THE CONCEPTION AND STRUCTURE OF THE PRODUCTION-DESTRUCTION OF ORGANIC MATTER MODEL; VERIFICATION TESTS FOR THE GULF OF GDAŃSK

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Abstract

This paper presents a concept and detailed mathematical formulation of the Production and Destruction of Organic Matter Model designed for the description of the biogeochemical cycles in the coastal environment. A short review is given on *state-of-the-art* in the ecological modelling in the North Sea and the Baltic Sea regions. The presented model takes into account three functional groups: phytoplankton, zooplankton, detritus and associated nutrient cycles (nitrogen, phosphorus, silicon). The dissolved oxygen is also included. The mass balance equations are closed for eleven state variables and are described explicitly.

Verification tests of the implementation of ProDeMO Model for the region of the Gulf of Gdańsk are discussed. The horizontally integrated 1D model with irregular grid spacing is applied for the Gdańsk Deep using the data from 1991. The influence of environmental conditions (solar radiation, nitrogen and phosphorus concentration, water temperature) on the rate of primary production and comparison of annual primary production with data derived from other sources are presented. Further, the same 1D approach is used to test the annual dynamics of two phytoplankton groups (diatoms, non-diatoms) and zooplankton biomass. The 2D depth integrated calculation for the Gulf of Gdańsk are presented using the same data set. The annual structure of total nitrogen and total phosphorus for two stations: P110 and P116 is discussed.

INTRODUCTION

Since 1970-ies there have been a lot of efforts to integrate the knowledge about marine ecological processes in a form of mathematical models. The ecological modelling method has a wide spectrum of applications: from a very short time scale, *e.g.* phytoplankton blooms, to long-term investigations and spatially from the local studies to whole seas (Lauenroth *et al*. 1983, Fransz *et al.* 1991). A modelling approach has been very often used in biogeochemical flux studies in the coastal environment. LOICZ Biogeochemical Modelling Guidelines underline that modelling of carbon, nitrogen and phosphorus cycles in the coastal systems is the „necessary requirement for meeting the overall goals and objectives of LOICZ" (Gordon *et al*. 1995).

Most of the classical ecological models use *the functional group approach* assuming that all individuals are identical within one group and react in the same way to external factors, *e.g.* the solar radiation. The functional groups are combined to biomass and usually represented by the concentration of chlorophyll *a* (algae groups) or organic carbon. In last decade, eco-modellers have tried to apply different approach assuming that all individuals are different (size, age) and able to choose their „own way" (Judson 1994). For example, Babovic and Barreta (1996) have investigated the influence of dynamic processes on local and seasonal interactions between three "intelligent agents": authotrophs, omnivores and carnivores.

An overview of models, developed for the North Sea, has been given by Fransz *et al*. (1991). The most recent work reflecting the present state of complex marine ecological modelling, ERSEM model, has been presented by Barretta *et al*. (1995) and applied for the North Sea. The ERSEM model simulates the large-scale seasonal dynamics of the trophic levels (from bacteria to fish) and the associated cycling of nutrients.

In the Baltic Sea, there have been a few attempts to study the different aspects of ecosystem by the use of ecological modelling method. Stigebrandt and Wulff (1987) have developed a horizontally integrated, time-dependent physico-biogeochemical (nitrogen cycle, oxygen conditions) model for the Baltic Proper. Further development have been undertaken by Savchuk and Wulff (1993) who gave more detailed biological description of autotrophs-heterotrophs interactions in the pelagic zone. A semi-empirical approach, where a remote sensing data from the North Atlantic and the Baltic Sea were assimilated in the ecosystem model, have been presented in the work of Semovski and Woźniak (1995). A similar approach to study the phytoplankton spring bloom in the Gulf of Gdańsk has been presented by Semovski *et al.* (1994). Also for this region, the Delwaq model has been adopted (van der Vat 1994). Witek *et al*. (1993) have applied the Sjöberg's model for the Gulf of Gdańsk, using the empirical data from 1987. They have studied the influence of water temperature on the primary production rate and zooplankton distribution concluding that the

further development in the structure of phytoplankton composition and zooplankton - higher predator interaction is needed in order to obtain more accurate representation of observed data.

Here, we present the structure with detailed mathematical description of the **Pro**duction-**De**struction of Organic Matter **Mo**del (ProDeMo). Then, some preliminary results for the Gulf of Gdańsk are given and discussed. The general objective of the ProDeMo model has been to describe the main biogeochemical cycles in the marine coastal environment. We do not include the benthic processes except for the nutrient regeneration in the sediment which is described implicitly. The classical functional group approach has been used. In the conception phase of the ProDeMo model, we considered the main processes controlling production of organic matter and the cycling of nutrients in the water column and tried to keep the model as simple as possible. The structure of the model is open: other functional groups (*e.g.* fish) might be added and the included ones might be divided (*e.g.* diatoms, dinoflagellates) into several subgroups. The external factors influencing the ProDeMo model are: the transport processes (advection, diffusion) most often supplied by the hydrodynamical models, solar radiation and external nutrient loading.

MODEL CONCEPT AND STRUCTURE

Three functional groups have been considered: phytoplankton, zooplankton and detritus as well as the cycles of three nutrients: nitrogen, phosphorus and silicon. The phytoplankton is composed of autotrophic organisms which may be divided into a few subgroups: *e.g.* diatoms, dinoflagellates, chlorophytes. The zooplankton is treated as one group of heterotrophic organisms grazing on authotrophs. Detritus pool consists of all dead material (dead primary and secondary producers, excrements) which further undergoes mineralization processes. There are four inorganic macronutrients included in the ProDeMo structure: nitrate nitrogen, ammonium nitrogen, phosphate phosphorus and silicate silicon. The inorganic form of carbon has not been included in the model structure as the one which does not limit growth of phytoplankton. Therefore, only the part of carbon cycle, phytoplankton – zooplankton - detritus, is described. The mass balance equations are closed for nitrogen, phosphorus and silicon in the water column. Finally, there are 11 non-conservative state variables and 11 derived quantities (direct proportion of non-conservative state variables) (Tab. 1). For each of them the mass balance equation contains two general terms: state variable = production processes - destruction processes.

The biogeochemical processes, which transform the state variables c_i from one form to another, have been described by the source/sink function $S(c_i)$ in the well known advection - dispersion equation:

$$\frac{\partial c_i}{\partial t} + \frac{\partial}{\partial x}(uc_i) + \frac{\partial}{\partial y}(vc_i) + \frac{\partial}{\partial z}(wc_i) =$$

$$= \frac{\partial}{\partial x}\{D_x \frac{\partial c_i}{\partial x}\} + \frac{\partial}{\partial y}\{D_y \frac{\partial c_i}{\partial y}\} + \frac{\partial}{\partial z}\{D_z \frac{\partial c_i}{\partial z}\} + S(c_i),$$

(1)

where:

c_i, state variable; t, time; u, v and w, components of velocity vector; D_x, D_y and D_z, diffusion coefficients in x, y and z directions, respectively; $S(c_i)$, source/sink function.

Table 1

State variables and derived quantities of the ProDeMO Model

State variables			Derived quantities		
Symbol	**Description**	**Unit**	**Symbol**	**Description**	**Unit**
[n-PHYT]	phytoplankton carbon for each group	[gC m^{-3}]	[PHYT]	total phytoplankton carbon	[gC m^{-3}]
[ZOOP]	zooplankton carbon	[gC m^{-3}]	[Chl a]	chlorophyll a	[gChla m^{-3}]
[DETR]	detritus carbon	[gC m^{-3}]	[N-PHYT]	phytoplankton nitrogen	[gN m^{-3}]
[N-NO3]	nitrate nitrogen	[gN m^{-3}]	[N-ZOOP]	zooplankton nitrogen	[gN m^{-3}]
[N-NH4]	ammonium nitrogen	[gN m^{-3}]	[N-TOT]	total nitrogen	[gN m^{-3}]
[N-DETR]	detritus nitrogen	[gN m^{-3}]	[P-PHYT]	phytoplankton phosphorus	[gP m^{-3}]
[P-PO4]	phosphate phosphorus	[gP m^{-3}]	[P-ZOOP]	zooplankton phosphorus	[gP m^{-3}]
[P-DETR]	detritus phosphorus	[gP m^{-3}]	[P-TOT]	total phosphorus	[gP m^{-3}]
[Si-SiO4]	silicate silicon	[gSi m^{-3}]	[Si-PHYT]	phytoplankton silicon	[gSi m^{-3}]
[Si-DETR]	detritus silicon	[gSi m^{-3}]	[Si-ZOOP]	zooplankton silicon	[gSi m^{-3}]
[DO]	dissolved oxygen	[gDO^{-3}m]	[Si-TOT]	total silicon	[gSi m^{-3}]

Mathematical representations of the biogeochemical processes ($S(c_i)$ in eq. 1) allow one to combine the ecological models with hydrodynamic and transport models (Vested *et al.* 1996).

PHYTOPLANKTON

Here, to simplify the model formulation, we assume that the phytoplankton biomass is composed only of one group. Differentiation of the phytoplankton composition, requires that another coefficient values are included in the mathematical representation due to the fact that each subgroup reacts differently to three environmental factors: light intensity, nutrient concentration and water temperature determining the growth rate. Also each subgroup behaves differently in the case of loss processes: respiration, grazing and sinking.

GROWTH

The main growth equation is:

$$G = G_{\max} \cdot G(T) \cdot G(I) \cdot G(B),$$

(2)

where:
G, total growth of phytoplankton at different depths [d^{-1}]; G_{max}, maximum phytoplankton growth rate [d^{-1}]; G(T), temperature function of phytoplankton growth [-]; G(I), light function of phytoplankton growth [-]; G(B), nutrient function of phytoplankton growth [-].

The temperature function is given by Riley and Stefan (1988):

$$G(T) = \exp\left\{\begin{array}{ll} 2.3\left(\dfrac{T - T_{opt}}{T_{opt} - T_{min}}\right)^2 & T \leq T_{opt} \\[3mm] 2.3\left(\dfrac{T - T_{opt}}{T_{max} - T_{opt}}\right)^2 & T > T_{opt} \end{array}\right\}, \tag{3}$$

where:
T_{opt}, optimum temperature of the phytoplankton growth [°C]; T_{min}, minimum temperature of the phytoplankton growth (growth is reduced by 90%) [°C]; T_{max}, maximum temperature of the phytoplankton growth (growth is reduced by 90%) [°C].

The influence of solar radiation on photosynthesis is given by the following functions (Steele 1975):

$$G(I) = \int_{z}^{z+Dz} \frac{1}{z} F(I_{PAR}(t,z))dz \ , \tag{4}$$

$$F(I_{PAR}(t,z)) = \frac{I_{PAR}(t,z)}{I_s}\exp\left[-\frac{I_{PAR}(t,z)}{I_s} + 1\right], \tag{5}$$

where:
$F(I_{PAR}(t, z))$, nondimensional function of relative photosynthesis [-]; $I_{PAR}(t, z)$, light intensity in *PAR* range (400–700 nm) [W m^{-2}]; I_s, optimum light intensity for phytoplankton growth [W m^{-2}]; t, time [d]; z, depth [m].

Above integration (eq. 4) is resolved analytically (Fransz *et al*. 1991) and usually mean daily light intensity $I_{PAR}(t, z)$ is used. Very often a *self shading effect* is applied to determine the penetration of light into the water column (Fransz *et al*. 1991).

The nutrient concentration limits the primary production rate according to the standard Michaelis-Menten expressions:

$$G(N) = \frac{\{[N\_NH4] + [N\_NO3]\}}{K_{MN} + \{[N\_NH4] + [N\_NO3]\}}, \tag{6}$$

$$G(P) = \frac{[P\_PO4]}{K_{MP} + [P\_PO4]} \ , \tag{7}$$

$$G(Si) = \frac{[Si\_SiO4]}{K_{MSi} + [Si\_SiO4]} , \tag{8}$$

where:
   $G(N)$, $G(P)$ and $G(Si)$ are limitation functions for inorganic nitrogen, phosphorus and silicon [-]; K_{MN}, K_{MP} and K_{MSi} are inorganic nitrogen, phosphorus and silicon half-saturation constants, respectively [$g\,m^{-3}$].

O'Neill *et al.* (1989) have reviewed and compared different formulas describing the nutrient limitation in ecological models. We have chosen the Liebig concept assuming that the growth rate is controlled by the minimum value among 6–8 expressions, so:

$$G(B) = \min \{G(N), G(P), G(Si)\}. \tag{9}$$

Finally, from the equations (2–9), the daily primary production PP_{daily} [gC m^{-2} d^{-1}] is described by:

$$PP_{daily} = \int_0^H (G \cdot [PHYT]) \, dz \ , \tag{10}$$

where:
   H is water depth [m].

The chlorophyll *a* concentration [*Chl a*] has been assumed to be proportional (fixed ratio) to the phytoplankton carbon. If more than one phytoplankton group is applied, the ratio between chlorophyll *a* and carbon in each group must be specified.

LOSS PROCESSES

Respiration
According to Baretta *et al.* (1988), the respiration rate of phytoplankton contains three terms: activity respiration, resting respiration and nutrient stress respiration. The activity respiration is assumed to be proportional to the phytoplankton growth rate (2). This assumption gives (Baretta *et al.* 1988):

$$R_{akt} = K_{Rakt} \cdot G_{max} \cdot G(T) \cdot G(I) \cdot G(B), \tag{11}$$

where:
    R_{act}, activity respiration rate [d^{-1}]; K_{Rakt}, the fraction of growth used for activity respiration [-].

The resting respiration depends on the water temperature and day length:

$$R_{rest} = D_{Rresr} \cdot Q_{Rrest}{}^{T-10} \cdot (1 - h(d)), \tag{12}$$

where:
    R_{rest}, resting respiration rate [d^{-1}]; D_{Rrest}, resting respiration rate at the temperature of 10 °C [d^{-1}]; Q_{Rrest}, temperature respiration constant [-]; T, water temperature [°C]; $h(d)$, relative day length [-].

The nutrient stress respiration is assumed to be proportional to the difference between the maximal (no nutrient limitation) potential growth rate and actual growth rate G (Varela *et al*. 1995):

$$R_{str} = K_{Rstr} \cdot G_{max} \cdot G(T) \cdot G(I) \cdot [1 - G(B)], \tag{13}$$

where:
    R_{str}, nutrient stress respiration rate [d^{-1}]; K_{Rstr}, nutrient stress respiration coefficient [–].

Thus the total respiration rate R [d^{-1}] is a sum of three mentioned rates:

$$R = R_{act} + R_{str} + R_{rest}. \tag{14}$$

Grazing by zooplankton

The carbon flux due to heterotrophic grazing of phytoplankton is based on the filtration rate concept rather than heterotrophic ratio concept (bioenergetic approach) (Savchuk and Wulff 1993), therefore we have assumed that:

$$D_Z = Fr \cdot [ZOOP], \tag{15}$$

where:
    D_Z, grazing rate by zooplankton [d^{-1}]; Fr, filtration [m^3 g[C-ZOOP]$^{-1}$d^{-1}].

The filtration function Fr is dependent on the food density and temperature in the following way (General description 1990):

$$Fr = \frac{G_Z \cdot Q_Z{}^{T-20}}{1 + \exp[a_{fr} - b_{fr} \cdot (P_{aval} \cdot [PHYT])]}, \tag{16}$$

where:
    G_Z, grazing coefficient [m^3 g[C-ZOOP]$^{-1}$d^{-1}]; Q_Z, grazing temperature constant [-];

T, temperature [°C]; a_{fr} and b_{fr}, filtration parameters [-] and [$m^3 g^{-1}$], respectively; P_{aval}, food availability constant [-].

The food density dependent filtration expression results in low grazing rate at low phytoplankton biomass increasing to high grazing for high content of the phytoplankton biomass. If the phytoplankton biomass consists of different sub-groups of algae, the total food pool for zooplankton must be described. Hence, the different food availability to zooplankton (P_{aval} constant) may be applied in eq. (16).

Sinking

Generally, it has been accepted that nutrient limitation conditions influence the sinking rate (Fransz *et al.* 1991). Therefore, two sinking rates are often used in modelling of phytoplankton dynamics: the standard one (maximum value) under no limitation conditions and the second in the case of deficiency of nutrients:

$$V_s = \begin{cases} V_{smax} & \text{if} [N] \geq N_h \\ V_{slim} & \text{if} [N] < N_h \end{cases},$$ (17)

where:
V_s, V_{smax} and V_{slim} are sinking velocity and maximum or under limitation conditions sinking velocity, respectively [md^{-1}]; [N] and N_h are nutrient concentration and threshold nutrient concentration, respectively [$g m^{-3}$].

The overall mass balance equation for any phytoplankton group is:

$$\frac{\partial [PHYT]}{\partial t} = \left(G - R - D_z - \frac{V_s}{\Delta z} \right) [PHYT],$$ (18)

where:
Δz is water depth [m].

ZOOPLANKTON

Zooplankton biomass consists of all heterotrophic organisms within a wide range of sizes which graze on autotrophs (phytoplankton subgroups). Thus, the model describes only the main flow of organic material between autotrophic producers and heterothrophic consumers and does not take into account different classes of zooplankton (micro-, mesozooplankton). The processes considered in zooplankton dynamics are: growth, respiration, excretion and mortality. Many of the mathematical descriptions of these processes have been based on, and adopted from „the standard organism" concept used in ERSEM (Baretta-Bekker *et al.* 1995).

GROWTH OF ZOOPLANKTON

We assume that the growth rate of zooplankton [ZOOP] is related directly to the grazing process by the filtration function Fr (eq. 15, 16) and to the assimilation of phytoplankton biomass, so:

$$G_{ZOOP} = Z_{As} \cdot Fr \cdot [PHYT],$$ (19)

where:
G_{ZOOP}, assimilation rate by zooplankton [d^{-1}]; Z_{as}, assimilation efficiency [-].

LOSSES OF ZOOPLANKTON

Respiration
Following Baretta-Bekker *et al.* (1995), the respiration includes two processes: activity respiration, which depends on growth rate and assimilation efficiency (eq. 19), and excretion and standing stock respiration being a function of water temperature *T*. The activity respiration is given by:

$$R_{ZAct} = G_{ZOOP} \cdot (1 - Z_{As})(1 - Ex),$$ (20)

where:
R_{ZAct}, zooplankton activity respiration rate [d^{-1}]; Ex, excreted fraction of food [-].

For standing stock respiration, the temperature effect is quantified in the following expression (Baretta-Bekker *et al.* 1995):

$$R_{ZSt} = D_{ZSt} \cdot Q_{ZSt}^{(T-10) \cdot 0.1},$$ (21)

where:
R_{ZSt}, standing stock respiration rate for zooplankton [d^{-1}]; D_{ZSt}, standing stock respiration at 10 °C [d^{-1}]; Θ_{ZSt}, temperature constant [-]; T, temperature [°C].

Thus, the total respiration rate for zooplankton is:

$$R_Z = R_{ZAc} + R_{ZSt}.$$ (22)

Excretion
The excretion process is defined as follows (Baretta-Bekker *et al.* 1995):

$$W_Z = G_{Zoop} \cdot (1 - Z_{As}) \cdot Ex,$$ (23)

where:
W_Z, is excretion rate for zooplankton [d^{-1}].

The equations (20) and (23) give the total non-assimilated fraction of food intake and *Ex* is a proportionality factor over the active respiration and excretion.

Mortality

The zooplankton mortality rate, defined by constant value L_Z [d^{-1}], includes all processes not describe explicitly in the zooplankton dynamics, *e.g.* natural mortality or grazing by predators. Therefore, L_Z rate may serve as the main calibration parameter to described zooplankton loss processes.

The final mass balance equation for zooplankton biomass is given by:

$$\frac{\partial[ZOOP]}{\partial t} = \left(G_Z - R_Z - W_Z - L_Z\right)[ZOOP].$$ (24)

DETRITUS

Detritus in our model is defined as the whole pool of dead organic material present in the water column with varying C:N:P:Si ratio. The detritus pool consists of material left by primary and secondary producers as a result of respiration and mortality, non-assimilated food, material excreted by zooplankton. The dead organic matter is decomposed to dissolved inorganic matter (mineralization) by bacteria, which are not considered in the ProDeMo model. The bacteria activity increase with water temperature, thus the mineralization of detritus carbon [*DETR*] has been defined as the water temperature dependent functions in the following form:

$$M_C = K_{mC} \cdot Q_{mC}^{\ T-20},$$ (25)

where:
M_C, detritus carbon mineralization rate [d^{-1}]; K_{mC}, detritus carbon mineralization coefficient [d^{-1}], Θ_{mC}, temperature mineralization constant for detritus carbon [-].

Sinking rate of detritus, V_{sD} [m d^{-1}], has a constant value in the whole water column.

$$\frac{\partial[DETR]}{\partial t} = R \cdot [PHYT] + \left(1 - Z_{As}\right) \cdot Fr \cdot [PHYT] \cdot [ZOOP]$$
$$+ \left(R_Z + W_Z + L_Z\right) \cdot [ZOOP] - \left(M_C + \frac{V_{sDETR}}{\Delta z}\right) \cdot [DETR].$$ (26)

NUTRIENTS

Generally, the mass balance equations are very similar for each nutrient: nitrogen, phosphorus and silicon. The inorganic, contained in living organisms and detritus, forms of nutrients have been considered. There are two main processes influencing the concentration of different forms of nitrogen, phosphorus and silicon: uptake by phytoplankton and mineralization. The ratios between carbon, nitrogen, phosphorus and silicon in living organisms have been assumed to be constant, therefore, only the phytoplankton and zooplankton carbon (Tab. 1) have been treated as the independent state variables. Contrary to the living organisms, C:N:P:Si ratio in detritus varies due to the different rates of nutrient mineralization (Radach and Lenhart 1995), thus the detritus forms of nitrogen, phosphorus and silicon have been included as the state variables. The mineralization of detritus nutrients has been described using the same form of function as for carbon (eq. 25) with different parameter values. In the case of nitrogen, also the nitrification and denitrification processes are included in the mass balance equations using the standard temperature dependent type of function (eq. 25). The assumption that ammonium is preferably taken up over the nitrate by the phytoplankton has been applied after Ambrose *et al.* (1986). In the phosphorus cycle, parametrisation of the sorption-desorption processes (equilibrium concept) has been used (Ambrose *et al.* 1986). Due to the factor f_{PIP} in eq. 33, the inorganic phosphorus adsorbed on suspended matter may sink and thus decrease the concentration of [*PO4*] in the water column. The total mass of nutrient is a sum of independent nutrient state variables (inorganic forms, detritus form) and derived quantities (content in living organisms) (Tab. 1). Pro-DeMo model does not describe nutrient regeneration in the benthic system, however, the fluxes of inorganic nutrients from the sediment to the water phase have been calculated implicitly. The assumption that nutrient flux from the sediment is proportional to the detritus flux to the sediment has been applied. In the case of nitrogen, it has been assumed that all inorganic nitrogen flux from sediment is realised in a form of ammonium nitrogen. Additionally, the inorganic nutrient flux is modulated by the dissolved oxygen content in near bottom water and by temperature:

$$S_N = \begin{cases} [DO] \le M_{DO} \Rightarrow S_{Nunox} \\ [DO] > M_{DO} \Rightarrow K_{mSN} \cdot Q_{mSN}^{T-20} \cdot \dfrac{[DO]}{M_{DO} + [DO]} \cdot (S_{NPHYT} + S_{NDETR}), \end{cases}$$

$$S_{NPHYT} = V_s \cdot [PHYT] \cdot a_{NCPHYT},$$
$$S_{NDETR} = V_{sD} \cdot [N\_DETR], \tag{27}$$

where:
S_N, nutrient flux from sediment to water [$g\,m^{-2}\,d^{-1}$]; S_{Nunox}, nutrient flux from sediment to

water under the anaerobic conditions $[\mathrm{g\,m^{2}\,d^{-1}}]$; K_{mSN}, proportionality factor for nutrient mineralization in the sediment [-]; Θ_{mSN}, temperature constant for nutrient mineralization in the sediment [-]; M_{DO}, threshold dissolved oxygen concentration for anaerobic conditions $[\mathrm{g\,m^{-3}}]$; S_{NPHYT}, flux of nutrient contained in phytoplankton to sediment $[\mathrm{g\,m^{-2}\,d^{-1}}]$; S_{NDETR}, flux of detritus nutrient to sediment $[\mathrm{g\,m^{-2}\,d^{-1}}]$; V_{s}, sinking rate for phytoplankton $[\mathrm{m\,d^{-1}}]$; V_{sD}, sinking rate for detritus $[\mathrm{m\,d^{-1}}]$; a_{NCPHYT}, nutrient to carbon ratio in phytoplankton [-].

The whole set of mass balance equations for three nutrients included in the ProDeMo model is presented below:

NITROGEN

$$\frac{\partial [N\_NO3]}{\partial t} = N_{\mathrm{Nitr}} \cdot [N\_NH4] - G \cdot [PHYT] \cdot a_{\mathrm{NC}} \cdot (1 - P_{\mathrm{NH4}}) - \\ - N_{\mathrm{Denitr}} \cdot [N\_NO3], \tag{28}$$

$$\frac{\partial [N\_NH4]}{\partial t} = M_{\mathrm{N}} \cdot [N\_DETR] - G \cdot [PHYT] \cdot a_{\mathrm{NC}} \cdot P_{\mathrm{NH4}} - \\ - N_{\mathrm{Nitr}} \cdot [N\_NH4] + \frac{S_{\mathrm{N}}}{\Delta z}, \tag{29}$$

$$P_{\mathrm{NH4}} = \frac{[N\_NH4] \cdot [N\_NO3]}{(K_{\mathrm{MN}} + [N\_NH4]) \cdot (K_{\mathrm{MN}} + [N\_NO3])} + \\ + \frac{[N\_NH4] \cdot K_{\mathrm{MN}}}{([N\_NO3] + [N\_NH4]) \cdot (K_{\mathrm{MN}} + [N\_NO3])}, \tag{30}$$

$$\frac{\partial [N\_DETR]}{\partial t} = R \cdot [PHYT] \cdot a_{\mathrm{NCPHYT}} (R_{\mathrm{Z}} + W_{\mathrm{Z}} + L_{\mathrm{Z}}) \times \\ \times [ZOOP] \cdot a_{\mathrm{NCZOOP}} - \left(M_{\mathrm{N}} + \frac{V_{\mathrm{sD}}}{\Delta z} \right) \cdot [N\_DETR], \tag{31}$$

$$[N\_TOT] = [N\_NO3] + [N\_NH4] + \\ + [N\_PHYT] + [N\_ZOOP] + [N\_DETR], \tag{32}$$

where:

N_{Nitr}, nitrification rate [d^{-1}]; N_{Denitr}, denitrification rate [d^{-1}]; M_{N}, nitrogen mineralization rate [d^{-1}]; a_{NCPHYT}, nitrogen to carbon ratio in phytoplankton [-]; a_{NCZOOP}, nitrogen to carbon ratio in zooplankton [-]; P_{NH4}, preference ammonium over nitrate nitrogen function [-]; S_{N}, inorganic nitrogen flux from sediment [g m^{-2} d^{-1}].

PHOSPHORUS

$$\frac{\partial [P\_PO4]}{\partial t} = M_{\text{P}} \cdot [P\_DETR] - G \cdot [PHYT] \cdot a_{\text{PCPHYT}} - $$
$$- \frac{V_{\text{sSUSP}}}{\Delta z} \cdot [P\_PO4] \cdot f_{\text{PIP}} + \frac{S_{\text{P}}}{\Delta z}, \tag{33}$$

$$\frac{\partial [P\_DETR]}{\partial t} = R \cdot [PHYT] \cdot a_{\text{PCPHYT}} + (R_{\text{Z}} + W_{\text{Z}} + L_{\text{Z}}) \times$$
$$\times [ZOOP] \cdot a_{\text{NPZOOP}} - \left(M_{\text{P}} + \frac{V_{\text{sD}}}{\Delta z} \right) \cdot [P\_DETR], \tag{34}$$

$$[P\_TOT] = [P\_PO4] + [P\_PHYT] +$$
$$+ [P\_ZOOP] + [P\_DETR], \tag{35}$$

where:

M_{P}, phosphorus mineralization rate [d^{-1}]; a_{PCPHYT}, phosphorus to carbon ratio in phytoplankton [-]; a_{PCZOOP}, phosphorus to carbon ratio in zooplankton [-]; f_{PIP}, fraction of adsorbed inorganic phosphorus [-]; V_{sSUSP}, sinking rate of suspended matter [m d^{-1}]; S_{P}, inorganic phosphorus flux from sediment [g m^{-2} d^{-1}].

SILICON

$$\frac{\partial [Si\_SiO4]}{\partial t} = M_{\text{Si}} \cdot [Si\_DETR] - $$
$$- G \cdot [PHYT] \cdot a_{SiCPHYT} + \frac{S_{\text{si}}}{\Delta z}, \tag{36}$$

$$\frac{\partial [Si\_DETR]}{\partial t} = R \cdot [PHYT] \cdot a_{\text{SiC}} + (R_{\text{Z}} + W_{\text{Z}} + L_{\text{Z}}) \times$$
$$\times [ZOOP] \cdot a_{\text{SiPZOOP}} - \left(M_{\text{Si}} + \frac{V_{\text{sD}}}{\Delta z} \right) \cdot [Si\_DETR], \tag{37}$$

$$[Si\_TOT] = [Si\_SiO4] + [Si\_PHYT] + \\ + [Si\_ZOOP] + [Si\_DETR], \tag{38}$$

where:
M_{Si}, silicon mineralization rate [d^{-1}]; $a_{SiCPHYT}$, silicon to carbon ratio in phytoplankton [-]; $a_{SiCZOOP}$, silicon to carbon ratio in zooplankton; S_{Si}, inorganic silicon flux from sediment [g m^{-2} d^{-1}].

DISSOLVED OXYGEN

In the case of dissolved oxygen mass balance calculations, all processes, except reaeration, are taken into account in other state variable mass balance equations: primary production, nitrification, denitrification, respiration of living organisms, mineralization, consumption by sediment. For each of these processes, the specific proportionality ratios have been applied.

REAERATION

The reaeration is a process causing the flux of oxygen from atmosphere to the water body through the surface of the sea. The higher is the concentration of dissolved oxygen in the sea, the less of it water body can absorb. Most of the models define reaeration as a function of the current velocity and wind velocity parameterising the sea surface dynamics. We have described the reaeration as follows (General description 1990):

$$R_{DO} = K_{DO} \cdot (C_{ST} - [DO]), \tag{39}$$

$$C_{ST} = 14.652 - S \cdot 0.0841 + T \cdot [S \cdot 0.00256 - 0.41022 + \\ + T \cdot (0.007991 - S \cdot 0.0000374 - T \cdot 0.000077774)], \tag{40}$$

$$K_{DO} = 1123200 \cdot \frac{V^{0.5}}{Dz^{1.5}} + \frac{W}{Dz}, \tag{41}$$

$$W = 0.728 \cdot W_v^{0.5} - 0.371 \cdot W_v + 0.0372 \cdot W_v^2, \tag{42}$$

where:
R_{DO}, reaeration rate [g m^{-3} d^{-1}]; K_{DO}, reaeration coefficient [d^{-1}]; C_{ST}, saturated concentration of dissolved oxygen [g m^{-3}]; S, salinity [PSU]; T, water temperature [°C]; W_v, wind velocity [m s^{-1}]; z, depth [m]; V, surface current velocity [m s^{-1}].

The overall mass balance equation for dissolved oxygen is expressed as:

$$\frac{\partial [DO]}{\partial t} = R_{DO} + G \cdot [PHYT] \cdot a_{OC} + N_{Denitr} \cdot [N\_NO3] \cdot a_{ONden} -$$
$$- R \cdot [PHYT] \cdot a_{OC} - R_Z \cdot [ZOOP] \cdot a_{OCZOOP} - \qquad (43)$$
$$- M_C \cdot [DETR] \cdot a_{OCDETR} - N_{Nit} \cdot [NH4] \cdot a_{ONnit} - \frac{S_C}{\Delta z} \cdot a_{OCDETR},$$

where:

S_C, inorganic carbon flux from sediment $[\mathrm{g\,m^{-2}\,d^{-1}}]$; a_{OC}, a_{OCZOOP} and a_{OCDETR} are oxygen to carbon ratios due to the production/respiration of phytoplankton, respiration of zooplankton and mineralization, respectively [-]; a_{ONden} and a_{ONnit} are oxygen to nitrogen ratio due to the denitrification and nitrification, respectively [-].

RESULTS: VERIFICATION TESTS OF PRODEMO MODEL APPLICATION FOR THE GULF OF GDAŃSK

The ProDeMo model has been applied in the 1D horizontally integrated case. A hydro-chemical measurements taken by the Institute of Meteorology and Water Management, Maritime Branch, at station P1 (the Gdańsk Deep) covering year 1991 have been used (Fig. 1). We have considered only one group of phytoplankton, thus we have excluded the silicon cycle, which is important when diatoms are taken into account separately.

We have assumed that the Gdańsk Deep is located far enough from the land to neglect the influence of horizontal inflow of nutrients, so there is no advective fluxes of nutrients. The only source of nutrients is the atmospheric deposition (Falkowska 1985).

The irregular gridspacing (0, 3, 5, 10, 15, 20, 30, ..., 100, 106 m) and timestep $\Delta t = 2\mathrm{h}$ have been used in the calculations. The only driving force in physical modelling is vertical mixing process. The vertical mixing coefficient K_z $[\mathrm{m\,s^{-2}}]$ is a function of wind friction, water temperature and salinity (Jędrasik 1995). The K_z values, as well as the temperature, have been defined at every grid depth for each month and interpolated by Furrier transformation for each day. Daily doses of solar radiation available for station in Gdynia have been converted to mean daily values of light intensity.

The influence of three environmental factors: solar radiation, temperature and nutrient concentrations on the primary production has been studied according to eq. (2). The annual distributions of nutrient concentrations have been derived directly from ProDeMo model and compared with monthly measurements. An example of the calibration is shown in Fig. 2. The model results have shown a good agreement with the observed values. The calculated concentration of nitrate nitrogen seems to be too high below 20 m depth. The increase of nutrient concentrations near bottom is caused by the fluxes from sediment and is too low in the case of phosphate phosphorus. Generally, the model results show

the reasonable coherence with measurements for nitrogen and phosphorus. The vertical distributions of phytoplankton biomass and primary production have a similar shape as those found in literature (Renk 1990).
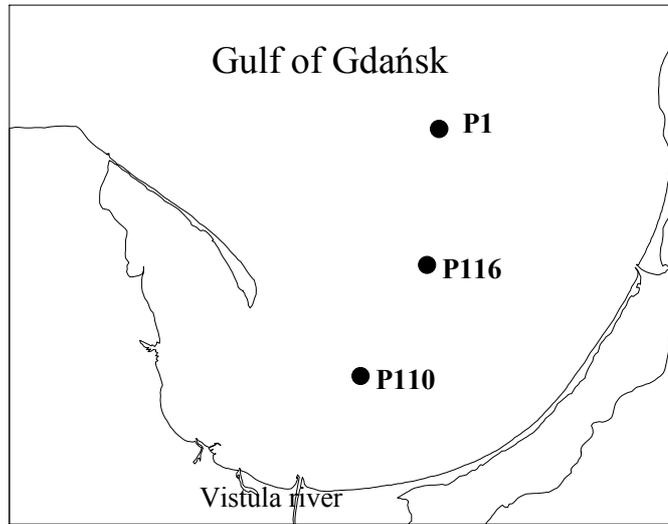

Fig. 1. The map of the Gulf of Gdańsk with the location of sampling stations

Each of nondimensional functions varies between 0 and 1 which represents the limitation and no limitation conditions, respectively. During the first three months of the year, the growth of phytoplankton is mostly limited by the low light intensity $G(I)$ and temperature $G(T)$, while the water is rich in nutrients $G(N)$ (Fig. 3). During the spring bloom, nutrients rapidly decrease and during the whole summer season nitrate nitrogen limits the primary production. The optimum light intensity for the primary production occurs at the beginning of summer (June), while the values of temperature are optimal during the late summer ($G(T) = 1$). The very high changes of $G(I)$ values (Fig. 3) are caused by difference in the light intensity which varies from day to day. The late summer regeneration processes, stimulated by high temperature, make the nutrients again available for phytoplankton growth.

The total effect of: solar radiation, temperature and nutrient concentrations on primary production rate is shown by expression G (eq. 2) whose lowest values correspond to the spring bloom and highest to late summer. Furthermore, the annual distribution of primary production has been calculated, according to eq. 10, and compared with observations (Fig. 4). The curve displays two peaks: first corresponding to the spring and second to autumn. The second peak seems to appear too late, but generally calculated values comply with the measurements. Also the shape of curve is similar to long-term mean distributions (Renk

1990). The calculated annual primary production in 1991 is about 40 % greater compared to the mean value (Renk 1993) (Tab. 2).
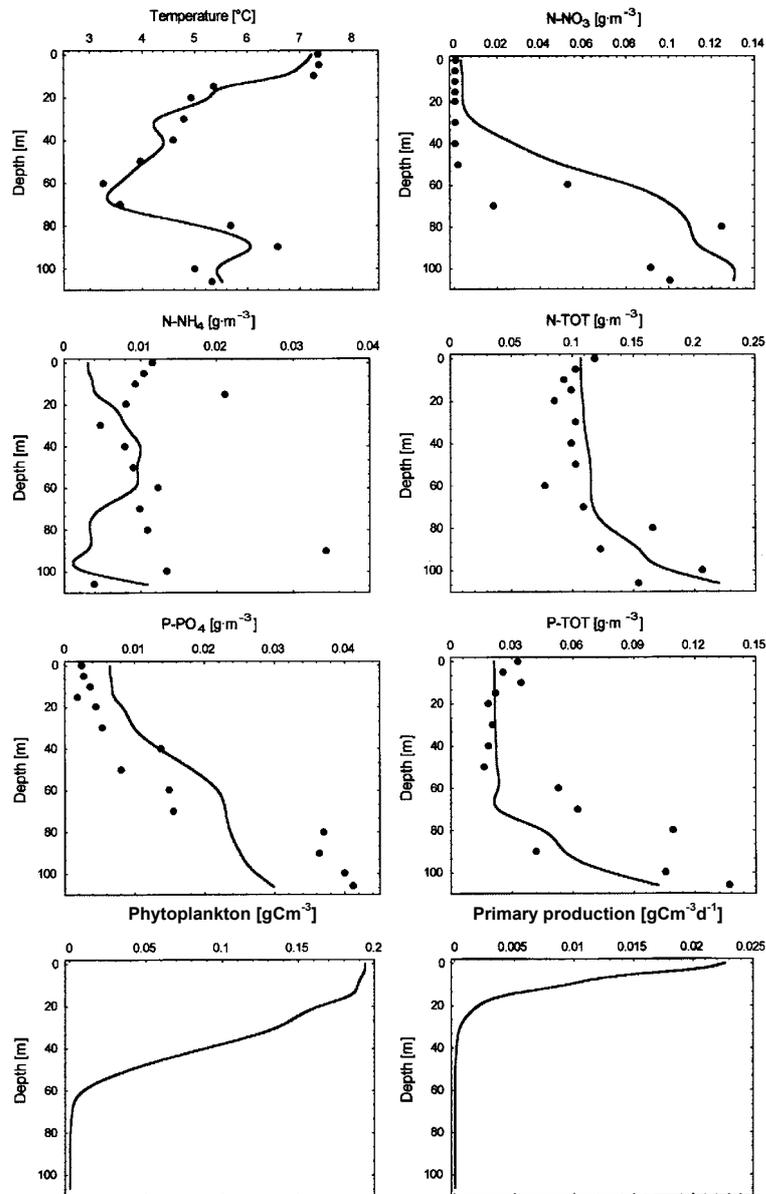

Fig. 2. Observed (points) (IMGW data) and computed (curves) values of modelled parameters for the station P1 on 25th May 1991

Annual primary production in the Gdańsk Deep (P1) according to different sources

Period	Value [gC m^{-2}y^{-1}]	Method	Reference
1991	239.4	calculated from the model	this study
1991	204.9	estimated from measurements	Renk *et al.* 1993
1992	153.5	estimated from measurements	unpublished
1987-1994	170.5	estimated from measurements	unpublished

The annual dynamics of two phytoplankton subgroups: diatoms, non-diatoms and zooplankton simulated by the ProDeMo model was compared with the input data set from 1994 covering the meteorological conditions in the Gulf of Gdańsk. The calculation results are presented in Fig. 5. Diatoms may grow at lower temperatures (eq. 3), so the spring bloom occurs in the middle of April. Non-diatom peak appears later due to the preference of higher temperature. The non-diatom biomass stays higher than diatoms during summer. Diatoms biomass increases again in autumn. Under the limitation conditions, the subgroups of phytoplankton compete between each other for inorganic nutrients. Zooplankton biomass increases with the increase of water temperature and reaches the maximum value 0.055 gC m^{-3} in summer. The modelled distribution of zooplankton gives the values which are in the same range as those published elsewhere (Witek 1995, Renk 1989).
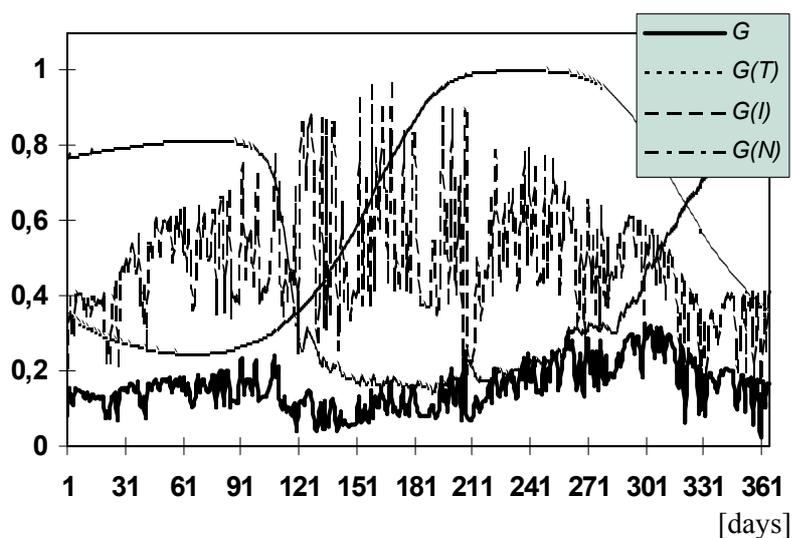

Fig. 3. The annual distribution of phytoplankton growth rates *G* and growth limitation functions of the solar radiation *G(I)*, temperature *G(T)* and nutrient concentrations *G(N)* in the surface layer in 1991

A simpler version of the ProDeMo model has been used in 2D vertically integrated application for the Gulf of Gdańsk. The application has been meant mainly to study the spatial and temporal nutrient dynamics (nitrogen, phosphorus) in the Gulf. Because the zooplankton functional group has been excluded, phytoplankton losses due to grazing by zooplankton has been defined as the externally driven function. The grazing has been assumed to be proportional to the zooplankton biomass distribution (Renk 1989). The wider description of this approach, as well as the calibration results have been given in Ołdakowski *et al.* (1994).
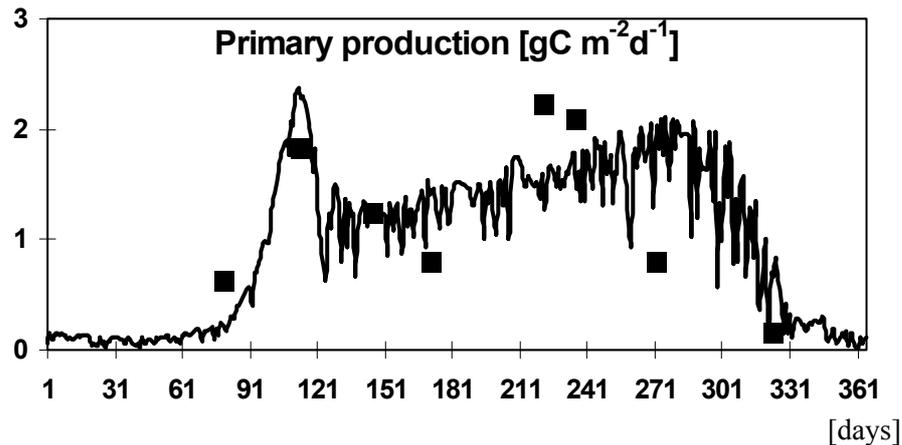

Fig. 4. The calculated (——) and measured (Renk *et al.* 1993, SFI data) (■) primary production in 1991 at station P1

Two stations, P110 located closer to the Vistula river and P116 located further to the open sea (Fig. 1), have been chosen to investigate the evolution of [*P-TOT*] and [*N-TOT*] structure in the Gulf. Generally, the mass balance was kept for both compounds (Fig. 6), however, there was a difference in a percentage distribution of organic (detritus, phytoplankton) and inorganic forms. Near the Vistula river mouth (P110), the values for both components were higher and the amplitudes of their fluctuations were also significant. The further from the Vistula river outlet, the smaller and smoother were the variations of their concentration caused by horizontal diffusion. Going from the shore toward the open sea, the values of [*P-TOT*] and [*N-TOT*] decreased due to dilution of the Vistula waters. The inorganic nitrogen compounds turned out to be the factor limiting primary production, however, phosphorus may also limit the growth of phytoplankton for a short time during the spring bloom (Ołdakowski *et al.* 1994). If unbound inorganic nitrogen (mineralization, advection) appeared in the water column during summer, it was immediately taken up by algae. The inorganic phosphorous was never depleted completely in summer and was transported across the Gulf into the open sea.
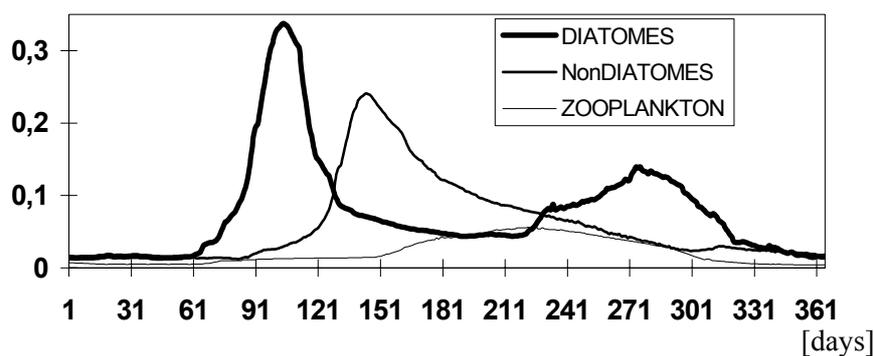
Fig. 5. Calculated annual distribution of biomass [gC m^{-3}] of zooplankton and two phytoplankton groups: diatoms and non-diatoms in 1994
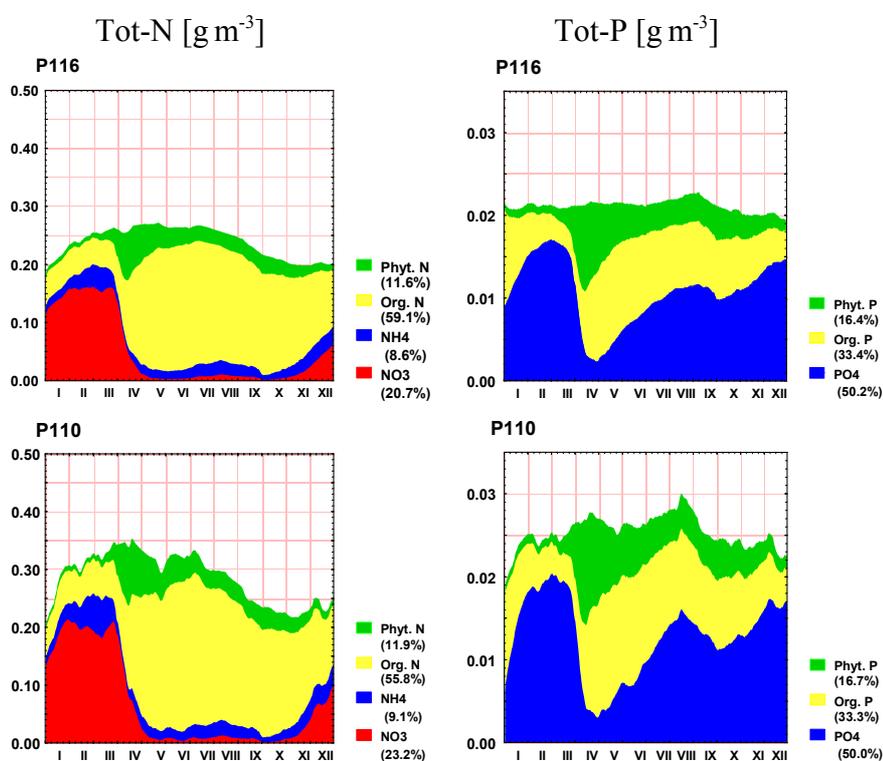

Fig. 6. Calculated annual structural distribution of total nitrogen and total phosphorus at two stations: P116 and P110 in 1991

Nutrients discharged by the Vistula river have the great influence on the ecological state of the Gulf of Gdańsk. Even during the strong limitation condi-

tions in summer, the influence of the Vistula river on nitrate nitrogen is very visible (Fig. 7). By the application of the 2D model, southern part of the Gulf and external part of Puck Bay have been found to be the most eutrophicated regions (Ołdakowski *et al*. 1994).
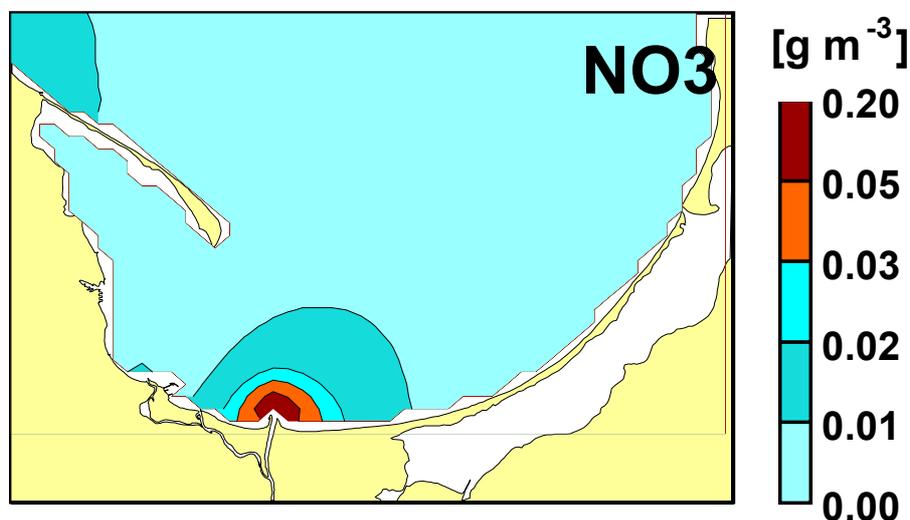

Fig. 7. Mean calculated summer nitrate nitrogen concentration in the Gulf of Gdańsk in 1991 in 0–60 m layer

CONCLUSIONS

Modelling of marine ecosystem is an interdisciplinary task, therefore it needs the close co-operation of scientists who deal with wide spectrum of physical and biological processes occurring in the marine environment. The conception and structure of the ProDeMo model seems to be an important attempt for the development of a complex ecological model for the Gulf of Gdańsk. The correctness of mathematical formulations of the model has been proven by first applications, especially in the case of nutrient-autotrophs dynamics, where data from field observations were available. Until now, ProDeMo model describes only the main interactions and matter cycle between inorganic and organic compounds, however, it provides a base for further studies on *e.g.* nutrient cycling in biotic phase, phytoplankton and zooplankton composition and its dynamics, benthic processes. The presented model seems to be very useful for biogeochemical flux calculations. By using the developed ecological model with aggregated transport model, a matter budget for the Gulf of Gdańsk can be calcu-

lated in a more complete way than based on field observations only as it has been done for other regions (Baretta *et al*. 1995, Gordon *et al*. 1995).

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