Numerical studies of the influence of the nutrient regeneration mechanism on the chlorophyll *a* concentration in a stratified sea

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Abstract

This paper presents numerical simulations of variability in such biological processes as nutrient uptake by phytoplankton, nutrient release, nutrient remineralisation within the water column and nutrients excreted by zooplankton, and the effect of these processes on the distribution functions of chlorophyll *a* and nutrient concentration in a stratified sea. The influence of these processes on the distribution functions was recorded in the changes in biological and chemical parameters, such as the factor limiting production increase, the maximum rate of production increase, the function characterising the vertical distribution of zooplankton and the coefficients n_z, n_f and n_e of the material being grazed. The numerical studies were carried out using a two–dimensional biological upper layer model (phytoplankton–phosphate) with a well-developed regeneration mechanism. This paper presents the vertical distributions of these biological characteristics in order to facilitate a better understanding of temporal changes, albeit under the assumption that the above processes are horizontally uniform. The calculations were made in an area of $0 \leq z \leq 20$ m with a vertical space step of 10 cm and a time step of 15 min. The complex experimental data, gathered during the international experiment PEX ′86, and subsequently by the International Council for the Exploration of the Sea, were used as the input data for the calculations.

1. Introduction

The objective of this work was to simulate the biological and chemical processes directly influencing the nutrient distribution function. They include the uptake of nutrients by phytoplankton, their release and remineralisation within the water column, and their excretion by zooplankton as dissolved metabolites.

The numerical studies were carried out using a simple but highly realistic biological model within a physical environment. This is the phytoplankton – phosphate biological upper layer model, which consists of two diffusion advection reaction equations for the phytoplankton biomass V and a single nutrient P in the water column, with source functions describing production and loss; it is described in greater detail in Dzierzbicka-Głowacka (1994a, 1996). The nutrient serves as both trigger and limiting agent for primary production. All organic material lost from the water column is immediately transported to the bottom, where it enters the detritus pool.

The aim was to make the model as simple as possible, so the phytoplankton was modelled using one state variable only. Phytoplankton naturally consists of many different species, each with different dynamic characteristics and contributing different proportions of biomass during the year. Our assumption in using the phytoplankton biomass is that the species composition is limited by the availability of species (two or three), hence the dynamic constants used are representative of the entire phytoplankton community; this has been done in many models of phytoplankton production (*e.g.* Riley *et al.*, 1949; Radach and Maier-Reimer, 1975; Radach, 1983; Taylor *et al.*, 1986; Tett *et al.*, 1986; Wolf and Woods, 1988). Recent models (Aksnes and Lie, 1990; Cochrane *et al.*, 1991) split phytoplankton into two or more groups.

The phytoplankton concentration is taken to be a dynamically passive physical quantity (*i.e.* it is incapable of making autonomous movements), and will henceforth be represented by the chlorophyll *a* concentration.

Bearing in mind the fact that the intention was to make the model as simple as possible, and also to avoid the necessity of including several nutrient components (as would have been necessary if nitrogen had been taken as nutrient), the model was based on phosphate. The chemistry of phosphorus, moreover, is considerably simpler than that of nitrogen (Raymont, 1980).

The biological model (Fig. 1) incorporates formulations of the primary production mechanism and of the mixed-layer regeneration mechanism in the lower layers. Primary producers sink, die and are utilised by zooplankton. Grazed phytoplankton are subdivided into three portions, the first contributing to zooplankton growth, the second being lost as faecal pellets and the third being excreted by zooplankton as dissolved metabolites, thereby replenishing the nutrient pool. A proportion of the material contributing

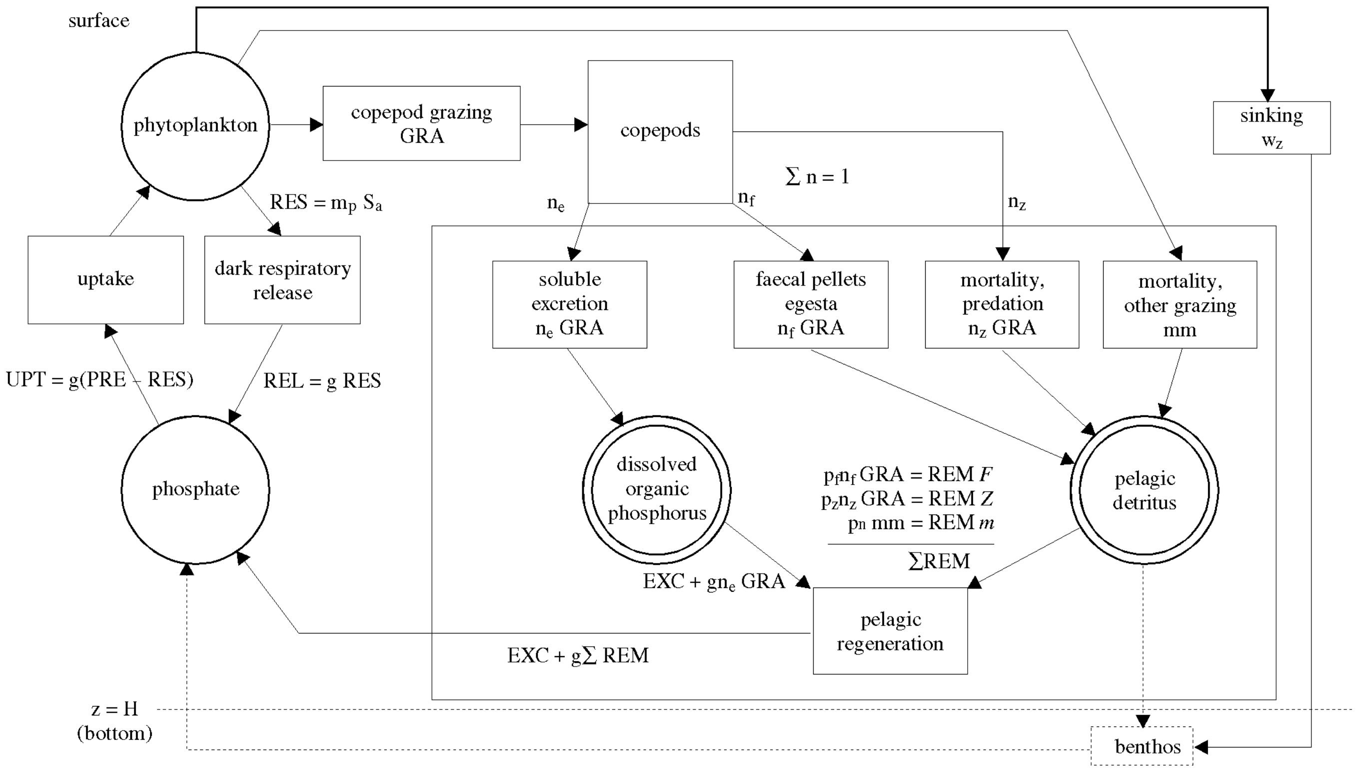

Fig. 1. Simplified phosphorus cycle of the biological upper layer model

to growth, represented by dead zooplankton, is assumed to be lost immediately. Certain proportions of both the faecal and the excreted material are immediately regenerated.

The time scale assumed for the sinking of faecal and dead material is of the order of a few days and is much shorter than that assumed for most regeneration processes, calculated in terms of weeks to months. Most of the detritus is thus deposited on the bottom where it collects as a detrital pool.

Only a small portion of detritus remains suspended in the water column. The effect of the microbial food web (Azam *et al.*, 1983) is parametrised by converting this portion of detrital material immediately into regenerated nutrients within the water column.

Thus, there are two pathways for the regeneration of pelagic and benthic nutrients, each with different time scales. The present model deals with only one pathway, the pelagic one. The availability of regenerated nutrients for production in the upper layers will be controlled by physical processes and the distance between the locations of regeneration.

2. The biological upper layer model

The present phytoplankton – phosphate model, as described in recent papers, takes the regeneration mechanism in the water column into consideration (Fig. 1), and consists of two, non-linearly coupled, second-order partial differential equations together with initial and boundary conditions. The details of the model can be found in the papers by Dzierzbicka-Głowacka (1994a, 1996).

The change in the local phytoplankton biomass concentration $V(x,z,t)$ is caused by turbulent diffusion $\mathrm{DIF}\,V$, sinking of algae SINK, production PRE, respiration RES, mortality $\mathrm{MOR}\,V$ and grazing by zooplankton GRA:

$$\frac{\partial V}{\partial t} = \mathrm{DIF}\,V - \mathrm{SINK} + \mathrm{PRE} - \mathrm{RES} - \mathrm{MOR}\,V - \mathrm{GRA}. \tag{1}$$

The time of local nutrient concentration $P(x,z,t)$ is determined by turbulent diffusion $\mathrm{DIF}\,P$, algal uptake UPT, remineralised dead phytoplankton, zooplankton faecal pellets and dead zooplankton REMI, zooplankton excretion EXC and nutrient release REL:

$$\frac{\partial P}{\partial t} = \mathrm{DIF}\,P - a\,(\mathrm{UPT} - \mathrm{REL} - \mathrm{REMI} - \mathrm{EXC}). \tag{2}$$

In eq. (2) for phosphate, all terms describing biological and chemical processes must be multiplied by the constant a (an empirical coefficient), which denotes the fixed ratio of phytoplankton carbon to chlorophyll a.

This paper will be restricted to a description of the regeneration mechanism in the water column.

Excretion of dissolved and particulate material is parametrised *via* the amount of grazed material: soluble zooplankton excreta are parametrised as

$$\mathrm{EXC} = g n_e \,\mathrm{GRA}, \tag{3}$$

with percentage n_e. Faecal pellet production is described by

$$\mathrm{FEC} = n_f \,\mathrm{GRA}, \tag{4}$$

and the zooplankton carcasses are described by

$$\mathrm{MOR}\, Z = n_z \,\mathrm{GRA}, \tag{5}$$

with percentages n_e, n_f and n_z of the material being grazed. For the sake of mass conservation it is assumed that $n_e + n_f + n_z = 1$. The constant g is the P:C ratio.

Remineralisation REMI within the water column by the 'microbial food web' is assumed for the proportions of dead phytoplankton $\mathrm{REM}\, m$, zooplankton $\mathrm{REM}\, Z$ and faecal pellets $\mathrm{REM}\, F$:

$$\mathrm{REM}\, m = p_m \,\mathrm{MOR}\, V, \tag{6}$$

$$\mathrm{REM}\, Z = p_z \,\mathrm{MOR}\, Z, \tag{7}$$

$$\mathrm{REM}\, F = p_f \,\mathrm{FEC}, \tag{8}$$

$$\begin{aligned} \mathrm{REMI} &= g\,(\mathrm{REM}\, m + \mathrm{REM}\, Z + \mathrm{REM}\, F) \\ &= g\,\{p_m \,\mathrm{MOR}\, V + (p_f n_f + p_z n_z)\mathrm{GRA}\}, \end{aligned} \tag{9}$$

with percentages p_m, p_z and p_f expressing those parts of dead phytoplankton, zooplankton and faecal material immediately remineralised in the water column as the parametrisation of the microbial food web.

It is assumed that phytoplankton grazing by zooplankton GRA is independent of the chemical state of the water. One dominant species among the zooplankton is responsible for consuming (80–90%) of the phytoplankton; possible changes in the numbers of this dominant species can be neglected within a given time interval, and the process is considered on a diurnal cycle. The rate of loss of phytoplankton mass is given in Daro (1980) and in Ciszewski *et al.*, (1983):

$$\mathrm{GRA} = g_w\,(x,z,t)\,V(x,z,t), \tag{10}$$

$$g_w = \{1 + a_w \cos\omega(t - t_0)\}\, f(x,z,t), \tag{11}$$

where a_w denotes the relative amplitude of zooplankton biomass changes, t_0 the time when the zooplankton concentration reaches a maximum, and $\omega = \Pi/12$. The function $f(x,z,t)$ in this equation defines an additional dimensional model of zooplankton distribution in the sea (Dzierzbicka-Głowacka 1994b, 1996).

Phytoplankton mortality MOR V is assumed to be proportional to the phytoplankton standing stock with a mortality rate of mm (Raymont, 1980; Sjöberg, 1980)

$$\mathrm{MOR}\,V = mm\,V(x,z,t). \tag{12}$$

Respiration in the dark consumes particulate organic matter. To conserve matter, the respiration term in the equation for phytoplankton must be balanced by a nutrient release term REL in the equation for phosphate. This term parametrises the contribution of respiration to the nutrient pool, given a fixed P:C ratio, $g\,(\mathrm{mmolP}\,(\mathrm{gC})^{-1})$:

$$\mathrm{REL} = g\,\mathrm{RES}. \tag{13}$$

Respiration RES consists of basic and photo-respiration, each being proportional to V (Ryther, 1956; Parsons *et al.*, 1977)

$$\mathrm{RES} = S_a(m_p^1 + m_p^2 \min\{d_I, d_P\})\,V(x,z,t), \tag{14}$$

where the basic dark respiration rate m_p^1 is a factor proportional to the maximum photosynthetic rate (Ryther, 1956), and the photo-respiration rate m_p^2 is a factor proportional to the rate of primary production. The rate of primary production PRE is formulated as in Radach (1983) or Tett *et al.* (1986) by following Liebig's law: the minimum limitation function for growth rate modification is taken to be

$$\mathrm{PRE} = S_a \min\{d_I, d_P\}\,V(x,z,t). \tag{15}$$

Here S_a is the maximum growth rate, d_I and d_P are the respective limiting functions for the photosynthetically available radiation and the nutrient:

$$d_I = \frac{S(x,z,t)}{S_a}, \quad d_p = \frac{P(x,z,t)}{P(x,z,t)+k_s}, \tag{16}$$

where k_s is the nutrient half-saturation constant,

$$S_a = \max S(x,z,t). \tag{17}$$

For a given concentration of a nutrient limiting photosynthesis, the coefficient S, defining the total primary production depends on the assimilation number A, determined from the Platt model (Platt *et al.*, 1980; Harrison *et al.*, 1985):

$$S(x,z,t) = aA(x,z,t)\sin\gamma, \tag{18}$$

where a is an empirical coefficient characterising the basin in question, expressing the mg of organic carbon in terms of mg of chlorophyll, and γ is the solar elevation at a given instant of time (GMT).

Nutrient uptake UPT appears in the equation for phosphate as

$$\mathrm{UPT} = g\,(\mathrm{PRE} - \mathrm{RES}), \tag{19}$$

for positive net production only.

3. Data for the simulation studies

The mathematical two-dimensional model of turbulent phytoplankton diffusion in a stratified sea, described in greater detail in Dzierzbicka-Głowacka (1994a, 1996), together with the regeneration mechanism mentioned in section 2 was used to simulate the influence of this process (through changes in the selected biological and chemical parameters) on the chlorophyll *a* and nutrient distributions in the water.

This paper presents the vertical distributions of the biological characteristics in order to facilitate a better understanding of temporal changes, albeit under the assumption that the above processes are horizontally uniform. The calculations were made in an area of $0 \le z \le 20$ m with a vertical space step of 10 cm and a time step of 15 min.

Comprehensive experimental data, collected during the PEX ′86 international scientific experiment of the Baltic states, and prepared and coordinated by the International Council for the Exploration of the Sea, were used as the input data. A detailed description of the experiment as well as the list of parameters measured, the geographical coordinates of the PEX ′86 polygon and the distribution of stations are given in the final report prepared by Dybern and Hansen (1989). The chlorophyll *a* and phosphate concentrations, measured at a standard depth at station AN1 at 04:00 h on 26 April 1986, were taken to be the initial concentrations. They are as follows:

$$\begin{array}{llll} z = \ \ 1 \text{ m} & V(\ 1, t_0) = 1.4 \ \ [\text{mgchl m}^{-3}] & P(\ 1, t_0) = 0.26 & [\text{mmolP m}^{-3}] \\ z = \ \ 5 \text{ m} & V(\ 5, t_0) = 1.45 \ [\text{mgchl m}^{-3}] & P(\ 5, t_0) = 0.22 & [\text{mmolP m}^{-3}] \\ z = 10 \text{ m} & V(10, t_0) = 1.41 \ [\text{mgchl m}^{-3}] & P(10, t_0) = 0.235 & [\text{mmolP m}^{-3}] \\ z = 20 \text{ m} & V(20, t_0) = 1.4 \ \ [\text{mgchl m}^{-3}] & P(20, t_0) = 0.36 & [\text{mmolP m}^{-3}]. \end{array}$$

The coefficients defining the assimilation number at an arbitrary depth were determined from measurements of the irradiation field at different depths in the 400–700 nm range. The values of these coefficients determined for the region studied (AN1) and on 26 April 1986 were presented in Dzierzbicka-Głowacka (1994a, 1996). The half-saturation value for phosphorus, described by the relationship (16), was adopted after Lehman *et al.* (1975) and Raymont (1980). Two values of this coefficient were used in the subsequent numerical analysis: $k_s = 0.12$ and $k_s = 0.32$ mmolP m^{-3}.

The coefficients defining regeneration and expressing those proportions of dead phytoplankton p_m, zooplankton p_z and faecal material p_f immediately remineralised in the water column are equal: $p_m = p_z = p_f = 0.2$ (Postma and Rommets, 1984). However, the coefficients describing the proportions of the material being grazed and regenerated as soluble excreta from zooplankton n_e, as faecal material n_f, and as dead zooplankton n_z are equal to $n_e = 0.33, n_f = 0.33$ and $n_z = 0.33$ (Steele, 1974). The values of coefficients a and g – the respective ratios of organic carbon to chlorophyll (C:chl) and of phosphorus to organic carbon (P:C) – were taken from the experimental data collected during PEX ′86 and are $a = 0.046$ gC $(\text{mgchl})^{-1}$ and $g = 0.3$ mmolP $(\text{gC})^{-1}$ (Dybern and Hamsen, 1989). The lack of experimental data (PEX ′86) meant that phytoplankton mortality and respiration had to be described with the aid of constant coefficients taken from the data published by Radach (1983); these were equal to $mm = 10^{-6}\ \text{s}^{-1}$ and $m_p = 1.56 \times 10^{-6}\ \text{s}^{-1}$ respectively. Grazing was determined by the function $f(z)$ describing zooplankton distribution as a linear, second-degree polynomial. The coefficient of relative amplitude of phytoplankton biomass variability a_w, and the coefficient of the time during which the maximum zooplankton concentration occurred in the upper sea layer t_0, both of which appear in the relationship describing grazing (11), were taken from Renk *et al.* (1983). These coefficients are equal to $a_w = 0.6$ and $t_0 = -3.25$ h. In all cases the numerical analysis was performed within a range of density variability $(0.99 \times 10^{-3} \le \rho \le 1.04 \times 10^{-3}\ \text{kg m}^{-3})$ acceptable with respect to the natural environment, and within an acceptable range of changes of module of the average vertical rate of suspension sedimentation $(2.2 \times 10^{-7} \le w_z \le 5.1 \times 10^{-7}\ \text{m s}^{-1})$.

The calculations were carried out for a constant value of the turbulent diffusion coefficient, *i.e.* $K_z = 10^{-4}\ \text{m}^2\ \text{s}^{-1}$ (uniform water mass).

The results of the numerical investigations into the effect of the processes described in section 2 (under selected biological and chemical conditions) on the plots and values of the chlorophyll a and nutrient concentration distribution functions in this region are presented in section 4.

Figs. 2–12 show the time variability distribution functions of chlorophyll a (a), nutrient concentration (b) nutrient uptake by phytoplankton (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f) at 06:00, 12:00, 18:00, 24:00 h and 06:00 h the next day.

4. Results of simulation studies

4.1. The influence of the factor limiting production increase on the variability of the biological characteristics investigated

The influence of the factor limiting production increase on the variability of the characteristics investigated was analysed on the assumption that $k_s = 0.12$ mmolP m^{-3}, $S_a = 4.5 \times 10^{-5}\ \text{s}^{-1}$ and $f(z) = 0.02\,z + 0.5$. The following assumption was made in the calculations:

case 1: nutrients are the limiting factor in primary production
(a significant loss from the nutrient pool is noted) (Fig. 2);

case 2: the nutrient concentration is large enough in the study area;
only production generated by photosynthesis takes place (Fig. 3).

In both cases, the distributions of chlorophyll *a* and nutrient concentrations and the other processes investigated are different with respect to shape and value.

The results show that after 24 h have elapsed the chlorophyll *a* concentration distribution function attains a value considerably higher in case 1 (Fig. 2a) than in case 2 (Fig. 3a). In both cases, the maximum of this function gradually moves to a shallower depth. The position of the chlorophyll *a* concentration maximum varies with depth from $h = 14$ m to $h = 10$ m (Figs. 2a and 3a). In case 1 this change in this function's maximum position occurs gradually throughout the day (Fig. 2a). In case 2, however, the change occurs abruptly after the elapse of 8 hours.

On the assumption that phytoplankton cell growth is controlled by the nutrient concentration in the water (case 1), the coefficients obtained for all the processes under investigation are higher in value than in case 2. This leads to a substantial rise in the chlorophyll *a* concentration.

The simulations showed that in both cases 1 and 2, nutrient uptake by phytoplankton and nutrient release depend largely on the shape and value of the chlorophyll *a* concentration distribution function (Fig. 2c, 2f and 3c, 3f).

Analysis of nutrient remineralisation in the water and of nutrient excretion by zooplankton shows that these processes increase considerably in intensity. In case 1, this increase takes place gradually throughout the day; in case 2, however, these processes accelerate abruptly and only at night (Figs. 3d and 3e). The calculations also indicate that remineralisation and excretion by zooplankton depend mainly on daytime primary production and on phytoplankton grazing by zooplankton during the night.

Throughout the experiment, when phytoplankton is ‘feeding on’ nutrients and there is sufficient light, the nutrient concentration distribution function in the deeper layer in case 1 (Fig. 2b) is much smaller than in case 2 (Fig. 3b). In the latter case, however, the nutrient concentration remains unchanged: it is already so high that nutrient uptake by phytoplankton scarcely affects it (Fig. 3b).

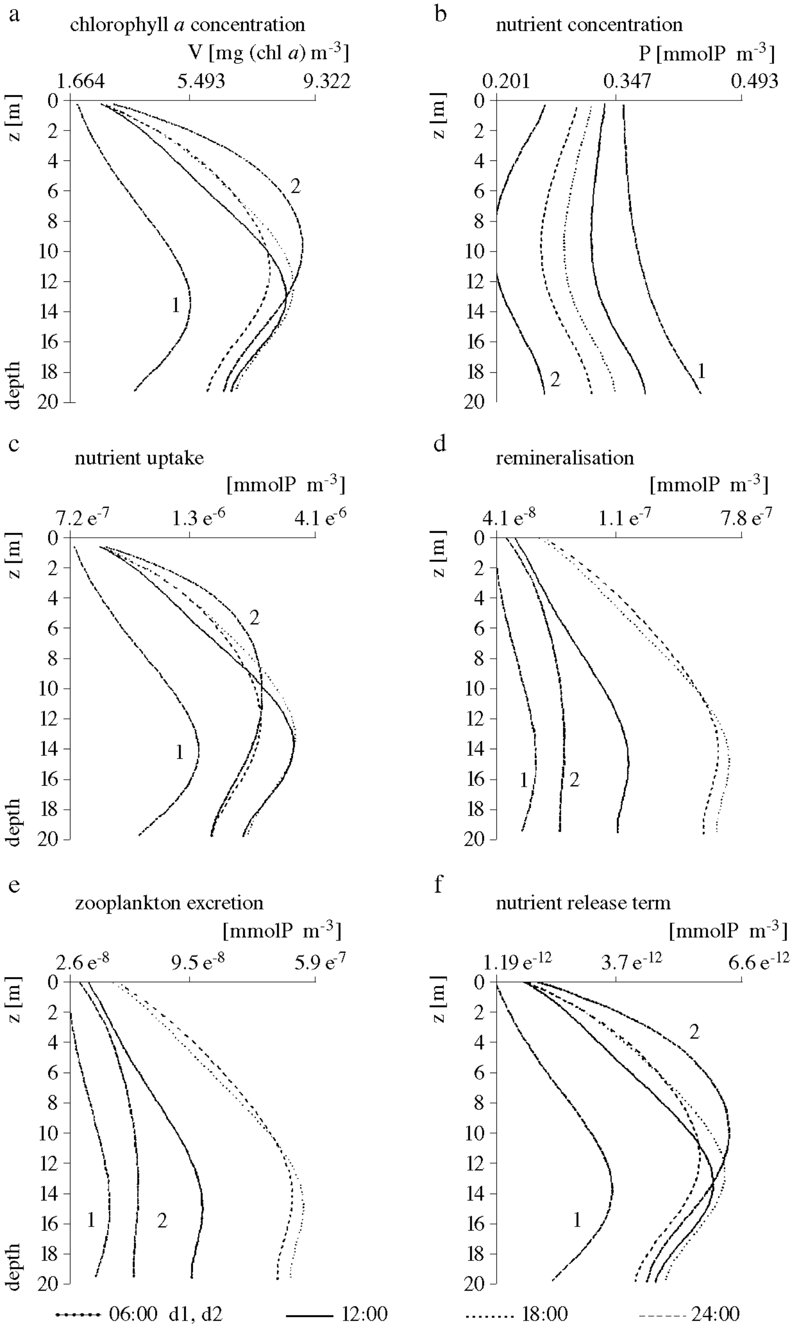

Fig. 2. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.12\,\mathrm{mmolP\,m^{-3}}$, $S_a = 4.5 \times 10^{-5}\,\mathrm{s^{-1}}$, $f(z) = 0.02\,z + 0.5$, and that nutrients are the limiting factor in primary production

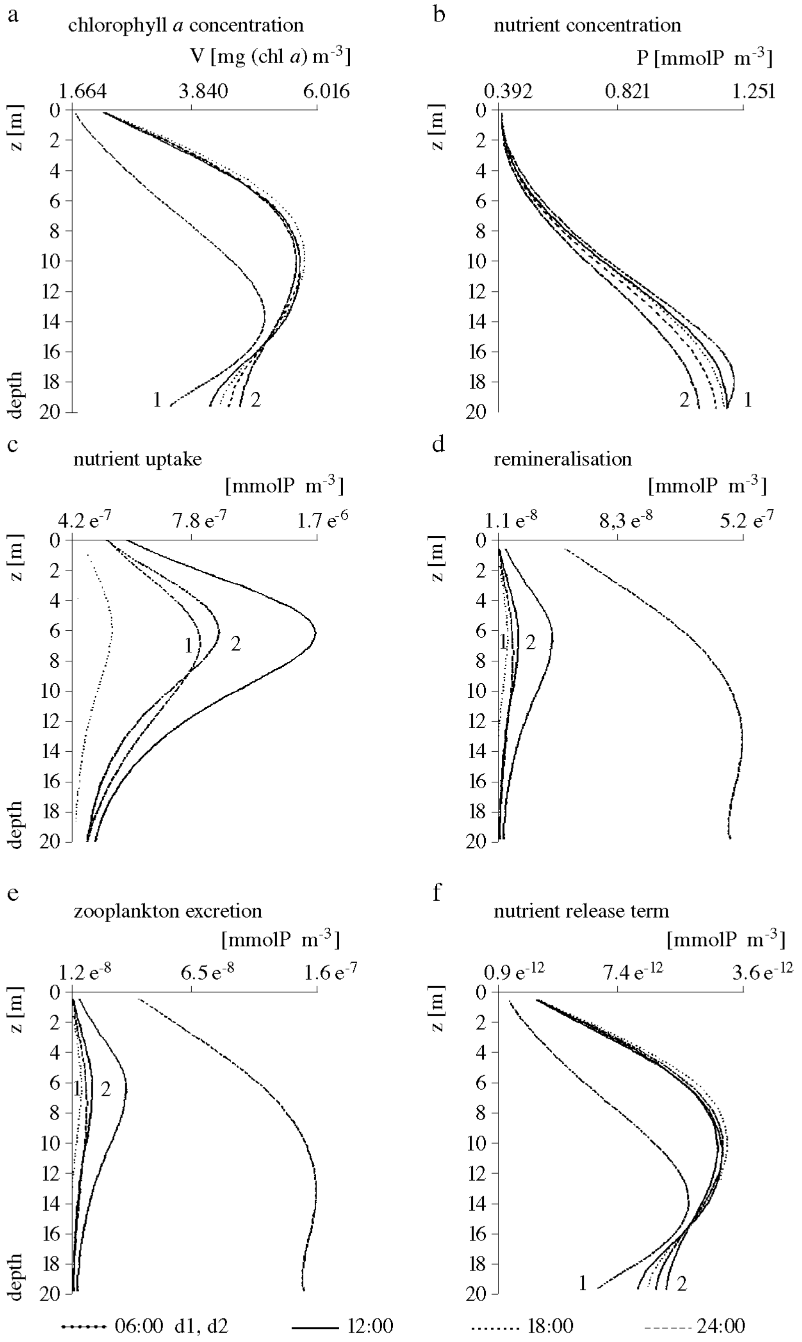

Fig. 3. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.12\,\mathrm{mmolP\ m^{-3}}$, $S_a = 4.5 \times 10^{-5}\ \mathrm{s^{-1}}$, $f(z) = 0.02\,z + 0.5$, and that only production generated by photosynthesis takes place

4.2. The influence of the maximum rate of production increase on the variability of the biological characteristics investigated, assuming that nutrients are the limiting factor in primary production

The following assumptions were made in the analysis of the maximum rate of production increase on the distributions of the chlorophyll *a* and nutrient concentrations controlled by the processes under scrutiny: nutrients are the limiting factor in primary production and $k_s = 0.32$ mmolP m^{-3}, $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$.

The calculations were carried out for three values of the maximum rate of production increase:

case 1: the maximum rate of production increase is equal to
$S_a = 10^{-4}$ s^{-1} (Fig. 4);

case 2: the maximum rate of production increase is equal to
$S_a = 4.5 \times 10^{-5}$ s^{-1} (Fig. 5);

case 3: the maximum rate of production increase is equal to
$S_a = 10^{-6}$ s^{-1} (Fig. 6).

The simulations show that changes in the maximum rate of production increase S_a have a considerable influence on the shapes and values of the chlorophyll *a* and nutrient concentration distribution functions. They show, moreover, that any increase in the value of S_a causes the chlorophyll *a* concentration to rise and the maximum of this function to move to a shallower depth. The position of this maximum changes with depth from $h = 14$ m to $h = 5$ m in case 1 (Fig. 4a) and to $h = 7$ m in case 2 (Fig. 5a). However, with respect to case 3 ($S_a = 10^{-6}$ s^{-1}) S_a causes the chlorophyll *a* concentration to decline and the maximum of this latter function to move from $h = 14$ m to $h = 16$ m (Fig. 6a). The value of S_a affects the variability of these processes to a considerable degree.

These simulations show that an increase in any of the investigated parameters (Figs. 4, 5 and 6), not just in the chlorophyll *a* concentration in cases 1 and 2, depends largely on the value of S_a. These functions increase in value as S_a does so.

The calculations also demonstrated that in all cases nutrient uptake by phytoplankton and nutrient release depend mainly on the shape of the dependent variable of phytoplankton distribution in the sea. In case 3, the intensity of these processes subsides throughout the numerical experiment (24 h) (Figs. 6c and 6f).

However, remineralisation varies exactly as in cases 1 and 2, *i.e.* this process intensifies during the daytime and slows down at night

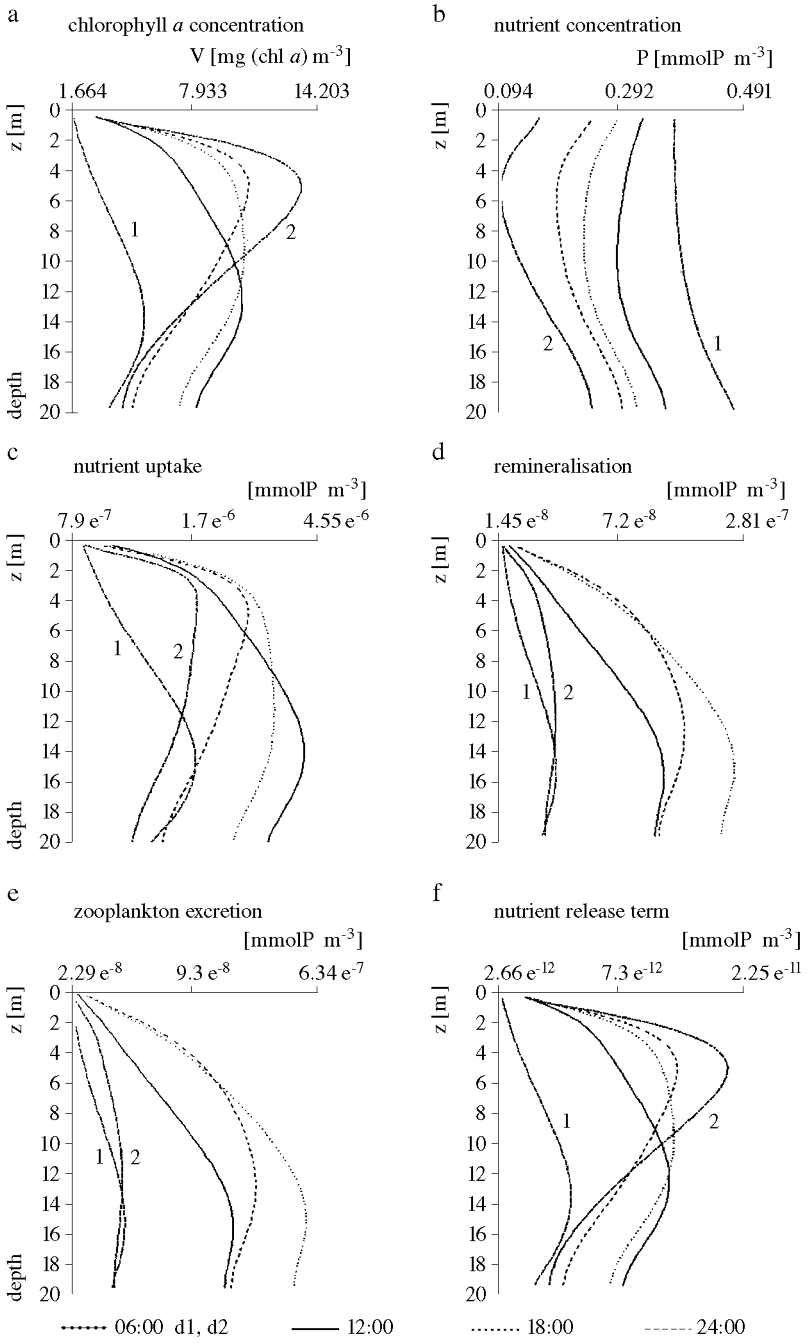

Fig. 4. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$, and that nutrients are the limiting factor in primary production and $S_a = 10^{-4}$ s^{-1}

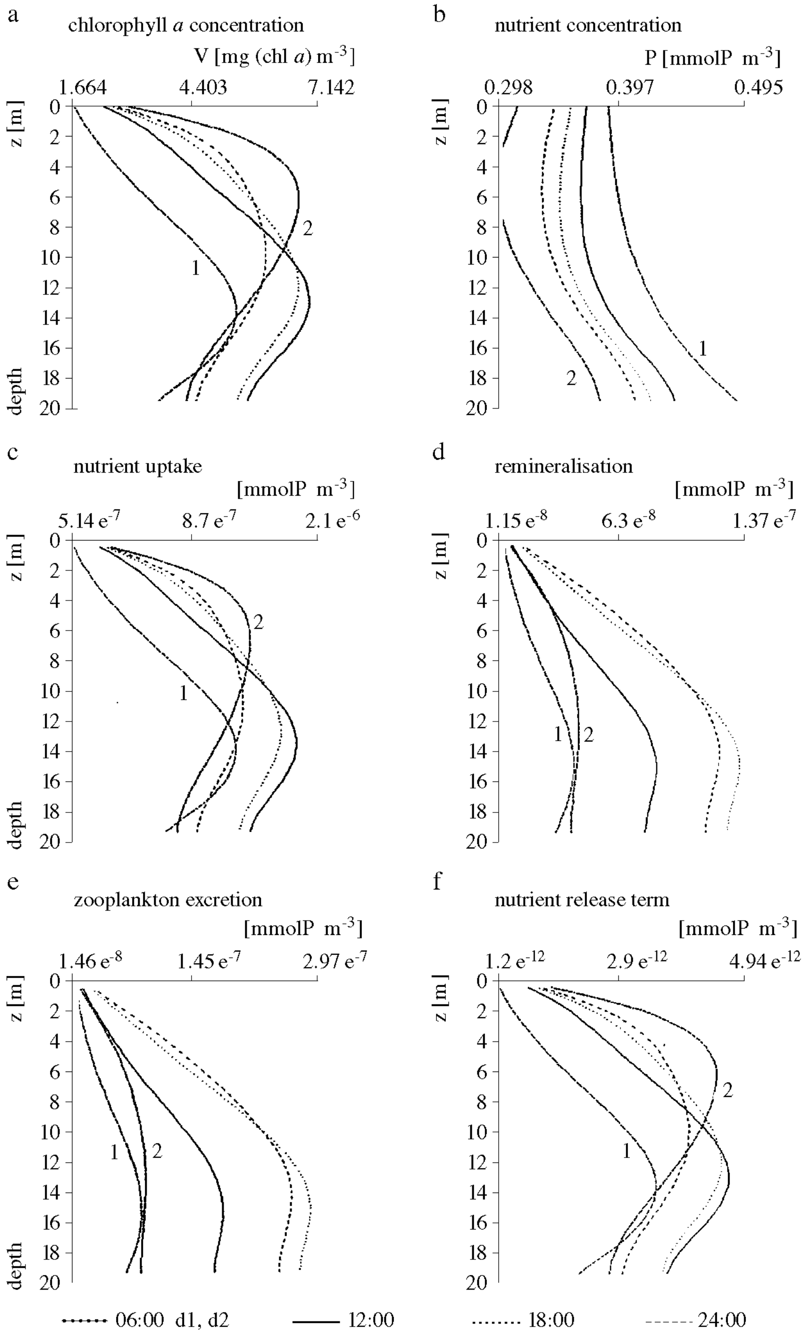

Fig. 5. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f) assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$, and that nutrients are the limiting factor in primary production and $S_a = 4.5 \times 10^{-5}$ s^{-1}

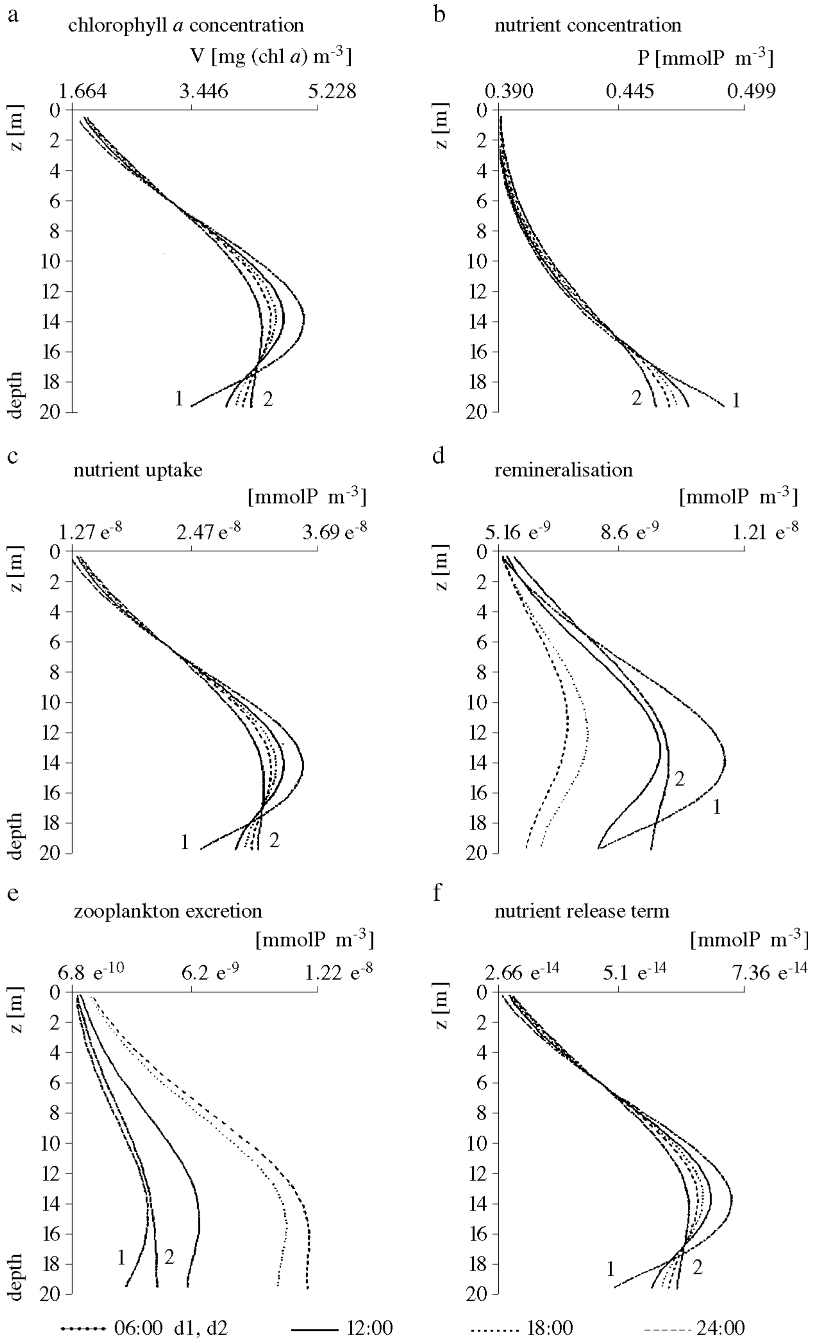

Fig. 6. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$, and that nutrients are the limiting factor in primary production and $S_a = 10^{-6}$ s^{-1}

(Figs. 4d and 5d). Quite the opposite situation obtains in case 3, when the maximum rate of production increase S_a is equal to $S_a = 10^{-6}$ s^{-1} (Fig. 6d) (*i.e.* remineralisation slackens off during the day and gathers momentum during the night). The simulations demonstrated the dominant influence of primary production on the nutrient remineralisation in both cases 1 and 2. However in case 3, this particular process depends chiefly on phytoplankton grazing by zooplankton.

The results of these studies have shown that nutrient concentrations drop considerably with rising values of S_a (Fig. 4b).

4.3. The influence of the maximum rate of production increase on the variability of the biological characteristics under investigation, assuming that only production by photosynthesis takes place

The calculations were carried out for three values of the maximum rate of production increase S_a (as in variant 2):
case 1: $S_a = 10^{-4}$ s^{-1} (Fig. 7);
case 2: $S_a = 10^{-6}$ s^{-1} (Fig. 8)
and it was assumed that only production due to photosynthesis takes place.

The results show the dominant influence of the value of S_a on the shape and value of the parameters under study, as in variant 2. The distributions shown in Figs. 7a and 8a demonstrate that the value of S_a has a crucial effect on the chlorophyll *a* concentration. This increases when S_a does so (Fig. 7a), which causes the maximum of the latter function to move towards the upper sea layers, *i.e.* to a depth of $h = 6$ m (Fig. 7a) and $h = 14$ m (Fig. 8a) in cases 1 and 2 respectively. The chlorophyll *a* concentration increases abruptly during the afternoon hours and the new level is maintained until the following day.

The calculations also demonstrated that in the situation illustrated in Fig. 7a, phytoplankton grazing does not have a very great effect on the chlorophyll *a* concentration field. The reverse situation obtains in case 2, when $S_a = 10^{-6}$ s^{-1}, which causes a decrease in phytoplankton concentration during the whole 24 h (Fig. 8a), as in variant 1. The lower value of this function means that the factor limiting production increase independently of the nutrient concentration and the quantity of light has little influence on the chlorophyll *a* concentration distribution.

However, in this case, the simulations show that phytoplankton grazing by zooplankton does have a decisive influence on the phytoplankton concentration field. This variant takes into account the fact that during the entire numerical experiment, phytoplankton absorbs light only when

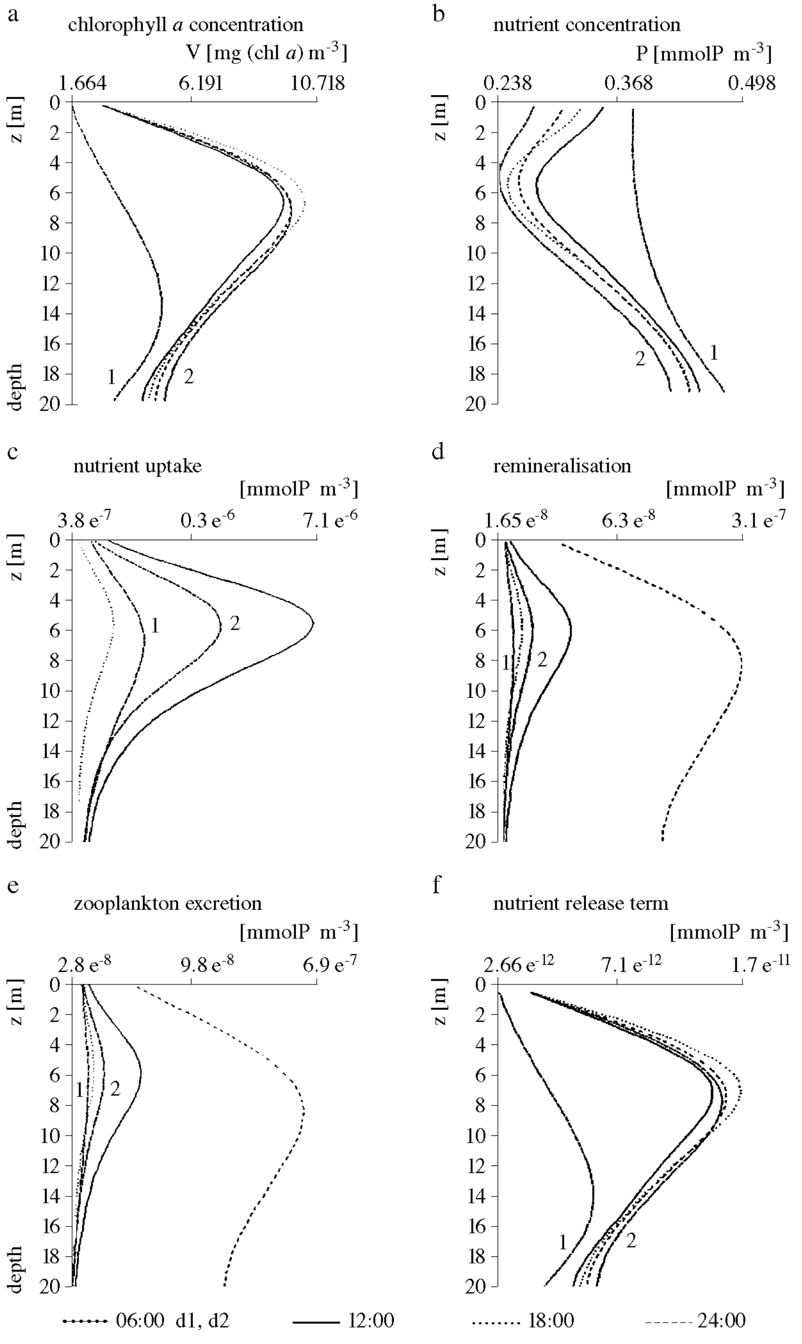

Fig. 7. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$, and that only production generated by photosynthesis takes place and $S_a = 10^{-4}$ s^{-1}

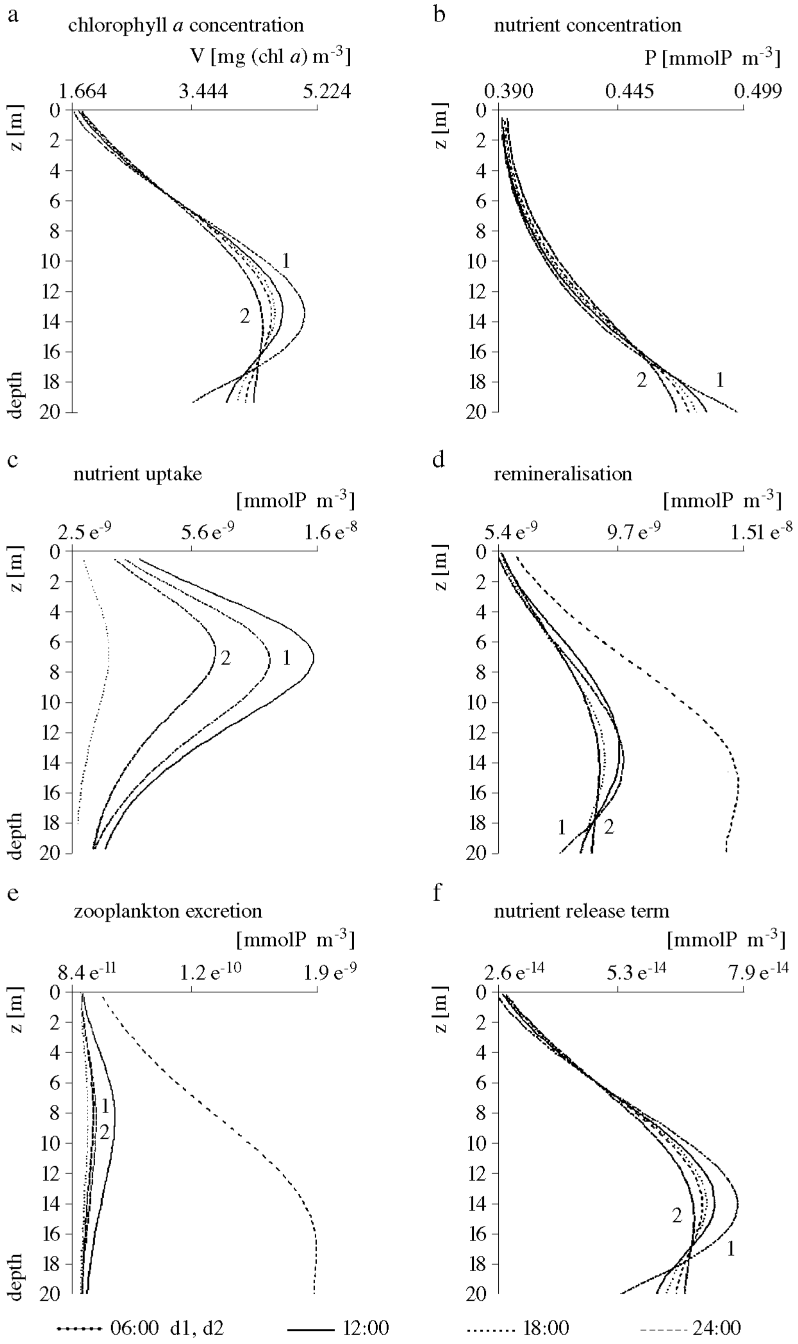

Fig. 8. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$, and that only production generated by photosynthesis takes place and $S_a = 10^{-6}$ s^{-1}

the nutrient level has reached saturation; it assumes, furthermore, that there is no nutrient uptake by phytoplankton at night.

The results (Figs. 7c and 8c) demonstrate that nutrient uptake depends to a considerable degree on the factor limiting production increase, *i.e.* on the light (variant 2).

In all cases the calculations showed a rapid increase in remineralisation during the night followed by a sudden decrease (Figs. 7d and 8d).

The distributions in Figs. 7b and 8b illustrate the changes in the nutrient concentration field. The nutrient concentration decreases with rising maximum rate of production increase. In this variant the decrease in this function is smaller than in variant 2.

4.4. The influence of phytoplankton grazing by zooplankton on the variability of the biological characteristics

The influence of phytoplankton grazing by zooplankton on the variability of the biological characteristics was analysed under the assumption that nutrients are the factor limiting production increase and $k_s = 0.32$ mmolP m^{-3}, $S_a = 4.5 \times 10^{-5}$ s^{-1}. Assuming further that grazing is horizontally uniform, the function $f(z)$ describing zooplankton distribution is linear and a second-degree polynomial. The coefficients of the polynomial can be determined either arbitrarily or from the experimental values of the grazing coefficient at the following depths:

- at the free surface corresponding to conditions of zooplankton survival in the water,
- at a depth equal to the thickness of the euphotic layer (the depth corresponding to the conditions during the phytoplankton bloom).

For the calculations, the following assumption was made:
case 1: $f(z) = 0.02\,z + 0.5$ (Fig. 9);
case 2: $f(z) = -0.00125\,z^2 + 0.05\,z + 0.5$ (Fig. 10).

The simulations showed that, particularly at night, grazing exerts a pronounced effect on the shape of the distribution function and the dependent variable of phytoplankton distribution in the sea.

During the evening the zooplankton migrate towards the upper sea layers in search of food, *i.e.* phytoplankton. Almost the entire phytoplankton production is grazed during the night hours, a fact reflected by the declining chlorophyll *a* concentration.

The position of the maximum of this function varies with depth from $h = 14$ m to $h = 12$ m (Fig. 9a) and to $h = 5$ m (Fig. 10a).

The results of the simulations indicate that the standing stock of phytoplankton has an important influence on these processes when compared

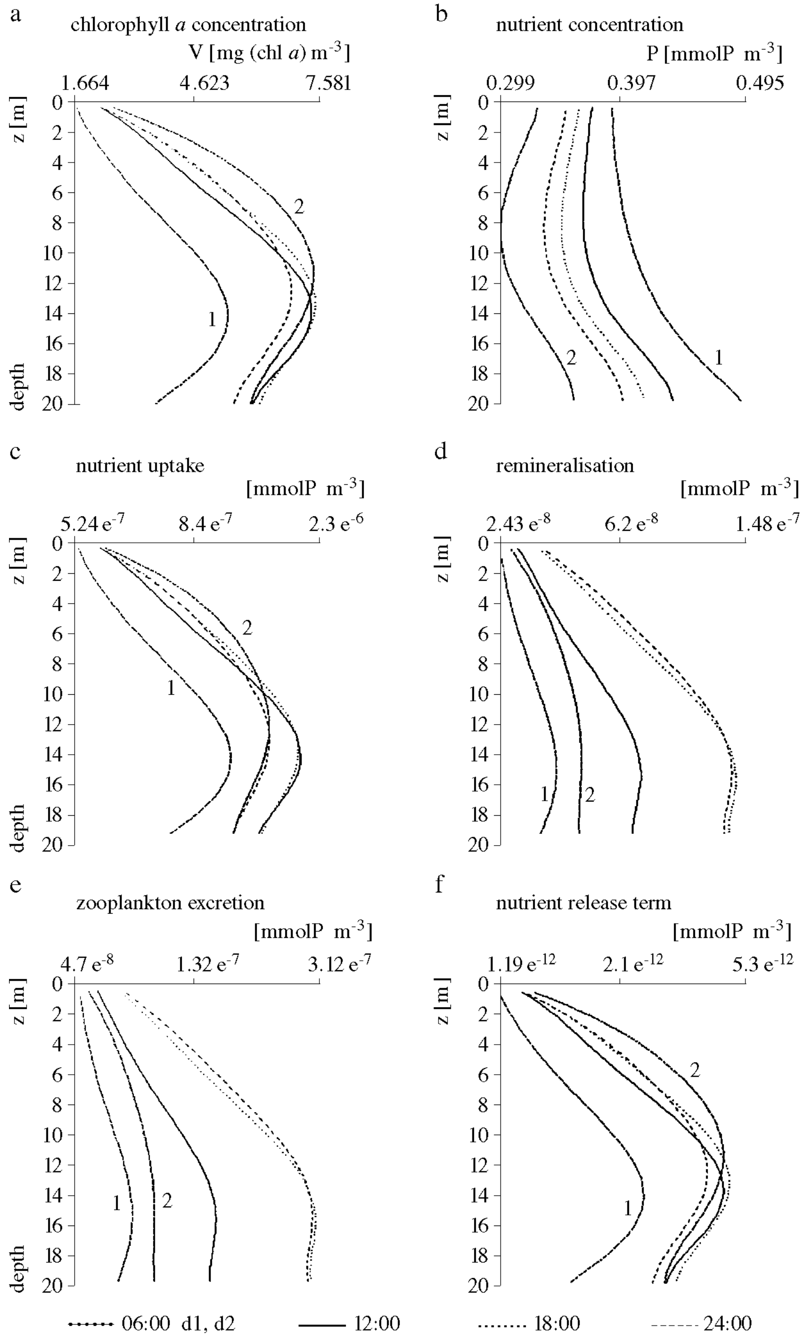

Fig. 9. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 4.5 \times 10^{-5}$ s^{-1}, and that nutrients are the limiting factor in primary production and $f(z) = 0.02\,z + 0.5$

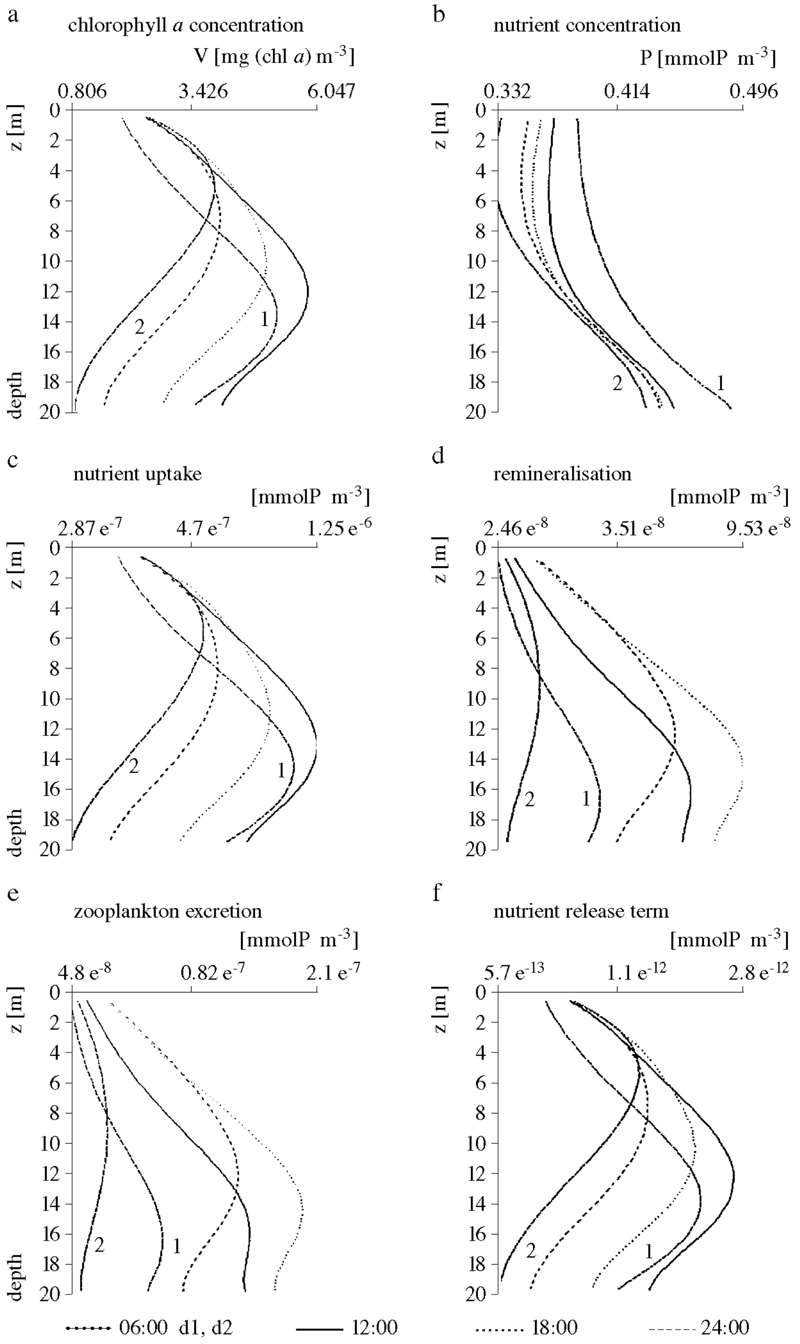

Fig. 10. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 4.5 \times 10^{-5}$ s^{-1}, and that nutrients are the limiting factor in primary production and $f(z) = -0.00125\,z^2 + 0.05\,z + 0.5$

with phytoplankton grazing. The increase in the grazing coefficient (case 2) causes the chlorophyll *a* concentration to fall (Fig. 10a), a fact reflected by the declining values of the parameters investigated (Figs. 10c, 10d, 10e and 10f), assuming that the coefficients n_z, n_f and n_e are constant in all cases.

The distributions in Figs. 9 and 10 illustrate nutrient uptake (Figs. 9c and 10c) and nutrient release, which are dependent largely on the shape of the distribution function and value of the chlorophyll *a* concentration.

The simulations show that phytoplankton grazing influences principally the variability of nutrient remineralisation (Figs. 9d and 10d) and nutrient excretion by zooplankton (Figs. 9e and 10e). Increased grazing during the night causes these other processes to intensify as well.

In all the cases, the nutrient concentration distributions (Figs 9b and 10b) differ to a very small degree with respect to their shapes and values.

The increase in the grazing coefficient (case 2) causes a decrease in the chlorophyll *a* concentration (Fig. 10a) and in the parameters studied (Figs. 10c, 10d, 10e and 10f), something that is reflected in the smaller loss of the nutrient concentration (Fig. 10b).

4.5. The influence of the coefficients n_z, n_f and n_e on the variability of the investigated biological characteristics

The influence of the coefficients n_z, n_f and n_e of the material being grazed on the variability of the processes investigated and the chlorophyll *a* and nutrient concentration was analysed under the assumption that $k_s = 0.32$ mmolP m^{-3}, $S_a = 4.5 \times 10^{-5}$ s^{-1}, $f(z) = 0.02\,z + 0.5$ and nutrients are the limiting factor in primary production. The simulations were carried out for different values of n_z, n_f and n_e:
case 1: $n_z = 0.13, n_f = 0.13$ and $n_e = 0.73$ (Fig. 11);
case 2: $n_z = 0.13, n_f = 0.73$ and $n_e = 0.13$ (Fig. 12).

The results indicate that changes in the values of n_z, n_f and n_e influence the parameters investigated only very slightly, with the exception of nutrient remineralisation and nutrient excretion by zooplankton (Figs. 11d, 11e and 12d, 12e). The increase in n_e and n_f, indicating those proportions of the material being grazed, regenerated as soluble excreta of zooplankton (case 1) and regenerated as faecal material (case 2), leads to respective increases in excretion (Fig. 11e) and remineralisation (Fig. 12d).

The intensification of these processes has little effect on the nutrient concentration field. The results of the numerical investigations (Fig. 11b and 12b) demonstrate that increasing excretion considerably reduces the nutrient concentration (Fig. 11b and 11e) more than increasing remineralisation does (Figs. 12b and 12d). As a result, the nutrient concentration field depends mainly on remineralisation in the water.

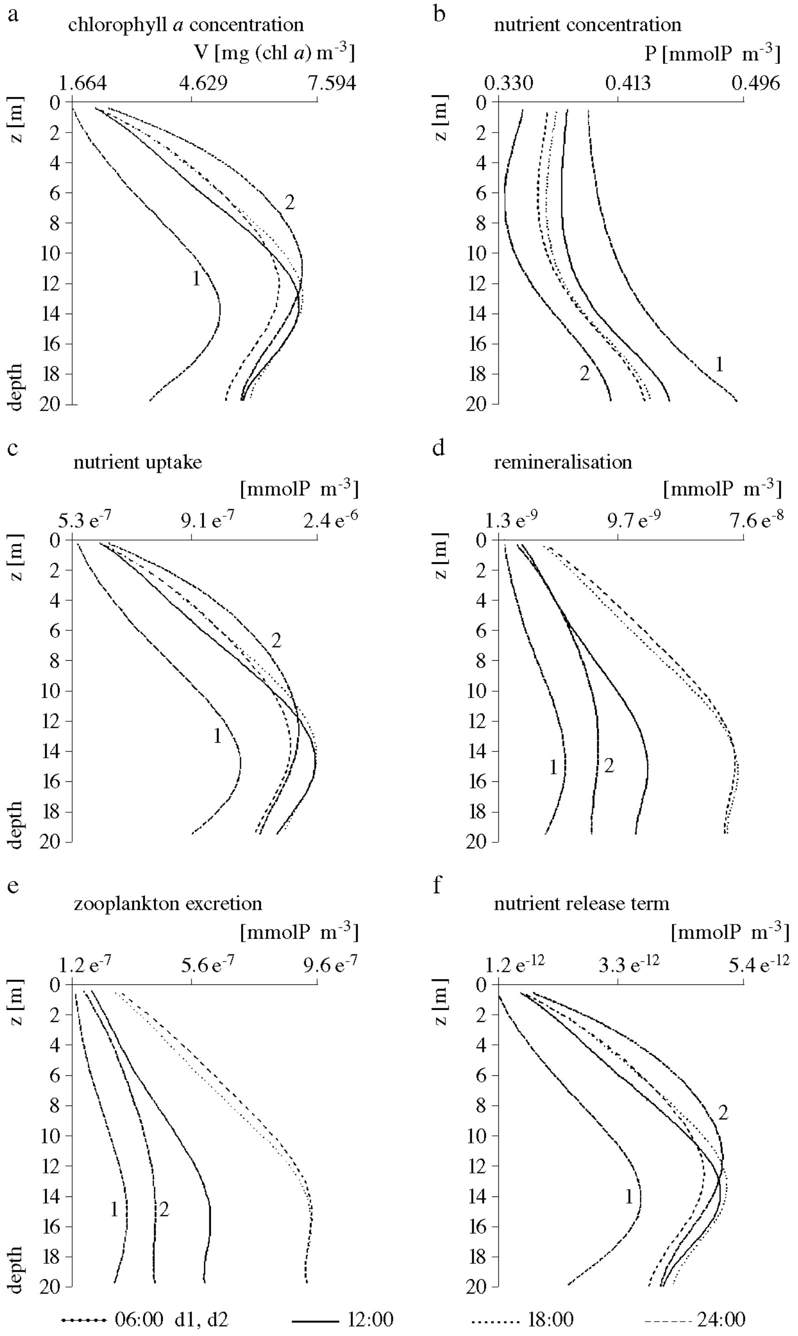

Fig. 11. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 4.5 \times 10^{-5}\mathrm{s}^{-1}$, $f(z) = 0.02z + 0.5$, and that nutrients are the limiting factor in primary production and $n_z = 0.13, n_f = 0.13, n_e = 0.73$

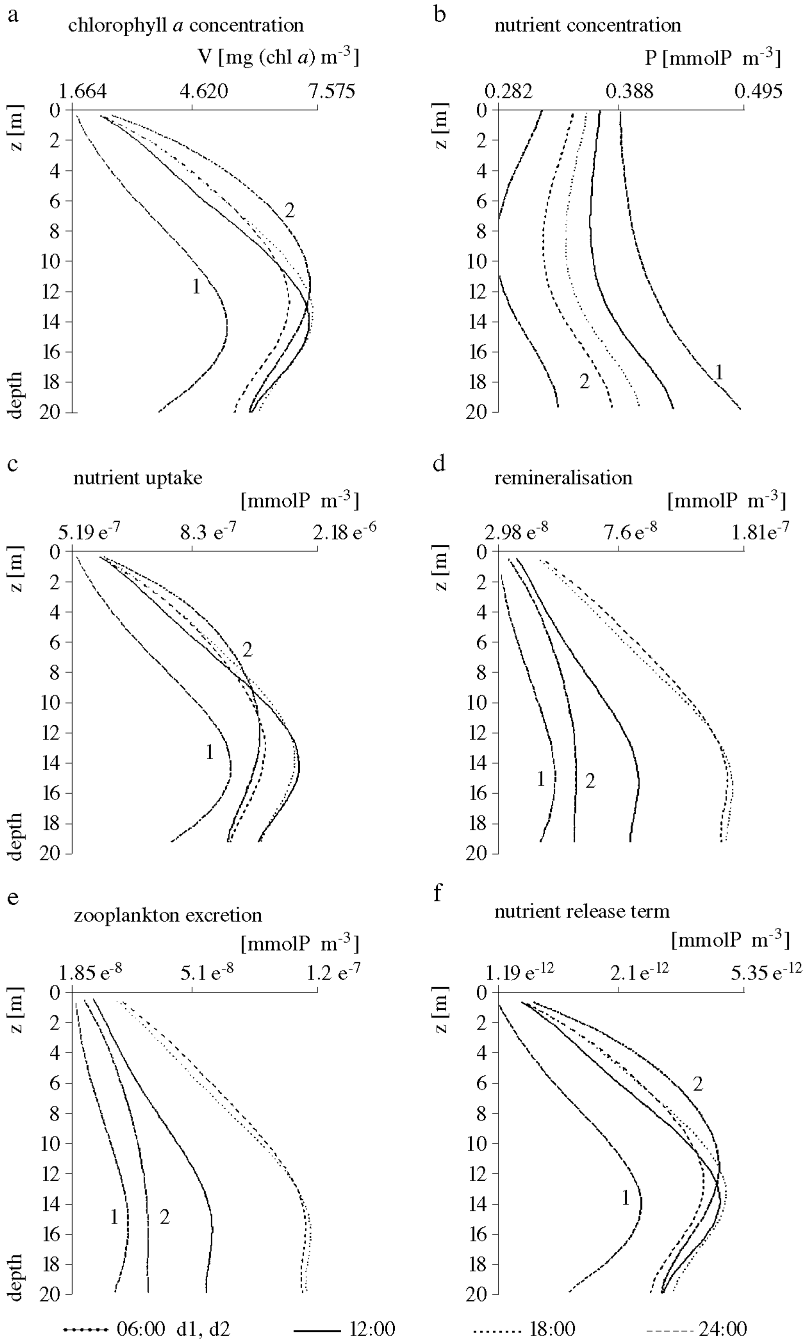

Fig. 12. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), nutrient uptake (c), nutrient remineralisation (d), nutrients excreted by zooplankton (e) and nutrient release (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 4.5 \times 10^{-5}$ s^{-1}, $f(z) = 0.02\,z + 0.5$, and that nutrients are the limiting factor in primary production and $n_z = 0.13, n_f = 0.73, n_e = 0.13$

5. Discussion

The simulating calculations showed that the changes in the selected biological and chemical parameters, *i.e.* the factor limiting production increase, the maximum rate of production increase, the function characterising the vertical distribution of zooplankton and the coefficients n_z, n_f and n_e of the material being grazed, immediately influence the processes investigated, which largely affect the shape and value of the distribution functions of chlorophyll a and nutrient concentrations.

This influence makes itself felt through the changes in the position of the maximum chlorophyll a concentration and the increase in value of this function in variants 1, 2 and 3 in all cases. The exception is case 3 (variants 2 and 3), when the maximum rate of production increase is equal to $S_a = 10^{-6}$ s^{-1}. The calculations demonstrate that the chlorophyll a concentration then decreases. This indicates that primary production does not have much influence on this function. However, phytoplankton grazing does affect the chlorophyll a concentration field to a significant degree.

The results of these simulations indicate that in areas where phytoplankton grazing is intensive (variant 4), there occur non–homogeneities in the chlorophyll a concentration distribution function owing to the decrease in chlorophyll a concentration.

However, with regard to the processes investigated, the numerical studies show that the selected biological and chemical parameters considerably influence the variability of these processes, which in turn act on the distributions of the chlorophyll a and nutrient concentrations.

Nutrient uptake by phytoplankton and nutrient release depend mainly on the shape and value of the chlorophyll a distribution function in the water; in the case of nutrient uptake this dependence is largely controlled by primary production.

The results of the numerical investigations demonstrate that the maximum rate of production increase S_a to a considerable extent establishes the magnitudes of the biological characteristics in question. Any increase in the value of S_a causes not only the chlorophyll a concentration to increase but also the processes investigated to intensify.

All the variants of these simulations show that remineralisation in the water column and excretion of dissolved metabolites by zooplankton increase considerably during the night. Moreover, the values of these parameters, increase with increasing phytoplankton grazing mainly during the night. However, in the variant 2 (cases 1 and 2), when the coefficient S_a increases in value, nutrient remineralisation and excretion by zooplankton depend largely on primary production.

The calculations indicate that during the entire numerical experiment, when phytoplankton is 'feeding on' nutrients and there is sufficient light, the nutrient concentration distribution function attains values considerably smaller than when production generated solely by photosynthesis takes place. Analysis of these numerical studies also demonstrates that this function decreases significantly as the maximum rate of production increase rises. However, increasing phytoplankton grazing does not cause the nutrient concentration to fall to such an extent.

The results of these numerical investigations show that changes in the values of the coefficients n_z, n_f and n_e of the material being grazed exert hardly any influence on the characteristics examined with the exception of nutrient remineralisation and zooplankton excreta. The increase in the value of coefficients n_e and n_f, which denote those parts of the material being grazed and regenerated as soluble zooplankton excreta or as faecal material leads to increasing excretion and remineralisation respectively; this is reflected by the changes in the nutrient concentration. The simulations indicate that as a result, nutrient remineralisation has a greater influence on the value of this function than on excretion by zooplankton.

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