INTERNAL REPORT 68

MODELING ANNUAL PHYTOPLANKTON-PHOSPHATE CYCLES

IN LAKE WASHINGTON: A FEASIBILITY STUDY

by

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Several numerical models have been developed recently to study seasonal variations of algal growth and nutrient concentrations in lakes. These include compartment or "box" models as well as vertically-integrated models of the distribution of various substances related to water quality. The present work was undertaken to assess the feasibility of constructing a different sort of model of deep, stratified lakes where the biological, physical, and chemical properties are continuous functions of space and time. Specifically, this paper describes the results of a "demonstration" numerical model of the annual cycles of algal and phosphate concentrations in Lake Washington near Seattle (Figure 1). It was consistent with this rather limited objective to use highly idealized representations of only the most prominent limnological processes. We recognize that a number of important features of lake ecology have not been included in the present work. However, we felt that valid conclusions regarding model feasibility could still be drawn if only those factors were included which were of overriding importance throughout all seasons.

Lake Washington was chosen for modeling since it has been the subject of limnological study in the past (Scheffer and Robinson, 1939) and because there are available adequate data for verification of a coarse time resolution analysis of primary production and nutrient cycling (see, for example, Edmondson et al., 1956; Comita and Anderson, 1959; Edmondson, 1972a, 1972b).

About a decade ago, Lake Washington was in a eutrophic state due to excessive nutrient enrichment from septic tank drainage and sewage treatment plant effluent. During the late 1950's and early 1960's, high phosphate levels prevailed at depth in the lake for the most part of the year, including the wintertime, and this condition was attended by high summertime chlorophyll a concentrations and low transparencies. These characteristic properties of the lake are illustrated in Figures 2 and 3. The exhibited data are from Edmondson (1972a), who also demonstrated a hyperbolic relation between the Secchi disc depth and the mean chlorophyll concentration in the uppermost 10 meters of the lake (Figure 3b). These data constitute evidence of certain interrelationships between biological activity, on the one hand, and the physio-chemical properties of the lake on the other. These should be reproduced at least qualitatively, if not quantitatively, by any numerical model of eutrophication.

With respect to its hydrography, the lake was assumed to be laterally homogeneous and thermally stratified in the vertical direction. Turbulent mixing in the vertical was described by an eddy diffusion coefficient \( K(z) \), where \( z \) is measured positive downward from the surface. In conformity with the observation that \( K \) attains minimal values below the epilimnion, the diffusion coefficient was assumed to decay exponentially with depth from the surface through the epilimnion to the vicinity of the thermocline (0-20 m):

\[
K = K_0 \exp\left(-\frac{z}{z_1}\right),
\]
where \( K_0 \) was assigned a nominal value of 2 cm\(^2\) sec\(^{-1}\). It has also been observed that the value of \( K \) near the thermocline of a first-class lake may fall by one or two orders of magnitude in the summertime when stratification is most pronounced (Hutchinson, 1957). Therefore, the effect of a midyear decrease of \( K \) at depth was included in the present study by varying \( z_1 \) from a wintertime value of 20 m to a summertime low of 5 m. It should be pointed out that such a specification of \( K \) can do nothing more than provide a rough estimate of the magnitudes and trends of diffusion effects. In order to obtain a more reliable description of eddy diffusion, it would be necessary to perform a thorough analysis of additional pertinent data, such as water temperature measurements. Finally, it was assumed that turbulent transport of algal cells and phosphate-phosphorus could be described by the same diffusion coefficient.

The standing stock of phytoplankton at time \( t \) was described by a concentration \( C(z,t) \) of chlorophyll \( a \) per m\(^3\). Phosphorus was assumed to be the only limiting nutrient and its abundance was described by a concentration \( P(z,t) \) of soluble phosphate per cubic meter. The processes which we assumed governed the dynamic interrelationship between chlorophyll \( a \) and phosphate are expressed by the equations

\[
\frac{\partial C}{\partial t} = \frac{\partial}{\partial z} \left( K \frac{\partial C}{\partial z} \right) - \frac{\partial}{\partial z} (w \cdot C) + F(z,t;P,C)C - G(z,t;C)H
\]  

(2)

and

\[
\frac{\partial P}{\partial t} = \frac{\partial}{\partial z} \left( K \frac{\partial P}{\partial z} \right) - V_m(z,t;P,C)C + S(z,t).
\]  

(3)

In equation (2), \( w \) is the sinking speed of an algal cell, \( F \) is the net specific primary production rate, \( G \) is a specific loss rate due to grazing by herbivores whose density \( H(z,t) \) is presumed to be measured, estimable, or otherwise known. In equation (3) \( V_m \) is a specific phosphate uptake rate and \( S(z,t) \) is a source term which describes the net input rate of phosphorus due to stream, river, and land drainage, inflow associated with sewage effluent, and outflow from the lake. The numerical model involves the solution of equations (2) and (3) in a relevant space-time domain, subject to initial distributions of \( C \) and \( P \) and appropriate boundary conditions at the lake surface and at depth.

Since this effort was primarily a feasibility study, we decided to use Edmondson's data of 1963 to prescribe a phosphate source concentration just below the thermocline. Thus, in Figure 2, the concentration \( P \) at about 20 m is seen to vary between 50 and 70 \( \mu \)g per liter over the course of the year. It was further assumed, as a rough approximation, that algal cells near the surface penetrate to the hypolimnion preferentially by sinking, rather than by turbulent mixing, particularly under conditions of stratification. This assumption is expressed by a zero-gradient condition on \( C \) at \( z = 20 \) m. Zero flux conditions were imposed on both the chlorophyll \( a \) and
phosphate concentrations at the surface. With these conditions, the function \( S \) in equation (3) can be set equal to zero (the phosphate source now being specified at a boundary), and the space domain of the model is the epilimnion-thermocline zone. As stated earlier, the time domain is taken to be the entire year 1963.

The net specific algal growth rate just below the water surface was assumed to depend upon the relative amount of sunlight available on a seasonal basis (i.e., hours of daylight per day), the temperature \( T \) of the epilimnion, and the amount of phosphate, in accordance with the relation

\[
F(0,t;P,C) = p_{\text{max}}(T) \frac{P}{P + K_m} \cdot \frac{t_d}{24},
\]

where \( p_{\text{max}} \) denotes the maximum rate at which plant carbon is synthesized per unit mass of plant carbon and where \( t_d \) is the number of daylight hours per day. The parameter \( K_m \) was assigned the value \( 1.0 \times 10^{-6} \text{ g-atom per liter (P)} \) on the basis of studies of phosphate-limited phytoplankton growth by Fuhs et al. (1972). The temperature dependence of the parameter \( p_{\text{max}} \) was expressed as

\[
p_{\text{max}} = 0.005 \exp(T/10).
\]

This particular functional form was inspired by measurements reported in a survey by Eppley (1972) of specific algal growth rates at different temperatures. The coefficient in the right-hand side of equation (5) was assigned from the aforementioned algal growth studies reported by Fuhs et al. (1972). Epilimnetic water temperatures were obtained from data acquired biweekly at a representative station (Madison Park) and are displayed in Figure 5. The value of \( t_d \) at the latitude of Lake Washington is readily obtained (from Tide Tables, for example) and ranges from 9 to 15 hours (see Figure 5). The net specific productivity at depth \( z \) was then calculated from the relation

\[
F(z,t;P,C) = F(0,t;P,C) \exp(-k_e(z)z),
\]

where the extinction coefficient \( k_e(z) \) varies with depth only as a result of self-shading:

\[
k_e(z) = k_1 + k_2 \int_0^z C(s) \, ds.
\]

The coefficients \( k_1 \) and \( k_2 \) were determined from a consideration of transparency data for Lake Washington and were found to be approximately 0.3 and 0.04, respectively.
In the present work, the effect of grazing by zooplankton has been omitted from the calculations because herbivore densities were unavailable at the time the computations were performed.

The sinking speed of algal cells was assigned a nominal value of 1/2 meter per day (see, for example, Smayda, 1970). The specific phosphate uptake rate \( V_m \) was expressed as a constant fraction \( B \) of the specific photosynthetic rate:

\[
V_m(z,t; P, C) = BF(z,t; P, C)
\]

where \( B \) denotes a representative value of the cellular phosphorus to chlorophyll a ratio (=3)(Strickland, 1965).

With the terms and coefficients defined as described above, equations (2) and (3) were solved numerically, beginning with specified depth distributions at the first of the year 1963. The space derivatives were expressed by centered differences, correct to the second order in \( \Delta z \), and evaluated midway between the \( n \)-th time step (where the variables are known) and the next step. Variables \( P \) and \( C \) in the coefficients were also evaluated midway between time steps by means of an iterative process. In summary, this procedure requires the iterative solution of two tridiagonal systems, which becomes a closed system of equations when the finite-difference forms of the boundary conditions are included. The solution of the systems is readily accomplished by using the Thomas algorithm.

In this very simple model, the actual "driving functions" of the system are the epilimnetic water temperatures, solar radiation, phosphate concentrations below the epilimnion, and the seasonal change in mixing coefficient. These input variables were prescribed on a weekly basis and the computations were performed with 50 time steps per week. The depth resolution of the model was taken to be one meter. All calculations were performed on a CDC 6400 at the University of Washington.

The results of the calculations for 1963 are presented in Figures 6 and 7. Figure 6 shows depth distributions of phosphate at approximately the same times of the year as the measured distributions in Figure 2. Figure 7 shows the time variations of the Secchi disc depth and mean chlorophyll a over the top 10 meters of the water column throughout the year. The over-simplified relationship between the growth rate and the nutrient uptake rate is partially responsible for the quantitative discrepancy between observed and calculated near-surface phosphate levels in late summer. However, the minimum Secchi disc depth and the peak values of mean chlorophyll concentration correspond reasonably well to those which were observed in midsummer of 1963 (Figure 3a).

Throughout much of the period of vigorous algal growth, near-surface gradients in the depth distribution of chlorophyll a are small enough so that, when \( z \) is not more than a few meters, the integral of \( C \) in
equation (7) can be replaced with $\bar{aC}$, where $\bar{C}$ denotes mean chlorophyll $a$ over the top 10 meters of the water column. An apparent Secchi disc depth $D_a$ can then be derived from the alternative form of equation (7):

$$D_a = \frac{1.7}{(k_1 + k_0 \bar{C})}.$$  

(9)

Figure 8 shows a plot of the apparent Secchi disc depth $D_a$ versus the mean chlorophyll $a$ concentration over the top 10 meters as calculated from equation (9). Not surprisingly, the trend of the curve follows closely the pattern of the data displayed by Edmondson (see Figure 4).

As a check of the sensitivity of the calculation to resident phosphate at depth, the computations were repeated using a constant phosphate concentration of 8 $\mu$g per liter ($PO_4$-P) below the thermocline. The results of these calculations are also shown in Figures 6 and 7 for comparison with data presented by Edmondson (1972a) for the year 1933 when phosphate input to the lake was low. The rather large discrepancy in the near-surface phosphate is due partly to the oversimplified relationship between growth and phosphate uptake rates and also to the inadequacy of the description of inflow, outflow, and turbulent diffusion of soluble phosphate. Despite the discrepancies, enough of the principal features of the data are reproduced by this simple model to justify the conclusion that it is feasible to construct continuous-variable models of algal-nutrient cycles in deep, stratified lakes.

A more realistic model would include a specification of the rate of inflow and distribution of externally supplied phosphate, the impact of zooplankton grazing, a description of boundary and bottom effects, and a treatment of vertical turbulent mixing consistent with available measurements of state variables, such as temperature. Models which include some of these effects are presently being developed. However, it is important to bear in mind that the hydrodynamic and biological processes which govern the growth of organisms in lakes are quite complicated and it is unlikely that numerical models of the sort which are currently available can serve as predictive devices. Nevertheless, such models can be useful as investigative tools in identifying and elucidating processes relevant to biological activity in lakes and assessing their relative importance under various circumstances.

ACKNOWLEDGMENTS

This work was supported in part by a National Science Foundation Grant to the Coniferous Forest Biome, International Biological Program, and in part by the Washington Sea Grant Program which is maintained by the National Oceanic and Atmospheric Administration, U.S. Department of Commerce. We are grateful to Professor W. T. Edmondson for discussing this problem with us and for providing some of his unpublished Lake Washington data obtained with support from the National Science Foundation. Thanks are also due to Mr. K. Claude Lee for his assistance with the computations and the preparation of this report.
REFERENCES


Figure 1  Map of Lake Washington.
Figure 2  Measured vertical distributions of phosphate in Lake Washington during the spring, summer, and fall of 1933 and 1963 (from Edmondson, 1972a).
Figure 3a  Mean chlorophyll $a$ in top 10 m during July and August (from Edmondson, 1972b).

Figure 3b  Depth of disappearance of Secchi disc during July and August. The horizontal line indicates the mean and the vertical line the range of the observations (from Edmondson, 1972b).
Figure 4. Relation between Secchi disc depth and mean chlorophyll $a$ in top 10 m for July and August, 1950, 1956/1959, 1962/1970 (from Edmondson, 1972a).
Figure 5. Variation of epilimnetic water temperature and hours of available sunlight during 1963.
Figure 6. Calculated distributions of phosphate in Lake Washington for 1933 and 1963.
Figure 7. Variation of calculated mean chlorophyll a in top 10 m and calculated apparent Secchi disc depth during 1933 and 1963.
Figure 8. Relation between Secchi disc depth and mean chlorophyll $a$ in top 10 m based on model calculations. The depth resolution was one meter.