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INTRODUCTION

A mathematical model was developed to simulate the nitrogen limited growth dynamics of phytoplankton in a stratified embayment. The representation of biological growth dynamics includes consideration of intracellular nutrient storage as well as the effects of temperature and light intensity. Several competing species can be represented simultaneously. Model hydrodynamics represent the effects of vertical mixing in the water column on the physical distribution of nutrients and phytoplankton. Sinking velocities of the cells are also included. The model was applied to Auke Bay, Alaska, and model responses are compared to data observed during the spring and summer of 1967.

GROWTH DYNAMICS

Biological Considerations

Nutrient enrichment studies have indicated that phytoplankton populations in natural environments are frequently limited by the unavailability of a particular nutrient in the water, but the relationship between the environmental concentration of this limiting nutrient and the instantaneous growth rate of the organisms is not completely understood. One of the factors influencing phytoplankton growth dynamics is the storage of intermediate metabolites in "pools" within the cells. This phenomenon has been observed frequently; however, little has been done to describe the mechanisms mathematically so that effects can be related to realistic problems.

Considerable success has been achieved in describing the uptake rates of nitrate and ammonia by Michaelis-Menten kinetics, and half-saturation constants (K_s) have been calculated for a number of phytoplankton species. (See Eppley et al., 1969; Eppley and Thomas, 1969; MacIsaac and Dugdale, 1969.) The relationship between environmental nutrient concentration and cell growth, on the other hand, does not appear to be so easily described. Observations over short periods of time have indicated, in some cases, relatively slow growth concurrent with rapid uptake and, in other cases, rapid growth in environments having low nutrient concentrations. (Eppley et al., 1969; Caperon, 1969.) The buildup of inorganic nitrogen and soluble amino acids in the cells has also been observed. (See Eppley and Coatsworth, 1968; Thomas and Krauss, 1955; Parsons et al., 1961.) Fuhs (1972) and others have noted similar responses with phosphorus uptake and observed the accumulation-rich storage compounds within the cells. Droop (1968) observed significant storage of vitamin B_{12} in the phytoplankton **Monochrysis lutheri.**

The traditional Monod (1949) model has been used extensively to describe phytoplankton dynamics. (See MacIsaac and Dugdale, 1969; Gates and Marlar, 1968; Shelef et al., 1971.) However, this one-compartment model lacks the flexibility to represent different rates of assimilation and growth or to accumulate intracellular storage products.

Attempts have been made to develop more realistic models. Caperon (1969) developed a two-compartment model that incorporated lag times in the uptake response of the cells to nitrate in the environment. Williams (1967) developed a two-compartment model that differentiates between "synthetic" and "structural/genetic" components. The model represents many interesting phenomena associated with growth dynamics but is not based on saturation kinetics. The excellent work by Droop (1968) results in a model distinguishing absorption, uptake, and growth rates. Growth rates are represented by saturation kinetics based on intracellular substrate concentrations. However, this model does not specifically distinguish between intracellular storage ("luxury substrate") and that which has been incorporated in the viable cell material.

The Biological Model

A model was developed to represent a phytoplankton population having the capacity to store nitrogen in a nitrate-limited environment. Only a general description of the model is presented here; a detailed description may be found in Grenney, Bella, and Curl (1973). Figure 1 is a schematic diagram of the nitrogen flow in the phytoplankton model. Environmental nitrate is taken up by the population and stored in an intracellular pool. This material is utilized by the cell to produce nitrogenous organics which provide the precursors for protein synthesis. The size of the phytoplankton population at any time is represented by the concentration of protein. Protein was chosen because of its close association with the major structural and functional components in a cell. It is the primary constituent of cell membranes, nuclear sap, and enzymes. Significant amounts of organic nitrogen may be excreted from the population to the environment. This material may be recycled as a nutrient source in two ways: Direct uptake by the cells, or bacterial decomposition to ammonia and nitrate. The latter recycling mechanism was not considered significant in this application. Reaction rates are based on Michaelis-Menten kinetics.

Interspecific Competition

Hutchinson (1967) suggested that the most important feature of phytoplankton associations is the presence of numerous species in each small sample taken from the environment. Usually one dominant species, one or two subdominant species, and, except in the case of extreme ecological conditions, at least several rare species, can be found in each small sample. This ability for numerous species to compete sucessfully in the same apparently homogeneous environment is a complex phenomenon which is not completely understood.

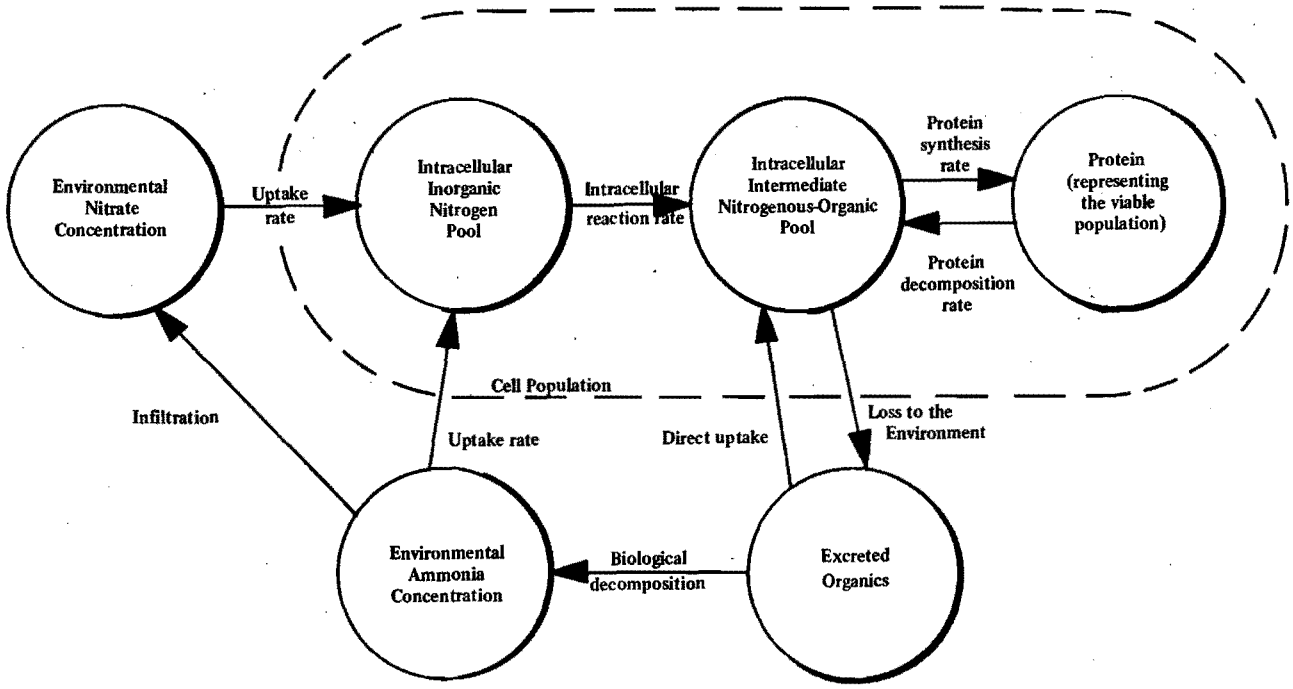


Figure 1. Schematic diagram showing the flow of nitrogen in the phytoplankton model.

Hutchinson (1967, p. 350) postulates: "In general we may expect that in the presence of suitable light and sources of C, N, P, S, K, Mg, Si, Na, Ca, Fe, Mn, Zn, Cu, B, Mo, Co, and V and the three vitamins thiamin, cyanocobalamin (B_{12}) and biotin nearly all algae can grow if the concentrations are correct and certain physical conditions are satisfied." It is reasonable to suppose that, for a specific combination of environmental equilibrium conditions, the one particular species having physiological characteristics that provide the greatest efficiency in energy and resource utilization will dominate the system. The concept of competitive exclusion (Hardin, 1960) postulates that the less efficient species will be gradually eliminated as resources required for their survival are depleted from the environment by the more efficient species. Coexistence at equilibrium conditions, therefore, could only occur when the more efficient species does not completely remove any one of the resources necessary to another less efficient species.

Several situations are conceivable in which coexistence could occur at some equilibrium condition. If the population size of the more efficient species is limited by some selective process, as, for example, selective predators or high sinking rates, then sufficient resources may remain to support a less efficient species. It is also possible that symbiotic relationships may exist between species, as in the case of the more efficient species requiring vitamins produced by a less efficient species. However, the large number and continual fluctuations of species found together in nature suggest that additional mechanisms are important in supporting such diversity (Hutchinson, 1961).

The continual variation in environmental conditions with time may be a major factor contributing to the observed phenomenon of numerous species coexisting in the same apparent isotropic environment. Thus, the species composition of a phytoplankton community never really attains competitive equilibrium, but is tending toward different equilibria at different times.

Many environmental forces are known to influence growth dynamics in natural systems. The intensities of these forces fluctuate widely, regularly or irregularly, with different periods and amplitudes, thus providing an unlimited number of intensity combinations as the system passes through time. At one point in time the combination of environmental conditions may be most suitable for one particular species and at another time most suitable for an entirely different species. Provided that a suitable combination occurs with sufficient frequency and duration, a species may be able to survive indefinitely.

Three species of competing algae were included in the model for this application. Coefficients for the growth parameters were obtained from the literature when available and otherwise were obtained by calibrating the model to observed data.

MODEL APPLICATION

The conceptual model discussed in the previous section was developed for systems in which exogenous influences (external environmental factors) were minimized. The systems were assumed to be at constant temperature and light in uniformly mixed environments. However, for realistic field applications, these biological models must be included as parts of larger models of the comprehensive system structure. Examples of methods for representing spatial distributions and variations in temperature, light, and turbulent mixing are presented in this section. The multi-compartment model previously discussed is used for growth dynamics of phytoplankton blooms. The model is applied to Auke Bay, Alaska, for purposes of example.

The general characteristics of Auke Bay, Alaska, are used in the model to represent the physical environment. However, no attempt has been made to quantitatively simulate a specific series of blooms.

Auke Bay is located in southeastern Alaska about 20 km northwest of the city of Juneau. It is a small embayment, with an area of approximately 11 km^2, off a system of large fjords which connect the open ocean. Depths of 40 to 60 m predominate in the upper end of the bay.

Water chemistry and biological data were collected at Auke Bay during the spring and summer of 1967 (Bruce, 1969). The water temperature, salinity, and certain nutrient concentrations were measured at the surface, 5, 10, 20, 30, and 50 m depths. These data revealed significant changes occurring in the water column during the spring bloom (April through June). The temperature increased progressively (from 3° to 13°C at the surface) and the salinity decreased (from 30 to 15 percent at the surface) resulting in a strongly stratified water column. During the same period, a succession of diatom blooms occurred. The nitrate, phosphate and silica concentrations in the upper 10 m were reduced markedly during the growth phase of the first bloom and remained at low levels through the summer. Nutrient concentrations below about 20 m were not significantly affected. The relative concentration of the nutrients in the epilimnion indicated that nitrate

was limiting. It is assumed for the purposes of this study that horizontal variations in the environment are negligible compared to the vertical gradients and that mechanisms in the bay can be generally represented by considering a typical water column.

The Model

General

The time-space distribution of materials suspended in the water of a channel with constant cross-sectional area is frequently represented by the following one-dimensional differential equation:

$$\frac{\partial C}{\partial T} = \frac{\partial}{\partial Z}\left(D \frac{\partial C}{\partial Z}\right) - \frac{\partial}{\partial Z}(UC) + S \quad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where C = concentration of material, T = time, Z = distance, D = dispersion coefficient, U = advective velocity and S = time rate of addition (or removal) of material. The first term on the right-hand side of Equation (1) is the dispersion term and represents the transport of materials due to mixing. The second term represents advective transport and the third term represents a source (or sink) for the material. An explicit, finite-difference scheme was developed for the solution of Equation (1). Following is a general summary of the model; however, specific techniques can be found in references (Grenney, 1972).

The water column is conceptualized as being divided into segments of equal depth ($\Delta Z = 1.5$m). Because no significant changes occurred in temperature, salinity, or nutrient concentration below 30 m, only the top 30 m of the water column were modeled. Each segment is a completely mixed subsystem and reactions within each segment are calculated over a finite-time interval ($\Delta T = 2$ hours).

During each ΔT the program proceeds through three specific steps. The first is to calculate the growth of each phytoplankton species and the resulting environmental nitrate removal independently in each segment. This step is accomplished by means of a subprogram of the multi-compartment model developed in the previous section. The second step is to advect the various phytoplankton species between segments in accordance with their respective sinking velocities. The third step is to disperse the environmental nitrate and the organisms between segments as a function of the dispersion coefficient at the interface. When suitable values ofΔX and ΔT are selected, this stepwise procedure has been shown to be efficient and to provide reasonably accurate solutions.

Growth

Growth as described by the multi-compartment model represents organisms growing at optimum levels of temperature and light in a laboratory. In the natural environment, however, variations in termperature and light will cause significant variations in the biological reaction rates.

Light

Light provides the ultimate source energy for the organisms and, therefore, affects the rates of the intracellular growth processes. There is evidence to indicate that the individual process rates are not affected to the same degree by light variations. Each of these reaction rates could be treated individually in the model if the proper functions were known; however, the influence of light on the net growth rate is considered to be of sufficient accuracy for the study. This is accomplished by multiplying the net growth rate at optimum light by a dimensionless factor, F_{ℓ}.

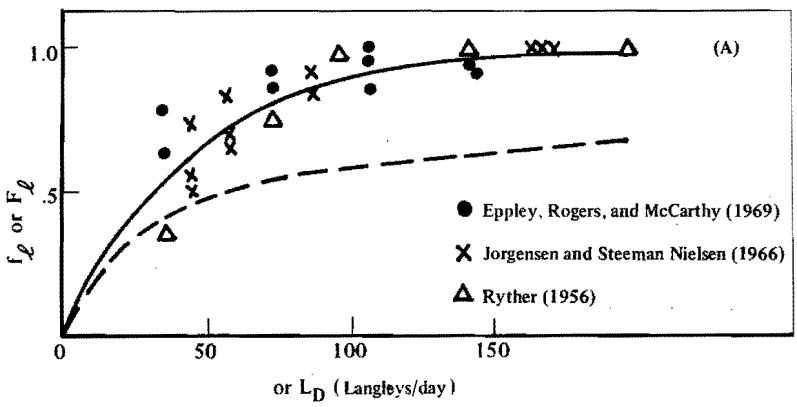
The attenuation of light with depth can be approximated by an exponential function:

$$\ell = \ell_s \exp(-kZ) \qquad (2)$$

where ℓ is the light intensity at depth Z and ℓ_s is the intensity at the surface. Auke Bay has a relatively shallow photic zone (1 percent light level) of about 12 meters which is represented in the model by using a value of k equal to 0.38 per meter.

Experimental evidence indicates that the photosynthetic rate increases with light intensity and will reach a constant, maximum rate for a particular range of intensities (Eppley et al., 1969; Ryther, 1956; Ryther and Yentsch, 1958; Sorokin and Krauss, 1958; Thomas, 1966; Yentsch and Lee, 1966). The photosynthetic rate is inhibited at light intensities above this optimum range. Some mathematical models have proposed linear variation of photosynthesis with light intensity (Steele, 1958; Riley, 1946); some have proposed a hyperbolic function (Chen, 1970; Middlebrooks and Porcella, 1971); and others have proposed an exponential function (DiToro et al., 1970). Relative photosynthetic rates for diatoms were calculated from the average curves reported in these references and are shown in Figure 2(A) where

$$f_{\ell} = \frac{P}{P_{max}} \qquad (3)$$



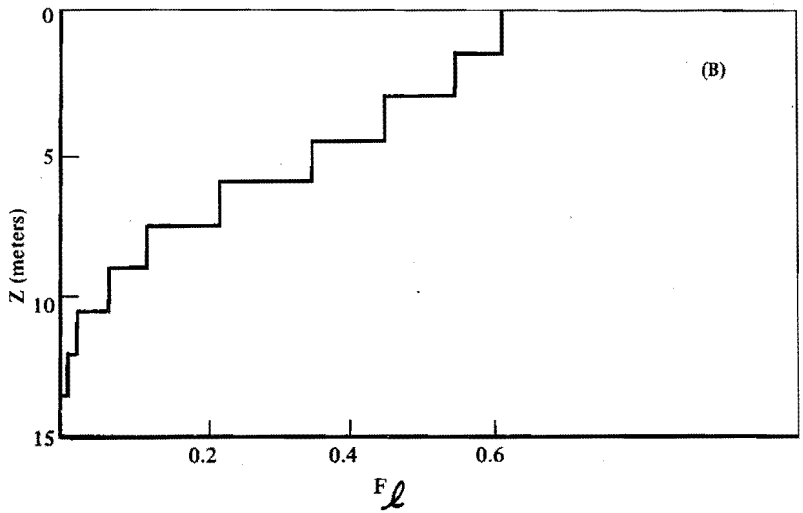


Figure 2. Relative effect of light intensity on growth.

P = photosynthetic rate at light intensity ℓ, and P_{max} = maximum photosynthetic rate. These data were fit by eye with the equation

$$f_\ell = 1 - \exp(-.0224\ell) \quad \ldots\ldots(4)$$

as shown by the solid line in Figure 2(A).

Figure 2(A) approximates the instantaneous growth rate, relative to the maximum, at a particular light intensity. During a 24-hour period the light intensity will vary drastically and, since instantaneous light intensities are not represented in the model, it is necessary to estimate an average daily value of f_ℓ from an average daily value of light intensity. The diurnal variation in light intensity on the surface can be approximated by the cosine law (Berry, 1945):

$$\ell = L \cos\left(\frac{\pi}{T_\ell} T\right), \quad -\frac{1}{2}T_\ell \leq T \leq \frac{1}{2}T_\ell \quad \ldots\ldots(5)$$

$$\ell = 0, \quad \text{otherwise} \quad \ldots\ldots(6)$$

where ℓ = instantaneous light intensity, T = time measured from local noon (days), T_ℓ = length of daylight period (days), L = light flux at noon (langleys per day). Substituting Equations (5) and (6) into Equation (4) gives:

$$f_\ell = 1 - \exp(-0.0224L \cos\theta), \quad -\frac{\pi}{2} \leq \theta \leq +\frac{\pi}{2} \quad \ldots\ldots(7)$$

$$f_\ell = 0 \quad \text{otherwise} \quad \ldots\ldots(8)$$

$$\theta = \frac{\pi}{T_\ell} T \quad \ldots\ldots(9)$$

The time average value of f_ℓ over a day can be represented as

$$F_\ell = \frac{\int_{-T_\ell/2}^{+T_\ell/2} \{1 - \exp[-0.22fL \cos(\frac{\pi}{T_\ell} T)]\}\, dT}{} \quad \ldots\ldots(10)$$

Equation (10) can be reduced to the form:

$$F_\ell = T_\ell - \frac{2T_\ell}{\pi} \int_0^{\pi/2} \exp(-0.224L \cos\theta)\, d\theta \quad \ldots\ldots(11)$$

The average length of the daylight period at Auke Bay during the study period was estimated to be about two-thirds day (Berry, 1945). The value of L can be estimated from the following equation:

$$L = \frac{L_D \pi}{2T_\ell} \quad \ldots\ldots(12)$$

where L_D = total langleys on the surface during the day. The integral in Equation (11) was solved numerically for various values of L_D and the results are shown as the dashed line in Figure 2(A).

The surface isolation (L_D) at Auke Bay during the study period averaged about 175 langleys per day (Bruce, 1969). Values of L_D were calculated at various depths by Equation (2) and then the dashed curve in Figure 2(A) was used to determine the average daily relative growth rate (F_ℓ). The resulting value of F_ℓ (shown in Figure 2(B)) were used in the model to represent the influence of light on the phytoplankton community.

Temperature

The variation in growth rate with temperature has been represented in mathematical models by exponential equations of the following general form:

$$\frac{\mu_1}{\mu_2} = K_\tau^{(\tau_1 - \tau_2)} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (13)$$

in which μ_1 and μ_2 = specific growth rates at temperatures τ_1 and τ_2 respectively and K_τ = a constant (Middlebrooks and Porcella, 1971; Riley and Von Arx, 1949). The justification for this approach is based on the observation that enzymatic reaction rates tend to increase exponential with temperature. A plot of saturated growth rate vs. temperature has been constructed from data from a number of sources (DiToro et al., 1970). These data were widely scattered, however, and no functional relationship was apparent.

The variation in growth rate as a function of temperature at constant light intensities has been reported for three species of tropical oceanic phytoplankton (Thomas, 1966), and the diatom, **Nitzchia closterium** (Spencer, 1966). These data were normalized by calculating the following dimensionless variables:

$$F_\tau = \frac{\mu}{\mu_{max}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (14)$$

$$\tau_r = \frac{\tau - \tau_0}{\tau_{max} - \tau_0} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (15)$$

where μ = growth rate occurring at temperature τ, μ_{max} = maximum possible growth rate, τ_{max} = the temperature at which μ_{max} first occurs, and τ_0 = temperature at which zero growth occurs. In some cases τ_0 and τ_{max} had to be extrapolated from the data. F_τ = the relative growth rate and τ_r = the fraction of the temperature range

between τ_0 and τ_{max}. Values of F_τ vs. τ_r are shown in Figure 3. These data were fit by the following second order polynomial,

$$F_\tau = 1.92\tau_r - 0.92\tau_r^2, \quad 0 \leq \tau \leq \tau_{max} \quad \ldots\ldots\ldots(16)$$

as shown by the solid curve in Figure 3.

The optimum temperature for cold water diatoms is probably in the neighborhood of 13° to 16°C (Hutchinson, 1967; Jorgensen and Nielsen, 1966) so values for τ_0 and τ_{max} were assumed to be 0° and 13°C respectively for the Auke Bay model. Average weekly temperatures were estimated from the field data for each segment in the water column at Auke Bay. These values were stored in a matrix in the computer memory for use in Equation (16) during each model run. The maximum temperature occurring in Auke Bay during the study period was 13°C, so the range of Equation (15) is sufficiently large.

Convection and Dispersion

If the organisms have a negative buoyancy, they will have a downward velocity relative to the water. This sinking velocity is designated by the symbol U in Equation (1) and represented the advection of organisms between segments in the model. Phytoplankton sinking velocities are related to the physiological state of the organism and to water density (Lund, 1959; Munk and Riley, 1952; Riley, 1965). However, at this time a functional relationship between cell storage and sinking velocities has not been defined and, therefore, U will be considered constant over the study period.

Methods have been developed to estimate the dispersion coefficients (D) at various depths in the water column from changes in the temperature or salinity profiles (Bella and Grenney, 1972; Orlob and Selna, 1970). These methods are based on the assumption that all of the vertical transport of heat or salinity in the water column can be represented by a diffusive-type expression. Consider any cross section in the water column at depth Z. Diffusive transport can be expressed by:

$$-\left(D \frac{\partial \theta}{\partial Z}\right)_Z = R_Z \quad \ldots\ldots\ldots(17)$$

where Z is the depth, Θ is the temperature (salinity), and R_Z is the rate change in total heat (salt mass) below depth Z. As an approximation one may write:

$$-(\overline{D})_Z \frac{[\theta_{(Z+\Delta Z/2)} - \theta_{(Z-\Delta Z/2)}]}{\Delta Z} = \frac{H_{(t)} - H_{(t+\Delta t)}}{\Delta t} \quad \ldots(18)$$

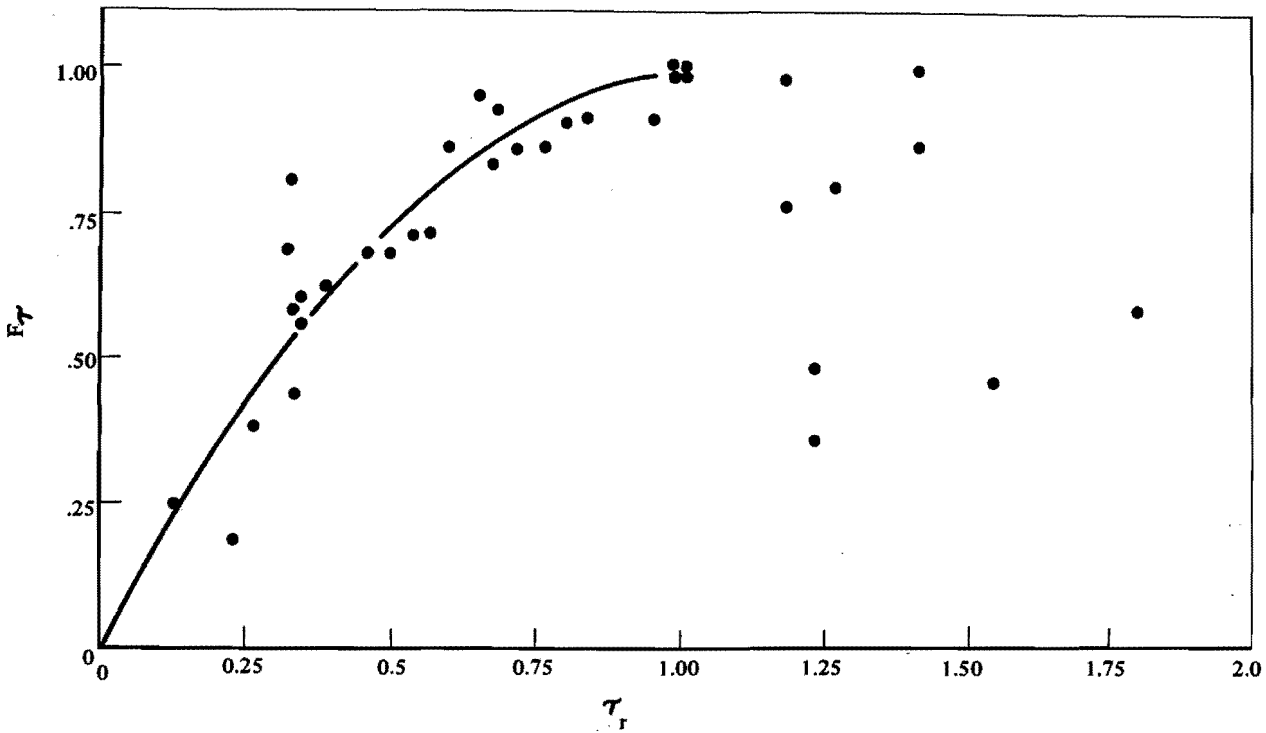


Figure 3. Relative effect of temperature on growth.

where Δt is a finite time interval, $H_{(t)}$ is the total heat (salt mass) below depth Z at the beginning of time interval Δt, and $H_{(t+\Delta t)}$ is the total heat below depth Z at the end of the time interval. The bars denote values averaged over the time interval. It is assumed that flux in or out of the water column can occur only at the upper boundary, i.e., the top segment.

Dispersion coefficients were calculated at each water column segment from average weekly temperature and salinity data for Auke Bay. Changes in the salinity profile did not occur in sufficient magnitude to calculate D until the first of May. Values of D calculated from the temperature profile from May to July were generally one and a half to three times larger than corresponding values calculated from the salinity profile. This relationship might be expected because no attempt was made to account for changes in the temperature profile due to the penetration of radiant energy. Also, error is undoubtedly introduced by the assumption in the estimating procedure that no horizontal flux into or out of the water column occurs except in the top segment. Values of D estimated from the salinity profile were used in the model for the period May to July. Values of D estimated from the temperature profile were used for the month of April. These values were adjusted down by factors of three-fourths to one-half in order to be consistent with the values calculated from the salinity data. The average weekly dispersion coefficients for each segment were stored in an array in the computer memory for use during the model runs.

Profiles were calculated from the estimated dispersion coefficients for the given boundary conditions in order to check the estimating procedure. Comparisons were made between the profile used to estimate the coefficients and the profile generated by the estimated coefficients. The salinity profiles agreed within 3 percent and the temperature profiles generally within 20 percent. The dispersion coefficients occurring at mid-April, mid-May and mid-June are shown in Figure 4. The curves show the same general shape as some estimated by similar methods for lakes and reservoirs (Bella, 1970; Orlob and Selna, 1970). In general, the dispersion coefficients estimated for Auke Bay are about four to five times larger than estimated for Lake Sammamish, Washington (Bella, 1970). The increasing stability of the water column through the spring bloom is indicated by the decreasing dispersion coefficients in Figure 4.

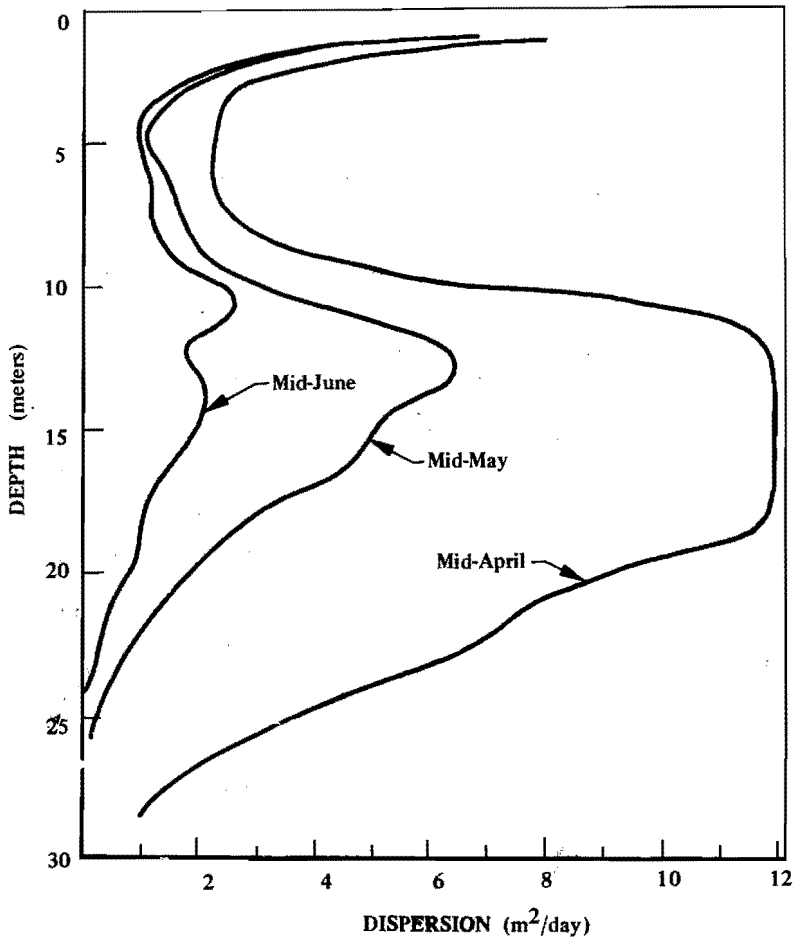


Figure 4. Vertical distribution of calculated dispersion coefficients in Auke Bay.

MODEL RESPONSES

Several runs were conducted in order to observe the time and space response of the model. The top 30 meters of a water column were modeled using a finite-time interval ΔT of two hours and segment depths ΔZ of one and one-half meters. The average weekly dispersion coefficients and temperatures estimated from Auke Bay data for each segment were stored in arrays in computer memory. A uniform daily surface insolation of 175 langleys and a 12 m photic zone were assumed to approximate Auke Bay conditions during the study period. The phytoplankton population was described by the multi-compartment model discussed in the previous section. Also the influence of light and temperature on growth are represented by the methods discussed previously.

The model indicated that phytoplankton populations decrease rapidly with increasing sinking velocity. For example, an increase in U from 0.33 to 1.0 meters per day results in an almost 67 percent decrease in the peak concentration. In all cases, the environmental nitrate concentrations were reduced to very low levels in the upper waters of the photic zone. Low sinking velocities resulted in significantly earlier blooms than high sinking velocities. A phytoplankton population cannot increase when the organisms are sinking out of the photic zone at an average rate equal to or greater than the growth rate. This condition apparently exists during the month of April for the case when $U = 1.0$ m/day. However, as the water warms the growth rate increases and apparently overtakes the sinking rate during the first week in May. When nutrients are depleted in the upper waters the population decreases rapidly.

Early in the season, the growth rates of the populations are limited by the cold temperatures. The model indicates that during these conditions the phytoplankton have a tendency to store large amounts of nutrient as N_1 and N_2. These intracellular nutrient pools are utilized for

growth as the water warms, and when they are depleted the growth rate declines. Intracellular storage reaches 75 percent of total cellular nitrogen when the growth rate is limited by temperature in nutrient rich water. As the season progresses, the water warms and the environmental nitrate decreases causing reduction in storage.

The combination of temperature, light, sinking-velocities may have a significant influence on the vertical distribution of the population especially during periods of low nutrient supply. As the season progresses nutrients are depleted in the upper segments of the water column and the growth rate falls below the sinking rate resulting in a decrease in the local population concentration. However, warming tends to increase the growth rate at the depths where intracellular nitrogen is available for growth and, thus, the maximum population has a tendency to occur at greater depths as the season progresses.

The Auke Bay spring blooms and nitrate concentrations for the spring of 1967 (Bruce, 1969) are shown in Figure 5. The nitrate was depleted in the surface water during the first bloom and remained at very low levels for the remainder of the spring. The nitrate concentrations at 10 m (near the bottom of the photic zone) decreased gradually indicating that nitrate at this depth provided a nutrient source during the entire sequence of blooms. Nitrate concentrations were not significantly changed at 20 m.

The solid line in Figure 5 is the model response for the total cell concentration in a two species system. Comparison of the model response with the field measured total cell count indicates reasonable agreement during the April-May bloom.

The nitrate concentrations at the surface and 10 m are very similar between the model and the observed values. At 20 m depth, the model shows significantly more change than the field data, a condition which might also be due to exaggerated biological activity in the model at low temperatures.

A closer correspondence between the model and the data could probably be obtained if the following information were known about the phytoplankton species in Auke Bay:

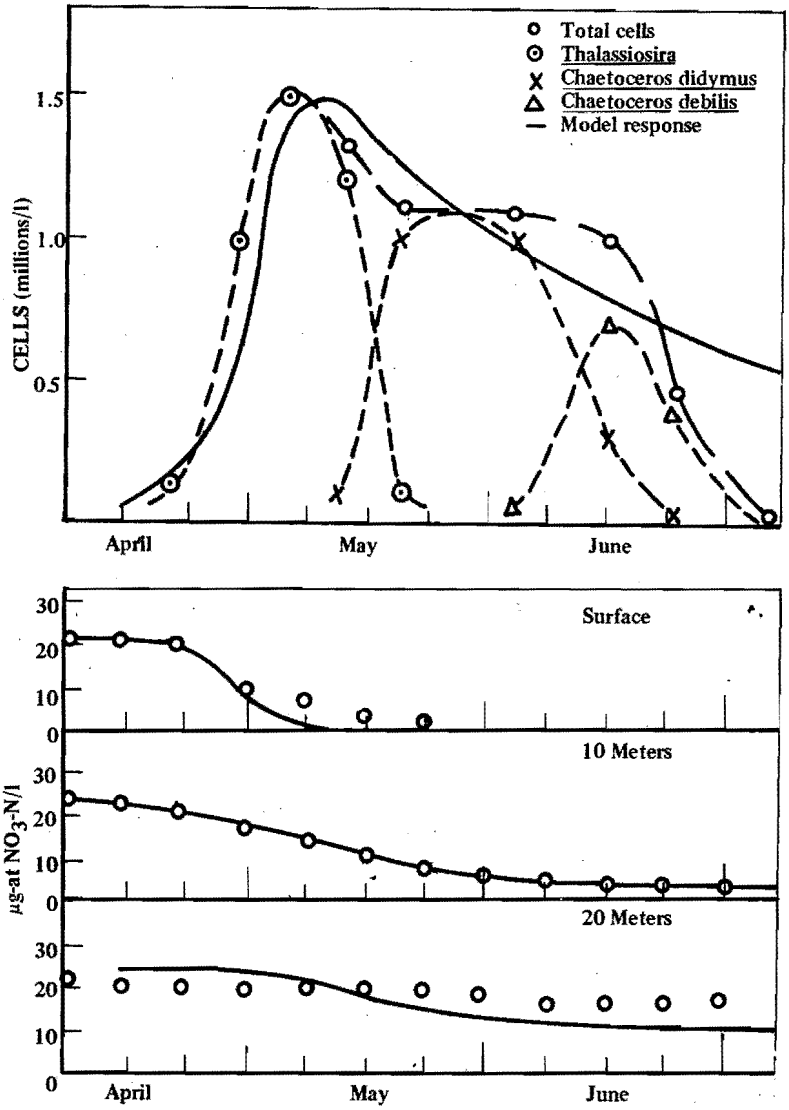


Figure 5. Auke Bay blooms, Spring 1967.

1. Better estimates of the parameters representing storage and growth characteristics of the specific phytoplankton in Auke Bay.

2. More knowledge about sinking velocities and their relationship to intracellular storage.

3. The inclusion of grazing in the model. Significant numbers of zooplankton were observed at the time of population decrease. The fact that grazers are not represented in the model may account for the discrepancy between field observations and model response toward the end of June.

CONCLUSIONS

Ecosystems are systems of living organisms in a physical chemical environment which have developed and adapted over long periods of time. As such, they present unique problems for quantitative description and prediction. Mathematical models can be powerful tools for analyzing these systems. Models are constructed for particular purposes and are subject to numerous limitations. Although it can be concluded that all models are less than perfect, their evaluation should only be based on characteristics in relation to their proposed use. In this regard an optimal balance between accuracy and practicability is sought, and, in fact, is often approached.

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