

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

**Population modelling
of *Acartia* spp.**

L. Dzierzbicka-Glowacka
et al.

Population modelling of *Acartia* spp. in a water column ecosystem model for the Southern Baltic Sea

L. Dzierzbicka-Glowacka¹, I. M. Żmijewska², S. Mudrak², J. Jakacki¹, and
A. Lemieszek²

¹Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland

²Institute of Oceanography, University of Gdańsk, Gdynia, Poland

Received: 9 November 2009 – Accepted: 9 December 2009 – Published: 5 January 2010

Correspondence to: L. Dzierzbicka-Glowacka (dzierzb@iopan.gda.pl)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

This paper describes numerical simulations of the seasonal dynamics of *Acartia* spp. in the Southern Baltic Sea. The studies were carried out using a structured zooplankton population model adapted to *Acartia* spp. The population model with state variables for eggs, nauplii, five copepodites stages and adults was coupled with a marine ecosystem model. Four state variables for the carbon cycle represent the functional units of phytoplankton, pelagic detritus, benthic detritus, and bulk zooplankton, which represent all zooplankton other than the structured population. The annual cycle simulated for 2000 under realistic weather and hydrographic conditions was studied with the coupled ecosystem–zooplankton model applied to a water column in the Gdańsk Gulf (Southern Baltic Sea). The vertical profiles of selected state variables were compared to the physical forcing to study differences between bulk and structured zooplankton biomass. The simulated population dynamics of *Acartia* spp. and zooplankton as one biomass state variable were compared with observations in the Gdańsk Gulf. Simulated generation times are more affected by temperature than food conditions except during the spring phytoplankton bloom. The numerical studies are a following step in understanding how the population dynamics of a dominant species in the Southern Baltic Sea interact with the environment.

1 Introduction

Copepods are generally considered the most important component in the marine pelagic ecosystem being grazers on phytoplankton and other protists, and prey for animals at higher trophic levels (Mauchline, 1998). Feeding studies of fish larvae by Last (1980) and Wiktor (1990) have shown that *Pseudocalanus*, *Acartia* and *Temora* nauplius and copepodid stages are important components of the diet of numerous species of fish (sprat and herring) in the Baltic Sea and adjacent waters, i.e. the North Sea and also the English Channel, as well as in Scotland, Nova Scotia and Canadian

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Arctic waters. Our knowledge of their life parameters (e.g. development time, growth rate, and egg production) provides fundamental information on the energy and matter transformation in pelagic food webs. These organisms play a dominant role in marine food webs and biogeochemical cycles.

5 Most models take into account only nutrients and phytoplankton (Fransz et al., 1991), probably because of the difficulty in representing the complex behaviour that exists among zooplankton species and also among the different zooplankton development stages. Models having one compartment for the whole zooplankton community are useful only for simulating ecosystem dynamics over the course of a few days (Wroblewski and Richman, 1987) or for a stable environment, but become meaningless for
10 long periods if the environment fluctuates. Although field workers consider population dynamics to be the minimum level of study, zooplankton population models are rarely included in ecosystem models. A study of copepod population dynamics was performed, for instance, by Francois Carlotti and several co-workers, who have worked
15 along the same lines, i.e. in the papers by Carlotti and Sciandra (1989), Carlotti and Nival (1992), Carlotti and Radach (1996) and Carlotti and Wolf (1998). These present a population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida), coupling individual growth and development, as well as of *Calanus finmarchicus* based on Lagrangian particles coupled with a 1-D ecosystem model. This type of study was
20 carried out for *Pseudocalanus* spp. by Fennel (2001), Dzierzbicka-Glowacka (2004, 2005a,b), Stegert et al. (2007), Moll and Stegert (2007). A similar study for *Acartia* spp. is presented in this paper.

25 The copepod model for *Acartia* spp. was calibrated by Dzierzbicka-Glowacka et al. (2009a,b) under the environmental conditions typical of the Southern Baltic Sea. The idea of establishing the combined effect of temperature and food concentration on the development and growth of the naupliar stage and copepodid stages (C1, C2, C3, C4, C5, C6) of *Acartia* spp. was presented. In this study the development time of copepods *Acartia* spp. in the changing environmental conditions in the Southern Baltic Sea also was modeled. It is important to investigate and identify the critical factors in

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



mathematical models of pelagic communities with a high-resolution zooplankton (herbivorous copepods) module as a top-down regulator which may play a significant role in marine ecosystems. The aim of this paper is to run the population model within an ecosystem model to study the impact of seasonal variations of food and temperature on *Acartia* spp. biomass in the Southern Baltic Sea.

Numerical experiments were executed as part of the grant supported by Polish State Committee of Scientific Research.

2 Southern Baltic Sea water column

The location of interest is a water column in the Southern Baltic Sea close to the P1 station in the open sea, 110 m water depth, 100 km from the shore, which is located in the middle of Gdańsk Deep (54°50' N 19°17' E; Fig. 1). At this depth the water column is characterized by permanent stratification. The halocline, which separates the surface water layer of 7.2 PSU salinity from the deep water layer of 11 PSU, is located at a depth of 60–80 m (Voipio, 1981). At deep-water station P1, the isotherm reached its maximum depth in February and March – down to 70 m. In the latter case the isotherm remained until the beginning of May. In April the thermocline began to form; it gradually reached increasingly greater temperature differences and greater depths until the end of July. The layer of colder waters, so called winter water or minimum temperature layer, occurred from February until the end of the year, at a depth of about 50–70 m. The temperature of these waters increased with time from about 0.5 to almost 4 °C, with the range extending both up- and downwards. Near-bottom waters of the Gdańsk Deep became gradually colder, from 6 °C at the beginning of the year to about 4 °C at the end. All mathematical simulations were performed for conditions characteristic of the P1 station.

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2.1 The ecosystem model structure

Recently, Dzierzbicka-Glowacka (2005b, 2006) developed a one-dimensional, ecosystem, upper layer model: 1-D CEM Coupled Ecosystem Model. This ecosystem model supplemented with the population dynamics submodel for copepods and a component for pelagic detritus was used to study the dynamics of *Pseudocalanus minutus elongates* in the Southern Baltic Sea (Dzierzbicka-Glowacka, 2005a,b). The 1-D CEM model reduced to a 1-D POC Particulate Organic Carbon Model with an equation for dead organic matter (pelagic detritus) is presented in Dzierzbicka-Gowacka et al. (2009c). The 1-D POC model is an ecosystem model able to simulate biogeochemical processes in the physical environment. The particulate organic carbon (POC) concentration was determined as the sum of phytoplankton and zooplankton biomasses and pelagic detritus concentrations.

The marine ecosystem model consists of a set of equations. These are all of the general form, i.e. equations of the diffusion type including the functions of gains and losses, expressing change in the pelagic variables. The temporal changes in the phytoplankton biomass are caused by primary production, excretion, mortality, grazing by zooplankton and sinking. The zooplankton biomass is affected by ingestion, excretion, faecal production, mortality, and carnivorous grazing. The changes in the pelagic detritus concentration are determined by input of: dead phytoplankton and zooplankton, natural mortality of predators, faecal pellets, and sinks: sedimentation, zooplankton grazing and decomposition. In this model nutrients are represented by two components: total inorganic nitrogen ($\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) and phosphate (PO_4^{3-}). Silica is not included, as it is not a critical parameter for the primary production, yet. In this paper bacteria were not explicitly simulated. Their activity only appeared implicitly in the parameterizations of the remineralization terms. Benthic detritus accumulated by sinking out of the water column, it was regenerated by bacterial action, and the resulting nutrients move upwards by turbulent diffusion. Bacteria will be considered in our next studies in which the dissolved organic carbon DOC will be modeled.

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The different sinks and sources for 1-D POC model are put together in Table 1 in Dzierzbicka-Gowacka et al. (2009c), while the mathematical formulation for biogeochemical processes in the model is presented in Appendices A–C in Dzierzbicka-Glowacka et al. (2009c) and Dzierzbicka-Glowacka (2005b). Results obtained by Dzierzbicka-Glowacka et al. (2009c) indicated that the 1-D POC model might be a useful tool for actual carbon cycle investigations and prediction of its changes. Comparison of measured and modeled POC (POC=Phyt+Zoop+DetrP) concentrations suggested appropriate functioning of the model (Fig. 2).

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

2.2 Copepod model for *Acartia* spp.

The copepod model (Dzierzbicka-Glowacka, 2009a) includes here the rate of transfer from stage i to the next ($i+1$). It consists of sixteen state variables with masses W_i and numbers Z_i for each of eight model stage, grouping stages to: the non feeding stages and eggs are represented by the stage – eggs-N2, following are the naupliar stages – N3–N6, then five copepodite stages – C1, C2, C3, C4, C5 and finally the adult stage – C6. For the each of eight model stage, mass W_i and number Z_i were calculated.

The changes in the stage-specific mean biomass, which is the algebraic sum of the products of the masses, W_i , and numbers, Z_i , of *Acartia* spp. for each of the model stages, are controlled by ingestion, egestion, metabolism, mortality, predation

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and transfer. Both processes, ingestion and transfer, depend on individual weights in successive stages using critical moulting masses, C_m , as described by Carlotti and Sciandra (1989). In this paper, the critical moulting mass is obtained by: $C_m = (C_k + \sqrt{2}C_r) / (1 + \sqrt{2})$, assuming that the half saturation value is equal $C_h = 2C_m - C_r$ (Moll and Stegert, 2007), which ensures that ingestion is not reduced before transfer starts and that the function $f m_i$ describing the limitation of ingestion rate as molting weight is $f m_i(C_h) = 0.5$ (Fig. 3b). The transfer rate TRN_i from stage i to the next $i+1$ is given by a sigmoidal function depending on the W_i and C_m with a reference weight, C_r , as a threshold mass, below which no transfer takes place and $TRN_i(C_m) = 0.5$ (Fig. 3b). This was not included in previous versions of the model (Dzierzbicka-Glowacka, 2005; Dzierzbicka-Glowacka et al., 2009a). The reference C_r and critical C_k masses are defined for each stage. The values of C_r and C_k derived from literature data (Ciszewski and Witek, 1977), were used for the weight-dependent function of ingestion.

The ingestion rate ING_i for specific developmental stages is dependent firstly on the maximum ingestion rate, secondly on available food $Food_j$ (Fig. 3a), thirdly on temperature T , following a constant Q_{10} (2.6) law (Fig. 3a) applicable to the temperature range of 5–18°C and fourthly on individual weight using C_m by the function $f m_i$ (Fig. 3b). Q_{10} was used to estimate the t_2 coefficient; consequently, the parameter t_2 had a value of 1.1. Coefficient t_1 was calculated so that $f t_e$ was equal to 1 at 15°C and, therefore, t_1 was equal to 0.239. Coefficients t_1 and t_2 were identical for all stages. Additionally, a parabolic threshold function $f t_2$ (with $T_0 = 18^\circ\text{C}$, $t_3 = 0.6$ and $K_1 = 1.3$) realizes a decrease at higher temperatures as a result of physiological depression. So, growth follows an exponential curve up to the optimal temperature of $\sim 18^\circ\text{C}$ and decreases for higher temperatures. Moulting to the next stage occurs when the critical moulting weight has been reached. During the molting process a small proportion of the weight is lost (Carlotti and Wolf, 1998). The food concentration $Food_j$ (equaling $\rho_{\text{Phyt}} = 60\%$ of phytoplankton biomass, $\rho_{\text{Zoop}} = 15\%$ of microzooplankton biomass and $\rho_{\text{DetrP}} = 25\%$ of

pelagic detritus concentration) for each stage i in this study is included:

$$ING_i = \sum_{j=1}^3 ING_{i,j} f m_j W_j \rho_j \quad (1)$$

with $ING_{i,j} = f_{\max,i} \left\{ 1 - \exp\left(\frac{-(Food_j - Food_o)}{k_{Food}}\right) \right\}$ and $\sum \rho_j = 1$.

The ingested food is portioned into growth and metabolic losses of respiration, excretion, and egestion and additionally for the population in moulting and reproduction.

The assimilation rate of 70% is generally considered as representative for copepods; hence the percentage of ingestion egested as fecal material, which immediately enter the detritus pool is 30%. Nauplii N1 and N2, which do not feed, are assumed to consume 20% of their weight per day for basic metabolism. For nauplii from N3 to N6, copepodites and adults, were assigned a minimum respiration rate of 4% of their weight per day, to which was added a respiration rate equal to 30% of the ingestion rate for active metabolism (see Dzierzbicka-Glowacka et al., 2009a). The ingestion rate decreases as weight reaches the critical weight of molt, because growth is limited by the exoskeleton. Here, it is assumed that the ingestion in one stage follows a negative parabolic function $f m_j$ when the weight exceeds the critical molting weight of stage i . Such a limitation does not occur in adults for which reproduction limits weight increase (see Carlotti and Sciandra, 1989).

In this study, the hypothesis that the food-saturated rate of production of egg matter is equivalent to the maximal specific growth rate of copepods was used for calculation of the number of eggs produced by each female during one day (Sekiguchi et al., 1980; McLaren and Leonard, 1995). The egg production rate was obtained as a function of growth rate, i.e. by multiplying $\exp GROWTH - 1$ by $W_{\text{female}}/W_{\text{egg}}$, assuming the growth rate to be that of the naupliar stage (Dzierzbicka-Glowacka et al., 2009b) and including here a transfer from adults to eggs. The number of juveniles is defined on the assumption that eggs are released by the adult female throughout some time span, J . The period of egg production for females of *Acartia bifilosa* from the Southern Baltic Sea

**Population modelling
of *Acartia* spp.**

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



varied with temperature from about 14 d at 20 °C up to about 1 month at 7 °C (Ciszewski and Witek, 1977). The efficiency term, X (=50%), was the conversion of biomass increase by the adult population into eggs, including the wasted growth in males. In this study the weight of an egg W_{egg} was taken to be 0.0305 $\mu\text{g C egg}^{-1}$ for *Acartia* (Ambler, 1985).

3 Results

This model described above was used in the numerical simulations of the seasonal dynamics of *Acartia* spp. in the Southern Baltic Sea (Gdańsk Deep). The simulation was carried out for 2000, when observations from several months including winter values, were available. The correlation of physical forcing and biological response of the main ecosystem state variables is shown in Fig. 4a and b.

Modeled temperature fields resulting from the physical model (as the output) (Fig. 4a) were used for the biogeochemical processes calculation. The simulated temperature began to increase at the end of March after day 88 and reached $\sim 18^\circ\text{C}$ in August. At the same time (March), vertical diffusion decreased (Fig. 4a). This led to thermal stratification, causing a high gradient within 30–40 m for most state variables. This stratification broke in September/October (day 273) with increasing vertical exchange. The destruction of the thermocline started in the late autumn. The depths of the upper layer, which were determined by the mixing intensity in the water column, showed that strong gradients in the nutrient concentration develop (Fig. 4b). The spring bloom in 2000 was triggered in mid-March, most likely. The bloom was initiated by the heating event and the extremely low winds. The end of permanent overturning of the water column in mid-March was the main cause that allowed the phytoplankton to start growing. The phytoplankton biomass reflected the nutrient availability, showing a strong nutrient-depleting spring bloom. The phytoplankton biomass was the highest in the surface layers and reached maximum in mid-April (day 101) with a peak of 450 mg C m^{-3} . Correlated with the phytoplankton bloom, nutrient depletion began and limited plankton

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



growth. The phytoplankton biomass was low in summer (July and August) most likely as a result of faster depletion of nutrients and the phytoplankton grazing by zooplankton.

The development of zooplankton followed the development of both phytoplankton and pelagic detritus. The start of the zooplankton increase took place in May, about six weeks after the beginning of the spring bloom. Biomass of zooplankton was characterized by the occurrence of two biomass peaks in a year, the main one – at the turn of June and July (ca. 160 mg C m^{-3}), and a smaller one, in August/September (ca. 100 mg C m^{-3}), (Fig. 4d). Pelagic detritus (Fig. 4e) was abundant mainly when the phytoplankton concentration exceeded 200 mg C m^{-3} , and its maximum concentration (ca. 590 mg C m^{-3}) was in the near surface layers. Detritus served as a zooplankton food source within the whole column during spring and autumn and was sinking through the water column supplying material to the bottom detritus pool. In early autumn a certain increase in phytoplankton biomass took place. It might have been related to an increase in the concentration of nutrients resulting from deeper mixing of the water column. The vegetation season ended in December, when the biomass of phytoplankton dropped to the starting level from January–February.

3.1 *Acartia* spp.

The vertical distributions shown in Fig. 5 demonstrate the annual biomass profiles for the selected state variables representing *Acartia* spp. stage dynamics. The four state variables for eggs: N2, naupliar stage, N3–N6, copepodite stage, C1–C5 (including five copepodite stages together) and finally the adult stage, C6 are presented. First, eggs occurred at the end of March according to the phytoplankton spring bloom and increasing temperature. In the present study, the embryonic duration D_e is estimated after Norrbin (1996) for *A. longiremis* which is similar to D_e of *A. clausi* (McLaren, 1978). Hence, the parameters of Bělehrádek's function a and α_e were determined as $a=1008$ and $\alpha_e=-8.701$, where a is a population specific constant, and α_e is related to the normal temperature regime for the species.

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Several generation peaks within the stage biomass variables can be observed during the development period of *Acartia* spp. throughout the year. The development assembles in the column water – mainly in the euphotic layer, where food – a mixture of phytoplankton, microzooplankton and small pelagic detritus – is available but also extends beyond the thermocline due to ingestion of dead organic matter. The highest proportion of all the developmental stages is found above the thermocline. In June a thermocline developed at a depth of 30 m; the temperature in the surface layer increased from 13 °C in June to 17 °C in July and 18.5 °C in August, before cooling started. In November the thermocline was destroyed. During the same time, most of the total biomass of *Acartia* spp. as the sum over four state variables, non-feeding, naupliar, copepodite and adult stages, is observed.

Figure 6 presents the simulated stage biomasses, which are the algebraic sum of the products of the weights, W_i , and numbers, Z_i , of each stage, as vertical mean values and also the number of *Acartia* spp. generations in the Southern Baltic Sea (Gdańsk Deep) is illustrated. The simulation starts with over wintering copepodites C4 and C5 and adults. The small maxima occurring in the distribution of the eggs-N2 stage are the result of a brood by successive females causing their numbers to increase. The strong increase in an available food concentration – mainly of phytoplankton biomass, in the spring bloom begins egg production. The hatching time at 4–6 °C is 20 d. Five complete distinct generations, from eggs to adults, developed throughout the year, the first beginning in mid-March. The stage duration for the first generation is 65 d. The development time of all the model stages was obtained by Eq. (4) given in Dzierzbicka-Glowacka et al. (2009a). During development of the second generation (51 d), surface temperature increases from 8 to 15 °C causing accelerated growth, while a drop in food concentration causes a retard. The third generation starts in the first half of July (day 191) and takes 47 d to complete as a result of the low food concentration (ca. 70 mg C m⁻³ in the upper 20 m layer) and the high surface temperature (15–18.5 °C). The total development time for the next generation is the shortest and assumes the value of 45 d similar to that of the third generation. During the fourth generation, tem-

**Population modelling
of *Acartia* spp.**L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



perature is lower, with a mean of ca. 2.5°C, than during the previous generation but the food supply concentration is higher, mean value of Food=120 mg C m⁻³ in the 50 m water column. This is equal to the surface value as a result of vertical mixing. Individuals of the fifth generation (day 283) are produced in the first half of October and reach adulthood at the end of the numerical simulation when there is a lack of food and a decrease in temperature.

The distribution shown in Fig. 6b presents the vertical mean total biomass, which is the algebraic sum of the vertical mean biomasses of all stages.

The total biomass of *Acartia* spp. is characterized by one main biomass peak at the end of August, and two smaller peaks. The first is slightly smaller, occurring during in the first half of July and the second small peak occurs in mid-October. The peak of biomass in August (ca. 15 mg C m⁻³) is mainly due to the high biomass of copepodites and adults of the third generation and the high egg production as a result of the very high numbers of adults of the previous generation. The high reproduction is a result of high temperature at this time. The smaller peaks of biomass (ca. 11 mg C m⁻³ and 5 mg C m⁻³, respectively) also are mainly due to the high biomass of copepodites and adults of the 2nd and 4th generations and the high egg production of the 1st and 3rd generations, respectively. However, the nauplii biomass of successive generations influence the peaks of the total biomass at the beginning of the growth.

The phytoplankton peak in September–October permits a new growth period for the 4th generation and females of this generation produce relatively small eggs to give a 5th generation in October–November.

4 Discussion

The Baltic zooplankton are composed of microzooplankton, mezozooplankton and macroplankton with characteristic ichthyoplankton forms. The dominant group of the Baltic zooplankton is made up of Copepoda, whose abundance may seasonally exceed even 80% of all zooplankters, but the next groups in a quantitative respect are Rotatoria

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and Cladocera. Among Copepoda the dominants are *Acartia bifilosa*, *Acartia tonsa*, *Temora longicornis* and *Pseudocalanus minutus elongatus* (Chojnacki and Antonczak, 2008). Cladocera are usually dominated by marine forms: *Podon polyphemoides*, *Bosmina coregoni maritime*, *Evadne nordmanni*, and out of fresh water species, found in the neritic zone and in estuaries: *Daphnia* spp. *Chydorus sphaericus*, *Bosmina coregoni*, *Bosmina longirostris*. Rotatoria are represented by the following genera: *Keratella*, *Brachionus* and *Synchaeta* (Wiktor and Żmijewska, 1985). Shallow coastal waters, particularly in sheltered bays and near river mouths, fertilized by the influence of rivers and organic pollutants entering the sea, are the areas richest in zooplankton in the Southern Baltic Sea (Chojnacki and Antonczak, 2008).

The most important species in the Gdańsk Gulf are copepoda: *Acartia* spp. (i.e. *A. bifilosa*, *A. longiremis* and *A. tonsa*), *Temora longicornis*, *Pseudocalanus minutus elongatus* and *Centropages hamatus* and cladocera: *Bosmina coregoni maritime* and *Podon polyphemoides*. Copepoda dominates numerically, while in the warm season Cladocera are subdominants. *P. m. elongatus* occurs in great abundance in the Gdańsk Deep, becomes dominant below 30 m, and is almost the only representative of mesozooplankton below the isohaline layer. In 1999 at the Gdańsk Deep, the predominant species were *Pseudocalanus minutus elongatus* and *Acartia longiremis* (see Maritime Branch Materials, IMGW 2000).

The structure of mezozooplankton in the Gdańsk Gulf in 2000 mainly consisted of four taxa: copepoda, cladocera, rotatoria and meroplankton; but in summer, biomass of cladocera was three times as high as copepod biomass (Mudrak, 2004). The predominant species were *Acartia bifilosa* during the entire year and *Bosmina coregoni maritime* in summer (Mudrak, 2004).

The results of the numerical simulations described here are compared to the mean monthly observed values (Fig. 7), assuming an organic carbon content of copepods $g\ C/g_{w.w.} = 0.064$ (Vinogradov and Shushkina, 1987).

The plankton material was collected monthly at eight stations in the Gdańsk Gulf during September 1999–August 2000, in three successive summer seasons of 1998,

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Population modelling
of *Acartia* spp.**L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



1999 and 2000 and during 20–25 May 1999 in diurnal cycles from the water column, which was divided into several layers. The hauls were made using a Copenhagen net (100 μm). Every single sample was prepared and analyzed according to standard methods (HELCOM). Numbers and biomass (in $\text{mg}_{w.w.} \text{m}^{-3}$) for selected species are given by Mudrak (2004). During May 1999 in the Gdańsk Deep, the vertical distributions of observed biomass in diurnal cycles were different, i.e. 0.02–1 mg C m^{-3} in the upper layer and 0.03–0.55 mg C m^{-3} in the lower layer for *Acartia* spp. The average value of the biomass in the whole column water at this time was 0.395 mg C m^{-3} for *Acartia* spp.

10 The monthly averages of *Acartia* spp. biomass (in $\text{mg}_{w.w.} \text{m}^{-3}$) in the summer season (July, August, September) in 1998, 1999 and 2000 from the eight stations in the Gdańsk Gulf (see Fig. 7) are given in Table 1. Analysis of the data set and in Mudrak (2004) showed that mesozooplankton concentration varied characteristically, being dependent on abiotic indicators of the environment.

15 The summer of 1999 was exceptionally sunny and sweltering. July was warmest month and the monthly average of water temperature in the Gdańsk Gulf exceeded 20 °C and was about 2–3 °C higher than the long-term mean value. However, in 2000, August was the warmest month and water temperature was similar to the long-term mean value. Temperatures at the stations (P1, J23) in the open sea were similar to those at So3, So2 and G2 inside the bay. At the end of summer, a decrease in water temperature was faster in the coastal region than in the open sea and in mid-October a sudden cooling of the western coastal water was caused by upwelling, which was still apparent at the end of November.

25 In 2000 at the all stations, biomass of *Acartia* spp. was relatively high. The highest values occurred in August at J23 (ca. 450 $\text{mg}_{w.w.} \text{m}^{-3}$), G1 (ca. 400 $\text{mg}_{w.w.} \text{m}^{-3}$) and G2 (ca. 380 $\text{mg}_{w.w.} \text{m}^{-3}$), whereas in 1999, the highest biomass occurred in July at the all stations, i.e. at So4 (ca. 270 $\text{mg}_{w.w.} \text{m}^{-3}$) and G1 (ca. 300 $\text{mg}_{w.w.} \text{m}^{-3}$). However, in 1998 at the all stations, biomass of *Acartia* spp. was relatively low. The highest values were noted in July at So1 (ca. 65 $\text{mg}_{w.w.} \text{m}^{-3}$), August at J23 (ca. 80 $\text{mg}_{w.w.} \text{m}^{-3}$) and

in September at So_2 (ca. $70 \text{ mg}_{w.w.} \text{ m}^{-3}$) – see Fig. 7 (biomass in mg C m^{-3}). At the stagnation time, biomass of *Acartia* spp. was from 1–3 $\text{mg}_{w.w.} \text{ m}^{-3}$ in February, 3–5 $\text{mg}_{w.w.} \text{ m}^{-3}$ in March to 4–6 $\text{mg}_{w.w.} \text{ m}^{-3}$ in November.

Figure 7 shows the results of numerical simulations and observed data for three successive regions of Gdańsk Gulf for total biomass of *Acartia* spp. (in mg C m^{-3}) as monthly averages in the upper 20 m layer. The highest biomass of *Acartia* spp. was ca. 40 mg C m^{-3} in mid-August. In the all months, the mean observed values are lower than mean obtained by the model; however, in August in 2000, the experimental data are most similar to the mean numerical results.

The simulation provided the development of four zooplankton model stages (Fig. 5) and additionally the total biomass as summed over all stages. The total biomass of *Acartia* spp. is compared to the total zooplankton biomass, which was modeled using the bulk formation.

The simulations show the general variations in investigated populations with time (Fig. 4b). The results show significant changes in phytoplankton biomass distribution, which took place in an area where there was a considerable increase in primary production. During the spring bloom, there is a substantial growth in phytoplankton biomass and then in pelagic detritus concentration, which thereafter fall as a result of the increase in zooplankton (Fig. 4b) and *Acartia* spp. (Fig. 5) biomasses. The growth of the total zooplankton biomass mostly depend on food. Generally speaking, the numbers of zooplankton in the upper layer are the highest, when the algal biomass and pelagic detritus concentrations there are large.

However, the later increase in *Acartia* spp. is caused by the increase in biomass of successive stages. This situation led to the substantial growth in the total biomass of *Acartia* spp. which is the algebraic sum of the products of weights W_i and numbers Z_j for modeled stages ($Z_{Acartia} = \sum_{i=\text{stages}} W_i Z_i$). These small maxima occurring in the distribution $Z_{Acartia}$ are the result mainly of egg production by each adult causing their numbers Z_j to increase.

**Population modelling
of *Acartia* spp.**L. Dzierzbicka-Glowacka
et al.[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

**Population modelling
of *Acartia* spp.**L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The influence of temperature and food concentration on the development of each of the model stages is similar, as described in Dzierzbicka-Glowacka et al. (2009). The annual cycle of the total biomass of *Acartia* spp. is the result of the above-mentioned parameters, but mainly due to temperature changes. The highest values of *Acartia* spp. biomass occur in the period of high temperatures, in summer, and in July and August, in the upper 20 m layer are ca. 30 and 40 mg C m⁻³, respectively. The values were higher in August than July as a result of higher temperature.

In the Gdańsk Gulf, cladocera only occurs from May to August; the other three taxa of mezozooplankton: copepoda, rotatoria and meroplankton in 1999 and 2000 occurred in different proportions during the whole year. From September to April, copepods dominated assuming 75–96% of total biomass mezozooplankton. In the period from May to August, the dominant groups were: in May – rotatoria (56%), June – cladocera (53%), July – copepoda (77%) and in August – cladocera (66%) (Mudrak, 2004). Proportional participation of copepoda in mezozooplankton, outside the dominant month, was not large – from 20% in June (min) to 32% in August (see Fig. 93 in Mudrak, 2004). Copepoda accounted for 24% of total mezozooplankton biomass in the entire area of Gdańsk Gulf, and exceeded 50% in the region of Puck Lagoon (M2) only.

The dominant part on score of copepoda biomass with exception in November and June played *Acartia* spp. They reached a maximum (98%) in September and minimum (23%) in June. However, in months of copepoda dynamic development, this participation reduces overbalance of *Temora longicornis* (in November – 52% and June – 66%) and in a less degree, *Centropages hamatus* (11%) and *Eurytemora* sp. (5%) in the coastal waters and *Pseudocalanus minutus elongatus* (15%) in the deep regions of the Gdańsk Gulf (see Fig. 116 in Mudrak, 2004).

An analysis of the above information and that given in Mudrak (2004) demonstrate, that the experimental total mezozooplankton biomass was characterized by two biomass peaks in a year, in June (ca. 130 mg C m⁻³) and August (ca. 80 mg C m⁻³), similar to the modeled zooplankton. These values are slightly lower than those of the total zooplankton biomass, which was modeled using the bulk formation because the

microzooplankton biomass was not included in the experimental data. Generally, the biomasses of total zooplankton and *Acartia* spp. biomass are in agreement with observations.

The next step in our modeling work is to study the impact of climate changes on the development of *Acartia* spp. in the Southern Baltic Sea through the impact of seasonal variations of food and temperature within the next few decades. This has not been investigated and the response of the marine ecosystem is unknown.

Acknowledgements. This research was carried out in support of a grant of the Polish State Committee of Scientific Research.

References

- Ambler, J. W.: Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* Dana, from East Lagoon, Galveston, Texas, Estuar. Coast. Shelf S., 20, 743–760, 1985.
- Carlotti, F. and Sciandra, A.: Population dynamics model of *Euterpina acutifrons* (Copepoda: Harpacticoida) coupling individual growth and larval development, Mar. Ecol. Prog. Ser., 56, 225–242, 1989.
- Carlotti, F. and Nival, P.: Model of copepod growth and development: moulting and mortality in relation to physiological processes during an individual moult cycle, Mar. Ecol. Prog. Ser., 84, 219–233, 1992.
- Carlotti, F. and Radach, G.: Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North Sea as revealed by a coupled one-dimensional model, Limnol. Oceanogr., 41(3), 522–539, 1996.
- Carlotti, F. and Wolf, K. U.: A Lagrangian ensemble model of *Calanus finmarchicus* coupled with a 1-D ecosystem model, Fish. Oceanogr., 7(3/4), 191–204, 1998.
- Chojnacki, J. C. and Antonczak, E.: Seasonal changes in the neritic zone mezozooplankton of Pomeranian Bay in 2000, EJPau, 11(4), 29, available online: <http://www.ejpau.media.pl/volume11/issue4/art-29.html>, 2008.
- Ciszewski, P. and Witek, Z.: Production of older stages of copepods *Acartia bifilosa* Giesb. and *Pseudocalanus elongatus* Boeck in Gdańsk Bay, Pol. Arch. Hydrobiol., 24, 449–459, 1977.

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Dzierzbicka-Glowacka, L.: Growth and development of copepodite stages of *Pseudocalanus* spp., J. Plankton Res., 26, 49–60, 2004.
- Dzierzbicka-Glowacka, L.: A numerical investigation of phytoplankton and *Pseudocalanus elongatus* dynamics in the spring bloom time in the Gdańsk Gulf, J. Mar. Sys., 53, 19–36, 2005a.
- 5 Dzierzbicka-Glowacka, L.: Modelling the seasonal dynamics of marine plankton in Southern Baltic Sea. Part 1. A Coupled Ecosystem Model, Oceanologia, 47(4), 591–619, 2005b.
- Dzierzbicka-Glowacka, L.: Modelling the seasonal dynamics of marine plankton in the Southern Baltic Sea. Part 2. Numerical simulations, Oceanologia, 48(1), 41–71, 2006.
- 10 Dzierzbicka-Glowacka, L., Lemieszek, A., and Żmijewska, I. M.: Parameterization of a population model for *Acartia* spp. in the Southern Baltic Sea. Part 1. Development time, Oceanologia, 51(2), 165–184, 2009a.
- Dzierzbicka-Glowacka, L., Lemieszek, A., and Żmijewska, I. M.: Parameterization of a population model for *Acartia* spp. in the Southern Baltic Sea. Part 2. Egg production, Oceanologia, 51(2), 185–201, 2009b.
- 15 Dzierzbicka-Glowacka, L., Kuliński K., Maciejewska, A., Osiński, R., Jakacki, J., and Pempkowiak J.: Particulate Organic carbon in the Southern Baltic Sea. Part 1. Numerical simulations and experimental data, J. Mar. Syst., submitted, 2009c.
- Fennel, W.: Modeling of copepods with links to circulation model, J. Plankton Res., 23, 1217–1232, 2001.
- 20 Fransz, H. G., Colebrook, J. M., Gamble, J. C., and Krause, M.: The zooplankton of the North Sea, Neth. J. Sea Res., 28(1/2), 1–52, 1991.
- Last, J. M.: The food of twenty species of fish larvae in the west-central North Sea, Fisheries Research Technical report, Lowestoft, 60, 44 pp., 1980.
- Maritime Branch Materials Institute of Meteorology and Water Management: Environmental conditions in the Polish zone of the Southern Baltic Sea during 1999, IMGW Gdynia, Institute of Meteorology and Water Management in Gdynia, Poland, 299 pp., 2000.
- 25 Mauchline, J.: The Biology of Calanoid Copepods, Academic Press, San Diego, 710 pp., 1998.
- McLaren, I. A.: Generation lengths of some temperate marine copepods: estimation, production and implications, J. Fish Res. Bd. Can., 345, 1330–1342, 1978.
- 30 McLaren, I. A. and Leonard, A.: Assessing the equivalence of growth and egg production of copepods, ICES J. Mar. Sci., 52, 397–408, 1995.
- Moll, A. and Stegert, C.: Modelling *Pseudocalanus elongatus* stage-structured population dynamics embedded in a water column ecosystem model for the northern North Sea, J. Marine

**Population modelling
of *Acartia* spp.**

L. Dzierzbicka-Glowacka
et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

Syst., 64, 35–46, 2007.

Mudrak, S.: Short- and long-term variability of zooplankton in coastal Baltic waters: using the Gulf of Gdańsk as an example, PhD Thesis, Gdańsk University, Gdynia, 328 pp. + Aneks, 2004 (in Polish).

5 Norrbin, M. F.: Timing of diapause in relation to the onset of winter in the high-latitude copepods *Pseudocalanus acuspes* and *Acartia longiremis*, Mar. Ecol. Prog. Ser., 142, 99–109, 1996.

Sekiguchi, H., McLaren, I. A., and Corkett, C. J.: Relationship between growth rate and egg production in the copepod *Acartia clausi* Hudsonica, Mar. Biol., 58, 133–138, 1980.

10 Stegert, C., Kreuz, M., Carlotti, F., and Moll, A.: Parameterisation of a zooplankton population model for *Pseudocalanus elongatus* using stage durations from laboratory experiments, Ecol. Modell., 206, 213–230, 2007.

Wiktor, K.: Zooplankton biomass in the coastal waters of Gdańsk Gulf, Oceanography, 12, 109–134, 1990 (in Polish).

15 Wiktor, K. and Żmijewska, M. I.: Zooplankton species composition and distribution in the waters of the inshore part of the Gulf of Gdańsk, Stud. Mater. Oceanol., 46, 64–114, 1985.

Wroblewski, J. S. and Richman, J. G.: The non-linear response of plankton to wind mixing events – implications for survival of larval northern anchovy, J. Plankton Res., 9, 103–123, 1987.

20 Vinogradov, M. E. and Shushkina E. A.: Functioning of plankton communities in the euphotic zone of the ocean, Nauka, Moskwa, 1987 (in Russian).

Voipio, A.: The Baltic Sea, Elsevier Scientific Publishing Company, Amsterdam, 123–143, 1981.

BGD

7, 55–82, 2010

Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Population modelling
of *Acartia* spp.**

L. Dzierzbicka-Glowacka
et al.

Table 1. Total biomass of *Acartia* spp. (in $\text{mg}_{w.w.} \text{m}^{-3}$) as monthly averages in the surface (0–10 m) or subsurface layer (10–20 m) in the summer season (July, August, September) in 1998, 1999 and 2000 from the eight stations in the Gdańsk Gulf (see Mudrak, 2004).

station	Total biomass of <i>Acartia</i> spp. (in $\text{mg}_{w.w.} \text{m}^{-3}$)		
	July 1998/1999/2000	August 1998/1999/2000	September 1998/1999/2000
J23	30/20/50	80/8/450	30/30/35
So1	65/70/160	10/70/50	20/60/10
So2	10/45/40	10/40/120	70/30/50
So3	15/70/60	15/20/100	25/5/10
So4	20/270/40	50/10/40	5/5/15
G1	5/300/90	20/80/400	20/60/10
G2	5/130/50	15/60/380	10/20/5
M2	10/40/–	15/20/30	10/40/20

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Population modelling
of *Acartia* spp.**

L. Dzierzbicka-Glowacka
et al.

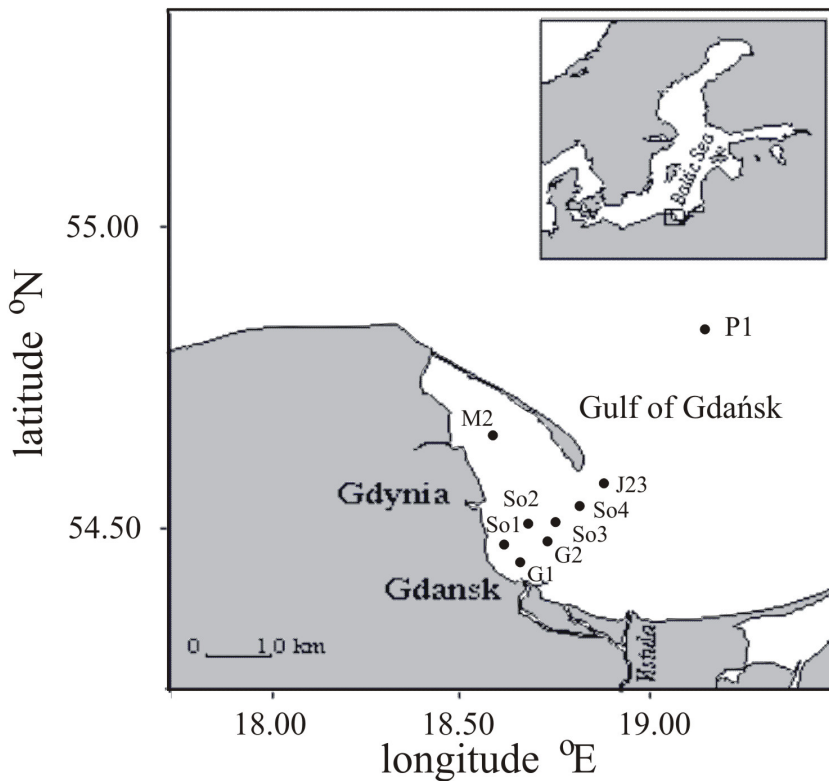


Fig. 1. Location of the sampling stations.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

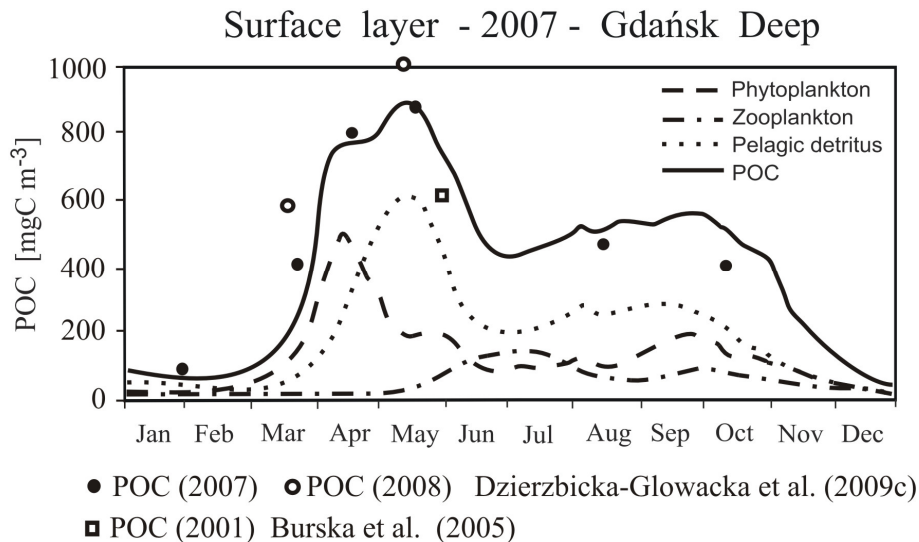


Fig. 2. Modelled POC seasonality presented against background of Phyt, Zoop and DetrP and in situ measured POC concentrations; solid line – POC, dashed line – phytoplankton, dash-dotted line – zooplankton, dotted line – pelagic detritus, full circles – data of POC from 2007, open circles – data of POC from 2008 (Dzierzbicka-Glowacka et al., 2009), open square – data of POC from 2001 (Burska et al., 2005).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Population modelling of *Acartia* spp.

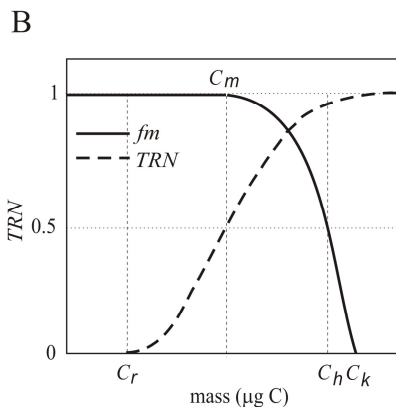
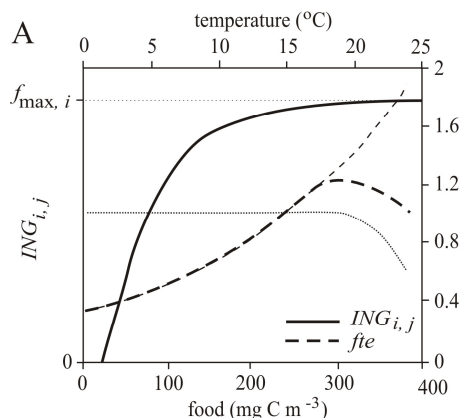
L. Dzierzbicka-Glowacka et al.

$$ING_{i,j} = f_{\max,i} \left\{ 1 - \exp\left(\frac{-(Food_j - Food_o)}{k_{Food}}\right) \right\}$$

$$fte = \hat{f}_1 \hat{f}_2 = \begin{cases} 1 & T \leq T_o \\ 1 - \left(\frac{T - T_o}{t_3 T_o}\right)^{K_1} & T \geq T_o \end{cases}$$

$$fm_i = \begin{cases} 1 & \text{if } W_i \leq C_m \\ 1 - \left(\frac{W_i - C_m}{C_k - C_m}\right)^2 & \text{if } W_i > C_m \end{cases}$$

$$TRN_i = \frac{(W_i - C_r)^{K_2}}{(W_i - C_r)^{K_2} + (C_m - C_r)^{K_2}} \text{ if } W_i > C_r$$



where: f_{\max} , $Food_o$, k_{Food} , C_k , C_r - Dzierzbicka-Glowacka et al. (2009a)
 $t_1=0.239$, $t_2=1.1$, $T_o = 18^\circ\text{C}$, $K_1=1.3$, $t_3=0.6$ $K_2 = 4$ (nauplii, copepodites, adults)
 $K_2 = 6$ (eggs)

Fig. 3. Diagrams of three parameters (Food, T , W) used in the copepod model for physiological process rates: ingestion rate depending on food availability (solid line, **A**), temperature (dashed, **A**) and weight (solid line, **B**) and transfer depending on weight (dashed, **B**).

Title Page	
Abstract	Introduction
Conclusions	References
Tables	Figures
◀	▶
◀	▶
Back	Close
Full Screen / Esc	
Printer-friendly Version	
Interactive Discussion	



**Population modelling
of *Acartia* spp.**

L. Dzierzbicka-Glowacka
et al.

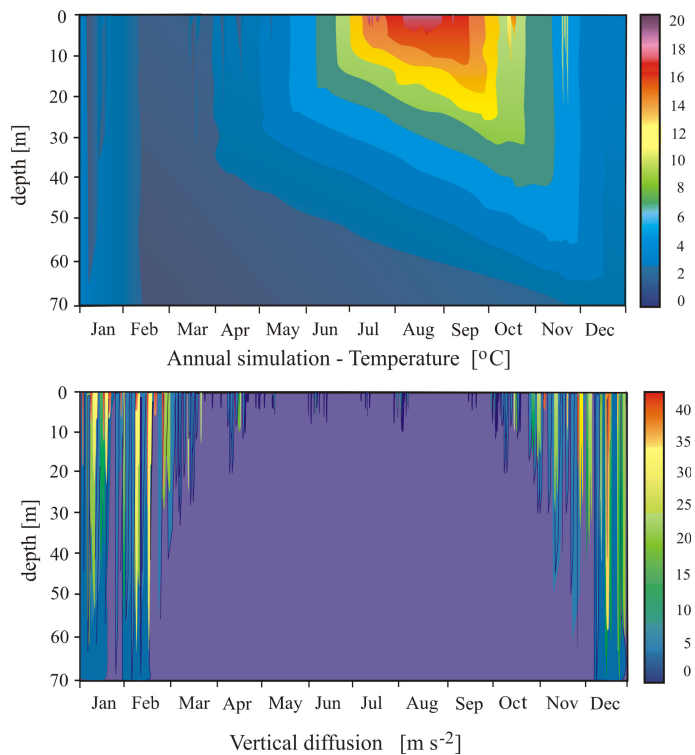


Fig. 4a. Model results for physical state variables.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Population modelling
of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

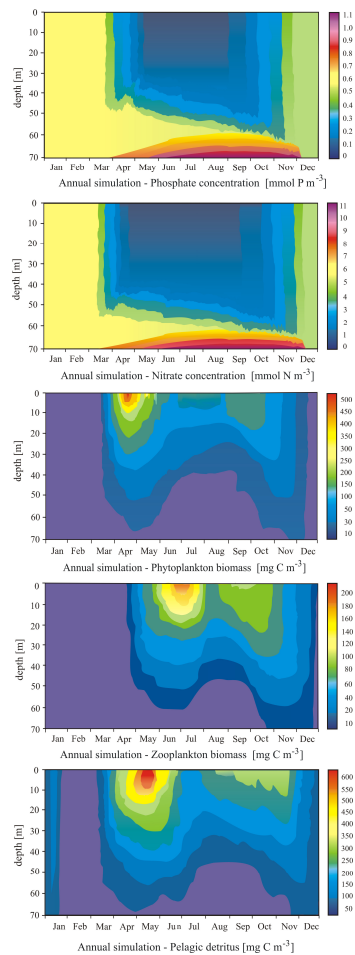


Fig. 4b. Model results for biological state variables.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka
et al.

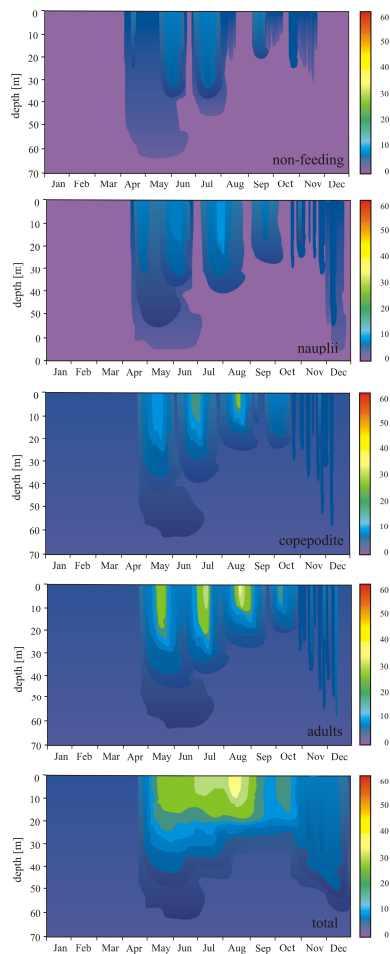


Fig. 5. Simulated annual profiles of four *Acartia* spp. groups representing: biomasses of eggs, nauplii, copepodites and adults and of total biomass of *Acartia* spp. (mg C m^{-3}).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



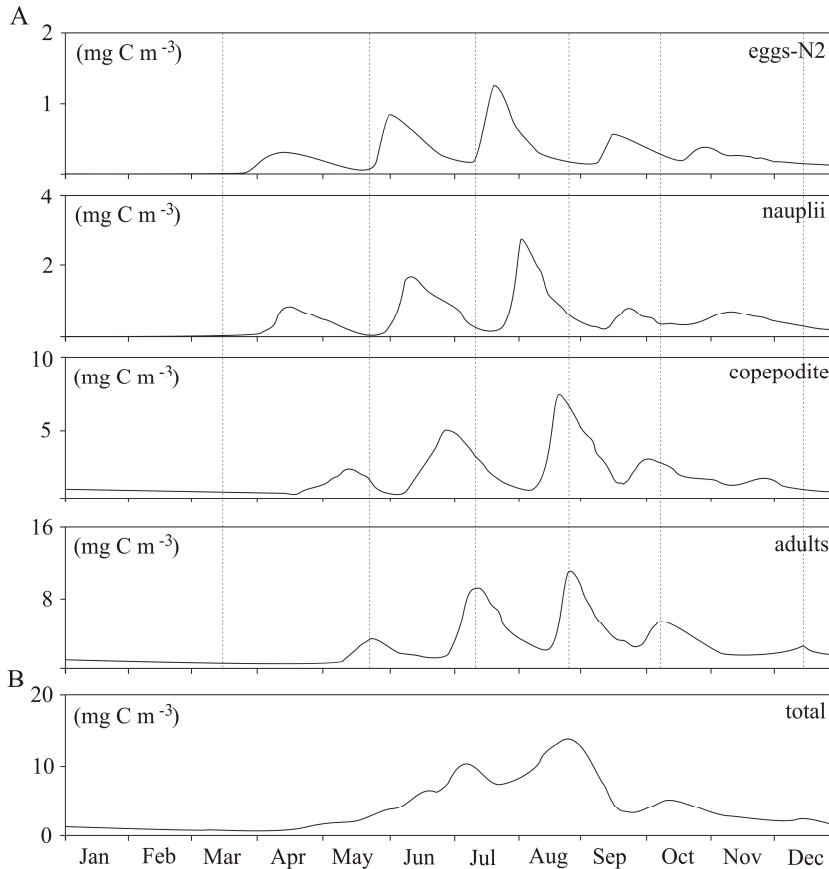


Fig. 6. Simulated *Acartia* spp. generations **(A)** vertical mean biomasses of eggs, nauplii, copepodites and adults (mg C m^{-3}), **(B)** total biomass as vertical mean concentrations; vertical lines indicate the durations of five generations.

BGD

7, 55–82, 2010

**Population modelling
of *Acartia* spp.**

L. Dzierzbicka-Glowacka
et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Population modelling of *Acartia* spp.

L. Dzierzbicka-Glowacka et al.

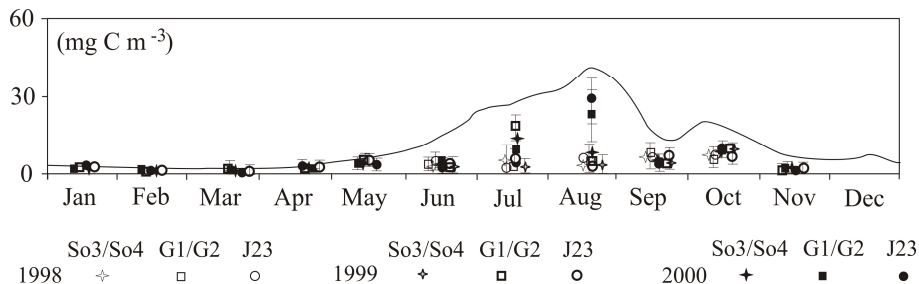


Fig. 7. Observed *Acartia* spp. biomass for the Gdańsk Gulf compared to simulated population (solid line) – based surface biomass concentrations 0–20 m (mg C m⁻³); full circles – data from J23 station, full squares – data from G1 and G2 stations, full stars – data from So3 and So4 stations from 2000; half-open circles – data from J23 station, half-open squares – data from G1 and G2 stations, half-open stars – data from So3 and So4 stations from 1999; open circles – data from J23 station, open squares – data from G1 and G2 stations, open stars – data from So3 and So4 stations from 1998.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

