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Seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia* spp. in the southern Baltic Sea (Gdańsk Deep) – numerical simulations

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Abstract. A population dynamics model for copepods is presented, describing the seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia* spp. in the southern Baltic Sea (Gdańsk Deep). The copepod model was coupled with a one-dimensional physical and biological upper layer model for nutrients (total inorganic nitrogen, phosphate), phytoplankton, microzooplankton, and an early juvenile of herring as a predator. In this model, mesozooplankton (herbivorous copepods) has been introduced as an animal having definite patterns of growth in successive stages, reproduction and mortality. The populations are represented by 6 cohorts in different developmental stages, thus assuming that recruitment of the next generation occurs after a fixed period of adult life. The copepod model links trophic processes and population dynamics, and simulates individual growth within cohorts and the changes in biomass between cohorts.

The simulations of annual cycles of copepods contain one complete generation of *Pseudocalanus* and two generations of *Acartia* in the whole column water, and indicate the importance of growth in the older stages of 6 cohorts of each species, to arrive at a total population biomass. The peaks of copepods' biomass are larger at the turn of June and July for *Pseudocalanus* and smaller in July for *Acartia*, lagging that of phytoplankton by ca. two mouths, due to the growth of cohorts in successive stages and egg production by females.

The numerical results show that the investigated species could not be the main factor limiting the spring phytoplankton bloom in the Gdańsk Deep, because the initial development was slow for *Acartia* and faster for *Pseudocalanus*, but the main development formed after the bloom, in both cases. The phytoplankton bloom is very important in the diet of the adults of the copepods, but it is not particularly important for the youngest part of new generation (early nauplii). However, the simulated microzooplankton biomass was enough high to conclude, in our opinion, that, in this case, it was a major cause in limiting phytoplankton bloom. The model presented here is a next step in understanding how the population dynamics of a dominant species in the southern Baltic Sea interact with the environment.

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1 Introduction

In the past, where zooplankton has been introduced into a model, factors such as filtering, respiration, and excretion rather often have been taken as fixed productions of the hypothetical biomass rather than being related to more detailed information on behaviour and metabolism. In the literature there are now considerable experimental data on these aspects for several species of zooplankton. This information can be used to provide some idea of the functional relations which could be used in a simulation of zooplankton response to variations in its environment. The development of such theoretical descriptions is critical to the inclusion of this animal, in more general simulations of ecosystems. Most of the models take into account only nutrient 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 developmental 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 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.

The considerations of herbivores as biomass show that useful deductions can be made. In particular, in studies of phytoplankton populations, it may be sufficient to use a single parameter for presenting the general concepts from this

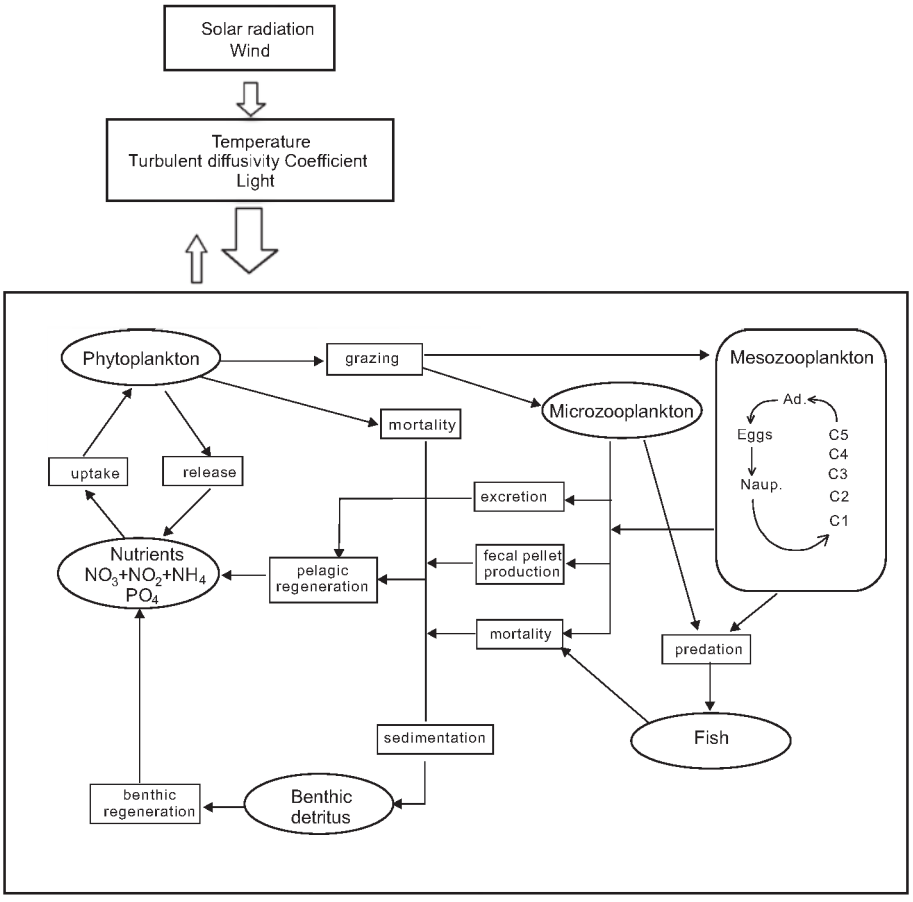

Fig. 1. Conceptual diagram of the coupled model.

point of view (Riley, 1965). Such studies of phytoplankton usually stress the effects of physical variables in changing the phytoplankton populations. These factors are certainly important, but they may have been overemphasised by the excessive simplicity of the portrayal of the herbivores. Thus, it is necessary to look at the probable intricacies that can arise from a more consistent consideration of growth, reproduction, and mortality of copepods in particular development stages. Steele and Henderson (1976) demonstrated that a comprehensive model of the food chain needs to take into account the population dynamics of herbivores for *Calanus finmarchicus* in the North Sea; this species dominates the biomass of zooplankton in spring and summer and shows clearly demarcated cohorts. The study of copepods population dynamics was made, for instance, by Francois Carlotti and several co-workers, who have worked along the same lines, i.e. in the papers by Carlotti and Sciandra (1989), Carlotti and Nival (1992), Carlotti and Radach (1996), Carlotti and Wolf (1998) and Radach et al. (1998) and here should be included the paper by Moll and Stegert (2007). This type of study for the southern Baltic Sea (Gdańsk Gulf) has been made by Dzierzbicka-Głowacka (2005a) for *P. elongatus* dynamics in the spring bloom time in the Gdańsk Gulf. However, growth ad development of copepodite stages of *Pseudocalanus* were presented by Dzierzbicka-Głowacka (2004a, b).

The aim of this paper is a description of the seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia* spp. at the Gdańsk Deep. A population dynamics model for copepods was coupled with a 1-D physical and biological model (Dzierzbicka-Głowacka, 2005b) and a simple 1-D prey-predator upper layer model (Dzierzbicka-Głowacka, 2006).

2 The coupled one-dimensional model

Recently, Dzierzbicka-Głowacka (2005b) developed a one-dimensional physical and biological upper-layer model. In our paper, we study the dynamics of *P. minutus elongatus* and *Acartia* spp. from the southern Baltic Sea (Gulf of Gdansk). We kept the structure of both simple models (Fig. 1) and added a component for pelagic detritus, which was not previosly represented.

Table 1. Differential equations for pelagic detritus and new processes; PDetr(z,t): detritus concentration, K_z: turbulent diffusion coefficient, w_z: phytoplankton sinking velocity, w_d: detritus sinking velocity, r_d: detritus remineralization rate.
$\frac{\partial \mathrm{PDetr}}{\partial t} = \frac{\partial}{\partial z}\left(K_z \frac{\partial \mathrm{PDetr}}{\partial z}\right) + \mathrm{MOR}_{PD} + \mathrm{FEC}_{TD} + \mathrm{MOR}_{TD} - w_d \frac{\partial \mathrm{PDetr}}{\partial z} - \mathrm{ING}_D - \mathrm{REMI}_D.$

Food available for mezozooplankton	$\mathrm{Foot}(z,t) = Phyt(z,t) + \mathrm{PDetr}(z,t)$
Inputs to the pelagic detritus equation	
with microzooplankton equation:	
Fecal pellet material	$\mathrm{FEC}_Z = n_f \mathrm{ING}_Z$
Carcasses material	$\mathrm{MOR}_Z = n_z \mathrm{ING}_Z$
with mesozooplankton equation given in Table 3	
Pelagic detritus equation	
Sinking of pelagic detritus	$w_d \frac{\partial \mathrm{PDetr}}{\partial z}$
Flux of dead phytoplankton	$\mathrm{MOR}_{PD} = p_p \mathrm{MOR}_P$
Flux of fecal pellets	$\mathrm{FEC}_{TD} = p_f(\mathrm{FEC}+\mathrm{FEC}_Z)$
Flux of dead zooplankton and fish	$\mathrm{MOR}_{TD} = p_z(\mathrm{MOR}+\mathrm{MOR}_Z)$
Copepod grazing on pelagic detritus	$\mathrm{ING}_D = \mathrm{ING}\frac{\partial \mathrm{PDetr}(z,t)}{\partial \mathrm{Foot}(t)}$
Remineralization of pelagic detritus	$\mathrm{REMI}_D = r_d \mathrm{PDetr}$
Nutrient equation	
Total remineralization	$\mathrm{REMI} = \mathrm{REMI}_D$
Benthic detritus equation	
Flux condition at the boundary for phytoplankton and detritus	$F_P(H) = -w_z Phyt(H,t) - w_d \mathrm{PDetr}(H,t)$

A one-dimensional Coupled Ecosystem Model consists of three submodels: meteorological, physical and biological. The meteorological component drives both of the 1-D models, and the output of the physical model is also used for driving the biological model. We do not discuss the meteorological and physical submodels, but focus on the biological submodel. This submodel combines two models: *nutrient-phytoplankton-zooplankton-detritus* and *prey-predator*, i.e. this model consists of seven mass conservation equations. There are six diffusion advection reaction equations for phytoplankton, micro- and mesozooplankton, and early juvenille fish biomass, and a double nutrient in the water column. The seventh equation, an ordinary differential equation, describes the development of detritus at the bottom. The equations, process formulations and parameter values of the ecosystem model are given by Dzierzbicka-Glowacka (2005b). However, the additional equations and processes relating to the model's pelagic detritus compartment are presented in Table 1.

The philosophy was to make the model as simple as possible as far as phytoplankton is concerned: phytoplankton is modelled with the aid of only one state variable. The phytoplankton concentration is taken as a dynamically passive physical quantity, i.e. it is incapable of making autonomous movements. The biological model incorporates formulations of the primary production mechanism and of the remineralization mechanisms within the mixed layer in the lower layers and at the bottom. Phytoplankton in the water is either grazed by zooplankton, small fish, or else it dies and sinks. The grazed phytoplankton can be divided into many groups: one contributes to zooplankton growth, another is deposited as faecal pellets, and a third is excreted by the zooplankton as dissolved metabolites, and is lost by mortality and predation. Organic detritus in the water column is either immediately remineralized or directly transported to the bottom, where it accumulates in a stock of benthic detritus. The concept of the detritus pool at the bottom has been 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 is parameterized by assuming a net remineralization rate for bottom detritus (Billen et al., 1991). In this model nutrients are represented by two components: total inorganic nitrogen (NO_3+NO_2+NH_4) and phosphate (PO_4). The pool of nutrients is enriched in many ways: through the remineralization of dead phytoplankton, zooplankton and fish, and feacal pellets; the release from phytoplankton, zooplankton and fish excretion and benthic regeneration. One state variable for microzooplankton is considered. Microzooplankton is defined as heterotrophic planktonic organisms from 10 to 500 μm SED (Spherical Equivalent Diameter), excluding heterotrophic nanoflagellates and naupliar/larval stages of larger zooplankton and of benthic organisms. The microzooplankton comprises ciliates and other heterotrophic protists, which are filter-feeders, feeding on phytoplankton. The fish is represented by earlier juvenile of herring *Clupea harengus* for 4–10 cm size class, where its growth rate is controlled by the encounter rate between consumer and prey. This component has been introduced into this model to determine a predation of zooplankton.

Table 2. Mathematical formulations of relationships used in the model; i: cohort; j: stage; if $W_{j-1}<W_i<W_j$, then $i=j$ for successive developmental stages j=1, 2 $\cdots$ 13; Foot: food concentration; T: temperature; W_i: weight; Z_i: number; B: predator biomass; g: growth rate of predator; W_{female}: weight of female; W_{egg}: weight of egg; K_z: turbulent diffusion coefficient; Ri: Richardson number.

Process	Units	Formulation
Growth		
Ingestion	μgC d^{-1}	$\text{ING}_i = fil_i\, fte_i\, fw_i$
Influence of food		$fil_i(\text{Foot}) = f_{i_{max}}\{1-\exp\left(\frac{-(Foot-Foot_o)}{k_{\text{Foot}}}\right)\}$
Influence of temperature		$fte_i(T) = t_1 t_2^T$
Allometric relation		$fw_i(W) = W_i^{\alpha}$
Fecal pellets	μgC d^{-1}	$\text{FEC}_i=(1-n_a)\text{ING}_i=n_f\text{ING}_i$
Metabolism	μgC d^{-1}	$\text{MET}_i=M_s+M_a$
Basic metabolism		$M_s = n_w W_i$
Active metabolism		$M_a = n_e A_i$, $A_i = n_a\text{ING}_i$
Egg matter	μgC d^{-1} female^{-1}	$\text{ProdEgg}_i = \exp(\text{GROWTH}) - 1$
Growth	μgC d^{-1}	GROWTH=ING$-$FEC$-$MET
Growth j=13	μgC d^{-1}	$\text{GROWTH}_{13}=\text{ING}_{13}-\text{FEC}_{13}-\text{MET}_{13}-$ProEgg
Dynamics		
Mortality	no. m^{-3} d^{-1}	$\text{MOR}_i=Z_i m_z$
Predation	no. m^{-3} d^{-1}	$\text{PRED}_i=\beta g B/W_i$
Migration	no. m^{-3} d^{-1}	$\text{MIG}_i=1+a_w\cos(\omega(t-t_o))f(z)$
Eggs	no. d^{-1} female^{-1}	$\text{EGG}_i=\frac{W_{\text{female}}}{W_{\text{egg}}}\text{ProdEgg}_i$, EGG=$X\,Z_{13}\int_J \text{EGG}_i$
Turbulent diffusion	m^2 s^{-1}	$K_z = 5\times10^{-4}(1+Ri)^{-2.5}+10^{-6}$

In this paper the mesozooplankton (herbivorous copepods) has been introduced into this model as animals having definite patterns of growth, reproduction, and mortality. Assume that two taxa of copepod *Pseudocalanus minutus elongatus* and *Acartia* spp. are present. The each species' population is represented as six cohorts with different developmental stages.

Planktonic copepods are the major food source for fish larvae in the period of development following the utilization of the larval yolk sac. They also form part of the basic diet of many adult pelagic fish. Feeding studies of fish larvae by Zalachowski et al. (1975) and Last (1978a, b, 1980) have shown that *Pseudocalanus*, *Acartia* and *Temora* nauplius and copepodid stages are important components of the diet of numerous species of fish 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 Arctic waters.

3 Submodel of population dynamics for investigated copepods

We consider that the mesozooplankton is composed of 6 cohorts with different ages of *P m. elongatus* and *Acartia* spp., with weights W_i and numbers Z_i; then

$\{Z_{\text{meso}}\} = \sum_{k=1}^{2}\sum_{i=1}^{6} W_i Z_i$, where

$$\frac{\partial W_i}{\partial t} = \text{ING}_i - \text{FEC}_i - \text{MET}_i \quad (1)$$

$$\frac{\partial Z_i}{\partial t} = \frac{\partial}{\partial z}\left(K_z\frac{\partial Z_i}{\partial z}\right) - \text{MIG}_i - \text{MOR}_i - \text{PRED}_i. \quad (2)$$

Equation (1) determines the change in weight of an individual copepod, taking developmental stages into consideration as the sum of its individual gains and losses of energy (GROWTH=ING$-$FEC$-$MET); equation (2) represents the effects of mortality, predation, and daily migration on a particular cohort as a function of numbers in that cohort in the appropriate development stage. If W_{egg} is the weight of the naupliar stage at which feeding starts and W_{female} is the weight of the adult, then for each cohort relations of the form Egg=$F(T, \text{Foot}, Z_{\text{female}}, W_{\text{female}}/W_{\text{egg}})$ indicate the requirements for some function defining recruitment Egg in terms as temperature T, food available, Foot, adults numbers, Z_{female}, and the ratio of adult to naupliar weight, $W_{\text{female}}/W_{\text{egg}}$.

Processes taken into account are presented in Table 2. Weight is controlled by growth, which depends on food and temperature. The growth rate is expressed in carbon mass units. The ingestion rate ING for specific developmental stages is dependent firstly on the food concentration according to a function fil_i and secondly on temperature, following a constant Q_{10} law fte_i. We use the allometric relation

expressed by Paffenhöfer (1971), fw_i, in which the maximal ingestion rate increases with weight during development. Egested matter is the part of ingested matter which is not assimilated and here is represented by fecal pellet production FEC. The quantity of egested matter is simply proportional to the ingestion rate with the percentage of ingestion egested as fecal material n_f. The total rate of metabolic loss (excretion rate) MET can be split into three components with different relations to the food uptake rate (see Steele and Mullin, 1977). M_s is assumed to be the resultant or basic metabolism, independent of food supply. The respiratory costs of foraging for and capturing food M_r should fall as the food concentration and, correspondingly, f(Food), rises. Finally, there is the cost of assimilating and biochemically transforming the food (specific dynamic action, M_a), proportional to the rate of assimilation A, which is computed as a constant fraction of the ingestion rate (e.g. Steele, 1974, who used A=0.7ING). We suppose as Wroblewski (1984) that excretion can be separated into 2 terms. The first (M_s) represents the basic metabolism and is proportional to weight. The second (M_a) refers to the active metabolism and is proportional to the ingestion rate.

The number of juveniles EGG is defined assuming that eggs are released by the female throughout some time span J. For mature adults, ingested matter is used for maintenance and reproduction (Sekiguchi et al., 1980). The reproductive rate per individual female of *Pseudocalanus* can be converted to the equivalent amount of egg matter per day as a percentage of female weight (see Corkett and McLaren, 1978; McLaren and Leonard, 1995). The efficiency term X is the conversion of increase in biomass by the adult population into eggs, including the wasted growth in the males.

The intensity of mortality MOR is determined as average mortality rate m_z; m_z at different food concentrations and temperatures for *Pseudocalanus* is given by Klein Breteler et al. (1995).

According to Mudrak (2004), the youngest development stages (nauplii) were usually found in subsurface layers (mostly between 10 and 20 m). They did not normally change their positions in the water column. Younger copepodids (C1-C2) showed strong diel vertical migration above the halocline, older copepodids (C4-C5) below the thermocline, when adults remained in the deepest part of the water column (near the bottom) (Mudrak et al., 2004). Therefore, here the migration process MIG, only for copepodids in the vegetation season, was described in a day-night cycle, where $f(z)$ is the vertical distribution of copepods in time t_o in which its maximum concentration occurs in the upper layer.

Predation PRED represents the losses incurred by Z_i. Its magnitude can be determined from the biomass of early juvenile herring on the assumption that the loss incurred by the prey concentration is proportional to the increase in the predator biomass.

The copepod population model simultaneously provides the time variations for the weights and the number of the six cohorts, and for the biomasses of each cohort for *Pseudocalanus minutus elongatus* and *Acartia* spp. in the whole column water in the southern Baltic Sea.

Copepod ingestion and egg-production rates vary in response to forcing from the physical and biological environments (Runge, 1984, 1985; Ambler, 1985; Peterson, 1988; Rothschild, 1988; Kleppel, 1992). In turn, the ingestion rate and diet are thought to affect growth, development and egg production (Roman, 1984; Stoecker and Egloff, 1987; Kleppel et al., 1991). The relationships between food concentration, composition, feeding and production have been difficult to quantify in natural food environments. Growth and development of copepods in different waters are determined mainly by temperature and food availability (Paffenhöfer and Harris, 1976; Corkett and McLaren, 1978; Vidal, 1980a, b; Thompson, 1982; McLaren et al., 1989; Klein Breteler et al., 1995; Witek, 1995; Koski et al., 1998; Dzierzbicka-Glowacka, 2004a, b). Egg production of copepods in nature is generally assumed to be food-limited, while juvenile growth often seems to be dependent on temperature alone (McLaren et al., 1969; Paffenhöfer and Harris, 1976; Thompson, 1976; Corkett and McLaren, 1978; Landry, 1983; Dzierzbicka-Glowacka and Zieliński, 2004). Some authors found correlations between copepod egg production and phytoplankton standing stock (e.g. Landry, 1978; Checkley, 1980; Durbin et al., 1983; Beckman and Petersen, 1986; Kiørboe and Johanson, 1986) while others did not (e.g. Bautista et al., 1994; Hay, 1995). In our opinion, these relations are not explicit and are hard to obtain. Food concentration clearly has no effect on egg production. Egg production for some species may be correlated with food availability at the same temperature.

Most of the coefficients used in the submodel are calculated from these results. Where data are lacking, coefficients are estimated from knowledge about similar species (see Appendix).

3.1 Assumptions of the model

The dynamical constants used in the biological model with the population dynamics submodel for the copepods investigated were determined mostly from data derived from the literature (see Tables 1 and 2 of Dzierzbicka-Glowacka, 2005b). The values of the parameters were chosen reasonably close to Baltic levels.

We need to make assumptions concerning the vertical distribution of the biological characteristics and the biology of the *Pseudocalanus* and *Acartia*:

(i) initial values as constants with depth were assumed (see Table 3);

(ii) the initial population of *Pseudocalanus* and *Acartia* had no eggs and no nauplii N1-N6;

Table 3. The initial values of biological characteristics investigated.

State variable	Symbol	Value	Units
Total inorganic nitrogen	$Nutr_N$	6	mmol m^{-3}
Phosphate	$Nutr_P$	0.6	mmol m^{-3}
Phytoplankton	Phyt	0.01	mgC m^{-3}
Microzooplankton	Z_{micro}	mgC m^{-3}	0.1 mgC m^{-3}
Pseudocalanus	Egg	0	ind. m^{-3}
	N1-N6	0	ind. m^{-3}
	C1	2300	ind. m^{-3}
	C2	1800	ind. m^{-3}
	C3	1300	ind. m^{-3}
	C4	900	ind. m^{-3}
	C5	500	ind. m^{-3}
	adults	300	ind. m^{-3}
	Z_{mezo}	4.2	mgC m^{-3}
Acartia	Egg	0	ind. m^{-3}
	N1-N6	0	ind. m^{-3}
	C1	1100	ind. m^{-3}
	C2	1000	ind. m^{-3}
	C3	900	ind. m^{-3}
	C4	700	ind. m^{-3}
	C5	400	ind. m^{-3}
	adults	300	ind. m^{-3}
	Z_{mezo}	2	mgC m^{-3}
Clupea harengus (3 cohorts)	B_1	30	mgC m^{-3}
	B_2	15	mgC m^{-3}
	B_3	7.5	mgC m^{-3}

(iii) the mean weight for specific development stages of species investigated were assumed after standard HELCOM (Hernroth, 1985) for Gdansk Deep.

We assume that the available food concentration for all the stages of the population of copepods investigated is the value of the food concentration (phytoplankton and other resources), as well as the notion that copepods feed continuously if there is food present. The products of mesozooplankton metabolism, which enter the nutrient model (i.e. excretion, remineralized fecal pellets and dead bodies), are evenly distributed throughout the upper layer (Table 4). The remaining fecal pellets and dead bodies fall immediately to the benthic detritus.

Predator is represented by early juvenile of herring *Clupea harengus* (4–10 cm). The Vistula Lagoon is an important spawning area for southern Baltic spring-spawning herring *Clupea harengus*. At the turn of winter and spring (in March), adults which migrate from the southern Baltic to the spawning are in the shallow and brackish water of the Vistula Lagoon (Fey, 2001). Herring in the Vistula Lagoon have three cohorts each year (Margoński, 2000). Larvae abundance in Vistula Lagoon in 1999 was observed in 495–128 individuals in 100 m^3. When young herring are about 40 to 50 mm, they undergo a metamorphosis, developing the morphological characteristics of adults; they are then identified as juveniles. Metamorphosis begins in June in Vistula Lagoon. Herring early juveniles emigrated from the Polish part of the Vistula Lagoon; the juveniles of the first cohort migrated in June, the second cohort in July, and the third cohort in August to the southern Baltic Sea. An early juvenile (ca. 40 mm) appears in the Gulf Gdańsk after two weeks, assuming that its velocity was ca. 4 cm s^{-1}, after Miller et al. (1988). Therefore, in these calculations it was assumed that, during the first half of the year, the predator biomass is B=0.

Table 4. Processes coupling the mesozooplankton submodel to the other components.

Total ingested material	$\mathrm{ING}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{ING}_{k,i}Z_{k,i}$
Total fecal pellet material	$\mathrm{FEC}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{FEC}_{k,i}Z_{k,i}$
Total cadaverous material	$\mathrm{MOR}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{MOR}_{k,i}W_{k,i}$
Total metabolic products	$\mathrm{MET}=\sum_{k=1}^{2}\sum_{i=1}^{6}\mathrm{MET}_{k,i}Z_{k,i}$

4 Results

The 1-D biological upper layer model described in Dzierzbicka-Glowacka (2005b), with the population dynamics submodel for copepods, was used in the numerical simulations of the seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia* spp. in the southern Baltic Sea. However, the experimental data relating to copepods were given by Maritime Branch Materials (IMGW 2000) and Mudrak (2004).

4.1 Numerical simulations

The flow field and water temperature used as the inputs of the biological submodel were reproduced by the physical submodel. However, wind stress, global radiation and the heat balance at the sea surface are determined from standard meteorological components for the location (54°52′ N, 19°10′ E) in Gdańsk Gulf for 1999. In Dzierzbicka-Glowacka (2005a) the spring phytoplankton and *Pseudocalanus elongatus* dynamic in the southern Baltic Sea at the two stations were simulated. Here we present the results of the biological parts of the model for 1999 at the Gdańsk Deep, as well as the simulation made with a dynamic population of *P m. elongatus* and *Acartia* spp.

4.1.1 Simulations of annual plankton cycle

Modeled temperature fields resulting from the physical model (as the output) (Fig. 2a) were used for the primary production, phytoplankton respiration and physiological processes of copepods calculation. The simulated temperature began to increase during the second half of March and

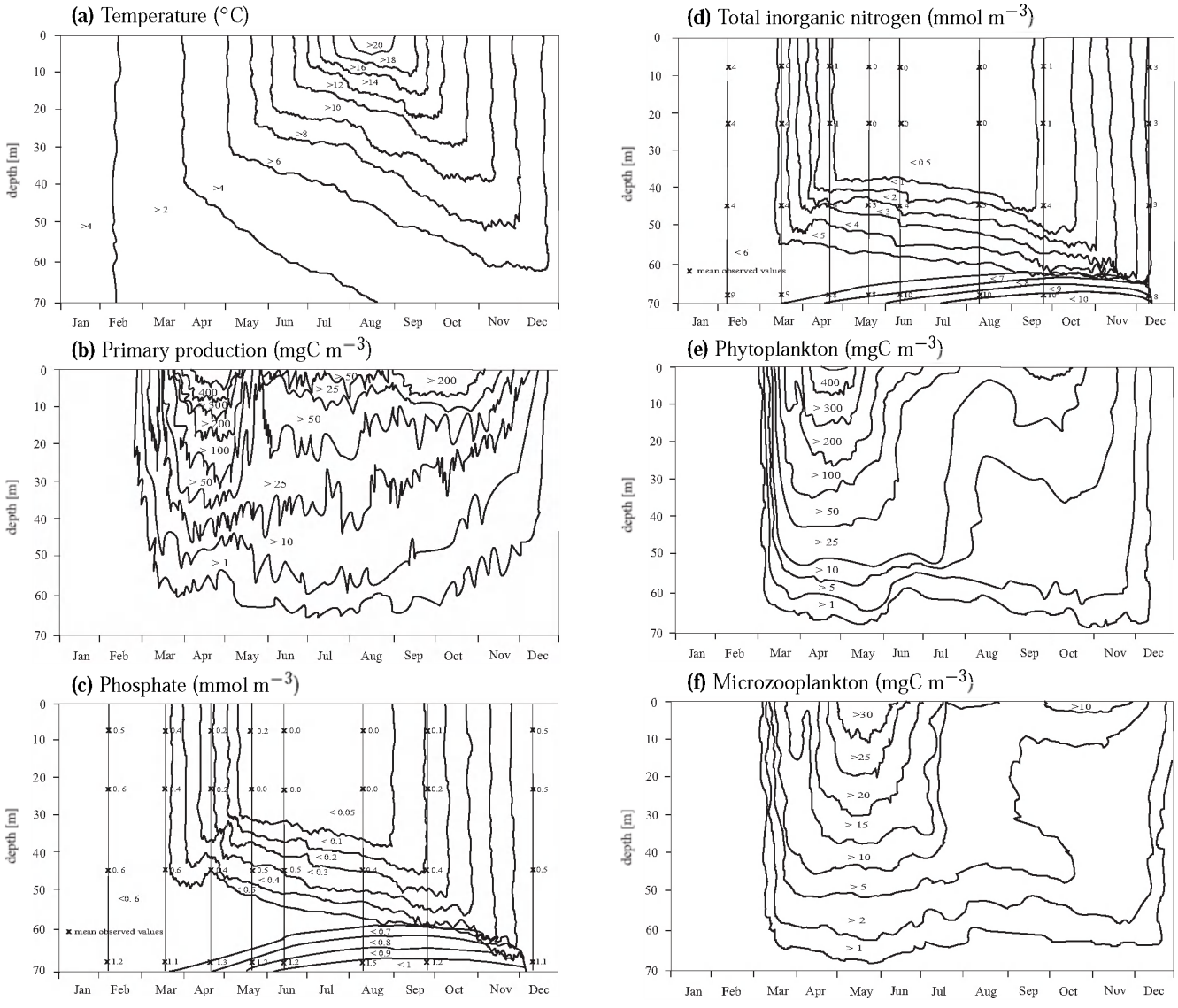

Fig. 2. Annual simulation. Simulated profiles of temperature **(a)**, primary production **(b)**, nutrients – total inorganic nitrogen **(c)** and phosphate **(d)**, phytoplankton **(e)**, microzooplankton **(f)**, small detritus **(g)**, mesozooplankton – *Pseudocalanus minutus elongatus* and *Acartia* spp. **(h)** and early juvenile of herring **(i)** at the Gdansk Deep in 1999.

Fig. 2. Continued.

reached ca. 21°C in August. The destruction of the thermocline starts in the late fall. Probably, the spring bloom in this year was triggered in the first half of March. The bloom is initiated by the heating event and the extremely low winds. The end of permanent overturning of the water column in mid-March in the main event allows the phytoplankton to start growing (Fig. 2b). The depths of the upper layer, which are determined by the mixing intensity in the water column, show that strong gradients in the nutrient concentration develop (Figs. 2c and d). The phytoplankton biomass (Fig. 2e) reflects the nutrient availability, showing a strong nutrient – depleting spring bloom. The phytoplankton biomass reached the mean maximum values ca. 400 mgC m^{-3} in the upper 10-m layer in the spring bloom. The highest value occurred in the second half of April and equaled ca. 530 mgC m^{-3} on the surface sea (Fig. 2e). This situation is caused by the high nutrient concentrations and daily global radiation in the last decade, focusing on March and April. The phytoplankton biomass was low in summer, from June till August, most likely as a result of a faster depletion of nutrients and the phytoplankton grazing by micro- and mesozooplankton. The development of microzooplankton was exactly correlated with the development of phytoplankton (Fig. 2f). Generally, the greatest amounts of microzooplankton occurred in the upper layer, in the periods of large biomass of algae. Biomass of microzooplankton was characterized by the occurrence of

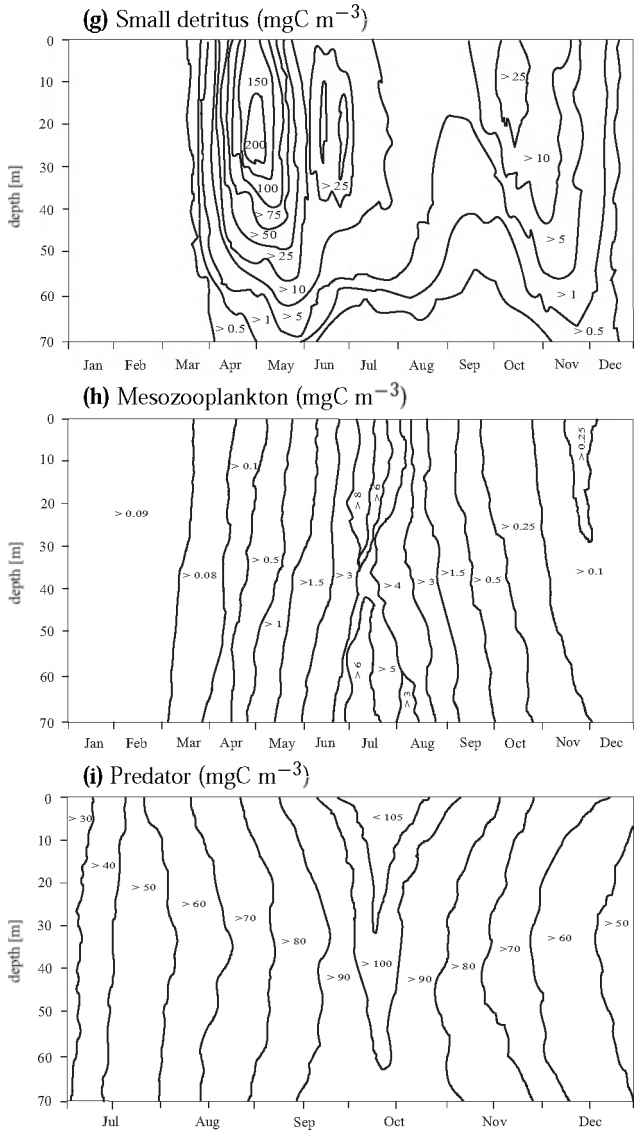

Fig. 2. Continued.

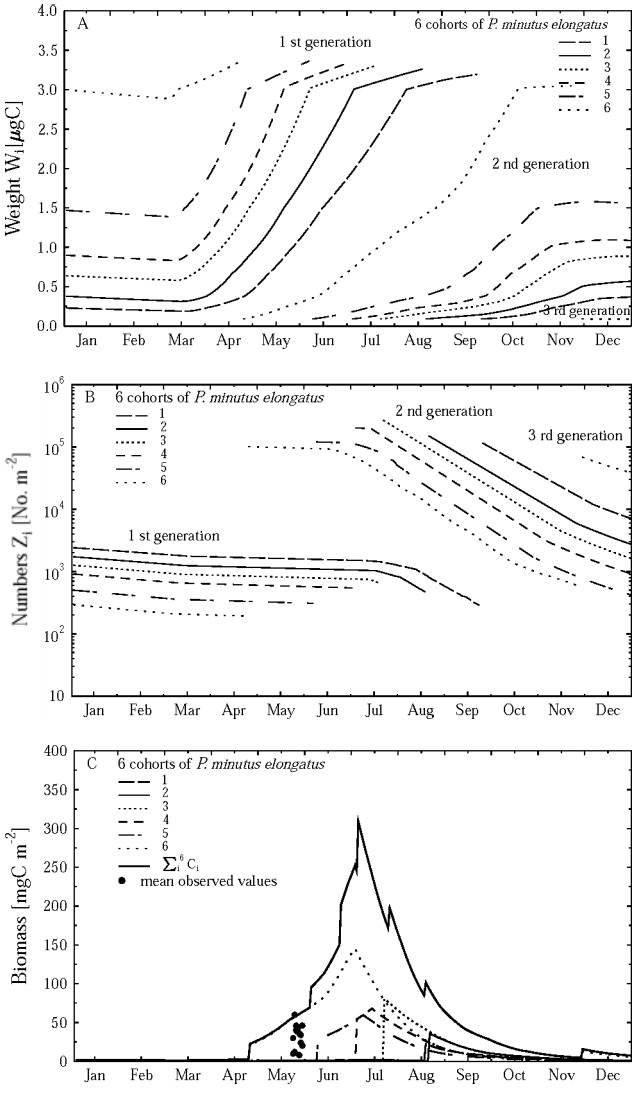

Fig. 3. *Pseudocalanus minutus elongatus.* Weights, W_i **(a)**, numbers, Z_i **(b)**, and biomass, $\sum W_i Z_i$ **(c)**, of six cohorts.

two biomass peaks in a year; at the turn of summer and autumn. A considerable increase in Z_{micro} took place in April, shortly after the beginning of the spring bloom. The microzooplankton biomass was ca. 30 mgC m^{-3} in the springtime; however, in the summertime, it fell below 10 mgC m^{-3}, with simultaneous decreasing phytoplankton biomass, and reappeared in early autumn with higher biomass. Small pelagic detritus (Fig. 2g) was abundant mainly when the phytoplankton concentration exceeded 200 mgC m^{-3}, and its maximum concentration was deeper than the 20 m layer.

The biomass of mesozooplankton, represent by *Pseudocalanus* and *Acartia*, increased in the first half of the year, reaching maximum values from ca. 8 mgC m^{-3} at the turn of June and July (Fig. 2h). This increase was mainly from growth in successive stages and egg production. In autumn a certain increase in phytoplankton biomass took place. *Phyt* remained stable, at a level slightly higher than in summer. It might have been related to the considerable reduction in the amount of micro- and mesozooplankton, as well as an increase in the concentration of nutrients resulting from deeper mixing of water. The vegetation season ended in December, when the biomass of phytoplankton dropped to a level from January–February. The early juvenile of herring biomass increased to ca. 60 mgC m^{-3} at the end of July, and 90 mgC m^{-3} at the end of August (Fig. 2i). The increase in predator biomass in July and August is additionally caused by the migration of second and third cohorts from the Vistula Lagoon. The highest biomass of early juvenile of herring occurred last summer (ca. 140 mgC m^{-3}), when prey concentration reached the second small maximum.

4.1.2 *Pseudocalanus minutus elongatus*

The distributions shown in Fig. 3 present the changes in values of weights W_i (Fig. 3a) and numbers Z_i (Fig. 3b), and the biomasses of six cohorts $W_i Z_i$ (Fig. 3c) of *Pseudocalanus*.

One complete distinct generation (6th cohort of 2nd generation) developed throughout the seven mouths, beginning in mid-April and ending in mid-November.

The peaks of the biomass (see Fig. 3c) were due to egg production, in mid-April – of 6th cohort of the 1st generation, at the turn of May and June – of 5th cohort, as well as to a high degree of 6th cohort biomass, in mid-June – of 4th cohort, as well as to a high degree of 6th cohort biomass and to a lower degree of 5th, at the turn June and July – of 3rd cohort, as well as to a high degree of 6th cohort biomass and to a lower degree of 4th and 5th, in mid-July – of 2nd cohort, as well as to a high degree of 6th cohort biomass and to a lower degree of 3rd, 4th and 5th cohorts biomass and at the first half of August – of 1st cohort, as well as 2nd, 3rd, 4th, 5th and 6th cohorts biomass of the 1st generation.

The phytoplankton peak in September permitted a new growth period for the second generation copepodite stages (visible mainly in the weight curves); and females of the 6th cohort produced a relatively small number of eggs to yield a third generation in November.

The total depth integrated biomass of *Pseudocalanus* is characterized by one peak biomass. The maximum total biomass (ca. 330 mgC m^{-2}) was at the turn of June and July (see Fig. 3c). Figure 3 clearly illustrates the overlap between the first and second generations. The second generation, present the first spawning, seemed to develop slowly and with a higher mortality.

During winter, the total biomass of *Pseudocalanus* slightly decrease, invisible at Fig. 3c, because of a weights decrease of individuals subject to lack of food (see Fig. 3a), as well as of a numbers decrease, because the weights and numbers of individuals decreased slightly owing to the lack of food and the low mortality. The biomass then increased as a result of a considerable increase in the individuals weight for the copepodite stages. In spring, the individuals became active and they grew by feeding on the phytoplankton bloom, and the adult females produced eggs. By combining the information on growth with the dynamics of individuals, we can affirm that most individuals had a lower growth rate during the naupliar and copepodite phases, with a low phytoplankton biomass in summer; subsequently, the copepodite stages resumed exponential growth with the rise of phytoplankton in September (Fig. 3a). Individuals of the 3rd generation were produced in November by the females of the 6th cohort of the 2nd generation, but they developed no farther than stage N3, due to a lack of food and the severe decrease in temperature. Growth curves stopped because of the death of individuals and which of the weights and numbers decreased. Any decrease in numbers was caused by mortality and at the second half of year, also by predation. The rate of mortality was high

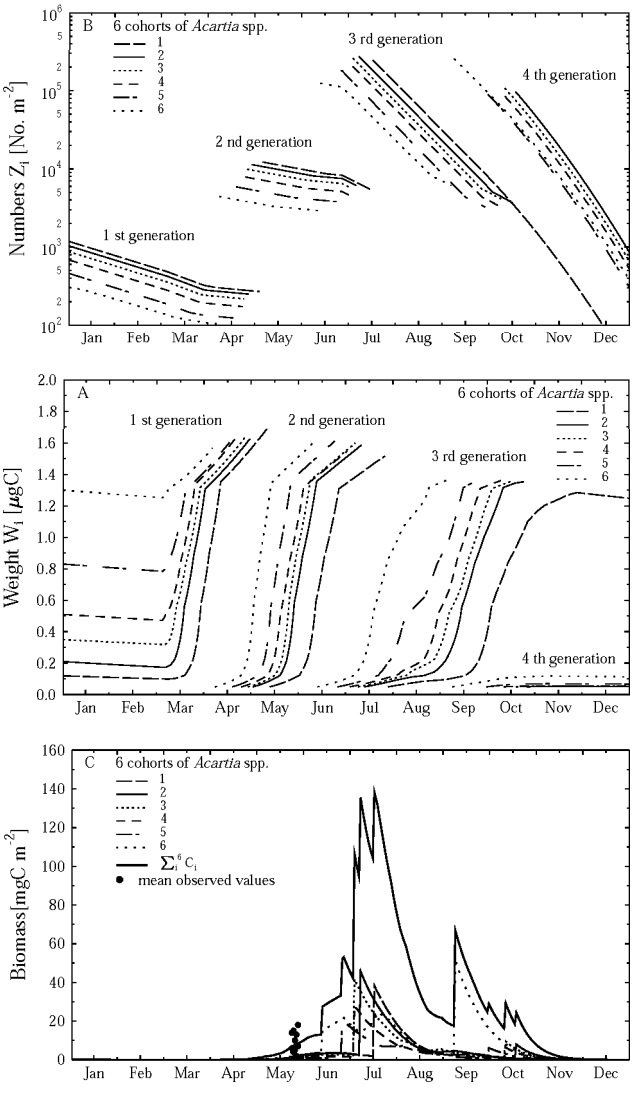

Fig. 4. *Acartia* spp. Weights, W_i **(a)**, numbers, Z_i **(b)**, and biomass, $\sum W_i Z_i$ **(c)**, of six cohorts.

in summer in the upper layer as a result of high temperature and low food concentration; however, in springtime, the rate was the lowest as a result of high food concentration and low temperature. Predation was the largest in October, when the predator biomass had a maximum value.

4.1.3 *Acartia* spp.

The distributions shown in Fig. 4 present the changes in values of weights W_i (Fig. 4a) and numbers Z_i (Fig. 4b) and the depth integrated biomasses of six cohorts and total biomass $\sum_{i=1}^{6} W_i Z_i$ (Fig. 4c) of *Acartia* spp.

Two complete distinct generations, from eggs to adults, for the first time – 6 cohorts of the 2nd generation, the second time – 5 cohorts of the 3rd generation, developed throughout the year, one beginning in April and the other

from mid-June to mid-July (see Figs. 4a and b). The total biomass of *Acartia* is characterized by two biomass peaks, in July – main, and small, in September. The peak of biomass in July (ca. 140 mgC m^{-2}, see Fig. 4c) was mainly due to the high egg production by adults of the 2nd generation (1st, 2nd, 3rd and 4th cohorts), as a result of the very high numbers of adults (Fig. 4b). Figures 4a and b clearly illustrates the overlap between generations. The 3rd generation, present from the first spawning in mid-June by the 6th cohort to the adults at the turn of August and September, as well as the first spawning at the turn June and July by the 5th, 4th, 3rd, and 2nd cohorts to the adults in September, seemed to developed slowly (Fig. 4a) and had a high predation rate (Fig. 4b), i.e. the total development time of the 6th cohort was 75 days and of the 2nd cohort – 90 days. The second peak of biomass in September (ca. 70 mgC m^{-2}, see Fig. 4c) was mainly due to the high egg production of adults of the 6th cohort of the 3rd generation (Fig. 4b), as a result of high temperature. The phytoplankton peak in September permitted a new growth period for the 3rd generation copepodite stages, and females of the 5th, 4th, 3rd, and 2nd cohorts of the 3rd generation produced relatively small eggs to give a 4th generation in October.

In the spring bloom, a substantial growth of phytoplankton biomass was observed which fell at the next stage as a result of an increase first in microzooplankton, and next in mesozooplankton biomass. This growth in biomass of successive cohorts of copepods is caused by an increase in body weight and egg production by each of the adults. This situation leads to the substantial growth in the total biomass, $\sum_{k=1}^{2}\sum_{i=1}^{6} W_i Z_i$, which is the algebraic sum of the products of the weights, W_i, and numbers, Z_i, of both species.

The biomass peak of *Pseudocalanus* appeared at the turn of June and July; however, the *Acartia* biomass was characterized by two biomass peaks in a year; in July and in September.

These small maxima occurring in the distributions of investigated species are the result mainly of a brood by successive cohorts, causing their numbers to increase. The calculations demonstrate that the growth of the weight of each cohort is mainly caused by temperature and a substantial increase in phytoplankton biomass. The body weight of copepods strongly increases in the spring bloom, because in the time the growth rate is higher as a result of larger phytoplankton biomass. In this period, temperature has also significant influence on the growth of *Pseudocalanus*, causing the growth rate tends to maximum.

4.2 Experimental data

The most important species in the Gdansk Gulf are *Acartia* spp. (i.e. *A. bifilosa*, *A. longiremis* and *A. tonsa*) and *Centropages hamatus*, *Temora longicornis*, and *Pseudocalanus minutus elongatus*. In the Gdańsk Deep a fourth species, *Pseudocalanus*, occurred in great abundance, where in a deeper layer, below 30 m, it became dominant, and below the isohaline layer – almost the only representative of mesozooplankton. In 1999 at the Gdańsk Deep, the predominant species were *Pseudocalanus minutus elongatus* and *Acartia longiremis* (see Maritime Branch Materials, IMGW 2000). The results of the numerical simulations described here are compared to the mean observed values, assuming an organic carbon content of copepods $gC/g_{w.w}$=0.064 (Vinogradov and Shushkina, 1987). The mean biomass of all copepods (8 species) in the whole column water in the Gdańsk Deep in 1999, was obtained Maritime Branch Materials, IMGW 2000, i.e. in March – ca. 20, April – ca. 45 , June – ca. 80 and August – ca. 100 $mg_{w.w}$ m^{-3} and it corresponds to 1.3, 2.9, 5.1 and 6.4 mgC m^{-3}. However, the mean biomass of investigated species calculated here was ca. two times lower than observed values, except in March; i.e. in March – ca. 0.1, April – ca. 1.2, June – ca. 2.8 and August – ca. 3.8 mgC m^{-3}.

The plankton material was also collected 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 analysed according to standard methods (HELCOM). Numbers of *P m. elongatus* and *Acartia* spp. for specific development stages were given by Mudrak (2004). During this period, the vertical distributions of observed biomass in diurnal cycles were different, i.e. in the 0.07–0.8 mgC m^{-3} range in the upper-euphotic layer and 0.1–0.9 mgC m^{-3} in the lower one for *Pseudocalanus* and 0.02–1 mgC m^{-3} in the upper layer and 0.03–0.55 mgC m^{-3} in the lower one for *Acartia*. The average value of the biomass in the whole column water in these days was 0.395 mgC m^{-3} for *Acartia* and 0.728 mgC m^{-3} for *Pseudocalanus*.

Figures 3c and 4c show the results of numerical simulations, as well as observed data for depth integrated biomass of investigated species. Depth integrated biomass was in the 1.8–42 mgC m^{-2} range for *Acartia* and in the 6–63 mgC m^{-2} range for *Pseudocalanus* at the end of May after experimental data. However, the mean observed values were 13 mgC m^{-2} for *Acartia* and 48 mgC m^{-2} for *Pseudocalanus* and they are slightly higher (ca. 25%) for *Acartia* and ca. 20% lower for *Pseudocalanus* than mean obtained here, i.e. the calculated mean biomass was ca. 10 mgC m^{-2} for *Acartia* and ca. 60 mgC m^{-2} for *Pseudocalanus*.

5 Discussion

The simulated biological characteristics (i.e. the inorganic nitrogen and phosphate concentrations, the phytoplankton biomass and depth integrated of *Pseudocalanus minutus elongatus* and *Acartia* spp. biomass) in the model were compared to the observations from the investigated water regions. Taking into consideration the fact that outputs of the meteorological submodel were obtained using meteorological data for 1999, the comparison of numerical results will be made

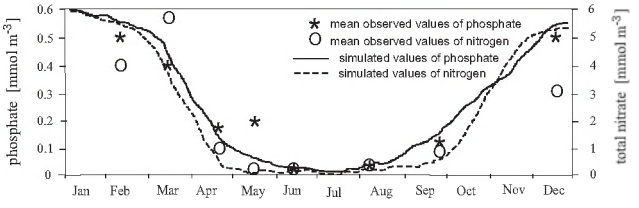

Fig. 5. Simulated and mean observed values of nutrient in the 15-m upper layer at the Gdańsk Deep in 1999.

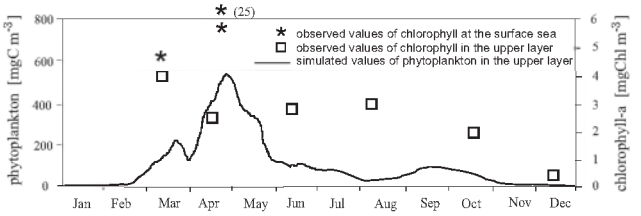

Fig. 6. Simulated values of phytoplankton biomass and mean observed values of chlorophyll-*a* in the upper layer at the Gdańsk Deep in 1999.

to the mean values of empirical data for 1999 on the basis of various authorities.

The outstanding problem concerns the quality of field data used to test such simulations. The problems of data arise from the fact that the variability in space and time of zooplankton is usually so great that any model that has the right orders of magnitude in its outputs will fit the data. Thus, even with models treating herbivores in some detail, the testing of these models may rest primarily upon the nutrient and phytoplankton levels, which can be measured with greater accuracy.

The results of the numerical simulations of phytoplankton biomass and nutrient concentration are in accordance with the in-situ observations. Comparing the nutrient concentration from the calculated and mean experimental data, the present results indicate that the difference in *Nutr* is ca. 20% in the wintertime, and ca. 5% in the summertime, in the upper layer (see Fig. 5); however, ca. 30% at the bottom (see Figs. 2c and d). The differences in the phytoplankton biomass between the modelled and mean observed values is equal to 5–20% in the 10-m upper layer and to 30% at the surface sea (see Fig. 6) and depend on both the month for which the calculations were made, as well on the C/Chl-*a* ratio for converting the simulated carbon contents to chlorophyll-*a*. In this paper, the calculations were made assuming the C/Chl-*a* ratio as a mean value for the southern Baltic Sea in the upper layer after Witek (1993) (see Fig. 7).

However, the obtained depth integrated biomass of copepods is different in relation to the mean value of the observation data. The differences are in the 20–30% range at the end of May, after experimental data given by Mudrak (2004). In our opinion, on the basis of data from IMGW (see Maritime Branch Materials, 2000), the total biomass of *Pseudocalanus* and *Acartia* computed here amount to ca. 50–60% of all the copepod biomasses in the Gdańsk Deep in 1999.

The results obtained here are different than those given by Mudrak (2004) and Maritime Branch Materials (2000), probably as a result of predation, which is proportional to the increase in predator biomass. During the first half of the year, predation was assumed to be zero because the predator biomass was equal to zero at this time; however, during the second half of the year, predation was considered, because, in our model, the predator is only represented by early juvenile herring. The high biomass of *Pseudocalanus* in May was due to initial numbers of adults which were too large and produced too many eggs in April (the efficiency term X was too high) and the biomass of *Acartia* in May was too low, due to initial numbers of adults which were too small and produced too little eggs in April (the efficiency term X was too low), and the mortality for *Pseudocalanus* was too low and a high number for *Acartia* in the springtime, as well as the low threshold for ingestion of food causing an early increase in weights. This situation could also be caused by migration, which, in our model, is of the same for copepodites of the investigated species.

In our model, the development of copepods adjusts to the dynamics of its food supply. The threshold of food concentration where copepods can survive seems to be an essential parameter at the beginning of the bloom and at the end of summer. The copepod biomass depends on physical and biological processes, such as phytoplankton growth, as well as mortality and predation. We established a low threshold for naupliar and copepodite stages. The simulations show that the zooplankton population clearly misses the phytoplankton bloom, if it is brief. One complete generation of *Pseudocalanus* develops in spring, summer and early autumn. Any increase in the *Pseudocalanus* population starts in the spring bloom time (Fig. 3c) but mainly formes at the turn of spring and summer from individuals of the second generation. Two complete generations of *Acartia* develop in spring and summer. In the case of *Acartia*, the initial growth in population takes place in May after the phytoplankton spring bloom (Fig. 4c). Total biomass of *Acartia* was characterized by the occurrence of two biomass peaks in a year; one in July, mainly formed from individuals of the second generation and another small peak in September, from individuals of the third generation. The numerical simulations show that the investigated species could not be the main factor limiting the phytoplankton spring bloom in the southern Baltic Sea, because the initial development was slow for *Acartia* and faster for *Pseudocalanus*, but the main development formed after the bloom. However, the simulated microzooplankton biomass was enough high (i.e. maximum value ca. 30 mgC m^{-3} in May) to conclude, in our opinion, that, in this case, it was the major cause limiting the spring bloom.

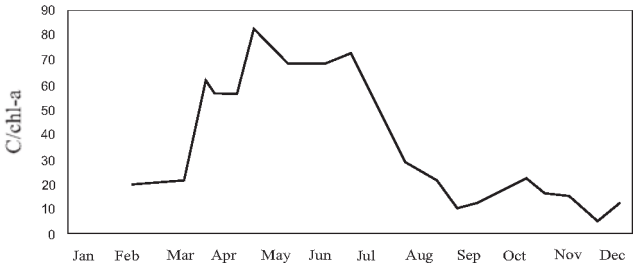

Fig. 7. Carbon-to-chlorophyll-*a* ratio in phytoplankton at a station in the Gdańsk Gulf in the 0–15 m layer (Witek, 1993).

The results are significant changes in the distributions of phytoplankton and zooplankton biomass which have taken place in an area of considerable increase in primary production. In the spring bloom time, a substantial growth of phytoplankton biomass is observed which falls slightly at the next stage, as a result of an increase in the zooplankton biomass, mainly the microzooplankton. The microzooplankton biomass reflects the phytoplankton availability, showing a strong increase with declining food concentration. However, later an increase in mesozooplankton biomass is caused by the weight growth of successive cohorts and also the egg production by each of the female. This situation leads to the substantial growth in the total biomass of the investigated species which is the algebraic sum of the products of the weights, W_i, and numbers, Z_i, ($Z_{\text{meso}} = \sum_{k=1}^{2} \sum_{i=1}^{6} W_{k,i} Z_{k,i}$). These small maxima occurring in the distributions of *Pseudocalanus* and *Acartia* are the results mainly of a brood by successive cohorts, causing their numbers Z_i to increase. Then, early juvenile of herring biomass growth tends to decrease in the micro- and mesozooplankton biomass. Any increase in the predator biomass depends not only on prey concentration but also on energy dissipation, which, in the upper mixed layer, is defined by wind speed. At low prey levels, the rate of mortality is higher than growth and a decrease in predator biomass is observed.

6 Conclusions

The work presents the idea of a 1-D Coupled Ecosystem Model with a high-resolution zooplankton (herbivorous copepods) module for two taxa (*Pseudocalanus* and *Acartia*) as a top-down regulator which may play a significant role in marine ecosystems. The zooplankton community is diverse, comprising large size differences and metabolic heterogeneity. It is therefore of importance to investigate and identify the critical factors. Such models are suitable as tools because hypotheses can be tested, and our understanding of the processes and dynamics can be evaluated. The copepod model links trophic processes and population dynamics, and simulates individual growth within cohorts and the changes in biomass between cohorts.

The population dynamics model for *Pseudocalanus* and *Acartia*, coupled with a 1-D Coupled Ecosystem Model presented in this work, can be utilized to study of the seasonal variability of the above species in the southern Baltic Sea (Gulf of Gdańsk). This paper is a next step in understanding how the population dynamics of a dominant species interact with the environment.

Appendix A

Adaptation of the submodel to investigated copepods

The parameters of the function *fil* – the dependence of the ingestion rate on the food concentration – are ($f_{i_{\max}}$), the maximal ingestion rate, (Foot_o), the minimal threshold food concentration which is the value of Foot at which GROWTH=0, and (k_{Foot}), the ingestion rate as $f_{i_{\max}}/k_{\text{Foot}}$ for Foot which is slightly greater than Foot_o (Steele and Mullin, 1977).

The ingestion rate depends on the developmental stage, food supply, temperature and weight of the animals. We assumed that the first two naupliar stages of *Pseudocalanus* and *Acartia* are unable to ingest particles; they are considered to live on reserves provided by the egg after Berggreen et al. (1988) for *Acartia tonsa*. For the other naupliar stages, N3-N6, we have extrapolated the coefficient $f_{i_{\max}}$, considering a similar increase as for C1. The values of $f_{i_{\max}}$ for C1 – adults were estimated after experimental data which were given by Ciszewski and Witek (1977) for *P. m. elongatus* at 5°C and *Acartia bifilosa* at 15°C from the Gdańsk Depth. The parameters (Foot_o) and (k_{Foot}) are given in Table A1.

The maximum ingestion rate in copepods has been shown to be temperature dependent, but the reported Q_{10} values differ widely (see Table A1). We use an intermediate value of 2.6 for *Acartia* to estimate the t_2 coefficient; consequently, our parameter t_2 has a value of 1.1. However, for *Pseudocalanus* a Q_{10} of 1.9 was assumed after Fennel (2001); hence, a t_2 has a value of 1.066. Coefficient t_1 is calculated so that fte is equal to 1 at 15°C for *Acartia* and 1 at 5°C for *Pseudocalanus* and, therefore, t_1 is equal to 0.239 and 0.726 for *Acartia* and *Pseudocalanus*, respectively. Coefficients t_1 and t_2 are identical for all stages. The assimilation rate (n_a) of 70% is generally considered as representative for copepods (Steele, 1974); hence, the percentage of ingestion egested as fecal material (n_f) is 30%. Supposing first that 30% (n_e) of the ingested matter is used for metabolism and is excreted, and second, that the ratio of the maximum ingestion rate to weight averages 20% (Sciandra, 1986), then a daily excretion rate of 6% of the weight may be attributed to the active metabolism. To adjust total metabolic losses to an average value of 10% of the weight per day (Corkett and McLaren, 1978; Miller and Landry, 1984), we estimate that excretory wastes, due to minimal metabolism (n_w), represent 4% of the body weight (Carlotti and Sciandra, 1989). The growth rate for copepodite stages of *Pseudocalanus* at

Table A1. Parameters used in the copepod submodel and given after some authors: Foot_o: threshold food concentration; Q_{10}: temperature coefficient; W_{egg}: weight of an egg; α: exponent of allometric relation; X: the sex ratio.

Parameter	Species	Value	Source
Foot_o	*Acartia hudsonica* (at the 4 temperatures)	30.5 mgC m^{-3} (at 4°C)	Wlodarczyk et al. (1992)
		11.6 mgC m^{-3} (at 8°C)	
		20.7 mgC m^{-3} (at 12°C)	
		16.4 mgC m^{-3} (at 16°C)	
	Acartia tonsa	45 mgC m^{-3}	Kiørboe et al. (1985)
		0.2–22 mgC m^{-3}	Piontkovski and Petipa (1976)
		5–10 mgC m^{-3}	Turner and Tester (1989)
	Acartia spp.	10 mgC m^{-3} (N3-N6, C1, C2)	in this paper
		20 mgC m^{-3} (C3-C6)	
	Pseudocalanus minutus elongatus	variable	in this paper after Dzierzbicka-Glowacka (2004a, b)
Q_{10}	*Centropages hamatus*	3.8	Kiørboe et al. (1982)
	Neonalanus plumchrus	5.4	Dagg and Wyman (1983)
	Eudiaptomus graciliodes	4.1	Christofferson and Jespersen (1986)
	Temora longicormis	2.4	Dam and Peterson (1988)
	Acartia hudsonica	1.88	Wlodarczyk et al. (1992)
	Acartia tonsa	1.4–3.9	Thompson et al. (1994)
	Acartia clause	1.6–3.3	Kremer and Nixon (1978)
	Acartia spp.	2.6	in this paper
	Pseudocalanus minutus elongatus	1.9	in this paper after Fennel (2001)
k_{Foot}	*Acartia*	28 mgC m^{-3} (N3-N6)	
		70 mgC m^{-3} (C1-C6)	in this paper
α	*Acartia*	0.7	Paffenhöfer (1971)
	Pseudocalanus	0.7	Paffenhöfer (1971)
W_{egg}	*Acartia*	0.0305 μgC	Ambler (1985)
	Pseudocalanus	0.14 μgC	Frost (1989)
X	*Acartia*	20%	in this paper
	Pseudocalanus	80%	in this paper

5°C and *Acartia* at 15°C is shown at Fig. A1 as a function of food concentration.

Here we obtained the number of eggs produced per female per day as a function of growth rate, i.e. multiplying exp GROWTH-1 by $W_{\text{female}}/W_{\text{egg}}$, assuming a maximum growth rate of *Pseudocalanus* for C5 and of *Acartia* for C1 (after McLaren and Leonard, 1995; Dzierzbicka-Glowacka, 2005c). The number of juveniles is defined on the assumtion that eggs are released by the adult female throughtout some time span J. For females from the southern Baltic Sea this value for *Acartia bifilosa* changed with temperature from 20°C to 7°C – from 2 weeks up to about 30 days; for *Pseudocalanus minutus elongatus* – species living in cooler waters than *Acartia* – was about 40 days at a temperature of 7°C and after about 2 months at a temperature of 3°C, after Ciszewski and Witek (1977). The wet weight adult of females is obtained after standard HELCOM (Hernroth, 1985), assuming the organic carbon content of copepods to be $gC/g_{w.w.}$=0.064 (Vinogradov and Shushkina, 1987).

Schmidt et al. (1998) found the mortality of *Acartia tonsa* in the southern Baltic Sea, ca. 7% in winter, 5% in autumn, and negligible in summer and spring (ca. 1%). We use the above value for *Acartia*. However, for *Pseudocalanus* the mortality rate (m_z), as a function of temperature and food concentration, is used after Klein Breteler et al. (1995).

The parameters of migration MIG are the relative amplitude of zooplankton concentration changes (a_w) and the time in which the maximum zooplankton concentration occurs (t_o). The values of 0.6 and 3.25 a.m. for a_w and t_o were estimated by Renk et al. (1983) on the basis of experimental data for the southern Baltic Sea. The vertical distribution of zooplankton in time t_o in the vegetation season was determined as a function of depth ($f(z)=-0.0003775z^2+0.62$) (Dzierzbicka-Glowacka, 1994). Figure A2 shows the diel migration as a function of depth at the following four times: 03:00 a.m., 08:00 a.m., 03:00 p.m. and 08:00 p.m.

We use a value of 5/3 for β in predation PRED; this means that 60% of the ingested food contributes to predator growth

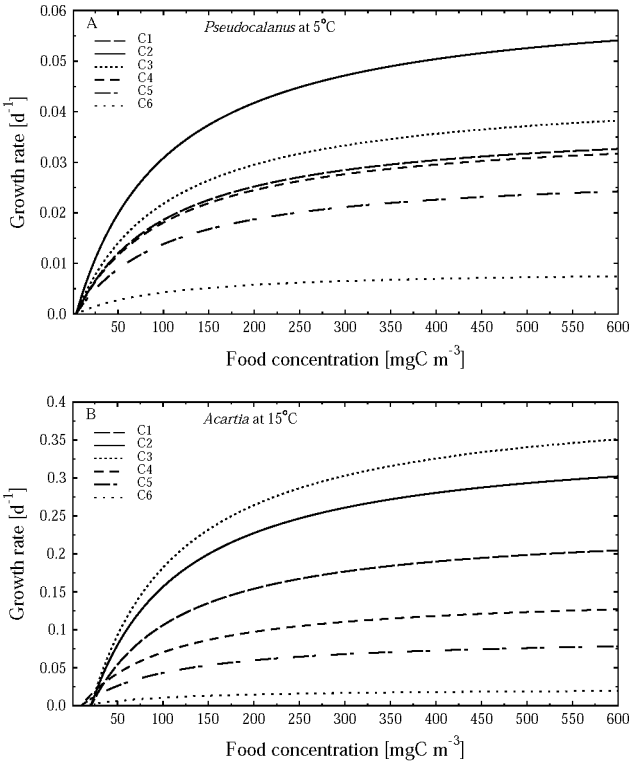

Fig. A1. Growth rate as a function of food concentration at 5°C for *Pseudocalanus minutus elongatus* **(a)** and at 15°C for *Acartia* spp. **(b)**.

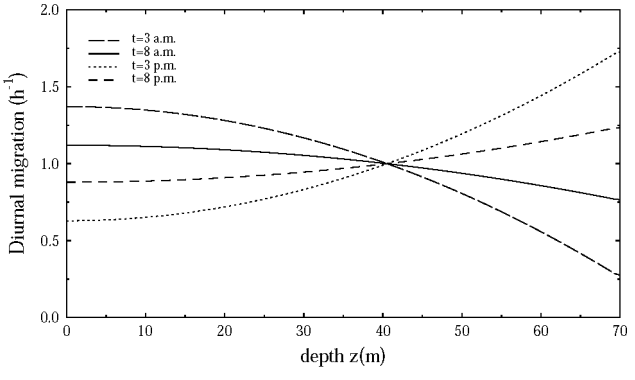

Fig. A2. Daily migration rate as a function of depth at 03:00 a.m., 09:00 a.m., 03:00 p.m. and 09:00 p.m.

and 40% is voided as fecal pellets and excreted material. The detailed description of the process is presented in the work of Dzierzbicka-Glowacka (2005b).

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