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**Evaluating a Mathematical Model  
for Predicting Lake Eutrophication**

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## PREFACE

The disposal of nutrient-containing wastes into fresh waters has resulted in a dramatic increase in problems of cultural eutrophication in the United States. If cultural eutrophication is to be prevented in existing and planned reservoirs, methods for monitoring and predicting water quality and biological community changes must be developed. The research reported here forms a part of a larger program-plan developed by the principal investigators for mass-balance analysis of productivity and community variation in fresh waters which we hope will eventually provide "water quality" information useful in basin-wide planning.

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## ABSTRACT

This research project developed a mathematical model of a lake ecosystem and then tested its ability to indicate what ecological changes—in particular eutrophication—would result from changes in the physical environment.

The model was developed using a digital computer. *In situ* enrichment experiments then were performed to assess the relationship between nutrient concentrations and the growth of phytoplankton. The investigation included an evaluation of the use of nonlinear parameter estimation in determining the model's growth constants. The model did demonstrate that it could provide useful qualitative information.

Field experiments did not, however, produce data suitable for quantifying the relationship between species diversity and nutrient addition showed that a diversity index holds little promise for use as a quantitative indicator of eutrophic conditions.

The field experiments and the study of parameter estimation indicate that *in situ* enrichment experiments will not provide adequate data for accurate determination of model parameters. Growth parameters can be estimated on the basis of careful laboratory experiments, but extrapolation of this data to field conditions proved questionable. For this reason and others, the researchers conclude that the principal application of lake ecosystem models is for qualitative determinations. Even for this limited use, the researchers caution that each such model must be carefully designed for each specific application.



## INTRODUCTION

Spurred primarily by the problem of cultural eutrophication—the increased productivity in natural waters due to artificial nutrient enrichment—investigators in various fields have presented models of phytoplankton production in freshwater lakes or impoundments (*Ref. 13, 11, 46, 29, 45*). Although a desirable goal is “a lake model which with obtainable inputs in any specific lake situation can be employed to predict the response of that lake to its various influents, and hence to disclose the necessary controls and monitoring programs for protecting the lake” (*Ref. 39*), none of the models yet presented can approach this goal.

The effectiveness of a model as a predictive tool is directly related to how well the model describes the natural environmental interactions, and from where and how the values for the parameters in the models are derived. While development of lake ecosystem models has been relatively straightforward and based on biological and physical principles, the matter of parameter estimation for the models has been largely neglected.

In most attempts at modeling a lake ecosystem, the biological growth parameters have been estimated using data from laboratory cultures. It is questionable whether values derived from experiments in artificial environments can be extrapolated to a natural environment. On the other hand, because of a multitude of complexities introduced in experiments under natural conditions, data from *in situ* experiments may be difficult to analyze. A combination of methods may be necessary in order to best approach the problem.

An area that has not been fully explored is the use of mathematically sound techniques for estimating growth parameters from either laboratory or *in situ* nutrient uptake data. The techniques which have been most widely used in the past may produce misleading results.

The research described here was designed 1) to develop a “reasonable” lake ecosystem model; 2) to conduct *in situ* nutrient enrichment experiments to provide data for calibration and testing of the model; and 3) to examine the feasibility of using parameter estimation techniques with field and laboratory phytoplankton data to determine the appropriate growth constants for use in a lake model.

In addition, the data collected from *in situ* nutrient enrichment experiments in Sugar Hollow Reservoir provided an evaluation of the utility of a species

diversity index in describing water quality, the parameter estimation techniques allowed testing of the ability to discriminate among several possible models of nutrient uptake, and the lake model yielded significant results regarding a possible explanation of the "paradox of the plankton" (Ref. 30) and the possibility that inhibition of photosynthesis at the surface of lakes may be due to nutrient limitation.

## BACKGROUND AND PREVIOUS WORK

There is a large and rapidly growing literature on lake ecosystem models (*see Ref. 39* for a recent compilation of papers). Most of these models are based on the continuity equation and are constructed by specifying particular forms for the source/sink terms in the equation.

In a phytoplankton model, the primary source term is growth. The relationship between phytoplankton growth and nutrient concentration is often modeled by a Monod expression which is a reasonable assumption since uptake response to various concentrations of macro- and micro-nutrients has been widely reported as fitting a rectangular hyperbola (*Ref. 5, 17, 20, 37, 26, 23, 8, 9, 47, 15, 16*).

Various models have been proposed that separate the process of nutrient uptake and growth (*Ref. 6, 7, 15, 16*). These types of models are supported by evidence of nutrient uptake in the dark, variations of cellular concentrations of nutrients, rapid uptake by nutrient-starved cells relative to growth rate, and luxury uptake of one nutrient which is present in excess while another nutrient limits growth (*Ref. 32, 47, 31, 34, 14, 22*). Most of these models rely on the Monod expression for substrate-nutrient limitation, and before any model can be used for predictive purposes the growth constants appearing in this expression must be estimated.

The data used for determining growth parameters are usually derived from single-species laboratory cultures. A laboratory population is subject to "unnatural" selective pressures and thus extrapolation of laboratory-derived constants to a natural community is questionable. Few *in situ* determinations of values for uptake parameters have been made and only whole community values have been reported (*Ref. 48, 17*). Several attempts were made in the course of this research to provide data from *in situ* experiments which could be used to calibrate a lake model. We were therefore led to examine methods of analyzing such data.

The most widely-used method for calculation of nutrient-uptake parameters is to use a linear transformation of the Monod expression and perform a least-squares fit on uptake data (*Ref. 5, 17, 26, 23, 21, 48, 15, 16*). Data from chemostat cultures are more easily analyzed by this technique than are data from batch cultures. However, by using finite-differences to estimate the uptake rates, batch-culture data have been used (*Ref. 17, 20, 37, 23, 21, 48, 15, 16*). Unless the sampling intervals are negligibly short, this use of batch-culture data neglects the fact that the nutrient concentration changes

with time; yet, when the sampling interval is too short, the rate of change of nutrient concentration would be insignificant or not measurable.

This traditional method of analyzing nutrient uptake data suffers from a number of drawbacks: estimates obtained through the use of transformed data may be biased; certain parameters which are independent in a dynamic model may not be independent in the associated steady-state model and hence may not be estimated from chemostat data; and certain models may differ only in their dynamic behavior. Again, chemostat data could not be analyzed to study the transient response of a phytoplankton population. Other methods of parameter identification have been proposed and used, but none of these methods directly fits a model (or equation) to a time series of data measured during a batch-culture experiment. Moreover, an assemblage of phytoplankton is made up of competing species and no method has been proposed to identify the growth and uptake parameters for each species in a whole community experiment. If "community values" are derived from such an experiment, use of the conventional regressions can easily give poor estimates of the growth parameters if the community is composed of dissimilar species (*Ref. 50*).

A method is available which overcomes the objections mentioned above. A growth curve of biomass, measured through the course of a batch-culture experiment, can be described by the solution to a differential equation which incorporates a nutrient-uptake model, and the parameters in the model equation can be estimated by fitting the solution to the time series of measured data. This is accomplished by using nonlinear parameter estimation, a procedure in which successive changes in the values of parameters are made until the solution of the differential equation converges to the closest fit of the model to the data. (The closeness of fit is a function of the difference between the model prediction of the dependent variable and the measured value—i.e., the experiment datum).

Sophisticated methods for parameter estimation are available for application to a lake model. Marquardt (*Ref. 38*), Fletcher and Powell (*Ref. 25*), and Bard (*Ref. 2, 3*) have presented methods especially suited to dynamic equations with multiple observed variables and with the parameters appearing in nonlinear fashion.



## A LAKE ECOSYSTEM MODEL

A model for phytoplankton growth can be derived by applying mass balance to a volume of lake water. A general form for this relationship is

$$\frac{\partial c}{\partial t} = \nabla \cdot (D \nabla c) - \nabla \cdot c \vec{v} + \sum S$$

where  $c$  = concentration of a dissolved or suspended constituent such as a nutrient or plankton species;  
 $D$  = diffusivity;  
 $\vec{v}$  = velocity;  
 $\sum S$  = sum of sources and sinks.

We have simplified this general form of the equation to include only changes in the vertical direction and to account for any vertical motion by using a dispersion coefficient. In this ecosystem model we consider several species of phytoplankton and herbivores. The gross production of the phytoplankton is controlled by incident radiation and by the concentration of two nutrients. Nutrient uptake is modeled using Michaelis-Menten (Monod) kinetics. The respiration term of the equation accounts for actual respiration as well as nutrient recycling by decomposers. The resulting equations are:

1) producer equation for species  $i$  ( $i=1, \dots, I$ );

$$\frac{\partial P_i}{\partial t} = A_i F P_i \frac{N1}{KM1_i + N1} \frac{N2}{KM2_i + N2} - R_i P_i - \sum_{j=1}^J G_j P_i H_j + \frac{\partial}{\partial z} \left\{ D_v \frac{\partial P_i}{\partial z} \right\}$$

2) herbivore equation for species  $j$  ( $j=1, \dots, J$ );

$$\frac{\partial H_j}{\partial t} = \sum_{i=1}^I E_j P_i G_j H_j \frac{HMAX_j - H_j}{HMAX_j} - R_j H_j - CARN_j H_j + \frac{\partial}{\partial z} (D_{vH} \frac{\partial H_j}{\partial z})$$

3) equation for nutrient N1,

$$\frac{\partial N1}{\partial t} = \sum_{i=1}^I (C1_i^P) (U_i^P) - \sum_{j=1}^J (C1_j^H) (U_j^H) + \frac{\partial}{\partial z} (D_v \frac{\partial N1}{\partial z})$$

4) equation for nutrient N2,

$$\frac{\partial N2}{\partial t} = - \sum_{i=1}^I (C2_i^P) (U_i^P) - \sum_{j=1}^J (C2_j^H) (U_j^H) + \frac{\partial}{\partial z} (D_v \frac{\partial N2}{\partial z})$$

where:

- F = input energy at depth z,  
P = concentration of phytoplankton,  
A = ability of the producers to utilize light through photosynthesis,  
N1 = concentration of nitrates in solution,  
N2 = concentration of phosphates in solution,  
KM1 = nitrate half-rate constant,  
KM2 = phosphate half-rate constant,  
R<sub>i</sub> = producer respiration rate,  
G = grazing rate of herbivore,  
H = concentration of herbivore,  
E = grazing efficiency,  
R<sub>j</sub> = herbivore respiration rate,  
HMAX = maximum herbivore concentration (carrying capacity),  
D<sub>v</sub> = dispersion coefficient,  
D<sub>VH</sub> = "dispersion" coefficient for herbivores  
C<sub>1</sub><sup>H</sup> = concentration of N1 in herbivore  
C<sub>1</sub><sup>P</sup> = concentration of N1 in phytoplankton,  
C<sub>2</sub><sup>P</sup> = concentration of N2 in phytoplankton,  
C<sub>2</sub><sup>H</sup> = concentration of N2 in herbivore,  
U<sub>i</sub><sup>P</sup> = net growth of phytoplankton =  

$$\frac{\partial P_i}{\partial t} - \frac{\partial}{\partial z} (D_V \frac{\partial P_i}{\partial z})$$
  
U<sub>J</sub><sup>H</sup> = net growth of herbivore =  

$$\frac{\partial H_j}{\partial t} - \frac{\partial}{\partial z} (D_{VH} \frac{\partial H_j}{\partial z})$$
  
CARN = grazing rate of carnivores.

Although we do not believe that a superior formulation has been presented elsewhere, several of the assumptions used to derive the above equations (and equations used by others) may be questioned. Neglect of advection and use of a vertical dispersion coefficient to account for all vertical motion may be undesirable, especially in a predictive model. Some workers consider formulations other than the Michaelis-Menten equation to be superior for describing nutrient-limited growth (for example, *Ref. 16, 8*). The linear relationship between light and photosynthesis has been questioned (*Ref. 49*). Although these (and other) assumptions may be invalid, we do not believe

that there is presently enough understanding of *in situ* growth kinetics to allow formulation of a better model. As will become clear, the four previous equations are structured so that useful qualitative information may be derived from their solution, and the validity of some of the assumptions may be examined using the model.

Solution of these four equations is accomplished by approximating the spatial derivatives by finite differences and by using a Runge-Kutta method to solve the resulting system of ordinary differential equations. The computer program used to implement the solution is listed and documented in Appendix I.



## CALIBRATION OF THE MODEL: FIELD EXPERIMENTS

After preliminary reconnaissance of a number of impoundments in the vicinity of Charlottesville, Virginia, Sugar Hollow Reservoir was chosen as the location for initial field studies (started mid-July, 1972). This reservoir is located at the edge of the Shenandoah National Park and serves as a water supply for the city of Charlottesville.

Sugar Hollow Reservoir normally has low concentrations of nutrients ( $< .1 \mu\text{g/l PO}_4\text{-P}$  and  $\sim 4 \mu\text{g/l NO}_3\text{-N}$ ), low primary productivity, a mean Secchi disc depth of 3 m, and a phytoplankton community of more than 15 major species. The average depth is 15 m and the depth of the thermocline in summer is about 3 m. The lake, therefore, has many characteristics of an oligotrophic impoundment.

A floating rack supporting 14 polyethylene bags was constructed and placed in the lake. The bags were open to the atmosphere and extended 3 m in depth. Besides two controls, combinations of high (0.5 mg/l) and low (0.3 mg/l) nitrate and high (0.1 mg/l) and low (0.05 mg/l) phosphate enrichments were made, in replicate, and growth was monitored. Phytoplankton, phosphate, nitrate, dissolved oxygen, chlorophyll-a, and light and dark bottle productivity were sampled at three depths every two days in each bag and in the lake. The experiment was continued for four weeks, until the productivity, chlorophyll-a, and nutrient concentrations reached equilibrium.

We had planned to use these data to estimate the growth coefficients for the various phytoplankton species and to verify the predictive capability of the ecosystem model. We found, however, that quantitative estimates could not be derived from these data. In addition, the polyethylene bags used in the field experiments during the first year's work were open to the atmosphere at the top and extended vertically through the thermocline. Effects observed in the bags were thus depth-averaged, and inferences regarding growth rate differences with depth and light availability were not possible.

However, these data were used to determine whether a species diversity index is a useful quantitative index of water quality or "trophic condition" of a reservoir. Mitchell and Buzzell (*Ref. 41*) attempted to quantify the relationship between a species diversity index and nutrient concentration. They used laboratory microcosms, contained in carboys, to quantitatively assess the effects of pollution and/or nutrient input in terms of the diversity index of the microcosm populations. They added nutrients in the un-

controlled form of a commercial grade garden fertilizer or sewage water. Mitchell (Ref. 40) also used this technique to analyze the effects of detergent input into aquatic systems. Mitchell's work has been criticized in the literature: it "contains both errors in logic and factual misrepresentations" and "The use of microcosms to simulate lakes has many faults" (Ref. 27). The *in situ* experiments in Sugar Hollow Reservoir were designed to overcome the defects in the approach taken by Mitchell.

Significant results from this study in which nutrients were added as an initial pulse are:

1. diversity initially decreases when nutrients are added to an oligotrophic lake in the form of phosphate and/or nitrate;
2. the decrease is very rapid;
3. the decrease is not correlated with either the nutrient added or its concentration;
4. diversity tends to increase after the initial decrease.

It can be concluded that there is an inverse relationship between nutrient additions and the diversity index of the phytoplankton. However, the relationship is a qualitative one. Considering this, it is unlikely that the diversity index can be used as a quantitative indicator of eutrophic conditions. Likewise, it would be most unlikely that the diversity index could be used to make quantitative predictions regarding the effects of nutrient additions on the aquatic community. (Ref. 44 will have further details of this study.)

In the summer of 1973 another attempt was made to use observed *in situ* species growth to determine the actual Michaelis-Menten growth constants for phytoplankton populations in the reservoir. Smaller, enclosed bags were used in this experiment, and data were collected every four hours. The results showed that uptake was very slow, and it was concluded that the standing crop in Sugar Hollow Reservoir was not great enough to provide meaningful nutrient variation in the short-term enrichment experiment.

To test this hypothesis, the experiment was repeated in the Rivanna River Reservoir, which has characteristics indicating that it has a much higher standing crop and productivity than Sugar Hollow. The Rivanna Reservoir exhibits problems associated with eutrophication.

The response in the bags in the Rivanna Reservoir was clearly more rapid and larger in magnitude than that in Sugar Hollow. However, the water in the Rivanna Reservoir was quite turbid and this interfered with the determination of nutrient concentrations. Consequently, although it was obvious that the enrichment caused rapid growth (and, by inference, uptake), quantitative measurements of nutrient concentrations could not be obtained and thus the data were unsuited for estimation of growth parameters.

From these field studies it is obvious that *in situ* experiments cannot be used to estimate phytoplankton growth parameters under some conditions, and that experiments must be very carefully tailored to the particular situation.





## PARAMETER ESTIMATION: METHODS

Although the field experiments did not provide data suitable for estimating growth coefficients for the model, the feasibility of using parameter identification techniques for such purposes was thoroughly investigated. We felt that insight might be gained regarding design of an *in situ* experiment to collect such data. Also, in the event that it should prove necessary to resort to laboratory culture data, the technique might still be required to estimate the parameters. Complete details of this portion of the research are given by Lederman (*Ref. 35*).

Data to test the parameter estimation technique were generated using the lake model, equations 2–5. The growth parameters  $V_m$ ,  $K_m$ , and  $R$ , were chosen from ranges of values given in the literature (*Ref. 13, 21*). For example, the value of  $V_m$  which was used for one simulation represents a doubling rate of  $1.1 \text{ day}^{-1}$  for constant light of  $500 \text{ Kcal m}^{-2} \text{ hr}^{-1}$  in the absence of nutrient limitation and respiration. The numerical value is

$$\frac{1 \cdot 1}{\text{day}} \times \frac{\text{day}}{24 \text{ hr}} \times \frac{\text{m}^2 \text{ hr}}{500 \text{ Kcal}} \approx .00009 \text{ m}^2 \text{ Kcal}^{-1}$$

High values of  $K_m$  were chosen as being representative of a eutrophic environment. The values for respiration were assumed to be a rate of reduction of biomass that would approximately halve the biomass in five days in a dark environment.

Parameter values for three different species (Table 1) were chosen and the simulations were run to equilibrium from the same initial conditions for biomass and nutrient. The total nutrient (the sum of the nutrient in biomass and in solution) for all simulations in this study was  $750 \text{ mg NO}_3\text{-N m}^{-3}$ . Simulations were made assuming both constant and diurnally varying light. The equilibrium values from the constant-light simulations were then used as initial conditions for simulations of constant-light, batch-enrichment experiments. The initial conditions for the diurnal-light, batch-enrichment simulations were taken as the values of biomass and nutrient at the end of the first dark period following the light period when values indicated equilibrium conditions. The initial nutrient level for each simulation was increased with four different levels of nutrients and the equations were integrated for 72 hours. Biomass and nutrient values representing experimental samples were taken each hour. The 24 “perfect” data sets were noise-corrupted with normally-distributed percent error with a mean of zero and a standard deviation of 10%. This standard error is representative of the chemical-measurement error to be expected over a large part of the range of magnitudes of experimental data (*Ref. 1*).

**TABLE 1**  
**Growth Parameters Used in Simulations**

SPECIES	$V_m$ $m^2 \text{ Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $hr^{-1}$
1	.00009	10.	.0035
2	.00019	14.	.003
3	.00029	20.	.0055

Similar computer experiments were run simulating batch culture experiments with two and three species. Three two-species combinations of the three species listed in Table 1 were chosen. The simulations were run for a diurnal light environment (this avoided exclusion of one of the species through competition). After 360 hours of simulation, the system had reached a dynamic equilibrium and the initial conditions for the enrichment runs were established. Four enrichment levels were again chosen and the simulations were run for 72 hours, with nutrient and the biomass of each species recorded for each hour.

This same procedure was used to generate data for a simulation of growth when three species are competing for the nutrient. A dynamic equilibrium was established and the values for each species and the nutrient in solution were used as initial conditions for the four enrichment simulations.

A five-species (Table 2) simulation was also run with the lake model, following the previous procedure but making only one enrichment run. However, instead of taking biomass measurements for each species, the community biomass and the nutrient in solution were recorded each hour. These data were noise-corrupted using the method described previously. The data were analyzed with the parameter estimation procedure to determine the feasibility of deriving community uptake values and to assess the meaning of the estimated values.

The feasibility of using parameter estimation techniques for determining phytoplankton growth constants was evaluated. A computer program parameter estimation package (*Ref. 3*) was used to back-calculate the parameter values from the simulated data, and the estimated values were compared with the known input values to the simulations. Parameters in a dynamic system (a number of coupled first-order differential equations) are easily handled with Bard's program through use of special sub-routines, some of which must be supplied by the user, so the program is well-suited for the phytoplankton-nutrient problem. The program uses a Gauss-Newton method with modifications (*Ref. 28, 18, 2, 10*) to maximize the likelihood function.

TABLE 2

Growth Parameters Used in the Community Simulation

SPECIES	$V_m$ $m^2 \text{ Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $\text{hr}^{-1}$
1	.00009	10.	.0025
2	.00014	15.	.003
3	.00019	13.	.0045
4	.00024	17.	.005
5	.00029	20.	.0055

## PARAMETER ESTIMATION: RESULTS AND DISCUSSION

The estimated values for the parameters for the single-species, constant-light data (perfect and noise-corrupted) are listed in Table 3. The enrichment levels in the table represent additions of 100, 250, 350, and 500 mg NO<sub>3</sub>-N m<sup>-3</sup>. An estimation run will be referred to by numbers representing the number of the species and the level of enrichment. Some of the simulation runs reached equilibrium within five hours, although a minimum of 10 hours of data was used. The values estimated from the perfect data were all very close to the true values. The standard deviations of the residual error (mean = 0) were in all cases less than 0.2 mg NO<sub>3</sub>-N m<sup>-3</sup> for a range of data from 1250 to less than 1 mg NO<sub>3</sub>-N m<sup>-3</sup>. For these runs, the standard deviations of the biomass and the nutrient residuals are the same. With perfect data, all the residuals represent estimation error, and the estimation error for the predicted nutrient values are the negative of the error for the biomass predictions. The parameter values estimated from the noise-corrupted data in most cases were of the correct order of magnitude for V<sub>m</sub> and K<sub>m</sub>. They cannot be considered close enough to the true values to be good estimates (the criterion for goodness being that the estimates for the three different species should show significantly different uptake values). The estimates for R were, in most cases, unacceptable. Two standard deviations of the residuals are given for the noise-corrupted data because each perfect datum was independently corrupted.

The results of the single-species, diurnal-data estimation runs are listed in Table 4. Seventy-two hours of data were first used in the estimation runs. Only species-1 estimations converged with this length of the time series data. A possible explanation for lack of convergence is that species 2 and 3 had relatively faster growth rates and thus reached a dynamic equilibrium in less than 72 hours. Smaller data sets were then used until the estimation procedure converged. Estimated parameter values for the perfect data were, in all but one case (species 3-500 enrichment), very close to the true values. The standard deviation of the residuals were all less than 0.3 mg NO<sub>3</sub>-N m<sup>-3</sup>. The values estimated from the noise-corrupted data were all of the correct order of magnitude, with the K<sub>m</sub> estimates being consistently the poorest. The estimated values for V<sub>m</sub> and R were similar within the four experiments for each species, and were different between species. The standard deviations of the residuals were within 10% of the means of samples in each run in most cases. For example, the mean of the samples in the run for species 3-500 enrichment was 1,052 mg NO<sub>3</sub>-N m<sup>-3</sup>.

Table 4 also contains the estimates from the community data. The estimated values are close to the average of the values for all the species in the run. The

TABLE 3  
Estimates for Single-Species, Constant-Light Data

SPECIES	Enrichment	PERFECT DATA			NOISE-CORRUPTED DATA			Standard Deviation of the Residuals	Hours of Data	
		$V_m$ $m^2 \text{ Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $hr^{-1}$	$V_m$ $m^2 \text{ Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $hr^{-1}$			
1	100	.00009	10.	.0035	.00011	14.9	.0034	136.	1.4	12
	250	.00009	10.	.0036	.00009	15.	$.4 \times 10^{-21}$	122.	9.	16
	350	.00009	10.	.0037	.00014	14.9	.019	92.	14.	20
	500	.000091	9.9	.0040	.00010	14.9	.0054	82.	12.1	25
2	100	.00019	14.2	.003	.00018	15.	.00044	86.	.64	10
	250	.00019	14.2	.003	.00016	15.	0.	117.	7.9	10
	350	.00019	14.2	.0031	.00017	15.	0.	66.	13.	10
	500	FAILED TO CONVERGE	14.2	.0031	.00022	21.7	.00019.	358.	7.4	10
3	100	.00030	23.3	.005	FAILED TO CONVERGE	FAILED TO CONVERGE	FAILED TO CONVERGE	FAILED TO CONVERGE	FAILED TO CONVERGE	10
	250	.000291	20.6	.00555	FAILED TO CONVERGE	FAILED TO CONVERGE	FAILED TO CONVERGE	FAILED TO CONVERGE	FAILED TO CONVERGE	10
	350	.00029	20.	.00562	.00033	15.	.019	110.	4.	10
	500	.00029	20.	.0058	.00022	.47	.000035	144.	75.	10

TABLE 4  
Estimates for Single-Species, Diurnal-Light Data

SPECIES	Enrichment	PERFECT DATA				NOISE-CORRUPTED DATA				Standard Deviations of the Residuals	Hours of Data
		$V_m$ $m^2 \text{ Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $hr^{-1}$	Standard Deviation of the Residuals	$V_m$ $m^2 \text{ Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $hr^{-1}$	Biomass		
1	100	.00009	9.82	.00349	.13	.00011	16.6	.0038	109.	2.2	72
	250	.00009	9.64	.0035	.19	.000088	6.8	.00397	137.	9.5	72
	350	.00009	9.76	.00348	.25	.000083	15.3	.0031	70.	9.5	72
	500	.00009	9.8	.00347	.29	.00010	14.9	.0046	105.	22.	72
2	100	.00019	14.1	.0035	.01	.00021	16.5	.00355	61.	3.2	12
	250	.00019	14.1	.003	.026	.00024	50.	.0028	80.	6.8	24
	350	.00019	14.	.003	.003	.00021	25.	.0029	90.	12.	24
	500	.00019	14.	.003	.003	.000197	70.	.0026	84.	26.	24
3	100	.00029	20.	.0055	.008	.00037	18.	.00556	69.	3.8	24
	250	.00029	20.	.0055	.03	.000296	55.	.0052	78.	10.	24
	350	.00029	20.	.0055	.016	.00037	99.	.0047	105.	12.	18
	500	.000286	15.5	.0055	.8	.00031	15.	.0055	88.	15.	36
Community				.02	.000156	15.3	.0037	127.	2.	36	

fit to the data was very good, with a residual standard of  $0.02 \text{ mg NO}_3\text{-N m}^{-3}$ . The values estimated from the noise-corrupted data correspond very well to the perfect-data estimates.

The results of the two-species estimation runs are given in Table 5. All the estimates were close to the true values, and the standard deviation of the residuals was less than  $0.4 \text{ mg NO}_3\text{-N m}^{-3}$  for all runs. Two of the runs never converged. A possible explanation is that the species combinations and the nutrient level may have been too small for a determination between the response of species 1 and 2. The uptake response of species 3 in the species 1,3-500 enrichment may have been so rapid relative to species 1 that the determination of values for species 1 was impossible. The estimated values for the three-species experiments (Table 6) were also close to the true values for the three runs that converged.

The estimated parameter values for the perfect data were generally very close to the true values. The usefulness of nonlinear parameter estimation to calibrate a nutrient uptake model was substantiated. The estimation technique, while generally useful, may not give reliable estimates with certain data sets. In this simulated-data study, each set of simulated data was independently used to estimate parameter values. Better estimates would be expected if the data from separate simulation runs were grouped together as input. Increasing the sample size permits better estimates of the population statistics and better maximum likelihood estimates. In some of the estimation runs, the sample size may have been so small that the distribution may not have been normal with mean of zero. The assumption, as previously stated, is that the errors are normally distributed, independent between samples, and have a mean of zero. For species 3-350 enrichment run, the mean of the residuals was 36 with a standard deviation of  $67 \text{ mg NO}_3\text{-N m}^{-3}$ .

While the fit of the uptake model to noise-corrupted data had residuals within the range of the imposed measurement error, difficulties were encountered with the estimation of different parameters in the constant-light and diurnal-light situations. The estimated respiration values for constant-light data were neither close to the correct values nor consistent within each species run. The true respiration rate is almost two orders of magnitude smaller than the true  $V_m$  and the noise in the data probably makes the effect of the respiration term hard to determine relative to uptake. In the diurnal runs, the estimates for  $V_m$  and  $R$  were fairly reliable. The estimated  $V_m$  and  $R$  values for all data sets were not only close to the true values, but also consistent for each species. In the diurnal experiments, the return of nutrient to the medium through respiration during low light and the dark period allowed  $R$  to be reliably estimated.



TABLE 5  
Estimates for Two-Species, Diurnal-Light Data

SPECIES	Enrichment	PERFECT DATA										Standard Deviation of the Residuals	Hours of Data	
		$V_m$ $m^2 \text{ Kcal}^{-1}$	$KM$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $hr^{-1}$	$V_m$ $m^2 \text{ Kcal}^{-1}$	$R$ $hr^{-1}$	$KM$ $\text{mg NO}_3\text{-N } m^{-3}$	$V_m$ $m^2 \text{ Kcal}^{-1}$	$R$ $hr^{-1}$	$KM$ $\text{mg NO}_3\text{-N } m^{-3}$	$R$ $hr^{-1}$			
1 and 2	100	FAILED TO CONVERGE												18
	250	.00009	10.	.0035	.0019	14.	.0035	.0019	14.	.003	.013			60
	350	.0000898	9.6	.00348	.00189	13.3	.00348	.00189	13.3	.003	.25			18
	500	.00009	10.	.0035	.0019	14.	.0035	.0019	14.	.003	.003			
1 and 3	100	.00009	10.	.0035	.00029	20.	.0035	.00029	20.	.0055	.01			18
	250	.00009	10.1	.0035	.00029	20.2	.0035	.00029	20.2	.0055	.03			18
	350	.00009	9.5	.0035	.000288	19.	.0035	.000288	19.	.00547	.38			60
	500	FAILED TO CONVERGE												
2 and 3	100	.00019	14.	.003	.00029	20.	.003	.00029	20.	.0055	.01			18
	250	.00019	14.2	.003	.00029	20.2	.003	.00029	20.2	.0055	.024			18
	350	.00019	14.16	.003	.00029	20.18	.003	.00029	20.18	.0055	.06			18
	500	.00019	14.25	.003	.00029	20.	.003	.00029	20.	.0055	.07			12

TABLE 6  
Estimates for Three-Species, Diurnal-Light Data

SPECIES	Enrichment	PERFECT DATA								Standard Deviations of the Residuals	Hours of Data	
		$V_m$ $m^2 \text{Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N m}^{-3}$	$R$ $\text{hr}^{-1}$	$V_m$ $m^2 \text{Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N m}^{-3}$	$R$ $\text{hr}^{-1}$	$V_m$ $m^2 \text{Kcal}^{-1}$	$K_m$ $\text{mg NO}_3\text{-N m}^{-3}$			$R$ $\text{hr}^{-1}$
1, 2, and 3	100	.00009	10.	.0035	.00019	14.	.003	.00029	20.	.0055	.01	18
	250	FAILED TO CONVERGE										
	350	.00009	9.67	.00348	.00019	13.5	.00297	.00029	19.3	.00548	.32	36
	500	.00009	10.	.0035	.00019	14.	.003	.00029	20.	.0055	.013	24

Diurnal data are better suited to calibration of the uptake model in terms of convergence, consistency, and reliability. The  $K_m$  estimates, however, are very poor for noise-corrupted data. It may be necessary to use both constant- and diurnal-light data in order to obtain good estimates of all parameters. The estimates of  $V_m$  and  $R$  from the diurnal data could be held constant in estimation runs made with the constant-light data so as to obtain a good estimate of  $K_m$ .

Although simulated data were employed in the present study, current laboratory techniques should allow meaningful experimental data to be collected. Obviously, statistical techniques such as nonlinear parameter estimation will be necessary in the analysis of phytoplankton data. From a simulation study, the investigator obtains information which can be later applied to experimental design and which can provide insight concerning the strengths and weaknesses of the method of analysis. Since a batch experiment is a mass-balanced system, the design of the measurements could be adjusted to decrease the magnitude of the measurement errors. Nitrate, assuming it is the limiting nutrient in the culture medium, can be precisely and accurately measured with an autoanalyzer. The precision of the sample measures can be maintained through frequent standardization of the entire range of the expected nitrate levels in the experiment. Measurement of biomass, total nitrogen in living phytoplankton cells, is a procedure that can be precisely and accurately carried out with a carbon-nitrogen analyzer. Biomass-nitrogen and nitrate-nitrogen could be measured through the course of the batch experiment. The levels of these two variables should be similar for part of the experiment. The experimenter can determine whether the sum of biomass-nitrogen and nitrate-nitrogen remains constant through the midrange of the time-series measurements. If so, the assumption of mass balance between the two variables is substantiated.

Nitrogen was used as an example because it has predictive relevance in lake ecosystem models since it is considered to be one of the most frequently limiting nutrients. Much experimental work has also been carried out on nitrate and ammonium limitation of algal cultures (*Ref. 8, 9*).  $^{15}\text{N}$  could also be used in batch experiments and the nutrient in solution could be measured at lower concentrations with greater repeatability and reliability than with standard nitrate analysis. Other nutrients such as phosphate and vitamin  $\text{B}_{12}$  can be labelled with radioactive phosphorous or cobalt and their concentrations easily determined by scintillation counting.

The application of nonlinear parameter estimation to multispecies batch-culture data, though easily and successfully applied to simulated data, may be infeasible for actual experimental data. The methods of chemical analysis

presently available cannot easily provide separate measures of the biomass for each species in an experiment. If this difficulty in measurement could be overcome, parameter estimation would be very useful in the recognition of species interactions. For example, the uptake parameters for two species could be estimated from single-species experiments. The uptake parameters for the two species could then be estimated from two-species experiments. The comparison of the single-species and the two-species estimates would be an indicator of the presence and degree of interactions.

Single measures or trophic-level measures of community parameters, while providing no information about each species' response, may be useful for qualitative prediction of growth yield or potential. Moreover, the results of the simulation study demonstrate that quantitative prediction could be possible through use of community uptake values. The parameters of each species in the simulated community of this study were such that each species had similar abilities to compete in a diurnal-light environment. It is not unreasonable that the "community estimates" for this case would be an average over all the species. However, this conclusion may not carry over to an actual ecosystem. The dynamics of different species may be different and, if so, should be described with the best model for each species. Also, a natural community is usually made up of a few dominant species and many subdominant species. Species succession and interactions may be such that the community parameter values would describe the uptake for only the experimental conditions and would be of limited predictive usefulness. Nevertheless, the measurement errors may be so large (especially from an *in situ* experiment with a natural community) that the community-parameter estimates would be the best available method for calibration of the primary trophic level in a lake ecosystem model.

The problem of model discrimination (i.e., determining the appropriate equation relating nutrient concentration to phytoplankton growth) was also addressed using parameter identification. Data were generated by solving a Monod-type growth equation and noise-corrupting the results. Numerical experiments were then performed to determine whether significant differences in the residuals were obtained when the generating model, a Caperon-type model (*Ref. 6*) and a logistic-type model were used for the estimation. A complete discussion is given by Lederman (*Ref. 35*).

The three models in this study predict dissimilar nutrient uptake responses by phytoplankton. Therefore, given perfect data, discrimination between models is possible. Discrimination between models given noise-corrupted data (the only case of practical importance) may be very difficult. The standard

deviations of the nutrient residuals were the only criterion for discrimination for the cases tested here. This brings into question the arguments of various investigators that their model is better than models proposed by other workers. Careful design of experiments may make discrimination possible, but this study indicates that the predictions of all models could result in similar fits to error-corrupted data. The results of this study also demonstrate that the criterion for discrimination should be expanded to take into account the reproducibility of parameter estimates between experiments (enrichment levels).



## EXAMPLE APPLICATIONS OF THE MODEL

We had originally planned to calibrate the lake model using data from *in situ* nutrient-enrichment experiments. However, as discussed above, we were unable to determine the pertinent growth parameters from the field data and our study of parameter estimation applied to nutrient uptake indicates that it may be impossible to design an experiment to accomplish this. Thus, some serious questions regarding the predictive utility of phytoplankton models may be raised. Nevertheless, such models reproduce observed behavior fairly well in some cases (*Ref. 13*) and the results from them definitely provide good qualitative information.

Several runs of the model were made to indicate the usefulness of this qualitative information and potential applications in real situations. Values of the parameters were chosen from those reported in the literature (*Ref. 13*). These values and the initial conditions for the five cases given below are listed in Appendix II.

The most significant results generated from solving the equations are:

- 1) The model produces a "realistic" sequence of events as shown in Figure 1 (e.g., a spring bloom and smaller fall bloom are predicted, with a different dominant species in each);
- 2) the response to nutrient enrichment is what would be expected—excess algal production followed by increased respiration in the hypolimnion;
- 3) stratification has a marked effect on the phytoplankton productivity; artificial destratification reduces the magnitude of the spring bloom and in certain instances would prevent anoxic conditions from developing in the hypolimnion; artificial stratification (e.g., from a thermal effluent) has the opposite effect;
- 4) diurnal light variation and vertical mixing suffice to maintain a large number of species in coexistence (Figure 2); this provides a possible explanation of "the paradox of the plankton" (*Ref. 30*);
- 5) nutrient depletion causes decreased production efficiency in the near-surface waters (Figure 3); this phenomenon has been observed in the field (*Ref. 48*) and has been attributed to direct light inhibition of photosynthesis. The model indicates that nutrient depletion is a possible alternate explanation.

Figure 1

Lake ecosystem simulation for a year.

Numerals 1, 2, and 3 refer to the three phytoplankton species, the H refers to the herbivore species, and N to nutrient. Note that the spring bloom is dominated by species 2 while the fall bloom is dominated by species 3. A diurnal cycle is superimposed on the annual cycle.



MG. NO3-N/CUBIC METER X 1000.

.1	.2	.3	.4	.5	PRODUCER 1
.1	.2	.3	.4	.5	PRODUCER 2
.1	.2	.3	.4	.5	PRODUCER 3
.1	.2	.3	.4	.5	HERBIVORES
.1	.2	.3	.4	.5	NITRATES

.....*					
H	1	3			N
H	1	23			N
H	1	3			N
H	1	3			N
.	1	3			N
.	1	23			N
.	1	3			N
720. HRS.*	1	32			N
.	1	3			N
.	1	3			N
.	1	32			N
.	1	3			N
.	1	3			N
.	1	32			N
.	1	3			N
.	1	3			N
.	1	3			N
.	1	3			N
1440. HRS.*	1	3	23 N		N
.	1	3	N3 2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
2160. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
2880. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
3600. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
4320. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
5040. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
5760. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
6480. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
7200. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
7920. HRS.*	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
.	1	3	2		N
8640. HRS.*	1	3	2		N



Figure 2

Simulation for five phytoplankton with diurnally varying light showing a dynamic interaction in which all the species co-exist.

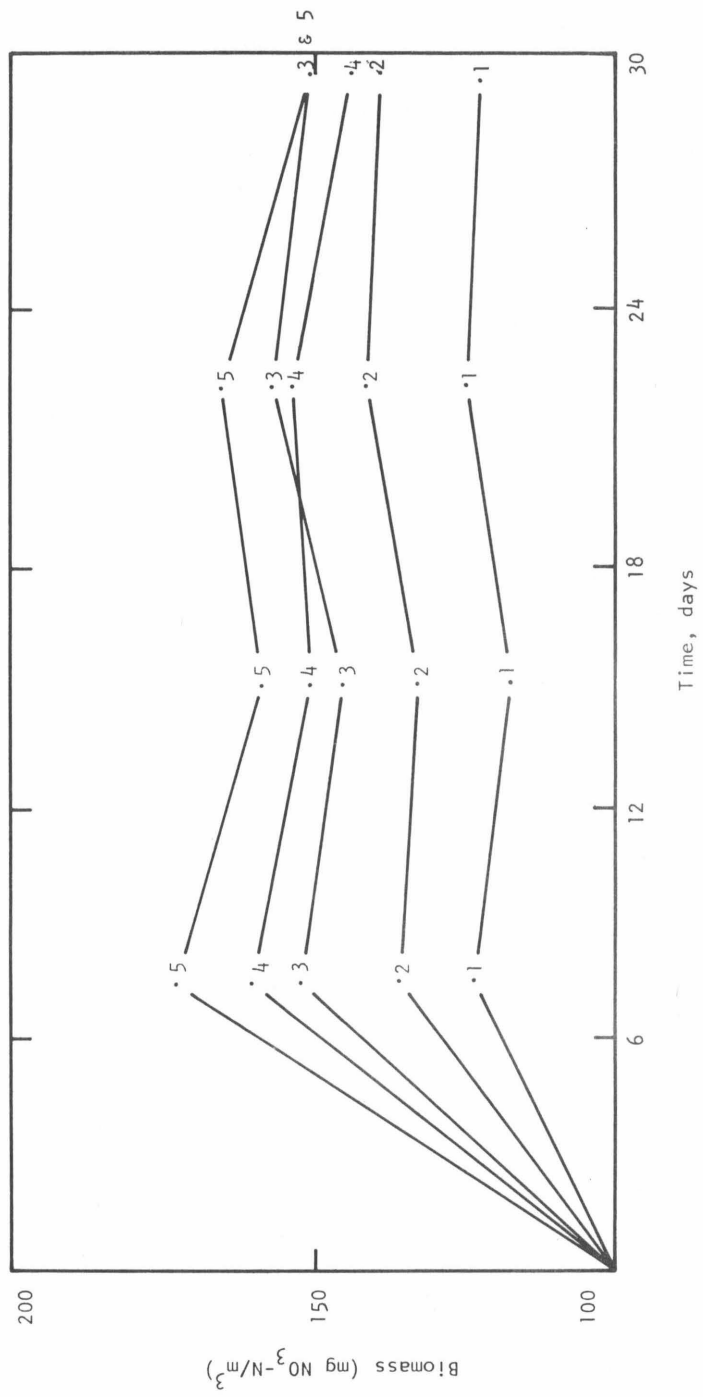
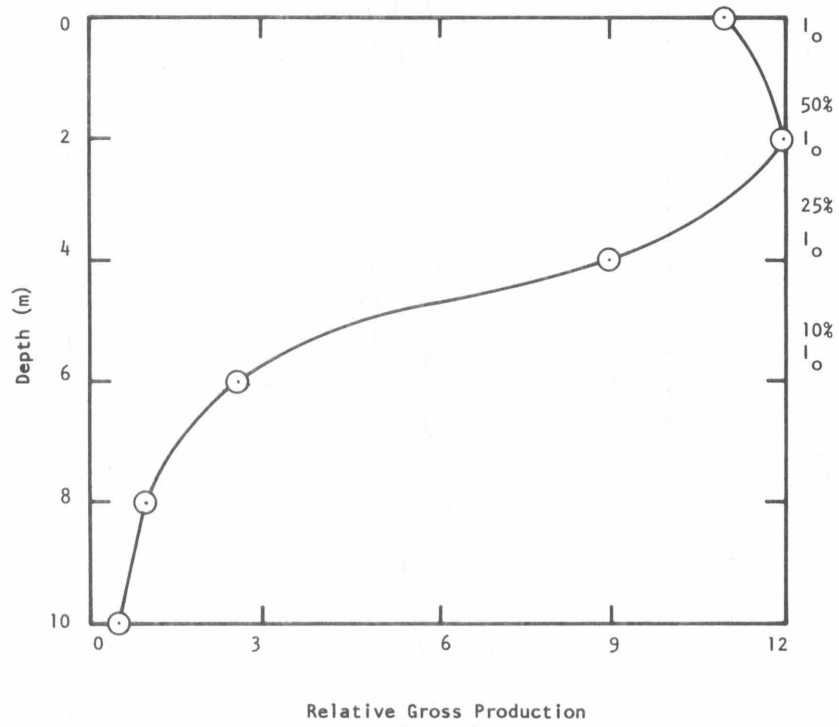


Figure 3.

Relative gross production for 12 hours vs depth for simulation of nutrient-limited growth in a water column.



The first two results actually check only the reasonableness of the model; many alternative model formulations would predict similar behavior (*Ref. 12*). The effects of stratification have also previously been investigated using a phytoplankton model (*Ref. 36*).

The last two results, however, have not been reported. The possibility of environmental variability negating competitive exclusion has been suggested (*Ref. 30*), and models have indicated that seasonal variation does allow a number of species to co-exist (*Ref. 33*). The results of this model show that short-term environmental changes also allow a number of species to co-exist.

The fifth result listed above has important implications regarding interpretation of measurements of primary productivity. If nutrient depletion can be important in open waters, then it would surely influence light-dark bottle measurements of productivity (*Ref. 19*). Also, any model that incorporated a light inhibition function would produce erroneous predictions if the decrease in production were due to nutrient limitation rather than the assumed light limitation.



## SUMMARY

1. The lake ecosystem model produces a "realistic" sequence of events (e.g., a spring bloom and smaller fall bloom are predicted).
2. The response to nutrient enrichment is what would be expected—excess algal production followed by increased respiration in the hypolimnion.
3. Stratification has a marked effect on the phytoplankton productivity; artificial destratification reduces the magnitude of the spring bloom and in certain instances would prevent anoxic conditions from developing in the hypolimnion; artificial stratification (e.g., from a thermal effluent) has the opposite effect.
4. Diurnal light variation and vertical mixing suffice to maintain a (large) number of species in coexistence; this provides a possible explanation of "the paradox of the plankton" (Ref. 30).
5. Nutrient depletion causes decreased production efficiency in the near-surface waters; this phenomenon has been observed in the field (Ref. 48) and has been attributed to direct light inhibition of photosynthesis. The model indicates that nutrient depletion is a possible alternate explanation.
6. *In situ* enrichment experiments showed that diversity initially decreases when nutrients are added to an oligotrophic lake in the form of phosphate and/or nitrate; the decrease is very rapid; the decrease is not correlated with either the nutrient added or its concentration; diversity tends to increase after the initial decrease.
7. It can be concluded that there is an inverse relationship between nutrient additions and the diversity index of the phytoplankton; however, the relationship is a qualitative one. Considering this, it is unlikely that the diversity index can be used as a quantitative indicator of eutrophic conditions.
8. The usefulness of nonlinear parameter estimation to calibrate a nutrient uptake model for one species was established. However, adequate data cannot be obtained from *in situ* experiments, and careful laboratory experiments using both constant and diurnal light conditions are necessary to obtain good estimates of all parameters.

9. The application of nonlinear parameter estimation to multispecies batch-culture data, though easily and successfully applied to simulated data, is probably infeasible for actual experimental data.
10. Discrimination to choose the "best" model among several alternatives was shown to be very difficult; results show that the criteria for discrimination should include the reproducibility of parameter estimates between experiments.



## CONCLUSIONS

The lake ecosystem model which was developed predicts effects of biological changes in an impoundment in response to various changes in the physical environment and can provide qualitative information which may be of considerable value in planning situations. However, this research has indicated that there are severe problems associated with using lake ecosystem models to quantitatively predict the effects of nutrient enrichment. Several investigators (*Ref. 11*) have proposed using such models for planning purposes, but our work has shown that predictions based upon these models must be viewed with skepticism.

The most difficult aspect of verifying the models is in determining "correct" growth parameters. Our field experiments and study of parameter estimation indicate that *in situ* enrichment experiments will not provide adequate data for accurate determination of the parameters. The fact that a very important parameter—the half-saturation constant—can be grossly misestimated from poorly-chosen data demonstrates that model "calibration" using field data is unwarranted. Although growth parameters can be estimated using careful laboratory experiments, extrapolation to field conditions is questionable.

Therefore, even if model predictions compare reasonably well with field observations, predictions of changes in response to other hypothetical environmental conditions should be used only in a qualitative or semi-quantitative manner. Results of models extrapolated to different conditions should not be used for precise management decisions.



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**APPENDIX I**  
**FORTRAN COMPUTER PROGRAM**

This program was written by T. Lederman and W. Keene as part of a research project supervised by G. Hornberger and M. Kelly. The work was supported by the Department of Interior, Office of Water Research and Technology Grant A-045-VA. The purpose of this project was to develop a model to study problems associated with lake eutrophication. The program is a digital computer simulation of the interactions among two limiting nutrients, 1-15 producer species, and 1-3 herbivore species in a vertically mixed one-dimensional lake. The model consists of mass balance equations and incorporates Michaelis-Menten growth mechanics.

Many models of phytoplankton growth have been developed. The review by Patten (*Ref. 42*) summarizes the earlier attempts and presents criticisms of them. More recent models which parallel our work include those reported by Chen and Orlob (*Ref. 11*), DiToro *et al.* (*Ref. 13*), and Grenney (*Ref. 29*).

The following growth equations are given for quiescent water.

Producer equation for species  $i$  ( $i=1, \dots, I$ ):

$$\frac{dP_i}{dt} = A_i F P_i \left( \frac{N_1}{KM_1 + N_1} \right) \left( \frac{N_2}{KM_2 + N_2} \right) - R_i P_i - \sum_{j=1}^J G_j P_i H_j$$

where: F = input energy at the lake surface  
P = concentration of phytoplankton  
A = ability of the producers to utilize F through photosynthesis  
N1 = concentration of nitrates in solution  
N2 = concentration of phosphates in solution  
KM1 = nitrate disassociation constant  
KM2 = phosphate disassociation constant  
R = producer respiration rate  
G = grazing rate of herbivore  
H = concentration of herbivore

This equation incorporates Michaelis-Menten uptake dynamics. The general form of the Michaelis-Menten term is:

$$\frac{N}{KM+N}$$

where: N = nutrient in solution  
 KM = disassociation constant

It can be seen that as N decreases, the term approaches zero; the rate of this approach being dependent on Km. A detailed discussion of Michaelis-Menten growth mechanics is given by Eppley *et al.* (Ref. 21) and Dugdale (Ref. 17). In the case of two nutrients, as N1 becomes large its term approaches 1 and N2 becomes limiting. This form thus approximates Liebig's law of the minimum.

Herbivore equation for species j(j=1, . . . ,J):

$$\frac{dH_j}{dt} = \left( \sum_{i=1}^I E_j P_i G_j H_j \left( \frac{HMAX_j \cdot H_j}{HMAX_j} \right) \right) - R_j H_j - CARN_j H_j$$

where: E = grazing efficiency  
 R = herbivore respiration rate  
 HMAX = maximum herbivore concentration  
 (carrying capacity)  
 CARN = grazing rate of carnivores

The logistic term (Hmax–H/Hmax) is used to limit herbivore growth at some theoretical maximum limit. This is unrealistic because it does not deal directly with the limiting factor. It was used because the dynamics of limiting factors, such as density dependency, are not well understood.

Nutrient equation:

$$\frac{dN}{dt} = \sum_{i=1}^I C_i^P \left( - \frac{dP_i}{dt} \right) + \sum_{j=1}^J C_j^H \left( - \frac{dH_j}{dt} \right)$$

where: C = concentration of nutrient (either nitrates or phosphates) in the phytoplankton or herbivore

Vertical dispersion is treated by finite differencing over the depth interval. The general form of the equation is:

$$\frac{d}{dz} D \frac{dc}{dz}$$

The finite difference approximation is developed as follows:

$$D_{n-1/2} \approx (D_n + D_{n-1}) / 2$$

$$D_{n+1/2} \approx (D_{n+1} + D_n) / 2$$

$$D \frac{dC}{dz} \Big|_{n+1/2} \approx D_{n+1/2} \left( \frac{C_{n+1} - C_n}{\Delta z} \right)$$

$$D \frac{dC}{dz} \Big|_{n-1/2} \approx D_{n-1/2} \left( \frac{C_n - C_{n-1}}{\Delta z} \right)$$

$$\frac{d}{dz} \left( D \frac{dC}{dz} \right) \approx \frac{D_{n+1/2} \left( \frac{C_{n+1} - C_n}{\Delta z} \right) - D_{n-1/2} \left( \frac{C_n - C_{n-1}}{\Delta z} \right)}{\Delta z}$$

$$\approx \left( \frac{1}{\Delta z} \right)^2 [D_{n+1/2} C_{n+1} - (D_{n+1/2} + D_{n-1/2}) C_n + (D_{n-1/2} C_{n-1})]$$

where:  $D_n$  = dispersion rate at depth  $n$   
 $C_n$  = concentration of mixed material at depth  $n$   
 $\Delta z$  = depth interval

The term represents an input due to mixing and takes on positive or negative values depending on the concentration gradient.

Boundary conditions require a modification of the above equations. Since material is not lost to the atmosphere, the surface layer is only mixed with the layer below it. This condition is met by the following equations:

$$\begin{aligned} D_{n+1} &= D_{n-1} \\ C_{n+1} &= C_{n-1} \end{aligned}$$

Material can be transported across the bottom into the sediment and vice versa. This is treated as a source and sink term in the equation. Due to a lack of time and information, we were unable to incorporate this transport into our simulation. The source and sink terms in the equations were set to zero and consequently dispersion at the bottom and surface is treated in a similar manner.

Mixing is the first step toward including effects of water motion. In this model the dispersion coefficient must handle all effects. Thus, the general mass balance equations are:

$$\frac{\partial P_{n,i}}{\partial t} = A_i F P_{n,i} \left( \frac{N1}{KM1_i + N1} \right) \left( \frac{N2}{KM2_i + N2} \right) - R_i P_{n,i} - \left( \sum_{j=1}^J G_j P_{n,i} H_{n,j} \right) + \left( \frac{1}{\Delta z} \right)^2 \left( (D_{n+1/2,i} P_{n+1,i}) - (D_{n+1/2,i} + D_{n-1/2,i}) P_{n,i} + (D_{n-1/2,i} P_{n-1,i}) \right)$$

where:  $D_{n,i}$  = dispersion rate for producers at depth  $n$ ;  
 $P_{n,i}$  = concentration of the  $i$ th producer species at depth  $n$ ;  
 $H_{n,j}$  = concentration of the  $j$ th herbivore species at depth  $n$ ;

$$\frac{\partial H_{n,j}}{\partial t} = \left( \sum_{i=1}^I E_j G_j P_{n,i} H_{n,j} \left( \frac{HMAX_j - H_{n,j}}{HMAX_j} \right) \right) - R_j H_{n,j} - CARN_j H_{n,j} + \left( \frac{1}{\Delta z} \right)^2 \left( (D_{n+1/2,j} H_{n+1,j}) - (D_{n+1/2,j} + D_{n-1/2,j}) H_{n,j} + (D_{n-1/2,j} H_{n-1,j}) \right)$$

where:  $D_{n,j}$  = dispersion rate for the  $j$ th herbivore species at depth  $n$ ;

$$\frac{\partial H_{n,j}}{\partial t} = \sum_{i=1}^I C_i \left( \frac{\partial P_{n,i}}{\partial t} \right) + \sum_{j=1}^J C_j \left( \frac{\partial H_{n,j}}{\partial t} \right) + \left( \frac{1}{\Delta z} \right)^2 \left( (D_{n+1/2} N_{n+1}) - (D_{n+1/2} + D_{n-1/2}) N_n + (D_{n-1/2} N_{n-1}) \right)$$

Since the equations are solved at discrete depths, consideration has been made to attenuation with depth of the available surface light. Light attenuation results from the effects of producer self-shading, sediment, and the water itself. The equation is:

$$F_n = F_{n+1} e^{-(KW+KS+KB)\Delta Z}$$

where:  $F_n$  = light flux at the depth being considered  
 $F_{n+1}$  = light flux at one depth interval above  
 $KW$  = water attenuation coefficient  
 $KB$  = biological attenuation coefficient  
 $\Delta Z$  = depth interval

The above system of equations is coupled nonlinear partial differential equations, for which the solution must be numerical. There is a variety of methods of solution from which to choose. Most work has been in finite-difference solutions. We chose to finite-difference the spatial derivative, thereby reducing the problem to one of solving a system of ordinary differential equations. A Runge-Kutta technique, which is a widely-used method in ecological modeling, was used for the time variable.

## ASSUMPTIONS, LIMITING OR RESTRICTIVE FACTORS

- 1) Phytoplankton follow Michaelis-Menten growth mechanics.
- 2) The nutrient per unit biomass in both the producer and herbivore is constant. The ratio of nitrate to phosphate is 15:1.
- 3) Grazing is linearly related to the plant biomass.
- 4) There are no effects due to vertical migration of the herbivores.
- 5) There is a maximum carrying capacity for the herbivores.
- 6) There are no temperature effects on the system except those implied in the seasonal variation of the dispersion rates.
- 7) There are no decomposers, and the nutrient egested by the herbivore is immediately available to the phytoplankton.
- 8) There is no lateral motion—all mixing is vertical.
- 9) No transport occurs across the surface boundary.
- 10) There is no shading due to the herbivores.
- 11) Light is unidirectional—there is no scattering.
- 12) There is no differential absorption of light.
- 13) The sediment attenuation coefficient is treated as a constant.
- 14) The maximum time step was estimated empirically at half an hour. Rate coefficients are in inverse hours; this restriction is advisable in order to maintain reasonable numerical accuracy.
- 15) There is no carnivore storage; this biomass is returned to the nutrient in solution.





## DEFINITIONS AND VALUES OF CONSTANTS

- F Average monthly incident radiation values for the southeast United States were obtained from Odum (*Ref. 42*). A fourth order polynomial equation was fit to the data and used in the program to generate average hourly light values ( $\text{kcal/m}^2/\text{hr}$ ) on a 24-hour-a-day basis.
- A A value for the ability of each producer to absorb the incident light was derived such that  $A \times F$  when  $F$  equals  $180 \text{ kcal/m}^2/\text{hr}$  gave a doubling time of approximately one day.
- RP, RH A respiration rate was obtained such that in the absence of growth, the producer biomass was reduced one half in five days. The same respiration rate was used for the herbivore.
- KM1,  
KM2 Dissociation constants for nitrate and ammonium were given by Eppley *et al.* (*Ref. 21*). Under conditions of high nitrate concentrations, higher KM values would be expected. Due to a lack of data for freshwater systems, two values of 4 and 6 microgram-atoms N/l or 4000 and 6000 microgram-atoms  $\text{N/m}^3$ , the unit volume used in the simulation, was chosen. KM values for phosphate were set at an arbitrary low value (10 and 20 microgram-atoms  $\text{P/m}^3$ ). The present study is only concerned with the effects of nitrates; the low phosphate KM helps retard the effect of the phosphate Michaelis-Menten term and therefore keeps phosphates from becoming limiting.
- CP1,  
CH1 All standing crop concentrations used are in microgram-atoms.
- CP2,  
CH2 nitrate/ $\text{m}^3$ . The concentrations of nitrate in both the producer (CP1) and the herbivore (CH1) are therefore 1. By assuming a constant ratio of nitrate to phosphate of 15:1, a value of 0.07 was consequently used for CP2 and CH2.
- N1,  
N2,  
NT1,  
NT2 A high total nitrate concentration (NT1) of 20,000 microgram-atoms nitrate/ $\text{m}^3$  was used as a realistic value for a eutrophic situation. An unrealistically high total phosphate concentration (NT2) of 5,000 microgram-atoms phosphate/ $\text{m}^3$  was used to retard

the limiting effect of the phosphate Michaelis-Menten term. The nutrient in solution (N) was obtained by the following equation:

$$\text{Nutrient in solution} = (\text{total nutrient}) - (\text{nutrient in biomass})$$

- G A grazing rate was derived by assuming a filtering rate of 1 liter/day/gram herbivore. This gives a rate of 0.000042/hr on a  $\text{m}^3$  basis.
- E The efficiency is assumed to be 0.1.
- HMAX The herbivore carrying capacity is assumed to be the point at which all the nitrate is bound in the herbivore biomass. Therefore, HMAX equals the average total nitrate, or 20,000 microgram-atoms  $\text{N}/\text{m}^3$ .
- D Dispersion rates were taken from Bella (*Ref. 4*). His values ranged from  $1 \text{ cm}^2/\text{sec}$  ( $0.4\text{m}^2/\text{hr}$ ) for turnover conditions to  $0.1 \text{ cm}^2/\text{sec}$  ( $0.036\text{m}^2/\text{hr}$ ) for low mixing conditions. These values were used as an order of magnitude indicator of the dispersion rates. Phytoplankton and nutrients were mixed at the same rate at each depth, with low mixing across the thermocline (when it was present). The dispersion rate for the herbivores was the same at all levels, and it was equal to the producer-nutrient dispersion above the thermocline. This partially accounts for the effects of vertical migration and predation. Dispersion values were changed every month to account for seasonal variation. It would obviously be better to use changing dispersion rates based on seasonal temperature changes, but information on the dispersion-temperature relationship is not readily available. Between October and March complete mixing occurred. The dispersion rate equaled  $0.4\text{m}^2/\text{hr}$  at all depths. Between April and June the lake was highly stratified. The dispersion rates above the thermocline (which was between 3 and 4 m) was  $0.144 \text{ m}^2/\text{hr}$ .
- KW An attenuation coefficient of 0.02 is used. This value is typical of clear water ( $0.018 = \text{KW}$  for distilled water).
- KS A sediment and dissolved material attenuation coefficient of 0.1 is used and is assumed to be constant throughout the year.
- KB The biological attenuation coefficient was assumed to have a value of 1 at a producer concentration of 50,000 microgram-atoms nitrate/ $\text{m}^3$ . KB varies with the concentration of the producer biomass by the following relationship:

$$KB = CLIGHT \sum_{i=1}^I P_i$$

where: CLIGHT = a constant relating KB with P.  
A CLIGHT value of 0.00002 was calculated from this relationship. This value may be too low, in that a KB value of 1 would be more likely to occur at a concentration of 25,000 microgram-atoms nitrate/m<sup>3</sup>.

A listing of the FORTRAN computer program follows.

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58      PROGRAM LAKERK(INPUT,OUTPUT,PUNCH,TAPE5=INPUT)
          RAM LAKERK(INPUT,OUTPUT,PUNCH,TAPE5=INPUT)
          THIS PROGRAM SIMULATES A VERTICALLY MIXED LAKE WITH A PLANKTON
          COMMUNITY CONSISTING OF A VARIABLE NUMBER OF PHYTOPLANKTON AND
          HERBIVORE SPECIES AND 2 LIMITING NUTRIENTS USING MICHAELIS-MENTEN
          GROWTH MECHANICS
          C      TH MECHANICS          LIMITING NUTRIENTS USING MICHAELIS-MENTEN
          C      THE INPUT VARIABLES ARE READ IN THE FOLLOWING ORDER
          C      ASTERISKS INDICATE SEPARATE DATA CARDS
          C      ASTERISKS INDICATE SEPARATE DATA CARDS          ELIS-MENTEN
          C      READ THE NUMBERS OF SPECIES AND THE RUN TIMING VARIABLES
          C      THE NUMBERS OF SPECIES AND THE RUN TIMING VARIABLES      N
          *****
          C      NUMBP=NUMBER OF PHYTOPLANKTON SPECIES
          C      NUMBH=NUMBER OF HERBIVORE SPECIES
          C      TIMEO=RUN STARTING TIME (HOURS)
          C      ENDT=RUN TERMINATION (HOURS)
          C      DT=RUNGE-KUTTA CALCULATION INTERVAL (HOURS)
          C      TPRNT=COMMUNITY PRINT INTERVAL (HOURS)
          C      SPRNT=SPECIES PRINT INTERVAL (HOURS)
          C      CGRAPH=GRAPH STORAGE INTERVAL (HOURS)
          C      CPLOT=PLOT STORAGE INTERVAL (HOURS)
          *****
          C      READ THE LAKE AND LIGHT ATTENUATION PARAMETERS
          C      THE LAKE AND LIGHT ATTENUATION PARAMETERS
          *****
          C      KS=ATTENUATION COEFFICIENT FOR TOTAL SUSPENDED AND DISSOLVED

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C MATERIAL
C KW=WATER ATTENUATION COEFFICIENT
C DEEP=DEPTH OF THE LAKE (METERS)
C DZ=DEPTH INTERVAL (METERS)
C CLIGHT=CONSTANT RELATING KB WITH 9P
*****
C READ THE PLCT ROUTINE PARAMETERS *****
C THE PLCT ROUTINE PARAMETERS *****
*****
C IXX=NUMBER OF VARIABLES TO BE PLOTTED IN TERMS OF NITRATES
C LAYA,LAYB=DEPTHS AT WHICH THE VALUES TO BE PLOTTED ARE STORED
C XVAL=INTERVAL (HOURS) AT WHICH X AXIS LABELS ARE TO BE PRINTED
C NOTE - XVAL MUST BE EVENLY DIVISIBLE BY CPL0T
*****
C VMAX=MAXIMUM VALUE FOR EACH VARIABLE PLOTTED
C HMAX=MAXIMUM VALUE FOR THE DIVERSITY INDEX
*****
C LABEL=ALPHANUMERIC NAME OF EACH VARIABLE TO BE PLOTTED
*****
C P=ALPHNUMERIC SINGLE LETTER FOR EACH VARIABLE TO BE PLOTTED
*****
C READ THE NAME, GROWTH PARAMETERS, AND INITIAL BIOMASS VALUES OF
C EACH PHYTOPLANKTON SPECIES (REPEAT FOR EACH SPECIES)
C EACH PHYTOPLANKTON SPECIES (REPEAT FOR EACH SPECIES)
*****
C NAMEP1,NAMEP2=ALPHANUMERIC STORAGE FOR THE NAME OF EACH PHYTO-

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C C PLANKTON SPECIES
C C A=ABILITY OF EACH PHYTOPLANKTON SPECIES TO UTILIZE F IN PHOTOSYNTHESIS
C C (SQ. M./KCAL)
C C RP=RESPIRATION RATE FOR EACH PHYTOPLANKTON SPECIES (/HR.)
C C KM1=MICHAELIS-MENTEN DISASSOCIATION CONSTANT FOR NITRATES FOR
C C EACH PHYTOPLANKTON SPECIES (MG. N03-N/CU. M.)
C C KP2=MICHAELIS-MENTEN DISASSOCIATION CONSTANT FOR PHOSPHATES FOR
C C EACH PHYTOPLANKTON SPECIES (MG. P04-P/CU. M.)
C C CP1=CONCENTRATION OF N03 IN EACH PHYTOPLANKTON SPECIES
C C (MG. N03-N/MG. N03-N)
C C CP2=CONCENTRATION OF P04 IN EACH PHYTOPLANKTON SPECIES
C C (MG. P04-P/MG. N03-N)
C C *****
C C BF=PHYTOPLANKTON BICMASS FOR EACH SPECIES AT EACH DEPTH
C C (MG. N03-N/CU. M.)
C C *****
C C READ THE NAME, GROWTH PARAMETERS, AND INITIAL BICMASS VALUES OF
C C EACH HERBIVORE SPECIES (REPEAT FOR EACH SPECIES)
C C EACH HERBIVORE SPECIES (REPEAT FOR EACH SPECIES)
C C *****
C C NAMEH1,NAMEH2=ALPHANUMERIC STORAGE FOR THE NAMES OF EACH HERBIVORE
C C SPECIES
C C EFF=GRAZING EFFICIENCY FOR EACH HERBIVORE SPECIES (AMOUNT
C C ASSIMILATED/AMOUNT GRAZED)
C C GRAZ=GRAZING RATE FOR EACH HERBIVORE SPECIES (CU. M./MG. N03-N/HR.)
C C RH=RESPIRATION RATE FOR EACH HERBIVORE SPECIES (/HR.)
C C CH1=CONCENTRATION OF N03 IN EACH HERBIVORE SPECIES

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C      (MG. N03-N/MG. N03-N)
C      CH2=CONCENTRATION OF P04 IN EACH HERBIVORE SPECIES
C      (MG. F04-P/MG. N03-N)
C      BMAX=CARRYING CAPACITY FOR EACH HERBIVORE SPECIES
C      (MG. N03-N/CU. M.)
*****
C      CARN=LOSS RATE FOR EACH HERBIVORE SPECIES WHICH ACCOUNTS FOR GRAZING
C      BY CARNIVORES (/HR.)
*****
C      BH=HERBIVORE BIOMASS FOR EACH SPECIES AT EACH DEPTH
C      (MG. N03-N/CU. M.)
*****
C      READ THE INITIAL TOTAL NUTRIENT VALUES
C      THE INITIAL TOTAL NUTRIENT VALUES
*****
C      NT1=TOTAL N03 AT EACH DEPTH (MG. N03-N/CU. M.)
*****
C      NT2=TOTAL P04 AT EACH DEPTH (MG. P04-P/CU. M.)
*****
C      READ THE INITIAL DISPERSION RATES
C      THE INITIAL DISPERSION RATES
*****
C      DRP=DISPERSION RATE BETWEEN EACH 2 DEPTHS FOR ALL PHYTOPLANKTON
C      SPECIES (SQ. M./HR.)
*****
C      DN=DISPERSION RATE BETWEEN EACH 2 DEPTHS FOR BOTH NUTRIENTS (SQ.

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```

C M./HR.)
C *****
C DBH=DISPERSION RATE BETWEEN EACH 2 DEPTHS FOR EACH HERBIVORE
C SPECIES (SQ. M./HR.) (REPEAT FOR EACH SPECIES)
C *****
C ALL READ STATEMENTS AFTER THESE INPUT THE SUBSEQUENT MONTHLY
C DISPERSION RATES
C DISPERSION RATES R THESE INPUT THE SUBSEQUENT MONTHLY
C DISPERSION RATES R THESE INPUT THE SUBSEQUENT MONTHLY
C THE FOLLOWING IS AN ALPHABETIZED LIST OF ALL VARIABLES USED IN THE
C PROGRAM (EXCLUDING THE INPUT VARIABLES DESCRIBED ABOVE) HE
C PROGRAM (EXCLUDING THE INPUT VARIABLES DESCRIBED ABOVE) HE
C AVE=AVERAGE NT1 FOR ALL DEPTHS IN THE LAKE (MG. N03-N/CU. M.)
C BLANK=ALPHANUMERIC CONSTANT FOR A BLANK
C BION1=TOTAL N03 IN THE FLANKTON BIOMASS (MG. N03-N/CU. M.)
C BION2=TOTAL P04 IN THE PLANKTON BIOMASS (MG. P04-P/CU. M.)
C CLEAN=STORAGE FOR THE POSITION OF THE PLOTTED POINTS SO THAT
C THEY MAY LATER BE #ERASED#
C COMBP,COMBH,COMN1,COMN2=COMPUTATIONAL VARIABLES USED IN THE
C RUNGE-KUTTA CALCULATIONS REPLACING BP, BH, N1, AND N2
C DELTBH=NET HERBIVORE CHANGE FOR EACH SPECIES AT EACH DEPTH
C (MG. N03-N/CU. M./HR.)
C DELTBP=NET PRODUCER CHANGE FOR EACH SPECIES AT EACH DEPTH
C (MG. N03-N/CU. M./HR.)
C DOT=ALPHANUMERIC CONSTANT FOR A DOT
C DMIX=DEPTHS AT WHICH DISPERSION RATES ARE INPUTTED (METERS)
C DP=CHANGE IN BP OVER THE CALCULATION INTERVAL (DT)
C F=AVERAGE LIGHT FLUX AT A SPECIFIC DEPTH (KCAL/SQ. METER/HR.)

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C FO=AVERAGE LIGHT FLUX AT THE SURFACE (KCAL/SQ. M./HR.)  
 C GRAPH=ARRAY USED TO STORE TNET FOR ALL DEPTHS, AT A SPECIFIED  
 C TIME (CGRAPH)  
 C GRAZBH=TOTAL AMOUNT GRAZED FROM EACH HERBIVORE SPECIES AT EACH  
 C DEPTH (MG. NO3-N/CU. M./HR.)  
 C GRAZBP=TOTAL AMOUNT GRAZED FROM EACH PHYTOPLANKTON SPECIES AT EACH  
 C DEPTH (MG. NO3-N/CU. M./HR.)  
 C GROSS=INSTANTANEOUS GROSS PRODUCTIVITY FOR EACH PHYTOPLANKTON  
 C SPECIES AT EACH DEPTH (MG. NO3-N/CU. M./HR.)  
 C GROWBH=TOTAL ASSIMILATION BY EACH HERBIVORE SPECIES AT EACH DEPTH  
 C (MG. NO3-N/CU. M./HR.)  
 C HEAR=SHANNON INFORMATION MEASURE  
 C IGRAPH=COUNTER OF THE NUMBER OF TIMES TNET VALUES WERE STORED  
 C ISTOP=COUNTER OF THE NUMBER OF LINES TO BE PLOTTED  
 C IU,IW,IX,IY,IZ=VARIABLES DEPENDENT ON LDEPTH WHICH ALLOW INPUTTING  
 C DIFFERENT LAKE DEPTHS  
 C KB= BIOLOGICAL ATTENUATION COEFFICIENT  
 C KBP,KBH,KN1,KN2=THE RUNGE-KUTTA VARIABLES  
 C LAYN=FORMAL PARAMETER IN PLOT FOR LAYA OR LAYB  
 C LDEPTH=NUMBER OF DEPTH INCREMENTS (DEFP/DZ)  
 C LINE=ARRAY THAT STORES THE POINTS FOR EACH LINE OF PLOT  
 C MIXBH=INPUT OF EACH HERBIVORE SPECIES TO EACH DEPTH DUE TO MIXING  
 C (MG. NO3-N/CU. M./HR.)  
 C MIXBP=INPUT OF EACH PHYTOPLANKTON SPECIES TO EACH DEPTH DUE TO MIXING  
 C (MG. NO3-N/CU. M./HR.)  
 C MPT=FORMAL PARAMETER IN PLOT FOR IXX  
 C NET=INSTANTANEOUS NET PRODUCTIVITY FOR EACH PHYTOPLANKTON SPECIES  
 C AT EACH DEPTH (MG. NO3-N/CU. M.)

C N1=N03 IN SOLUTION AT EACH DEPTH (MG. N03-N/CU. M.)  
 C N2=P04 IN SOLUTION AT EACH DEPTH (MG. P04-P/CU. M.)  
 C PRODBP=GROSS PRODUCTION FOR EACH PHYTOPLANKTON SPECIES OVER THE  
 C CALCULATION INTERVAL AT EACH DEPTH (MG. N03-N/CU. M./HR.)  
 C Q=THE VALUE OF Y (TIME) AS IT CHANGES OVER THE RUNGE-KUTTA  
 C CALCULATION INTERVAL  
 C RESBH=RESPIRATION FOR EACH HERBIVORE SPECIES AT EACH DEPTH  
 C (MG. N03-N/CU. M./HR.)  
 C RESBP=RESPIRATION FOR EACH PHYTOPLANKTON SPECIES AT EACH DEPTH  
 C (MG. N03-N/CU. M./HR.)  
 C STAR=ALPHANUMERIC CONSTANT FOR AN ASTFRISK  
 C STORA=ARRAY USED TO STORE TBIOP, TBI0H, AND N1 FOR A SPECIFIED  
 C DEPTH (LAYA), AT A SPECIFIED TIME (CPL0T)  
 C STORB=ARRAY USED TO STORE TBIOP, TBI0H, AND N1 FOR A SPECIFIED  
 C DEPTH (LAYB), AT A SPECIFIED TIME (CPL0T)  
 C SUM=VARIABLE USED IN CALCULATING DIVERSITY (HBAR)  
 C TBI0H=TOTAL HERBIVORE BICMASS AT EACH DEPTH (MG. N03-N/CU. M.)  
 C TBIOP=TOTAL PRODUCER BICMASS AT EACH DEPTH (MG. N03-N/CU. M.)  
 C TCC=COMMUNITY PRINT TIMER (HOURS)  
 C TCS=SPECIES PRINT TIMER (HOURS)  
 C TDISP=NEW DISPERSION READ TIMER (HOURS)  
 C TGRAPH=STORE INTERVAL TIMER FOR THE GRAPH ROUTINE (HOURS)  
 C TGROSS=INSTANTANEOUS TOTAL GROSS PRODUCTIVITY AT EACH DEPTH  
 C (MG. N03-N/CU. M./HR.)  
 C TNET=INSTANTANEOUS TOTAL NET PRODUCTIVITY AT EACH DEPTH  
 C (MG. N03-N/CU. M./HR.)  
 C TFLOT=STORE INTERVAL TIMER FOR THE PLOT ROUTINE (HOURS)  
 C TIME=TIME (HOURS)

```

C      TCTAL=SUM OF NT1 FOR ALL DEPTHS IN THE LAKE
C      VAL=FORMAL PARAMETER IN PLOT FOR STORA OR STORB
C      YVAL=VALUE OF EACH Y AXIS LABEL IN PLOT
C      XFACT=VARIABLE MULTIPLIED WITH XVAL TO GIVE THE HOURS OF THE X AXIS
C      LABEL IN PLOT
C      XVALC=X AXIS INCREMENT COUNTER IN PLOT
C      Y=YEARLY TIMER (HOURS)
C      ARLY TIMER (HOURS)   COUNTER IN PLOT   HE HOURS OF THE X AXIS
C      ARLY TIMER (HOURS)   COUNTER IN PLOT   HE HOURS OF THE X AXIS
C      COMMON/AA/EP(15,13),BH(3,13),NET(15,13),GROSS(15,13)
C      COMMON/AB/DN(13),DBH(3,13),IY,IZ,CLIGHT,KS,KW,Y,FO
C      COMMON/AC/N1(13),N2(13),NT1(13),NT2(13),F(13),HBAR(13),DMIX(10)
C      COMMON/AD/KM1(15),KM2(15),A(15),RP(15),CP1(15),CP2(15)
C      COMMON/AE/EFF(3),GRAZ(3),RH(3),BHMAX(3),CH1(3),CH2(3),CARN(3)
C      COMMON/BA/TBIOP(13),TBIOH(13),TGROSS(13),TNET(13),DBP(13)
C      COMMON/BB/NAMEP1(15),NAMEP2(15),NAMEH1(3),NAMEH2(3)
C      COMMON/PT/P(7),VMAX(7),LABEL(7)
C      COMMON/GR/GRAPH(13,30)
C      COMMON/L/FAMP,PI
C      DIMENSION STORA(7,300),STORB(7,300)
C      REAL KM1,KM2,KB,KW,KS,NET,N1,N2,NT1,NT2,HMAX
C      REAL L1,L2,L3
C      INTEGER P
C      GER P
C      T,N1,N2,NT1,NT2,HMAX
C      READ (5,10) NUMBP,NUMBH,TIMEO,ENDT,DT,TPRNT,SPRNT,CGRAPH,CPLOT
C      READ (5,13) KS,KW,DEEP,DZ,CLIGHT
C      LDEPTH=IFIX(DEEP)/DZ
C      IU=LDEPTH+1

```

```

66      IW=LDEPTH+2
        IX=LDEPTH+3
        IY=LDEPTH+4
        IZ=LDEPTH+5
        READ(5,7)  IXX,LAYA,LAYB,XVAL
        READ(5,36) (VMAX(I),I=1,IXX),HMAX
        READ(5,37) (LABEL(I),I=1,IXX),LABEL(7)
        READ(5,38) (P(I),I=1,IXX),P(7)
        DO 1 I=1,NUMBF
          READ (5,11) NAMEP1(I),NAMEP2(I),A(I),RP(I),KM1(I),KM2(I),CP1(I),
1          CP2(I)
          READ (5,12) (BP(I,J),J=2,IW)
          CONTINUE
          DO 2 I=1,NUMBH
            READ (5,11) NAMEH1(I),NAMEH2(I),EFF(I),GRAZ(I),RH(I),CH1(I),
1            CH2(I),BHMAX(I)
            READ (5,32) CARN(I)
            READ (5,12) (BH(I,J),J=2,IW)
            CONTINUE
            READ (5,12) (NT1(I),I=2,IW)
            READ (5,12) (NT2(I),I=2,IW)
            READ (5,12) (DBP(I),I=3,IW)
            READ (5,12) (DN(I),I=3,IW)
            DO 3 I=1,NUMBH
              READ (5,12) (DBH(I,J),J=3,IW)
              CONTINUE
              INUE      BH(I,J),J=3,IW      F(I),GRAZ(I),RH(I),CH1(I),
3              PRINT 39

```

```

PRINT 14
PRINT 8
PRINT 15
PRINT 16, DEEP
PRINT 17, NUMBP
PRINT 18, NUMBH
PRINT 19
PRINT 20
PRINT 21
PRINT 22
DO 4 I=1,NUMBP
PRINT 23,NAMEP1(I),NAMEP2(I),A(I),RP(I),KM1(I),KM2(I),CP1(I),
1 CP2(I)
4 CONTINUE
PRINT 24
PRINT 25
PRINT 26
DO 5 I=1,NUMBH
PRINT 27, NAMEH1(I),NAMEH2(I),EFF(I),GRAZ(I),RH(I),CH1(I),C+2(I),
1 BHMAX(I),CARN(I)
5 CONTINUE
PRINT 28
PRINT 29
PRINT 30, KS,KW,DZ,CLIGHT
PRINT 31
T 31 W,DZ,CLIGHT I),GRAZ(I),RH(I),CH1(I),CH2(I),
OMIX(1)=DZ/2.
DO 9 K=2,LDEPTH

```

```

68
9      DMIX(K)=DMIX(K-1)+DZ
      (K)=DMIX(K-1)+DZ
      PRINT 33,(DMIX(I),I=1,LODEPTH)
      DO 6 I=1,NUMBH
      PRINT 34, NAMEH1(I),NAMEH2(I),(DBH(I,IY-J),J=2,IU)
      CONTINUE
      PRINT 35, (DN(IY-I),I=2,IU)
      T 35, (DN(IY-I),I=2,IU)
      (I,IY-J),J=2,IU)
      FORMAT(3I5,F10.2)
      FORMAT(10X*MIXED LAKE ASSUMING MICHAELIS-MENTEN GROWTH MECHANICS*)
      FORMAT (2I4,7F10.0)
      FORMAT (2A10,6F10.0)
      FORMAT (11F7.0)
      FORMAT (5F10.0)
      FORMAT (//5X*THIS MODEL SIMULATES THE PLANKTON COMMUNITY OF A ONE
      10 DIMENSIONAL VERTICALLY*)
      FORMAT (//58X*INITIAL CONCITIONS*//)
      FORMAT (5X*LAKE DEPTH =*F5.1* METERS*)
      FORMAT (5X*NUMBER OF PHYTOPLANKTON SPECIES =*I3)
      FORMAT (5X*NUMBER OF HERBIVORE SPECIES =*I3)
      FORMAT (5X*ALL BIOMASS VALUES ARE IN (MG. NO3-N/CU. M.)*
      1 /)
      1
      20 FORMAT(11X*PRODUCER*15X*A*10X*RP*11X*KM1*14X*KM2*16X*CP1*18X*CP2*)
      21 FORMAT(12X,*SPRICES*12X*(SQ. M.*5X*(/HR.)*4X*(MG. NO3-N/*7X *(MG.
      1 P04-P/*4X*(MG. NO3/MG. NC3)*5X*(MG. P04/MG. NO3)*)
      22 FORMAT(14X*NAME*14X*/KCAL)*19X*CU. M.)*9X*CU. M.)**)
      23 FORMAT (5X,2A10,F12.6,F11.4,F14.1,F17.1,F19.3,F21.3)
      24 FORMAT(/11X*HERBIVORE*12X*EFF*8X*GRAZ*8X*RH*12X*CH1*18X*CH2*13X

```

```

1  *9HMAX*8X*CARN*)
25  FORMAT(12X*SPECIES*20X*(CU. M./MG.*3X*(/HR.))*2X*(MG. NO3/MG. NO3)*
14X*(MG. PO4/MG. NO3)*5X*(MG. NO3-N/*3X*(/HR.))*
26  FORMAT(14X*NAME*22X*NO3-N/CU. M.)*55X*CU. M.)*
27  FORMAT(5X,2A10,F10.2,F14.7,F9.4,F14.3,F21.3,F19.1,F12.5)
28  FORMAT (/10X*KS*10X*KW*10X*DZ*18X*CLIGHT*)
29  FORMAT(31X*(METERS)*9X*(CU. M./MG. NO3-N)*
30  FORMAT (1X,3F12.3,F24.7)
31  FORMAT (/5X*HERBIVORE DISPERSION RATES (DBH) (SQ. M./HR.))*
32  FORMAT (F10.0)
33  FORMAT(12X,*SPECIES*,6X,10(F7.1,* M.*))
34  FORMAT (5X,2A10,10F10.4)
35  FORMAT (/5X,*NUT. DISPERSION (DN)*,10F10.4//)
36  FORMAT(7F10.0)
37  FORMAT(7A10)
38  FORMAT(7A1)
39  FORMAT(1H1)
    AT(1H1)
    AT(1H1)
    AT(1H1)
    AT(1H1)
    SION (DN)*,10F10.4//)
    SION (DN)*,10F10.4//)
    SION (DN)*,10F10.4//)
    SION (DN)*,10F10.4//)
    SION (DN)*,10F10.4//)
    SION (DN)*,10F10.4//)
    )*
    )*
    )*
    )*
    )*
    )*
C  INITIALIZATION
    IALIZATION
    TIME=TIMEO
    Y=TIME
    TDISP=AMOD(TIME,720.)
    TCC=0.0
    TCS=0.0

```

```

TOTAL=0.
TPLOT=0.
ISTOR=0
IGRAPH=0
TGRAPH=0.
PI=3.1415926535898
DBP(2)=DBP(3)
DRP(IX)=DBP(IW)
DN(2)=DN(3)
DN(IX)=DN(IW)
DO 45 I=1,NUMPH
DBH(I,2)=DBH(I,3)
DBH(I,IX)=DBH(I,IW)
CONTINUE
      INUE      I,IW)
C      CALCULATE THE LIGHT FOR THIS HOUR
CALL LIGHT(Y,L1,L2,L3,DT)
FO=L1
      1
      1
      1,L2,L3,DT)
      1,L2,L3,DT)
C      CALCULATE THE INITIAL LIGHT, NUTRIENT IN SOLUTION, AND GROSS AND
      NET PRODUCTIVITY VALUES FOR EACH DEPTH
      NET PRODUCTIVITY VALUES FOR EACH DEPTH
      GROSS AND
DO 50 J=2,IW
TRI0H(IY-J)=TRIOP(IY-J)=BION1=RION2=0.
TGROSS(IY-J)=TNET(IY-J)=SUM=0.
DO 47 I=1,NUMEP
TRIOP(IY-J)=TRIOP(IY-J)+8P(I,IY-J)

```

45

C

C



```

47      BION1=9ION1+CP1(I)*9P(I,IY-J)
      BION2=9ICN2+CF2(I)*8P(I,IY-J)
      CONTINUE
      DO 49 I=1, NUMBH
      TBIOH(IY-J)=TBIOH(IY-J)+BT(I,IY-J)
      BION1=3ION1+CH1(I)*BH(I,IY-J)
      BION2=3ION2+CH2(I)*BH(I,IY-J)
      CCNTINUE
49      N1(IY-J)=N1(IY-J)-BION1
      N2(IY-J)=N2(IY-J)-BION2
      KB=CLIGHT+TBICP(IY-J)
      F(IY-J)=F(IZ-J)*EXP(-(KW+KS+KB)*DZ)
      F(IM)=FO
      DO 48 I=1, NUMEP
      GROSS(I,IY-J)=F(IY-J)*A(I)*RP(I,IY-J)*(N1(IY-J)/(N1(IY-J)+KM1(I)))
      * (N2(IY-J)/(N2(IY-J)+KM2(I)))
1      TGROSS(IY-J)=TGROSS(IY-J)+GROSS(I,IY-J)
      NET(I,IY-J)=GROSS(I,IY-J)-RP(I)*BP(I,IY-J)
      TNET(IY-J)=TNET(IY-J)+NET(I,IY-J)
      (IY-J)=TNET(IY-J)+NET(I,IY-J)
      -J)/(N1(IY-J)+KM1(I))
      CALCULATE DIVERSITY INDEX AND AVERAGE TCTAL NO3
      UULATE DIVERSITY INDEX AND AVERAGE TOTAL NO3
      SUM=SUM+(BP(I,IY-J)/TBICP(IY-J))*(ALOG(BP(I,IY-J)/TBICP(IY-J)))
      CONTINUE
48      HRAR(IY-J)=-SUM
      CONTINUE
50      INUE M P(IY-J)*(ALOG(BP(I,IY-J)/TBICP(IY-J)))
      TOTAL=TOTAL+(NT1(2)+NT1(IM))/2.0

```

```

72      DO 55 N=3,IU
          TOTAL=TOTAL+NT1(N)
          CONTINUE
          AVE=TOTAL/FLOAT(LDEPTH)
          TOTAL/FLOAT(LDEPTH)
          PRINT INITIAL VALUES
          T INITIAL VALUES
          CALL PRCOMM (TIME,DZ,LDEPTH,IU,IW,IY,AVE)
          CALL PRSPEC (TIME,TIMEO,IU,IW,IY,NUMRP,NUMBH,DZ)
          PRSPEC (TIME,TIMEO,IU,IW,IY,NUMPP,NUMBH,DZ)
          PRSPEC (TIME,TIMEO,IU,IW,IY,NUMPF,NUMBH,DZ)
          C      BEGIN SIMULATION
          N SIMULATION          IU,IW,IY,NUMRP,NUMBH,DZ)
          N SIMULATION          IU,IW,IY,NUMPP,NUMBH,DZ)
          C      READ AND PRINT NEW DISPERSION RATES AT THE BEGINNING OF EACH MONTH
          AND PRINT NEW DISPERSION RATES AT THE BEGINNING OF EACH MONTH
          IF (TIME.EQ.0.0) GO TO 140
          IF (TDISP.LT.720.) GO TO 140
          TDISP=AMCD(TIME,720.)
          DO 65 I=1,NUMRP
          PUNCH 12,(BP(I,J),J=2,IW)
          READ (5,12) (DBP(I),I=3,IW)
          READ (5,12) (DN(I),I=3,IW)
          DO 90 I=1,NUMBH
          PUNCH 12,(BH(I,J),J=2,IW)
          READ (5,12) (DBH(I,J),J=3,IW)
          CONTINUE
          DRP(2)=DBP(3)
55
C
C
C
60
65
90

```

```

DBP(IX)=CRP(IW)
DN(2)=DN(3)
DN(IX)=DN(IW)
DO 70 I=1, NUMBH
DBH(I,2)=DBH(I,3)
DBH(I,IX)=DBH(I,IW)
CONTINUE
70      INUE      I, IW)
PRINT 31
PRINT 33, (DMIX(I), I=1, LDEPTH)
DO 95 I=1, NUMBH
PRINT 34, NAMEH1(I), NAMEH2(I), (DBH(I, IY-J), J=2, IU)
95      CONTINUE
PRINT 35, (DN(IY-I), I=2, IU)
T 35, (DN(IY-I), I=2, IU)
T 35, (DN(IY-I), I=2, IU)
140    CALL RK(NUMBP, NUMBH, LDEPTH, IU, IW, DT, AVE, DZ, IX)
        RK(NUMBP, NUMBH, LDEPTH, IU, IW, DT, AVE, DZ, IX)
        RK(NUMBP, NUMBH, LDEPTH, IU, IW, DT, AVF, DZ, IX)
        INCREMENT CCOUNTERS      TH, IU, IW, DT, AVE, DZ, IX)
        Y=Y+DT
        IF (Y.EQ.8640.) Y=0.
        TDISP=TDISP+DT
        TPLOT=TFLOT+DT
        IF (Y.GT.8640.) Y=TDISP
        TGRAPH=TGRAPH+DT
        TIME=TIME+DT
C

```

```

74      TCS=TCS+DT
      TCC=TCC+DT
      TCC+DT
C      COMMUNITY VALUES ARE PRINTED AFTER EACH COMMUNITY PRINT INTERVAL
C      (TPRNT)
      (TPRNT) ES APE PRINTED AFTER EACH COMMUNITY PRINT INTERVAL
      IF(TCC.LT.TPRNT) GO TO 155
      DC 153 N=2, IW
      SUM=0.0
      DO 152 I=1, NUMRP
152     SUM=SUM+(BP(I,N)/TRIOF(N))*(ALOG(RP(I,N)/TBIOP(N)))
      HBAR(N)=-SUM
153     CONTINUE
      CALL PRCOMM (TIME,DZ,LDEPTH,IU,IW,IY,AVE)
      TCC=0.0
      0.0      IME,DZ,LDEPTH,IU,IW,IY,AVE)  OP(N))      T INTERVAL
C      SPECIES VALUES ARE PRINTED AFTER EACH SPECIES PRINT INTERVAL (SPRNT)
      IES VALUES ARE PRINTED AFTER EACH SPECIES PRINT INTERVAL (SPRNT)
155     IF(TCS.LT.SPRNT)GO TO 160
      CALL PRSPEC (TIME,TIME0,IU,IW,IY,NUMRP,NUMBH,CZ)
      TCS=0.0
      0.0      IME,TIME0,IU,IW,IY,NUMRP,NUMBH,DZ)      TERVAL (SPRNT)
C      THE VALUES TO BE PLOTTED ARE STORED IN STORA AND STORB AFTER EACH
C      STORE INTERVAL (CPLCT)
      STORE INTERVAL (CPLCT)      D IN STORA AND STORB AFTER EACH
160     IF(TPLOT.LT.CPLOT) GO TO 170
      TPLOT=0.
      ISTORE=ISTOR+1

```

```

STORA(1, ISTCR)=BP(1, LAYA)
STORA(2, ISTCR)=BP(2, LAYA)
STORA(3, ISTCR)=BP(3, LAYA)
STORA(4, ISTCR)=BH(1, LAYA)
STORA(5, ISTCR)=N1(LAYA)
STORB(1, ISTCR)=TBIOP(LAYA)
STORB(2, ISTCR)=RH(1, ISTCR)
STORB(3, ISTCR)=N1(LAYA)
      B(3, ISTCR)=N1(LAYA)
C   TOTAL NET PRODUCTIVITY VALUES ARE STORED IN GRAPH AFTER EACH STORE
C   INTERVAL (CGRAPH)
170  IF(TGRAPH.LT.CGRAPH) GO TO 200
    TGRAPH=0.
    IGRAPH=IGRAPH+1
    DO 180 K=2, IW
      GRAPH(K, IGRAPH)=TNET(K)
    CONTINUE
180  INJE      )=TNET(K)          STORED IN GRAPH AFTER EACH STORE
    IF(TIME.NE.ENDT) GO TO 60
    IME.NE.ENDT) GO TO 60      STORED IN GRAPH AFTER EACH STORE
    IME.NE.ENDT) GO TO 60      STORED IN GRAPH AFTER EACH STORE
    CALL PLCT(ISTCR, STORA, IXX, IW, LAYA, XVAL, C'PLOT, HMAX, DZ)
    IXX=3
    VMAX(1)=VMAX(2)=VMAX(3)=750.
    P(1)=1HP
    P(2)=1HH
    P(3)=1HN

```

```

LABEL (1)=10HPRODUCERS
LABEL (2)=10MHERBIVORES
LABEL (3)=10HNITRATES
CALL PLOT(ISTCR,STORB,IXX,IW,LAYA,XVAL,CPLLOT,HMAX,DZ)
PLOT(ISTCR,STORB,IXX,IW,LAYA,XVAL,CPLLOT,HMAX,DZ)
STOP
END
SUBROUTINE LIGHT(Y,L1,L2,L3,DT)
OUTINE LIGHT(Y,L1,L2,L3,DT) XVAL,CPLLOT,HMAX,DZ)
REAL L1,L2,L3
L1,L2,L3 ,L3,DT) XVAL,CPLLOT,HMAX,DZ)
L1,L2,L3 ,L3,DT) XVAL,CPLLOT,HMAX,DZ)
X=Y*.01
FAMP=1.55236 + X*(-.0190516 +X*(.00877981 +X*(-.000211877 + X*
1 (.00000130746)))
FAMP=FAMP*100.
=FAMP*100. 516 +X*(.00877981 +X*(-.000211877 + X*
L1=SIN(3.1415926535898*Y/12.)*FAMP
IF(L1.LE.0.0) L1=0.0
L2=SIN(3.1415926535898*(Y+DT/2.)/12.)*FAMP
IF(L2.LE.0.0) L2=0.0
L3=SIN(3.1415926535898*(Y+DT)/12.)*FAMP
IF(L3.LE.0.0) L3=0.0
3.LE.0.0) L3=C.0 Y+DT)/12.)*FAMP *(-.000211877 + X*
3.LE.0.0) L3=0.0 Y+DT)/12.)*FAMP *(-.000211877 + X*
RETURN
END
SUBROUTINE FLCT(MPT,VAL,IX,IW,LAYN,XVAL,CPLLOT,HMAX,DZ)

```

```

C THIS ROUTINE PLOTS TBIOP, TBIOH, AND N1 VALUES AS A FUNCTION OF
C TIME FOR A SPECIFIC DEPTH.
  TIME FOR A SPECIFIC DEPTH.
  DIMENSION VAL(7,MPT), CLEAN(7), LINF(101), YVAL(7)
  COMMON/PT/P(7), VMAX(7), LABEL(7)
  INTEGER CLEAN, LINE, P, DOT, BLANK, STAR
  REAL HMAX
  DATA DOT, BLANK, STAR/1H, 1H, 1H*/
  DATA DOT, BLANK, STAR/1H, 1H, 1H*/
  R (7) CTION OF
  100 FORMAT(//////1H1)
  101 FORMAT(17X,5(16X,F4.1),5X,A10)
  102 FORMAT(/35X,*MG. NO3-N/CUBIC METER X 1000.*)
  103 FORMAT(15X,101A1)
  104 FORMAT( 5X,F5.0,* HRS.*,101A1)
  105 FORMAT(35X,*SHANNON INFORMATION MEASURE: DIVERSITY INDEX - 0*,5X,
1 *DEPTH =*,I2,* METERS*/)
  ASURE: DIVERSITY INDEX - 0*,5X,
  XVALC=XFACT=0.0
  C=XFACT=0.0
  RS*/)
  ASURE: DIVERSITY INDEX - 0*,5X,
  PRINT 100
  LAY=IABS(LAYN-IW)*IFIX(DZ)
  IABS(LAYN-IW)*IFIX(DZ)
  PRINT 102
  DO 109 I=1,IX
  DO 108 J=1,5
  YVAL(J)=VMAX(I)/5000.*FLCAT(J)
  108 CONTINUE

```

```

78      109      PRINT 101, (YVAL(J), J=1, 5), LABEL(I)
          CCONTINUE
          INUE      L(J), J=1, 5), LABEL(I)
          DO 110 J=2, 101
          LINE(J)=DOT
          M=MOD(J-1, 20)
          IF(M.EQ.0) LINE(J)=STAR
110      CONTINUE
          LINE(1)=DOT
          PRINT 103, LINE
          T 103, LINE
          DO 111 J=2, 101
          LINE(J)=BLANK
          (J)=BLANK
          DO 116 K=1, MPT
          XVALC=XVALC+CPL0T
          DO 112 IP=1, IX
          IF(VAL(IP, K).GT.VMAX(IP)) VAL(IP, K)=VMAX(IP)
          J=100.*((VAL(IP, K)-VMAX(IP))/VMAX(IP)+1.0)+1.5
          LINE(J)=P(IP)
          CLEAN(IP)=J
111      CONTINUE
          LINE(1)=DOT
          (1)=DOT
          IF(XVAL.NE.XVALC) GO TO 113
          XFACT=XFACT+1.0
          LINE(1)=STAR
          XVALC=0.0
112
          IP))/VMAX(IP)+1.0)+1.5
          GO TO 113

```



```

X=XFACT*XVAL
PRINT 104,X,LINE
GO TO 114
  O 114      NE
113 PRINT 103,LINE
  T 103,LINE
114 DO 115 LJ=1,IX
  ICLEAN=CLEAN(LJ)
  LINE(ICLEAN)=BLANK
115 CONTINUE
  INUE      LANK
  LINE(1)=DOT
116 CONTINUE
  INUE      LANK
  RETURN
END
SUBROUTINE GRAPHN(IM,IGRAPH)
  OUTINE GRAPHN(IM,IGRAPH)
C   GRAPHN PRINTS NET PRODUCTIVITY VALUES FOR EACH DEPTH. VALUES
C   WERE STORED AFTER EACH CGRAPH INTERVAL (CGRAPH=TGRAPH)
  STORED AFTER EACH CGRAPH INTERVAL (CGRAPH=TGRAPH)
  COMMON/GR/GRAPH(13,30)
  DIMENSION LINE(117)
  INTEGER DOT
  DATA DOT/1H./
  DOT/1H./
  GRAPH INTERVAL (CGRAPH=TGRAPH)
710 FORMAT (1H1,8X,117A1)
720 FORMAT (////9X,*,*,11F10.2,5X,*,*)

```

```

80      740  FORMAT (//////9X,117A1)
          AT (//////9X,117A1)
          DO 700 I=1,117
          LINE(I)=DOT
            (I)=DOT
          PRINT 710,LINE
            T 710,LINE
          DO 730 J=1,IGRAPH
          PRINT 720,(GRAPH(I,J),I=2,IW)
          CONTINUE
            INUE      PH(I,J),I=2,IW)
          PRINT 740,LINE
            T 740,LINE
          RETURN
          END
          SUBROUTINE PRCOMM (TIME,DZ,LDEPTH,IU,IW,IY,AVE)
            OUTINE PRCOMM (TIME,DZ,LDEPTH,IU,IW,IY,AVE)
            PRCOMM PRINTS VALUES BY DEPTH FOR SPECIES DIVERSITY,LIGHT,
            PRODUCER COMMUNITY BIOMASS AND GROSS AND NET PRODUCTION,
            HERMIVORE COMMUNITY BIOMASS, TOTAL NUTRIENT, AND NUTRIENT IN
            SOLUTION. ALSO PRINTED ARE AVERAGE TOTAL NUTRIENT AND PRODUCER
            DISPERSION VALUES FOR BETWEEN DEPTHS.
            DISPERSION VALUES FOR BETWEEN DEPTHS.
            DISPERSION VALUES FOR BETWEEN DEPTHS.
            DISPERSION VALUES FOR BETWEEN DEPTHS.
            COMMON/AC/N1(13),N2(13),NT1(13),NT2(13),F(13),H8AR(13),DMIX(10)
            COMMON/BA/TRIOP(13),TRIOH(13),TGROSS(13),TNET(13),DBP(13)
            REAL N1,N2,NT1,NT2
            N1,N2,NT1,NT2      F(13),TGROSS(13),TNET(13),DBP(13)

```

```

67  FORMAT(/5X,*COMMUNITY VALUES*)
68  FORMAT(/26X,10(F7.1,* M.*))
69  FORMAT (5X*PRODUCER DISP. (DRP)*10F10.3)
70  FORMAT(8X,*TIME*,10X,*SHANNON*,3X,*LIGHT*,7X,*GROSS*,9X,*NET*,
1  4X,*PRODUCER*,3X,*HERBIVORE*,5X,*NUT 1*,5X,*NUT 2*,5X,
2  *TOTAL*,5X,*TOTAL*)
71  FORMAT(5X,*{(HOURS)*,3X,*DEPTH*,4X,*INDEX*,2X,*ENERGY*,2X,
1  *PRODUCTION*,2X,*PRODUCTION*,5X,*BIOMASS*,5X,*BIOMASS*,4X,
2  *IN SOL*,4X,*IN SOL*,5X,*NUT 1*,5X,*NUT 2*//)
72  FORMAT(4X,2F8.2,F9.4,F8.2,4F12.4,4F10.2)
73  FORMAT(5X,*AVE. TOTAL NUT. 1 =*F11.5)
    AT(5X,*AVE. TOTAL NUT. 1 =*F11.5)
    PRINT 57
    PRINT 70
    PRINT 71
    DEPTH=J.0
    DO 74 I=2,IM
    PRINT 72,TIME,DEPTH,HBAR(IY-I),F(IY-I),TGROSS(IY-I),TNET(IY-I),
1  TBIOP(IY-I),TBIOH(IY-I),N1(IY-I),N2(IY-I),NT1(IY-I),NT2(IY-I)
    DEPTH=DEPTH+DZ
    CONTINUE
    PRINT 58, (DMIX(I),I=1,LDEPTH)
    PRINT 59, (DBP(IY-I),I=2,IU)
    PRINT 73,AVE
    T 73,AVE (IY-I),I=2,IU      -I),N2(IY-I),NT1(IY-I),NT2(IY-I)
    RETURN
    END
SUBROUTINE PRSPEC (TIME,TIMEO,IU,IM,IY,NUMBP,NUMEH,DZ)

```

```

82 C PRSPEC PRINTS VALUES FOR ALL SPECIES AT EACH DEPTH FOR PRODUCER
C BIOMASS, NET PRODUCTION, GROSS PRODUCTION, AND HERBIVORE BIOMASS
ASS, NET PRODUCTION, GROSS PRODUCTION, AND HERBIVORE BIOMASS
ASS, NET PRODUCTION, GROSS PRODUCTION, AND HERBIVORE BIOMASS
COMMON/AA/8P(15,13),BH(3,13),NET(15,13),GROSS(15,13)
COMMON/BB/NAMEP1(15),NAMEP2(15),NAMEH1(3),NAMEH2(3)
DIMENSION DEPTH(13)
REAL NET
NET H(13) EP2(15),NAMEH1(3),NAMEH2(3) RE BIOMASS
FORMAT (//5X,*SPECIES VALUES*,10X,*TIME =*,F8.2/)
FORMAT(5X,2A10)
FORMAT (18X,*BIOMASS*,5X,11F9.2)
FORMAT (9X,*GROSS PRODUCTION*,5X,11F9.2)
FORMAT (11X,*NET PRODUCTION*,5X,11F9.2/)
FORMAT(1H1,56X,*RESULTS*///)
FORMAT (30X,11(F6.1,* M.*))
AT (30X,11(F6.1,* M.*)) F9.2/ 8.2/ RE BIOMASS
DEPTH(1)=0.
DO 88 I=2,IU
DEPTH(I)=DEPTH(I-1)+DZ
H(I)=DEPTH(I-1)+DZ *) F9.2/ 8.2/ RE BIOMASS
PRINT 81, TIME
PRINT 87, (DEPTH(I), I=1, IU)
DO 89 J=1, NUMBP
PRINT 82, NAMEP1(J), NAMEP2(J)
PRINT 83, (EP(J, IY-I), I=2, IW)
PRINT 84, (GROSS(J, IY-I), I=2, IW)

```

```

89 PRINT 85,(NET(J,IY-I),I=2,IM)
CONTINUE
DO 90 J=1,NUMPH
PRINT 82,NAMEH1(J),NAMEH2(J)
PRINT 83,(BH(J,IY-I),I=2,IM)
90 CONTINUE
IF (TIME.EQ.TIMEO) PRINT 86
TIME.EQ.TIMEO) PRINT 86
RETURN
END
SUBROUTINE RK(NUMBP,NUMBH,LDEPTH,IU,IM,DT,AVE,DZ,IX)
OUTLINE RK(NUMBP,NUMBH,LDEPTH,IU,IM,DT,AVE,DZ,IX)
RK CALCULATES NEW PRODUCER, HERBIVORE, NO3, AND P04 VALUES OVER THE
C CALCULATION INTERVAL (DT), ALL EQUATIONS ARE TREATED SIMULTANEOUSLY
C BY THIS METHOD.
C HIS METHOD.
COMMON/AA/EP(15,13),BH(3,13),NET(15,13),GROSS(15,13)
COMMON/AB/DN(13),DBH(3,13),IY,IZ,CLIGHT,KS,KW,Y,FO
COMMON/AC/N1(13),N2(13),NT1(13),NT2(13),F(13),HBAR(13),IMIX(10)
COMMON/AD/KM1(15),KM2(15),A(15),RP(15),CP1(15),CP2(15)
COMMON/AE/EFF(3),GRAZ(3),RH(3),BHMAY(3),CH1(3),CH2(3),CARN(3)
COMMON/BA/TBIOP(13),TBICH(13),TGROSS(13),TNET(13),DBP(13)
COMMON/L/FAMP,PI
DIMENSION COMBP(15,13),CCMBH(3,13),COMN1(13),COMN2(13)
DIMENSION GROWBH(3),GRAZBP(15),PRODBP(15),RESBP(15),DELTBP(15)
DIMENSION RESBH(3),DELTBH(3),DP(15,13),GRAZBH(3)
REAL KS,KW,KB
REAL KBP(4,15,13),KBH(4,3,13),KN1(4,13),KN2(4,13),MIXBP(15)

```

```

REAL MIXBH(3), KM1, KM2, NET, N1, N2, NT1, NT2
REAL L1, L2, L3
      L1, L2, L3
      T, N1, N2, NT1, NT2
C INITIALIZATION
      IALIZATION
      T, N1, N2, NT1, NT2
TOTAL=0.
R=S=T=U=0.
      T=U=0.
      T, N1, N2, NT1, NT2
C DERIVE VALUES FOR EACH K
      VE VALUES FOR EACH K
      1, NT2
DO 595 K=1,4
C CALCULATE THE LIGHT FOR THIS HOUR
CALL LIGHT(Y, L1, L2, L3, DT)
FO=L1
IF (K.EQ.2.OR.K.EQ.3) FO=L2
IF (K.EQ.4) FO=L3
DO 150 L=2, IW
KR=CLIGHT*TRIOP(IY-L)
F(IY-L)=F(IZ-L)*EXP(-(KW+KS+KB)*DZ)
F(IW)=FO
150 CONTINUE
DO 480 N=1, IX
480 TRIOP(N)=0.0
      P(N)=0.0
      +KS+KB)*DZ)
C DERIVE VALUES FOR EACH DEPTH
      VE VALUES FOR EACH DEPTH
DO 590 N=2, IW
IF (N.EQ.IW) GO TO 526

```

```

IF (K.EQ.4) GO TO 518
IF (K.EQ.2.OR.K.EQ.3) GO TO 509
K.EQ.2.OR.K.EQ.3) GO TO 509
C    NORMAL CONDITIONS FOR K1
      AL CCNDITIONS FOR K1
DO 500 I=1,NUMBP
COMBP(I,N+1)=BP(I,N+1)
500  TRIOP(N+1)=TRIOP(N+1)+BP(I,N+1)
DO 501 J=1,NUMBH
501  COMBH(J,N+1)=BH(J,N+1)
      COMN1(N+1)=N1(N+1)
      COMN2(N+1)=N2(N+1)
IF (N.NE.2) GO TO 550
      N.NE.2) GO TO 550 (I,N+1)
C    BOTTOM CONDITIONS FOR K1
      OM CONDITIONS FOR K1
DO 502 I=1,NUMBP
COMBP(I,N)=BP(I,N)
502  TRIOP(N)=TRIOP(N)+BP(I,N)
DO 503 J=1,NUMBH
503  COMBH(J,N)=BH(J,N)
      COMN1(N)=N1(N)
      COMN2(N)=N2(N)
GO TO 523
      O 523
C    NORMAL CONDITIONS FOR K2 AND K3
      AL CCNDITIONS FOR K2 AND K3
509  DO 510 I=1,NUMBP

```

```

510 COMBP(I,N+1)=KBP(K-1,I,N+1)/2.+BP(I,N+1)
    TBIOP(N+1)=TBIOP(N+1)+BP(I,N+1)
    DO 511 J=1,NUMBH
511 COMBH(J,N+1)=KBH(K-1,J,N+1)/2.+BH(J,N+1)
    COMN1(N+1)=KN1(K-1,N+1)/2.+N1(N+1)
    COMN2(N+1)=KN2(K-1,N+1)/2.+N2(N+1)
    IF (N.NE.2) GO TO 550
    N.NE.2) GO TO 550
    N.NE.2) GO TO 550 2.+N2(N+1)
C BOTTOM CONDITIONS FOR K2 AND K3
    OM CONDITIONS FOR K2 AND K3
    DO 512 I=1,NUMBP
512 COMBP(I,N)=KBP(K-1,I,N)/2.+BP(I,N)
    TBIOP(N)=TBIOP(N)+BP(I,N)
    DO 513 J=1,NUMBH
513 COMBH(J,N)=KBH(K-1,J,N)/2.+BH(J,N)
    COMN1(N)=KN1(K-1,N)/2.+N1(N)
    COMN2(N)=KN2(K-1,N)/2.+N2(N)
    GO TO 523
    O 523 -1,N)/2.+N2(N)
C NORMAL CONDITIONS FOR K4
    AL CONDITIONS FOR K4
518 DO 519 I=1,NUMBP
519 COMBP(I,N+1)=KBP(K-1,I,N+1)+BP(I,N+1)
    TBIOP(N+1)=TBIOP(N+1)+BP(I,N+1)
    DO 520 J=1,NUMBH
520 COMBH(J,N+1)=KBH(K-1,J,N+1)+BH(J,N+1)
    COMN1(N+1)=KN1(K-1,N+1)+N1(N+1)
    COMN2(N+1)=KN2(K-1,N+1)+N2(N+1)

```



```

IF (N.NE.2) GO TO 550
N.NE.2) GO TO 550
C   BOTTOM CONDITIONS FOR K4
    OM CONDITIONS FOR K4
DO 521 I=1,NUMBP
COMBP(I,N)=KBP(K-1,I,N)+BP(I,N)
521  TBIOP(N)=TBIOP(N)+BP(I,N)
DO 522 J=1,NUMBH
COMBH(J,N)=KBH(K-1,J,N)+BH(J,N)
522  COMN1(N)=KN1(K-1,N)+N1(N)
    COMN2(N)=KN2(K-1,N)+N2(N)
    2(N)=KN2(K-1,N)+N2(N)
C   BENTHOS CONDITIONS FOR ALL K-S
    HOS CONDITIONS FOR ALL K-S
DO 524 I=1,NUMBP
COMBP(I,N-1)=COMBP(I,N+1)+R
524  TBIOP(N-1)=TBIOP(N-1)+CCMBP(I,N-1)
DO 525 J=1,NUMBH
COMBH(J,N-1)=COMBH(J,N+1)+S
525  COMN1(N-1)=COMN1(N+1)+T
    COMN2(N-1)=COMN2(N+1)+U
GO TO 550
    O 550    N2(N+1)+U
C   SURFACE CONDITIONS FOR ALL K-S
    ACE CONDITIONS FOR ALL K-S
DO 527 I=1,NUMBP
526  COMBP(I,N+1)=COMBP(I,N-1)
527  TBIOP(N+1)=TBIOP(N+1)+BP(I,N+1)

```

```

88      DO 528 J=1, NUMBH
528      GOMBH(J,N+1)=COMBH(J,N-1)
        COMN1(N+1)=COMN1(N-1)
        COMN2(N+1)=COMN2(N-1)
        2(N+1)=COMN2(N-1)
        2(N+1)=COMN2(N-1)
C      INITIALIZATION
        IALIZATION
550      DO 555 J=1, NUMBH
555      GROWBH(J)=0.
        BION1=0.
        BION2=0.
        2=0.
        BH
C      EQUATIONS
        TIONS
C      CALCULATE GROSS PRODUCTION, RESPIRATION, AND MIXING FOR EACH
        PRODUCER SPECIES
C      PRODUCER SPECIES CN, RESPIRATION, AND MIXING FOR EACH
        DO 565 I=1, NUMBP
        PRODBP(I)=F(N)*A(I)*COMBP(I,N)*(COMN1(N)/(KM1(I)+COMN1(N)))*
1      (CCMN2(N)/(KM2(I)+CCMN2(N)))
        RESBP(I)=RP(I)*COMBP(I,N)
        MIXBP(I)=(1./DZ)**2.*(DBP(N+1)*COMBP(I,N+1)-(DBP(N+1)+DBP(N))*
1      COMBP(I,N)+DBP(N)*COMBP(I,N-1))
        COMBP(I,N)+DBP(N)*COMBP(I,N-1))
C      CALCULATE THE GRAZING OF EACH HERBIVORE SPECIES ON EACH PRODUCER
        SPECIES AND THE GROSS PRODUCTION OF EACH HERBIVORE SPECIES
C      SPECIES AND THE GROSS PRODUCTION OF EACH HERBIVORE SPECIES

```

```

GRAZBP(I)=0.
DO 560 J=1,NUMBH
  GRAZBP(I)=GRAZBP(I)+GRAZ(J)*COMBP(I,N)*COMBH(J,N)
  GROWBH(J)=GROWBH(J)+EFF(J)*GRAZ(J)*COMP(I,N)*COMBH(J,N)*
    ((BHMAX(J)-COMBH(J,N))/BHMAX(J))
1 CONTINUE
560 INUE      )-COMBH(J,N))/BHMAX(J))      ) *COMBH(J,N) *
C CALCULATE THE NET CHANGE OF EACH PRODUCER SPECIES AND THE TOTAL
C NET CHANGE OF EACH NUTRIENT BOUND IN THE PRODUCER BIOMASS
C NET CHANGE OF EACH NUTRIENT BOUND IN THE PRODUCER BIOMASS
DELTBP(I)=PRODBP(I)-RESBP(I)-GRAZBP(I)
BION1=BION1+DELTBP(I)*CP1(I)
BION2=BION2+DELTBP(I)*CP2(I)
CONTINUE
565 INUE      LTRP(I)*CP2(I)      P(I)      E PRODUCER BIOMASS
C CALCULATE THE RESPIRATION, LOSS DUE TO GRAZING, AND MIXING FOR EACH
C HERBIVORE SPECIES. ADD THE TOTAL NET CHANGE OF EACH NUTRIENT
C BOUND IN THE HERBIVORE BIOMASS TO THE TOTAL NET CHANGE OF EACH
C NUTRIENT BOUND IN THE PRODUCER BIOMASS
C NUTRIENT BOUND IN THE PRODUCER BIOMASS      HANGE OF EACH
DO 570 J=1,NUMBH
  RESBH(J)=RH(J)*COMBH(J,N)
  MIXBH(J)=(1./DZ)**2.*(DBH(J,N+1)*COMBH(J,N+1)-(DBH(J,N+1)+
    DBH(J,N))*COMBH(J,N)+DBH(J,N)*COMBH(J,N-1))
1 DELTRH(J)=GROWBH(J)-RESBH(J)
  BION1=BION1+DELTBP(I)*CH1(J)
  BION2=BION2+DELTBP(I)*CH2(J)
CONTINUE
570

```

```

90 C      PERFORM FOURTH ORDER RUNGE-KUTTA CALCULATIONS
      OR4 FOURTH ORDER RUNGE-KUTTA CALCULATIONS
      DO 575 I=1,NUMBP
575     KRP(K,I,N)=DT*(DELTBP(I)+MIXRP(I))
      DO 580 J=1,NUMRH
580     KBH(K,J,N)=DT*(DELTBH(J)+MIXBH(J))
      KN1(K,N)=DT*(-BION1+((1./DZ)**2.*(DN(N+1)*COMN1(N+1)-(DN(N+1)+
1      DN(N))*COMN1(N)+DN(N)*COMN1(N-1))))
      KN2(K,N)=DT*(-BION2+((1./DZ)**2.*(DN(N+1)*COMN2(N+1)-(DN(N+1)+
1      DN(N))*COMN2(N)+DN(N)*COMN2(N-1))))
590     CONTINUE
595     CONTINUE
      INUE      MN2(N)+DN(N)*COMN2(N-1)))
      INUE      MN2(N)+DN(N)*COMN2(N-1)))
C      INITIALIZATION
      DO 610 N=2,IW
      BION1=0.
      BION2=0.
      TEIOP(N)=0.
      TBIOH(N)=0.
      TNET(N)=0.
      TGROSS(N)=0.
      SUM=0.
      0.
      N)*COMN2(N-1)))
C      CALCULATE NEW VALUES FOR EACH DEPTH
      UULATE NEW VALUES FOR EACH DEPTH
      MN2(N+1)-(DN(N+1)+
      MN2(N+1)-(DN(N+1)+

```

```

C      NUTRIENT IN SOLUTION
      NUTRIENT IN SOLUTION
N1(N)=N1(N)+1./6.*((KN1(1,N)+2.*KN1(2,N)+2.*KN1(3,N)+KN1(4,N))
N2(N)=N2(N)+1./6.*((KN2(1,N)+2.*KN2(2,N)+2.*KN2(3,N)+KN2(4,N))
)=N2(N)+1./6.*((KN2(1,N)+2.*KN2(2,N)+2.*KN2(3,N)+KN2(4,N))
BIOMASS, GROSS PRODUCTION, AND NET PRODUCTION FOR EACH PRODUCER
SPECIES
SPECIES      UCTION, AND NET PRODUCTION FOR EACH PRODUCER
DO 600 I=1,NUMBP
DP(I,N)=1./6.*(KBP(1,I,N)+2.*KBP(2,I,N)+2.*KBP(3,I,N)+KBP(4,I,N))
BP(I,N)=BP(I,N)+DP(I,N)
GROSS(I,N)=F(N)*A(I)*BP(I,N)*(N1(N)/(KM1(I)+N1(N)))+(N2(N)/(KM2(I)
1 +N2(N)))
NET(I,N)=GROSS(I,N)-RP(I)*BP(I,N)
I,N)=GROSS(I,N)-RP(I)*BP(I,N)
TOTAL PRCDUCER BIOMASS, GROSS PRODUCTION, AND NET PRODUCTION
TOTAL PRCDUCER BIOMASS, GROSS PRODUCTION, AND NET PRODUCTION
TBIOP(N)=TBIOP(N)+BP(I,N)
TGROSS(N)=TGROSS(N)+GROSS(I,N)
TNET(N)=TNET(N)+NET(I,N)
(N)=TNET(N)+NET(I,N)      PRODUCTION, AND NET PRODUCTION
TOTAL NUTRIENT BOUND IN THE PRODUCER BIOMASS
TOTAL NUTRIENT BOUND IN THE PRODUCER BIOMASS      PRODUCTION
BION1=BION1+BP(I,N)*CP1(I)
BION2=BION2+BP(I,N)*CP2(I)
600 CONTINUE
INUE      (I,N)*CP2(I)      RODUCER BIOMASS      PRODUCTION
C      HERBIVORE BIOMASS FOR EACH SPECIES, TOTAL HERBIVORE BIOMASS,

```

```

92      C      AND NUTRIENT BOUND IN THE TOTAL PLANKTON BIOMASS
      AND NUTRIENT BOUND IN THE TOTAL PLANKTON BIOMASS
      DO 605 J=1,NUMBH
      BH(J,N)=BH(J,N)+1./6.*(KBH(1,J,N)+2.*KBH(2,J,N)+2.*KBH(3,J,N)+
1      KBH(4,J,N))
      TBIOH(N)=TBIOH(N)+BH(J,N)
      BION1=BION1+BH(J,N)*CH1(J)
      BION2=BION2+BH(J,N)*CH2(J)
605      CONTINUE
      INUE      (J,N)*CH2(J)      2.*KBH(2,J,N)+2.*KBH(3,J,N)+
      TOTAL NUTRIENT
      TOTAL NUTRIENT      J)      2.*KBH(2,J,N)+2.*KBH(3,J,N)+
      NT1(N)=N1(N)+BION1
      NT2(N)=N2(N)+BION2
610      CONTINUE
      INUE      ION2      J)      2.*KBH(2,J,N)+2.*KBH(3,J,N)+
      CALCULATE AVERAGE NO3 IN THE WATER COLUMN
      ULA TE AVERAGE NO3 IN THE WATER COLUMN      ,N)+2.*KBH(3,J,N)+
      TOTAL=TOTAL+(NT1(2)+NT1(IW))/2.
      DO 620 N=3,IU
      TOTAL=TOTAL+NT1(N)
620      CONTINUE
      AVE=TOTAL/FLOAT(LDEPTH)
      TOTAL/FLOAT(LDEPTH)      COLUMN      ,N)+2.*KBH(3,J,N)+
      RETURN
      END
      3      1      0.      8640.      .5      240.      240.      9000.      120.
      .1      .02      10.      2.      .0005

```

	5	7	6	720.	500.	500.	500.	500.	500.
500.									
PRODUCER 1	500.								500.
123HN									
PRODUCER 1					.00024	.005	17.	0.0	1.0
100.	100.	100.	100.	100.	100.	100.	100.	0.0	0.0
PRODUCER 2					.00019	.003	14.	0.0	1.0
100.	100.	100.	100.	100.	100.	100.	100.	0.0	0.0
PRODUCER 3					.00029	.0055	20.	0.0	1.0
100.	100.	100.	100.	100.	100.	100.	100.	0.0	0.0
HERBIVORES					.1	.00025	.004	1.0	0.0
.00042									750.
50.	50.	50.	50.	50.	50.	50.	50.		
750.	750.	750.	750.	750.	750.	750.	750.		
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.4	.4	.4	.4	.4	.4	.4	.4		
.0036	.0036	.0036	.0036	.0036	.074	.144	.144		
.0036	.0036	.0036	.0036	.074	.144	.144	.144		
.144	.144	.144	.144	.144	.144	.144	.144		
.0036	.0036	.0036	.0036	.074	.144	.144	.144		





**APPENDIX II**  
**INITIAL CONDITIONS AND PARAMETERS**  
**FOR EXAMPLE APPLICATIONS**

A summary of the initial conditions and parameters used in the example problems is presented on the following pages. This summary is complete for examples 1, 2, and 3. The parameters for five species as listed in Table 2 were used for examples 4 and 5.

The dispersion values were set at .144, .107, .04, .007, and .004 m<sup>2</sup>/hr at depths of 1,3,5,7, and 9m respectively.

THIS MODEL SIMULATES THE PLANKTON COMMUNITY OF A ONE DIMENSIONAL VERTICALLY MIXED LAKE ASSUMING MICHAELIS-MENTEN GROWTH MECHANICS

INITIAL CONDITIONS

LAKE DEPTH = 10.0 METERS  
 NUMBER OF PHYTOPLANKTON SPECIES = 3  
 NUMBER OF HERBIVORE SPECIES = 1  
 ALL BIOMASS VALUES ARE IN (MG. NO3-N/CU. M.)

PRODUCER SPECIES NAME	A (SQ. M. /KCAL)	RP (/HR.)	KM1 (MG. NO3-N/ CU. M.)	KM2 (MG. PO4-P/ CU. M.)	CP1 (MG. NO3/MG. NO3)	CP2 (MG. PO4/MG. NO3)
PRODUCER 1	.000240	.0050	17.0	.0	1.000	.000
PRODUCER 2	.000190	.0630	14.0	.0	1.000	.000
PRODUCER 3	.000290	.0055	20.0	.0	1.000	.000

HERBIVORE SPECIES NAME	EFF	GRAZ (CU. M./MG. NO3-N/CU. M.)	RH (/HR.)	CH1 (MG. NO3/MG. NO3)	CH2 (MG. PO4/MG. NO3)	BHMAX (MG. NO3-N/ CU. M.)	CARN (/HR.)
HERBIVORES	.10	.000250	.0043	1.000	.000	750.0	.00042

KS	KW	DZ (METERS)	CLIGHT (CU. M./MG. NO3-N)
.100	.020	2.000	.000500

HERBIVORE DISPERSION RATES (DBH) SPECIES	1.0 M.	3.0 M.	5.0 M.	7.0 M.	9.0 M.
HERBIVORES	.4000	.4000	.4000	.4000	.4000

NUT. DISPERSION (DN)
.4000



RESULTS

COMMUNITY VALUES		SHA:INON	LIGHT	GROSS	NET	PRODUCER	HERBIVORE	NUT 1	NUT 2	TOTAL	TOTAL
(HOURS)	DEPTH	INDEX	ENERGY	PRODUCTION	PRODUCTION	BIOMASS	BIOMASS	IN SOL	IN SOL	NUT 1	NUT 2
50.00	.00	1.0985	77.25	3.0011	2.2499	167.2263	53.6566	529.12	1.00	750.00	1.00
50.00	2.00	1.0984	51.53	1.9651	1.2278	164.2150	53.5668	532.22	1.00	750.00	1.00
50.00	4.00	1.0984	34.57	1.2703	.5604	158.3457	53.3505	538.30	1.00	750.00	1.00
50.00	6.00	1.0983	23.33	.8228	.1422	152.0539	53.0981	544.85	1.00	750.00	1.00
50.00	8.00	1.0982	15.83	.5406	-.1183	147.4110	52.9054	549.68	1.00	750.00	1.00
50.00	10.00	1.0981	10.75	.3628	-.2880	145.6559	52.8342	551.51	1.00	750.00	1.00
PRODUCER DISP. (DBP)		1.0 M.	3.0 M.	5.0 M.	7.0 M.	9.0 M.					
AVE. TOTAL NUT. 1 =		.400	.400	.400	.400	.400					
		750.00000									

SPECIES VALUES TIME = 50.00

	.0 M.	2.0 M.	4.0 M.	6.0 M.	8.0 M.	10.0 M.
PRODUCER 1						
BIOMASS	54.36	53.38	51.47	49.42	47.90	47.33
GROSS PRODUCTION	.98	.64	.41	.27	.18	.12
NET PRODUCTION	.70	.37	.16	.02	-.06	-.12
PRODUCER 2						
BIOMASS	56.51	55.70	54.11	52.40	51.14	50.66
GROSS PRODUCTION	.81	.53	.35	.23	.15	.10
NET PRODUCTION	.64	.36	.18	.07	-.00	-.05
PRODUCER 3						
BIOMASS	56.35	55.13	52.76	50.23	48.37	47.66
GROSS PRODUCTION	1.22	.79	.51	.33	.21	.14
NET PRODUCTION	.91	.49	.22	.05	-.05	-.12
HERBIVORES						
BIOMASS	53.66	53.57	53.35	53.10	52.91	52.83

COMMUNITY VALUES												
TIME (HOURS)	DEPTH	SHANNON INDEX	LIGHT ENERGY	PRODUCTION	GROSS PRODUCTION	NET PRODUCTION	PRODUCER BIOMASS	HERBIVORE BIOMASS	NUT 1 IN SOL	NUT 2 IN SOL	TOTAL NUT 1	TOTAL NUT 2
100.00	.00	1.0980	133.53		2.9510	2.5256	94.7256	50.4588	604.82	1.00	750.00	1.00
100.00	2.00	1.0980	95.80		2.0590	1.6457	92.1856	50.3928	607.42	1.00	750.00	1.00
100.00	4.00	1.0979	69.00		1.4153	1.0211	88.0747	50.2269	611.70	1.00	750.00	1.00
100.00	6.00	1.0978	49.90		.9735	.5989	83.8763	50.0290	616.09	1.00	750.00	1.00
100.00	8.00	1.0976	36.20		.6791	.3191	80.7404	49.8734	619.39	1.00	750.00	1.00
100.00	10.00	1.0975	26.29		.4852	.1311	79.4580	49.8147	620.73	1.00	750.00	1.00
PRODUCER DISP. (DBP)			1.0 M.	3.0 M.	5.0 M.	7.0 M.	9.0 M.					
AVE. TOTAL NUT. 1 =			.400	.400	.400	.400	.400					
			750.00000									

SPECIES VALUES										
TIME = 100.00										
	.0 M.	2.0 M.	4.0 M.	6.0 M.	8.0 M.	10.0 M.				
PRODUCER 1										
BIOMASS	30.02	29.21	27.91	26.57	25.57	25.17				
GROSS PRODUCTION	.94	.65	.45	.31	.22	.15				
NET PRODUCTION	.79	.51	.31	.18	.09	.03				
PRODUCER 2										
BIOMASS	32.34	31.65	30.52	29.36	28.50	28.14				
GROSS PRODUCTION	.80	.56	.39	.27	.19	.14				
NET PRODUCTION	.70	.47	.30	.18	.11	.05				
PRODUCER 3										
BIOMASS	32.37	31.33	29.65	27.94	26.67	26.15				
GROSS PRODUCTION	1.21	.84	.57	.39	.27	.19				
NET PRODUCTION	1.04	.67	.41	.24	.12	.05				
HERBIVORES										
BIOMASS	50.46	50.39	50.23	50.03	49.87	49.81				

COMMUNITY VALUES		SHANNON	LIGHT	GROSS	NET	PRODUCER	HERBIVORE	NUT 1	NUT 2	TOTAL	TOTAL
TIME	DEPTH	INDEX	ENERGY	PRODUCTION	PRODUCTION	BIOMASS	BIOMASS	IN SOL	IN SOL	NUT 1	NUT 2
(HOURS)											
150.00	.00	1.0972	154.28	2.1290	1.8643	58.9683	44.6628	646.37	1.00	750.00	1.00
150.00	2.00	1.0972	114.67	1.5270	1.2716	56.9524	44.6259	648.42	1.00	750.00	1.00
150.00	4.00	1.0972	85.48	1.0769	.8354	53.9630	44.5342	651.50	1.00	750.00	1.00
150.00	6.00	1.0971	63.89	.7606	.5326	51.0672	44.4246	654.51	1.00	750.00	1.00
150.00	8.00	1.0969	47.86	.5450	.3271	48.9147	44.3378	656.75	1.00	750.00	1.00
150.00	10.00	1.0968	35.88	.4007	.1870	47.9873	44.3049	657.71	1.00	750.00	1.00
PRODUCER DISP. (DBP)		1.0 M.	3.0 M.	5.0 M.	7.0 M.	9.0 M.					
AVE. TOTAL NUT. 1 = 750.00000			.400	.400	.400	.400					

SPECIES VALUES TIME = 150.00

	.0 M.	2.0 M.	4.0 M.	6.0 M.	8.0 M.	10.0 M.
PRODUCER 1						
BIOMASS	18.21	17.59	16.66	15.77	15.10	14.81
GROSS PRODUCTION	.66	.47	.33	.24	.17	.12
NET PRODUCTION	.57	.38	.25	.16	.09	.05
PRODUCER 2						
BIOMASS	20.18	19.63	18.81	18.00	17.40	17.14
GROSS PRODUCTION	.58	.42	.30	.21	.15	.11
NET PRODUCTION	.52	.36	.24	.16	.10	.06
PRODUCER 3						
BIOMASS	20.58	19.73	18.49	17.30	16.41	16.03
GROSS PRODUCTION	.89	.64	.44	.31	.22	.16
NET PRODUCTION	.78	.53	.34	.22	.13	.07
HERBIVORES						
BIOMASS	44.66	44.63	44.53	44.42	44.34	44.30









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