Numerical analysis of the influence of grazing on the two-dimensional distribution function of the phytoplankton concentration in a stratified sea

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Mathematical model
Stratified sea
Phytoplankton
Grazing

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Abstract

This paper presents the results of simulated phytoplankton grazing by zooplankton and the influence of this process on the distribution function of chlorophyll *a* concentration in a stratified sea. The salinity, temperature and density functions of the sea are known. The process of grazing is described by a two-dimensional function in a day-night system. The investigation was carried out at various times of hydrodynamic instability. The results suggest that, to a certain extent, grazing camouflages the stratification of the water basin. It was observed that grazing was responsible for the shape of the vertical fluorescence profiles of chlorophyll *a* under natural conditions to the same extent as dynamic processes and the input of solar energy. The numerical analysis of grazing and the hydrodynamic instabilities presented in this paper shows that in the distribution of chlorophyll *a* concentration the phenomenon of 'patchiness' occurs as a result of the processes described above.

1. Introduction

Theoretical and experimental investigations on the turbulent diffusion of marine phytoplankton indicate that, apart from the mechanisms *tuning* the stratified structure of density and seawater velocity fields, the process is fundamentally influenced by the chemical parameters of seawater and the related biological properties of the benthos in a water region. A significant factor influencing the shape of the phytoplankton distribution function in a stratified sea is the grazing of phytoplankton by zooplankton (Radach *et al.*, 1984). Under natural conditions this process is prevalent and determines the concentration of phytoplankton at different depths.

Both this process and the existing relationships with the processes of respiration and mortality of phytoplankton are still poorly recognized and difficult to investigate *in situ*.

The published data on these problems are scarce and concern selected water regions and phytoplankton species (Daro, 1980; Ciszewski *et al.*, 1983). A knowledge of this process is necessary for the mathematical modelling of a marine ecosystem, and in particular for modelling the effect of the dynamic parameters of water masses on the chlorophyll *a* distribution function in the upper sea layer.

Dzierzbicka and Zieliński (1988) attempted to model grazing and to determine its influence on the vertical chlorophyll *a* distribution function in a water region of uniform density.

The influence of grazing on the phytoplankton concentration distribution function is described by a two-dimensional function in a day-night cycle. Grazing was described on the basis of a two-dimensional mathematical-physical model of the time-space changes in chlorophyll *a* concentration in a density-stratified sea (Dzierzbicka-Głowacka, 1992).

2. Mathematical model

Assumptions:

- the basin's properties change in both the horizontal and the vertical,
- the horizontal K_x and vertical K_z turbulent diffusion of phytoplankton and nutrients is described by coefficients characterizing the water masses,
- the rate of primary production P_r depends mainly on the quantity of solar energy reaching the basin,
- the quantity of solar energy varies with depth; it depends on the optical properties of the water and is constant in a horizontal cross-section,
- the rate of plankton translocation u depends on the physical and dynamic properties of the water masses,
- the nutrient content of the water varies in both the horizontal and the vertical,
- the rate of regeneration R_v and assimilation of nutrients R_p by the phytoplankton depends on the initial concentrations of nutrients and phytoplankton and is constant in a horizontal cross-section,
- grazing of phytoplankton by zoopolankton g_w is described by a two-dimensional function in a day-night cycle.

The model described in this paper was created for a horizontally stratified sea, on the assumption that the water mass flux is horizontal, parallel to the x axis, and that its average velocity depends on depth only, *i.e.* $u = u(z)$. Hence, the field-of-flux velocity is stationary and homogeneous along the x axis. The influence of the vertical gradient of the horizontal velocity $\partial u/\partial z$ on phytoplankton and nutrient concentrations in the turbulent flux studied by the author is controlled by a turbulent mixing process, the intensity of which depends on the Richardson number.

When the density distribution is absolutely stable, upwelling and downwelling of water masses is impossible. The vertical component of the water flow velocity is thus approximately equal to zero and nutrients are not transferred along the z axis. The mean settlement velocity of a phytoplankton suspension in stagnant water can be approximately described by Stoke's equation (Dera, 1992).

Employing the constraints and assumptions described above, the mathematical model of two-dimensional turbulent diffusion of phytoplankton and nutrients in the top layer of the sea takes the following form:

$$\begin{aligned} \frac{\partial V}{\partial t} &= \frac{\partial}{\partial x}\left(K_x \frac{\partial V}{\partial x}\right) + \frac{\partial}{\partial z}\left(K_z \frac{\partial V}{\partial z}\right) - \vec{w}\frac{\partial V}{\partial z} + \pi_1 V \\ \frac{\partial P}{\partial t} &= \frac{\partial}{\partial x}\left(K_x \frac{\partial P}{\partial x}\right) + \frac{\partial}{\partial z}\left(K_z \frac{\partial P}{\partial z}\right) + \pi_2 V, \end{aligned} \tag{1}$$

where

$$\begin{aligned} \pi_1 &= P_r(x,z,t) - g_w(x,z,t) - m(x,z,t) - R(x,z,t), \\ \pi_2 &= R_p(x,z,t) - R_v(x,z,t), \\ K_x &= 0.0103 \times l^{1.15} \quad \text{(Okubo and Ozmidov, 1970)} \\ K_\rho &\cong K_T \cong 5 \times 10^{-4}(1 + Ri)^{-2.5} + 10^{-6} \quad \text{(Peters } et\ al.\text{, 1988)}, \\ K_z &= K_\rho \cong K_T \quad \text{(Druet and Zieliński, 1994)}, \end{aligned}$$

l – the average spatial scale, *i.e.* the step of the spatial numerical lattice, in this case equal to 100 m,

Ri – the Richardson number; in this case values of Ri lie within the range $1.5 \times 10^{-1} \leq Ri \leq 2 \times 10^{1}$ for which coefficient K_z was calculated,

$V = V(x,z,t)$ – chlorophyll *a* concentration at point (x, z) and in time t,

$P = P(x,z,t)$ – nutrient concentration at point (x, z) and in time t,

$\vec{u} = (\vec{u}, 0, \vec{w})$ – horizontal and vertical components of the mean phytoplankton transfer rate.

The following initial and boundary conditions supplement equation system (1):
for $t = 0$

$$\begin{aligned} V(x,z,0) &= V_0(x,z) = V_0(z) \\ P(x,z,0) &= P_0(x,z) = P_0(z), \end{aligned} \tag{2}$$

for $z = 0$ (free surface)

$$\begin{aligned} wV(x,0,t) &= K_x \frac{\partial V(x,0,t)}{\partial x} + K_z \frac{\partial V(x,0,t)}{\partial z} \\ \frac{\partial P(x,0,t)}{\partial z} &= 0, \end{aligned} \tag{3}$$

for a depth $z = 2z_e$ (double the depth of the euphotic zone)

$$\begin{aligned} wV(x,2z_e,t) &= K_x \frac{\partial V(x,2z_e,t)}{\partial x} + K_z \frac{\partial V(x,2z_e,t)}{\partial z} \\ P(x,2z_e,t) &= P_1(x,2z_e) = \text{const.} \end{aligned} \tag{4}$$

Equation system (1) with conditions (2), (3) and (4) can be solved numerically using the Crank-Nicholson method in a rectangular region R: $0 \le x \le X, 0 \le z \le Z$ by dividing this region with a two-dimensional net of variable spacing $1 \le i \le N, 1 \le j \le M$ (Potter, 1973). The differential equation system obtained at each time step is a system of non-uniform algebraic equations that can be solved using the successive overrelaxation method utilizing the Gauss-Seidel formulations.

The most important physical, biological and chemical processes influencing phytoplankton behaviour have been included in the model (*e.g.* Dzierzbicka-Głowacka, 1992; Druet and Zieliński, 1994).

3. Grazing of phytoplankton by zooplankton

Utilizing the results of studies on zooplankton grazing of phytoplankton (Daro, 1980; Ciszewski *et al.*, 1983), a modified model was conceived in this work, assuming that:

- grazing does not depend on the chemical state of seawater,
- there is a dominant zooplankton species, responsible for 89–90% of the phytoplankton mass consumed,

- potential changes in zooplankton concentration during the numerical experiment are negligible,
- the spatial distribution of zooplankton can be described by a $f(x,z,t)$ function,
- the grazing process is described in a day-night cycle.

Consequently, the grazing coefficient can be calculated as

$$\begin{aligned} \{grazing\} &= g_w(x,z,t)\,V(x,z,t) \\ g_w(x,z,t) &= \{1 + a_w cos(\omega(t-t_0))\}\,f(x,z,t), \end{aligned} \tag{5}$$

where

a_w – relative amplitude of zooplankton biomass changes,
t_0 – time in which the maximum zooplankton concentration occurs,
t – arbitrary time,
$\omega = \frac{2\pi}{T}$; $T = 24$ h,
$f(x,z,t)$ – a function characterizing the spatial distribution of zooplankton.

It was assumed that the function $f(x,z,t)$ (created by this author) describing the grazing process in space can be presented as the product of two exponential functions of variables x and z

$$f(x,z,t) = h(x,t)\,k(z,t), \tag{6}$$

$$h(x,t) = W_p(t)\,\alpha\ \exp((-W_r(x-x_i)^2), \tag{7}$$

$$k(z,t) = \exp(q(x,t)), \tag{8}$$

$$q(z,t) = a_0(t) + a_1(t)\,z + a_2(t)\,z^2 + ... \tag{9}$$

On adopting the assumption that grazing is horizontally uniform, the function describing grazing can be given as

$$\begin{aligned} h(x,t) = 1; &\qquad k(z,t) = q(z,t) \\ f(x,z,t) = f(z,t) &= a_0(t) + a_1(t)\,z + a_2(t)\,z^2 + ... \end{aligned} \tag{10}$$

where

α – coefficient of proportionality, responsible for the zooplankton count,
W_p – coefficient defining the percentage of the phytoplankton mass consumed,
W_r, x_i – coefficients characterizing zooplankton distribution in the horizontal plane.

The coefficients in the polynomial can be determined by adopting arbitrary or experimental values of the grazing coefficient at the following depths for $z = 0$ (free sufrace)

$$g_w(x, 0, t) = g_{w0}(t),$$

for $z = z_i$ (arbitrary depth)

$$g_w(x, z_i, t) = g_{wi}(t),$$

for $z = z_e$ (depth of the euphotic zone)

$$g_w(x, z_e, t) = g_{we}(t) = 1,$$

where

$g_{w0}(t)$ – grazing coefficient at the free surface corresponding to the conditions of zooplankton survival in the water of the basin examined,

$g_{wi}(t)$ – grazing coefficient at depth z_i in time t.

These assumptions apply to the approximation of the mass of phytoplankton grazed by zooplankton and do not elucidate the process itself, its dynamics or its relations with the dynamic and chemical properties of seawater. However, it is at present the only possible way of modelling this process. Lack of detailed data and poor recognition of the conditions of this process renders impossible a more precise mathematical description corresponding to the conditions *in situ.* These difficulties can be eliminated through the selection of suitable values of the coefficients in eq. (5), but the time period cannot exceed 48 h. A description of the method of estimating these coefficients based on experimental data acquired by various methods can be found in Radach *et al.* (1984).

4. Results of calculations

Investigations on the effect of grazing on the chlorophyll a concentration in a stratified sea were carried out using the model mentioned in section 2 and described in greater detail in Dzierzbicka-Głowacka (1992).

The following form of the function $f(x, z, t)$ describing the spatial distribution of zooplankton (eqs. (6) – (11)) was assumed in the analysis. The values of the coefficients of this function were chosen arbitrarily by assuming certain values of the grazing coefficient for $z = 0$ (free sea surface) and $z = 20$ (depth of the euphotic zone in the Gulf of Gdańsk), and by assuming $t = t_0$.

The values of the coefficients a_w and t_0 (eq. (5)) used in this paper were determined experimentally for the southern Baltic and are equal to $a_w = 0.6$ and $t_0 = -3.25$ h (Renk *et al.*, 1983).

Empirical data identical to those in Dzierzbicka-Głowacka (1992) were used to calculate the effects of light, mortality and respiration of phytoplankton, as well as regeneration and assimilation of nutrients by phytoplankton on the chlorophyll a distribution function.

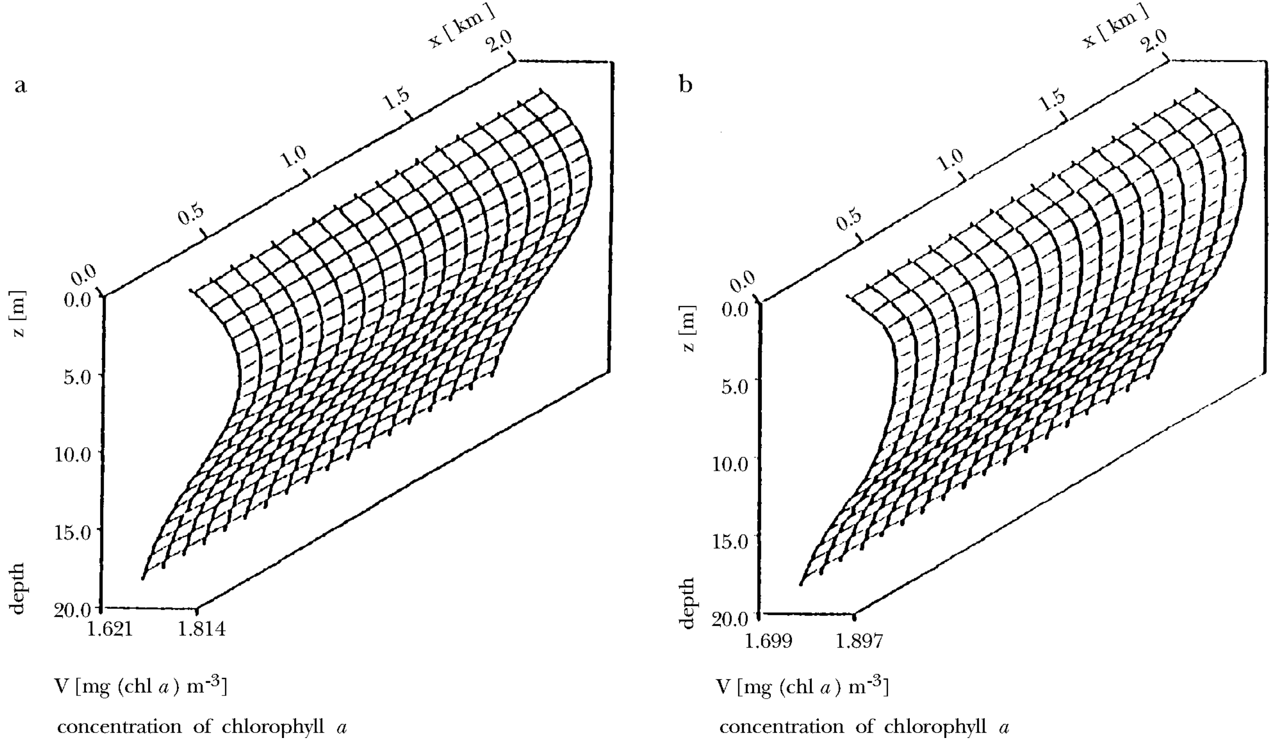
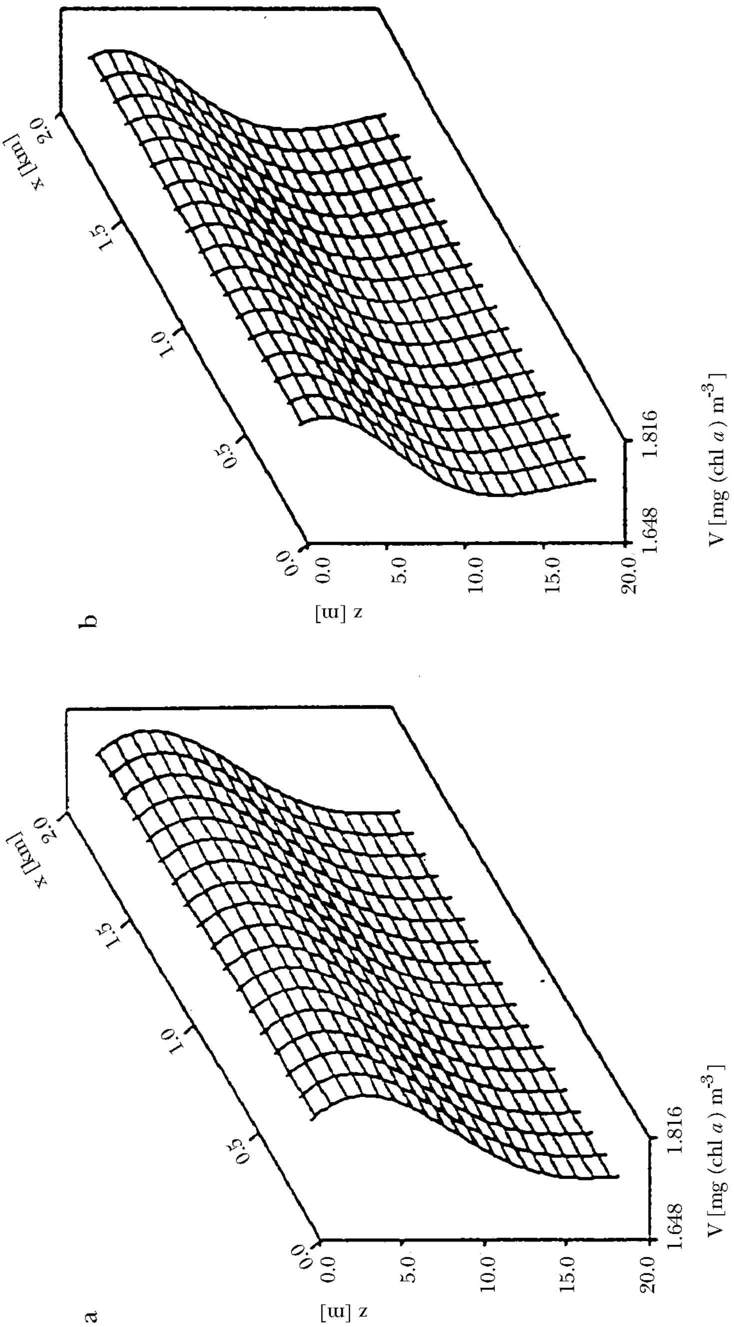


Fig. 1. Chlorophyll a distribution function in a uniform water mass ($K_z = 10^{-6}\,\mathrm{m}^2\,\mathrm{s}^{-1}$, $w_z = 5 \times 10^{-7}\,\mathrm{m\,s}^{-1}$), with grazing determined by a constant value of $g_w = 0$ (a), $g_w = 0.3$ (b)


b
x [km]
0.0
0.5
1.0
1.5
2.0
z [m]
0.0
5.0
10.0
15.0
20.0
V [mg (chl a) m-3]
1.648
1.816
a
x [km]
0.0
0.5
1.0
1.5
2.0
z [m]
0.0
5.0
10.0
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20.0
V [mg (chl a) m-3]
1.648
1.816

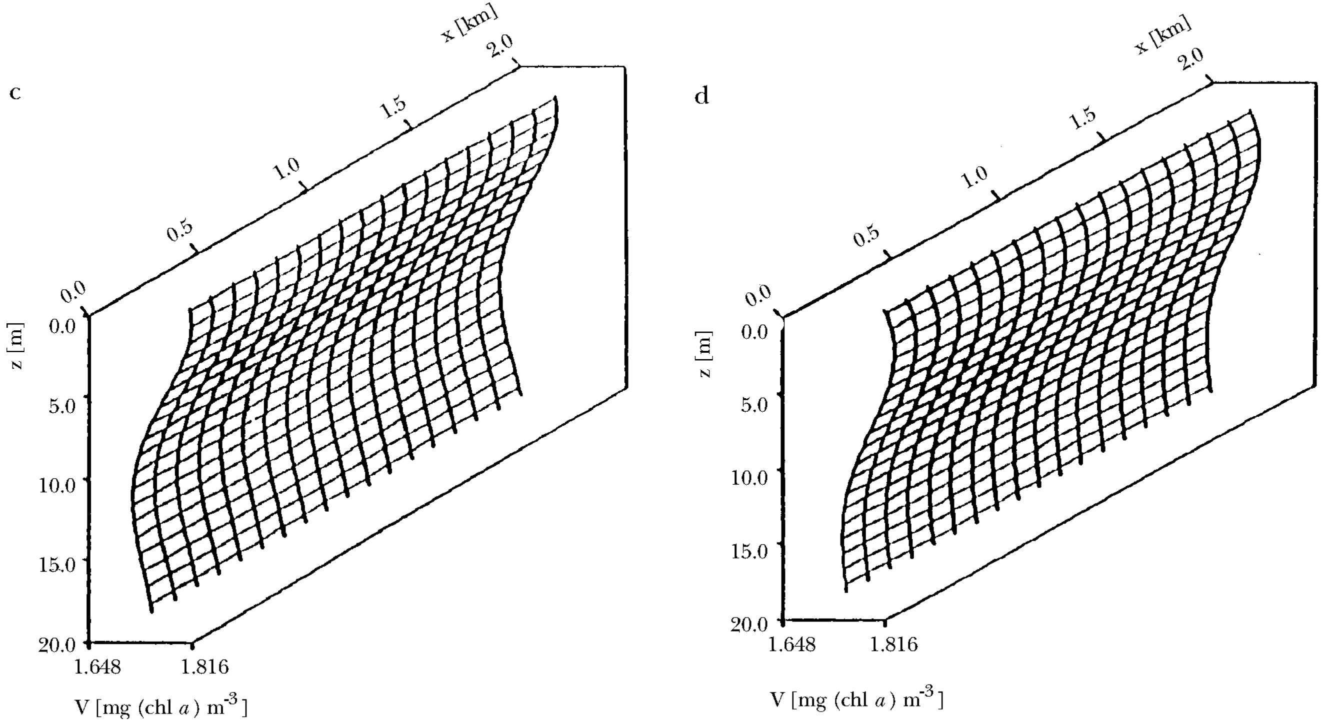


Fig. 2. Calculated time-dependence of chlorophyll a concentration for $t = 1600$ h (a), $t = 2200$ h (b), $t = 0200$ h (c), $t = 0800$ h (d), assuming that the local grazing coefficient is a variable of time and space described by a 2nd degree function $f(x, z, t) = a_0(t) + a_1(t)\, z + a_2(t)\, z^2$

The initial vertical distribution of chlorophyll *a* concentration was determined experimentally during the PEX–86 experiment and was assumed to be constant in all the cases analysed.

The calculations were carried out for two values of the turbulent diffusion coefficient, *i.e.* $K_z = 10^{-6}\,\mathrm{m^2\,s^{-1}}$ (uniform water mass) and $K_z = 5 \times 10^{-4}(1 + Ri)^{-2.5} + 10^{-6}$ (non-uniform water mass), and assuming that phytoplankton settle at a mean rate of $w = 5.1 \times 10^{-7}\,\mathrm{m\,s^{-1}}$ – the value calculated according to Stoke's formula (Dera, 1992).

The results of numerical investigations into the effect of the assumed dynamic conditions and grazing, characterizing the investigated water region, on the function of chlorophyll *a* distribution in this region are presented in graphical form in Figs. 1–5.

The reference point for this analysis is the case for which $g_w = 0$ (Fig. 1a, $t = 0800$ h). This is an imaginary case; nevertheless, it allows the absolute grazed mass produced in the marine environment to be estimated.

Case 1

For the calculations, the following assumption was made: $f(x,z,t) = k(z,t) = q(z,t)$, when $h(x,t) = 1$, *i.e.* the process is horizontally homogeneous.

$$g_{w0} = 0.3 - 0.5 \quad \text{for} \quad z = 0\,\mathrm{m},$$
$$g_{we} = 0.9 - 1.0 \quad \text{for} \quad z = 20\,\mathrm{m}.$$

The values of coefficient g_{we} relate to periods of phytoplankton blooms when these are grazed by one or two dominant types of zooplankton. The average grazing coefficient from the 0.3–0.9 range refer to the most common conditions occurring in nature, *i.e.* between two blooms. The minimum value of $g_w = 0.3$ refers to the conditions which allow zooplankton to survive in the marine environment (Fig. 1b, $t = 1500$ h). Fig. 2 gives some idea of the influence of simulated grazing on the chlorophyll *a* distribution function in the day-night cycle.

$$g_{w0} = 0.3, \quad g_{we} = 0.9 \quad \text{for} \quad t = 1600\,\mathrm{h} \qquad \text{(Fig. 2a)},$$
$$g_{w0} = 0.5, \quad g_{we} = 1.0 \quad \text{for} \quad t = 2200\,\mathrm{h} \qquad \text{(Fig. 2b)},$$
$$g_{w0} = 0.5, \quad g_{we} = 0.9 \quad \text{for} \quad t = 0200\,\mathrm{h} \qquad \text{(Fig. 2c)},$$
$$g_{w0} = 0.3, \quad g_{we} = 0.9 \quad \text{for} \quad t = 0800\,\mathrm{h} \qquad \text{(Fig. 2d)}.$$

The local grazing coefficient changes in time and space and is described by a second degree function:

$$f(z) = q(z, 16.00) = -0.00107z^2 + 0.07z + 0.3 \qquad \text{(Fig. 2a)},$$
$$f(z) = q(z, 22.00) = -0.005z^2 + 0.1z + 0.5 \qquad \text{(Fig. 2b)},$$
$$f(z) = q(z, 2.00) = -0.00125z^2 + 0.05z + 0.5 \qquad \text{(Fig. 2c)},$$

$$f(z) = q(z, 8.00) = -0.00107z^2 + 0.07z + 0.3 \qquad \text{(Fig. 2d)}.$$

In consecutive hours the shape and values of the chlorophyll *a* distribution are different, and the maximum changes occur within the 1–5 m depth range.

Case 2

In the calculations, the grazing coefficient was taken to be the product of two exponential functions, $f(x, z, t) = h(x, t) \times k(z, t)$, described by formulas 6 – 9. Fig. 3 shows the results of the calculated phytoplankton grazing by the zooplankton in the day-night cycle. For the water masses described in section 2, zooplankton rises to the upper water layers (euphotic layer) in the evening, in accordance with the grazing theory. That is why almost all the phytoplankton is consumed by the zooplankton at night. Fig. 3a shows the chlorophyll *a* distribution at 1800 h at which 10–20% of the phytoplankton mass was grazed at depths from 15 m to 20 m. The horizontal dimension was 800 m to 1200 m.

$$h(x, t) = 0.015 \times 10^2 \times \exp\left(-0.002(x - 1000)^2\right),$$

$$k(z, t) = \exp\left(-0.5(20 - z)\right).$$

Fig. 3b shows the situation at 2100 h when zooplankton moved upwards and grazed 20–40% of the phytoplankton mass at depths from 5 m to 10 m in the same area as in Fig. 3a.

$$h(x, t) = 0.05 \times 10^2 \times \exp\left(-0.002(x - 1200)^2\right),$$

$$k(z, t) = \exp\left(-0.00175z^2 + 0.07z + 0.03\right).$$

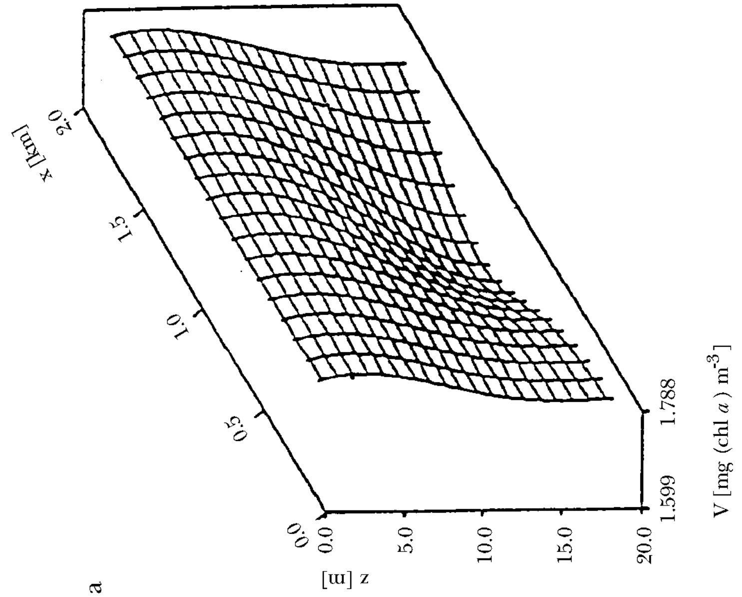
Fig. 3c shows the situation at midnight, when zooplankton grazed about 70% of the phytoplankton mass in the surface layers.

$$h(x, t) = 0.07 \times 10^2 \times \exp\left(-0.002(x - 1400)^2\right),$$

$$k(x, t) = \exp(-0.005z^2 + 0.1z + 0.5).$$

The distribution shown in Fig. 3d shows the increase in chlorophyll *a* concentration at 0300 h. This increase is due to the downward movement of zooplankton, which causes the decrease in the g_w coefficient. In this case, the shapes and values of the chlorophyll *a* distribution vary significantly in both the vertical and horizontal when compared with case 1, in which the differences are only vertical. The differences in chlorophyll *a* concentrations in case 2 in consecutive hours vary from 10% to 40% and they differ significantly in the day-night cycle.

The following assumption was made to show the influence of phytoplankton grazing by zooplankton moving horizontally and upwards on the a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1.5
2.0
z [m]
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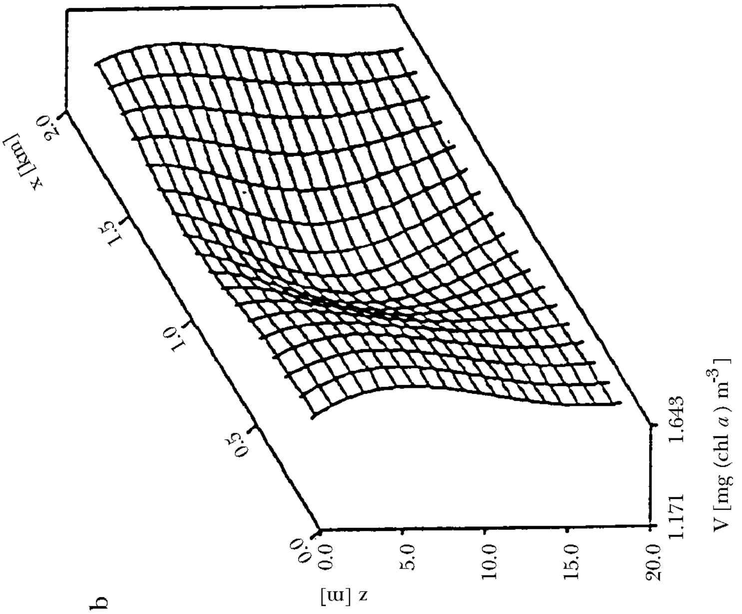
15.0
20.0
1.599
1.788
V [mg (chl a) m^{-3}]

b


x [km]
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1.0
1.5
2.0
z [m]
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5.0
10.0
15.0
20.0
1.171
1.643
V [mg (chl a) m^{-3}]

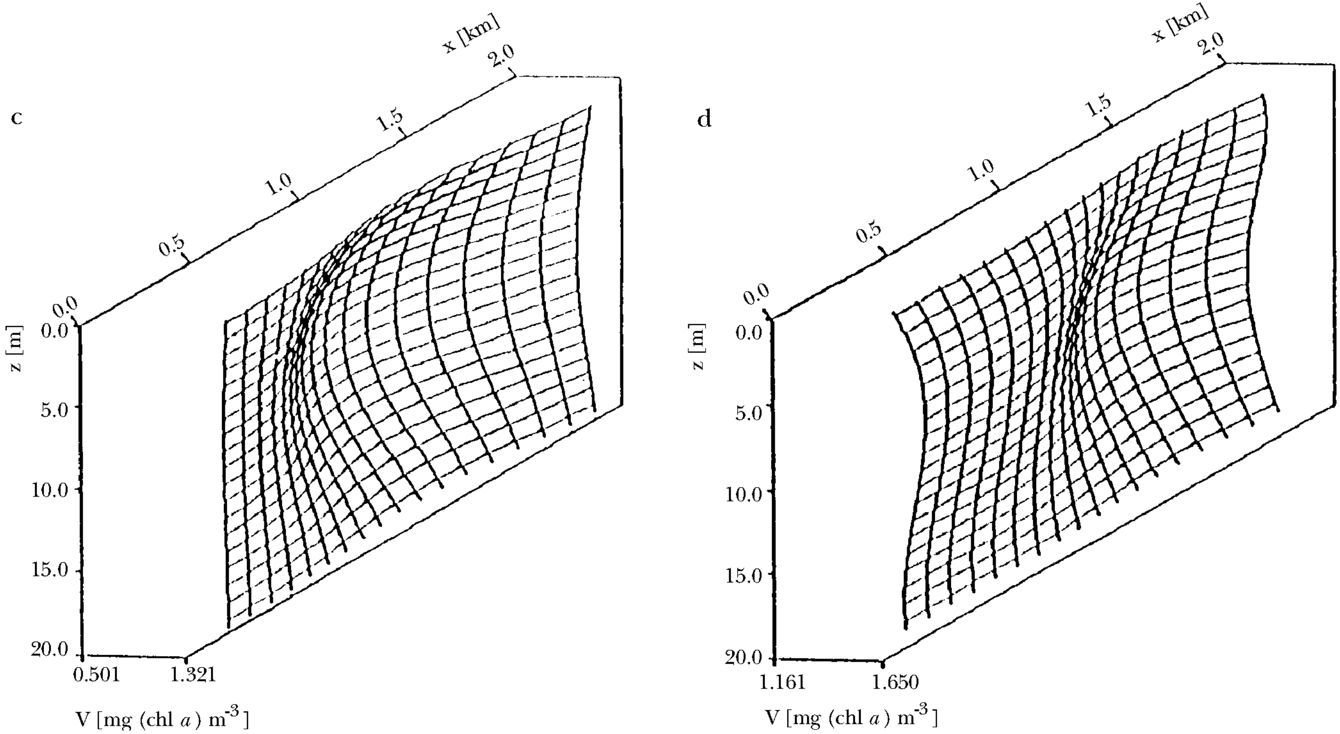
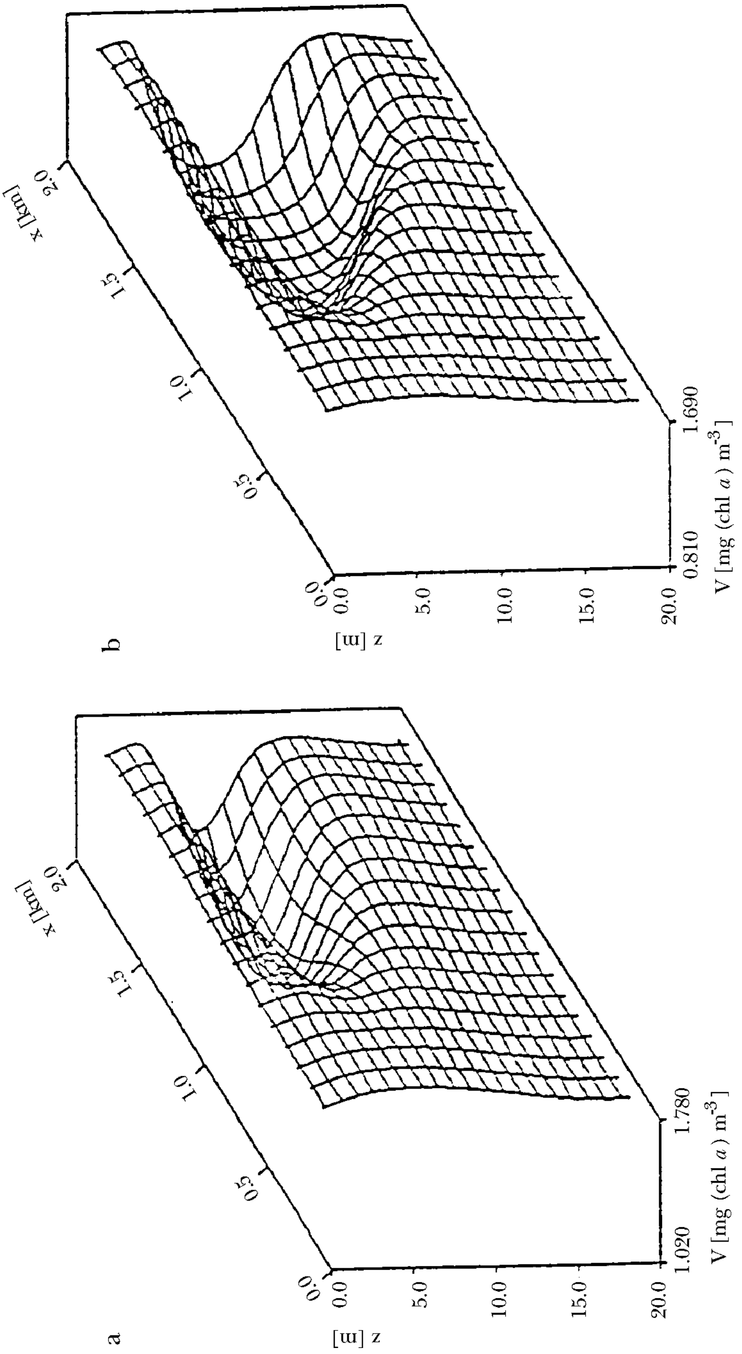


Fig. 3. Spatial distribution of chlorophyll a concentration for $t = 1800$ h (a), $t = 2100$ h (b), $t = 2400$ h (c), $t = 0300$ h (d) assuming that the local grazing coefficient is a time–space variable and can be represented by the product of two functions $f(x,z,t) = h(x,t)\,k(z,t)$


b
x [km]
2.0
1.5
1.0
0.5
0.0
z [m]
0.0
5.0
10.0
15.0
20.0
0.810
1.690
V [mg (chl a) m-3]
a
x [km]
2.0
1.5
1.0
0.5
0.0
z [m]
0.0
5.0
10.0
15.0
20.0
1.020
1.780
V [mg (chl a) m-3]

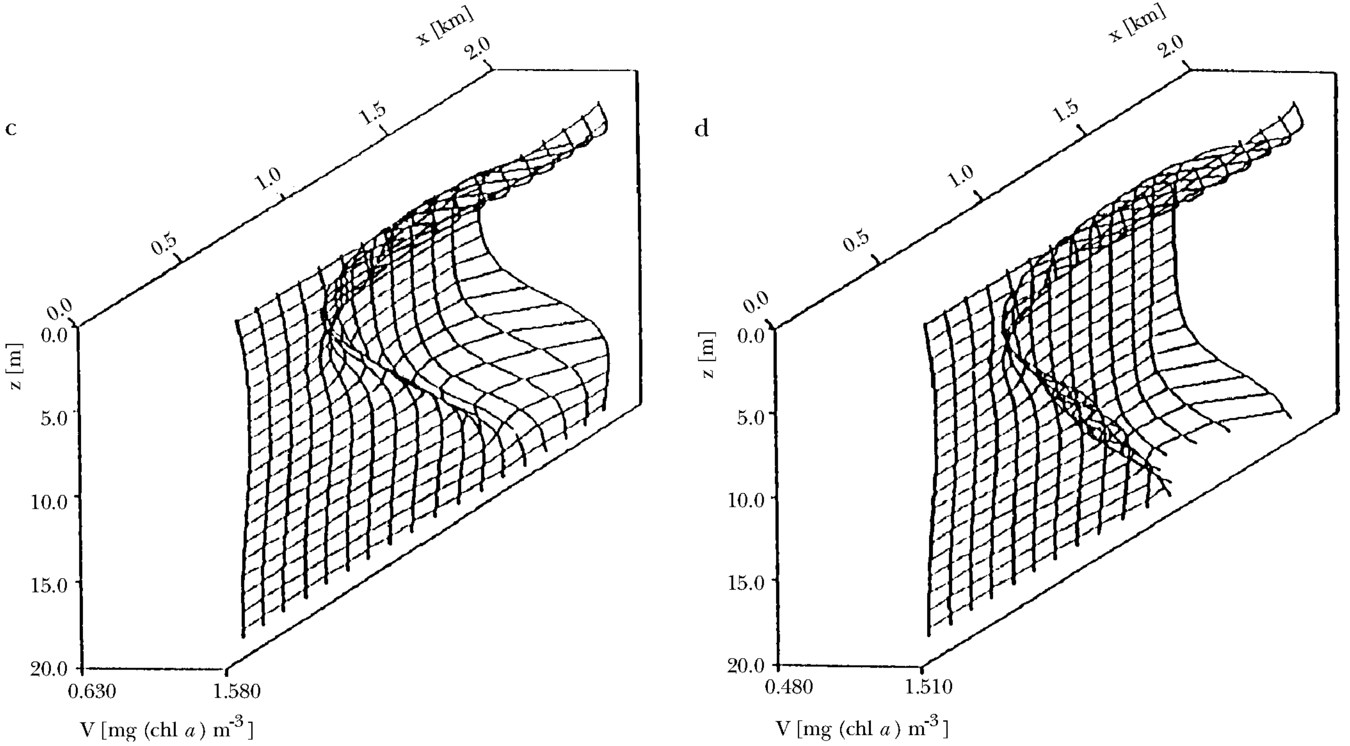
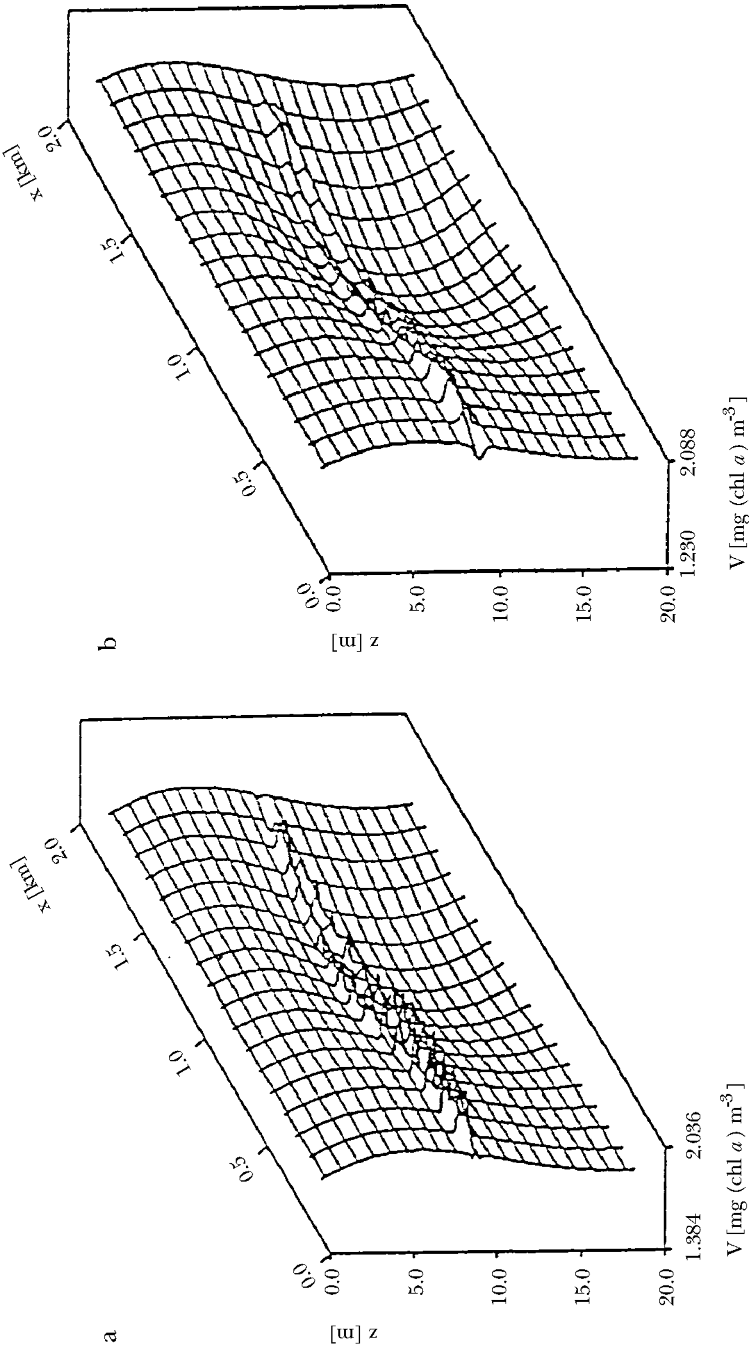


Fig. 4. Spatial distribution of chlorophyll a concentration for $t = 2100$ h (a), $t = 2300$ h (b), $t = 0100$ h (c), $t = 0300$ h (d), assuming that zooplankton moves in a horizontal direction x at a depth increasing with time


b
x [km]
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1.5
1.0
0.5
0.0
z [m]
0.0
5.0
10.0
15.0
20.0
1.230
2.088
V [mg (chl a) m-3]
a
x [km]
2.0
1.5
1.0
0.5
0.0
z [m]
0.0
5.0
10.0
15.0
20.0
1.384
2.036
V [mg (chl a) m-3]

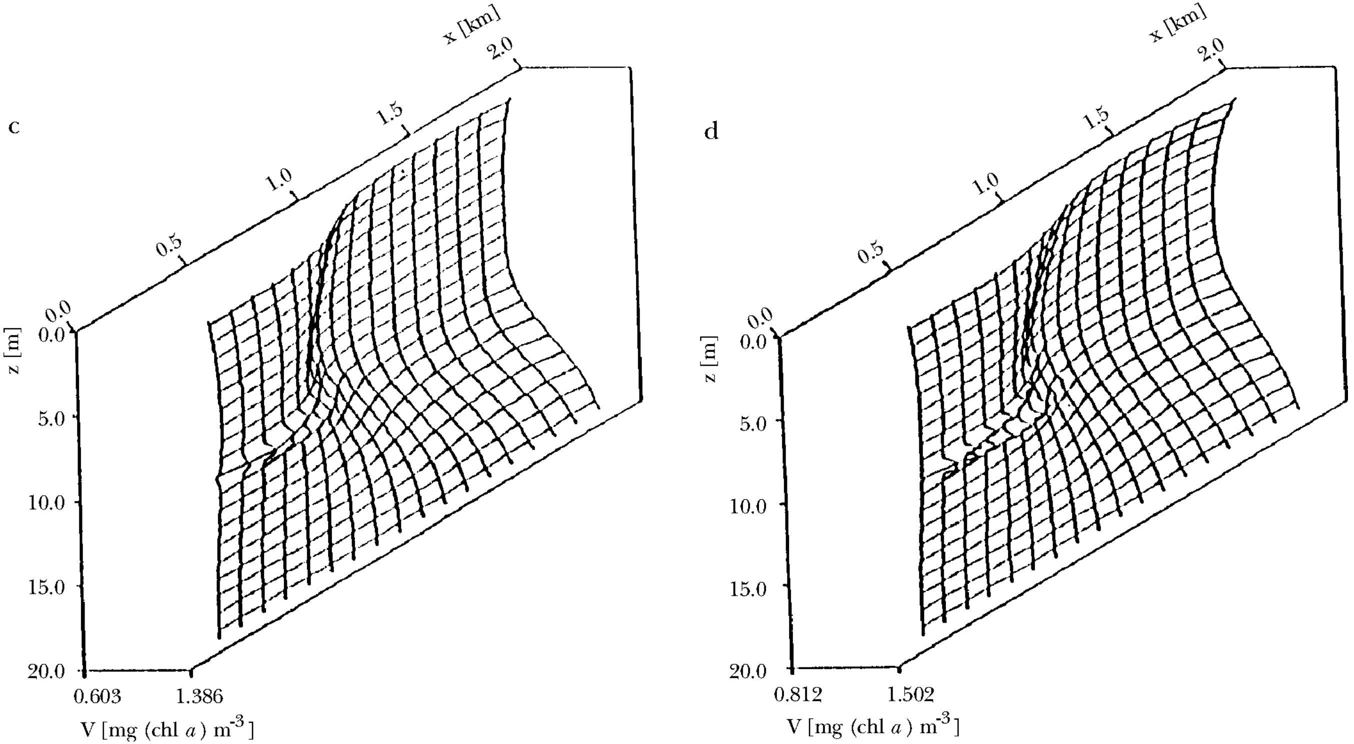

Fig. 5. Influence of the time of hydrodynamic instability appearance on chlorophyll *a* distribution for $t = 1900$ (a), $t = 2100$ h (b), $t = 2300$ h (c), $t = 0100$ h (d)

chlorophyll concentration described by the concentration distribution function

$$f(x,z,t) = 10^{-2} \times x \times \exp\Big(-0.005(x-800)^2\Big)(-0.005z^2 + 0.1z + 0.5)$$

$$\text{for} \qquad 900 \le x \le 2000\,\mathrm{m}.$$

Fig. 4 shows the chlorophyll a concentration distribution function at night: Fig. 4a t = 2100 h, Fig. 4b t = 2300 h, Fig. 4c t = 0100 h, Fig. 4d t = 0300 h. For both cases 1 and 2 it is obvious that in areas of intensive phytoplankton grazing there occur non-homogeneities in the chlorophyll a concentration distribution function due to the decrease in chlorophyll a concentration.

Fig. 3a shows the distribution function of chlorophyll a concentration and how it was modified by grazing at 1800 h. under the following conditions $f(x,z,t) = h(x,t)k(z,t)$.

$$h(x,t) = 0.025 \times 10^2 \times \exp\left(-0.002(x-1000)^2\right),$$

$$k(x,t) = \exp(-0.5(20-z)).$$

On the assumption that in the water masses described earlier (section 3) grazing occurs as in case 2 (see Fig. 3), the mixing layer theory predicts a hydrodynamic instability at a depth of 10 m for a period of 8 minutes. This instability occurs at 1900 h (Fig. 5a), at 2100 h (Fig. 5b), at 2300 h (Fig. 5c) and at 0100 h (Fig. 5d). The distributions shown in Fig. 5 show these differences caused by the hydrodynamic instabilities. With the increase in grazing the influence of unstable layers on the chlorophyll a concentration is relatively smaller owing to the greater zooplankton concentration in the surface layers during the late night hours.

5. Conclusions

Computer simulations show that the process of phytoplankton grazing by zooplankton should be considered in a day-night cycle, assuming that there is a dominant zooplankton species in the basin studied. An analysis of this process shows that the grazing intensity changes depending on the assumed form of the spatial zooplankton distribution function $f(x,z,t)$. The calculations have shown that, for all shapes of the function, its coefficients should provide values of chlorophyll concentrations ensuring survival of the zooplankton throughout the day-night cycle. They have also shown that to a large extent grazing masks the dynamic processes associated with the emergence of hydrodynamic instabilities.

References

Ciszewski P., Ochocki S., Pydel H., Renk H., 1983, *Diel changes in zooplankton distribution at the Gdańsk Deep*, Pol. Ecol. Stud., 9, 361–372.

Daro M. H., 1980, *Field study of the diel feeding of a population of Calanus finmarchiens at the end of a phytoplankton bloom*, Meteor. Forschungsergeb. A, 22, 123–137.

Dera J., 1992, *Marine physics*, Elsevier, Amsterdam–Oxford–New York–Tokyo, 515 pp.

Druet C., Zieliński A., 1994, *Modelling the fine structure of the phytoplankton concentration in a stably stratified sea*, Oceanol. Acta, 17 (1), 79–88.

Dzierzbicka L., Zieliński A., 1988, *Numerical analysis of the influence of the grazing effect on phytoplankton distribution function in a stratified sea*, Proc. XVI Conf. Baltic Oceanographers, Institute of Marine Research, Kiel, 1, 353–266.

Dzierzbicka-Głowacka L. 1992, *A two–dimensional mathematical model describing the phytoplankton distribution function in a stratified sea*, Ecol. Pol., 40, 479–496.

Okubo A., Ozmidov R. W. 1970, *Empiricheskaya zavisimost koefficienta gorizontalnoy turbulentnoy difuzy v okeane ot masshtaba yavleniya*, Izv. Akad. Nauk SSSR, Fiz. Atm. Okeana, 6, 534–536.

Peters H., Gregg M. C., Toole M. I., 1988, *On the parametrization of equatotial turbulence*, J. Geophys. Res., 93, 216–225.

Potter D., 1973, *Computation physics*, J. Wiley, London–New York–Sydney–Toronto, 278 pp.

Radach G., Berg I., Heinemann B., Krause M., 1984, *On the relation of primary production to grazing during the Fladen Ground Experiment 1976*, [in:] *Flow of energy and materials in marine ecosystems*, M. J. R. Fasham (ed.), Plenum Press, London–New York–Tokyo, 597–625.

Renk H., Ochocki S., Pytel H., 1983, *Short–term fluctuations of primary production and chlorophyll a concentration in the Gdańsk Deep*, Pol. Ecol. Stud., 9, 341–359.