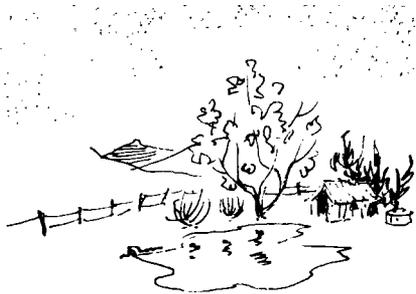


EDITORIAL NOTE: This article--the first general description of the Biome lake model to be published in a journal--is presented in SIMULATION in anticipation of the interest that the diverse readership will have in such a comprehensive model. It is the product of 25 scientists, associated with seven schools, who worked together on a lake ecology project of the Eastern Deciduous Forest Biome, U.S. International Biological Program. Software for the generalized lake ecosystem model CLEAN (described herein) is outlined by five of the coauthors in a sequel article that begins on page 51 of this issue. NF



Richard A. Park



# A generalized model for simulating lake ecosystems\*

## SUMMARY

CLEAN, a generalized lake-ecosystem model with strong ecological realism, has been developed in response to one aspect of the growing need for models suitable for helping man to manage his environment. The model currently consists of twenty-eight ordinary differential equations which represent approximately sixteen compartments, including attached aquatic plants, phytoplankton, zooplankton, bottom-dwelling aquatic insects, fish, suspended organic matter, decomposers, sediments, and nutrients. These equations can be linked in any meaningful combination to simulate a given point in a lake (a separate model for lake circulation is available to represent spatial variations

\* Contribution No. 152 from the Eastern Deciduous Forest Biome, U.S. International Biological Program.

## AUTHORS OF THIS PAPER

The coauthors of this paper are associated with the Eastern Deciduous Forest Biome, U.S. International Biological Program. They represent the two aquatic sites in the project, Lake George, New York, and Lake Wingra, Wisconsin, and the central modeling staff from Biome headquarters at Oak Ridge National Laboratory. Richard Park (see photo left) is a geologist and systems ecologist who has responsibility for coordinating the aquatic modeling effort in the Biome. Robert O'Neill is a systems ecologist and is modeling and science coordinator for the Biome, with responsibility for three terrestrial sites as well as the aquatic sites. He is assisted in the central modeling staff by Henry Shugart and Robert Goldstein, who are also systems ecologists, and by Raymond Booth and J. B. Mankin, who are systems analysts. Jay Bloomfield is an environmental engineer and microbiologist, Joseph Koonce is a systems ecologist, and Don Scavia is an environmental engineer. The remaining coauthors have contributed by developing specific parts of the lake model and by evaluating the model. They include ecologists, microbiologists, hydrologists, systems analysts, physical limnologists, environmental engineers, statisticians, and mathematicians.

and to couple simulations of different regions of the lake). Subprogram functions exist for each principal physiological and ecological process, and a submodel for lake water balance is presently being implemented. The program is written in FORTRAN for UNIVAC and IBM time-sharing systems.

The model has provided intuitively realistic simulations and has given us insight into the effects of nutrient enrichment on the functioning of the lake ecosystem as a whole. Sensitivity analysis has indicated priorities for further studies to obtain more precise estimates of parameters. Also, evaluation of the logic and organization of the model by experimenting with it are providing information to use in planning new experimental approaches. CLEAN is presently being tested using data from Lake George, New York, and Lake Wingra, Wisconsin.

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## INTRODUCTION

Many lake ecosystems are endangered by man's activities. Siltation from improper land use, waste heat from power stations, and pollution by oil, pesticides, and herbicides are all causing serious alterations of the natural environment. Probably nutrient enrichment from improper use of fertilizer and from the discharge of sewage is the most critical for lake ecosystems. Eutrophication resulting from nutrient enrichment may improve fishing, but it can also increase the population of undesirable species of fish, and of foul-tasting and odor-producing algae, and produce unsightly algal scum. In severe cases, eutrophication can deplete dissolved oxygen to the point of killing large numbers of fish. Unfortunately, total removal of nutrients from sewage is costly; further, as recreational developments spread along lakeshores there is more sewage to treat.

The pressing need for enlightened management of our lake ecosystems is made more critical by the difficulty of predicting the consequences of man-induced perturbations. The lake is a complex system with large numbers of biological, chemical, and physical components. Interactions among these components are characteristically nonlinear and involve intricate feedback loops. Desirable changes in one component of the system may trigger a complex chain of effects which results in deterioration of the total system.

The complexity of the lake ecosystem and the growing need for proper management of this natural resource has placed a high priority on large-scale integrated approaches to the problem. This paper outlines and presents a set of equations for a generalized lake ecosystem model. The model is the result of the joint efforts of a team of aquatic specialists and systems modelers. It is designed as a diagnostic tool to study the effects of nutrient enrichment and other perturbations on the ecosystem. It has been structured to permit studying a wide range of lake systems by appropriately changing parameter values and driving variables.

The present model is not without historical precedent. Most present-day efforts, including this model, have been influenced by the work of Riley and his colleagues.<sup>1-5</sup> Steele<sup>6-8</sup> has also had an important influence on the development of aquatic models. Following from these early studies, models have become more complex, paralleling advances in computer technology and ecological theory. Parker<sup>9</sup> modeled the relationships among phytoplankton, zooplankton, and fish. Chen<sup>10</sup> presented a model for simulating an ecosystem with phytoplankton, zooplankton, fish, detritus, biological oxygen demand (BOD), nutrients, and oxygen. Williams<sup>11</sup> demonstrated the applicability of computer simulation using data from Lindeman's classic study.<sup>12</sup> Our own modeling effort has been influenced in particular by the extensive literature review and formulations of DiToro, O'Connor, and Thomann.<sup>13</sup>

The model described here is known as CLEAN (Comprehensive Lake Ecosystem ANalyzer). It represents an advance over previous models in that individual ecological processes are represented in greater detail. Furthermore, the model's equations encompass a broader spectrum of the processes of lake-ecosystem dynamics. Incorporation in the CLEAN model of detailed information about these processes has been made possible by the close collaboration among diverse specialists and generalists within the

Eastern Deciduous Forest Biome, International Biological Program. Many of the formulations used to describe the biological interactions in CLEAN are derived from formulations previously developed for TEEM, a terrestrial ecosystem energy model developed by Shugart, Goldstein, O'Neill and Mankin.<sup>14</sup>

The model is being developed as a collection of submodels, each focusing on a specific component of the ecosystem. Specialists in ecology and limnology have contributed their insights into the processes most familiar to them and have participated in collecting data needed to implement the model. Although the theoretical structure of the model is still greatly simplified, it conforms to what is currently known in the applicable sciences. Several of the submodels are simplifications of more extensive process models developed in the Biome.

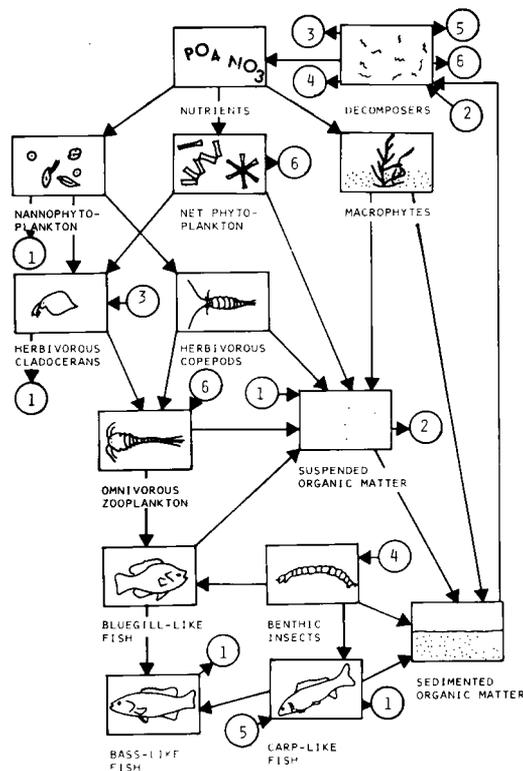


Figure 1 - Ecosystem components forming submodels in CLEAN (numbers identify common points)

## STRUCTURE

The present model is formulated as 28 coupled ordinary differential equations representing the most important compartments of the lake ecosystem (Figure 1). Detailed interactions are indicated in Figure 2. Allowances were made in programming the model to accommodate additional components as required; these will include submodels for lake water balance (described below) and for additional types of fish and organisms that live on the lake bottom. Currently, the driving variables include incident solar radiation, water temperature, nutrient loadings, wind or changes in barometric pressure, and influx of dissolved and particulate organic material from the terrestrial system surrounding the lake. In addition, a separate circulation model is available to be run in conjunction with CLEAN.



CLEAN employs modular programming so that a user may execute a specific submodel or link any meaningful combination of submodels as required for a specific simulation. Furthermore, a separate subprogram function is created for each process (such as respiration), permitting the process formulations to be altered quickly and easily. The result is a greatly compressed program as most of the biological processes occur repeatedly in the model with only changes in parameter values.

The modular structure greatly expedites submodel development and testing. As submodels are initially implemented, they represent a wide range of biological sophistication. Therefore, it is important that the submodels be accessible both individually and in varied combinations to permit evaluations of specific terms in them and to make it easier to calibrate them and to use them.

CLEAN has been implemented in interactive mode in FORTRAN for both UNIVAC and IBM time-sharing systems. Parameters and initial conditions can be edited on-line, and driving variables can be changed readily by using an internal CHART function. Thus, the program makes it convenient to run experiments on the model and to update the model as new knowledge develops in this rapidly advancing field.

#### DESCRIPTION OF COMPONENTS IN CLEAN

To simplify the task of presenting a detailed description of the submodels of CLEAN, the equations that make up the submodels are presented as a series of tables. The text presents a simplified description of the important factors in each of the submodels, and cites references for the process models which served as the basis for developing CLEAN.

$$P_{\text{net},m} = (1-x) \left[ \frac{P_{\text{max},m}}{\kappa_1} \ln \left( \frac{A + I_0 \exp[-z(\epsilon + \kappa_2 B_p)]}{A + I_0 \exp[-z(\epsilon + \kappa_2 B_p) - \kappa_1 F]} \right) \cdot f(T)g(V) \right] - \rho_f F \quad 1.1$$

$P_{\text{net},m}$  = Net primary production (quantity of material fixed by photosynthesis and available for plant growth)

$x$  = Fraction of photosynthetic product excreted from plant and lost

$P_{\text{max},m}$  = Maximum photosynthetic rate (under conditions of optimal light, temperature, and nutrients)

$\kappa_1$  = Coefficient for light extinction due to plant leaves

$A$  = Light saturation coefficient (at light intensity  $A$ , photosynthesis rate =  $1/2 P_{\text{max},m}$ )

$I_0$  = Light intensity at water surface (driving or extrinsic variable which varies during the year)

= Water depth

= Coefficient for light extinction due to water

= Coefficient for light extinction due to phytoplankton biomass

= Phytoplankton biomass

= Leaf area index (total surface of leaves suspended over a unit area of lake bottom)

$V$  = Water current velocity

$g(V)$  = Function of water current velocity necessary to renew nutrients in boundary zone of plant,  $\leq 1.0$

$T$  = Temperature, °C

$f(T)$  = Function of temperature (see Table 3);  $\leq 1.0$

$\rho_f$  = Respiration rate of plant leaves; a function of temperature

$$dL/dt = L^* \delta(t_p) + G_L - (R_L + M_L) \quad 1.2$$

$$\delta = \begin{cases} 1, & t = t_p \\ 0, & \text{otherwise} \end{cases} \quad 1.21$$

$L$  = Biomass of plant leaf tissue

$t$  = Time

$t_p$  = Time for initial plant growth in spring, based on cumulative effect of temperature during early spring

$L^*$  = Initial biomass pulse of arbitrarily small value

$G_L$  = Growth of new leaf tissue

$R_L$  = Leaf respiration

$M_L$  = Leaf mortality (sloughing of entire leaves)

Table 1  
Macrophytes

Macrophytes<sup>15</sup> (Table 1)

Macrophytes are aquatic plants which are generally rooted in the lake sediment and which grow toward the lake surface. Growth of these plants depends on photosynthesis (Equation 1.1) which enables macrophytes to utilize solar energy, carbon dioxide, and water to form complex carbohydrate molecules. The model considers a maximum photosynthetic rate  $P_{max}$ , which is reduced by suboptimal levels of light, temperature, and available carbon. The shading effects of algae and macrophytes and absorption of light by the water and by material suspended in it attenuate light as depth increases. The model incorporates this effect and the depth distribution of photosynthetic macrophyte tissue by integrating the photosynthetic rate over the leaf-area index, yielding Equation 1.1. A portion of the photosynthetic

material is lost through respiration and extracellular secretion ("excretion"). The remaining photosynthate forms a pool of carbohydrates  $S$ , which is then drawn upon for plant growth and metabolism.

Incremental changes (Equation 1.2) in leaf biomass  $L$  result from growth of new tissue  $G_L$ , metabolic losses  $R_L$ , and leaf sloughing  $M_L$ . Growth of new tissue (Equation 1.3) is a function of leaf biomass and proceeds asymptotically to an optimal leaf-area index as long as the available carbohydrates exceed a minimum level  $S_0$ . The optimal leaf-area index (Equation 1.4) is that ratio of leaf-surface area to lake-surface area which results in maximum net photosynthesis.<sup>16</sup> A leaf-area index greater than the optimum results in reduced net gain due to self-shading and the metabolic cost of maintaining additional biomass. Loss by cellular respiration of leaf

$$G_L = \lambda L \left( 1 - \frac{L}{nF_{opt}} \right) \left( \frac{S - S_0}{S_1 + S - S_0} \right) v(nF_{opt} - L) v(S - S_0) \quad 1.3$$

$$v(a) = \begin{cases} 0, & a \leq 0 \\ 1, & a > 0 \end{cases} \quad 1.31$$

$\lambda$  = Fractional increase in leaf biomass per unit time

$n$  = Units of leaf biomass per unit leaf area

$F_{opt}$  = Optimal leaf area index

$S$  = Stored pool of carbohydrates resulting from photosynthesis

$S_0$  = Minimal level of carbohydrates reserved for overwintering

$S_1$  = Carbohydrate level at which growth is 1/2 maximum

$$F_{opt} = \frac{1}{\kappa_1} D v(D) \quad 1.4$$

$$D = \kappa n \left( \frac{I_0 \{ P_{max} (1 - \chi) g(V) f(T) - \rho_f \} \exp[-z(\epsilon + \kappa_2 B_D)]}{A \rho_f} \right)$$

$$R_L = \rho_L L v[\nu(S_0 - S) + \nu(F - F_{opt})] \quad 1.5$$

$\rho_L$  = Fraction of leaf biomass lost by respiration per unit time, a function of temperature

$$M_L = \gamma_1 L [\nu(t - t_1) \nu(t_2 - t) + \nu(t - t_3) \nu(t_4 - t)] - \gamma_2 L \nu(F - F_{opt}) \quad 1.6$$

$\gamma_1$  = Fraction of leaf biomass sloughed per unit time during sloughing periods

$\gamma_2$  = Fraction of leaf biomass sloughed per unit time when  $F_{opt}$  is exceeded by  $F$

$t_1$  to  $t_2$  = Initial period of sloughing

$t_3$  to  $t_4$  = Subsequent period of sloughing

$$dR/dt = G_R - R_R v \quad 1.7$$

$R$  = Biomass of roots

$G_R$  = Growth of root tissue

$R_R$  = Root respiration

$$G_R = \mu R \left( 1 - \frac{R}{R_{max}} \right) \left( \frac{S - S_0}{S_1 + S - S_0} \right) v(S - S_0) \quad 1.8$$

$\mu$  = Fractional growth of root biomass per unit time

$$R_R = \rho_R R v(S_0 - S) \quad 1.9$$

$$dS/dt = P_{net,m} - \rho_R R v(S - S_0) - \rho_L L v(S - S_0) v(F_{opt} - F) - \alpha(G_L + G_R) \quad 1.10$$

$\alpha$  = Inverse efficiency of conversion of labile carbohydrates to leaf and root biomass

Table 1 (continued)  
Macrophytes

structural material (Equation 1.5) is proportional to leaf biomass; it occurs only if the carbohydrate pool is below the minimal level  $S_0$ , or if active growth of leaves is occurring. Leaf sloughing for macrophytes in Lake Wingra (Equation 1.6) occurs primarily during two periods of the year, although the mechanisms causing the loss are not well understood; in addition, if leaf area exceeds the optimal leaf-area index, sloughing occurs.

Changes in root biomass (Equation 1.7) also involve growth of new tissue and the respiratory cost of maintaining the existing biomass. Growth of new tissue (Equation 1.8) proceeds at a rate proportional to the root biomass up to a maximum value as long as sufficient carbohydrates are available. Cellular respiration of root structural material (Equation 1.9) is proportional to root biomass, but this form of loss ceases when available carbohydrates exceed the minimal level  $S_0$  (Equation 1.9).

#### Phytoplankton<sup>17,18</sup> (Table 2)

In addition to the larger attached macrophytes discussed above, there are also many species of floating algae, which are known collectively as phytoplankton. Again, net photosynthesis is considered as the difference between a maximum rate  $P_{\max}$ , modified by suboptimal conditions and a respiration rate (2.2). The combined limitations of light and nutrients are represented as a normalized factor that is mathematically analogous to the inverse of the total effect of electrical resistors in parallel. Grazing is a function of zooplankton biomass, temperature, and capturability as discussed below (Equation 3.1). Excretion is considered as proportional to net photosynthesis (Equation 2.3), and nonpredatory mortality is taken to be the sinking rate as a function of temperature (Equation 2.4). In the current implementation of CLEAN, two phytoplankton groups are distinguished: nanophytoplankton (extremely small) and net (larger) phytoplankton (Figure 1), corresponding to two major subdivisions of the algal community.



#### Feeding term<sup>14,16</sup> (Table 3)

Most interactions between living components of the lake ecosystem take the form of feeding relationships, i.e., one population is utilizing another as a food supply. This relationship forms a nonlinear linkage which is extremely important to the overall dynamics of the system. Therefore, it must be carefully formulated.

Equation 3.1 shows the dependence of the feeding rate on the biomass of consumers  $B_j$  and the biomass of the food supply  $B_i$ . The relationship is modified by a food preference term  $w_{i,j}$  to differentiate between feeding rates on different types of food. As food supply becomes very abundant, the  $w_{i,j}$  term becomes dependent only on the mass of consumers of each type in relation to their available food supplies. Alternatively, as consumer populations become very large in relation to the food supply, feeding is dependent only upon the available food supply, with a limit on the population of consumers being imposed by a minimum food supply,  $B_{\min,j}$ . At intermediate biomass densities, the feeding rate is dependent on the biomass of both interacting populations. The ecological theory and mathematical implications of the nonlinear linkage have been explored in other papers.<sup>19-21</sup>

Table 2  
Phytoplankton

$$dB_p/dt = (P_{\text{net},p} - G_{p,z} - U_p - M_p)B_p \quad 2.1$$

$G_{p,z}$  = Rate of grazing of zooplankton on phytoplankton

$U_p$  = Excretion rate of phytoplankton

$M_p$  = Nongrazing mortality rate of phytoplankton

$$P_{\text{net},p} = (P_{\max,p} \frac{1}{\prod_i [\Sigma 1/\mu_i]} - R_p) f(T) \quad 2.2$$

$$\mu_1 = \left[ \frac{2.71828 \phi_p}{\epsilon + \kappa_2 B_p} \right] \cdot \left[ \exp\left(\frac{-I_0}{I_s \phi_p} \exp\left[-z\left(\epsilon + \frac{\kappa_2 B_p}{z}\right)\right]\right) - \exp\left(\frac{-I_0}{I_s \phi_p}\right) \right] \quad 2.21a$$

$$\mu_i = \frac{C_i}{N_i + C_i}; \quad i = 2, 3, \dots, n \quad 2.21b$$

$R_p$  = Respiration

$\mu_i$  =  $i$ th limiting factor;  
 $\mu_1$  = light;  $\mu_i$ ,  $i \neq 1$ , = nutrients

$C_i$  = Concentration of nutrient  $i$

$N_i$  = Concentration of nutrient  $i$  at which photosynthesis rate =  $\frac{1}{2}P_{\max,p}$

$I_s$  = Saturated light intensity (light intensity above which photosynthesis is maximum)

$\phi_p$  = Photoperiod (fraction of light in a 24 hour period)

$$U_p = \begin{cases} \alpha P_{\text{net},p}; & P_{\text{net},p} \geq 0 \\ 0 & ; P_{\text{net},p} < 0 \end{cases} \quad 2.3$$

$\alpha$  = Fraction of net photosynthate lost per unit-time

$$M_p = bT \quad 2.4$$

$b$  = Fraction of algal biomass dying or sinking to lake bottom per unit of time and temperature

$$R_p = R_{\max} V^X e^{X(1-V)} \quad 2.5$$

$$R_{\max} = KP_{\max,p}$$

See 3.2 for  $V$  and  $X$

Table 3  
Trophic interaction or feeding term

$$C_{i,j} = C_{\max_j} H_{j,C} \cdot \left( \frac{w_{i,j} (B_i - B_{\min_i})}{Q_j^{z+r} B_j^{z+r} w_{i,j} (B_i - B_{\min_i})} \right) \quad 3.1$$

$$H_{j,n} = a_{j,n} \left( b_{j,n} \frac{(K_j - B_j)}{K_j} + 1 \right) c_{j,n} \quad 3.11$$

- $C_{i,j}$  = Consumption of  $i$ th prey by  $j$ th organism
- $Q_j^{z,r}$  = Environmental and population interaction coefficients
- $w_{i,j}$  = Coefficient relating preference, availability, capturability, etc., of  $i$  as a food for  $j$
- $K_j$  = Carrying capacity of ecosystem for predator  $j$
- $a_{j,n}$  = Correction factor for behavioral effects on the  $n$ th process (e.g.,  $n=C$  for consumption,  $R$  for respiration,  $M$  for mortality,  $F$  for fishing,  $G$  for gamete production) for the  $j$ th organism
- $b_{j,n}$  = Correction factor for effects of age structure of population on  $n$ th process
- $c_{j,n}$  = Correction factor for physiological effects on  $n$ th process

For example:

$$c_{z,C} = f(T) = V^x \exp[X(1-V)] \quad 3.2$$

where  $z$  denotes zooplankton and  $C$  consumption

$$V = \frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \quad 3.21$$

$$X = \frac{W^2 [1 + \sqrt{(1 + 40/W)}]^2}{400} \quad 3.22$$

$$W = (\ln S_Q) (T_{\max} - T_{\text{opt}}) \quad 3.23$$

$T_{\max}$  = Upper lethal temperature

$T_{\text{opt}}$  = Optimum temperature (temperature at which rate is maximum)

$S_Q$  =  $Q_{10}$  value (factor in log range by which rate is increased for a  $10^\circ\text{C}$  increase in temperature)

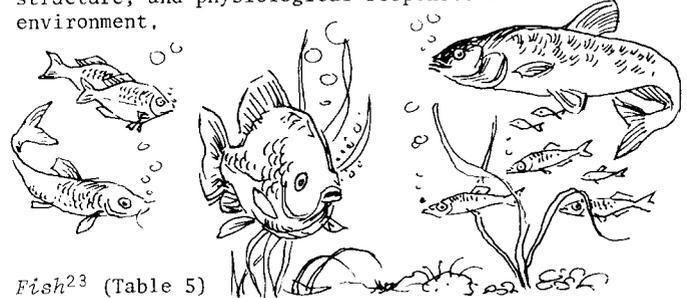
( $C_{j,k}$  = Consumption of  $j$ th organism by  $k$ th predator)

The adult feeding rate  $C_{i,j}$  is considered to be a complex function of temperature. The rate increases exponentially up to a potential maximum  $C_{\max}$  at an optimal temperature  $T_{\text{opt}}$ . At higher temperatures, the rate rapidly decreases until a lethal temperature is reached and the organism dies. Behavioral characteristics  $a_j$  also modify the feeding rate. For example, some animals may go into hibernation below some critical temperature, causing feeding to fall to zero.

The feeding rate  $C_{i,j}$  is defined as adult feeding rate and must be modified to account for the presence of immature organisms in the population. The age-structure correction factor is  $b_j$ , which appropriately increases the feeding rate to account for juveniles. As the population reaches its maximum possible density  $K_j$ , reproduction is greatly reduced, resulting in a population composed primarily of adults. Therefore, the magnitude of the correction factor is decreased to zero as the "carrying capacity" of the ecosystem is approached. This construct has proven to be satisfactory for predators in the upper levels of the predator-prey food chain, but we are presently replacing it with a better formulation for populations subject to heavy predation.

#### Zooplankton<sup>22</sup> (Table 4)

The next step in the food chain consists of small invertebrate animals known collectively as zooplankton (Figure 1). Three groups are distinguished in the model: calanoid copepods (which feed on phytoplankton), cladocerans (which feed on both phytoplankton and suspended particulate organic matter), and omnivorous zooplankton which can feed on other zooplankton as well as on phytoplankton and particulate organic matter. Multiple food supplies are incorporated in the model through a summation over individual feeding terms as shown in Equation 4.1. In a similar manner, predation on the zooplankton is represented by another summation over all potential consumer populations. Defecation and metabolic excretion are represented by the product of the feeding term and appropriate constants. Respiratory and mortality losses are presented as proportional to the biomass, with appropriate modifications for behavior, age structure, and physiological responses to the environment.



Fish<sup>23</sup> (Table 5)

Fish populations in the lake ecosystem are divided into three categories: a bluegill-like generalized predator feeding on zooplankton and benthic (bottom-dwelling) insect larvae; a carp-like scavenger; and a bass-like predator that consumes other fish. For each of these categories, model equations closely resemble the zooplankton model (4.1). Additional loss terms are included to account for the metabolic cost  $s_2$  of food digestion and utilization, incorporation of material into eggs and sperm, and losses due to fishing pressure by man. Equation 5.2 also introduces the concept of density-dependent stress due to overcrowding.

Table 4  
Zooplankton

$$\frac{dB_z}{dt} = \sum_{i=1}^n C_{i,z} - \sum_{k=1}^m C_{z,k} - (R_z + U_z + F_z + M_z) \quad 4.1$$

$B_z$  = Biomass of zooplankton

$R_z$  = Respiration rate

$U_z$  = Rate of metabolic excretion

$F_z$  = Rate of egestion (elimination of unassimilated materials)

$M_z$  = Rate of nonpredatory mortality

(with  $a_{z,C}$ ,  $b_{z,C}$ ,  $c_{z,C}$  in  $C_{i,z}$ )

$$F_z = \sum_{i=1}^n f_{i,z} C_{i,z} \quad 4.2$$

$f_{i,z}$  = Fraction of food supply  $i$  consumed but not assimilated by zooplankton

$$R_z = R_{\max} H_{z,R} B_z \quad 4.3$$

(with  $a_{z,R}$ ,  $b_{z,R}$ ,  $c_{z,R}$  in  $H_{z,R}$ )

$$U_z = u_z \sum_{i=1}^n C_{i,z} \quad 4.4$$

$u_z$  = Fraction of food assimilated and subsequently excreted

$$M_z = Z_M H_{z,M} B_z \left( \frac{d_{z,M} B_z}{K_j} + 1 \right) \quad 4.5$$

$d_{z,M}$  = Density-dependent term for increased mortality due to overcrowding

$Z_M$  = Natural rate of adult mortality

Table 5  
Fish

$$\frac{dB_f}{dt} = \sum_{i=1}^n C_{i,f} - \sum_{k=1}^m C_{f,k} - (F_f + R_f + U_f + G_f + M_f + C_{f,man}) \quad 5.1$$

$B_f$  = Biomass of fish

$R_f$  = Respiration rate

$U_f$  = Metabolic excretion rate

$G_f$  = Rate of gamete production

$M_f$  = Rate of nonpredatory mortality

$C_{f,man}$  = Mortality rate due to fishing

$F_f$  = Egestion rate

$$R_f = s \sum_{i=1}^n C_{i,f} + H_{f,R} B_f \left( 1 + \frac{d_{f,R}}{K_f} B_f \right) \quad 5.2$$

(with  $a_{f,R}$ ,  $b_{f,R}$ ,  $c_{f,R}$  in  $H_{f,R}$ )

$s$  = Metabolic cost of food digestion and utilization

$d_{f,R}$  = Density-dependent term for increased respiration due to overcrowding

$$F_f = \sum_{i=1}^n f_{i,f} C_{i,f} \quad 5.3$$

$f_{i,f}$  = Fraction of  $i$ th ingested food that is not assimilated

$$U_f = u_f \sum_{i=1}^n C_{i,f} \quad 5.4$$

$u_f$  = Fraction of assimilated food that is excreted

$$G_f = H_{f,G} Z_G \kappa_G B_f \quad 5.5$$

(with  $a_{f,G}$ ,  $b_{f,G}$ ,  $c_{f,G}$  in  $H_{f,G}$ )

$Z_G$  = Instantaneous rate of gamete mortality

$\kappa_G$  = Fraction of adult biomass in gametes at spawning

$c_{f,G}$  = Temperature switch permitting spawning between a maximum and minimum temperature

$$M_f = Z_M H_{f,M} B_f \left( \frac{d_{f,M} B_f}{K_f} + 1 \right) \quad 5.6$$

(with  $a_{f,M}$ ,  $b_{f,M}$ ,  $c_{f,M}$  in  $H_{f,M}$ )

$Z_M$  = Rate of adult natural mortality

$$C_{f,man} = Z_F H_{f,F} B_f \quad 5.7$$

(with  $a_{f,F}$ ,  $b_{f,F}$ ,  $c_{f,F}$  in  $H_{f,F}$ )

$Z_F$  = Rate of adult mortality due to fishing

Table 6  
Bottom-dwelling organisms (benthos)

$$dB_{b_j}/dt = \sum_i C_{i,b_j} + I_{b_j} - (R_{b_j} + F_{b_j} + H_{b_j} + X_{b_j} + P_{b_j} + M_{b_j} + \frac{FC_{b_j,k}}{k}) \quad 6.1$$

$R_{b_j}$  = Respiration

$$= R_{\max b_j} H_{b_j,R} \left( 1 + \frac{d_{b_j,R} B_{b_j}}{K_{b_j,R}} \right) B_{b_j} \quad 6.11$$

$$H_{b_j,n} \begin{cases} a_{b_j,n} = \text{Physiological effects due to dissolved oxygen for } n = M, C, R \\ b_{b_j,n} = \text{Correction term for effect of mean weight on process; replaces } \left( b_{b_j,n} \frac{(K_j - \bar{w}_j)}{K_j} + 1 \right) \\ = \alpha \bar{w}_{b_j}^{\beta-1}; \alpha, \beta \text{ fitted coefficients} \\ c_{b_j,n} = \text{Physiological effects due to } T \text{ for } n = M, C, R \\ B_{b_j} = \text{Biomass of benthos in } j\text{th size class: } j = 1 \text{ for instars 1-3; } j = 2 \text{ for 4th instar} \\ d_{b_j,n} = \text{Effects due to crowding on } n\text{th process} \end{cases}$$

$F_{b_j}$  = Egestion

$$= \sum_i f_{i,b_j} C_{i,b_j} \quad 6.12$$

$f_{i,b_j}$  = Fraction of  $i$ th food not assimilated (i.e., egested)

$U_{b_j}$  = Excretion

$$= u_{b_j} \sum_i C_{i,b_j} \quad 6.13$$

$u_{b_j}$  = Fraction of assimilated food excreted

$X_{b_j}$  = Exuviation

$$= x_{b_j} B_{b_j} \quad 6.14$$

$x_{b_j}$  = Fraction of biomass exuviated

$M_{b_j}$  = Nonpredatory mortality

$$= Z_{b_j} H_{b_j,M} \left( 1 + \frac{d_{b_j,M} B_{b_j}}{K_{b_j,M}} \right) B_{b_j} \quad 6.15$$

$Z_{b_j}$  = Instantaneous rate of nonpredatory mortality

$d_{b_j,M}$  = Increase in mortality due to density-dependent factors (overcrowding)

$K_{b_j}$  = Carrying capacity of ecosystem

$I_{b_j}$  = Influx into class. For  $j = 1$ , = egg-laying =  $iW_e$ ; for  $j = 2$ , = maturation of 3rd instars into 4th =  $F_{b_1}W_3$ . 6.16

$i$  = Number of eggs that hatch =  $f(N_{b_1}, N_{b_2})$

$W_e$  = Average weight of an egg

$F_{b_1}$  = Number of molting 3rd instars (maturing into 4th)

$W_3$  = The critical weight of a 3rd instar at which molting is induced

$P_{b_j}$  = Promotion out of class. For  $j = 1$ , maturation of 3rd instar into 4th (=  $I_{b_2}$ ); for  $j = 2$ , = emergence of 4th instars to adults, =  $e_b W_c$ . 6.17

$e_b$  = Number of emerging insects

$$= \begin{cases} 0 & ; \bar{w}_{b_j} < \bar{w}_e \\ N_{b_j} \kappa_1 (\exp(\kappa_2 (\bar{w}_{b_j} - \bar{w}_e)) - 1) & ; \bar{w}_{b_j} \geq \bar{w}_e \end{cases} \quad 6.18$$

$\bar{w}_{b_j}$  = Mean weight of  $j$ th size class

$\bar{w}_e$  = Critical population mean weight to begin emergence

$W_c$  = Actual organism's weight to induce emergence

$\kappa_1, \kappa_2$  = Fitted coefficients

$$dN_{b_j}/dt = \frac{1}{\bar{w}_{b_j}} \left( -M_{b_j} - \sum_i C_{i,b_j} + k \right) + \frac{I_{b_j}}{\bar{w}_k} - \frac{P_{b_j}}{\bar{w}_k} \quad 6.2$$

$N_{b_j}$  = Numbers of  $j$ th class of benthos

$\bar{w}_{b_j}$  = Mean weight of  $j$ th class

$W_k = \begin{cases} W_e; & k=1 \text{ (1st size class)} \\ W_3; & k=2 \end{cases}$

$Y_k = \begin{cases} W_3; & k=1 \\ W_c; & k=2 \end{cases}$

Benthos<sup>24,25</sup> (Table 6)

The changes in biomass (Equation 6.1) and numbers (Equation 6.2) for bottom-dwelling (benthic) insect larvae are considered separately for two size classes. The first three larval stages (instars) are included in one size class and the final larval stage in a second class; adults and eggs constitute two additional size classes.



The formulation for biomass changes resembles the approach used for zooplankton (Table 4) and fish (Table 5), with feeding rate balanced against respiration, excretion, mortality, and other loss terms. An additional term is added to the benthos equation to account for material lost as the larvae shed the

outer covering (exoskeleton) during molt. Terms are also added to account for input and output from one size class to another; these factors include egg-laying, maturation from one larval size class to the other, and metamorphosis into adults and subsequent emergence from the lake.

The addition of a numbers equation permits the calculation of mean weight so that the processes of respiration, feeding, predation, and promotion (maturation and emergence of adults) can be made functions of mean weight. The numbers equation includes those terms from the biomass equation that represent discrete changes in numbers of individuals; each term is divided by mean weight in order to convert from weight to numbers.

Maturation and emergence are considered a function of a particular size class. As weight increases above a critical level, the probability of promotion increases exponentially. Nonpredatory mortality considers the effect of overcrowding, which causes increased mortality as the population approaches carrying capacity (determined as the maximum number of individuals that can occupy a unit area without touching). Respiration, feeding, and nonpredatory mortality are also affected by the dissolved oxygen level, which is often near critically low levels for maintenance of the bottom-dwelling organisms.

Decomposition (conversion of dead plant and animal material to inorganic forms) occurs in the water column and in bottom sediments. The process can be considered as occurring in two stages. First, particles of organic matter  $B_p$  are made soluble by hydrolysis. The resultant dissolved organic matter  $B_{DOM}$  serves as substrate for decomposers (fungi, bacteria, and protozoans)  $B_d$ . As byproducts of their metabolism, these decomposers produce inorganic carbon, nitrogen, phosphorus, and dissolved organic matter that is not readily subject to further biodegradation. The decomposer-particulate-matter aggregate also serves as a food source for zooplankton, benthic insect larvae, and bottom-feeding fish.

The equations for particulate (Equation 7.2) and dissolved (Equation 7.3) organic matter consist of fluxes associated with animal and plant losses of organic matter (particularly by death, elimination of waste materials, and leaf sloughing), terms for inputs from outside the lake ecosystem, and flux terms due to decomposer activity. The decomposer equation (Equation 7.1) contains uptake, respiration, excretion, and mortality terms. The set of three equations is considered to represent processes both within the water column and within the sediments.

Decomposer uptake of dissolved organic matter follows simple saturation kinetics (Equation 7.4), except that a certain amount  $DOM_{min}$  of the dissolved material is deemed unusable. Uptake is

Table 7  
Decomposition

$$dB_{d_i}/dt = V_{d_i} - (R_{d_i} + U_{d_i} + S_{d_i} + M_{d_i} + \sum_j C_{p_i,j} B_j) \quad 7.1$$

- $B_{d_i}$  = Biomass of the  $i$ th decomposer group
- $V_{d_i}$  = Rate of uptake of organic materials
- $R_{d_i}$  = Respiration rate
- $U_{d_i}$  = Rate of excretion of inorganic and refractory organic materials
- $S_{d_i}$  = Rate of sedimentation (or resuspension)
- $M_{d_i}$  = Rate of mortality due to lysis (disintegration), inactivation, and micropredators

$$dB_{p_i}/dt = I_{p_i} + \sum_j F_j + \sum_j K_{p,M_j} M_j + S_{p_i} - (H_{p_i} + \sum_j C_{p_i,j}) B_j \quad 7.2$$

- $B_{p_i}$  = Mass of the  $i$ th Particulate Organic Matter (POM) compartment
- $I_{p_i}$  = External loading of POM
- $F_j$  = Defecation rate of the  $j$ th consumer group
- $K_{p,M_j}$  = Input rate of POM due to nonpredatory mortality
- $S_{p_i}$  = Rate of sedimentation (or resuspension)
- $H_{p_i}$  = Hydrolysis rate
- $C_{p_i,j}$  = Rate of grazing by  $j$ th consumer group

$$dB_{DOM_i}/dt = I_{DOM_i} + \sum_{j=1}^n U_j + \sum_j K_{p,M_j} M_j + H_{p_i} + D_{DOM_i} - V_{d_i} \quad 7.3$$

- $B_{DOM_i}$  = Mass of the  $i$ th Dissolved Organic Matter (DOM)
- $I_{DOM_i}$  = External loading of  $i$ th DOM
- $U_j$  = Excretion rate of organics by the  $j$ th biotic group
- $K_{p,M_j}$  = Input rate of DOM due to nonpredatory mortality
- $D_{DOM_i}$  = Diffusion rate of  $i$ th organic between sediment and water

$$V_{d_i} = V_{max,d_i} a_{d_i} v^{c_{d_i,v}} V \left( \frac{B_{DOM_i} - DOM_{min_i}}{K_{DOM_i} + B_{DOM_i} - DOM_{min_i}} \right) B_{d_i} \cdot v \left( B_{DOM_j} - DOM_{min_j} \right) \quad 7.4$$

- where  $i$  =  $i$ th decomposer group,  $j$  =  $j$ th DOM group
- $V_{max,d_i}$  = Maximum uptake rate
- $c_{d_i,v}$  = Effect of temperature on uptake (see Equation 3.2)
- $a_{d_i,v}$  = Effect of dissolved oxygen
- $1 + K_{V,O_2} v(O_{2,min} - O_2)$  7.41
- $DOM_{min_j}$  = DOM level below which uptake is negligible

- $K_{DOM_i}$  = Half-saturation constant for uptake
- $O_{2,min}$  = Oxygen level for anaerobic uptake
- $K_{V,O_2}$  = Change in uptake due to anaerobic conditions
- $R_{d_i} = R_{max,d_i} a_{d_i,R} B_{d_i} + K_{resp,d_i} V_{d_i}$  7.5
- $R_{max,d_i}$  = Maximum endogenous respiration rate
- $K_{resp,d_i}$  = Constant for effect of uptake on respiration

$$U_{d_i} = \sum_j v(O_{2,min} - O_2) (V_{d_i} - R_{d_i}) v_j (V_{d_i} - R_{d_i}) \quad 7.6$$

$u_j$  = Percent of net assimilation which is excreted for  $j$ th compound

$$H_{p_j} = H_{max,p_j} c_{p_j,H} a_{p_j,H} h_{p_j,H} \left( \frac{B_{d_i}}{K_{spv_j} B_{p_j} + B_{d_i} + K_{POM_j}} \right) B_{p_j} \quad 7.7$$

- $H_{max,p_j}$  = Maximum hydrolysis rate
- $h_{p_j,H}$  = Effect of pH on hydrolysis
- $\exp \left[ - \left( \frac{pH - pH_{opt}}{\sigma} \right)^2 \right]$  7.71

- $K_{spv_j}$  = Available surface area parameter
- $K_{POM_j}$  = Saturation constant for hydrolysis
- pH = pH of water or interstitial water in sediment
- $pH_{opt}$  = Optimum pH for hydrolysis
- $\sigma$  = pH "bandwidth" constant for hydrolysis
- POM = Particulate Organic Matter

$$S_{d_i} = \psi_{d_i} \exp[K_{sed,d_i} (\Delta T/\Delta z)] \frac{\Delta P_{bar}}{\Delta t} B_{d_i} \quad 7.8$$

- $\Delta T/\Delta z$  = Maximum vertical thermal gradient
- $\Delta P_{bar}/\Delta t$  = Change in barometric pressure over past day
- $K_{sed,d_i}$  = Thermal gradient constant
- where  $B_{d_i}$  is either water or sediment compartment depending on the sign of  $\frac{\Delta P_{bar}}{\Delta t}$

$$D_{DOM_i} = K_{DIF} (B_{DOM_i} - B_{DOM_{i+1}}) \quad 7.9$$

- $K_{DIF}$  = Boundary layer resistance coefficient
- DOM = Dissolved Organic Matter

$$M_{d_i} = K_{d_i,M} a_{d_i,M} B_{d_i} C_{d_i,M} \quad 7.10$$

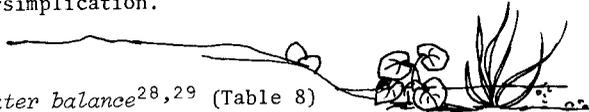
$K_{d_i,M}$  = Nonmacro predatory mortality

changed by a fraction  $K_V, O_2$  under anaerobic conditions. Respiration losses from the decomposers are considered proportional to decomposer biomass, modified by temperature and the amount of dissolved oxygen. Grazing rates on the decomposer-particulate substrate have already been considered in the models for the individual grazers (see Tables 3-6).

The rate of hydrolysis of particulate organic matter is dependent on water temperature, acidity/alkalinity (pH), dissolved oxygen, and the amount of organic matter and decomposers (Equation 7.7). The parameter  $K_{gp}$  is a function of the mean available surface area of particulate matter. The complex hydrolysis term produces a flux proportional to particulate concentration when decomposers are abundant, proportional to decomposers when organic matter is abundant, and proportional to both at intermediate concentrations.

Through metabolic excretion the decomposers produce organic byproducts and remineralize phosphorus and nitrogen. The rate of this process is considered a function of uptake and respiration (Equation 7.6), and the excretion of organics increases significantly with low concentrations of oxygen. The refractory dissolved organic matter might be considered as a carbon source for methane-producing bacteria, but this process is ignored in the present version of the model.

The rate of sedimentation of particulate organic matter is a function of the potential for vertical mixing, as indicated by the thermal gradient, and wave agitation (Equation 7.8). Wave agitation is a result of wind stress; however, in order to make the model more general, we have considered using the change in barometric pressure as a driving variable for wave agitation instead of wind.<sup>27</sup> This also permits simulation of the resuspension of sediment when wave base intersects the lake bottom at a particular time. Further study is being conducted to determine if this construct is adequate, or if it is an oversimplification.



Lake-water balance<sup>28,29</sup> (Table 8)

The hydrology of the lake basin is of interest in that it affects transport of nutrients into the lake, the nutrient concentrations in the lake, and the wash-out from the lake of both nutrients and plankton. A separate hydrological transport model has been developed to predict nutrient loadings<sup>29</sup>; output from this model can be used to drive CLEAN. Experience with WNGRA2, the site-specific version of CLEAN for Lake Wingra, has been quite encouraging.<sup>31</sup> At present, a water-balance submodel for lakes is being incorporated into CLEAN.

Positive terms include precipitation, surface inflow, and groundwater inflow. Negative terms include surface outflow, evaporation, and groundwater outflow. Inflow and outflow rates may be expressed as functions of lake stage so that the effects of water-level fluctuations, particularly in recent impoundments, can be simulated. Several formulations for calculating evaporation have been used, including one that corrects for the horizontal transport of energy by water currents. Groundwater flow may be determined empirically using data from observational wells. In lake basins having little contribution from groundwater (e.g., rock basins) groundwater flow can be

Table 8  
Lake water balance

$$\frac{dV}{dt} = (p-e)A(E) + Q_s f(E) + \sum_{i=1}^n \left[ K_i \left( \frac{w_i - E}{D_i} \right) L_i [m_{0i} + \alpha(w_i - w_{0i})] \right] - K(t) \quad 8.1$$

- $V$  = Volume of lake water
- $A(E)$  = Lake surface area as a function of lake stage,  $E$
- $p$  = Precipitation rate
- $e$  = Evaporation rate
- $Q_s$  = Surface inflow rate
- $f(E)$  = Elevation-dependent correction factor for inflow
- $n$  = Number of observation wells
- $K_i$  = Saturated hydraulic conductivity at observation well  $i$
- $w_i$  = Elevation of groundwater table at well  $i$
- $E$  = Lake level
- $D_i$  = Distance of well  $i$  from lake
- $L_i$  = Effective length of aquifer along the shoreline associated with well  $i$
- $m_{0i}$  = Base value for effective saturated thickness
- $\alpha$  = Parameter which characterizes dependence of  $m$  on  $w$
- $w_{0i}$  = Index elevation
- $K_3(t)$  = Known time-series of outflow

simplified or neglected. The outflow term shown in Equation 8.1 refers to conditions of known outflow. For other situations, such as flow over an ungated spillway or natural stream drainage, an appropriate expression can be substituted.

#### Lake-circulation and substance-transport

Wind-driven currents, lake oscillations, and heat transfer across the air-water boundary are of importance to the aquatic ecosystem in that they transport and diffuse nutrients and particulate materials (including influents, organic matter, plankton, and resuspended sediments) from one region of the lake to another. Therefore, the modeling program would not be complete without some means of predicting lake motions. A separate circulation model has been developed as a part of the research effort at Lake Wingra<sup>32</sup> (see Table 9). Because CLEAN was formulated as a point model to minimize

Table 9  
Lake circulation  
and substance transport

Mass conservation

$$\frac{\partial}{\partial t} (U\bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial y} (V\bar{H})_{k-\frac{1}{2}} + \omega_{k-1} - \omega_k + \frac{\partial Z_{k-1}}{\partial t} - \frac{\partial Z_k}{\partial t} = 0$$

Momentum conservation

a)  $x$ -component

$$\begin{aligned} & \frac{\partial}{\partial t} (U\bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial x} (\alpha_1 U^2 \bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial y} (\alpha_2 UV\bar{H})_{k-\frac{1}{2}} - f[V\bar{H}]_{k-\frac{1}{2}} + [\omega\bar{U}]_{k-1} - [\omega\bar{U}]_k \\ & = -H_{k-\frac{1}{2}} \left( \frac{\partial}{\partial x} \left[ g\eta + \frac{P_g}{\rho_0} \right] + P_{x,k-\frac{1}{2}} \right) + \frac{\partial}{\partial x} \left( [A_{mH}]_{k-\frac{1}{2}} \frac{\partial}{\partial x} (U\bar{H})_{k-\frac{1}{2}} \right) + \frac{\partial}{\partial y} \left( [A_{mH}]_{k-\frac{1}{2}} \frac{\partial}{\partial y} (U\bar{H})_{k-\frac{1}{2}} \right) \\ & \quad + \left( A_{mU} \frac{\partial \bar{U}}{\partial z} \right)_{k-1} - \left( A_{mU} \frac{\partial \bar{U}}{\partial z} \right)_k \end{aligned} \quad 9.2$$

b)  $y$ -component

$$\begin{aligned} & \frac{\partial}{\partial t} (V\bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial x} (\alpha_2 UV\bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial y} (\alpha_3 V^2 \bar{H})_{k-\frac{1}{2}} + f[U\bar{H}]_{k-\frac{1}{2}} + [\omega\bar{V}]_{k-1} - [\omega\bar{V}]_k \\ & = H_{k-\frac{1}{2}} \left( \frac{\partial}{\partial y} \left[ g\eta + \frac{P_g}{\rho_0} \right] + P_{y,k-\frac{1}{2}} \right) + \frac{\partial}{\partial x} \left( [A_{mH}]_{k-\frac{1}{2}} \frac{\partial}{\partial x} (V\bar{H})_{k-\frac{1}{2}} \right) + \frac{\partial}{\partial y} \left( [A_{mH}]_{k-\frac{1}{2}} \frac{\partial}{\partial y} (V\bar{H})_{k-\frac{1}{2}} \right) \\ & \quad + \left( A_{mV} \frac{\partial \bar{V}}{\partial z} \right)_{k-1} - \left( A_{mV} \frac{\partial \bar{V}}{\partial z} \right)_k \end{aligned} \quad 9.3$$

Heat conservation

$$\begin{aligned} & \frac{\partial}{\partial t} (T\bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial x} (\beta_1 U\bar{T}H)_{k-\frac{1}{2}} + \frac{\partial}{\partial y} (\beta_2 V\bar{T}H)_{k-\frac{1}{2}} + [\omega\bar{T}]_{k-1} - [\omega\bar{T}]_k \\ & = \frac{\partial}{\partial x} \left( [A_{HT}]_{k-\frac{1}{2}} \frac{\partial}{\partial x} (T\bar{H})_{k-\frac{1}{2}} \right) + \frac{\partial}{\partial y} \left( [A_{HT}]_{k-\frac{1}{2}} \frac{\partial}{\partial y} (T\bar{H})_{k-\frac{1}{2}} \right) + \left( A_{HT} \frac{\partial \bar{T}}{\partial z} \right)_{k-1} - \left( A_{HT} \frac{\partial \bar{T}}{\partial z} \right)_k + \phi_{k-\frac{1}{2}} \end{aligned} \quad 9.4$$

Substance (dissolved or particulate) conservation

$$\begin{aligned} & \frac{\partial}{\partial t} (C\bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial x} (\delta_1 UC\bar{H})_{k-\frac{1}{2}} + \frac{\partial}{\partial y} (\delta_2 VC\bar{H})_{k-\frac{1}{2}} + [\omega\bar{C}]_{k-1} - [\omega\bar{C}]_k - [\omega_{SS}\bar{C}]_{k-1} + [\omega_{SS}\bar{C}]_k \\ & = \frac{\partial}{\partial x} \left( [A_{SC}]_{k-\frac{1}{2}} \frac{\partial}{\partial x} (C\bar{H})_{k-\frac{1}{2}} \right) + \frac{\partial}{\partial y} \left( [A_{SC}]_{k-\frac{1}{2}} \frac{\partial}{\partial y} (C\bar{H})_{k-\frac{1}{2}} \right) + \left( A_{SC} \frac{\partial \bar{C}}{\partial z} \right)_{k-1} - \left( A_{SC} \frac{\partial \bar{C}}{\partial z} \right)_k + S_{k-\frac{1}{2}} \end{aligned} \quad 9.5$$

where

$Z_0 = \eta(x, y, t)$  = free water surface

$Z_k = -h_k$  = location of rigid intermediate levels (layer boundaries)

$Z_n = -h(x, y)$  = lake bottom

$H_{k-\frac{1}{2}} = Z_{k-1} - Z_k$  = layer thickness

$k = 1, 2, 3, \dots, N$  = index denoting particular level (layer boundary) below water surface ( $k = 0$ )

$x, y$  = horizontal coordinates in plane of equilibrium lake water surface

$z$  = vertical coordinate perpendicular to equilibrium water surface, positive upwards

$t$  = time

$$U_{k-\frac{1}{2}} = \frac{1}{H_{k-\frac{1}{2}}} \int_{Z_k}^{Z_{k-1}} u dz = \text{layer-averaged } x\text{-component of velocity}$$

$$V_{k-\frac{1}{2}} = \frac{1}{H_{k-\frac{1}{2}}} \int_{Z_k}^{Z_{k-1}} v dz = \text{layer-averaged } y\text{-component of velocity}$$

$u, v,$  and  $w$  = horizontal and vertical velocity components in  $x, y,$  and  $z$  directions at  $(x, y, z)$

$\alpha_1, \alpha_2, \alpha_3$  = coefficients resulting from variation of velocity over layer thickness

$$\omega_k = w_k - \left[ u_k \frac{\partial Z_k}{\partial x} + v_k \frac{\partial Z_k}{\partial y} \right] - \frac{\partial Z_k}{\partial t} = \text{velocity (vertical) relative to level } k$$

note that  $\omega_0 = 0, \omega_n = 0$

$f$  = Coriolis parameter =  $2\Omega \sin \phi$  (where  $\Omega$  = angular rotation rate of earth,  $\phi$  = latitude)

$$\bar{U}_k = \frac{1}{2} (U_{k-\frac{1}{2}} + U_{k+\frac{1}{2}}) = \text{average velocity of } x\text{-component between layers}$$

$$\bar{V}_k = \frac{1}{2} (V_{k-\frac{1}{2}} + V_{k+\frac{1}{2}}) = \text{average velocity of } y\text{-component between layers}$$

$g$  = gravitational constant

$P_g$  = atmospheric pressure on water surface

$\rho_0$  = reference water density

Table 9 (continued)  
Lake circulation  
and substance transport

$$P_{x_{k+\frac{1}{2}}} - P_{x_{k-\frac{1}{2}}} = g \left( \frac{H_{k+\frac{1}{2}} + H_{k-\frac{1}{2}}}{2} \right) \frac{\partial}{\partial x} \left[ \frac{c_k}{\rho_0} \right] = x\text{-component of horizontal pressure gradient due to temperature variations}$$

where

$$P_{x_{\frac{1}{2}}} = gH_{\frac{1}{2}} \frac{\partial}{\partial x} \left[ \frac{c_{\frac{1}{2}}}{\rho_0} \right]; \text{ note that the same expression holds for the } y\text{-component when } x \text{ is replaced by } y.$$

$\sigma_k = \psi(\bar{T}_k)$  = equation of state (relating density changes to temperature changes)

$A_{m_h}$  = horizontal turbulent-diffusion coefficient for momentum

$A_{m_v}$  = vertical turbulent-diffusion coefficient for momentum

$$\left[ A_{m_v} \frac{\partial \bar{U}}{\partial z} \right]_k = 2A_{m_v} \left[ \frac{U_{k-\frac{1}{2}} - U_{k+\frac{1}{2}}}{H_{k-\frac{1}{2}} + H_{k+\frac{1}{2}}} \right] = x\text{-component of vertical momentum transfer due to turbulent shear;}$$

$$\text{note that } \left[ A_{m_v} \frac{\partial \bar{U}}{\partial z} \right]_0 = \frac{\tau_{sx}}{\rho_0} \text{ and } \left[ A_{m_v} \frac{\partial \bar{U}}{\partial z} \right]_N = \frac{\tau_{bx}}{\rho_0}$$

$\tau_{sx}, \tau_{sy}$  =  $x, y$  components of wind shear stress on water surface

$\tau_{bx}, \tau_{by}$  =  $x, y$  components of bottom shear stress

$$\left[ A_{m_v} \frac{\partial \bar{V}}{\partial z} \right]_k = 2A_{m_v} \left[ \frac{V_{k-\frac{1}{2}} - V_{k+\frac{1}{2}}}{H_{k-\frac{1}{2}} + H_{k+\frac{1}{2}}} \right] = y\text{-component of vertical momentum transfer due to turbulent shear;}$$

$$\text{note that } \left[ A_{m_v} \frac{\partial \bar{V}}{\partial z} \right]_0 = \frac{\tau_{sy}}{\rho_0} \text{ and } \left[ A_{m_v} \frac{\partial \bar{V}}{\partial z} \right]_N = \frac{\tau_{by}}{\rho_0}$$

$$T_{k-\frac{1}{2}} = \frac{1}{H_{k-\frac{1}{2}}} \int_{z_k}^{z_{k-1}} T dz = \text{layer-averaged temperature}$$

$T$  = water temperature at  $(x, y, z)$

$\bar{T}_k = \frac{1}{2}(T_{k-\frac{1}{2}} + T_{k+\frac{1}{2}})$  = average temperature between layers

$\beta_1, \beta_2, \beta_3$  = coefficients resulting from variation of temperature and velocity over layer thickness

$A_{h_h}$  = horizontal turbulent-diffusion coefficient for heat

$A_{h_v}$  = vertical turbulent-diffusion coefficient for heat

$$\left[ A_{h_v} \frac{\partial \bar{T}}{\partial z} \right]_k = 2A_{h_v} \left[ \frac{T_{k-\frac{1}{2}} - T_{k+\frac{1}{2}}}{H_{k-\frac{1}{2}} + H_{k+\frac{1}{2}}} \right] = \text{vertical heat transfer due to turbulent diffusion;}$$

$$\text{note that } \left[ A_{h_v} \frac{\partial \bar{T}}{\partial z} \right]_0 = Q_0 \text{ and } \left[ A_{h_v} \frac{\partial \bar{T}}{\partial z} \right]_N = 0.$$

$Q_0$  = net rate of heat absorption at water surface

$$\phi_{k-\frac{1}{2}} = \frac{1}{H_{k-\frac{1}{2}}} \int_{z_k}^{z_{k-1}} \phi dz = \text{net rate of heat absorption within a layer}$$

$\phi$  = rate of internal radiation absorption at any depth

$$C_{k-\frac{1}{2}} = \frac{1}{H_{k-\frac{1}{2}}} \int_{z_k}^{z_{k-1}} C dz = \text{layer-averaged concentration of substance}$$

$C$  = concentration of dissolved or particulate material

$\delta_1, \delta_2, \delta_3$  = coefficients resulting from variation of concentration and velocity over layer thickness

$\bar{C}_k = \frac{1}{2}(C_{k-\frac{1}{2}} + C_{k+\frac{1}{2}})$  = average concentration between layers

$A_{s_h}$  = horizontal turbulent-diffusion coefficient for substance

$A_{s_v}$  = vertical turbulent-diffusion coefficient for substance

$$\left[ A_{s_v} \frac{\partial \bar{C}}{\partial z} \right]_k = 2A_{s_v} \left[ \frac{C_{k-\frac{1}{2}} - C_{k+\frac{1}{2}}}{H_{k-\frac{1}{2}} + H_{k+\frac{1}{2}}} \right] = \text{vertical transfer of substance due to turbulent diffusion;}$$

$$\text{note that } \left[ A_{s_v} \frac{\partial \bar{C}}{\partial z} \right]_0 = -(\omega_{ss} \bar{C})_0, \text{ no flux through water surface, and that}$$

$$\left[ A_{s_v} \frac{\partial \bar{C}}{\partial z} \right]_N + (\omega_{ss} \bar{C})_N = E_N$$

$E_N$  = net flux of material into suspension at lake bottom

$\omega_{ss}$  = settling velocity of substance

$\mathcal{E}_{k-\frac{1}{2}}$  = net rate of substance production in layer

computational time, it does not seem advisable to couple it directly to a two- or three-dimensional circulation model such as this, except where the spatial distributions of ecosystem components are of critical interest.

At present the lake circulation model is being used to predict transient two-dimensional motion in Lake Wingra for different wind patterns, assuming homogeneous (isothermal) conditions. The predicted transport rates can then be plugged into CLEAN or the site-specific version, WNGRA2, in order to couple simulations for different regions of the lake. However, the circulation model is formulated in such a way that CLEAN can be run as a part of it and used to generate net production rates and concentrations of substances. Thus, if needed, there could be a hierarchy of models, with CLEAN operating as a part of the lake circulation model.

To model lake motions, the conservation laws for mass (Equation 9.1), momentum (Equations 9.2 and 9.3), heat (Equation 9.4), and substance mass (Equation 9.5) are written for a lake which is comprised of an arbitrary number  $N$  of horizontal layers of different thicknesses. These equations include horizontal and vertical transport of energy and turbulent diffusive transport of momentum, heat, and substance throughout the lake and describe the temporal and spatial variations in velocity, temperature, and concentration averaged over each layer at a particular horizontal location. The lake motions represented in the model are driven by wind shear, atmospheric pressure gradients, and heat absorption and are subject to shoreline and bottom boundary conditions. The model equations must be solved simultaneously because of the coupling between the conservation laws.



#### EXPERIMENTATION AND ANALYSIS

The mathematical equations are instructive in that they represent a formal, unambiguous statement of our understanding of ecosystem dynamics. Experimentation with the model and sensitivity analysis then assist in drawing out the implications of these equations. In particular, running simulations and checking the results for intuitive reasonableness have been invaluable in the continuing process of evaluating the model and improving it.

Individual submodels, in some cases more detailed than those versions incorporated in CLEAN, have been subjected to intensive testing for internal consistency and for accuracy of prediction. The results of these detailed studies will be reported in a series of technical publications.<sup>20,33,34</sup> Numerous combinations of submodels have also been investigated. The most extensive experimentation has involved components representing the open-water portion of the ecosystem. These include two phytoplankton, two herbivorous zooplankton, omnivorous zooplankton, bluegill-like fish, bass-like fish, particulate and dissolved organic matter, decomposers, and phosphate. This open-water version of CLEAN demonstrates the utility of the more important nonlinear feedback terms in the model; it also exhibits important functional dissimilarities between two groups of phytoplankton and among three groups of zooplankton — groups that are lumped together in many simulation models.

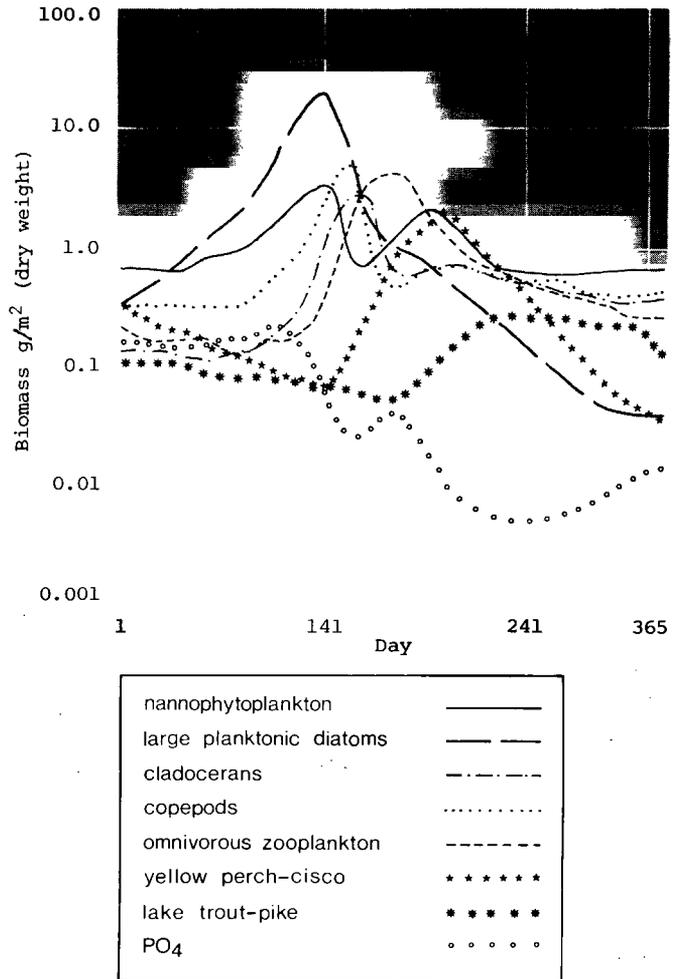


Figure 3 - Simulated seasonal changes in the open-water ecosystem. This and the following figures are for the south end of Lake George, New York.

CLEAN has been run using data from a number of lakes; however, most experimentation has been with data from the intensive research sites, Lake George and Lake Wingra. Biomass values predicted for a typical year at the south end of Lake George are presented in Figure 3. Parameters for the state variables are set to correspond to the principal groups endemic to Lake George; thus, the "net phytoplankton" are large planktonic diatoms, "bluegill-like fish" are principally yellow perch and cisco, and "bass-like fish" are principally lake trout and pike.

The predicted levels are of the same magnitude as the observed levels, but at the present stage of calibration the model seems not to be predicting seasonal patterns with sufficient accuracy to be satisfactory (e.g., Figures 4a and 4b). Unfortunately, given the inherent sampling and transformation errors in the available data, it is not possible to test the adequacy of the model rigorously. However, inspection of the output and consideration of the ecologic basis for the model suggests some general conclusions about the way in which the model behaves.

In spring, as light ceases to be a limiting factor in the model, the phytoplankton can utilize the nutrients that have accumulated during the winter with the

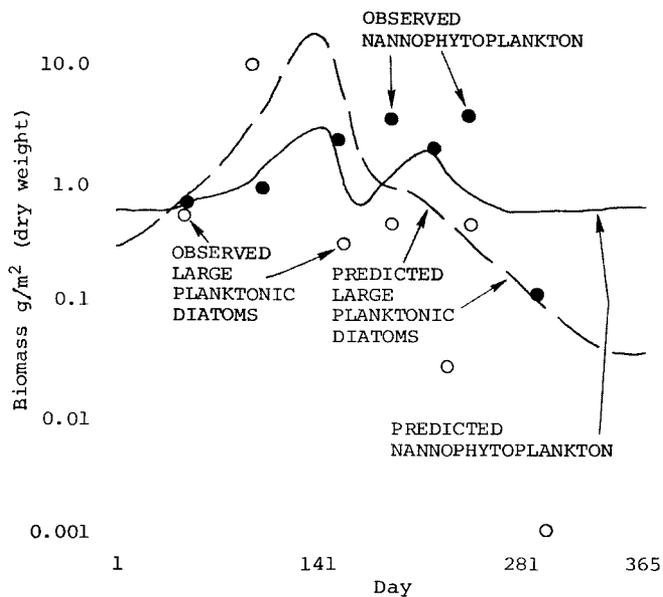


Figure 4a - Comparison of predicted and observed nannophytoplankton and large planktonic diatoms. Open circles represent observed large diatom biomass and closed circles represent observed nannophytoplankton biomass; legend for predicted patterns same as in Figure 3. Data courtesy of H. H. Howard.

large diatoms increasing most rapidly because the optimum water temperature for them is lower than for smaller species and they require less light. The large diatom and nannophytoplankton populations both reach a peak in the latter part of May and then "crash" as available phosphate is depleted and grazing by zooplankton is intensified.

During the summer the biomass moves up the food chain, with the model exhibiting fairly realistic time lags, depending on the position of each group in the food chain. Herbivorous cladocerans and copepods differ somewhat in their seasonal abundancies because of differences in their maximum growth rates and their ability to feed on large diatoms. Omnivorous zooplankton feed on the herbivorous zooplankton and are eaten in turn by yellow perch and cisco. Lake trout and pike increase in biomass during the latter part of summer, feeding on yellow perch and cisco, which decline precipitously in the simulation in response to the increased predation. Nannophytoplankton increase following the decline of the herbivorous zooplankton, but the large diatoms continue to decline because the available phosphate level is suboptimal for their requirements. Thus, the model output represents the combined effects of a number of ecological relationships. This behavior of the model is reasonable and is useful for environmental management, although continued refinement is clearly desirable.

Whereas on-line experimentation with the model can give a "feel" for the dynamics of the model, sensitivity analysis is more useful in indicating specific parameters which must be known with greater accuracy to ensure fully satisfactory simulations. A range of values, rather than precise estimates, is available for most parameters because of the difficulty of

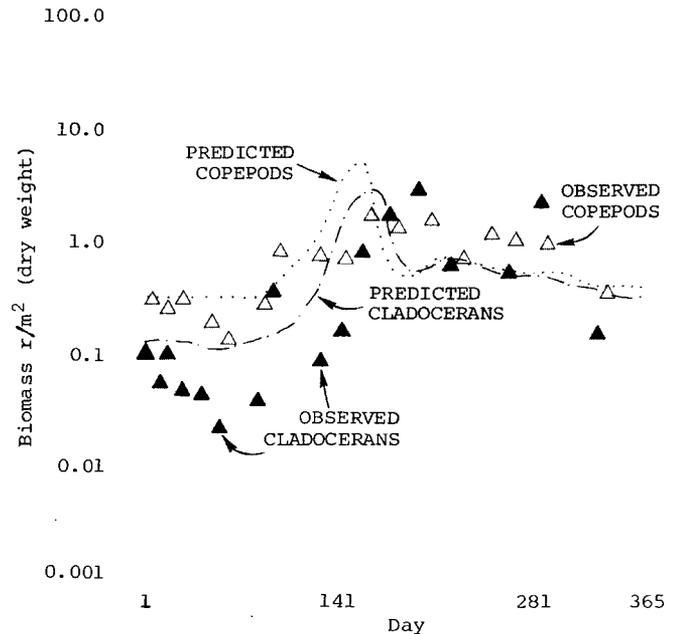


Figure 4b - Comparison of predicted and observed herbivorous zooplankton. Open triangles represent observed herbivorous copepod biomass and closed triangles represent observed cladoceran biomass; legend for predicted patterns same as in Figure 3.

measuring biological processes. Within the estimated range, sensitivity can be determined readily by response-surface methodology.<sup>35</sup>

A normalized parameter for rate of change,

$$K(t) = \frac{dB_i}{B_i(t) dt}$$

is determined from field data by a spline function technique<sup>36</sup> and compared to the value of  $K(t)$  predicted by the model. Sums of squares of differences between measured and predicted values of  $K(t)$  are calculated utilizing a fractional factorial combination of the largest and smallest values in the range of each parameter. This produces a set of sums of squares and corresponding parameter values. Stepwise linear regression then is used to fit the sum of squares to a full quadratic model of individual parameters. The relative sensitivities of the simulation model to the parameters are indicated by the  $F$ -values of the parameters in the regression equation.

Such an analysis has revealed the open-water model to be particularly sensitive to maximum photosynthesis rates, respiration constants, phytoplankton sinking coefficients, and phosphate limitations. Grazing components are most sensitive to food preference, maximum feeding rates, and optimal temperature. On the other hand, the model appears relatively insensitive to the level of light saturation, metabolic excretion rates, and correction factors for the age structures of the several populations. This information is now being used in setting priorities for further studies to obtain more precise estimates of the most sensitive parameters.

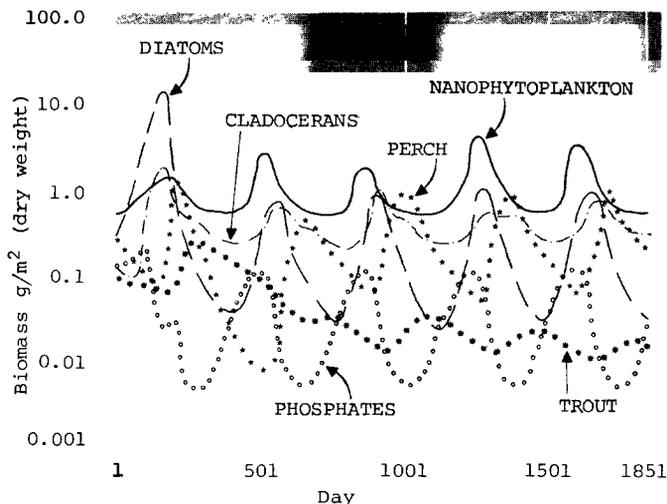


Figure 5 - Simulated 5-year patterns of selected components of the open-water ecosystem. Legend same as in Figure 3.

The stability of the model can be established readily through examination of a five-year simulation based on the same parameters and driving variables as used for the one-year simulation described above (Figure 5). However, there is transient response in the first year. Large diatoms exhibit a large spring peak only in the first year, and lake trout-pike eventually reach a lower level in equilibrium with the yellow perch-cisco population.

The diatom response is a manifestation of an unrealistic time lag in the regeneration of available phosphate: without suitably high phosphate levels early in the spring, the simulated diatoms cannot reach the observed levels using reasonable values for the parameters. Presumably this difficulty with the model will be resolved when more precise parameter estimates are available for the decomposer component, causing phosphate to be simulated more realistically. It is likely that the lake trout-pike simulation seeks a lower equilibrium because the model is over-simplified. The open-water version of CLEAN does not provide for seasonal differences in predation brought about by the growth of macrophytes that serve as cover, nor does it presently account for the massive restocking of lake trout from hatcheries. With these additions the two groups of fish will not be as intensely coupled and will probably maintain more realistic long-term dynamics.

Experimentation with CLEAN in forecasting lake eutrophication is instructive. For example, by symbolically doubling the input of phosphate into the south end of Lake George, we get some rather interesting results compared to the "normal" simulation (Figure 6). In the perturbed simulation large diatoms become half again as abundant, whereas the nanophytoplankton (which compete with them) are slightly less abundant than "normal" in the spring. However, the nanophytoplankton become significantly more abundant than "normal" in the late summer peak. The predicted spring increase in large diatoms seems to be realistic and is of particular interest in that these diatoms include taste- and odor-producing forms that seriously degrade the quality of the water as perceived by tourists and cottage owners.

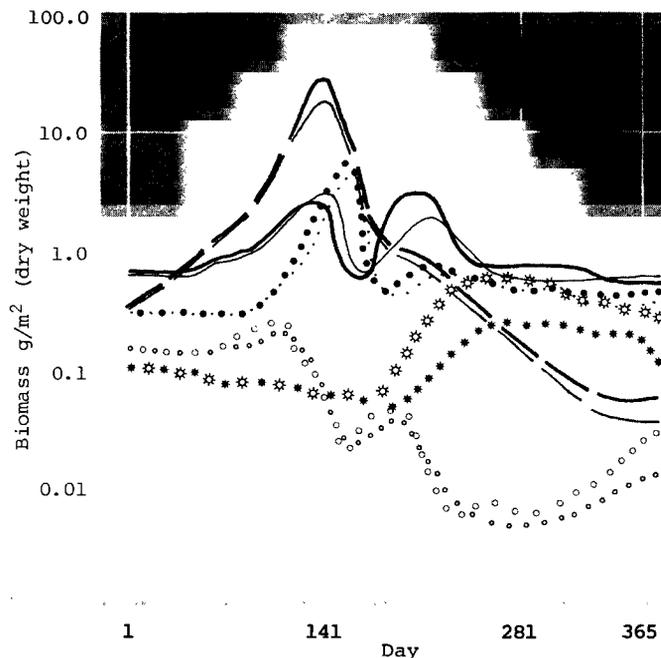


Figure 6 - Comparison of simulated seasonal patterns of selected ecosystem components for normal and doubled phosphate loadings. Inset shows 5-year patterns for lake trout-pike.

On the plus side, lake trout and pike become almost three times as abundant (or big) as before, representing the transfer of biomass up to the higher levels of the food chain. This, too, is realistic for a lake in an intermediate stage of eutrophication.

Over the course of a five-year simulation (see inset in Figure 6) the discrepancy between levels of fish in the normal and perturbed systems becomes even more pronounced, although this probably reflects the inadequacies of the present model, as discussed above.

Interestingly enough, available phosphate levels are almost the same in the normal and perturbed simulations, reflecting the rapid uptake of phosphate by phytoplankton and underscoring the fact that available phosphate levels are not a suitable index to eutrophication. Thus, even in its present stage of development, CLEAN exhibits good potential as a tool for environmental management.

## REFINEMENTS AND EVALUATION

Individual submodels have been tested and found capable of satisfactorily predicting the dynamics of their respective subsystems. However, model constructs are imperfect representations of the real world, and a continuing effort is therefore required to improve these models. For example, various formulations for the limitations of light and nutrients on photosynthesis are being examined. In addition to the mean resistance construct, used in Equation 2.2, a minimum function

$$\min (\mu_{\text{light}}, \mu_{\text{PO}_4}, \mu_{\text{N}}, \mu_{\text{C}})$$

has produced excellent results. We have also experimented with a multiplicative function

$$\mu_{\text{light}} \cdot \mu_{\text{PO}_4} \cdot \mu_{\text{N}} \cdot \mu_{\text{C}}$$

which seems to limit photosynthesis more severely than is actually observed in nature. Ultimately, the choice of a single formulation may depend on the development of new laboratory procedures to determine the nature of the limitation process more accurately.

A principal advantage of large-scale interdisciplinary research is feedback from model analysis to provide redirection for research. This is particularly important in working with complex ecosystems where interaction among components can often lead to counterintuitive results. Initial research has emphasized the dynamics of individual components. Much has been learned from the subsystem models, and this knowledge is rapidly being incorporated into the model. In turn, on-line simulation with the model is yielding valuable insight into whole-system functionalities and is setting the stage for new laboratory approaches and field programs which emphasize the interfaces between components.

From the inception of the present study there has been a well-defined strategy for evaluating the ecosystem model. Lake Wingra is a shallow, nutrient-rich lake and is partially surrounded by a city. However, Lake George is a large, relatively nutrient-poor lake with extensive undeveloped shorelines—although the south end is undergoing eutrophication as the area is increasingly developed. By changing

site constants and substituting the appropriate values of the driving variables, various hierarchical versions of CLEAN can be used for either lake (as well as for other lakes for which there are suitable data). Therefore, a model calibrated for Lake Wingra can be evaluated for the totally different conditions at Lake George, as well as for intermediate conditions. From such testing we are presently identifying and generalizing those formulations and parameter values which appear to be unique to a single lake or stage or eutrophication. Ideally, the model should be able to describe the dynamics of both lake ecosystems merely by using the appropriate site constants and driving variables.

Data have been collected from both lakes for four years; so the model can be evaluated on a yearly basis, yielding a model responsive to minor variations in driving variables. We have already found that ecosystem dynamics can be affected by seemingly unimportant annual events that trigger replacement of one organism by another, with important effects on the ecosystem. Recognition of these time-varying effects as well as site-specific effects permits us to develop versions of the model with high resolution but limited generality and versions that are less accurate but more widely applicable. For example, WNGRA2<sup>36</sup> has proved to be useful in examining the impact that changes in the drainage basin have on Lake Wingra. At the other end of the scale, we are presently generalizing the parameters so that CLEAN can be applied to arctic and alpine lakes as well. Such flexibility, which is inherent in the modular structure of CLEAN, is necessary if simulation is to be used as an effective tool in answering the diverse problems facing environmental management.

## ACKNOWLEDGEMENT

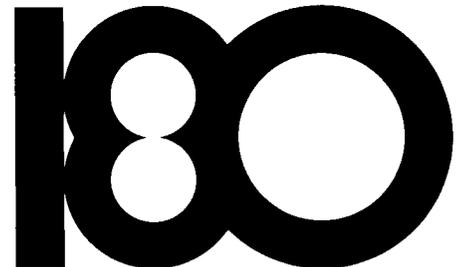
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