INTERNAL REPORT 95

A TEMPORAL-SPATIAL MODEL FOR STUDYING NUTRIENT CYCLING DYNAMICS OF A PHYTOPLANKTON PRODUCTION SYSTEM

PART I--DEVELOPMENT OF MODEL

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Table of Contents

List of Figures

1. Introduction

Since the task of most scientific disciplines is to endeavor
to understand the dynamic nature of systems by discovering and
defining functional relationships among their components, con-
trolled experiments are and will continue to be the predominant
scientific tool used for studying the dynamics of physical and
biological processes. The scientifically most important aspect
of a controlled experiment, which distinguishes it from the al-
ternative of merely monitoring measurable qualities of a system
in its natural environment, is the facility for systematically and
meaningfully varying the measurable qualities of some components
of the system in order to study their relationship to the behavior
of other components. There are, however, limits on the complexity
of systems which may be effectively studied exclusively with
controlled experiments. For systems which are defined in terms
of a large number of components it is economically unfeasible or
technically impossible to study more than a limited proportion
of the components in a controlled experiment, and of the components
selected for study only a much smaller proportion can be effectively
varied systematically. Scientific study of these complex systems
must rely more heavily upon techniques for monitoring the system
in its natural environment. Although the behavior of a large
number of components may usually be measured simultaneously by
using monitoring techniques, there do not exist analytic procedures
which have the capability of using this information to unravel the
array of functional relationships which effectively define the
dynamics of the system. There do, however, exist useful analytic
tools for studying the behavior of complex systems. A system
model is an analytic tool for combining the results from controlled
experiments with monitoring data, through the use of scientific
hypotheses, to mathematically describe a simulated system which
possesses dynamic properties similar to the actual system under
consideration. Controlled experiments are performed to discover
and define sub-models which describe the type of functional

relationships among small collections of components. These sub-models are defined in terms of meaningful parameters whose magnitude may be assessed from monitoring data. If insufficient empirical evidence is available to satisfactorily define functional relationships between some components then scientific hypotheses based upon logical assumptions are substituted for experimental results. Collections of sub-models are analytically linked together, by employing scientific hypotheses, to form a system model. In its abstract mathematical form many dynamic properties of the simulated system may be determined through analytical analysis. Additionally, by employing high speed computers, meaningful experiments may be performed with the entire simulated system which would otherwise be unfeasible. Thus intelligently constructed system models may be employed as a scientific tool for studying complex systems in a systematic manner.

The first step in constructing a model is to define the constituents of the process being examined. For complex systems the definition of the constituent components will depend upon the adoption of a specific conceptualization of the system. A number of different conceptualizations have been used for defining ecological systems; among them are: a thermodynamic approach, a mass or energy transport approach, a mass or energy budget approach, and approaches for studying successional changes in species composition. The second step in building a model is to formulate a set of scientific questions concerning the dynamics of the system previously conceptualized. Only those components of the system which will bear upon these questions will be included within an analytic description. The purpose of a system model is analogous to the objectives of a controlled experiment; a set of well defined questions or hypotheses are to be explored. There is no final step in the model building process. As with all research endeavors, more questions are raised than answered. A model thus evolves as our depth of perception of the system grows.

The subsequent sections describe the development of a system model for studying the processes of phytoplankton production and nutrient cycling in a freshwater lake. The next section provides a conceptualization of the ecological system and defines the constituent components which will be necessary in order to address the list of questions formulated in the third section. In the fourth section, the physical and biological hypotheses, which define the relationships among the components, are stated precisely in terms of mathematical equations. These sets of equations comprise an analytical description of the simulated system. Since the resulting system of equations are too complicated to be solved analytically, the fifth section is devoted to outlining numerical procedures for obtaining solutions. The sixth section is devoted to a study of model behavior. This section describes how the model may be used to increase our understanding of the dynamics of the system and how it can be useful in guiding research effort.

2. Conceptualization of Ecological System

The role of sound conceptualization and meaningful questions in the modelling process is discussed in Eggers and Male (1972). Included in this paper is a conceptualization of an aquatic ecosystem which could serve as the framework for a substantial system analysis. A more complete discussion of the essential elements which comprise a phytoplankton production-nutrient cycling system will be given here.

The concentration of phytoplankton in freshwater lakes may be viewed as a component of a system, but it is obvious to an ecologist that a large number of systems could be defined which admitted this variable as a component. If the objective of a scientific study is to understand the reasons for temporal fluctuations in photosynthetic production then only those factors which appreciably affect the concentration of phytoplankton or the rate of photosynthetic production need to be defined as components of the system. If instead, the objective of a study is to predict temporal fluctuations in photosynthetic production then dynamical models of each of the components which affect phytoplankton production must also be constructed. It should be clear that this objective would cause the magnitude of a research investigation to snowball and because of its massive proportions it would necessarily draw attention away from the scientific pursuit of studying those phenomena which are little understood. Nevertheless, many interesting aspects of ecological systems can be studied only by integrating dynamic models for several components. The modelling tools developed here incorporate features from both of the foregoing approaches. Emphasis is placed on the study of dynamical trends the ecological system will follow when essential components of the system are varied systematically. This process will allow a scientific assessment of the role and relative importance which various components have in controlling the direction and rate of change of the system.

Considered as a component of an ecological system the individual algal cells comprising a community of phytoplankton are envisaged as suspended particles which are at the mercy of prevailing currents. The cells exhibit certain buoyancy properties which will cause them either to sink toward the bottom of the lake or rise to the surface. Through the physiological processes of photosynthesis and reproduction a community of algae has the capability of utilizing resources available in its physical environment to increase its mass. The rate at which these growth processes may proceed is dependent upon the abundance of the necessary resources subject to certain limits on the physiological capability of the cells. The physiological process of respiration, the physical processes of sinking and mixing by water currents, and the biological process of grazing by zooplankton and bacterial decomposition may contribute to a reduction in the concentration of phytoplankton at any point in the lake. Since physical factors such as intensity of solar radiation, temperature, rate of mixing, rate of sinking, and concentration of essential nutrients all exhibit prominent vertical variation within a lake, it is expected that the phytoplankton production dynamics would vary vertically as well. For these reasons the phytoplankton community will be characterized by its vertical concentration profile. The total rate of production for a typical column of water would thus be represented by the integral, from the surface to the bottom, of the vertical profile of production per unit volume. Since each of the aforementioned factors vary temporally as well as spatially our task will be to identify functional relationships which describe the manner in which the vertical profiles for the physical factors determine the vertical profile for production rate of the phytoplankton. The solution of the resulting system of differential equations will be a useful tool for evaluating both the temporal and spatial dynamics of phytoplankton production.

The sinking rate of particles in a liquid is known to depend upon the specific gravity of the substance, its geometric shape, and upon the viscosity of the liquid. However, since various species of algae possess some capability for regulating their specific gravity, since the diversity of shapes of algal cells is almost as great as the variety of species, and since the viscosity of water is a function of temperature, it would require rather sophisticated models to study the sinking rate of a community of phytoplankton. If interest is centered primarily upon production dynamics it would be foolish to pursue detailed models for sinking rate until it had been satisfactorily demonstrated that it was a controlling factor upon production. One method for acquiring this insight is to assume a constant average sinking rate for the community and then systematically vary the sinking rate in an experiment with the simulated system.

Eddy diffusivity currents are created any time the velocity of a liquid exceeds certain limits. Small packages of water are transported perpendicular to the direction of the current with a momentum which depends upon the velocity of the liquid. The minimal velocity for establishing eddy diffusivity currents in a lake is very small, therefore these eddy currents are always present. These packages of water carry with them their distinguishing characteristics which include heat content, dissolved solids, and suspended particles including phytoplankton. The ecological importance of eddy diffusivity currents is that they are a mechanism for mixing in the water column. Their effect on a vertical concentration profile is to tend to equalize concentrations in neighboring layers of water, i.e., to decrease the concentration gradient. Diffusion has the same effect upon concentration gradients but this process is thousands of times slower than eddy diffusivity mixing. The rate of effective mixing depends directly upon density gradients in the water column; if packages of dense water are transported up into a layer of less dense water they will tend to sink back to their former density

level, and if packages of lower density water are transported down into layers of greater density they will tend to buoy up to their former density level. Thus negative density gradients (essentially temperature gradients in freshwater lakes) impart stability to the water column. Wind is, in most cases, the principle force for creating currents which sustain eddy mixing. Although models may be constructed which relate the effective rate of eddy mixing to density gradients and wind action, the first step in the investigation of this ecological system will be to determine the role and importance of mixing for controlling the system's behavior.

The amount of solar radiation reaching a specified depth in a lake depends upon the amount of radiation passing through the lake surface, the depth, and the light extinction properties of the water. The light extinction properties are defined by the constant light absorption properties of distilled water and the concentration of dissolved and suspended solids. The concentration profile of dissolved and suspended material has been used to characterize different lakes and also exhibits seasonal variation within each lake. Since photosynthetic rate depends directly upon the amount of solar radiation reaching algae chloroplasts, and since algal cells are indeed suspended particles which can increase the extinction of light in the water column, it is important to view the relationship between phytoplankton concentration profiles and light extinction in the water column as a density dependent mechanism for population control. In addition, it would be of ecological interest to determine what effects various temporal patterns of surface solar radiation have upon the behavior of the system.

Phytoplankton growth rate has been observed to depend upon the concentration of certain nutrients such as nitrate and phosphate. Algal cells remove these nutrients from the water column and to some extent recycle them back into the water column in

order to carry out the processes of reproduction and photosynthesis. The concentration profile of these nutrients is a function of the rate profiles for nutrient uptake and recycling, eddy mixing, allochthonous input and outflow, invertebrate excreation, and bacterial decomposition. In many freshwater lakes the availability of essential nutrients is a severely limiting factor upon primary production, but the relationships among the biological, chemical, and mechanical processes which control the conservation and recycling of these nutrients is not clearly understood. One of the principle objectives of the modelling tools developed here will be to shed some light on these interrelations.

Many other components of a nutrient cycling-phytoplankton production system could be defined, but the conceptualization provided thus far is sufficient for addressing many relevant questions.

3. Relevant Questions

The following list of questions by no means exhausts the usefulness of the model; to the contrary, the list will indubitably expand as the study of model behavior progresses.

Can the rate of eddy diffusivity mixing control the timing or magnitude of phytoplankton blooms?

Is eddy diffusivity mixing a principal mechanism for supplying phosphorus to the potentially most productive surface waters of a lake?

Since wind action is the principal force which drives eddy diffusivity currents, can the fetch of a lake (which is determined by the size and shape of a lake basin) significantly affect the dynamics of the system, i.e., can major differences between different lakes be attributed to the morphological characteristics of the lakes' basins?

If bottom sediment release is a potentially important source of phosphorus to phytoplankton, then how important is the average depth of a lake basin in determining the rate at which this nutrient is transported to the surface waters?

Are the dynamics of the phosphorus — phytoplankton system sensitive to small variations in the force of eddy diffusivity mixing, i.e., how accurately and how often must the force of mixing be measured in order to assure specified levels of predictive capability?

How does the development of a summer density gradient in the water column affect the phosphorus - phytoplankton cycling system? Is the productivity of different lakes related to the extent and timing of their thermal stratification? How accurately and how often must thermal profiles be measured to assure a specified level of predictive capability?

Is the sinking rate of phytoplankton a significant factor for determining the behavior of a phytoplankton-nutrient cycling system? Can sinking phytoplankton function as a prominent trap for phosphorus?

What is the relative importance of the following nutrient cycling mechanisms for maintaining a temporally balanced system: autolytic and mechanical release of nutrients by phytoplankton; variable carbon to phosphorus ratios of phytoplankton; ingestion and excreation by zooplankton; sediment release and eddy diffusivity mixing processes; limnetic bacterial decomposition cycling processes; allochthonous inflow and outflow of nutrients? How does the relative importance of these cycling mechanisms depend upon the physical characteristics of the lake basin and the behavior of the community of organisms which have evolved there?

How does the extinction coefficient for light in the water column affect the phytoplankton production system? Can seasonal variation in turbidity explain a significant proportion of variation in production rate? Can differences in the production dynamics of different lakes be partially explained by their inherent differences in turbidity?

To what extent does self-shading by phytoplankton define the carrying capacity of the environment?

How much of the differences in the production dynamics of different lakes may be explained by differences in the pattern and intensity of solar radiation reaching the lake surface; in particular, what are the effects of cloud cover, fog, and physical obstructions such as mountains?

Are the conventional Michaelis-Menton models, which are used to relate relative photosynthetic rate to nutrient concentration, satisfactory when the water column is viewed as a phytoplankton production-nutrient cycling system instead of just a phytoplankton production system? In particular, should the nutrient storage capabilities of phytoplankton be viewed as a nutrient conservation mechanism or a trap for nutrients?

4. Description of Model

The concentration of phytoplankton carbon and the concentration of phosphorus are assumed to vary with time and depth according to the model

(1) $$\frac{\partial x}{\partial t} = \frac{\partial}{\partial z}(K\frac{\partial x}{\partial z}) - s\frac{\partial x}{\partial z} + f$$

(2) $$\frac{\partial v}{\partial t} = \frac{\partial}{\partial z}(K\frac{\partial v}{\partial z}) - \alpha f$$

where

t is time in days,

z is depth from surface in meters,

$x(t,z)$ is phytoplankton carbon concentration in mg m^{-3},

$v(t,z)$ is phosphorus concentration in mg m^{-3},

$K(z)$ is coefficient of eddy diffusivity in $m^2 day^{-1}$,

s is sinking rate of phytoplankton in m day^{-1},

$f(t,z,x,v)$ is net photosynthetic rate in mg $m^{-3} day^{-1}$,

α is phosphorus to carbon ratio of phytoplankton,

$(K\frac{\partial x}{\partial z})$ is net rate at which phytoplankton pass a horizontal surface of area one m^2, at depth z, due to vertical mixing by eddy diffusivity currents in mg $m^{-2} day^{-1}$.

The boundary conditions are taken to be

(3) $K\frac{\partial x}{\partial z} - sx = 0$ at z = 0 (the surface); the assumption is that there is no phytoplankton mixing or sinking through the surface

(4) $K\frac{\partial x}{\partial z} - sx = -sx$ at z = z_b (the bottom); the assumption is that there is no phytoplankton mixing through the bottom, but phytoplankton disappear from the population when they sink to the bottom

(5) $\frac{\partial v}{\partial z} = 0$ at z = 0; no mixing of phosphorus through the surface

(6) $v(t,z_b) = v_b$ (a constant); the assumption is that some unidentified mechanism maintains a constant phosphorus concentration on the bottom.

The coefficient of eddy diffusivity is assumed to decrease exponentially through the water column according to the equation

(7) $$K(z) = K_0 \exp\{-K_1 z\}.$$

The parameter K_0 is the rate of mixing at the surface ($m^2 day^{-1}$) and the parameter K_1 regulates the rate of decrease. The assumption of exponential decline is not unreasonable and has in fact been observed in some lakes. In any case this model will serve as a flexible vehicle for studying the effects of eddy mixing upon the system. If mixing can be demonstrated to appreciably affect system behavior then the model can be made more realistic by incorporating the influence of wind and density gradients.

Net photosynthetic rate is assumed to depend upon solar radiation intensity and concentration of phosphorus according to the equation

(8) $$f(t,z,x,v) = f_{max} \cdot [\frac{R(t,z)}{R_{opt}} \exp\{1 - \frac{R(t,z)}{R_{opt}}\}] \cdot [\frac{v}{H+v}] \cdot x$$

where

f_{max} is saturated relative net photosynthetic rate in day^{-1}; the maximum photosynthetic rate per unit mass of phytoplankton carbon which can be expected under optimal phosphorus and light conditions,

$R(t,z)$ is solar radiation reaching depth z at time t in K cal $m^{-2} day^{-1}$,

R_{opt} is solar radiation level which produces the saturated net relative photosynthetic rate in K cal $m^{-2} day^{-1}$,

$[\frac{R}{R_{opt}} \exp\{1 - \frac{R}{R_{opt}}\}]$ is proportional reduction in net relative photosynthetic rate attributed to solar radiation of level R; as a function of R this term behaves according to the following graph
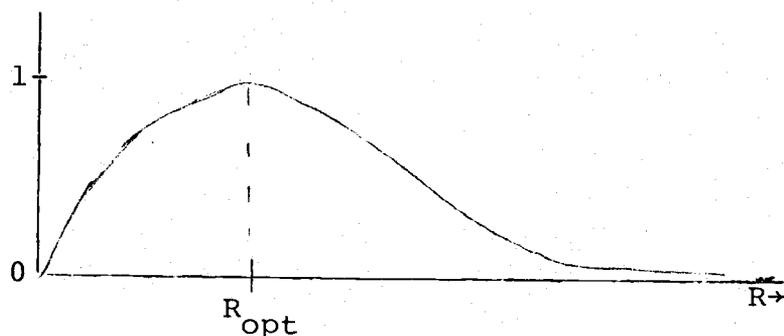
H is Michaelis-Menton half saturation constant for carbon uptake
rate versus phosphorus concentration; units are mg m^{-3},

$[\frac{v}{H+v}]$ is proportional reduction of saturated net relative
photosynthetic rate attributed to phosphorus concentra-
tion; as a function of v this term behaves according to
the following graph
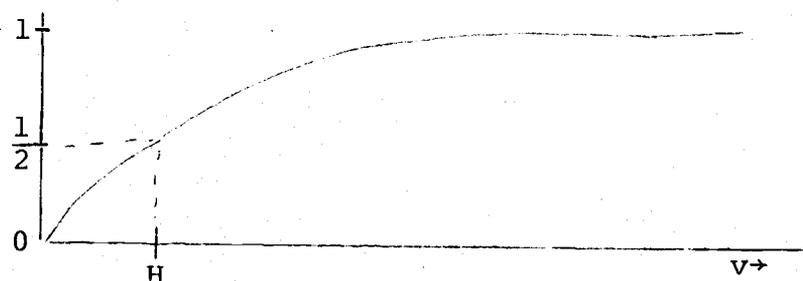
In (8) it is implicitly assumed that the effects of light and
nutrient operate independently upon net relative photosynthetic
rate. Since the present formulation does not separate the processes
of photosynthesis and respiration this extension of the model is
imminent.

The intensity of solar radiation reaching any depth is
assumed to depend upon the surface solar radiation, the specified
depth, and the phytoplankton concentration profile according to the
expression

$$(9) \qquad R(t,z) = I_0(t)\exp\{-B_1 z - B_2 \int_0^z x(t,y)dy\}$$

where

$I_0(t)$ is surface solar radiation at time t in K cal $m^{-2}day^{-1}$,

B_1 is extinction coefficient for lake water devoid of phyto-
plankton,

B_2 is extinction coefficient for phytoplankton,

$\int_0^z x(t,y)dy$ is amount of phytoplankton carbon above the depth z in mg m^{-2}.

This model is derived from the assumption that the vertical gradient of light intensity at any depth is proportional to the concentration of substances dissolved and suspended in the water.

For purposes of studying model behavior the temporal pattern of surface solar radiation is initially assumed to behave according to the expression

$$(10) \qquad I_0(t) = 1500[\sin(\frac{2\pi(t-81.25)}{365}) + 1].$$

5. Solution of Equations

The following implicit scheme for approximating equations (1) and (2) by finite difference equations has been adopted. Let

(11) $z = (i-1)(\Delta z) = (i-1)h$ for $i = 1,2,\ldots,N+1$,

where $z_b = Nh$

and

(12) $t = (j-1)(\Delta t) = (j-1)k$ for $j = 1,2,\ldots$.

Since $\frac{\partial}{\partial z}(K\frac{\partial x}{\partial z}) = (\frac{\partial K}{\partial z})(\frac{\partial x}{\partial z}) + K\frac{\partial^2 x}{\partial z^2}$ we can rewrite (1) and (2) as

(13) $$\frac{\partial x}{\partial t} = K\frac{\partial^2 x}{\partial z^2} + (\frac{\partial K}{\partial z} - s)\frac{\partial x}{\partial z} + f$$

(14) $$\frac{\partial v}{\partial t} = K\frac{\partial^2 v}{\partial z^2} + (\frac{\partial K}{\partial z})(\frac{\partial v}{\partial z}) - \alpha f .$$

A finite difference approximation for (13) at $t = jk$ and $z = (i-1)h$ is

(15) $$(x_i^{j+1} - x_i^j)/k = K_i(x_{i-1}^{j+1} - 2x_i^{j+1} + x_{i+1}^{j+1})/h^2$$
$$+ (\frac{\partial K}{\partial z} - s)_i(x_{i+1}^{j+1} - x_{i-1}^{j+1})/2h + f_i^{j+1}$$

where

$x_i^j = x((j-1)k,(i-1)h)$

$K_i = K((i-1)h)$

and

$f_i^j = f((j-1)k,(i-1)h,x_i^j,v_i^j)$.

To evaluate f_i^{j+1} we approximate it by its first degree Taylor expansion about the point $((i-1)h,x_i^j,v_i^j)$;

(16) $f_i^{j+1} \doteq f_i^j + \frac{\partial f}{\partial x}\Big|_i^j (x_i^{j+1}-x_i^j) + \frac{\partial f}{\partial v}\Big|_i^j (v_i^{j+1}-v_i^j)$

where $\frac{\partial f}{\partial x}\Big|_i^j = \frac{\partial f}{\partial x}((j-1)k,(i-1)h,x_i^j,v_i^j)$.

When we substitute (16) into (15) and rearrange we obtain

$$(17) \quad \left[\frac{1}{2h}\left(\frac{\partial K}{\partial z}-s\right)_i - \frac{1}{h^2}K_i\right]x_{i-1}^{j+1} + \left[\frac{1}{k} + \frac{2K_i}{h^2} - \frac{\partial f}{\partial x}\Big|_i^j\right]x_i^{j+1}$$

$$+ \left[-\frac{1}{2h}\left(\frac{\partial K}{\partial z}-s\right)_i - \frac{1}{h^2}K_i\right]x_{i+1}^{j+1}$$

$$= f_i^j + \left[\frac{1}{k} - \frac{\partial f}{\partial x}\Big|_i^j\right]x_i^j + \frac{\partial f}{\partial v}\Big|_i^j(v_i^{j+1}-v_i^j)$$

Finite difference approximations for the boundary conditions at the surface and the bottom are

$$(18) \quad 0 = \left(K\frac{\partial x}{\partial z} - sx\right)\Big|_1^{j+1} \doteq \frac{K_1}{2h}(x_2^{j+1} - x_0^{j+1}) - sx_1^{j+1}$$

$$\text{or } x_0^{j+1} = x_2^{j+1} - \frac{2hs}{K_1}x_1^{j+1}$$

and

$$(19) \quad 0 = \frac{\partial x}{\partial z}\Big|_{N+1}^{j+1} \doteq (x_{N+2}^{j+1} - x_N^{j+1})/2h$$

$$\text{or } x_{N+2}^{j+1} = x_N^{j+1} \; .$$

Imposing the boundary conditions on equations (17) we can rewrite the finite difference equations as a tridiagonal system of linear equations:

$$(20) \quad \begin{bmatrix} V_1 & W_1 & & & & & \\ U_2 & V_2 & W_2 & & & & \\ & U_3 & V_3 & W_3 & & & \\ & & & \cdot & & & \\ & & & \cdot & & & \\ & & & \cdot & & & \\ & & & & U_N & V_N & W_N \\ & & & & & U_{N+1} & V_{N+1} \end{bmatrix} \cdot \begin{bmatrix} x_1^{j+1} \\ x_2^{j+1} \\ x_3^{j+1} \\ \cdot \\ \cdot \\ \cdot \\ x_N^{j+1} \\ x_{N+1}^{j+1} \end{bmatrix} = \begin{bmatrix} \xi_1 \\ \xi_2 \\ \xi_3 \\ \cdot \\ \cdot \\ \cdot \\ \xi_N \\ \xi_{N+1} \end{bmatrix}$$

where

$$V_1 = \frac{1}{k} + \frac{2K_1}{h^2} - \left.\frac{\partial f}{\partial x}\right|_1^j - \frac{s}{K_1}\left(\frac{\partial K}{\partial z} - s\right)_1 + \frac{2s}{h}$$

$$W_1 = -\frac{2}{h^2}K_1$$

$$U_i = \frac{1}{2h}\left(\frac{\partial K}{\partial z} - s\right)_i - \frac{1}{h^2}K_i$$

$$V_i = \frac{1}{k} + \frac{2K_i}{h^2} - \left.\frac{\partial f}{\partial x}\right|_i^j \qquad\qquad \text{for } i = 2,\ldots,N$$

$$W_i = \frac{-1}{2h}\left(\frac{\partial K}{\partial z} - s\right)_i - \frac{1}{h^2}K_i$$

$$U_{N+1} = \frac{-2}{h^2}K_{N+1}$$

$$V_{N+1} = \frac{1}{k} + \frac{2K_{N+1}}{h^2} - \left.\frac{\partial f}{\partial x}\right|_{N+1}^j$$

and

$$\xi_i = f_i^j + \left[\frac{1}{k} - \left.\frac{\partial f}{\partial x}\right|_i^j\right]x_i^j + \left.\frac{\partial f}{\partial v}\right|_i^j (v_i^{j+1} - v_i^j) \qquad (i = 1,\ldots,N+1).$$

A similar finite difference approximation leads to an analogous tridiagonal system of linear equations for the phosphorus model. Primes will be used to identify the corresponding terms:

$$V_1' = \frac{1}{k} + \frac{2K_1}{h^2} + \alpha\left.\frac{\partial f}{\partial v}\right|_1^j$$

$$W_1' = -\frac{2K_1}{h^2}$$

$$U_i' = \frac{1}{2h}\left.\frac{\partial K}{\partial z}\right|_i - \frac{K_i}{h^2}$$

$$V_i' = \frac{1}{k} + \frac{2K_i}{h^2} + \alpha\left.\frac{\partial f}{\partial v}\right|_i^j \qquad\qquad \text{for } i = 2,\ldots,N$$

$$W_i' = -\frac{1}{2h}\left.\frac{\partial K}{\partial z}\right|_i^{j+1} - \frac{K_i}{h^2}$$

$$U'_{N+1} = 0$$

$$V'_{N+1} = 1$$

and

$$\xi'_i = -\alpha f^j_i + \left[\frac{1}{k} + \alpha \frac{\partial f}{\partial v}\Big|^j_i\right] v^j_i - \alpha \frac{\partial f}{\partial x}\Big|^j_i (x^{j+1}_i - x^j_i) \qquad (i = 1, \ldots, N)$$

$$\xi'_{N+1} = v_b \; .$$

These two systems of equations may be solved iteratively beginning with an initial guess for the differences $(v^{j+1}_i - v^j_i)$ $(i = 1, \ldots, N+1)$ and initial conditions for the phytoplankton and phosphorus concentration profiles, i.e., $x(0,z) = g_x(z)$ and $v(0,z) = g_v(z)$.

6. Process of Studying Model Behavior

In order to obtain numerical solutions to the proposed equations, numerical estimates or hypotheses must be given for each of the parameters. The subsequent list of values come partially from research at Lake Samamish, Washington and partially from literature survey. These parameter values will be used to demonstrate a typical simulation. The eventual plan is, of course, to systematically vary some of these parameters in order to study model behavior.

Description of Parameter	Value in Simulation	Source
z_b - depth of water column	17.5 m	Average depth of Lake Samamish
Δz - vertical depth increments used for approximation	.35 m	Determined to be satisfactory for scientific analysis
Δt - time increment used for approximation	one day	
s - sinking rate for community of phytoplankton	.5 m day^{-1}	A guess; according to Hutchinson's (1967) survey somewhere between 2 and 18 day^{-1} would be more realistic
K_0 - coefficient of eddy diffusivity at the surface	1.5 m^{2}day^{-1}	Summarized from Hutchinson (1957)
K_1	.0514	A guess
B_1 - coefficient of light extinction for lake water devoid of phytoplankton	.3	Lake Samamish
B_2 - coefficient of light extinction for phytoplankton	.0004	A guess; B_1 and B_2 yield a combined extinction coefficient which is representative of Lake Samamish
R_{opt} - solar radiation intensity required for saturated growth rate	1084 K cal m^{-2}day^{-1}	Lake Samamish

Description of Parameter	Value in Simulation	Source
H - Michaelis-Menton half saturation constant for phosphorus versus carbon uptake	3.0 mg m^{-3}	Lake Samamish
f_{max} - saturated relative net photosynthetic rate	2.5	An educated guess based upon data from Lake Samamish
α - phosphorus to carbon ratio of phytoplankton by weight	$.09$	Lake Samamish
$g_x(z)$ - initial concentration profile for phytoplankton	40 mg m^{-3} from surface to bottom	Winter conditions for Lake Samamish
$g_v(z)$ - initial concentration profile for phosphorus	12 mg m^{-3} from surface to bottom	Winter conditions for Lake Samamish
v_b - phosphorus concentration maintained on the water-sediment interface	12 mg m^{-3}	Winter conditions for Lake Samamish

In section 4 we made precise (not necessarily correct) assumptions concerning the functional relationship between the rates of change of phytoplankton and phosphorus concentrations and several components, i.e., vertical concentration gradients, mixing rates, sinking rates, photosynthetic rates, and nutrient uptake rates. If these equations are additionally constrained by specified initial and boundary conditions then there exist unique functions of time and depth which satisfy these hypotheses. The numerical techniques outlined in section 5 are a procedure for finding these unique solutions. The result of a simulation can thus be represented by graphs, with respect to time and depth, of the phytoplankton and phosphorus concentrations. Some of the results from a 50 day simulation, beginning with light conditions representative of January 1, are demonstrated in Figures 1 through 4. Figures 5 through 7 are included to aid interpretation of Figures 1 through 4.

Figure 1 shows phytoplankton concentration profiles at 5 day intervals. In Figure 2 are phosphorus concentration profiles; some profiles were omitted because of their proximity to others. Figure 3 shows net production rate profiles. If the phytoplankton concentration profiles are integrated from the surface to the bottom at each time step then the total amount of phytoplankton in a water column with one square meter surface is obtained. The temporal behavior of the integrated profiles is given in Figure 4. Figure 5 represents the assumed temporal behavior of surface solar radiation. Figure 6 is the proportional reduction in photosynthetic rate at the surface, as measured by carbon uptake rate, attributed to solar radiation intensity, i.e., the function in Figure 5 is substituted into the expression

$$\frac{R}{R_{opt}} \exp\{1 - \frac{R}{R_{opt}}\} \quad .$$

Figure 7 is the assumed Michaelis-Menton relationship between phosphorus concentration and proportional reduction in carbon uptake rate.

The simulation depicts a system characterized by an initial decline in both the phytoplankton and phosphorus concentrations, a subsequent bloom of the algae population and then a population crash which never recovers. At the beginning of the time period the relative photosynthetic rate is insufficient to maintain the algae population against the force of sinking. Since the photosynthetic rate is small (due to low solar radiation levels), the phosphorus uptake rate is small, so that the phosphorus concentration profile does not decline rapidly with time. As the amount of solar radiation increases the relative photosynthetic rate increases to the point where a bloom is possible. The phosphorus concentration profile now begins to drop rapidly. Since the force of mixing is evidently insufficient to supply phosphorus to the surface waters at the rate at which it is being assimilated, the relative photosynthetic rate declines and leads to a population crash.

Although more interesting results will be gleaned from the model when a systematic plan for varying the parameters is implemented, a few general conclusions can be inferred from this single simulation.

Light intensity and phosphorus concentration are definitely major controlling forces upon phytoplankton production. This observation is trite, but draws attention to the fact that the proposed model is certainly a useful tool for studying the effects of various temporal patterns of light and turbidity, and evaluating the role and importance of various mechanisms for cycling nutrients. The simulated system is obviously deficient in mechanisms for cycling phosphorus so that this topic should receive increased attention. The role of phytoplankton sinking as a prominant mechanism for draining phosphorus from the surface waters is emphasized by the simulation. It is difficult to draw many conclusions regarding the mixing rate from a single simulation but it is evident that this mechanical process for circulating nutrients does not function rapidly enough to sustain a growing phytoplankton population. Although the light intensity is greatest at the lake surface the net production rate and even the relative net production rate may be greatest at a deeper level.
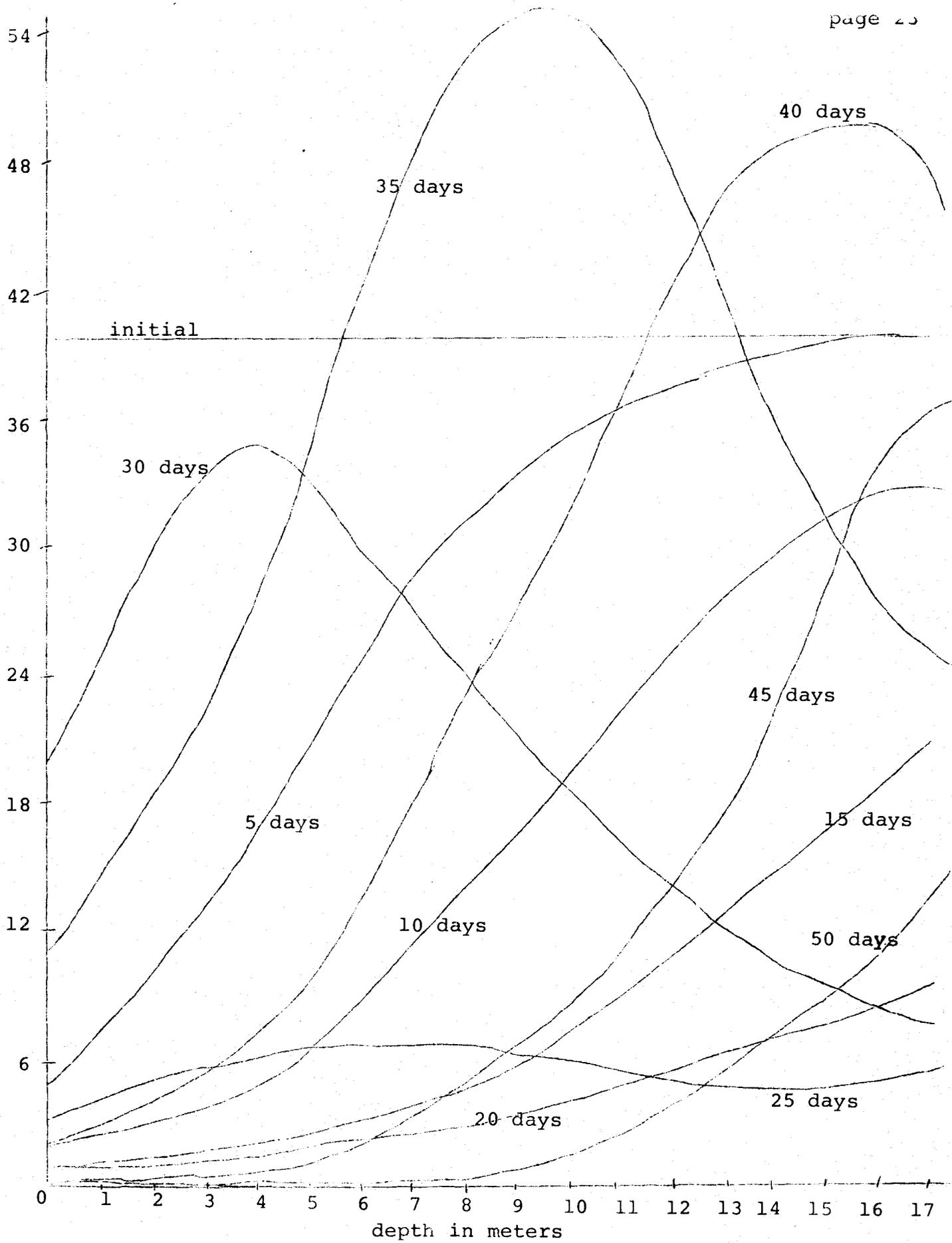
Figure 1.   Phytoplankton Concentration Profiles in mg carbon per m^3.

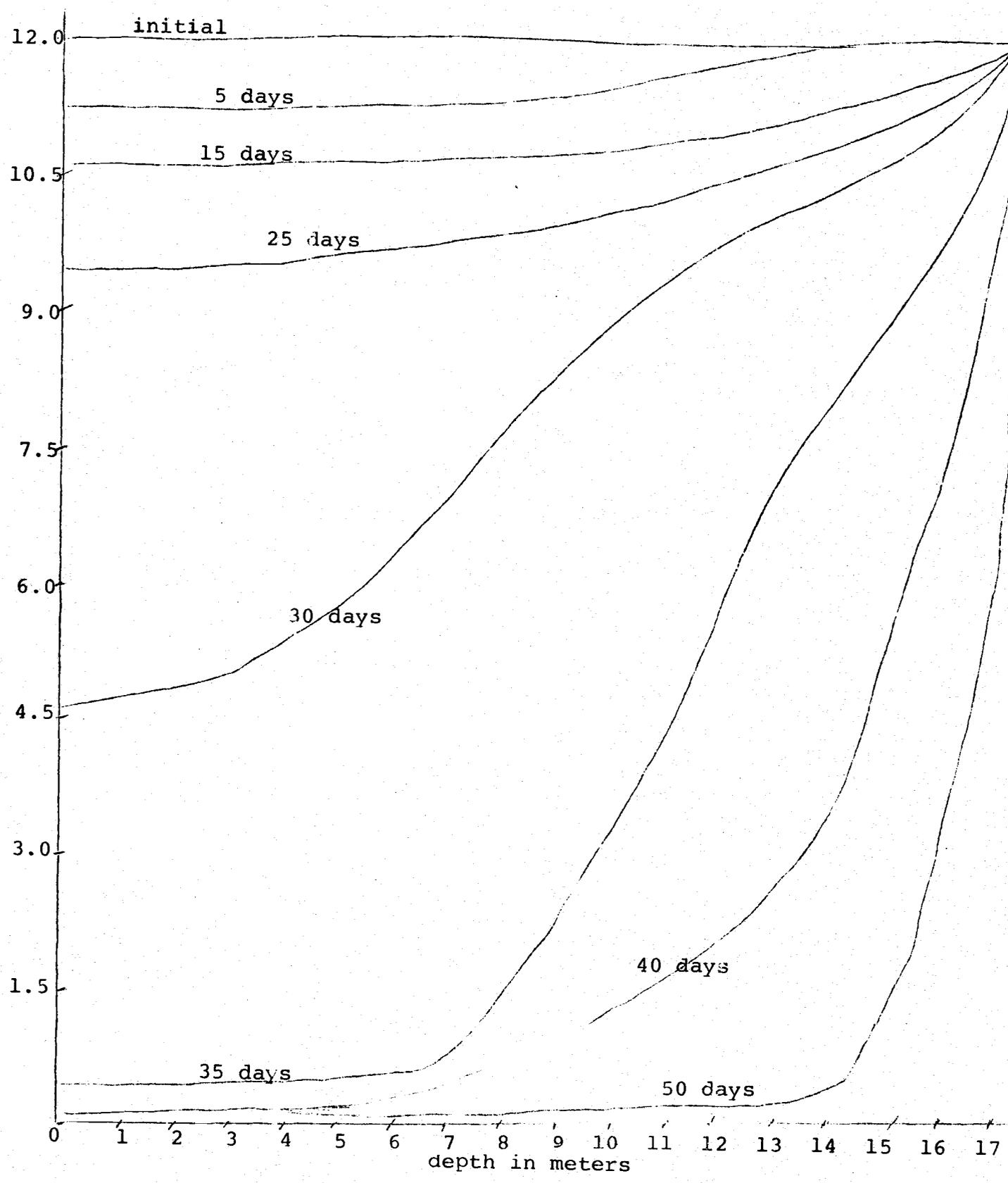Figure 2. Phosphorus concentration profiles in milligrams per cubic meter.

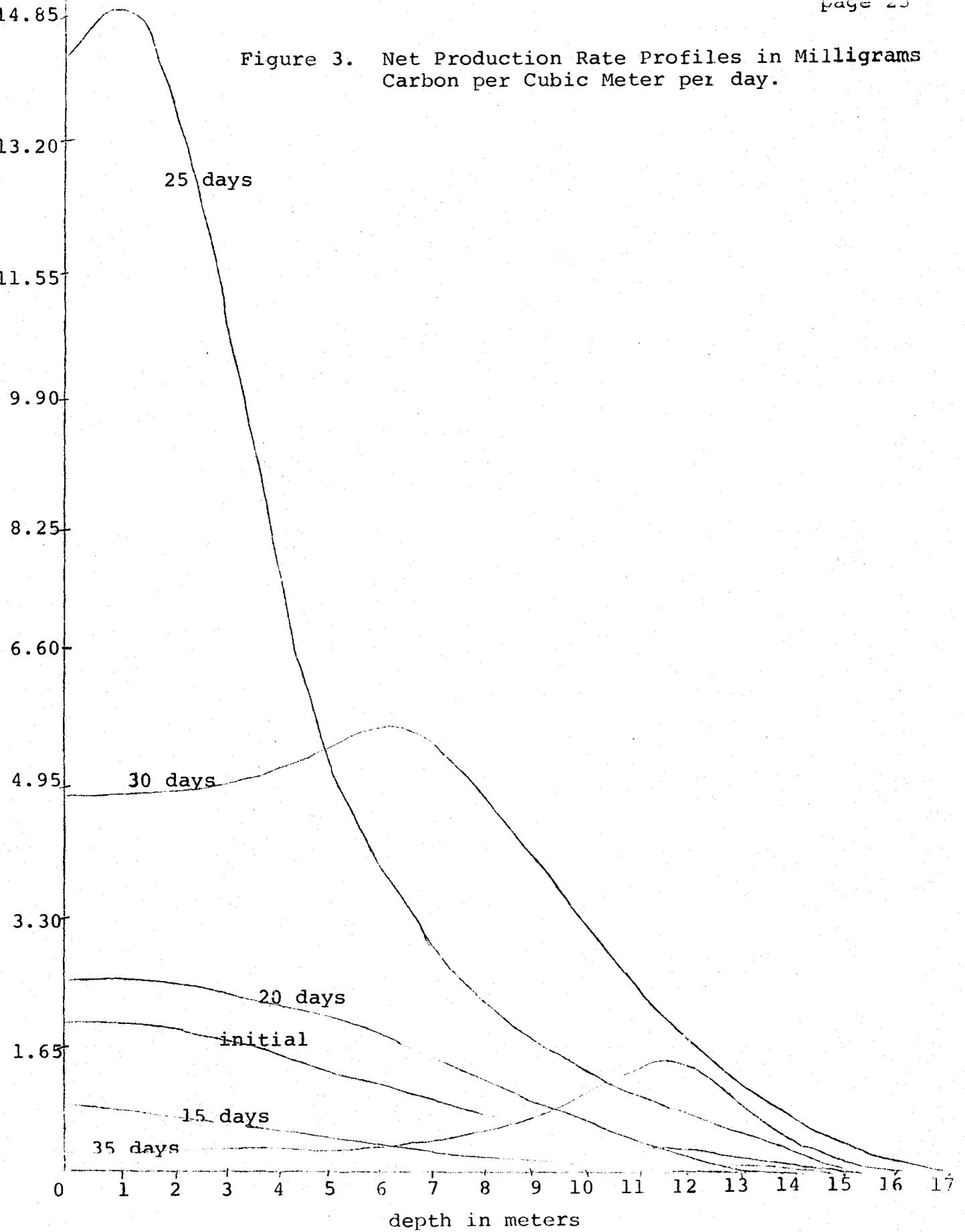Figure 3. Net Production Rate Profiles in Milligrams Carbon per Cubic Meter per day.

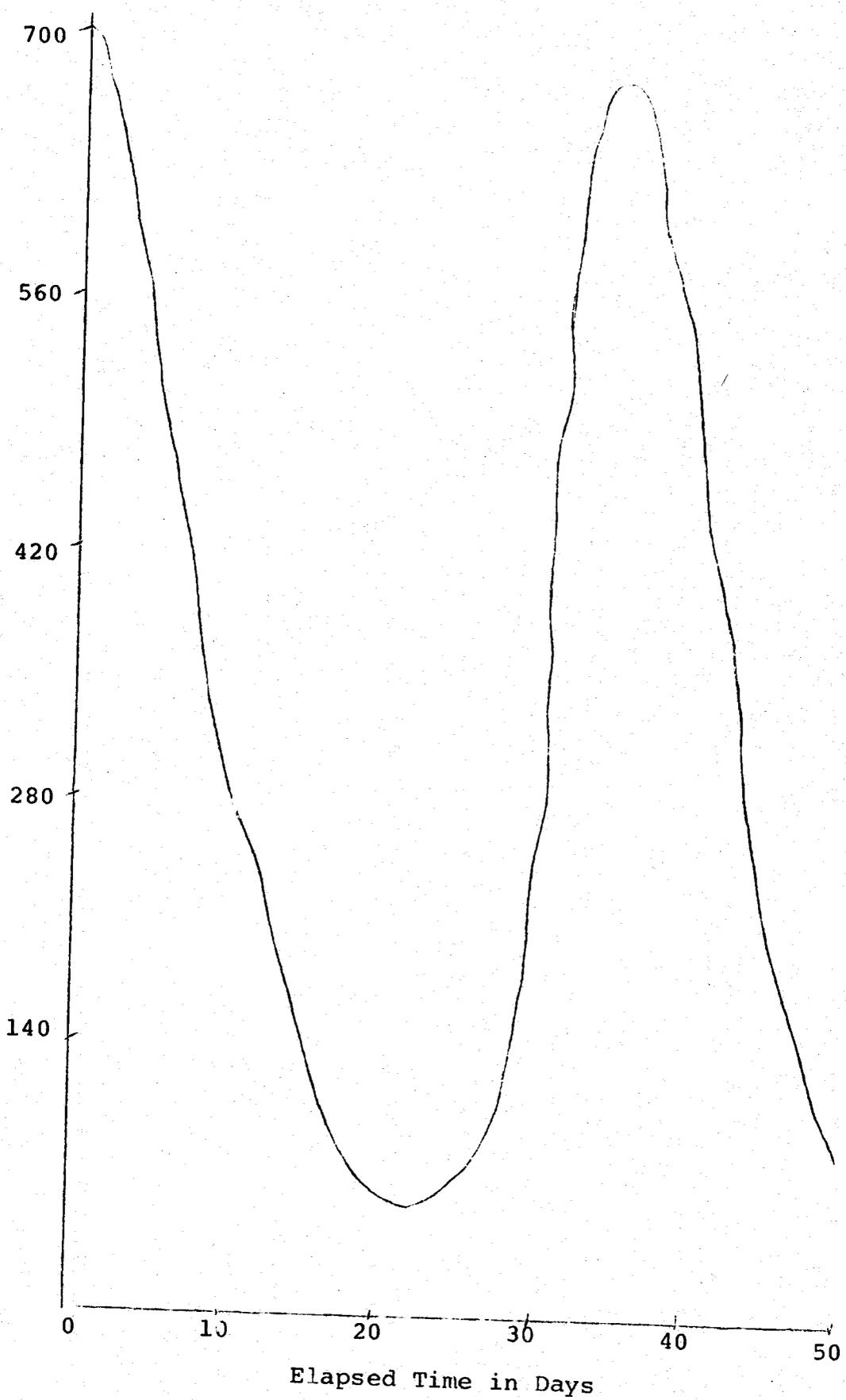Figure 4.   Total Phytoplankton in Milligrams per Square Meter

Elapsed Time in Days

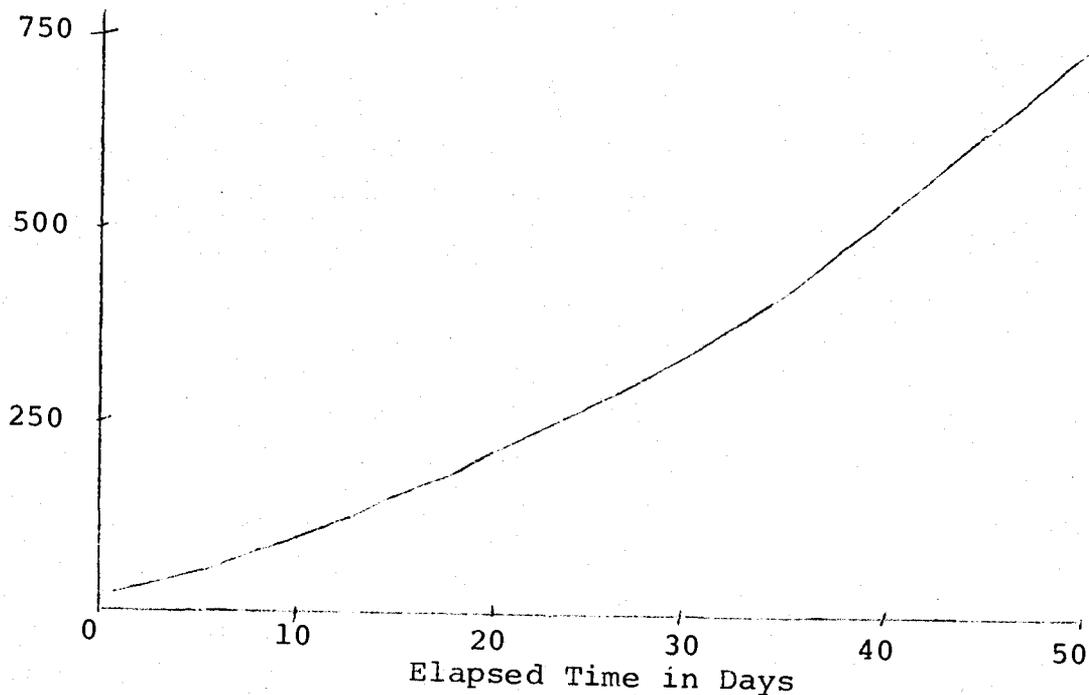Figure 5.   Solar Radiation in Kilocalories per Square Meter
            per Day

Elapsed Time in Days

Figure 6.   Proportional Reduction in Carbon Uptake Rate at
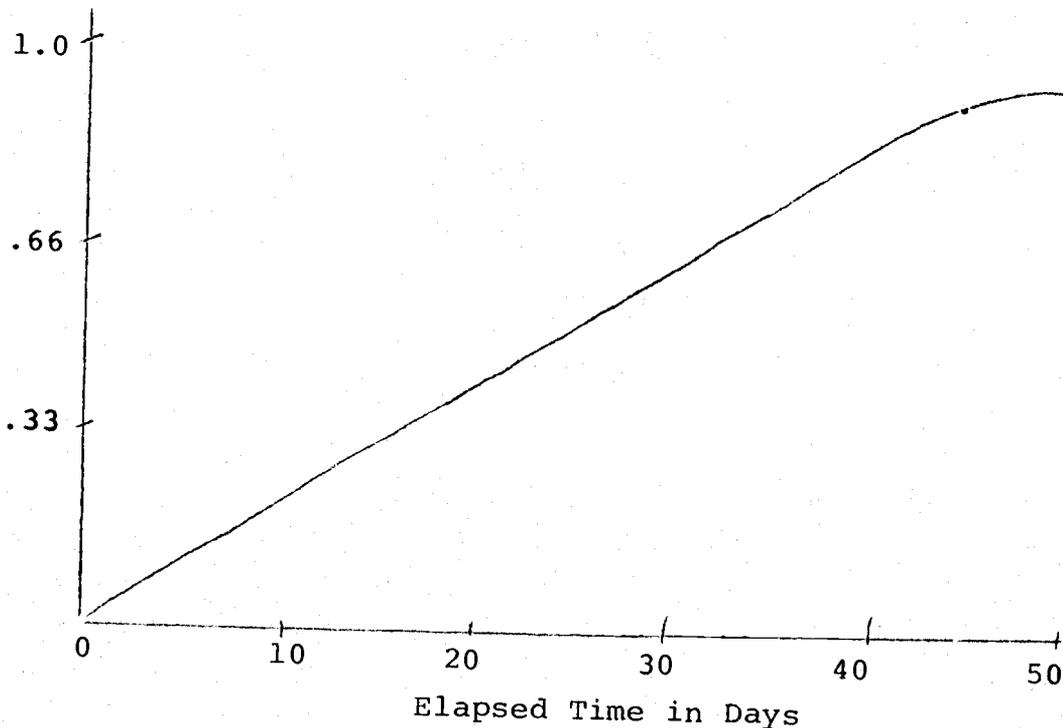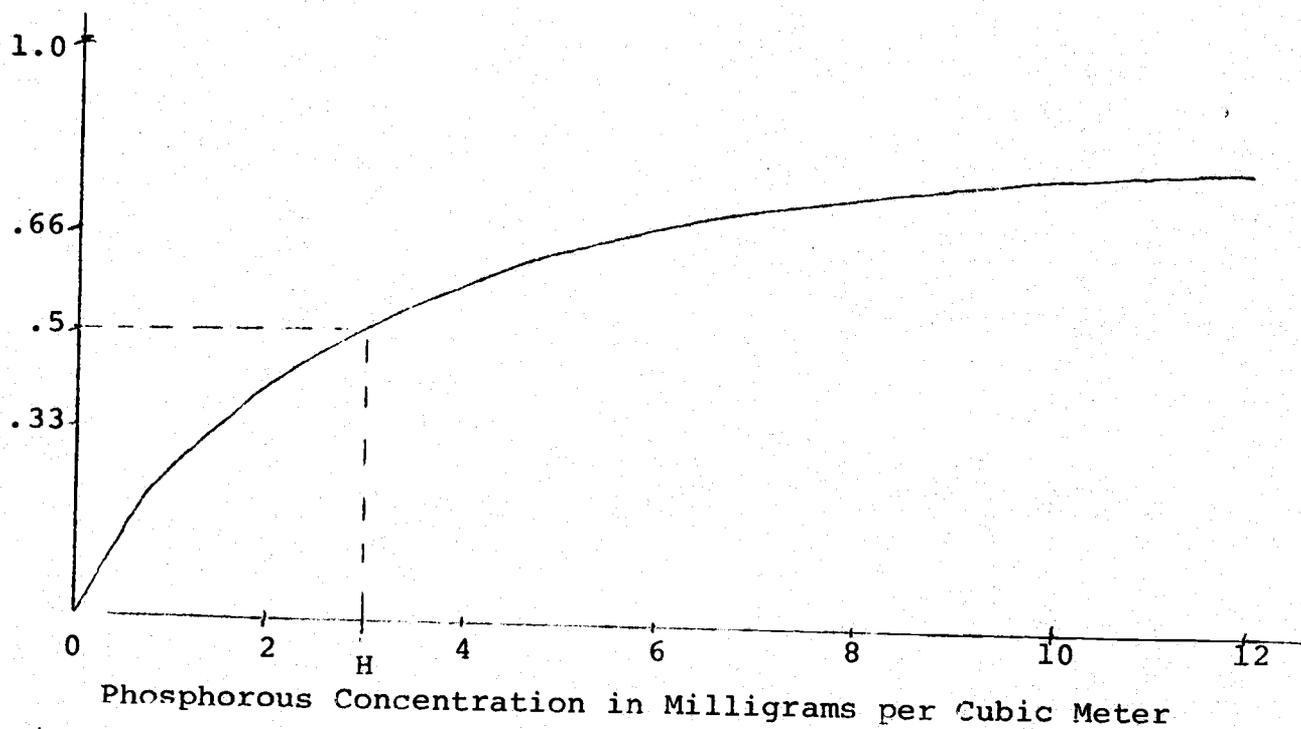   the Lake Surface Attributed to Solar Radiation Inte

Elapsed Time in Days

Figure 7. Michaelis-Menton Relation Between Phosphorus
Concentration and Proportional Reduction in Carbon
Uptake Rate; H = 3.0 mg m^{-3}.

Phosphorous Concentration in Milligrams per Cubic Meter

7. Acknowledgments

8. Literature Cited

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