

Modelling the fine structure of the phytoplankton concentration in a stably stratified sea

Mathematical model
Stratified sea
Turbulent diffusion
Phytoplankton

Modèle mathématique
Stratification verticale
Diffusion turbulente
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ABSTRACT

The paper presents a one-dimensional mathematical model describing the vertical distribution of chlorophyll *a* and nutrients in a stratified sea. The model takes into account the most important physical, chemical and biological processes controlling the evolution of this function.

This model was tested with data obtained *in situ* during the Baltic research expedition of R/V *Prof. Siedlecki* in 1980. The vertical distributions of temperature field, chlorophyll *a* and nutrient concentrations were taken as initial conditions for various simulations.

The results of numerical simulations explained the influence of biological processes on the variability of phytoplankton concentration in time and space under various dynamic conditions. The variable dynamic conditions were simulated by the change of intensity of the layer-mixing processes, achieved by superimposing on a constant vertical shear a variable structure of the vertical distribution of the Brunt-Väisälä frequency.

This study reveals that the Richardson number values decrease and the values of the turbulent mass exchange coefficient increase with the increase of the vertical velocity gradient.

For values of vertical shear greater than $0.1 \text{ ms}^{-1} \text{ m}^{-1}$, microscale interbeddings are completely mixed. Under the same hydrodynamic conditions various chlorophyll *a* concentration distributions may be obtained, depending on the initial concentration of nutrients.

Hydrodynamic conditions, initial distributions of chlorophyll *a* and nutrient concentrations play a basic role where the microstructure of these functions is concerned.

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RÉSUMÉ

Modélisation de la répartition verticale du phytoplancton dans une mer stratifiée

Nous présentons dans cette étude les bases d'un modèle mathématique unidimensionnel décrivant la fonction de distribution de la concentration de chlorophylle *a* et des substances biogènes dans une mer stratifiée. Nous avons pris en considération dans ce modèle les principaux processus physiques, chimiques et biologiques contrôlant l'évolution de cette fonction. Le modèle a été testé avec la base de données obtenues *in situ* au cours des campagnes océanographiques du navire de recherche *Prof. Siedlecki* en Mer Baltique pendant l'année 1980.

Les conditions initiales des simulations du modèle sont les profils verticaux observés de la température, de la concentration de chlorophylle *a* et de la concentration des substances biogènes. Ces répartitions déterminent de façon significative, au temps initial $t = 0$, les conditions de la formation des processus de mélange turbulent.

Les résultats des simulations numériques ont permis d'expliquer l'influence des facteurs biogènes sur les variations du phytoplancton dans le temps et dans l'espace, sous des conditions dynamiques variables. Les conditions dynamiques variables ont été simulées en faisant varier l'intensité des processus de mélange. Nous avons obtenu ces variations en superposant à un cisaillement vertical constant, une structure verticale variable de la répartition de la fréquence de Brunt-Väisälä.

Ce travail a démontré que les valeurs du nombre de Richardson diminuent avec l'accroissement vertical du gradient de vitesse, alors que les valeurs du coefficient d'échange turbulent de masse augmentent.

Les stratifications micro-échelles se mélangent entièrement lorsque le cisaillement vertical est supérieur à $0,1 \text{ ms}^{-1} \text{ m}^{-1}$. Dans des conditions hydrodynamiques identiques, on obtient différentes distributions verticales de la concentration de chlorophylle *a* selon la concentration initiale des substances biogènes.

Les conditions hydrodynamiques et les distributions initiales de concentration de chlorophylle et de substances biogènes jouent un rôle important dans la formation de la structure à micro-échelle de ces fonctions.

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INTRODUCTION

The last ten years have witnessed a tangible increase in research into the spatial and temporal effect of the dynamic properties of a vertically stratified sea and of nutrients on the variability of the phytoplankton concentration field.

Visible progress has been made both in empirical studies and in mathematical modelling (*e.g.* Radach and Mair-Reimer, 1975; Lewis *et al.*, 1983; Bigg *et al.*, 1989; Ondrusek *et al.*, 1991). Nevertheless, the problem of constructing an adequate mathematical-physical representation of actual phenomena in a vertically stratified sea is still a long way from being satisfactorily solved, whether from the theoretical or from the practical standpoint. Some of the difficulties faced by oceanographers in this respect are inherent in the problem itself; others stem from the mathematical modelling.

They are exacerbated as the spatial and temporal variability of the phenomena under study and the vertically layered fine structure of the velocity, density, temperature and salinity fields in a marine basin become reduced in scale. In this regard, the fine stratification of hydrophysical fields affecting the concentration of marine plankton is a particularly important factor governing hydrobiological processes. Thin interlayers with characteristically steep vertical density gradients are mostly laminar layers in which the exchange of heat, mass and momentum is incomparably smaller than in turbulent layers. The absolute stability of such an interlayered pycnocline would preclude the vertical transfer of oxygen, nutrients and suspended particles

through the water, were it not for the hydrodynamic, fine-scale reconstruction of the thermohaline structure of the density jump layer that occurs during the vertical transfer of mass and energy. On the other hand, it is well known that if an ocean basin constituted a homogeneous medium with respect to the spatial distribution of hydrophysical features, zooplankton could not exist there, since the uniform distribution of food resources thereby produced would mean that the amount of energy expended by zooplankton animals in search of food would be far greater than the quantity gained from its consumption. Therefore a layered structure of hydrophysical fields, as well as its variability (diurnal, seasonal) in time and space, is essential for hydrobiological processes to occur. The sources of the turbulent mixing that occurs within this structure alter in time and space both the concentration of suspensions and nutrients and the thermodynamic characteristics of the fields, thereby leading to variability in the location of regions providing optimum conditions for the incubation and growth of the different stages of marine organisms.

Such studies can be performed by means of mathematical modelling based on the differential equations of exchange and transfer processes in a set of local Euler coordinates.

This work is a continuation of research, the preliminary results of which were published in 1988 (Druet and Zielinski, 1988; Druet *et al.*, 1988). The present paper seeks to explain the influence of a variety of nutrients on the growth and variability of the phytoplankton concentration in time and space under changing dynamic conditions of fine-scale, stably-stratified density and velocity fields of water masses in the sea.

MODEL DESCRIPTION

The concentration of phytoplankton cells is considered per unit volume, with a number of cells sufficiently large to permit statistical averaging, but small enough in comparison with the surrounding analogous volumes for differential equations to be applicable.

The phytoplankton concentration is a dynamically passive physical quantity and depends on:

- the hydrodynamic state of the environment (transfer and exchange of mass in the aquatic medium);
- the temperature, salinity and oxygenation of the water;
- the intensity of underwater illumination (photosynthesis);
- the concentration of nutrients (phosphates, carbon, ammonia, nitrates, nitrites, *etc.*);
- the physiological capability of phytoplankton to take up nutrients;
- the regeneration of nutrients excreted by zooplankton into the water;
- losses due to phytoplankton mortality; and
- losses due to the grazing of phytoplankton by zooplankton.

Conservation equations for phytoplankton biomass and for nutrient concentration take the form:

$$\begin{aligned} \frac{\partial \bar{v}}{\partial t} + \frac{\partial}{\partial x_i} (\bar{u}_i \bar{v}) - \frac{\partial}{\partial x_i} (K_v \frac{\partial \bar{v}}{\partial x_i}) - \Pi_1 \bar{v} &= 0 \\ \frac{\partial \bar{B}}{\partial t} + \frac{\partial}{\partial x_i} (\bar{u}_i \bar{B}) - \frac{\partial}{\partial x_i} (K_B \frac{\partial \bar{B}}{\partial x_i}) - \Pi_2 \bar{v} &= 0 \end{aligned} \quad (1)$$

where $\bar{v} = \bar{v}(x, y, z, t)$ denotes the mean concentration of suspended matter at point x_i and time t ;

$\bar{B} = \bar{B}(x, y, z, t)$ denotes the mean concentration of nutrients at point x_i and time t ;

$\bar{u} = \bar{u}(u, v, w, t)$ denotes the vector of the mean velocity of advective transfer of suspended matter and nutrients at point x_i and time t ;

K_v and K_B are coefficients of the locally isotropic exchange of mass of suspended matter and nutrients;

Π_1 and Π_2 are coefficients of biological interaction terms (production and consumption) in a concentration of suspended matter. The units of the defined variables are given in the Table.

If the suspended matter is non-living, *e. g.* mineral, the second equation in system (1) can be ignored.

The set of equations (1) can be solved provided the following initial and boundary conditions are assumed:

- for $t = 0$ distributions \bar{v} and \bar{B} are known:

$$\begin{aligned} \bar{v}(x, y, z, 0) &= \bar{v}_0(x, y, z) \\ \bar{B}(x, y, z, 0) &= \bar{B}_0(x, y, z) \end{aligned} \quad (2)$$

- on the ordinate $z = 0$ (free sea surface):

$$\bar{u}_i \bar{v} = K_v \left(\frac{\partial \bar{v}}{\partial x_i} \right); \quad \frac{\partial \bar{B}}{\partial z} = 0 \quad (3)$$

- on the ordinate $z = H^e$ (double the thickness of the euphotic zone of the sea):

$$\bar{u}_i \bar{v} = K_v \left(\frac{\partial \bar{v}}{\partial x_i} \right) \quad (4)$$

$$\bar{B} = \bar{B}_1 = \text{const}$$

The transfer and exchange of phytoplankton biomass and nutrients

Fundamental to the present modelling study is the assumption of an absolutely stable vertical distribution of the average sea water density in the studied region. This means that the mean density and salinity of the water increase and the mean temperature falls with depth. It is against such a hydrological background that the fine-scale stratification of density and flow velocity fields, generated by turbulent, quasi-turbulent, quasi-laminar and laminar mixing, is played out. The source of these processes in a region with a hydrostatically absolutely stable density distribution could be:

- wind friction on the free sea surface and the transfer of momentum into the basin;
- Langmuir circulations in the field of drift flows co-acting with wind-generated waves on the free sea surface;
- Kelvin-Helmholtz instability;
- refraction of internal waves, or
- the collapse and transformation of turbulent patches.

The Kelvin-Helmholtz hydrodynamic instability and the refraction of internal waves are the only internal sources of mixing when the density distribution in the water is absolutely stable. In such a situation there can be neither convective mixing, generated by an unstable temperature distribution when the salinity and density distributions are stable (thermal inversion), nor the "salty finger" phenomenon that accompanies an unstable salinity distribution when the temperature and density distributions are stable. Therefore, the hydrodynamic state of mass transfer and exchange in the various intervals of a stably stratified density distribution can be defined by means of two quantities:

- the vertical distribution of the square of the Brunt-Väisälä frequency:

$$N^2 = -g \frac{\partial \bar{\rho}}{\partial z} \quad (5)$$

where $\bar{\rho}$ denotes the average density and g is the acceleration due to gravity;

- the spatial distribution of the average flow velocity representing the advection process:

$$u_i \equiv \begin{pmatrix} \bar{u} & \bar{v} & \bar{w} \end{pmatrix} (x, y, z, t) \quad (6)$$

When the density distribution is absolutely stable, there can be no upwelling or downwelling of water masses. Therefore the vertical component of the water flow velocity $\bar{w} \approx 0$ (one-dimensional model), and nutrients are not moved along the z axis.

The mean velocity of settlement of suspension in stagnant water can be approximately described in the following manner:

Table

Quantities, definitions, values of constant and units as used in the model.

Quantity	Definition	Value	Unit
A_0	Coefficient determined experimentally for a given basin	44.53	$\frac{\text{mgC}}{\text{mgChl } a \text{ day}}$
A_s	Assimilation number	variable	$\frac{\text{mgC}}{\text{mgChl } a \text{ day}}$
a_A	Empirical coefficient	$1.479 \cdot 10^{-4}$	$\frac{\text{mgCm}^2}{\text{mgChl } a \text{ J}}$
\bar{B}	Phosphate concentration at point z and time t	variable	$\mu\text{mol P m}^{-3}$
$B_{0.5}$	Half saturation constant for phosphate	0.12	$\mu\text{mol P m}^{-3}$
b_A	Empirical coefficient	$8.45 \cdot 10^{-6}$	$\frac{\text{mgCm}^2}{\text{mgChl } a \text{ J}}$
C/P_s	Ratio of organic carbon to phosphorus in algae	0.3	$\frac{\mu\text{molP}}{\text{gC}}$
C_G	Grazing coefficient	variable	s^{-1}
C_M	Mortality rate	10^{-6}	s^{-1}
C_R	Respiration constant	$1.56 \cdot 10^{-6}$	s^{-1}
D_{oz}^0	Dose of solar energy reaching the free surface of sea	$7.709 \cdot 10^6$	$\frac{\text{J}}{\text{m}^2\text{day}}$
d	Particle diameter	variable	m
K_p	Local vertical turbulent coefficient	variable	m^2s^{-1}
m_c	Conversion factor of mg of organic carbon to mg of chlorophyll	0.046	$\frac{\text{mgChl } a}{\text{gC}}$
N	Local Väisälä-Brunt frequency	variable	s^{-1}
q	Relative amplitude of changes in zooplankton biomass	0.6	none
Q_f	Percentage of regenerated phosphorus from zooplankton excretion	0.1	none
Q_w	Percentage of grazed phytoplankton appearing as zooplankton excretion	0.33	none
Ri	Richardson number	variable	none
T_r^0	Coefficient of solar energy transmission through the free surface	0.94	none
T_r^z	Coefficient of solar energy transmission trough at the depth z	variable	none
t_0	Time in which maximum concentration of zooplankton occurs	3.25	hour
\bar{v}	Chlorophyll-a concentration in point z and time t	variable	mg m^{-3}
μ	Coefficient of dynamic viscosity of water	0.14	$\text{kgm}^{-1}\text{s}^{-1}$
ρ	Average density of sea water	(0.99-1.04)	kgm^{-3}
ρ_s	Average density of phytoplankton	$1,1 \cdot 10^3$	kgm^{-3}

$$\bar{w}_s(z) = \frac{g[(\bar{\rho}_s - \bar{\rho}(z)) d^2]}{18\mu} \quad (7)$$

where $\bar{\rho}_s$ is the average density of suspended phytoplankton in unit volume;

μ the coefficient of dynamic viscosity of water;

d particle diameter.

The settling velocity \bar{w}_s is unknown for the horizontal translatory movement of an aquatic medium in motion.

For this reason, a number of workers (*e.g.* Lerman *et al.* 1977) have suggested that the vertical transport of suspensions causes the zooplankton to form aggregates filtering food items from the sea water.

Knowing the vertical distributions of the Brunt-Väisälä frequency and the horizontal component of the average velocity vector $\sqrt{(u^2 + v^2)} = u(z)$ at any point x_i and time t, we can evaluate the Richardson number, characterizing the state of development of turbulent mixing at that point:

$$Ri = \left(\frac{N}{\frac{\partial \bar{u}(z)}{\partial z}} \right)^2 \quad (8)$$

When $Ri < 0.25$, we will be dealing with a developing state of turbulent mixing. This process is initiated when, in the presence of internal waves, a stream of laminar flow reaches a state of hydrodynamic instability manifested as overturning with a dimension on the Thorpe scale (Thorpe, 1973) of:

$$l_{Th} \approx \left(\frac{\varepsilon}{3N^3} \right)^{1/3} \quad (9)$$

where ε is the rate of dissipation of the kinetic energy of overturning.

The thickness of a turbulent patch formed in this way will grow with time if the sources powering the hydrodynamic instability continue to exist. With the passage of time, the turbulent patch will spread both horizontally and vertically. Since at a given depth the mechanism of hydrodynamic instability always generates a whole succession of turbulent patches in a horizontal plane, these structures will join up as they spread to produce a horizontal turbulent interlayering of the water. After the sources giving rise to mixing have ceased to act, the inertial forces of the moving volumes of water continue to prevail over frictional and density buoyancy forces. It is for these reasons that for some time, even in the condition $Ri > 0.25$, the thickness of the turbulent interlayering will increase to reach a maximum at the instant that the Richardson number attains a value known as the Thorpe number (Garrett and Munk, 1972):

$$Ri = Th \approx 0.4 \pm 0.1 \quad (10)$$

This quantity is given by:

$$h_{Th} = \frac{(\Delta \bar{u})_0}{3.2 N_0} \quad (11)$$

where $(\Delta \bar{u})_0$ and N_0 are the velocity differences between the top and bottom of the turbulent interlayering and the Brunt-Väisälä frequency respectively, when $Ri = Th$.

Thorpe's investigations (1973) indicate that when a time $t_0 \approx 4t_1$ (where $t_1 \approx 1-2$ mn) has elapsed from the instant when hydrodynamic instability comes into existence, horizontal turbulent interlayering occurs which reaches a state of complete development when relationship (11) is satisfied.

When sources cease to supply energy to the mixing processes and the state $Ri \approx Th$ has been reached, the turbulent interlayering begins to collapse, becoming thinner but longer with time. This process arises because the motion of volume elements in the turbulent patch becomes polarized. Homogeneous mixtures are never produced by the overturn mechanism. The heavier volume elements that are raised and the lighter ones that are depressed will, if centrifugal forces of inertia disappear, tend towards hydrostatic equilibrium. In the final stage of this process, which occurs at a time $t \approx 30 N^{-1}$ (Wu, 1969) after the state $Ri = Th$ has been reached, thin laminar interlayers are formed.

When the expansion-contraction cycle of turbulent interlayering is in full swing, the intensity of turbulent mixing varies with time, depending on the relationship between the work of density buoyancy forces damping the turbulence and the work of inertial forces increasing it. This relationship is represented by the Richardson number. The coefficients of turbulent mass exchange in equations (1) should therefore be inversely proportional to the Richardson number. Among the various estimators of this dependence, the representation by Peters *et al.* (1988) deserves special attention because of its practicability.

It is valid for the upper layer of a stratified sea down to a depth of 100 m, *i. e.* to a depth in excess of twice the thickness of the euphotic layer:

$$K_p \approx 5.10^{-4} (1 + Ri)^{-2.5} + 10^{-6} \quad (12)$$

This estimator does not satisfy the boundary conditions for $Ri \rightarrow 0$ and $Ri \rightarrow \infty$. Nevertheless, verification studies have indicated that in the conditions of an actual stratified ocean, the estimates given by this formula are correct. We assume that locally isotropic turbulent diffusion of passive suspended matter (\bar{v}) and of passive mixture (\bar{B}) takes place in the same way as density diffusion, and can write that $K_p = K_v = K_B$.

Production and loss of phytoplankton biomass

The factor determining the extent of production is the solar radiation penetrating the basin. The quantity of energy carried by this radiation into the euphotic zone of the sea depends on the optical properties of the water, and permits marine photosynthesis to occur. The efficiency of this production source of phytoplankton biomass will be directly dependent on the amount of solar energy absorbed by the phytoplankton, defined by the characteristics of the underwater light field. This amount is governed by the concentration of the phytoplankton itself and the composition and absorptive properties of its pigments. The above relationships were represented by Radach (1983) as a formula describing the rate of primary production:

$$V_p(x_i, t) = V_{max} [\min(\alpha_s, \alpha_B)] \bar{v}(x_i, t) \quad (13)$$

where V_{max} denotes the maximum rate of production increase while α_s and α_B are coefficients restricting this increase because of the quantity of light available for a given concentration of nutrients. The coefficients are given by formulae:

$$\alpha_s = \frac{C_p(x_i, t)}{V_{max}}, \quad \alpha_B = \frac{\bar{B}(x_i, t)}{B(x_i, t) + B_{0.5}} \quad (14)$$

where $B_{0.5}$ is the nutrient half-saturation constant

The concentration of biogenic substances in sea water can be described by phosphorus because of the ratio C:P:N is constant for the Baltic Sea (Koblentz-Mishke and Vedeniev, 1977; Koblentz-Mishke, 1988; Mordasova, 1976). For given nutrient concentrations, the coefficient C_p defines the total primary production and is given by the Platt model (Harrison *et al.*, 1985) in the form:

$$C_p(x_i, t) = m_c A_s(x_i, t) \sin(\gamma_s) \quad (15)$$

where m_c is an empirical coefficient characterizing the investigated basin and γ_s is the solar elevation at a given instant of time (GMT) calculated from the relationship:

$$\sin(\gamma_s) = \sin(\varphi)\sin(\delta) + \cos(\varphi)\cos(\delta)\cos\left[t_{\text{GMT}}\left(\frac{\Pi}{12}\right) - \Pi + \lambda\right] \quad (16)$$

where $\varphi = 56^\circ 25' \text{N}$ is the geographical latitude, $\lambda = 18^\circ 37' \text{E}$ the angle of longitude and $\delta = 16^\circ$ the solar declination.

The assimilation number A_s is given by:

$$A_s(x_i, t) = A_0 \{1 - \exp[-a_A D_{\text{Oz}}(x_i, t) A_0^{-1}]\} \exp[-b_A D_{\text{Oz}}(x_i, t) A_0^{-1}] \quad (17)$$

where a_A, b_A are empirical coefficients adapting the assimilation number to the natural conditions of the basin in question.

The amount of solar energy reaching the requisite depth z is given by Dera (1992):

$$D_{\text{Oz}}(x_i, t) = D_{\text{Oz}}^0(t) T_r^0 \cdot T_r^z \quad (18)$$

where D_{Oz}^0 is the amount of solar energy reaching the free sea surface and T_r^0 and T_r^z are the coefficients of solar energy transmission across the free surface and within the water down to a depth z .

In summary, the rate of phytoplankton biomass production during photosynthesis for a given state of nutrient saturation is given by:

$$V_p(x_i, t) = C_p(x_i, t) \cdot \bar{v}(x_i, t) \quad (19)$$

Part of the photosynthetic energy is utilized in producing dissolved oxygen, which disappears from the water column during respiration. Hence, the real increment in primary production per unit of time will be lower than the rate of production given by (13) by a quantity (Parsons *et al.*, 1977):

$$V_R(x_i, t) = C_R \cdot \bar{v}(x_i, t) \quad (20)$$

where $C_R = m_R V_{\text{max}}$ and m_R is the respiration constant.

A second factor reducing the phytoplankton biomass is its natural mortality whose effect, however, is poorly understood. Some workers (Raymont, 1980; Sjöberg, 1980) assume a linear relationship between mortality and phytoplankton concentration:

$$V_M(x_i, t) = C_M \bar{v}(x_i, t) \quad (21)$$

where C_M is the mortality rate of phytoplankton cells. In the sea, this coefficient usually takes very small values and is determined as an average value for all the phytoplankton species occurring in the basin.

Another process causing significant losses in the biomass of phytoplankton is its consumption by zooplankton. If it is assumed that: a) this process is independent of the chemical state of the water; b) one dominant species among the zooplankton is responsible for 80-90 % of the phytoplankton consumed; c) possible changes in the numbers of this dominant species can be neglected within a given interval of time; and d) consumption is considered on a diurnal cycle, the rate of loss of the phytoplankton mass can be given by (Daro, 1980; Ciszewski *et al.*, 1983):

$$V_G(x_i, t) = C_{\text{GR}}(x_i, t) \cdot \bar{v}(x_i, t) \quad (22)$$

where C_{GR} is the grazing coefficient given by

$$C_{\text{GR}}(x_i, t) = \{1 + q \cos[\omega(t - t_0)]\} f_G(z) \quad (23)$$

$f_G(z) = q_0 + q_1 \cdot z + q_2 \cdot z^2 + \dots$ is a polynomial describing the vertical distribution of zooplankton concentration whose relative amplitude of change q reaches a maximum after time $t = t_0$ and $\omega = \Pi/12$.

The amplitudes q_1 in the polynomial $f_G(z)$ can be evaluated from experimental data defining the consumption coefficient C_{GR} at three depths:

- on the free surface ($z = 0$): $C_{\text{GR}}(0, t) = C_{\text{GR}}^0(t)$;
- at any intermediate depth ($z = z_n$): $C_{\text{GR}}(z_n, t) = C_{\text{GR}}^z(t)$;
- at the depth equal to the thickness of the euphotic zone ($z_H = 0.5 H^e$): $C_{\text{GR}}(z_H, t) = 1$.

Taking expressions (19-22) into consideration, the gain and loss coefficient of phytoplankton biomass occurring in the first equation of set (1) will take the form:

$$\Pi_1 = C_p(x_i, t) - [C_R + C_M + C_{\text{GR}}(x_i, t)] \quad (24)$$

The values of coefficients C_p and C_{GR} are determined from formulas (15) and (23). On the other hand, coefficients C_M and C_R are constants, representing long-term averages for the growing season in a particular marine basin.

The coefficient Π_2 in the equations (1) depends on the difference between the quantity of nutrients taken up by the phytoplankton cells from the surroundings and their amount excreted by zooplankton, either in soluble form or as faeces sinking to the sea bed. These sediments undergo rapid bacterial conversion and mineralization. Thus a certain quantity of nutrients replenishing their concentration field is released back into the environment. The quantity of nutrients taken up by phytoplankton cells can be expressed as (Radach, 1983):

$$B_p(x_i, t) = C/P_s [V_p(x_i, t) - V_R(x_i, t)] \quad (25)$$

where C/P_s is a constant, denoting the ratio of organic carbon (C) to phosphorus (P_s).

On the other hand, the quantity of regenerated nutrients depends on the biomass consumed and can be given by (Stigebrandt and Wulff, 1987):

$$B_R(x_i, t) = C/P_s Q_f Q_w \cdot V_G(x_i, t) \quad (26)$$

where Q_f denotes the percentage of matter regenerated as phosphate and Q_w the percentage of consumed matter that has been excreted.

The difference between B_p and B_R , divided by the phytoplankton biomass concentration, is given by the coefficient:

$$\Pi_2 = C/P_s \{C_p(x_i, t) - [C_R + Q_f Q_w C_{\text{GR}}(x_i, t)]\} \quad (27)$$

MODEL RESULTS AND DISCUSSION

Methodology of numerical calculations and initial assumptions

Let us assume that in an absolutely stable sea all the hydrophysical, hydrochemical and hydrobiological characteristics remain unchanged in a horizontal plane, *i. e.* that:

$$x_R = z, \partial/\partial x = \partial/\partial y = 0, \partial/\partial z \neq 0$$

and taking the above considerations into account, equations (1) simplify to the form:

$$\begin{aligned} \partial \bar{v} / \partial t + \partial / \partial z (\bar{w}_s \bar{v}) - \partial / \partial z (K_z^p \partial \bar{v} / \partial z) - \Pi_1 \bar{v} &= 0 \\ \partial \bar{B} / \partial t + \partial / \partial z (K_z^p \partial \bar{B} / \partial z) - \Pi_2 \bar{v} &= 0 \end{aligned} \quad (28)$$

The initial and boundary conditions (2-4) are reduced to the form:

$$\text{- for } t = 0: \bar{v}(z, 0) = \bar{v}_0(z), \bar{B}(z, 0) = \bar{B}_0(z) \quad (29)$$

$$\text{- for } z = 0: \bar{w}_s \bar{v} = K_z^p (\partial \bar{v} / \partial z), \partial \bar{B} / \partial z = 0 \quad (30)$$

$$\text{- for } z = -H: \bar{w}_s \bar{v} = K_z^p (\partial \bar{v} / \partial z), \bar{B} = B_1 = \text{const} \quad (31)$$

The set of equations (28) with boundary conditions (29-31) and equations (24), (27) were solved numerically on the basis of the well-known Crank-Nicholson method (Potter, 1982). This method is absolutely convergent and is characterized by second order with respect to the time and space discretization steps.

The programme of computations has been prepared in such a way that at any time and space step it is possible to:

- read off any experimentally determined temperature profile;
- analyze this profile along the computation lattice and determine those sections where hydrodynamic instability (turbulent mixing) occurs;
- change the value of the space step in those study areas where hydrodynamic instability occurs;
- determine the coefficient of turbulent diffusion corresponding to the current state of internal turbulence; and
- carry out computations at any moment in time, starting at any instant during the day.

The variation in the Richardson number (Ri) is the basis for defining the zones of hydrodynamic instability, assuming that the velocity gradient of vertical flow $\bar{u}(z)$ is constant ($\partial \bar{u} / \partial z = \text{const}$). The areas of turbulent mixing located on this basis must again be analysed numerically in accordance with the above procedure, assuming that over the distance $\Delta z = z_i - z_{i-1}$ from the point of hydrodynamic instability the value of the linear quantization step changes from $\Delta z = 10$ cm to $\Delta z = 1$ cm. Thus are determined the vertical distributions of the turbulent diffusion coefficient (K_i) = f(Ri) according to dependence (11). The computations with step $\Delta z = 1$ cm are realized in layers of turbulent mixing whose thickness is increased from top and bottom by a value $\Delta z = 10$ cm.

At any point between nodes of the computation lattice (x_{i-1}, x_i or x_i, x_{i+1}), the values of R_i, \bar{v} and B are determined from the values of these quantities at the nodes using a second-degree approximation polynomial.

This model was tested with comprehensive empirical data obtained *in situ* during the Baltic research expedition of R/V Prof. Siedlecki in 1980.

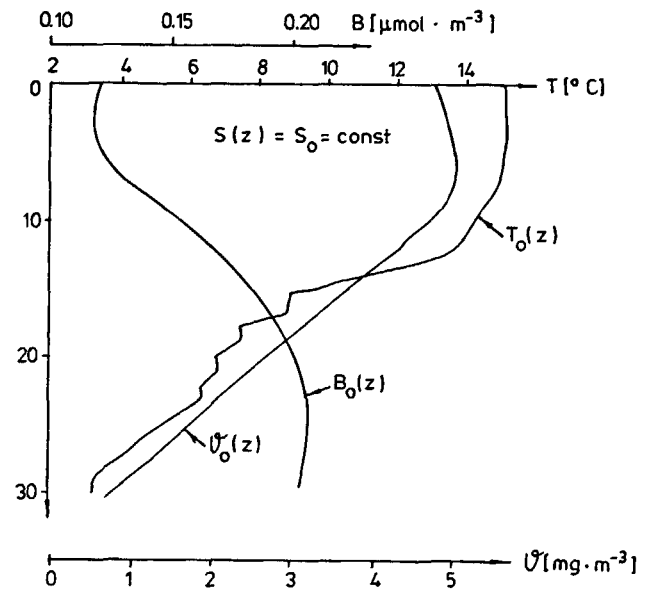


Figure 1

Initial z-axis distributions of temperature (T_0), nutrient concentration (B_0) and chlorophyll a concentration (v_0) when $\partial \bar{v} / \partial z = 0$.

Results of simulation studies

The simulation studies with the numerical model described above are carried out with real, vertical initial distributions of temperature $T_0(z)$, chlorophyll concentration $\bar{v}_0(z)$ and nutrient concentration $\bar{B}_0(z)$ (Fig. 1). The temperature

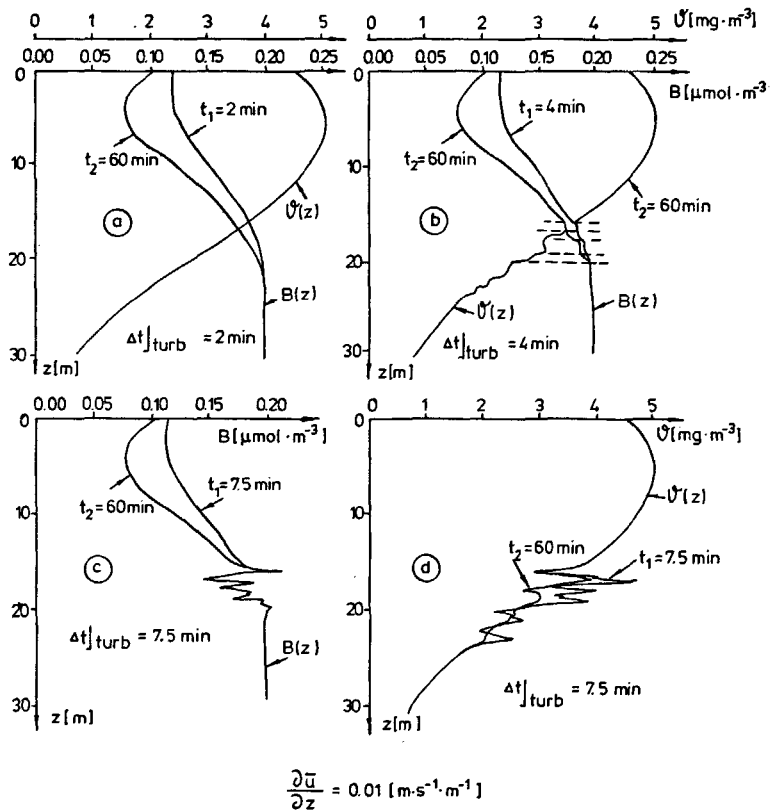


Figure 2

The influence of nutrient concentration (\bar{B}) and the duration of turbulent mixing ($\Delta t / \text{turb}$) on the structure of the vertical distribution of chlorophyll a concentration (\bar{v}).

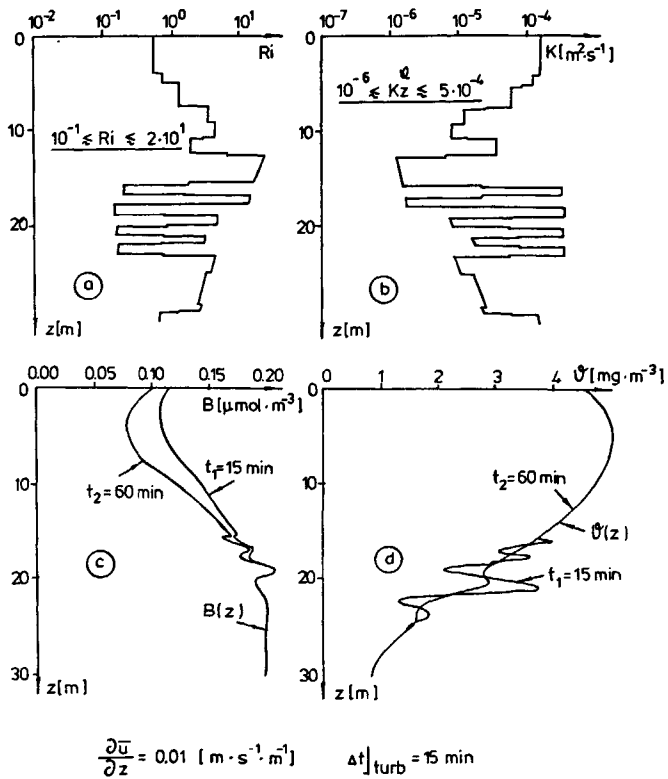


Figure 3
The influence of turbulent processes and laminar mixing (R_i , K) and nutrient concentration (\bar{B}) on the structure of the vertical distribution of chlorophyll a ($\bar{\psi}$) concentration when $\partial\bar{u}/\partial z = 0.01 \text{ ms}^{-1}/\text{m} = \text{const}$.

distribution is given directly by the vertical density distribution $\rho(z)$ and the Brunt-Väisälä frequency $N(z)$ for a homogeneous and constant salinity distribution $S(z) = S_0 = \text{const}$. Hence, at $t = 0$ of turbulent mixing generation, the initial conditions are defined by the distributions shown in Figure 1.

The intensity of laminar mixing can be simulated by superimposing on the vertical shear ($\partial\bar{u}/\partial z = \text{const}$) a variable structure of the vertical distribution of the Brunt-Väisälä frequency.

The production source coefficients in equations (24), (27) and other are given in the Table.

By solving the set of equations (28) with the aid of the initial and boundary conditions (29-31) and the assumptions made earlier, we obtain a simulated variability of vertical distributions $\bar{\psi}(z)$ and $\bar{B}(z)$ in time (t) along depth (z). Figure 2 shows the results of simulations performed under the assumption that $\partial\bar{u}/\partial z = 0.01 \text{ ms}^{-1}/\text{m} = \text{const}$, $R_i(z)$ and $K_z(z)$ are given in the form of the distributions shown in Figure 3 (a and b), and the time of action of the hydrodynamic sources of mixing (t_1) lasts for $t_1 = 2 \text{ mn}$, $t_1 = 4 \text{ mn}$ and $t_1 = 7.5 \text{ mn}$. The distributions in Figure 2 illustrate the state of the concentration field after a time t_1 and after a time $t_2 = 60 \text{ mn}$ from the instant hydrodynamic instability occurred. During the entire experiment phytoplankton “feeds on” light and nutrients (nutrients are consumed continuously). However, fine-scale stratification in its concentration field only begins to appear after a time $t_1 = 4 \text{ mn}$, becoming the more distinct,

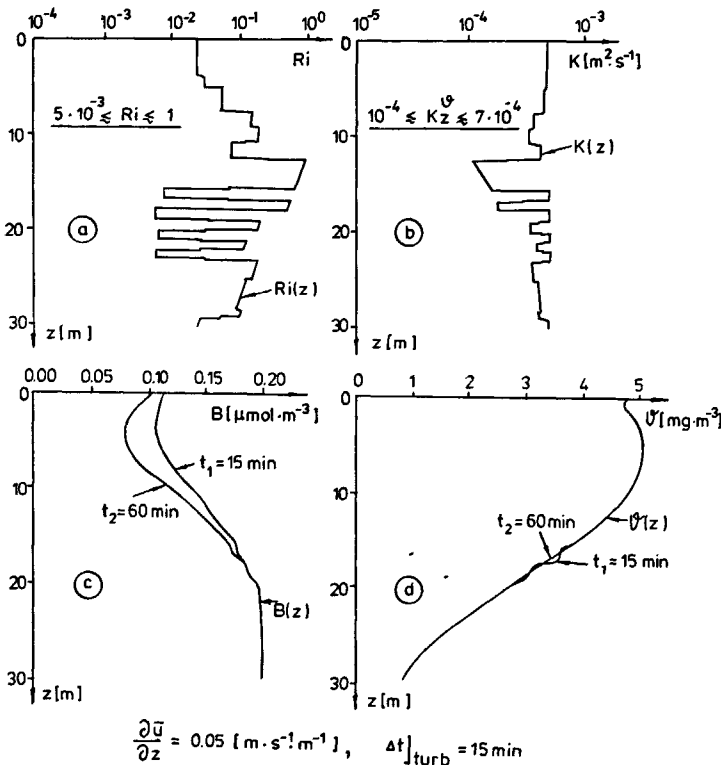


Figure 4
The influence of turbulent processes of laminar mixing (R_i , K) and nutrient concentration (\bar{B}) on the structure of the vertical distribution of chlorophyll a ($\bar{\psi}$) concentration when $\partial\bar{u}/\partial z = 0.05 \text{ ms}^{-1}/\text{m} = \text{const}$.

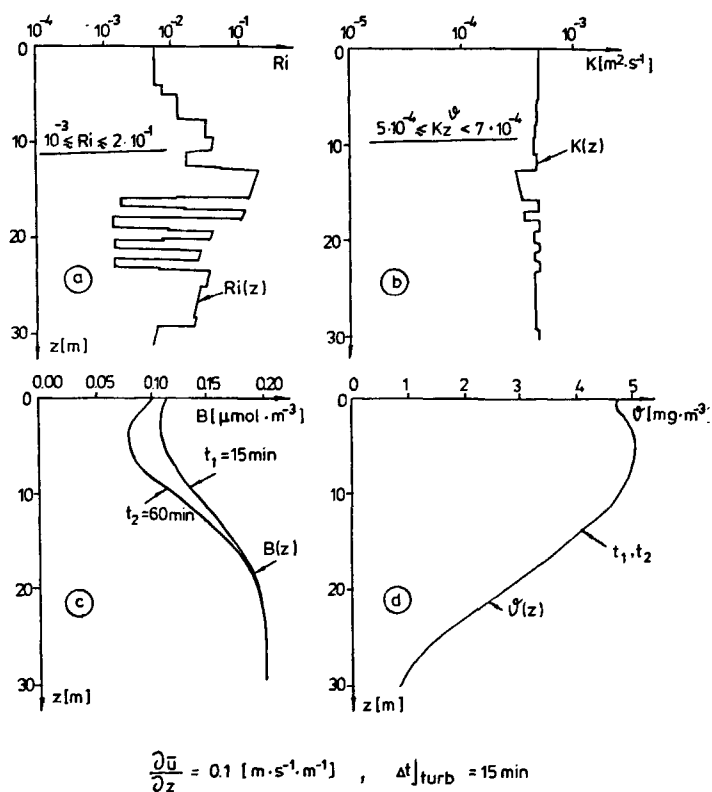


Figure 5
The influence of turbulent processes of laminar mixing (R_i , K) and nutrient concentration (\bar{B}) on the structure of the vertical distribution of chlorophyll a ($\bar{\psi}$) concentration when $\partial\bar{u}/\partial z = 0.1 \text{ ms}^{-1}/\text{m} = \text{const}$.

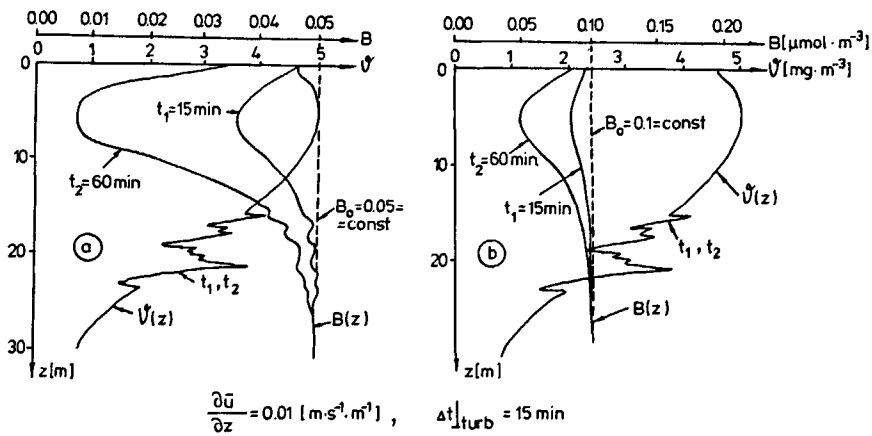


Figure 6

The influence of the initial nutrient concentration (B_0) on the structure of the vertical concentration distribution $\bar{B}(z)$ and $\bar{v}(z)$.

the longer the source of hydrodynamic mixing lasts. Clearly, the fine-scale changes in the distribution of concentration $\bar{v}(z)$ induce opposite changes in the concentration distribution $\bar{B}(z)$, because the higher the phytoplankton biomass concentration, the greater the decrease in nutrient concentration.

Figures 3-5 show the increasing intensity of turbulent mixing sources and the decrease in fine-scale heterogeneities in distributions $\bar{v}(z)$ and $\bar{B}(z)$ under the influence of an increase in the vertical shear. As this gradient steepens the Richardson number decrease while the coefficient of turbulent mass exchange increases, *i. e.* laminar mixing processes increase in intensity.

When $\partial\bar{u}/\partial z = 0.1 \text{ ms}^{-1}/\text{m}$, fine-scale interlayering is completely mixed.

These simulations have shown that fine-scale stratification in the concentration fields \bar{v} and \bar{B} depend largely on the state of the turbulent mixing processes in the layers. Nevertheless the extent of nutrient saturation in the environment of phytoplankton cells plays a significant part in their functioning. It is for these reasons that the structure of the phytoplankton biomass concentration may correspond to the identical but independent structure of the nutrient concentration field. Figure 6 illustrates two cases of $\bar{v}(z)$ and $\bar{B}(z)$ structure formation, assuming that the initial distribution $\bar{B}(z) = \bar{B}_0 = \text{const}$. At low saturation, hydrodynamic processes govern stratification and are principally responsible for producing the fine-scale structure $\bar{B}(z)$. On the other hand, if the growth of phytoplankton cells is governed by - for example - 50 % nutrient saturation, their concentration is so great that the intake of the mass of nutrients by the stratified structures of plankton concentration do not cause any losses giving rise to stratification in field $\bar{B}(z)$. Comparison of distributions $\bar{B}(z)$ on Figures 6 a and 6 b shows that under

the same hydrodynamic conditions ($\partial\bar{u}/\partial z = 0.01$) they differ considerably because of the difference in initial nutrient concentration ($B_0 = 0.05 \mu\text{mol}\cdot\text{m}^{-3}$ and $B_0 = 0.1 \mu\text{mol}\cdot\text{m}^{-3}$).

CONCLUSION

The one-dimensional model of diffusion of suspensions and biogenic substances in the sea presented here can be utilized for numerical investigations on space-time changes in the vertical distribution of chlorophyll *a* concentration.

The presented results of numerical investigations concerning the effect of chemical and dynamic processes on the shape and absolute value of the function of vertical distribution of chlorophyll *a* concentration in the sea depths reveal that these processes are responsible for the observed *in situ* shape of vertical profiles of phytoplankton concentration to the same extent as solar energy influx. However, it is difficult at the present stage of investigation to establish which of the mentioned processes prevails and to what extent it limits the shape of the function of chlorophyll *a* concentration at depth.

The existing mutual relationships between these processes require further investigations leading to more precise determination of the coefficient occurring in the model and describing these processes.

This statement applies particularly to the development of investigations on the diurnal grazing cycle of phytoplankton and on changes in nutrient concentration in this cycle. Lack of these data precludes full numerical analysis of this phenomena, as well as analysis in longer intervals.

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