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MATHEMATICAL MODELING OF PHYTOPLANKTON BIOMASS

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This paper demonstrates how the main factors such as light, temperature, nutrients, respiration, sedimentation, grazing and toxic compounds that affect the growth of phytoplankton are taken into account in constructing phytoplankton models. Such models are based on the accumulated knowledge and data relating to water bodies. They are used in order to improve understanding of ecosystems and to make predictions. Natural ecosystems are complex and the models that are abstractions of these systems therefore include numerous state variables, forcing functions and parameters. The problem of dividing the total phytoplankton into functional groups is dealt with and an example of a possible division is given. Further, the theoretical aspects of constructing phytoplankton models are discussed. Phytoplankton models appear to be capable of correctly simulating the average concentrations of phytoplankton biomass and to some extent its dynamics.

Index words: Phytoplankton models, mathematical models, ecological models, simulation models, water quality prediction.

1. INTRODUCTION

Phytoplankton biomass affects the water quality of water bodies in many ways. It influences the concentrations of dissolved oxygen and nutrients, biological oxygen demand, pH and turbidity. Decay of phytoplankton mass can decrease the concentration of dissolved oxygen to such an extent that aerobic aquatic life is inhibited. Some species of phytoplankton produce odours, cause bad taste in fish and may even secrete toxic chemicals to the water. These phenomena decrease the suitability of water as a source of drinking water and for recreational purposes.

A large number of water quality models have been presented for the evaluation of the effects of phytoplankton (e.g. Riley 1946, 1965, Russel 1975, Kremer and Nixon 1975, Lehman et al. 1975, Jørgensen 1976, Nyholm 1978, Benndorf and Recknagel 1982). In these models the factors such as light, temperature, nutrients and grazing that affect the growth of phytoplankton are taken into account. The relationship between the factors interacting in the ecosystem are presented with mathematical equations. In nature there are numerous factors that affect the growth of phytoplankton and the models are therefore rather complicated and generally include many state variables, forcing functions and parameters.

Mathematical models are simplifications and abstractions of reality. In modeling an aquatic ecosystem the knowledge available from the system is processed into a usefully organized form. Models are built to provide a synthesis of the scientific principles of aquatic ecosystems and the observed data. They are used as a research tool for indicating directions for investigation or as a management tool e.g. as an aid in planning. A modeller organizes existing data and must decide what information to include in the model.

The factors that determine how correctly the model simulates nature are the correctness of the simplification of the natural ecosystem into a model, the validity of the mathematical equations, division of the phytoplankton into groups, estimation of the parameters and the historical data available for calibrating and validating the model. Orlob (1983) and Beck and van Straten (1983) have discussed the methods and problems encountered in constructing water quality models. Patten (1968) and Schwartzman and Bentley (1979) presented literature reviews on phytoplankton models.

The objectives of this paper are to review briefly the main factors that affect the growth of phytoplankton and to provide examples of how these factors are mathematically taken into account in phytoplankton models. The modeling literature is vast and therefore the examples are limited in number and present only the main mechanisms, of which a great number of modifications exist. Models including stochastic components are not included. In addition the theory and the mechanisms used in constructing phytoplankton models are discussed, with special reference to selected models.

2. FACTORS AFFECTING PHYTOPLANKTON GROWTH

2.1 The basic equation

In natural water bodies the growth rate of phytoplankton is smaller than the maximal growth rate, because nutrient concentrations, prevailing temperature and light intensity are not optimal. The overall growth of phytoplankton is a function of the growth rate and death rate, which in turn are functions of various factors of the aquatic ecosystem. The growth of phytoplankton can be simulated with the general equation (Eq. 1).

$$\frac{dP}{dt} = (G_p - D_p)\,P \qquad (1)$$

G_p = growth rate
D_p = death rate
P = concentration of phytoplankton biomass

By taking into account the various factors such as light, temperature, nutrients, respiration and grazing that affect the growth rate, equation 1 can be developed further (Eq. 2).

$$G_p = G_m\,(N, L, T) \qquad (2)$$

G_m = maximal growth rate of phytoplankton, a function of nutrients (N), light (L) and temperature (T)

Death rate (D_p) can be divided into the terms of respiration, sedimentation and grazing.

$$D_p = R_p + S_p + F_p \qquad (3)$$

R_p = respiration rate
S_p = sedimentation rate
F_p = grazing rate

By substituting equations (2) and (3) to equation (1) a general equation (Eq. 4) for the simulation of phytoplankton is obtained.

$$\frac{dP}{dt} = (G_p - R_p - S_p - F_p)\,P \qquad (4)$$

The terms of this equation are treated more closely in subsequent sections.

2.2 Nutrients

Phosphorus, nitrogen and silicon are the most frequently simulated nutrients in phytoplankton models. In some models carbon is also included. Micronutrients such as metals or other growth factors are generally not included although in certain environmental conditions they may limit the growth of phytoplankton (Benoit 1957). Simulation of nutrients includes various processess that are important in the cycling of nutrients, e.g. uptake by phytoplankton, mineral-

ization, excretion, release of nutrients from sediments, nitrogen fixation, nitrification and denitrification etc.

Michaelis-Menten-type expressions are typically used for the simulation of nutrients. In some models e.g. Lehman et al. 1975, DiToro et al. 1975, Michaelis-Menten-type formulae are written for each factor limiting the growth of phytoplankton and the formulae are multiplied by each other (Eq. 5). In other models e.g. Scavia and Park 1976, Gaume and Duke 1975, Kinnunen et al. 1982, the smallest value of formulae written in this way are used in calculating the growth rate (Eq. 6). Jørgensen (1983b) presented various mechanisms of taking into account the interactions of several factors limiting the growth of phytoplankton.

$$G_p = \left(\frac{P}{K_1+P}\right)\left(\frac{N}{K_2+N}\right)\left(\frac{C}{K_3+C}\right) G_m \qquad (5)$$

$$G_p = \mathrm{Min}\left[\left(\frac{P}{K_1+P}\right)\left(\frac{N}{K_2+N}\right)\left(\frac{C}{K_3+C}\right)\right] G_m \qquad (6)$$

P = phosphorus concentration
N = nitrogen concentration
C = carbon concentration
K_1 = half saturation constant for phosphorus
K_2 = half saturation constant for nitrogen
K_3 = half saturation constant for carbon

A third method, in which the growth of phytoplankton is considered as a two-phase process in which the uptake of nutrients into a cell and phytoplankton growth are treated separately, was used e.g. by Bierman (1976). The growth of phytoplankton was simulated in his model by taking the smallest of the following three functions written for phosphorus, nitrogen and silicon, respectively:

$$G_p = \mathrm{Min}\begin{cases} G_m\, f(T)\, f(L)\left\{1-\exp\left[-0.693\,(P/P_0-1)\right]\right\} \\ G_m\, f(T)\, f(L)\,\dfrac{(N-N_0)}{KNCELL+(N-N_0)} \\ G_m\, f(T)\, f(L)\,\dfrac{SCM}{KSCM+SCM} \end{cases} \qquad (7)$$

KNCELL = intracellular half saturation constant for nitrogen-dependent growth (mol N per cell)
KSMC = half saturation constant for silicon-dependent growth (mol Si l^{-1})
P = moles of phosphorus per phytoplankton cell
P_o = minimum stoichiometric level of phosphorus per phytoplankton cell (mol per cell)
N = moles of nitrogen per phytoplankton cell
N_o = minimum stoichiometric level of nitrogen per phytoplankton cell (mol per cell)
SCM = silicon concentration in water (mol l^{-1})
f(T) = temperature correction factor
f(L) = light correction factor
T = temperature ^oC

The traditional Michaelis-Menten-type expression does not include a feed-back mechanism and it is therefore a special case of Bierman's equation (Eq. 7) and assumes that the nutrient storage in the phytoplankton cell is constant.

Although Michaelis-Menten type expressions are frequently used in modeling their use has also been critized (Mar 1976, Li 1983).

2.3 Light

Increase in light intensity stimulates the growth of phytoplankton up to a certain optimum, after which the growth rate decreases due to photoinhibition (Fig. 1). This general pattern is valid for all species of phytoplankton although there is variation between different species. Many of

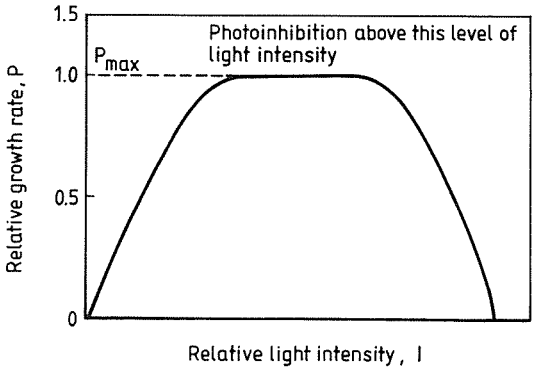

Fig. 1. The relationship between light intensity (I) and phytoplankton growth rate (P).

the equations that describe this relationship have been written for the linear part of the light-saturation curve, up to illumination levels at which photoinhibition begins. Other equations take into account the inhibitive effect of high light intensity. Smith (1936) presented the following equation for the linear part of the curve:

$$p\,(p_{max}^2 - p^2)^{-\frac{1}{2}} = aI \qquad (8)$$

p = photosynthetic rate
p_{max} = maximum photosynthetic rate
a = a constant which determines the initial slope of the curve at low light level
I = intensity of light

The curve fits well with the data obtained in experiments with a freshwater vascular plant. This equation was used e.g. by Talling (1957). Steele's (1962) equation includes the inhibitive effects of high light intensities.

$$p = p_{max}\, aIe^{1-aI} \qquad (9)$$

In this equation the inhibition is initiated by the exponentially decreasing term. The equation includes two parameters, a and p_{max}, which depend on the photosynthetic yield at low light intensities and at optimum light intensity.

Jassby and Platt (1976) applied eight different mathematical formulations of the photosynthesis-light curve for phytoplankton up to and including light saturation. Seven of the equations were selected from the literature and they included e.g. the equations of Smith (1936), Steele (1962) and a Michaelis-Menten-type equation. One of the equations was the hyperbolic tangent function (Eq. 10) developed by the authors:

$$p = p_{max} \tanh \frac{aI}{p_{max}} \qquad (10)$$

The criterion for the validity of these equations was their ability to describe data with minimum number of parameters. All the equations were rewritten in terms of two common parameters α (mg C [mg Chl a]$^{-1}$ h^{-1} W^{-1} m^{-2}), the slope of the light-saturation curve in the linear range and p_{max} (mg C [mg Chl a]$^{-1}$ h^{-1}), the specific photosynthetic rate at saturation level. The equations were fitted to the data gathered in 188 duplicate experiments. It was found that with this data the best overall agreement was obtained with the hyperbolic tangent function and Smith's (1936) equation. The worst agreement was obtained with the Michaelis-Menten-type of expression and Steele's (1962) equation. The last two equations, however, are widely used in phytoplankton ecology.

Additional equations that take into account the inhibitive effects of excessive illumination have been presented e.g. by Vollenweider (1965), Parker (1974) and Lehman et al. (1975).

Vollenweider (1965) presented the following equation, which is Smith's (1936) equation modified by the addition of an inhibition term:

$$p = p_{max} \frac{aI}{\sqrt{1+(aI)^2}} \left(\frac{1}{\sqrt{1+(\alpha I)^2}}\right)^n \qquad (11)$$

Different combinations of values of α and n (total number, generally 1 or 2) generate a family of curves which may fit experimental data.

Parker (1974) presented two empirical equations and applied them to three sets of data. Both equations fitted the data set equally well. He concluded that the simpler equation (Eq. 12) with three parameters should be preferred to the more complex equation with four parameters.

$$p = p_{max}\left[\frac{I}{I_{opt}} \exp\left(1-\frac{I}{I_{opt}}\right)\right]^{\alpha} \qquad (12)$$

For the use of the model the three parameters I_{opt}, α and P_{max} must be estimated.

Lehman et al. (1975) presented the following relationship between light and the growth of phytoplankton on the basis of the function of Steele (1962):

$$p(I) = p_{max}\left(\frac{I}{I_{opt}}\right) \exp\left(1-\frac{I}{I_{opt}}\right) \qquad (13)$$

p(I) = rate of photosynthesis at the light intensity (I)
p_{max} = maximum rate of photosynthesis
I = ambient light intensity
I_{opt} = optimum light intensity for photosynthesis

Both the appearance of surface inhibition and the correlation between light attenuation and photosynthesis are predicted by the model.

Lehman et al. (1975) formulated the equation (14) for photosynthetic carbon fixation reduced

by end product inhibition. However, it is uncertain whether the end product inhibition functions in nature.

$$p(I,C) = \frac{C_m - C}{C_m - C_o} \; p(I) \qquad (14)$$

$p(I)$ = determined by equation (13)
C_m = maximum carbon content in the cell
C = carbon content in the cell
C_o = limiting carbon content for cell growth

The equations describing the relationship between light saturation and photosynthesis are integrated over time and depth to calculate the average daily photosynthesis for the euphotic zone.

2.4 Temperature

Temperature affects chemical and biological reactions and this effect must be taken into account in modeling. The general pattern of the effect of temperature on process rates is described by a curve which first increases exponentially with increasing temperature, reaches an optimum and then begins to decline after the optimum (Fig. 2). This phenomenon closely resembles the effect of light intensity on phytoplankton growth (Fig. 1).

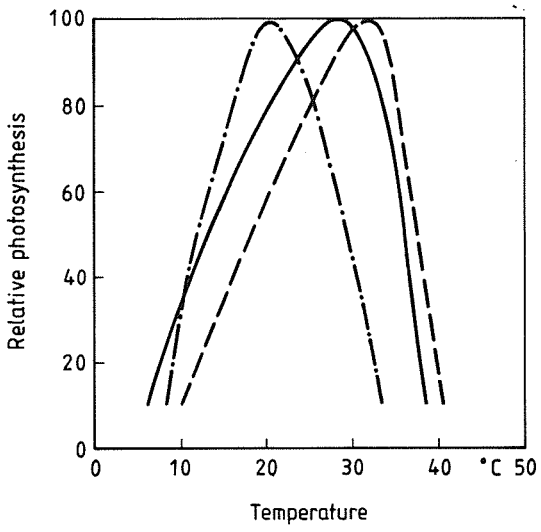

Fig. 2. The relationship between temperature and relative photosynthesis with three hypothetical algal species.

Several different equations have been used to simulate the effect of temperature on biological reactions. Some of these equations describe only the rising exponential part of the curve, whereas others describe the whole curve including the values for optimum, maximum and minimum temperatures for the processes studied.

In ecological modeling perhaps the most widely used of the equations that do not consider an optimum temperature is the equation of Streeter and Phelps (1925):

$$G_p(T) = G_{p(20)}\Theta^{(T-20)} \qquad (15)$$

$G_p(T)$ = growth rate at temperature T°C
$G_{p(20)}$ = growth rate at 20°C
Θ = empirical constant
T = prevailing temperature

This equation has been used in several models e.g. by Gaume and Duke (1975), DiToro et el. (1979) and DiToro and Matystik (1980). It gives reasonably good results in the temperature area below the optimum value.

However the van't Hoff's expression is the traditional equation for taking into account the effect of temperature on chemical and biological reactions. Benedict and Carlson (1970) studied the relationship between the equations of Streeter-Phelps (1925) and van't Hoff. They found that the empirical temperature coefficient theta of Streeter and Phelps can be interpreted in terms of the van't Hoff's equation and showed that in reality theta is not a constant but is a decreasing function of temperature. In practical work the use of the Streeter-Phelps equation is acceptable, as the error is less than ten percent.

Goldman and Carpenter (1974) used the Arrhenius equation to take into account the effect of temperature on algal growth. The Arrhenius equation (Eq. 16) was originally developed to describe the dependence of chemical reaction rates on temperature:

$$k = A\, e^{-E/RT} \qquad (16)$$

k = reaction rate
A = constant d^{-1}
E = activation energy cal mol^{-1}
R = gas constant cal $^{o}K^{-1}$ mol^{-1}
T = temperature ^{o}K

This equation can be applied to chemical reactions in which activation energy can be determined. When it is applied to biological reactions the term E/R must to be substituted with a constant typical for each process.

Lassiter and Kearns (1974) developed the following equation which includes the optimum and maximum temperatures:

$$k_T = k_{opt}\, e^{a(T - T_{opt})} \left[\frac{T_{max} - T}{T_{max} - T_{opt}}\right]^{a(T_{max} - T_{opt})} \quad (17)$$

k_T = rate of biological reaction
T_{opt} = optimum temperature
k_{opt} = rate at the optimal temperature
T = prevailing temperature
T_{max} = maximum temperature

Lehman et al. (1975) presented the following equations:

$$k_T = k_{opt} \exp\left(-2.3\frac{T - T_{opt}}{T_{max} - T_{opt}}\right) \text{ for } T > T_{opt} \quad (18)$$

$$k_T = k_{opt} \exp\left(-2.3\frac{T - T_{opt}}{T_{opt} - T_{min}}\right) \text{ for } T \leq T_{opt} \quad (19)$$

These equations are a somewhat inexact approach to the Arrhenius equation.

Scavia and Park (1976) presented an equation taking into account the optimum, maximum and minimum temperatures. Their equation was further developed by Groden (1977) and Park et al. (1979). Frisk and Nyholm (1980) developed a general temperature correction based on the equation of Streeter and Phelps (1925) which was used e.g. by Kinnunen et al. (1982).

Problems in correcting the reaction rates for temperature are the selection of the correct equation and estimation of the true optimum, maximum and minimum temperatures for the process being studied. For large functional groups of phytoplankton these values are somewhat arbitrary. However, the literature contains some data on the growth rates of individual phytoplankton species at different temperatures (Canale and Vogel 1974, Jørgensen 1979), which can be used in modeling.

2.5 Respiration

The groups of organisms that are typically included in phytoplankton models are phytoplankton and zooplankton. They consume oxygen in respiration, which must be taken into account in simulating the growth of organisms and the oxygen balance of a water body. On the other hand phytoplankton produces oxygen to water.

Riley (1946) included the respiration rate in his model and assumed it to be a function of temperature:

$$R_T = R_o\, e^{rT} \quad (20)$$

R_T = respiration rate at temperature T^oC
R_o = respiration rate at 0^oC
r = constant expressing the rate of change of the respiratory rate with temperature, typically 0.069

A modification of this equation was used e.g. by Lehman et al. (1975) and DiToro and Matystik (1980). A typical mechanism for the modeling of respiration, used in various models, is:

$$R = R_{max}\, f(T)\, P \quad (21)$$

R = respiration rate
R_{max} = maximum respiration rate, function of temperature
P = concentration of phytoplankton biomass

The empirical expression of the relationship between the respiration rate and body weight of an organism has been given e.g. by Norstrom et al. (1976) and Jørgensen (1983a):

$$R = aW^b \quad (22)$$

R = respiration rate
W = weight of an organism
a and b = constants

The weights of individual organisms cannot be determined in modeling. The total weight of the phytoplankton biomass is therefore estimated and respiration is assumed to be proportional to the biomass.

Modeling of respiration is difficult because it is affected not only by temperature but also by

the size of an organism, its physiological state, activity and degree of acclimatization. Two separate respiration rates are often used. The first is the active respiration rate which is used when the cells are actively growing and the second, passive respiration rate is used for non-growing cells (Gaume and Duke 1975). Both of these rates are functions of temperature.

2.6 Sedimentation

Sedimentation of phytoplankton is affected by various factors such as vertical turbulence, vertical density distribution, nutrient depletion, species composition and the physiological state of the phytoplankton species. In some circumstances the sedimentation velocity may be zero or the cells may move upwards towards the surface of the lake. In rivers and estuaries where the water transport occurs along the longitudinal axis of the flow, sedimentation may be insignificant. Sedimentation of phytoplankton is simulated with a first order reaction, which is a gross simplification. In some models the sedimentation rate is assumed to be constant. In the models which do not include the death rate of phytoplankton, the removal of phytoplankton from the euphotic zone is included in sedimentation. In a detailed model, sedimentation should be calculated separately for each functional group and it should be a function of all the factors affecting sedimentation, including e.g. viscosity of the water. In some cases the rate of sedimentation is determined by calibration.

2.7 Grazing by zooplankton

In most models phytoplankton is assumed to be grazed by herbivorous zooplankton. The grazing rate is decreased by low concentration of phytoplankton and sub-optimal temperatures. Simulations of phytoplankton and herbivorous zooplankton are strongly interrelated.

Herbivorous zooplankton is modeled with the same type of expressions as those used for phytoplankton. The factors affecting changes in zooplankton biomass are growth rate, respiration and grazing. A typical equation for the simulation of zooplankton is the following:

$$\frac{dZ}{dt} = (G_z - D_z)\, Z \qquad (23)$$

G_z = gross specific growth rate
D_z = death rate
Z = zooplankton concentration

The specific growth rate of zooplankton is assumed to be a function of several factors, typically of phytoplankton concentration, ingestion or grazing rate, temperature and assimilation efficiency.

DiToro and Matystik (1980) presented the following equation for the growth rate of herbivorous zooplankton:

$$G_z = K_{zp}\ A\, F_z\, P \qquad (24)$$

$$\text{where } A = \frac{A_{max}\, K_A}{K_A + P} \qquad (25)$$

$$\text{and } F_z = F_{zmax} \left(\frac{T}{20}\right) \frac{K_p}{K_p + P} \qquad (26)$$

G_z = growth rate of herbivorous zooplankton
K_{zp} = stoichiometric ratio of zooplankton to phytoplankton
A = assimilation efficiency
A_{max} = maximum assimilation efficiency
F_z = grazing rate
F_{zmax} = maximum grazing rate
P = concentration of phytoplankton
K_A = half saturation constant for assimilation efficiency
K_p = half saturation constant for the grazing
T = temperature ^oC

This Michaelis-Menten-type approach has earlier been used in other models as well, e.g. by Bierman (1976). Modifications of this equation, with additions of different zooplankton groups and preference factors for various phytoplankton groups, have been presented (e.g. Canale et al. 1976, Kinnunen et al. 1982).

There are several factors which affect the zooplankton death rate, such as predation by other zooplankton or fish, respiration, mortality due to of non-optimal conditions and natural mortality, all of which are functions of water temperature. One expression for zooplankton death rate is:

$$D_z = R_z + F_z \qquad (27)$$

R_z = respiration rate, a function of temperature
F_z = zooplankton grazing

It was earlier assumed that zooplankton grazes all the phytoplankton from a certain volume of water after a certain time, regardless of the initial phytoplankton concentration. Subsequently, it has been observed that the feeding rate depends on the density of phytoplankton (McMahon and Rigler 1965, Richman and Rogers 1969, Frost 1972). In these cited papers, investigations were carried out concerning the preying of different species of zooplankton on various algal or bacterial cells in laboratory experiments. For example, *Calanus helgolandicus* preys on synchronously growing populations of the marine diatom *Ditylum brightwellii* (Richman and Rogers 1969), and *Daphnia magna* prey on *Escherichia coli, Chlorella vulgaris* and *Tetrahymena pyriformis* (McMahon and Rigler 1965). Frost (1972) and McCauley (1985) investigated the effects of the size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus.* In all these experiments it was found that the ingestion rate increased linearly with increasing prey cell concentration up to a certain maximum level, after which ingestion rate remained the same with further increase in cell concentration. The results of both batch and continuous cultures were in agreement (Frost 1972).

Mullin et al. (1975) attempted to fit models to different sets of data described in the literature, among others to the data of Frost (1972). They found that the rectilinear model fitted better to the data of Frost (1972) than the Michaelis-Menten curve, although the differences were small. Mullin et al. (1975) stated that »The rectilinear and curvilinear presentations (or models) arise from slightly different concepts of the ingestion process. In the former, there is assumed to be no interference between particles in the capture-ingestion mechanism until the critical concentration is reached, and the rate at which water is swept clear of food is constant within this range of concentrations. In the latter, the degree of interference increases continuously as the concentration of particles increases so that the rate of ingestion decelerates».

The assumption that zooplankton ceases to feed on phytoplankton when the concentration of phytoplankton is low would imply that there is a refuge for phytoplankton where it is not preyed. This approach has been used and it has been found to improve the temporal stability of the model. Theoretically it may be assumed that if the cost in energy for zooplankton is high in relation to the non-feeding metabolic rate, it is advantageous to cease preying when the concentration of food is low (Mullin et al. 1975). Furthermore, there are certain species, such as very large cells of green algae and colonial blue-green algae, that are unsuitable as prey for zooplankton.

The equations written for grazing often include a parameter called digestive efficiency, which determines how much of the consumed phytoplankton biomass is converted to zooplankton. It is often assumed that zooplankton feeds not only on phytoplankton but also on detritus. These models include a preference factor that defines the proportions in which the food sources are used.

On the basis of the investigations referred to above, the ingestion rate of zooplankton preying on phytoplankton is of a type presented in Fig. 3. Equations describing this type of curve are e.g. the Ivlev (1966) equation (Eq. 28)

$$R = R_{max} (1-e^{kq}) \qquad (28)$$

R = raily ratio
R_{max} = maximum raily ratio
q = food concentration
k = constant

or the Michaelis-Menten-type expression, see Eq. (26)

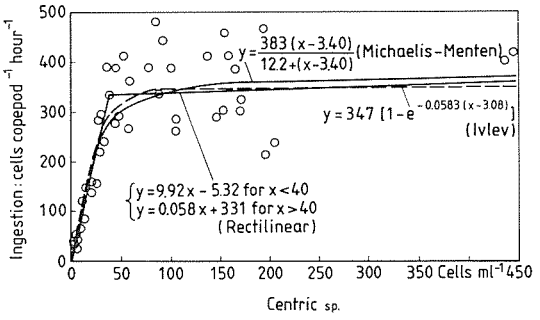

Fig. 3. Example of the grazing of phytoplankton by zooplankton. Ingestion of the *Centric* sp. by *Calanus* according to the data of Frost (1972, Fig. 4). The equations are the leastsquares best fit rectilinear, Ivlev and Michaelis-Menten models. (from Mullin et al. 1975, redrawn).

Another method is to fit two lines to observations in order to obtain a rectilinear model (Fig. 3).

A threshold value below which zooplankton cease to feed on phytoplankton can be introduced e.g. to Ivlev's (1966) equation, which then becomes

$$R = R_{max} [1-e^{-k (q - q_o)}] \quad (29)$$

q_o = the feeding threshold

A threshold value was used e.g. by Kinnunen et al. (1982).

Kuparinen (1985) proposed that in aquatic ecosystems there is an energy flow from phytoplankton through exudates and bacteria to microzooplankton. These interactions may be important, but they are not generally taken into account in the models at their present stage of development.

2.8 Toxic compounds

The development of models taking into account the impact of toxic substances is nowadays rather important. However, due to several difficulties encountered in simulating toxic processes, only a few models describing quantitatively the distribution and effects of toxic substances have been presented.

Toxic compounds discharged into water bodies have toxic and inhibitive effects on the growth of phytoplankton. These effects can be expressed:

$$M = M_N + \beta C_T \quad (30)$$

M = total mortality
M_N = natural mortality
β = toxicity coefficient
C_T = concentration of the toxic substance

Another method of taking into account toxic and inhibitive effects is simply to decrease the growth rate of phytoplankton or to increase its death rate or sedimentation rate. Jørgensen (1983a) presented in detail the simulation of the distribution and effects of toxic substances in rivers and lakes.

3. DIVISION OF PHYTOPLANKTON INTO FUNCTIONAL GROUPS

In this paper the phytoplankton system and nomenclature of Tikkanen (1986) is used. It differs somewhat from the older nomenclature used in previous papers (Kinnunen et al. 1982, Niemi and Eloranta 1984).

The total phytoplankton biomass in a body of water consists of different species of algae. The large systematic groups of algae are by no means homogenous. There are numerous examples of differences in ecology within the systematic groups. For example the blue-green algae, *Cyanophyceae* or *Cyanobacteria,* can be divided into species that cause algal blooms and species that do not. Some of the bloom-forming species assimilate atmospheric nitrogen. Of the *Chlorophyta* the species of *Chlorococcales,* especially *Scenedesmus,* are more often found in eutrophic than in oligotrophic waters. *Euglenophyceae* are mainly typical of eutrophic waters. *Chromophyta* are important in Finnish natural waters, in particular species of *Diatomophyceae* are often abundant and they form a considerable part of the biomass of the total phytoplankton. *Diatomophyceae* is a heterogenous group with regard to nutrient concentrations: cell numbers of *Biddulphiales* increase more with eutrophication than those of *Bacillariales* (Heinonen 1980).

Light and temperature cause wide seasonal variations in the distribution of phytoplankton. Phytoplankton is not distributed evenly in the water mass. It occurs in those parts of the water body where its requirements for growth are met. As a consequence, the composition and distribution of phytoplankton varies from lake to lake. A detailed survey of the quantity and composition of phytoplankton in Finnish inland waters was carried out by Heinonen (1980).

It is necessary to consider how to divide the phytoplankton into groups to be used in models. The ultimate objective should be to define the groups at the lowest possible taxonomical level. In practice, however, the division is always a compromise between small, well defined groups for which there is sufficient information for the determination of parameters, and larger, more heterogeneous groups about which less is known for the estimation of parameters. A certain division of phytoplankton should be applicable to a certain type of lake. It cannot be universally valid. Exact estimation of parameters for large

heterogeneous groups is probably not possible. One alternative is to divide phytoplankton into groups according to the size of the species (e.g. Gaume and Duke 1975). However, this is restricted by large annual and spatial variations in the size of algal cells. The best method would be to define groups according to their ecology. For Finnish lakes the following groups could be considered:

1. *Dinophyceae*
2. *Cryptophyceae*
3. *Chrysophyceae*
4. Nano- and picoplankton (< 20 μm)
5. *Chlorococcales*
6. Blue-green algae that cause algal blooms (e.g. *Microcystis, Anabaena, Aphanitzomenon)*
7. Other blue-green algae
8. *Diatomophyceae*
9. *Euglenophyceae*
10. *Desmidiales*

The three first groups are taxonomical and contain species that move with flagella. Groups 5, 8, 9 and 10 are also taxonomical. *Chlorococcales* and *Euglenophyceae* are typical of eutrophic lakes. *Desmidiales* are often found in oligotrophic and acid lakes. *Diatomophyceae* form a considerable part of the total phytoplankton biomass and should therefore be considered as one functional group. The other groups are not based on taxonomy. Group four is formed on the basis of the size of plankton, while groups 6 and 7 are based on the importance of *Cyanophyta* in water bodies. From the practical point of view the simulation of group 6 is important. The same groups that are used for calculating the species quotients could be used in modeling, because it has been observed that the quotients reflect the trophic state of a water body (e.g. Heinonen 1980). The groups that are used in the quotients are e.g. *Cyanophyta, Desmidiales,*

Table 1. Biomasses (mg l^{-1}) of phytoplankton groups and total phytoplankton in the northern lake Päijänne in 1975–1977. Data from Granberg et al. 1976, Granberg and Selin 1977 and Granberg et al. 1978 were processed in the National Board of Waters, Finland.

			Chromophyta				
Date	Cyanophyta	Chlorophyceae	Biddulphiales	Bacillariales	Total chromophyta	Cryptophyceae	Total phytoplankton biomass
1975							
6.6	.01	.02	.23	.03	.29	.94	1.26
24.6	0	.04	.41	.03	.48	.38	.90
22.7	0	.21	.68	.17	1.25	.63	2.10
27.8	.05	.12	1.49	.14	1.65	.19	2.02
10.9	.05	.11	3.76	.52	4.31	.17	4.64
25.9	.04	.05	6.77	.26	7.04	.07	7.19
1976							
19.5	.01	0	–	–	.01	.02	.05
1.6	0	.27	.33	.04	.56	2.56	3.33
22.6	.01	.21	1.98	.24	2.25	.08	2.55
12.7	–	.03	.52	.01	.59	.71	1.33
16.8	.07	.14	.65	.06	.84	.88	1.93
15.9	.03	.03	1.08	.02	1.14	.07	1.27
1977							
18.5	–	0	–	–	0	.01	.02
8.6	0	.01	2.00	.07	2.46	1.46	3.92
27.6	.03	.05	.11	.06	.45	.45	.98
12.7	–	.13	4.77	.26	6.63	1.08	7.84
8.8	.01	.08	1.50	.06	2.21	.37	2.67
7.9	.04	.03	2.76	.03	2.85	.15	3.07

– = species of phytoplankton of this group not recorded
0 = biomass so small that it is regarded as zero

Biddulphiales (Centrales) and *Bacillariales* (Pennales).

In the FINNECO-model the use of ten functional phytoplankton groups is possible but it requires detailed data of the species composition and biomass of phytoplankton of a case study lake.

Bierman (1976) simulated four groups, namely *Diatoms*, *Chlorophyta*, blue green algae (nitrogen fixing) and blue green algae (non-nitrogen fixing). The groups differed in their requirements for nutrients, growth rates, sinking rates and grazing pressure.

The application of the FINNECO-model to lake Päijänne, central Finland, is an example of the division of total phytoplankton into functional groups (Kinnunen et al. 1982). The biomasses of phytoplankton groups were measured several times during three consecutive years (Table 1). On the basis of this data the most dominant groups, *Chromophyta* and *Cryptophyceae*, were taken as functional groups. Later, an additional group entitled »other phytoplankton» was included in the model. Estimation of the parameters for these groups was carried out on the basis of earlier applications of the model, literature data and calibration.

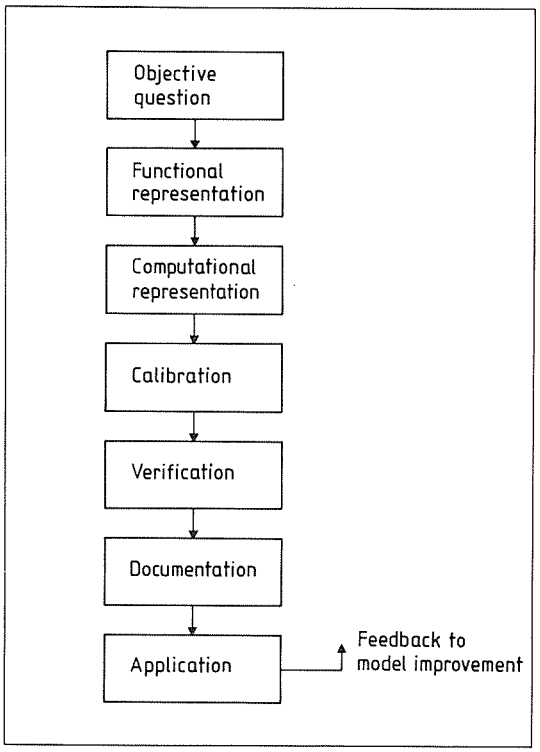

Fig. 4. Model process development.

4. MODEL CONSTRUCTION

The construction of a phytoplankton model can be divided into different stages, such as setting of goals and objectives for model development, functional and computational representation, calibration, verification, documentation and application (Fig. 4). Other stages are parameter estimation and sensitivity analysis.

In the modeling literature the objectives of the model construction are seldom stressed sufficiently. The model objective could be e.g. to investigate the effects of wastewaters on a water body. The objective question might then be: what will be the effect of phosphorus discharged from the wastewater treatment plant on the growth of phytoplankton in the recipient water body. Given these goals, an appropriate model can be constructed and answers to the question can be obtained. The goals and objectives of the model determine to a large extent what will be the conceptualization and functional representation of the model.

Large models have a modular-hierarchical structure. They are typically constructed by defining a number of sub-systems or sub-models which are constructed first. The identification of sub-systems can be accomplished by the so called top-down approach, in which the system with its environment is considered as a whole and the system is divided into smaller and smaller subsystems until sufficient resolution is achieved. Model structure can also be identified by proceeding in the opposite direction by bottom-up approach. Using a hierarchical approach, the objective of the model can be divided into subobjectives fulfilled by respective submodels (Fig. 5). Three hierarchical levels are obtained: firstly the system that is being observed, secondly the environment of this system that is the next system in the upper level and thirdly the subsystem of the system under observation (Fig. 6).

A strategy for the construction of a model could be the following (Overton 1977):

- specify the model objectives as a list of model specifications
- identify sub-models and sub-objectives
- construct and validate submodels
- assemble the sub-models into the complete model and validate
- seek answers to the objective question
- examine the general behaviour of the model: identify behaviours of interest
- using sensitivity analysis, identify the structure and parameters that are causal for the behaviour of interest
- validate the causal structures and parameters

For calibration, the model is applied to a water body and the real set of data and parameters are calibrated so that the model produces the observed data. Parameter estimation is a problem in large models because the number of parameters is great and there are no exact measurements of the values of all of them. Parameter estimation leads to the question of the concept of equilibrium of ecosystems. One could ask wheather the values of parameters are constants in nature or whether they vary according to the season or some other factor. The parameters that are functions of temperature, e.g. decay rates of many substances or the growth rates of phytoplankton groups, in fact show seasonal variation because temperature varies with the season.

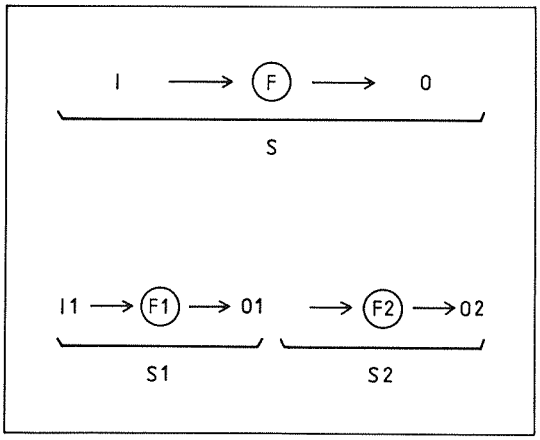

Fig. 5. Decomposition of a system S represented by a function F with input I and output O, into sub-systems S1 and S2.

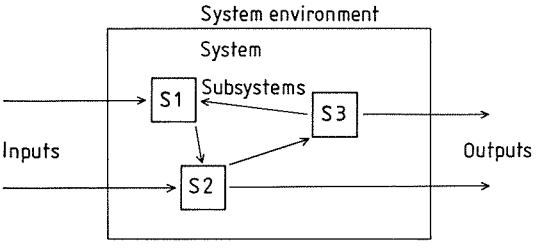

Fig. 6. Division of a system into three hierarchical levels: a system under observation, its sub-systems (S1, S2 and S3) and the system of its environment.

The sensitivity of the model can be investigated by changing the values of one or more parameters at a time, making a computer run and comparing the results with the earlier results obtained with the former values of the same parameters. Sensitivity analysis can be carried out e.g. by the Monte Carlo method (Fedra 1983) or by other methods (e.g. Liepmann and Stephanopoulos 1985).

Verification of the model must be accomplished with data which are independent of calibration. The model should behave in a certain manner in a certain region of behavioral space, predictable according the data available and the assumptions made. The model should be applicable to other systems that differ somewhat from the original system for which it was developed; there should be a certain tolerance in the model behaviour. A model can be verified separately for various systems, but it cannot be verified in the sense that it is universally valid. Verification must be considered in relation to the objectives given for the model. Although not universally valid, the model may turn out to be adequate for the purpose for it was constructed, and therefore be used for this particular purpose.

Documentation of the model should give the necessary data so that other users can apply the model. Application of the model to new case study areas can provide information that can be used to improve the structure of the model.

5. DISCUSSION

Construction of ecological models requires a holistic approach, in which the total behaviour of the ecosystem is studied. In phytoplankton modeling this implies certain simplifications in the

processes operating in the system and further simplifications of the complicated structure of the taxonomical groups of algae. The main factor influencing the structure of the model is the objective question — i.e. the question to which an answer is sought with the model. Other factors that must be considered are the correct hierarchical structure, degree of aggregation, selection of forcing functions and state variables and the correct level of resolution in the model structure. After solving these questions the conceptual and diagrammatic model can be constructed and based on this mathematical model. A mathematical model is programmed for a computer and after gathering the data test runs can be carried out. The final computer model also includes additional factors such as the algorithms used, the length of the simulation step and the technique according to which the equations affecting the functioning of the model are solved.

A model is derived on the basis of all the available information gathered from the system under study. After application of the model the output is compared with observations made from the real system. It is assumed that the reality — the real ecosystem being studied — is reflected in observations and the output of the model is made to fit to the observations in calibration (Fig. 7). Observations, however, include errors due to several factors, e.g. because of temporal and spatial variations in the water quality in water bodies and errors due to sampling, transportation and inadequate analyses. On the other hand the simulated results include errors due to the nature of models, their structure and the values of the parameters. As the simulated results are made to agree with the observations, the observations are in a way regarded as correct, absolute values that represent the reality and the errors included in the observations are therefore transferred to the model and taken to the values of its parameters. In the verification of the model these errors are reflected in the values of the new output, and if the new set of observations used for verification is obtained during a period of different temporal or spatial conditions, or if the observations include different errors due to e.g. transportation, the agreement between the model output and observations is not good.

The correctness of this type of comparison can be argued at length. In simulating complicated and sensitive groups of organisms such as phytoplankton the types of errors referred to

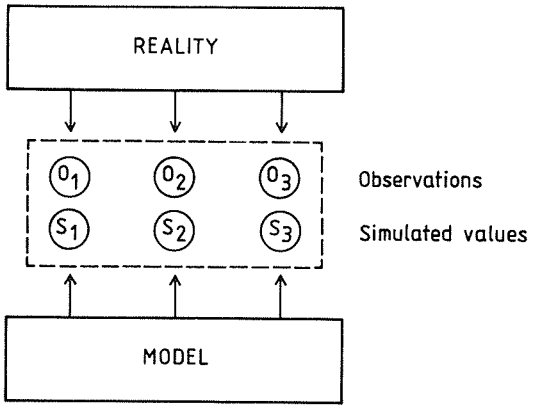

Fig. 7. A model and reality. Observations are assumed to present reality and model output is made to agree with them in the calibration.

may be significant. A more correct comparison could be achieved by taking into account the error limits of the observations, if possible (e.g. Bierman 1976). Naturally, there are numerous other factors, both in the ecosystem under study and in the model produced, that affect the agreement between the observations and the model output, but this question has some theoretical interest in modeling philosophy.

Niemi (1979) simulated total phytoplankton and found that the model was capable of simulating comparatively well the general level of phytoplankton. During calibration the observed phytoplankton maxima at the end of June could be generated. With the verification data, however, the model could not produce the observed maxima, but only simulated the average concentration without distinct peaks. This is often the case with other models as well. The parameters used in calibrating phytoplankton appear not to be capable of producing the dynamic variations occurring in phytoplankton populations. Simulation of different phytoplankton groups may help to produce the observed pattern of phytoplankton variation. Bierman (1976) could simulate four distinct maxima for four phytoplankton groups by using chlorophyll-a as a measure of phytoplankton. However, in his work only one maximum was produced for each algal group.

Kinnunen et al. (1982) simulated three groups of phytoplankton, namely: *Chrysophyta, Pyrrophyta* and a third group entitled »other phytoplankton with the characteristics of blue-green algae». In calibration the model could be

made to produce the two maxima of the first groups. When the model was run with two other independent sets of data, the simulated results were in rather good agreement with the observations.

These few examples illustrate the general conclusion that correct simulation of phytoplankton dynamics is difficult, although the models calculate the average level of algal concentration. Simulation results depend on numerous factors both in the ecosystem modeled and in the model itself. The models described, however, are typical phytoplankton models and the results obtained with them are typical of phytoplankton models at their present stage of development.

There are several parameters governing the growth of phytoplankton that can be used in phytoplankton calibration. The most important of these are e.g. half-saturation constants of nutrients and light, the temperature correction factor and temperature tolerance limits, settling rates, growth and death rates and active and passive respiration rates. Furthermore the parameters of zooplankton that affect the concentrations of phytoplankton, e.g. the threshold concentration of phytoplankton below which zooplankton ceases to feed, are also important. By estimating the corr values of these parameters the model can be made to produce the observations in calibration. The adequacy of calibration is always a compromise and depends e.g. on the objective question of the model and the calibration criteria, which are generally difficult to define in a complicated model. The question arises of how good the agreement between the model output and observations must be before the model can be considered valid for the purpose for which it was constructed. Universal verification for a phytoplankton model is impossible. In the simulation of phytoplankton it becomes evident that most of the reactions active in the ecosystem, e.g. water movements, chemical reactions of nutrients and exogenous variables such as light and temperature, affect the growth of algae. Phytoplankton simulation is therefore sensitive to a certain extent to most of the factors active in the ecosystem. It is thus evident that the simulation of phytoplankton cannot in all circumstances be as accurate as might be wished. On the other hand the present level of success in phytoplankton modeling shows that the most important reactions of the ecosystems are relatively correctly taken into account, because in spite of all their simplifications and approximations phytoplankton models calculate the average level of phytoplankton and even to some extent the general pattern of its annual variation.

The numerous mechanisms affecting the algae in aquatic ecosystems have complicated interactions. The development of phytoplankton models therefore requires more thorough analysis of these mechanisms, investigation of the correct hierarchical structure, development of submodels, reduction of the present parameters into groups of key parameters, and probably the introduction of stochastic components to the presentation of e.g. meteorological phenomena and other data that must be obtained in making predictions.

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TIIVISTELMÄ

Kasviplanktonmallit ovat matemaattisia malleja, jotka kuvaavat kasviplanktonin reaktioita vesiekosysteemissä. Niihin on sisällytetty tärkeimmät kasviplanktonin kasvuun vaikuttavat tekijät kuten valo ja lämpötila. Tällaiset mallit ovat yleensä monimutkaisia ja niissä on suuri joukko ulkoisia muuttujia, tilamuuttujia ja parametreja. Malleja laaditaan tutkimustarkoituksiin haluttaessa laatia synteesi vesiekosysteemeistä olemassa olevasta tietämyksestä sekä vedenlaatuennusteiden tekemiseen käytännön vesiensuojelutehtäviä varten.

Tässä työssä on tarkasteltu tärkeimpiä kasviplanktonmalleissa vaikuttavia tekijöitä, joita ovat: ravinteet, valo, lämpötila, respiraatio, sedimentaatio ja eläinplanktonin aiheuttama predaatio. Luonnonolosuhteissa nämä tekijät tai osa

niistä pienentävät kasviplanktonin maksimaalista kasvunopeutta. Ravinteiden ja usein myös valon vaikutus otetaan huomioon Michaelis-Menten tyyppisillä yhtälöillä. Lämpötilan vaikutus kemiallisiin ja biologisiin tekijöihin otetaan huomioon eri tyyppisillä yhtälöillä, joista yleisin on Streeterin ja Phelpsin (1925) happimallissaan käyttämä yhtälö. Kasviplanktonin respiraatio oletetaan yleensä maksimaalisen respiraation, lämpötilan ja kasviplanktonbiomassan funktioksi. Levien sedimentaationopeus käsitellään yleensä yksinkertaisella tavalla olettamalla se vakioksi. Osa eläinplanktonista käyttää kasviplanktonia ravintonaan. Tähän ilmiöön vaikuttavat mm. lähes kaikki eläinplanktonin kasvuun vaikuttavat tekijät kuten kasviplanktonin määrä ja koko, ravinnonoton tehokkuus ja lämpötila. Malleja varten on selvitettävä eläin- ja kasviplanktonmäärien välinen riippuvuus. Useissa malleissa predaation oletetaan lakkaavan kasviplanktonmäärän pienentyessä tiettyä rajaa alhaisemmaksi.

Kasviplanktonin jakaminen toiminnallisesti saman tyyppisiin ryhmiin on yksi malleja laadittaessa esille tulevia kysymyksiä, joita tässä työssä on tarkasteltu. Lisäksi esitetään ehdotus mahdolliseksi jaoksi ja annetaan esimerkki, kuinka tällainen jako on eräissä malleissa tehty.

Kasviplanktonmallien laatimiseen sisältyy monia periaatekysymyksiä, jotka tulevat esille kaikissa ekologisissa malleissa. Tällaisia ovat mm. mallille asetettavien vaatimusten pohdinta, oikean rakenteen valinta, mallin kehittäminen käsitteellisestä mallista tietokoneelle ohjelmoitavaksi malliksi, kalibrointi ja verifiointi.

Kasviplanktonmalleilla pystytään niiden tämänhetkisessä kehitysvaiheessa laskemaan kasviplanktonin keskimääräisiä pitoisuuksia ja karkealla tasolla myös vuodenaikaisvaihtelua.

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