Numerical studies of the influence of the benthic detritus pool on the chlorophyll *a* concentration in a stratified sea

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Abstract

This paper presents the numerical simulations of variability of biological processes such as phytoplankton bottom flux, remineralisation of detritus, detrital material sedimenting out of the water column onto the bottom and the benthic detritus pool, as well as 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 nutrient half-saturation constant and the function characterising the vertical distribution of zooplankton. The numerical studies were carried out using a phytoplankton–phosphate–detritus biological model with a well–developed regeneration mechanism. This paper presents the vertical distributions of biological characteristics to facilitate a better understanding of temporal changes but on the assumption that the above processes are horizontally uniform. The calculations were made in an area $0 \leq z \leq 20$ m with a vertical space step of 10 cm and a time step of 15 min. The complex experimental data, gathered during the PEX′86 international scientific experiment of the Baltic states, and subsequently by the International Council for the Exploration of the Sea, were used as the input data for the calculations.

1. Introduction

The aim of this work was to simulate the benthic regeneration processes directly influencing the detritus pool at the bottom, and largely affecting the distribution functions of nutrient and chlorophyll *a* concentrations.

The numerical studies were carried out using a biological model with a well-developed regeneration mechanism described in Dzierzbicka-Głowacka and Zieliński (1997).

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.

In order to make the model as simple as possible, and to avoid the inclusion of a number of nutrient components (as would be necessary if nitrogen were the reference nutrient), the model was based on phosphate; the chemistry of phosphorus is considerably simpler than that of nitrogen (Raymont, 1980).

The simplified phosphorus cycle in the biological model (Fig. 1) incorporates formulations of the primary production mechanism and of the regeneration mechanism within the mixed layer, in the lower layers and at the bottom.

Phytoplankton in the water is either grazed by zooplankton or else it dies and sinks. Grazed phytoplankton contributes to zooplankton growth, is lost as faecal pellets, and is excreted by zooplankton as dissolved metabolites, so replenishing the nutrient pool. A proportion of the material contributing to growth, representing dying zooplankton, is assumed to be lost immediately. Proportions of both the faecal and the excreted material are immediately regenerated.

Most of the detrital material sediments onto the bottom, where it collects as a detrital pool (Billen *et al.*, 1991). Only a small portion of detritus remains suspended in the water column, where it is immediately regenerated. The majority sediments onto the bottom, where it is re-worked by bacteria and other organisms. The concept of the detrital pool at the bottom has been introduced to create a log in the remineralisation of most of the upper layer with nutrients. This complex process is parametrised by assuming a net remineralisation rate for bottom detritus (Billen *et al.*, 1991).

Thus, there are two pathways for the regeneration of pelagic and benthic nutrients, each on a different time scale. The present model deals with both pelagic and benthic pathways.

The availability of the regenerated nutrient for production in the upper layers will be controlled by the physical processes and the distance between the locations of regeneration.

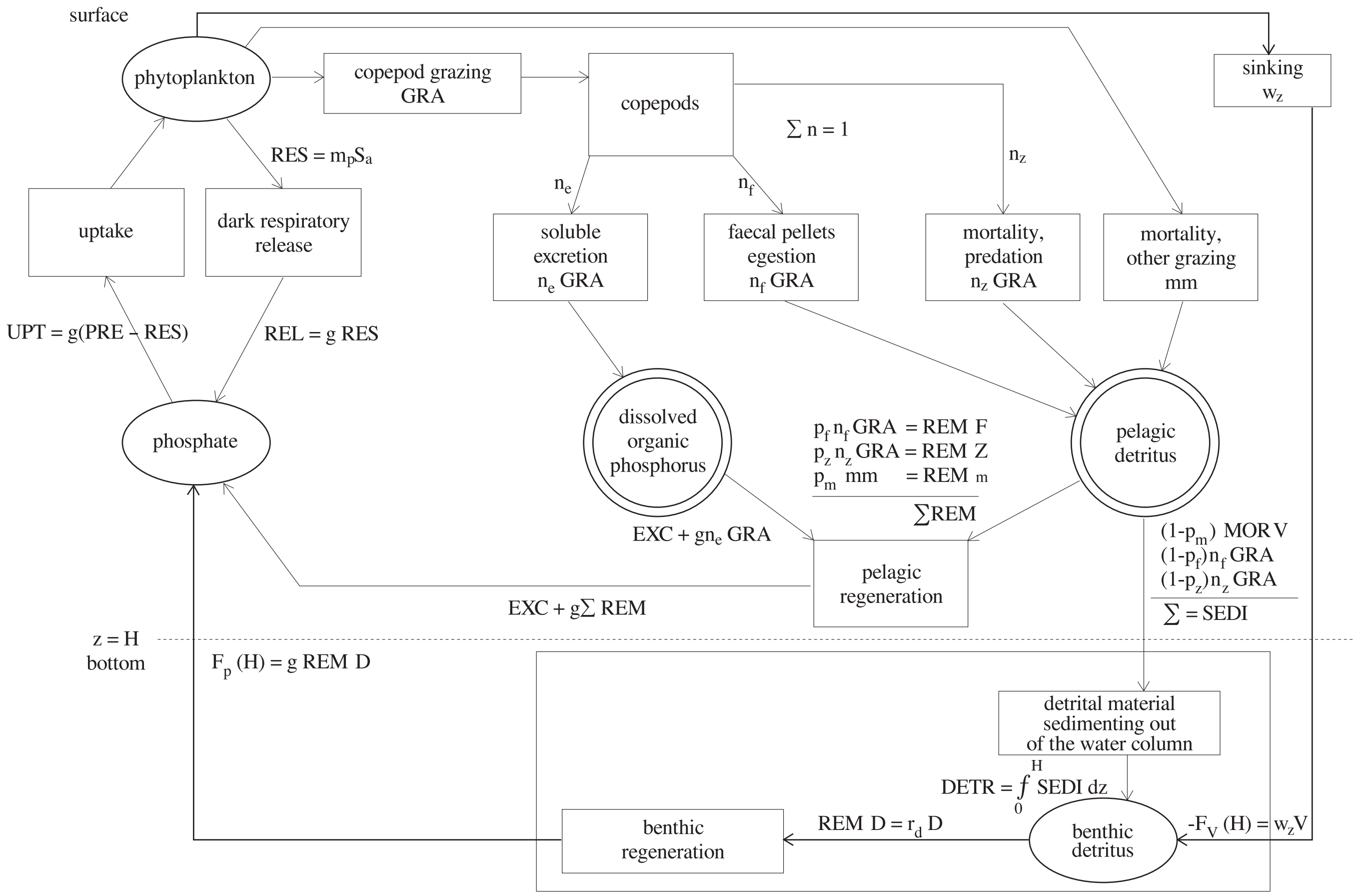

Fig. 1. Simplified phosphorus cycle of the biological upper layer model (notation on p. 372)

The pools (state variables) and processes in the biological model V–P–D are restricted to the following: the phytoplankton standing stock V and phosphate P in the water column serve as time and depth-dependent pools. Detritus D is a time-dependent pool at the bottom. All three pools are prognostic state variables. Underwater light, however, is calculated as a diagnostic variable, and several other variables also serve as diagnostic state variables. Thus the number of degrees of freedom is kept relatively small. The zooplankton standing stock is prescribed and serves as a forcing variable. Bacteria are not explicitly simulated as prognostic variables: their activity only appears implicitly in the parametrisations of the remineralisation terms. Benthic detritus accumulates by sinking out of the water column. It is regenerated by bacterial action, and the resulting phosphate diffuses upwards by turbulent diffusion.

2. The phytoplankton–phosphate–detritus biological model

The present phytoplankton–phosphate model with a well-developed regeneration mechanism, as described in a recent paper (Dzierzbicka-Głowacka and Zieliński, 1997), takes the benthic detritus pool equation into consideration (Fig. 1). The V–P–D model consists of two nonlinearly coupled, partial second-order differential equations and one ordinary first-order differential equation, together with modified initial and boundary conditions.

The change in local phytoplankton biomass concentration $V(z,t)$ is caused by turbulent diffusion DIF V, sinking of algae SINK, production PRE, respiration RES, mortality 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 the local nutrient concentration $P(z,t)$ is determined by turbulent diffusion DIF P, uptake by algae UPT, remineralised dead phytoplankton, zooplankton faecal pellets and dead zooplankton REMI, and by 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 a fixed ratio of phytoplankton carbon to chlorophyll a.

Finally, the time change of the detritus pool at the bottom $D(t)$ is determined by the flux of phytoplankton $F_V(H)$ and of detrital material sedimenting out of the water column onto the bottom DETR and remineralisation of detritus REM D:

$$\frac{dD}{\partial t} = -F_V(H) + \mathrm{DETR} - \mathrm{REM}\,D, \tag{3}$$

where $\mathrm{REM}\,D$ is converted into a flux of phosphate, released back into the overlying water column, according to the boundary conditions.

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

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

$$\mathrm{EXC} = g n_e \,\mathrm{GRA}, \tag{4}$$

with percentage n_e. Faecal pellet production is described by

$$\mathrm{FEC} = n_f \,\mathrm{GRA}, \tag{5}$$

and the zooplankton carcasses are described by

$$\mathrm{MOR}\,Z = n_z \,\mathrm{GRA}, \tag{6}$$

with percentages n_e, n_f and n_z of the material being grazed. For the sake of mass conservation we assume $n_e + n_f + n_z = 1$. 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 $\mathrm{REM}\,F$:

$$\mathrm{REM}\,m = p_m \,\mathrm{MOR}\,V, \tag{7}$$

$$\mathrm{REM}\,Z = p_z \,\mathrm{MOR}\,Z, \tag{8}$$

$$\mathrm{REM}\,F = p_f \,\mathrm{FEC}, \tag{9}$$

$$\begin{aligned}\mathrm{REMI} &= g\,(\mathrm{REM}\,m + \mathrm{REM}\,Z + \mathrm{REM}\,F)\\ &= g\,\{p_m \mathrm{MOR}\,V + (p_f n_f + p_z n_z)\mathrm{GRA}\},\end{aligned} \tag{10}$$

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

Most dead, excreted and sinking material finally ends up in the benthic detritus pool. Their contributions are:

$$\begin{aligned}\mathrm{SEDI} &= (1-p_m)\,\mathrm{MOR}\,V + (1-p_f)\,\mathrm{FEC} + (1-p_z)\,\mathrm{MOR}\,Z\\ &= (1-p_m)\,\mathrm{MOR}\,V + \{(1-p_f)n_f + (1-p_z)n_z\}\mathrm{GRA}.\end{aligned} \tag{11}$$

Benthic detritus varies according to the input of detrital algal material from the water column, and loss by remineralisation. Remineralisation at the bottom is assumed to be proportional to the amount of benthic detritus available:

$$\mathrm{REM}\,D = r_d D, \tag{12}$$

where r_d denotes the remineralisation rate of benthic detritus and D the detritus concentration.

The detrital material sedimenting out of the water column enters the equation as

$$\mathrm{DETR} = \int_0^H \mathrm{SEDI}\, dz. \tag{13}$$

SEDI is given by eq. (11).

Sedimentation of living phytoplankton provides a net gain to the detritus pool. The flux of algae across the bottom boundary is taken to be a source term in the detritus eq. (3). The remineralised detritus is then transported back as phosphate into the water column by upward diffusion. The latter mechanism is cast into the form of a boundary condition for the nutrient, which couples the phosphate eq. (2) and the detritus eq. (3).

On the basis of the available bibliographical information, the rate of primary production is defined in the model by the equation given by Radach (1983):

$$\mathrm{PRE} = S_a \mathrm{min}\{d_i, d_p\} V(z,t), \tag{14}$$

where S_a denotes the maximum rate of production increase, while d_i and d_p are factors limiting production increase (the light available at a given concentration of nutrients). The coefficients are given by the formulae

$$d_i = \frac{S(z,t)}{S_a}, \quad d_p = \frac{P(z,t)}{P(z,t) + k_s}, \tag{15}$$

where k_s is the nutrient half-saturation constant and $S_a = \max S(z,t)$.

For a given concentration of the nutrient limiting photosynthesis, the coefficient S, which defines the total primary production, depends on the assimilation number A (Dzierzbicka-Głowacka, 1994b, 1996):

$$S(z,t) = aA(z,t) \sin\gamma, \tag{16}$$

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

The details of the other physical, biological and chemical processes can be found in the papers by Dzierzbicka-Głowacka (1994b, 1996) and Dzierzbicka-Głowacka and Zieliński (1997).

Initial and boundary conditions

The following initial and boundary conditions are supplementary to the equation system (1)–(3): the initial vertical distributions of chlorophyll *a*

V and phosphate P are known:

$$\begin{aligned} V(z,0) &= V_0(z) \qquad && 0 \le z \le Z, \\ P(z,0) &= P_0(z) && 0 \le z \le Z, \\ D(t=0) &= D_0 = 0. && \end{aligned} \tag{17}$$

For phytoplankton and phosphate we assume there are no fluxes across the sea surface ($z = 0$), which means that

$$\begin{aligned} F_V(0) &\equiv K_z^V \frac{\partial V(z,t)}{\partial z} - w_z V(z,t) = 0, \\ F_P(0) &\equiv K_z^P \frac{\partial P(z,t)}{\partial z} = 0. \end{aligned} \tag{18}$$

Phytoplankton can sink out of a water column of depth $z = h$, resulting in a flux condition at the interior interface

$$F_V(h) \equiv K_z^V \frac{\partial V(z,t)}{\partial z} - w_z V(z,t). \tag{19}$$

When assuming that the turbulent flux

$$F_V^T(H) \equiv K_z^V \frac{\partial V(z,t)}{\partial z} = 0 \tag{20}$$

ceases at the bottom, we get the bottom flux condition

$$F_V(H) \equiv -w_z V(z,t). \tag{21}$$

This flux $F_V(H)$ enters the benthic detritus equation as a source term. At the bottom there is a flux of phosphate into the water column across the interface $z = H$:

$$F_P(H) \equiv K_z^P \frac{\partial P(z,t)}{\partial z} \neq 0. \tag{22}$$

Phosphate provided from the benthic detritus pool enters the bottom boundary condition for phosphate as

$$F_P(H) \equiv K_z^P \frac{\partial P(z,t)}{\partial z} = g\,\mathrm{REM}\,D. \tag{23}$$

Thus the boundary condition provides the mechanism of replenishing the water column with phosphate resulting from benthic remineralisation. If turbulent mixing is strong enough to reach the bottom layers, the full water column becomes homogenous with respect to phosphate.

3. Data for the simulation studies

The two-dimensional phytoplankton–phosphate mathematical model, described in greater detail in Dzierzbicka-Głowacka (1994b, 1996) with a well-developed regeneration mechanism (Dzierzbicka-Głowacka and Zieliński, 1997) was used to simulate the influence of the processes investigated (through changes in the selected biological and chemical parameters) on the chlorophyll a and nutrient distributions in the water.

The V–P–D model (eq. (3)) describing detritus accumulation at the bottom modifies the initial conditions.

This paper presents the vertical distributions of biological characteristics to facilitate a better understanding of temporal changes, but only on the assumption that the above processes are horizontally uniform. The calculations were made in an area $0 \le z \le 20$ 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 $t = 6$ 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 for 26 April 1986 were presented in Dzierzbicka-Głowacka (1994a, 1996). The half-saturation constant for phosphate was adopted after Lehman *et al.* (1975) and Raymont (1980): $k_s = 0.32$ mmolP m^{-3}. The constant k_s is the concentration of limiting nutrient in the medium at which $S = S_{\max}/2$, where S is the specific growth rate and $S_{\max}$ is the maximum specific growth rate of the population under the prevailing environmental conditions.

The coefficients defining the regeneration process expressing those parts of dead phytoplankton p_m, zooplankton p_z and faecal material p_f, which are immediately remineralised in the water column are equal and amount to $p_m = p_z = p_f = 0.2$ (Postma and Rommets, 1984). However, the remineralisation rate of benthic detritus is equal to $r_d = 0.0167$ d^{-1} (Radach *et al.*, 1990).

The coefficients describing those parts of the material being grazed and regenerated as soluble zooplankton excreta n_e, faecal material n_f, and 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, defining 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; they are $a = 0.046$ gC $(\text{mgchl})^{-1}$ (Kaczmarek, personal communication) and $g = 0.3$ mmolP $(\text{gC})^{-1}$ (Radach *et al.*, 1983).

The lack of experimental data (PEX′86) meant that phytoplankton mortality and respiration were described with the aid of constant coefficients taken from the data published by Radach (1983); they 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 linear and a second-degree polynomial. The coefficient of relative amplitude of phytoplankton biomass variability a_w, and the coefficient of time during which the maximum zooplankton concentration occurred in the upper sea layer t_0, both of which appear in the relationship describing grazing Dzierzbicka-Głowacka (1994b), were taken from Renk *et al.* (1983). These coefficients are $a_w = 0.6$ and $t_0 = -3.25$ h. In all the cases the numerical analysis was performed within a range of density variability $(0.99 \times 10^{-3} \le \rho \le 1.04 \times 10^{-3}$ 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 $(2.2 \times 10^{-7} \le w_z \le 5.1 \times 10^{-7}$ m s$^{-1})$.

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

Figs. 2–16 show the time variability distribution function of chlorophyll a (a) and nutrient concentration (b) and the processes investigated: bottom flux of phytoplankton (c), remineralisation of detritus (d), detrital material sedimenting out of the water column onto the bottom (e) and the detritus pool at the bottom (f).

4. Results of simulation studies

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 are presented in this section.

These selected biological and chemical parameters, *i.e.* the factor limiting production increase, the maximum rate of production increase, the nutrient half-saturation constant and the function characterising the vertical distribution of zooplankton, are responsible for the shape and value of the chlorophyll a and nutrient concentration distribution functions.

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

The influence of the factor limiting production increase on the variability of the characteristics investigated was analysed under the assumption that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}$ s^{-1} and $f(z) = 0.0352\,z + 0.3$. The following assumptions were 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, distributions of chlorophyll *a* and nutrient concentrations and the other processes investigated are different with respect to shape and value.

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 in the deeper layer.

Analysis of the bottom flux of phytoplankton $F_V(H)$ (Fig. 2c) and the detrital material sedimenting out of the water column onto the the bottom DETR (Fig. 2e) shows that these processes increase considerably in intensity and are directly dependent on the chlorophyll *a* concentration. In case 1, this increase takes place during the daytime; however, at night, the value of the detritus pool DETR falls, while the value of $F_V(H)$ remains unchanged.

The results of the simulations show that when only production generated by photosynthesis takes place (case 2), the value of $F_V(H)$ (Fig. 3c) and the detritus pool DETR (Fig. 3e) rises substantially during the early morning and afternoon; however, the the bottom flux of phytoplankton $F_V(H)$ drops considerably during the evening and the night, and the detritus pool DETR decreases abruptly in size during the evening hours and then remains unchanged during the night.

Throughout the experiment, when phytoplankton is 'feeding on' nutrients and there is sufficient light, the nutrient concentration distribution function in case 1 (Fig. 2b) is smaller than in case 2 (Fig. 3b). The uptake of nutrients by phytoplankton scarcely affects their concentration, since they are replenished by the benthic detritus pool (Fig. 2f) through nutrient

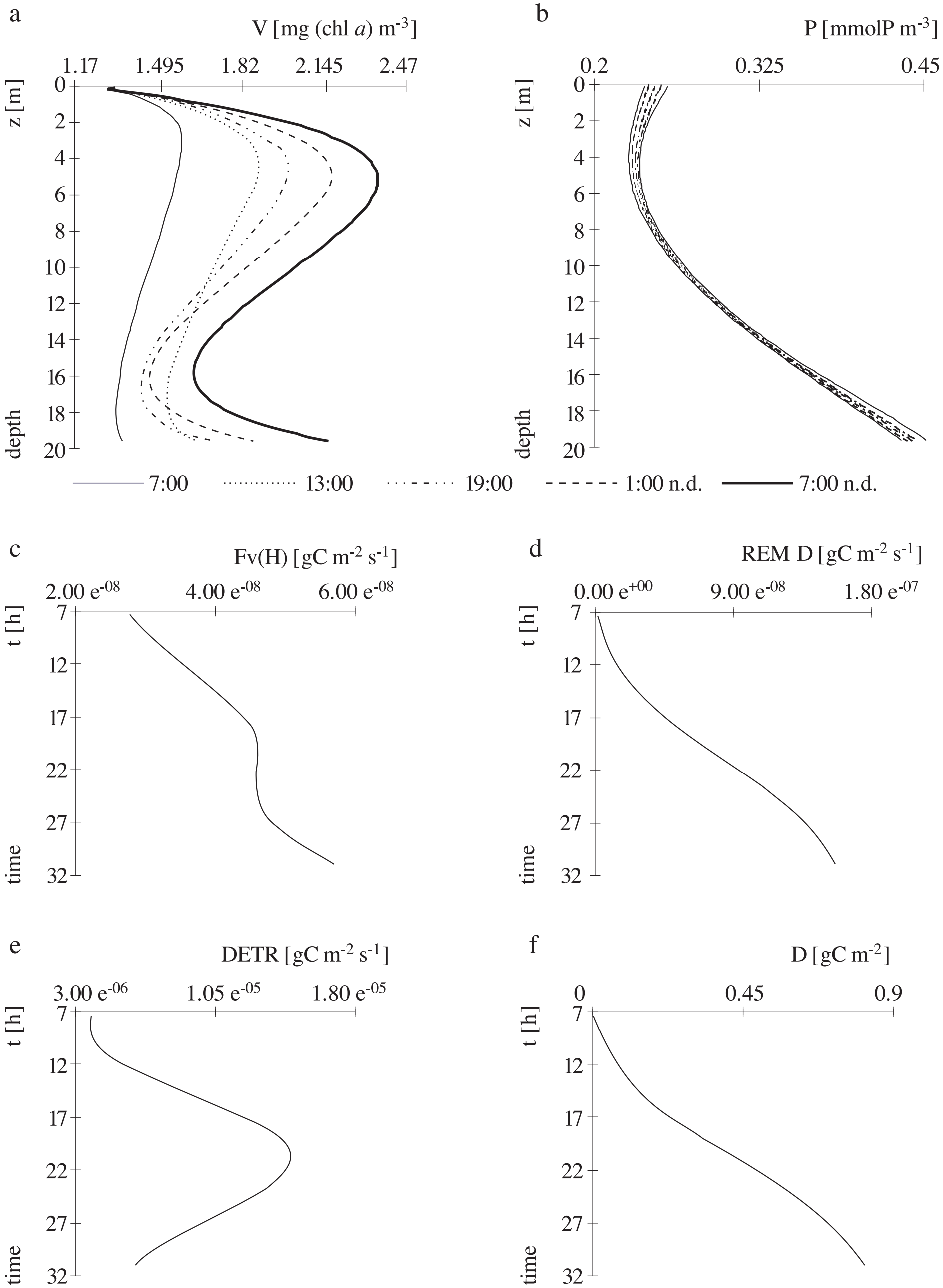

Fig. 2. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom *n* (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}\,\mathrm{s}^{-1}$, $f(z) = 0.0352\,z + 0.3$ and nutrients are the limiting factor in primary production (notation on p. 372)

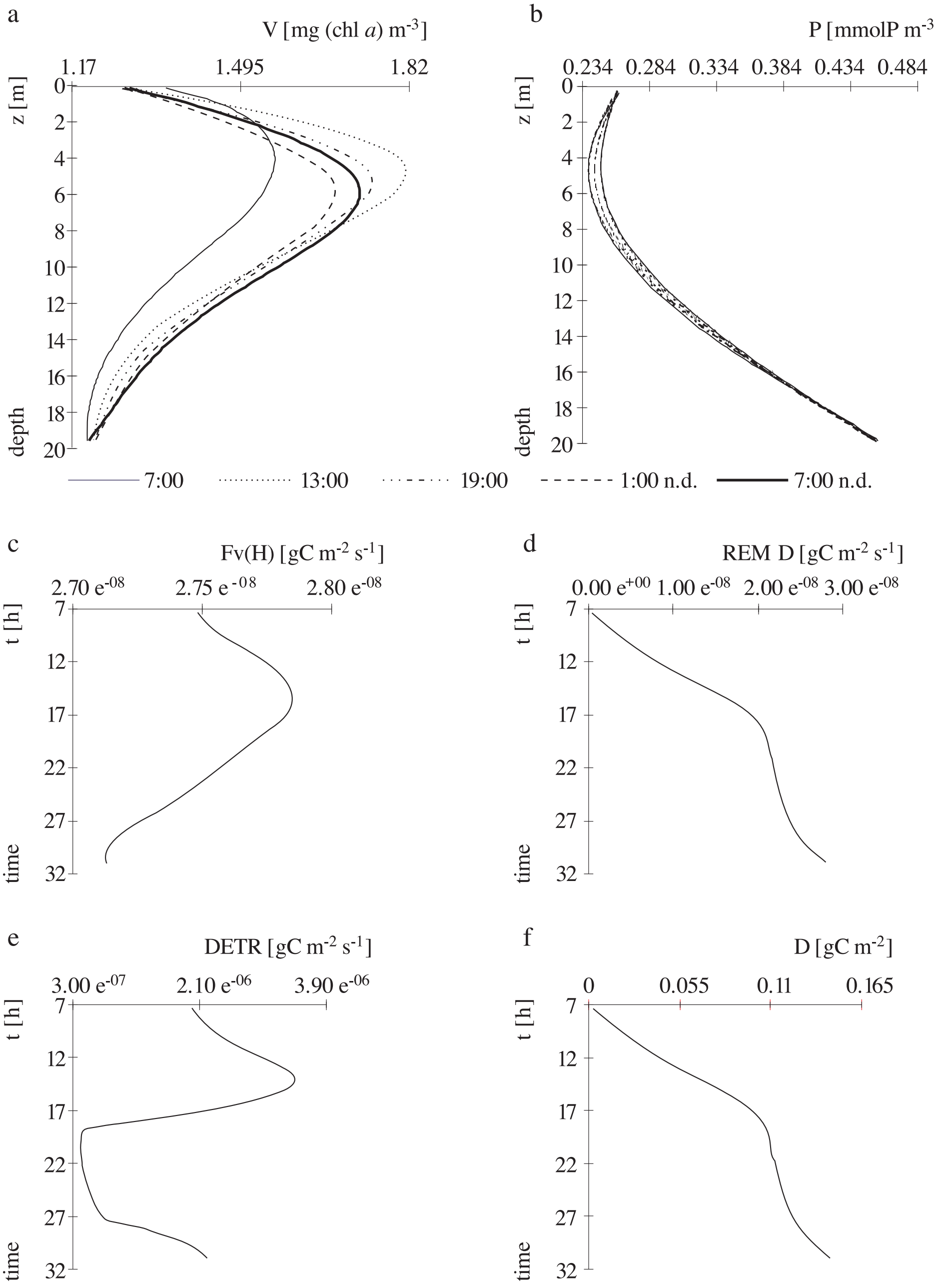

Fig. 3. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}\,\mathrm{s}^{-1}$, $f(z) = 0.0352\,z + 0.3$ and only production generated by photosynthesis takes place

remineralisation at the bottom (Fig. 2d). This process attains a higher value in case 1 than in case 2, and leads to a substantial rise in the chlorophyll *a* concentration in the deeper layer (case 1, Fig. 2a) through phytoplankton grazing. This increase depends mainly on the nutrient uptake.

The calculations demonstrated that when the nutrient concentration is large enough in the study area, the benthic detritus does not influence the chlorophyll *a* concentration.

The simulations show that the distribution function of chlorophyll *a* interacts with the benthic detritus pool in case 1; however, in case 2 this effect does not occur.

4.2. The influence of the maximum rate of production increase on the variability of the characteristics investigated, assuming that nutrients are the factor limiting 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}, $K_z = 10^{-4}\ \mathrm{m}^2\ \mathrm{s}^{-1}$ and $f(z) = 0.0352\,z + 0.3$.
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 $S_a = 10^{-6}\ \mathrm{s}^{-1}$ (Fig. 4);
case 2: the maximum rate of production increase is equal to $S_a = 4.5 \times 10^{-5}\ \mathrm{s}^{-1}$ (Fig. 5);
case 3: the maximum rate of production increase is equal to $S_a = 10^{-4}\ \mathrm{s}^{-1}$ (Fig. 6).

The simulations show that changes in the maximum rate of production increase S_a have a considerable influence on the shapes and value of the chlorophyll *a* and nutrient concentration distribution functions and on the variability of the processes investigated. They show, moreover, that any increase in the value of coefficient S_a causes the chlorophyll *a* concentration to rise (Figs. 5a and 6a) in case 2 and 3. However, with respect to case 1 ($S_a = 10^{-6}\ \mathrm{s}^{-1}$) S_a causes the chlorophyll *a* concenrtation to decline (Fig. 4a). 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 parameters studied (Figs. 5 and 6), not just in the chlorophyll *a* concentration in cases 2 and 3, depends largely on the value of S_a. These functions increase in value as S_a does so.

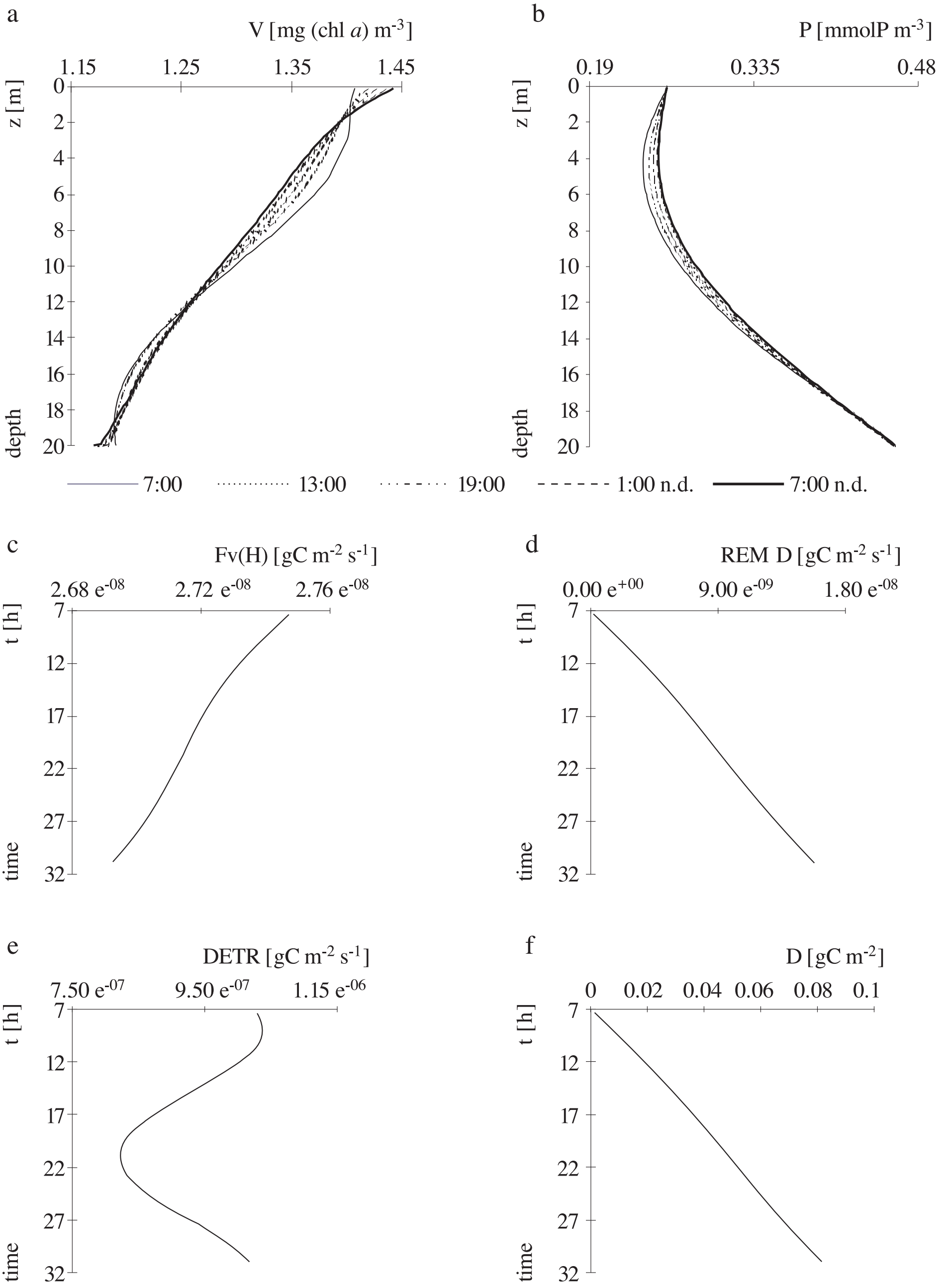

Fig. 4. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = 0.0352\,z + 0.3$, nutrients are the limiting factor in primary production and $S_a = 10^{-6}\,\mathrm{s}^{-1}$

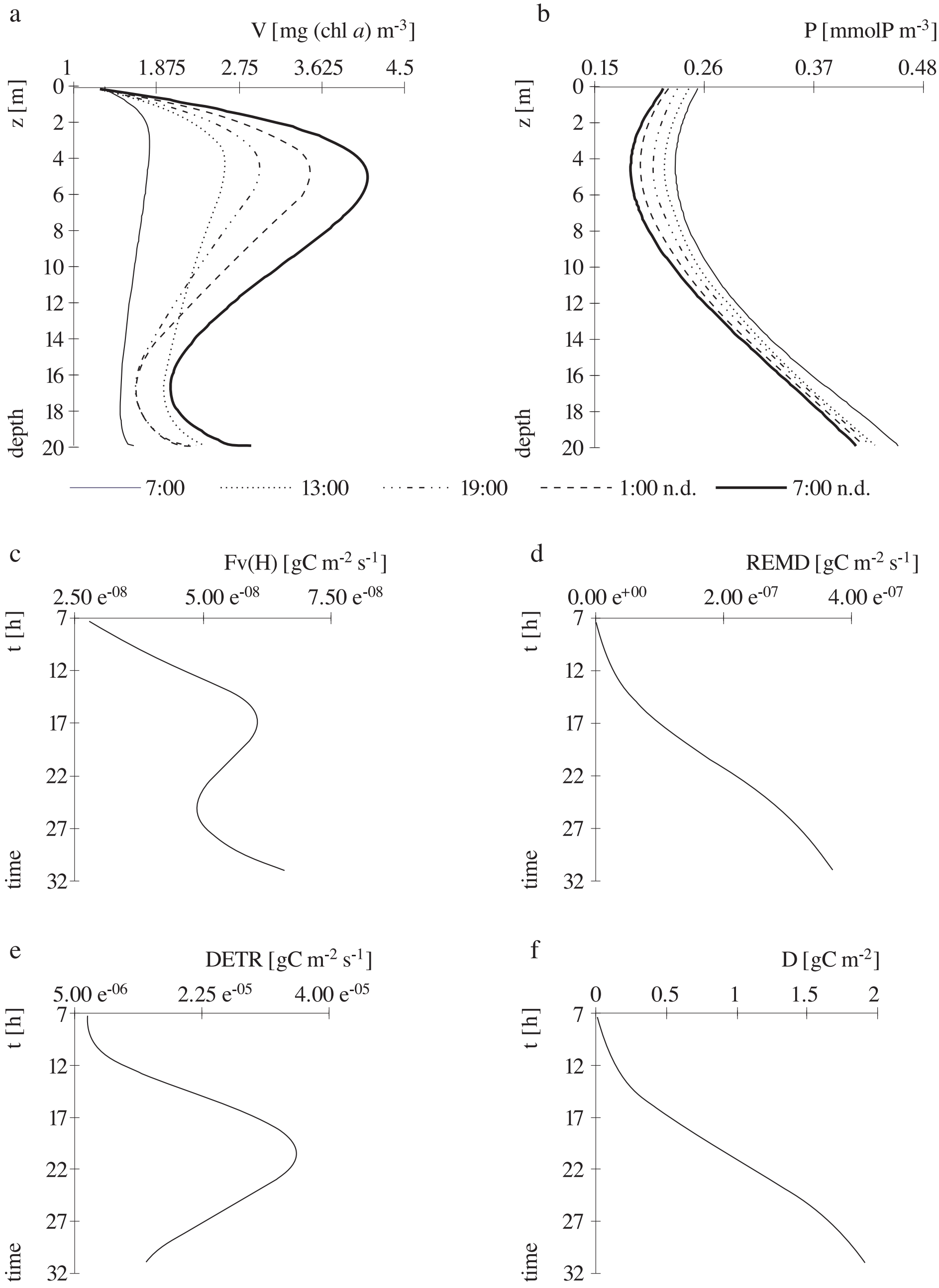

Fig. 5. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = 0.0352\,z + 0.3$, nutrients are the limiting factor in primary production and $S_a = 4.5 \times 10^{-5}\,\text{s}^{-1}$

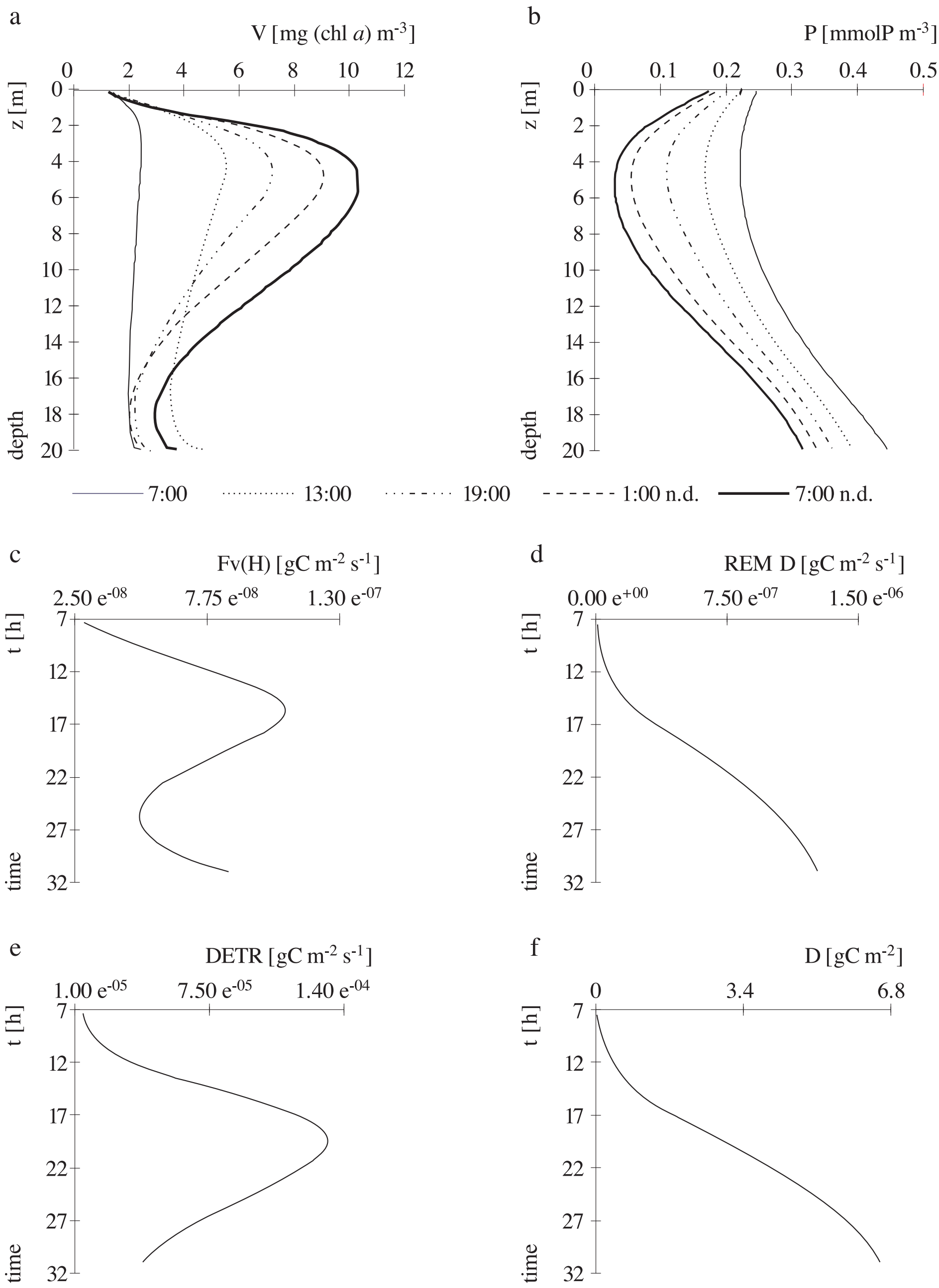

Fig. 6. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = 0.0352\,z + 0.3$, nutrients are the limiting factor in primary production and $S_a = 10^{-4}\,\mathrm{s}^{-1}$

The calculations also demonstrated that, in case 3 ($S_a = 10^{-4}$ s^{-1}) the increase in the chlorophyll a concentration brings about a much larger increase in the benthic detritus pool D (Fig. 6f) than in case 2 ($S_a = 4.5 \times 10^{-5}$ s^{-1}). Furthermore, this increase in the amount of benthic detritus causes remineralisation at the bottom to increase (Fig. 6d), more so in case 3 (Fig. 6d) than in case 2 (Fig. 5d).

In case 3, when the maximum rate of production increase S_a is equal to $S_a = 10^{-4}$ s^{-1} and nutrients are the limiting factor in primary production, nutrient uptake by phytoplankton reaches very large values. This gives rise to a considerably lower value of the nutrient concentration distribution function (Fig. 6b).

The simulations show that in case 1, when the maximum rate of production increase S_a is equal to $S_a = 10^{-6}$ s^{-1}, the bottom flux of phytoplankton $F_V(H)$ (Fig. 4c) declines with time; the detritus pool DETR (Fig. 4e) decreases in magnitude throughout the day, after which it gradually increases again. In this situation, the benthic detritus pool D (Fig. 4f) increases insignificantly in size.

4.3. Influence of the maximum rate of production increase on the variability of the biological characteristics investigated, assuming that only production generated by photosynthesis takes place

The calculations were carried out for three values of the maximum rate of production increase S_a (as in variant 4.2):
case 1: $S_a = 10^{-6}$ s^{-1} (Fig. 7);
case 2: $S_a = 4.5 \times 10^{-5}$ s^{-1} (Fig. 8);
case 3: $S_a = 10^{-4}$ s^{-1} (Fig. 9),
and it was assumed that only production generated by photosynthesis takes place.

The results of numerical investigations show the predominant influence of the value of S_a on the shape and value of the parameter under study, as in variant 2. The distributions shown in Figs. 7a, 8a and 9a demonstrate that the value of S_a has a crucial effect on the chlorophyll a concentration. Any increase in S_a causes the chlorophyll a concentration distribution to increase (Fig. 8a and 9a). This function increases more abruptly during the afternoon hours in this variant than in variant 4.2.

The reverse situation obtains in case 1, when $S_a = 10^{-6}$ s^{-1}, which causes a decrease in phytoplankton concentration (Fig. 7a), as in variant 4.2. The lower value of this function means that the factor limiting production increases independently of the nutrient concentration, and the quantity of light has little influence on the chlorophyll a concentration distribution.

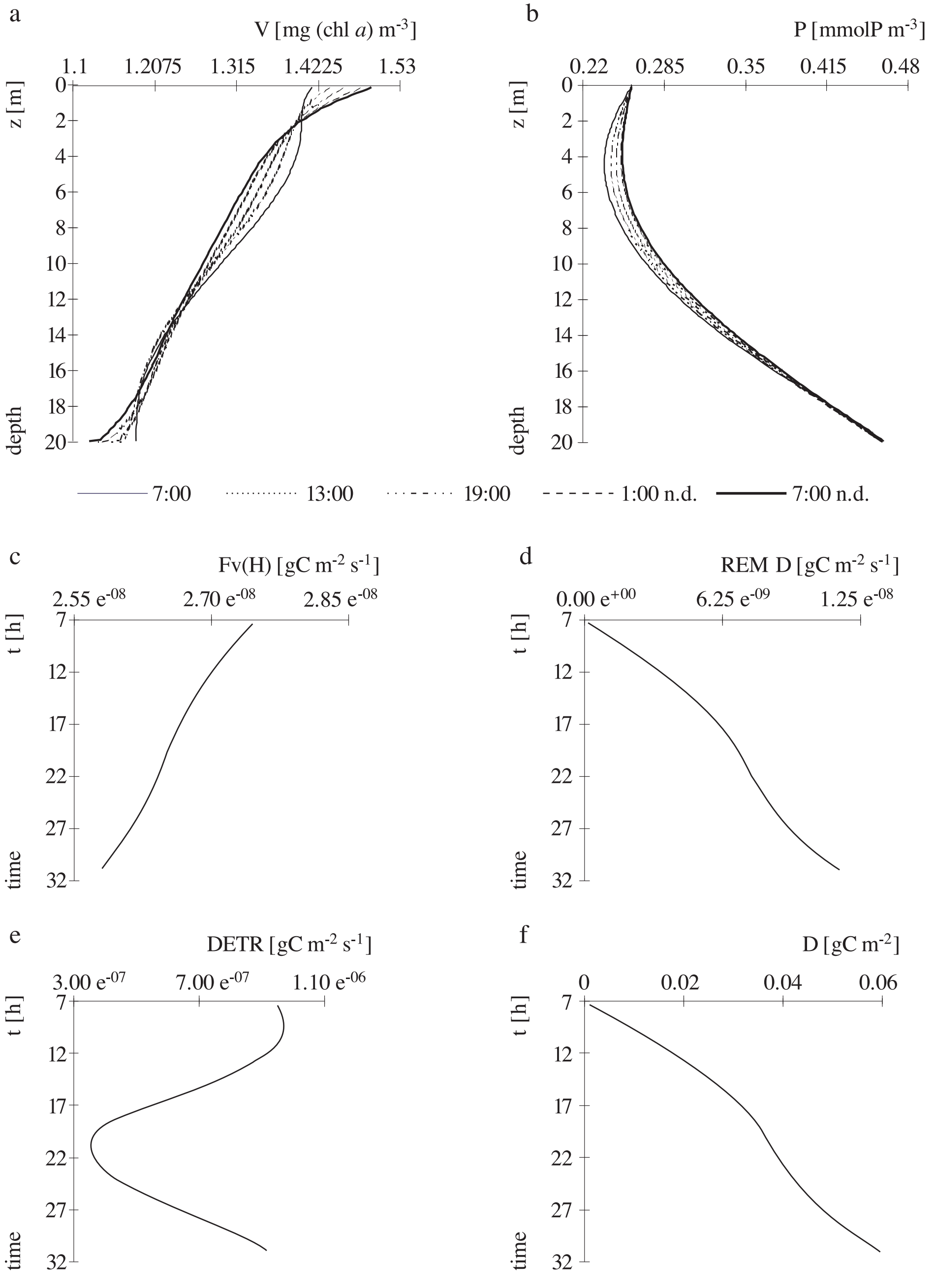

Fig. 7. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom *n* (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = 0.0352\,z + 0.3$, only production generated by phytosynthesis takes place and $S_a = 10^{-6}\,\mathrm{s}^{-1}$

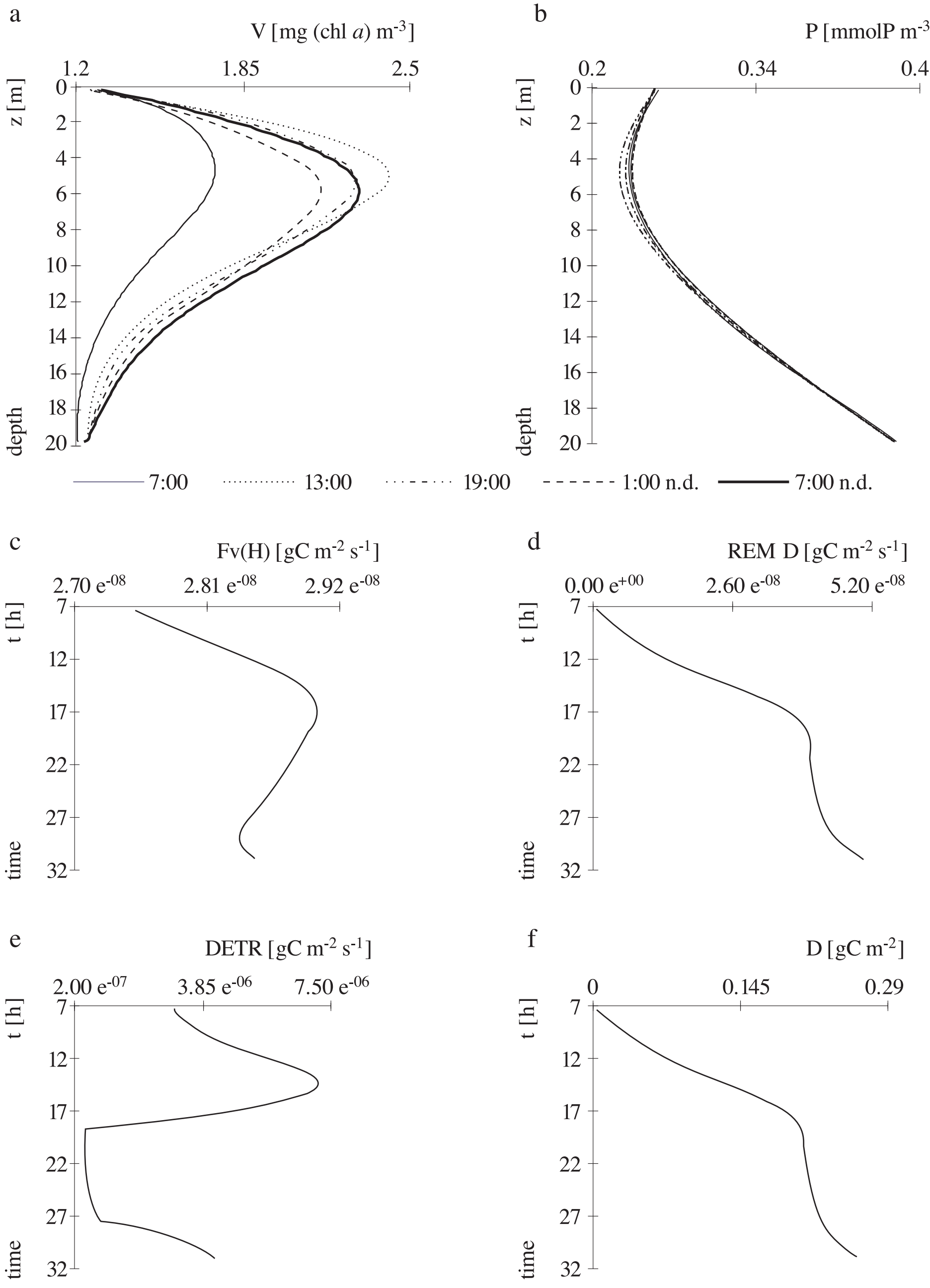

Fig. 8. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = 0.0352\,z + 0.3$, only production generated by phytosynthesis takes place and $S_a = 4.5 \times 10^{-5}\,\mathrm{s}^{-1}$

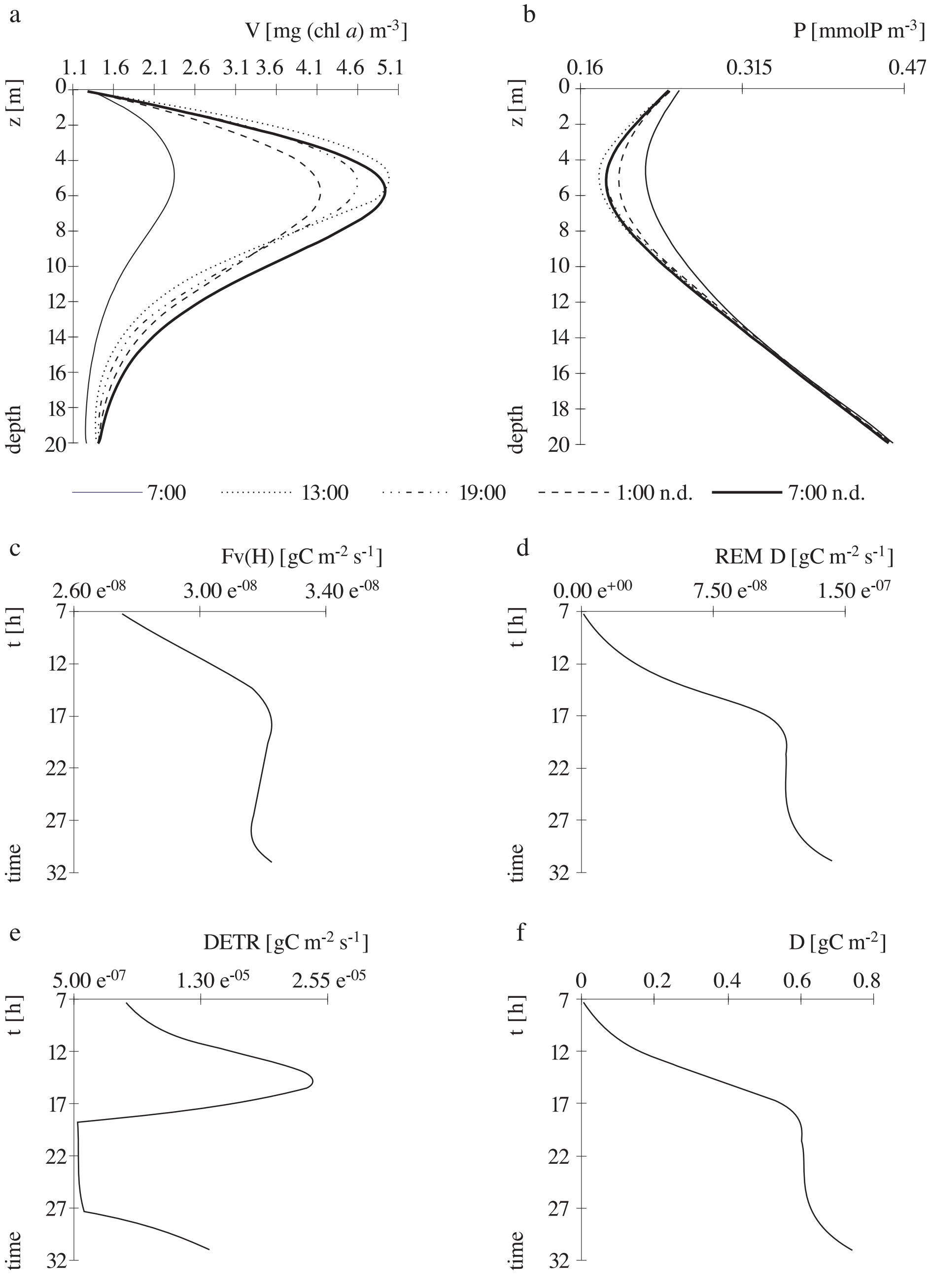

Fig. 9. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $f(z) = 0.0352\,z + 0.3$, only production generated by phytosynthesis takes place and $S_a = 10^{-4}\,\mathrm{s}^{-1}$

However, in this case, the simulations show that phytoplankton grazing by zooplankton does have a decisive influence on the chlorophyll *a* concentration field.

The simulations demonstrate that an increase in any of the investigated parameters (Figs. 7, 8 and 9) depends largely on the value of S_a. These functions increase in value as S_a does so. In this variant the increase in these functions is smaller than in variant 4.2 (Figs. 4, 5 and 6).

4.4. The influence of the nutrient half-saturation constant k_s on the variability of the investigated biological characteristics

The influence of the nutrient half-saturation constant k_s on the variability of the processes investigated and the chlorophyll *a* and nutrient concentration was analysed under the assumption that $K_z = 10^{-6}$ m^2 s^{-1}, $S_a = 23.1 \times 10^{-6}$ s^{-1}, $f(z) = 0.0352\,z + 0.3$ and nutrients are the limiting factor in primary production.

The simulations were carried out for different values of k_s:

case 1: the nutrient half-saturation constant is equal to
$k_s = 0.12$ mmolP m^{-3} (Fig. 10);

case 2: the nutrient half-saturation constant is equal to
$k_s = 0.6$ mmolP m^{-3} (Fig. 11).

The results indicate that, in all the cases, the chlorophyll *a* and nutrient concentration distributions and the parameters investigated differ to a very small degree with respect to their shapes. However, these functions are very different in value. The increase in the nutrient half-saturation constant k_s (case 2) causes a decrease the chlorophyll *a* concentration (Fig. 11a), something that is reflected by the declining values of the parameters investigated: the bottom flux of phytoplankton $F_V(H)$ (Fig. 11c) and the detrital material sedimenting out of the water column onto the bottom DETR (Fig. 11e). This means that these processes are directly dependent on the chlorophyll *a* concentration. However, the simulations show that a decrease in their values $F_V(H)$ and DETR leads to a substantial decline in the benthic detritus pool D (Fig. 11f) in comparison with case 1 (Fig. 10f).

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

The influence of the phytoplankton grazing by zooplankton on the variability of the biological characteristics was analysed under the assumption that nutrients are the factor limiting production increase, where $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}$ s^{-1} and $K_z = 10^{-4}$ m^2 s^{-1}.

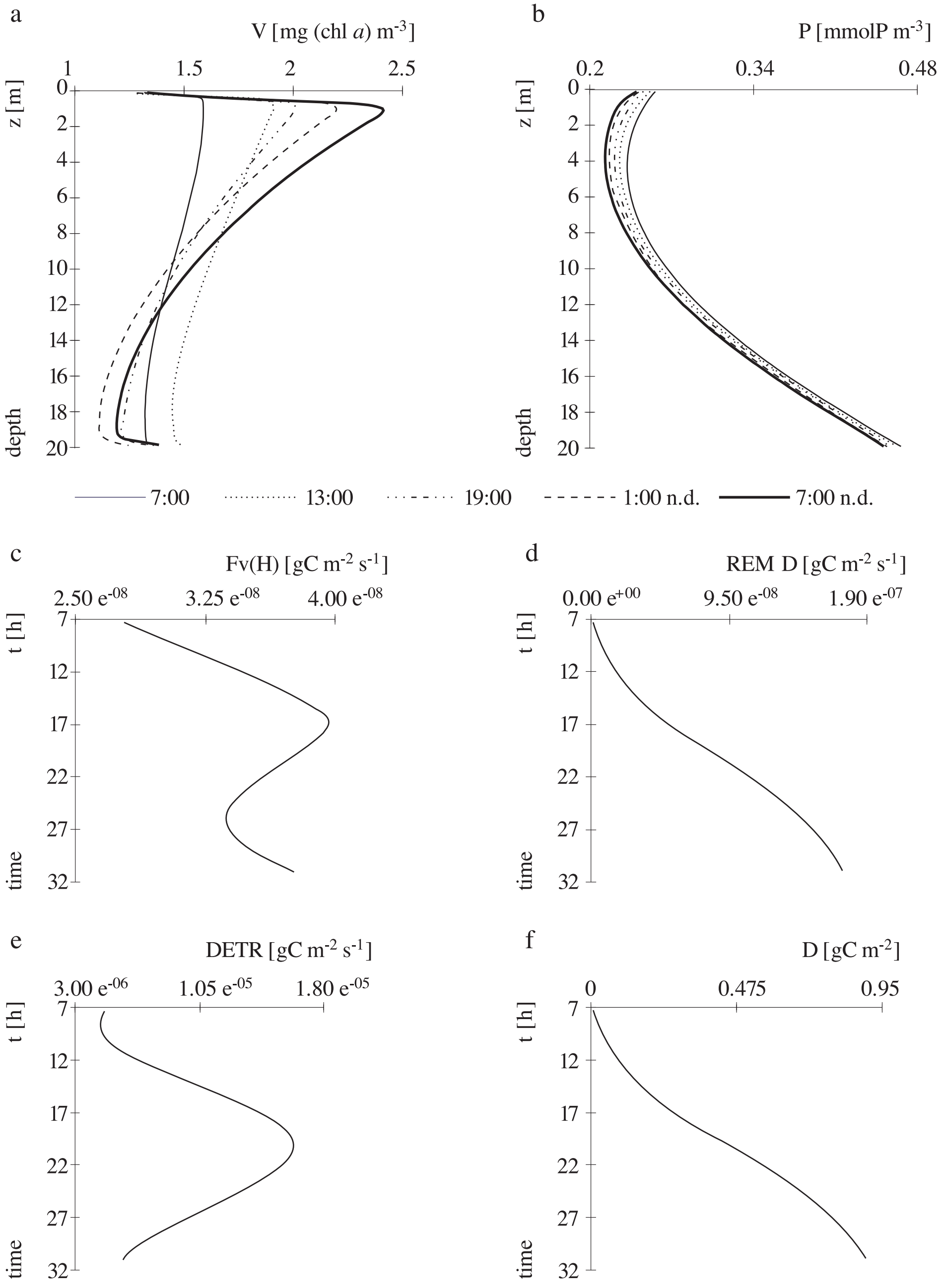

Fig. 10. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $f(z) = -0.00125\, z^2 + 0.05\, z + 0.5$, $K_z = 10^{-6}\,\mathrm{m^2\,s^{-1}}$, $S_a = 23.1 \times 10^{-6}\,\mathrm{s^{-1}}$, nutrients are the limiting factor in primary production and $k_s = 0.12$ mmolP $\mathrm{m^{-3}}$

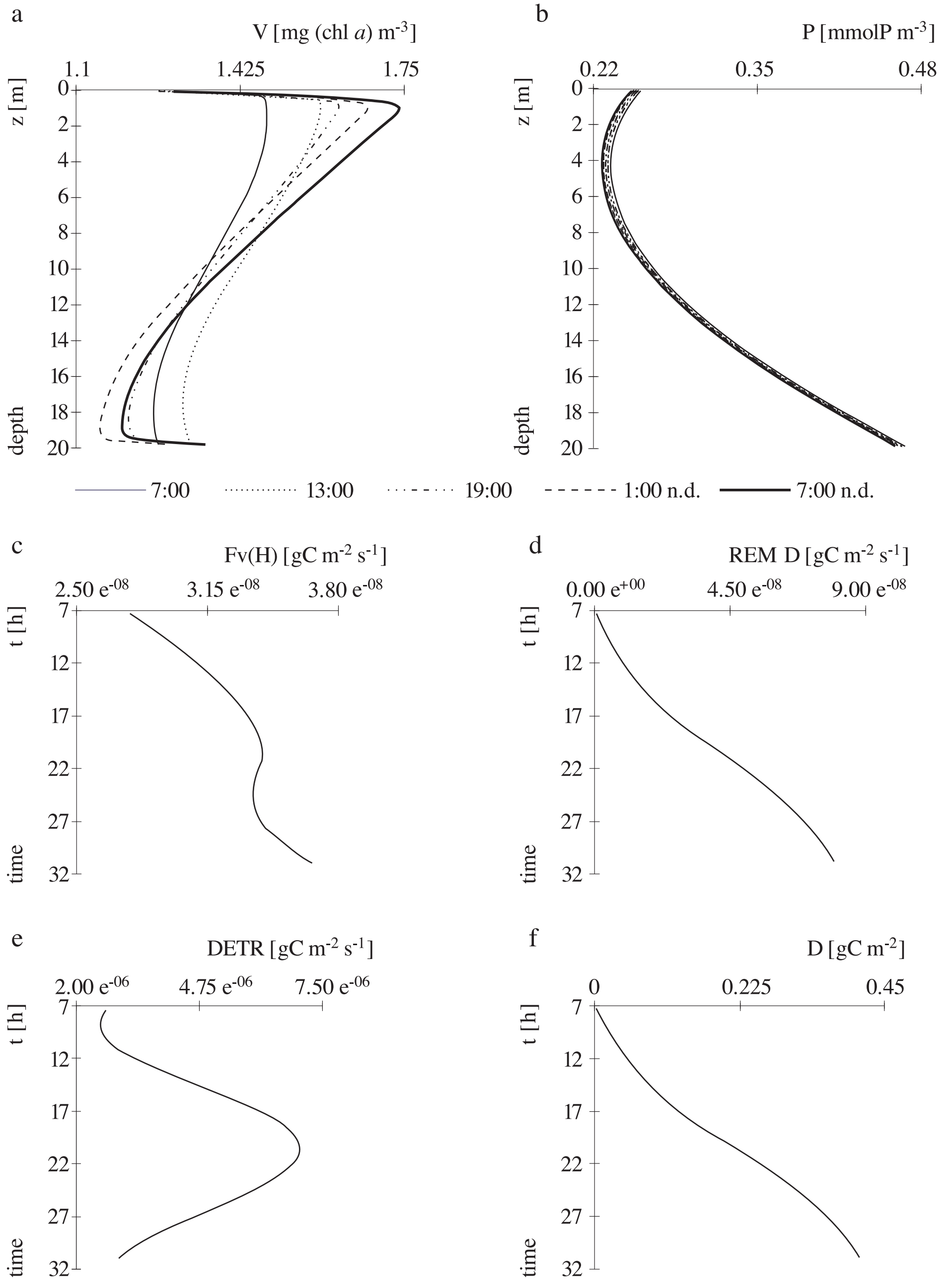

Fig. 11. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $f(z) = -0.00125\,z^2 + 0.05\,z + 0.5$, $K_z = 10^{-6}$ m^2 s^{-1}, $S_a = 23.1 \times 10^{-6}$ s^{-1}, nutrients are the limiting factor in primary production and $k_s = 0.6$ mmol(P) m^{-3}

Assuming further that grazing is horizontally uniform, the function $f(z)$ describing zooplankton distribution is linear and a second-degree polynomial (variant 4.5 A) or constant (variant 4.5 B). The coefficients of the polynomial can be determined either arbitrarily or from the experimental values of grazing coefficient at the following depths:

- at the free surface corresponding to the 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).

Variant A

For the calculations, the following assumption was made:
case 1: $f(z) = 0.02\,z + 0.5$ (Fig. 12);
case 2: $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$ (Fig. 13).

In all cases, the results of the simulations indicate that changes in the values of the function $f(z)$ describing zooplankton distribution exert hardly any influence on the characteristics examined with the exception of the bottom flux of phytoplankton $F_V(H)$ (Figs. 12c and 13c) which depend directly on the chlorophyll *a* concentration.

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 (Figs 12a and 13a).

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 (Dzierzbicka-Głowacka, 1996).

The distributions in Figs. 12a and 13a illustrate the considerable increase in the chlorophyll *a* concentration in the deeper layer.

This situation indubitably determines the influence of the benthic detritus pool D (Figs. 12f and 13f) through the remineralisation of detritus REM D (Figs. 12d and 13d) on the nutrient concentration distribution (Figs. 12b and 13b) (this situation did not occur in our earlier papers, which did not include the model V–P of the eq. (3) for benthic detritus D). However, this function does affect the chlorophyll *a* concentration through nutrient uptake by phytoplankton.

In all the cases, the nutrient concentration distributions (Figs. 12b and 13b) differ to a very small degree with respect to their shapes and values. The calculations also demonstrated that an increase in nutrient concentration appears in the deeper layer as in case of the chlorophyll *a* concentration.

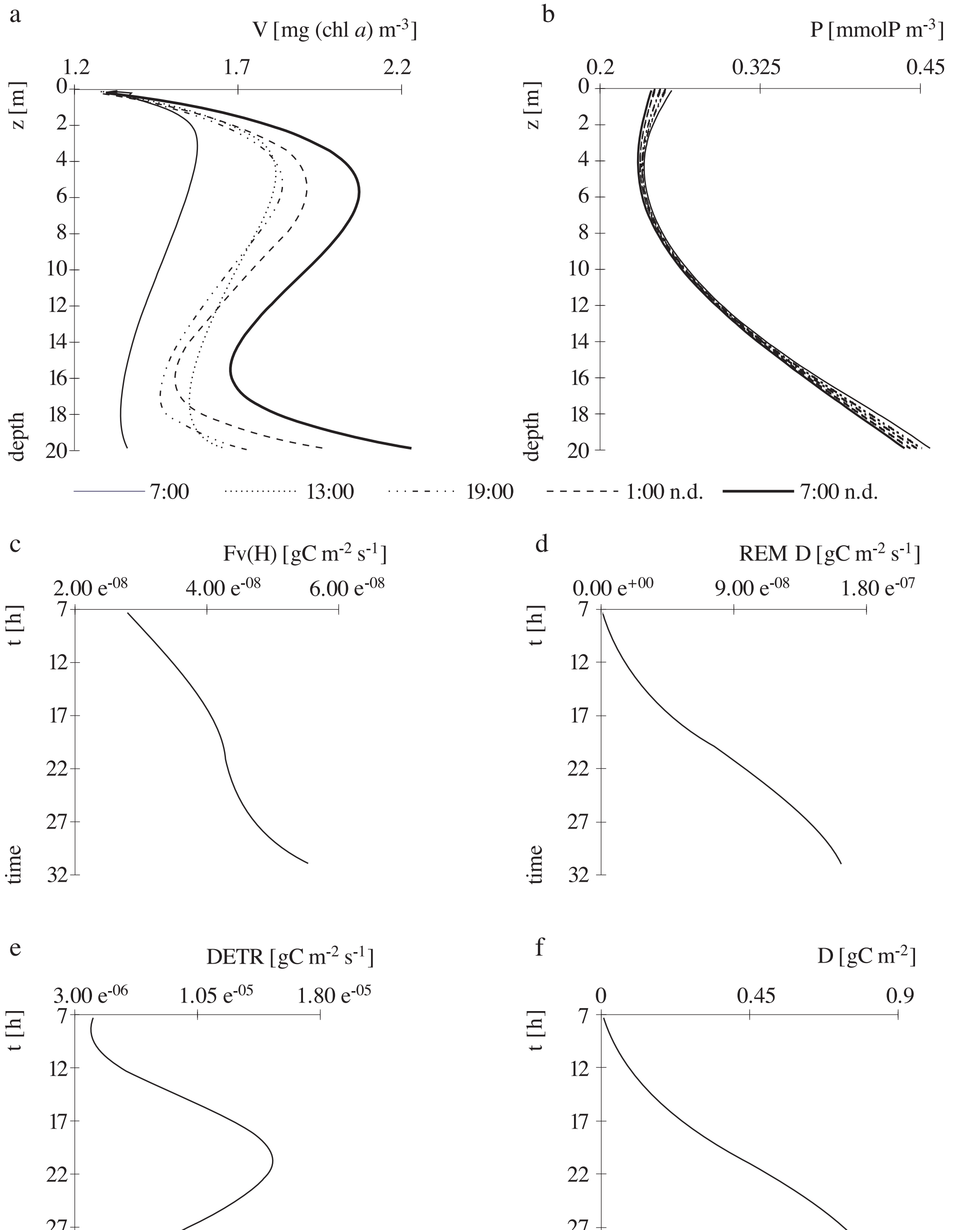

Fig. 12. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}\,\mathrm{s}^{-1}$, $f(z) = 0.02\,z + 0.5$ and nutrients are the limiting factor in primary production

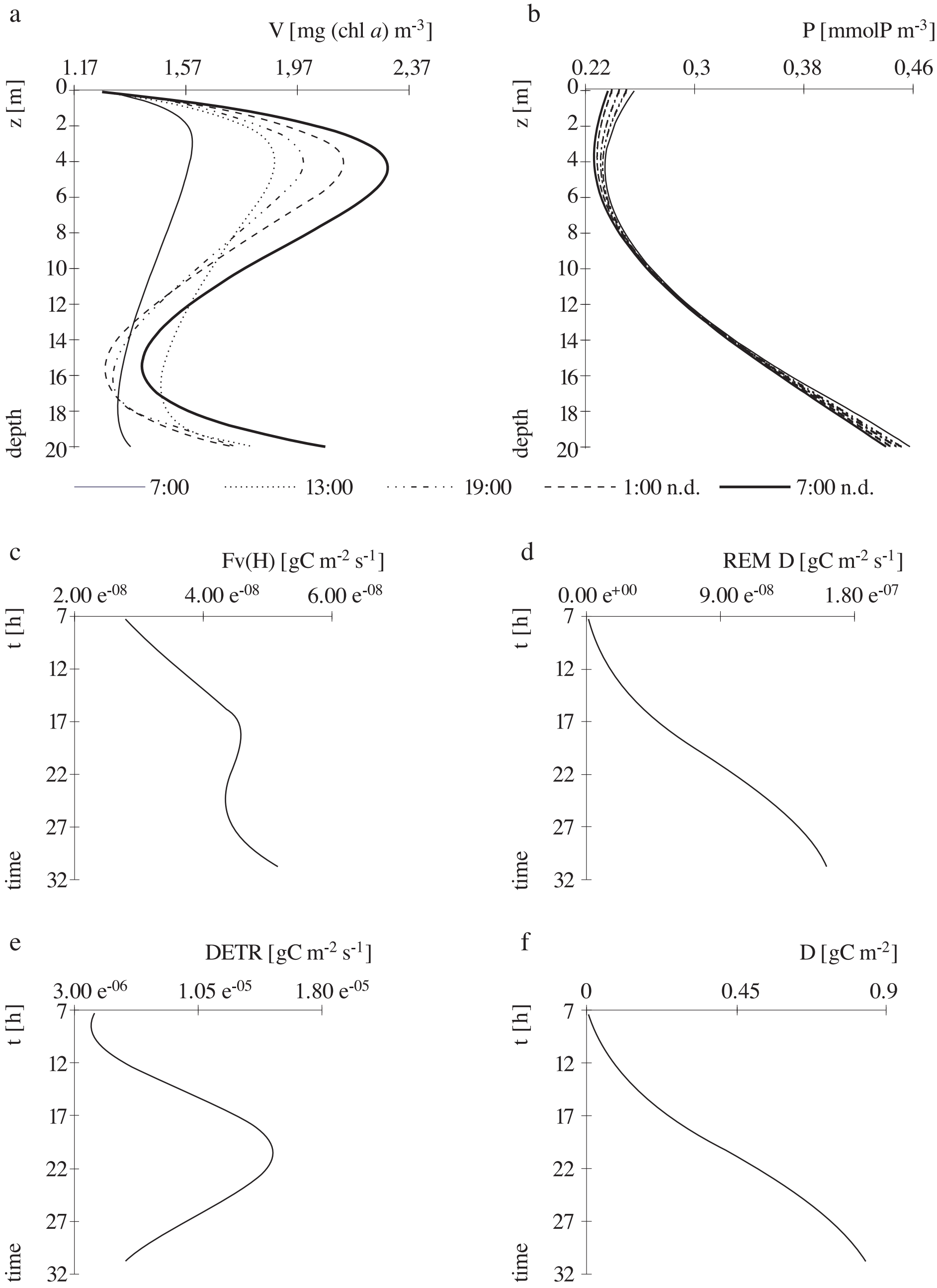

Fig. 13. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}\,\mathrm{s}^{-1}$, $f(z) = -0.00175\,z^2 + 0.07\,z + 0.15$ and nutrients are the limiting factor in primary production

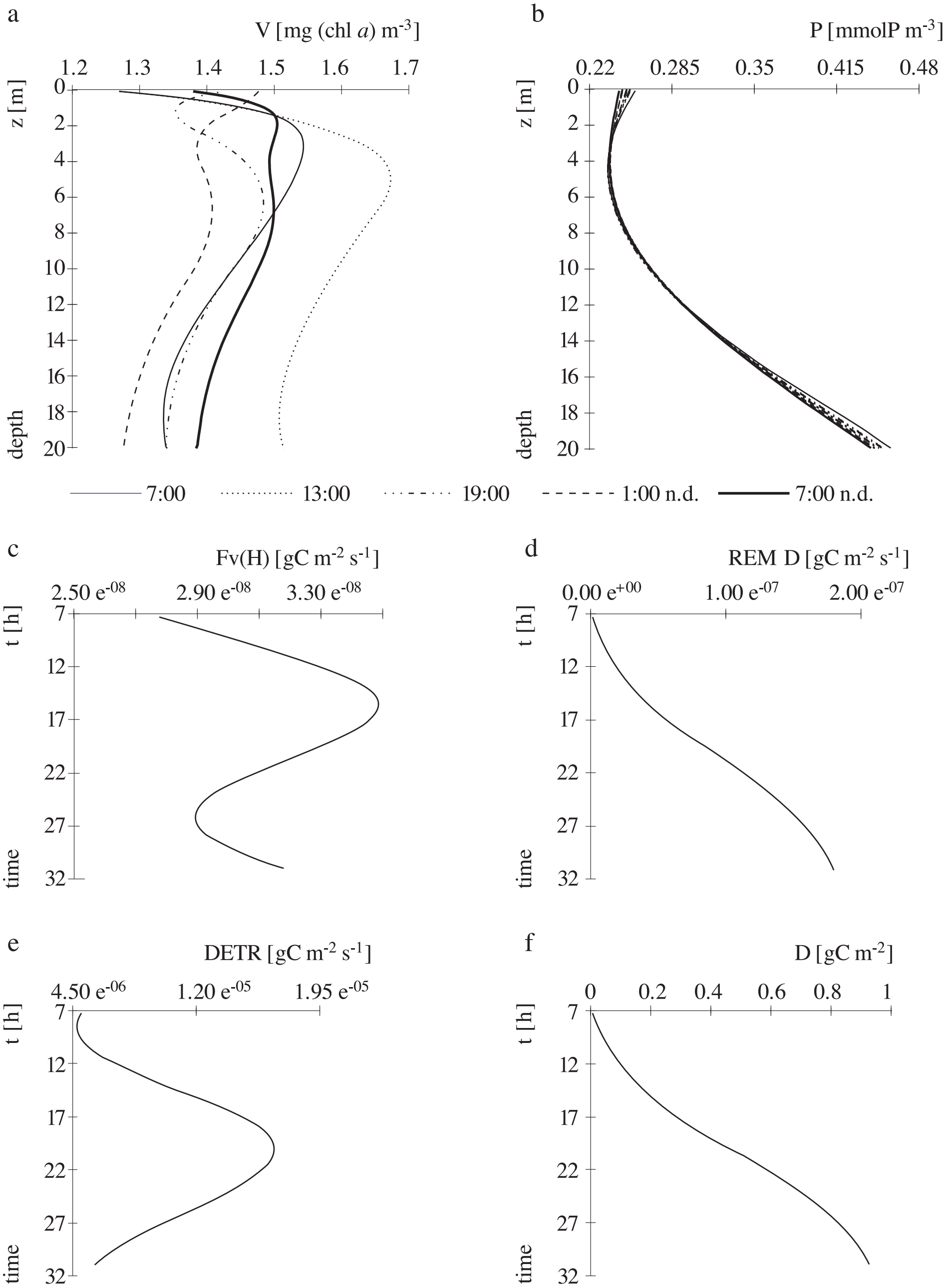

Fig. 14. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}\,\mathrm{s}^{-1}$, $f(z) = 0.9$ and nutrients are the limiting factor in primary production

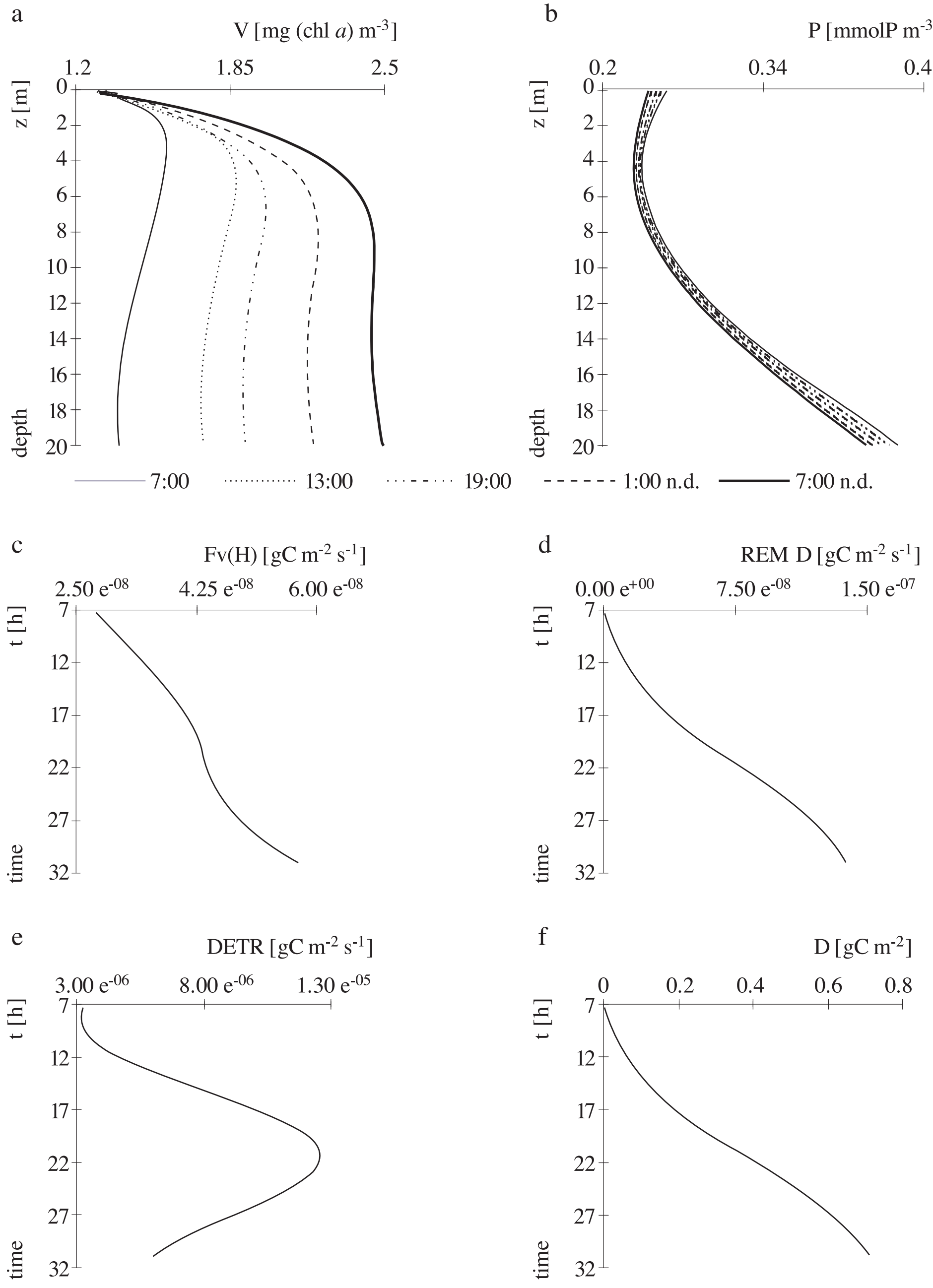

Fig. 15. Simulated biological characteristics: chlorophyll a concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom n (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}\,\mathrm{s}^{-1}$, $f(z) = 0.5$ and nutrients are the limiting factor in primary production

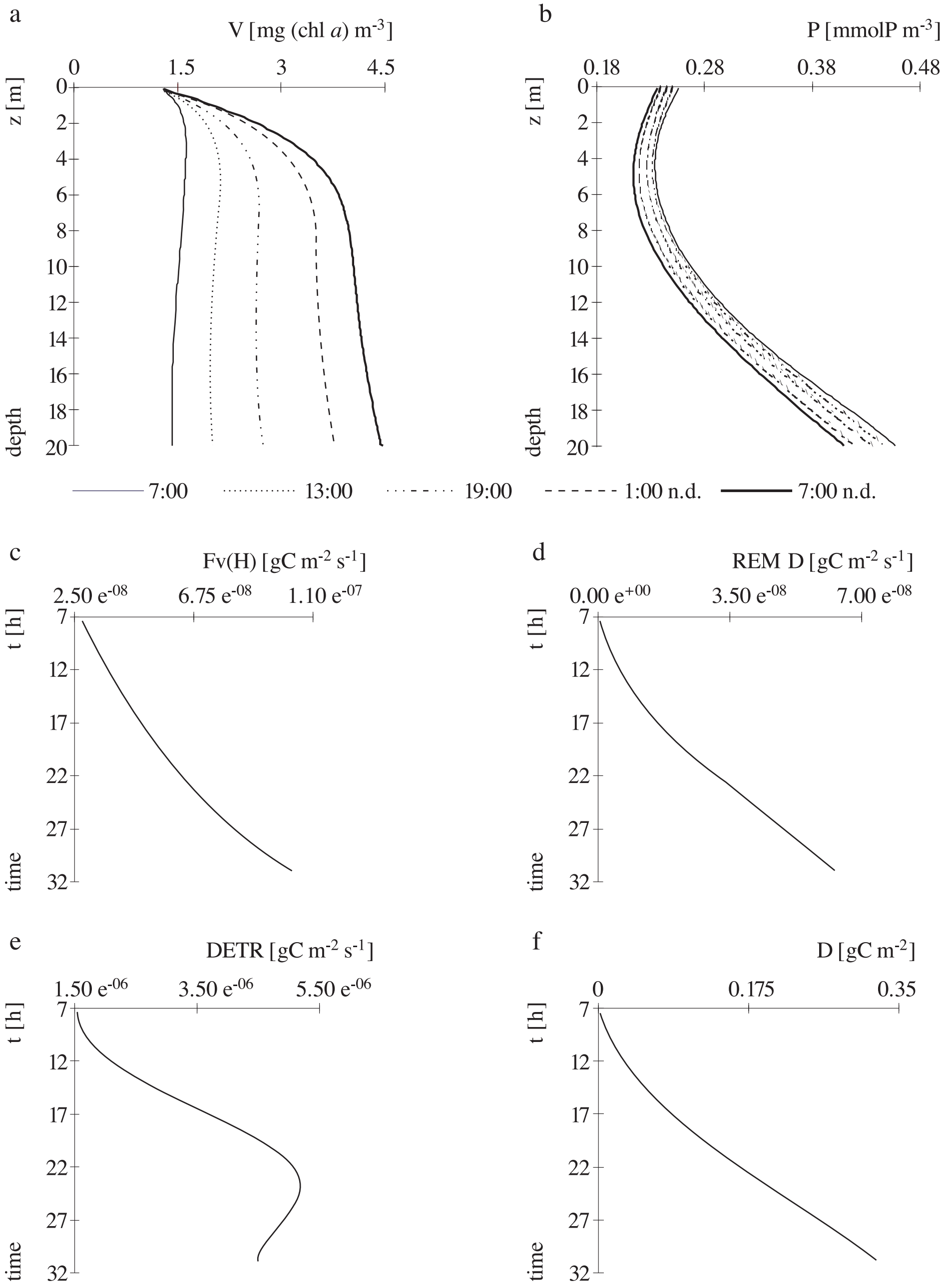

Fig. 16. Simulated biological characteristics: chlorophyll *a* concentration (a), nutrient concentration (b), bottom flux of phytoplankton (c), remineralisation of benthic detritus (d), detrital material sedimenting out of the water column onto the bottom *n* (e) and detritus pool at the bottom (f), assuming that $k_s = 0.32$ mmolP m^{-3}, $S_a = 23.1 \times 10^{-6}\,\mathrm{s}^{-1}$, $f(z) = 0.1$ and nutrients are the limiting factor in primary production

Variant B

For the calculations, the following assumption was made:
case 1: $f(z) = 0.9$ (Fig. 14);
case 2: $f(z) = 0.5$ (Fig. 15);
case 3: $f(z) = 0.1$ (Fig. 16).

The influence of the value of $f(z)$ describing the zooplankton distribution on the variability of the characteristics investigated was analysed under the same assumption as in variant A.

In all cases, the distribution of chlorophyll *a* concentration varies widely in shape and value. This applies principally to case 1, where the vertical distribution of zooplankton is equal to $f(z) = 0.9$, indicating that phytoplankton grazing is intensive (90% of its biomass) throughout the water column (Fig. 14a).

The results of these simulations indicate that the chlorophyll *a* concentration depends mainly on phytoplankton grazing in case 1. However, in cases 2 and 3, where $f(z)$ decreases in value, primary production has a considerable influence on the distribution function of chlorophyll *a* concentration, causing its value to increase.

The simulations show that the increase in the grazing coefficient causes a decrease in the chlorophyll *a* concentration (Figs. 14a, 15a and 16a) and an increase in the parameters studied with the exception of bottom flux of phytoplankton $F_V(H)$ (Figs. 14c, 15c and 16c).

This increase in the parameters investigated (Figs. 14d, 14e, 14f, 15d, 15e, 15f and 16d, 16e, 16f) is caused by the detrital material sedimenting out of the water column onto the bottom DETR, which depends mainly on the value of the grazing coefficient.

5. Discussion and conclusion

The simulating calculations showed that the changes in the values of selected biological and chemical parameters, *i.e.* the factor limiting production increase, the maximum rate of production increase, the nutrient half-saturation constant and the function characterising the vertical distribution of zooplankton, directly influence the processes investigated, which largely affect the shape and value of the distribution functions of chlorophyll *a* and nutrient concentrations.

1. The results of the numerical studies demonstrate that, when phytoplankton cell growth is controlled by the nutrient concentration in the water (variant 4.1, case 1), the values of all the processes investigated, *i. e.* the bottom flux of phytoplankton $F_V(H)$, the remineralisation of detritus REM D, the detrital material sedimenting out of the water

column onto the bottom DETR and benthic detritus pool D, are higher than in case 2 (variant 4.1), where the production generated by photosynthesis takes place.

This leads to a substantial rise in the chlorophyll a concentration in the deeper part of the layer. The increase in this function is due to the nutrient concentration, which at the bottom of this basin depends on benthic regeneration.

The simulations indicate in this case (variant 4.1) that the distribution function of chlorophyll a concentration interacts with the benthic detritus.

In case 2 (variant 4.1), however, during the entire numerical experiment when phytoplankton is 'feeding on' light and sufficient nutrients are present, the chlorophyll a concentration influences the processes investigated, but the reverse does not occur, *i. e.* the processes investigated have no effect on the chlorophyll a concentration.

2. The results of the numerical investigations show that the maximum rate of production increase S_a establishes to a considerable extent the magnitudes of the biological characteristics in question. In all cases, the increase in the value of S_a causes an increase in the chlorophyll a concentration. The exception is case 1 (variant 4.2 and 4.3) when the maximum rate of production increase is equal to $S_a = 10^{-6}$ s^{-1}. The calculations demonstrate that the chlorophyll a concentration decreases.

   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, phytoplankton grazing by zooplankton does affect the phytoplankton concentration field to a significant degree.

   The simulating calculations show that the increase in the value of S_a causes not only the processes investigated to intensify. This increase is much higher in the case when nutrients are the factor limiting primary production (variant 4.2).

3. The nutrient half-saturation constant has a considerable influence on the variability of the characteristics investigated. The calculations indicate that the increase in the value of k_s causes the primary production to decrease and a consequent decline in the the chlorophyll a concentration. The decrease in this function leads to a substantial fall in the processes studied.

4. The results of these simulations show that in areas where phytoplankton grazing is intensive, non-homogeneities occur in the chlorophyll a concentration distribution function owing to the decrease in chlorophyll a concentration.

   In variant 4.5A in all cases where the function $f(z)$ describing zooplankton distribution is linear and a second-degree polynomial, phytoplankton grazing by zooplankton does not have a very great effect on the characteristics examined with the exception of the bottom flux of phytoplankton $F_V(H)$, which depends closely on the chlorophyll a concentration. However, in variant 4.5B, where $f(z)$ is constant, the shape and value of the chlorophyll a concentration distribution function is very different. Analysis of the numerical studies also demonstrates that the chlorophyll a concentration decreases with a rising grazing coefficient. Moreover, the values of this increase with intensifying phytoplankton grazing with the exception of $F_V(H)$. The simulations indicate that as a result, grazing phytoplankton has a greater influence on the benthic detritus pool than on chlorophyll a concentration.

5. The results of the numerical investigations show that taking into consideration eq. (3), describing the temporal variations in the detritus pool at the bottom, in the V–P–D model is an important aspect in modelling the chlorophyll a concentraction distribution function in the water.

   The numerical studies and the computer simulations indicated the dominant influence of primary production and phytoplankton grazing on the variability of the biological characteristics investigated.

References

Billen G., Lancelot C., Maybeck M., 1991, *N, P, and Si retention along the aquatic continuum formland to ocean*, [in:] *Ocean margin processes in global change*, R. F. C. Mantoura, J. M. Martin and R. Wollast (eds.), Phys., Chem. and Earth Sci. Res. Rep., John Wiley and Sons, Chichester, 9, 19–44.

Dzierzbicka-Głowacka L., 1994a, *Mathematical modelling of the chlorophyll a distribution function in a stratified sea*, Ph. D. thesis, Uniw. Gdańsk, Gdynia, (in Polish).

Dzierzbicka-Głowacka L., 1994b, *Numerical analysis of the influence of the grazing on the two-dimensional distribution function of the phytoplankton concentration in a stratified sea*, Oceanologia, 36 (2), 155–173.

Dzierzbicka-Głowacka L., 1996, *Mathematical modelling of chlorophyll a concentration in a stratified medium*, Oceanologia, 38 (2), 153–193.

Dzierzbicka-Głowacka L., Zieliński A. 1997, *Numerical studies of the influence of the nutrient regeneration mechanism on the chlorophyll a concentration in a stratified sea*, Oceanologia, 39 (1), 55–82.

Dybern B., Hansen H. P., 1989, *International Council for the Exploration of the Sea*, Cooperat. Res. Rep., Copenhagen, 163 pp.

Lehman I. T., Botkin D. B., Likens G. E., 1975, *The assumptions and radionales of a computer model of phytoplankton population dynamics*, Limnol. Oceanogr., 20, 343–364.

Postma H., Rommets J. W., 1984, *Variations of particulate organic carbon in the central North Sea*, Neth. J. Sea Res., 18, 31–50.

Potter D. (ed.), 1982, *Computation physics*, John Wiley and Sons, London–New York–Sydney–Toronto, 278 pp.

Radach G., 1983, *Simulations of phytoplankton dynamics and their interaction with other system components during FLEX '76*, [in:] *North Sea dynamics*, J. Sündermann and W. Lenz (eds.), Springer Verlag, Berlin–Heidelberg–New York, 584–632.

Radach G., Berg J., Hagmeier E., 1990, *Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at Helgoland and LV Elbe I in the German Bight*, Cont. Shelf Res., 10, 305–328.

Raymont J. E., 1980, *Plankton and productivity in the oceans. Phytoplankton*, Pergamon Press, Toronto, 1, 489 pp.

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

Steele J. H., 1974, *The structure of marine ecosystems*, Harvard Univ. Press, Cambridge, 128 pp.

Appendix

1. Notation

Symbol	Description
DETR	detrital material at the bottom
DIF P	turbulent diffusion of nutrients
DIF V	turbulent diffusion of phytoplankton
EXC	excretion of dissolved metabolic products
FEC	faecal pellet production
$F_{P(z)}$	flux condition at the boundary for nutrients
$F_{V(z)}$	flux condition at the boundary for phytoplankton
GRA	copepod grazing
MOR V	phytoplankton mortality
MOR Z	zooplankton mortality
PRE	gross primary production
REL	nutrient release during dark respiration
REM D	remineralisation of benthic detritus
REMI	total remineralisation in the water column
REM F	remineralisation of faecal pellets
REM m	remineralisation of dead phytoplankton
REM Z	remineralisation of dead zooplankton
RES	total respiration
SEDI	losses of particulate material from the water column (MOR V + FEC + MOR Z) to the bottom
SINK	sinking of living algae
UPT	nutrient uptake
a	C:Chl ratio
A	assimilation number
D	detritus concentration
d_i	light limitation factor
d_p	nutrient limitation factor
f	function describing zooplankton distribution
g	P:C ratio
k_s	half-saturation constant for phosphate
K_z	turbulent diffusion coefficient
n_e	percentage of ingestion, regenerated as soluble zooplankton excreta

Notation (continued)

Symbol	Description
n_f	percentage of ingestion egested as faecal material
n_z	percentage of ingestion ending up as dead zooplankton
P	nutrient concentration
p_f	percentage of remineralised faecal material in the water column
p_m	percentage of remineralised dead organic matter in the water column
p_z	percentage of remineralised dead zooplankton in the water column
r_d	remineralisation rate of benthic detritus
S_a	maximum growth rate
w_z	sinking velocity of phytoplankton
V	phytoplankton concentration

2. Algorithm of the V–P–D model solution

Equation system (1)–(2) with conditions (17)–(23) is solved numerically by using the indirect Crank-Nicholson method (Potter, 1982) in an area of $0 \leq z \leq Z$ by digitising this region with a variable step δ into (i) elements (the number of elements fulfils the condition $1 \leq i \leq n$. The detailed algorithm of the solution to the V–P model can be found in Dzierzbicka-Głowacka (1994b). In this method the first and second equation of equation system (1)–(2) with appropriate initial and boundary conditions for $i = 1$ and $i = n$, can be written in the form:

$$V_1^{t+1} = V_1^t \left\{ \Delta t(\alpha_1 - \mathrm{GRA}_1 \alpha_1) + 1 \right\}, \tag{24}$$

$$P_1^{t+1} = P_1^t + \Delta t V_1^t a \beta_1, \tag{25}$$

where
$\alpha_1 = \mathrm{PRE}_1 - \mathrm{MOR}\, V_1 - \mathrm{RES}_1$,
$\beta_1 = \mathrm{REL}_1 + \mathrm{REMI}_1 + \mathrm{EXC}_1 - \mathrm{UPT}_1$.

$$V_n^{t+1} = \frac{V_{n-1}^{t+1} w_n + V_n^t \left(1 + \alpha_n \Delta t(1 - \mathrm{GRA}_n) - w_n\right) + V_{n-1}^t w_n}{1 + w_n}, \tag{26}$$

$$P_n = P_n^t + a \left(gr_d \Delta t D^t + V_n^t \Delta t \beta_n \right), \tag{27}$$

where
$\alpha_n = \mathrm{PRE}_n - \mathrm{MOR}\, V_n - \mathrm{RES}_n$,
$\beta_n = \mathrm{REL}_n + \mathrm{REMI}_n + \mathrm{EXC}_n - \mathrm{UPT}_n$.

The third equation, an ordinary differential equation, describes the development of detritus at the bottom and is solved on the basis of the well-known Euler method (Potter, 1982):

$$\frac{dD}{\partial t} + f(D, t) = 0, \tag{28}$$

where $D(t) = D$,

$$f(D, t) \equiv -w_z V(H, t) + r_d D(t) - \mathrm{DETR}(t). \tag{29}$$

Eq. (28) can be integrated the time grid over a certain time interval Δt:

$$D^{m+1} = D^m - \int_{t^m}^{t^{m+1}} f(D, t) \Delta t, \tag{30}$$

when $\Delta t = t^{m+1} - t^m$.

For the simple ordinary differential equations we use the indirect method, in which the integral in the eq. (29) is second order, introducing the average values of the function f at the time between the time levels t^m and t^{m+1}:

$$D^{m+1} = D^m - \left\{ f\left(D^m, t^m\right) + f\left(D^{m+1}, t^{m+1}\right) \right\} \frac{\Delta t}{2}. \tag{31}$$

Substituting f from the eq. (28) in eq. (30) and applying the initial condition from eq. (17) ($D(t=0) = D_o = 0$), we obtain eq. (31)

$$\begin{aligned} D^{m+1} &= \frac{D^m \left(1 - r_d \frac{\Delta t}{2}\right) + w_z(H) \frac{\Delta t}{2} \left(V^m + V^{m+1}\right)}{1 + r_d \frac{\Delta t}{2}} + \\ &+ \frac{\frac{\Delta t}{2} \left(\mathrm{DETR}^m + \mathrm{DETR}^{m+1}\right)}{1 + r_d \frac{\Delta t}{2}}, \end{aligned} \tag{32}$$

which is the sought-after solution to eq. (3).

This method is a second order one; it remains for us to designate the stability criterion. Assuming that the dependent variable D^m at the time t^m is encumbered with error ε^m, the error of the dependent variable D^{m+1} can be found. With eq. (30) we get

$$\begin{aligned} D^{m+1} &+ \varepsilon^{m+1} = D^m + \\ &+ \varepsilon^m \left\{ f\left(D^m + \varepsilon^m, t^m\right) + f\left(D^{m+1} + \varepsilon^{m+1}, t^{m+1}\right) \right\} \frac{\Delta t}{2}. \end{aligned} \tag{33}$$

The function f can be expanded at the Taylor series round D^m for $D = D^m + \varepsilon^m$ if the error ε^m is small enough.

$$f(D^m + \varepsilon^m, t^m) = f(D^m, t^m) + \frac{\partial f}{\partial D} |_m \, \varepsilon^m + O(\varepsilon^m). \tag{34}$$

Using eqs. (30) and (3) we get the following terms for the transfer of the slight error:

$$\begin{aligned} \varepsilon^{m+1} &= \varepsilon^m - \frac{\partial f}{\partial D} |_m \, \frac{\Delta t}{2} \varepsilon^m + O(\varepsilon^m) + \\ &+ \frac{\partial f}{\partial D} |_{m+1} \, \frac{\Delta t}{2} \varepsilon^{m+1} 1 + O(\varepsilon^{m+1}), \end{aligned} \tag{35}$$

$$\varepsilon^{m+1} \left(1 + \frac{\partial f}{\partial D} |_{m+1} \, \frac{\Delta t}{2}\right) = \varepsilon^m \left(1 - \frac{\partial f}{\partial D} |_m \, \frac{\Delta t}{2}\right), \tag{36}$$

$$\varepsilon^{m+1} = \varepsilon^m \frac{1 - \frac{\partial f}{\partial D} |_m \, \frac{\Delta t}{2}}{1 + \frac{\partial f}{\partial D} |_{m+1} \, \frac{\Delta t}{2}}. \tag{37}$$

The coefficient of amplification g takes the form:

$$g = \frac{1 - \frac{\partial f}{\partial D}\,\big|_m\, \frac{\Delta t}{2}}{1 + \frac{\partial f}{\partial D}\,\big|_{m+1}\, \frac{\Delta t}{2}}. \tag{38}$$

The modulus of coefficient g is smaller than that for equations $\left(\frac{\partial f}{\partial D} > 0\right)$; therefore this method is absolutely stable at every time step.