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**A Dynamic Model of
Phytoplankton Populations
in Natural Waters**

by

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I. Introduction

The quality of natural waters can be markedly influenced by the growth and distribution of phytoplankton. Utilizing radiant energy, these microscopic plants assimilate inorganic chemicals and convert them to cell material which, in turn, is consumed by the various animal species in the next trophic level. The phytoplankton, therefore, are the base of the food chain in natural waters and their existence is essential to all aquatic life.

The quality of a body of water can be adversely affected if the population of phytoplankton becomes so large as to interfere with either water use or the higher forms of aquatic life. In particular, high concentration of algal biomass cause large diurnal variations in dissolved oxygen which can be fatal to fish life. Also the growths can be nuisances in themselves especially when they decay and either settle to the bottom or accumulate in windrows on the shoreline. Phytoplankton can cause taste and odor problems in water supplies and in addition, contribute to filter clogging in the water treatment plant.

The development of large populations of phytoplankton and, in some cases, larger aquatic plants can be accelerated by the addition of nutrients which result from man's activities or natural processes. The resulting fertilization provides more than ample inorganic nutrients with the resulting development of excessive phytoplankton. This sequence of events is commonly referred to as eutrophication.

Generally, the management of water systems subjected to accelerated eutrophication because of waste discharges has been largely subjective. Extensive programs of nutrient removal have been called for with little or no quantitative predictions of the effects of such treatment programs. A quantitative methodology is required to estimate the effect of proposed treatment programs that are planned to restore water quality, or to predict the effects of expected future nutrient discharges. This methodology should include a model of the phytoplankton population which approximates the behavior of the phytoplankton in the water body of interest and, therefore, can be used to test the effects of the various control procedures available. In this way, rational planning and water quality management can be instituted with at least some degree of confidence that the planned results will actually be achieved.

This paper presents a phytoplankton population model in natural waters. This model is constructed on the basis of the principle of conservation of mass. This is an elementary physical law which is satisfied by macroscopic natural systems. The use of this principle is dictated primarily by the lack of any more specific physical laws which can be applied to these biological systems. An alternate conservation law, that of conservation of energy, can also be used. However, the details of how mass is transferred from species to species is better understood than the corresponding energy transformations. The mass interactions relate among other factors to the kinetics of the populations and it is to this that the majority of the paper is devoted to exploring.

Conservation of mass has been successfully applied to the modeling of the dissolved oxygen distribution in natural waters as well as the distribution of salinity and other dissolved substances. The resulting models have proved useful in guiding engineering and management decisions concerned with the efficient utilization of the water resources and the protection of their quality. It is felt that the phytoplankton model presented herein can serve a similar purpose by providing a basis for predicting the effects of nutrient control programs on the eutrophication of natural waters.

Thus, the primary purpose of this paper is to introduce a quantitative model of phytoplankton population dynamics in natural waters. It is within this problem context that the simplifications, assumptions, and generally the structure of the model is formulated. An attempt is made to make the equations representative of the biological mechanisms while still retaining a sufficient simplicity so that the result is tractable and useful.

II. Review of Previous Models

The initial attempts to model the dynamics of a phytoplankton population have been based on a version of the law of conservation of mass in which the hydrodynamic transport of mass is assumed to be insignificant. Let $P(t)$ be the concentration of phytoplankton mass at time t in a suitably chosen region of water. The principle of conservation of mass can be expressed as a differential equation

$$\frac{dP}{dt} = S$$

where S is the net source or sink of phytoplankton mass within the region. If hydrodynamic transport is not included then the rate at which P increases or decreases depends only on the internal sources and sinks of phytoplankton in the region of interest.

The form of the internal sources and sinks of phytoplankton is dictated by the mechanisms which are assumed to govern the growth and death of phytoplankton. Fleming (1939)⁽⁴⁴⁾ postulated that spring diatom flowering in the English Channel is described by the equation:

$$\frac{dP}{dt} = [a - (b + ct)] P$$

where P is the phytoplankton concentration, a is a constant growth rate and $(b + ct)$ is a death rate due to the grazing of zooplankton. The zooplankton population which is increasing due to its grazing results in an increasing death rate which is approximated by the linear increase of the death rate as a function of time.

A less empirical model has been proposed by Riley⁽⁴⁴⁾ (1946) based on the equation:

$$\frac{dP}{dt} = [P_h - R - G] P$$

where P_h is the photosynthetic growth rate, R is the endogenous respiration rate of the phytoplankton and G is the death rate due to zooplankton grazing. A major improvement in Riley's equation is the attempt to relate the growth rate, the respiration rate, and the grazing to more fundamental environmental variables such as incident solar radiation, temperature, extinction coefficient, and observed nutrient and zooplankton concentration. As a consequence the coefficients of the equations are time variable since the environmental parameters vary throughout the year. This precludes an analytical solution to the equation and numerical integration methods must be used. Three separate applications (40, 41, 47) of these equations to the near-shore ocean environment have been made and the resulting agreement with observed data is quite encouraging.

A complex set of equations, proposed by Riley, Stommel and Bumpus⁽⁴⁶⁾ (1949) first introduced the spatial variation of the phytoplankton with respect to depth into the conservation of mass equation. In addition, a conservation of mass equation for a nutrient (phosphate) was also introduced, as well as simplified equations for the herbivorous and carnivorous zooplankton concentrations. The phytoplankton and nutrient equations were applied to twenty volume elements which extended from the surface to well below the euphotic zone. In order to simplify the calculations a temporal steady-state was assumed to exist in each

volume element. Thus the equations apply to those periods of the year during which the dependent variables are not changing significantly in time. Such conditions usually prevail during the summer months. The results of these calculations were compared to observed data and again the results were encouraging.

Steele⁽⁵⁵⁾ (1956) found that the steady-state assumption did not apply to the seasonal variation of the phytoplankton population. Instead he used two volume segments to represent the upper and lower water levels and kept the time derivatives in the equations. Thus both temporal and spatial variations were considered. In addition, the differential equations for phytoplankton and zooplankton concentration were coupled so that the interactions of the populations could be studied, as well as the nutrient-phytoplankton dependence. The coefficients of the equations were not functions of time however so that the effects of time varying solar radiation intensity and temperature were not included. The equations were numerically integrated and the results compared to the observed distribution. Steele applied similar equations to the vertical distribution of chlorophyll in the Gulf of Mexico.⁽⁵⁶⁾

The models proposed by Riley et. al. and Steele are basically similar. Each consider the primary dependent variables to be the phytoplankton, zooplankton and nutrient concentration. A conservation of mass equation is written for each species and the spatial variation is incorporated by considering finite volume elements which interact due to vertical eddy diffusion and downward advective transport of the phytoplankton. Their equations differ in some details (for example,

the growth coefficients that were used and the assumptions of steady state) but the principle is the same. In addition, these equations were applied by the authors to actual marine situations and their solutions compared to observed data. This is a crucial part of any investigation discussion wherein the assumptions that are made and the approximations that are used are difficult to justify a priori.

The models of both Riley and Steele have been reviewed in greater detail by Riley (44) in a discussion of their applicability and possible future development. The difficulties encountered in formulating simple theoretical models of phytoplankton-zooplankton population models were discussed by Steele(57).

Other models have been proposed which follow the outlines of the equations discussed above. Equations with parameters that vary as a function of temperature, sunlight, and nutrient concentration have been presented by Davidson and Clymer(12) and simulated by Cole(8). A set of equations which model the population of phytoplankton, zooplankton and a species of fish in a large lake have been presented by Parker(38). The application of the techniques of phytoplankton modeling to the problem of eutrophication in rivers and estuaries has been proposed by Chen and Orlob(7). The interrelations between the nitrogen cycle and the phytoplankton population in the Potomac Estuary has been investigated using a feed-forward - feed-back model of the dependent variable, which interact linearly following first order kinetics(62).

The formulations and equations presented in the subsequent sections are modifications and extensions of previously presented

equations which incorporate some additional physiological information on the behavior of phytoplankton and zooplankton populations. In contrast to the majority of the applications of phytoplankton models which have been made previously, the equations presented in the subsequent sections are applied to a relatively shallow reach of the Sacramento River and the estuary further downstream. The motivation for this application is an investigation of the possibility of excessive phytoplankton growths as environmental conditions and nutrient loadings are changed in this area. Thus the primary thrust of this investigation is to produce an engineering tool which can be used in the solution of engineering problems to protect the water quality of the region of interest.

III. Phytoplankton System Interactions

The major obstacle to a rigorous quantitative theory of phytoplankton population dynamics is the enormous complexity of the biological and physical phenomena which influence the population. It is necessary, therefore, to idealize and simplify the conceptual model so that the result is a manageable set of dependent systems or variables and their interrelations. The model considered in the following sections is formulated on the basis of three primary dependent systems: the phytoplankton population, whose behavior is object of concern; the herbivorous zooplankton population, which are the predators of the phytoplankton, that is, they utilize the available phytoplankton as a food supply; and the nutrient system, which represents the nutrients, primarily inorganic substances, that are required by the phytoplankton during growth. These three systems are affected not only by their interactions, but also by external environmental variables. The three principal variables considered in this analysis are temperature, which influences all biological and chemical reactions, dispersion and advective flow which are the primary mass transport mechanisms in a natural body of water, and solar radiation, the energy source for the photosynthetic growth of the phytoplankton.

In addition to these external variables, the effect of man's activities on the systems is felt predominately in the nutrient system for which sources of the necessary nutrients may be the result of, for example, inputs of wastewater from municipal and industrial discharges or agricultural runoff. The man-made waste loads are in most cases the primary control variables which are available to affect changes in the phytoplankton and zooplankton systems. A schematic representation of these systems and their interrelations is presented in fig. 1.

In addition to the conceptual model which isolates the major interacting systems, a further idealization is required which sets the lower and upper limits of the temporal and spatial scales being considered. Within the context of the problem of eutrophication and its control, the seasonal distribution of the phytoplankton is of major importance so that the lower limit of the temporal scale is on the order of days. The spatial scale is set by the hydrodynamics of the water body being considered. For example, in a tidal estuary the spatial scale is on the order of miles whereas in a small lake it is likely a good deal smaller. The upper limits for the temporal and spatial extent of the model are dictated primarily by practical considerations such as the length of time for which adequate information is available and the size of the computer being used for the calculations.

These simplifying assumptions are made primarily on the basis of an intuitive assessment of the important features of the systems being considered and the experience gained by previous attempts to address these and related problems in natural bodies of water. The basic principle to be applied to this conceptual model, which can then be translated into mathematical terms, is that of conservation of mass.

IV. Conservation of Mass

The principle of conservation of mass is the basis upon which the mathematical development is structured. Alternate formulations, such as those based on the conservation of energy, have been proposed. However, conservation of mass has proved a useful starting point for many models of the natural environment.

The principle of conservation of mass simply states that the mass of the substance being considered within an arbitrarily selected volume must be accounted for by either mass transport into and out of the volume or as mass produced or removed within the volume. The transport of mass in a natural water system is due primarily to two phenomena: dispersion, which is caused by tidal action, density differences, turbulent diffusion, wind action, etc; and advection due to a unidirectional flow, for example the fresh water flow in a river or estuary, or the prevailing currents in a bay or a near shore environment. The distinction between the two phenomena is that, over the time scale of interest, dispersive mass transport mixed adjacent volumes of water so that a portion of the water in adjacent volume elements is interchanged and the mass transport is proportional to the difference in concentrations of mass in adjacent volumes. Advective transport, however, is transport in the direction of the advective flow only. In addition to the mass transport phenomena, mass in the volume can increase due to sources within the volume. These sources represent the rate of addition or removal of mass per unit time per unit volume by chemical and biological processes.

A mathematical expression of conservation of mass which includes the terms to describe the mass transport phenomena and the source term is a

partial differential equation of the following form:

$$\frac{\partial P}{\partial t} = \nabla \cdot E \nabla P - \nabla \cdot Q P + S_P \quad (1)$$

where $P(x, y, z, t)$ is the concentration of the substance of interest, e.g. phytoplankton biomass, as a function of position and time; E is the diagonal matrix of dispersion coefficients; Q is the advective flow rate vector; S_P is the vector whose terms are the rate of mass addition by the sources and sinks; and ∇ is the gradient operator. This partial differential equation is too general to be solved analytically and numerical techniques are used in its solution.

An effective approximation to eq. (1) is obtained by segmenting the water body of interest into n volume elements of volume V_j ; and representing the derivatives in eq. (1) by differences. Let V be the $n \times n$ diagonal matrix of volumes V_j ; A , the $n \times n$ matrix of dispersive and advective transport terms; S_P , the n vector of source terms S_{Pj} , averaged over the volume V_j ; and P , the n vector of concentrations P_j , which are the concentrations in the volumes; Then the finite difference equations can be expressed as a vector differential equation:

$$\dot{VP} = AP + VS_P \quad (2)$$

where the dot denotes a time derivative. The details of the application of this version of the dispersion advection equation to natural bodies of water has been presented by Thomann⁽⁶¹⁾ and reviewed by O'Connor et al.⁽³⁵⁾

The main interest in this report is centered on the source terms S_{Pj} for the particular application of these equations to the phytoplankton population in natural water bodies. It is convenient to express the

source term of phytoplankton, S_{pj} , as a difference between the growth rate, G_{pj} , of phytoplankton and their death rate D_{pj} , in the volume V_j . That is:

$$S_{pj} = (G_{pj} - D_{pj}) P_j \quad (3)$$

where G_{pj} and D_{pj} have units $[\text{day}^{-1}]$. The subscript P identifies the quantities as referring to phytoplankton; the subscript j refers to the volume element being considered. The balance between the magnitude of the growth rate and death rate determines the rate at which phytoplankton mass is created or destroyed in the volume element V_j . Thus the form of the growth and death rates as functions of environmental parameters and dependent variables is an important element in a successful phytoplankton population model.

V. Phytoplankton Growth Rate

The growth rate of a population of phytoplankton in a natural environment is a complicated function of the species of phytoplankton present and their differing reactions to solar radiation, temperature and the balance between nutrient availability and phytoplankton requirements. The complex and often conflicting data pertinent to this problem has been recently reviewed by Hutchinson (1967)⁽²³⁾, Strickland (1965)⁽⁵⁹⁾, Lund (1965)⁽²⁸⁾ and Rayment (1963)⁽³⁹⁾. The available information is not sufficiently detailed to specify the growth kinetics for individual phytoplankton species in natural environments. Hence, in order to accomplish the task of constructing a growth rate function a simplified approach is followed. The problem of different species and their associated nutrient and environmental requirements is not addressed. Instead the population is characterized as a whole by a measurement of the biomass of phytoplankton present. Typical quantities used are the chlorophyll concentration of the population; the number of organisms per unit volume; or the dry weight of the phytoplankton per unit volume⁽⁶⁵⁾. With a choice of biomass units established, the growth rate expresses the rate of production of biomass as a function of the important environmental variables. The environmental variables to be considered below are light, temperature and the various nutrients which have been shown to be necessary for phytoplankton growth.

Light and Temperature

Consider a population of phytoplankton, either a natural association or a single species culture, and assume that the optimum or saturating light intensity for maximum growth rate of biomass is present and illuminates all the cells, and further that all the necessary nutrients are

present in sufficient quantity so that no nutrient is in short supply. For this condition the growth rate that is observed is called the maximum or saturated growth rate, K' . Measurements of K' (base e) as a function of temperature are shown in fig. 2 and listed in Table I. The experimental conditions under which these data were collected appear to meet the requirements of optimum light intensity and sufficient nutrient supply. The data presented are selected from larger groups of reported values and they represent the maximum of these reported growth rates. The presumption is that these large values reflect the maximum possible growth rates achievable. From an ecological point of view it is necessary to consider the species most able to compete, and, in terms of growth rate, it is the species with the largest growth rate which will predominate. A straight line fit to this data appears to be a crude but reasonable approximation of the data relating saturated growth rate K' to temperature, T :

$$K' = K_1 T \quad (4)$$

where K_1 has values in the range $0.10 \pm 0.025 \text{ day}^{-1} \text{ } ^\circ\text{C}^{-1}$. This coefficient indicates an approximate doubling of the saturated growth rate for a temperature change from 10°C to 20°C in accordance with the generally reported temperature dependence of biological growth rates. The optimum temperature for algal growth appears to be in the range between 20° and 25°C although thermophilic strains are known to exist⁽¹⁹⁾. At higher temperatures there is usually a suppression of the saturated growth rate and the straight line approximation is no longer valid. It should also be noted that the scatter in the data in fig. 2 is sufficiently large so that the linear dependence on temperature and also the magnitude of K' can vary considerably in particular situations.

In the natural environment the light intensity to which the phytoplankton are exposed is not uniformly at the optimum value but it varies as a function of depth due to the natural turbidity present and as a function of time over the day. Thus the phytoplankton in the lower layers are exposed to intensities below the optimum and those at the surface may be exposed to intensities above the optimum so that their growth rate would be inhibited. Figure 3^{b,c,d} from Ryther⁽⁴⁹⁾ are plots of the photosynthesis rate normalized by the photosynthesis rate at the optimum or saturating light intensity versus the light intensity, I , incident on the populations. Figure 3a is a plot of function

$$F(I) = \frac{I}{I_s} \exp \left[-\frac{I}{I_s} + 1 \right] \quad (5)$$

for $I_s = 2000$ ft. - candles, proposed by Steele⁽⁵⁷⁾ to describe the light dependence of the growth rate of phytoplankton.

The similarity between this function and data from Ryther is sufficient to warrant the use of this expression to express the influence of non-optimum light intensity on the growth rate, of phytoplankton. Other workers have suggested different forms for this relationship⁽⁵⁰⁾⁽⁶⁴⁾. These variations approximately follow the shape of eq. (5) for low light intensities but differ for the region of high light intensities, usually by not decreasing after some optimum intensity is reached. In particular, Tamiya et. al.⁽⁶⁰⁾ have investigated the growth rate of Chlorella ellipsoidea to various light and temperature regimes. The saturated growth rates as a function of temperature are included in fig. 2. The influence of varying light intensity fits the function:

$$F(I) = \frac{I}{I + K'/\alpha} \quad (6)$$

where K' is the saturated growth rate and α is a constant ($\alpha = 0.45 \text{ day}^{-1} \text{ kilolux}^{-1}$). However since K' is a function of temperature the saturating light intensity for eq. (6) is also a function of temperature. Similar data obtained by Sorokin et al.⁽⁵³⁾ using a high temperature strain of Chlorella pyrenoidosa support the temperature dependence of the saturating light intensity for chlorella. Therefore in using eq. (5) a temperature dependent light saturation intensity may be warranted.

At this point in the analysis the effect of the natural environment on the light available to the phytoplankton must be included. Eq. (5) expresses the reduction in the growth rate due to non-optimum light intensity. This expression can therefore be used to calculate the reduction in growth rate to be expected at any intensity. However, this is too detailed a description for conservation of mass equations which deal with homogeneous volume elements, V_j , and the growth rate within these elements. What is required is averages of the growth rate over the volume elements.

In order to calculate the light intensity which is present in the volume V_j , the light penetration at the depth of water where V_j is located must be evaluated. The rate at which light is attenuated with respect to depth is given by the extinction coefficient k_e . That is, at a depth z , the intensity at that depth, $I(z)$, is related to the surface intensity, I_0 , by the formula:

$$I(z) = I_0 \exp(-k_e z) \quad (7)$$

where $z = 0$ is the water surface and is positive downward. Thus the reduction of the saturated growth rate at any depth z due to the non-

optimum light intensity present is given by eq. (7), substituted into eq. (5):

$$F [I(z)] = \frac{I_0 e^{-k_e z}}{I_s} \exp \left[- \frac{I_0 e^{-k_e z}}{I_s} + 1 \right] \quad (8)$$

To apply this equation to the finite volume elements, within which it is assumed that the phytoplankton concentration is uniform, it is necessary to average this reduction factor throughout the depth of the volume element V_j . Let H_{0j} and H_{1j} be the depths of the surface and bottom respectively of the volume element V_j . For example if the volume element V_j extends from the water surface to the bottom of the body of water, then $H_{0j} = 0$ and H_{1j} is the water depth at the location of V_j . For the sake of simplicity, it is assumed that this is the case. If $H_{0j} \neq 0$ a straightforward generalization of the following average is required.

In addition to an average over depth, it is also expedient to average the phytoplankton growth rate over a time interval. Since the time scale within which this analysis is addressed is the week-to-week change in the population over a year, a daily average is appropriate. For simplicity, it is assumed that the incident solar radiation as a function of time over a day is given by the function:

$$\begin{aligned} I_0(t) &= I_a & 0 < t < f \\ &= 0 & f < t < 1 \end{aligned} \quad (9)$$

where f is the daylight fraction of the day (i.e. the photo period) and I_a is the average incident solar radiation intensity during the photo period.

Let r_j be the reduction in growth rate due to nonoptimum light conditions in volume V_j , averaged over depth and time. Then r_j is given by

$$r_j = \frac{1}{H_j} \int_0^{H_j} \frac{1}{T} \int_0^t \frac{I_a e^{-k_{ej}z}}{I_s} \exp \left[\frac{-I_a e^{-k_{ej}z}}{I_s} + 1 \right] dt dz \quad (10)$$

where $T = 1$ day, the time averaging interval, and $H_{1j} = H_j =$ the depth of segment V_j and k_{ej} is the extinction coefficient in V_j . The result is

$$r_j = \frac{e t}{k_{ej} H_j} e^{-\alpha_{1j}} - e^{-\alpha_{0j}} \quad (11)$$

where

$$\alpha_{1j} = \frac{I_a}{I_s} e^{-k_{ej} H_j} \quad (12)$$

$$\alpha_{0j} = \frac{I_a}{I_s}$$

The integral given by eq. (10) is a form of an integral used by Steeman Nielson (1952), Talling (1957), Ryther and Yrmtsch (1957), Vollenweider (1958)⁽⁶⁴⁾, and, in particular, Steele (57), for the purpose of relating an instantaneous rate (e.g. growth, photosynthesis, etc.) to an average day rate and an average depth rate.

The reduction factor r_j is a function of the extinction coefficient k_{ej} of the volume V_j . However the extinction coefficient is a function of the phytoplankton concentration present if their concentration is large.

Thus an important feedback mechanism exists which can have a marked effect on the growth rate of phytoplankton. As the concentration of phytoplankton in a volume element increases, the extinction coefficient, particularly at the green wavelengths, starts to increase. This mechanism is called self-shading. The most straightforward approach to including this effect into the growth rate expression is to specify the extinction coefficient as a function of the phytoplankton concentration:

$$k_{ej} = k'_{ej} + h(P_j) \quad (13)$$

where k'_{ej} is the extinction coefficient due to other causes and k_{ej} includes the phytoplankton's contribution. The function $h(P_j)$ has been investigated by Riley (43) who found that it can be approximated by:

$$h(P_j) = 0.0088 P_j + 0.054 P_j^{2/3} \quad (14)$$

where P_j has the units $\mu\text{g/l}$ chlorophyll_a concentration and h has units m^{-1} . A more recent investigation (51) shows that this relationship applies to coastal waters of Oregon for a range in chlorophyll_a concentration of from 0 to 5.0 mg Chl_a/m³.

A theoretical basis for this relationship is the Beer-Lambert law which expresses the extinction coefficient in terms of the concentration of light absorbing material. For dense algal cultures, this law has been experimentally verified (37). A similar relationship based on this law has been proposed by Chen et al. (7) from the data of Azad and Borchardt (3):

$$h(P_j) = 0.17 P_j \quad (15)$$

for h in m^{-1} and P_j , the phytoplankton concentration is mg/l of dry

weight. This expression gives value comparable to eq. (14) for a reasonable conversion factor for the units involved.

To summarize the analysis to this point, the saturated growth rate K' has been estimated from available data and its temperature dependence established. The reduction to be expected from non-optimum light intensities has been quantified and used to calculate the reduction in growth rate, r_j , to be expected in each volume element V_j as a function of the extinction coefficient and the depth of the segment. The mechanism of self-shading has been included by specifying the chlorophyll dependence of the extinction coefficient. It remains to evaluate the effect of nutrients on the growth rate.

Nutrients

The effects of various nutrient concentrations on the growth of phytoplankton has been investigated and the results are quite complex. As a first approximation to the effect of nutrient concentration on the growth rate it is assumed that the phytoplankton population in question follow Monod growth kinetics with respect to the important nutrients. That is, at an adequate level of substrate concentration, the growth rate proceeds at the saturated rate for the temperature and light conditions present. However at low substrate concentration the growth rate becomes linearly proportional to substrate concentration. Thus for a nutrient with concentration N_j in the j^{th} segment the factor by which the saturated growth rate is in the j^{th} segment reduced is: $N_j/(K_m + N_j)$. The constant, K_m , which is called the Michaelis or half saturation constant, is the nutrient concentration at which the growth rate is half the saturated growth rate. There exists an increasing body of experimental evidence to

support the use of this functional form for the dependence of the growth rate on the concentration of either phosphate (16), nitrate, or ammonia (17) if only one of these nutrients is in short supply. An example of this behavior, using the data from Ketchum (24), is shown in fig. (4a) for the nitrate uptake rate as a function of nitrate concentration and in fig. (4b) for the phosphate uptake as a function of phosphate concentration. These results are from batch experiments. Similar results from chemostat experiments, which seem to be more suitable but more lengthy for this type of analysis, have also been obtained. Table II is a listing of measured and estimated Michaelis constants for ammonia, nitrate, phosphate. The estimates are obtained by taking one third the reported saturation concentration of the nutrients. These measurements and estimates indicate that the Michaelis constant for phosphorous is approximately 10 $\mu\text{g-P/l}$ and for inorganic nitrogen forms in the range from 1.0 to 100 $\mu\text{g-N/l}$ depending on the species and its previous history.

The data on the effects of the concentration of other inorganic nutrients on the growth rate is less complete. Since algae use carbon dioxide as their carbon source during photosynthesis this is clearly a nutrient which can reduce the growth rate at low concentrations (25). Reported saturation concentration for *Chlorella* is $< 0.1\%$ atmospheres (34).

The silicate concentration is a factor in the growth rate of diatoms for which it is an essential requirement. The saturated growth rate concentration is in the range of 50 - 100 $\mu\text{g Si/l}$ (59).

There are a large number of trace inorganic elements which have been implicated in the growth processes of algae among which are iron for which a Michaelis constant of 5 $\mu\text{g/l}$ for reactive iron has been reported (18)

manganese, calcium, magnesium and potassium⁽²⁸⁾. However the significance of these elements in the growth of phytoplankton in natural waters is still unclear. Trace organic nutrients have also been shown to be necessary for most species of algae: 83% of the strains studied require vitamin B₁₂, 53% require thiamine and 10% require biotin⁽¹⁵⁾. Presumably these nutrients are available in sufficient quantities on natural waters so that their concentration does not appreciably affect the growth rate.

In the preceding discussion of nutrient influences on the growth rate it is tacitly assumed that only one nutrient is in short supply and all the other nutrients are plentiful. This is sometimes the case in a natural body of water. However it is also possible that more than one nutrient is in short supply. The most straightforward approach to formulating the growth rate reduction due to a shortage of more than one nutrient is to multiply the saturated growth rate by the reduction factor for each nutrient. As an example, the data from Ketchum⁽²⁴⁾, for the rate of phosphate absorption as a function of both phosphate and nitrate concentration, can be satisfactorily fit with a product of two Michaelis Menton expressions. The resulting fit, obtained by a multiple non-linear regression analysis, is shown in fig. (5). The Michaelis constants that result are $28.4 \mu\text{g NO}_3 - \text{N/}$ and $30.3 \mu\text{g PO}_4 - \text{P/}$, with a saturated absorption rate of $15.1 \times 10^{-8} \mu\text{g PO}_4 - \text{P/cell-hr.}$ This approximation to the growth rate behavior as a function of more than one nutrient must be regarded as only a first approximation, however, since the complex interactions between the nutrients which have been reported is neglected.

The result of the above investigation is the following growth rate

expression: For the case of one limiting nutrient, N, with Michaelis constant K_m , the growth expression for the rate in the j^{th} segment is:

$$G_{Pj} = K_1 T_j \left(\frac{2.718 f}{k_{ej} H_j} (e^{-\alpha_{1j}} - e^{-\alpha_{0j}}) \right) \left(\frac{N_j}{K_m + N_j} \right) \quad (16)$$

in which eqs. (4) and (11) have been combined. This is the functional form that is used subsequently in the applications of these equations to natural phytoplankton populations.

VI. Comparison to Other Growth Rate Expressions

The most extensive investigation of the relationship between the growth rate of natural phytoplankton populations and the significant environmental variables, within the context of phytoplankton models, is that of Riley et. al. (1949)⁽⁴⁶⁾. The expression which results from their work is:

$$\log \left[\frac{G_p}{K' I_0 - G_p} \right] = 22.884 + \log v_p - \log I_0 - \frac{6573.8}{T'} \quad (17)$$

where G_p is the growth rate (day⁻¹), $K' = 7.6$, I_0 = average daily incident solar radiation (ly/min.), T' = temperature in °K, and v_p is the nutrient reduction factor for phosphate concentration, N_p , defined as:

$$\begin{aligned} v_p &= 1.0 & N_p &> 0.55 \text{ mg-at./m}^3 \\ v_p &= (0.55)^{-1} N_p & N_p &< 0.55 \text{ mg-at./m}^3 \end{aligned} \quad (18)$$

In order to compare this expression with that in the previous section, let the nutrient reduction factor be replaced by a Michaelis-Menton expression.

$$v_p = \frac{N_p}{K_{mp} + N_p} \quad (19)$$

where K_{mp} is the Michaelis constant for phosphate. To be comparable to equation (16), K_{mp} should equal approximately 0.20 mg-at/m³ (6.2 mg-P/m³). Using eq. (19) for v_p , the growth rate expression becomes:

$$G_p = K' I_0 \left[\frac{\eta(T)}{\eta(T) + I_0} \right] \left[\frac{N_p}{K_m \left[\frac{I_0}{\eta(T) + I_0} \right] + N_p} \right] \quad (20)$$

where

$$\eta(T) = 10 \left[\frac{22.9 (T) - 336.4}{T + 273} \right] \quad (21)$$

and T is temperature in degrees centigrade. To compare this expression with that proposed in the previous section, consider first the nutrient saturated growth rate as a function of solar radiation intensity and temperature. The equations are compared in Fig. (6a) as a function of total daily solar radiation, for three temperatures. The dotted line is eq. (20) and the solid line is the product of eqs. (4) and (5). The rate expressions are comparable, although two differences are apparent: in Riley's expression the effect of temperature is less pronounced in the 15°C to 25°C range and effect of higher daily average solar radiation intensities is opposite (i. e. tends to increase the rate) to that of eq. (5) based on Steele's expression. The growth rate equations averaged over depth, are compared in fig. (6b). The depth average rate resulting from Riley's expression is:

$$G_P = \frac{K' \eta(T)}{k_e H} \ln [1 + I_0 / \eta(T)] \quad (22)$$

which is compared to eq. (16). The differences are now more pronounced. In particular the higher growth rates at lower light intensities given by eq. (16) is reflected in the increased depth average growth rate. This is not unexpected since the majority of the population is exposed to lower light levels at the lower depths. Also the dependence on temperature is quite different, being linear in the case of eq. (16) but practically suppressed in eq. (22).

An interesting feature of Riley's eq. (20) is the multiplication of the Michaelis constant by an expression which depends on temperature and light intensity. The effect is to lower the Michaelis constant at high temperatures and at high light intensity levels which seems to be a reasonable behavior for a phytoplankton population.

More elementary growth rate formulations have been proposed which do not span the range of conditions attempted in eqs. (16) and (20). In particular a common proposal is to make the growth rate linearly proportional to the various environmental variables. For example, Davidson and Clymer (1966)⁽¹²⁾ assumed that the growth rate is proportional to incident solar radiation, temperature and nutrient concentration below a limiting value. Also, Parker (1968)⁽³⁸⁾ assumed that the growth rate is proportional to phosphate concentration and photo period and a temperature factor given by $\exp(- (T - 18.)^2/18.)$. This temperature factor is quite different from all others proposed and greatly magnifies the effect of temperature on the growth rate. For example at $T = 18^\circ\text{C}$ the factor equals 1.0, whereas at $T = 9^\circ\text{C}$ the factor drops to 0.01, a one-hundred fold decrease, compared to approximately a two-fold decrease predicted by eqs. (16) and (20). This exaggerated effect seems to be unrealistic.

A complete investigation of the environmental influences on the growth rate is still to be made. In particular it has been emphasized that there is an interaction between nitrogen and phosphorous limitations as well as other effects which influence the phytoplankton growth rate. Also, these effects are different for differing species. The species dependent effects are important in the problem of the seasonal succession of phytoplankton species.

For any particular application, it is advisable to investigate the growth rate of the already existing population as the resulting expression may differ significantly from the general overall behavior as described by eqs. (16) and (20). Also in dealing with natural associations of species of phytoplankton the various constants which result from such an investigation can be considered to be averages over the population and so they represent in some average way the population behavior as a whole.

VII. Phytoplankton Death Rate

Numerous mechanisms have been proposed which contribute to the death rate of phytoplankton: endogenous respiration rate, grazing by herbivorous zooplankton, a sinking rate, and parasitization⁽¹⁹⁾. The first three mechanisms have been included in previous models for phytoplankton dynamics and they have been shown to be of general importance.

Endogenous Respiration

The endogenous respiration rate of phytoplankton is the rate at which the phytoplankton oxidize their organic carbon to carbon dioxide per unit weight of phytoplankton organic carbon. Respiration is the reverse of the photosynthesis process and as such contributes to the death rate of the phytoplankton population. If the respiration rate of the population as a whole is greater than the photosynthesis or growth rate, there is a net loss of phytoplankton carbon and the population biomass is being reduced in size. The respiration rate as a function of temperature has been investigated and some measurements are presented in fig. (7) and Table III. A straight line seems to give an adequate fit of the data; that is, $\text{Respiration Rate} = K_2 T$. For the respiration rate in days^{-1} and T in $^{\circ}\text{C}$, the value of K_2 is in the range $.005 \pm .001$. The lack of any more precise data precludes exploring the respiration rates dependence on other environmental variables. However an important interaction has been suggested by Lund⁽²⁸⁾. During nutrient depleted conditions, "many algae pass into morphological or physiological resting stages under such unfavorable conditions. Resting stages are absent in Asterionella formosa and this is why a mass death occurs in the nutrient

depleted epilimnion after the vernal maximum." In terms of the respiration rate, the resting stage corresponds to a lowering of the respiration rate as the nutrient concentrations decrease. Thus a Michaelis-Menton expression for the respiration rate nutrient dependence may also be required and this dependence should be investigated experimentally. This mechanism is quite significant from a water quality point of view since the deaths of algae after a bloom is of primary concern in protecting the quality of natural bodies of water. The resulting mass of dead algal cells become a sink of dissolved oxygen which can dangerously lower the available oxygen for fish and other aquatic animals.

Grazing by Zooplankton

The interaction between the phytoplankton population and the next trophic level, the herbivorous zooplankton is a complex process for which only a first approximation can be given. A basic mechanism by which zooplankters feed is by filtering the surrounding water and clearing it of whatever phytoplankton and detritus is present. Thus the presence of zooplankton contribute to the death rate of phytoplankton since many species of zooplankton prey on phytoplankton as a food source. The filtering or grazing rate of some species of zooplankton have been measured and are presented in Table IV. The grazing rate is sometimes reported as a volume of water filtered per unit time per individual. In order to be applicable to a natural zooplankton population consisting of differing species, these grazing rates are converted to a filtering rate per unit biomass of zooplankton and denoted by C_g . A convenient biomass unit for zooplankton concentration is their dry weight. As can be seen from Table IV the resulting values of C_g vary considerably. This variation

is not unexpected since the measurement of grazing rates of zooplankters is a difficult procedure and subject to large variations in the estimates.

Variations of the filtering rate due to temperature change have been reported⁽²⁾. Examples of this variation is presented in fig. (8) for four species of genus Daphnia, a small crustacea⁽⁵⁾; two species of Acartia; and two species of Centropages, both copepods. The copepods show a marked grazing rate temperature dependence while the grazing rates of the Daphnia do not vary as markedly. The filtering rate also varies as a function of the size of the phytoplankton cell being ingested⁽³²⁾, the concentration of phytoplankton⁽³¹⁾ and the amount of particulate matter present⁽⁶⁾. Selective grazing of certain phytoplankton species, has also been reported⁽⁵⁾. The complexity of this aspect of phytoplankton mortality is such that the use of one grazing coefficient to represent the process must be viewed as a first approximation. However, since this mathematical expression does represent a physiological mechanism that has been investigated and for which reported values of C_g are available, this approximation is a realistic first step. Also, it is difficult to see, aside from refinements as to temperature and phytoplankton concentration dependence, what further improvements could be made in the formulation so long as the phytoplankton and zooplankton population are represented by a biomass measurement which ignores the species present and their individual characteristics. For simplicity in this investigation, the grazing rate is assumed to be a constant. The death rate of phytoplankton due to the grazing by zooplankton is given by the expression $C_g Z_j$, where Z_j is the concentration of herbivorous zooplankton biomass in the j^{th} volume element.

For models of the phytoplankton populations in coastal oceanic waters and in lakes the sinking rate of phytoplankton cells is an important contribution to the mortality of the population. The cells have a net downward velocity and they eventually sink out of the euphotic zone to the bottom of the water body. This mechanism has been investigated and included in phytoplankton population models⁽⁴⁶⁾⁽⁷⁾. However for the application of these equations to a relatively shallow vertically well mixed river or estuary, the degree of vertical turbulence is sufficient to eliminate the effect of sinking on the vertical distribution of phytoplankton.

Therefore, considering only the phytoplankton respiration and the predation by zooplankton the death rate of zooplankton is given by the equation:

$$D_{Pj} = K_2 T + C_g Z_j \quad (23)$$

and for a zooplankton biomass concentration Z_j the mortality rate can be calculated from this equation.

This completes the specification of the growth and death rates of the phytoplankton population in terms of the physical variables: light and temperature; the nutrient concentrations; and the zooplankton present. With these variables known as a function of time it is possible to calculate the phytoplankton population resulting throughout the year. However the zooplankton population and the nutrient concentrations are not known a priori since they depend on the phytoplankton population which develops. That is, these systems are interdependent and cannot be analyzed separately. It is therefore necessary to characterize both the zooplankton population

and the nutrients in mathematical terms in order to predict the phytoplankton population which would develop in a given set of circumstances.

VIII. The Zooplankton System

As indicated in the previous section, the zooplankton population exerts a considerable influence on the phytoplankton death rate due to its feeding on the phytoplankton. In some instances it has been suggested that this grazing is the primary factor in the reduction of the concentration of phytoplankton after the spring bloom. In the earlier attempts to model the phytoplankton system, the measured concentration of zooplankton biomass was used to evaluate the phytoplankton death rate due to grazing. However, it is clear that the same arguments used to develop the equation for the conservation of phytoplankton biomass can be applied directly to the zooplankton system. In particular the source of zooplankton biomass S_{Zj} within a volume element V_j can be given as the difference between a zooplankton growth rate G_{Zj} and a zooplankton death rate D_{Zj} . Thus the equation for the source of zooplankton biomass, which is analogous to equation (3), is:

$$S_{Zj} = (G_{Zj} - D_{Zj}) Z_j \quad (24)$$

where G_{Zj} and D_{Zj} have units day^{-1} and Z_j is the concentration of zooplankton carbon in the volume element V_j . The magnitude of the growth rate in comparison to the death rate determines whether the net rate of zooplankton biomass production in V_j is positive, indicating net growth rate, or negative, indicating a net death rate.

As in the case of the phytoplankton population, the growth and death rates, and in fact the whole life cycle of individual zooplankters, are complicated affairs with many individual peculiarities. The surveys by Hutchinson⁽²³⁾ and Raymont⁽³⁹⁾ gives detailed accounts of their complex

biology. It is, however, beyond the scope of this paper to summarize all the differences and species dependent attributes of the many zooplankton species. The point of view adopted is macroscopic with the population characterized in units of biomass. The resulting growth and death rates can be thought of as averages over the many species present. These simplifications are made in the interests of providing a model which is simple enough to be manageable, and yet representative of the overall behavior of the populations.

Growth Rate

The grazing mechanism of the zooplankton provides the basis for the growth rate of the herbivorous zooplankton, G_{Zj} . For a filtering rate C_g the quantity of phytoplankton biomass ingested is $C_g P_j$ where P_j is the phytoplankton biomass concentration in V_j . To convert this rate to a zooplankton growth rate, a parameter which relates the phytoplankton biomass ingested to zooplankton biomass produced, that is, a utilization efficiency, a_{ZP} , is required. However, this utilization efficiency or yield coefficient is not a constant. The reason is that at high phytoplankton concentrations, the zooplankton do not metabolize all the phytoplankton that they graze, but rather they excrete a portion of the phytoplankton in undigested or semi-digested form⁽⁴¹⁾. Thus the utilization efficiency is a function of the phytoplankton concentration. A convenient choice for this functional relationship is $a_{ZP} K_{mP} / (K_{mP} + P_j)$ so that the growth rate for the zooplankton population is:

$$G_{Zj} = a_{ZP} C_g K_{mP} \left(\frac{P_j}{K_{mP} + P_j} \right) \quad (25)$$

The resulting growth rate has the same form as that postulated for the

nutrient - phytoplankton relationship, namely a Michaelis-Menton expression with respect to phytoplankton biomass. In fact the argument which is used to justify its use in equation (16) can be repeated in this context. The difference is that in this case the substrate or nutrient is phytoplankton biomass, and the microbes are the zooplankton. The Michaelis constant K_{MP} is the phytoplankton biomass concentration at which the growth rate G_{Zj} is one-half the maximum possible growth rate $a_{ZP}C_gK_{MP}$. The fact that at high phytoplankton concentrations the zooplankton growth rate saturates was incorporated by Riley (1947)⁽⁴¹⁾ in the first model proposed for a zooplankton population.

The assimilation efficiency of the zooplankton at low phytoplankton concentrations, a_{ZP} , which is the ratio of phytoplankton organic carbon utilized to zooplankton organic carbon produced has been estimated by Conover⁽¹¹⁾ for a mixed zooplankton population. The results of 26 experiments gave an average of 63% and a standard deviation of 20%. Other reported values are within this range. Experimental values for K_{MP} , which in effect set the maximum growth rate of zooplankton, are not available and would probably be highly species dependent. Perhaps a more effective way of estimating K_{MP} is to first estimate the maximum growth rate at saturating phytoplankton concentrations, $a_{ZP}C_gK_{MP}$, and then calculate K_{MP} . Growth rates for copepods through their life cycle average 0.18 day⁻¹ (33). For the Georges Bank population, Riley used 0.08 day⁻¹ (41) for the maximum zooplankton growth rate. For a value of the grazing coefficient C_g of 0.5 l/mg-dry wt.-day and an assimilation coefficient of 65% the Michaelis constant for zooplankton assimilation, K_{MP} ranges between 0.25 and 0.55 mg-dry wt./l of phytoplankton biomass. However these values

should only be taken as an indication of the order of magnitude of K_{mp} . It is probable that its value can vary substantially in different situations.

The fact that the growth rate reaches a maximum or saturates is an important feature of the formulation of the zooplankton growth rate since in some cases the phytoplankton concentration during part of the year exceeds that which the zooplankton can effectively metabolize. If the zooplankton growth rate is not limited in some way and, instead, is assumed simply to be proportional to the phytoplankton concentration, as proposed in simpler models, the resulting zooplankton growth rate during phytoplankton blooms can be very much larger than is physiologically possible for zooplankton, an unrealistic result. The saturating growth rate also has implications in the mathematical properties of the resulting equations. In particular the behavior differs significantly from the classical Volterra Predator-Prey equations⁽²⁷⁾. This is discussed further in a subsequent section.

The growth of the zooplankton population as a whole, of which the herbivorous zooplankton are a part, is complicated by the fact that some zooplankters are carnivorous or omnivorous. Thus the nutrient for the total population should include not only phytoplankton but also organic detritus as a food source since this is also available to the grazing zooplankton. However for cases where the phytoplankton are abundant and the growth rate saturates for the significant growing periods, the simplification introduced by ignoring the detritus is probably acceptable.

Death Rate

The death rate of herbivorous zooplankton is thought to be due

primarily to the same mechanisms that cause the death of the phytoplankton, namely, endogenous respiration and predation by higher trophic levels. The endogenous respiration rate of zooplankton populations has been measured and the results of some of these experiments are presented in fig. (9) and Table V.

It is clear from these measurements that the respiration rate of zooplankters is temperature dependent. It is also dependent on the weight of the zooplankter in question and its life cycle stage⁽⁹⁾. As a first approximation, a straight line dependence is adequate and the endogenous respiration rate is given by the equation: respiration rate = $K_3 T$ where $K_3 = 0.2 \pm 0.1$ (day °C)⁻¹. The conversion from the reported units to a death rate is made by assuming that 50% of the zooplankton dry weight represents the carbon weight and that carbohydrate (CH₂O) is being oxidized. The data are somewhat variable and serve only to establish a range of values within which the respiration rate of a natural zooplankton association might be expected.

The death rate due to predation by the higher trophic levels, specifically the carnivorous zooplankton, has been considered by previous models in a more or less empirical way. The complication resulting from another equation and the uncertainty as to the mechanisms involved are quite severe at this trophic level. In particular it is probable that an equation for organic detritus is necessary to adequately describe the available food. Hence it is expedient to break the casual chain at this point and assume that the herbivorous zooplankton death rate due to all other causes is given by a constant, the magnitude of which is to be determined empirically. The severity of this assumption can be tested by

examining the sensitivity of the solutions of the phytoplankton and zooplankton equations to the magnitude of this constant. Hence the resulting zooplankton death rate is given by

$$D_{Zj} = K_3 T + K_4 \quad (26)$$

where K_4 is empirically determined.

With the growth and death rates given by eqs. (25) and (26) respectively, the source term for herbivorous zooplankton biomass is given by eq. (24). The conservation of mass equation which describes the behavior of Z_j is given by eq. (2) with Z_j as the dependent variables replacing P_j and S_{Zj} replacing S_{Pj} as the source terms.

This completes the formulation of the equations which describe the zooplankton system. What remains to be formulated is the equations for the nutrient system.

IX. The Nutrient System

The conservation of mass principle is applied to the nutrients being considered in the same way as it has been previously applied to the phytoplankton and zooplankton biomass within a volume segment. The number of mass conservation equations required is equal to the number of nutrients that are explicitly included in the growth rate formulation for the phytoplankton. For the sake of simplicity the formulation for only one nutrient is discussed below.

The source term S_{Nj} in the conservation of mass equation for the concentration of the nutrient N_j in the j^{th} volume segment V_j is the sum of all sources and sinks of the nutrient within V_j . The primary interaction between the nutrient system and the phytoplankton system is the reduction or sink of nutrient due to phytoplankton growth. The rate of increase of phytoplankton biomass is $G_{pj}P_j$. To convert this assimilation rate to the rate of utilization of the nutrient, the ratio of biomass production to net nutrient assimilated is required. Over a long time interval, this ratio approximates the nutrient to biomass ratio of the phytoplankton population. For example if the nutrient being considered is total inorganic nitrogen and the phytoplankton biomass is characterized in terms of dry weight, then this ratio is the nitrogen to dry weight ratio of the population. For both nitrogen and phosphorus these ratios have been studied for a number of phytoplankton species and natural associations. An example of this information is presented in Table VI, condensed from Strickland⁽⁵⁹⁾. If a_{NP} is the nutrient to phytoplankton biomass ratio of the population, then the sink of the nutrient due to phytoplankton growth is $a_{NP}G_{pj}P_j$.

A secondary interaction between the biological systems and the nutrient systems is the excretion of nutrients by the zooplankton and the release of nutrients in an organic form by the death of phytoplankton and zooplankton. The excretion mechanism has been considered by Riley⁽⁴⁵⁾ in a generalization of the equations of Steele. The rates of phosphorus excretion has also been measured experimentally⁽³⁰⁾. Using the formulation for zooplankton growth rate proposed in section VIII, the rate of nutrient excretion is the rate grazed, $a_{NP}C_gP_jZ_j$, minus the rate metabolized $a_{NP}C_zZ_j$; that is, the excretion rate is:

$$a_{NP}C_gZ_jP_j \left(1 - \frac{a_{ZP} K_{mP}}{K_{mP} + P_j} \right) \quad (27)$$

At high phytoplankton concentrations almost all the grazed phytoplankton is excreted since the bracketed term in eq. (27) approaches unity.

There is a difficulty, however, in using this term directly as a source of nutrient. To illustrate this difficulty assume that the nutrient is inorganic nitrogen. The excreted nitrogen, however, is in organic form and a bacterial decomposition into the inorganic forms must precede the utilization by the phytoplankton. The same is true for the nutrient released by the death of phytoplankton, $a_{NP}K_2TP_j$, and that released by the death of zooplankton, $a_{NZ}K_3TZ_j$, where a_{NZ} is the nutrient to zooplankton biomass ratio. Therefore, strictly speaking, a conservation of mass equation for the organic form of the nutrient is required. The organic form is then converted to the inorganic form. For the case of nitrogen, the kinetics of this conversion have been investigated and applied to stream and estuarine situations⁽⁶²⁾. If the conversion rate is large by

comparison to the other rates in the phytoplankton and zooplankton equations, then the direct inclusion of these sources is approximately correct.

The sources of nutrients due to man-made inputs, such as wastewater discharges and agricultural runoff, are included explicitly into the source term since these sources are usually the major control variables available to influence the biological systems. An extensive review of the magnitude and relative importance of these sources of nutrients, primarily nitrogen and phosphorus, has recently been made⁽⁶⁵⁾. A useful distinction is made between diffuse sources, such as agricultural runoff loads and groundwater infiltration which are difficult to measure and control; and point sources such as wastewater discharges from municipal and industrial sources for which more information is available. The nitrogen and phosphorus loads from agricultural runoff are quite variable, and depend on many variables such as soil type, fertilizer application, rainfall, and irrigation practice. The nutrient sources from point loads can be estimated more directly. For example, the nutrient load from biologically treated municipal wastewater is in the order of 10 g/capita-day total nitrogen and 2 g/capita-day total phosphorus. It is interesting to note that the ratio of per capita phosphorus to physiologically required phosphorus is approximately 2 to 3, the excess being primarily due to detergent use. Industrial loads can also be important, especially effluents from food processing industries. If the required loading rates are available their loads should be included in the nutrient mass balance equations. In particular if the investigation of the phytoplankton population is directed at the probable effects of increasing or decreasing the nutrient load, these loads must be explicitly identified and their magnitude assessed.

Let W_{Nj} be the rate of addition of the nutrient to the j^{th} volume element. This source is then included as a component in the nutrient source term in the mass balance equation.

An important additional source of inorganic nutrients which may influence the availability of nutrients is the interaction of the overlying water with either the underlying mineralstrata if exposed or whatever sediment is present. These interactions can complicate the source term but they should be included if they add significantly to the available nutrient.

The source term which results from the inclusion of the phytoplankton utilization sink, the zooplankton excretion and the mortality sources, and the man-made additions, is:

$$N_j = \frac{W_{Nj}}{V_j} - a_{NP} G_{Pj} P_j + a_{NP} C_{Zj} P_j \left[1 - \frac{a_{ZP} K_{mP}}{K_{mP} + P_j} \right] + a_{NP} K_2 T P_j + a_{NZ} K_3 T Z_j \quad (1)$$

Whatever additional sources and sinks that contribute can be added to the source term as needed. With the source term formulated the conservation of nutrient mass equation is given by eq. (2) with N_j as the dependent variable replacing P_j and S_{Nj} replacing S_{Pj} .

X The Equations of the Model

In the previous sections the equations for phytoplankton and zooplankton biomass and nutrient concentration within one volume element have been formulated. The resulting equations are an attempt to describe the kinetics of the growth and death of the phytoplankton and zooplankton populations and their interaction with the nutrients available. The form of the equations for the volume V_j are as follows:

$$\dot{P}_j = [G_{Pj}(P_j, N_j, t) - D_{Pj}(Z_j, t)] P_j = S_{Pj}(P_j, Z_j, N_j, t) \quad (29)$$

$$\dot{Z}_j = [G_{Zj}(P_j, t) - D_{Zj}(t)] Z_j = S_{Zj}(P_j, Z_j, t) \quad (30)$$

$$\dot{N}_j = S_{Nj}(P_j, Z_j, t) \quad (31)$$

where G_{Pj} and D_{Pj} are given by equations (16) and (23), G_{Zj} and D_{Zj} are given by equations (25) and (26) and S_{Nj} by equation (28). The dependence of the growth and death rates on the concentration of the three dependent variables and time is made explicit in the above notation.

These equations describe only the kinetics of the populations in a single volume elements V_j . However, in a natural water body there exists significant mass transport as well. The mass transport mechanisms can be conveniently represented by the matrix A with elements a_{ij} . If for particular segments i and j the matrix element a_{ij} is non-zero, then the volume segments V_i and V_j interact and mass is transported between the two segments. Letting P , Z , and N be the vectors of elements P_j , Z_j , and N_j ; and letting S_P , S_Z , S_N be the vectors of elements S_{Pj} , S_{Zj} ,

and S_{Nj} , the conservation of mass equations for the three systems including the mass transport and kinetic interactions are:

$$\dot{V}P = AP + VS_P \quad (32)$$

$$\dot{V}Z = AZ + VS_Z \quad (33)$$

$$\dot{V}N = AN + VS_N \quad (34)$$

where V is the diagonal matrix of the volumes of the segments. These are the equations which form the basis for the phytoplankton population model. The detailed formulation and evaluation of the mass transport matrix has been discussed elsewhere⁽⁶¹⁾ (35) (36).

The form of the above equations make explicit the linear and non-linear portions of the equations. In the equation for P , the phytoplankton biomass, the concentration P_j , in the volume element V_j , is linearly coupled to the other P_k 's through the matrix multiplication by A . However, there is no nonlinear interaction between P_j and any other P_k , $k \neq j$. The reason is that the transport processes are described by linear equations. It is usually the case, however, that the A matrix is a function of time, since at least the advective terms usually vary in time. The nonlinear terms in the vector S_P involve P_j itself and the corresponding Z_j and N_j . Hence the P equation is coupled to the Z and N through this term. Note, however, that P_j is not coupled to the Z_k and N_k , $k \neq j$, in any other segment, so that the coupling takes place only within each volume segment.

Therefore the nonlinearities provide the coupling between the phytoplankton, zooplankton and nutrient systems. This coupling is

accomplished within each volume and does not extend beyond the volume boundary. The coupling among the volumes is accomplished by the linear transport interaction represented by the matrix A . This matrix may be time varying but its elements are not functions of the phytoplankton, zooplankton or nutrient concentrations. Hence in many ways these equations behave linearly. In particular their spatial behavior is unaffected by the nonlinear source terms. However, the temporal behavior and the relationships between each P_j , Z_j and N_j are distinctly nonlinear.

XI Comparison to Lotka - Volterra Equations

The classical theory of predator prey interaction as formulated by Volterra involves two equations which express the growth rate of the prey and the predator⁽²⁷⁾. Within the context of phytoplankton and zooplankton population the prey is the phytoplankton and the predator the zooplankton. In the notation of the previous sections, for a one volume system, the Lotka-Volterra equations are:

$$\frac{dP}{dt} = (G_P - D_P^I) P - C_g PZ \quad (35)$$

$$\frac{dZ}{dt} = -D_Z Z + a_{ZP} C_g PZ \quad (36)$$

where all the coefficients, G_P , D_P^I , C_g , D_Z and a_{ZP} are assumed to be constants and $G_P > D_P^I$. This is a highly simplified situation since, as indicated previously, the growth and death rates are functions of time and, in the case of the phytoplankton growth rate, of the phytoplankton and nutrient concentrations as well. However for a situation with adequate nutrients and low initial phytoplankton concentration, the non-linear interactions is small initially, and the time variation of G_P can be small during the summer months. In any case the analysis of this simplified situation is quite instructive.

Although no analytical solution is available for these simplified equations, their properties are well understood⁽¹³⁾. In particular the equations have two sets of singular points corresponding to the solution of the righthand side of eqs. (35) and (36) equated to zero: the trivial solutions $P^* = 0$, $Z^* = 0$ and

$$P^* = \frac{D_Z}{a_{ZP} C_g}, \quad Z^* = \frac{G_P - D'_P}{C_g} \quad (37)$$

A perturbation analysis of eqs. (35) and (36) about this singular point shows that the solutions whose initial conditions are close to P^* , Z^* , oscillate sinusoidally about this singular point. Hence no constant solution is possible. The prey and predator populations continually oscillate and are out of phase with each other. When the predator predominates the prey is reduced, which in turn causes the predator to die for lack of food, which allows the prey to proliferate for lack of predator, which then causes the predator to grow because of the prey available as a food supply and so on. The interesting feature is that these oscillations continue indefinitely.

The classical Lotka-Volterra equations assume an isolated population with no mass transport into or out of the volume being considered. To simulate the effect of mass transport into the volume, assume that an additional source term of phytoplankton biomass exists and has constant magnitude P_0 . For this situation the equations become:

$$\frac{dP}{dt} = (G_P - D'_P) P - C_g PZ + P_0 \quad (38)$$

$$\frac{dZ}{dt} = D_Z Z + a_{ZP} C_g PZ \quad (39)$$

The nontrivial singular point for these equations is:

$$P^* = \frac{D_Z}{a_{ZP} C_g}; \quad Z^* = \frac{a_{ZP} P_0}{D_Z} + \frac{(G_P - D'_P)}{C_g} \quad (40)$$

A perturbation analysis about this singular point yields a second order linear ordinary differential equation whose characteristic equation has the roots λ_1 , and λ_2 where:

$$\lambda_{1,2} = - \frac{a_{ZP} P_0 C_g}{2 D_Z} \pm \sqrt{\left[\frac{a_{ZP} P_0 C_g}{2 D_Z} \right]^2 - a_{ZP} C_g P_P - (G_P - D_P) D_Z} \quad (41)$$

Since for $P_0 > 0$ these roots have negative real parts, this singular point is a stable focus and the steady state values given by eq. (40) are approached either by a damped sinusoid or an exponential⁽¹³⁾. Note that for $P_0 = 0$, the classical case, the roots are purely imaginary and the oscillation persists indefinitely.

This analysis suggests that the effect of transport into the system stabilizes the behavior of the equations and in particular allows the solutions to achieve a constant solution. This is in marked contrast to the behavior of the classical Lotka-Volterra equations.

Another modification, which has been introduced into the zooplankton equations, changes the behavior of the proposed equations in contrast to the Lotka-Volterra equations. It has been argued that the zooplankton growth rate due to grazing must approach its maximum value when the phytoplankton population becomes large since the zooplankters cannot metabolize the continually increasing food that is available. Thus the growth rate $a_{ZP} C_g PZ$ is replaced by $a_{ZP} C_g ZP K_{mP} / (P + K_{mP})$ where K_{mP} is a Michaelis constant for the reaction. The equations then become:

$$\frac{dP}{dt} = (G_P - D_P)P - \frac{C_g PZ}{P + K_{mP}} + P_0 \quad (42)$$

$$\frac{dZ}{dt} = -D_z Z + \frac{a_{zp} C_{zp} Z P K_{mp}}{P + K_{mp}} \quad (43)$$

The non-zero singular points are:

$$P^* = \frac{D_z K_{mp}}{a_{zp} C_{zp} K_{mp} - D_z} \quad (44)$$

$$Z^* = \frac{P_0}{C_g P^*} + \frac{(G_p - D_p)}{C_g} \quad (45)$$

This solution reduces to the previous situation, eq. (40), for large K_{mp} . This is expected since for K_{mp} large with respect to P , the expression $K_{mp}/(P + K_{mp})$ approaches one. However an interesting modification from classical predator prey behavior occurs if the following condition is met:

$$a_{zp} C_{zp} K_{mp} = D_z + \epsilon \quad (46)$$

where ϵ is a small positive number. For this condition, P^* is large and positive. What happens in this case is that the zooplankton population, although it continues to grow exponentially cannot grow quickly enough to terminate the phytoplankton growth by grazing, and the phytoplankton continue to grow exponentially until P^* is reached. Of course in the actual situation, for which G_p is not a constant, other phenomena such as nutrient depletion and self-shading exert their effect and the growth may be stopped sooner. However the point is that if the growth rate of zooplankton at a phytoplankton concentration equal to the

Michaelis constant K_{mp} is only slightly larger than their death rate D_z then the zooplankton alone do not rapidly terminate the bloom.

This condition is an important dividing line for the possible behavior of the phytoplankton-zooplankton equations set forth in the previous sections. In particular it indicates what must be true for a system wherein the zooplankton are a significant feature in the resulting phytoplankton solution. However if eq. (46) is satisfied then the zooplankton are not the dominant control of the phytoplankton population.

XIII Application - San Joaquin River

As an example of the application of the equations proposed herein, consider the phytoplankton and zooplankton population observed at Mossdale Bridge on the San Joaquin River in California during the two years 1966-1967. Mossdale is located approximately 40 miles from the confluence of the San Joaquin and the Sacramento Rivers. The data presented below have been supplied to the authors by the Department of Water Resources, State of California⁽¹⁴⁾, as part of an ongoing project to assess the effects of proposed nutrient loads and flow diversions on the water quality of the San Francisco Bay Delta. A more complete report of this investigation will be forthcoming⁽³⁶⁾.

In order to simplify the spatial segmentation and the calculations, a one-volume segment is chosen for the region of the San Joaquin for which Mossdale is representative. The volume of this segment is, of course, somewhat arbitrary and a more representative spatial segmentation would remove this uncertainty. However it is instructive to consider the behavior of the solution of this simplified model.

The nutrient data available indicates that phosphate, bicarbonate, silicate, calcium and magnesium are available at concentrations well above the levels for which it has been suggested that these nutrients limit growth. Only the ammonia and nitrate concentrations are low and they both decrease markedly during the 1966 spring bloom. Hence these nutrients must be considered explicitly. To simplify the computations the ammonia and nitrate nitrogen are combined and the nutrient considered is total inorganic nitrogen.

There is some uncertainty concerning the magnitude and the temporal variation of the inorganic nitrogen load being discharged to the system during the time interval of interest. For lack of a better assumption the inorganic nitrogen load W_N being discharged into the volume is assumed to be a constant, the magnitude of which is determined by comparison to the observed inorganic nitrogen concentration data at Mossdale.

The variation of the environmental variables being considered namely temperature, solar radiation, and advective flow in the San Joaquin during the two-year period of interest and the straight line approximations that are used directly in the numerical computation are shown in fig. (10). The influent advective flow which is assumed to have constant concentrations of phytoplankton and zooplankton biomass and inorganic nitrogen, is routed through the volume. Since Mossdale is located above the saline portion of the San Joaquin, no significant dispersive mass transfer is assumed to exist by comparison to the advective mass transfer.

The equations which represent this one segment model are:

$$\dot{P} = (G_P - D_P) P + \frac{Q}{V} (P_0 - P) \quad (47)$$

$$\dot{Z} = (G_Z - D_Z) Z + \frac{Q}{V} (Z_0 - Z) \quad (48)$$

$$\dot{N} = -a_{NP} G_P P + \frac{W_N}{V} + \frac{Q}{V} (N_0 - N) \quad (49)$$

where $Q = Q(t)$ is the advective flow entering and leaving the volume; V is the volume of the segment; P_0 , Z_0 , and N_0 are the phytoplankton, zooplankton and inorganic nitrogen concentration of the flow entering the

volume. The remaining terms have been defined previously by eqs. (16), (23), (25) and (26). In the nutrient equation only the direct source of inorganic nitrogen, W_N , has been included; the organic feedback terms representing excreted nitrogen etc., eq. (28), have been dropped. Since the magnitude of W_N is uncertain and is assigned by comparison of observed data and computed model output these feedback terms can be thought of as being incorporated in the value obtained for W_N .

The solution of eqs. (47), (48) and (49) requires numerical techniques. For such nonlinear equations, it is usually wise to employ a simple numerical integration scheme which is easily understood and pay the price of increased computational time for execution rather than using a complex, efficient, numerical integration scheme where unstable behavior is a distinct possibility. A variety of simple methods are available for integrating a set of ordinary first order differential equations. In particular the method of Henn⁽²⁶⁾ is effective and stable. It is self-starting and consists of a predictor and a corrector step. Let $y = f(t,y)$ be the vector differential equation and let h be the step size. The predictor is that of Euler: with y_0 the initial condition vector at t_0 the predictor value of y at $t_0 + h = t_1$ is:

$$y_1^* = y_0 + h f(t_0, y_0) \quad (50)$$

The corrector value is simply

$$y_1 = y_0 + \frac{h}{2} [f(t_0, y_0) + f(t_1, y_1^*)] \quad (51)$$

That is, the corrector uses the predictor value at t_1 to estimate the

slope at t_1 which is averaged with the slope at t_0 to provide the slope of the straight line approximation. A variation of this method is discussed at some length by Hamming⁽²²⁾.

Another simple two-step method is that of Runge⁽²⁶⁾. The Euler predictor is used with a half step integration.

$$y_{\frac{1}{2}}^* = y_0 + \frac{h}{2} f(t_0, y_0) \quad (52)$$

and this value of y is used to estimate the slope at the midpoint of the interval, which is then used as the slope of the straight line approximation:

$$y_1 = y_0 + h f(t_0 + \frac{h}{2}, y_{\frac{1}{2}}^*) \quad (53)$$

Both of these methods are second order methods, being accurate to terms of order Δt^2 in a comparison of Taylor series expansions of the exact and approximate values, and both methods require two derivative evaluations per step. The method of Runge has been used in the calculations presented below.

The equations themselves are programmed for solution using a continuous simulation language and a digital computer. The language, in this case CSMP/1130, is based on a block diagram, analog computer, representation of the differential equations. The flexibility of these languages which allow changes in the equation structure to be made easily is an asset in modeling complex systems.

The biomass variables used in the calculations are total cell counts for the phytoplankton and rotifer counts for the zooplankton. The rotifer

population represented the large majority of the zooplankton present on a weight basis as well. In order to relate these variables to comparable units a series of conversion factors have been used. The phytoplankton count - chlorophyll concentration ratio was measured. However the carbon - chlorophyll or dry weight - chlorophyll conversions are unknown. Hence the conversion to an organic carbon basis is made rather arbitrarily. However the carbon to chlorophyll ratio which results, see Table VII, is within the range reported in the literature. The same problem exists with the rotifer counts to rotifer carbon conversion; the value used is given in Table VII.

The comparison of the model output and the observed data for the two year period for which data is available is shown in fig 11. The parameter values used in the equations are listed in Table VII.

It is clear from both the data and the model results that a classical predator prey situation is observed in 1966: the spring bloom of phytoplankton due to a favorable temperature and light intensity provides the food for the zooplankton which then reduce the population during the summer. The decrease of the zooplankton and the subsequent slight secondary bloom of phytoplankton complete the cycle for the year. It is not clear, however, from a casual inspection of the data, whether the zooplankton population terminated the phytoplankton growth, as in classical predator prey situations, or whether the nutrient concentration dropped to a limiting value that reduced the growth rate, or a combination of the two. This point is elaborated in the next section.

The situation in 1967 is quite different. No significant phytoplankton growth is observed until late in the year. The controlling variable

in this case is the large advective flow during the spring and summer of 1967, see fig.10, which effectively washes out the population in the region. Only when the flow has sufficiently decreased so that a population can develop do the phytoplankton show a slight increase. However the dropping temperature and light intensity level terminate the growth for the year.

XIII Growth Rate - Death Rate Interactions

The behavior of the equations which represent the phytoplankton, zooplankton and nutrient systems in one volume can be interpreted in terms of the growth and death rates of the phytoplankton and zooplankton. The equations are as before:

$$\frac{dP}{dt} = (G_P - D_P) P + \frac{Q}{V} (P_o - P) \quad (54)$$

$$\frac{dZ}{dt} = (G_Z - D_Z) Z + \frac{Q}{V} (Z_o - Z) \quad (55)$$

where P_o and Z_o are the concentrations of phytoplankton and zooplankton carbon in the influent flow, Q . A more suggestive form for these equations is:

$$\frac{dP}{dt} = \left[G_P - \left(D_P + \frac{Q}{V} \right) \right] P + \frac{Q}{V} P_o \quad (56)$$

$$\frac{dZ}{dt} = \left[G_Z - \left(D_Z + \frac{Q}{V} \right) \right] Z + \frac{Q}{V} Z_o \quad (57)$$

A complete analysis of the properties of these equations is quite difficult since the coefficients of P and Z are time variable and also functions of P and Z . However the behavior of the solution becomes more accessible if the variation of these coefficients are studied as a function of time. The expressions $G_P - (D_P + Q/V)$ and $G_Z - (D_Z + Q/V)$ can be considered the net growth rates for phytoplankton and zooplankton. The advective or flushing rate, Q/V , is included in these expressions since it acts as a death rate in one segment system.

The sign and magnitude of the net growth rate controls the behavior of the solution. For a linear equation, for which the net growth rate is not a function of the dependent variable (i.e. P or Z), the type of solution obtained depends on the sign and magnitude of the net growth rate. That is, for the equation

$$\frac{dP}{dt} = \alpha P + \frac{Q}{V} P_0 \quad (58)$$

where α , Q and V are constant the solution is

$$P(t) = P(0) e^{\alpha t} + P_0 \frac{Q}{\alpha V} (e^{\alpha t} - 1) \quad (59)$$

For α negative, that is, for a negative net growth rate, the solution tends to the steady state value $P_0 Q / |\alpha| V$. However for α positive, the solution grows exponentially without limit. Thus for α negative but $|\alpha|$ small, or for α positive, the solution becomes large; whereas for α negative but $|\alpha|$ large the solution stays small. Hence the behavior of the solution can be inferred from the plots of the net growth rates. Fig. 12a is a plot of the following terms from the 1966 Mossdale calculation: G_p without the Michaelis Menton multiplicative factor included, i.e. the growth rate at nutrient saturation denoted by $G_p(I, T)$; G_p itself denoted by $G_p(N, I, T)$; i.e. the growth rate considering the nutrient effects. The net growth rate $G_p - (D_p + Q/V)$ is also plotted. Similarly in Fig. 12b, the growth rate of zooplankton, G_z ; the mortality rate D_z and the flushing rate $Q(t)/V$ as well as the net growth rate $G_z - (D_z + Q/V)$ is plotted.

The analysis of the 1966 model calculations can now be made by inspecting these figures. The net growth rate for the phytoplankton $G_p - (D_p + Q/V)$ becomes positive at $t = 85$ days due to an increase in G_p , the result of rising temperature and light intensity, and a decrease in Q/V as the advective flow decreases. The positive net growth rate of the population causes their numbers to increase exponentially fast until the nutrient begins to be in short supply. This is evidenced by the departure of the G_p curve from the G_p at nutrient saturation curve. At the same time the D_p curve is showing a marked increase due to the increased zooplankton population and their grazing. The result is that the net growth rate becomes zero and then negative as the zooplankton reduce the phytoplankton population by grazing. The growth of the zooplankton can be analyzed in a similar fashion using Fig. 12b. The net growth rate becomes positive when the phytoplankton population is large enough to sustain the zooplankters. Then the zooplankton grow until they have reduced the phytoplankton population to a level where they are no longer numerous enough to sustain the zooplankton. The net zooplankton growth rate then becomes negative and the population diminishes in size. This small zooplankton population no longer exerts a significant effect on the death rate of the phytoplankton, D_p , and its value decreases causing the net phytoplankton growth rate to become positive again and the smaller autumn bloom results. The decreasing temperature and light intensity and the increasing advective flow then effectively terminate the bloom as the year ends.

XIV Summary and Conclusions

A model of the dynamics of phytoplankton populations based on the principle of conservation of mass has been presented. The growth and death kinetic formulations of the phytoplankton and zooplankton have been empirically determined by an analysis of existing experimental data. Mathematical expressions which are approximations to the biological mechanisms controlling the population are added to the mass transport terms of the conservation equation for phytoplankton, zooplankton and nutrient mass in order to obtain the equations for the phytoplankton model. The resulting equations are compared to two years of data from the tidal portion of the San Joaquin River, California. Similar comparisons have been made for the lower portion of Delta and will be reported elsewhere. (37)

It is recognized that certain parameters in the model have been estimated from the data which are then used to demonstrate the veracity of the model. The parameters used in the verification were either obtained from prototype measurements or estimated from the range of values reported in the literature. The refinement of the later set of parameters was made by comparing the observed 1966 data and calculated results. The model was further verified by applying the parameters obtained in the 1966 analysis to the data of the following year. The parameter values finally used were all within the ranges of reported literature values. The agreement achieved between the available data and the model calculations is sufficiently encouraging to prompt further effort in this direction.

The primary aim of this investigation, that of presenting a useful model as a component in solution of the eutrophication problems, in our opinion, has been achieved. The resulting equations are admittedly complex and require numerical methods for solution. It is anticipated as with all modeling activities the structure presented herein will be expanded and modified in the future to incorporate additional features of the eutrophication phenomena. However, the initial application of these equations to an actual problem area with specific eutrophication problems has been sufficiently successful to support its engineering use as a preliminary step in the assessment of a potential or actual eutrophication problem.

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TABLE I
MAXIMUM GROWTH RATES AS A FUNCTION OF TEMPERATURE

Reference	Organism	Temperature °C	Saturated Growth Rate K' (base _e , day ⁻¹)
(60)	Chlorella ellipsoidea (Green Alga)	25. 15.	3.14 1.2
(68)	Nannochloris atomus (marine flagellate)	20. 10.	2.16 1.54
(54)	Nitzschia closterium (marine diatom)	27. 19. 15.5 10.	1.75 1.55 1.19 0.67
(46)	Natural Association	4. 2.6	0.63 0.51
(34)	Chlorella pyrenoidosa	25.	1.96
(34)	Scenedesmus quadricauda	25.	2.02
(52)	Chlorella pyrenoidosa	25	2.15
(52)	Chlorella vulgaris	25	1.8
(52)	Scenedesmus obliquus	25	1.52
(52)	Chlamydomonas reinhardtii	25	2.64
(53)	Chlorella pyrenoidosa	10	0.2
	(synchronized culture)	15	1.1
	(high temperature strain)	20	2.4
		25	3.9

TABLE II
MICHAELIS CONSTANTS FOR NITROGEN AND PHOSPHORUS

Reference	Organism	Nutrient	Michaelis Constant ($\mu\text{g/l}$ as N or P)
(63)	<i>Chaetoceros gracilis</i> (marine diatom)	PO_4	25.
(18)	<i>Scenedesmus gracile</i>	total N	150.
		total P	10.
(45)	Natural Association	PO_4	6. (*)
	<i>Microcystis Aeruginosa</i> (Blue-Green)	PO_4	10. (*)
(20)	<i>Phaeodactylum tricornutum</i>	PO_4	10.
(21)	Oceanic Species	NO_3	1.4 - 7.0
	" "	NH_3	1.4 - 5.6
(21)	Neritic Diatoms	NO_3	6.3 - 28.
	" "	NH_3	7.0 - 120.
(21)	Neritic or Littoral Flagellates	NO_3 NH_3	8.4 - 130. 7.0 - 77.
(29)	Natural Association Oligotrophic	NO_3 NH_3	2.8 1.4 - 8.4
(29)	Natural Association Eutrophic	NO_3 NH_3	14. 18.

(*) Estimated

TABLE III
ENDOGENOUS RESPIRATION RATES OF PHYTOPLANKTON⁽¹⁶⁾

Organism	Temperature °C	Endogenous Respiration Rate (Day ⁻¹) (base _e)
Nitzschia closterium	6.	.035
	35	.170
Nitzschia closterium	20	.08
Coscinodiscus excentricus	16	.075
	16	0.11
Natural Association	2.	0.03
	18.	0.12
	2.0	0.024 ± 0.012
	17.9	0.110 ± 0.007

TABLE IV
GRAZING RATES OF ZOOPLANKTON

Ref.	Organism	Reported Grazing Rate	Grazing Rate (1/mg. dry wt.-day)
<u>Rotifer</u>			
(23)	Brachionus calyciflorus	0.05 - 0.12 (b)	0.6 - 1.5
<u>Copepod</u>			
(46)	Calanus sp.	67 - 208 (a)	0.67 - 2.0
(1)	Calanus finmarchicus	27 (b)	0.05
(33)	Rhincalanus nasutus	98 - 670 (b)	0.3 - 2.2
(2)	Centropages hamatus		0.67 - 1.6
<u>Cladocera</u>			
(67)	Daphnia sp.		1.06
(5)	Daphnia sp.		0.2 - 1.6
(48)	Daphnia magna	81 (b)	0.74
(31)	Daphnia magna	57 - 82 (b)	0.2 - 0.3
<u>Natural Association</u>			
(46)	Georges Bank	80 - 110 (a)	0.8 - 1.10

(a) ml/mg wet wt. - day

(b) ml/ animal - day

TABLE V

ENDOGENOUS RESPIRATION RATE OF ZOOPLANKTON

Ref.	Organism	Plotting Symbol	Temperature °C					Respiration Rate ml O ₂ /mg. dry weight - day				
(4)	Cladocera	X	18.	4								
			14.2	2.7								
(4)	Copepods	+	18	4								
			12.2	3.8								
(4)	Copepods	■	18	16	12	8	4					
			8.2	6.5	5.2	4.1	3.4					
(44)	Galanus finmarchicus	▲	20	15	10	4						
			4.2	2.3	1.4	1.3						
(9)	Diaptomus leptopus	▼	25	20	15	10	5					
			12.1	7.4	5.3	2.8	2.5					
(9)	D. clavipes	●	25	20	15	10	5					
			12.5	8.5	5.1	2.4	1.8					
(9)	D. siciloides	□	25	20	15	10	5					
			21.	13.5	7.8	5.5	4.8					
(9)	Diaptomus sp.	○	25	20	15	10	5					
			4.3	3.0	2.1	1.7	1.1					

TABLE VI
 DRY WEIGHT PERCENTAGE* OF CARBON, NITROGEN AND PHOSPHORUS IN PHYTOPLANKTON (59)

Phytoplankter	% Carbon		% Nitrogen		% Phosphorus	
	Average	Range	Average	Range	Average	Range
Myxophyceae	36.	(28.-45.)	4.9	(4.5-5.8)	1.1	(0.8-1.4)
Chlorophyceae	43.	(35.-48.)	7.8	(6.6-9.1)	2.9	(2.4-3.3)
Dinophyceae	43.	(37.-47.)	4.4	(3.3-5.0)	1.0	(0.6-1.1)
Chrysophyceae	40.	(35.-45.)	8.4	(7.8-9.0)	2.1	(1.2-3.0)
Bacillariophyceae	33.	(19.-50)	4.9	(2.7-5.9)	1.1	(0.4-2.0)

*The units are (mg of carbon, nitrogen, or phosphorus)/(mg dry weight of phytoplankton) x 100%.

TABLE VII
PARAMETER VALUES FOR THE MOSSDALE MODEL

Notation	Description	Parameter Value
K_1	Saturated growth rate of phytoplankton	0.1 day ⁻¹ °C
I_s	Light Saturation Intensity for phytoplankton	300. ly/day
k'_e	Extinction Coefficient	4.0 m ⁻¹
H	Depth	1.2 m
K_m	Michaelis constant for total inorganic nitrogen	0.025 mg - N/l
f	Photoperiod	0.5 + sin (0.0172(t - 165.)) day
K_2	Endogenous respiration rate of phytoplankton	0.005 day ⁻¹ °C ⁻¹
C_g	Zooplankton grazing rate	0.13 l/mg - C - day
P_o	Influent phytoplankton chlorophyll concentration	5.0 µg - Chl/l
a_{ZP}	Zooplankton conversion efficiency	0.6 mg - C/mg - C
K_{mP}	Phytoplankton Michaelis constant	60. µg - Chl/l
D_Z	Zooplankton death rate	0.075 day ⁻¹
Z_o	Influent zooplankton carbon concentration	0.05 mg - C/l
a_{NP}	Phytoplankton nitrogen-carbon ratio	0.17 mg - N/mg - C
C/Chl	Phytoplankton carbon to total chlorophyll ratio	50. mg - C/mg - Chl
N_o	Influent total organic nitrogen concentration	0.1 mg - N/l
W_N	Direct discharge rate of nitrogen	12500. lbs/day
V	Segment volume	9.7 x 10 ⁸ ft. ³
Phytoplankton total cell count/phytoplankton		100 cells/ml = 1.75 µg-Chl/l
Zooplankton count/zooplankton carbon ratio		10 ⁴ No./l = 1.30 mg - C/l

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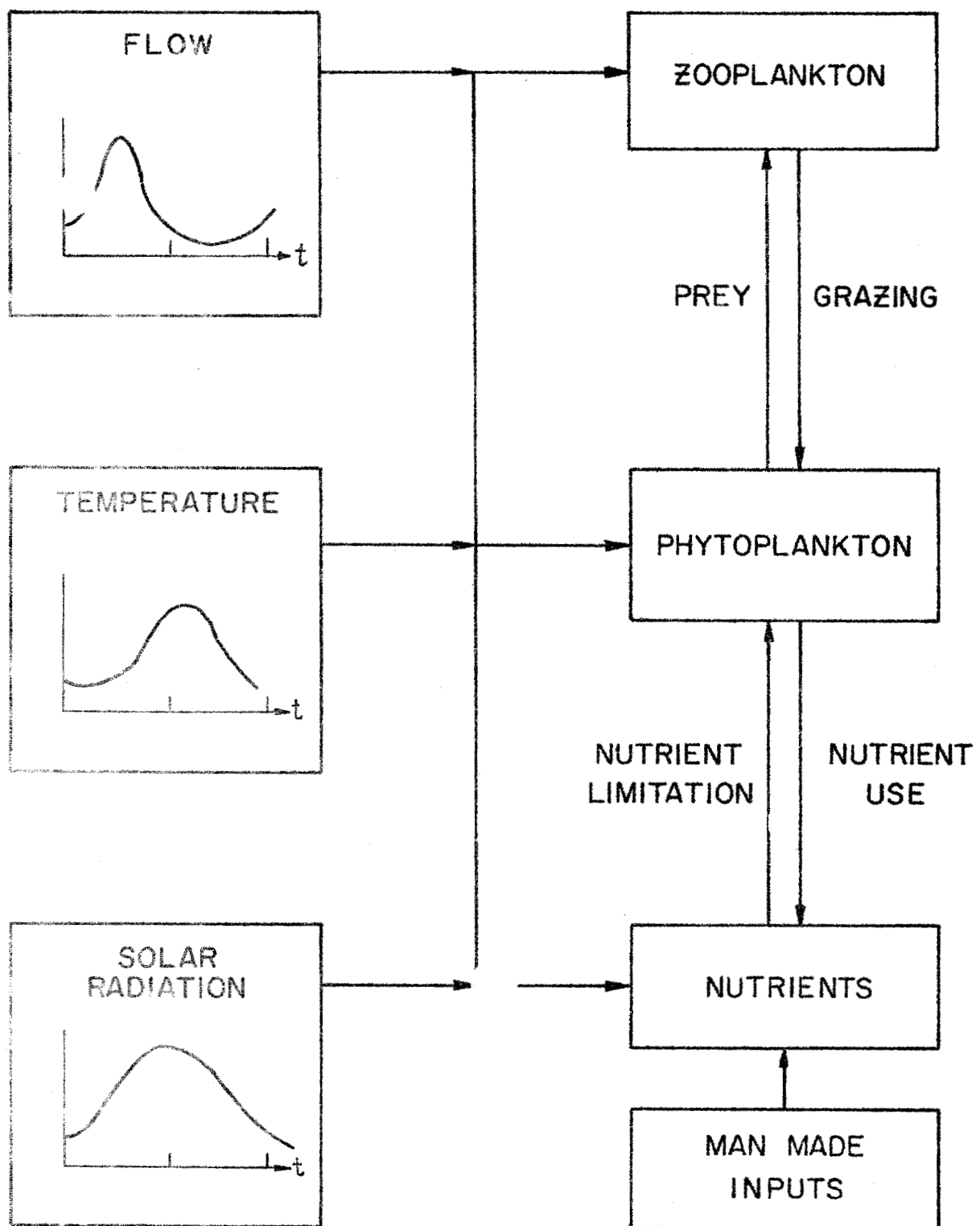


Fig. 1. Interactions: environmental variables and the phytoplankton, zooplankton, and nutrient systems.

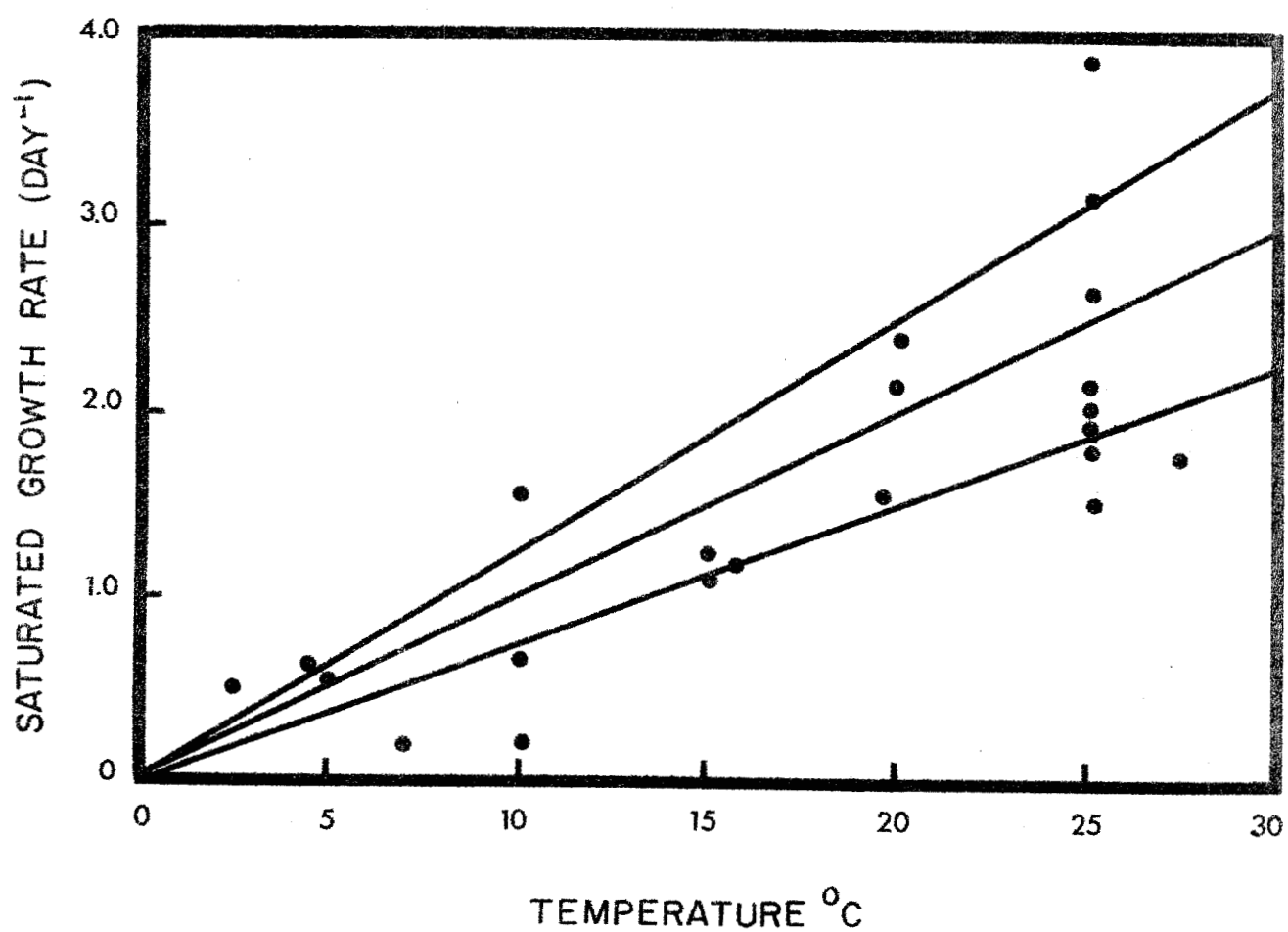


Fig. 2. Phytoplankton saturated growth rate (base e) as a function of temperature.

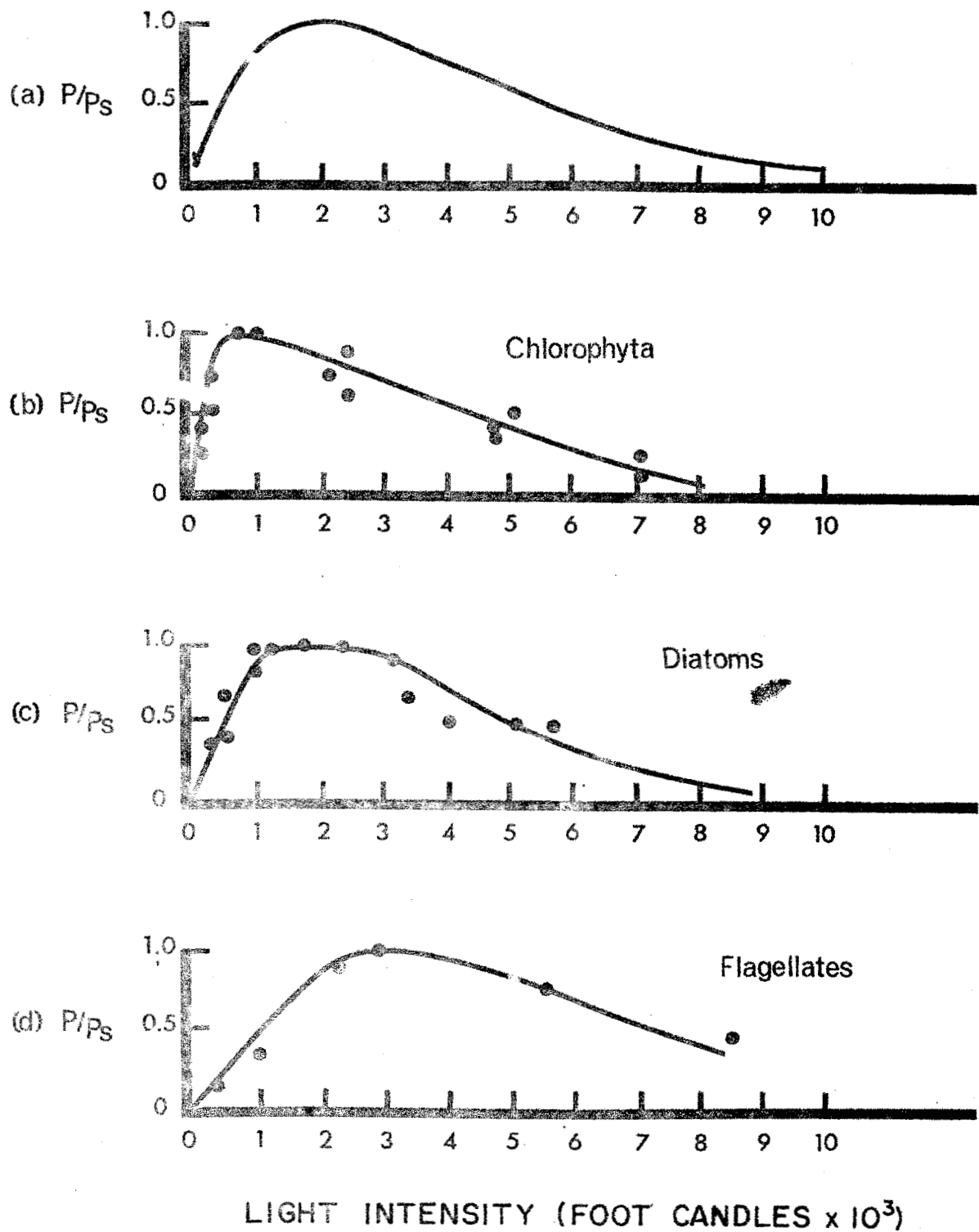


Fig. 3. Normalized rate of photosynthesis versus incident light intensity: (a) Theoretical curve after Steele⁽⁵⁷⁾; (b,c,d) Data after Ryther⁽⁴⁹⁾.

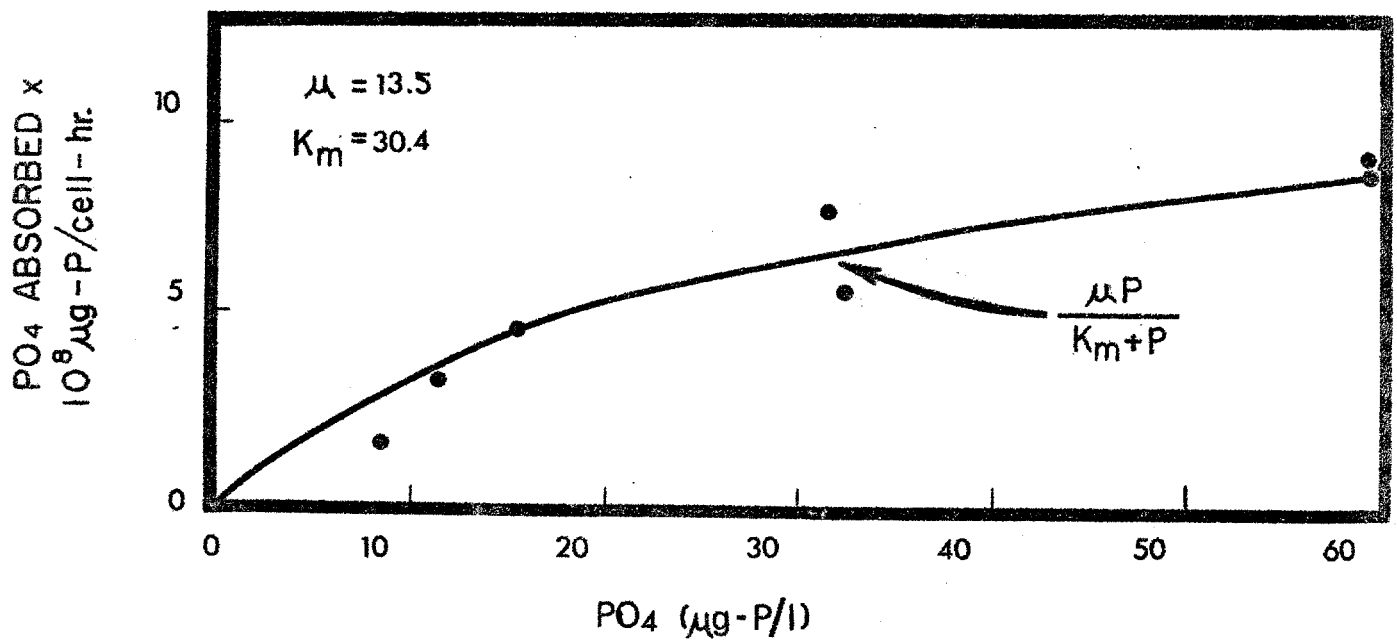
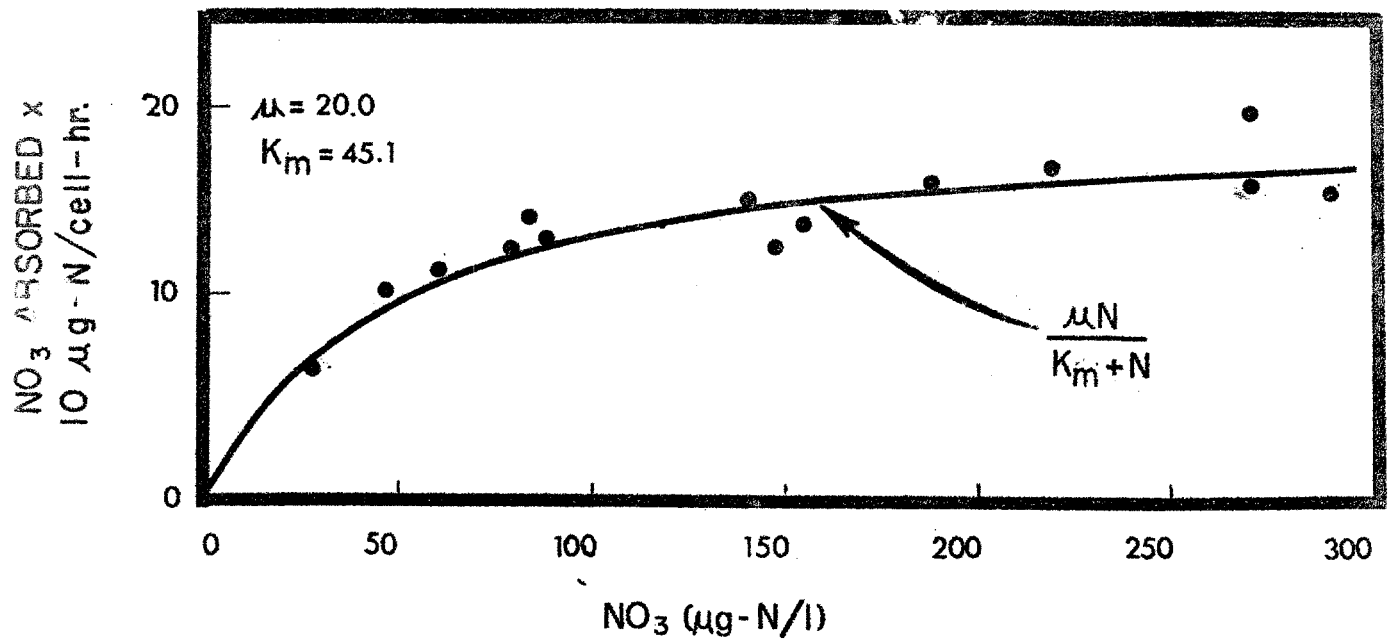


Fig. 4. Nutrient absorption rate as a function of nutrient concentration: comparison of Michaelis-Menton theoretical curve with data from Ketchum. (24)

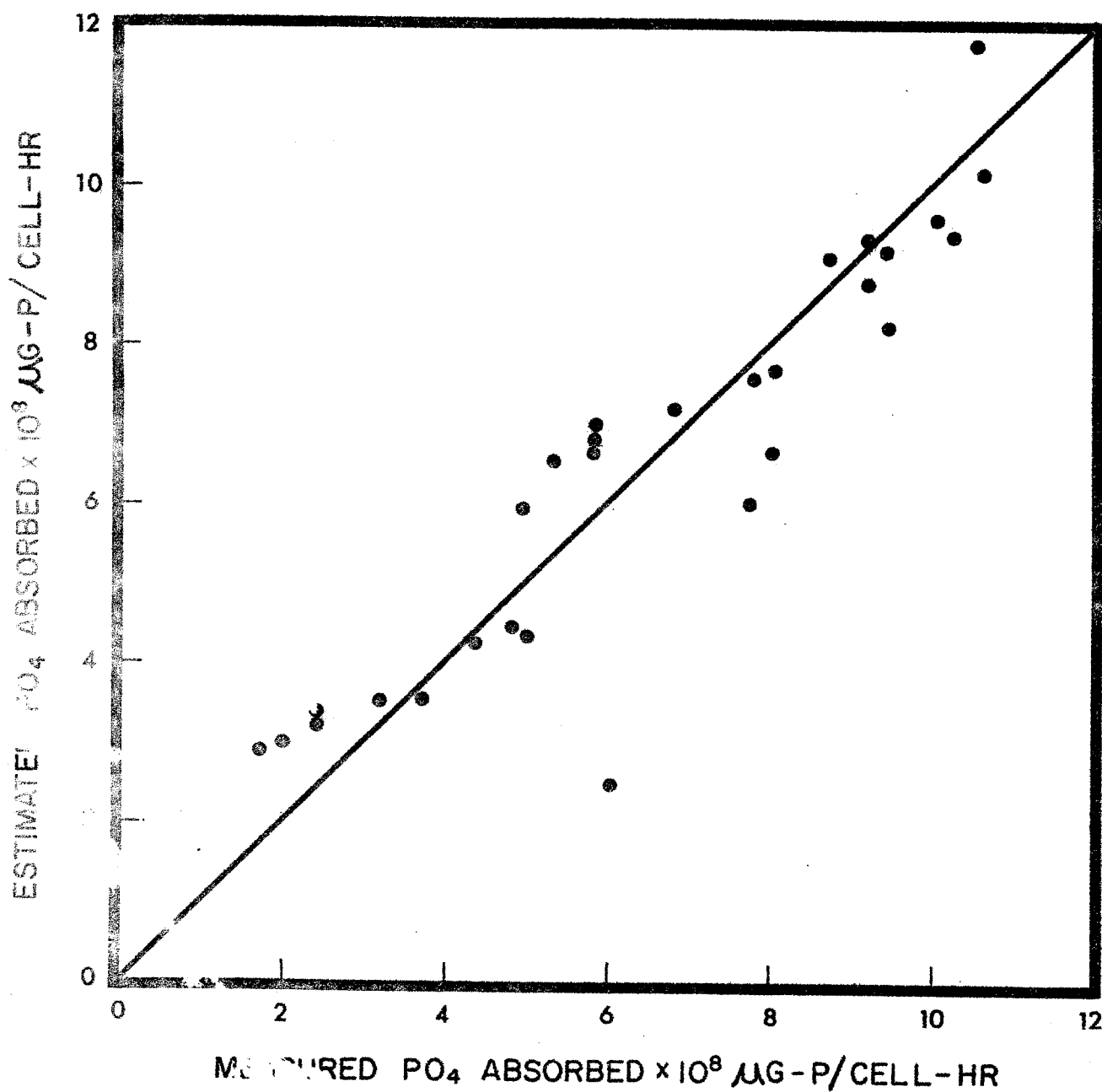


Fig. 5. Measured phosphate absorption rate, after Ketchum⁽²⁴⁾ versus phosphate absorption rate estimated using $\frac{1}{4}N_1N_2/(K_{m1} + N_1)(K_{m2} + N_2)$ where N_1 is the nitrate and phosphate concentration.

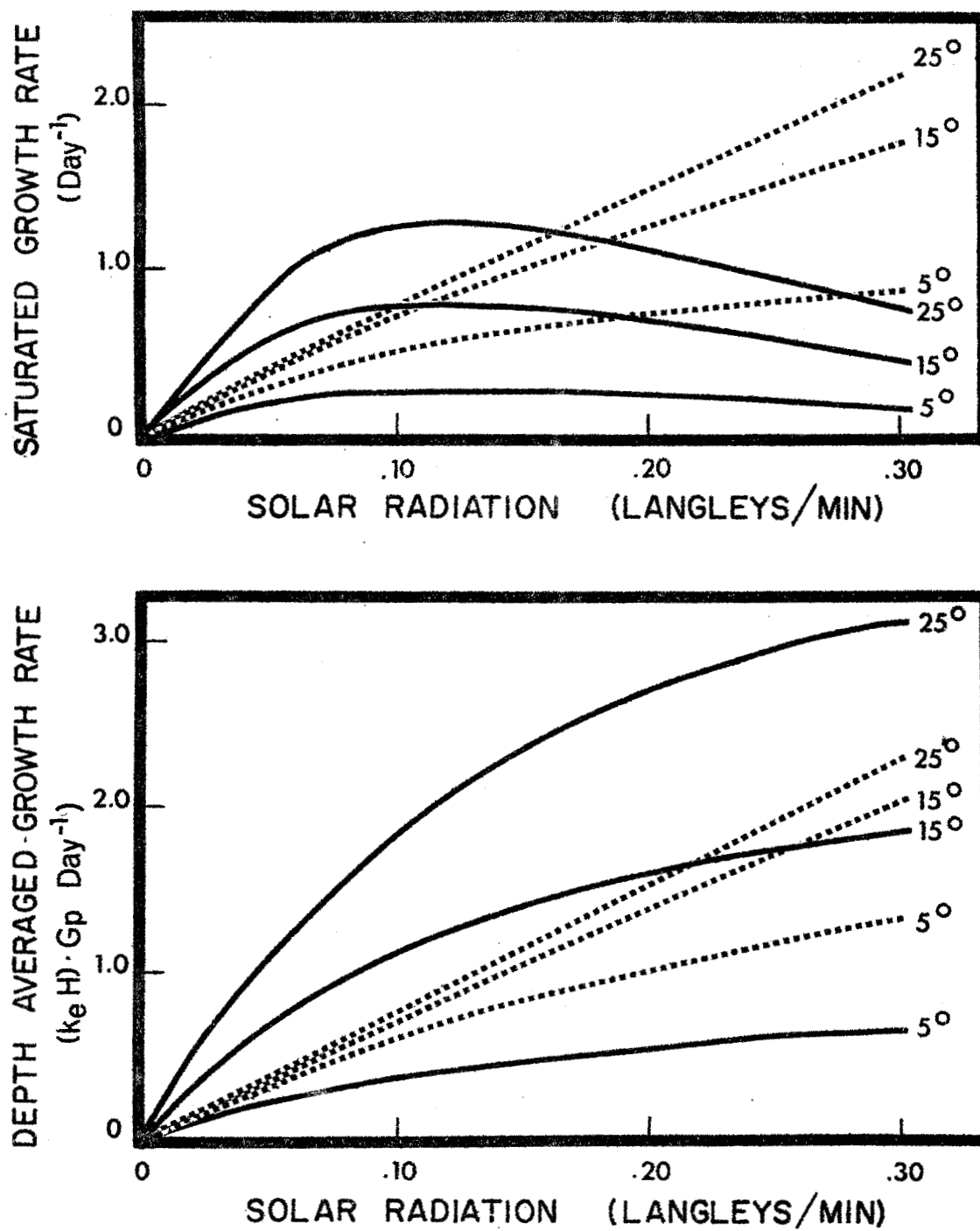


Fig. 6. Comparison of phytoplankton growth rates as a function of incident solar radiation intensity and temperature.

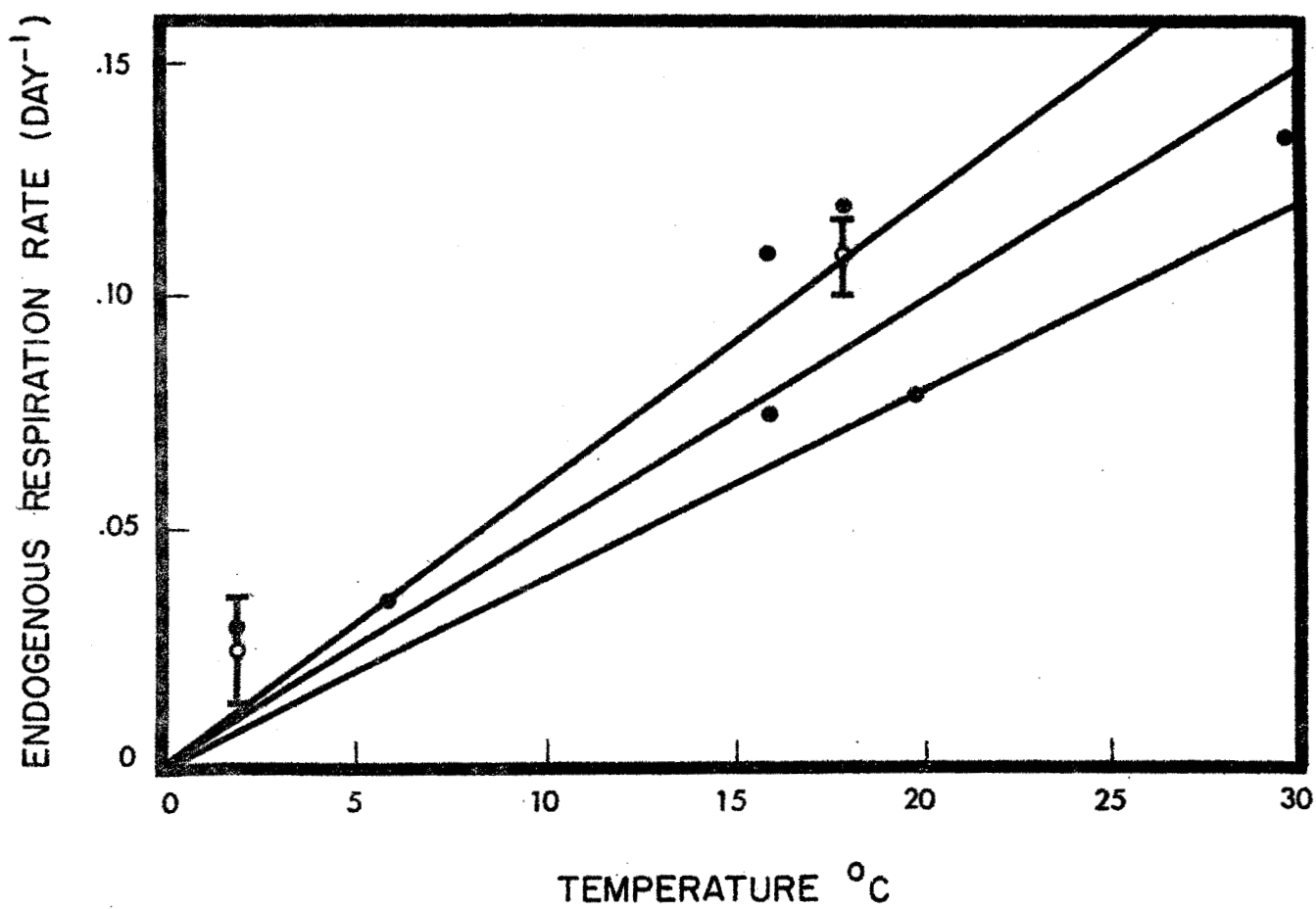


Fig. 7. Endogenous respiration rate of phytoplankton versus temperature after Riley (46).

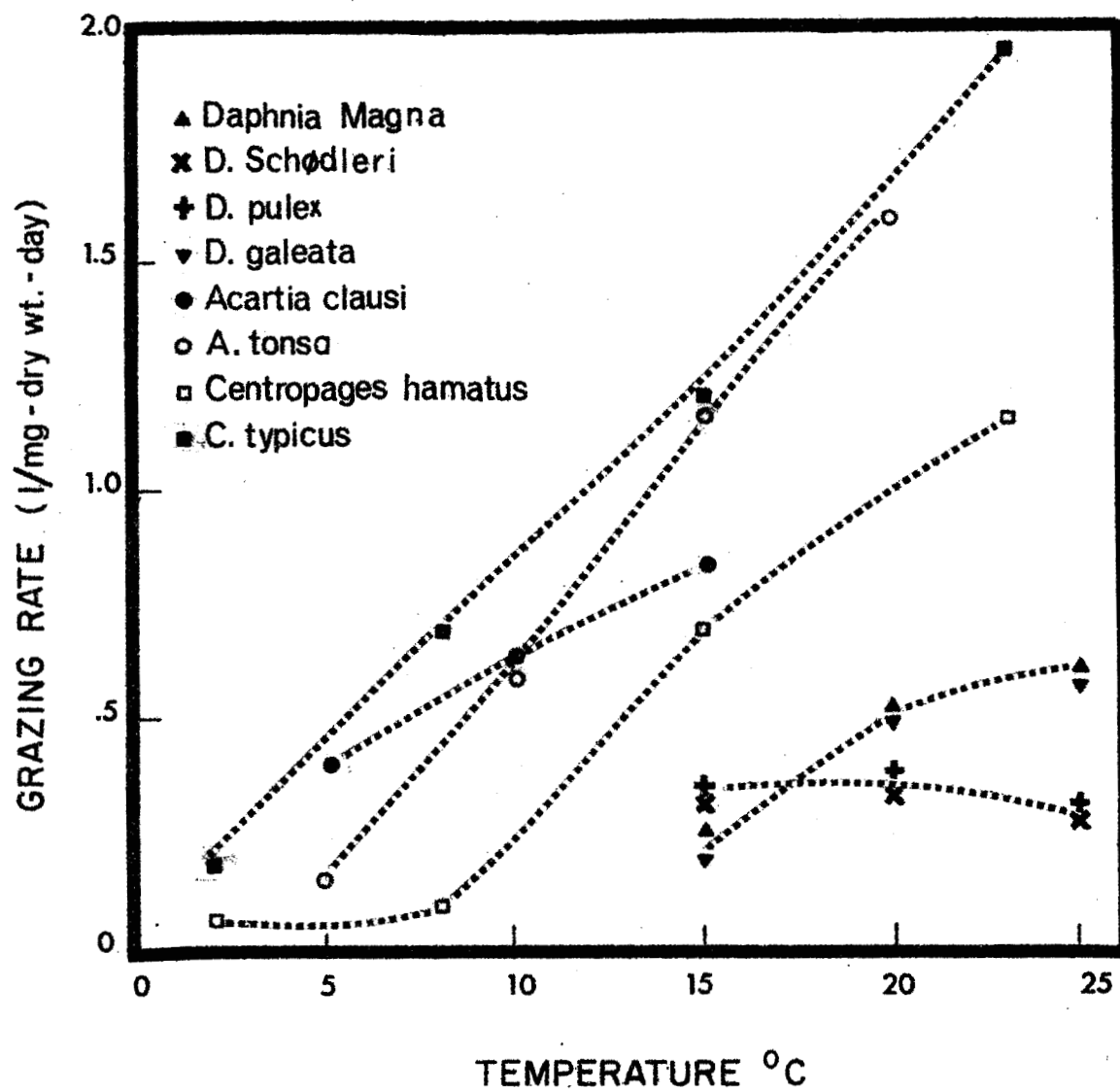


Fig. 8. Grazing rates of zooplankton versus temperature

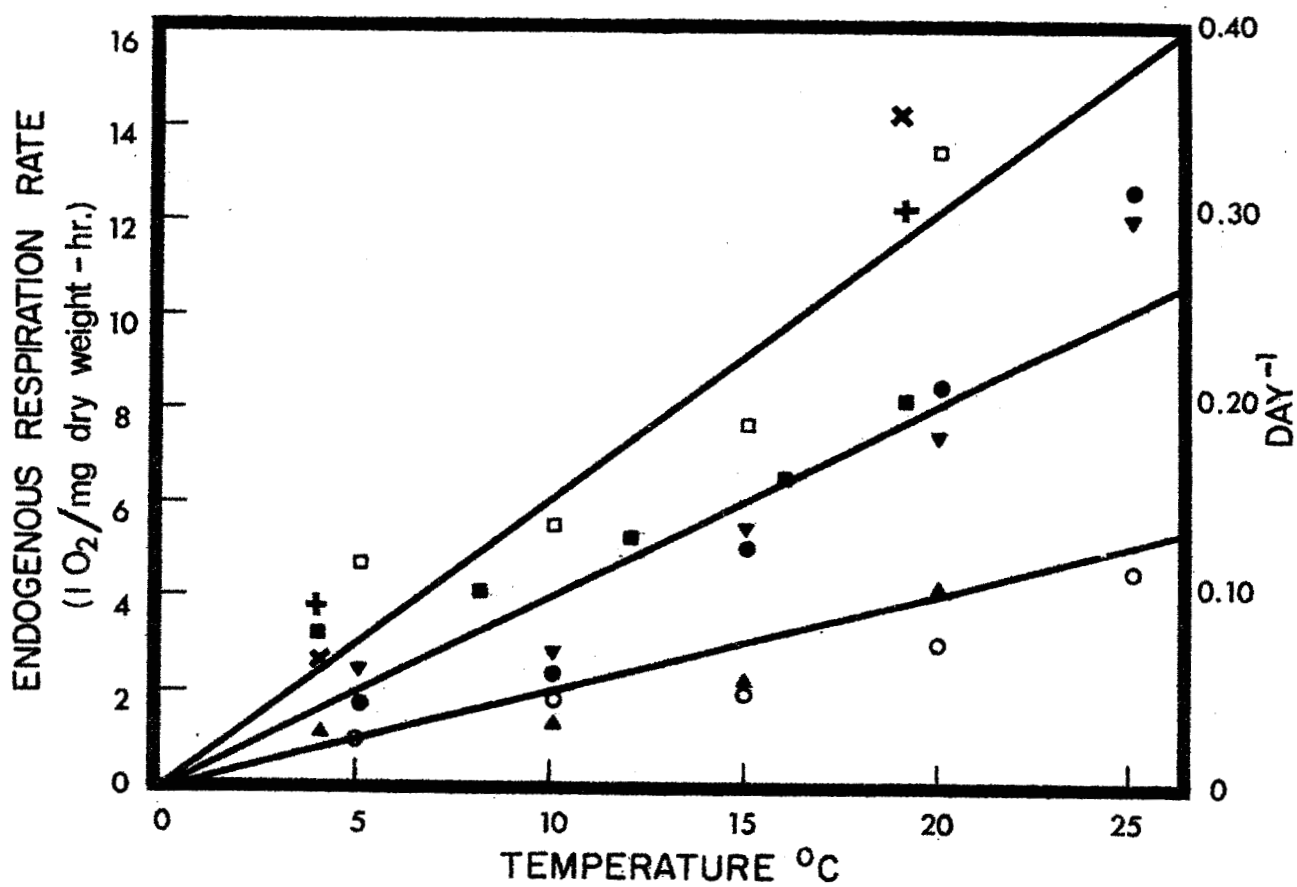


Fig. 9. Endogenous respiration rate of zooplankton versus temperature.

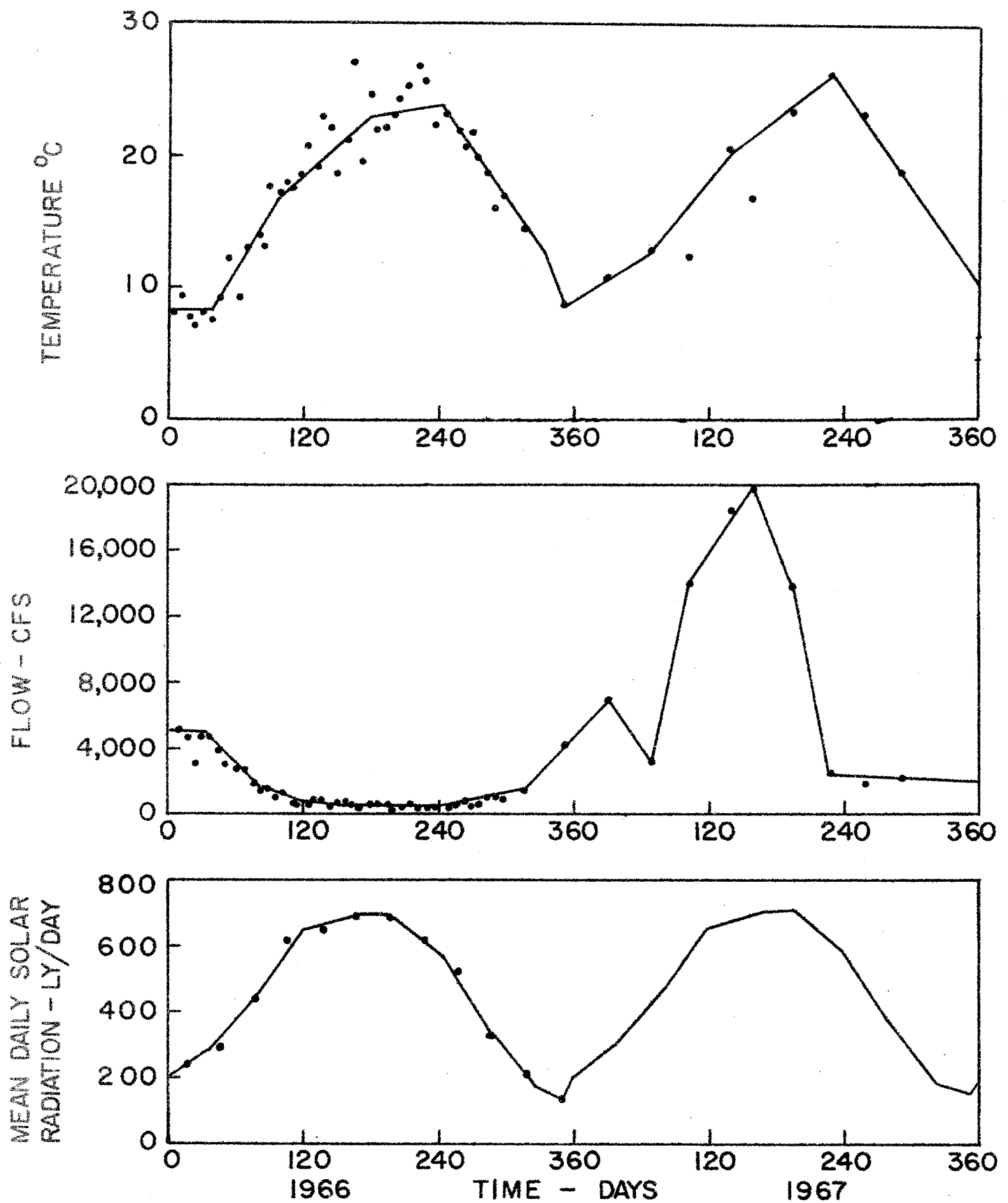


Fig.10. Temperature, flow and mean daily solar radiation.
San Joaquin River, Mossdale, 1966-1967.

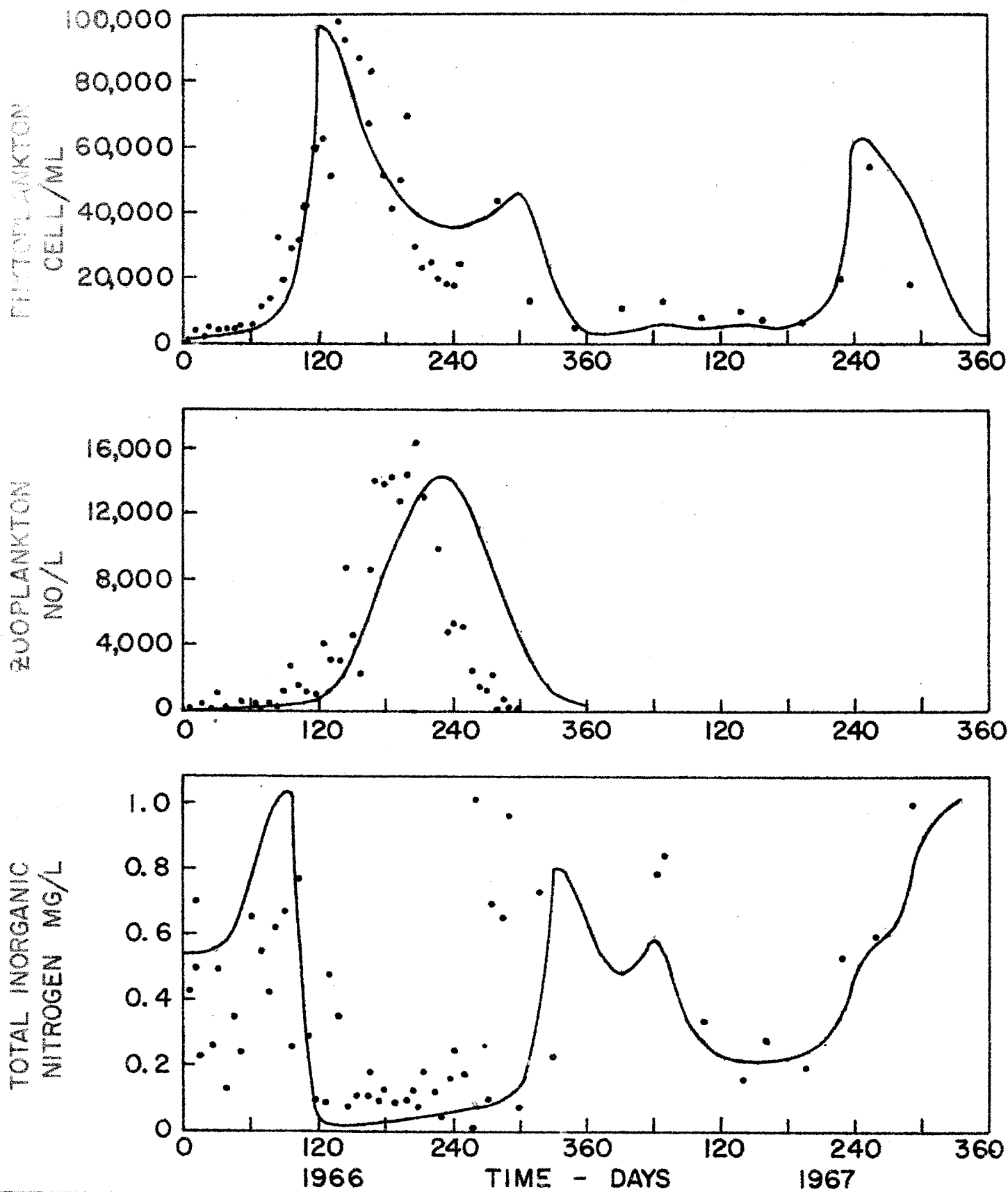


Fig.11. Phytoplankton, zooplankton, and total inorganic nitrogen. Comparison of theoretical calculations and observed data. San Joaquin River, Mossdale, 1966-1967.

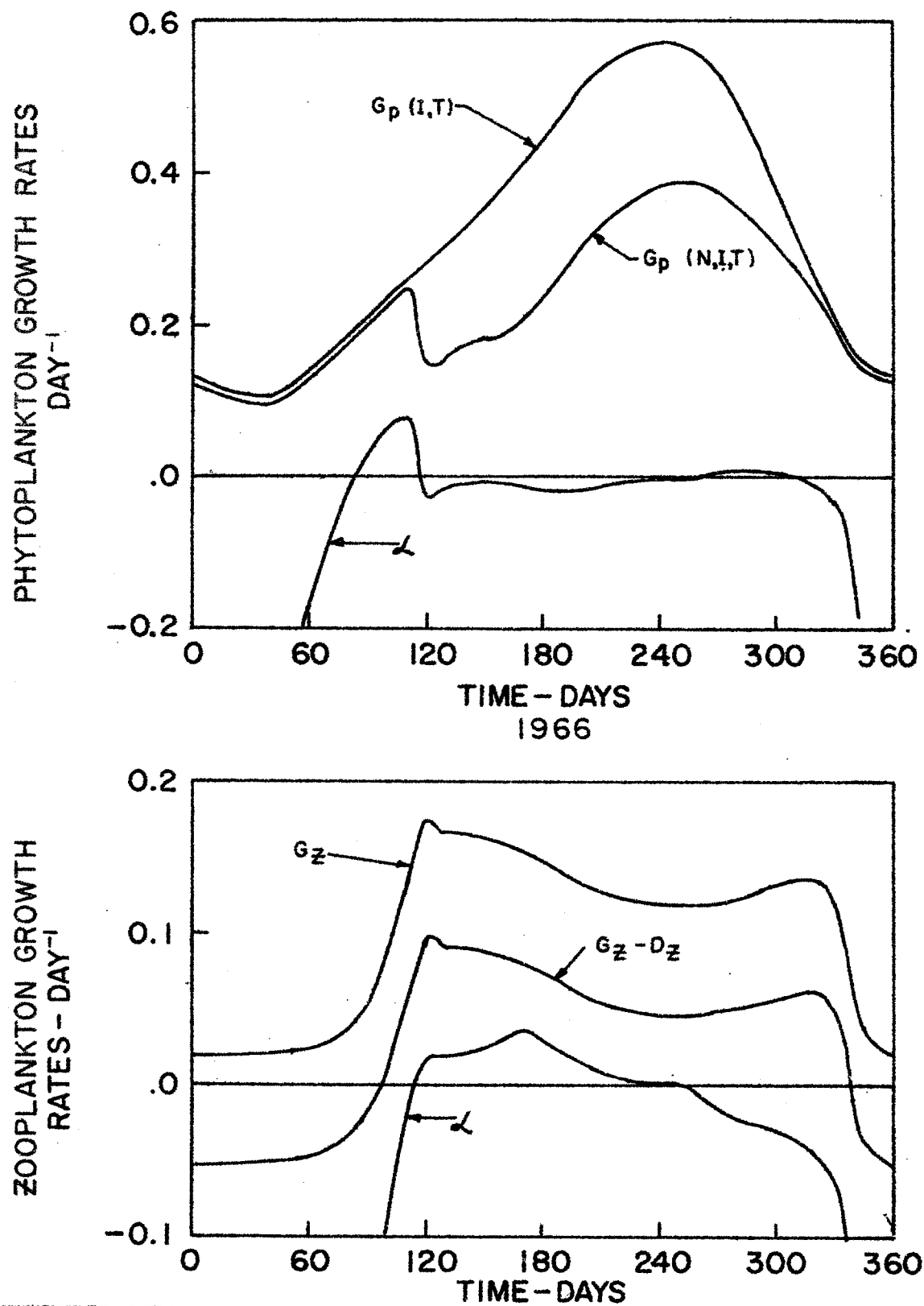


Fig.12. Theoretical growth rates for phytoplankton and zooplankton populations.