

**Particulate organic carbon
in the southern Baltic Sea:
numerical simulations and
experimental data***

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Abstract

Particulate Organic Carbon (POC) is an important component in the carbon cycle of land-locked seas. In this paper, we assess the POC concentration in the Gdańsk Deep, southern Baltic Sea. Our study is based on both a 1D POC Model and current POC concentration measurements. The aim is twofold: (i) validation of simulated concentrations with actual measurements, and (ii) a qualitative assessment of the sources contributing to the POC pool.

The POC model consists of six coupled equations: five diffusion-type equations for phytoplankton, zooplankton, pelagic detritus and nutrients (phosphate and total inorganic nitrogen) and one ordinary differential equation for detritus at the

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bottom. The POC concentration is determined as the sum of phytoplankton, zooplankton and pelagic detritus concentrations, all expressed in carbon equivalents. Bacteria are not simulated in this paper.

The observed large fluctuations of POC concentrations are attributed to its appreciable seasonal variability. The maximum concentration of POC varied between 870 mgC m^{-3} in May and 580 mgC m^{-3} in September, coinciding with the period of maximum dead organic matter and phytoplankton biomass concentrations. The results of the numerical simulations are in good agreement with observed values. The difference between the modelled and observed POC concentrations is equal to 3–28% and depends on the month for which the calculations were made, although no time trend of the difference is observed. The conclusion is that the numerical simulations are a sufficiently good reflection of POC dynamics in the Baltic.

1. Introduction

Organic matter is a minor component of sea water. The concentration of organic compounds in the ocean is less than 3 mg dm^{-3} , and in coastal areas the concentration seldom exceeds 15 mg dm^{-3} . Despite its low concentration, however, organic matter plays an important role in establishing the properties of sea water and the processes taking place there. The former include, for example, water colour and the speciation of chemical trace constituents, the latter, light scattering and the migration and bioavailability of heavy metals (Hedges 2002). The concentration of organic carbon (OC) in sea water is a measure of the organic matter content. It is assumed that OC constitutes 45% of OM, although other proportions have been reported (Chester 2003).

For practical purposes, organic matter is most often separated into particulate (POM) and dissolved (DOM) species. Although the DOM/POM ratio can vary quite widely, its value in coastal areas is from 4 to 6. Particulate organic carbon (POC) is a measure of particulate organic matter (POM) in the marine environment (Wangersky 1977). POM is defined as suspended organic matter that remains on $0.2\text{--}1.0 \mu\text{m}$ pore filters during the filtering of sea water (Turnewitsch et al. 2007). Nominally, therefore, POM consists of phyto- and zooplankton cells, detritus and bacteria. In relation to the concentrations of dissolved carbon species (both inorganic – DIC and organic – DOC), POC makes up rather a small part of the total carbon pool. Nonetheless, in spite of the low concentrations, POM plays a key role in many natural processes occurring in the marine environment. The most significant of these seems to be the downward vertical transport of chemical substances (e.g. C, N, P, heavy metals, organic pollutants) in the water column. Degradation of POM supplies DOC, which provides

a substrate for biota (Haitzer et al. 1999, Hedges 2002, Chester 2003, Kuliński & Pempkowiak 2008).

Basically, POM originates directly or indirectly from primary production (Turnewitsch et al. 2007). Thus it is often used to describe the ‘biological pump’ mechanisms (e.g. Rost & Riebesell 2004, Sabine et al. 2004). From sea water, live phytoplankton absorbs dissolved CO₂, which is utilized in photosynthesis and the calcification of their skeletons. Both processes cause the partial pressure of CO₂ to decrease, which leads to an imbalance between the CO₂ concentrations in the sea water and the atmosphere; as a result, there is an uptake of atmospheric CO₂ to the water column. Part of the CO₂ that is turned into biomass is ultimately remineralized back to inorganic carbon forms, whereas the remainder is buried in marine sediments. In this way POM participates in the transport of carbon to the bottom sediments. ‘Biological pump’ mechanisms are especially significant in northern hemisphere shelf seas, where intensive phytoplankton blooms induce the uptake of atmospheric CO₂ (de Haas et al. 2002, Thomas et al. 2004).

The actual POC concentration depends on the equilibrium between POM sources and sinks (Chester 2003, Doney et al. 2003). The processes supplying organic matter to seawater are especially intensive in coastal areas and land-locked seas. This is attributed to the elevated supply of nutrients from the shore, which enhances primary productivity. The Baltic is one such coastal sea: it is one of the most productive marine ecosystems in the world, potentially capable of acting as a highly efficient natural CO₂ sequestrator (Thomas et al. 2005). As a result, POC concentrations in the Baltic are 3–4 times higher than in the oceans (Pempkowiak 1985, Grzybowski & Pempkowiak 2003, Kuliński & Pempkowiak 2008).

Because of the natural variability of POC, however, the quantification of the factors influencing organic matter concentrations in sea water is a complex process. The experimental assessment of POC distribution and long-term changes in the organic matter content of seawater are difficult. In the case of the latter, only a survey lasting several decades can provide realistic results.

But this difficulty can be overcome if mathematical models are applied to simulate the POC concentration in sea water. With such a model one can simulate POC distribution dynamics in the water column; it might even be possible to predict POC changes from changes in the factors affecting POC sources and sinks. Hence, the aim of the present study was to develop and validate a POC model for the Baltic Sea. Given the abundance of experimental data relating to the Gdańsk Deep (southern Baltic), this basin was considered to be the most suitable testing ground in this respect. All

the calculations were based on data relevant to this region, and the model was validated on the basis of literature data and in situ POC measurements. This particular model is based on the 1D model developed by Dzierzbicka-Głowacka (2005).

2. Material and methods

2.1. Study site

Water samples for POC measurements were collected using a GO-FLO Water Sampler (General Oceanics) at station P1 during r/v 'Oceania' cruises in 2007 and 2008. Station P1 (110 m water depth, 100 km offshore) is located in the middle of the Gdańsk Deep (54°50'N 19°17'E; Figure 1). At this depth the water is permanently stratified. The halocline separating the surface water layer (7.2 PSU) from the deep water layer (11 PSU) lies at 60–80 m depth (Voipio (ed.) 1981). In February and March at station P1, the depth of the mixed layer reached its maximum (70 m), where it remained until the beginning of May. In April the thermocline began to form, gradually encompassing ever greater temperature differences and depths until the end of July. The layer of colder waters, the so-called winter water or minimum temperature layer, occurred from February until the end of the year, at a depth of 50–70 m. The temperature of these waters

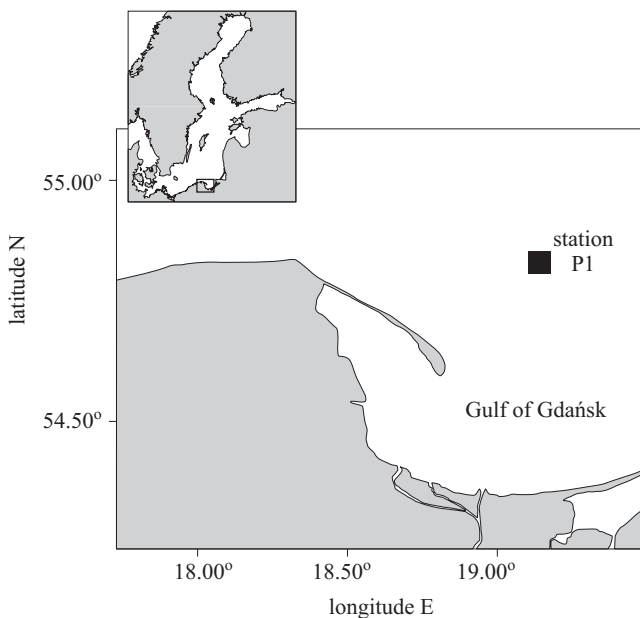


Figure 1. Location of the sampling station

increased with time from about 0.5 to almost 4°C, the amplitude extending both up- and downwards. The near-bottom waters of the Gdańsk Deep gradually became colder, from 6°C at the beginning of the year to about 4°C at the end. All the mathematical simulations were performed for the conditions characteristic of station P1.

2.2. Analytical method for POC

The water samples were passed through precombusted MN GF 5 (0.4 µm pore size) glass fibre filters and frozen (−20°C) before analysis for POC. In the laboratory the POC samples were dried at 60°C for 24 h and weighed (0.01 mg accuracy), after which they were homogenized in 20 ml of Milli Q water and ultrasonically disintegrated. To remove carbonates, samples were acidified with 1M HCl to pH=2 and purged with argon for 2 min. to remove CO₂. Analyses were done in a ‘HyPerTOC’ analyser (Thermo Electron Corp., the Netherlands) using high-temperature oxidation (680°C) with a Pt catalyst and non-dispersive infrared detection. The calibration line used for the POC concentration analysis was obtained using potassium hydrogen phthalate as standard. All the results were corrected by blank measurements. QC was assured by analysing known amounts of POC. Recovery was 97% (RSD = 4%; n = 5). The precision of the actual sample measurements, characterized by RSD, was 7.2% (n = 5).

2.3. The model structure

Recently, Dzierzbicka-Głowacka (2005) developed a one-dimensional, upper-layer ecosystem model, the 1D CEM Coupled Ecosystem Model. This model, supplemented by the population dynamics submodel for copepods and a component for pelagic detritus, was used to study the dynamics of *Pseudocalanus minutus elongates* and *Acartia* spp. in the southern Baltic Sea (Dzierzbicka-Głowacka et al. 2006). In that paper, the model was modified and used to calculate the seasonal variations of POC in the southern Baltic Sea.

The biological part of the model was embedded in the existing 3D hydrodynamic model of the Baltic Sea. Described in project ECOOP IP WP 10.1.1, the sea-ice model (POPCICE) was used to incorporate biological equations in a plankton system. Some basic information about the POPCICE coupled sea-ice model now follows. It is based on the Parallel Ocean Program (POP) and Community Ice Code models, both of which are from the Los Alamos National Laboratory (LANL). POPCICE was forced using European Centre for Medium-Range Weather Forecasts (ECMWF) data. It uses the following external data (ERA 40 reanalysis): 2 m temperature; 2 m dew point; long and short wave radiation; 10 m wind

speed and air-ocean wind stress; ocean model time step – 480 s; ice model time step – 1440 s. The horizontal resolution of the ice and ocean model is ~ 9 km (1/12 degree), and the vertical resolution (ocean model) is 21 levels (for the Baltic Sea ~ 12 levels).

The basis for any ecological simulation is the three-dimensional, time-dependent hydrodynamic model (POPCICE for the Baltic Sea), which provides the velocities, diffusion coefficients and the temperature on a temporal and spatial scale that resolves the atmospherically induced variability mentioned above. Here, we do not discuss the meteorological and physical models, but focus on the biological submodel.

The biological part of the 1D CEM Coupled Ecosystem Model (Dzierzbicka-Głowacka 2005), reduced to a 1D POC Model with an equation for dead organic matter (pelagic detritus), consisted of six coupled equations: five diffusion-type equations for phytoplankton, zooplankton, pelagic detritus and nutrients (phosphate and total inorganic nitrogen), and an ordinary differential equation for the detritus at the bottom. In this paper, the POC concentration was determined as the sum of phytoplankton, zooplankton and pelagic detritus concentrations:

$$\frac{\partial POC(z, t)}{\partial t} = \frac{\partial Phyt(z, t)}{\partial t} + \frac{\partial Zoop(z, t)}{\partial t} + \frac{\partial DetrP(z, t)}{\partial t}. \quad (1)$$

Phytoplankton was modelled with the aid of only one state variable. The phytoplankton concentration was taken to be a dynamically passive physical quantity, i.e. it was incapable of making autonomous movements. Cyanobacteria blooms were not incorporated separately at this stage of the model development. The fact that cyanobacteria activity is less intense in the open sea than in the near-shore zone (Voss et al. 2005) provided additional motivation for choosing station P1 for the present studies. Phytoplankton in the water was either grazed by zooplankton, or else died and sank. The grazed phytoplankton biomass was divided into four portions: one contributed to zooplankton growth, another was deposited at the bottom as faecal pellets, and a third was excreted by the zooplankton as dissolved metabolites. The fourth and final portion was lost due to mortality and predation. One state variable for zooplankton (mesozooplankton) was considered as it ingested both phytoplankton and pelagic detritus. The closure term of the model system was the zooplankton grazed by predators. Here, predation on zooplankton was defined after Steele & Henderson (1992): it is assumed to be proportional to the zooplankton biomass (see Appendix A). The 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 bacterivorous, herbivorous, omnivorous and carnivorous species. Yet nearly all models incorporating zooplankton consider the entire catch to be herbivores feeding in the upper layers of the sea. There are good reasons for this: the mesozooplankton are the largest group of zooplankton, processing as they do nearly all of the primary production (Mudrak 2004). In turn, they (or their faeces and excreta) are the predominant source of food for the rest of the system. Being a top-down regulator, zooplankton may play a significant role in marine ecosystems (Mudrak 2004). In this model, higher trophic levels are not included because of their insignificant effect on POC concentration (Andersson & Rudehäll 1993). Organic detritus in the water column was either immediately remineralized or transported directly to the bottom, where it accumulated in the stock of benthic detritus. The concept of the detritus pool at the bottom was introduced to create a lag in the remineralization of the majority of detritus and the eventual replenishment of the upper layer with nutrients. This complex process was parameterized by assuming a net remineralization rate for bottom detritus (Billen et al. 1991). In this model, nutrients were represented by two components: total inorganic nitrogen ($\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) and phosphate (PO_4^{3-}). The pool of nutrients was enriched in many ways: through detritus decomposition, release from phytoplankton, zooplankton and predator excretion, and benthic regeneration. In this paper bacteria were not explicitly simulated. Their activity only appeared implicitly in the parameterizations of the remineralization terms. Benthic detritus accumulates by sinking out of the water column; it is regenerated by bacterial action, and the resulting nutrients move upwards by turbulent diffusion.

Mathematically, the pelagic variables of the particulate organic carbon model can be described by a second-order partial differential equation:

$$\frac{\partial S}{\partial t} + (u_i + w_S) \frac{\partial S}{\partial x_i} = \frac{\partial}{\partial x_i} \left(K_i \frac{\partial S}{\partial x_i} \right) + F_S, \quad (2)$$

where S denotes model variables, u_i the velocity components, w_S ($= w_p; w_d$) the sinking velocity of phytoplankton or pelagic detritus, K_i the kinematic viscosity and F_S the biogeochemical sources and sinks of the variables.

The different sources and sinks F_S for the 1D POC Model are set out in Table 1 and the diagram in Figure 2. The mathematical formulations for the biogeochemical processes in the model are presented in Appendices A–C.

Table 1. Sinks and sources for the pelagic variables in the POC model

Variable (S)	Sink	Source	Explanation
phytoplankton <i>Phyt</i>	<i>EXCP</i>		phytoplankton excretion
	<i>MORP</i>		natural mortality
	<i>GRP</i>		zooplankton grazing
	<i>SINP</i>		phytoplankton sinking
		<i>PRP</i>	primary production
zooplankton <i>Zoop</i>	<i>EXCZ</i>		zooplankton excretion
	<i>PRED</i>		carnivorous grazing
	<i>FEC</i>		faecal pellets
	<i>MORZ</i>		natural mortality
		<i>GRZ</i>	zooplankton grazing
pelagic detritus <i>DetrP</i>	<i>SIND</i>		detritus sinking
	<i>DECP</i>		detritus decomposition
	<i>GRD</i>		zooplankton grazing
		<i>MORP</i>	natural mortality of phytoplankton
		<i>MORZ</i>	natural mortality of zooplankton
		<i>FEC</i>	faecal pellets
		<i>MORD</i>	natural mortality of predators
nutrients <i>Nutr</i>		<i>UPT</i>	nutrient uptake by phytoplankton
		<i>EXCP</i>	phytoplankton excretion
		<i>EXCZ</i>	zooplankton excretion
		<i>EXCD</i>	predator excretion
		<i>DECP</i>	detritus decomposition
benthic detritus <i>DetrB</i>	<i>REGD</i>		remineralization
		<i>SINP</i>	phytoplankton sedimentation
		<i>SIND</i>	detritus sedimentation

2.3.1. Forcing

The model simulations were carried out for the period 1995–2000. The modelled global radiation at the sea surface was obtained for each time step on the basis of the relation given by Rozwadowska & Isemer (1998) and Dzierzbicka-Głowacka (2005). The oceanographic forcing needed in the biological production model was adopted in the following way. Firstly, time- and space-dependent turbulent diffusion rates resulting from the simulation of the physical upper layer dynamics were introduced into the biological model by the diffusion term. Secondly, the photosynthetically available radiation (PAR) at the sea surface $I_o(I_o(t) = \varepsilon Q_g)$ was identified as $\varepsilon(\varepsilon = 0.465(1.195 - 0.195T_{cl}))$, where T_{cl} was the cloud transmittance function (Czyszek et al. 1979) of the net short-wave radiation flux. Photosynthesis is regulated by the light limitation factor f_I , which is defined by the underwater light intensity. The global radiation enters the source term

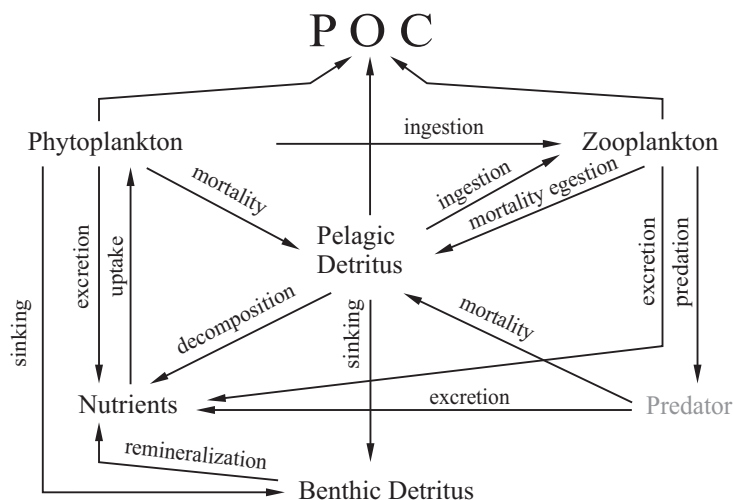


Figure 2. Conceptual flow diagram of the POC model

(primary production) in the phytoplankton equation (see Dzierzbicka-Głowacka 2005).

The flow field and water temperature used as ecosystem model inputs were reproduced by the 3-D hydrodynamic IO PAS-POPCICE model, which is now running for the period 1960–2000 (see project ECOOP IP WP10). The model was forced using daily-averaged reanalysis and operational atmospheric data (ERA-40) derived from the European Centre for Medium-Range Weather Forecasts (ECMWF). The interpolated output of the hydrodynamic model was used as the input in the ecosystem model, since in the simulated area the dynamic characteristics remain almost unchanged in the horizontal plane in comparison to the vertical changes. Hence, the magnitudes of the lateral import/export are lower, and the above assumption is justified.

2.3.2. Initial values

It was assumed that the starting-point of the numerical simulations would be the end of 1995 and that the final state of each year would be the starting point of the next year.

As phytoplankton values for January and December were sparse, a constant value of 10 mgC m^{-3} (Witek 1995) was applied. The model is not sensitive to the initial phytoplankton concentration, owing to the long simulation period (from January) preceding the spring bloom (April/May). The initial zooplankton biomass was obtained according to data by Witek (1995) as $Zoop = 1 \text{ mgC m}^{-3}$ with a maximum growth rate of 0.3 day^{-1} ,

derived as the average between the maximum growth rate of ciliates – equal to 0.4 day^{-1} – and that of heterotrophic dinoflagellates – equal to 0.14 day^{-1} . For copepods, on the other hand, the mean value for three copepods – *Pseudocalanus minutus elongates*, *Acartia* spp. and *Temora longicornis* – was taken (ca 0.3 day^{-1}). The initial values for nutrients were taken from the Institute of Meteorology and Water Management (IMGW) database as the average values for January: total inorganic nitrogen – $Nutr_N = 6 \text{ mmol m}^{-3}$ and phosphate – $Nutr_P = 0.6 \text{ mmol m}^{-3}$. These values were assumed to be constant with depth. Data for the detritus content at the bottom were not available, and the instantaneous sinking of detritus is a more arbitrary model assumption. The initial detritus content in the subsurface water layer was prescribed as 100 mgC m^{-2} . However, a constant value of 50 mgC m^{-3} for pelagic detritus was assumed throughout the water column.

2.3.3. Calibration of the model

The model was tested over a wide range of variability in the physical, biological and chemical parameters measured in the sea. The calibration was based on a comparison of the simulation results with the relevant environmental data from 1995–1996. The values of the coefficients adopted were such as to render the simulations as similar as possible to the observed seasonal distribution of nutrients, the annual cycle of primary production, and the annual variation in phytoplankton and zooplankton. Measurement data made available by the Institute of Oceanology in Sopot (IO PAN) and the Institute of Meteorology and Water Management in Gdynia (IMGW) were used for this purpose. Station P1 in the Gdańsk Deep was the principal measuring station at the calibration stage and for the validation.

The parameters adopted for the comparisons were the concentrations of total inorganic nitrogen, phosphate phosphorus and water temperature measured at the standard depths (2.5, 7.5, 10, 15, 20, 30, 40, 50, 60 and 70 m) at monthly intervals during 1995–96, except for phytoplankton biomass, which was compared several times per year.

The calibration of the 1D model enabled its sensitivity to be analysed. The changes in the optimum light intensities and temperatures affected the time of appearance and intensity of the phytoplankton bloom, the nutrient depletion and the phytoplankton biomass. Finally, a table of coefficients was obtained (Appendix C) to supplement the equations describing biogeochemical processes in southern Baltic waters (Appendices A–B).

2.3.4. Comparison of model results with measurements

The modelled values were compared with those measured at the surface layer and at 60 m depth. The seasonal vertical distribution of calculated and measured parameters in 1999 was analysed (Figure 3). In the surface layer, the modelled nutrients (total inorganic nitrogen and phosphate) concentrations were in accordance with the measurements (see Appendix D). Summer measurements indicated, however, that nitrogen $Nutr_N$ was fully depleted down to 50 m and phosphate $Nutr_P$ to 40 m,

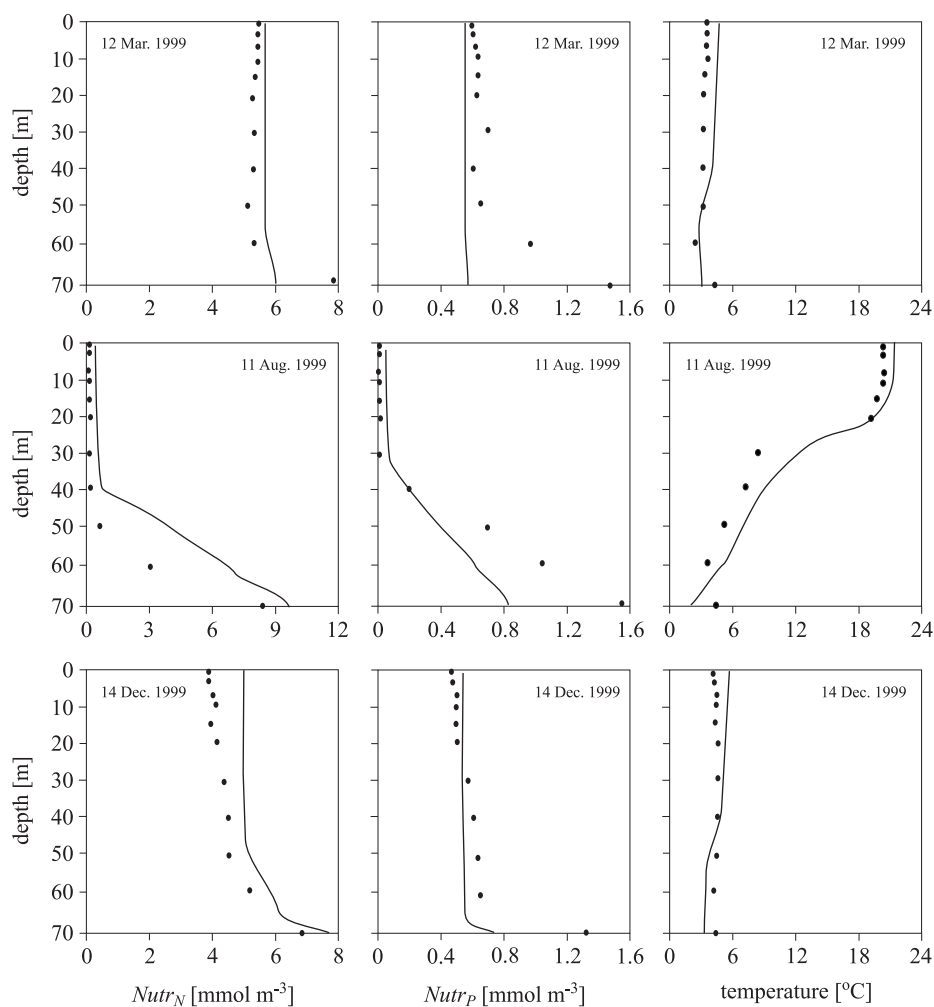


Figure 3. Seasonal variability in 1999 of measured vertical distributions (dots) and modelled parameters (line): total inorganic nitrogen $Nutr_N$, phosphate $Nutr_P$ and temperature in the Gdańsk Deep at station P1

whereas according to the model, $Nutr_N$ was depleted down to 40 m and $Nutr_P$ to 30 m. Moreover, the modelled distribution of $Nutr_N$ and $Nutr_P$ at 70 m did not agree well with observations. The modelled vertical water temperature distributions were consistent with observations. Apart from their variability in particular periods, the modelled results were analysed at the water surface and at 60 m depth (Figures 4 and 5). Comparison of the surface distributions of the above parameters and the phytoplankton biomass during 1995–2000 demonstrated the recurrence of annual cycles (Figure 4). This indicated that the model was functioning properly. In each of these years, there was a regular summer depletion of nutrients $Nutr_N$ and $Nutr_P$. The modelled values of the total inorganic nitrogen and phosphate

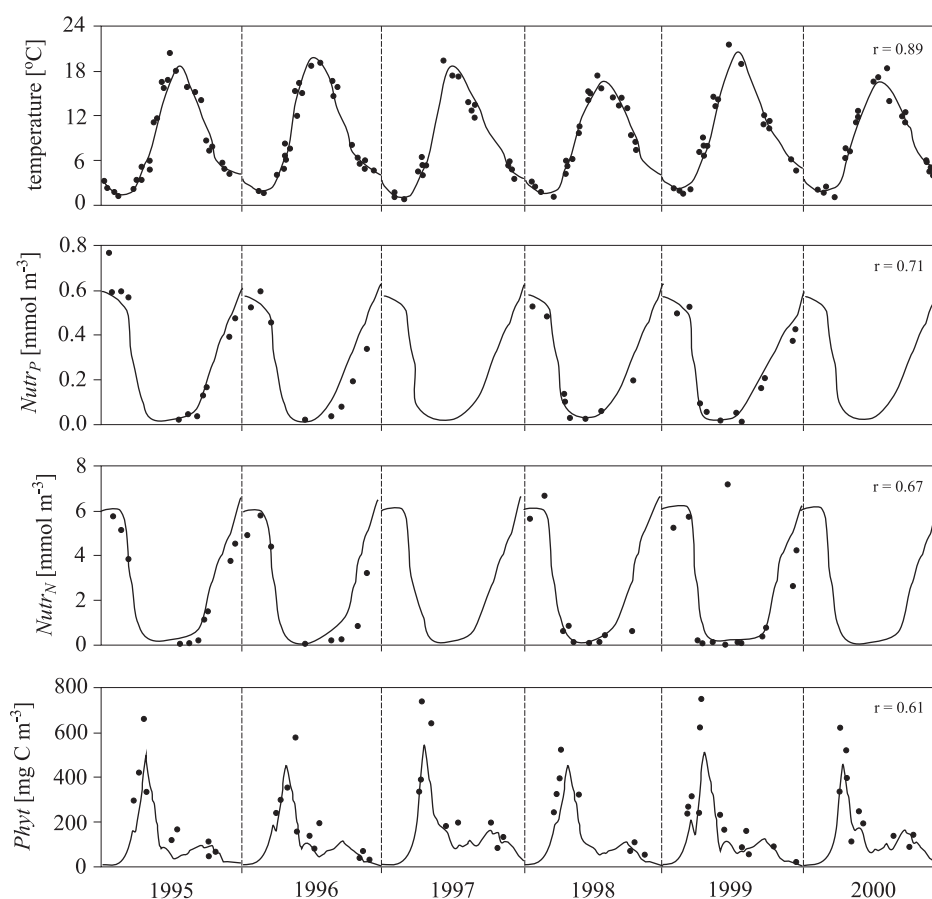


Figure 4. Temporal distribution (1995–2000) of measured (dots) and modelled (line) parameters: temperature, phosphate $Nutr_P$, total inorganic nitrogen $Nutr_N$ and phytoplankton biomass $Phyt$ in the Gdańsk Deep at 0 m depth

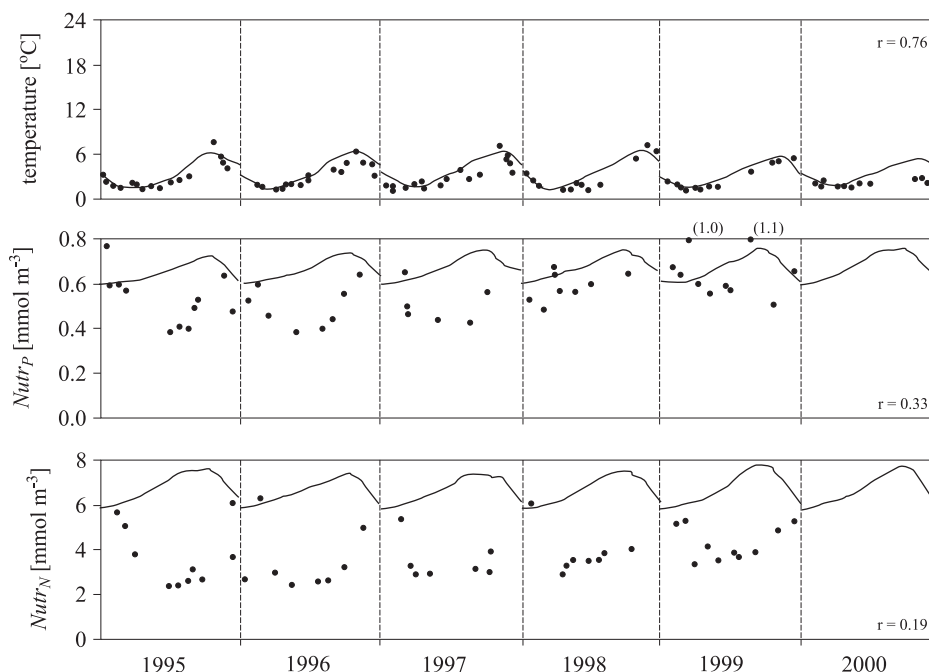


Figure 5. Temporal distribution (1995–2000) of measured (dots) and modelled (line) parameters: temperature, phosphate $Nutr_P$ and total inorganic nitrogen $Nutr_N$ in the Gdańsk Deep at 60 m depth

resembled the observations, with respective correlation coefficients of 0.67 and 0.71. However, at 60 m depth these values were considerably lower (Figure 5) – this was due to the assumed bottom layer depth. The modelled temperatures at these depths were in accordance with the measurements. The simulated phytoplankton biomass was compared with the chlorophyll *a* concentration (measured in the 10 m layer) and the corresponding carbon to chlorophyll *a* ratio in phytoplankton in the Gulf of Gdańsk in the 0–15 m layer (Witek (ed.) 1993). The simulation of phytoplankton was judged to be the weakest, despite a statistically significant correlation coefficient of 0.61.

The simulations and measurements in 1995–2000 were compared. With respect to all the parameters, the correlations of the observed regularities decreased from the surface to the bottom. The correlations for the layers from the surface down to 50 m for $Nutr_P$ and to 60 m for $Nutr_N$ were quite good ($r > 0.5$) during late winter and autumn and down to 40 m ($r > 0.4$) in summer. The consistency of the calculated values with measured distribution was particularly good with regard to temperature. These

results also testified to the fact that the environmental conditions did not change radically and that the simulated processes were regular.

The Pearson product-moment correlation coefficient was used to compare the model results with the measurements.

3. Results of the model simulations

The 1D POC Model described above was used in the numerical simulations of the seasonal dynamics of POC in the Gdańsk Deep (southern Baltic Sea) for 2007, when observations from several months including winter values were available. The hydrodynamic forcing calculated by the 1D physical submodel (see Dzierzbicka-Głowacka 2005) was included by

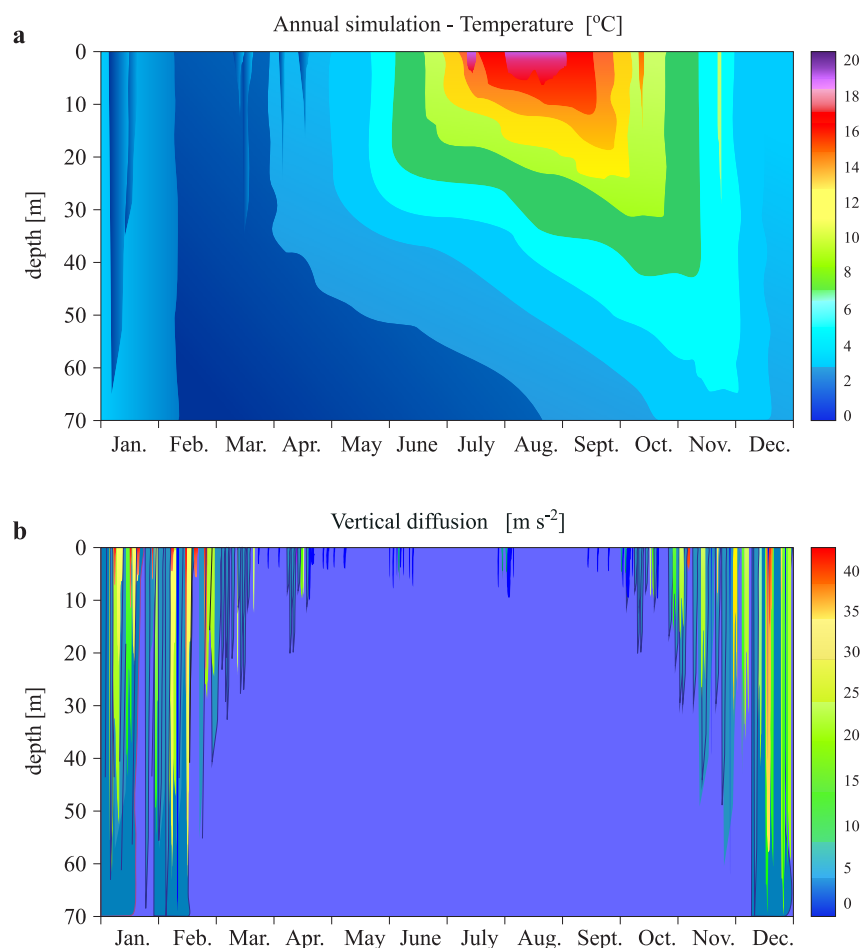


Figure 6. Model results for physical state variables (2007)

means of temperature and turbulent diffusion forcing data files (Figure 6). The correlation between physical forcing and the biological response of the main ecosystem state variables is shown in Figure 7.

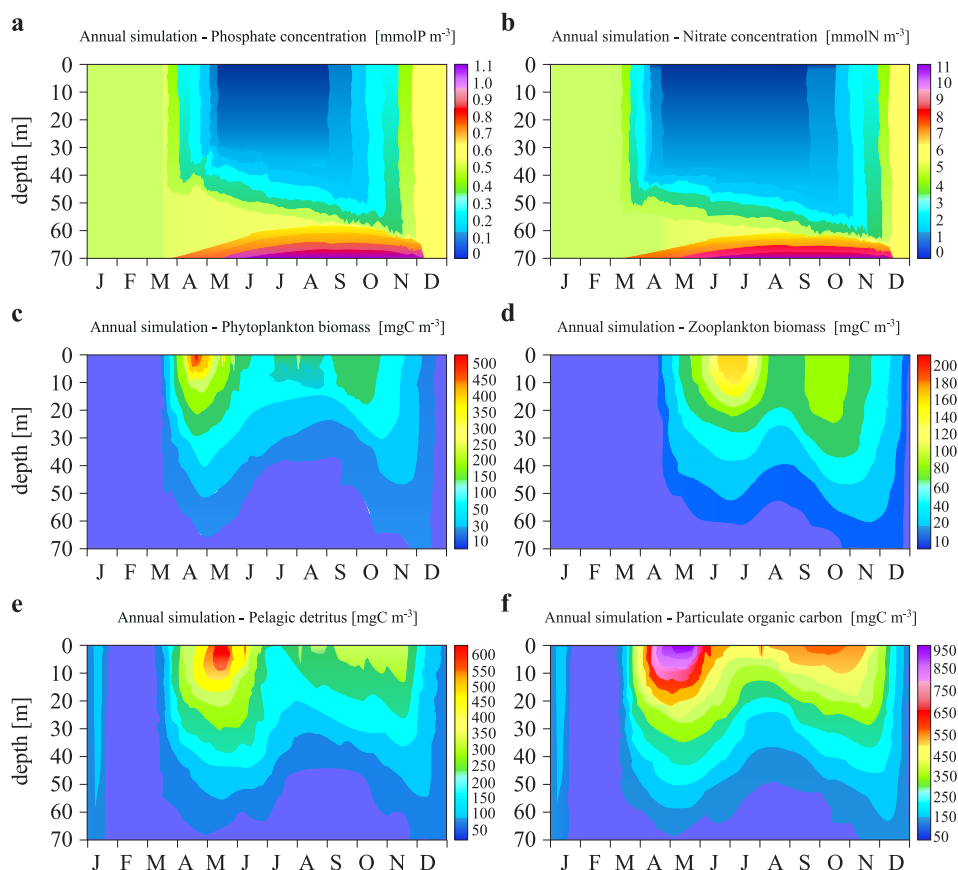


Figure 7. Model results for biological state variables (2007)

The modelled temperature fields resulting from the physical model (as the output) (Figure 6a) were used for calculating the biogeochemical processes. The simulated temperature began to increase in mid-March and reached ca 19°C in August. At the same time (March), vertical diffusion decreased (Figure 6b), which led to thermal stratification, causing a strong gradient within 30–40 m for most state variables. This stratification began to break up in the first half of October (day 283) with increasing vertical exchange, and by late autumn it was no longer in evidence. The upper layer depths determined by the mixing intensity in the water column are exemplified by the development of the strong nutrient concentration

gradients (Figures 7a and 7b). The spring bloom in 2007 most likely began in the first half of March, having been initiated by the warming up of the sea and the extremely light winds. The end of the intensive mixing of the water column in mid-March was the main reason why the phytoplankton started growing (Figure 7c). The phytoplankton biomass was a reflection of nutrient availability, showing a strong nutrient-depleting spring bloom. The phytoplankton biomass was the highest in the surface layers and reached a maximum in early April with a peak of 490 mgC m^{-3} . Correlated with the phytoplankton bloom, the nutrient depletion began to limit plankton growth. The phytoplankton biomass was low in summer (July and August), most likely as a result of nutrient deficiency and phytoplankton grazing by zooplankton.

The development of zooplankton was correlated exactly with temperature and followed the development of both phytoplankton and pelagic detritus. Generally, the largest numbers of zooplankton occurred in the upper layer, during the high-temperature period. Zooplankton started to increase in May, about six weeks after the beginning of the spring bloom. The zooplankton biomass was characterized by two peaks in the year – the main one in late June and early July (ca 160 mgC m^{-3}), and a smaller one in the second half of September (ca 100 mgC m^{-3}) (Figure 7d). Pelagic detritus (Figure 7e) was abundant mainly when the phytoplankton concentration exceeded 200 mgC m^{-3} , and its maximum concentration (ca 600 mgC m^{-3}) was in the near-surface layers. Detritus served as a zooplankton food source throughout the column during spring and autumn, sinking through it to replenish the bottom detritus pool. In early autumn a certain increase in phytoplankton biomass took place: this may have been related to the increase in nutrient concentration resulting from the deeper mixing of the water column. The growing season ended in December, when the phytoplankton biomass dropped to the starting level of January–February.

The simulation yielded the total concentration of POC as the sum of phytoplankton, zooplankton and pelagic detritus concentrations. The vertical profiles, presented in Figure 7f in the form of annual cycles, showed an increase in POC concentration (ca 870 mgC m^{-3}) due to the spring bloom, its decrease in response to the depletion of phytoplankton biomass and pelagic detritus, and the second peak in autumn. In the second half of the year, surface POC concentrations remained at the same average value (ca 490 mgC m^{-3}) until November.

3.1. Modelled vs. measured POC comparison

The simulated annual cycle of POC was compared to field observations, the available data referenced in the literature being merged from several sources. The results of the measured POC concentrations in the surface layer varied from $103 \pm 12 \text{ mgC m}^{-3}$ in winter 2007 to $1032 \pm 33 \text{ mgC m}^{-3}$ in the late spring of 2008 (Table 2, Figure 8). The measured POC concentrations were somewhat higher than the calculated ones, except the autumn data (Figure 8). However, the POC concentration – the sum of detritus, phytoplankton and zooplankton – may have fluctuated with high temporal and spatial resolution, which was demonstrated by the high variability of the measured phytoplankton and zooplankton biomasses (Figure 8). Despite the discrepancies between the observed and modelled

Table 2. Measured surface POC concentrations at station P1

Sampling year	Day of the year	POC [mg m^{-3}]	Reference
2007	31	103 ± 12	present study
2008	82	600 ± 39	present study
2007	85	423 ± 21	present study
2007	111	812 ± 24	present study
2008	137	1032 ± 33	present study
2007	143	873 ± 41	present study
2001	154	670*	Burska et al. 2005
2007	290	410 ± 19	present study

*mean surface POC concentration from 27 sampling data collected during 30.05.2001–06.06.2001 at station P1; min: 290 mg m^{-3} ; max: 1430 mg m^{-3} .

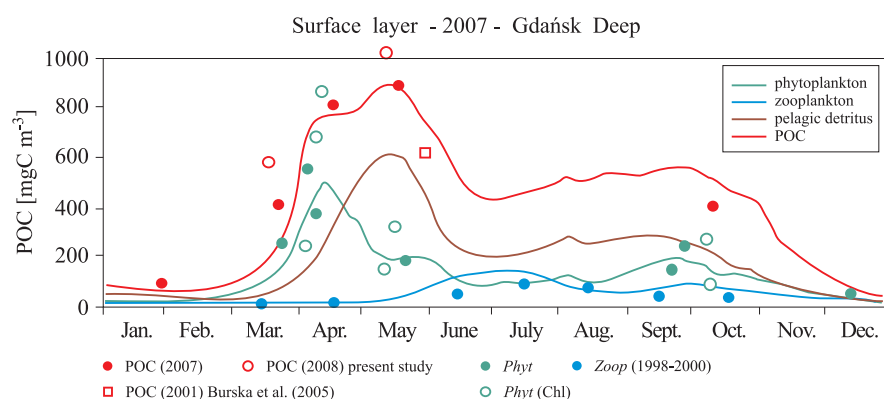


Figure 8. Modelled POC seasonality presented against the background of *Phyt*, *Zoop* and *DetrP* and in situ measured POC concentrations

biomass data of the POC components, the former were well reflected by the numerical simulations with respective correlation coefficients of 0.62 and 0.81 for phytoplankton and zooplankton in the upper 10 m layer (Figures 4, 8; see also Appendix D). Considerable fluctuations of POC concentrations were confirmed for the Gdańsk Deep, e.g. by Burska et al. (2005) (Table 2, Figure 8), who measured POC in 27 surface sea water samples taken at station P1 on 8 consecutive days in late spring 2001; the POC in these samples ranged from 290 to 1430 mgC m^{-3} . This is a further indication that the experimental approach to establishing temporal and spatial POC distributions must be based on prolonged and extended measuring programmes.

Experimental POC data collected in March 2008 suggest that the phytoplankton bloom started earlier in that year than in 2007. Such interannual shifts have been observed in the Baltic Sea (Voipio (ed.) 1981): they are a response to different temporary environmental conditions determining phytoplankton growth, i.e. nutrient availability, light and water temperature. On the other hand, the extremely high POC concentrations noted in May 2008 ($1032 \pm 33 \text{ mgC m}^{-3}$) indicated that phytoplankton activity was more intensive than in the same period in 2007.

Since the downward export of organic matter is an important POC sink, modelled and measured POC vertical distributions were compared (Figure 9). This was done for two crucial seasons – the end of April (2008) and late May/early June (2001) – when POC fluctuations are at their highest (Figure 8). In both cases there was a distinct decrease in

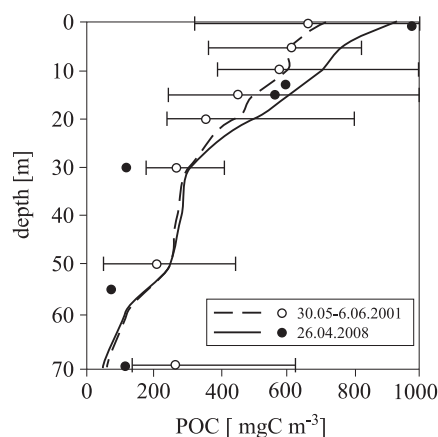


Figure 9. Observed (dots/circles) and modelled (solid/broken lines) POC vertical distributions on 26.04.2008 (present study) and 30.05.2001–06.06.2001 (Burska et al. 2005)

POC concentration from ca 950 mgC m⁻³ (April 2008) and 630 mgC m⁻³ (May/June 2001) in the upper layer to ca 50 mgC m⁻³ farther down in the water column. This is the result both of POC mineralization in the water column and of accelerated vertical sinking due to the aggregation of the organic matter particles. Comparison of vertical modelled and measured POC concentration profiles reveals satisfactory numerical reproducibility, especially in the upper water layers (0–25 m), but the deeper the water, the poorer the coincidence for both datasets. This is clearly manifested in the April 2008 profiles, where the differences were the greatest: these could be explained by time-shifts in the spring bloom development. The modelled data, unlike the measured POC, suggest a more advanced stage of the spring bloom, resulting in a more advanced downward export of biomass. There are also some discrepancies at 70 m depth. The underestimation of modelled POC concentrations in both calculations could be due to the accumulation of sinking detritus at the pycnocline caused by the water salinity gradient, which is not included in the model description.

4. Discussion

As a rule, mathematically simulated data are only an approximation of environmental processes. However, a properly validated model provides substantial knowledge as regards the spatial and temporal resolutions of processes, which is very difficult to obtain from in situ measurements.

The results indicate that the 1D POC Model could be a useful tool for investigating the current carbon cycle and predicting its changes. Some of the discrepancies observed could be the result of the dynamism of ecosystem changes. Model output is directly dependent on external forcing: since this is related to the average state of the ecosystem at a given instant, the variability of the modelled results also reflect average POC concentrations. It must be borne in mind, however, that experimental POC concentration data reflect only a temporary state, i.e. the one at the time of sampling. This was demonstrated by the experiment performed by Burska et al. (2005) (see Figure 9), who noted considerable hour-on-hour variations in POC at one station (P1) during sampling. Moreover, the lack of cyanobacteria as a separate phytoplankton group in the model could affect POC concentrations, especially during summer. However, this should be limited to temporary cyanobacteria bloom events. Another explanation of these discrepancies might be the absence of a contribution from bacteria at this stage of the model's development. Literature data suggest that up to 10–15% of the whole primary production could be attributed to bacteria biomass (Kuosa & Kivi 1989, Lignell 1990). However, the appropriate parameterization in the model of bacteria-governed processes

is difficult, because there is insufficient relevant literature data. Despite these limitations, however, comparison of measured and modelled POC concentrations suggests that the model is functioning properly.

Since only a few historical data sets of POC concentrations were available and temporal POC dynamics were high, it was difficult to assess whether there was any long-term trend in POC concentrations in the Baltic. Pempkowiak et al. (1984) measured POC concentrations of 690 mgC m^{-3} in the Gdańsk Deep in August 1983, a value some 40% higher than those measured in the same period in 2007. However, this was just a single concentration that may not have been representative of the area or of the season. Andersson & Rudehäll (1993) reported lower POC concentrations in all seasons (267, 231 and 166 mgC m^{-3} in spring, summer and autumn respectively) except winter (99 mgC m^{-3}), when both the calculated (this study) and reported data were comparable. However, the above investigations were carried out 15 years before ours in the central Bothnian Sea, a region where primary production is less than in the southern Baltic (Voipio (ed.) 1981, after Lassig et al. 1978).

Further activities with regard to POC modelling require both model validation and model improvement. Work aiming to improve model validation is in progress: this is focusing on both vertical resolution in the water column and spatial resolution in other Baltic Sea regions. Moreover, bacteria, another important factor influencing POC, should be taken into consideration in subsequent model improvements: this could eliminate the underestimation of POC in spring, when their biomass is the largest.

A well-tuned and properly functioning 1D POC Model will supply a substantial amount of information regarding the spatial and temporal variability of POC in the Baltic. This is particularly important, since POC is the decisive component in the processes responsible for the proper functioning of the ecosystem: vertical transport of chemical elements, biological pump functioning, eutrophication, bottom anoxia events, fisheries etc. However, one must remember that, depending on the season, POC constitutes from only ca 2% in winter to ca 25% during the spring bloom of the total organic carbon content in the water column (e.g. Pempkowiak et al. 1984, Ferrari et al. 1996, Grzybowski & Pempkowiak 2003, Kuliński & Pempkowiak 2008). Hence, extending the existing model of dissolved organic carbon concentration will provide significant information about the variability of the whole organic carbon content.

References

- Andersson A., Rudehäll Å., 1993, *Proportion of plankton biomass in particulate organic carbon in the northern Baltic Sea*, Mar. Ecol. Prog.-Ser., 95, 133–139.

- Billen G., Lancelot C., Maybeck M., 1991, *N, P and Si retention along the aquatic continuum from land to ocean*, [in:] *Ocean margin process in global change*, R. F. C. Mantoura, J. M. Martin & R. Wollast (eds.), Phys. Chem., Earth. Sci. Res., Rep. 9, 19–44.
- BMEPC – Baltic Marine Environment Protection Commission, 1983, *Guidelines for the Baltic monitoring programme for the second stage*, BSEP 12, Helsinki Commiss.
- Burska D., Pryputniewicz D., Falkowska L., 2005, *Stratification of particulate organic carbon and nitrogen in the Gdańsk Deep (southern Baltic Sea)*, *Oceanologia*, 47 (2), 201–217.
- Czyszek W., Wensierski W., Dera J., 1979, *Solar radiation energy inflow and absorption in Baltic water*, *Stud. Mater. Oceanol.*, 26, 105–140, (in Polish).
- Chester R., 2003, *Marine geochemistry*, 2nd edn., Blackwell Sci., London, 506 pp.
- De Haas H., van Weering T. C. E., de Stigter H., 2002, *Organic carbon in shelf seas: sink or sources, processes and products*, *Cont. Shelf Res.*, 22, 691–717.
- Doney S. C., Linsay K., Moore J. K., 2003, *Global ocean carbon cycle modeling*, [in:] *Ocean biogeochemistry*, M. J. R. Fasham (ed.), Springer-Verl., Berlin, Heidelberg, 217–238.
- Dzierzbicka-Głowacka L., 2005, *Modelling the seasonal dynamics of marine plankton in the southern Baltic Sea. Part 1. A Coupled Ecosystem Model*, *Oceanologia*, 47 (4), 591–619.
- Dzierzbicka-Głowacka L., 2006, *Modelling the seasonal dynamics of marine plankton in the southern Baltic Sea. Part 2. Numerical simulations*, *Oceanologia*, 48 (1), 41–71.
- Dzierzbicka-Głowacka L., Bielecka L., Mudrak S., *Seasonal dynamics of Pseudocalanus minutus elongatus and Acartia spp. in the southern Baltic Sea (Gdańsk Deep)*, *Biogeosciences*, 3 (4), 635–650.
- Eidler L. (ed.), 1979, *Recommendation on methods of marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll*, *Baltic Mar. Biol. Publ. No. 5*, 38 pp.
- Ferrari G. M., Dowell M. D., Grossi S., Targa C., 1996, *Relationship between the optical properties of chromophoric dissolved organic matter and total concentration of dissolved organic carbon in the southern Baltic Sea region*, *Mar. Chem.*, 55 (3–4), 299–316.
- Grasshoff K., Ehrhardt M., Kremling K. (eds.), 1983, *Methods of seawater analysis*, 2nd. edn., Verlag Chem., Weinheim, 419 pp.
- Grzybowski W., Pempkowiak J., 2003, *Preliminary results on low molecular weight organic substances dissolved in the waters of the Gulf of Gdańsk*, *Oceanologia*, 45 (4), 693–704.
- Haitzer M., Höss S., Traunspurger W., Steinberg C., 1999, *Relationship between concentration of dissolved organic matter (DOM) and the effect of DOM on the bioconcentration of benzo[a]pyrene*, *Aquat. Toxicol.*, 45 (2–3), 147–158.

- Hedges J. I., 2002, *Why dissolved organics matter*, [in:] *Biogeochemistry of marine dissolved organic matter*, D. A. Hansell & C. A. Carlson (eds.), Elsevier Sci., San Diego, 1–33.
- Jeffrey S. W., Humphrey G. F., 1975, *New spectrophotometric equations for determining chlorophylls a, b, c in higher plants, algae and natural phytoplankton*, *Biochem. Physiol. Pflanzen*, 1967, 191–194.
- Kuliński K., Pempkowiak J., 2008, *Dissolved organic carbon in the southern Baltic Sea: Quantification of factors affecting its distribution*, *Estuar. Coast. Shelf Sci.*, 78 (1), 38–44.
- Kuosa H., Kivi K., 1989, *Bacteria and heterotrophic flagellates in the pelagic carbon cycle in the northern Baltic Sea*, *Mar. Ecol. Prog.-Ser.*, 53, 93–100.
- Lassig J., Leppänen J.-M., Niemi Å., Tamelander G., 1978, *Phytoplankton primary production in the Gulf of Bothnia 1972–1975 as compared with other parts of the Baltic Sea*, *Finn. Mar. Res.*, 244, 101–115.
- Lignell R., 1990, *Excretion of organic carbon by phytoplankton: its relation to algal biomass, primary productivity and bacterial secondary productivity in the Baltic Sea*, *Mar. Ecol. Prog.-Ser.*, 68, 85–99.
- IMGW, 1996–1999, *Environmental conditions in the Polish zone of the southern Baltic Sea during 1995 (...1998)*, B. Cyberska, Z. Lauer & A. Trzosińska (eds.), *Mater. Oddz. Mor. Inst. Meteorol. Gosp. Wod.*, Gdynia, (in Polish with English summ.).
- IMGW, 2000, *Environmental conditions in the Polish zone of the southern Baltic Sea during 1999*, W. Krzyński, E. Łysiak-Pastuszek & M. Miętus (eds.), *Mater. Oddz. Mor. Inst. Meteorol. Gosp. Wod.*, Gdynia, 299 pp., (in Polish with English summ.).
- Mudrak S., 2004, *Short- and long-term variability of zooplankton in coastal Baltic waters: using the Gulf of Gdańsk as an example*, Ph.D. thesis, Gdańsk Univ., Gdynia, 328 pp. + Annex, (in Polish).
- Pempkowiak J., 1985, *The input of biochemically labile and resistant organic matter to the Baltic Sea from the Vistula River*, [in:] *Transport of carbon and minerals in major world rivers*, Pt. 3, E. T. Degens, S. Kempe & R. Herrera (eds.), *Mitt. Geol.-Paläont. Inst. Univ. Hamburg, SCOPE/UNEP Sonderbd.*, 58, 345–350.
- Pempkowiak J., Widrowski M., Kuliński W., 1984, *Dissolved organic carbon and particulate carbon in the southern Baltic in September, 1983*, *Proc. 14th Conf. Baltic Oceanogr.*, IMGW, Gdynia, 699–713.
- Rost B., Riebesell U., 2004, *Coccolithophores and the biological pump: responses to environmental changes*, [in:] *Coccolithophores: from molecular processes to global impact*, H. R. Thierstein & J. R. Young (eds.), Springer, Berlin, 99–125.
- Rozwadowska A., Isemer H.-J., 1998, *Solar radiation fluxes at the surface of the Baltic Proper. Part 1. Mean annual cycle and influencing factors*, *Oceanologia*, 40 (4), 307–330.
- Sabine C. L., Feely R. A., Gruber N., Key R. M., Lee K., Bullister J. L., Wanninkhof R., Wong C. S., Wallace D. W. R., Tilbrook B., Millero F. J., Peng T.-H., Kozyr

- A., Ono T., Rios A. F., 2004, *The oceanic sink for anthropogenic CO₂*, *Science*, 305 (5682), 367–371.
- Steele J. H., Henderson E. W., 1992, *The role of predation in plankton models*, *J. Plankton Res.*, 14 (1), 157–172.
- Thomas H., Bozec Y., de Baar H. J. W., Elkalay K., Frankignoulle M., Schiettecatte L.-S., Kattner G., Borges A. V., 2005, *The carbon budget of the North Sea*, *Biogeosciences*, 2 (1), 87–96.
- Thomas H., Bozec Y., Elkalay K., de Baar H. J. W., 2004, *Enhanced open ocean storage of CO₂ from shelf sea pumping*, *Science*, 304 (5673), 1005–1008.
- Turnewitsch R., Springer B. M., Kiriakoulakis K., Vilas J. C., Arístegui J., Wolff G., Peine F., Werk S., Graf G., Waniek J. J., 2007, *Determination of particulate organic carbon (POC) in seawater: the relative methodological importance of artificial gains and losses in two glass-fiber-based techniques*, *Mar. Chem.*, 105 (3–4), 208–228.
- Voipio A. (ed.), 1981, *The Baltic Sea*, Elsevier Sci., Amsterdam, 418 pp.
- Voss M., Emeis K.-C., Hille S., Neumann T., Dippner J. W., 2005, *Nitrogen cycle of the Baltic Sea from an isotopic perspective*, *Global Biogeochem. Cy.*, 19, GB3001, doi:10.1029/2004GB002338.
- Wangersky P. J., 1977, *The role of particulate matter in the productivity of surface waters*, *Helgol. Mar. Res.*, 30 (1), 546–564.
- Witek Z., 1995, *Biological production and its utilization within a marine ecosystem in the western Gdańsk basin*, *Sea Fish. Inst.*, Gdynia, 145 pp., (in Polish).
- Witek Z. (ed.), 1993, *Structure and function of marine ecosystem in Gdańsk Gulf on the basis of studies performed in 1987*, *Stud. Mater. Oceanol.*, 63 (Mar. Biol. 9), 5–125.

Appendix A

Parameterization of the POC model

F_S	Mathematical formula
primary production	$PRP = g_{Chl} f_{\max} f_{\min} F_I Phyt$
zooplankton grazing	$GRZ = GRP + GRD,$ $GRP = g_{\max} r s_P \times$ $\times \frac{Phyt^2}{k_g(p_P Phyt + p_d DetrP) + p_P Phyt^2 + p_d DetrP^2} Zoop,$ $GRD = g_{\max} r s_d \times$ $\times \frac{DetrP^2}{k_g(p_P Phyt + p_d DetrP) + p_P Phyt^2 + p_d DetrP^2} Zoop$
mortality of phytoplankton	$MORP = m_p Phyt$
excretion of phytoplankton	$EXCP = e_a PRP$
faecal pellets	$FEC = f GRZ$
excretion of zooplankton	$EXCZ = e_z GRZ$
mortality of zooplankton	$MORZ = m_z Zoop$
detrital decomposition	$DECP = m_{dec} \exp(c_{dec} T) DetrP$
predation by other zooplankton	$PRED = p_{\max} \frac{Zoop}{k_z + Zoop} Zoop$
predator mortality	$MORD = m_d PRED$
excretion by predator	$EXCD = (1 - m_d) PRED$
algal uptake	$UPT = g_{P/N} PRP$
benthic regeneration	$REGD = q_{P/N} r_b \exp(rtT) DetrB$

Appendix B

Functional responses in the biogeochemical sinks and sources of the ecosystem model

Functional response	
light limiting factor	$f_I = \frac{I_{PAR}}{I_{opt}} \exp\left(1 - \frac{I_{PAR}}{I_{opt}}\right)$
available light	$I_{PAR} = I_o \exp(-kz)$, $k = 0.17 + 25(g_{Chl}Phyt)$ g _{Chl} (gChl/gC) for the Gulf of Gdańsk*
optimal light for phytoplankton growth	$I_{opt} = 313.64 + 19.56T$ for the southern Baltic Sea
maximum phytoplankton growth	$f_{max} = 1.5865 \exp(0.075T)$ for the southern Baltic Sea
nutrient limiting factor	$f_N = \frac{Nutr_N}{K_N + Nutr_N}$, $f_P = \frac{Nutr_P}{K_P + Nutr_P}$
combined nutrient limiting factor	$f_{min} = \sqrt{f_N f_P}$
relative supply of phytoplankton	$r_{sP} = \frac{p_P Phyt}{p_P Phyt + p_d DetrP}$
relative supply of detritus	$r_{sd} = \frac{p_d DetrP}{p_P Phyt + p_d DetrP}$

* see Figure 10, after Witek (ed.) (1993).

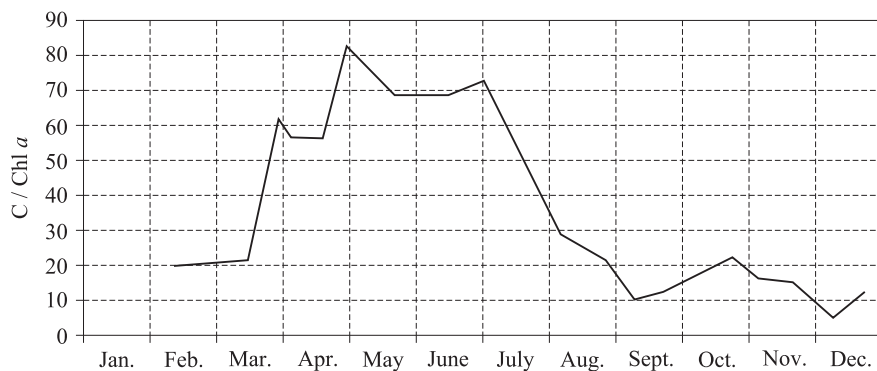


Figure 10. Carbon-to-chlorophyll *a* ratio in plankton at a station in the 0–15 m layer of the Gulf of Gdańsk (54°33.9'N; 18°40.8'E), 1987 (Witek (ed.) 1993). The experimental data determine the inflection points of the curve

Appendix C

Constants used in the model

Constant	Value	Unit	Designations/Comments
c_{dec}	0.15	$^{\circ}\text{C}^{-1}$	temperature coefficient for <i>DEC</i>
ea	0.26	–	percentage <i>PRP</i> , regenerated as phytoplankton excretion
ez	0.3	–	percentage ingestion, regenerated as zooplankton excretion
f	0.3	–	percentage ingestion, egested as zooplankton faecal production
g_{\max}	0.3	day^{-1}	maximum zooplankton grazing
g_{N}	0.0157	mmolN/mgC	N/C ratio in <i>Phyt</i>
g_{P}	0.000612	mmolP/mgC	P/C ratio in <i>Phyt</i>
k_g	50	mgC m^{-3}	half-saturation constant for zooplankton grazing
K_{N}	0.18	mmolN m^{-3}	nitrogen half-saturation constant
K_{P}	0.1	mmolP m^{-3}	phosphate half-saturation constant
k_z	1	mgC m^{-1}	half-saturation constant for carnivorous grazing
md	0.3	–	percentage predation, ending up as dead zooplankton predators
m_{dec}	0.002	day^{-1}	maximum decomposition rate of detritus
mp	0.05	day^{-1}	natural mortality rate of phytoplankton
mz	0.05	day^{-1}	natural mortality rate of zooplankton
p_d	0.25	–	zooplankton preference for detritus
p_{\max}	0.1	day^{-1}	maximum predation rate
p_p	0.75	–	zooplankton preference for phytoplankton
q_{N}	0.015	mmolN/mgC	N/C ratio in <i>DetrB</i>
q_{P}	0.00167	mmolP/mgC	P/C ratio in <i>DetrB</i>
rb	0.005	day^{-1}	maximum benthic mineralization rate
rt	0.005	$^{\circ}\text{C}^{-1}$	temperature coefficient for <i>REGD</i>
w_d	3	day^{-1}	pelagic detritus sinking
w_p	0.5	m day^{-1}	phytoplankton sinking

Appendix D

Analytical methods parameters used for comparison with model results

The physical, chemical and biological investigations were conducted following the guidelines for the HELCOM Baltic Monitoring Programme (COMBINE, <http://www.helcom.fi/ec.html>), including the quality assurance requirements and the methods recommended in the HELCOM MORS and EMEP programmes.

The data on inorganic nitrogen and phosphate contents were obtained from the Marine Branch of the Institute of Meteorology and Water Management in Gdynia (IMGW 1996–1999, 2000). The measurements were made using the spectrophotometric methods of Morris & Riley (nitrate), Bendschneider & Robinson (nitrite), Murphy & Riley (phosphate), and the indophenol method (ammonia) (Grasshoff et al. (ed.) 1983) on board the vessel during research cruises.

The samples (chlorophyll and phytoplankton) collected in 1995–1998 from discrete depths were pooled by mixing water portions from the following depths: 0, 5, 10 and 15 m; 15, 20, 25 and 30 m. Since 1999, however, samples have been collected from only two depths – 0–10 m and 10–20 m – using a PCV hose from on board ship. The chlorophyll concentration was measured spectrophotometrically (Edler (ed.) 1979, BMEPC 1983), and Whatman GF/F filters were used to remove suspended matter. The entire chlorophyll concentration was measured and, separately, the concentration of the fraction remaining in the water after filtration through 25 μm mesh gauze. Extraction of chlorophyll was carried out at room temperature with a 90% aqueous solution of acetone. The calculations were done according to the formulae of Jeffrey & Humphrey (1975). Samples for phytoplankton were preserved with Lugol's solution and analysed under an inverted microscope.

The mesozooplankton material was collected monthly at eight stations in the western part of the Gulf of Gdańsk from July 1998 until September 2000. Because the samples for some months were missing (for meteorological or technical reasons), the data for the whole year was pooled (September 1999–August 2000) in order to examine the seasonal variability of mesozooplankton in this area (Mudrak 2004). In addition, mesozooplankton material was collected from 20 to 25 May 1999 in diurnal cycles from station P1 (Gdańsk Deep) in order to investigate the short-term variability of this material in the water column (Mudrak 2004). Hauls were made using a closing Copenhagen net (50 cm diameter, 100 μm mesh size) from the water column, which was divided into several layers. The biological material

collected was preserved in 4% formaldehyde, and every single sample was prepared and analysed according to HELCOM standard methods in the laboratory (www.helcom.fi).

Figure 8 shows the results of numerical simulations (blue line) and observed data (blue dots) for the total mesozooplankton biomass (in mgC m^{-3}) in the Gulf of Gdańsk as monthly averages in the upper 10 m layer.