Parameterisation of a population model for *Acartia* spp. in the southern Baltic Sea. Part 1. Development time*

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(southern Baltic Sea)

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Abstract

The copepod model (see Dzierzbicka-Głowacka 2005b), reduced to a zero-dimensional population model (Fennel 2001, Stegert et al. 2007), is calibrated for *Acartia* spp. under the environmental conditions typical of the southern Baltic Sea. Most of the coefficients used in the model are taken from the literature, containing values from various published studies and parameters derived for similar species. The parameters for growth are presented in Part 1; those for population dynamics are given in Part 2. Ingestion rates, which are dependent on developmental stage, food supply, temperature and weight of the animals, are estimated for *Acartia bifilosa* at 15°C from the Gdańsk Deep after the experimental data of Ciszewski

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& Witek (1977). In Part 1 the model presents the change in mean individual mass in successive stages. Quantitative formulae are obtained describing the effects of temperature and food concentration on the development time of *Acartia* spp. for each of the model stage groups. The generation time during the seasons in the upper layer of the Gdańsk Deep is also determined. The simulations computed here are similar to the experimental results. Part 2 (Dzierzbicka-Głowacka et al. 2009 – this issue) will evaluate egg production as a function of the above-mentioned parameters, temperature and food availability.

1. Introduction

Planktonic copepods are a major food source for fish larvae in the period of development once the larval yolk sac has been used up. They also form part of the basic diet of many adult pelagic fish. Feeding studies of fish larvae by Załachowski et al. (1975) and Last (1978a,b, 1980) have shown that *Pseudocalanus*, *Acartia* and *Temora* naupliar and copepodid stages are important dietary components of numerous fish species in the Baltic Sea and adjacent waters, i.e., the North Sea and the English Channel, as well as in Scottish, Nova Scotian and Canadian Arctic waters.

In this study the development and population dynamics of copepods *Acartia* spp. in the changing environmental conditions of the southern Baltic Sea has been modelled. Knowledge of the population dynamics of copepods – a major food source for young fish – is essential for forecasting purposes, and a number of such models have been produced recently. This type of study was carried out for *Pseudocalanus* spp. (Fennel 2001, Dzierzbicka-Głowacka 2005a,b, Stegert et al. 2007).

Experiments on the ingestion rate of *Acartia* spp. suggest that this parameter is directly proportional to food concentration and that it is strongly influenced by food quality. The feeding of *Acartia* spp. has also been found to accelerate with temperature. However, the combined effect of food concentration and temperature as a function of these two parameters on growth and stage duration has not been established for *Acartia* spp. in the southern Baltic Sea. This is a key statement, since it is the motivation and justification for the present study. Part 1 of this series of articles discusses the relationships between the investigated variables (mean weight and development time) and temperature and food concentration, which were found by adapting a population model following the appropriate transformation of literature data.

In Part 2 (Dzierzbicka-Głowacka et al. 2009 – this issue) the numbers of eggs produced per female per day will be calculated. In Part 1 the hypothesis (Sekiguchi et al. 1980) that the food-saturated rate of production of egg matter is equivalent to the maximum specific growth rate of copepods will be applied.

2. Copepod model

The copepod model (see Dzierzbicka-Głowacka 2005b), reduced to a zero-dimensional population model (see Fennel 2001, Stegert et al. 2007), consists of sixteen state variables with masses W_i and numbers Z_i for each of eight model stages, grouped as follows: eggs-N2 – non-feeding stages and eggs; N3–N6 – naupliar stages; C1, C2, C3, C4, C5 – the five copepodid stages; C6 – the adult stage. Each of the eight model stages consists of two equations (for each age class-cohort, two state variables represent the mass W_i and the number Z_i of individuals):

$$\frac{\partial W_i}{\partial t} = ING_i - FEC_i - MET_i, \tag{1}$$

$$\frac{\partial Z_i}{\partial t} = -MOR_i - PRED_i. \tag{2}$$

Equation (1) enables the change in weight of an individual copepod during its developmental stages to be calculated as the sum of its individual gains and losses of energy ($GROWTH = ING - FEC - MET$); equation (2) represents the effects of mortality and predation in a given cohort as a function of the numbers in that cohort in the appropriate developmental stage. Equations for each state variable are formulated by employing the critical mass concept of Carlotti & Sciandra (1989). It defines a specific stage i by a mass W_i within the values $CW_{i-1} < W_i \leq CW_i$: hence, these critical masses CW_i have to be defined for each stage. Extreme values CW_i, derived from literature data (Ciszewski & Witek 1977), were used for the weight-dependent function of ingestion.

The initial weight of the spawned eggs is set at 0.0305 μgC egg^{-1} (Ambler 1985). The animals do not feed at this stage. Embryonic development depends on the actual temperature and time, in accordance with Bělehrádek's function (see Table 1 – embryonic duration).

All individuals in stages N3 to adult feed, have metabolic expenditures and grow. A constant proportion of adults are ovigerous females.

The different biological processes controlling growth and population dynamics are presented in Figure 1. The processes taken into account are presented in Table 1 and a list of abbreviations used in the model is given in Table 2.

Weight is characterised by growth, which depends on food and temperature, and can be expressed by stage duration, a state variable controlling the moulting process. The growth rate is expressed in carbon mass units.

The ingestion rate ING for specific developmental stages is dependent firstly on the food concentration $Food$ according to the function fil_i and

Table 1. Mathematical formulae for the relationships used in the model; i – stages, $Food$ – food concentration, T – temperature, W_i – weight, CW_i – critical weight, Z_i – number, W_{egg} – weight of egg, W_{female} – weight of female, B – predator biomass, g – growth rate of predator

Process	Units	Formulae
growth	μgC d^{-1}	$GROWTH = ING - FEC - MET$
growth $i = Ad$	μgC d^{-1}	$GROWTH_{Ad} = ING_{Ad} - FEC_{Ad} - MET_{Ad} - ProdEgg$
ingestion	μgC d^{-1}	$ING_i = fil_i fte_i fw_i fm_i$
influence of food		$fil_i = f_{i,\max}\left\{1 - \exp\left(\frac{-(Food - Food_o)}{k_{Food}}\right)\right\}$
influence of temperature		$fte_i = t_1 t_2^T$
allometric relation		$fw_i = W_i^{\alpha}$
limitation as moulting weight		$fm_i = \begin{cases} 1 & \text{if } W_i < CW_i \\ 1 - \frac{(W_i - CW_i)^2}{(CW_{i+1} - W_i)^2} & \text{if } W_i \geq CW_i \end{cases}$
faecal pellets	μgC d^{-1}	$FEC_i = (1 - n_a) ING_i = n_f ING_i$
metabolism	μgC d^{-1}	$MET_i = M_s + M_a$
basic metabolism		$M_s = n_w W_i$
active metabolism		$M_a = n_e ING_i$
egg matter	μgC d^{-1} female^{-1}	$ProdEgg = \exp GROWTH_{nauplii} - 1$
embryonic duration	d	$D_e = a(T + \alpha_e)^b$
dynamics		
mortality	no. m^{-3} d^{-1}	$MOR_i = m_z Z_i$
predation	no. m^{-3} d^{-1}	$PRED_i = \beta g B / W_i$
eggs	no. female^{-1} d^{-1}	$EGG = XZ_{Ad} \int_J Egg$; $Egg = \frac{W_{female}}{W_{egg}} \times ProdEgg$

Table 2. List of abbreviations used in the model

Parameters	Units	Definitions
α	dl	exponent of allometric relation
α_e	dl	temperature coefficient
a	dl	population specific constant
β	dl	coefficient of proportionality for predation
b	dl	slope of the line D_e, constant $b = -2.05$
B	μgC m^{-3}	predator biomass
CW_i	μgC	critical weight
D_e	d	embryonic matter
Egg	no. egg female^{-1} d^{-1}	numbers of eggs
FEC	μgC d^{-1}	faecal pellets
$Food$	μgC m^{-3}	food concentration
$Food_o$	μgC m^{-3}	minimal threshold food concentration
$f_{i,\max}$	d^{-1}	maximum ingestion rate
g	d^{-1}	growth rate of predator
ING	μgC d^{-1}	ingestion
J	d	time span
k_{Phyt}	μCg m^{-3}	half-saturation constant
MET	μC d^{-1}	metabolism
MOR	no. m^{-3} d^{-1}	mortality
m_z	d^{-1}	morality rate
n_a	dl	assimilation efficiency (0.7)
n_e	dl	coefficient of proportionality
n_f	dl	percentage of ingestion egested as faecal material
n_w	d^{-1}	routine excretion rate
$PRED$	μgC d^{-1}	predation
$ProdEgg$	μgC d^{-1} female^{-1}	egg matter
t_1	dl	temperature coefficient
t_2	dl	temperature coefficient
W_{egg}	μgC	weight of egg
W_{female}	μgC	weight of female
W_i	μgC	weight
Z_{Ad}	no. m^{-3}	number of adults
Z_i	no. m^{-3}	number
X	dl	sex ratio

dl – dimensionless.

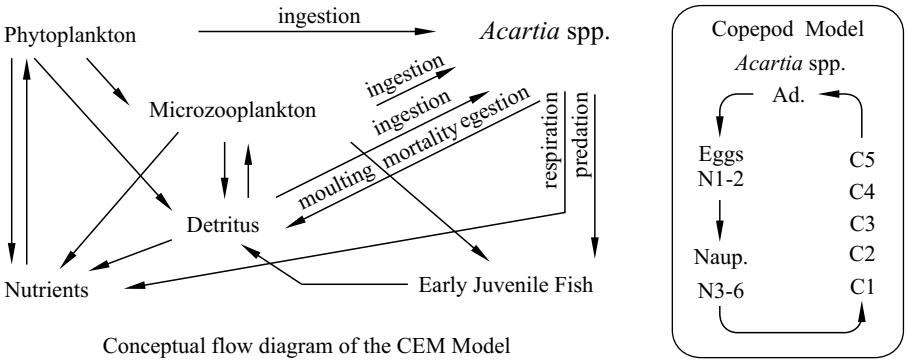

Figure 1. Conceptual flow diagram of the CEM Model with a copepod model for *Acartia* spp.

secondly on temperature T, following the constant Q_{10} (temperature coefficient) law fte_i. The allometric relation, expressed by Paffenhöfer (1971), is fw_i, in which the maximum ingestion rate increases with weight during development. The function fm_i concerns the copepod's mode of life during the moulting cycle. Moulting to the next stage occurs when the 'critical moulting weight' has been reached. During the moulting process a small proportion of the weight is lost (Carlotti & Wolf 1998); this was not included in previous versions of my model (Dzierzbicka-Głowacka 2005, Dzierzbicka-Głowacka et al. 2006).

The assimilated matter is considered to be a constant proportion of ingested matter, the difference being represented by faecal pellets FEC, which immediately enter the detritus pool. Metabolic MET expenditure is divided into two components: basic M_s and active M_a metabolism.

The number of juveniles EGG is defined on the assumption that eggs are released by the female during a time span J. Mature adults use ingested matter for maintenance and reproduction (Sekiguchi et al. 1980). The reproductive rate per individual female can be converted to the equivalent amount of egg matter per day as a percentage of female weight (see Corkett & McLaren 1978, McLaren & 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.

Mortality MOR is determined as the average mortality rate m_z, which depends on food and temperature.

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 next section describes the model details for growth processes; the corresponding details for population dynamics will be given in Part 2.

3. Adaptation of the copepod model to *Acartia* spp. from the Gulf of Gdańsk

The parameters of the function fil, i.e. the dependence of the ingestion rate on the food concentration, are $f_{i,\max}$ – the maximum ingestion rate, $Food_o$ – the minimal threshold food concentration (i.e. the value of $Food$ at which $GROWTH = 0$), and k_{Food} – the ingestion rate, as $f_{i,\max}/k_{Food}$ for $Food$ is slightly greater than $Food_o$ (Steele & Mullin 1977).

It was assumed that the first two naupliar stages of *Acartia* are unable to ingest particles; they are thought to survive on reserves provided by the egg (see Berggreen et al. (1988) for *A. tonsa*). For the other naupliar stages, N3–N6, the coefficient $f_{i,\max}$ was extrapolated on the assumption of a similar increase as for C1. The values of $f_{i,\max}$ for C1 – adults were estimated from experimental data given by Ciszewski & Witek (1977) for *A. bifilosa* at 15°C from the Gdańsk Deep.

Wlodarczyk et al. (1992) determined threshold food concentrations for *A. hudsonica*; they corresponded to carbon concentrations of 30.5, 11.6, 20.7 and 16.4 mgC m^{-3}, and were not significantly different at four temperatures: 4, 8, 12 and 16°C. The value of $Food_o$ was comparatively high in *A. tonsa* fed on the small alga *Rhodomonas baltica* (45 mgC m^{-3} – Kiørboe et al. 1985) but low for large species like the dinoflagellate *Gymnodinium fissum* (0.2–22 mgC m^{-3}, Piontkovskii & Petipa 1976). Turner & Tester (1989) made extensive measurements of feeding by *A. tonsa* females in natural assemblages dominated by diatoms and dinoflagellates. Their studies suggest thresholds from 5 to 10 mgC m^{-3}.

In this study a threshold food concentration $Food_o$ of 20 mgC m^{-3} was selected for the larger copepodid C3–C5 and adult stages, and a lower threshold of 10 mgC m^{-3} for nauplii (N3–N6) and smaller copepodids. However, the half-saturation coefficients, k_{Food}, ranged from 28 mgC m^{-3} for the nauplii to 70 mgC m^{-3} for the copepodids and adults (see Verity & Smayda 1989 – their data suggest that k_{Food} ranges from 60 to 75 mgC m^{-3}).

The maximum ingestion rate increases exponentially with temperature following a Q_{10} varying from 1.4 to 3.9 for *A. tonsa* (Thompson et al. 1994), from 1.6 to 3.3 for *A. clausi* (Kremer & Nixon 1978), and 1.88 for *A. hudsonica* (Wlodarczyk et al. 1992).

In the present study an intermediate value of 2.6 for *Acartia* was used to estimate coefficient t_2: consequently, this has a value of 1.1. Coefficient t_1

is calculated so that fte is equal to 1 at 15°C for *Acartia*; t_1 is therefore equal to 0.239. Coefficients t_1 and t_2 are identical for all stages.

The exponent α of the allometric relation between weight and ingestion generally lies between 0.6 and 0.8 for copepods (Paffenhöfer 1971). Here a value of 0.7 was adopted for all the stages.

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

An assimilation rate n_a of 70% is generally considered representative of copepods (Steele 1977); hence the percentage of ingestion egested as faecal material n_f is 30%. Nauplii N1 and N2, which do not feed, are assumed to consume 20% of their weight per day for basic metabolism n_w. Nauplii from N3 to N6, copepodids 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 n_e.

Experimental studies have shown that some species of crustaceans with normal development stop eating just before and during the moulting period (Paffenhöfer 1971). Paffenhöfer & Harris (1976) observed a slowing down of feeding activity in *Temora longicornis* before the moult to C1 and before the last moult to adult. Presumably, ingestion decreases as the weight reaches the critical moulting weight, because growth is limited by the exoskeleton. Here, it is assumed that ingestion in one stage follows a negative parabolic function fm_i when the weight exceeds the critical moulting weight of stage i, CW_i. Such a limitation does not occur in adults for which reproduction limits weight increase (see Carlotti & Sciandra 1989).

Bělehrádek's function has been used extensively to describe the embryonic duration of *Acartia* species (McLaren 1978) under adequate food conditions. In the present study, the embryonic duration D_e was estimated after Norrbin (1996) for *A. longiremis*, the value of which is similar to the 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.

4. Results

The system of differential equations (1) and (2) for each of the eight model stages was solved using the Crank-Nicolson method of numerical integration with a time step of 900 s. The model gave the rates of the biological processes and the values of state variables in each age class for every stage at any time.

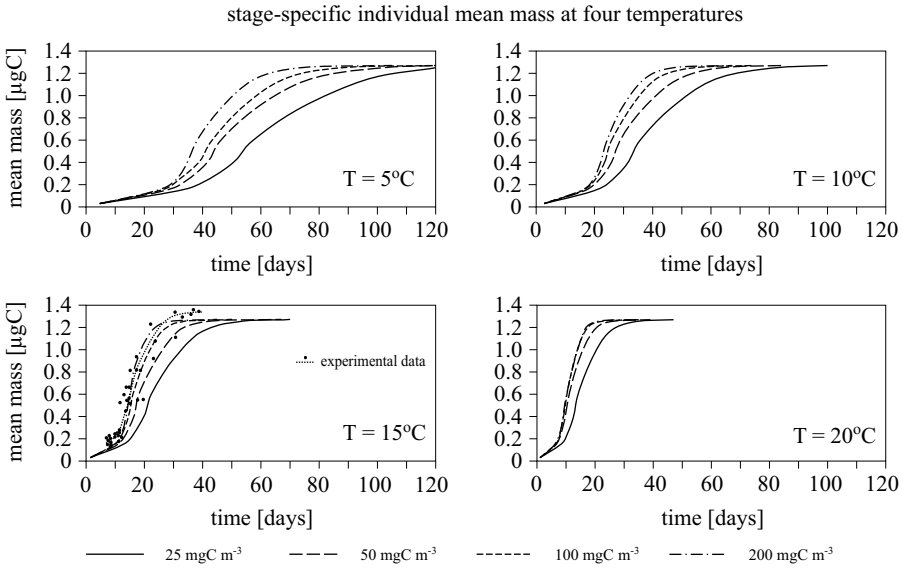

Figure 2. Growth of *Acartia* spp. from the southern Baltic Sea. Simulated mean individual body mass W_i [μgC] as a function of time [days] for 5°C, 10°C, 15°C and 20°C at selected food concentrations: 25 mgC m^{-3}, 50 mgC m^{-3}, 100 mgC m^{-3} and 200 mgC m^{-3}. Experimental data of the mean body mass after Ciszewski & Witek (1977) (dotted line)

It was used to simulate the effect of temperature and food on the development of *Acartia* spp. at temperatures 5, 10, 15 and 20°C for different food levels of 25, 50, 100 and 200 mgC m^{-3}.

The change in mean mass reflects the growth of individuals, and the model enables the mean individual mass in successive stages to be presented. Figure 2 illustrates the temporal development of the simulated mean mass of *Acartia* spp. for selected food concentrations at the four temperatures. The simulated growth reaches a maximum between copepodid stages C2 and C3 (see Figure 3). The effect of food concentration on the mean mass is small in the naupliar stage, but is more pronounced in later developmental stages than in the early copepodids. This interaction decreases with increasing temperature. At 20°C (Figure 2d), for concentrations > c. 180 mgC m^{-3}, there is no marked influence because of the saturation of the ingestion process formulated by the function fil_i (see Table 1). Between 20 and 180 mgC m^{-3}, growth is strongly affected by the variation in food level. Growth rates are reduced, in particular at concentrations < 40 mgC m^{-3} for model stage N3–C1 and $<$150–180 mgC m^{-3} in the given temperature range for the other stages. However, for very low food levels (< 20 mgC m^{-3}), the copepods die before developing fully.

The effect of temperature is very evident. Generally, temperature is hypothesised to influence several processes involved in the metabolism, such as filtration, ingestion and excretion, or more general processes, such as growth or development. The results show that the effect of temperature

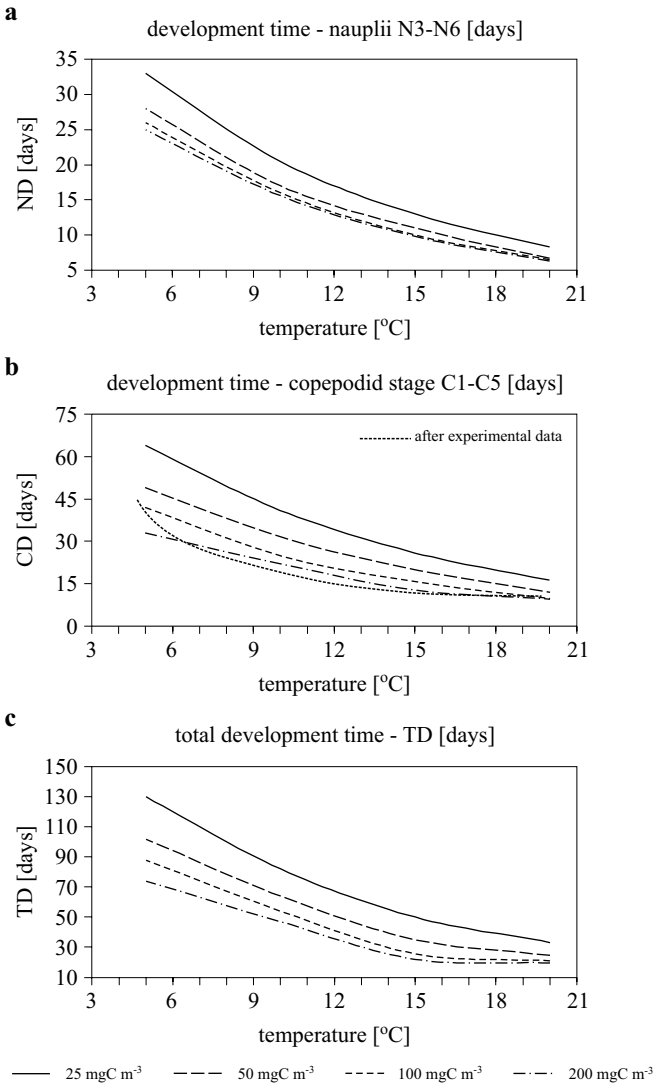

Figure 3. Relationships between the development time for each of the model stages of *Acartia* spp. from the southern Baltic Sea [days] and temperature T [°C] at different food concentrations: 25 mgC m^{-3}, 50 mgC m^{-3}, 100 mgC m^{-3} and 200 mgC m^{-3}; (a) naupliar stage, (b) copepodid stage C1–C6, (c) total development time and (d) all copepodid stages separately (C1, C2, C3, C4, C5, C6). Experimental data after Ciszewski & Witek (1977) (dotted line)

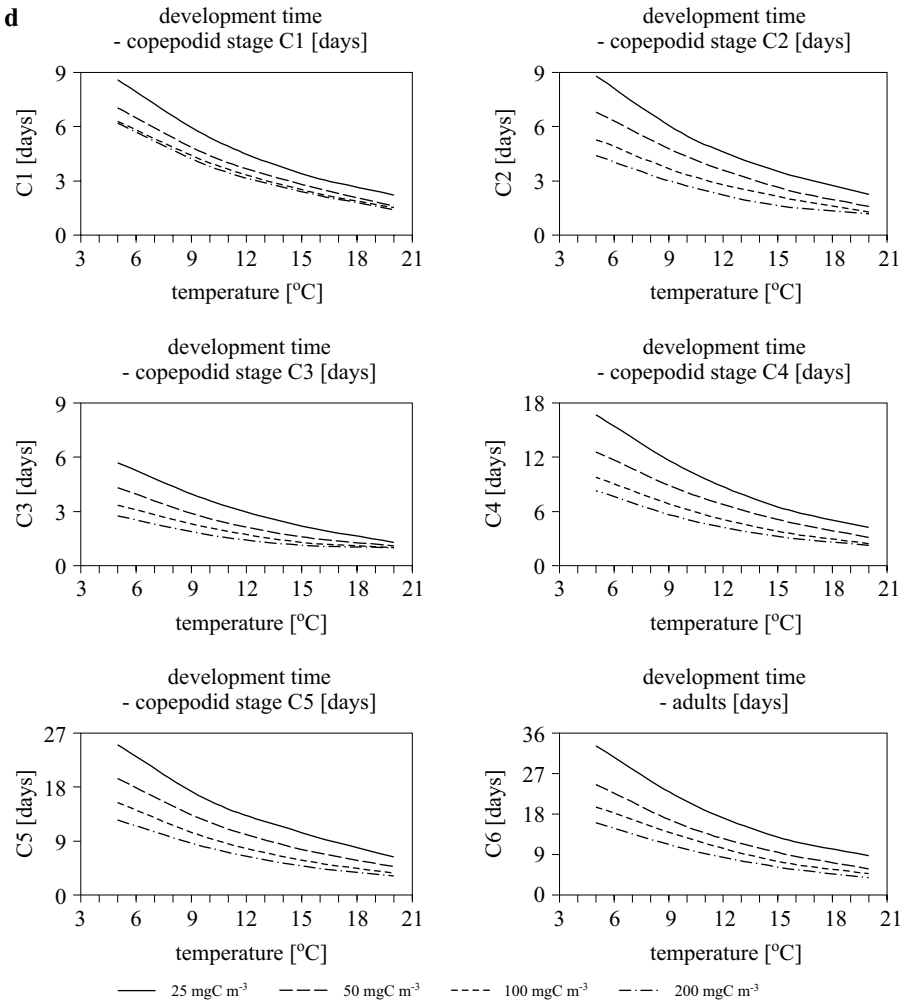

Figure 3. (*continued*)

on ingestion only, which has an indirect effect on excretion and assimilation, is sufficient to simulate correctly the action of temperature on the rate of development.

The development of individuals from eggs to adults was manifested by a change in the total stage duration as a function of both temperature and food concentration. The development of *Acartia* spp. for the investigated stages computed with equation (1) was used to obtain the stage duration. According to growth rate and weight data, the stage durations of *Acartia* spp. for the model stages were obtained by numerical solution of polynomials of unknown degrees. The polynomials at the given temperature

and food concentration were described by

$$W_i(1+g_i)^n(1+g_i)^d = W_{i+1}, \tag{3}$$

where W_i is the mean body weight for successive copepodid stages, g_i is the growth rate, and $D = n + d$ is the stage duration (e.g. when $n = 5$ and $d = 0.36$, then $D = 5.36$ days), and D is an unknown quantity. Transformation of these data yields a linear relationship between the logarithm of temperature and stage duration at selected food levels:

$$D = a \ln T + b. \tag{4}$$

The values of a, b and the correlation coefficient at food levels 25, 50, 100, 200 and max mgC m^{-3} were calculated; the correlation coefficients were in the 0.89–0.98 range. Then coefficients a and b were also described as a function of food concentration by means of a linear-log regression. The regression equations with the correlation coefficients are given in Table 3.

By substituting a and b in equation (4) for the equations in Table 3, the stage duration for each of the model stages of *Acartia* spp. becomes

Table 3. The coefficients a and b of equation (3) describing the stage duration D (in days) as a function of food concentration $Food$ (in mgC m^{-3}); $\mathbf{D = a \ln T + b}$

Duration	$a = a_1 \log\ Food + b_1$	r	$b = a_2 \log\ Food + b_2$	r
naupliar stage	$a = 27.20 \log Food - 106.19$	0.978	$b = -0.2486 \log Food + 4.4239$	−0.935
copepodid stage	$a = 16.05 \log Food - 55.57$	0.978	$b = -54.76 \log Food + 190.84$	−0.976
C1	$a = 1.065 \log Food - 5.891$	0.895	$b = -3.860 \log Food + 20.58$	−0.903
C2	$a = 2.301 \log Food - 7.760$	0.975	$b = -7.882 \log Food + 26.86$	−0.973
C3	$a = 1.787 \log Food - 5.504$	0.974	$b = 5.770 \log Food + 18.314$	−0.971
C4	$a = 4.509 \log Food - 14.9$	0.970	$b = -14.92 \log Food + 50.365$	−0.960
C5	$a = 7.090 \log Food - 23.296$	0.979	$b = -23.15 \log Food + 77.74$	−0.971
C6	$a = 8.716 \log Food - 29.12$	0.976	$b = -29.36 \log Food + 99.19$	−0.966
Total time	$\mathbf{a = 27.20 \log Food - 106.19}$	**0.978**	$\mathbf{b = -95.75 \log Food + 366.93}$	**−0.972**

a function of both food concentration from 25 mgC m^{-3} to excess and temperature in the 5–20°C range.

The stage duration curves for the total development time ($D = TD$), the development times for the copepodid stage ($D = CD$) and the naupliar stage ($D = ND$) are shown in Figure 3. The curves illustrate the effects of interactions between temperature and food concentration on the total stage duration of *Acartia* spp. The effect of temperature (non-limiting food conditions) is manifested as follows: at 5°C the first adults appeared after 58 days, at 10°C after 37 days, at 15°C after 22 days and at 20°C after only 15.9 days. The total development time decreases with increasing temperature, which is a consequence of the greater ingestion with temperature according to the function fte_i. Increasing the food supply shortened the stage durations. At 15°C the function $fte_i = 1$, total development took about 52 days at 25 mgC m^{-3} and 28 days at 200 mgC m^{-3}, which corresponds almost to food saturation. The differences in generation time TD were less at higher food concentrations ($\Delta TD \approx 5$ days between 100 and 200 mgC m^{-3}) than at lower ones ($\Delta TD \approx 12$ days between 25 and 50 mgC m^{-3}). The changes occurring in the total development time with variations in temperature and food concentration were more pronounced at low temperatures (< 10°C) and low food levels.

Figure 4 illustrates the effect of food composition and temperature on the total development time of *Acartia* spp. during the seasons in the upper 20 m layer in the Gdańsk Deep. The temperature and food concentration (equalling 60% of the phytoplankton biomass, 15% of the microzooplankton biomass and 25% of the pelagic detritus concentration) used in this paper are mean values from the last 5 years (2001–05) (data from the 1DCEM model – Dzierzbicka-Głowacka et al. 2006), which were obtained using another formula for primary production (Renk 2000). For the population of *Acartia* spp., food – a mixture of phytoplankton and detritus – results in an available food concentration that increases considerably to 235 mgC m^{-3} at the beginning of April, but drops to 80 mgC m^{-3} by the end of June. The comparatively high food level is sustained during the summer. When the temperature reaches its maximum, the food concentration assumes a value of about 135 mgC m^{-3} by the end of August.

The influence of temperature and food concentration on the duration of each of the model stages is similar, as described above. The annual cycle of the total development time is the result of the above-mentioned parameters, but mainly temperature. The stage duration is inversely related to temperature. *Acartia* spp. lives longer at lower than higher temperatures. When the population is starving, the total development time is c. 135 days

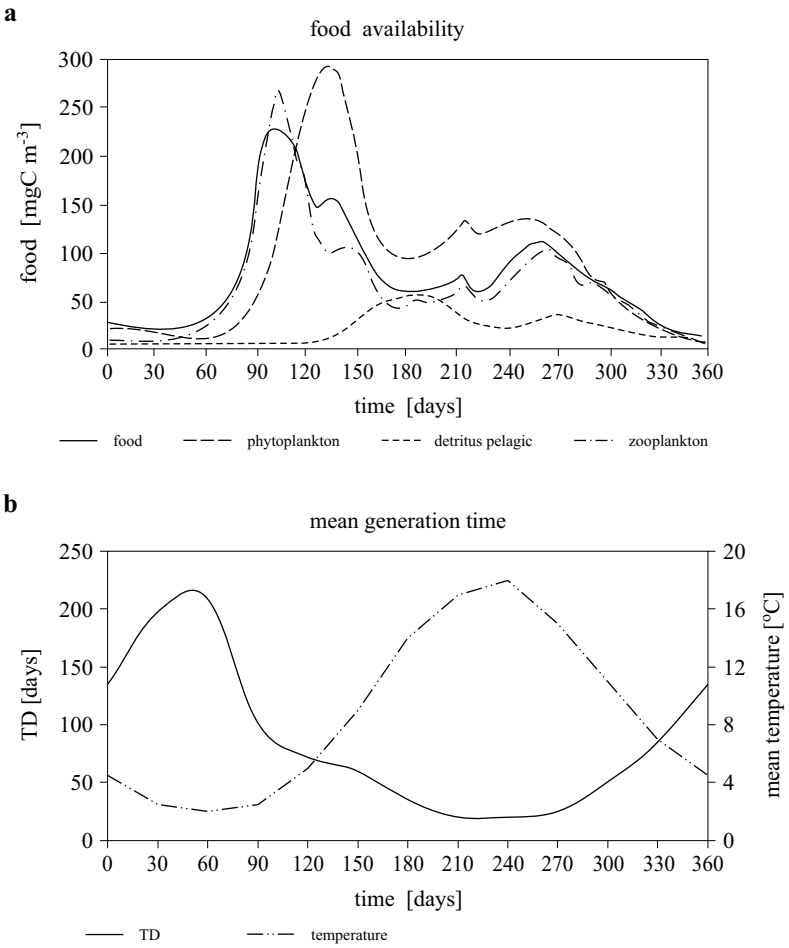

Figure 4. Simulated forcing and development of zooplankton for the annual cycle in the Gdańsk Deep; (a) mean food availability, (b) mean generation time of *Acartia* spp.

at 4.5°C at the beginning of the year and c. 209 days at 2°C at the end of February. However, at 4.5°C it drops to 100 days when the food concentration rises to high values, at which the growth rate tends to become constant during the spring bloom. Hence, at low temperatures and food concentrations, the individual only reaches maturity after some considerable time (200 days). This situation is observed in winter (February). But at high temperatures and a sufficiently high food concentration ($T = 18$°C and $Food = 135$ mgC m^{-3}), copepods can reach maturity after just 20 days. During the summer, stage duration anticorrelates with food supply and temperature. At the end the of the summer, reduced amounts of food

and maximum water temperatures result in an extension of the development time beyond the critical time, which is the minimum time for the total development of one complete generation (from eggs to adults).

5. Discussion

Several interactions of broad biological and ecological significance were obtained in the present study. An attempt was made to formulate some general statements about developmental processes in *Acartia* spp. in the southern Baltic Sea by combining the experimental data in Ciszewski & Witek (1977) with those from other papers (see section 3). The population model formulations for a typical copepod life cycle were adapted from Dzierzbicka-Głowacka (2005b, 2006) in that the moulting process was added.

An important interaction is the one resulting from the effects of temperature and food concentration on growth.

On the basis of material collected in the Gulf of Gdańsk (Baltic Sea), Ciszewski & Witek (1977) calculated the growth rate of *Acartia bifilosa*. The water in the experimental vessels was changed every 2 days, and fresh water was filtered through 64 μm gauze. The frequent changes of water in the experimental vessels enabled the food composition to be kept similar to that in the marine environment. Depending on the season when the experiment took place, the phytoplankton concentration in the sea varied from 100 000 cells dm^{-3} in February up to 5 000 000 cells dm^{-3} in April and back to 250 000 cells dm^{-3} in October. The main sources of food were *Kirchneriella obesa*, *Microcystis aemginosa*, *Euglena* sp., *Navicula* sp. and *Gymnodinium* sp. The growth rate of *A. bifilosa* obtained by those authors was 21% for C1, 31% for C2, 36% for C3, 13% for C4, 8% for C5 and 2% of body weight day^{-1} for adults at 15°C. The copepodids grew at different rates, depending on age. The inflexion on Figure 2 (dotted line), drawn to a great approximation among the points, is sigmoid. Body weight increase in the youngest copepodids of *A. bifilosa* was relatively slow, but growth was intensive in the 4–12 μg body wet weight range ($\approx$ 0.256–0.768 μgC). The growth rate of older specimens decreased gradually. The weight of adult copepods stabilised at the level of 18–20 μg wet weight ($\approx$ 1.152–1.28 μgC). The development time of the copepodid stages in *A. bifilosa* decreased from about 27 days to 11.5 days with a temperature rise from 7°C to 20°C. Correspondingly, adults completed their growth during 30 days and 2 weeks, respectively (after Ciszewski & Witek 1977).

The changes in mean mass, reflecting the growth of the individuals computed here (black lines), are similar to the experimental data (dotted line) given by Ciszewski & Witek (1977) for a temperature of 15°C and a food concentration of c. 200 mgC m^{-3} (see Figure 2). The simulated

growth of *Acartia* spp. increases rapidly with rising temperature in the 5–20°C range but less so with a food concentration from 25 mgC m^{-3} to excess ($\approx$ 200 mgC m^{-3}).

For the different temperatures, the curves of population mean mass are sigmoidal, suggesting the more or less exponential growth in the naupliar and early copepodid stages (C1–C4), followed by saturation as the adults appear. Similar curves were previously drawn by Miller et al. (1977) for *A. clausi* and *A. tonsa*. These authors demonstrated that several species of the copepod genus *Acartia* completed each moult-to-moult phase of the life cycle over a constant period of time. They also showed that the increase in mass during each phase was a nearly constant fraction of the weight at the beginning of the stage and that growth in *Acartia* is exponential in time throughout most of the life cycle. In the present study, stage duration was found to be a useful indicator for assessing the quality of the simulation. The development times for the copepodid stages of *Acartia* spp. (CD) under conditions of excess food computed here resemble the earlier results given by Ciszewski & Witek (1977) at much the same range of temperature (see Figure 3b – dotted line); the small difference in CD is due to the difference in food concentration. The present study has also demonstrated that the development time for each of the model stages of *Acartia* spp. is a function of both temperature in the 5–20°C range and food concentration from 25 mgC m^{-3} to excess, rising with decreasing temperature and food concentration in the studied ranges. Particularly at lower food concentrations, the stage duration became progressively longer with each further developmental stage. At the highest food concentration the stage durations CD and ND were similar (c. 20 days at low temperatures and c. 7 days at high ones). The generation time curves run almost parallel and there were only small differences between the curves at the higher food levels. Klein Breteler et al. (1995) made similar findings in experiments with *Temora longicornis*, *Acartia clausi* and *Pseudocalanus elongatus*. *A. clausi* from the North Sea was bred 3 times from naupliar stages N1 and N2 to maturity at 5, 10, 15 and 20°C and 4 different portions of autotrophic and heterotrophic food (Klein Breteler & Schogt 1994). These authors obtained relations, described by Bělehrádek's function, between development time and temperature for different food levels. These relations predict a generation time of about 50 days under spring bloom conditions and slightly less during summer due to food limitation. Miller et al. (1977) stated that the median time required for the development of *A. clausi* from Jakle's Lagoon was 12 days at 20°C; for *A. tonsa* from Chesapeake Bay it was 20 days at 12°C, 11 days at 15°C, 7.5 days at 20°C, 4.9 days at 25.5°C and 4 days at 30.7°C.

In this study, the simulated total development time (TD) of *Acartia* spp. from the southern Baltic Sea is in the 75–50 days range during the spring bloom time, i.e. at 6–10°C with an excess of food, and is similar to TD given by Klein Breteler & Schogt (1994). TD obtained here is half as long during summer, i.e. about 25 days in the 16–20°C temperature range, but twice as long as TD for *Acartia clausi* and three times as long as TD for *A. tonsa* after Miller et al. (1977).

6. Conclusions

This paper discusses the modelling of the combined effect of temperature and food concentration on growth and stage duration of *Acartia* spp. in the southern Baltic Sea. It presents a comprehensive description of the parameterisation of a copepod model for *Acartia* spp. to represent realistic development. The copepod model enabled the mean individual mass in successive stages to be calculated for selected food concentrations at four temperatures. On the basis of quantitative expressions describing the effects of the above parameters on the development time for each of the model groups, the total stage duration of *Acartia* spp. from the Gdańsk Deep was obtained for the modelled temperature and available food concentration (food consisting of phytoplankton, microzooplankton and pelagic detritus). Simulated generation times were affected mostly by temperature, to a lesser degree by food availability. The calculations also suggest that three complete generations (from eggs to adults) of *Acartia* spp. from the Gdańsk Deep can develop during a single year in the upper layer. The individuals of the second generation develop more rapidly as a result of the mainly high temperature. Such population models are suitable as tools because hypotheses can be tested, and our understanding of processes and dynamics can be evaluated. Zooplankton has characteristic growth and development rates that are important in ecosystem dynamics and should be considered in ecosystem models. This paper is a further step towards understanding the population dynamics of one of the dominant species in the Baltic Sea and how it interacts with the environment.

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