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

Part 1. P–V–Z–D model

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Abstract

This paper presents a nutrient–phytoplankton–zooplankton–detritus biological model with a fully-developed regeneration mechanism with respect to the daily migration of zooplankton. The P–V–Z–D model consists of two partial differential equations of the diffusion type for the concentration of nutrients and phytoplankton, and two ordinary differential equations for the concentration of zooplankton and the benthic detritus pool, together with initial and boundary conditions.

1. Introduction

The modelling of marine ecosystems has tended to concentrate on two trophic levels, the phytoplankton and the fish. In the former case this has been possible because the plant material could be considered conceptually and measured analytically as a single unit. In the latter case the major commercial fish species were treated one by one, mainly in relation to the effects of fishing on stock abundance; the relevant data were supplied by the fishing industry.

Usually, herbivores or benthic detritus feeders are included in simulation modelling only as a means of supplying or disposing of biological matter required by those parts of the ecosystem treated as the central components. For the benthos there is, so far, no evidence of a change in this attitude, but the zooplankton are at present considered as mere consumers rather than as organisms having certain patterns of growth, reproduction and mortality. Thus the parameters of population dynamics – fecundity, age structure, age, specific birth and death rates – are more important in determining the behaviour of an ecosystem than the simpler concepts of the flow of organic matter.

However, there are still certain limitations which must be imposed here. Zooplankton are a very heterogeneous group, defined by the method of collection rather than by their position in the food web. Any net haul, and particularly a series of hauls with different mesh sizes, is likely to contain bacteriovorous, 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 single group in the zooplankton, so practically all the primary production must literally pass through them. In turn, they (or their faeces and excreta) are the predominant source of food for the rest of the system. There is also a less satisfactory reason, namely, the lack of information on the abundance of other groups within the plankton such as microzooplankton, carnivores, and the deep-water communities of the open ocean. In particular, there is little experimental data on the feeding behaviour or metabolism of these populations.

In view of the above, the main attention below is focused on the pelagic herbivores as one of the principal links in the food chain (Mullin, 1963).

2. Zooplankton as biomass

It is simplest to begin with the general interactions between nutrients P, phytoplankton V and the herbivorous zooplankton Z. A schematic representation gives

$$\frac{dP}{dt} = -\text{phytoplankton uptake}\,(P,\,V) + \text{zooplankton excretion}\,(Z), \tag{1}$$

$$\frac{dV}{dt} = \text{phytoplankton growth}\,(P,\,V) - \text{zooplankton grazing}\,(V,\,Z), \tag{2}$$

$$\frac{dZ}{dt} = \text{zooplankton growth}\,(V,\,Z) - \text{predation}\,(Z). \tag{3}$$

It can be seen that the zooplankton has an effect on all three trophic levels. The terms containing Z are not simple functions, just as the other terms are not, as is known from previous work. All this requires knowledge of the kinetics of metabolism at each trophic level. Yet this is often not available, particularly for the zooplankton and particularly when only data concerning the biomass (*i.e.* wet weights, dry weights, or organic matter in net hauls) are available.

These considerations of herbivores as biomass show that useful deductions can be made. Especially in studies of phytoplankton populations, it may be sufficient to use a single parameter for grazing; the general concepts from this point of view have already been reviewed (Riley, 1963). Such studies of phytoplankton usually stress the effects of physical variables in changing the phytoplankton populations. These factors are certainly important, but Cushing (1959) and others have pointed out that they may have been overemphasised by the excessive simplicity of the portrayal of the herbivores. Thus it is necessary to look at the probable intricacies that can arise from a more consistent consideration of grazing, growth, metabolism, reproduction and mortality in copepods.

3. Zooplankton as animals

Equation (3) can be expanded to

$$\frac{dZ}{dt} = \text{ingestion} - \text{defecation} - \text{metabolism} - \text{predation}. \tag{4}$$

Assume Z is composed of i cohorts of copepods with weights W_i and numbers Z_i; then

$$Z = \sum W_i Z_i, \tag{5}$$

$$\frac{dZ}{dt} = \sum \left(W_i \frac{dZ_i}{dt} + Z_i \frac{dW_i}{dt} \right), \quad \text{and} \tag{6}$$

by comparison with eq. (4),

$$\frac{dW_i}{dt} = \frac{1}{Z_i}(\text{ingestion} - \text{defection} - \text{metabolism}), \tag{7}$$

$$-\frac{dZ_i}{dt} = \frac{1}{W_i}\,(\text{predation}). \tag{8}$$

Eq. (7) determines the change in weight of an individual copepod as the sum of its individual gains and losses and losses of energy; eq. (8) 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 $W0$ is the weight of the naupliar stage at which feeding starts and WN is the weight of the adult, then for each cohort relations of the form

$$Z0 = F\left(V,\, ZN,\, \frac{WN}{W0}\right) \tag{9}$$

indicate the requirements for some function defining recruitment $Z0$ in terms of food available, adult numbers ZN and the ratio of adult to naupliar weight. The function includes not merely reproductive capacity but also the mortality before the feeding naupliar stage is reached.

4. The biological P–V–Z–D model

In this paper the zooplankton (herbivorous copepods) has been introduced into the model as 'biomass'.

The present nutrient–phytoplankton–zooplankton–detritus model is based partly on the papers by Dzierzbicka-Głowacka (1994a, 1996) and Dzierzbicka-Głowacka and Zieliński (1997a,b). The P–V–Z–D model consists of two nonlinearly coupled, partial second-order differential equations and two ordinary first-order differential equations, together with initial and boundary conditions.

The change in local nutrient concentration $P(z,\, t)$ is determined by turbulent diffusion K_z, uptake by algae UPT, remineralised dead phytoplankton, zooplankton faecal pellets and dead zooplankton REMI, and by zooplankton excretion EXC and nutrient release REL:

$$\frac{\partial P}{\partial t} = \frac{\partial}{\partial z}\left(K_z \frac{\partial P}{\partial z}\right) - \mathrm{UPT} + \mathrm{REL} + \mathrm{REMI} + \mathrm{EXC}. \tag{10}$$

The temporal changes in the local phytoplankton biomass concentration $V(z,\, t)$ are caused by turbulent diffusion K_z, sinking of algae w_z, production PRE, respiration RES, mortality MOR V and grazing by zooplankton GRA

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

The temporal changes in the local zooplankton biomass concentration $Z(z,\, t)$ are defined by ingestion (= grazing) GRA, zooplankton faecal pellets FEC, metabolism MET and predation (= mortality) MOR Z

$$\frac{\partial Z}{\partial t} = \mathrm{GRA} - \mathrm{FEC} - \mathrm{MET} - \mathrm{MOR}\, Z. \tag{12}$$

Finally, the temporal changes in the detritus pool at the bottom $D(t)$ are determined by the flux of phytoplankton $F_V(H)$ and that of detrital material sedimenting out of the water column onto the bottom DETR and remineralisation of detritus REM D

$$\frac{dD}{\partial t} = -F_V(H) + \mathrm{DETR} - \mathrm{REM}\, D, \tag{13}$$

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

Primary production

Based on the available literature, the rate of primary production is defined in the model by the equation given by Radach (1983)

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

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, 1994a, 1996):

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

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

The assimilation number A, the ratio of production (amount of assimilated carbon) to the concentration of chlorophyll, was determined on the basis of the Platt model (Platt *et al.*, 1980; Harrison *et al.*, 1985), and depends on η, the amount of solar energy reaching the free surface of the study area

$$A(z,t) = \phi(1 - \exp[-\alpha\eta(z,t)/\phi])\exp\left(-\beta\eta(z,t)/\phi\right), \tag{17}$$

where α, β, ϕ are empirical coefficients approximating the assimilation number to the natural conditions of the basin in question.
The amount of solar energy reaching depth z is given by Dera (1992)

$$\eta(z,\, t) = \eta_o T_{z,\, vis}(z,\, t), \tag{18}$$

where η_o is the amount of solar energy reaching the free sea surface.
The $T_{z,\, vis}$ total downward irradiance transmission coefficient in the 400–700 nm range is described by the following formula (Woźniak, 1993):

$$T_{z,vis}(z,t) = \int\limits_{400\,\mathrm{nm}}^{700\,\mathrm{nm}} f_E(\lambda, z=0)\exp\left(-\int\limits_{0}^{z} k_d(\lambda, z, V)dz\right)d\lambda\,, \tag{19}$$

where f_E is the virtually constant relative function of the solar incident irradiance (Dera, 1992; Woźniak, 1993), and k_d is 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 (Woźniak and Pelevin, 1991).

Respiration of phytoplankton

In fact, the metabolic processes in plants are accompanied by katabolic 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 values of the losses due to respiration. Respiration RES consists of basic and photo-respiration, each being proportional to V (Ryther, 1956; Parsons *et al.*, 1977)

$$\mathrm{RES} = \mathrm{RES}^n + \mathrm{RES}^d = m_v^n S_a V(z,t) + m_v^d S_a \min\{d_i, d_p\} V(z,\,t), \tag{20}$$

where the basic dark respiration rate is m_v^n as a proportionality factor to the maximum photosynthetic rate (Ryther, 1956) and the photo-respiration rate is m_v^d as a proportionality factor to the rate of primary production.

Nutrient release

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

$$\mathrm{REL} = g\,\mathrm{RES}. \tag{21}$$

Nutrient uptake

The quantity of nutrient uptake by phytoplankton cells can be expressed as (Radach, 1983)

$$\mathrm{UPT}^d = g\,(\mathrm{PRE} - \mathrm{RES}^d) \tag{22}$$

for positive net production only and for photo-respiration. However, for dark respiration, nutrient uptake is proportional to the rate of primary production.

$$\mathrm{UPT}^n = g\,(S_a V(z,\,t) - \mathrm{RES}^n), \tag{23}$$

where the constant g is the P:C ratio.

Phytoplankton mortality

The natural phytoplankton mortality is a process which results in some losses in biomass. It was assumed that mortality is directly proportional to the phytoplankton concentration (Raymont, 1980; Sjöberg, 1980)

$$\mathrm{MOR}\,V = mmV(z,\,t). \tag{24}$$

Phytoplankton grazing

Phytoplankton grazing by zooplankton GRA is assumed to be independent of the chemical composition of the water. One dominant species among the zooplankton is responsible for 80–90% of the phytoplankton consumed, possible changes in the numbers of this dominant species can be neglected within a given interval of time, and the process is scaled on a diurnal basis. The intensity of phytoplankton grazing GRA is proportional to the zooplankton biomass Z (Renk *et al.*, 1983):

$$\mathrm{GRA} = g_w(z,\, t)Z(z,\, t). \tag{25}$$

The coefficient of phytoplankton grazing by zooplankton g_w denotes the amount of phytoplankton grazed by the zooplankton biomass at a constant phytoplankton concentration:

$$g_w = \{1 + a_w \cos\omega(t - t_0)\} f(z) \frac{\mathrm{PRE}_o}{Z_o}, \tag{26}$$

where Z_o is the mean zooplankton biomass averaged over 24 hours, PRE_o denotes the mean primary production rate at the midday sun culmination, a_w is the relative amplitude of zooplankton biomass changes, t_0 is the time when the maximum zooplankton concentration occurs, and $\omega = \Pi/12$. The function $f(z)$ characterises the vertical distribution of the grazing process (Dzierzbicka-Głowacka, 1994b, 1996).

Assimilation

The true gain to a feeding zooplankter is the organic matter that is assimilated from the gut, rather than that ingested. The measurement of the efficiency of assimilation (assimilation/ingestion) is surprisingly difficult and the results of the estimations are quite variable (Conover, 1964). The apparently simple, direct measurement of assimilation using radioisotopic tracers can be hard to interpret (*e.g.* Conover and Francis, 1973), and the quantitative recovery of faeces is very difficult.

Lacking reliable information, it seems that the assimilation A could be computed either as a constant fraction of the ingestion rate, GRA (*e.g.* Steele (1974), who used $A = 0.7$ GRA), or as a fraction of GRA which decreases as GRA increases. For example (Mullin, 1963),

$$A = 0.3\,\mathrm{GRA}\left(3.0 - \frac{\mathrm{GRA}}{\mathrm{GRA}_m}\right). \tag{27}$$

This equation establishes an efficiency which approaches 90% for low values of GRA and decreases to 60% near the maximum ingestion rate GRA_m.

Respiration of zooplankton

The major metabolic loss of organic matter from a population is undoubtedly through respiration, and for purposes of modelling the zooplankton, respiration and excretion can probably be considered to be the same process. The total rate of metabolic loss MET can be split into three components with different relations to the food uptake rate GRA. There is assumed to be a basic resting metabolism M_s independent of food supply. The respiratory costs of foraging and capturing food M_r should decrease as the food concentration and, correspondingly, $f(V)$, increases. Finally, there is the cost of assimilating and biochemically transforming the food (specific dynamic action M_a), proportional to A:

$$\mathrm{MET} = M_s + M_r + M_a. \tag{28}$$

It is known that the respiratory rate varies with food availability (Marshall, 1973; Steele, 1974). In experiments with a wide range of food supply concentrations, Mullin and Brooks (1970) found that the ratio of growth to food intake was relatively constant. These results suggest that M_a is a prevailing component. In his model of a simple phytoplankton–zooplankton ecosystem, Steele (1974) found it important for the stability of the system that respiration by the zooplankton be proportional to ingestion, in effect making M_r and M_a the major components of MET.

Excretion

Soluble zooplankton excretion is parametrised by metabolism costs as

$$\mathrm{EXC} = g\,\mathrm{MET} = g\,(M_s + n_e A), \tag{29}$$

with the percentage of ingestion n_e regenerated as soluble zooplankton excreta.

Faecal pellets

Faecal pellet production is described by

$$\mathrm{FEC} = n_f \mathrm{GRA}, \tag{30}$$

with the percentage of ingestion n_f evaluated as faecal material.

Zooplankton mortality

The carcasses of zooplankton are described by

$$\mathrm{MOR}\,Z = n_z \mathrm{GRA}, \tag{31}$$

with the percentage of ingestion n_z ending up as dead zooplankton.

Remineralisation within the water column

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

$$\mathrm{REM}\,m = p_m \mathrm{MOR}V, \tag{32}$$

$$\mathrm{REM}\,Z = p_z \mathrm{MOR}\,Z, \tag{33}$$

$$\mathrm{REM}\,F = p_f \mathrm{FEC}, \tag{34}$$

$$\begin{aligned}\mathrm{REMI} &= g\,(\mathrm{REM}\,m + \mathrm{REM}\,Z + \mathrm{REM}\,F)\\ &= g\,\{p_m \mathrm{MOR}\,V + (p_f n_f + p_z n_z)\mathrm{GRA}\},\end{aligned} \tag{35}$$

with the percentages p_m, p_z and p_f corresponding to the component of dead phytoplankton, dead zooplankton and faecal material, which are immediately recycled in the water column.

Pelagic detritus sedimentation

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

$$\begin{aligned}\mathrm{SEDI} &= (1-p_m)\mathrm{MOR}\,V + (1-p_f)\mathrm{FEC} + (1-p_z)\mathrm{MOR}\,Z\\ &= (1-p_m)\mathrm{MOR}\,V + \{(1-p_f)n_f + (1-p_z)n_z\}\mathrm{GRA}.\end{aligned} \tag{36}$$

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

$$\mathrm{DETR} = \int\limits_0^H \mathrm{SEDI}\,dz. \tag{37}$$

SEDI is given by eq. (36).

Remineralisation at the bottom

Benthic detritus varies according to the input of algal detritus from the water column, and loss by remineralisation. At the bottom, the latter process is assumed to be proportional to the amount of benthic detritus available

$$\mathrm{REM}\,D = r_d D, \tag{38}$$

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

Sedimentation of living phytoplankton provides a net gain to the detritus pool. The flux of algae across the bottom boundary is taken as a source term in the detritus eq. (4). 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. (1) and the detritus eq. (4).

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 (1997a,b).

Initial and boundary conditions

The following initial and boundary conditions supplement equation system (10)–(13): the initial vertical distributions of chlorophyll *a* V, phosphate P and zooplankton Z are known:

$$
\begin{aligned}
V(z,0) &= V_o(z) \qquad 0 \le z \le H,\\
P(z,0) &= P_o(z) \qquad 0 \le z \le H,\\
Z(z,0) &= Z_o(z) \qquad 0 \le z \le H,\\
D(t=0) &= D_o = 0\,.
\end{aligned}
\tag{39}
$$

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

$$
\begin{aligned}
F_V(0) \equiv K_z^V \frac{\partial V(z,t)}{\partial z} - w_z V(z,\,t) &= 0\\
F_P(0) \equiv K_z^P \frac{\partial P(z,\,t)}{\partial z} &= 0\\
F_Z(0) &= 0.
\end{aligned}
\tag{40}
$$

Phytoplankton can sink out of the water column of depth $z = h$, resulting in a flux condition at the interior interface; however, for zooplankton we assume there is no flux into the water column and at the bottom

$$
\begin{aligned}
F_V(h) &\equiv K_z^V \frac{\partial V(z,t)}{\partial z} - w_z V(z,t)\\
F_Z(h) &= F_Z(H) = 0.
\end{aligned}
\tag{41}
$$

When assuming that the turbulent flux

$$F_V^T(H) \equiv K_z^V \frac{\partial V(z,t)}{\partial z} = 0 \tag{42}$$

ceases at the bottom, we obtain the bottom flux condition

$$F_V(H) \equiv -w_z V(z,t). \tag{43}$$

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 $z = H$:

$$F_P(H) \equiv K_z^P \frac{\partial P(z,\,t)}{\partial z} \neq 0. \tag{44}$$

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

$$F_P(H) \equiv K_z^P \frac{\partial P(z,\,t)}{\partial z} = g\,\mathrm{REM}\,D. \tag{45}$$

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 entire water column becomes homogeneous with respect to phosphate.

5. Conclusions

The present nutrient–phytoplankton–zooplankton–detritus P–V–Z–D model consists of two nonlinearly coupled, partial second-order differential equations of the diffusion type for the concentration of nutrients P and phytoplankton V and two ordinary first-order differential equations for the concentration of zooplankton Z and benthic detritus pool D, together with initial and boundary conditions.

The system of equations (10)–(13) with conditions (39)–(45) is solved numerically by using the indirect Crank-Nicholson method (Potter, 1982) in an area of $0 \leq z \leq H$ by digitising this region with a variable step δ into (i) elements. This method is a second-order one, absolutely stable at every time and space step. The detailed algorithm of the solution to the V–P model can be found in Dzierzbicka-Głowacka (1994b, 1996).

The phytoplankton concentration is assumed to be a dynamically passive physical entity (*i.e.* it is incapable of making autonomous movements) which depends on:

- the hydrodynamic state of the environment (K_z, w_z);
- the intensity of natural production sources PRE;
- losses caused by phytoplankton respiration RES;
- losses caused by phytoplankton mortality MOR V;
- losses due to phytoplankton grazing by zooplankton GRA;
- the physiological nutrient uptake by phytoplankton UPT;
- nutrient regeneration REMI from zooplankton excretion EXC;
- detritus remineralisation processes REM D through the nutrient uptake UPT.

The turbulent vertical diffusion coefficients for both phytoplankton and nutrients are assumed to be equal in this model, and are estimated in the same way as the diffusion of a passive admixture (Druet and Zieliński, 1993).

The P–V–Z–D model is an open model which can be used to study the influence of different hydrodynamic, biological and chemical processes on the distribution of functions investigated on larger scales.

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Appendix

1. Notation

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
MET – metabolic loss
MOR V – mortality of phytoplankton
MOR Z – mortality of zooplankton
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 the percentage of grazed material at the depth z
g – P:C ratio
k_s – half-saturation constant for phosphate
K_z – turbulent diffusion coefficient
M_s – standard metabolism
n_e – percentage of ingestion, regenerated as soluble excretion of zooplankton
n_f – percentage of ingestion egested as faecal material

n_z – percentage of ingestion ending up as dead zooplankton
P – nutrient concentration
PP – a coefficient denoting the mean intensity of primary production
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
t_o – coefficient of the time during which the maximum phytoplankton grazing occurred
w_z – sinking velocity of phytoplankton
Z – zooplankton concentration
V – phytoplankton concentration

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

In this method the first and second equation of equation system (10)–(13) with appropriate initial and boundary conditions for $i = 1$ and $i = n$, can be written in the form

$$V_1^{t+1} = V_1^t\,\{\Delta t(\alpha_1 - \mathrm{GRA}_1\alpha_1) + 1\}, \tag{46}$$

$$P_1^{t+1} = P_1^t + \Delta t V_1^t a\beta_1, \tag{47}$$

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

$$V_n^{t+1} = \frac{V_{n-1}^{t+1}w_n + V_n^t\,(1 + \alpha_n\Delta t(1 - \mathrm{GRA}_n) - w_n) + V_{n-1}^t w_n}{1 + w_n}, \tag{48}$$

$$P_n = P_n^t + a\left(gr_d\Delta t D^t + V_n^t\Delta t\beta_n\right), \tag{49}$$

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 describes the distribution function of zooplankton concentration, and in this method for $(1 \le i \le n)$ can be written as

$$Z_i^{t+1} = Z_i^t + \Delta t V_i^t\,\{\mathrm{GRA}_i(1 - n_f - n_z) - \mathrm{MET}_i\}. \tag{50}$$

The fourth equation of the equation system (10)–(13), an ordinary differential equation, describes the development of detritus at the bottom, and for $i = n$ can be written in the form:

$$D^{t+1} = \frac{D^t\left(1 - r_d\frac{\Delta t}{2}\right) + w_z(H)\frac{\Delta t}{2}\left(V_n^t + V_n^{t+1}\right) + \frac{\Delta t}{2}\left(\mathrm{DETR}^t + \mathrm{DETR}^{t+1}\right)}{1 + r_d\frac{\Delta t}{2}} \tag{51}$$

which is the sought-after solution to eq. (13).