

THE VERTICAL STRUCTURE
OF PHYTOPLANKTON GROWTH DYNAMICS
A MATHEMATICAL MODEL

by

G. RADACH,

*Sonderforschungsbereich 94 Meeresforschung Hamburg
Universität Hamburg*

and

E. MAIER-REIMER

*Institut für Meereskunde
Universität Hamburg*

ABSTRACT

A phytoplankton model is presented which includes the physical processes of turbulent diffusion, sinking, light penetration and the biological processes of photosynthesis, respiration, mortality, nutrient uptake, and regeneration.

The model predicts the variations of phytoplankton, nutrients and light in the vertical space dimension and in time. The photosynthesis rate is taken as dependent on light and nutrients. Light inhibition is included. In all light computations, the self-shading effect of phytoplankton and the daily variations of light intensity are taken into account.

Simultaneously with the vertical distributions of phytoplankton and nutrients, integrated balance equations for nutrients and phytoplankton, and several related variables such as compensation depth, the depth of the euphotic zone, the effective photosynthesis and loss rates are considered. These additional computations illustrate the mass transfer through the system and summarize the order of magnitude of metabolic processes.

The model is applied to a series of cases obtained by varying individual parameters about a standard reference case, thereby enabling a discussion of the significance of the various parametrisations involved.

Self-shading of phytoplankton and the inclusion of a diurnally varying surface light intensity turn out to be essential features which should be incorporated in a model describing the vertical structure of phytoplankton dynamics.

1. INTRODUCTION

There are many mathematical models to describe plankton growth dynamics. The authors start from very different points of view concerning the components which should be incorporated as the most important ones into a model. The models reviewed by PATTEN (1968) partly refer to the growth dynamics of phytoplankton alone (RILEY, 1946; STRICKLAND, 1960), or incorporate the limiting influence of nutrients and of their changes in time or of light intensity (e.g. SVERDRUP et al., 1942; SVERDRUP, 1953; STEELE, 1958; STEELE, 1962; VOLLENWEIDER, 1965). Other

authors take additional components of the ecosystem into account, such as herbivorous or carnivorous plankton and fish (RILEY, 1947; RILEY, STOMMEL and BUMPUS, 1949; CUSHING, 1959; STEELE, 1965 and RILEY, 1965).

The more components of the ecosystem are included, the simpler the functional relations between the components need to be in order to retain tractable differential equations. For this reason many of the models are restricted to functional relations between quantities averaged over space or time coordinates. In PATTEN's notation the first are the $\partial B/\partial t$ -models, the latter are usually restricted to $\partial B/\partial z$ -models (B = biomass).

A general mathematical formulation of the problem including dependent variables (phytoplankton, nutrients, and light intensity etc.) both in space and time (e.g. RILEY et al.) is rarely presented. A few authors, e.g. RILEY et al., STRICKLAND, consider the environmental conditions which are caused by the dynamics of the ocean : vertical and horizontal turbulent diffusion of the components of the ecosystem, and convection resulting from existing currents. Recently this research field has extended considerably. Complex models have been set up for estuaries (e.g. DI TORO et al., 1971) and upwelling areas (e.g. O'BRIEN and WROBLEWSKI, 1973). VINOGRADOV et al. (1972) presented a numerical model which includes nine dependent variables : phytoplankton, nutrients, detritus, bacteria, small herbivorous, large herbivorous, omnivorous and carnivorous plankton, light intensity. A comparison of their numerical results with measurements (fig. 4 of VINOGRADOV et al.) shows that only the lower members of the food chain are reproduced well at that moment (40 days after starting the computation) although an elaborated theory for the higher members of the food chain is incorporated in the model. This may be taken as an indication that the interrelationships of the phytoplankton and a nutrient need to be studied very thoroughly before adding other members of the ecosystem to the model.

It is known that many of the environmental variables such as currents, turbulent mixing, temperature, and nutrients may have a vertical structure. Light intensity in the upper tens of meters of the euphotic zone always has a strong vertical structure. Vertical turbulent diffusion is a very important process in phytoplankton growth dynamics because it determines the residence time of phytoplankton in the euphotic zone and supplies the upper layer with nutrients from below (GILLBRICHT, 1955; ANDERSON and BANSE, 1961; DI TORO, 1974). Thus, a model of the pelagic ecosystem cannot be satisfactorily developed on the assumption of vertical homogeneity of the variables mentioned. Similarly, the attempt to model a pelagic system with vertically integrated conservation equations leads to difficult parametrization problems with respect to the assumed vertical structure.

It appears therefore that the simplest realistic model will have to describe, as a minimum, the time development and vertical structure of a few essential variables in a horizontally homogenous water mass, i.e. at least biomass of phytoplankton, one limiting nutrient and underwater light intensity. The model we propose is suited to study interactions of physical processes such as turbulent diffusion, sinking of phytoplankton and light penetration with the biological processes of photosynthesis, respiration, grazing, nutrient uptake and excretion.

We assume that the photosynthesis rate depends on light and nutrients; light inhibition is included. In computing the light intensity, we take the self-shading effect of the phytoplankton and the daily variations of the light intensity into account.

For the sake of simplicity, no prognostic equations for other components (herbi-

vorous, carnivorous plankton) are incorporated in the model, although there are no mathematical complications in including them. This may be regarded as a shortcoming, but we thought it more important to study the behaviour of the basic regime of phytoplankton, nutrients, and light in different situations in detail (especially the effects of small changes of the controlling parameters) before extending the model.

The problem leads to a system of second order nonlinear partial differential equations, which are integrated numerically.

In addition to the complete solutions we consider vertically and time integrated balance equations. In general, the integrated layer is the euphotic zone itself, or a layer including the euphotic zone. These additional computations describe the mass transfer through the system caused by diffusion and sinking. They show the relevance of variations of physical origin as compared with those caused by biological processes. Additional characteristic variables, such as compensation depth, depth of the euphotic zone, effective photosynthesis rate, and effective loss rates, are also found to be useful in summarizing the evolution of the system.

2. A MATHEMATICAL MODEL

The numerical experiments described in the following sections are based upon two nonlinearly coupled second order partial differential equations for the concentration of phytoplankton P and one limiting nutrient N , both variables depending on time t and depth z ,

$$2.1 \quad \frac{\partial P}{\partial t} = A_v \frac{\partial^2 P}{\partial z^2} + (R_P^+ - R_P^-) P - w_s \frac{\partial P}{\partial z}$$

$$2.2 \quad \frac{\partial N}{\partial t} = A_v \frac{\partial^2 N}{\partial z^2} + (R_N^+ - R_N^-) P$$

and a first order ordinary differential equation for light intensity

$$2.3 \quad \frac{dI}{dz} = -k(z) I,$$

using the following symbols :

$\frac{\partial}{\partial t}$ partial time derivative

$\frac{\partial}{\partial z}$ partial vertical derivative

A_v vertical eddy diffusion coefficient

R_P^+ photosynthesis rate

R_P^- biological loss rate

w_s sinking velocity

R_N^+ nutrient regeneration rate

R_N^- nutrient uptake rate

$k(z)$ extinction coefficient

The appendix summarizes the symbols used in the treatment.

The extinction coefficient k is assumed to be dependent on depth z , i.e. on the vertical structure of suspended material and especially on phytoplankton (self-shading). The equations for P and N are diffusion equations with biologically determined source and sink terms. Taking the non-continuous character of the individual plankton cell into account, the equations must be regarded as equations of distribution probabilities.

A basic assumption is that all horizontal gradients are negligible, and that there is no mean vertical motion w of the water

$$2.4 \quad \frac{\partial P}{\partial x} = \frac{\partial P}{\partial y} = \frac{\partial N}{\partial x} = \frac{\partial N}{\partial y} = w = 0.$$

The vertical eddy diffusion coefficient A_v is taken to be constant and equal for phytoplankton and nutrients. For special simulation problems A_v can depend on the stratification as would be necessary for the study of interaction processes of phytoplankton dynamics with thermocline dynamics. The vertical diffusion coefficient used in this model is a compromise and should be replaced by a better mechanism of turbulence when available.

The sinking velocity w_s of phytoplankton is taken to be constant, too.

If any functional dependence of e.g. temperature should be given, temperature itself could easily be introduced into the model as a prescribed temperature field.

For the photosynthesis rate R_P^+ and the mortality rate R_P^- , as well as the related terms of nutrient uptake R_N^+ and nutrient regeneration rate R_N^- , we assume factorized forms :

$$2.5 \quad R_P^+ = r_P r_N r_I$$

$$2.6 \quad R_P^- = m_P m_T + m_L$$

r_P is the optimum photosynthesis rate; r_N (nutrient limitation) and r_I (light inhibition) take values between 0 and 1. Similarly, m_P is the respiration rate multiplied with the factor m_T (dependence of respiration on temperature). Since we neglect temperature in turbulent diffusion, in all experiments we choose $m_T = 1$. All other biological losses as, for instance, grazing by higher trophic levels, are represented by the mortality rate m_L . Consequently, m_L represents the effect of « forcing functions ». Obviously the constants r_P and m_P have to depend on the species of the phytoplankton under consideration. It should be emphasized that the factorial representation implies independent limitation by the occurring variables.

The nutrient uptake rate R_N^- is assumed proportional to the photosynthesis rate with a proportionality factor g :

$$2.7 \quad R_N^- = g R_P^+.$$

Regeneration of nutrients is determined by the mortality rate. A loss of phytoplankton leads to an immediate gain of nutrients; but only part of the nutrients consumed is regenerated. A time shift as caused, for instance, by detritus is not included :

$$2.8 \quad R_N^+ = f_N g R_P^-.$$

For special functional relationships and values of the constants see section 3.

To get a closed mathematical problem we have to prescribe initial and boundary conditions. The vertical distributions of phytoplankton and nutrients have to be defined at the beginning of the time interval in which the processes are to be

computed. To get a model which reproduces the real situation, these profiles should be measured very accurately. Then we have to introduce into the model :

$$2.9 \quad P(z, t) = P_0(z) \quad \text{and}$$

$$2.10 \quad N(z, t) = N_0(z) \quad \text{for } t = 0.$$

We assume that no mass transport occurs across the sea surface, i.e. the processes leading to an exchange of mass, cancel each other. For phytoplankton this leads to

$$2.11 \quad w_s P(0, t) = A_v \frac{\partial P}{\partial z}(0, t).$$

In the case of no sinking velocity this reduces to

$$2.12 \quad w_s(z=0) = 0 \quad \text{and} \quad \frac{\partial P}{\partial z}(z=0) = 0.$$

In the present computation we use (2.11). For nutrients we use the condition

$$2.13 \quad \frac{\partial N}{\partial z}(z=0, t) = 0.$$

We solve the equations (2.1) to (2.3) for a layer ($0 \leq z \leq h$) which is at least twice the euphotic zone. Consequently, we assume that below this layer the plankton concentration $P(h, t)$ is very small. Thus we may prescribe

$$2.14 \quad w_s P(h, t) = A_v \frac{\partial P}{\partial z}(h, t) \quad \text{or} \quad P(h, t) = 0 \quad \text{or} \quad \frac{\partial P}{\partial z}(h, t) = 0$$

for a sufficient large depth h . The layer below $z = h$ is assumed to be rich of nutrients. Therefore we assume :

$$2.15 \quad N(h, t) = N_0(h) = \text{const.}$$

For the equation for light intensity we have to prescribe the surface value

$$2.16 \quad I(0, t) = I_0(t).$$

3. CHOICE OF FUNCTIONAL RELATIONS AND PARAMETERS

To get a realistic phytoplankton model the functional relations needed in the model must be chosen carefully. At present time, no validation of the model by natural conditions seems possible because we know of no experiment from which all these relations and constants have been derived for one bounded region and one bounded time interval. So our computations represent a theoretical approach. In literature many relations are given concerning single aspects of the limitation problem. We base our simulations mainly on functions and data given by STEELE (1958), RILEY (1965), and DUGDALE (1967).

In the simulations the units of phytoplankton P and phosphate as the limiting nutrients N are g carbon/ m^3 and mg -at. phosphorus/ m^3 .

(a) *Photosynthesis rate* R_p^+ :

Most models using a non-constant rate consider the influence of light and/or

nutrient limitation on photosynthesis (e.g. RILEY, 1946; TALLING, 1957; STEELE, 1962; STEELE, 1964, VOLLENWEIDER, 1965), using factorized forms of the growth rate: $R_p^+ = r_p r_N r_I$, where r_p is a constant optimum photosynthesis rate, r_N and r_I are limiting factors due to nutrients and light. The limiting factor of nutrients (without a threshold), r_N , is modelled in a very simple form by

$$3.1 \quad r_N = \begin{cases} \eta N & \text{for } N < 2N_1 \\ 1 & \text{for } N \geq 2N_1 \end{cases}$$

with $\eta = 2.5 \text{ m}^3/\text{mg-at. } p$ and $N_1 = 0.2 \text{ mg-at. } p/\text{m}^3$, following RILEY (1965), or using a MICHAELIS-MENTEN expression

$$3.2 \quad r_N = \frac{N}{N + N_1},$$

following DUGDALE (1967).

For r_I we assume (STEELE, 1962)

$$3.3 \quad r_I = \left(\frac{I}{I_{\text{opt}}} \right)^{1 - \frac{I}{I_{\text{opt}}}},$$

I_{opt} being the light intensity corresponding to optimum photosynthesis. STEEMANN NIELSEN and HANSEN (1959) have shown that different values of I_{opt} may exist for phytoplankton in different depths (« light » and « shade » plankton). These effects of light adaption are neglected, and as a first approximation we choose I_{opt} constant and independent of depth.

Fig. 2a and 2b show the photosynthesis rate R_p^+ using (3.3) and (3.1) or (3.2) resp. Fig. 1a shows r_I for various values of $I_{\text{max}}/I_{\text{opt}}$, i.e. for various optimal depths for $k = 0.04 \text{ m}^{-1}$.

(b) *Biological loss rate* R_p^- :

STEEMANN NIELSEN and HANSEN (1959) relate the respiration rate to the maximum photosynthesis rate with a fixed ratio of about 5 to 10 per cent. For a first approximation we assume a constant value for the respiration rate of $m_p = 0.035 \text{ day}^{-1}$ (STEELE, 1958; RILEY, 1965), which has to be related to the maximum effective photosynthesis rate of 0.35 day^{-1} (see sections 5, 6).

For m_T we then have to take 1.0. The loss rate m_L describing mainly zooplankton grazing should include herbivorous plankton H [gC/m^3] and its grazing rate G [$m^3/gC/day$], $m_L = GH \text{ day}^{-1}$.

Neglecting the dynamics of herbivorous plankton we get $R_p^- \approx 0.1 \text{ day}^{-1}$ (independent of depth) assuming a mean zooplankton concentration of 0.02 gC/m^3 and a grazing coefficient $G = 3.4 \text{ m}^3/gC/day$ (RILEY 1965). Thus, in the simulations we use the value 0.1 day^{-1} .

(c) *Sinking velocity* w_s :

We consider the values 0, 1, 2, 3, 4, 5 m/day. RILEY (1965) reports the values 3 and 6 m/day. In a more refined model, w_s should be dependent on nutrients (STEELE and YENTSCH, 1960).

(d) *Nutrient regeneration* R_N^+ *and nutrient uptake* R_N^- :

For g RILEY (1965) obtains $0.774 \text{ mg-at. } p/gC$. We performed simulations

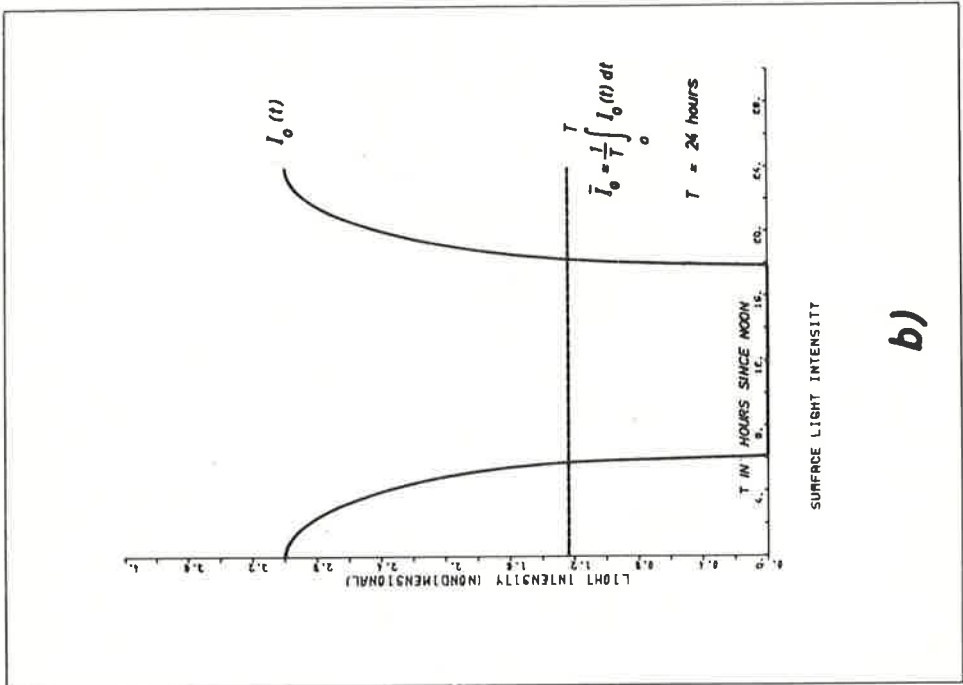
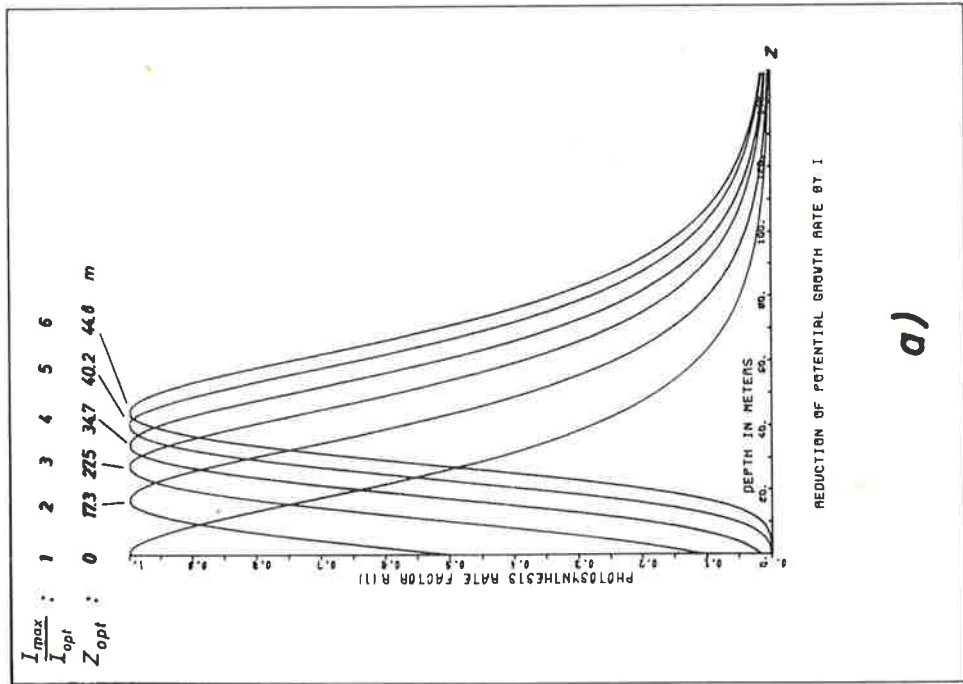


Fig. 1

a) Reduction of the potential growth rate by the light intensity factor : r_I is plotted vs. various maximum surface light intensities.
 b) Surface light intensity : diurnally varying and averaged over 24 hours, $I_0(t)$ and \bar{I}_0 resp.

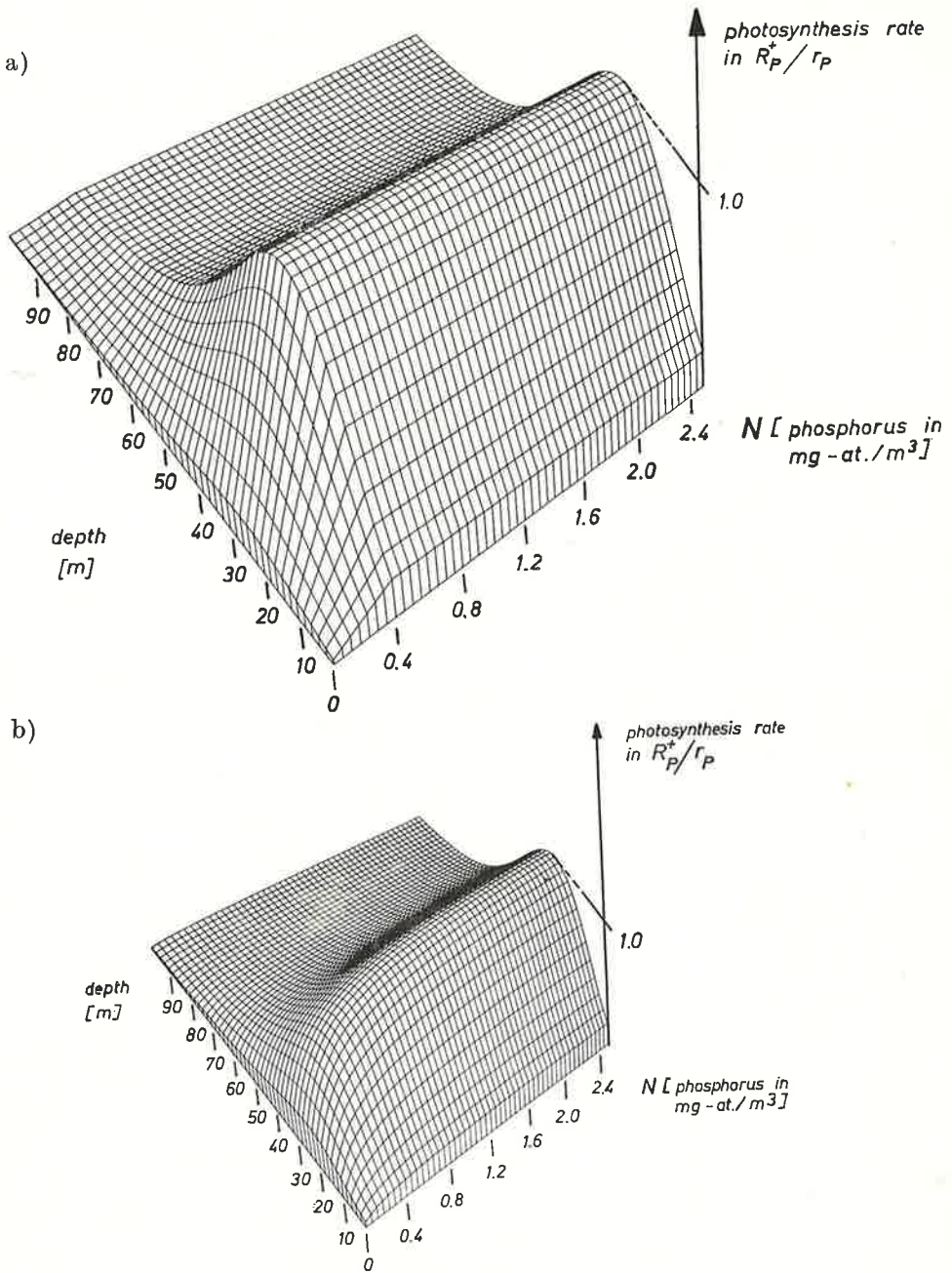


Fig. 2. — Photosynthesis rate R_P^+ vs. nutrient concentration N and depth under light conditions without self-shading (extinction coefficient $k_0 = 0.04 \text{ m}^{-1}$): a) using (3.1), b) using (3.2).

with g ranging from 0.10 to 1.00 mg-at. p/gC . The regeneration rate depends on the total carbon consumed by the herbivorous plankton represented by GHP. The phosphorus content of the food for herbivores is $gGHP$. Assuming that 85 % of the phosphorus in the total loss is regenerated (RILEY, 1965), we have $R_N^+ = f_N \cdot g \cdot (m_P + GH) = 0.066 \text{ day}^{-1}$. For f_N , values ranging from 0.40 to 1.00 were chosen.

(e) *Vertical eddy diffusion coefficient A_v* :

Most authors use mixing rates m instead of vertical eddy diffusion to get first order equations. They consider a two-layered system. The mixing rate is defined as the ratio of the exchanged mass per day from upper layer to lower layer to the total upper layer mass. The relation between mixing rate and eddy diffusion coefficient follows from the solution of the differential equation for the diffusion of a substance $S(z, t)$ (e.g. P or N)

$$\frac{\partial S}{\partial t} = A_v \frac{\partial^2 S}{\partial z^2}$$

with the initial conditions

$$S(z, 0) = 0 \text{ for } z > H'$$

$$S(z, 0) = S_0 = \text{const. for } z \leq H'$$

and the boundary conditions

$$S(-\infty, t) = S_0, S(\infty, t) = 0.$$

If A_v is not too large, we may assume

$$S(-\infty, t) = S(0, t) = S_0.$$

At the beginning of the diffusion ($t = 0$) the total mass of the substance S is $S_0 \cdot H'$. The solution of this initial-boundary-value-problem is (FRANK—MISES, 1961, p. 536)

$$S(z, t) = 0.5 S_0 \left(1 + \operatorname{erf} \left\{ -\frac{z - H'}{2\sqrt{A_v t}} \right\} \right)$$

where erf denotes the error function. The mixing rate m is

$$3.5 \quad m = -\frac{\int_{H'}^{\infty} S(z, t_0) dz}{S_0 H'}$$

with $t_0 = 1$ day. Evaluation of this formula by numerical integration gives the correspondence of m and A_v as shown in fig. 3, for example for an upper layer with 100 m thickness :

$$A_v = 6 \text{ cm}^2/\text{sec} \hat{=} m = 0.06,$$

$$A_v = 100 \text{ cm}^2/\text{sec} \hat{=} m = 0.30.$$

STEELE (1958) and RILEY (1965) gave mixing rates m between 0.02 and 0.06. For all considered depths of the upper layer we have to choose A_v less than $10 \text{ cm}^2/\text{sec}$.

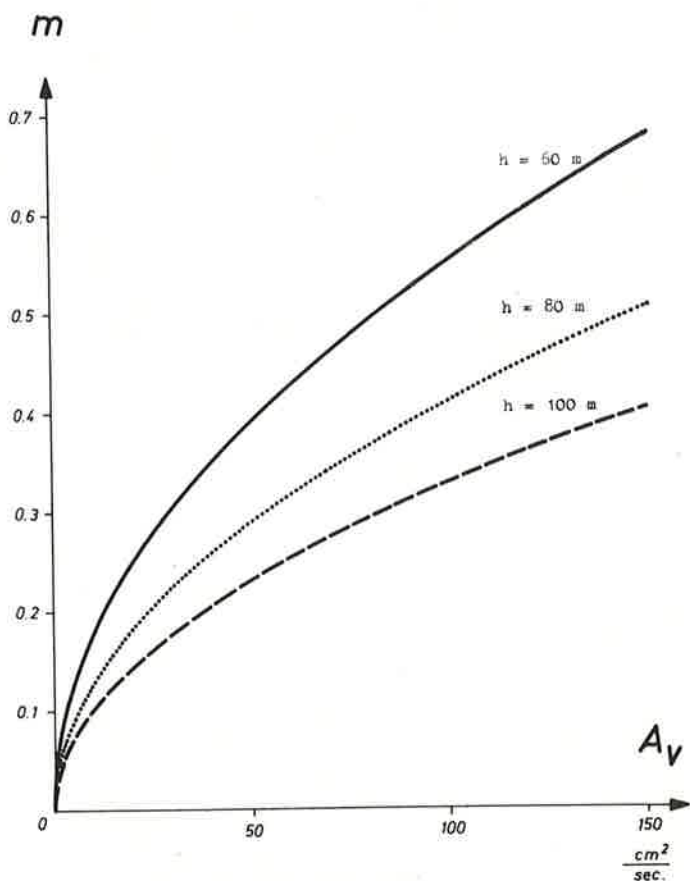


Fig. 3. — Mixing factor m vs. turbulent mixing coefficient A_v for various depths of the mixed layer.

(f) *Extinction coefficient $k(z)$* :

The extinction coefficient $k(z)$ summarizes the effects of inorganic suspended material, organic detritus and living plankton. The effect of detritus may be responsible for an amount up to about 65 % of the total extinction (GILLBRICHT, 1959). For the Fladen Ground area, however, STEELE and BAIRD (1961) found no signs of « dead » chlorophyll. Moreover, detritus is effectively zero in March and April and builds up to about a quarter or a half of the organic matter in autumn (STEELE and BAIRD, 1965). Thus, for the three months of simulation, say April, May and June, we concentrate on the investigation of the effect of selfshading. For this purpose we assume $k(z) = k(P)$.

RILEY (1956) gave an empirical relation between extinction and the chlorophyll content of phytoplankton

$$3.6 \quad k(P) = k_0 + k_1 \text{Chl} + k_2 (\text{Chl})^{2/3}$$

where $k_0 = 0.04 \text{ m}^{-1}$, $k_1 = 0.0088 \text{ m}^2 (\text{mg chlorophyll})^{-1}$, and $k_2 = 0.054 \text{ m} (\text{mg}$

chlorophyll)^{-2/3}. This relation was confirmed by SMALL and CURL (1968). As the units of phytoplankton we use are gC/m³, the formula has to be converted by

$$3.7 \quad \text{weight of C} = k_c \text{ weight of Chl}$$

STEELE (1956) gave the equivalence $k_c = 54 \text{ gC/gChl}$. HARVEY (1950) gave $k_c = 27 \text{ gC/gChl}$. For our simulations we vary k_c between 10 and 110 gC/gChl. Fig. 4 shows the relation (3.6) for various values for k_c ranging from 0 to 1.5 gC/m³ of plankton.

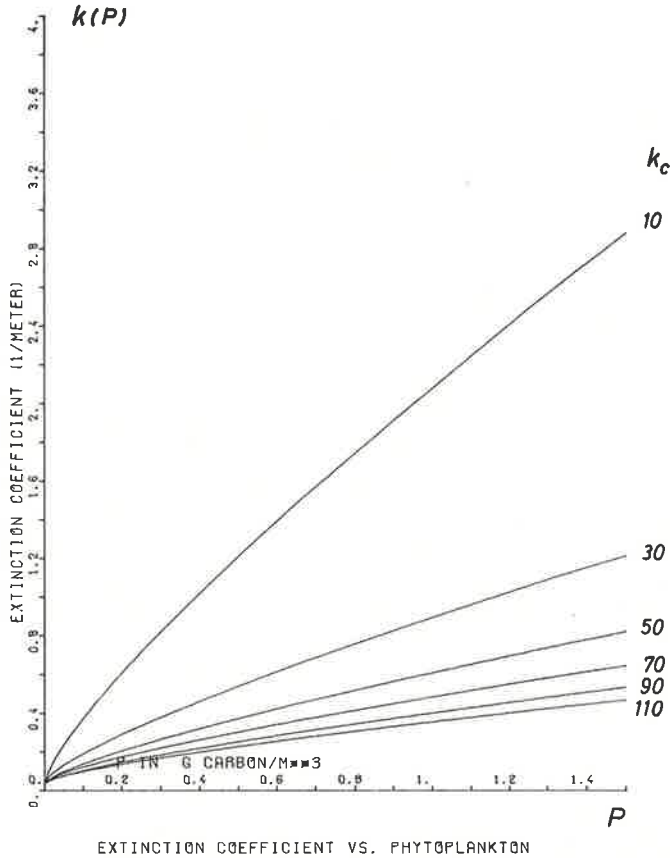


Fig. 4. — Extinction coefficient $k(P)$ for various values of the chlorophyll/carbon ratio : $k_c = 10; 30; 50; 70; 90; 110 \text{ gC/gChl}$.

(g) *Initial values for P and N :*

RILEY (1965) based his computations for N at $t = 0$ on the values 0.4, 0.7 and 1.5 mg-at. phosphorus/m³. STEELE (1956) gave measured values of 1 mg-at. P/m³ for the Northern North Sea in April. For $P(z, 0)$, in most computations, we chose a linear relation

$$P(z, 0) = 0.02 \left(1 - \frac{z}{100 \text{ m}} \right) H (100 \text{ m} - z) \text{ gC/m}^3$$

with the Heaviside function $H(x)$ defined by

$$H(x) = \begin{cases} 1 & \text{for } x > 0 \\ 0 & \text{for } x \leq 0. \end{cases}$$

This profile is similar to that observed in the Northern North Sea at the end of winter (STEELE, 1956; STEELE and BAIRD, 1965).

(h) *Daily variations of light intensity :*

To solve the equation (2.3) for light intensity we prescribe

$$3.8 \quad I_0(t) = I_0(t) = I_{\max} H(\cos \sigma t) \cdot \cos^{1/3} \sigma t$$

with $\sigma = 2\pi \text{ day}^{-1}$, and I_{\max} being the light intensity at the sea surface at noon. The expression takes into account the relative short dawn compared with the day length.

We assume I_{opt} to be constant. Consequently, we only have to prescribe the ratio I_{\max}/I_{opt} . At noon this ratio corresponds to a depth z_{opt} of maximum photosynthesis defined by

$$\exp \left\{ - \int_0^{z_{\text{opt}}} k(P) dz \right\} = \frac{I_{\text{opt}}}{I_{\max}}.$$

We chose $I_{\max}/I_{\text{opt}} = 3$, corresponding in clear water to an optimum depth of 27.5 m. Fig. 1 shows the graph of the function (3.8) and the mean value averaged over 24 hours.

The numerical simulation experiments were carried out with the values of parameters as given in Table I. A basic computation was carried out with the italic values of the parameters. In all additional simulations we changed only one of the parameters. So the figures give insight only into a restricted neighbourhood around the central « point » of the multidimensional « parameter space ». As a general feature of nonlinear equations, solutions may be quite different from those shown here if the central point is chosen alternatively.

TABLE I

Values of the parameters used in the simulations

r_p	0.5	1.0	1.5	2.0	3.0	4.0	5.0	day ⁻¹
$R_{\overline{P}}$	0.05	0.1	0.2	0.3	0.4	0.5		day ⁻¹
$\frac{I_{\max}}{I_{\text{opt}}}$	1	2	3	4	5			
A_v	1	2	3	5	10	20		cm ² /sec
w_s	0	0.5	1	2	3	4	5	m/day
g	0.3	0.45	0.6	0.774	0.9	1.05		mg-at.p/gC
f_N	0.4	0.55	0.7	0.85	1.0			
k_c	10	30	50	70	90	110		gC/gChl
$P_0(0)$	0.01	0.02	0.05	0.1	0.2	0.3		gC/m ³
$N_0(z)$	0.2	0.6	1.0	1.4	1.8	2.2		mg-at.p/m ³

4. BALANCE EQUATIONS

The computations yield vertical profiles from which new variables may be derived which give insight into the physical and biochemical mass transfer through the system.

Integrating the phytoplankton and nutrient equations (2.1) and (2.2) over a horizontal unit area, over the depth h' of a layer including the euphotic zone and over time, we obtain

$$\begin{aligned} & \int_0^T \int_0^{h'} \frac{\partial P}{\partial t} dz dt = \int_0^{h'} [P(z, T) - P(z, 0)] dz = \bar{P}_T - \bar{P}_0 \\ & = \int_0^T \int_0^{h'} A_v \frac{\partial^2 P}{\partial z^2} dz dt + \int_0^T \int_0^{h'} R_{\bar{P}}^+ P dz dt - \int_0^T \int_0^{h'} R_{\bar{P}}^- P dz dt - \int_0^T \int_0^{h'} w_s \frac{\partial P}{\partial z} dz dt \\ & = \int_0^T \left[A_v \frac{\partial P}{\partial z}(h', t) - A_v \frac{\partial P}{\partial z}(0, t) \right] dt + \bar{P}_+ - \bar{P}_- - \int_0^T [w_s P(h', t) - w_s P(0, t)] dt \end{aligned}$$

or, in abbreviated notation,

$$4.1 \quad \bar{P}_T - \bar{P}_0 = P_A^{h'} - P_A^0 + \bar{P}_+ - \bar{P}_- - P_w^{h'} + P_w^0.$$

The turbulent transfer across the surface P_A^0 and the sinking at the sea surface P_w^0 compensate each other because of the vanishing net flux, expressed by the boundary condition (2.11). Therefore the net gain (or loss) of phytoplankton from the beginning $t = 0$ up to $t = T$, $\bar{P}_T - \bar{P}_0$, is the sum of the loss of phytoplankton through turbulence and sinking at the lower boundary, i.e. $P_A^{h'}$ and $P_w^{h'}$, the gross photo synthesized biomass \bar{P}_+ and the gross loss of biomass by respiration and grazing \bar{P}_- in the whole water column above h' .

The integration of the conservation equation for nutrients (2.2) yields

$$4.2 \quad \int_0^T \int_0^{h'} \frac{\partial N}{\partial t} dz dt = \bar{N}_T - \bar{N}_0 = N_A^{h'} - N_A^0 + f_N \bar{P}_- - g \bar{P}_+.$$

Due to the boundary condition (2.13) the term N_A^0 vanishes. So the net gain (or loss) of nutrients $\bar{N}_T - \bar{N}_0$ during the time from $t = 0$ to $t = T$ consists of the nutrients gained by turbulent mixing at the lower boundary $N_A^{h'}$, the consumed nutrients $\bar{N}_- = g \bar{P}_+$ and the regenerated nutrients $\bar{N}_+ = f_N g \bar{P}_-$ during the same time interval.

The equations (4.1) and (4.2) may serve for computations of the different balance terms which are involved in the metabolic processes during the period for which the equations (2.1) and (2.2) are integrated numerically. An example of these balance considerations is given in section 6 where the balance terms are computed in dependence on turbulent mixing and sinking velocity.

5. RELATED DEPENDENT VARIABLES

From the vertical plankton profiles we can derive further interesting variables.

The tickness of the euphotic zone can be computed as a function of time. The lower boundary of the euphotic zone is defined here as the depth z_{eu} where light intensity has decreased to 1 % of the surface value. Self-shading of phytoplankton

reduces the thickness of the euphotic zone during the plankton bloom. Approaching the quasistationary phase after the bloom the euphotic zone slowly increases again.

Other characteristic depths of interest are, for instance, the compensation depth z_{com} where photosynthesis and biological loss compensate each other, or the depth $z_{1/2}$ which divides the water column in two parts with the same plankton content etc.

Quantities of more interest are given by the effective rates of photosynthesis and respiration which may be defined as follows: Given a vertical distribution of plankton $P(z, t)$ at time t , the photosynthesis would result in a gross gain of plankton at time $t + \Delta t$ under the assumption that all other processes are ignored (losses, turbulent diffusion, sinking). The new distribution $P(z, t + \Delta t)$ at the time $t + \Delta t$ would yield a plankton content $\bar{P}(t + \Delta t)$ in the water column

$$5.1 \quad \bar{P}(t + \Delta t) = \int_0^{h'} P(z, t + \Delta t) dz = \int_0^{h'} P(z, t) dz + \int_0^{t+\Delta t} \int_0^{h'} R_P^+ P(z, \tau) dz d\tau \\ = \bar{P}(t) + \Delta P^+.$$

The effective (gross) photosynthesis rate r_P^{eff} for the considered water column of depth h' is then defined by

$$5.2 \quad P(t + \Delta t) = P(t) \exp(r_P^{eff} \Delta t)$$

Thus:

$$5.3 \quad r_P^{eff} = \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \ln \left\{ 1 + \frac{1}{\bar{P}(t)} \int_t^{t+\Delta t} \int_0^{h'} R_P^+ P(z, \tau) dz d\tau \right\}.$$

In general, h' will be the depth of the euphotic zone. Analogous definitions for the effective loss rates, nutrient regeneration, and uptake rates can be formulated.

We see from eq. (2.5), (3.2) and (3.3) that the effective production rate turns out to be an averaged quantity dependent on the whole history of phytoplankton in the time interval between t and $t + \Delta t$. As a consequence of daily variation in light intensity, the choice of $\Delta t = 1$ day will yield effective rates different from those derived with Δt in the order of minutes.

On the other hand, even with a fixed Δt the vertical structure of plankton and light intensity will yield locally different rates, the effective rate for the whole water column being an averaged quantity.

In a thoroughly mixed system, the effective rate for a layer of the depth h' can be expressed in terms of the local rate necessary for a plankton model with vertical variability. Then we have $P(z, t) = P(t)$ and $r_N(z, t) = r_N(t)$. For very small time intervals Δt we may assume approximately $r_N(t) = r_N = \text{constant}$. Then (5.3) becomes

$$5.4 \quad r_P^{eff} = \frac{1}{\Delta t} \ln \left\{ 1 + \frac{r_P r_N \bar{r}_I}{\bar{P}(t)} \int_t^{t+\Delta t} \bar{P}(t') dt' \right\},$$

and together with (5.2) we get after some computation

$$5.5 \quad r_P^{eff} = r_P r_N \bar{r}_I \quad \text{with} \quad \bar{r}_I = \frac{1}{h'} \int_0^{h'} r_I(z) dz < 1.$$

In this special case, (5.5) could be used in vertically integrated models. In general, the local optimum production rate is large compared to the effective rate because the limitations are included in the effective rate in an averaged form. Normally, measurements of photosynthesis rates are carried out over intervals of hours. In our model we use time steps of the order of minutes. In order to get realistic effective rates, we use instantaneous optimum rates r_P ranging from 1 to 6 per day (O'BRIEN and WROBLEWSKI (1973) used similar values in their model).

Questions of this kind lead to the difficult problem of parametrisation of vertical structures to get the constants needed in vertically integrated models for studying the horizontal structure of phytoplankton. This problem appears to be not solvable at present state because even the physical processes in the upper layer cannot be parameterized adequately.

6. RESULTS OF SIMULATIONS

The results are based upon the parameter values given in Table I. We investigate the processes in a water column extended to a depth of 250 meters. The balance considerations refer to the upper 111 meters, corresponding to the euphotic zone for $k = 0.04 \text{ m}^{-1}$.

As mentioned before, most of the parameter values have been derived for the Northern North Sea (Fladen Ground area). Nearly all computations include the daily variations of light intensity using (3.8). However, most of the figures do not show explicitly the daily variations because the values of the variables are plotted only once a day, at noon.

It should be stressed that this model (like many ecological models) needs testing against more extensive field measurements than are presently available.

6.1. *Plankton and nutrient distribution for Fladen Ground data*

The dynamics of phytoplankton and the limiting nutrient phosphorus — shown in figs. 5c), 5d), 6c), 6d), 7 and 8 — result from the standard run with the Fladen Ground data (italic parameter values of Table 1). The whole time interval of 90 days may be subdivided into three sections with different regimes (fig. 5c), 6c)). In the first days unlimited growth is shown till, after about 25 days, a maximum of the plankton bloom is reached. Nutrient limitation begins in a shallow surface layer and causes a decay of growth. In the last period a quasistationary equilibrium state is reached. Over the whole time interval the nutrient concentration is affected only in the upper 50 meters. At the end of the computation the minimum nutrient concentration is $0.26 \text{ mg-at. } \mu\text{m}^3$. The weak turbulent diffusion ($A_v = 3 \text{ cm}^2 \text{ sec}^{-1}$) cannot support the upper layer sufficiently with nutrients from below, and the bloom slowly breaks down. The general features are in a fairly good accordance with the measurements given by STEELE (1956) and STEELE and BAIRD (1965) regarding the strong simplification of the model.

6.2. *Transport of matter through the system*

The related balance terms for the standard run are shown in fig. 6c) and d) over 90 days. For the chosen parameter set the dominant processes in phytoplankton growth dynamics are photosynthesis and losses due to respiration and grazing (fig. 6c)). While the plankton content after 90 days is of the order of $10 \text{ } \mu\text{C}/\text{m}^2$, each

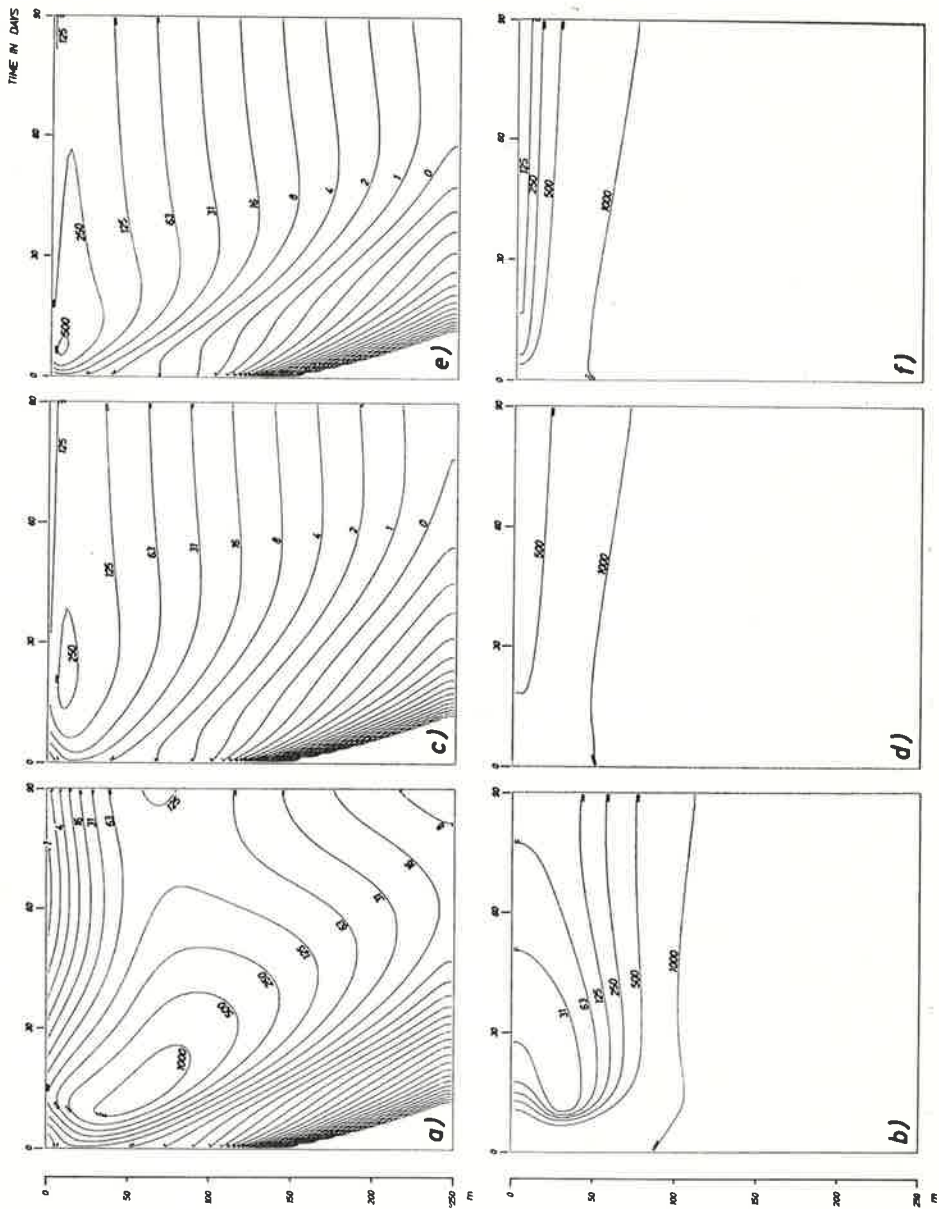


Fig. 5. — Development of the phytoplankton and the nutrient concentrations P resp. N over 90 days and a depth range of 250 m. Run 2 : Dynamics with diurnal light variations and without self-shading : a) phytoplankton, b) phosphorus; run 1 : dynamics with light variations and self-shading : c) phytoplankton, d) phosphorus; run 3 : dynamics with averaged light intensity and self-shading : e) phytoplankton, f) phosphorus (neighbouring isopleths differ by the factor 2).

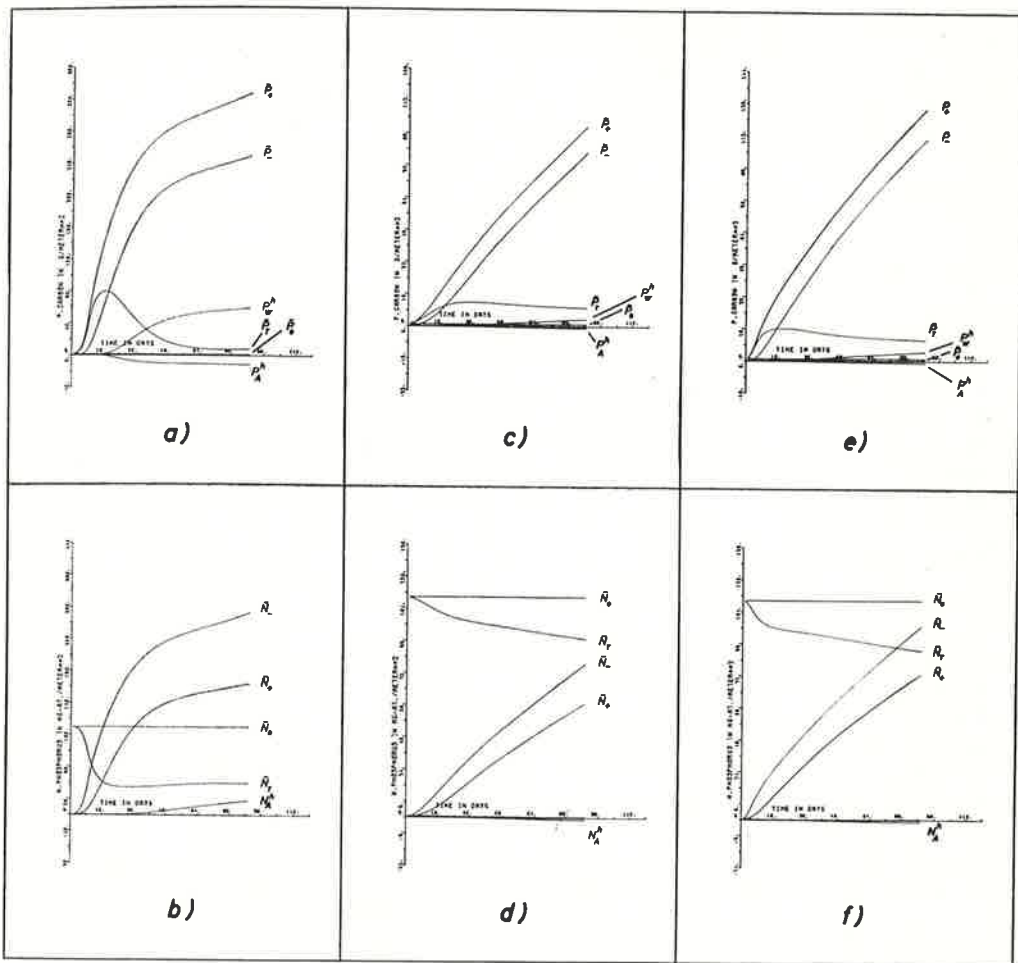


Fig. 6. — Terms of phytoplankton and nutrient balance equations in their time dependence over 90 days in the upper 111 m : Run 2 : Dynamics with diurnal light variations and without self-shading : a) phytoplankton, b) phosphorus; run 1 : dynamics with diurnal light variations and self-shading : c) phytoplankton, d) phosphorus; run 3 : dynamics with averaged light intensity and self-shading : e) phytoplankton, f) phosphorus. P_{10}^h = integrated loss of biomass through the lower boundary due to sinking; P_A^h = corresponding loss of biomass due to turbulent diffusion; \bar{P}_T = biomass of the plankton in the water column at $t = T$; \bar{P}_+ = integrated photosynthesized biomass in the water column; \bar{P}_- = integrated loss of biomass due to metabolic processes and grazing; the line parallel to the t -axis represents the initial biomass in the water column \bar{P}_0 . \bar{N}_T = phosphorus content in the water column at $t = T$; \bar{N}_0 = initial phosphorus content in the water column; \bar{N}_+ = integrated gain due to phosphorus regeneration; \bar{N}_- = integrated loss due to phosphorus uptake.

of the gain and loss terms, \bar{P}_+ and \bar{P}_- , sum up to a multiple of this value namely 100.5 and 87.7 gC/m^2 . Thus, the mean photosynthesis and loss per day in the water column of 111 meters are 1.1 and 0.97 $gC/m^2/day$, leading to a net biotic mean gain of 142 $mgC/m^2/day$. The amount of diffused plankton at $z = 111$ meters is vanishingly small; after 90 days 0.94 gC/m^2 has been diffused out of the layer. Sinking of phytoplankton yields a loss of 3.6 gC/m^2 at $z = 111$ m.

Analogous features are shown by the nutrient balance terms in fig. 6d). The integrated uptake of 77.8 $mg-at. p/m^2$ is compensated to a large amount by the regeneration of 57.7 $mg-at. p/m^2$. The contribution of turbulent diffusion may surprise: in 90 days 1.0 $mg-at. p/m^2$ leaves the layer. The explanation is given by the sinking of phytoplankton which supplies the lower part of the upper layer with regenerated nutrient. Consequently, in a depth of about 100 meters a local maximum of nutrient is established. From this maximum, nutrient is diffused downwards across $z = 111$ m. Obviously, this effect results from the special choice of 111 m. It would not appear, e.g. at 50 or 200 m. The diffusion is not strong enough to redistribute this maximum and to fill the gap of nutrient in the upper 20 meters. However, this part of the diffusion in the interior of the layer does not occur in the variable N_A^p . A considerable amount of the initially available nutrient has been taken up in 90 days (see Table 2). The net biotic loss of the nutrient is 0.223 $mg-at. p/m^2/day$.

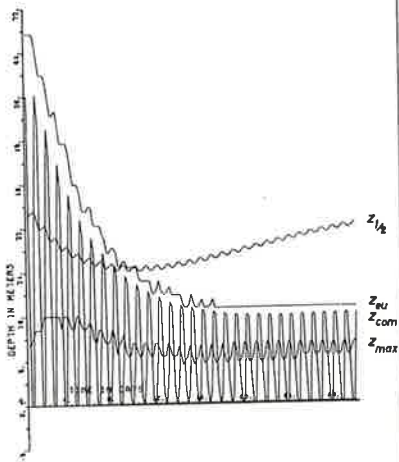
6.3. Related depths and rates

The depths mentioned in section 5 and the depth z_{max} of maximum plankton concentration are shown as a function of time over 30 days in fig. 7a) and over 90 days in fig. 7b) for the standard run 1. In general the depths $z_{1/2}$, z_{eu} , z_{max} and z_{com} diminish during the bloom. The depth of the euphotic zone remains 17 m from the 16th to the 33rd day and increases again to 22 m till the end of the computation after 90 days. z_{com} and z_{max} reach their minimum during the bloom at 15 m and 8 m. They increase again till they reach 20.8 m and 11.25 m, at the end of 90 days (fig. 7b)). The depth $z_{1/2}$ indicates the three regimes very clearly: during the strong growth in the first days the plankton content above $z_{1/2}$ increases, so $z_{1/2}$ has to decrease. During the beginning of the nutrient limitation plankton sinks down, and $z_{1/2}$ has to follow. The quasistationary phase is characterized by a constant $z_{1/2}$.

The computation of effective gain and loss rates as defined in section 5 yields values which are of the order of values derived from measurements. RILEY (1965) reports a value of 0.3 day^{-1} for the gross production rate on a daily basis. In the standard run the maximum effective gross production rate r_P^{eff} takes the same value and decreases to 0.1 day^{-1} after 30 days under nutrient limitation. This value remains unaltered during the quasistationary phase (fig. 7d)). The instantaneous rates, however, are sometimes much greater. The maximum value of 0.75 day^{-1} decreases to 0.225 day^{-1} during 30 days (fig. 7c)).

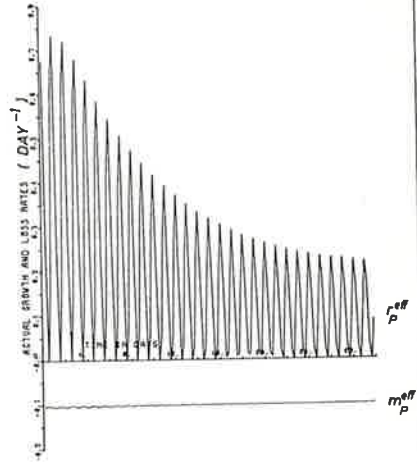
Fig. 7. — Related dependent variables in their time dependence over 30 days for the standard run 1: $z_{1/2}$ = depth dividing the water column into two columns of equal content of biomass; z_{max} = depth of maximum plankton concentration; z_{eu} = depth of the euphotic zone; z_{com} = compensation depth.

- diurnal variations of the characteristic depths over 30 days;
- values of the characteristic depths at noon, over 90 days;
- instantaneous effective gain and loss rates e_P^{eff} , m_P^{eff} ;
- effective gain and loss rates integrated over 1 day.



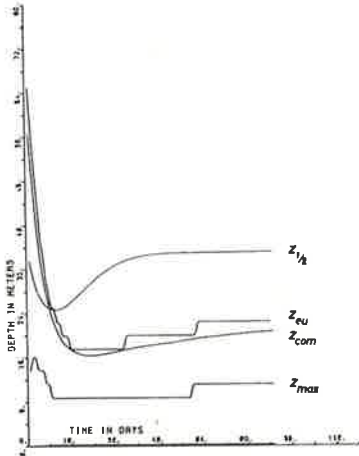
CHARACTERISTIC DEPTHS
DIURNAL VARIATIONS OVER 30 DAYS

a)



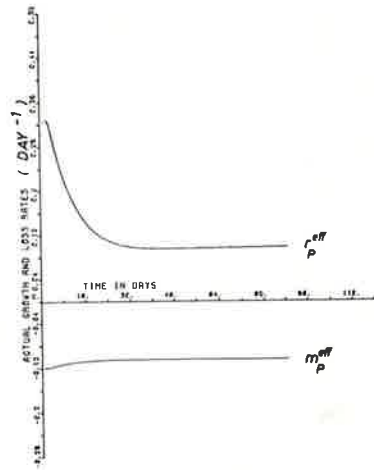
EFFECTIVE RATES
(INSTANTANEOUS)

c)



CHARACTERISTIC DEPTHS
VALUES AT NOON OVER 90 DAYS

b)



EFFECTIVE RATES
(INTEGRATED OVER 1 DAY)

d)

TABLE II

Balance terms

	after 30 days			31st-90th day			after 90 days		
	run 1	run 2	run 3	run 1	run 2	run 3	run 1	run 2	run 3
	in : gC/m ²								
phytoplankton balance :									
\bar{P}_T	12.2	50.4	14.9	—	—	—	9.3	8.7	10.3
\bar{P}_0	1.1	1.1	1.1	—	—	—	1.1	1.1	1.1
\bar{P}_+	36.0	232.4	55.1	64.5	96.1	71.7	100.5	328.5	126.8
\bar{P}_-	24.3	156.7	40.3	63.4	93.5	71.7	87.7	250.2	112.0
P_A^w	0.4	19.2	0.7	3.2	40.0	3.7	3.6	59.2	4.4
P_A^h	-0.2	-7.3	-0.3	-0.7	-4.2	-0.8	-0.9	-11.5	-1.1
production $\bar{P}_+ - \bar{P}_-$	11.7	75.7	14.8	1.1	2.6	0.0	12.8	78.3	14.8
in : mg-at.p/m ²									
nutrient balance :									
\bar{N}_T	98.0	34.4	93.7	—	—	—	88.9	39.6	84.4
\bar{N}_0	110.0	110.0	110.0	—	—	—	110.0	110.0	110.0
\bar{N}_+	16.0	103.1	26.5	41.7	61.5	47.2	57.7	164.6	73.7
\bar{N}_-	27.8	179.9	42.6	50.0	74.3	55.5	77.8	254.2	98.1
N_A^h	-0.1	1.3	-0.2	-0.9	17.9	-1.0	-1.0	19.2	-1.2

6.4. *Plankton dynamics without self-shading*

The effect of self-shading of phytoplankton is found to be non-negligible. Repeating the standard run 1 with the extinction coefficient $k = 0.04 \text{ m}^{-1}$ instead of (3.6) we obtained (run 2) the significantly modified results shown in fig. 5a), b) and 6a), b). The supply of phytoplankton with light energy is much larger than in the standard run (fig. 5c), d) and 6c), d)). Consequently, phytoplankton growth is stronger and occurs in greater depths. The maximum phytoplankton concentration of 1.39 gC/m^3 is reached after 12.2 days (compared to 0.308 gC/m^3 after 22.2 days in the standard run). The maximum sinks down to 60-80 meters, following the nutrient. Thus the standing stock of phytoplankton can be maintained only at a depth where uptake, regeneration and nutrient supply by turbulent diffusion from below are balanced. In the last days of this simulation, a second weak maximum occurs (fig. 5a)). After the strong limitation of growth, the turbulent diffusion partly filled up the gap in the nutrient distribution of the upper layer and built the basis for a second bloom. The balance terms (fig. 6a), b)) provide a better understanding of the dynamics than the plankton and nutrient distributions of fig. 5a), b). In the balance for phytoplankton the loss by sinking and turbulent diffusion play an important role. Biotic gain and loss take values which are multiples of the values for the standard run. A comparison of the balance terms after 30 and 90 days is given in Table II.

6.4. *Plankton dynamics for a mean surface light intensity*

In run 3 the variable surface light intensity (3.8) was replaced by its average value over 24 hours (fig. 1a)). From the figs. 5e), f) and 6e), f) we see that the dynamics are similar to those of the standard run 1, but there is a stronger growth. Except for the large values of plankton concentration, the second characteristic feature is the early occurrence of the maximum. The larger plankton values correspond to smaller nutrient values as compared with run 1. Differences can be detected between the balance terms in fig. 6e), f) as compared to fig. 6c), d). The main features are the steep ascent of plankton biomass in the initial phase and the corresponding strong nutrient limitation nearly from at the beginning. Figures for the balance terms are given in Tab. II.

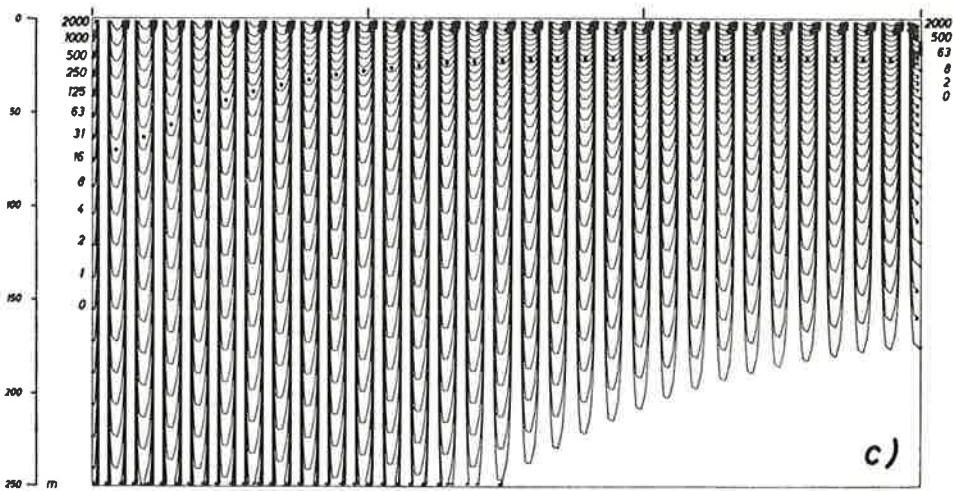
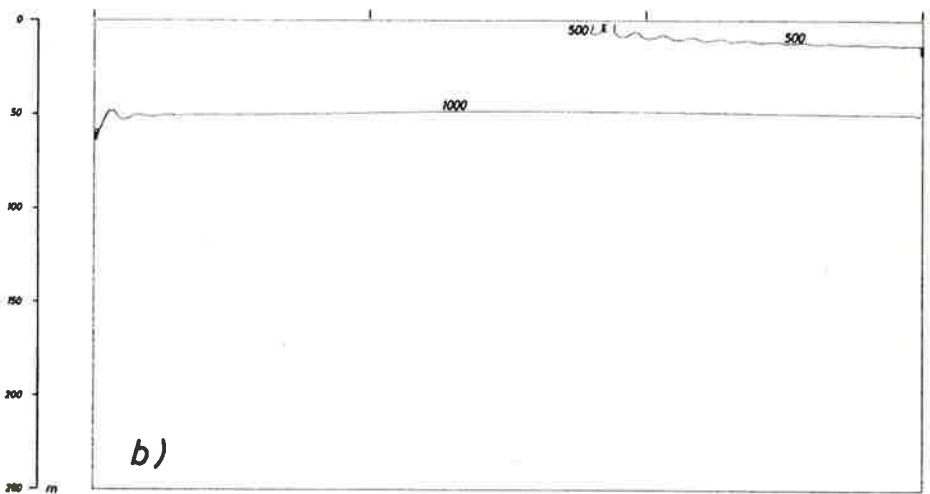
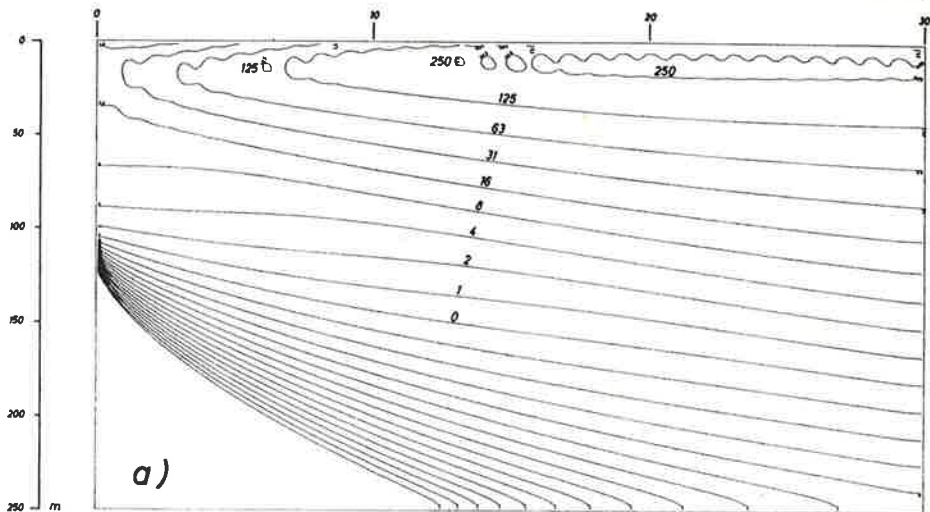
6.5. *Diurnal variations of phytoplankton and nutrient concentrations and light intensity in the water*

The existence of daily varying surface light intensity affects nearly all variables : light intensity in the water; phytoplankton concentration through the photo-synthesis rate; nutrient concentration through the different uptake (= growth in this model); the various characteristic depths which are based on production processes, and, of course, the effective rates.

To give an impression of the diurnal variations of these variables, the first 30 days of the standard run 1 are presented with a higher resolution in time (figs. 8 and 7a), b)). The dotted line in fig. 8c) marks the lower boundary of the euphotic zone. As the loss rate $R_{\bar{p}}$ is assumed to be time-independent, diurnal variations of plankton and nutrients occur only in the euphotic zone.

6.6. *Dependence of the balance terms on eddy diffusion and sinking velocity*

The balance terms after 30 days of computation are shown in figs. 9 and 10



(note the different scaling) as functions of the vertical turbulent diffusion and sinking velocity. The plankton content in the water column above $z = 111$ m is the greatest for small w_s ; it is smallest for small diffusion and large sinking velocities (fig. 9a)). The values for the net gain of plankton due to photosynthesis, respiration and grazing $\bar{P}_+ - \bar{P}_-$ are of the same magnitude. Thus, they are the dominant processes in plankton dynamics based on the standard parameter set. The effectivity E_P of growth of planktonic organisms may be measured by the ratio $E_P = (\bar{P}_+ - \bar{P}_-)/\bar{P}_+$. About 29 to 35 % of the gross photosynthesized plankton survive. For the system considered here the effectivity is the greatest for large eddy diffusion coefficients, but decreases with increasing sinking velocity except for very small diffusion coefficients (fig. 9c)). The integrated loss of plankton due to sinking (fig. 9d)) increases with increasing w_s , but not independent of diffusion. For low diffusion the effect of sinking is smaller than for large diffusion. The reason is that high diffusion distributes the plankton over the whole water column. Consequently, more of the plankton can sink across the interface $z = 111$ m. The integrated loss of plankton due to turbulent diffusion increases for increasing values of the eddy diffusion coefficient, but not independent of sinking velocity (fig. 9e)). For a fixed A_v the balance term $-P'_A$ (loss) increases with increasing w_s . The case that phytoplankton bloom is suppressed, is not included in the considered range for A_v .

The terms of the nutrient balance equation vary in accordance with the terms of the plankton balance equation (fig. 10). The nutrient content depends mainly on the value of sinking velocity. \bar{N}_T is smallest for $w_s = 0$ m/day and A_v about $5 \text{ cm}^2 \text{ sec}^{-1}$; it is largest for small eddy diffusion coefficients and large sinking velocities (fig. 10a)). The integrated gain (or loss) of nutrient N due to turbulent diffusion is vanishingly small (between 0 and 3 % of the initial nutrient content, fig. 10b)). For values of the eddy diffusion coefficient less than $5 \text{ cm}^2 \text{ sec}^{-1}$ only negative values appear. This means that nutrient is diffused out of the layer considered. The reason for this was mentioned earlier in section 6.2 : an intermediate nutrient maximum caused by sinking of phytoplankton out of the euphotic zone is smoothed. The integrated net loss of nutrient due to nutrient uptake and regeneration represents the main loss from the initial nutrient content (fig. 10c)). The effectivity E_N of these processes may be characterized by the variable $E_N = (\bar{N}_- - \bar{N}_+)/\bar{N}_-$. About 43 % of the nutrient consumed by the plankton have been taken up and remain unavailable for consumption (referred to the 30th day).

The dynamics expressed by these balance terms are, of course, altered by choosing a different set of biological parameters. Nevertheless, figs. 9 (and 10) show certain characteristic features of the interactions which can be identified — with appropriate modification — under a wide variety of conditions.

Fig. 8. — Development of the phytoplankton and the nutrient and the underwater light intensity over 30 days for the upper 250 m plotted with the resolution of the daily variations :

a) phytoplankton concentration

b) nutrient concentration

c) light intensity in the water; the dotted line denotes the lower boundary of the euphotic zone

(neighbouring isopleths differ by the factor 2)

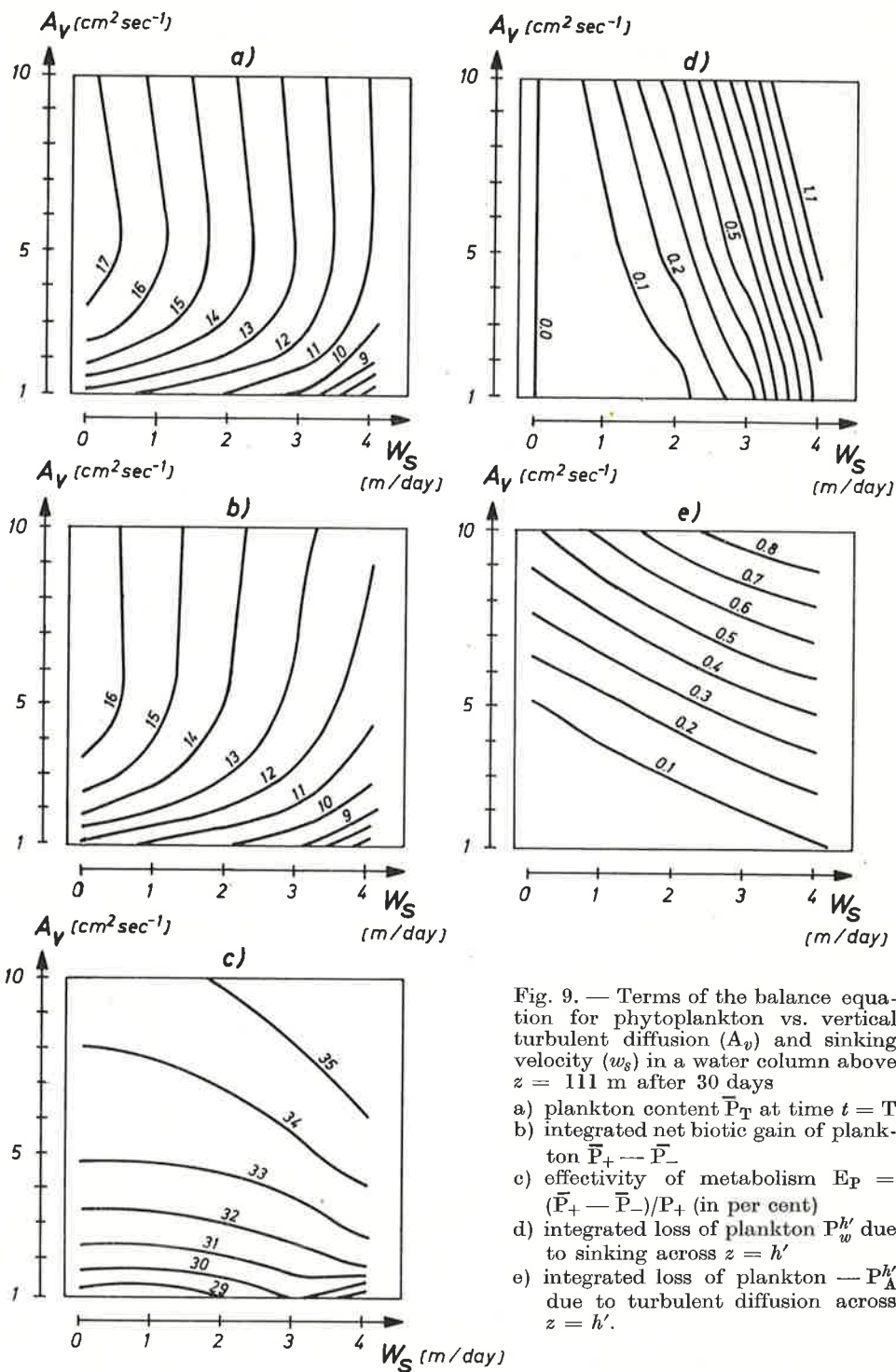


Fig. 9. — Terms of the balance equation for phytoplankton vs. vertical turbulent diffusion (A_v) and sinking velocity (w_s) in a water column above $z = 111$ m after 30 days

a) plankton content \bar{P}_T at time $t = T$
 b) integrated net biotic gain of plankton $\bar{P}_+ - \bar{P}_-$
 c) effectivity of metabolism $E_p = (\bar{P}_+ - \bar{P}_-)/P_+$ (in per cent)
 d) integrated loss of plankton $P_w^{h'}$ due to sinking across $z = h'$
 e) integrated loss of plankton $-P_A^{h'}$ due to turbulent diffusion across $z = h'$.

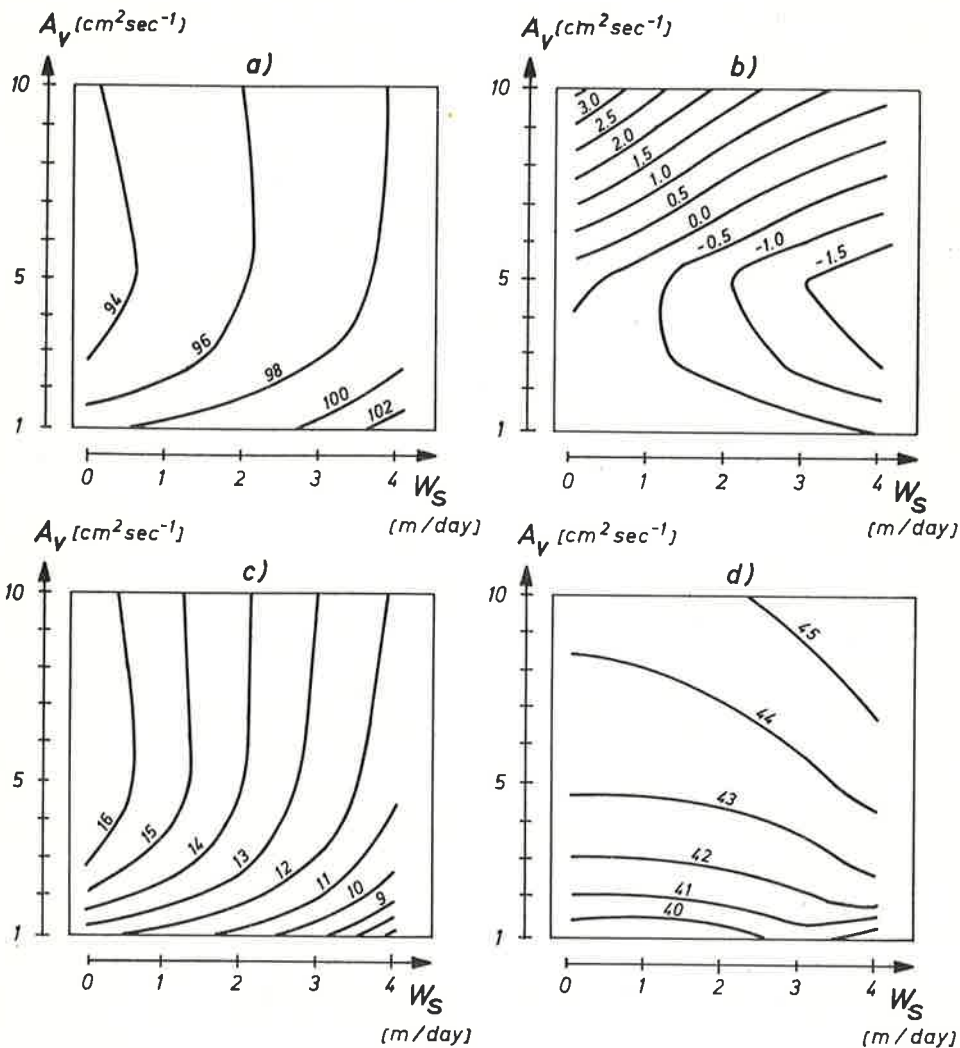


Fig. 10. — Terms of the balance equation for phosphorus vs. vertical turbulent diffusion (A_V) and sinking velocity (w_S) in a water column above $z = h' = 111$ m after 30 days

a) nutrient content \bar{N}_T at time $t = T$

b) integrated gain of nutrients $N_A^{h'}$ due to turbulent diffusion across $z = h'$

c) integrated net loss of nutrient due to uptake and regeneration $\bar{N}_- - \bar{N}_+$

d) effectivity of nutrient consumption $E_N = (\bar{N}_- - \bar{N}_+)/\bar{N}_-$ (in per cent).

6.7. Sensitivity of the solutions to parameter variations

In order to test the effects of variations of the ten parameters involved in the model, we performed several runs with one of the parameters changed, but fixing the other nine parameters at the values used in the standard run 1. Figs. 11, 12 and 13 show lines of equal concentrations of phytoplankton and nutrient as well as of equal light intensity as functions of depth and the varied parameter. The vertical scale of the graphs corresponds to the upper 111 m. This is the depth the balance considerations are related to. All diagrams refer to the 30th day of computation.

The importance of turbulent diffusion appears clearly in fig. 11a). Phytoplankton concentration has an optimum for an eddy diffusion coefficient $A_v = 5 \text{ cm}^2/\text{sec}$. For smaller A_v strong limitation occurs in the upper 15 m, and the euphotic zone is affected. For large values of the eddy diffusion coefficient the maximum concentration is lower, but the entire column takes part in the dynamics. Nutrient concentration is not limiting, but the consumption of nutrient has an effect even on the deeper region.

The maximum plankton concentration occurs at the surface for vanishing sinking velocity. As w_s increases the depth of the maximum increases and the maximum value itself decreases (fig. 11b)). Consequently, the limitation is strongest for the smallest values of w_s . For large w_t the lower boundary of the euphotic zone is deeper than for small w_t .

Changing the conversion factor g yields remarkable changes in the plankton and nutrient profiles. The euphotic zone remains nearly unaffected. With increasing g the phytoplankton concentration decreases due to the lack of sufficient nutrient in the upper layer. The nutrient limitation becomes stronger for increasing g , as expected.

Strong effects follow from changing the optimum photosynthesis and biological loss rates, r_p and R_p , shown by figs. 12a) and b). Small values of the photosynthesis rate leave nearly homogeneous small plankton concentrations throughout the layer, accompanied by nearly homogeneous unaltered nutrient concentrations. With increasing assimilation rate r_p the plankton grows faster, nutrient becomes rapidly limiting (from $r_p = 2 \text{ day}^{-1}$) and the euphotic zone remains nearly 20 meters thick (from $r_p = 2 \text{ day}^{-1}$). Increasing loss rates R_p cause strongly decreasing plankton concentrations, the maximum moving down from 15 m to nearly 30 m. Consequently, nutrient limitation occurs only for small values of the loss rate (less than 0.1 day^{-1}). The euphotic zone increases rapidly for increasing values of R_p .

Changing the initial nutrient concentration also yields strong effects. The plankton grows more rapidly. The deviation of the nutrient concentration from the prescribed initial value is strongest for high values of $N(z, 0) = N_0(z) = \text{const.}$ (fig. 12c)).

Increasing the regeneration coefficient f_N increases the plankton concentration. This is accompanied by a decreased loss of nutrients in the upper 15 m. The process is not so important that self-shading is affected (fig. 13a)).

The prescription of the ratio $I_{\text{max}}/I_{\text{opt}}$ corresponds to a prescription of the optimum depth for photosynthesis (see fig. 1a)). By increasing the ratio $I_{\text{max}}/I_{\text{opt}}$, the optimum depth is lowered. Nutrient limitation is most severe for an optimum depth of about 30 m. The plankton maximum increases with an increasing ratio because the light intensity available for phytoplankton growth increases.

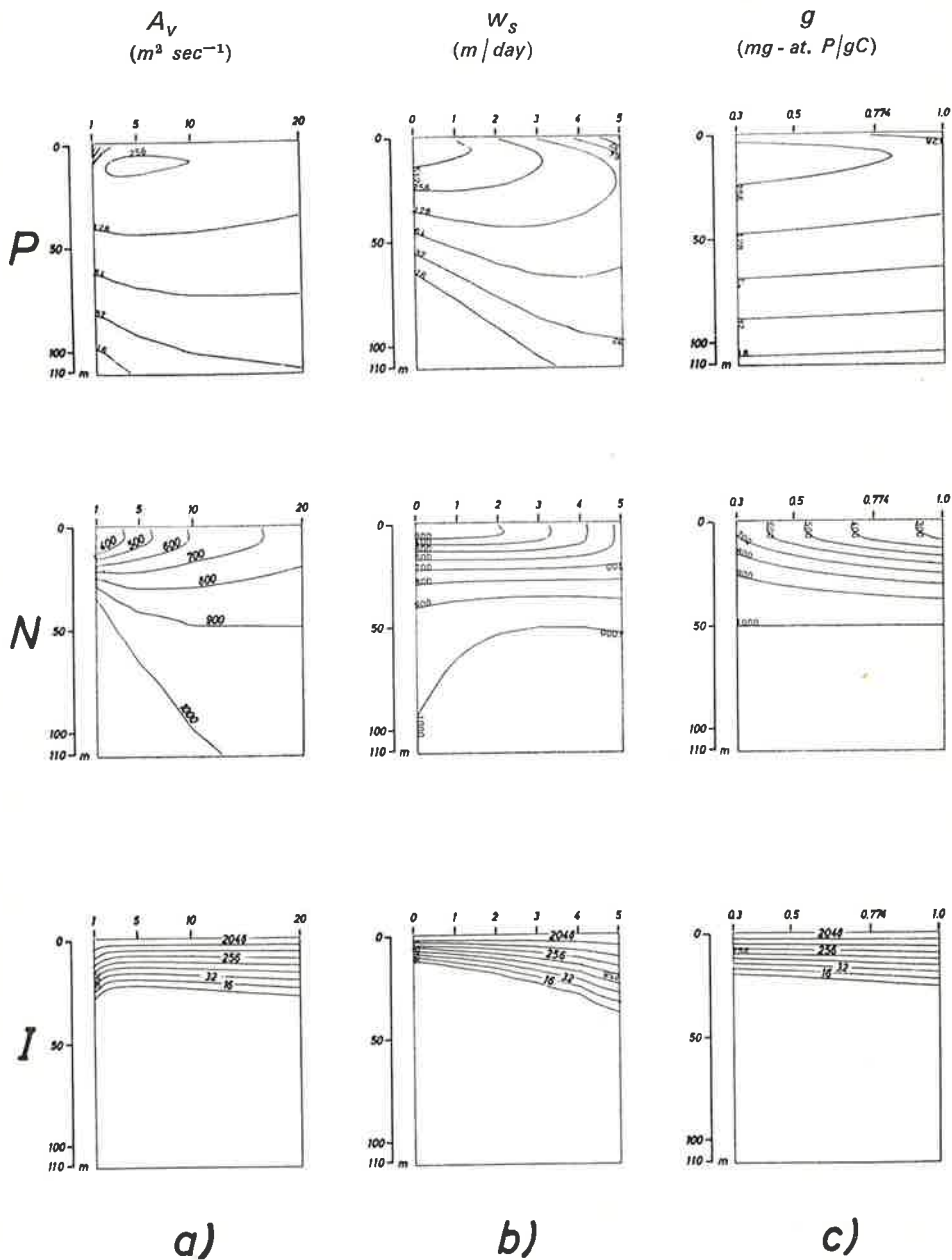


Fig. 11. — Vertical distributions of phytoplankton P, nutrient concentrations and underwater light intensity I after 30 days for various values of different parameters over a depth range of 111 m.
 a) eddy diffusion coefficient A_v
 b) sinking velocity w_s
 c) conversion factor g .

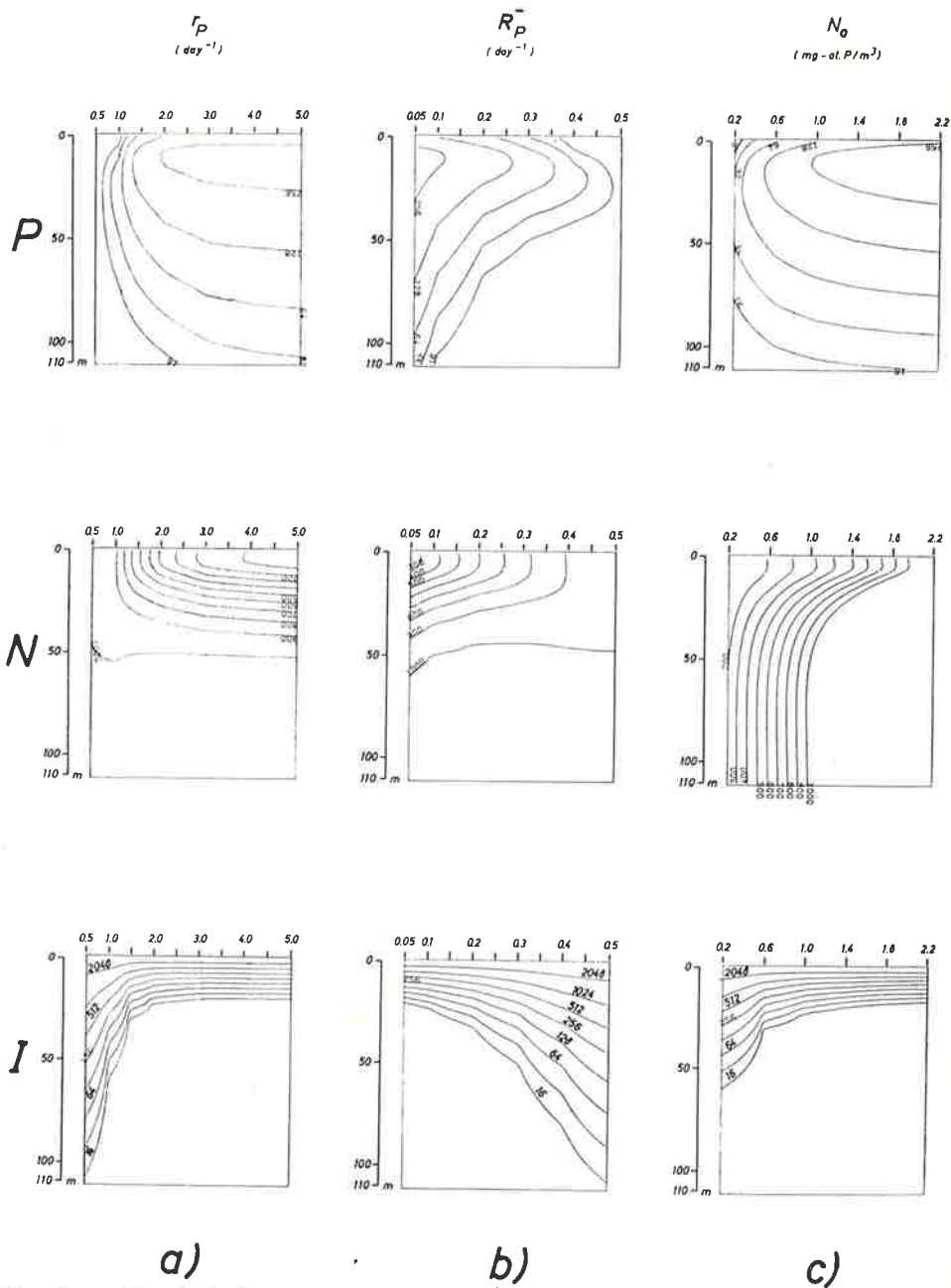


Fig. 12. — Vertical distributions of phytoplankton and nutrient concentrations and underwater light intensity after 30 days for various values of different parameters over a depth range of 111 m.

- a) optimum photosynthesis rate r_P
 b) biological loss rate $m_P + m_L$
 c) initial nutrient concentration $N_0(z)$.

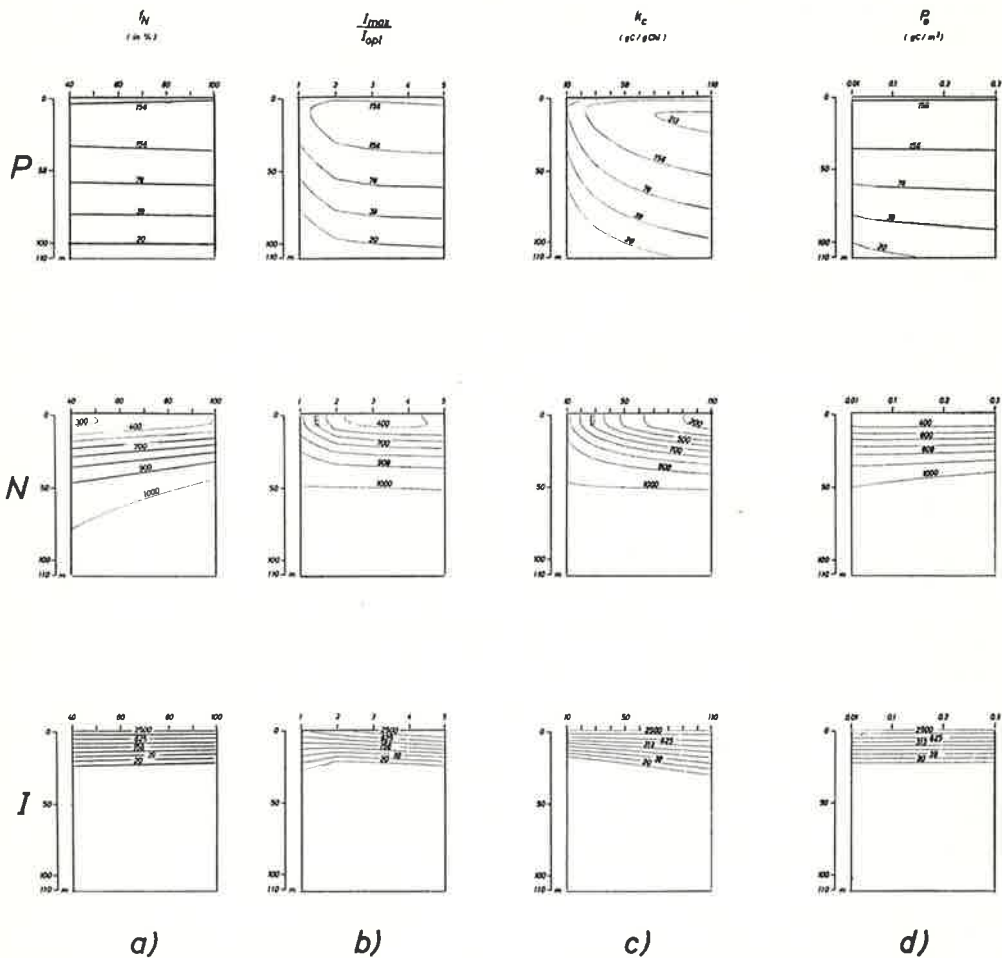


Fig. 13. — Vertical distributions of phytoplankton and nutrient concentrations and underwater light intensity after 30 days for various values of different parameters over a depth range of 111 m.

- a) regeneration coefficient f_N
- b) light intensity ratio I_{\max}/I_{opt}
- c) self-shading coefficient k_c
- d) initial plankton concentration at the surface $P_0(0)$.

The self-shading coefficient k_c seems to be important not only for the phytoplankton concentration but also for nutrient consumption and underwater light intensity as a consequence of growth of phytoplankton (fig. 13c)). The stronger the effect of self-shading ($k_c = 10 \text{ gC/gChl}$), the less plankton can develop; the nutrient content remains on a high level and the euphotic zone is very shallow. Decreasing self-shading makes the plankton develop strongly, combined with strong nutrient limitation and an increasing euphotic zone.

The initial plankton concentration in the water column turns out to be nearly without effect on the profiles after 30 days of simulation. Looking at the balance terms

within the 30 days (not shown) we recognize that the dynamics appear quite different for different initial concentrations.

Summarizing the results of the 30th day we can distinguish two classes of the parameters; the parameters r_P , R_P , A_v , w_s , k_c and N_0 effect the dynamics significantly, whereas the parameters g , f_N , I_{\max}/I_{opt} and P_0 have only minor influence.

7. CONCLUSIONS

A two-dimensional theoretical model, which incorporates the interactions between physical and biological processes, has been developed to describe the time dependent vertical structure of phytoplankton and a limiting nutrient (phosphorus). Self-shading of phytoplankton turns out to be an important process in phytoplankton dynamics and should not be neglected. Without self-shading, the plankton concentration would increase more rapidly making the nutrient limitation appear too strong and the maximum phytoplankton concentration occur at too great a depth. At least in the second half of the simulated time interval detritus will influence light extinction. Thus, detritus should be incorporated in the relationship for the extinction coefficient as a time-dependent (measured or computed) variable. Applying the model to a real situation measured vertical profiles of the extinction coefficient should be used.

The prescription of a mean surface light intensity instead of a diurnally varying one seems to be an oversimplification. The maximum phytoplankton concentration using a mean surface light intensity occurs in half the time compared to that using a diurnal variation.

Balance equations have been derived as a convenient summary of the mass transfer in the phytoplankton-nutrient system. For the given parameter ranges, based on biological measurements made in the Northern North Sea, the biological processes of photosynthesis, respiration and grazing were more important than the physical processes of turbulent diffusion and sinking. This is in accordance with the results obtained previously (STEELE, 1956; Table I).

However, a detailed comparison of our simulations with existing data is not possible for at least two reasons. First, the present model does not simulate a thermocline due to the simple concept of turbulent diffusion involved.

The changes of vertical turbulent diffusion in time and space during the establishment of the seasonal thermocline in spring should be introduced to get a better representation of the interactions of the physical and biological processes. For this purpose the physical processes acting in the upper layer should be clarified. This has not, as yet, been done adequately, but is the aim of several experiments.

Secondly, the vertical profiles, parameters and functional relations used for validating the model should be measured during the same experiment. We expect that measurements of this kind in a bounded area over a fixed time interval will be available after Fladen Ground Experiment '76 in the Northern North Sea is completed.

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APPENDIX

A_D	vertical eddy diffusion coefficient (cm^2/sec)
B	biomass
E_P	effectivity of phytoplankton production
E_N	effectivity of nutrient consumption
f_N	regeneration coefficient for the nutrient N
g	conversion factor : nutrient = $g \cdot$ phytoplankton
G	grazing rate of herbivorous plankton ($\text{m}^3/\text{gC}/\text{day}$)
h	depth of the considered water column (m)
h'	depth of a layer including the euphotic zone, for balance considerations (m)
H	herbivorous plankton concentration (gC/m^3)
H'	depth of an upper layer with homogeneously distributed substance S (m)
$H(x)$	Heaviside function
I	underwater light intensity
I_{max}	maximum surface light intensity
I_{opt}	optimum light intensity for photosynthesis
$I_0(t)$	surface light intensity
$k, k(z)$	extinction coefficient (m^{-1})
k_c	conversion factor : phytoplankton = $k_c \cdot$ chlorophyll
k_0, k_1, k_2	coefficients in the relation for the extinction coefficient k
m	mixing rate
m_L	loss rate of phytoplankton due to all causes except respiration
m_P	respiration rate
m_T	functional dependence of the respiration rate on temperature
m_P^{eff}	effective loss rate due to respiration and grazing
N	concentration of the limiting nutrient ($\text{mg phosphorus}/\text{m}^3$)
$N_0(z)$	initial distribution of the nutrient
N_1	half-saturation constant in the nutrient limitation function
\bar{N}_0	nutrient content at $t = 0$ in the water column of depth h'
N_A^0	integrated gain (loss) of nutrients due to turbulent diffusion across $z = 0$ (dummy variable)
$N_A^{h'}$	integrated gain (loss) of nutrients due to turbulent diffusion across $z = h'$
\bar{N}_T	nutrient content at $t = T$ in the water column of depth h'
\bar{N}_+	integrated gain of nutrient due to regeneration
\bar{N}_-	integrated loss of nutrient due to uptake
p	phosphorus
P	phytoplankton concentration (gC/m^3)
\bar{P}	vertically integrated phytoplankton content of a water column (gC/m^2)
\bar{P}_0	plankton content in the water column of depth h' for $t = 0$
$P_0(z)$	initial distribution of phytoplankton
P_A^0	integrated loss of plankton due to turbulent diffusion across $z = 0$ (dummy variable)
$P_A^{h'}$	integrated loss of plankton due to turbulent diffusion across $z = h'$
\bar{P}_T	phytoplankton content in the water column of depth h' for $t = T$
P_w^0	integrated loss of plankton due to sinking across $z = 0$
$P_w^{h'}$	integrated loss of plankton due to sinking across $z = h'$
\bar{P}_+	integrated gain of phytoplankton due to photosynthesis
\bar{P}_-	integrated loss of phytoplankton due to respiration and grazing

r_I	light limitation function for photosynthesis
r_N	nutrient limitation function for photosynthesis
r_P	optimum photosynthesis rate
r_P^{eff}	effective photosynthesis rate
R_N^+	nutrient regeneration rate
R_N^-	nutrient uptake rate
R_P^+	photosynthesis rate
R_P^-	biological loss rate
S	substance for which diffusion laws hold
S_0	initial value of S for $t = 0$ in the upper layer
t	time
t_0	arbitrary time
T	time which the balance considerations are based on
w	mean vertical velocity of the water
w_s	sinking velocity of phytoplankton (m/day)
x	horizontal space dimension, eastwards
y	horizontal space dimension, northwards
z	vertical space dimension = depth, downwards
z_{com}	compensation depth
z_{eu}	depth of the euphotic zone
z_{max}	depth of the maximum phytoplankton concentration
z_{opt}	depth corresponding to the optimum light intensity
$z_{1/2}$	depth dividing the considered water column in two parts of equal plankton content
$\frac{\partial}{\partial t}$	partial time derivative
$\frac{\partial}{\partial z}$	partial vertical derivative
$\frac{\partial}{\partial x}, \frac{\partial}{\partial y}$	partial horizontal derivatives
Δt	small time interval
σ	frequency for surface light intensity
τ	integration variable

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