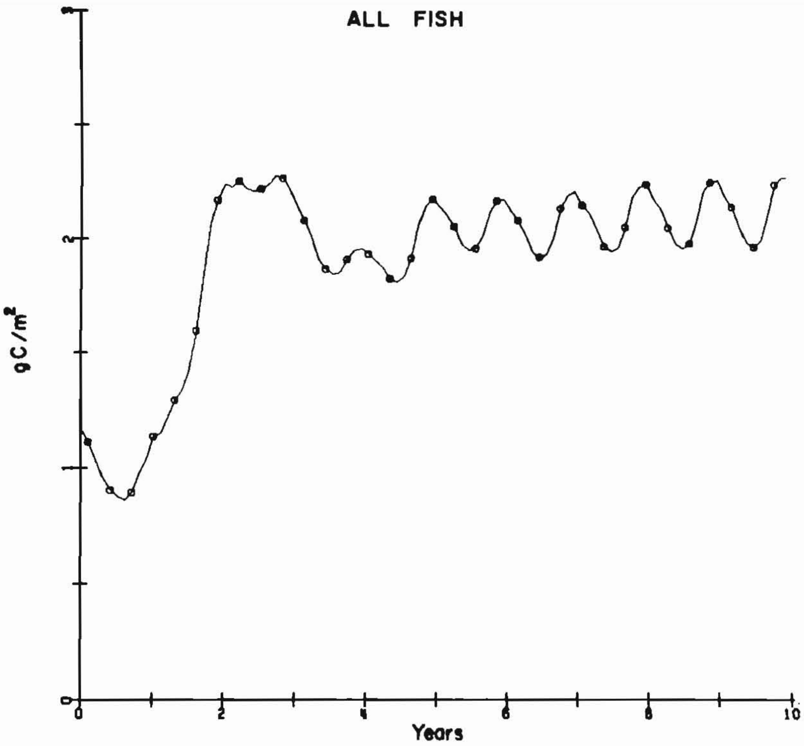


Figure 32. Simulated changes in biomass of the fish population under undisturbed conditions for 10 years

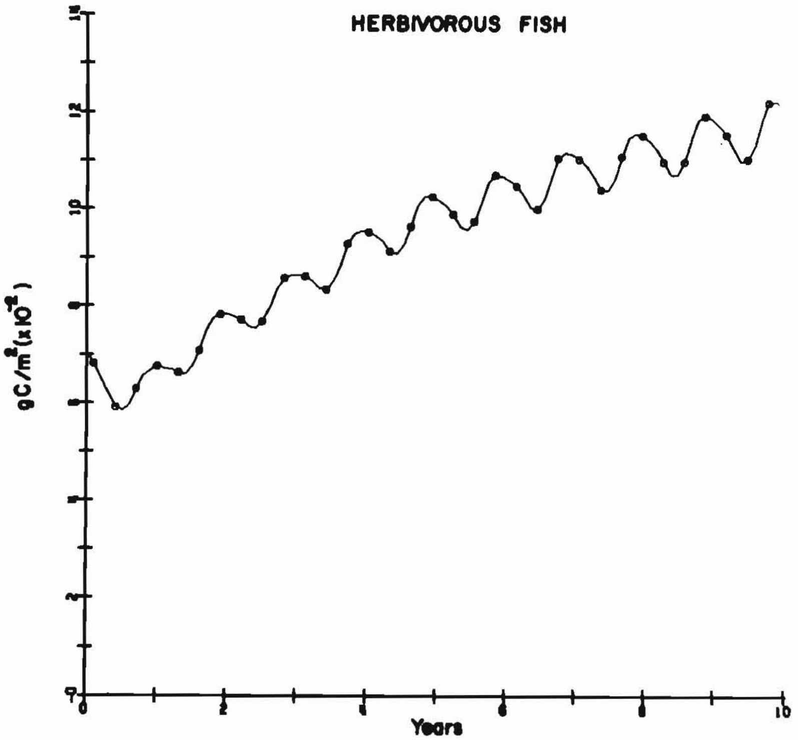


Figure 33. Simulated changes in biomass of the herbivorous fish population under undisturbed conditions for 10 years

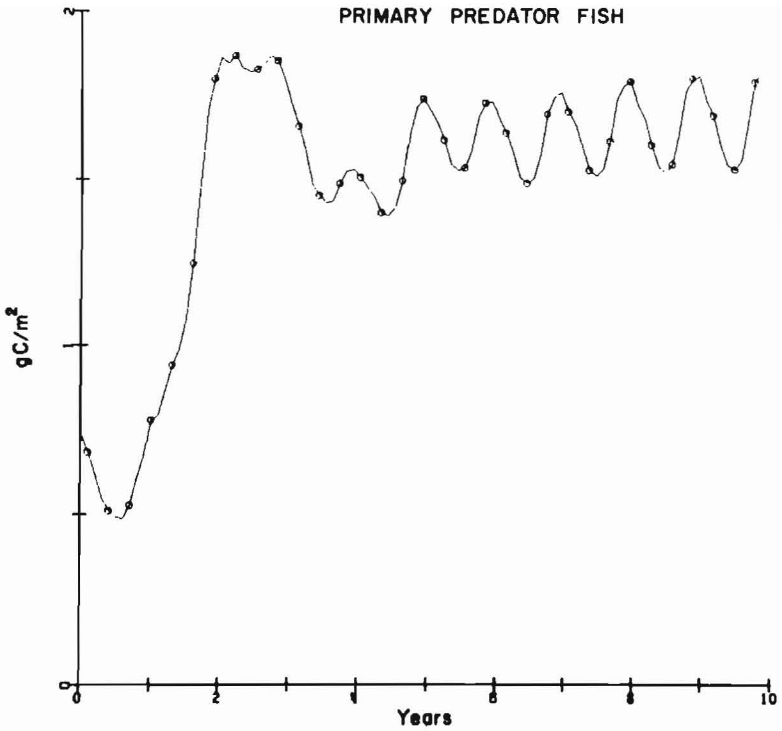


Figure 34. Simulated changes in biomass of the primary predator fish population (both young and adult) under undisturbed conditions for 10 years

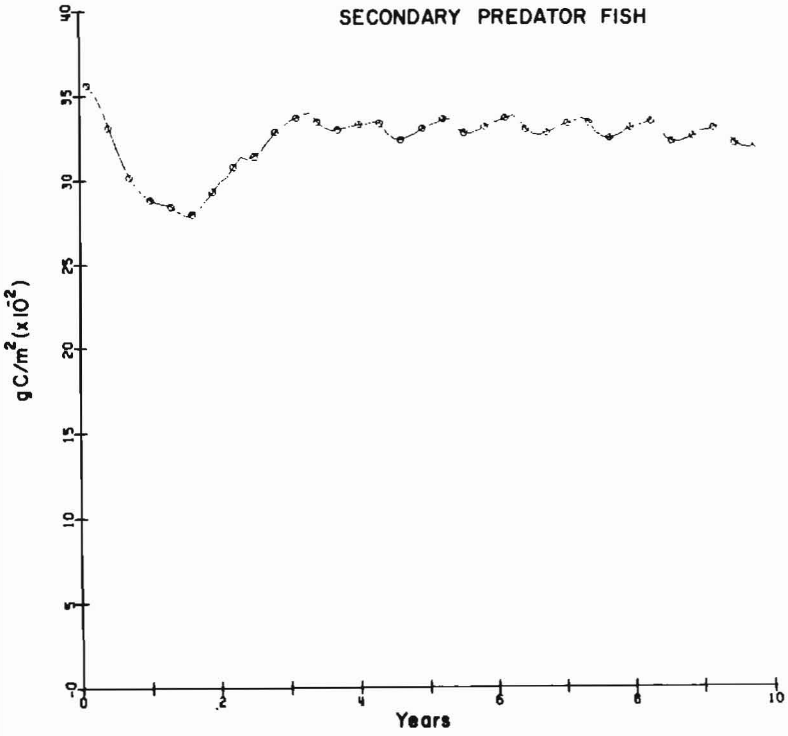


Figure 35. Simulated changes in biomass of the secondary predator fish population under undisturbed conditions for 10 years

the early instability of the zooplankton and benthic invertebrate populations. Seasonal variations are damped in the secondary predator fish, and this group does not show an increase in biomass.

82. Simulations of changes in orthophosphate in the epilimnion and in the hypolimnion are shown in Figures 36 and 37, respectively. No data are available for verification of these simulations, since concentrations during most of the simulation remain below the limits of detection of the analyzer used by the Orange County Pollution Control Department. Levels never rose above this concentration in Lake Conway during the study year. The simulations show decreases in both the epilimnion and the hypolimnion in the spring and a second decrease in the hypolimnion in late summer. Despite the fact that mixing is programmed to occur from late summer to midwinter (one complete turnover occurs each month during this period), the two layers maintain distinct patterns. Detritus (Figure 38) doubled over the 10-year period.

83. The present model is an approximation of ecological relationships in Lake Conway, but does not yet represent these conditions as closely as is desired. Zooplankton are the only group whose simulated pattern of seasonal changes in biomass is unrealistic; complete data for several other groups were not available when this report was written, however. Although simulated patterns of change in macrophytes and in phytoplankton are consistent, the annual productivity and respiration rates rise considerably higher than the levels measured and programmed for the initial year. This discrepancy affects both uptake and release of phosphorus and may account for the increases seen in epipelic algae and in all the animals except the secondary predator fish.

84. The importance of the epipelic algae to the stability of the model appeared during earlier simulations, when phosphorus released by the epipelic algae during respiration was inadvertently doubled. This led to a five-fold increase in herbivorous fish biomass, a decrease in benthic invertebrate biomass (to half the level reached in the simulation discussed above), and a dramatic decrease in secondary predator fish. When the model has been stabilized to produce a 10-year steady state simulation, a structured set of sensitivity analyses will be

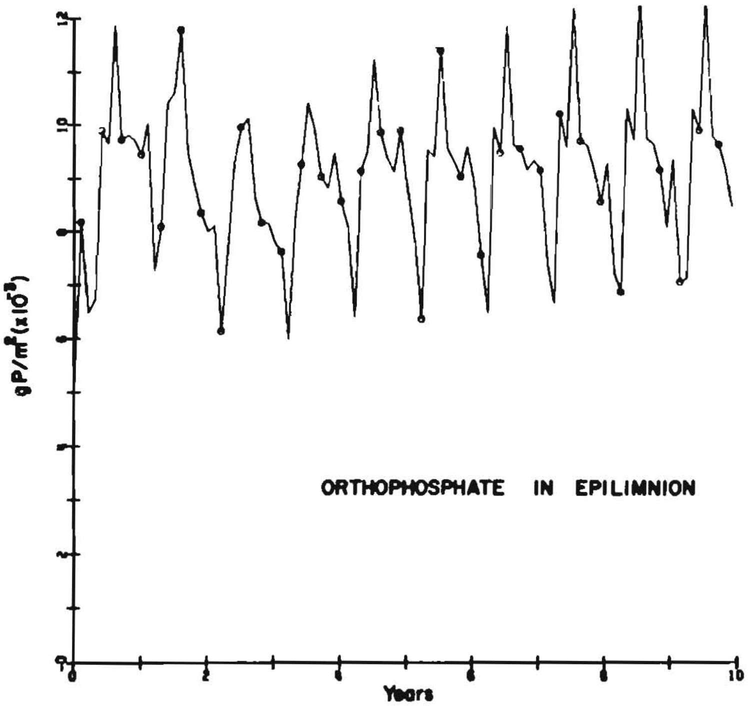


Figure 36. Simulated changes in levels of orthophosphate in the epilimnion under undisturbed conditions for 10 years

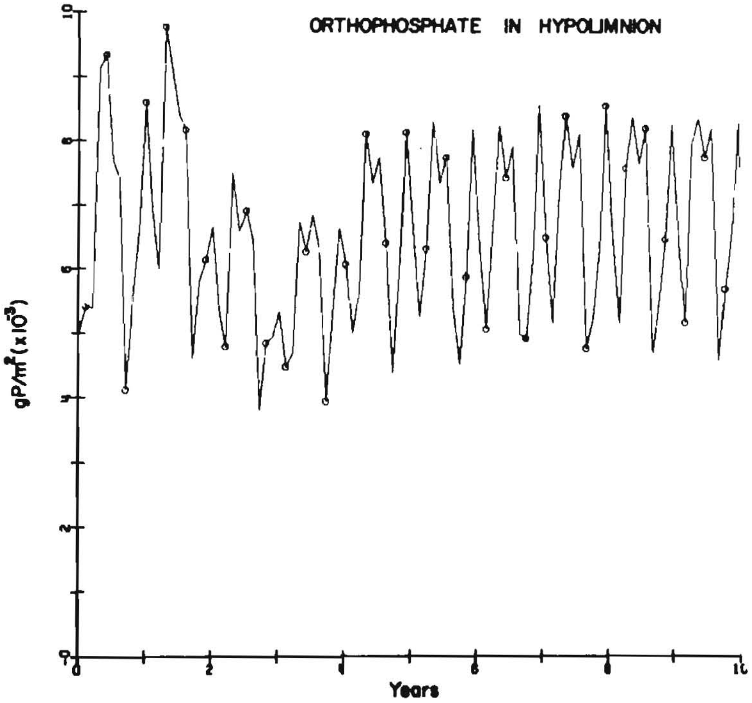


Figure 37. Simulated changes in levels of orthophosphate in the hypolimnion under undisturbed conditions for 10 years

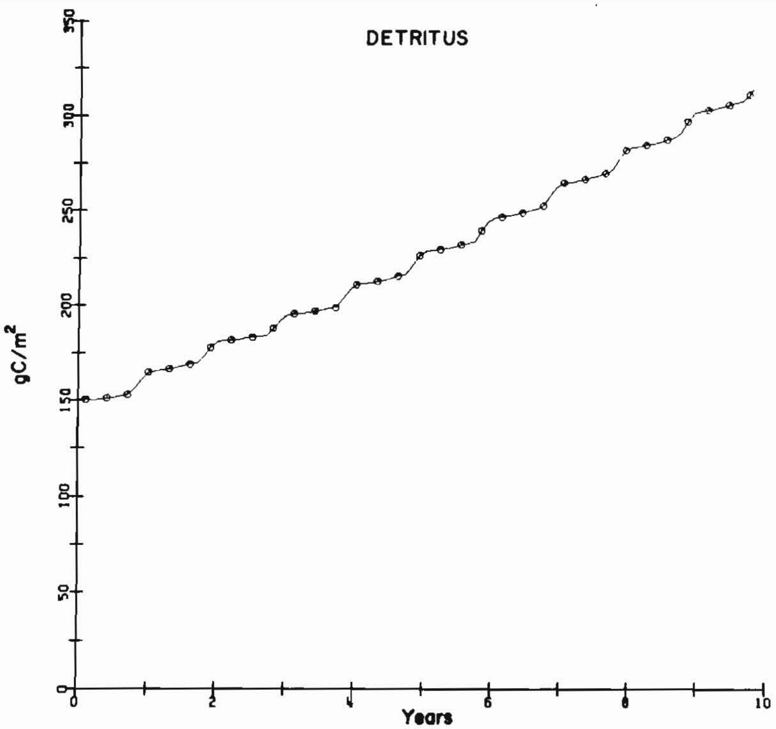


Figure 38. Simulated changes in amount of detritus in Lake Conway under undisturbed conditions for 10 years

conducted to evaluate the effect of changes in each component on the stability of other components and of the entire model.

PART IV: SIMULATED INTRODUTION OF WHITE AMUR

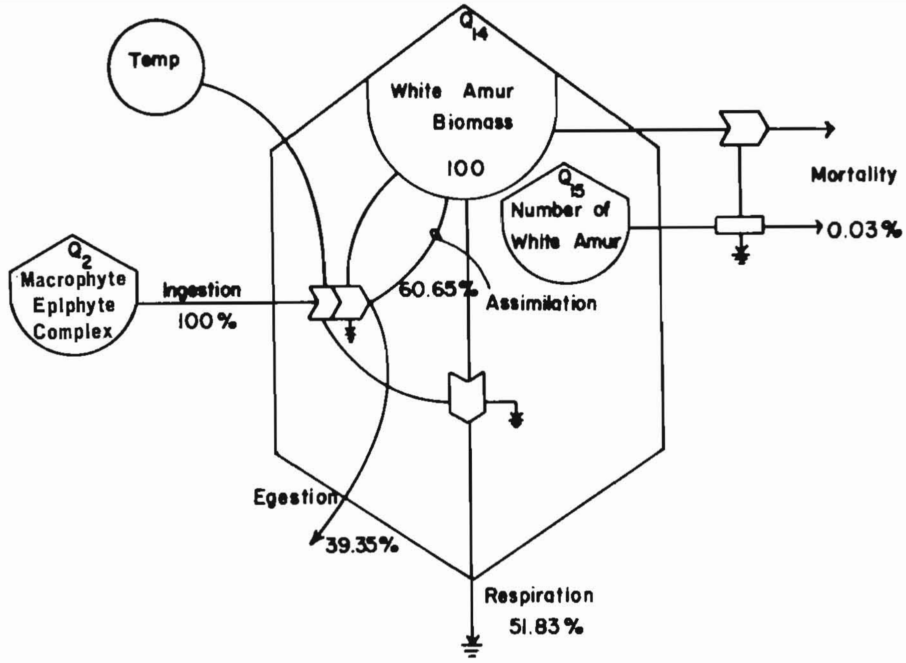
Dynamics of White Amur Population

85. Much of the published information on the white amur exists in Russian literature. Many of the studies that have been done on basic biological features of the white amur have been translated and summarized by Fischer and Lyakhnovich,[9] whose interpretation is used in this analysis.

86. Growth efficiency data for white amur are shown in Table 7. The first set of data summarizes the opinion of Fischer and Lyakhnovich[9] that three distinct growth phases are discernible in white amur: during the first 2 years, fish can double their weight within a year; from the second to fifth year, growth efficiency is 3 percent, and body weight may increase as much as 30 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. Variability in the second set of data listed is due primarily to different weeds which were fed the fish to determine weed-specific growth efficiencies.[88]

87. Weight-specific digestion rates are listed in Table 8. Fischer and Lyakhnovich[9] summarize data showing that daily growth increases vary from 29 percent of initial body weight in fry to 2 percent in young fish and 0.07 percent in mature fish.

88. The white amur component of the model is shown in Figure 39. The values are percentages of ingested food, assuming that the fish eat 100 percent of their body weight daily. Fischer and Lyakhnovich[9] report assimilation efficiencies ranging from 31.2 percent of ingestion to 90.1 percent; an average of 60.65 percent is used in the model. They also estimate that 85.5 percent of assimilated food is lost as respiration or death. The age-varying growth rates are incorporated into the model by adjusting respiratory losses from 85.5 percent for a young fish to 100 percent for a 5- to 6-year-old fish, or one which weighs 10 kg. Fischer and Lyakhnovich[9] indicate that fish can reach a size of 32 kg, but that leveling off generally occurs closer to 10 kg.



$$\dot{Q}_{14} = K_{141} \cdot K_{142} \cdot K_{143} \cdot Q_{14} \cdot Q_2 \cdot T_1 - K_{144} \cdot Q_{14} \cdot T_1 - K_{151} \cdot Q_{14} \cdot Q_{14} / Q_{15}$$

$$Q_{15} = - K_{151} \cdot Q_{15}$$

Figure 39. Inputs and outputs affecting biomass and number of white amur. (Egestion and assimilation are expressed as percentages of food ingested, respiration is expressed as percentage of food assimilated. Mortality is expressed as the daily rate of loss of numbers of fish)

89. Feces and dead white amur are assumed to sink to the sediment with some remineralization of the latter releasing into the hypolimnion.

Simulated Effects of White Amur

90. The introduction of 7000 white amur, estimated to weigh 450 g each, was simulated with the Lake Conway ecosystem model. Changes in the number and biomass of the fish are shown in Figures 40 and 41, respectively. The death rate of the fish is constant, reducing them to about 43 percent of their initial level in 10 years. Biomass increases rapidly, however, until the second year. Decrease in biomass of vascular plants is evident in the second year after introduction (Figure 42),

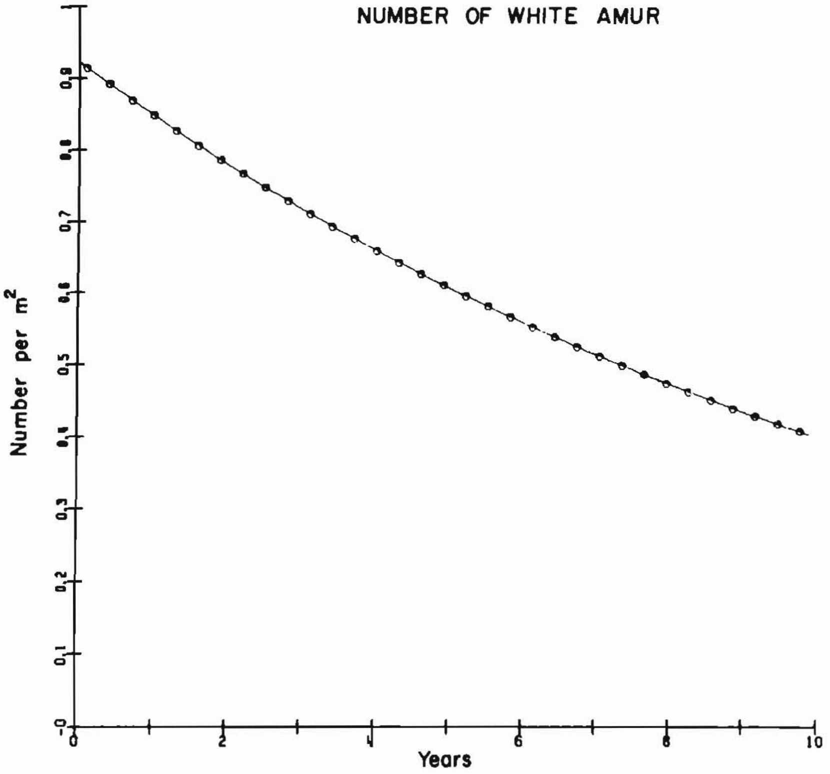


Figure 40. Simulated changes in total number of white amur for 10 years after their introduction

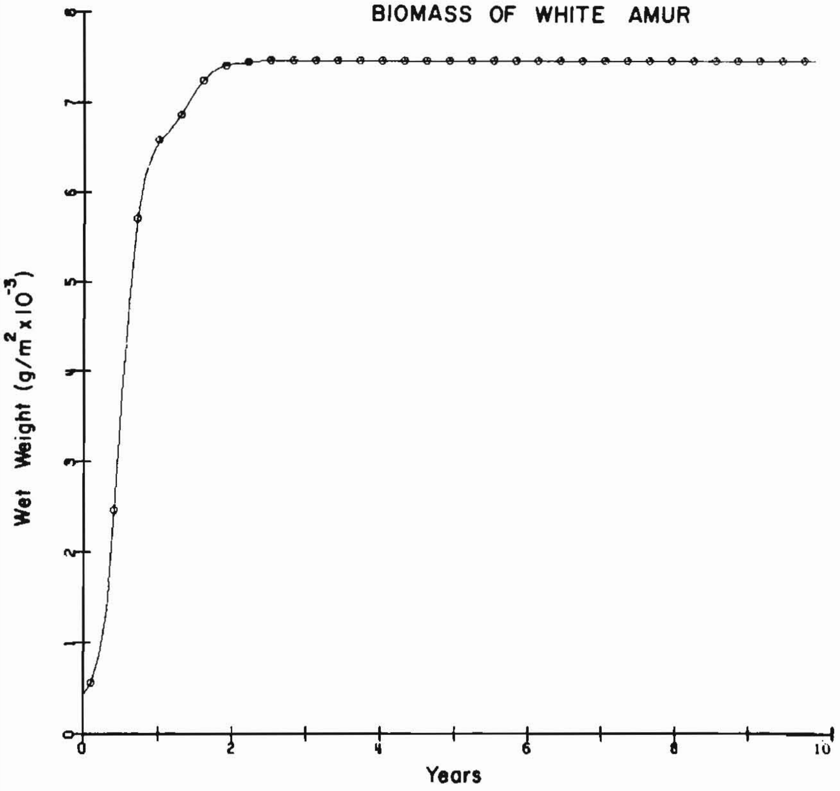


Figure 41. Simulated changes in total biomass of white amur for 10 years after their introduction

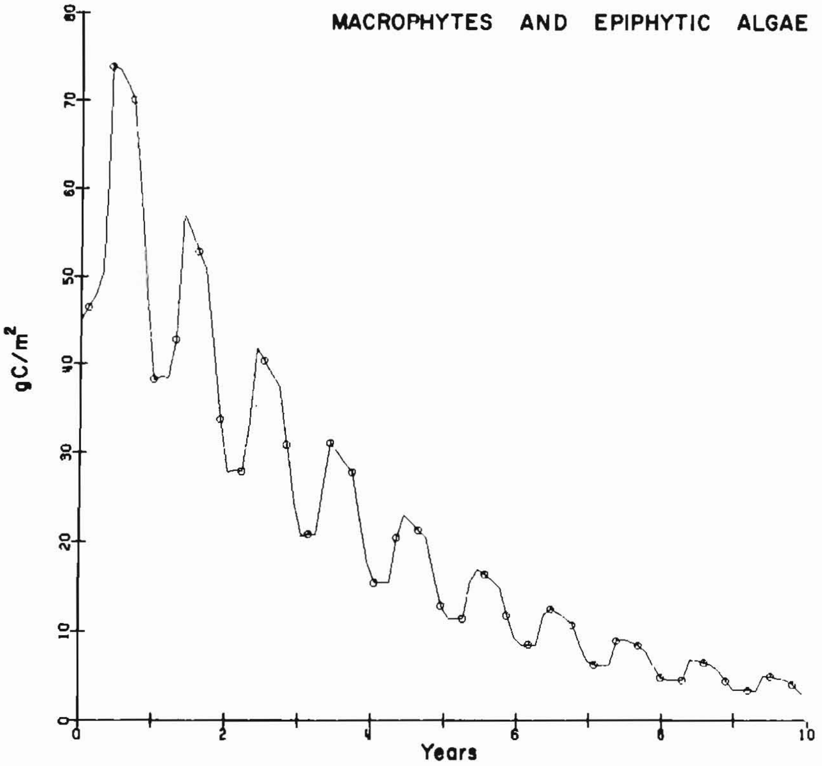


Figure 42. Simulated changes in biomass of macrophytes and epiphytic algae for 10 years after the introduction of white amur

and only 10 percent of the initial amount of biomass remains by the ninth year. This decrease in biomass slows the pumping of nutrients from the sediment, causing a decrease in orthophosphate levels in the epilimnion (Figure 43), which in turn leads to a decrease in phytoplankton levels (Figure 44). Increased light availability permits the epipelic algae to increase in biomass (Figure 45), although phosphorus levels in the hypolimnion (Figure 46) are somewhat decreased by the lower input from the epilimnion during turnover.

91. Zooplankton are much reduced by the fifth year (Figure 47), presumably as a result of the decrease in their primary food source, phytoplankton. Benthic invertebrates increase (Figure 48), however, in response to the increased biomass of epipelic algae. Fish populations as a whole increase toward the end of the 10-year period (Figure 49). Herbivorous fish do not show a dramatic change in biomass (Figure 50). Primary predator fish decrease somewhat (Figure 51). Secondary predator

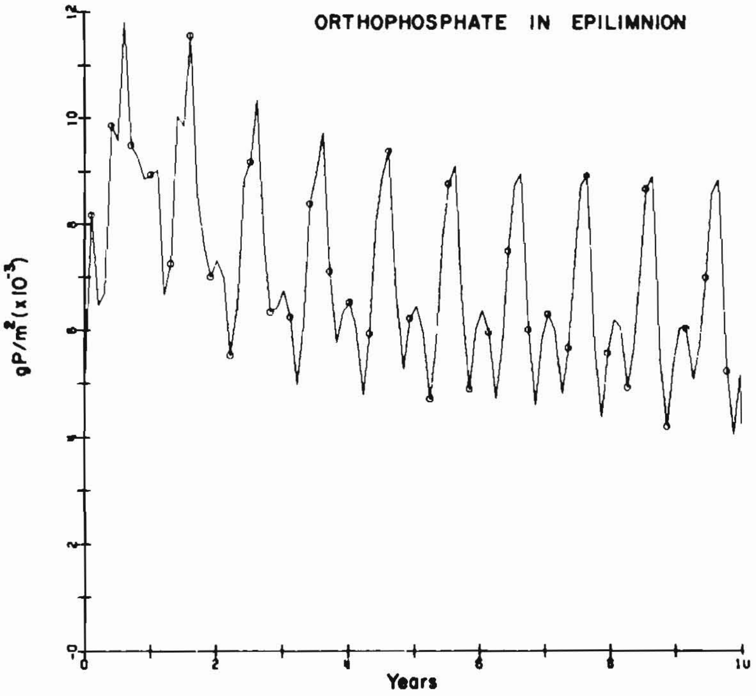


Figure 43. Simulated changes in the level of orthophosphate in the epilimnion for 10 years after the introduction of white amur

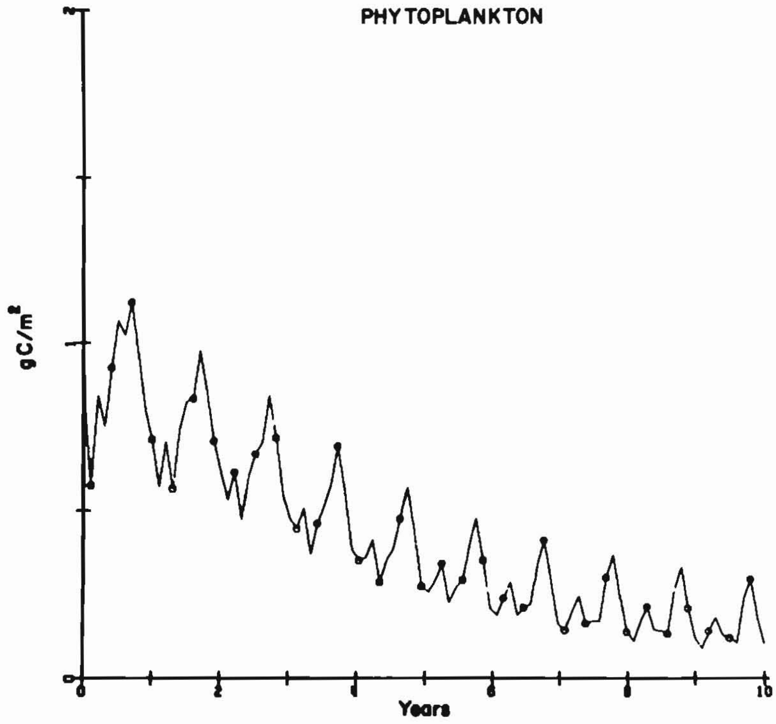


Figure 44. Simulated changes in the biomass of phytoplankton for 10 years after the introduction of white amur

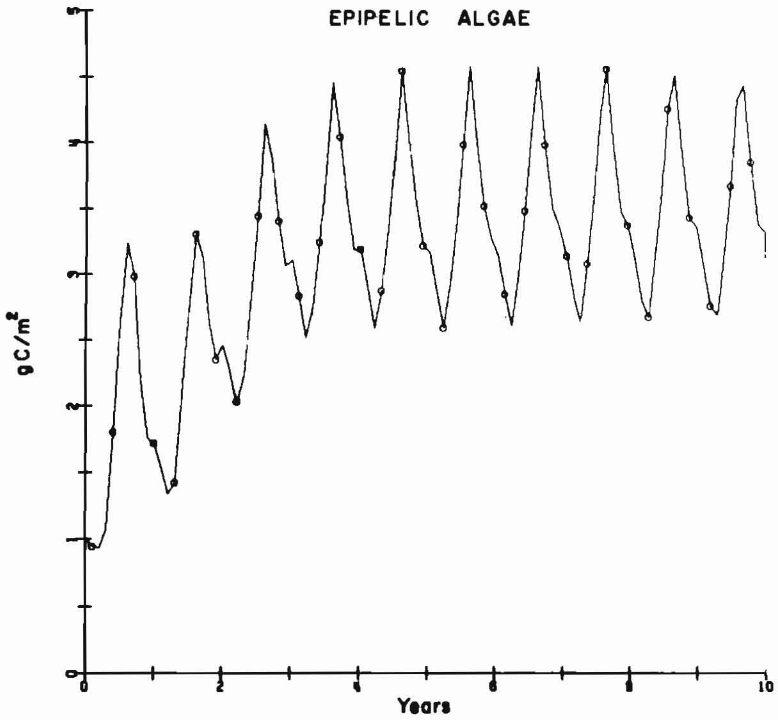


Figure 45. Simulated changes in the biomass of epipelic algae for 10 years after the introduction of white amur

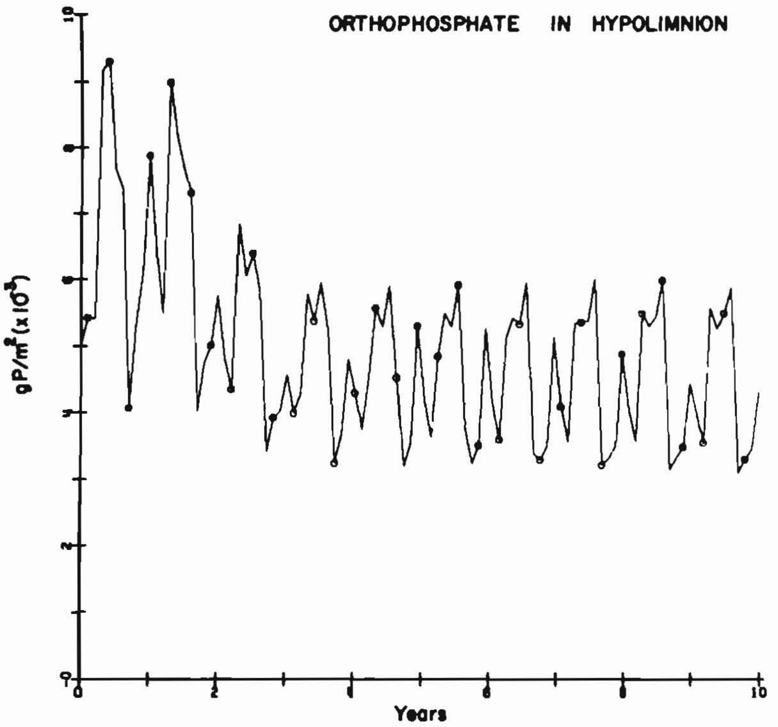


Figure 46. Simulated changes in the level of orthophosphate in the hypolimnion for 10 years after the introduction of white amur

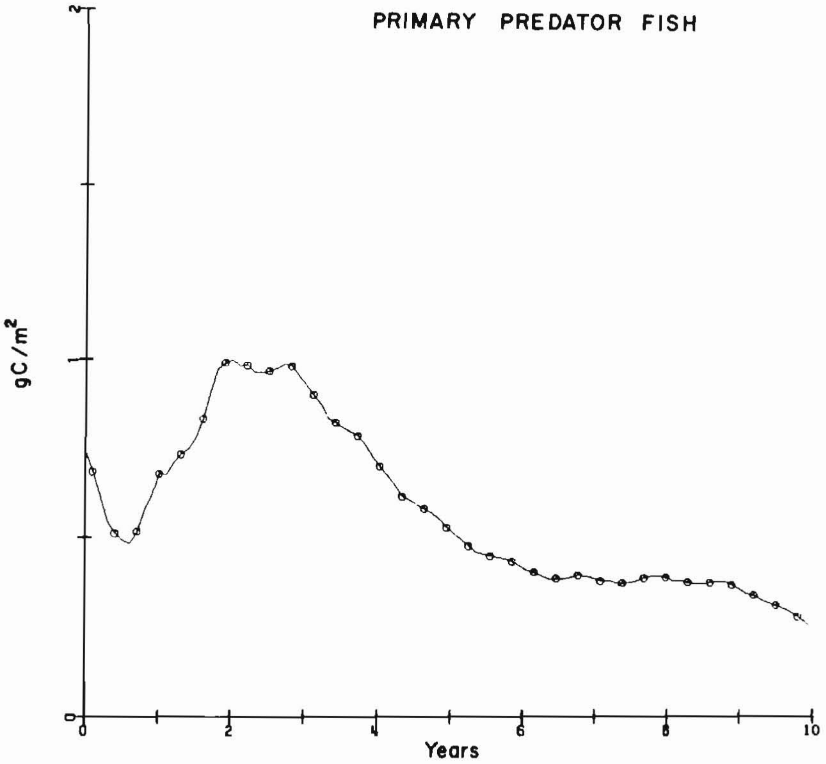


Figure 51. Simulated changes in biomass of the primary predator fish population for 10 years after the introduction of white amur

fish, which feed heavily on benthic invertebrates and other fish, increase significantly (Figure 52) as the cover is removed. After an initial rise, the amount of detritus decreases (Figure 53).

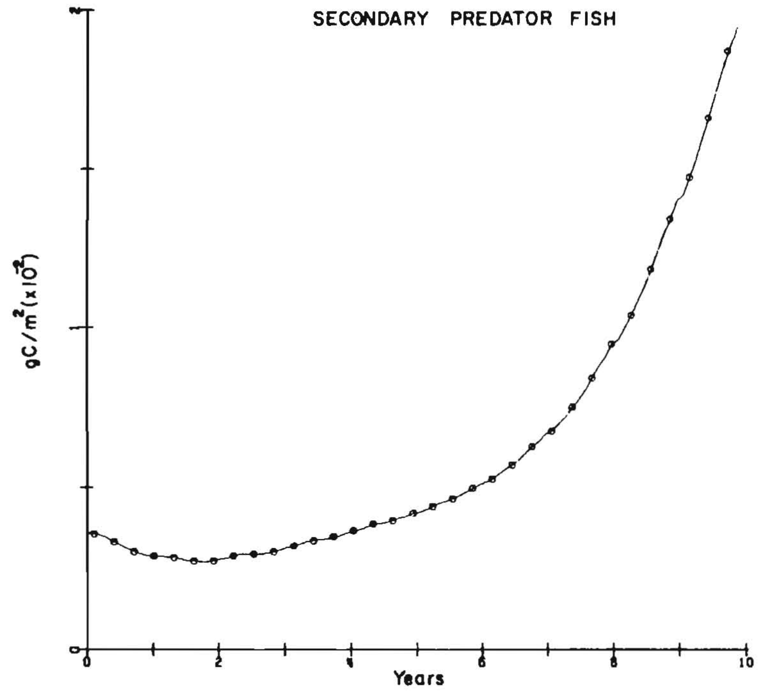


Figure 52. Simulated changes in biomass of the secondary predator fish population for 10 years after the introduction of white amur

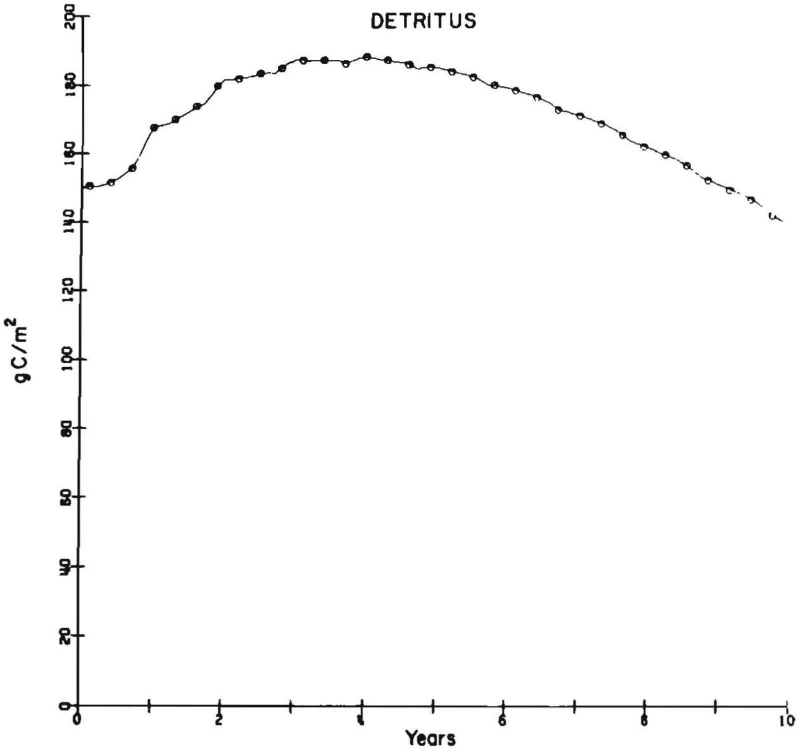


Figure 53. Simulated changes in the amount of detritus in Lake Conway for 10 years after the introduction of white amur

PART V: CONCLUSIONS

92. The Lake Conway ecosystem model as presently formulated contains those state variables which are believed to be essential for describing seasonal and long-term changes in a southeastern lake ecosystem. In the final model, the magnitude of change of the state variables will be determined by conditions in Lake Conway, but the nature and rates of interactions among these state variables should be common to lake ecosystems throughout the region. Predictions could therefore be made of the effect of the white amur on conditions in another lake, given certain morphological, climatological, and biological data about the lake.

93. The current inadequacy of nutrient relationships within the model prevents the model as it is now formulated from being used for sound prediction. Many of the discrepancies between data and simulation can be attributed to treatment of relationships between nutrient availability and productivity. Other discrepancies, such as the failure of the model to produce the standing crop of macrophytic plants that is known to exist, can be investigated experimentally by measuring different growth parameters. Correction of the difficulty with the zooplankton component can be made by testing different assumptions in the model. Other discrepancies may appear or be resolved when all the data from the other research teams have been provided.

94. It is interesting to note the effects of the white amur on the current ecosystem model and to speculate on the significance of the simulated outcome. The increase in epipelic algae may be a phenomenon that is specific to stratified lakes. In a shallower lake or pond, epipelic algae might compete directly with phytoplankton for nutrients, although they would still be shaded by both phytoplankton and macrophytic plants. Singh et al.[88] mention the disappearance of Spirogyra sp. from a 0.04-ha nursery pond after introduction of the white amur. It is doubtful that the algae were consumed. Stevenson mentions that white amur did not eat the Spirogyra sp. that was fed to the fish. Persistence of the algae in this case was presumably due to the continued

feeding of fish meal, which would have sustained it.[12] In such situations, epipelic algae and phytoplankton may well be using the same resources, and neither will survive when a major nutrient source such as macrophytes is removed.

95. The decreases in phytoplankton and zooplankton predicted by the model are corroborated by Terrell,[90] who reported a decrease in phytoplankton and zooplankton in acidic, soft-water ponds to which white amur had been added for weed control tests. He attributed this to precipitation of orthophosphate, iron, and magnesium by organic acids.

96. Stott et al.[91] report that bream in ponds stocked with white amur showed faster growth rates than in control ponds. Production of bass, crappie, and bluegill in an Arkansas lake seemed to increase after introduction of white amur; results for gizzard shad were ambiguous.[92] In the same study, it was noted that phytoplankton and zooplankton blooms frequently result in eutrophic situations when a high stocking rate of white amur causes weeds to be removed rapidly. In cases such as this, input of nutrients from runoff or groundwater seepage may be large enough to dominate the lake after the macrophytes are removed and no longer exert shading or allelopathic effects on the phytoplankton. Stott et al.[91] notes that such a bloom may result "in extremely rich lakes" even when low stocking rates are used. The level of stocking itself probably has little effect.

97. Sutton[93] suggests that white amur release the nutrients tied up in aquatic macrophytes, making them available for other organisms. However, it appears more likely that the fish remove these nutrients almost permanently from use. If sediment respiration exceeds production, long-term use of the white amur may reduce the quantity of sediment on which a crop of submersed macrophytes depends, reversing the successional trends that allowed the weeds to proliferate in the first place. If the assumptions used in the model for nutrient cycling are valid--and many of them are supported in the literature--the model predicts the disappearance of sediment, a parameter that is difficult to measure in situ and would require years to observe. This will be an important component to observe in the Lake Conway model after it has been improved.

98. If successful, the model will therefore serve two purposes: short-term prediction of the effects of white amur on the plants and animals in a lake ecosystem, and long-term prediction of the effects of the fish on the trophic state of the lake itself.

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Table 1

Annual Productivity of Four Lakes and Contributions of Phytoplankton and Macrophytes

Lake and Investigators	Characteristics	Annual Productivity g C/m^2 per year	Range g C/m^2 per day Phytoplankton/ Macrophytes
Lake Wingra, Wisc. (Adams and McCracken[3])	Large, alkaline lake. Littoral zone = 31 percent of lake area; *Myriophyllum* predominates	847 (13.8 percent due to macrophytes)	No data/0-10.8
Sangwin Pond, England (Goulder[4])	Small, shallow gravel pit, enriched. *Ceratophyllum* predominates	1700 (35.3 percent due to macrophytes)	5-12/0-7
Lake Conway, Fla. (this study)	Warm temperate, enriched lake. Littoral zone = 39 percent of lake area; *Nitella* predominates in deep littoral zone, *Potamogeton* and *Vallisneria* in shallow littoral	900 (30 percent due to macrophytes)	0-5/0-9
Lake Lanao, Philippines (Lewis[5])	Large, deep tropical lake	640 (phytoplankton production)	0-5/No data

Table 2

Relative Productivity and Respiration Rates for Submersed Macrophytes at Three Different Temperatures

Temperature T , °C	NP*	R**	GPP†
10	0.72	0.55	0.73
20	1.00	0.74	1.00
30	0.62	1.00	0.93

---

* Net photosynthesis, based on data for Hydrilla, Potamogeton, and Vallisneria.[19]

** Respiration function: $0.63 \times e^{0.03 \cdot T}$

† Gross primary productivity (NP + R); values have been converted to a relative scale.

Table 3

Food Preferences of Herbivorous Fish Found in Lake Conway

Fish	Major Food Items	References
Dorosoma petenense (threadfin shad)	Plankton, benthic invertebrates, detritus	Carlander,[44] Swingle,[45] Burns[46]
D. cepedianum (gizzard shad)	Zooplankton, phytoplankton	Carlander,[44] Cromer and Marzolf[47]
Ictalurus nebulosus (brown bullhead)	Benthic invertebrates, detritus, algae, plants, insects, fish, fish eggs	Carlander,[44] Emig[48]
I. catus (white catfish)	Benthic invertebrates, macrophytes, snails, filamentous algae, detritus	McLane,[49] Miller[50]
Notemigonus crysoleucas (golden shiner)	Phytoplankton, zooplankton, benthic invertebrates	Carlander,[44] McKechnie[51]
Notropis petersoni (coastal shiner)	Filamentous algae and other plants, insect larvae, and nymphs	McLane[49]
Jordanella floridae (flagfish)	Algae and other vegetation	McLane[49]
Erimyzon sucetta (lake chubsucker)	Filamentous algae, other plant matter, detritus, benthic invertebrates	McLane[49]

Table 4

Food Preferences of Adult Primary Predator Fish Found in Lake Conway

Fish	Major Food Items	References
Fundulus seminolis (seminole killifish)	Benthic invertebrates, seeds of aquatic plants	McLane[49]
Lucania goodei (bluefin killifish)	Benthic invertebrates	McLane[49]
Labidesthes sicculus (brook silverside)	Insects and crustaceans	Ewers and Boesel,[52] McLane[49]
Enneacanthus gloriosus (blue-spotted sunfish)	Insect larvae, small crustaceans	Chable,[53] McLane[49]
Lepomis gulosus (warmouth sunfish)	Benthic invertebrates, small fish	Hubbell[54]
L. macrochirus (bluegill)	Zooplankton, benthic invertebrates, crustaceans, aquatic plants	Chable,[53] Emig,[55] Flemer and Woolcott,[56] Huish[57]
L. microlophus (redear sunfish)	Benthic invertebrates	Emig,[58] Huish[57]
L. marginatus (dollar sunfish)	Zooplankton, benthic invertebrates	Chable,[53] McLane[49]
Etheostoma fusiforme (swamp darter)	Benthic invertebrates, zooplankton	McLane[49]
Noturus gyrinus (tadpole madtom)	Zooplankton, benthic invertebrates	Carlander,[44] McLane[49]
Heterandria formosa (least killifish)	Benthic invertebrates, zooplankton, filamentous algae	McLane[49]
Fundulus chrysotus (golden topminnow)	Benthic invertebrates, zooplankton	McLane[49]
Gambusia affinis (mosquitofish)	Insects, zooplankton, filamentous algae	McLane[49]
L. punctatus (spotted sunfish)	Insects, crustaceans	Chable[53]
Ictalurus natalis (yellow bullhead)	Benthic invertebrates, zooplankton, aquatic plants	McLane,[49] Miller[59]
Aphredoderus sayannus (pirate perch)	Benthic invertebrats, zooplankton, aquatic plants	McLane[49]

Table 5

Food Preferences of Secondary Predator Fish Found in Lake Conway

Fish	Major Food Items	References
Lepisosteus platyrhincus (Florida gar)	Fish, crustaceans, insects	Carlander,[44] Crumpton[60]
Esox niger (chain pickerel)	Fish	Buntz,[61] Carlander[44]
Micropterus salmoides (largemouth bass)	Fish, crustaceans, benthic invertebrates	Emig,[62] McLane[49]
Pomoxis nigromaculatus (black crappie)	Fish, benthic invertebrates	Goodson,[63] Huish[57]
Lepisosteus osseus (longnose gar)	Fish, benthic invertebrates	Crumpton,[60] Lagler and Hubbs[64]
Amia calva (bowfin)	Fish, benthic invertebrates, zooplankton	Lagler and Hubbs[64] McLane[49]
Esox americanus (redfin pickerel)	Benthic invertebrates, fish	McLane[49]

Table 6

Phosphorus Budget for Lake Conway

Month	Rainfall* cm	Total Phosphorus Input** g/m^2, from Rainfall	Citrus† Runoff	Urban†† Runoff	Total Monthly Input from All Sources g TP/m^2 per mo
January	12	0.0053	0.0023	0.0297	0.0373
February	7	0.0031	0.0014	0.0175	0.0220
March	11	0.0048	0.0021	0.0273	0.0342
April	7	0.0031	0.0014	0.0175	0.0220
May	12	0.0053	0.0023	0.0297	0.0373
June	17	0.0075	0.0033	0.0423	0.0531
July	16	0.0070	0.0031	0.0395	0.0496
August	18	0.0079	0.0035	0.0447	0.0561
September	29	0.0128	0.0056	0.0720	0.0904
October	3	0.0013	0.0006	0.0073	0.0092
November	2	0.0009	0.0004	0.0049	0.0062
December	7	0.0031	0.0014	0.0175	0.0220
TOTAL	141	0.0621	0.0274	0.3499	0.4394

---

* Precipitation data from Reference 73.

** Shannon and Brezonik report an average concentration of 0.044 g total phosphorus/m^3 in rain.[74] For runoff from citrus and urban lands, they report average total phosphorus loadings of 0.018 and 0.11 g/m^2 per year, respectively. Monthly loading rates from land sources were determined by using the following formula:

Monthly increment = (area of land type in basin) × (yearly loading rate) × (percent of total precipitation which occurred during that month)

This equation assumes that runoff from the land is immediate and directly proportional to the rain which falls upon it.

† The area of citrus lands in the drainage basin is 11.254×10^6 m^2 (E. Blancher, personal communication).

†† The area of urban lands in the drainage basin is 23.47×10^6 m^2 (E. Blancher, personnal communication).

Table 7

Growth Efficiencies of White Amur of Different Ages and Weights

Age, years	Weight, g	Growth Food Intake* percent
0-2	--	10**
2-5	--	--†
5-6	--	--**
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 are calculated from wet weights of both food and fish.

** Data summarized in Fischer and Lyakhnovich.[9]

† Data from Singh et al.[88]

†† Ages estimated from data summarized by Fischer and Lyakhnovich.[9]

Table 8

Daily Weight-Specific Digestion Rates of White Amur

Initial Wet Weight, g	Daily Food Intake, g	Intake Biomass, percent
1000	115-1350	12-135*
2000	500-2300	25-115*
--	--	30*
--	--	30-130**

* From data summarized by Fischer and Lyakhnovich.[9]

** Stott.[89]

APPENDIX A: PROGRAM LISTING FOR THE LAKE CONWAY MODEL

```
INITIAL

*STATE VARIABLES
INCON ICFN=9.21E-4
INCON ICFB=.4182
INCON ICBI=1.73
INCON ICDT=150.
INCON ICEP=1.
INCON ICHF=.07
INCON ICPEPI=.005
INCON ICPF1=.74
INCON ICPF2=.36
INCON ICPHYP=.005
INCON ICPP=.84
INCON ICTU=30.
INCON ICVP=45.
INCON ICZP=.21

*BENTHIC INVERTEBRATE CONSTANTS
CONST KBI1=1.
CONST KBI2=8.28E-3
CONST KBI3=1.26
CONST KBI4=.4
CONST KBI5=.1
PARAM BIASSM=.689

*DETRITUS CONSTANTS
CONST KJ=21.75
CONST KK=10.87

*EPIPELIC ALGAE CONSTANTS
CONST K1EP=313.48
CONST K2EP=3.2
CONST K5EP=1.34
PARAM EPMEFF=.10
PARAM EP50=350.0

*HERBIVOROUS FISH CONSTANTS
CONST KHF1=.462
CONST KHF2=.183
CONST KHF3=3.41E-3
CONST KHF4=.153
CONST KHF5=.121
CONST KHF6=1.
CONST KHF7=1.5
CONST KHF8=.1
CONST KHF9=.1
PARAM HFASSM=.69
      KPHHF1=2.44E-4

*HYPOLIMNETIC PHOSPHORUS CONSTANTS
CONST KPHYP1=.06
CONST KPHYP2=100.
PARAM PEPX=.009
PARAM PHYPX=.005
CONST KC2P=.01
CONST PCTPIF=.5

*KC2P*PCTPIF IS THE AMOUNT OF NON REFRACTORY P IN A FISH;KC2P CONVERTS
*  FISH CARBON TO PHOSPHORUS; 50 PERCENT OF THIS IS AVAILABLE FOR
*  REMINERALIZATION

*LIGHT FUNCTION CONSTANTS
CONST KC=.949
CONST KD=-.456
CONST KI=-.28
CONST KM=-.43
PARAM REFLCT=.05
CONST Z=2.0

*PHYTOPLANKTON CONSTANTS
CONST K1PP=372.
CONST K2PP=.76
CONST K4PP=36.
```

```
CONST K6PP=10.
CONST K7PP=.195
CONST K8PP=.805
CONST K9PP=0.
PARAM PPMEFF=.0098
PARAM PP50=14597.

*THE AMOUNT OF PHOSPHORUS RELEASED FROM DEAD PHYTOPLANKTON IS EQUAL TO
*  75 PERCENT OF THAT AVAILABLE. THE OTHER 25 PERCENT IS ACCOUNTED FOR
*  IN ZOOPLANKTON EXCRETION

*PRIMARY PREDATOR FISH CONSTANTS
CONST KPF11=.85
CONST KPF12=7.07E-3
CONST KPF13=4.
CONST KPF14=.318
CONST KPF15=1.7E-2
CONST KPF16=3.8
CONST KPF17=.1
PARAM P1ASSM=.8
CONST KPHP11=2.44E-4

*SECCNDARY PREDATOR FISH CONSTANTS
CONST KPF21=.298
CONST KPF22=.166
CONST KPF23=2.98E-2
CONST KPF24=.1
CONST KPF25=.6
CONST KPF26=5.95E-2
PARAM PF2ASM=1.

*TUBER CONSTANTS
CONST KTU1=1.5
CONST KTU2=16

*VASCULAR PLANT CONSTANTS
CONST K1VP=2.2E-2
CONST K3VP=.58
CONST K6VP=.1
CONST K7VP=.05
CONST K8VP=.65
CONST K9VP=.7
CONST KCAL2C=.11
PARAM VPMEFF=.1426
PARAM VP50=2726.48

*WHITE AMUR CONSTANTS
CONST K1FN=.0833
CONST K1FB=1.94
CONST K2FB=1.0
CONST K3FB=.6065
CONST KW2C=.036
CONST KPHFB1=2.44E-4
*YOUNG PRIMARY PREDATOR FISH CONSTANTS
CONST KYNG1=3.53E-2
CONST KYNG2=1.4E-2
CONST KYNG3=2.62E-4
CONST KYNG4=3.37E-2
CONST KYNG5=8.96E-3
CONST KYNG6=.106
CONST KYNG7=8.
CONST KYNG8=3.76E-2
CONST KYNG9=.1
PARAM YNGASM=.69
      KPHYG1=2.44E-4
*ZOOPLANKTON CONSTANTS
CONST KZP1=4.
CONST KZP2=9.57
CONST KZP4=.142
CONST KZP5=6.5
PARAM ZPASSM=.47


*OTHER CONSTANTS AND PARAMETERS
PARAM KOXIC=6.4
PARAM KOVR1=3.01
PARAM KOVR=1.37
```

```
FUNCT DCY=0.0,0.,0.1,1.,0.2,2.,0.3,3.,0.4,4.,...
          0.5,5.,0.6,6.,0.7,7.,0.8,8.,0.9,9.,...
          1.0,0.,1.1,1.,1.2,2.,1.3,3.,1.4,4.,...
          1.5,5.,1.6,6.,1.7,7.,1.8,8.,1.9,9.,...
          2.0,0.,2.1,1.,2.2,2.,2.3,3.,2.4,4.,...
          2.5,5.,2.6,6.,2.7,7.,2.8,8.,2.9,9.,...
          3.0,0.,3.1,1.,3.2,2.,3.3,3.,3.4,4.,...
          3.5,5.,3.6,6.,3.7,7.,3.8,8.,3.9,9.,...
          4.0,0.,4.1,1.,4.2,2.,4.3,3.,4.4,4.,...
          4.5,5.,4.6,6.,4.7,7.,4.8,8.,4.9,9.,...
          5.0,0.,5.1,1.,5.2,2.,5.3,3.,5.4,4.,...
          5.5,5.,5.6,6.,5.7,7.,5.8,8.,5.9,9.,...
          6.0,0.,6.1,1.,6.2,2.,6.3,3.,6.4,4.,...
          6.5,5.,6.6,6.,6.7,7.,6.8,8.,6.9,9.,...
          7.0,0.,7.1,1.,7.2,2.,7.3,3.,7.4,4.,...
          7.5,5.,7.6,6.,7.7,7.,7.8,8.,7.9,9.,...
          8.0,0.,8.1,1.,8.2,2.,8.3,3.,8.4,4.,...
          8.5,5.,8.6,6.,8.7,7.,8.8,8.,8.9,9.,...
          9.0,0.,9.1,1.,9.2,2.,9.3,3.,9.4,4.,...
          9.5,5.,9.6,6.,9.7,7.,9.8,8.,9.9,9.,...
          10.0,0.,10.1,1.

FUNCT SN=0.,61.4E3,.85,71.40E3,1.64,134.8E3,2.5,165.0E3,3.32,84.00E3,...
         4.16,113.0E3,5.0,150.0E3,5.84,143.0E3,6.69,113.9E3,7.51,...
         108.0E3,8.33,71.4E3,9.15,93.0E3,10.,61.4E3

FUNCT DG1=0.,.58,.53,.55,1.38,.85,2.3,.84,3.04,1.0,4.07,.99,4.95,.90,...
          5.74,.800,6.39,.950,7.38,.97,8.15,.88,9.93,.65,10.,.58

FUNCT DG2=0.,.20,.53,.20,1.38,.25,2.3,.25,3.04,.47,4.07,.49,4.95,.60,...
          5.74,.670,6.39,.570,7.38,.50,8.15,.32,9.93,.21,10.,.20
FUNCT DG3=0.,.92,.53,.90,1.38,1.0,2.3,.99,3.04,.98,4.07,.97,4.95,.95,...
          5.74,.920,6.39,.950,7.38,.96,8.15,.99,9.93,.94,10.,.92

FUNCT DG4=0.,.64,.53,.52,1.38,.76,2.3,.78,3.04,.91,4.07,.94,4.95,1.0,...
          5.74,1.06,6.39,1.03,7.38,.98,8.15,.80,9.93,.65,10.,.64

FUNCT DG6=0.,.36,.53,.34,1.38,.52,2.3,.55,3.04,.82,4.07,.87,4.95,1.1,...
          5.74,1.24,6.39,1.03,7.38,.97,8.15,.60,9.93,.38,10.,.36

FUNCT ORTHO=0.,.0145,.85,.0086,1.64,.0133,2.5,.0086,3.32,.0145,4.16,...
            .0207,5.0,.0193,5.84,.0219,6.69,.0353,7.51,.0036,8.33,...
            .0024,9.15,.0086,10.0,.0145

FUNCT PERCNT=0.0,.85,1000.,.888,2000.,.915,3000.,.94,4000.,.96,5000.,...
      .97,6000.,.98,7000.,.99,8000.,.995,9000.,.998,1.E4,1.,1.E5,1.

FUNCT ZPT=(0.,.66),(.53,.65),(1.38,.77),(2.3,.76),(3.04,.89),...
          (4.07,.91),(4.95,.97),(5.74,1.),(6.39,.94),(7.38,.92),...
          (8.15,.79),(9.93,.67),(10.,.67)

FUNCT BIT=(0.,.45),(.53,.45),(1.38,.58),(2.3,.7),(3.04,.85),...
          (4.07,.89),(4.95,.96),(5.74,1.),(6.39,.98),(7.38,.96),...
          (8.15,.77),(9.93,.51),(10.,.51)

FUNCT FSHT=(0.,.35),(.53,.35),(1.38,.67),(2.3,.7),(3.04,.91),...
           (4.07,.93),(4.95,.98),(5.74,1.),(6.39,.97),(7.38,.96),...
           (8.15,.75),(9.93,.41),(10.,.41)

FUNCT HEIGHT=(0.0,2.0),(5.18,1.9),(9.69,1.8),(12.78,1.7),(15.3,1.6),...
      (17.67,1.5),(19.82,1.4),(21.84,1,3),(23.74,1.2),(25.31,1.1),...
      (26.52,1.),(27.73,.9),(28.52,.8),(28.97,.7),(29.32,.6),...
      (29.51,.5),(29.58,.4),(29.6,.3),(200.,.2)

FUNCT SHADE=(0.,1.),(150.,.01)

FUNCT BLOCK=(0.,1.),(150.,.5)

FUNCTION PLANTS=(0.,2.),(45.,1.),(130.,1.),(200.,.5)

FUNCT ORGLC1=(0.,.01),(15.,.14),(30.,.18),(45.,.14),(60.,.01),(100.,.01)
FUNCT ORGLC2=(0.,.01),(5.,.14),(10.,.18),(15.,.14),(20.,.01),(100.,.01)

DYNAMIC

      TIMEX=AFGEN(DCY,TIME)
      SUN=AFGEN(SN,TIMEX)
      OPINPT=AFGEN(ORTHO,TIMEX)
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```
       T1PP=AFGEN(DG1,TIMEX)
       T2PP=AFGEN(DG2,TIMEX)
       T1EP=AFGEN(DG1,TIMEX)
       T2EP=AFGEN(DG1,TIMEX)
       TIVP=AFGEN(DG3,TIMEX)
       T2VP=AFGEN(DG4,TIMEX)
       T2NC=AFGEN(DG6,TIMEX)

       ZPRIME=AFGEN(HEIGHT,VP)
       RATIO=AFGEN(PERCNT,I)
       VPSHD1=AFGEN(SHADE,VP)
       VPSHAD=AFGEN(BLOCK,VP)

ZPTEMP=AFGEN(ZPT,TIMEX)
FSHTMP=AFGEN(FSHT,TIMEX)
BITEMP=AFGEN(BIT,TIMEX)
CPPRLS=AFGEN(ORGLC1,GPPPP)
CEPRLS=AFGEN(ORGLC2,GPPEP)

*THE PLANT EQUATIONS INCLUDE THE FOLLOWING VARIABLES
*   GPPXX IS GROSS PRIMARY PRODUCTIVITY
*   XXRESP IS RESPIRATION
*   XXHERB IS LOSS OF BIOMASS DUE TO HERBIVORY
*   XXLEAC IS LEACHING OF DISSOLVED ORGANIC CARBON
*   CXXRLS CONTROLS ACTIVE SECRETION OF ORGANIC COMPOUNDS.  IT
*       IS GREATEST AT INTERMEDIATE LEVELS OF PRODUCTIVITY.
*SUBMERSED VASCULAR PLANT-EPIPHYTIC ALGAE COMPLEX (VP)

       VP=INTGRL(ICVP,GPPVP+SPROUT-VPRESP-SLOUGH-PRFORM-VPHERB)
       GPPVP=K1VP*VPLITE*VP*(VPMEFF/(1.+VPLITE/VP50))*T1VP*KCAL2C
       VPLITE=SUN*(1.-REFLCT)*(KC*EXP(KD*ZPRIME+KI*ZPRIME*PP/Z))

*VPLITE IS THE LIGHT AVAILABLE FOR VP PHOTOSYNTHESIS AND IS A
*  FUNCTION OF THE HEIGHT OF THE VP AND THE OPTICAL PROPERTIES OF H20
*VPMAX IS THE MAXIMUM OBSERVED BIOMASS OF VP
*VPMEFF IS THE MAXIMUM PHOTOSYNTHETIC EFFICIENCY OF VP
*VP50 IS THE LIGHT INTENSITY AT WHICH 50 PERCENT OF VPMEFF OCCURS
*REFLECT IS THE DECIMAL PERCENT OF SOLAR ENERGY WHICH IS REFLECTED
*   AND CHANGES SEASONALLY
*ZPRIME CORRELATES CUMULATIVE VP BIOMASS WITH THE DISTANCE FROM THE
*   TOP OF THE CANOPY TO THE WATER SURFACE; THE SECOND TERM IN THE
*   EXPONENT CALCULATES SHADING OF VP BY PHYTOPLANKTON

       VPRESP=K3VP*VP*T2VP
       VPHERB=BIXVP+HFXVP+YNGXVP+ZPXVP+KW2C*FCNSMP

*SLOUGH=SLOUGHING OF LEAVES AND OTHER PLANT PARTS
       SLOUGH=K6VP*VP+K9VP*VP*DIE
       FALL=IMPULS(.75,1.)
       DIE=PULSE(.25,FALL)

*P04-P LEACHING BY VP (VPPLCH)
       VPPLCH=KC2P*VPRESP*.5

*SLOUGHED MATERIAL WHICH REACHES THE SEDIMENTS (VP2SED)
       VP2SED=K8VP*SLOUGH

*P04-P RELEASED UPON DECAY OF SLOUGHED MATERIAL IN H20 COLUMN (PSLUF)
       PSLUF=KC2P*K7VP*SLOUGH

*FORMATION AND GERMINATION OF PROPAGULES AFFECT
* VASCULAR PLANT BIOMASS IN THE SPRING AND FALL

*TUBERS (TU)
       TU=INTGRL(ICTU,PRFORM-SPROUT)
       PRFORM=DIE*KTU1*VP
       SPROUT=BIRTH*KTU2*TU

*PHYTOPLANKTON
       PP=INTGRL(ICPP,GPPPP-PPRESP-PPLEAC-PPHERB-SINKNG)
       GPPPP=K1PP*PPLITE*(PPMEFF/(1.+PPLITE/PP50))*PEPI*T1PP*KCAL2C*PP

*PPLITE IS THE LIGHT AVAILABLE FOR PP PHOTOSYNTHESIS AND IS A FUNCTION
*   OF THE OPTICAL PROPERTIES OF H20, SELFSHADING, AND SHADING BY VP
*PPMEFF IS THE MAXIMUM PHOTOSYNTHETIC EFFICIENCY OF PHYTOPLANKTON
*PP50 IS THE LIGHT INTENSITY AT WHICH 50 PERCENT OF PPMEFF OCCURS
*THE EXPONENT TERM REPRESENTS SELF SHADING;VPSHAD=SHADING BY VP
       PPLITE=SUN*(1.-REFLCT)*K2PP*EXP(KM*PP)*VPSHAD
```

```
       PPRESP=K4PP*T2PP*PP
       PPLEAC=CPPRLS*GPPPP
       PPHERB=ZPXPP+HFXPP+YNGXPP

*SINKNG=SETTLING OUT OF PHYTOPLANKTON
       SINKNG=K6PP*PP

*PP2SED=THE PERCENTAGE OF SINKING PHYTOPLANKTON WHICH REACHES
*THE SEDIMENT
       PP2SED=K8PP*SINKNG

*PO4-P RELEASED UPON DECAY OF SINKING PHYTOPLANKTON=PSINK
       PSINK=KC2P*(SINKNG-PP2SED)*.5
       PPPART=K7PP*K6PP*PP

*EPIPELIC ALGAE (EP)
       EP=INTGRL(ICEP,GPPEP-EPRESP-EPLEAC-EPHERB-EPMORT)
       GPPEP=K1EP*EPLITE*(EPMEFF/(1.+EPLITE/EP50))*PHYPO*T1EP*KCAL2C*EP

*EPMEFF IS THE MAXIMUM PHOTOSYNTHETIC EFFICIENCY OF EP
*EP50 IS THE LIGHT INTENSITY AT WHICH 50 PERCENT OF PPMEFF OCCURS

*EPLITE IS THE LIGHT AVAILABLE FOR EP PHOTOSYNTHESIS AND IS A
*  FUNCTION OF THE OPTICAL PROPERTIES OF H2O, AND SHADING BY VP AND PP
       EPLITE=SUN*(1.-REFLCT)*EXP(KD*Z+KM*PP)*VPSHD1

       EPRESP=K2EP*T2EP*EP
       EPLEAC=CEPRLS*GPPEP
       EPHERB=ZPXEP+HFXEP+PF1XEP+YNGXEP

*EPMORT=MORTALITY OF EPIPELIC ALGAE
       EPMORT=K5EP*EP

*THE ANIMAL EQUATIONS INCLUDE THE FOLLOWING VARIABLES
*  XXASSM*XXFOOD (OR XXXASM*XXXFD) IS THE AMOUNT OF FOOD ASSIMILATED
*  XXRESP (OR XXXRSP) IS THE METABOLIC RATE
*  XXPRED (OR XXXPRD) IS THE LOSS DUE TO PREDATION

*THE ABILITY OF A PREDATOR TO CAPTURE ITS PREY IS IN PART DEPENDENT ON
*  THEIR RELATIVE ABILITIES TO FUNCTION AT THE AMBIENT TEMPERATURE
       BIZP=BITEMP/ZPTEMP
       FSHBI=FSHTMP/BITEMP
       FSHZP=FSHTMP/ZPTEMP


*BENTHIC INVERTEBRATES (BI)
       BI=INTGRL(ICBI,BIASSM*BIFOOD-BIRESP-BIPRED)

       BIFOOD=BIXZP+BIXVP+BIXDT
       BIEATN=BIASSM*BIFOOD
       BIXZP=KBI1*BI*ZP*BIZP*BITEMP
       BIXVP=KBI2*BI*VP*BITEMP
       BIXDT=KBI3*BI*BITEMP

       BIRESP=KBI4*BI*BITEMP
       BIPRED=HFXBI+PF1XBI+YNGXBI+PF2XBI
       BIEGEX=(1.-BIASSM)*BIFOOD
       PHBIEE=KC2P*BIEGEX

*HERBIVOROUS FISH (HF)
       HF=INTGRL(ICHF,HFASSM*HFFOOD-HFRESP-HFPRED)

       HFFOOD=HFXEP+HFXPP+HFXVP+HFXDT+HFXBI+HFXZP
       HFEATN=HFASSM*HFFOOD
       HFXEP=KHF1*EP*HF*FSHTMP
       HFXPP=KHF2*PP*HF*FSHTMP
       HFXVP=KHF3*VP*HF*FSHTMP
       HFXDT=KHF4*HF*FSHTMP
       HFXBI=KHF5*HF*BI*FSHBI*FSHTMP
       HFXZP=KHF6*HF*ZP*FSHZP*FSHTMP

       HFRESP=KHF7*HF*FSHTMP
       HFPRED=KPF22*HF*PF2*FSHTMP*COVER
       HFEGEX=(1.-HFASSM)*HFFOOD
       PHHFEE=KPHHF1*HFEGEX
```

```
*PRIMARY PREDATOR FISH (PF1)
       PF1=INTGRL(ICPF1,P1ASSM*PF1FD+GROWTH-BREED-PF1PRD-PF1RSP)

       PF1FD=PF1XBI+PF1XVP+PF1XZP+PF1XEP
       PF1ETN=P1ASSM*PF1FD
       PF1XBI=KPF11*BI*PF1*FSHBI*FSHTMP
       PF1XVP=KPF12*VP*PF1*FSHTMP
       PF1XZP=KPF13*ZP*PF1*FSHTMP*FSHZP
       PF1XEP=KPF14*EP*PF1*FSHTMP

       PF1RSP=KPF16*PF1*FSHTMP
       PF1PRD=KPF21*PF2*PF1*FSHTMP*COVER

       PF1EGX=(1.-P1ASSM)*PF1FD
       PHP1EE=KC2R*PF1EGX

*  BREED AND GROWTH REFER TO REPRODUCTION AND RECRUITMENT OF PRIMARY
*    PREDATOR FISH                                   .
       GROWTH=KYNG7*YNG*FSHTMP
       BREED=KPF15*PF1*BIRTH/DELT
       BIRTH=PULSE(.1,SPRING)
       SPRING=IMPULS(.3,1.)

*YOUNG PRIMARY PREDATOR FISH
       YNG=INTGRL(0.,BREED+YNGASM*YNGFD-GROWTH-YNGRSP-YNGPRD)

       YNGFD=YNGXEP+YNGXPP+YNGXVP+YNGXDT+YNGXBI+YNGXZP
       YNGETN=YNGASM*YNGFD
       YNGXEP=KYNG1*EP*YNG*FSHTMP
       YNGXPP=KYNG2*PP*YNG*FSHTMP
       YNGXVP=KYNG3*VP*YNG*FSHTMP
       YNGXDT=KYNG4*YNG*FSHTMP
       YNGXBI=KYNG5*YNG*BI*FSHTMP*FSHBI
       YNGXZP=KYNG6*YNG*ZP*FSHTMP*FSHZP

       YNGRSP=KYNG8*YNG*FSHTMP

       YNGPRD=KPF23*PF2*YNG*FSHTMP*COVER
       YNGEGX=(1.-YNGASM)*YNGFD
       PHYNGE=KC2P*YNGEGX
       ALLHF=PF1+YNG
       ALLF=HF+PF1+PF2+YNG

*SECONDARY PREDATOR FISH (PF2)
       PF2=INTGRL(ICPF2,PF2ASM*PF2FD-PF2RSP-PF2DTH)
       PF2FD=PF1PRD+HFPRED+YNGPRD+PF2XBI
       PF2XBI=KPF24*BI*PF2*FSHTMP*FSHBI*COVER
       PF2ETN=PF2ASM*PF2FD
       COVER=AFGEN(PLANTS,VP)
       PF2RSP=KPF25*PF2*FSHTMP

*  PF2DTH IS THE DEATH RATE OF SECONDARY PREDATOR FISH
       PF2DTH=KPF26*PF2*FSHTMP

*ZOOPLANKTON (ZP)
       ZP=INTGRL(ICZP,ZPASSM*ZPFOOD-ZPRESP-ZPPRED)

       ZPFOOD=ZPXEP+ZPXPP+ZPXVP
       ZPEATN=ZPASSM*ZPFOOD
       ZPXEP=KZP1*EP*ZP*ZPTEMP
       ZPXPP=KZP2*PP*ZP*ZPTEMP
       ZPXVP=KZP4*VP*ZP*ZPTEMP

       ZPRESP=KZP5*ZP*ZPTEMP
       ZPPRED=BIXZP+PF1XZP+HFXZP+YNGXZP
       ZPEGEX=(1.-ZPASSM)*ZPFOOD
       PHZPEE=KC2R*ZPEGEX*.25

*EPILIMNETIC PHOSPHORUS EQUATIONS
PEPI=INTGRL(ICPERI,OPINPT+VPPLCH+PSLUF+KC2P*(PPLEAC+PPRESP*.5-GPPPP)...
               +PHZPEE+PHHFEE+PHP1EE+PHYNGE+PHFBEE+TRNOVR*(PHYPO-PEPI))

*HYPOLIMNETIC PHOSPHORUS EQUATIONS
PHYPO=INTGRL(ICPHYP,KC2P*KK*T2NC*ANOXIC+KPHYP1*KC2P*KJ*T2NC*AEROBC...
               +PSLUF+PSINK-KC2P*(GPPEP-(EPRESP*.5)-EPLEAC-...
               (EPMORT*.5))+PHBIEE+KC2P*PCTPIF*(PF2DTH+KHF9*HFRESP...
               +KPF17*PF1RSP+YNGRSP+FMORT)+TRNOVR*(PEPI-PHYPO))
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```
*WHITE AMUR EQUATIONS
*FN=FISH NUMBER,FB=TOTAL FISH BIOMASS, I=BIOMASS/INDIVIDUAL,
*FCNSMP=CONSUMPTION OF AQUATIC PLANTS BY THE WHITE AMUR
*FASSIM=PERCENT OF CONSUMPTION WHICH IS ASSIMILATED
*FRESP=RESPIRATION OF THE WHITE AMUR
*FMORT=DIE-OFF OF THE WHITE AMUR

       FN=INTGRL(ICFN,-K1FN*FN)
       FB=INTGRL(ICFB,FASSIM-FRESP-FMORT)
       FCNSMP=K1FB*K2FB*FB*VP*FSHTMP
       FASSIM=K3FB*FCNSMP
       FEGEX=KW2C*(FCNSMP-FASSIM)
       PHFBEE=KPHFB1*FEGEX
       FRESP=K5FB*FB*FSHTMP
       FMORT=K1FN*FN*I
*VARIABLE COEFFICIENT K5FB ADJUSTS RESPIRATORY LOSSES ACCORDING TO THE
*  RATIO OF ((FRESP+FMORT)/FASSIM). THE RATIO VARIES BETWEEN 0.85 FOR
*  A 0-2 YEAR OLD FISH AND 1.0 FOR A 5-6 YEAR OLD FISH
       K5FB=(RATIO*FASSIM-FMORT)/(FB*FSHTMP)
       I=FB/FN

       ANOXIC=AND(AN,OXIC)
       AN=COMPAR(TIMEX,2.2)
       OXIC=COMPAR(KOXIC,TIMEX)
       AEROBC=NAND(AN,OXIC)
       TRNOVR=IOR(ISTRM1,ISTRM2)
       ISTRM1=AND(TRN1,OVR1)
       TRN1=COMPAR(TIMEX,2.49)
       OVR1=COMPAR(KOVR1,TIMEX)
       ISTRM2=EOR(TRN,OVR)
       TRN=COMPAR(TIMEX,7.5)
       OVR=COMPAR(KOVR,TIMEX)

*DETRITUS EQUATIONS
       DT=INTGRL(ICDT,.9*SLOUGH+PP2SED+.75*ZPEGEX+BIEGEX+HFEGEX+...
          PF1EGX+YNGEGX+KBI5*BIRESP+KHF8*HFRESP+KPF17*PF1RSP+...
          KYNG9*YNGRSP+PF2DTH-HFXDT-BIXDT-YNGXDT+FEGEX+FMORT-DETRSP)
       DETRSP=KJ*T2NC*AEROBC+KK*T2NC*ANOXIC


NOSORT

*THE FOLLOWING EQUATIONS SCALE THE PRINTOUT SO THAT THE MINIMUM IS ZERO

       IF(TIME-10.)1,2,2
1      FISH=ALLF
       FISHNO=FN
       FISHBI=FB
       VASC=VP
       PHYTO=PP
       ALGAE=EP
       INVERT=BI
       ZOOPL=ZP
       HERBF=HF
       PREDF1=PF1
       PREDF2=PF2
       YOUNG=YNG
       DETRTS=DT
       PHOS1=PEPI
       PHOS2=PHYPO
       ALLPF1=ALLHF
       GO TO 3
2      FISH=0.
       FISHBI=0.
       FISHNO=0.
       VASC=0.
       PHYTO=0.
       ALGAE=0.
       INVERT=0.
       ZOOPL=0.
       HERBF=0.
       PREDF1=0.
       PREDF2=0.
       YOUNG=0.
       DETRTS=0.
       PHOS1=0.
       PHOS2=0.
       ALLPF1=0
3      CONTINUE
```

```
TERMINAL
METHOD RECT
TIMER DELT=1.E-3,FINTIM=10.10,OUTDEL=.101
END
STOP

ENDJOB
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APPENDIX B: EXPLANATION OF TERMS USED IN THE PROGRAM*

Term in Equation in Figure 12	Term in Computer Program	Explanation
	Phytoplankton (Q_1)	
$K_{11} \cdot S \cdot (1 - R) \cdot K_{12} \cdot e^{-K_{13} \cdot Q_1} \cdot f_2Q_2$	K1PP*PPLITE	Availability of light
$\frac{K_{14}}{1 + S \cdot (1 - R) \cdot K_{12} \cdot e^{-K_{13} \cdot Q_1} \cdot f_2Q_2 \cdot K_{15}}$	$\frac{\mathrm{PPMEFF}}{\mathrm{1 + PPLITE/PP50}}$	Photosynthetic rate at available light level
Q_{11}	PEPI	Level of orthophosphate in epilimnion
T_8	T1PP	Effect of temperature on photosynthesis
K_{27}	KCAL2C	Conversion from kilocalories to carbon for photosynthesis
Q_1	PP	Phytoplankton biomass
$fY \cdot$ (product of above terms)	CPPRLS*GPPPP (PPLEAC)	Leaching of organic carbon; rate varies with rate of photosynthesis
$K_{17} \cdot T_9 \cdot Q_1$	K4PP*T2PP*PP (PPRESP)	Respiration rate
$Q_1 \cdot K_{63} \cdot Q_6 \cdot T_1$	KHF2*PP*HF*FSHTMP (HFXPP)	Consumption by herbivorous fish
$Q_1 \cdot K_{43} \cdot Q_4 \cdot T_5$	KZP2*PP*ZP*ZPTEMP (ZPXPP)	Consumption by zooplankton
$Q_1 \cdot K_{83} \cdot Q_8 \cdot T_1$	KYNG2*PP*YNG*FSHTMP (YNGXPP)	Consumption by young primary predator fish
$K_{18} \cdot Q_1$	K6PP*PP (SINKNG)	Settling of phytoplankton to sediments

Term in Equation in Figure 11	Term in Computer Program	Explanation
	Macrophytes and Epiphytic Algae (Q_2) and Tubers (Q_{13})	
$K_{21} \cdot S \cdot (1 - R) \cdot \left[K_1 \cdot e^{-(K_2Z'+K_3Z' \cdot Q_1/Z)}\right]$	K1VP*VPLITE	Availability of light
$\frac{E_{Q_2}}{1 + L_{Q_2}/L_{Q_{2-50}}}$	$\frac{\mathrm{VPMEFF}}{\mathrm{1 + VPLITE/VP50}}$	Photosynthetic rate at available light level
Q_2	VP	Macrophyte biomass
T_{10}	T1VP	Effect of temperature on photosynthesis
K_{27}	KCAL2C	Conversion from kilocalories to carbon for photosynthesis
$fY \cdot K_{132} \cdot Q_{13}$	BIRTH*KTU2*TU (SPROUT)	Tuber germination in spring

(Continued)

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* A program listing for the Lake Conway model is given in Appendix A.

Term in Equation in Figure 11	Term in Computer Program	Explanation
	Macrophytes and Epiphytic Algae (Q_2) and Tubers (Q_{13}) (Continued)	
$K_{24} \cdot Q_2 \cdot T_{11}$	K3VP*VP*T2VP (VPRESP)	Respiration rate
$K_{25} \cdot Q_2 - fY \cdot K_{26} \cdot Q_2$	K6VP*VP + K9VP*VP*DIE (SLOUGH)	Normal sloughing rate of leaves, with additional fall pulse
$K_{131} \cdot Q_2 \cdot fY$	DIE*KTU1*VP (PRFORM)	Tuber formation in fall
$Q_2 \cdot K_{53} \cdot T_6 \cdot Q_5$	KBI2*BI*VP*BITEMP (BIXVP)	Consumption by benthic invertebrates
$Q_2 \cdot K_{64} \cdot T_1 \cdot Q_6$	KHF3*VP*HF*FSHTMP (HFXVP)	Consumption by herbivorous fish
$Q_2 \cdot K_{84} \cdot T_1 \cdot Q_8$	KYNG3*VP*YNG*FSHTMP (YNGXVP)	Consumption by young primary predator fish

Term in Equation in Figure 13	Term in Computer Program	Explanation
	Epipelic Algae (Q_3)	
$K_{31} \cdot S \cdot (1 - R) \cdot e^{-(K_2 Z + K_7 \cdot Q_1)} \cdot f_3 Q_2$	K1EP*EPLITE	Availability of light
$\frac{E_{Q_3}}{1 + LQ_3/LQ_{3-50}}$	$\frac{\text{EPMEFF}}{1 + \text{EPLITE/EP50}}$	Photosynthetic rate at available light level
Q_{12}	PHYPO	Level of orthophosphate in hypolimnion
T_8	T1EP	Effect of temperature on photosynthesis
K_{27}	KCAL2C	Conversion from kilocalories to carbon for photosynthesis
Q_3	EP	Biomass of epipelic algae
$fY \cdot$ (product of above terms)	CEPRLS*GPPEP (EPLEAC)	Leaching of organic carbon; rate varies with rate of photosynthesis
$K_{33} \cdot T_8 \cdot Q_3$	K2EP*T2EP*EP(EPRESP)	Respiration rate
$K_{34} \cdot Q_3$	K5EP*EP(EPMORT)	Death rate
$Q_3 \cdot K_{42} \cdot T_5 \cdot Q_4$	KZP1*EP*ZP*ZPTEMP (ZPXEP)	Consumption by zooplankton
$Q_3 \cdot K_{62} \cdot T_1 \cdot Q_6$	KHF1*EP*HF*FSHTMP (HFXEP)	Consumption by herbivorous fish
$Q_3 \cdot K_{75} \cdot T_1 \cdot Q_7$	KPF14*EP*PF1*FSHTMP (PF1XEP)	Consumption by adult primary predator fish
$Q_3 \cdot K_{82} \cdot T_1 \cdot Q_8$	KYNG1*EP*YNG*FSHTMP (YNGXEP)	Consumption by young primary predator fish

Term in Equation in Figure 16	Term in Computer Program	Explanation
	Zooplankton (Q_4)	
$K_{41} \cdot Q_4 \cdot T_5 \cdot ((K_{42} \cdot Q_3) + (K_{43} \cdot Q_1) + (K_{44} \cdot Q_2))$	ZPASSM*ZPFOOD	Food assimilated by zooplankton (epipelic algae, phytoplankton, and macrophytes)
$K_{45} \cdot Q_4 \cdot T_5$	KZP5*ZP*ZPTEMP (ZPRESP)	Respiration rate

(Continued)

Term in Equation in Figure 16	Term in Computer Program	Explanation
	Zooplankton (Q_4) (Continued)	
$Q_4 \cdot K_{52} \cdot Q_5 \cdot T_3 \cdot T_6$	KBI1*BI*ZP*BITEMP^2/ZPTEMP (BIXZP)	Consumption by benthic invertebrates
$Q_4 \cdot K_{74} \cdot Q_7 \cdot T_1 \cdot T_4$	KPF13*ZP*PF1*FSHTMP^2/ZPTEMP (PF1XZP)	Consumption by adult primary predator fish
$Q_4 \cdot K_{67} \cdot Q_6 \cdot T_1 \cdot T_4$	KHF6*HF*ZP*FSHTMP^2/ZPTEMP (HFXZP)	Consumption by herbivorous fish
$Q_4 \cdot K_{87} \cdot Q_8 \cdot T_1 \cdot T_4$	KYNG6*YNG*ZP*FSHTMP^2/ZPTEMP (YNGXZP)	Consumption by young primary predator fish

Term in Equation in Figure 18	Term in Computer Program	Explanation
	Benthic Invertebrates (Q_5)	
$K_{51} \cdot Q_5 \cdot T_6 \cdot ((K_{52} \cdot Q_4 \cdot T_7) + (K_{53} \cdot Q_2) + K_{54})$	BIASSM*BIFOOD	Food assimilated by benthic invertebrates (zooplankton, macrophytes, and detritus)
$K_{54} \cdot Q_5 \cdot T_6$	KBI4*BI*BITEMP(BIRESP)	Respiration rate
$Q_5 \cdot K_{66} \cdot Q_6 \cdot T_1 \cdot T_3$	KHF5*HF*BI*FSHTMP^2/BITEMP (HFXBI)	Consumption by herbivorous fish
$Q_5 \cdot K_{72} \cdot Q_7 \cdot T_1 \cdot T_3$	KPF11*BI*PF1*FSHTMP^2/BITEMP (PF1XBI)	Consumption by adult primary predator fish
$Q_5 \cdot K_{86} \cdot Q_8 \cdot T_1 \cdot T_3$	KYNG5*YNG*BI*FSHTMP^2/BITEMP (YNGXBI)	Consumption by young primary predator fish
$Q_5 \cdot K_{95} \cdot Q_9 \cdot T_1 \cdot T_3 \cdot FQ_2$	KPF24*BI*PF2*(FSHTMP^2/BITEMP)*COVER (PF2XBI)	Consumption by secondary predator fish

Term in Equation in Figure 19	Term in Computer Program	Explanation
	Herbivorous Fish (Q_6)	
$K_{61} \cdot T_1 \cdot Q_6 \cdot ((K_{62} \cdot Q_3) + (K_{63} \cdot Q_1) + (K_{64} \cdot Q_2) + K_{65} + (K_{66} \cdot Q_5 \cdot T_2) + (K_{67} \cdot Q_4 \cdot T_3))$	HFASSM*HFFOOD	Food assimilated by herbivorous fish (epipelic algae, phytoplankton, macrophytes, detritus, benthic invertebrates, and zooplankton)
$K_{68} \cdot Q_6 \cdot T_1$	KHF7*HF*FSHTMP(HFRESP)	Respiration rate
$K_{93} \cdot Q_6 \cdot Q_9 \cdot T_1 \cdot fQ_2$	KPF22*HF*PF2*FSHTMP*COVER (HFPRED)	Consumption by secondary predator fish

Term in Equation in Figure 20	Term in Computer Program	Explanation
	Primary Predator Fish: Adult (Q_7) and Young (Q_8)	
$K_{71} \cdot Q_7 \cdot T_1 \cdot ((K_{72} \cdot Q_5 \cdot T_2) + (K_{73} \cdot Q_2) + (K_{74} \cdot Q_4 \cdot T_4) + (K_{75} \cdot Q_3))$	P1ASSM*PF1FD	Food assimilated by adult primary predator fish (benthic invertebrates, macrophytes, zooplankton, and epipelic algae)
$K_{88} \cdot Q_8 \cdot T_1$	KYNG7*YNG*FSHTMP (GROWTH)	Growth of young fish into adult group
$K_{76} \cdot Q_2 \cdot fY$	KPF15*PF1*BIRTH/DELT(BREED)	Birth of young fish
$K_{92} \cdot Q_9 \cdot Q_7 \cdot T_1 \cdot fQ_2$	KPF21*PF2*PF1*FSHTMP*COVER (PF1PRD)	Consumption of adult primary predator fish by secondary predator fish
$K_{77} \cdot Q_7 \cdot T_1$	KPF16*PF1*FSHTMP(PF1RSP)	Respiration rate

(Continued)

Term in Equation in Figure 20	Term in Computer Program	Explanation
Primary Predator Fish: Adult (Q_7) and Young (Q_8) (Continued)		
$K_{81} \cdot Q_8 \cdot T_1((K_{82} \cdot Q_3) + (K_{83} \cdot Q_1) + K_{84} \cdot Q_2)$ $+ (K_{85} \cdot Q_{10}) + (K_{86} \cdot Q_5 \cdot T_2) + (K_{87} \cdot Q_4 \cdot T_3))$	YNGASM*YNGFD	Food assimilated by young predator fish (epipelic algae, phytoplankton, detritus, benthic invertebrates, and zooplankton)
$K_{89} \cdot Q_8 \cdot T_1$	KYNG8*YNG*FSHTMP(YNGRSP)	Respiration rate
$K_{94} \cdot Q_8 \cdot Q_9 \cdot T_1 \cdot fQ_2$	KPF23*PF2*YNG*FSHTMP*COVER (YNGPRD)	Consumption of young primary predator fish by secondary predator fish

Term in Equation in Figure 21	Term in Computer Program	Explanation
Secondary Predator Fish (Q_9)		
$K_{91} \cdot T_1 \cdot Q_9 \cdot ((K_{92} \cdot Q_7) + (K_{93} \cdot Q_6 \cdot T_1 \cdot fQ_2)$ $+ (K_{94} \cdot Q_8 \cdot T_1 \cdot fQ_2) + (K_{95} \cdot Q_5 \cdot T_1 \cdot T_3 \cdot fQ_2))$	PF2ASM*PF2FD	Food assimilated by secondary predator fish (young and adult primary predator fish, herbivorous fish, and benthic invertebrates)
$K_{96} \cdot Q_9 \cdot T_1$	KPF25*PF2*FSHTMP (PF2RSP)	Respiration rate
$K_{97} \cdot Q_9 \cdot T_1$	KPF26*PF2*FSHTMP (PF2DTH)	Death rate

Term in Equation in Figure 22	Term in Computer Program	Explanation
Detritus (Q_{10})		
$K_{121} \cdot T_1 \cdot fY$	KK*T2NC*ANOXIC	Release of orthophosphate from sediments when hypolimnion is anaerobic
$K_{122} \cdot T_1 \cdot fY$	KJ*T2NC*AEROBC	Release of orthophosphate from sediments when hypolimnion is aerobic

Term in Equation in Figure 23	Term in Computer Program	Explanation
Orthophosphate in Epilimnion (Q_{11})		
$fY \cdot K_R$	OP1NPT	Orthophosphate entering as rainfall and runoff
K_p	KC2P	Carbon to phosphorus ratio in organic matter
$(Q_{12} - Q_{11}) \cdot fY$	TRNOVR*(PHYPO-PEPI)	Mixing between epilimnion and hypolimnion during isothermal periods

Term in Equation in Figure 39	Term in Computer Program	Explanation
White Amur: Biomass (Q_{14}) and Number (Q_{15})		
$K_{141} \cdot K_{142} \cdot K_{143} \cdot Q_{14} \cdot Q_2 \cdot T_1$	K1FB*K2FB*K3FB*FB*VP*FSHTMP (FASSIM)	Assimilation rate of macrophytes
$K_{144} \cdot Q_{14} \cdot T_1$	K5FB*FB*FSHTMP(FRESP)	Respiration rate
$K_{151} \cdot Q_{15} \cdot Q_{14}/Q_{15}$	K1FN*FN*FB/FN(FMORT)	Mortality rate

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 1: Baseline studies; 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, Gainesville, Fla. Vicksburg, Miss. : U. S. Waterways Experiment Station ; Springfield, Va. : available from National Technical Information Service, 1979.
75, [19] p. : ill. ; 27 cm. (Technical report - U. S. Army Engineer Waterways Experiment Station ; A-78-2, Report 1, v.7)
Prepared for U. S. Army Engineer District, Jacksonville, Jacksonville, Fla., and Office, Chief of Engineers, U. S. Army, Washington, D. C., under Contract No. DACW39-76-C-0019.
References: p. 69-75.

1. Aquatic plant control. 2. Ecosystems. 3. Lake Conway.

(Continued on next card)

Ewel, Katherine C
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4. Lakes. 5. Models. 6. White amur. I. Fontaine, Thomas D., joint author. II. Florida. University, Gainesville. School of Forest Resources and Conservation. III. United States. Army. Corps of Engineers. IV. United States. Army. Corps of Engineers. Jacksonville District. V. Series: United States. Waterways Experiment Station, Vicksburg, Miss. Technical report ; A-78-2, Report 1, v.7.
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