An algorithm for calculating the concentration of phytoplankton in a stratified sea with respect to the daily migration of zooplankton. Part 2. Numerical simulation

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Abstract

The numerical studies were carried out using a (nutrient–phytoplankton–zooplankton–detritus) biological model with a well-developed regeneration block. This paper presents the time-dependent vertical distributions of biological characteristics (concentrations nutrients, phytoplankton and zooplankton and benthic detritus pool) on the assumption that the horizontal distribution of these parameters is uniform. The calculations were made in an area $0 \leq z \leq 20$ m with a vertical scale step of 10 cm and a time scale step of 15 min. The experimental data, gathered during the PEX′86 international scientific experiment of the Baltic states, and those by the International Council for the Exploration of the Sea, were used as the input data for the calculations.

1. Introduction

The nutrient–phytoplankton–zooplankton–detritus model, described in part 1 (section 4) and in greater detail in Dzierzbicka-Głowacka (1996) with a fully-developed regeneration mechanism (Dzierzbicka-Głowacka and Zieliński, 1997a,b) that takes account of the daily migration of zooplankton, was used to simulate the influence of selected biological parameters on the phytoplankton, zooplankton and nutrient distributions and benthic detritus pool.

These parameters were the factor limiting production increase, the maximum rate of production increase, the nutrient half-saturation constant, the coefficient denoting the mean intensity of primary production, the function describing the percentage of grazed material at every depth and the coefficient of the time during which the maximum grazing phytoplankton occurred.

The simplified phosphorus cycle in the P–V–Z–D biological model (Fig. 1) incorporates formulations of the primary production, grazing phytoplankton by zooplankton and regeneration within the mixed layer, at the lower depths and at the bottom.

This paper presents the time-dependent vertical distributions of the biological characteristics 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 resolution of 10 cm and a time resolution of 15 min.

2. Data for the simulation studies

The phytoplankton, zooplankton and phosphate concentrations for $0 \leq z \leq 20$ m at $t = 6.00$ h were taken to be the initial concentrations. They are as follows:

$$V(z, t_o) = 0.0644 \text{ gC m}^{-3};$$

$$Z(z, t_o) = 0.789 \text{ gC m}^{-3};$$

$$P(z, t_o) = 0.36 \text{ mmolP m}^{-3}.$$

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 measured in the study area (AN1) on 26 April 1986 are presented elsewhere (Dzierzbicka-Głowacka, 1994a, 1996). A detailed description of the experiment as well as the list of parameters measured, the geographical coordinates of the PEX′86 experimental area stations and their distribution are given in the final report by Dybern and Hansen (1989). The half-saturation constant for phosphate, $k_s = 0.32$ mmolP m^{-3}, was adopted from Lehman *et al.* (1975) and Raymont (1980).

The coefficients related to the regeneration process, which describe those fractions of dead phytoplankton p_m, zooplankton p_z, and faecal material p_f, which are immediately recycled in the water column are approximately equal (0.2; Postma and Rommets, 1984). The remineralisation rate for benthic detritus, r_d is 0.0167 d^{-1} (Radach *et al.*, 1990).

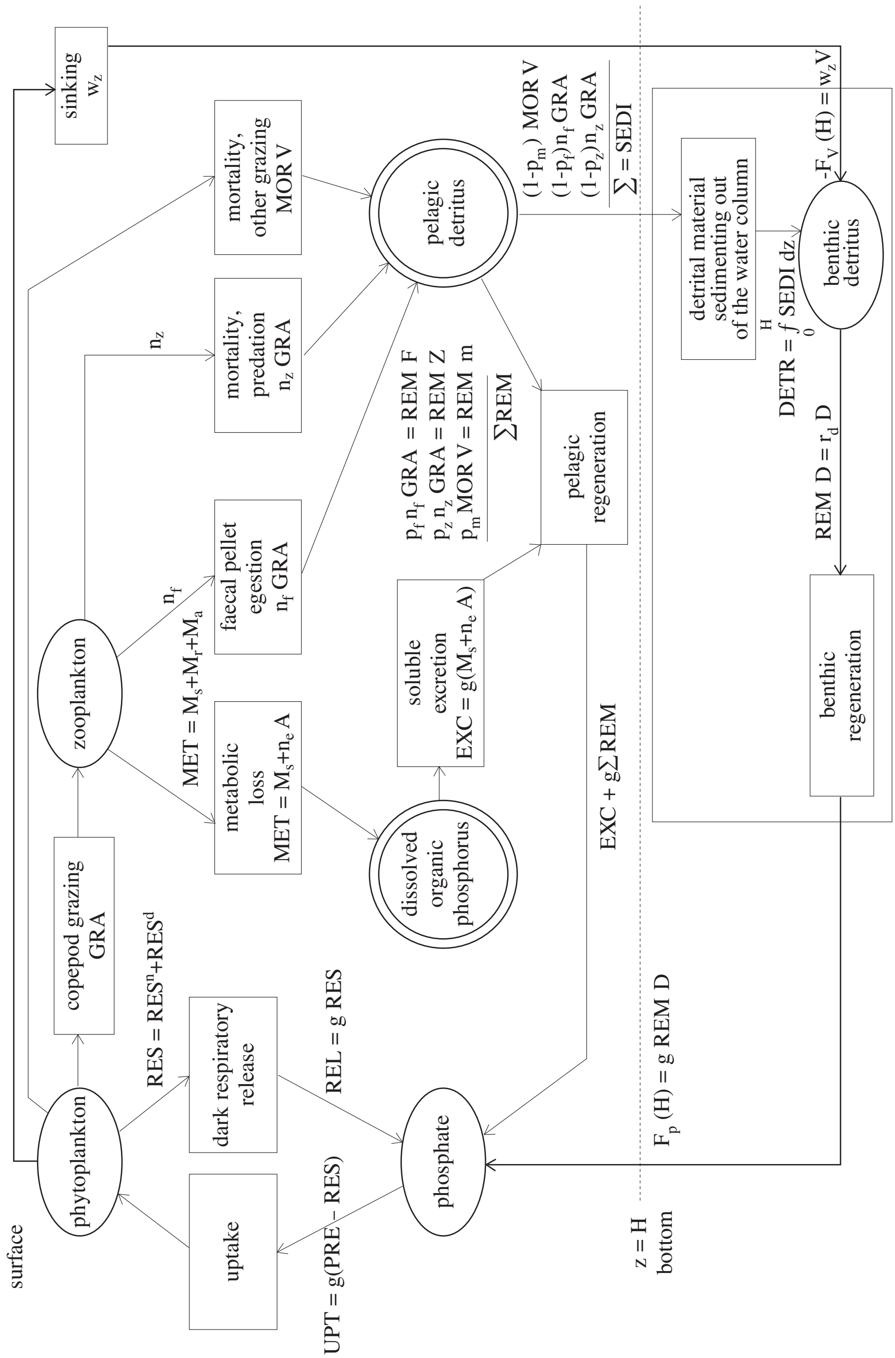

Fig. 1. Simplified phosphorus cycle of the biological upper layer model

The coefficients defining the material grazed and regenerated as soluble excretion of zooplankton n_e, faecal material n_f and dead zooplankton n_z are assumed equal to be 0.33 Steele (1974). The coefficient defining the basic metabolism M_s is 5×10^{-6}. The ratios of organic carbon to chlorophyll (C:Chl) a and of phosphorus to organic carbon (P:C) g were measured experimentally during the PEX′86; they average 0.046 gC $(\mathrm{mgChl})^{-1}$ for a (Kaczmarek, personal communication) and 0.06944 mmolP $(\mathrm{gC})^{-1}$ for g (Radach, 1983).

Because of the lack of experimental data (PEX′86), the phytoplankton mortality and respiration rates were described with the use of the constant coefficients taken from the data by Radach and Moll (1993); they were mm $= 5 \times 10^{-7}$ s^{-1} and $m_v^n = 0.1$, $m_v^d = 0.05$ respectively.

The coefficient of relative amplitude of the phytoplankton biomass variability a_w and the coefficient of time during which the maximum zooplankton concentration occurred in the upper layer t_0 used earlier by Dzierzbicka-Głowacka (1994b) were taken from Renk *et al.* (1983). These coefficients are 0.6 and 23.25 h respectively. 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}) characteristic of natural ecosystems, and within a realistic range of the changes of the average vertical suspension sedimentation rate ($2.2 \times 10^{-7} \le w_z \le 5.1 \times 10^{-7}$ m s^{-1}).

The calculations were carried out for the constant 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 the zooplankton (a), phytoplankton (b), nutrient concentration (c) and detritus pool at the bottom (d).

3. Results of simulation studies

The results of the numerical simulation of the effect of selected biological and chemical conditions on the behaviour of the zooplankton, phytoplankton and nutrient concentration distribution functions and the benthic detritus pool are presented in this section.

These parameters, namely, the factor limiting production increase, the maximum rate of production increase S_a, the nutrient half-saturation constant k_s, the coefficient PP denoting the mean production rate, the function $f(z)$ describing the percentage of grazed material at the depth z, and the coefficient of time t_o during which the maximum phytoplankton grazing occurs, are responsible for the shape and values of the zooplankton, phytoplankton and nutrient concentration distribution functions.

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

The influence of the nutrient half-saturation constant k_s on the variability of biological characteristics was analysed, given that K_z is 10^{-4} m^2 s^{-1}, S_a is 1.5×10^{-5} s^{-1}, $f(z)$ is $-0.00175\,z^2 + 0.08\,z + 0.15$, the primary production is nutrient-limited and the coefficient PP denotes the mean primary production rate ($PP = \frac{P}{(P+k_s)} S_a V(z,t)$, where the mean nutrient concentration is 0.36 mmolP m^{-3}).

The simulations were carried out for different values of k_s:

case 1: $k_s = 0.12$ mmolP m^{-3} (Fig. 2);

case 2: $k_s = 0.36$ mmolP m^{-3} (Fig. 3);

case 3: $k_s = 0.6$ mmolP m^{-3} (Fig. 4).

Given that the phytoplankton growth is controlled by the nutrient concentration, all the distributions of zooplankton and nutrient concentrations were different with respect to shape and value. The results show that the phytoplankton distributions and benthic detritus pool are almost identical in shape but differ quantitatively.

Analysis of the zooplankton distributions (Fig. 2a) shows that this function decreases during the daytime in case 1 ($k_s = 0.12$ mmolP m^{-3}); however, during the evening hours and at night, this function increases. The results of the simulations show that at night, when the nutrient half-saturation constant k_s is equal to 0.36 mmolP m^{-3}, the increase in the function of the zooplankton distribution (Fig. 3a) is smaller compared to case 1. However, in case 3 ($k_s = 0.6$ mmolP m^{-3}), the simulations show a decrease in the zooplankton concentration during the entire numerical experiment (Fig. 4a).

The calculations demonstrated that an increase in the value of coefficient k_s (case 3) results in a decrease of the primary production, which is reflected by the declining values of the phytoplankton and zooplankton concentrations (Figs. 2b, 3b, 4b and 2a, 3a, 4a). This means that phytoplankton grazing is directly dependent on the primary production through the coefficient PP.

The simulations show that the benthic detritus pool D (Figs. 2d, 3d and 4d) drop with rising values of the nutrient half-saturation constant k_s. This decrease is caused by pelagic sedimentation which depends largely on the phytoplankton grazing rate.

The results of these studies have shown that an increase in coefficient k_s results in a decrease of the phytoplankton nutrient uptake; however, this decrease causes an increase in nutrient concentration.

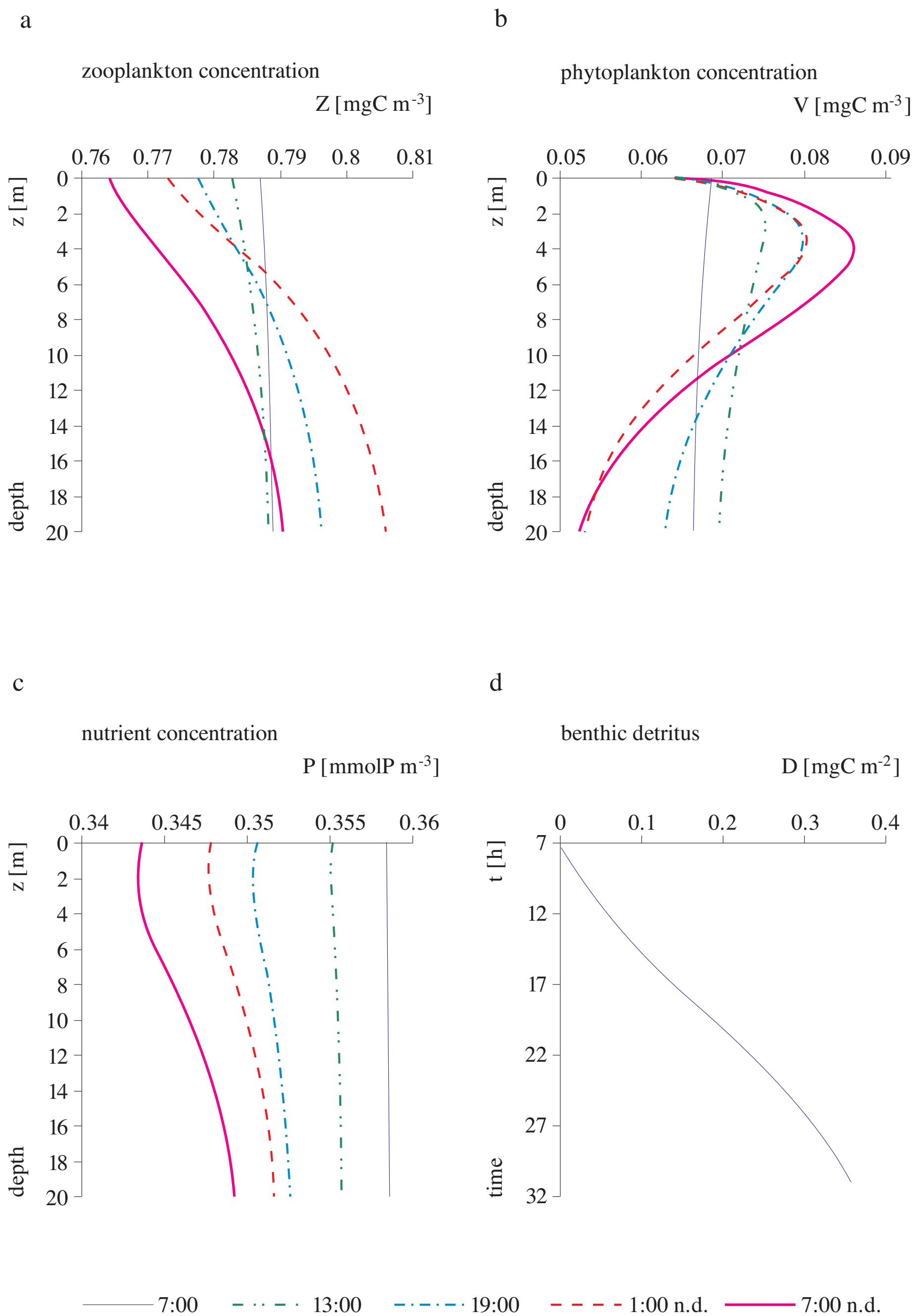

Fig. 2. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m^2\ s^{-1}}$, $S_a = 1.5 \times 10^{-5}\ \mathrm{s^{-1}}$, that nutrients are the limiting factor in primary production, and $k_s = 0.12$ mmolP m^{-3}

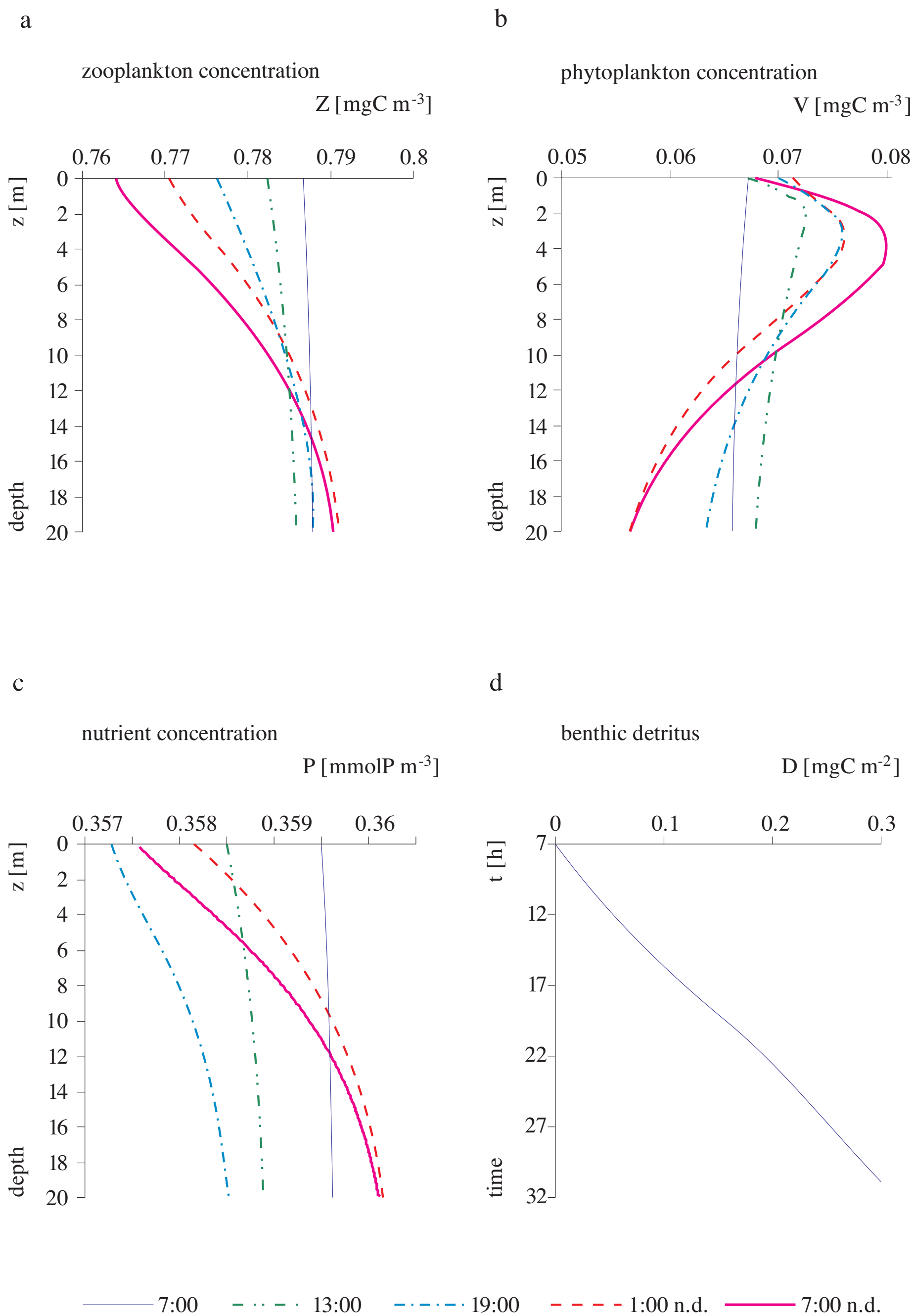

Fig. 3. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, that nutrients are the limiting factor in primary production, and $k_s = 0.36$ mmolP m^{-3}

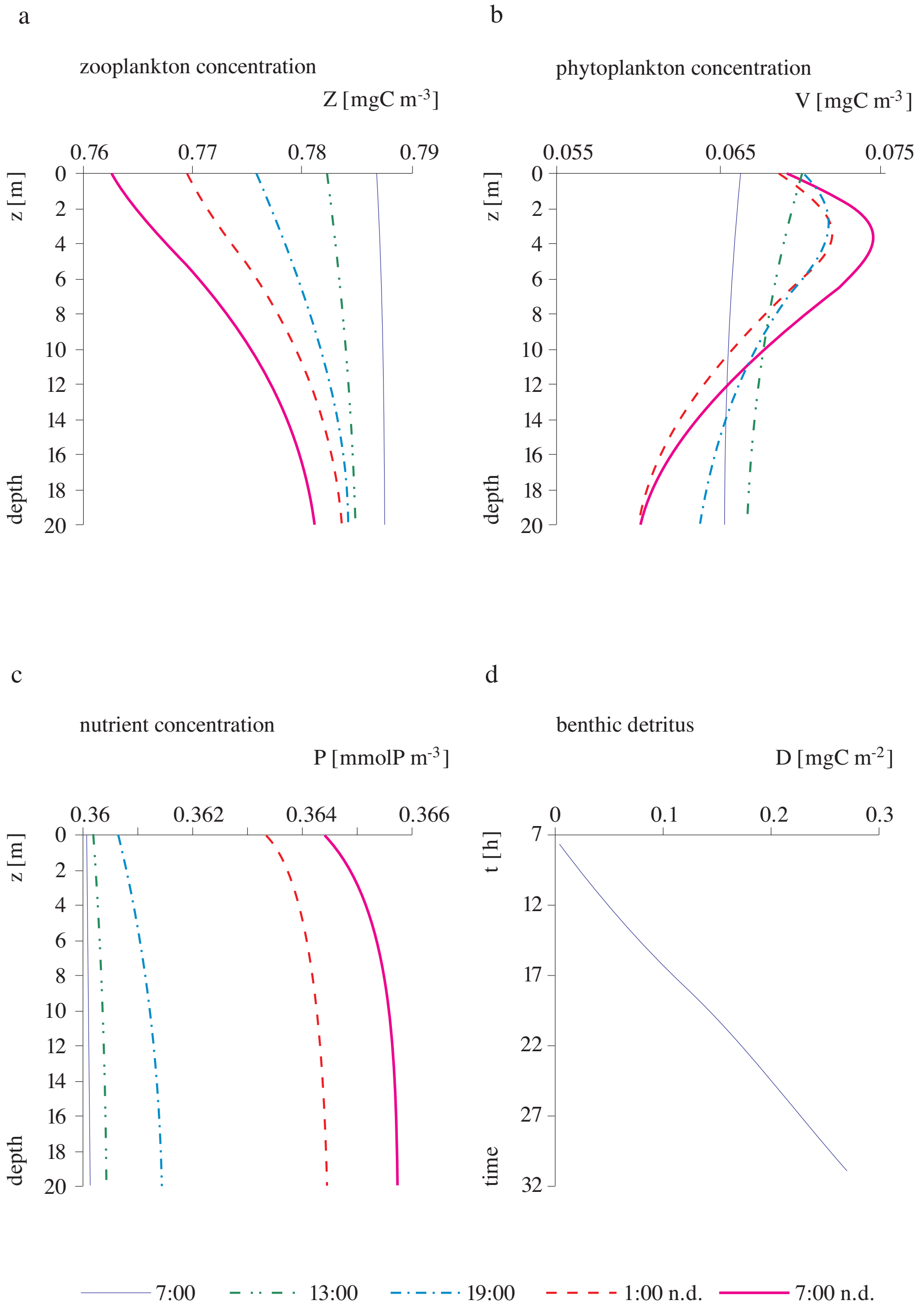

Fig. 4. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m}^2\ \mathrm{s}^{-1}$, $S_a = 1.5 \times 10^{-5}\ \mathrm{s}^{-1}$, that nutrients are the limiting factor in primary production, and $k_s = 0.6$ mmolP m^{-3}

3.2. The influence of the coefficient PP on the variability of the characteristics investigated

The influence of the coefficient PP, denoting the mean primary production, on the processes investigated, was analysed assuming that $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, $f(z) = -0.00175\, z^2 + 0.08\, z + 0.15$ and that the photosynthesis is the only source of pelagic primary production. The following assumptions were made in the calculations:
case 1: $PP = 0.75\ S_a V(z,t)$ (Fig. 5);
case 2: $PP = 0.5\ S_a V(z,t)$ (Fig. 6);
case 3: $PP = 0.375\ S_a V(z,t)$ (Fig. 7).

The results indicate that the changes in PP exert hardly any influence on the characteristics examined with the exception of the zooplankton (Figs. 5a, 6a and 7a). They show, moreover, that any increase in the value of PP causes the zooplankton concentration to rise considerably during the evening and the night in the deeper layer (Figs. 5a and 6a) in cases 1 and 2. However, with respect to case 3 ($PP = 0.375\ S_a$), PP causes the zooplankton concentration to decline gradually throughout the experiment (Fig. 7a). This means that the phytoplankton grazing by zooplankton is directly dependent on the coefficient PP. Its increase causes an increase in grazing, which is evidenced by a rise in the zooplankton abundance and a scarcely detectable decrease in phytoplankton density during the night (Figs. 5b, 6b and 7b).

The simulations show that elevated values of PP stimulate only a weak response from the benthic detritus pool (Figs. 5d, 6d and 7d).

The calculations have also demonstrated that, in the situation illustrated in Figs. 5c, 6c and 7c, the changes in PP do not have any noticeable effect on the nutrient concentration field. All the values of this function fall during the afternoon. However, when phytoplankton is 'feeding on' light and the nutrient concentration is high enough, the nutrient uptake rate by phytoplankton is very low, particularly at night, and hardly influences their concentrations. In such a situation, the simulations show that the nutrient pool increases substantially during the night.

3.3. The influence of the function $f(z)$ on the variability of biological characteristics

The influence of phytoplankton grazing by zooplankton through the function $f(z)$, which describes the portion of grazed material at depth z on the variability of the biological characteristics, was analysed assuming that the photosynthesis is only source of primary production and that $S_a = 1.5 \times 10^{-5}$ s^{-1}, $K_z = 10^{-4}$ m^2 s^{-1} and $PP = 0.5\ S_a$.

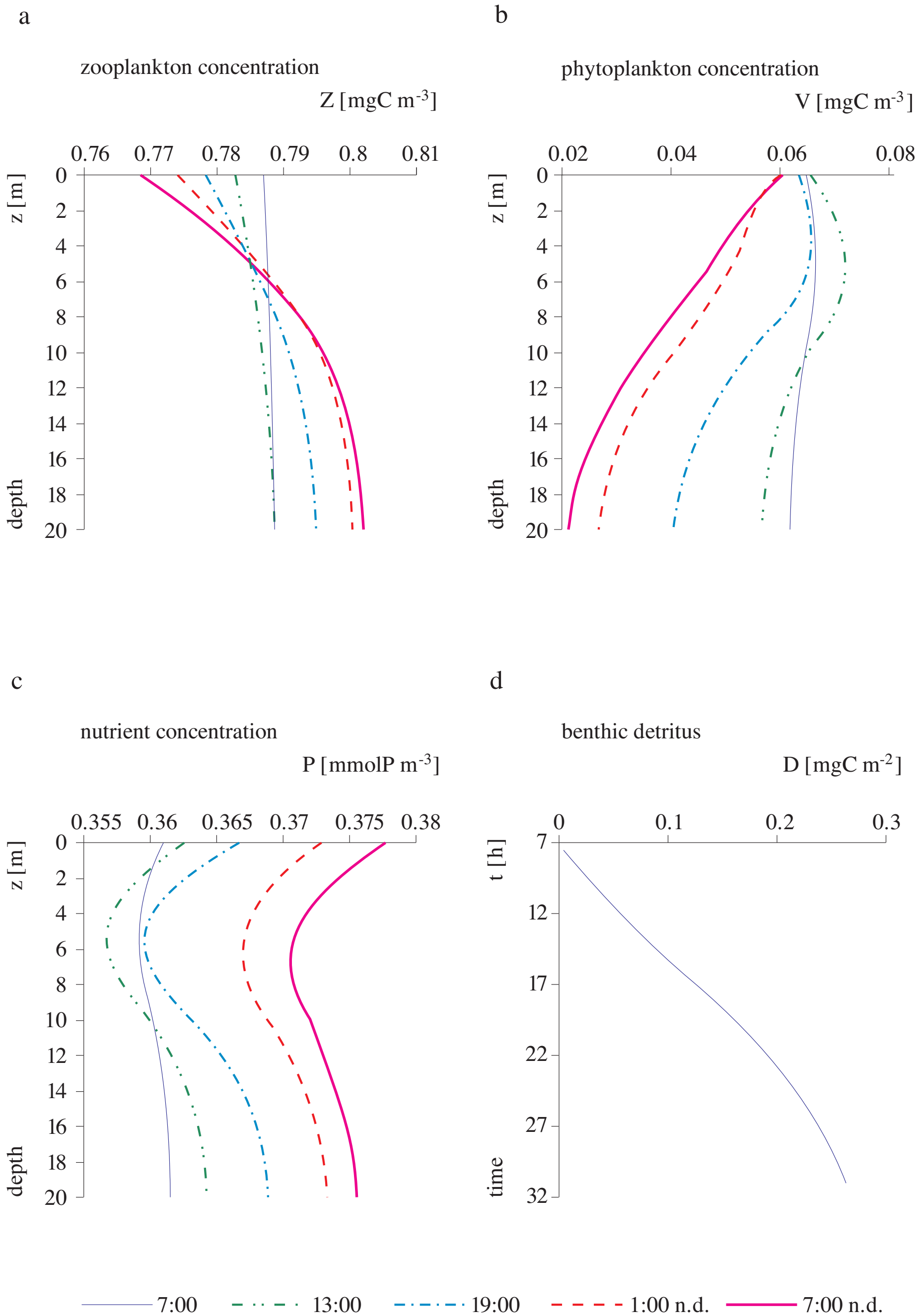

Fig. 5. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m^2\ s^{-1}}$, $S_a = 1.5 \times 10^{-5}\ \mathrm{s^{-1}}$, that only production generated by photosynthesis takes place, and $PP = 0.75\ S_a$

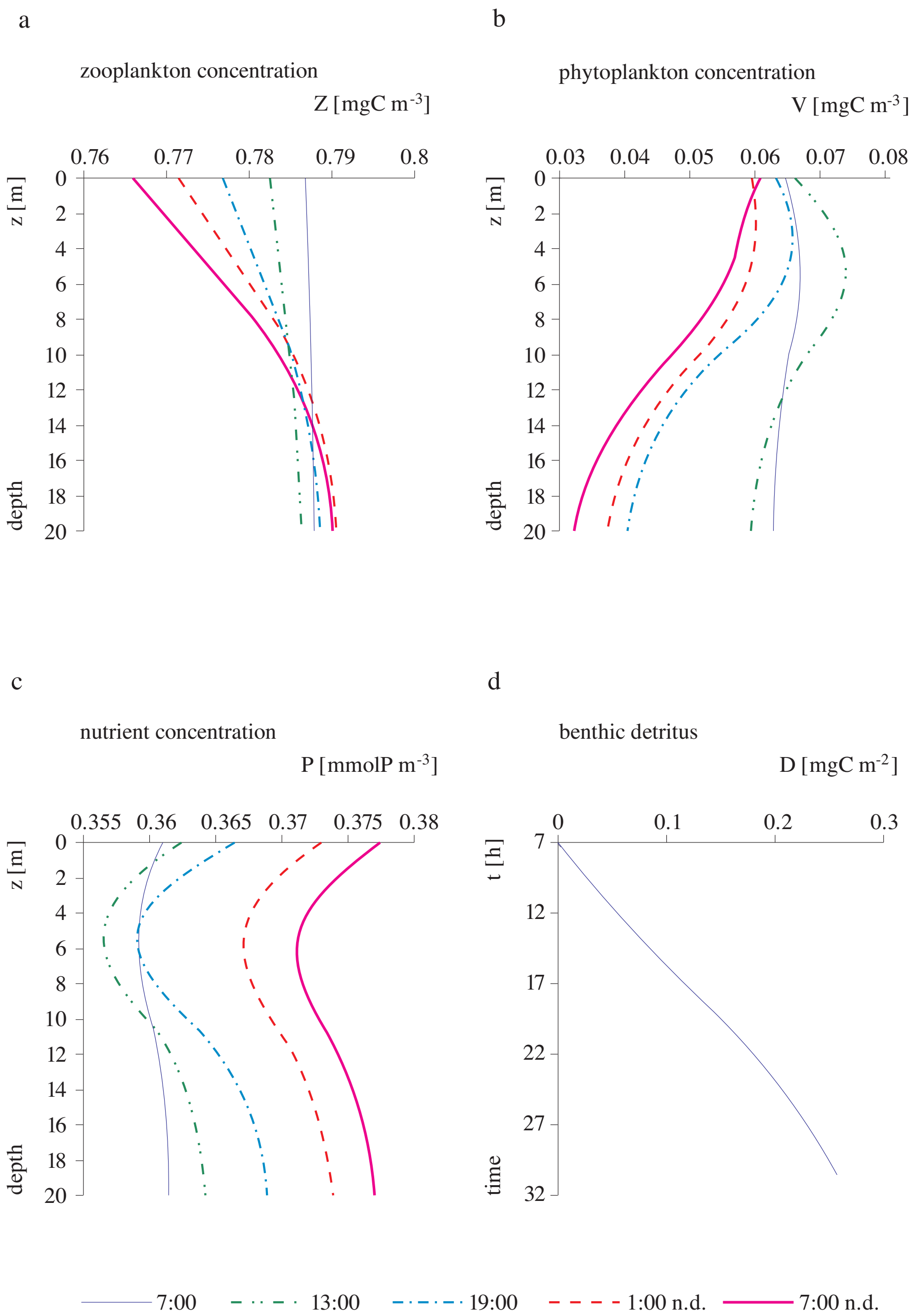

Fig. 6. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, that only production generated by photosynthesis takes place, and $PP = 0.5\ S_a$

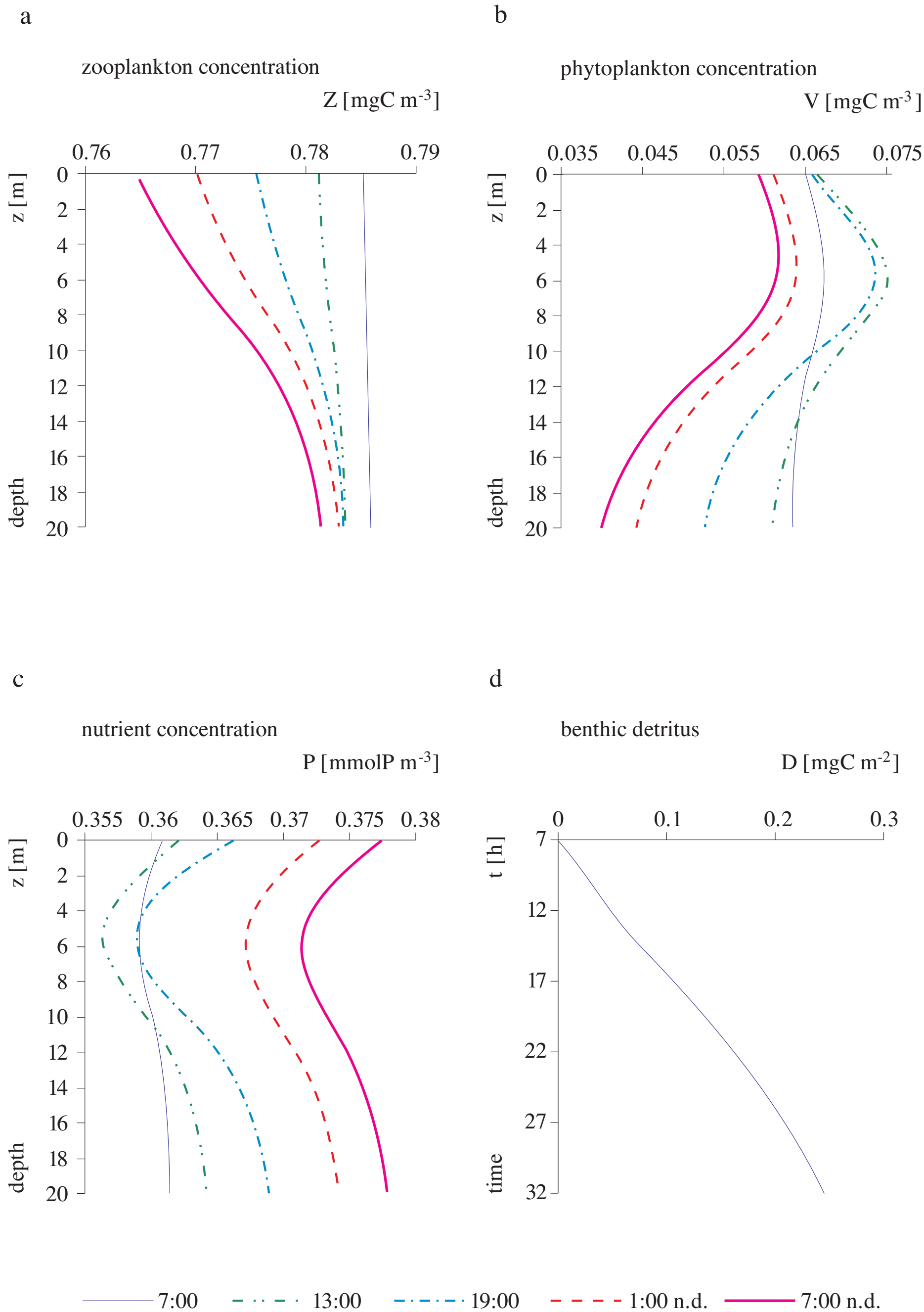

Fig. 7. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, that only production generated by photosynthesis takes place, and $PP = 0.375\ S_a$

The calculations were carried out for two variants: function $f(z)$ is linear and a second-degree polynomial (variant A), or constant (variant B).

The coefficients of the polynomial can be determined either arbitrarily or from the experimentally derived grazing coefficient at the following depths:

- at the free surface corresponding to the conditions of zooplankton survival,
- 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 assumptions were made:
case 1: $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$ (Fig. 6);
case 2: $f(z) = 0.02\ z + 0.5$ (Fig. 8).

In all cases, the results suggest that the changes in function $f(z)$ exert hardly any influence on the nutrient distribution (Figs. 6c and 8c) and benthic detritus pool (Figs. 6d and 8d). The simulation showed that grazing does, however, exert an effect on the shape of curves the phytoplankton (Figs. 6b and 8b) and zooplankton (Figs. 6a and 8a) distribution functions.

During the evening (assuming that $t_o = 20.25$ h) the zooplankton migrate up to the sea surface in search of food. Almost all phytoplankton production is grazed during the night hours, which is evidenced by the declining phytoplankton concentration (Figs. 6b and 8b) and the rising zooplankton concentration (Figs. 6a and 8a).

The calculations also demonstrated that a decrease in the phytoplankton density and an increase in the zooplankton density occurs in the deeper layer. These changes are more conspicuous in case 1 than in case 2.

Variant B

For the calculations, the following assumptions were made:
case 1: $f(z) = 0.9$ (Fig. 9);
case 3: $f(z) = 0.1$ (Fig. 10).

The influence of $f(z)$ was analysed under the same assumptions as in variant A.

The simulated distributions of phytoplankton and zooplankton vary widely in shape and value. In case 1, the value of $f(z)$ is equal to 0.9, indicating that phytoplankton grazing is intense (90% of its biomass) throughout the water column. The phytoplankton concentration here depends mainly on grazing. During the evening and night, the value of this function (Fig. 9b) drops considerably and the zooplankton concentration rises (Fig. 9a).

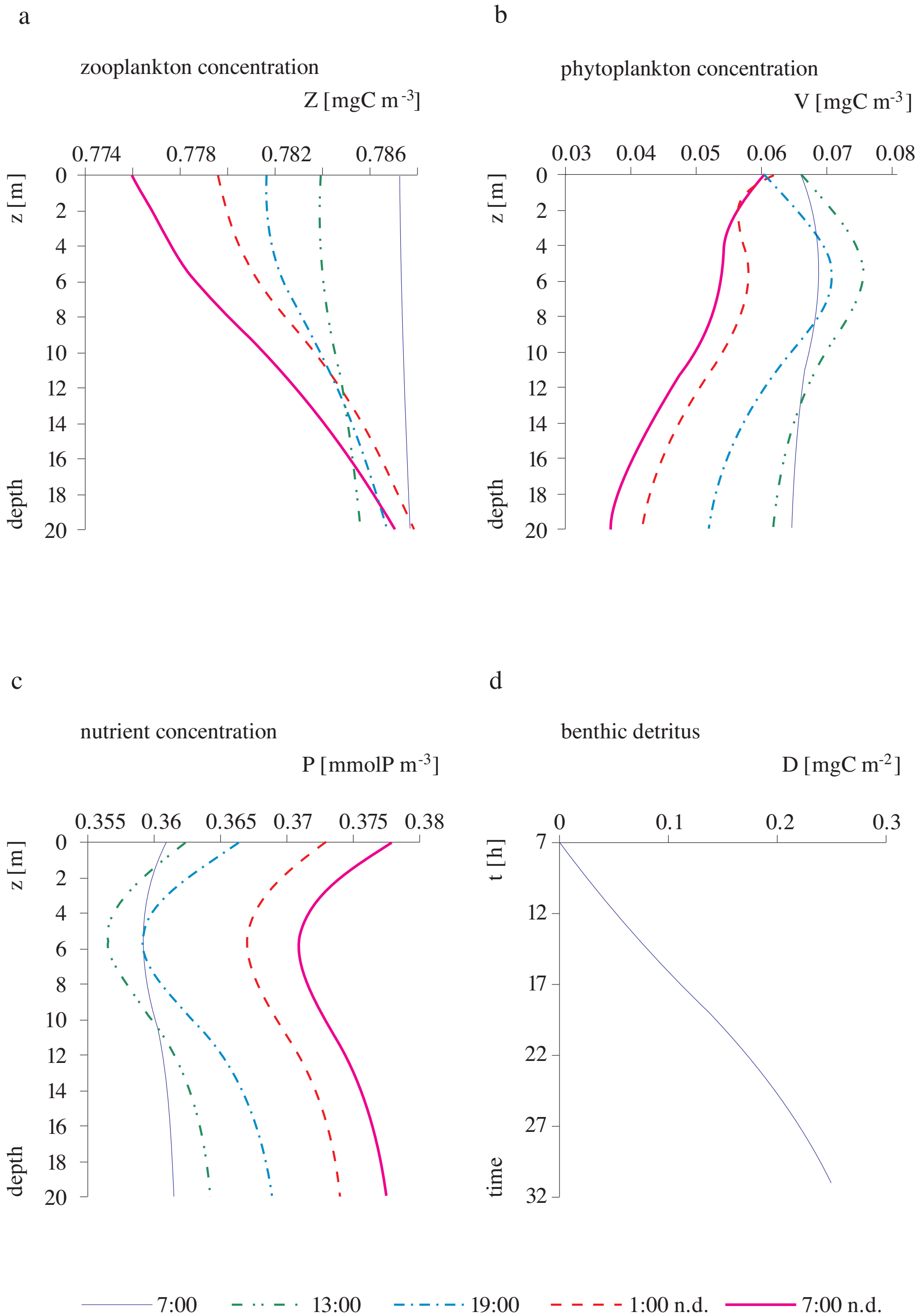

Fig. 8. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = 0.02\ z + 0.5$, $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, that only production generated by photosynthesis takes place, and $PP = 0.5\ S_a$

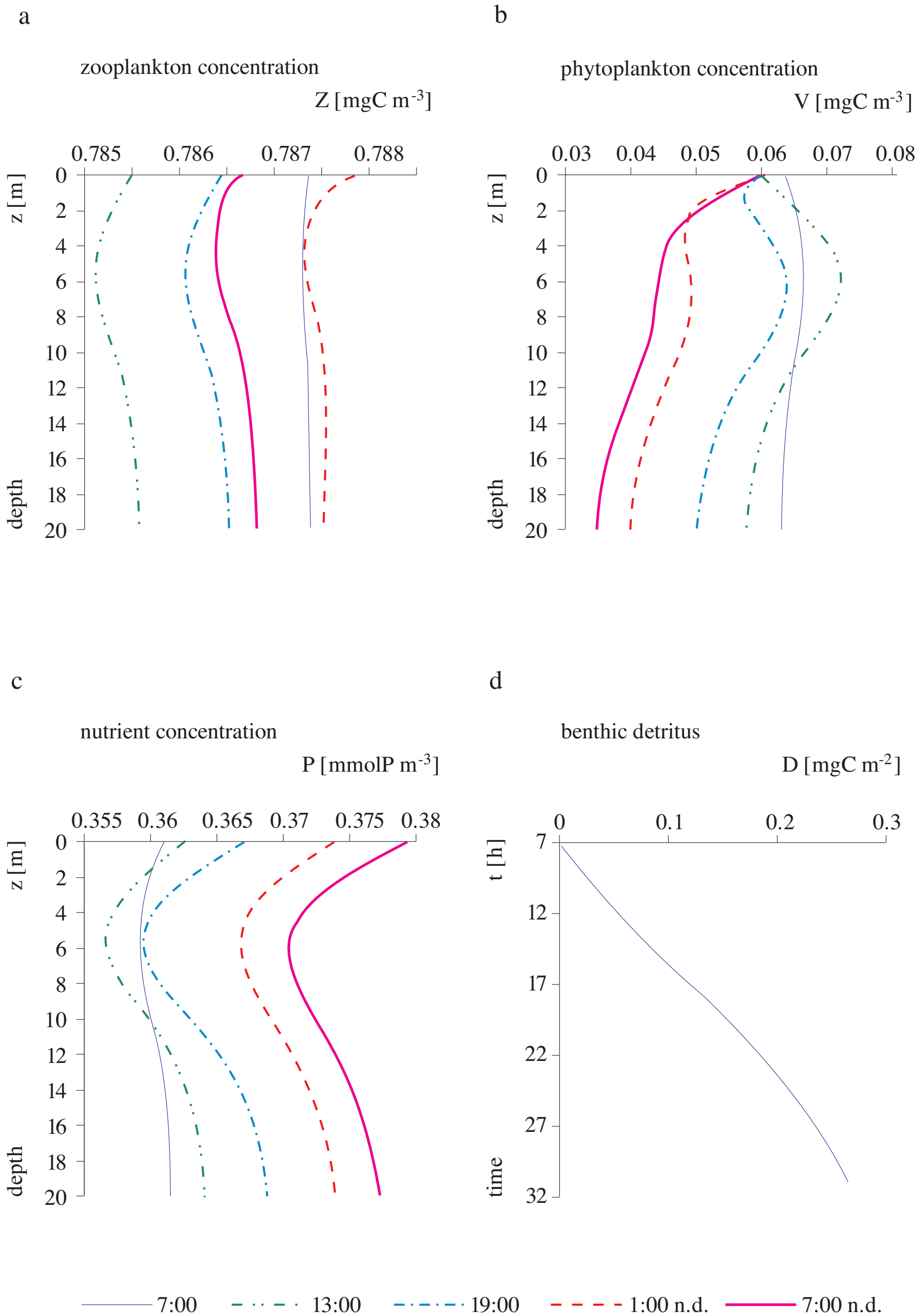

Fig. 9. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = 0.9$, $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, that only production generated by photosynthesis takes place, and $PP = 0.5\ S_a$

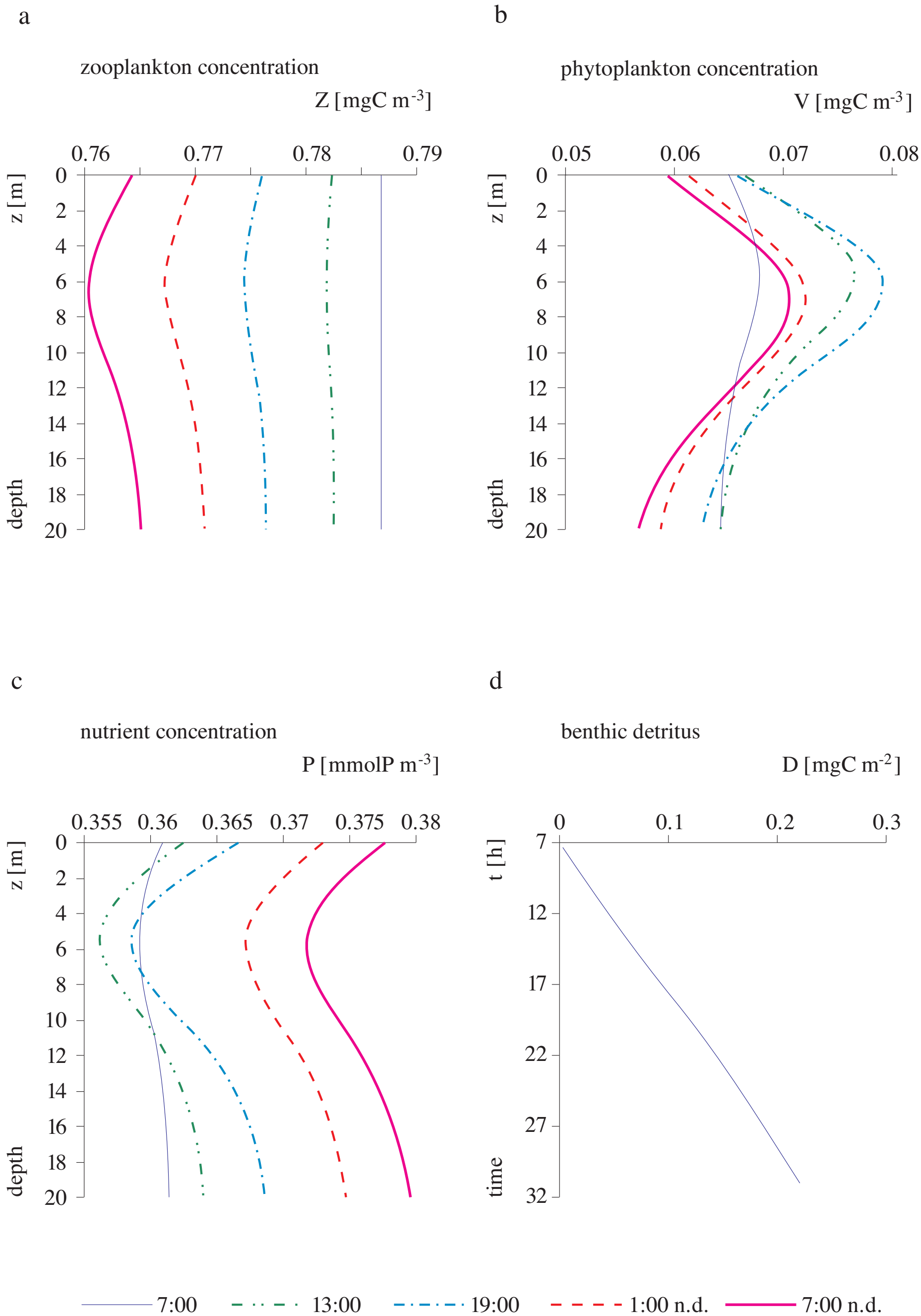

Fig. 10. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = 0.1$, $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, that only production generated by photosynthesis takes place, and $PP = 0.5\ S_a$

However, in case 2, primary production brings about a distinct increase in the concentration of phytoplankton (Fig. 10b), and a day-long decrease in that of zooplankton (Fig. 10a).

The simulations show that the increase in the grazing coefficient causes a decrease in the phytoplankton concentration (Figs. 9b and 10b) and an increase in the zooplankton concentration (Figs. 9a and 10a) and the benthic detritus pool (Figs. 9d and 10d). The latter is due to pelagic sedimentation, which depends mainly on the value of the grazing coefficient.

3.4. The influence of the coefficient of time t_o on the variability of the characteristics investigated

The influence of the coefficient of time t_o at which the maximum phytoplankton grazing occurs on the variability of the biological characteristics investigated was analysed on the assumption that the primary production is nutrient-limited, and $k_s = 0.36$ mmolP m^{-3}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, $K_z = 10^{-4}$ m^2 s^{-1} and $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$.

The calculations were carried out for four values of t_o:
case 1: $t_o = 3.25$ h (Fig. 11);
case 2: $t_o = 9.25$ h (Fig. 12);
case 3: $t_o = 15.25$ h (Fig. 13);
case 4: $t_o = 21.25$ h (Fig. 14).

The changes in t_o always exert a considerable influence on the characteristics investigated with the exception of the benthic detritus pool.

In case 1, when $t_o = 3.25$ h, during the late night hours, the zooplankton migrate up to the sea surface in search of food. Nearly all phytoplankton production is grazed during the early morning, this fact being evidenced by the declining phytoplankton concentration (Fig. 11b).

The results indicate that, in this situation, the zooplankton and nutrient concentrations increase considerably in the deeper layers during the late night hours and early in the morning; however, during the daytime, the values of these functions fall (Figs. 11a and 11c).

In case 2 ($t_o = 9.25$ h), in the morning and at noon, the zooplankton and nutrient densities (Figs. 12a and 12c) rise markedly, and the phytoplankton concentration decreases (Fig. 12b).

In case 3 ($t_o = 15.25$ h), an increase in the zooplankton and nutrient concentrations (Figs. 13a and 13c) occurs during the afternoon and evening hours; however, the distribution function of phytoplankton concentration falls (Fig. 13b) at this time.

The analysis of these functions shows that during the night and morning hours, the zooplankton density and nutrients concentration decrease (Figs. 13a and 13c), whereas the phytoplankton number rises (Fig. 13b).

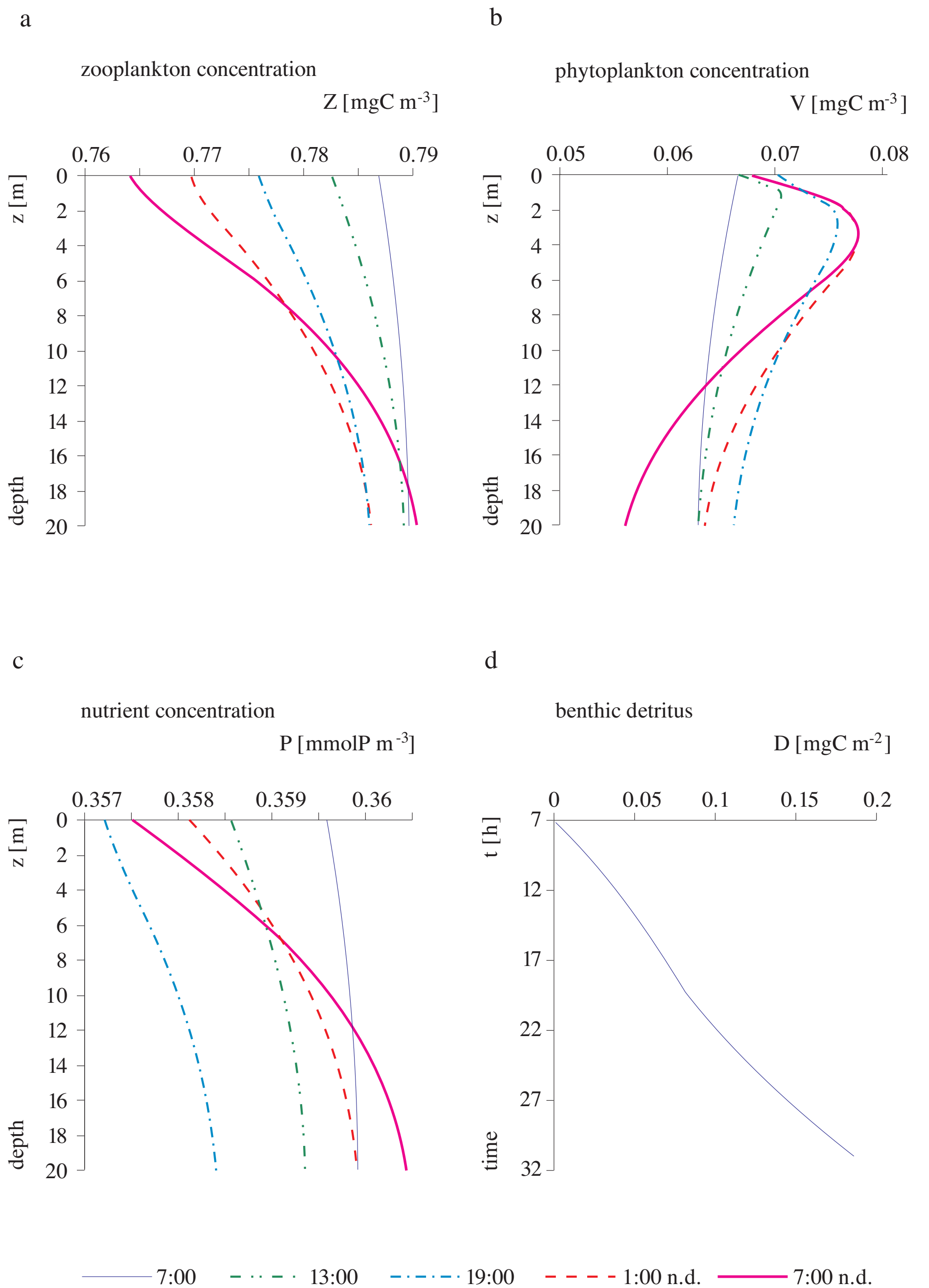

Fig. 11. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}$ m^2 s^{-1}, $S_a = 1.5 \times 10^{-5}$ s^{-1}, that nutrients are the limiting factor in primary production, and $k_s = 0.36$ mmolP m^{-3}, $t_o = 3.25$ h

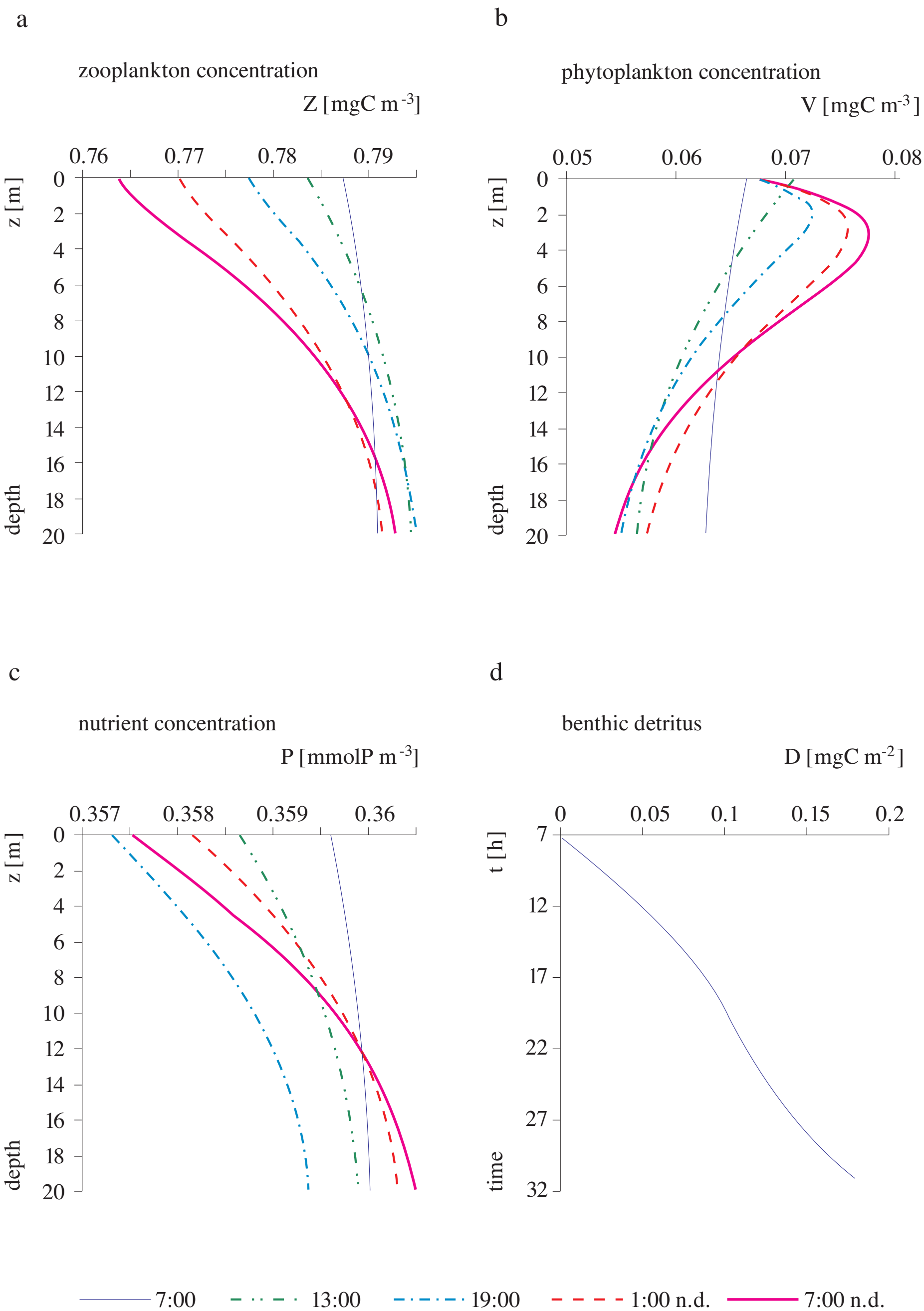

Fig. 12. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m}^2\ \mathrm{s}^{-1}$, $S_a = 1.5 \times 10^{-5}\ \mathrm{s}^{-1}$, that nutrients are the limiting factor in primary production, and $k_s = 0.36$ mmolP m^{-3}, $t_o = 9.25$ h

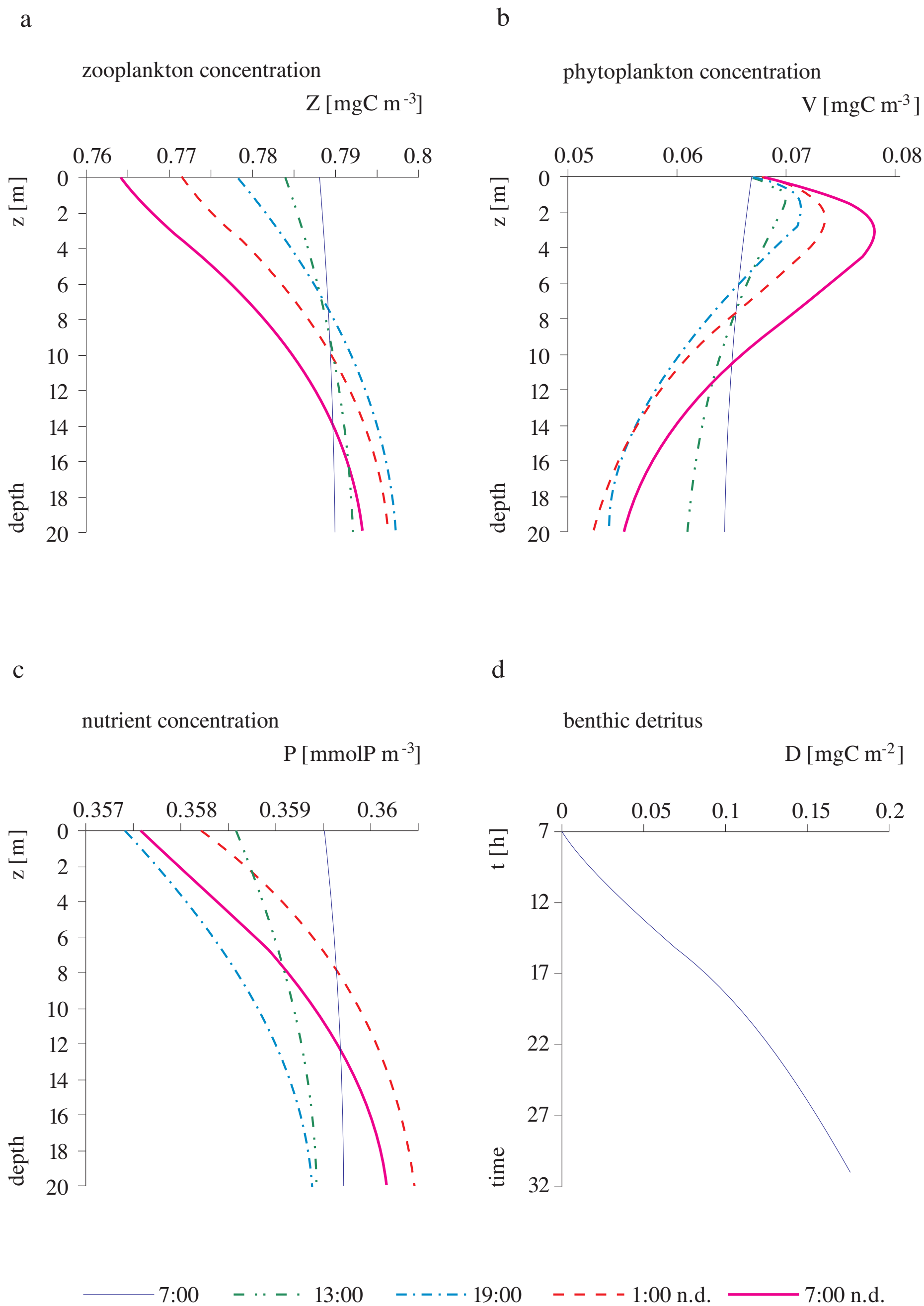

Fig. 13. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m^2\ s^{-1}}$, $S_a = 1.5 \times 10^{-5}\ \mathrm{s^{-1}}$, that nutrients are the limiting factor in primary production, and $k_s = 0.36$ mmolP m^{-3}, $t_o = 15.25$ h

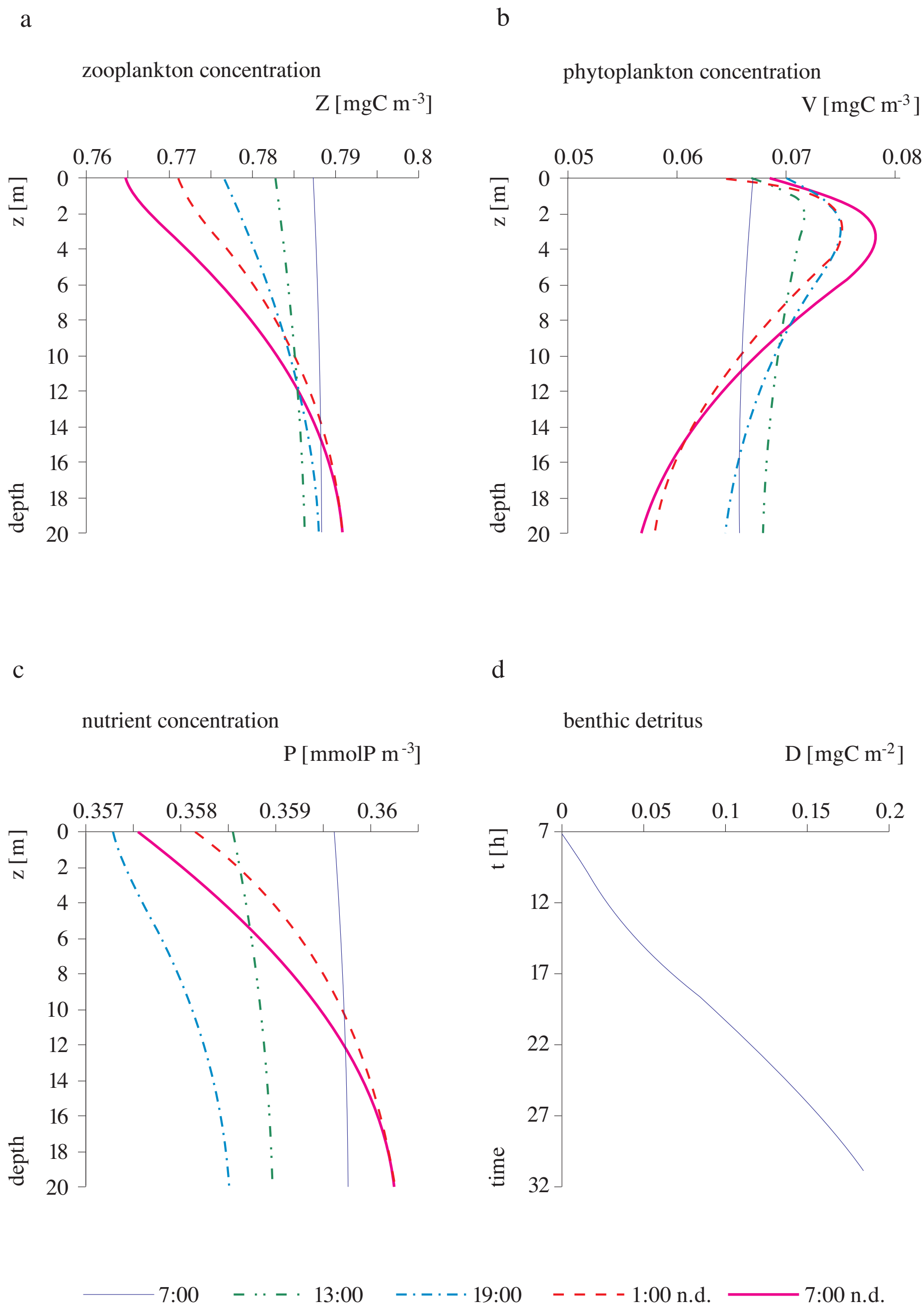

Fig. 14. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m^2\ s^{-1}}$, $S_a = 1.5 \times 10^{-5}\ \mathrm{s^{-1}}$, that nutrients are the limiting factor in primary production, and $k_s = 0.36$ mmolP m^{-3}, $t_o = 21.25$ h

In case 4, when $t_o = 21.25$ h, the calculations also demonstrated that an increase in the zooplankton and nutrient concentrations (Figs. 14a and 14c) occurs at the deeper layer in the evening and at night, while the phytoplankton concentration decreases (Fig. 14b).

However, a decrease in the distribution functions of the zooplankton and nutrient concentrations (Figs. 14a and 14c) and an increase in the phytoplankton concentration function (Fig. 14b) are noted during the daytime.

Therefore, phytoplankton grazing by zooplankton always has a significant influence on the variability of the characteristics investigated, during the daytime and at night, through the coefficient of time t_o.

The calculations demonstrated that in case 2, when the maximum phytoplankton grazing takes place in the morning and at noon, grazing does have a decisive influence on the characteristics investigated.

3.5. The influence of the maximum rate of production increase on the variability of the characteristics investigated

The following assumptions were made in the analysis of the maximum rate of production increase on the variability of the characteristics controlled by the processes under scrutiny: only production generated by photosynthesis takes place, $PP = 0.5\ S_a$, $K_z = 10^{-4}\ \mathrm{m}^2\ \mathrm{s}^{-1}$ and $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$.
The calculations were carried out for three values of the maximum rate of production increase:
case 1: $S_a = 10^{-6}\ \mathrm{s}^{-1}$ (Fig. 15);
case 2: $S_a = 1.5 \times 10^{-5}\ \mathrm{s}^{-1}$ (Fig. 6);
case 3: $S_a = 10^{-4}\ \mathrm{s}^{-1}$ (Fig. 16).

The simulations show that changes in S_a have a considerable influence on the functions investigated. Moreover, any increase in S_a causes the phytoplankton concentration to rise during the daytime in cases 2 and 3; however, at night, the value of this function falls (Figs 6b and 16b). The calculations also demonstrated that in case 1, S_a causes the phytoplankton concentration to diminish right through the day (Fig. 15b).

These simulations show that the magnitude of S_a exerts a significant influence on the processes under investigations. The zooplankton concentration increases as S_a does: during the night in case 2 (Fig. 6a), and during the entire numerical experiment when S_a is equal $10^{-4}\ \mathrm{s}^{-1}$ (case 3) (Fig. 16a). In case 1 ($S_a = 10^{-6}\ \mathrm{s}^{-1}$), the very low S_a causes the zooplankton concentration to fall right through the day (Fig. 15a).

An increase in S_a causes the nutrient concentration to decline during the entire numerical experiment in case 3 (Fig. 16c). However, in case 1

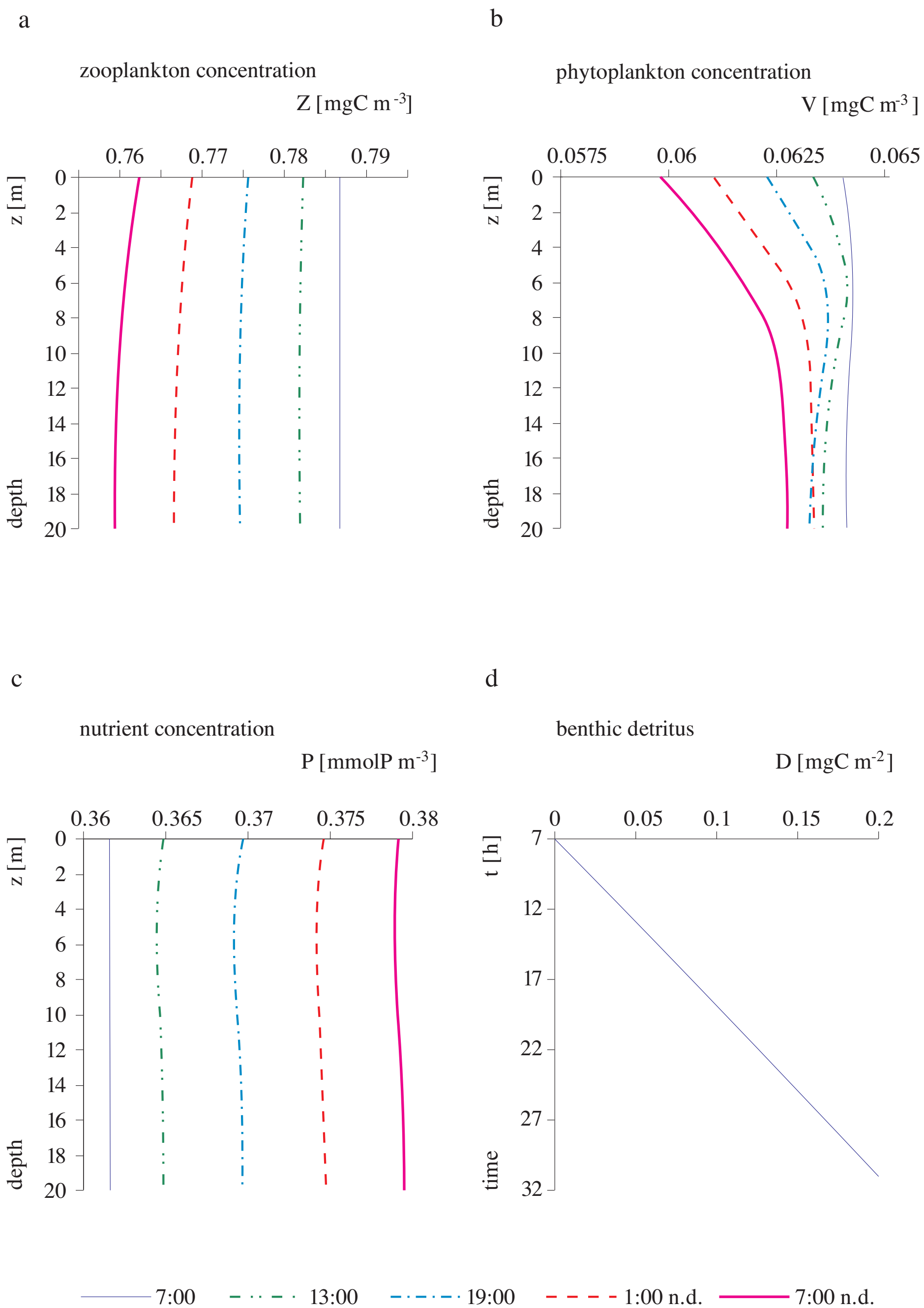

Fig. 15. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m}^2\ \mathrm{s}^{-1}$, $S_a = 10^{-6}\ \mathrm{s}^{-1}$, that only production generated by photosynthesis takes place, and $PP = 0.5\ S_a$

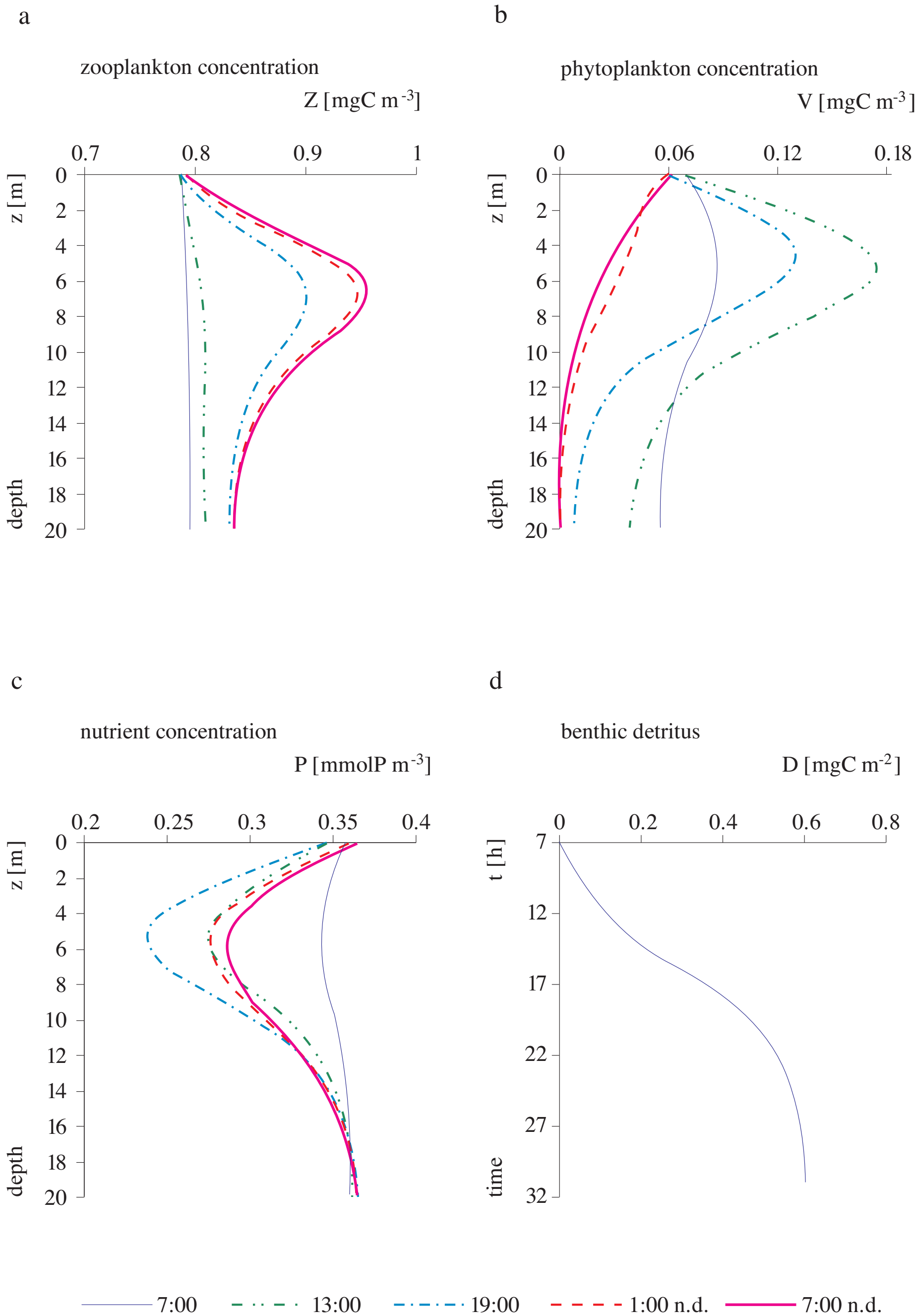

Fig. 16. Simulated biological characteristics (a), (b), (c) and (d) assuming that $f(z) = -0.00175\ z^2 + 0.08\ z + 0.15$, $K_z = 10^{-4}\ \mathrm{m}^2\ \mathrm{s}^{-1}$, $S_a = 10^{-4}\ \mathrm{s}^{-1}$, that only production generated by photosynthesis takes place, and $PP = 0.5\ S_a$

($S_a = 10^{-6}$ s^{-1}), the simulations show a slight increase in the value of this function (Fig. 15c). In case 2 ($S_a = 1.5 \times 10^{-5}$ s^{-1}), the nutrient concentration decreases during the noon hours; however, the value of this function rises in the evening and at night (Fig. 6c).

To a great extent, the value of S_a influences the benthic detritus pool. The increase in S_a causes the benthic detritus pool to increase (Figs. 16d and 6d). In case 3 ($S_a = 10^{-4}$) the increase in the phytoplankton concentration brings about a much larger increase in the benthic detritus pool (Fig. 16d) than in case 2 ($S_a = 1.5 \times 10^{-5}$ s^{-1}).

The results of the numerical simulations demonstrate the overwhelming influence of S_a on all the parameters examined here, suggesting that the nutrient concentration is the factor limiting primary production, as in version 5. The value of S_a has a crucial effect on the levels of the phytoplankton and zooplankton concentrations. Any increase in S_a causes these functions to increase as in version 5. The reverse situation is observed in case 1, when $S_a = 10^{-6}$ s^{-1}, which stimulates a decrease in the phytoplankton and zooplankton densities, as in version 5. The lower value of these functions means that the factor limiting production increases independently of the nutrient concentration, and the light levels have little influence on the phytoplankton and zooplankton distributions. However, in this case, phytoplankton grazing by zooplankton does have a decisive influence on the phytoplankton and zooplankton concentration fields.

4. Discussion and conclusions

The simulation experiments have shown that the changes in the values of selected biological parameters (*i.e.* the factor limiting production increase, the maximum rate of production increase S_a, the nutrient half-saturation constant k_s, the coefficient PP denoting the mean primary production rate, the function $f(z)$ describing the percentage of the material consumed at every depth 'z', and the coefficient of the time t_o during which the maximum grazing phytoplankton occurs), do influence the shape and value of the distribution functions of the zooplankton, phytoplankton and nutrient concentrations, and the benthic detritus pool.

- The coefficient PP in the two cases, *i.e.* version 1 – nutrients are the factor limiting primary production (through the nutrient half-saturation constant), and version 2 – only production generated by photosynthesis takes place, has a considerable influence on the variability of the characteristics investigated. When phytoplankton cell growth is controlled by the nutrient concentration in the water, the calculations indicate that the increase in the value of the nutrient half-saturation constant causes the primary production to decrease and a consequent decline in the phytoplankton and zooplankton concentrations. The decrease in these functions leads to a substantial falls in the benthic detritus pool. However, the increase in the value of k_s causes the distribution function of nutrient concentration rises through the decrease in the uptake of nutrients by phytoplankton. In the case when, during the entire numerical experiment, the phytoplankton 'feeds on' light and sufficient nutrients are present, any decrease in the value of PP causes a decrease in the zooplankton concentration and the benthic detritus pool, but only a very small increase in phytoplankton concentration.

- The maximum rate of production increase S_a establishes to a considerable extent the magnitudes of the biological characteristics. In all cases, the increase in the value of S_a causes an increase in the phytoplankton and zooplankton concentrations and the benthic detritus pool, too. The exception is case 1 (version 5) when S_a is equal to 10^{-6} s^{-1}. The calculations demonstrate that the phytoplankton and zooplankton concentrations decrease. This decrease means that the factor limiting production increase independently of the nutrient concentration and the quantity of light has little influence on these functions. However, phytoplankton grazing by zooplankton does affect the phytoplankton and zooplankton fields to a significant degree.

- In areas where phytoplankton grazing is intensive, non-homogeneities occur in the phytoplankton and zooplankton concentration distribution functions owing to a decrease in phytoplankton concentration and an increase in zooplankton concentration. In version 3A in all cases where the function $f(z)$ is linear and a second-degree polynomial, phytoplankton grazing by zooplankton does not have a very great effect on the nutrient concentration or the benthic detritus pool. However, in version 3B, where function $f(z)$ is constant, the shape and value of the phytoplankton and zooplankton distribution functions are very different. Analysis of the numerical studies also demonstrates that the phytoplankton concentration decreases and the zooplankton concentration increases with a rising grazing coefficient. Moreover, the increase in the value of $f(z)$ causes the benthic detritus pool to increase. The simulations indicate that as a result, grazing phytoplankton has a greater influence on the benthic detritus pool than on the phytoplankton concentration.

- The changes in the value of the coefficient of time t_o exert a pronounced effect on the variability of the investigated characteristics, both during the daytime and at night. The calculations indicate that at the time t_o, phytoplankton grazing by zooplankton does affect the phytoplankton concentration field to a greater degree than the primary production both in day light and in darkness.
- Phytoplankton grazing, through the value of the function $f(z)$ and the coefficient of time t_o, exerts the greatest influence on the zooplankton and phytoplankton distribution functions. Moreover, the calculations indicate that the values of these functions depend to a significant degree on the primary production through the maximum rate of production increase S_a and the nutrient half-saturation constant k_s.
- The results of the numerical investigations show that taking into consideration eq. (3), which describes the temporal variations in the value of zooplankton distribution, in the P–V–Z–D model is an important aspect in modelling the phytoplankton concentration distribution function in the water.

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