Numerical studies of the influence of food ingestion on phytoplankton and zooplankton biomasses

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Abstract

This paper presents the numerical simulations of the influence of food ingestion by a herbivorous copepod on phytoplankton and zooplankton biomasses (PZB) in the sea. The numerical studies were carried out using the *phytoplankton--zooplankton-nutrient-detritus* **PhyZooNuDe** biological upper layer model. This takes account both of fully developed primary production and regeneration mechanisms and of daily migration of zooplankton. In this model the zooplankton is treated not as a 'biomass' but as organisms having definite patterns of growth, reproduction and mortality. Assuming also that {**Zoop**} is composed of i cohorts of copepods with weights W_i and numbers Z_i, then $\{Zoop\} = \sum W_i Z_i$. The **PhyZooNuDe** model consists of three coupled, partial second-order differential equations of the diffusion type for phytoplankton, zooplankton and nutrients, and one ordinary first-order differential equation for the benthic detritus pool, together with initial and boundary conditions. The calculations were made during 90 days (April, May and June) for the study area P1 (Gdańsk Deep) in an area $0 \leq z \leq 20$ m with a vertical space step of 0.1 m and a time step of 300 s. The simulation given here demonstrated the importance of food ingestion by zooplankton in that it can alter the nature of the interactions of plants and herbivores. The analysis of these numerical studies indicate that the maximal ingestion rate and the half-saturation constant for grazing strongly affect the magnitude of the spring bloom and the cyanobacterial bloom, and also the total zooplankton biomass.

1. Introduction

In the past, when zooplankton were introduced into a model, factors such as filtering, respiration and excretion were often taken to be fixed productions of the hypothetical biomass rather than being related to more detailed information on behavior and metabolism. In the literature there are now considerable amounts of experimental data on these aspects for several species of zooplankton. This information can be used to give some idea of the functional relations which could be used in a simulation of the response of zooplankton to variations in their environment. The development of such theoretical descriptions is critical to the inclusion of these animals *qua* animals in more general simulations of ecosystems.

Zooplankton are at present regarded as mere consumers rather than as organisms having certain patterns of growth, reproduction and mortality. Thus the parameters of population dynamics – fecundity, age structure, specific birth and death rates – are more important in determining the behavior of an ecosystem than the simpler concepts of the flow of organic matter.

Zooplankton are a very heterogeneous group, and are defined by the method of collection rather than by their position in the food web. Any net haul, and particularly a series of hauls using nets of different mesh sizes, is likely to contain bacterivorous, herbivorous, omnivorous and carnivorous species. Yet nearly all models incorporating zooplankton consider the entire catch to be herbivores feeding in the upper layers of the sea. There are good reasons for this: herbivorous copepods are the largest group of zooplankton, and nearly all primary production must be processed by them. In turn, they (or their feces and excreta) are the predominant source of food for the rest of the system (Steele & Mullin 1977).

The parameters of zooplankton population dynamics – fecundity, age structure, specific birth and death rates – are more important in determining the behavior of an ecosystem than the simpler concepts of the flow of organic matter. The aim of this study is to determine the impact of selected parameters of food ingestion by herbivorous copepods on the phytoplankton and zooplankton biomass (PZB). In the numerical studies the maximal ingestion rate and half-saturation constant for grazing were taken into consideration.

2. Zooplankton as animals

The actual gain to a feeding zooplankter is the organic matter that is assimilated from the gut rather than what has been ingested, which is only partially utilized. Therefore, the energy balance equation for zooplankton is

somewhat different than for phytoplankton. It includes several parameters, i.e. ingestion of organic matter, defecation, metabolic loss and excretion, and reproduction. The equation for zooplankton can be expanded to (Dzierzbicka-Głowacka & Zieliński 1998a, b, Dzierzbicka-Głowacka 2000):

$$\frac{d\{Zoop\}}{dt} = \text{ingestion} - \text{defecation} - \text{metabolism} - \text{predation}. \tag{1}$$

Assume {**Zoop**} is composed of i cohorts of copepods with weights W_i and numbers Z_i; then:

$$\{Zoop\} = \sum W_i Z_i, \tag{2}$$

$$\frac{d\{Zoop\}}{dt} = \sum \left(W_i \frac{dZ_i}{dt} + Z_i \frac{dW_i}{dt} \right) \tag{3}$$

by comparison with equation (1):

$$\frac{dW_i}{dt} = \frac{1}{Z_i}(\text{ingestion} - \text{defecation} - \text{metabolism}), \tag{4}$$

$$\frac{dZ_i}{dt} = -\frac{1}{W_i}(\text{predation}). \tag{5}$$

Eq. (4) determines the change in weight of an individual copepod as the sum of its individual gains and losses of energy; eq. (5) represents the effects of predation on a particular cohort as a function of numbers in that cohort, assuming that all death is due to predation.

If WI is the weight of the naupliar stage at which feeding starts and WF is the weight of the adult, then for each cohort relations of the form:

$$\text{ZI} = f\left(\{Phyt\}, \text{ZF}, \frac{\text{WF}}{\text{WI}} \right) \tag{6}$$

indicate the requirements for some function defining recruitment ZI in terms of food available, adult numbers ZF, and the ratio of adult to naupliar weight. The function includes not only reproductive capacity but also any mortality before the feeding naupliar stage is reached (Steele & Mullin 1977).

Eqs. (4)–(6) form the basis for the portrayal of zooplankton as animals.

Food ingestion by zooplankton

This model considers food ingestion by those species – mainly crustaceans – that remove relatively small immobile particles by capturing them on a meshwork of coarse setae. Here, the ingestion rate is defined as the rate of intake per unit time per animal. This is a function of both the food concentration and the weight of the animal (Mullin & Brooks 1970):

$$\text{ING} = fil(\{Phyt\})W^{\alpha}. \tag{7}$$

The value of α has not been exactly determined but is assumed equal to 2/3 (Paffenhöfer 1971). Natural phytoplankton can provide a wide

selection of possible sizes of food items but, as in the experiments, the first approximation is to assume that all sizes of copepods are feeding on one total population, $\{Phyt\}$, defined in biomass units such as $\mathrm{gC\,m^{-3}}$. There are three functions used to define $fil(\{Phyt\})$ (Steele & Mullin 1977):

$$fil(\{Phyt\}) = \begin{cases} g_{\max}\frac{\{Phyt\}-\{Phyt\}_0}{k_{Phyt}} & \text{for } \{Phyt\}_0 \leqslant \{Phyt\} < K_R, \\ g_{\max} & \text{for } \{Phyt\} \geqslant K_R, \end{cases} \tag{8}$$

where $\{Phyt\}_0 + k_{Phyt} = K_R$,

$$fil(\{Phyt\}) = g_{\max}\left\{1 - \exp\left(\frac{-(\{Phyt\} - \{Phyt\}_0)}{k_{Phyt}}\right)\right\}, \tag{9}$$

$$fil(\{Phyt\}) = g_{\max}\frac{\{Phyt\} - \{Phyt\}_0}{k_{Phyt} + \{Phyt\} - \{Phyt\}_0}. \tag{10}$$

In all three, $fil(\{Phyt\}) = 0$ when $\{Phyt\} \leqslant \{Phyt\}_0$.

Each relation depends on three constants and satisfies the same three conditions:

1. $fil(\{Phyt\}) = 0$ when $\{Phyt\} = \{Phyt\}_0$.
2. $fil(\{Phyt\}) = g_{\max}\frac{\{Phyt\}-\{Phyt\}_0}{k_{Phyt}}$ for $\{Phyt\} > \{Phyt\}_0$.
3. $fil(\{Phyt\}) \longrightarrow g_{\max}$ as $\{Phyt\} \longrightarrow \infty$.

These correspond to three facets of experimental studies of ingestion:

1. There may or may not be a threshold $\{Phyt\}_0$ below which the animals do not feed.
2. When feeding starts, the ingestion rate increases in proportion to the increase in food concentration.
3. As food concentration rises to high values, the ingestion rate tends to become constant.

The best choice between these relations is in doubt. One reason for this is that there are still many simplifications implicit in these formulas, for example, the maximal ingestion rate $g_{\max}$ is not independent of the feeding of the animal prior to the measurement.

More controversial is the fact that $\{Phyt\}_0 > 0$. Feeding experiments with unialgal cultures in the laboratory usually yield very low values or zero. On the other hand, studies in which a natural assemblage of particulate matter is the source of food indicate that feeding ceases at a threshold concentration, $\{Phyt\}_0$, significantly different from zero (Parsons et al. 1984). This latter finding is teleologically attractive because it provides the phytoplankton with a refuge in low density, so that they cannot be grazed to extinction. This is a technical necessity in many models of phytoplankton–herbivore interactions (Steele & Mullin 1977).

Not all sizes of particles are equally accessible to a zooplankton organism as food. Thus k_{Phyt} in eqs. (8)–(10) is probably related directly to the relative sizes of the zooplankton and the particles. The morphology of the food collecting organs sets upper and lower limits to the size of particles which can be captured and ingested. For zooplankton trapping particles in a mucous net, these morphological constraints seem to be of primary importance in determining which particles will be ingested and which will not. Morphological constraints are also important for setous feeders such as copepods. It is often the case that an increase in bodily size, with a corresponding increase in feeding appendages, is correlated with an increase in the maximum size of particle which can be eaten, but does not necessarily reduce the ability to feed on small particles (Steele & Mullin 1977).

3. The PhyZooNuDe Model

The numerical studies were carried out using the *phytoplankton-zooplankton-nutrient-detritus* **PhyZooNuDe** biological upper layer model. This model consists of four mass conservation equations. There are three partial differential equations of the diffusion type for the concentration of phytoplankton and zooplankton as organisms, and a single nutrient in the water column. The fourth equation, an ordinary differential equation, describes the deposition of detritus at the bottom. All losses of organic material in the water column are immediately transported to the bottom, where they enter the detritus pool.

Since there is a lack of information on quantities, especially on feeding behavior or the metabolism of other groups within the plankton such as the microzooplankton, the carnivores and the deep plankton communities, this paper places emphasis on pelagic herbivores as part of the food chain from nutrients and phytoplankton to the benthic detritus pool.

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. The grazed phytoplankton can be divided into three groups: the first contributes to zooplankton growth, the second is deposited as fecal pellets, and the third is excreted by the zooplankton as dissolved metabolites, thereby replenishing the nutrient pool. Contributing to zooplankton growth, the first group is directly dependent on losses, and is represented by egg production and dying zooplankton. The fecal and excreted material are regenerated immediately.

Most of the detrital material is deposited on the bottom, where it collects as a detrital pool. Only a small portion of detritus remains suspended in

the water column, where it is immediately regenerated. The majority falls to the bottom, where it is reworked by bacteria and other organisms. The concept of the detrital pool at the bottom has been introduced to create a lag in the remineralization and possible replenishment of the upper layer with nutrients. This complex process is parameterized by assuming a net remineralization rate for bottom detritus. Hence, there are two pathways for the regeneration of pelagic and benthic nutrients, each with different time scales (Billen et al. 1991). The present model covers both pelagic and benthic pathways.

3.1. Equations of the PhyZooNuDe model

The phytoplankton {**Phyt**}, zooplankton {**Zoop**}, nutrients {**Nutr**} and benthic detritus {**Detr**} are included in the numerical model **PhyZoNuDe** as shown in Fig. 1.

The state variables obey the following equations, which include diffusion and biochemical processes (Dzierzbicka-Głowacka 2001):

$$\frac{\partial\{Phyt\}}{\partial t} + (w+w_z)\frac{\partial\{Phyt\}}{\partial z} = \frac{\partial}{\partial z}\left(K_z\frac{\partial\{Phyt\}}{\partial z}\right) + \mathrm{PRE} - \mathrm{RES} - \mathrm{MOR}_P - \mathrm{GRA}, \tag{11}$$

$$\frac{\partial\{Zoop\}}{\partial t} + w\frac{\partial\{Zoop\}}{\partial z} = \frac{\partial}{\partial z}\left(K_z\frac{\partial\{Zoop\}}{\partial z}\right) + \mathrm{ING} - \mathrm{FEC} - \mathrm{MET} - \mathrm{PRED}, \tag{12}$$

$$\frac{\partial\{Nutr\}}{\partial t} + w\frac{\partial\{Nutr\}}{\partial z} = \frac{\partial}{\partial z}\left(K_z\frac{\partial\{Nutr\}}{\partial z}\right) - \mathrm{UPT} + \mathrm{REL} + \mathrm{REMI} + \mathrm{EXC}, \tag{13}$$

$$\frac{d\{Detr\}}{dt} = -F_{Phyt}(H) + \mathrm{D} - \mathrm{REMD}. \tag{14}$$

Let us assume that the zooplankton {**Zoop**} is composed of i cohorts of copepods with weights W_i and numbers Z_i; then:

$$\{Zoop\} = \sum W_i Z_i, \tag{15}$$

$$\frac{\partial\{Zoop\}}{\partial t} = \sum\left(W_i\frac{\partial Z_i}{\partial t} + Z_i\frac{\partial W_i}{\partial t}\right), \tag{16}$$

and by comparison with (12):

$$\frac{\partial W_i}{\partial t} = \frac{1}{Z_i}(\mathrm{ING} - \mathrm{FEC} - \mathrm{MET}), \tag{17}$$

$$\frac{\partial Z_i}{\partial t} = \frac{1}{W_i}\left(\frac{\partial}{\partial z}\left(K_z\frac{\partial Z_i}{\partial z}\right) - w\frac{\partial Z_i}{\partial z} - \mathrm{PRED}\right). \tag{18}$$

The origin of the Cartesian coordinate system is set at the sea surface of the basin with the z-axis directed upwards, w_z denotes the sinking

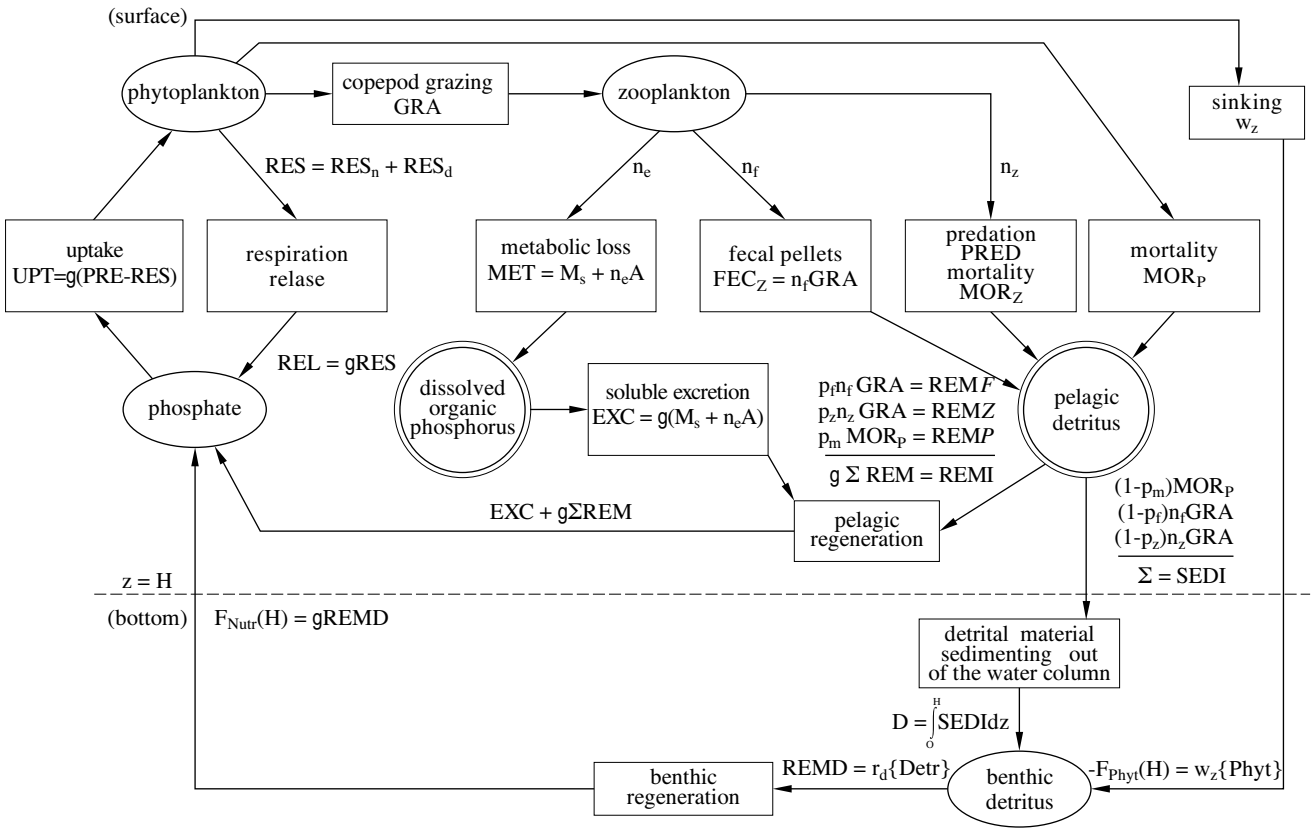

Fig. 1. Simplified phosphorus cycle of the biological upper layer model of the marine ecosystem (Dzierzbicka-Głowacka & Zieliński 1998b)

speed of phytoplankton, and K_z denotes the turbulent diffusion coefficient. However, the flow field, water temperature and salinity were reproduced by the prognostic numerical simulation technique using hydrographic climatological data (Jankowski, personal communication).

The biochemical terms used in eqs. (11)–(18) are listed in Appendix.

Phytoplankton

The phytoplankton was modelled using one state variable only. Natural phytoplankton consists of many different species, each with its own dynamic characteristics and contributing varying proportions of biomass during the year. Our assumption in using phytoplankton biomass is that the species composition regulates itself according to the availability that the dynamical constants used are representative of the whole phytoplankton community. 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 carbon concentration.

The phytoplankton biomass {**Phyt**} is affected by primary production PRE, respiration RES, mortality MOR_P, and grazing by zooplankton GRA. The primary production PRE is calculated from the minimum of the nutrient and light limitation functions d_N and d_I (eq. (24)) (Radach 1983, Radach & Moll 1993) and the assimilation number d_A; d_A is the maximum photosynthetic rate, i.e. the ratio of production (amount of assimilated carbon) to the concentration of chlorophyll, and for the Gdańsk Deep is described by the trigonometric polynomial (eq. (29)) (Renk & Ochocki 1999). d_I is used to calculate the photosynthetic rate for the saturation irradiance E_S (the irradiance at which the photosynthesis rate is the highest) and the irradiance at depth z, $E(z,t)$ (eq. (25)). $E(z,t)$ is dependent on η_d, the average daily dose of irradiation PAR (eq. (27)) (Renk & Ochocki 1998, 1999) and on k_d, the sum of components responsible for the attenuation of irradiance by pure water, phytoplankton and other optically active admixtures, which was calculated from Woźniak's bio-optical classification of natural waters (eq. (28)) (Woźniak & Pelevin 1991). For nutrient limitation the Michaelis-Menten formula is applied with k_{Nutr} as the half-saturation constant (eq. (25)). According to eq. (30), phytoplankton growth is also dependent on water temperature and salinity. Metabolic processes in plants are accompanied by catabolic processes such as respiration. Therefore, the true net increase in primary production (i.e. in the phytoplankton biomass) per time unit is lower by the losses due to respiration (Parsons et al. 1984). Respiration RES consists of basic and photo-respiration (eq. (31)), each being proportional to the phytoplankton biomass $\{Phyt\}$ (Ryther 1956, Parsons et al. 1984). The

basic dark respiration rate is m_P^n, a factor proportional to the maximum photosynthetic rate (Ryther 1956), and the photo-respiration rate is m_P^d, a factor proportional to the rate of primary production (Radach & Moll 1993). The natural phytoplankton mortality MOR_P is a process which results in some losses in biomass. It was assumed that mortality is directly proportional to the phytoplankton biomass $\{Phyt\}$ (Raymont 1980, Sjöberg 1980) with a mortality rate of m_P (eq. (32)). Phytoplankton grazing by zooplankton GRA is assumed to be proportional to a copepod biomass {Zoop} at a rate of $fil(\{Phyt\})$ (eq. (33)), but this rate is a function of the phytoplankton biomass with a threshold $\{Phyt\}_0$, below which grazing ceases, and of the half-saturation constant k_{Phyt} (Steele & Mullin 1977), where $g_{\max}$ denotes the maximal ingestion rate.

Zooplankton

In this model the zooplankton {**Zoop**} is treated not as a biomass but as organisms having definite patterns of growth, reproduction and mortality. Assuming further that $\{Zoop\}$ is composed of i cohorts of copepods with masses W_i and numbers Z_i, then $\{Zoop\} = \sum W_i Z_i$.

The ingestion rate ING is defined as the rate of food intake per unit time per animal, the coefficient of food selection being given by τ (eq. (34)). This is a function $fil(\{Phyt\})$ of both the food concentration $\{Phyt\}$ and the animal's weight W_i (eq. (35)), and takes a value of α, which is equal to 2/3 (Paffenhöfer 1971). The rate of assimilation A is computed as a constant fraction of the ingestion rate (eq. (36)) (e.g. Steele (1974) who used $A_i = 0.7\mathrm{ING}_i$). The major metabolic loss of organic matter from a population is undoubtedly through respiration, and for modelling zooplankton, respiration and excretion, can probably be regarded as the same process. The total rate of metabolic loss MET can be split into three components with different relations to the food uptake rate ING. M_s is assumed to be the resultant or basic metabolism, independent of food supply. The respiratory costs of foraging for and capturing food M_r should fall as the food concentration and, correspondingly, $fil(\{Phyt\})$, rises. Finally, there is the cost of assimilating and biochemically transforming the food (specific dynamic action, M_a), proportional to A (eq. (36)). The number of juveniles is defined on the assumption that eggs are released by the adult female as a single brood, continuously throughout some time span J. The simplest assumption is that the female, instead of utilizing assimilated food for growth, uses it for egg production. However, the males feed at the same rate as females and do not produce eggs. So, if WN is the adult weight for the species and ZN the number at time t, egg production EGG (eq. (37)) is the figure given by Steele & Mullin (1977). The efficiency term

X is the conversion of the biomass increase in the adult population into eggs, including the 'wasted' growth in the males.

The intensity of predation PRED depends on numbers in the individual stages (eq. (38)), where $pred_{\max}$ is the maximum rate of predation and Z_0 the zooplankton threshold for predation.

Nutrients

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 is considerably simpler than that of nitrogen (Raymont 1980).

The nutrient concentration {**Nutr**} is determined by algal uptake UPT, remineralized dead phytoplankton, zooplankton fecal pellets and dead zooplankton REMI, and by zooplankton excretion EXC and nutrient release REL.

Respiration in the dark consumes particulate organic matter. For matter to be conserved, the respiration term in the equation for phytoplankton must be balanced by a nutrient release term REL in the equation for phosphate. This term parameterizes the contribution of respiration to the nutrient pool, assuming a fixed P : C ratio g (eq. (39)). Nutrient uptake by phytoplankton cells UPT is assumed to occur for positive net production only and for photo-respiration (eq. (40)). Remineralization REMI within the water column by the 'microbial food web' is assumed for proportions of dead phytoplankton REMP (eq. (44)), dead zooplankton REMZ (eq. 45)) and fecal pellets REMF (eq. (46)), with the percentages p_m, p_z and p_f corresponding to the components of dead phytoplankton, dead zooplankton and fecal material, which are immediately recycled in the water column (eq. (47)) (Dzierzbicka-Głowacka & Zieliński 1997a, b). Excretion of dissolved and particulate material is parameterized via the amount of grazed material. Soluble zooplankton excretion EXC is parameterized by the metabolism costs MET (eq. (41)) with the percentage of ingestion, n_e, regenerated as soluble zooplankton excreta. The total fecal pellet production FEC is described by eq. (42), with the percentage of ingestion, n_f, evaluated as fecal material. The carcasses of zooplankton MOR$_Z$ are described by eq. (43), with the percentage of ingestion, n_z, ending up as dead zooplankton (Radach & Moll 1993).

Benthic detritus

Benthic detritus {**Detr**} varies according to the input of algal detritus from the water column D, and loss by remineralization at the bottom

REMD. Remineralization REMD is assumed proportional to the amount of benthic detritus available at the remineralization rate of benthic detritus r_d (eq. (50)) (Radach et al. 1984). The detrital material sedimenting out of the water column D consists of contributions from dead phytoplankton, fecal pellets and dead zooplankton, which are not remineralized in the water column (eq. (49)).

Sedimentation of living phytoplankton provides a net gain to the detritus pool (eq. (48)). The flux of algae across the bottom boundary is taken as a source term in the detritus equation (14). The remineralized 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 links the phosphate equation (13) with the detritus equation (14).

3.2. Initial and boundary conditions

The following initial and boundary conditions supplement the equation system (11)–(18): the initial vertical distributions of phytoplankton $\{Phyt\}$, phosphate $\{Nutr\}$, zooplankton $\{Zoop\}$(i cohorts of copepods with weights W_i and numbers Z_i) and detritus pool $\{Detr\}$ are known:

$$\begin{aligned}
\{Phyt\}(z,0) &= \{Phyt\}_0(z) \qquad 0 \le z \le H,\\
W_i(z,0) &= W_i^0(z) \qquad 0 \le z \le H,\\
Z_i(z,0) &= Z_i^0(z) \qquad 0 \le z \le H,\\
\{Zoop\}(z,0) &= \sum_1^k W_i^0 Z_i^0,\\
\{Nutr\}(z,0) &= \{Nutr\}_0(z) \qquad 0 \le z \le H,\\
\{Detr\}(t=0) &= \{Detr\}_0 = 0 \qquad z = H.
\end{aligned} \tag{19}$$

The vertical gradients of phytoplankton, zooplankton and phosphate concentration flux are zero at the sea surface ($z = 0$) and at the sea bottom ($z = H$) for zooplankton.

$$\begin{aligned}
F_{Phyt}(0) \equiv K_z \frac{\partial\{Phyt\}(z,t)}{\partial z}\bigg|_{z=0} - w_z\{Phyt\}(0,t) = 0,\\
F_{Nutr}(0) \equiv K_z \frac{\partial\{Nutr\}(z,t)}{\partial z}\bigg|_{z=0} = 0,\\
F_{Zoop}(0) \equiv \zeta K_z \frac{\partial\{Zoop\}(z,t)}{\partial z}\bigg|_{z=0} = 0.
\end{aligned} \tag{20}$$

However, the bottom flux condition for phytoplankton, phosphate and zooplankton is given as:

$$F_{Phyt}(H) \equiv -w_z\{Phyt\}(H,t), \tag{21}$$

$$F_{Nutr}(H) \equiv K_z \frac{\partial\{Nutr\}(z,t)}{\partial z}\bigg|_{z=H} = g\mathrm{REMD}, \tag{22}$$

$$F_{Zoop}(H) \equiv \zeta K_z \frac{\partial\{Zoop\}(z,t)}{\partial z}\bigg|_{z=H} = 0. \tag{23}$$

This flux $F_{Nutr}(H)$ enters the benthic detritus equation as a source term. The boundary condition (22) mechanism by which the water column is replenished with phosphate resulting from benthic remineralization.

The system of equations (11)–(18) with conditions (19)–(23) is solved numerically; the detailed algorithm of the solution to the **PhyZooNuDe** model can be found in Dzierzbicka-Głowacka (2000).

4. Numerical simulation

The **PhyZooNuDe** biological upper layer model, described in Section 3, was used in the numerical simulations of the influence of food ingestion on the temporal changes in the vertical distributions of phytoplankton carbon {**Phyt**}, zooplankton {**Zoop**} and nutrient-phosphorus {**Nutr**}, as well as of the numbers Z_i and masses W_i of i cohorts of a herbivorous copepod in the sea. But the emphasis here is on the herbivore component, in order to obtain the influence on phytoplankton distributions of zooplankton distributions as organisms with definite patterns of growth, reproduction, and predation.

The aim in this Section is not to generalize but to describe some of the consequences of the earlier discussion in one example of the model. It is neither possible nor desirable to include all the aspects of zooplankton population structure and metabolism. This example concerns problems arising from variations in the depth distribution of nutrients and zooplankton and the way these affect the response of the phytoplankton.

The first simplification is to assume that only one species of copepod is present, defined by an initial weight WI and a final adult weight WF. The population is represented as six cohorts; this assumes a second simplification, namely, that recruitment of the next generation occurs after a fixed period of adult life. The initial and final weights used here (WI = 0.2 μgC; WF = 100 μgC) are meant to approximate a *Calanus* species (Steele & Mullin 1977). The period from start of adult life to recruitment, 10 days, is derived from the data for $Calanus\ finmarchicus$, whose egg laying pattern approximates to the concept of a single brood.

Growth of body weight is expressed as $0.7(1-n_e)\mathrm{ING}_i - M_s W_i^{0.7}$, assuming that 30% of the ingested food is voided as particulate feces, which

are immediately regenerated. Of the food assimilated, a fraction n_e is used for food processing. The nutrient content associated with the n_e and M_s terms is returned to the system, too.

Nutrient limitation is introduced with the relation $\min\{d_I, d_P\}$. To simulate regeneration from the bottom, the nutrients in the deepest layers are added, or else the area is further restricted.

The parameters used in the numerical model are listed in Table 1 (with references). See Table 2 for the list of symbols.

Given these relations, the vertical distributions of nutrients (phosphorus), phytoplankton carbon and zooplankton are obtained for initial values which are constant with depth:

$$\{Phyt\}(z,t_0) = 0.01 \text{ gC m}^{-3},$$
$$\{Nutr\}(z,t_0) = 0.6 \text{ mmolP m}^{-3},$$
$$\{Detr\}(H,t_0) = 0.0 \text{ gC m}^{-2}.$$
$$Z_1(z,t_0) = 0.1 \times 10^3 \text{ m}^{-2}, \quad W_1(z,t_0) = 100 \ \mu\text{gC},$$
$$Z_2(z,t_0) = 0.7 \times 10^3 \text{ m}^{-2}, \quad W_2(z,t_0) = 40 \ \mu\text{gC},$$
$$Z_3(z,t_0) = 1.5 \times 10^3 \text{ m}^{-2}, \quad W_3(z,t_0) = 10 \ \mu\text{gC},$$
$$Z_4(z,t_0) = 4.0 \times 10^3 \text{ m}^{-2}, \quad W_4(z,t_0) = 3 \ \mu\text{gC},$$
$$Z_5(z,t_0) = 25 \times 10^3 \text{ m}^{-2}, \quad W_5(z,t_0) = 0.8 \ \mu\text{gC},$$
$$Z_6(z,t_0) = 40 \times 10^3 \text{ m}^{-2}, \quad W_6(z,t_0) = 0.2 \ \mu\text{gC}.$$

Values of the parameters reasonably close to levels found in Baltic waters (Gdańsk Deep) were closen. The studies were carried out for the study area P1 (54°50′N, 19°20′E) over 90 days (April, May and June).

The calculations were made in an area $0 \le z \le 20$ m with a vertical resolution of 0.1 m and a time resolution of 300 s.

The figures show the time variability distribution of the phytoplankton biomass $\{Phyt\}$ and total zooplankton biomass $\{Zoop\}$ Figs. 2–15 for different values of $g_{\max}$ and k_{Phyt}. The results of these studies refer to a selected level, in the study area, i.e. at 5 m depth. This is the average value for the three months (April, May and June), when the primary production attains a maximum and conditions for zooplankton reproduction are the most favourable. In this case production of eggs is much greater than at other levels, and the life-time of the specified cohort is shorter.

The following parameters were tested in the sensitivity analysis: the maximal ingestion rate $g_{\max}$ and the half-saturation constant for grazing k_{Phyt}. These parameters are responsible for the shape and values of the distributions investigated. The tested values for each parameter are given below.

Table 1. Parameters used in this numerical model and their references

Symbols	Value	References
Δz	0.1 [m]	
Δt	300 [s]	
H	20 [m]	
K_z	10^{-6} [$m^2\ s^{-1}$]	
g	0.6944 [mmolPO_4–P$(gC)^{-1}$]	Radach et al. (1984)
α	34.31 [$C_{org}(Chl\,a)^{-1}$]	Renk (2000)
$\{Phyt\}$	variable [$gC\,m^{-3}$]	
d_A	variable [mgC$(mgChl\,h)^{-1}$]	Renk 2000
E_S	218 [$kJ\,m^{-2}\ h^{-1}$]	Renk & Ochocki (1999)
$E(z,t)$	variable [$kJ\,m^{-2}\ h^{-1}$]	Renk & Ochocki (1999)
$\{Phyt\}_0$	0.05 [$gC\,m^{-3}$]	Dzierzbicka-Głowacka (2001)
$g_{\max}$	variable [day^{-1}]	
k_{Phyt}	variable [$gC\,m^{-3}$]	
m_P	0.05 [day^{-1}]	Radach & Moll (1993)
m_P^n	0.1	Radach & Moll (1993)
m_P^d	0.05	Radach & Moll (1993)
T	variable [°C]	
$\{Nutr\}$	variable [mmolPO_4–P$(gC)^{-1}$]	
k_{Nutr}	0.32 [mmolPO_4–P$(gC)^{-1}$]	Raymont (1980)
n_e	0.33	Radach & Moll (1993)
n_f	0.33	Radach & Moll (1993)
n_z	0.33	Radach & Moll (1993)
p_f	0.2	Postma & Rommets (1984)
p_p	0.2	Postma & Rommets (1984)
p_z	0.2	Postma & Rommets (1984)
$\{Zoop\}$	variable [$gC\,m^{-2}$]	
Z_i	variable [m^{-2}]	
W_i	variable [μgC]	
$pred_{\max}$	3 [day^{-1}]	Dzierzbicka-Głowacka (2000)
$Z_{\max}$	40×10^3 [m^{-2}]	Dzierzbicka-Głowacka (2000)
Z_0	0.001×10^3 [m^{-2}]	Dzierzbicka-Głowacka (2000)
$\{Detr\}$	variable [$gC\,m^{-2}$]	
r_d	0.0167 [day^{-1}]	Radach et al. (1990)

Table 2. List of symbols used in Table 1

Symbols	Quantity
Δz	depth resolution
Δt	time step
H	water depth
K_z	turbulent diffusion coefficient
g	P : C ratio
α	C_{org} : Chl a
$\{Phyt\}$	phytoplankton concentration
d_A	assimilation number
eta_d	average daily doses of irradiation PAR
E_S	saturation irradiance
$E(z,t)$	irradiance at depth z
k_d	light attenuation coefficient
$\{Phyt\}_0$	phytoplankton threshold for grazing
$g_{\max}$	grazing rate
k_{Phyt}	half-saturation constant for grazing
m_P	mortality rate
m_P^n	percentage basic respiration
m_P^d	percentage photorespiration
T	water temperature
T_0	mean temperature
$\{Nutr\}$	phosphate concentration
k_{Nutr}	half-saturation constant for phosphate
n_e	percentage of ingestion, regenerated as soluble excretion of zooplankton
n_f	percentage of ingestion egested as fecal material
n_z	percentage of ingestion ending up as dead zooplankton
p_f	percentage of remineralized fecal material in the water column
p_p	percentage of remineralized dead organic matter in the water column
p_z	percentage of remineralized dead zooplankton in the water column
$\{Zoop\}$	zooplankton biomass
Z_i	numbers of i cohorts
W_i	weights of i cohorts
$pred_{\max}$	maximum rate of predation
$Z_{\max}$	maximum number of zooplankton
Z_0	zooplankton threshold for predation
$\{Detr\}$	detritus concentration
r_d	remineralization rate of benthic detritus

The influence of the maximal ingestion rate $g_{\max}$ on the variability of the phytoplankton and zooplankton biomasses (PZB)

The influence of the maximal ingestion rate $g_{\max}$ on the variability of the phytoplankton and zooplankton biomasses (PZB) was analyzed for two values of the k_{Phyt} half-saturation constant for grazing. The following assumptions were made in the calculations:

case 1. for $k_{Phyt} = 0.1$ gC m^{-3}
$g_{\max} = 0.7$; 0.68; 0.67; 0.66; 0.65; 0.645 d^{-1}

case 2. for $k_{Phyt} = 0.2$ gC m^{-3}
$g_{\max} = 1$; 0.9; 0.8; 0.78; 0.75; 0.745 d^{-1}.

$g_{\max}$ affected the magnitude of the total PZB to a considerable extent. The smaller the value of $g_{\max}$, the larger the magnitude of PZB. The intensity of growth of PZB is different in the period considered than during the entire numerical experiment and is due to the magnitude of the half-saturation constant for grazing k_{Phyt}.

The simulations show that, in case 1 for $k_{Phyt} = 0.1$ gC m^{-3}, a decrease in $g_{\max}$ resulted in an increase in the magnitude of the summer bloom, mainly a cyanobacterial bloom, and the total zooplankton biomass in June. When this value was decreased from 0.7 d^{-1} to 0.65 d^{-1}, the magnitude of the cyanobacterial bloom as well as the total zooplankton biomass increased gradually Figs. 2–4; i.e. the phytoplankton biomass increased four times ($\{Phyt\}_{0.7} \simeq 0.12$ gC m^{-3} and $\{Phyt\}_{0.65} \simeq 0.48$ gC m^{-3}) and the total zooplankton biomass increased about five times ($\{Zoop\}_{0.7} \simeq 0.22$ gC m^{-2}

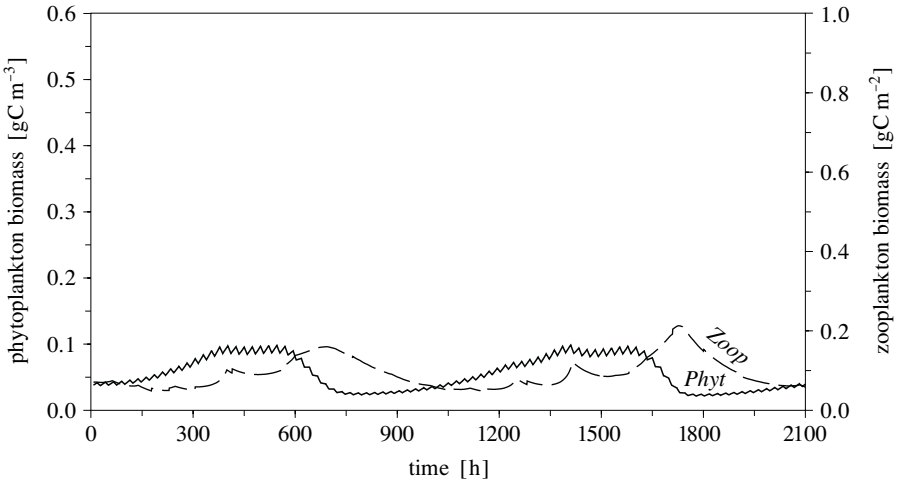

Fig. 2. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.7 d^{-1}, k_{Phyt}=0.1 gC m^{-3}

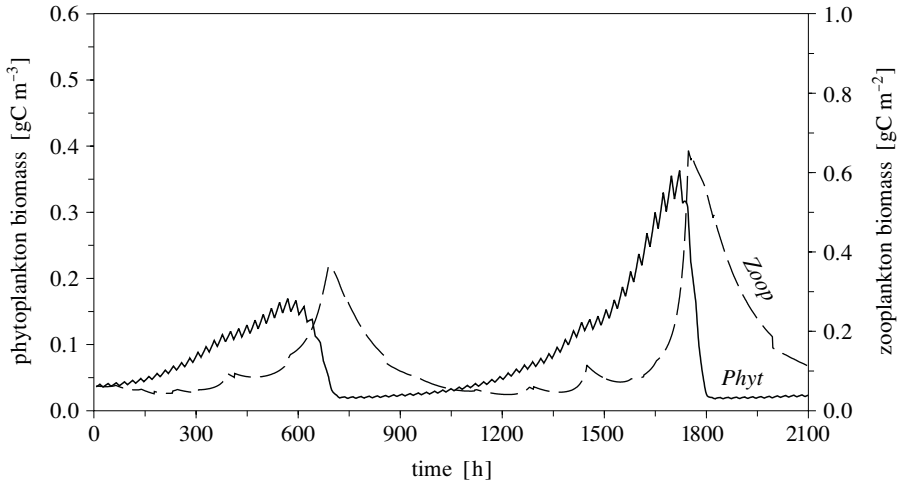

Fig. 3. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.66 d^{-1}, k_{Phyt}=0.1 gC m^{-3}

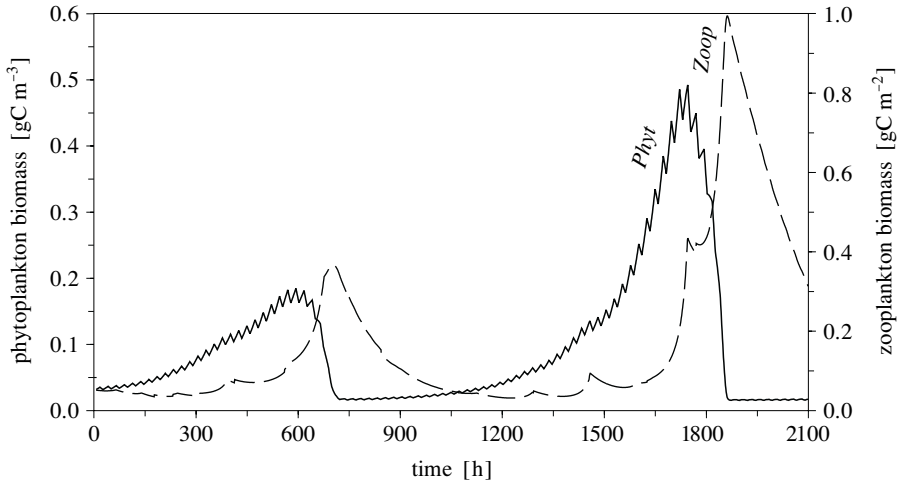

Fig. 4. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.65 d^{-1}, k_{Phyt}=0.1 gC m^{-3}

and $\{Zoop\}_{0.65} \simeq 1.08$ gC m^{-2}). When $g_{\max}$ was reduced to 0.645 d^{-1}, the PZB increased to $\{Phyt\} \simeq 0.65$ gC m^{-3} for the cyanobacterial bloom and to $\{Zoop\} \simeq 1.6$ gC m^{-2} for the total zooplankton biomass (Fig. 5).

However, in April, a decrease in $g_{\max}$ from 0.7 d^{-1} to 0.66 d^{-1} caused the spring bloom and total zooplankton biomass to grow slowly; i.e. for $g_{\max} = 0.7$ d^{-1} the following values were obtained: $\{Phyt\} \simeq 0.12$ gC m^{-3}

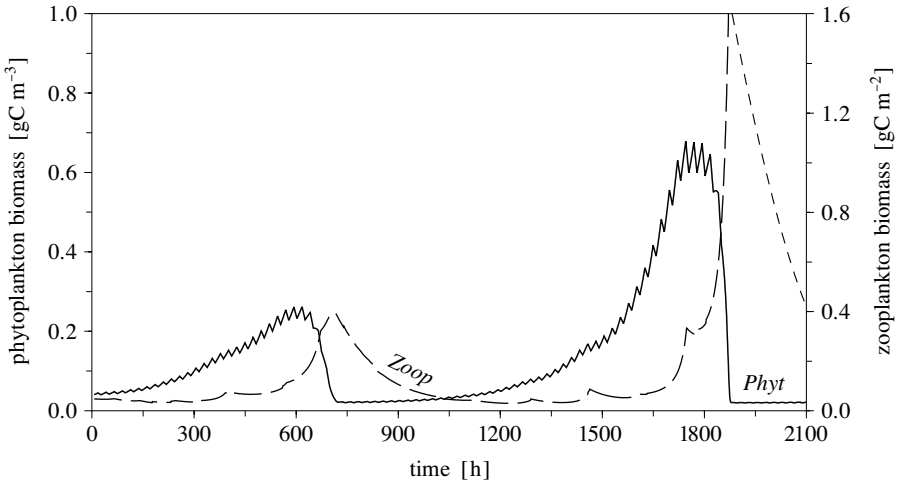

Fig. 5. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.645 d^{-1}, k_{Phyt}=0.1 gC m^{-3}

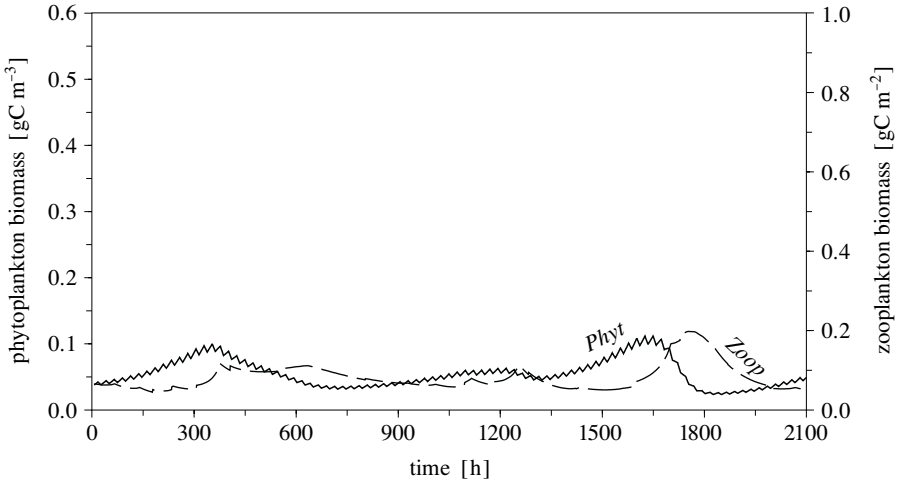

Fig. 6. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=1 d^{-1}, k_{Phyt}=0.2 gC m^{-3}

and $\{Zoop\} \simeq 0.22$ gC m^{-2}, and for $g_{\max} = 0.66$ d^{-1} : $\{Phyt\} \simeq 0.18$ gC m^{-3} and $\{Zoop\} \simeq 0.38$ gC m^{-2} (Fig. 3). When $g_{\max}$ was decreased to 0.645 d^{-1}, there was a scarcely detectable increase to $\{Phyt\} \simeq 0.24$ gC m^{-3} for the spring bloom and to $\{Zoop\} \simeq 0.4$ gC m^{-2} for the total zooplankton biomass (Fig. 5). Varying the maximal ingestion rate below a value of 0.66 d^{-1} in case 1 did not significantly affect the variability of the April magnitudes.

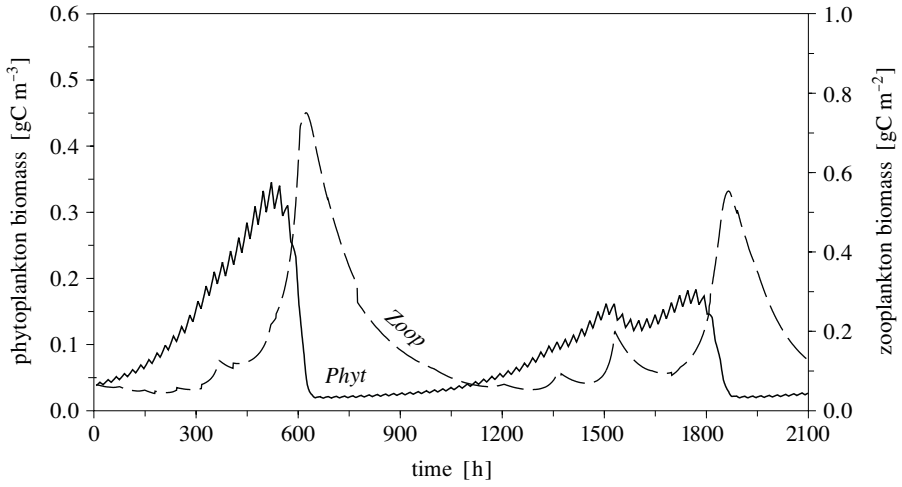

Fig. 7. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.8 d^{-1}, k_{Phyt}=0.2 gC m^{-3}

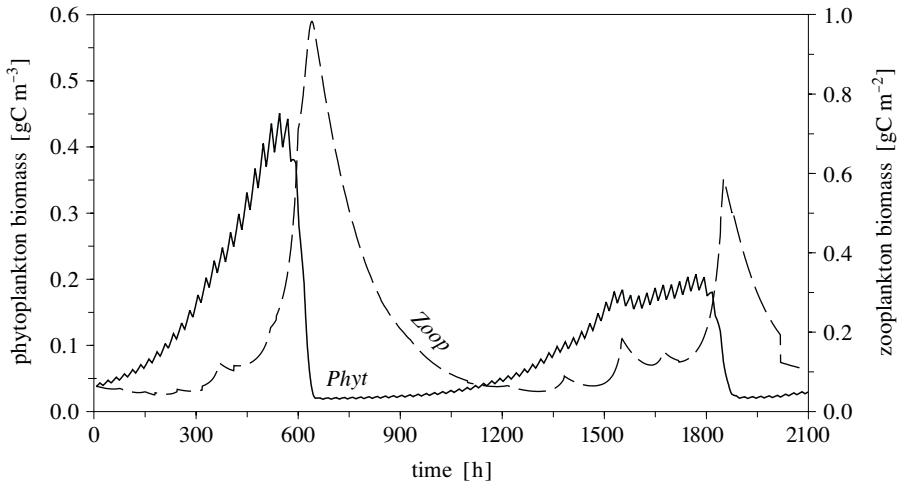

Fig. 8. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.78 d^{-1}, k_{Phyt}=0.2 gC m^{-3}

The calculations also demonstrated that, in case 2 for $k_{phyt} = 0.2$ gC m^{-3}, a decrease in the maximal ingestion rate gave rise to larger PZB in April. When this value was decreased from $g_{\max} = 1.00$ d^{-1} to 0.78 d^{-1}, the magnitude of the spring bloom increased about four times and the total zooplankton biomass increased about seven times Figs. 6 and 8. When $g_{\max}$ was decreased to 0.745^{-1} PZB increased about seven times to

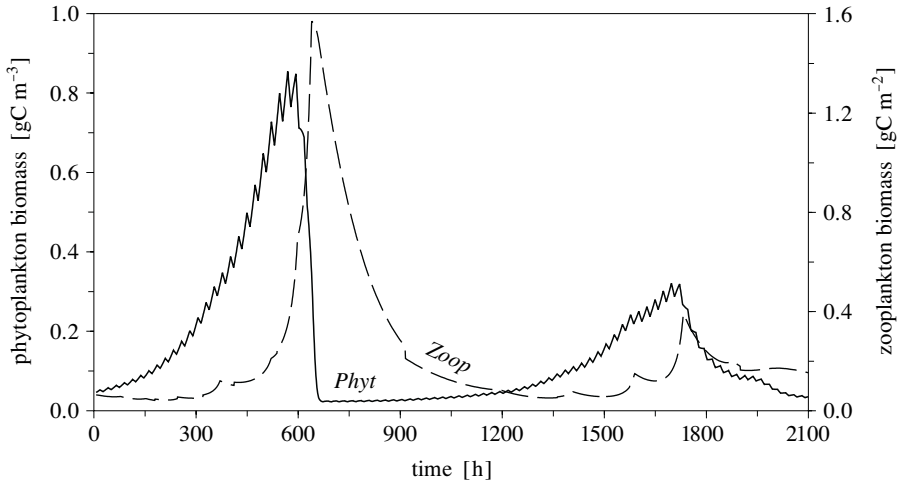

Fig. 9. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.75 d^{-1}, k_{Phyt}=0.2 gC m^{-3}

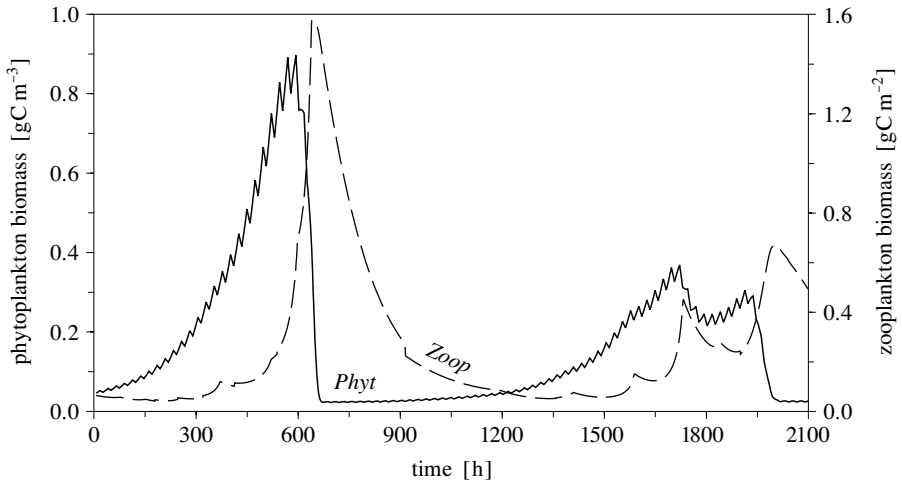

Fig. 10. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.745 d^{-1}, k_{Phyt}=0.2 gC m^{-3}

$\{Phyt\} \simeq 0.82$ gC m^{-3} for the spring bloom and about eleven times to $\{Zoop\} \simeq 1.6$ gC m^{-2} for the zooplankton biomass (Fig. 9). These values are overestimated for the study area.

However, the June simulations show that values of $g_{\max}$ reduced from 1 d^{-1} to 0.8 d^{-1} generate only a weak response from the cyanobacterial bloom and total zooplankton biomass Figs. 6 and 7 ($\{Phyt\} \simeq 0.1$ gC m^{-3}

and $\{Zoop\} \simeq 0.2\ \mathrm{gC\,m^{-2}}$). Whereas when $g_{\max}$ was decreased to $0.78\ \mathrm{d^{-1}}$, the cyanobacterial bloom increased by a factor of two and the total zooplankton biomass by a factor of three: $\{Phyt\} \simeq 0.2\ \mathrm{gC\,m^{-3}}$ and $\{Zoop\} \simeq 0.6\ \mathrm{gC\,m^{-2}}$. The subsequent drop in value of $g_{\max}$ to $0.75\ \mathrm{d^{-1}}$ caused the phytoplankton biomass to increase by 50 percent and the zooplankton biomass to decrease by approximately 33 percent, i.e. $\{Phyt\} \simeq 0.3\ \mathrm{gC\,m^{-3}}$ and $\{Zoop\} \simeq 0.4\ \mathrm{gC\,m^{-2}}$ respectively (Fig. 9). When $g_{\max}$ was reduced to $0.745\ \mathrm{d^{-1}}$, the cyanobacterial bloom and total zooplankton biomass rose to $\{Phyt\} \simeq 0.4\ \mathrm{gC\,m^{-3}}$ and $\{Zoop\} \simeq 0.7\ \mathrm{gC\,m^{-3}}$ respectively (Fig. 10).

The calculations show the general variations in the distributions of PZB with respect to time. The results demonstrate significant changes in the distributions of PZB (two distinct maxima $\{Phyt\}$ and $\{Zoop\}$), which take place in an area of considerable increase in primary production and food ingestion respectively. The substantial growth in phytoplankton biomass falls as a result of the considerable increase in zooplankton biomass. This growth is caused by the increase in body weight W_i through the rise in ingestion and also the production of single clutches of eggs by each adult. This situation leads to a real growth in the total zooplankton biomass, which is the algebraic sum of the products of weights W_i and numbers Z_i ($\{Zoop\} = \sum W_i Z_i$).

The results indicate that the changes in $g_{\max}$ exert hardly any influence on the characteristics examined. The decrease in $g_{\max}$ causes a general increase in the ingestion rate $fil(\{Phyt\}) = g_{\max}(\{Phyt\} - \{Phyt\}_0)/(\{Phyt\} - \{Phyt\}_0 + k_{Phyt})$ in the specified period of time, i.e. for $k_{Phyt} = 0.1\ \mathrm{gC\,m^{-3}}$ (case 1), the growth in $fil(\{Phyt\})$ occurs in April as well as in June, but is larger in the latter month. However, for $k_{Phyt} = 0.2\ \mathrm{gC\,m^{-3}}$ (case 2), two distinct maxima on the distribution of $fil(\{Phyt\})$ occur in both April and June. In this case, however, the increase is larger in April than in June.

It seems that the decrease in $g_{\max}$ should cause a decrease in $fil(\{Phyt\})$. But this does not happen, because the determination of food ingestion is explicitly dependent on the value of $g_{\max}$ as well as implicitly through the phytoplankton biomass $\{Phyt\}$, namely through grazing, where the coefficient $g_{\max}$ occurs. The results of the numerical investigations indicate that the phytoplankton biomass has a greater influence on the ingestion rate $fil(\{Phyt\})$ through the value of the expression $(\{Phyt\} - \{Phyt\}_0)/(\{Phyt\} - \{Phyt\}_0 + k_{Phyt})$ than the coefficient $g_{\max}$. Analysis of these simulations indicates that the distinct maxima occurring on the distributions of phytoplankton and zooplankton appear at the same time as the maxima on the distribution of food ingestion. This happens because

the phytoplankton biomass affects the zooplankton biomass to a significant degree through the ingestion of food. This then affects the phytoplankton biomass, or these magnitudes influence one another.

The influence of the half-saturation constant for grazing k_{Phyt} on the variability of the phytoplankton and zooplankton biomasses (PZB)

The half-saturation constant for grazing k_{Phyt} exerted a significant effect on the magnitude of the phytoplankton biomass and the total zooplankton biomass. The influence of the coefficient k_{Phyt} on PZB was analysed assuming a selected value of the maximal ingestion rate $g_{\max} = 0.67$ d^{-1}.

The following assumptions were made in the calculations: the half-saturation constant for grazing is equal to $k_{Phyt} = 0.9$; 0.1; 0.11; 0.115; 0.117; 0.119; 0.121; 0.123 d^{-1}.

The calculations demonstrated that, for $g_{\max} = 0.67$ d^{-1}, if k_{Phyt} was increased from 0.09 gC m^{-3} to 0.115 gC m^{-1}, PZB increased in April as well as in June (Figs. 11 and 12). This growth was larger in June than in April. The magnitude of the spring bloom rose about three times i.e. $\{Phyt\}_{0.09} \simeq 0.1$ gC m^{-3} and $\{Phyt\}_{0.115} \simeq 0.28$ gC m^{-3}, and the cyanobacterial bloom increased about four times i.e. $\{Phyt\}_{0.09} \simeq 0.15$ gC m^{-3} and $\{Phyt\}_{0.115} \simeq 0.6$ gC m^{-3} (Figs. 11 and 12 respectively). However, the magnitude of the total zooplankton biomass increased about three times in April i.e. $\{Zoop\}_{0.09} \simeq 0.2$ gC m^{-2} and $\{Zoop\}_{0.115} \simeq 0.6$ gC m^{-2}, and four

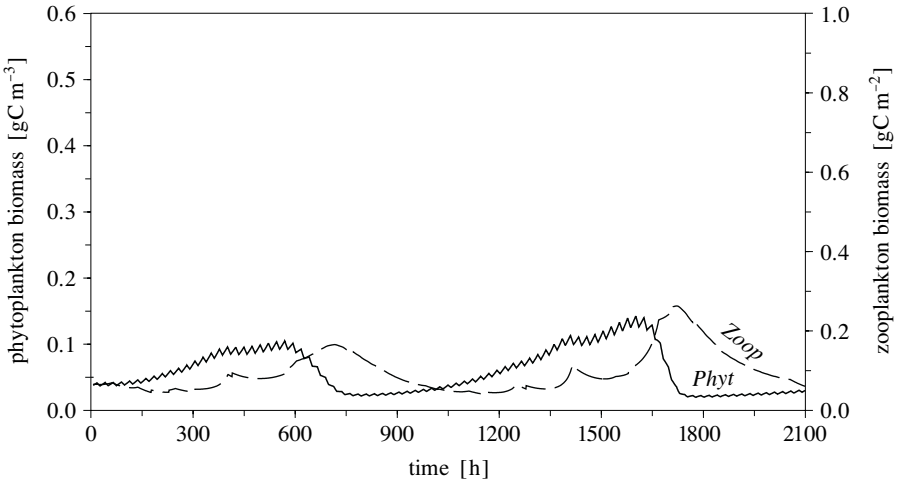

Fig. 11. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.67 d^{-1}, k_{Phyt}=0.09 gC m^{-3}

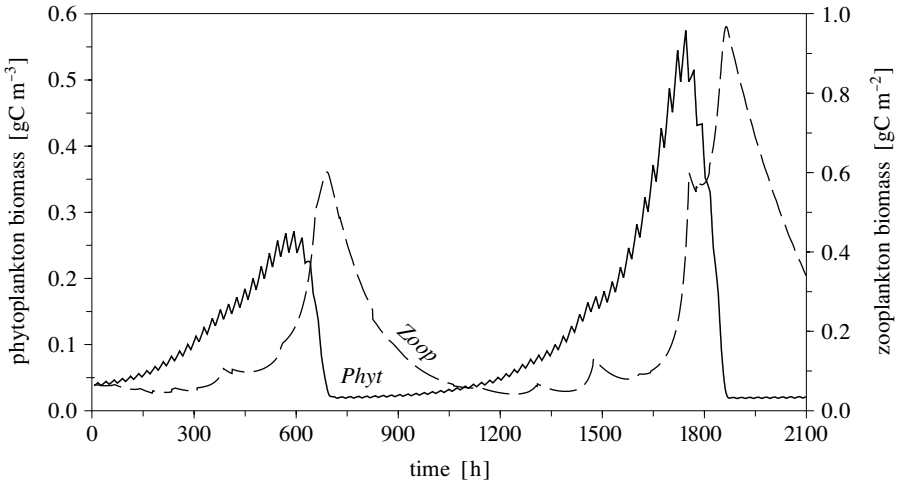

Fig. 12. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.67 d^{-1}, k_{Phyt}=0.115 gC m^{-3}

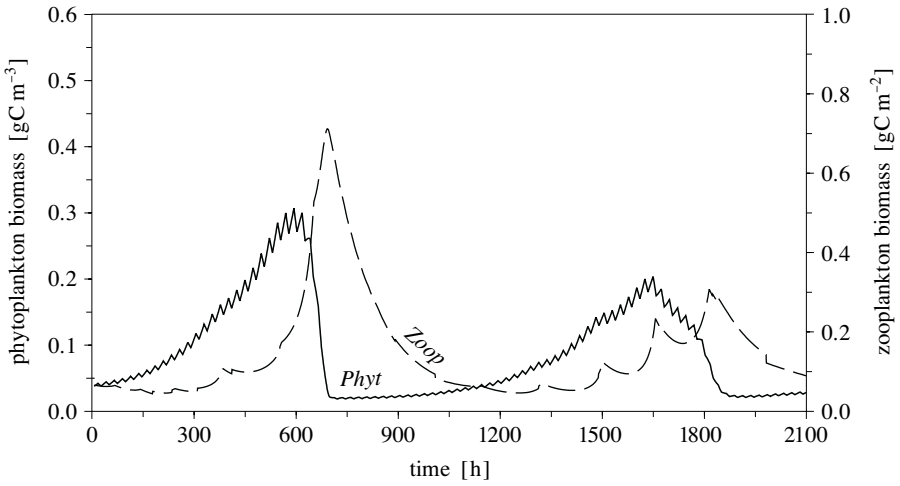

Fig. 13. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.67 d^{-1}, k_{Phyt}=0.119 gC m^{-3}

times in June i.e. $\{Zoop\}_{0.09} \simeq 0.25$ gC m^{-2} and $\{Zoop\}_{0.115} \simeq 1$ gC m^{-2} (Figs. 11 and 12 respectively). When k_{Phyt} was increased to 0.119 gC m^{-3} the magnitude of the cyanobacterial bloom and the total biomass of heterotrophs in June decreased considerably, i.e. $\{Phyt\}_{0.119} \simeq 0.2$ gC m^{-3} and $\{Zoop\}_{0.119} \simeq 0.3$ gC m^{-2} (Fig. 13). However, the simulations show that varying the value of k_{Phyt} in the range from 0.115 to 0.119 generates

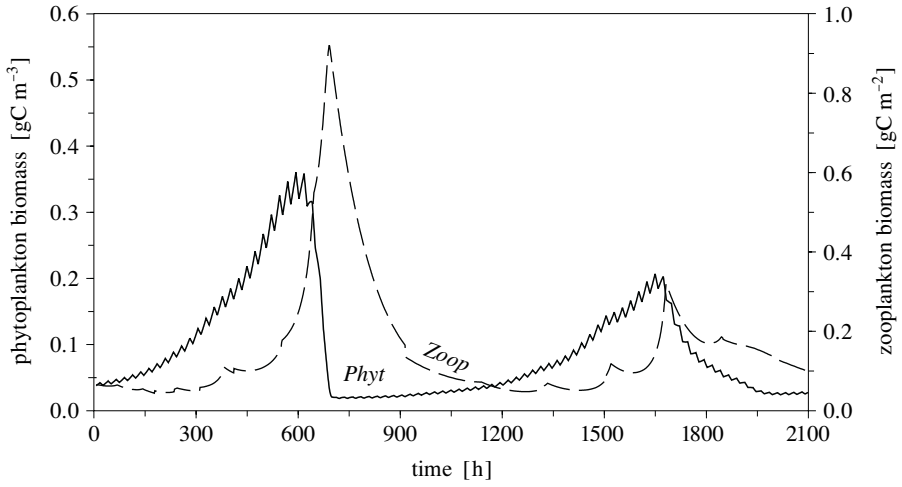

Fig. 14. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.67 d^{-1}, k_{Phyt}=0.121 gC m^{-3}

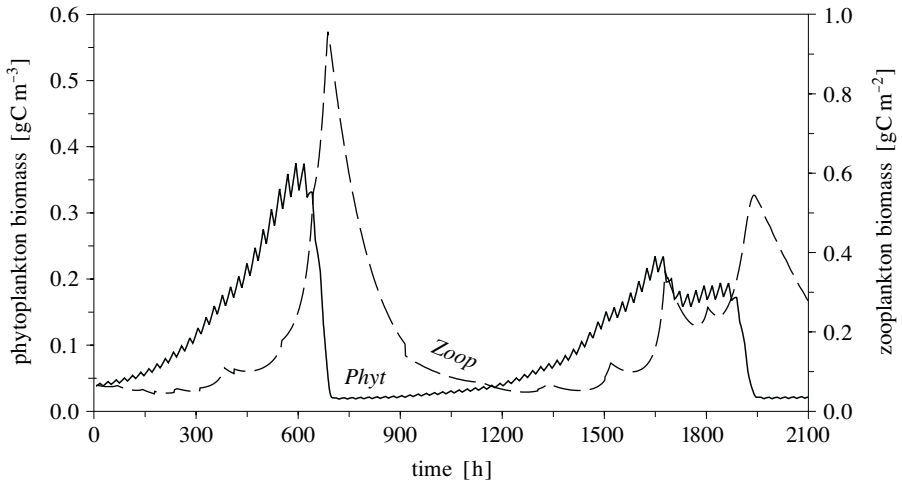

Fig. 15. Phytoplankton $\{Phyt\}$ and zooplankton $\{Zoop\}$ biomasses for 90 days when $g_{\max}$=0.67 d^{-1}, k_{Phyt}=0.123 gC m^{-3}

only a weak response from the spring bloom and the total zooplankton biomass in April, i.e. $\{Phyt\}_{0.119} \simeq 0.3$ gC m^{-3} and $\{Zoop\}_{0.119} \simeq 0.68$ gC m^{-2} respectively (Fig. 13). The results indicate that in the subsequent increase, the value of k_{Phyt} causes the total zooplankton biomass to rise significantly in April, with a smaller increase in the spring bloom, i.e. for $k_{Phyt} = 0.121$ gC m^{-3}, $\{Phyt\} \simeq 0.35$ gC m^{-3} and $\{Zoop\}$

$\simeq 0.9$ gC m^{-2} (Fig. 14). However, in June for $k_{Phyt} = 0.121$ gC m^{-3}, the increase in the distribution of PZB comes to a stop (Fig. 14). When the value of k_{Phyt} was increased to 0.123 the cyanobacterial bloom and the total zooplankton biomass in June increased, i.e. $\{Phyt\} \simeq 0.25$ gC m^{-3} and $\{Zoop\} \simeq 0.58$ gC m^{-2} respectively (Fig. 15). In April, however, the magnitudes investigated remained at the same level as when k_{Phyt} $= 0.121$ gC m^{-3}.

The half-saturation constant should be considered in that range of values for which the calculated PZB take real values in the study area.

The calculations of the numerical simulations demonstrated that changes in k_{Phyt} have a considerable influence on PZB. Moreover, any increase in k_{Phyt} causes PZB to rise or drop alternately in the period under consideration.

Increasing k_{Phyt} should cause the ingestion rate $fil(\{Phyt\})$ to decrease, but this does not take place. This situation is hard to explain. The half-saturation constant k_{Phyt} has a double influence on the ingestion rate, to be precise, on the expression $(\{Phyt\} - \{Phyt\}_0)/(\{Phyt\}$ $- \{Phyt\}_0 + k_{Phyt})$. This expression is directly dependent on the value of k_{Phyt}. It is also indirectly dependent on this value through the phytoplankton biomass $\{Phyt\}$, that is, via the process of grazing, where the coefficient k_{Phyt} occurs.

Analysis indicates that the distinct maxima (peaks) occurring on the distributions of phytoplankton and zooplankton appear at the same time as the maxima on the distribution of the ingestion rate. This happens because PZB affect each other.

5. Concluding remarks

The simulation experiments have shown that the changes in the values of selected parameters of food ingestion, i.e. the maximal ingestion rate $g_{\max}$ and the half-saturation constant for grazing k_{Phyt}, influence the shape and value of the distribution of PZB.

These investigations show this influence to be non-unique.

- The smaller the maximal ingestion rate, the larger the magnitudes of PZB. The intensity of this growth is different in the period considered than during the entire numerical experiment. This is due to the value of the half-saturation constant for grazing. There is a considerable increase in both phytoplankton biomass and total zooplankton biomass in April for $k_{Phyt} = 0.2$ gC m^{-3} and in June for $k_{Phyt} = 0.1$ gC m^{-3}.

- The increase in the value of the half-saturation constant for grazing for a specific maximal ingestion rate causes PZB to rise or drop alternately in the period considered.

The analysis of these numerical studies indicates that the half-saturation constant for grazing has a very great influence on the magnitudes investigated. The value of coefficient k_{Phyt}, which occurs in equations (8)–(10), is probably related directly to the relative sizes of the zooplankton and the particles. This value of k_{Phyt} sets upper and lower limits to the size of particles which can be captured and ingested.

The calculations clearly indicate for which value of k_{Phyt}, for the given period and study area P1, the increases in phytoplankton and zooplankton biomasses are retarded, i.e. when saturation is reached. A subsequent small increase in k_{Phyt} interrupts this state and the distributions of the magnitudes investigated undergo a change.

We do not know much of this variation is associated with physical fluctuations, and how much is due to the inherent characteristics of the population structure and to metabolic and behavioral processes in the animals. The simulation given here is intended to demonstrate the importance of food ingestion parameters, since they can alter the nature of the interactions between plants and herbivores.

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Appendix

Parameters of the PhyZooNuDe model:

Phytoplankton

$$\mathrm{PRE} = \alpha d_A \min\{d_I, d_N\} d_T d_S \{Phyt\}, \tag{24}$$

$$d_I = \frac{E(z,t)}{E_S} \exp\left[1 - \frac{E(z,t)}{E_S}\right], \quad d_N = \frac{\{Nutr\}}{\{Nutr\} + k_{Nutr}}, \tag{25}$$

$$E(z,t) = \frac{\eta_d}{\lambda}\left(1 + \cos\frac{2\pi t}{\lambda}\right) \exp\left(-k_d(\lambda) z\right), \tag{26}$$

$$\eta_d = 8.67 - 8.29\cos\left(\omega x - 3.03\right) + 0.69\cos\left(2\omega x - 5.80\right), \tag{27}$$

$$k_d(\lambda) = k_w + Chl_a\left[C_1(\lambda)\exp(-a_1(\lambda) Chl_a + k_{d,n}(\lambda)\right], \tag{28}$$

$$d_A = 3.63 - 2.30\sin\left(\omega x + 0.70\right) + 0.69\sin\left(2\omega x - 0.45\right), \tag{29}$$

$$d_T = \frac{T}{T_{opt}} \exp\left(1 - \frac{T}{T_{opt}}\right), \quad d_S = \frac{S}{S_{opt}} \exp\left(1 - \frac{S}{S_{opt}}\right), \tag{30}$$

$$\begin{aligned} \mathrm{RES} &= \mathrm{RES}_n + \mathrm{RES}_d \\ &= d_A\left(m_P^n + m_P^d \min\{d_I, d_N\}\right) d_T \{Phyt\}, \end{aligned} \tag{31}$$

$$\mathrm{MOR}_P = m_P \{Phyt\}, \tag{32}$$

$$\begin{aligned} \mathrm{GRA} &= g_{\max} \frac{\{Phyt\} - \{Phyt\}_0}{\{Phyt\} - \{Phyt\}_0 + k_{Phyt}} \{Zoop\} \\ &\quad \text{for} \quad \{Phyt\} > \{Phyt\}_0. \end{aligned} \tag{33}$$

Zooplankton as animals

$$\mathrm{ING}_i = \tau fil(\{Phyt\}) W_i^{\alpha}, \tag{34}$$

$$\begin{aligned} fil(\{Phyt\}) &= g_{\max} \frac{\{Phyt\} - \{Phyt\}_0}{\{Phyt\} - \{Phyt\}_0 + k_{Phyt}} \\ &\quad \text{for} \quad \{Phyt\} > \{Phyt\}_0, \end{aligned} \tag{35}$$

$$\mathrm{MET}_i = M_s + M_r + M_a = M_s + n_e A_i, \quad A_i = n_a \mathrm{ING}_i, \tag{36}$$

$$\mathrm{EGG} = X \int_J \mathrm{ZF} \left(\frac{dW}{dt} \right)_{W=\mathrm{WF}} dt, \tag{37}$$

$$\mathrm{PRED} = pred_{\max} \left\{ 1 - \exp \left(pred_{\max} \frac{Z_i - Z_0}{Z_{\max} - Z_0} \right) \right\}. \tag{38}$$

Nutrients

$$\mathrm{REL} = g\mathrm{RES}, \tag{39}$$

$$\mathrm{UPT} = g(\mathrm{PRE} - \mathrm{RES}), \tag{40}$$

$$\mathrm{EXC} = g\mathrm{MET} = g(M_s + n_e A), \tag{41}$$

$$\mathrm{FEC}_Z = n_f \mathrm{GRA}, \tag{42}$$

$$\mathrm{MOR}_Z = n_z \mathrm{GRA}, \tag{43}$$

$$\mathrm{REM}P = p_p \mathrm{MOR}_P, \tag{44}$$

$$\mathrm{REM}Z = p_z \mathrm{MOR}_Z, \tag{45}$$

$$\mathrm{REM}F = p_f \mathrm{FEC}_Z, \tag{46}$$

$$\begin{aligned} \mathrm{REMI} &= g(\mathrm{REM}P + \mathrm{REM}Z + \mathrm{REM}F) \\ &= g\{p_p \mathrm{MOR}_P + (p_f n_f + p_z n_z)\mathrm{GRA}\}. \end{aligned} \tag{47}$$

Benthic detritus

$$\begin{aligned} \mathrm{SEDI} &= (1-p_p)\mathrm{MOR}_P + (1-p_f)\mathrm{FEC}_{Zoop} + (1-p_z)\mathrm{MOR}_{Zoop} \\ &= (1-p_p)\mathrm{MOR}_P + \{(1-p_f)n_f + (1-p_z)n_z\}\mathrm{GRA}, \end{aligned} \tag{48}$$

$$D = \int_0^H \mathrm{SEDI} dz, \tag{49}$$

$$\mathrm{REMD} = r_d\{Detr\}. \tag{50}$$