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*Regular research paper*

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# EFFECTS OF PHYTOPLANKTON MORTALITY CAUSED BY UNPREDICTABLE CONDITIONS – NUMERICAL SIMULATIONS

ABSTRACT: The influence of episode of density-independent mortality on the time-space variability of phytoplankton distribution in the near surface layer of a stratified sea is the aim of this paper. The mortality of phytoplankton in unpredictable conditions, like a spill of crude oil or other chemicals is considered. The numerical simulations were carried out using a biological model of upper layer with a developed primary production and regeneration mechanisms and of daily migration of zooplankton. In such cases an increase in the mortality rate intensifies the decrease in phytoplankton biomass. Such a situation can on occasion lead to phytoplankton extinction, and hence to irreversible changes in its distribution area.

KEY WORDS: phytoplankton, mortality, unpredictable conditions, modelling

## 1. INTRODUCTION

Biomass of phytoplankton, i.e. small and passive organisms, incapable of making autonomous movements, is affected by certain processes like: turbulent diffusion, sinking, primary production, respiration, natural mortality, and grazing.

Mortality of phytoplankton can be mainly modelled via two pathways: grazing by zooplankton which is density-dependent and other kinds of mortality, usually density-independent, like cell lysis. It is in case of sudden and unpredictable appearance in the habitat of toxic pollution like a spill of crude oil or other chemicals.

The main objective of this paper is the numerical simulation of the effect of an unpredictable mortality agent like the pollution patch dispersing in the upper (euphotic) layer of sea and affecting the phytoplankton biomass. The biological model of upper layer {*nutrient – phytoplankton – detritus*} with developed mechanisms of primary production and regeneration given by Dzierzbicka-Głowacka (1994) was used in the numerical studies. This model consists of three mass conservation equations. There are two diffusion-advection-reaction equations for phytoplankton and nutrient. The third equation, an ordinary differential one, describes the development of detritus deposited at the bottom.

Phytoplankton is modelled by only one state variable. In nature, phytoplankton consists of many different species, each with different dynamical characteristics and contributing differently to the biomass over the year. However, my assumption concerning the biomass of the whole phytoplankton community is that the species composition is regulated by the availability of nutrients. Therefore the dynamic constants used in the model are representative of the whole phytoplankton community. It is practised in many models of phytoplankton production (e.g. Radach and Moll 1993, Tamsalu and Ennet 1995, Svansson 1996, Dzierzbicka-Głowacka 1994, 2000).

The formulations of the primary production mechanism and of the remineralization mechanism within the mixed layer are incorporated into the biological model. Phytoplankton is either grazed by zooplankton or it dies and sinks. Grazed phytoplankton is subdivided into three portions; the first contributes to zooplankton growth, the second is lost as faecal pellets, and the third is excreted by zooplankton as dissolved metabolites, so replenishing the nutrient pool. A part of the material contributing to growth is assumed to be lost immediately, representing dying zooplankton. Parts of both the faecal and the excreted material are immediately remineralized. The assumed time scale – a few days – of sinking of the faecal and dead material is much shorter than the time scales for most of the remineralization processes, which usually take weeks to months (Billen *et al.* 1991). Therefore most of the detrital material is deposited on the bottom where it constitutes a detrital pool.

In this model nutrients are represented by two components: total inorganic nitrogen ($NO_3$ + $NO_2$ + $NH_4$) and phosphates ($PO_4$). The nutrients serve both as a trigger and as a limiting agents for primary production. The concept of the detrital pool at the bottom has been introduced to create a lag in remineralization of the majority of detritus and the eventual replenishment of the upper layer with nutrients. This complex process is parameterised by assuming a net remineralization rate for bottom detritus (Billen *et al.* 1991).

I hypothesize that this model with a high-resolution module for phytoplankton mortality is sufficiently complex for the simulation the variation of the phytoplankton biomass in unpredictable conditions.

## 2. MATHEMATICAL MODEL

The principal assumptions of the two-dimensional model describing the function of phytoplankton distribution with depth in a stratified sea are defined as follows:

1. the physical, chemical and biological processes, below-mentioned in equations (1)–(4), have been selected on the basis of the publications (e.g. Stigebrandt and Wulff 1987, Fransz *et al.* 1991, Radach and Moll 1993, Svansson 1996, Tamsalu 1998, Dzierzbicka-Głowacka 2000);
2. in the model area ($0 < x < 2000$ m, $0 < z < 20$ m), which is described in section 4:
   – the coordinate system is situated at the free surface (the $z$ axis is directed vertically downwards, and the $x$ and $y$ axes are directed eastwards and northwards respectively);
   – the vertical distribution of seawater density is absolutely stable i.e. the vertical density and salinity increase, while the temperature decreases with depth;
3. the study area is uniform towards the $y$ axis, but non-uniform towards the $x$ and $z$ axes ($\partial/\partial y=0$; $\partial/\partial x\neq 0$; $\partial/\partial z\neq 0$) of all variables.

On condition that the water density distribution is absolutely stable, neither upwelling nor downwelling can occur. Therefore, the vertical component of flow velocity is nearly zero and nutrients are not transferred along the $z$ axis but, in the upper layer, are eventual replenishment as a result of benthic remineralisation.

In the equation for nutrients, expressions describing the vertical and horizontal advection are omitted, while in the equation for phytoplankton vertical advection is neglected. Nevertheless, it is assumed that suspended matter can settle and that the sinking velocity $w_z$ in the water is described by Stokes' formula (Dera 1992). In this paper all the assumptions have been made for a stratified sea, i.e. the water-mass flux is horizontal, parallel to the $x$ axis, and its average velocity is depth-dependent i.e. $u = u(z)$. Hence, the flow velocity field is stationary and uniform along the $x$ axis. The influence of the vertical gradient of the horizontal velocity $\partial u/\partial z$ on phytoplankton and nutrient concentrations in a turbulent flux is controlled by a turbulent mixing process. The rate of this process depends on the value of the turbulent diffusion coefficient in the vertical $K_z$; it is directly dependent on the Richardson number $Ri$.

Applying the constraints described above, the mathematical model resolves itself into a system of four equations, three partial equations of the diffusion type for the concentration of phytoplankton and two nutrients and one an ordinary differential equation, describes the dynamics of detritus deposited at the bottom. The functions of biomass production and loss are the functions describing the sources of distributions of phytoplankton, nutrients and detritus.

The system of equations is as follows:

- the changes in local nutrient concentration (for total inorganic nitrogen $N_N$ and phosphates $N_P$) is determined by horizontal and vertical turbulent diffusion $K_x$ and $K_z$, algal uptake UPT, nutrient influx $F_{\mathrm{inf}}$, remineralized dead phytoplankton, zooplankton faecal pellets and dead zooplankton REMI, and by zooplankton excretion EXC and nutrient release REL.

$$\frac{\partial\{N_P\}}{\partial t}=\frac{\partial}{\partial x}\left(K_x\frac{\partial\{N_P\}}{\partial x}\right)+\frac{\partial}{\partial z}\left(K_z\frac{\partial\{N_P\}}{\partial z}\right)-\mathrm{UPT_P}+F_{\mathrm{inf\,P}}+\mathrm{REL_P}+\mathrm{REMI_P}+\mathrm{EXC_P} \tag{1}$$

$$\frac{\partial\{N_N\}}{\partial t}=\frac{\partial}{\partial x}\left(K_x\frac{\partial\{N_N\}}{\partial x}\right)+\frac{\partial}{\partial z}\left(K_z\frac{\partial\{N_N\}}{\partial z}\right)-\mathrm{UPT_N}+F_{\mathrm{inf\,N}}+\mathrm{REL_N}+\mathrm{REMI_N}+\mathrm{EXC_N} \tag{2}$$

– the temporal changes in the phytoplankton biomass $P$ is affected by horizontal and vertical turbulent diffusion $K_x$ and $K_z$, sinking of algae $w_z$, primary production PRE, respiration RES, mortality $\mathrm{MOR_P}$, and grazing by zooplankton GRA.

$$\frac{\partial\{P\}}{\partial t}+u\frac{\partial\{P\}}{\partial x}+w_z\frac{\partial\{P\}}{\partial z}=\frac{\partial}{\partial x}\left(K_x\frac{\partial\{P\}}{\partial x}\right)+\frac{\partial}{\partial z}\left(K_z\frac{\partial\{P\}}{\partial z}\right)+\mathrm{PRE}-\mathrm{RES}-\mathrm{MOR_P}-\mathrm{GRA} \tag{3}$$

– the temporal changes in the detritus pool at the bottom $D$ are determined by the flux of phytoplankton $FP$ and that of detrital material sedimenting out of the water column onto the bottom DETR and remineralisation of detritus REMD.

$$\frac{d\{D\}}{dt}=-F_P(H)+\mathrm{DETR}-\mathrm{REMD} \tag{4}$$

The coefficient of horizontal turbulent diffusion $K_x$ is assumed constant and dependent, according to the Okubo model (1976), on the spatial scale $l$ of such diffusion

$$K_x=0.0103\times l^{1.15} \quad (\mathrm{m^2s^{-1}}) \tag{5}$$

In this two-dimensional model the scale $l$ is identified with the horizontal step of the numerical grid Δ.

Dependent on the stratification and the vertical gradient in flow velocity (through the value of the Richardson number $Ri$), the coefficient of vertical turbulent diffusion $K_z$ is determined from the Peters, Gregg and Toole (1988) formula for a non-uniform sea

$$K_z=5\times10^{-4}(1+Ri)^{-2.5}+10^{-6} \tag{6}$$

Coefficient $K_z$ is assumed constant in the $10^{-6}$–$10^{-3}$ $\mathrm{m^2s^{-1}}$ range for calculations made for a basin with constant density.

The biological terms used in Eqs. (1)–(4) are given in Appendix. The significance of symbols used in Appendix are given in Table 1 and the dynamical constants used in the biological model are listed in Table 2. The detailed descriptions of the processes having the influence on the source/sink functions are presented in Dzierzbicka-Głowacka (2000, 2005a, b).

The system equations is solved with the following initial and boundary conditions:

for $t=0$ (the initial vertical distributions $P_o$, $N_P$, $N_N$ and $D_o$ are known):

$$\begin{aligned}
&\{P\}(x,z,0)=\{P\}_o && 0\le z\le H && 0\le x\le X\\
&\{N_N\}(x,z,0)=\{N_N\}_o && 0\le z\le H && 0\le x\le X\\
&\{N_P\}(x,z,0)=\{N_P\}_o && 0\le z\le H && 0\le x\le X\\
&\{D\}(0)=\{D\}_o=0 && z=H && 0\le x\le X
\end{aligned} \tag{7}$$

for $z = 0$ (free surface):

$$K_z \frac{\partial \{P\}(x,z,t)}{\partial z}\bigg|_{z=0} - w_z \{P\}(x,z,t)\big|_{z=0} = 0$$

$$K_z \frac{\partial \{N_N\}(x,z,t)}{\partial z}\bigg|_{z=0} = 0$$

$$K_z \frac{\partial \{N_P\}(x,z,t)}{\partial z}\bigg|_{z=0} = 0 \quad (8)$$

for $z$ = H (double the depth of the euphotic layer):

$$F_P(H) \equiv -w_z \{P\}(x,z,t)\big|_{z=H}$$

$$K_z \frac{\partial \{N_N\}(x,z,t)}{\partial z}\bigg|_{z=H} = g_N \mathrm{REMD}$$

$$K_z \frac{\partial \{N_P\}(x,z,t)}{\partial z}\bigg|_{z=H} = g_P \mathrm{REMD} \quad (9)$$

This flux $F_P(H)$ enters the benthic detritus equation as a source term. The boundary condition (9) provides the mechanism of replenishing the water column with nutrients resulting from benthic remineralisation.

for $x = 0$

$$K_x \frac{\partial \{P\}(x,z,t)}{\partial x}\bigg|_{x=0} - u\, \{P\}(x,z,t)\big|_{x=0} = 0$$

$$N_N(x,z,t) = n(x,z);\ N_P(x,z,t) = p(x,z) \quad (10)$$

for $x$ = X

$$K_x \frac{\partial \{P\}(x,z,t)}{\partial x}\bigg|_{x=X} - u\, \{P\}(x,z,t)\big|_{x=X} = 0$$

$$N_N(x,z,t) = n(x,z);\ N_P(x,z,t) = p(x,z) \quad (11)$$

These conditions imply that the phytoplankton suspension and the nutrients are neither transferred from the euphotic layer to the near-water layer of the atmosphere nor to the water masses situated below a depth equal to twice the thickness of the euphotic layer. Although this is an arbitrary constraint, it does not fundamentally affect the qualitative description of these processes.

## 3. PHYTOPLANKTON MORTALITY

Natural phytoplankton mortality is a process leading to losses in its biomass. It is assumed that mortality is directly proportional to the phytoplankton biomass with a mortality rate $m$ (Raymont 1980, Sjöberg 1980)

$$\mathrm{MOR_P} = m\, P(x, z, t) \quad (12)$$

Unpredictable mortality events have also been taken into account in the model in that mortality is regarded as being dependent not only on the mortality factor but also on the function describing the spatial distribution $Sm$ of the dispersion of pollution patch.

$$MOR_P = m(1 + S_m(\mathrm{x, z, t}))\, P(x, z, t) \quad (13)$$

where

$S_m(x, z, t) = S_x(x, t) S_z(z)$

$S_x(x, t) = W_s(t)\, \beta \exp(-[p_s(x-x_i)^2])$

$S_z(z) = \exp(y(z))$,

$y(z) = b_o + b_1 z + b_2 z^2 + \ldots\ldots,$

where $W_s$ is the coefficient defining the percentage loss of phytoplankton biomass, β is the coefficient of proportionality specifying the degree of contamination, $p_s$ is the coefficient defining the spatial distribution of pollutants in the horizontal plane, and $b_o$, $b_1$, $b_2$ are the coefficients defining the spatial distribution of pollutants in the vertical plane. The value of the factors in the above equations can be determined either arbitrarily or on the basis of measurements of pollutant concentrations at various depths.

## 4. NUMERICAL SIMULATIONS

The biological model {*nutrient – phytoplankton – detritus*}, described in greater detail in Dzierzbicka-Głowacka (1994, 2000) was used to simulate the effect of the mortality of phytoplankton on the distribution field of phytoplankton biomass in the upper layer of sea. The differential equation system obtained at each time step is a system of non-uniform algebraic equations that can be solved using the successive overrelaxation method utilizing the Gauss-Seidel formulations. This model was tested for a wide range of the value, of physical, biological and chemical parameters which can occur in the marine environment (Dzierzbicka-Głowacka 1994). Here the calculations were made in a rectangular region XZ in a vertical section of dimensions 2000 m and 20 m, with a time step of 900 s a vertical space step of 0.1 m, and a horizontal space step of 100m.

The flow field and water temperature used in the biological model were reproduced by the prognostic numerical simulation technique using hydrographic climatological data (Jankowski, personal communication). The three-dimensional σ-coordinate baroclinic model (Jankowski 2002) is based on the Princeton Ocean Model (POM code). The details concerning the numerical schemas used in the POM can be found in the work of Mellor (1993). For more information on the hydrodynamic model, which results were used as the inputs to the biological model, the reader is referred to the work of Jankowski (2002). The dynamical constants used in the biological model are listed in Table 1 and were determined mostly from data derived from the literature (Raymont 1980, Stigebrandt and Wulff 1987, Radach and Moll 1993, Witek 1993, Renk 2000, Dzierzbicka-Głowacka 2000). In choosing values of the parameters reasonably close to levels found in Baltic waters, the numerical studies were made at station in Gulf Gdańsk – at Gdańsk Deep (Witek 1993, Witek 1995, IMGW 2000).

The phytoplankton and nutrient concentrations for $0 \le z \le 20$ m at $t_o = 6.00$ a.m. as constants with depth were assumed on the basis of interpolation of empirical data for 10 years, 1980–1990 at the beginning of March, and were taken to be the initial concentrations. They are as follows:

$P(z, t_o) = 64$ mg C m$^{-3}$;

$N_P(z, t_o) = 0.36$ mmol P m$^{-3}$;

$N_N(z, t_o) = 1$ mmol N m$^{-3}$;

$D(t_o) = 0.1$ g C m$^{-2}$

The influence of the mortality on the changes in time of phytoplankton biomass distribution function was analysed under the assumption that zooplankton grazing of phytoplankton is constant and GRA = 0.3{$Z$} where $Z(z, t) = 40$ mg C m$^{-3}$.

In the literature, the rate of phytoplankton mortality in the natural environment is given as m = $10^{-7}$, $5\times10^{-7}$, $10^{-6}$ s$^{-1}$, its magnitude means what part of biomass is lost per one second. The values are adequate to different periods of occurrence of various species of phytoplankton and they were determined on the basis on *in situ* measurements in the time of blooming and appearance of predominant species (Raymont 1980, Sjöberg 1980). These data present the mean values of mortality rate in time intervals not greater than two weeks. They are suitable for physical and chemical conditions in the water of the basin examined for the numerical studies in the given time period – one day. Natural phytoplankton mortality does not have a great effect on the phytoplankton biomass in the situation when catastrophic increase in mortality is caused by spreading of pollution. Therefore, in this paper, the numerical simulations were made of the influence of the mortality of phytoplankton in unpredictable conditions like the dispersing of a patch of crude oil or other chemicals in the distribution field of phytoplankton biomass in the upper layer of sea.

For this analysis, the calculations were made for two cases, in which the mortality rate in unpredictable conditions of pollution patch is $m\beta = 10^{-2}$ s$^{-1}$ and the function $S_m$ describing the spatial dispersing of polluted patch is presented as the product of two exponential functions of variables $x$ and $z$, $S_x$ and $S_z$:

Case 1

$$S_x = W_s\, 10^4 \exp(-[0.002\,(x - x_i)^2])\ \text{for}\ 5 < W_s < 50 \quad (14)$$

$$S_z = \exp(0.05\,z)$$

Case 2

$$S_x = W_s\, 10^4 \exp(-[0.004\,(x - x_i)^2])\ \text{for}\ 5 < W_s < 60 \quad (15)$$

$$S_z = \exp(0.005\,z)$$

The results of the numerical investigations of the effect of the described process of mortality in unpredictable conditions on the shapes and values of the phytoplankton biomass are presented in Figs. 1 and 2. Figure 1 shows the distributions of phytoplankton biomass in the period of 12 hours at t = 8.00 (Fig. 1A), 13.00 (Fig. 1B) and 18.00 (Fig. 1C) in the case 1. The shapes and values of the phytoplankton distribution vary significantly in both the vertical and horizontal zones. Phytoplankton biomass decreases about from 15% at first of 100 m to 5% at a distance of 2000 m after two hours (Fig. 1A), from 35 to 20 % after seven hours (Fig. 1B), and after twelve hours from 80% at first of 100 m to 50% at a distance of 2000 m (Fig. 1C) on the surface layer. However, Fig. 2 demonstrates the distributions of the investigated characteristic in the period of 7 hours at t = 8.00 (Fig. 2A), 11.00 (Fig. 2B) and 13.00 (Fig. 2C) in the case 2. In this case, the changes with depth in phytoplankton biomass are weak in comparison with case 1. The differences are mainly in horizontal zone and decrease in phytoplankton biomass varies in consecutive hours from 15% at first of 100 m to 9% at a distance of 2000 m after two hours (Fig. 2A), from 35 to 20% after five hours (Fig. 2B) and from

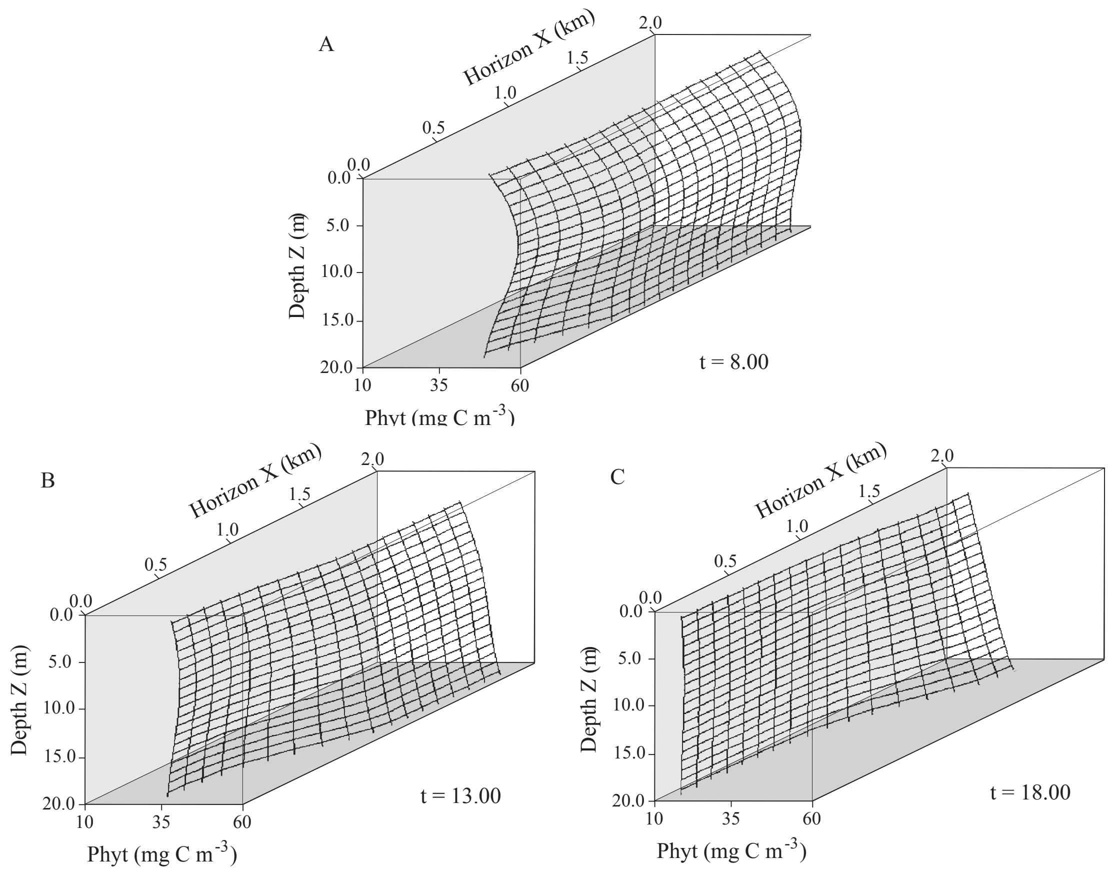


Fig. 1. The spatial distribution of phytoplankton biomass *Phyt* (mg C m$^{-3}$) in the period of 12 hours given for $t$ = 8.00 (A), 13.00 (B) and 18.00 (C) under the assumption that the unpredictable mortality agent is described by equation: $S_m = W_s \beta \exp(-[p_s(x-x_i)^2])\exp(y(z))$, where the coefficient $W_s$ defining the percentage loss of phytoplankton biomass is in the range $5 < W_s < 50$, $\beta = 10^4$ is the coefficient of proportionality specifying the degree of contamination (i.e. mortality rate is $10^{-2}$ s$^{-1}$), $p_s = 0.002$ is the coefficient defining the spatial distribution of pollutants in the horizontal plane, and $y(z) = 0.05z$ is the function defining the spatial distribution of pollutants in the vertical plane.
The decrease in phytoplankton biomass is considerable higher in the upper part of the surface mixed layer than in lower one and after 12 hours at a distance of 2000 m from appearance of the dispersion of water pollution episode is from *c.* 80 to 50% in relation to initial biomass.

65% at first of 100 m to 35% at a distance of 2000 m after seven hours (Fig. 2C) in the whole column water. In the case 2, the mortality rate is higher than in case 1. Hence, the phytoplankton biomass is relatively smaller in the case 2 than in the case 1, i.e. after seven hours the decrease in phytoplankton biomass is from 35 to 20% in case 1 and from 65 to 30% in case 2. For both cases 1 and 2 it is obvious that, as passage of time, in comparison with the stationary case, the intensive changes in distribution of phytoplankton biomass is caused by the phytoplankton mortality. The increase of phytoplankton mortality can lead to phytoplankton extinction in this area when the coefficient of mortality will attain value of 1 and the primary production value of 0. The above statement bases on the expansion of polluted patch in the surface layer which causes decreased transparency of sea water and increased toxicity, which in turn cause the decrease of photosynthesis rate.

Basing on the mortality process defined by Eq. (8), and knowing the time and horizontal coordinates of the appearance of the front of the polluted patch we can calculate a mean velocity of dispersion of polluted

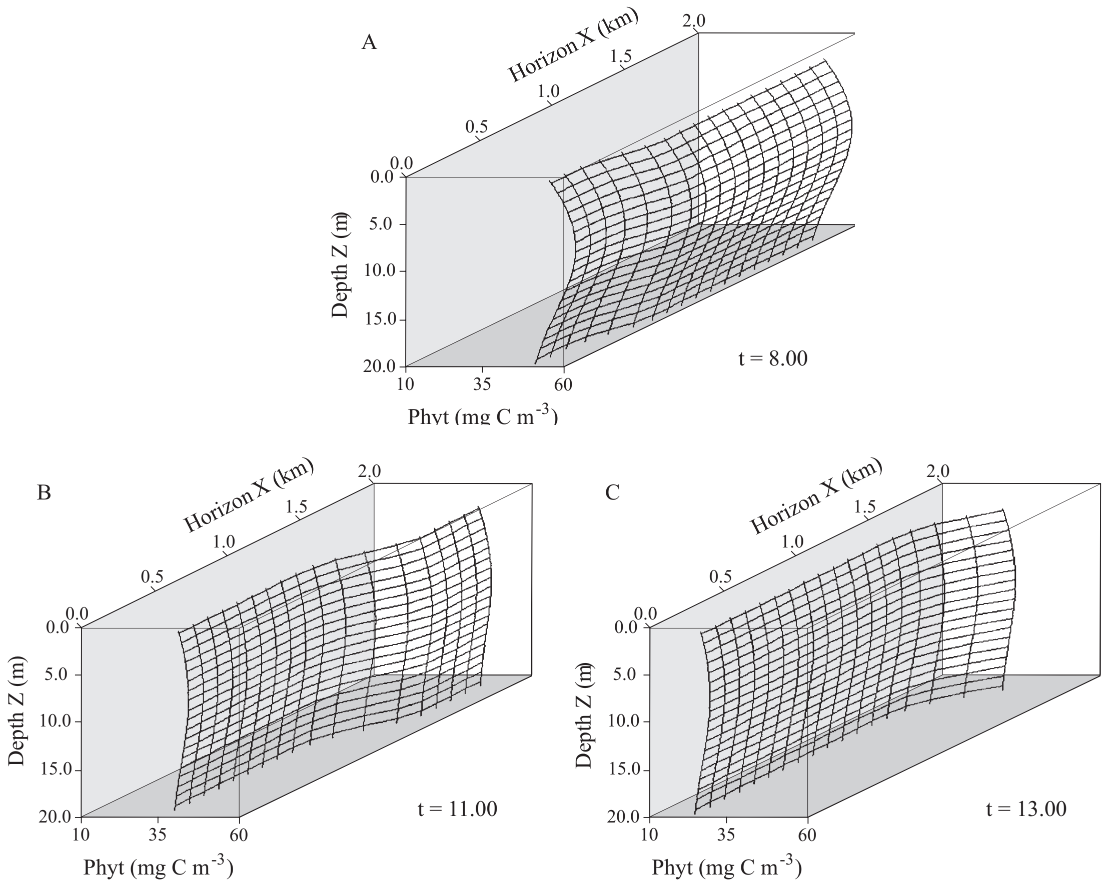


Fig. 2. The spatial distribution of phytoplankton biomass *Phyt*(mg C m$^{-3}$) in the period of 7 hours given for $t$ = 8.00 (A), 11.00 (A), and 13.00 (C) under the assumption that the unpredictable mortality agent is described by equation $S_m = W_s \beta \exp(-[p_s(x-x_i)^2])\exp(y(z))$, where the coefficient $W_s$ defining the percentage loss of phytoplankton biomass is in the range $5 < W_s < 60$, $\beta = 10^4$ is the coefficient of proportionality specifying the degree of contamination (i.e. mortality rate is $10^{-2}$ s$^{-1}$), $p_s = 0.004$ is the coefficient defining the spatial distribution of pollutants in the horizontal plane, and $y(z) = 0.005z$ is the function defining the spatial distribution of pollutants in the vertical plane.
The decrease in phytoplankton biomass is regular in a both zones and after 7 hours at a distance of 2000 m from appearance of the dispersion of water pollution episode is from *c.* 65 to 35% in relation to initial biomass.

patch masses. Also knowing a mean velocity of dispersion of these masses we can compute the time in which the front of the polluted water masses come up to a certain range. In agreement with above, a mean velocity of translocation of the polluted water masses is about 3.33 cm $s^{-1}$ in the whole column water in the case 1 and 6.67 cm $s^{-1}$ in the surface layer in the case 2. Hence, in the case 2, this velocity is greater twice than in case 1 and the degree of pollution is significantly higher.

## 5. CONCLUSION

The main aim of this paper, i.e. to simulate the effect of the mortality rate on the distribution of phytoplankton biomass in polluted environment was achieved by working out:

– the biological model in the upper layer {*nutrient – phytoplankton – detritus*} determining the changes in time of the phytoplankton biomass, nutrients concentration and detritus pool concentrations, as well as

– the sub-model describing the spatial distribution of the dispersing pollution patch.

Knowing the values of parameters of the function describing the effect of unpredictable mortality agent, we can obtain the mean velocity and the time in what the front of the of pollution patch dispersing in the water reaches a certain place. We also can qualify the percentage loss and time needed for the considerable decrease of the phytoplankton biomass caused by the mortality in these unpredictable conditions.

Mortality as the result of violent unpredictable changes in the environment (such as water pollution episode) can lead to a catastrophic increase in the mortality rate and in turn it causes a sudden decrease in the phytoplankton biomass in the period of several hours. Occasionally such a situation can lead to local phytoplankton extinction, and hence to irreversible changes in that area.

The 2D biological model of upper layer with a module for mortality presented in this paper may have a practical use in forecasting ecological changes in unpredictable conditions like the presence of a patch of crude oil or other chemicals.

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## APPENDIX. PARAMETERS OF THE BIOLOGICAL MODEL

### NUTRIENTS:

$$\mathrm{REL} = g\mathrm{RES}, \quad \mathrm{UPT} = g(\mathrm{PRE} - \mathrm{RES})$$

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

$$\mathrm{FEC}_Z = n_f\,\mathrm{GRA}, \quad \mathrm{MOR}_Z = n_z\,\mathrm{GRA}$$

$$\mathrm{REM}P = p_p\,\mathrm{MOR}_P, \quad \mathrm{REM}Z = p_z\,\mathrm{MOR}_Z, \quad \mathrm{REM}F = p_f\,\mathrm{FEC}_Z$$

$$\mathrm{REMI} = g(\mathrm{REM}P + \mathrm{REM}Z + \mathrm{REM}F) = g\{p_p\,\mathrm{MOR}_P + (p_f n_f + p_z n_z)\mathrm{GRA}\}$$

$$F_{\mathrm{inf}} = F_{\mathrm{inf},o}\exp(-0.1z)$$

### PHYTOPLANKTON:

$$\mathrm{PRE} = \sin\gamma d_A\, d_I \min\{d_P, d_N\}\{P\}$$

$$d_I = \frac{E}{E_o}\exp\left(1 - \frac{E}{E_o}\right), \quad d_P = \frac{\{N_P\}}{\{N_P\} + k_{Nutr\,P}}, \quad d_N = \frac{\{N_N\}}{\{N_N\} + k_{Nutr\,N}}$$

$$E_o = 313.64 + 19.56\,T; \quad d_A = 1.385 + 0.238\,T$$

$$E = \frac{\eta_d}{d}\exp(-K_d z)\left(1 + \cos\frac{2\pi t}{d}\right)$$

$$\eta_d = 8.67 + 8.29\cos(\omega x - 3.03) + 0.69\cos(\omega x - 5.80)$$

$$\mathrm{RES} = \mathrm{RES}_n + \mathrm{RES}_d = d_A\left(m_P^n + m_P^d \min\{d_I, d_N\}\right)\{P\}$$

$$\mathrm{MOR}_P = m_P\{P\}$$

$$\mathrm{GRA} = g_{\max}\frac{\{P\} - \{P\}_0}{\{P\} - \{P\}_0 + k_{Phyt}}\{Z\} \text{ for } \{P\} > \{P\}_0$$

### BENTHIC DETRITUS:

$$\mathrm{SEDI} = (1 - p_p)\mathrm{MOR}_P + (1 - p_f)\mathrm{FEC}_Z + (1 - p_z)\mathrm{MOR}_Z = (1 - p_p)\mathrm{MOR}_P + \{(1 - p_f)n_f + (1 - p_z)n_z\}\mathrm{GRA}$$

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

$$\mathrm{REMD} = r_d\{D\}$$

APPENDIX

Table 1. List of symbols used.

| Symbol | Meaning |
|---|---|
| $K_x$, $K_z$ | Horizontal and vertical turbulent diffusion coefficient |
| $g = g_N$ | C/N ratio in eq. for $N_N$ |
| $g = g_P$ | C/P ratio in eq. for $N_P$ |
| $g_{Chl}$ | C/Chl-*a* ratio |
| $\{P\}$ | Phytoplankton biomass |
| $d_A$ | Assimilation number |
| $E_o$ | Saturation irradiance |
| $E$ | Irradiance at depth $z$ |
| $H_d$ | Average daily doses of irradiation PAR |
| $\{P\}_o$ | Phytoplankton threshold for grazing |
| $g_{\max}$ | Maximum grazing rate |
| $k_{Phyt}$ | Half-saturation constant for grazing |
| $m_P$ | Mortality rate for *{Phyt}* |
| $m_p^n$ | Percentage basic respiration |
| $m_p^d$ | Percentage photorespiration |
| $\{N\}_N$ | Total inorganic nitrogen concentration |
| $\{N\}_P$ | Phosphate concentration |
| $k_{NutrN}$, $k_{NutrP}$ | Half-saturation constant for nutrient (*N* and *P*) |
| $n_e$ | Percentage of ingestion regenerated as soluble excretion of zooplankton |
| $n_f$ | Percentage of ingestion egested as fecal material |
| $n_z$ | Percentage of ingestion ending finally 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 |
| $\{Z\}$ | Zooplankton biomass |
| $\{D\}$ | Detritus concentration |
| $r_d$ | Remineralization rate of benthic detritus |

APPENDIX

Table 2. Dynamical constants in the biological model.

| Symbol | Value | Unit |
|---|---|---|
| $g_{\max}$ | 0.5 | $day^{-1}$ |
| $g_N$ | 0.0157 | mmol N $(mg\ C)^{-1}$ |
| $g_P$ | $0.612\times10^{-3}$ | mmol P $(mg\ C)^{-1}$ |
| $g_{Chl}$ | 34.31 | mg C $(mg\ Chl)^{-1}$ |
| $k_{Phyt}$ | 100 | mg C $m^{-3}$ |
| $k_{NutrN}$ | 0.1 | mmol N $m^{-3}$ |
| $k_{NutrP}$ | 0.06 | mmol P $m^{-3}$ |
| $m_P$ | 0.05 | $day^{-1}$ |
| $m_p^n$ | 0.1 | |
| $m_p^d$ | 0.05 | |
| $n_e$ | 0.33 | |
| $n_f$ | 0.33 | |
| $n_Z$ | 0.33 | |
| $p_f$ | 0.2 | |
| $p_P$ | 0.2 | |
| $p_Z$ | 0.2 | |