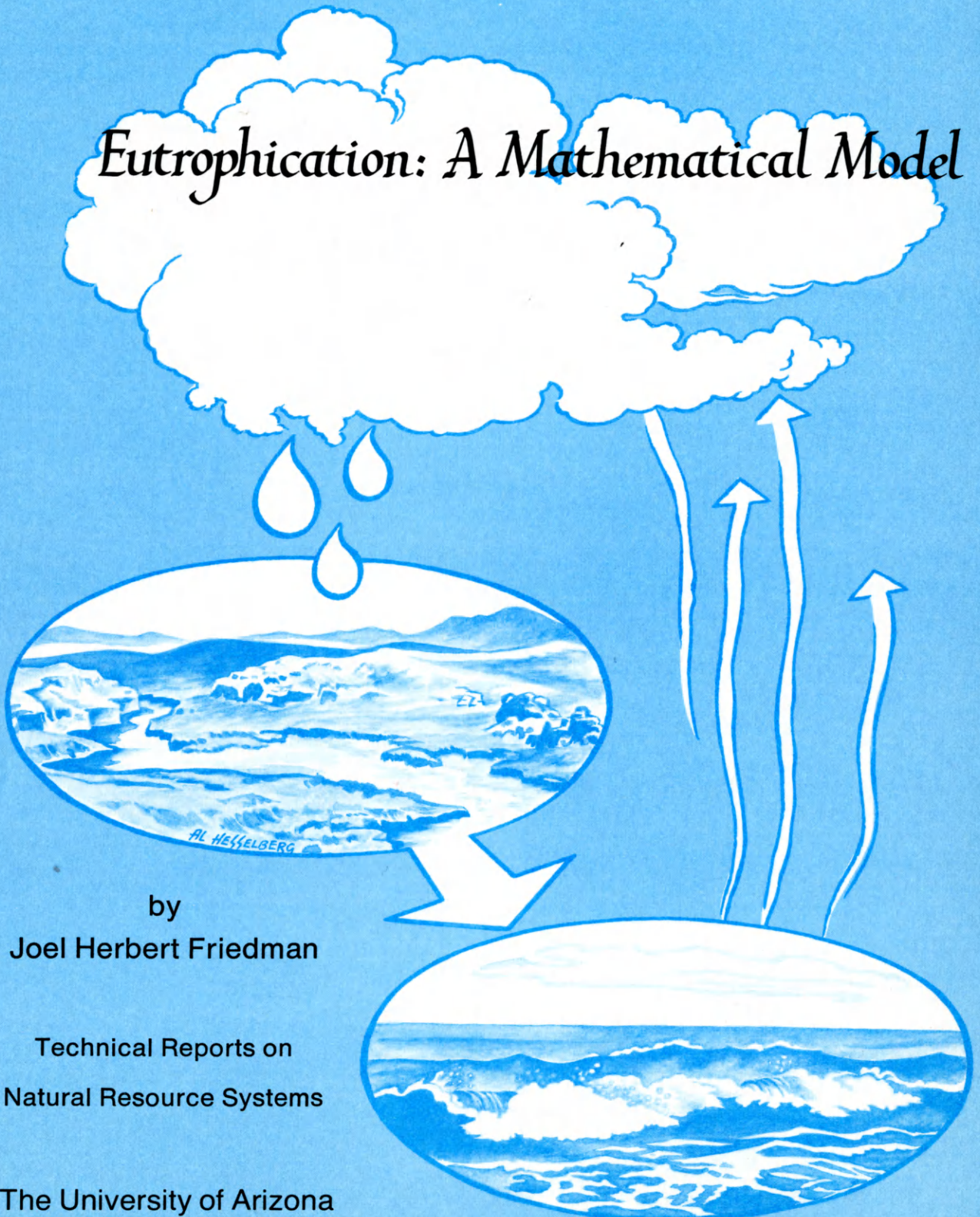


Eutrophication: A Mathematical Model



by
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Natural Resource Systems

The University of Arizona
Tucson, Arizona 85721

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PREFACE

This report constitutes the Master of Science thesis of the same title completed by the author in May, 1973, and accepted by the Department of Systems and Industrial Engineering. It is the result of a joint research project on "Decision analysis of watershed management alternatives," supported in part by the United States Department of the Interior, Office of Water Resources Research, as authorized under the Water Resources Research Act of 1964.

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ABSTRACT

Various approaches to modeling phytoplankton-zooplankton-nutrient interactions have been investigated. A stochastic birth-death model was developed to describe changes in phytoplankton and zooplankton population levels at a given point. The stochastic birth-death model was combined with a deterministic mass balance of limiting nutrient concentration to form an over-all system theoretic model that enables one to use Monte Carlo simulation to study the problem of eutrophication. A comparison made between this modeling approach and the standard differential equation approach suggested that further investigation was desirable, particularly in the area of model calibration.

CHAPTER 1

MOTIVATION

As man's power to affect his environment increases, so does his destructive potential. It thus becomes increasingly more important for man to be able to evaluate the probable results of a given set of actions. One area in which this evaluation is now becoming necessary is that of eutrophication.

Eutrophication (National Academy of Sciences 1969) refers to a natural or artificial addition of nutrients to a body of water as well as the effects of increased nutrients. Although inherently a natural process relating directly to the aging of a lake, it can be greatly accelerated by man. Limnologists are uncertain as to whether consequences of natural eutrophication parallel those of eutrophication accelerated by man, or whether eutrophication is reversible within a reasonable time span. This latter uncertainty underscores the urgent need to understand eutrophication and to be able to predict the effects of artificially adding nutrients to lakes, streams and rivers.

A brief look at some of the causes and consequences of accelerated eutrophication will serve to further

emphasize the critical need for a better understanding of the eutrophication process. Artificial causes of excess nutrients include human sewage, industrial wastes, drainage from farm lands, and runoff from urban areas. With increased population and industrial growth, coupled with intensified agricultural production and increased usage of shore properties, we can see that the number of potential sources of excess nutrients that cause eutrophication is rapidly growing. The consequences of accelerated eutrophication stem largely from excessive algal growth which destroys the balance of life in an aquatic ecosystem. Algal scums and undesirable odors may be produced, thereby greatly affecting the recreational use of the lake (Hasler 1947). Some species of algae may modify the taste of the water so as to affect its use as a water supply, such as in the case of a population of *Synedra* in Lake Skaneateles near Syracuse, New York (Jackson and Meier 1966). The excess algae may attract annoying insects such as the Clear Lake gnat that inhabits Lake County, California, as reported by Lindquist and Deonier (1942). An algal mass may die, sink to the bottom, and deplete a significant portion of the dissolved oxygen at lower levels, thus tending to adversely affect fish populations (Richards 1967). This combination of severe consequences and potentially larger sources of excess nutrients provide

sufficient motivation for a large-scale attack on the problem of eutrophication.

Having established a firm motivation for studying eutrophication, we will continue by briefly summarizing some of the literature relevant to modeling of eutrophication (Chapter 2). We will then examine a generalized aquatic ecosystem and the simplifications and approximations required for modeling purposes (Chapter 3); and, finally, after giving an introduction to stochastic processes (Chapter 4), we will develop a system theoretic model of eutrophication (Chapter 5). Conclusions and suggestions for further work are contained in Chapter 6.

CHAPTER 2

LITERATURE REVIEW

Our literature review will be divided into two sections. First, we will concern ourselves with past attempts at modeling eutrophication, and then we will examine the past uses of Monte Carlo simulation as applied to biological situations.

Previous modeling attempts have usually been based upon the conservation of mass expressed in terms of a set of simultaneous differential equations. The earliest extensive investigation of phytoplankton population dynamics using this approach is that of Riley, Stommel, and Bumpus (1949). They obtain the expression:

$$\log \left(\frac{G_p}{k' I_0 - G_p} \right) = 22.884 + \log v_p - \log I_0 - \frac{6573.8}{T'}$$

where

G_p is the growth rate of phytoplankton (/day),

k' is 7.6,

I_0 is the average daily incident solar radiation (langleys/minute),

T' is the water temperature in degrees Kelvin, and

v_p is the nutrient reduction factor defined in terms of the phosphate concentration N_p as follows:

$$v_p = 1.0 \text{ if } N_p > .55 \text{mg.-at./m}^3$$

$$= \frac{N_p}{.55} \text{ if } N_p \leq .55 \text{mg.-at./m}^3$$

Their work involved the assumption of a steady state environment, thus severely limiting the applicability of the model.

Considerable work has been reported since then. Davidson and Clymer (1966) developed from mass balance considerations a set of differential equations of the form:

$$\frac{1}{P} \dot{P} = K_1 N^{\text{LIM}} - K_2 Z - K_3 - K_4 T$$

$$\frac{1}{Z} \dot{Z} = K_5 P - K_6$$

$$\dot{N} = K_7 - K_8 P, \quad N \geq 0$$

$$T = K_9 - K_{10} \cos(\pi t/6)$$

$$I = K_{11} - K_{12} \cos(\pi t/6)$$

where

P is the phytoplankton population density,

Z is the zooplankton population weight density,

N is the limiting nutrient concentration,

T is the water temperature in degrees Centigrade,

I is the incident solar radiation,

N^{LIM} is the nutrient limited from above,

t is the time in months, zero at Jan. 1, and

K_i are constants.

Chen and Orlob (1968, 1972) developed a set of differential equations based on the conservation of mass. Their model explicitly includes such factors as bacterial decomposition of detritus, a division of algae into two groups by size, and the toxicity of the water. A division of the lake into horizontal slices permits modeling such factors as vertical migration and thermal gradients.

DiToro, O'Connor, and Thomann (1970) also use a set of differential equations based on the conservation of mass. Their model is based largely on the previous models of Riley et al. (1949) and Steele (1965) and is used to describe a shallow reach of the Sacramento River and a downstream estuary. Park and Wilkinson (1971) adopt the same approach and apply the model to Lake George in New York. In their application, more than one nutrient was considered, and zooplankton were divided into two categories, herbivorous and carnivorous.

Everett (1972) uses multiple linear regression to study the chemical and biological properties of Lake Mead in Arizona.

None of these models incorporate stochastic fluctuations, and most of them are based on a differential equation approach. Since we will be applying a stochastic model and running a Monte Carlo simulation, it seems appropriate to discuss briefly some of the biological applications of stochastic models and Monte Carlo techniques.

Stochastic models are frequently useful because ordinarily it is impossible to observe all of the details of the phenomena of interest, yet enough external manifestations of the phenomena can be observed so as to create a stochastic model. Neyman and Scott (1959) developed a stochastic model of the competition between two species of flour beetles. If the species shared the same habitat, inevitably one species or the other would become extinct, but not always the same species. Obviously, a deterministic model was insufficient for this case. Bartlett (1957) used Monte Carlo techniques to generate artificial realizations of this competitive case as well as the classical predator-prey interaction and other related processes. The classical predator-prey interaction is of particular interest because in the deterministic case there exists an equilibrium cycle, while in the stochastic case extinction occurs with probability one.

Engstrom-Heg (1970) uses Monte Carlo techniques to examine the effect of treating the coefficients of a time difference equation model of population interactions as varying randomly because of climatic fluctuations. Beyer, Harris, and Ryan (1972) use Monte Carlo simulation to examine the extinction probability of the wolf population in the Isle Royale biome. The success with which these stochastic models have been applied is encouraging. The

results of Beyer et al. (1972), for instance, showed that their model had good predictive value for up to ten years.

This brief review of the literature seems to indicate a twofold advantage of a stochastic model over the deterministic differential equation model that is so prevalent. The first advantage is exemplified by cases where there is either insufficient information about the phenomenon of interest or some inherent randomness in the process that makes it impossible to create a deterministic model. The second advantage arises from the simplicity of the Monte Carlo technique as compared to solving a system of nonlinear differential equations. The second advantage is the prime motivating factor for our model. We can now proceed to the discussion of our model of eutrophication.

CHAPTER 3

CONCEPTUAL MODEL

We will begin by discussing the simplified conceptual aquatic model given in Figure 1. It is easy to devise much more complicated conceptual models (Everett 1972, and Park and Wilkinson 1971), but it is necessary to take a simplified approach because of the lack of a concrete understanding of all of the aquatic ecosystem interactions. We lump together all species of phytoplankton into one group, and all species of zooplankton into another group because efforts at modeling specific species of either are still in their infancy. Such factors as phytoplankton affinity for certain types of nutrients and zooplankton affinity for certain types of phytoplankton are largely responsible for these modeling difficulties.

Frequently in other models the zooplankton group is divided into two categories: the herbivorous zooplankton which rely on phytoplankton for their sustenance, and the carnivorous zooplankton which prey upon the herbivorous zooplankton. The uncertainty involved in the feeding mechanisms at this and higher trophic levels (DiToro et al. 1970) encourages the modeler to break the food chain at the herbivorous zooplankton level and assume that the

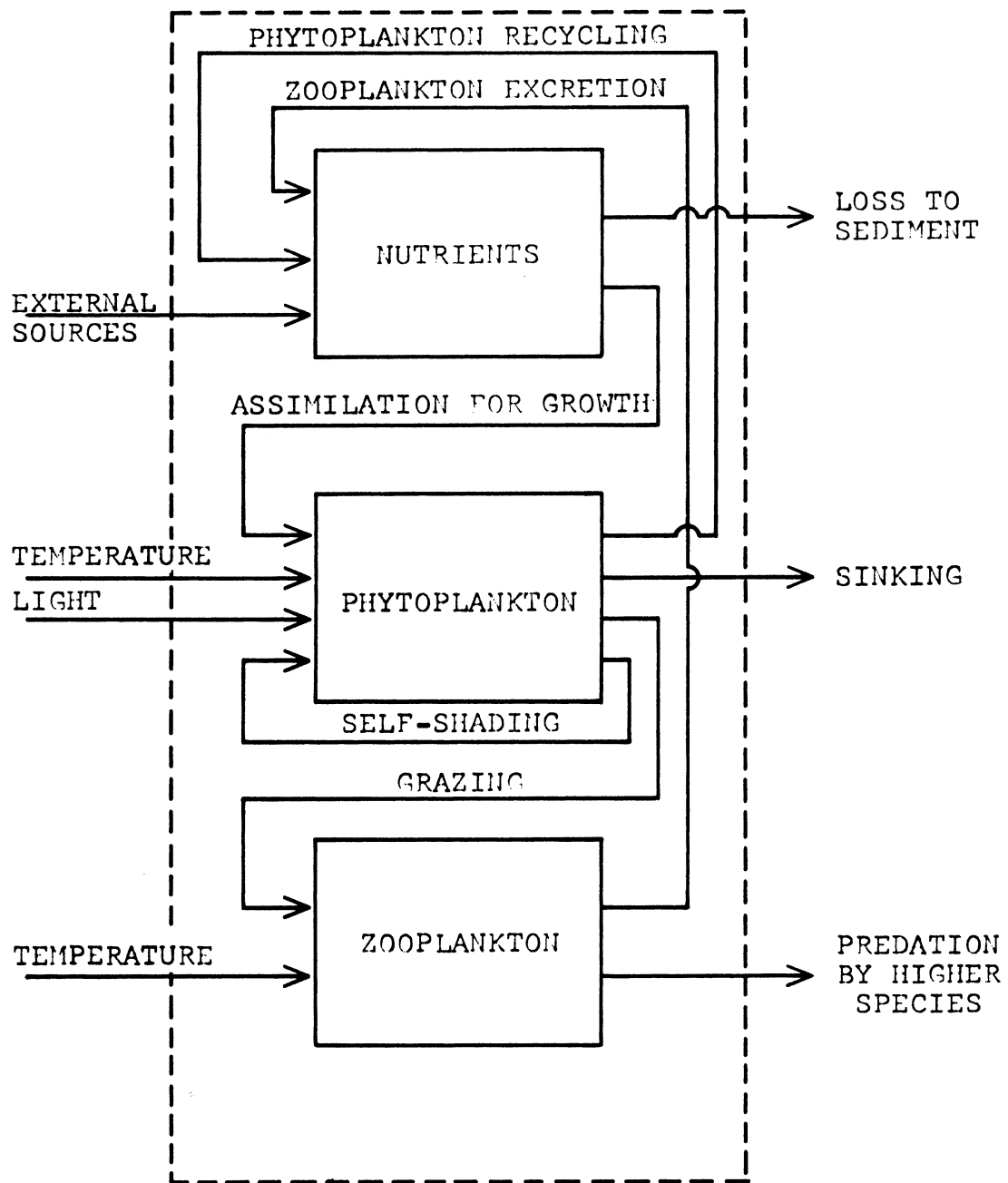


Figure 1. Simplified Aquatic Model

herbivorous zooplankton death rate is a constant. The model can be modified very easily to include higher species for cases where this assumption is not valid.

The arrow leading from phytoplankton to nutrients in Figure 1 also represents a simplification. Actually, the phytoplankton contribute to the amount of dead and decaying organic matter known as detritus. The detritus is acted upon by bacteria to form basic nutrients. The detritus also acts as a food supply for the herbivorous zooplankton. Since the interactions between bacteria and detritus are not well understood, and the detritus usually represents only a small part of the zooplankton food supply, it is convenient to assume immediate conversion of dead phytoplankton into nutrients. Here again the model can be easily modified to include detritus and bacteria as part of the state vector.

Our conceptual model also includes only one limiting nutrient. Hutchinson (1967) gives a list of elements required by phytoplankton that includes C, N, O, P, S, K, Mg, Ca, Si, Na, Fe, Mn, Zn, Cu, B, Mo, Co, and V, in addition to chemical compounds containing these elements. Our assumption is that all of the nutrients, except for the one limiting nutrient, are always in sufficient supply for maximum phytoplankton growth. Depending upon the

particular aquatic ecosystem under consideration, the limiting nutrient could vary. In some cases, however, the model would have to be modified to include additional nutrients. For instance, Park and Wilkinson (1971) found by using regression analysis at Lake George, New York, that ammonia, as well as phosphates, tended to limit phytoplankton growth.

The actual model that we will develop in Chapter 5 can be generalized very easily to include more than one nutrient and to include a division of the phytoplankton and zooplankton into a number of distinct groups. For simplicity, the case will be considered with one limiting nutrient, and all phytoplankton and zooplankton are lumped together into separate respective groups as the diagram in Figure 1 indicates.

Finally, we are imagining that all of these interactions occur within a volume of water at a specified depth in a lake or oceanic region in which the phytoplankton, zooplankton, and limiting nutrients are distributed homogeneously. The phytoplankton and zooplankton populations are characterized by the total number of organisms, whereas the nutrients are characterized by the total mass. It would be necessary to link together a number of these "point" models together to model a large body of water. In such a linkage, it is necessary to consider

the self-shading effect wherein phytoplankton growth at higher levels inhibits the light from traveling to the lower levels, thereby lowering the growth rate of the phytoplankton population at the lower levels.

Having discussed the simplifications inherent in the formulation of the conceptual model, we can now proceed to explain in detail the interactions between the limiting nutrient supply, the phytoplankton population, and the zooplankton population. Each of these groups will be discussed separately.

Phytoplankton Population

The changes in the size of a population of phytoplankton result from a complicated combination of a number of factors. The primary environmental variables which we will consider are water temperature, available light, and the balance between nutrient availability and phytoplankton requirements. Most species of phytoplankton react differently with respect to each of these environmental variables; so, by lumping all species together, we are only approximating the effect that these variables have on the actual phytoplankton. We will first examine the effect of these environmental variables on the phytoplankton birth rate and then on the phytoplankton death rate.

Since a complete investigation of environmental effects on phytoplankton birth rate has not yet been made,

we must choose from among a number of possible forms of the functional dependence of the rate on each of the environmental variables. In the case of water temperature, a number of different forms have been suggested. Both Davidson and Clymer (1966) and DiToro et al. (1970) suggest a linear dependence. On the other hand, Riley et al. (1949) suggest a complicated dependence on temperature resulting in a less pronounced dependence on temperature than the linear case, and Parker (1968) suggests a temperature factor that is normally distributed with a mean of 18° Centigrade and a variance of 64, resulting in a much more pronounced dependence than the linear case. We will adopt the Davidson and Clymer and DiToro et al. approach wherein the rate of increase of phytoplankton population is proportional to water temperature. The major limitation of this approach would seem to be at higher temperatures. Beyond a certain point, the effect of raising the temperature is to inhibit phytoplankton growth rather than to enhance it. In a situation where high water temperatures are likely to occur, some modified temperature dependent term would be desirable.

We will now examine the effect of solar radiation on phytoplankton growth. We first need to evaluate the light intensity (Li) in langleys/hour at a specified depth as a function of the surface solar radiation (solrad).

The light is attenuated in the following way:

$$I_i = \text{solrad} \cdot \exp(-k_{\text{extinct}} \cdot \text{depth})$$

where k_{extinct} is the extinction coefficient of light.

This extinction coefficient is not a constant because of the previously mentioned self-shading effect. Riley (1956) has investigated the self-shading effect and found that k_{extinct} can be approximated in the following way:

$$k_{\text{extinct}} = k_{\text{extinct}_0} + .0088c + .054c^{2/3}$$

where k_{extinct₀} is the extinction coefficient with no algae present and c is the chlorophyll concentration in micrograms per liter. Chen and Orlob (1968) have proposed a simpler form for the extinction coefficient that agrees reasonably well with Riley's:

$$k_{\text{extinct}} = k_{\text{extinct}_0} + .17 \cdot \text{phy} \cdot \text{mass} / \text{volume}$$

where phy is the phytoplankton population size in numbers of organisms, p_{mass} is the average phytoplankton mass in milligrams of dry weight per organism, and volume is the volume of water to be modeled. For the point model we will assume that the phytoplankton concentration is uniform at all depths in order to calculate the extinction coefficient. However, by creating a point model for each depth and appropriately linking them together, we would be able to evaluate the extinction coefficient at each depth, thereby representing the self-shading effect more precisely.

The effect of light intensity itself on phytoplankton growth is not completely understood. Davidson and Clymer (1966) suggested a linear dependence of growth rate on light intensity below a certain limiting value. Chen and Orlob (1972) treat growth rate as being proportional to $Li/(Li+k_1)$ where Li is light intensity and k_1 is a constant. Steele (1965) suggests a dependence proportional to $Li \cdot (\exp(1-Li/I_s))/I_s$ where I_s is a constant equal to 2000 foot candles. Since high light intensities tend to inhibit phytoplankton growth, Steele's form seems to be more desirable. We have plotted it in Figure 2, along with some laboratory data from Ryther (1956) to illustrate the effect of high light intensities. The data from Ryther seems to indicate some differences between the various types of phytoplankton with respect to the dependence of their growth rate on incident light. Since we are lumping together all species of phytoplankton, this is another area in which improvement can be made by a more definitive breakdown of phytoplankton.

Thus far we have examined the dependence of the phytoplankton growth rate on incident light and water temperature. We still need to consider the effect of the limiting nutrient supply.

As DiToro et al. (1970) point out, there is a reasonably large body of laboratory data that supports the

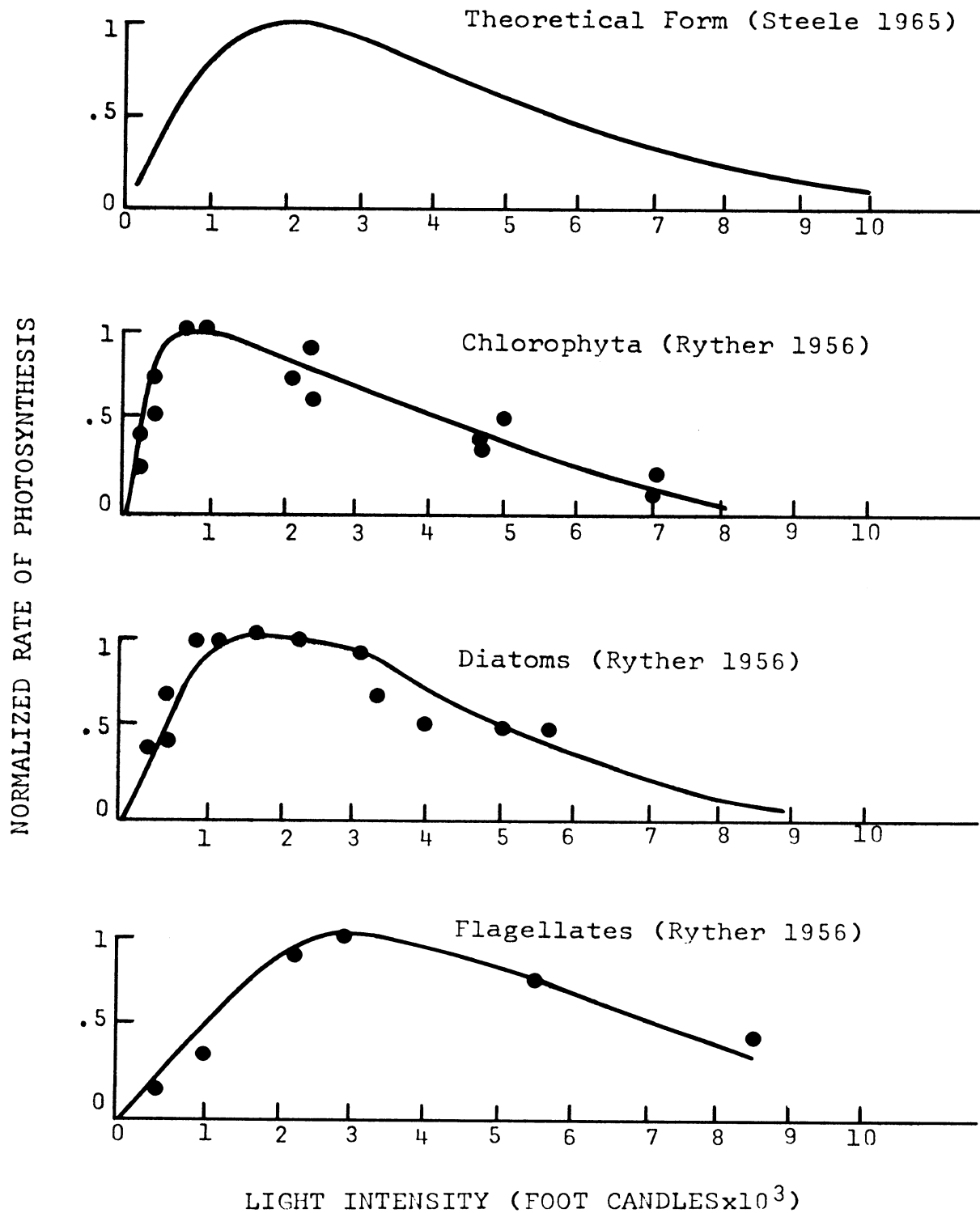


Figure 2. Normalized Rate of Photosynthesis versus Light Intensity

theory that growth rate is proportional to $c_{nut}/(c_{nut} + k_{nut})$ when the limiting nutrient assumption is justifiable where c_{nut} is the limiting nutrient concentration and k_{nut} is the Michaelis or half saturation constant which is the nutrient concentration at which the growth rate is half the saturated growth rate for fixed environmental conditions. The work of Dugdale (1967) verifies this for the case of phosphorus as the limiting nutrient, whereas the work of Eppley, Rogers, and McCarthy (1969) verifies it for the cases where either nitrate or ammonia is the limiting nutrient.

We therefore have the following functional form for the phytoplankton population growth rate ($p_{birthrate}$) as a function of water temperature (t), concentration of limiting nutrient ($nut/volume$), incident solar radiation ($solrad$), depth below surface ($depth$), phytoplankton population size (phy), average mass of phytoplankton organism (p_{mass}), volume of water to be modeled ($volume$), and the extinction coefficient without any phytoplankton ($k_{extinct_0}$):

$$p_{birthrate} = [k_{temp} \cdot t] \left(\frac{nut/volume}{nut/volume + k_{nut}} \right) \left(\frac{Li}{I_s} \cdot \exp\left(1 - \frac{Li}{I_s}\right) \right)$$

where

$$Li = solrad \cdot \exp(-k_{extinct_0} \cdot depth), \quad \text{and} \\ k_{extinct} = k_{extinct_0} + .17 \cdot phy \cdot p_{mass} / volume.$$

In order to complete our discussion of the phytoplankton population, we need to consider the possible ways in which the population can decrease. A number of possible mechanisms have been suggested that contribute to the death rate of phytoplankton. Endogenous respiration, by which organic carbon is converted into carbon dioxide, is used most frequently in other models. Since we are dealing in terms of actual numbers of phytoplankton cells rather than biomass, we need not consider endogenous respiration. The remaining mechanisms usually included in other models are grazing by herbivorous zooplankton and sinking of phytoplankton.

Grazing of phytoplankton by zooplankton is a very complex interaction which we will attempt to view in a very simplistic way, thus obtaining only a first order approximation. Many species of zooplankton feed by filtering a volume of water, thereby trapping any phytoplankton or detritus in that volume. DiToro et al. (1970) have reviewed the literature on zooplankton grazing and noted that the filtering rate varies among species of zooplankton as well as with water temperature, phytoplankton concentration, species and size of individual phytoplankton, and amount of particulate matter present. We will assume, along with DiToro et al. (1970), Chen and Orlob (1972), and many others, that the filtering rate per zooplankton

organism in terms of volume of water filtered per unit time is a constant, namely, kgraze. Therefore, the death rate of the phytoplankton population is

$$kgraze \cdot zoo \cdot phy / volume$$

where

zoo is the total number of zooplankton organisms,
phy is the total number of phytoplankton organisms,
volume is the volume of water in the region to be modeled.

Sinking of phytoplankton cells is a negligible factor in estuaries of rivers that are well mixed, but is a necessary factor in lake or coastal oceanic situations. We will assume a sinking rate proportional to water temperature (t) for simplicity, whereas in reality the sinking coefficient (k_{sink}) should depend upon currents, thermal gradients, and the size of the individual phytoplankton. We thus will use an average phytoplankton sinking rate of $k_{sink} \cdot t \cdot phy$. This completes our discussion of the factors controlling the size of the phytoplankton population.

Zooplankton Population

We need to include the zooplankton population in our model because of its interaction with the phytoplankton population. In some cases it has been suggested (DiToro et al. 1970) that zooplankton grazing of

phytoplankton is the primary factor leading to the reduction of phytoplankton population following a bloom.

As in the case of phytoplankton, there are many different species that make up the population with widely differing life cycles. Hutchinson (1967) gives an excellent summary of the complexities involved in zooplankton biology. We will treat the population very generally by developing a birth rate and a death rate that represents an average over the species of zooplankton that are present.

We will assume that zooplankton birth rate is a function of water temperature and food supply. It may be that other factors such as photoperiod and nutrient concentration are also significant factors, as suggested by Parker (1968), but the evidence is not conclusive. Based upon the work of Richman (1958) and others, a linear dependence of reproductive rate upon phytoplankton concentration seems reasonable. Results reported by Edmondson (1946) and Parker (1968) seem to indicate that for many species there is an optimal temperature for reproduction. We adopt Parker's assumption that the birth rate is proportional to a term akin to a normal distribution that accounts for temperature variability. We therefore obtain the following expression for the zooplankton birth rate:

$$z_{\text{birthrate}} = z_{\text{con}} \cdot \exp \left(-\frac{1}{2} \left(\frac{t - t_{\text{opt}}}{t_{\sigma}} \right)^2 \right) \cdot \text{phv}$$

where

zcon is a constant,

topt is the optimal temperature for reproduction, and

tg describes the "variance" of the temperature dependence term.

The death rate of herbivorous zooplankton is caused primarily by predation by higher level animals such as carnivorous zooplankton and fish, and by poisoning. Since we are not including fish in our model as part of the state vector, it is most convenient to treat the death rate as a constant (zdeathrate) which is to be determined empirically.

Our view of the zooplankton life cycle is necessarily oversimplified. We are ignoring aging and the associated dependence of birth and death rates on age as well as carnivorous zooplankton. Nonetheless, these assumptions are reasonably standard in that they also appear in the models developed by DiToro et al. (1970), Davidson and Clymer (1966), and Chen and Orlob (1972), among others.

Limiting Nutrient Supply

Having dealt with the factors that lead to changes in phytoplankton and zooplankton population sizes, we can now proceed to consider the factors leading to a change in the amount of the limiting nutrient. For this paper, we

will assume a limiting nutrient other than carbon. The model can be modified slightly by including nutrient sources based on zooplankton and phytoplankton respiration if an application is desired with carbon as the limiting nutrient, since respiration increases the supply of carbon.

The most obvious addition to the nutrient supply comes from external sources. The largest contributor in most cases is probably domestic sewage in either its raw or treated form. Industrial and agricultural effluent and natural sources also provide nutrients. The external source of nutrients is especially important because it represents the major source of control for the entire system with respect to level of eutrophication. Other possible alternative control measures based upon modifying the lake environment to make it less desirable for phytoplankton growth usually have the drawback of making the lake unsuitable for recreation. Examples of this type of control are increasing the acidity of the lake (Brock 1973), or decreasing the light transmitted to the euphotic zones where the algae predominate (Hergenrader and Hammer 1973). Controlling the incoming nutrients thus seems to be the simplest form of control.

Nutrients are, however, also generated within the system in a few different ways. The most important of these results from the residue of grazing of phytoplankton

by zooplankton (nzooexcr). This occurs because the zooplankton cannot metabolize all of the phytoplankton that they graze and must excrete some. Excrement from higher trophic levels such as fish (nother) is also included in our model.

Since we are not keeping track of fish populations explicitly in our model, we will treat the excrement from higher trophic levels as a constant source of input of limiting nutrient. We cannot, however, deal with the contribution from zooplankton excretion as simply. The mass of phytoplankton grazed is the product of the average mass of a phytoplankton cell (pmass) and the number of phytoplankton cells ingested (pgrazed). Dividing this product by the nutrient to biomass ratio (npratio) of phytoplankton yields the amount of nutrient that would be generated if none of the phytoplankton mass were to be utilized by the zooplankton. The fraction of phytoplankton mass utilized can be approximated (DiToro et al. 1970) by

$$\frac{\text{zooconveff} \cdot \text{kmp}}{\text{kmp} + (\text{phy}/\text{volume})}$$

where

zooconveff is the conversion efficiency of the zooplankton at low phytoplankton concentrations, and

kmp is the Michaelis-Menton constant for phytoplankton which is the phytoplankton biomass concentration at which the zooplankton growth rate is half the maximum possible

growth rate. Therefore, mass balance considerations allow us to express the nutrient addition due to zooplankton excretion as follows:

$$nzooexcr = \frac{pgrazed \cdot pmass}{npratio} \left(1 - \frac{zooconveff \cdot kmp}{kmp + (phy/volume)} \right) .$$

Previously we noted that changes in phytoplankton and zooplankton population sizes are dependent upon environmental variables. In the case of nutrient addition from zooplankton excretion, we noted that the dependence is upon the amount of grazing that occurred. This difference is significant because it implies that changes in the amount of the limiting nutrient are not independent of changes in phytoplankton and zooplankton population sizes. Thus, in our model, we will use Monte Carlo simulation to generate changes in phytoplankton and zooplankton population size but will calculate changes in the amount of limiting nutrient in a deterministic fashion based upon the results of the Monte Carlo simulation.

In addition to sources of nutrients, there are also nutrient sinks. The dominant factor resulting in a decrease of nutrient level is the nutrient usage for growth of the phytoplankton population. Another term that is significant in some cases is the loss of nutrients to the underlying sediment or in water flowing out of the lake.

The amount of limiting nutrient utilized for phytoplankton growth ($n_{\text{phytoassim}}$) is simply the additional mass of created phytoplankton multiplied by the nutrient to biomass ratio of phytoplankton. The amount of nutrient lost to the sediment (n_{sedloss}) is assumed to be a constant fraction of the total nutrients per time unit. Therefore,

$$n_{\text{sedloss}} = n_{\text{utlossrate}} \cdot n_{\text{ut}}$$

This completes our discussion of the conceptual model and the interaction between the zooplankton population, phytoplankton population, and limiting nutrient supply. Before converting our conceptual model into a system theoretic model (Chapter 5), we will give an introduction to the stochastic aspects of the model (Chapter 4).

CHAPTER 4

STOCHASTIC MODEL

We will consider a stochastic model of a two-species population where x and y represent the respective sizes of the two populations. The state of the system at any time can be represented by the ordered pair (x,y) . The system can change state as a result of either births or deaths of either species. Migrations will not be considered, although they do not pose any additional difficulties. We will assume that these births and deaths are independent events that individually satisfy the following four assumptions of the Poisson process:

- (1) The probability of exactly one event occurring in the time interval $(t, t+\delta t)$ is $r\delta t - o(\delta t)$;
- (2) The probability of more than one event occurring in the time interval $(t, t+\delta t)$ is $o(\delta t)$;
- (3) The probability of zero events occurring in the time interval is $1 - r\delta t + o(\delta t)$; and
- (4) The above probabilities are independent of the state changes of the system during an interval of time $(T, T+\Delta T)$ where $\Delta T \gg \delta t$.

The usual form (Bharucha-Reid 1960) for the last assumption is that the probabilities in the first three

assumptions are totally independent of the state of the system. Since our birth and death rates are somewhat state dependent, we need the modified form given above where ΔT is chosen such that the probability that there is a significant percentage change in a state within the time interval is arbitrarily close to zero. In practice, it is convenient to attempt a simulation with a prescribed value of ΔT and examine the results to check the validity of the fourth assumption rather than trying to derive an analytical expression for ΔT . With a proper choice of ΔT , if the state changes within the time interval do not appreciably change the birth and death rates, then we can treat these rates as constants that depend only upon the state at the beginning of the time interval.

A consequence of these four assumptions is that the probability of exactly k events of a given type occurring within the interval $(T, T+\Delta T)$ follows a Poisson distribution:

$$p(k,r) = \frac{(r\Delta T)^k}{k!} \exp(-r\Delta T) \quad .$$

Let r_{x+} and r_{y+} be the respective birth rates of the two species, and r_{x-} and r_{y-} the respective death rates. If the system is in the state (x,y) at time T , the probability $\text{Pr}((x,y), (x+a,y+b), \Delta T)$ of a transition to a state $(x+a,y+b)$ at time $T+\Delta T$ can be evaluated as follows:

$$\text{Pr}((x,y),(x+a,y+b),\Delta T)=$$

$$\left(\sum_{i=a}^x p(i,r_{x+}) \cdot p(i-a,r_{x-}) \right) \left(\sum_{j=b}^y p(j,r_{y+}) \cdot p(j-b,r_{y-}) \right)$$

It is not, however, practical to evaluate these probabilities in order to obtain a transition matrix, since the transition probabilities are not stationary in time, and the transition matrix is infinite dimensional. Instead, we will develop a Monte Carlo simulation of the system. Since we know the distributions of the number of births and deaths of each species within a time interval $(T, T+\Delta T)$ as a function of the state at time T , we can generate values from these distributions to simulate the number of births and deaths occurring in the time interval, and then very simply calculate the state at time $T+\Delta T$. We can then recalculate the birth and death rates for the next time interval in terms of the state at time $T+\Delta T$, and proceed with our simulation. The accuracy of our simulation relative to assumption number four can be improved by reducing the size of ΔT . The limit of reducing the size of ΔT would involve recalculation of the birth and death rates after each birth or death, which is the standard Monte Carlo simulation procedure. Since we will be dealing with phytoplankton and zooplankton populations whose sizes will normally be extremely large,

this standard procedure is infeasible for a practical simulation.

We will modify the above two-species stochastic population model for application to the description of phytoplankton-zooplankton interactions by introducing the limiting nutrient supply into the state vector. This is necessary because the phytoplankton birth rate depends very strongly upon the limiting nutrient supply as discussed in Chapter 3. Since changes in limiting nutrient supply depend to a large extent upon births and deaths of phytoplankton, we cannot treat the nutrient "births" and "deaths" as events independent of phytoplankton births and deaths. We will, therefore, treat the limiting nutrient supply in a deterministic fashion as described below.

After our simulation generates the number of births and deaths of each species in a given time interval $(T, T+\Delta T)$, we will calculate the changes in nutrient supply based upon these events as well as other contributing factors such as external nutrient inputs. This enables us to calculate the limiting nutrient supply at time $T+\Delta T$ in terms of the state and input at time T .

We are now prepared to describe our model in rigorous system theoretic terms. The terminology used in the model in the following chapter is from Wymore (1972).

Appendix A contains a brief summary of the systems definitions and concepts relevant to an understanding of the model for the convenience of the reader.

CHAPTER 5

SYSTEM THEORETIC MODEL

From the previous description of phytoplankton-zooplankton-nutrient interactions, it becomes apparent that any model we develop lacks analytical tractability primarily because of the nonstationary character of the transition rates. We therefore must develop a model which lends itself readily to computer simulation in order to have a useful model. The following system theoretic form of the model was chosen because it illustrates both the biological interactions and the logic of the Monte Carlo simulation in a reasonably concise, clear, and rigorous fashion. A finite state machine model is insufficient because there are an infinite number of possible states of the system. References will be made to some constants and functions which are explained below and which were previously discussed in Chapter 3.

The function POISSON(x) is defined uniquely by the following relationships:

- (1) $\text{POISSON}(x) \in \text{FUNCTIONS}([0,1], \text{NONNEGATIVE INTEGERS})$;
- (2) For every $r \in \text{REALS}[0,1]$,
$$\sum_{k=0}^{(\text{POISSON}(x))(r)-1} \exp(-x) \frac{x^k}{k!} < r < \sum_{k=0}^{(\text{POISSON}(x))(r)} \exp(-x) \frac{x^k}{k!} .$$

If r is a random observation from a uniform distribution on $[0,1]$, then $\text{POISSON}(x)$ is a random observation from a Poisson distribution with parameter x by the inverse transformation method of generating values from a probability distribution (Hillier and Lieberman 1970). In Appendix B we discuss an alternative scheme for generating observations from a Poisson distribution when the mean is large, based on the normal approximation to the Poisson.

The following constants and functions are also used:

zbirthrate = growth rate function for zooplankton
(organisms/hr.-organism)

zdeathrate = assumed constant value of the fraction
of zooplankton lost to predation by
higher species, poisoning, etc.
(organisms/hr.-organism)

pbirthrate = growth rate function for phytoplankton
population (organisms/hr.-organism)

ksink = phytoplankton sinking coefficient (/hr.-°C)

kgaze = zooplankton grazing rate (liters/organism-hr.)

pmass = average mass of phytoplankton organism (grams)

npratio = nutrient to biomass ratio of phytoplankton

volume = volume of water in section to be modeled
(liters)

kphytoresp = phytoplankton respiration coefficient
(/hr.-°C)

nutlossrate = fraction of total nutrients lost to
sediment per hour

depth = distance below surface of section to be
modeled

zooconveff = conversion efficiency of zooplankton at
low phytoplankton concentrations

kmp = Michaelis-Menton constant for phytoplankton

We will define a system LAKE=(S,P,F,M,T,σ) as a
discrete system as follows:

(1) S=ZOOPLANKTON×PHYTOPLANKTON×NUTRIENTS

where

ZOOPLANKTON=PHYTOPLANKTON=NONNEGATIVEINTEGERS, and
NUTRIENTS=NONNEGATIVEREALS.

The units of the zooplankton components of the state are
number of organisms, whereas the nutrient component is
specified by weight.

(2) P=TEMPERATURE×LIGHT INTENSITY×NUTRIENT IN
×RANDOM₁×RANDOM₂×...×RANDOM₅

where TEMPERATURE=INTEGERS,LIGHT INTENSITY=NUTRIENT IN=
NONNEGATIVEREALS, and

RANDOM_i=REALS[0,1] for i∈INTEGERS[1,5].

The units of temperature and light intensity are respec-
tively degrees Centigrade and langleys per hour, while the

nutrient input is measured in grams, and the RANDOM_i are random numbers generated from a uniform $[0,1]$ distribution and for $(\text{zoo}, \text{phy}, \text{nut}) \in S$,

$$p = (t, Li, n, r_1, r_2, r_3, r_4, r_5) \in P,$$

$$(3) \quad (\sigma(c_p, l))(\text{zoo}, \text{phy}, \text{nut}) = \\ (\text{zoo} + \text{zbirth} - \text{zdeath}, \text{phy} + \text{pbirth} - \text{psink} - \text{pgrazed}, \\ \text{nut} + n + \text{nzooexcr} + \text{nother} - \text{nphyassim} - \text{nsedloss})$$

where

$$\text{zbirth} = (\text{POISSON}(\text{zbirthrate} \cdot \text{zoo}))(\text{r}_1),$$

$$\text{zdeath} = \text{Min}((\text{POISSON}(\text{zdeathrate} \cdot \text{zoo}))(\text{r}_2), \text{zoo}),$$

$$\text{pbirth} = \text{POISSON}(\text{pbirthrate} \cdot \text{phy})(\text{r}_3),$$

$$\text{psink} = (\text{POISSON}(t \cdot \text{ksink} \cdot \text{phy}))(\text{r}_4),$$

$$\text{pgrazed} = (\text{POISSON}(k_{\text{graze}} \cdot \text{zoo} \cdot \text{phy} / \text{volume}))(\text{r}_5),$$

$$\text{nzooexcr} = \left(\frac{\text{pgrazed}}{\text{npratio}} \right) \left(1 - \frac{\text{zooconveff} \cdot k_{\text{mp}}}{k_{\text{mp}} + (\text{phy} / \text{volume})} \right),$$

nother = nutrient release rate per hour by death and excretion of higher food chain elements,

$$\text{nphyassim} = \text{pbirth} \cdot \text{pmass} \cdot \text{npratio}$$

$$\text{nsedloss} = \text{nutlossrate} \cdot \text{nut}.$$

The above model is, of course, only a point model. For practical use, a number of point models should be used and linked together appropriately. In order to accomplish the linkage, migrations of phytoplankton, zooplankton, and nutrients from the vicinity of one point to another must be considered. These migratory terms must then be encompassed

into the state transition function σ either in a deterministic or stochastic fashion. Chen and Orlob (1972) consider vertical migration in their differential equations, and DiToro et al. (1970) consider horizontal migration in their model, both using a deterministic approach. Either of these approaches can be used in our system theoretic framework by defining systems for each point and coupling them. This completes our discussion of the system theoretic model.

CHAPTER 6

CONCLUSIONS

Model evaluation is an extremely important and extremely difficult part of the modeling process. The previously discussed model has not yet been applied to a real world situation, so our model evaluation will be restricted to comparisons between our model and other models that have been evaluated.

Basically, our model is a stochastic version of the differential equation model developed by DiToro et al. (1970). Differences occur because DiToro et al. (1970) concern themselves with biomass, whereas we keep track of number of organisms. Therefore, changes in state in our model occur as a result of births and deaths, while growth causes changes in state in the DiToro model. Since neither model distinguishes between growth and reproduction, this difference is not very significant.

Our approach to determining changes in nutrient level is also slightly different. We treat these changes as being a function of the changes in phytoplankton and zooplankton population levels rather than the population levels themselves. This difference is necessary for maintaining the mass balance viewpoint adopted by DiToro

et al. (1970). In the deterministic case, there is a one-to-one correspondence between changes in population levels and the actual levels, whereas in the stochastic case the one-to-one correspondence is between the mean rate of change of population and the actual population size.

The DiToro model has been applied to the tidal portion of the San Joaquin River in California. Several simplifying assumptions were made. In order to simplify computations, the entire area modeled was treated as one homogeneous volume, and ammonia and nitrates were both lumped into the category of inorganic nitrogen which was then considered to be the limiting nutrient. The inorganic nitrogen external input was treated as an empirically determined constant for lack of a better assumption.

The resulting model calibration over the years 1966 and 1967 was quite successful. The model results indicated a large spring phytoplankton bloom and secondary bloom in autumn during 1966 of about the proper magnitude, and only a single autumnal bloom in 1967 because of an earlier advective flow, also in proper agreement temporally as well as magnitude-wise. We can thus conclude that our basis for determining rates of change of population levels and nutrient levels seems reasonable.

The birth-death approach used in our stochastic model has never previously been used to describe phytoplankton-zooplankton interactions, but it has successfully been used in biological modeling. The same is true concerning Monte Carlo simulation. Beyer et al. (1972) set up a birth-death model describing wolf-moose-plant interactions and ran a Monte Carlo simulation, and Bartlett (1957) used a birth-death approach combined with Monte Carlo simulation to describe the competition between two species of flour beetles.

The above arguments suggest that our modeling approach may be valid. A conclusive demonstration of its validity must await application.

Several problems occur in attempting to apply such a model. Several of the constants such as k_{temp} , and t_0 have no physical basis and must be estimated empirically. Other constants such as zooplankton grazing rates are species dependent, and we are forced to use some sort of average grazing rate. The model also requires as input the water temperature, incident light intensity, and external nutrient supply at all times. These data are frequently unavailable, as the standard sampling technique is to measure all the variables of interest at most once every two to three weeks at diverse locations.

Since these problems are shared with the standard differential equation approach used by DiToro et al. (1970),

Chen and Orlob (1968, 1972), and many others, they do not represent a severe limitation upon our modeling approach.

Several conclusions can be drawn from our literature search and model development. We have found that system theory provides a clear and precise language for describing a complicated model. In addition, a computer simulation can easily be constructed from this form of the model.

We have formulated a stochastic model of phytoplankton-zooplankton interactions that seems to be an alternative approach to the standard simultaneous differential equation approach. A final comparison of the two approaches must await a real world application.

As indicated earlier, the simplest way of controlling excess algal growths seems to be limiting the external nutrient input. Monte Carlo simulation can be used to evaluate the effects of different amounts of nutrient inputs.

Finally, our model has indicated a deficiency in the type of data generally available. In order to calibrate our model or a differential equation model, it is necessary to have data taken much more frequently than once every two or three weeks.

Water temperature, solar radiation, and nutrients from external sources are inputs to the model. These

should be measured as frequently as deemed necessary to obtain an acceptable approximation to the actual input stream. The constants--p_{mass}, k_{temp}, k_{extinct}₀, k_{graze}, t_{opt}, t_σ, z_{con}, n_{other}, z_{ooconveff}, k_{mp}, n_{pratio}, n_{sedlossrate}, and k_{sink}--should either be estimated from the available literature or estimated empirically. Frequent measurements of the state are necessary in order to perform the empirical estimation and laboratory data might provide a satisfactory basis for this estimation in many cases.

Further work is, of course, necessary. As interactions between different species of phytoplankton and zooplankton as well as phytoplankton affinities for specific nutrients are understood, the state description can be modified to include each species separately. More work is also needed in the area of model calibration. Finally, a careful comparison should be made between the differential equation approach and the use of Monte Carlo simulation as a tool for studying the complicated problem of eutrophication.

APPENDIX A

INTRODUCTION TO SYSTEM THEORY

We will first describe the system theoretic notation and then delve into some of the important concepts relevant to our model. All of the material is condensed from Wymore (1972).

The symbol $\{\}$ will always enclose the definition of a set. The symbol Λ will denote the idea of subset. The symbol \times will denote a vector product. The symbols $[\]$ and $(\)$ denote closed and open intervals, respectively.

If B is a set and b is an element of B , we indicate this by $b \in B$. The set of all integers is denoted INTEGERS , and the set of all real numbers is denoted REALS . Descriptive prefixes are added to denote subsets of these sets (e.g., $\text{NEGATIVEREALS} = \{x: x \in \text{REALS}, x < 0\}$). Other subsets can be indicated by using the interval symbols (e.g., $\text{REALS}(q,s) = \{r: q < r < s\}$).

A function f defined on a set A with values in a set B is a set of ordered pairs such that:

- (1) $f \Lambda \{(a,b): a \in A, b \in B\}$;
- (2) if $a \in A$, then there exists $b = f(a) \in B$ such that $(a,b) \in f$; and

(3) if $(a', b') \in f$, and $(a^*, b^*) \in f$, and $a' = a^*$, then $b' = b^*$.

The set of all functions defined on A with values in B is denoted $\text{FUNCTIONS}(A, B)$.

Let B be a finite set not empty of sets not empty. It can then be expressed as $\{A_1, A_2, \dots, A_n\}$ for some $n \in \text{POSITIVEINTEGERS}$. The vector product of the sets in B is denoted $A_1 \times A_2 \times \dots \times A_n$ and is defined as follows:

$$A_1 \times A_2 \times \dots \times A_n = \{(a_1, a_2, \dots, a_n) : a_i \in A_i \text{ for all } i \in \text{INTEGERS}[1, n]\}.$$

Let A and B be sets not empty and $b \in B$. The function which is constant on A and equal to b is denoted c_b and defined as follows: $c_b = \{(a, b) : a \in A\}$. The identity function defined on A is denoted $\text{IDENTITY}(A)$ and defined as follows: $\text{IDENTITY}(A) = \{(a, a) : a \in A\}$. If $f \in \text{FUNCTIONS}(A, B)$ and $A' \subseteq A$, then the restriction of f to A' is denoted $\text{RESTRICTION}(f, A')$ and is defined as follows: $\text{RESTRICTION}(f, A') = \{(a, b) : a \in A', (a, b) \in f\}$. The function f is "onto" if for every $b \in B$ there exists $a \in A$ such that $(a, b) \in f$. This is denoted by $f \in \text{FUNCTIONS}(A, \text{onto}, B)$.

Let P be a set not empty, $f, g \in \text{FUNCTIONS}(\text{REALS}, P)$, $r \in \text{REALS}$. We then define the translation and segmentation operations as follows:

$$\text{TRANSLATION}(f, r) = \{(t, f(r+t)) : t \in \text{REALS}\}$$

$$\text{SEGMENTATION}(f,g)=\{(t,z):z=f(t) \text{ if } t<0, \\ z=g(t) \text{ if } t\geq 0\}$$

A set F is an admissible set of input functions with values in P if and only if: f is not empty, $F \in \text{FUNCTIONS}(\text{REALS}, P)$, and if $f, g \in F, r \in \text{REALS}$, then $\text{TRANSLATION}(f, r) \in F$, and $\text{SEGMENTATION}(f, g) \in F$. The set of all admissible input functions with values in P is denoted $\text{ADMISSIBLES}(P)$.

We will use all of these ideas in a definition of a system. A system is a six-tuple (S, P, F, M, T, σ) where:

- (1) S is a set not empty;
- (2) P is a set not empty;
- (3) $F \in \text{ADMISSIBLES}(P)$;
- (4) $M \in \text{FUNCTIONS}(S, S)$, $\text{IDENTITY}(S) \in M$;
- (5) $T \in \text{REALS}$, $0 \in T$;
- (6) $\sigma \in \text{FUNCTIONS}(F \times T, \text{onto}, M)$, and for every $f, g \in F, s, t \in T$ such that $s+t \in T$:
- (7) $\sigma(f, 0) = \text{IDENTITY}(S)$;
- (8) $\sigma(\text{TRANSLATION}(f, s), t)(f, s) = \sigma(f, s+t)$;
- (9) $\sigma(f, t) = \sigma(g, t)$ if $\text{RESTRICTION}(f, T[0, t]) = \text{RESTRICTION}(g, T[0, t])$ when $t \geq 0$;
- (10) $\sigma(f, t) = \sigma(g, t)$ if $\text{RESTRICTION}(f, T[t, 0]) = \text{RESTRICTION}(g, T[t, 0])$ when $t < 0$.

The elements of the six-tuple are interpreted as follows:

S is the set of states, P the set of inputs, F the set of input functions, M the set of state transitions, T the time scale, and σ the state transition function.

The model utilized in Chapter 5 is that of a discrete system; so, we will formally define a discrete system since it represents a considerable simplification over the above definition. A discrete system is a system that additionally satisfies the following requirements:

$$\{c_p : p \in P\} \subseteq F;$$

$T = \text{NONNEGATIVE INTEGERS}$, and for every $f \in F$, $t \in T$, $x \in S$

$$\sigma(f, t)(x)$$

$$= x \text{ if } t=0$$

$$= (\sigma(c_{f(t-1)}, 1))(\sigma(f(t-1))(x)) \text{ if } t \neq 0.$$

Discrete systems have the nice property that they are completely determined by specifying S, P , and $\sigma(c_p, 1)$ for every $p \in P$. F, M , and T follow from the definition of discrete system so they need not be specified in our model in Chapter 5.

APPENDIX B

NORMAL APPROXIMATION TO THE POISSON

Some cases will arise in our simulation where x , the parameter of the Poisson, is extremely large and it becomes computationally inefficient to compute $\text{POISSON}(x)$ by the definition given in Chapter 5. In those cases, a normal approximation to a Poisson distribution will be used because there are extremely efficient algorithms available for generating observations from a normal distribution (Marsaglia, MacLaren, and Bray 1964).

When x is large,

$$\sum_{k < x + b\sqrt{x}} \frac{x^k}{k!} \exp(-x)$$

can be approximated by the cumulative distribution function of the normal distribution (Feller 1968). Given a value of b as an observation from the standard normal distribution, the corresponding value from the Poisson is $x + b\sqrt{x}$ again by the inverse transformation method used in Chapter 5.

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