Parameterisation of a population model for *Acartia* spp. in the southern Baltic Sea. Part 2. Egg production*

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Abstract

The paper describes the modelling of egg production in *Acartia* spp. under changing environmental conditions in the southern Baltic Sea (Gdańsk Deep). The hypothesis (Sekiguchi et al. 1980) that the food-saturated rate of egg matter production is equivalent to specific growth rate of copepods is applied. The average number of eggs produced per day by one *Acartia* female is obtained as a function of growth rate, i.e. by multiplying $\exp g_{N3} - 1$ from the growth rate of the nauplius stage equation by W_{female}/W_{egg}. The copepod model, reduced to a zero-dimensional population model calibrated for *Acartia* spp. under the environmental conditions typical of the southern Baltic Sea, was used to determine the effects

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of temperature and food concentration on the growth rate of each of the model stages (see Part 1 – Dzierzbicka-Głowacka et al. 2009 – this issue). In this part, egg production as a function of the above parameters is evaluated. The rate of reproduction during the seasons in the upper layer of the Gdańsk Deep is also determined.

1. Introduction

Although adult male copepods may not feed, adult females certainly do. Yet they cannot grow in the usual sense after the final moult to adulthood. Paffenhöfer & Harris (1976) make a curious attempt to calculate growth rates of adults from '50% adult to full adult'. This may compound the effects of larger adults maturing later, oogenesis and possibly fat deposition; moreover, very small estimates of growth rate do not appear to be very useful. The most significant use of food by females is surely in egg production. It is possible to determine the potential rate of production of egg matter in the same terms that we have used for the growth of body dry weight (Corkett & McLaren 1978). Planktonic copepods (*Acartia*, *Pseudocalanus*, *Temora*) are important components of the diet of a number of different species of fish in the Baltic Sea and adjacent waters, i.e. the North Sea and the English Channel, as well as Scottish, Nova Scotian and Canadian Arctic waters.

The paper presents describes the population dynamics of *Acartia* spp. Copepods – their development (Part 1) and egg production (Part 2) – in the changing environmental conditions of the southern Baltic Sea. 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).

Part 1 described the relationships between the investigated variables (mean weight and development time) and temperature and food concentration, found by adaptation of a population model (Dzierzbicka-Głowacka et al. 2009 – this issue).

In the present work (Part 2), the combined effect of food concentration and temperature as a function of these two parameters on the number of eggs produced per female per day is established for *Acartia* spp. The hypothesis that the food-saturated rate of egg matter production is equivalent to the maximum specific growth rate of copepods was tested some years ago by Sekiguchi et al. (1980) for *Acartia clausi hudsonicus*, by Berggreen et al. (1988) for *Acartia tonsa*, by Fryd et al. (1991) for two *Centropages* species,

by McLaren & Leonard (1995) for four *Calanus* species and by Dzierzbicka-Głowacka (2005c) for two *Pseudocalanus* species.

Here we analyse studies of *Acartia* spp. to test the equivalence of growth rate and egg production. The main objective of this paper is to derive a quantitative expression to describe the egg production per day by *Acartia* females as a function of temperature and food concentration via the growth rate, which was obtained in Part 1. The calculations are made for *Acartia* spp. from the Gdańsk Deep (southern Baltic Sea).

2. Adaptation of the copepod model to *Acartia* spp.

The copepod model, reduced to the zero-dimensional population model presented in Part 1 (see Dzierzbicka-Głowacka et al. 2009), 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). The change in weight of an individual copepod with respect to its developmental stages is determined as the sum of its individual gains and losses of energy ($GROWTH = ING - FEC - MET$); the effects of mortality MOR and predation $PRED$ in a particular cohort are functions of the numbers in that cohort in the relevant developmental stage.

The different biological processes controlling growth and population dynamics are presented in Figure 1 and Table 1 in Part 1.

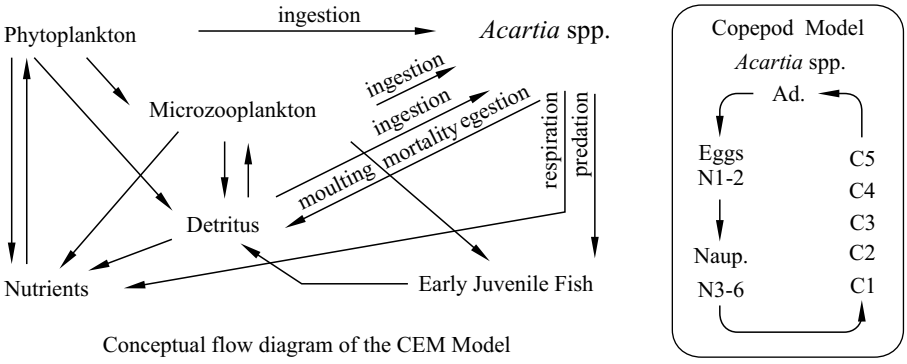

Figure 1. Conceptual flow diagram of the CEM Model with a copepod model for *Acartia* spp.

The literature provides copious experimental data on growth and egg production for different *Acartia* spp. This information can be used to obtain an idea of the functional relations between physiological rates and environmental parameters.

Most of the coefficients used in the population model were calculated from these results. Where data were lacking, coefficients were estimated from information about similar species. The section below describes the model details for egg production; the details regarding growth are given in Part 1.

2.1. Egg production rates

The relationships between food concentration, composition, feeding and egg production are difficult to quantify in natural food environments.

The egg production rate of *Acartia tonsa* increases sigmoidally with food concentration when a nutritious diet is offered in the laboratory (Kiørboe et al. 1985). Some authors found correlations between copepod egg production and the phytoplankton standing stock (e.g. Checkley 1980, Durbin et al. 1983, Beckman & Petersen 1986, Kiørboe & Johanson 1986, Schmidt et al. 1998), whereas others did not, e.g. (Bautista et al. 1994, Hay 1995). The importance of food quality for egg production is obvious since, firstly, the rate at which particles are captured and ingested by copepods depends on their size and shape (Vanderploeg et al. 1988) and, secondly, the composition of crustacean eggs includes a number of essential components (e.g. Harrison 1990, Pond et al. 1996) that different food sources may or may not supply. Even though food assimilation is the basis of any production, physiological rates are influenced by temperature, a factor that has been recognised as especially important. Hence, egg production is also a function of temperature; indeed, several authors have considered temperature as the principal parameter affecting egg production in the field (Uye & Shibuno 1992, White & Roman 1992).

In our opinion, however, these relations between egg production, and food supply and temperature are very hard to obtain.

The egg production of two species (*Acartia bifilosa* and *A. tonsa*) in the Pomeranian Bay, in the outer part of the Oder Estuary (southern Baltic Sea), was studied in 1994–95 by Schmidt et al. (1998). Rates were found to vary both seasonally and spatially.

In the present study, egg production rates (eggs female^{-1} d^{-1}) were obtained, on the basis of experimental data given by Schmidt et al. (1998), as a function of the Chl *a* concentration (mg m^{-3}). These were significantly positively correlated only in January 1995 ($Egg = 0.90846$ Chl $a^{0.91692}$, where the correlation coefficient r = 0.828 for *A. bifilosa*), when the total

phytoplankton biomass was lowest. In April 1995, egg production rates were almost constant (from 6.4 to 13.5, av. = 10.3 eggs female^{-1} d^{-1}) over a wide range of Chl *a* concentrations: to be precise: $Egg = (\text{Chl } a - 5)^2 + 9.28$, where r = 0.542 for *A. bifilosa*. A significant negative correlation was found for *A. bifilosa* in June/July 1995 ($Egg = -6.2537 \ln(\text{Chl } a) + 14.879$, r = −0.735). Moreover, egg production rates in this species were inversely correlated with Chl *a* in June/July 1994 ($Egg = 36.234 \exp(-0.10695 \text{ Chl } a)$, r = −0.743); this was also true for *A. tonsa* in June/July 1995 ($Egg = 13.468 \exp(-0.0793 \text{ Chl } a)$, r = −0.673). There was a negative, though not significant, relationship in September 1994 ($Egg = -2.2134 \ln(\text{Chl } a) + 9.525$, r = −0.696). Schmidt et al. (1998) also obtained the egg production rate for neighbouring areas of the southern Baltic Sea (from the extreme southwest of the Baltic to the Bornholms Gatt). As the results given by Schmidt et al. (1998) differ substantially for various areas of the southern Baltic Sea (see Table 1), they have not been taken into consideration for the description of egg production in *Acartia* spp. from the Gdańsk Deep.

Table 1. Data from August 1995: physical properties, Chl *a* concentration and egg production rate (EP) of *Acartia bifilosa* and *Acartia tonsa* at stations in the Pomeranian Bay (PB) and neighbouring areas (Mecklenburg Bay (MB), Arkona Sea (AS), Bornholms Gatt (BG)). Average Chl *a* concentration was integrated over the water column using discrete depths: 0, 2.5, 5, 10, 20 m and bottom (after Schmidt et al. 1998)

Area	Depth [m]	Temperature max [°C]	Chl *a* [mg m^{-3}]	EP ± SD [eggs female^{-1} d^{-1}]
PB	10	21	10	2.5 ± 1.9
PB	13	21	7	2.6 ± 2.1
PB	19	21	3	3.6 ± 2.3
BG	65	21	2	23.6 ± 8.2
AS	46	21	2.5	8.9 ± 4.8
AS	46	18	3	13.9 ± 7.6
AS	22	20	2.5	7.2 ± 4.1
MB	25	17	1.5	13.7 ± 6.8
MB	23	14	1.5	20.4 ± 8.2

In this study, the hypothesis that the food-saturated rate of egg matter production is equivalent to the maximum specific growth rate of copepods was the basis for calculating the number of eggs laid per day by one *Acartia* spp. female in the Gdańsk Deep. The egg production rate was

obtained as a function of growth rate, i.e. by multiplying exp $GROWTH$ -1 by W_{female}/W_{egg}, assuming the growth rate to be that of the N3 developmental stage of *Acartia* spp. from the Gulf of Gdańsk. The number of juveniles was defined on the assumption that eggs are released by the adult female throughout some time span J. The period of egg production for *Acartia bifilosa* females from the southern Baltic Sea varied with temperature from about 14 days at 20°C up to about 1 month at 7°C (Ciszewski & Witek 1977). The efficiency term X was the conversion of biomass increase by the adult population into eggs, including wasted growth in males. Here, a sex ratio X of 20% for *Acartia* females was assumed in accordance with experimental data from the Gdańsk Deep in May 1999 (Mudrak 2004). In this study the weight of an egg W_{egg} was taken to be 0.0305 μgC egg^{-1} for *Acartia* (Ambler 1985). The wet weight of adult females was obtained in accordance with the HELCOM standard (Hernroth 1985), assuming the organic carbon content of copepods $gC/g_{w.w.} = 0.064$ (Vinogradov & Shushkina 1987).

3. Results

To describe the potential egg production the following parameters are needed: (i) maximum growth rate for the second model stage, (ii) egg dry weight, (iii) weight of female and (iv) experimental temperature.

The model presented in Part 1 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 growth rates of *Acartia* spp. from the southern Baltic Sea were calculated for each of the eight model stages using equation (1) (see Part 1 – Dzierzbicka-Głowacka et al. 2009 – this issue).

The function $g_{\max}$ for the model naupliar stage ($g_{\max} = 0.0493 \exp(0.1046\ T)$, see Figure 2) can predict the food-saturated, temperature-dependent, specific production rate of egg matter by a female as $ProdEgg = \exp g_{\max} - 1$ (McLaren & Leonard 1995). Hence, the amount of egg matter produced per day as a percentage of female weight of *Acartia* spp. from the southern Baltic Sea using $g_{\max}$ is $ProdEgg = 0.0495 \exp(0.0964\ T)$ (Figure 2). The rate of production of egg matter, $ProdEgg$, obtained in this work as a function of temperature via the maximum growth rate (for N3–N6), for well-fed *Acartia* spp. females from the southern Baltic Sea (Gdańsk Deep), increases with rising temperature and assumes values from 0.08 to 0.4 μg μg^{-1} day^{-1} at temperatures from 5 to 20°C (Figure 2).

The potential daily growth rate can be converted to the equivalent maximum number of eggs produced per day by one female thus: $Egg = W_{female}/W_{egg}\ ProdEgg = 2.1169 \exp(0.0964\ T)$, assuming that W_{egg}

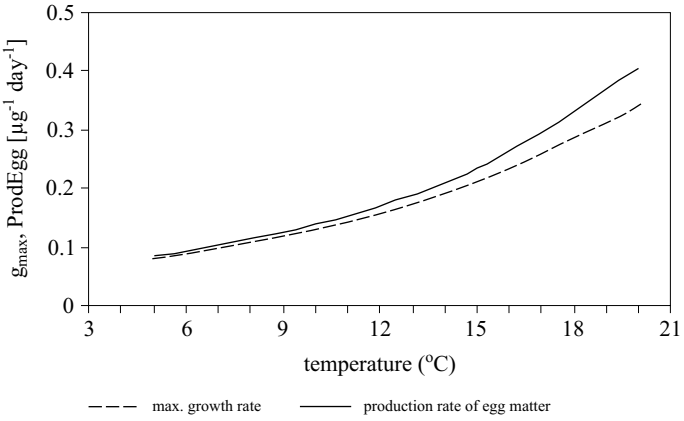

Figure 2. Temperature-dependent rate of production of egg matter as a proportion of the structural weight of well-fed female *Acartia* spp. from the southern Baltic Sea, using the maximum growth rate for the naupliar stage

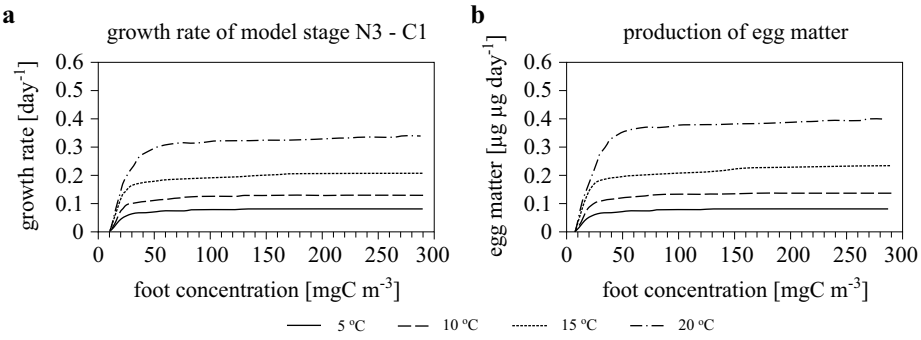

Figure 3. Relationships between food concentrations [mgC m^{-3}] and growth rate for the naupliar stage [day^{-1}] (a) and production of egg matter (b) of *Acartia* spp. from the southern Baltic Sea [days] for four temperatures T [°C]: 5°C, 10°C, 15°C and 20°C

and W_{female} are defined as above. Equation (1) (see Part 1 – Dzierzbicka-Głowacka et al. 2009 – this issue), which determines the growth of *Acartia* spp. (reduced by food limitation), was used to obtain the production rate of egg matter by a female: $ProdEgg = \exp GROWTH - 1$, where $GROWTH = f(Food,\ T)$ is the growth rate for the second model stage – N3–N6. Hence, taking $GROWTH$ for the specific developmental stage N3–N6 (see Figure 3a) into consideration, $ProdEgg$ for *Acartia* spp. females from the Gdańsk Deep, computed as a function of food concentration and temperature, is shown in Figure 3b.

The calculations demonstrate that $ProdEgg$ becomes less dependent on food concentration than on temperature, taking values from 0.059 to 0.085 μg μg^{-1} day^{-1} at 5°C and from 0.22 to 0.4 μg μg^{-1} day^{-1} at 20°C in the $25 - 300$ mgC m^{-3} food concentration range. However, successive values of $ProdEgg$ were used to determine the number of eggs produced per day by one female. Transformation of these data yields a relationship between the temperature and the number of eggs at selected food levels:

$$Egg = a \exp(bT). \tag{1}$$

The coefficients a, b and the correlation coefficients at selected food levels 25, 50, 100, 200 and max mgC m^{-3} were calculated; the correlation coefficients were in the $0.91 - 0.99$ range. The regression equations are given in Table 2. However, coefficients a and b were obtained as a function of food concentration by means of an exponential regression $a = 0.8482 Food^{0.1748}$ (r = 0.907) and a linear regression $b = -3 \times 10^{-6} Food + 0.091$ (r = 0.749).

Table 2. Egg production rates Egg [no. eggs female^{-1} day^{-1}] at four temperatures [°C] and for selected food levels $Food$ [mgC m^{-3}] obtained in this paper; the regression equations for Egg as a function of temperature for four food concentrations

$Food$	Temperature				Regression equations
	5	19	15	20	
25	2.206	3.562	5.745	8.0	$Egg = 1.4721 \exp(0.0869\,T)$
50	2.745	4.405	6.89	11.49	$Egg = 1.6996 \exp(0.0948\,T)$
100	3.037	4.902	7.28	12.26	$Egg = 1.9205 \exp(0.0916\,T)$
200	3.3	5.2	8.043	12.64	$Egg = 2.1166 \exp(0.0903\,T)$
max	3.312	5.22	8.11	12.66	$Egg = 2.1169 \exp(0.0964\,T)$

By substituting a and b in equation (1), Egg of *Acartia* spp. becomes a function of both food concentration from 25 mgC m^{-3} to excess and temperature in the $5 - 20$°C range:

$$Egg = 0.8482\, Food^{0.1748} \exp((-3 \times 10^{-6}\, Food + 0.091)\, T). \tag{2}$$

Figure 4 shows the set of egg production curves computed with equation (2). The figure clearly illustrates the effects of interactions between temperature and food concentration on the number of eggs produced per day by one *Acartia* spp. female.

The effect of temperature (non-limiting food conditions) is manifested as follows: females from the Gdańsk Deep produce c. 3.3 eggs per day at 5°C, c. 5.2 eggs at 10°C, 8.1 eggs at 15°C and 12.7 eggs at 20°C. Egg production

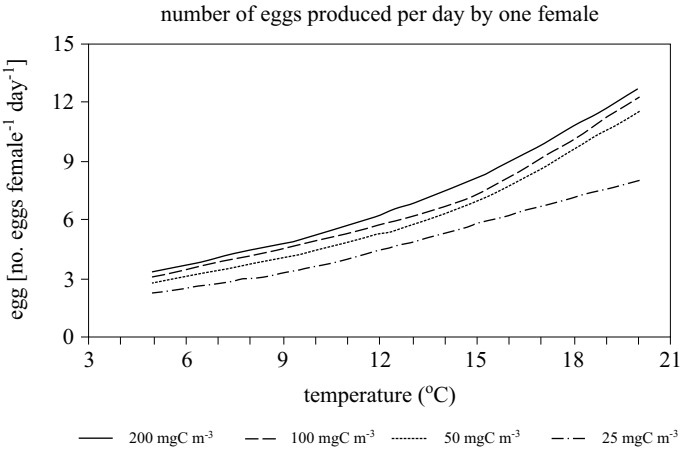

Figure 4. Relationships between the number of eggs produced per day by one female of *Acartia* spp. from the southern Baltic Sea [no. eggs day^{-1}] and temperature T [°C] for different food concentrations: 25 mgC m^{-3}, 50 mgC m^{-3}, 100 mgC m^{-3} and 200 mgC m^{-3}

grows as the temperature rises, which is a consequence of increasing growth with temperature, according to the function fte_i. A decreasing food supply reduced the number of eggs produced per day by one female. At 15°C, with $fte_i = 1$, c. 5.7 eggs were produced at 25 mgC m^{-3} and 8 eggs at 200 mgC m^{-3}, which corresponds almost to food saturation. The difference in egg production as a function of temperature $Egg = f(T)$ was less at lower food concentrations ($\Delta Egg \approx 5.8$ eggs for 25 mgC m^{-3}) than at higher ones ($\Delta Egg \approx 9.3$ eggs for 200 mgC m^{-3}). The changes occurring in egg production with variations in temperature and food concentration were more pronounced at high food levels ($\Delta Egg \approx 9.3$ eggs) and at high temperatures ($\Delta Egg \approx 4.6$ eggs) (see Table 2).

Figure 5 illustrates the effect of food composition and temperature on egg production in *Acartia* spp. during the seasons in the upper 20 m depth layer in the Gdańsk Deep. The temperature and the food concentrations (biomass phytoplankton – 60%, pelagic detritus – 25% and microzooplankton biomass – 15%) used in this paper are mean values of five-year data (2001–05) from the 1DCEM model (Dzierzbicka-Głowacka et al. 2006), which used a different formula for primary production (see Renk 2000). For the population of *Acartia* spp., food, comprising phytoplankton, microzooplankton and detritus, results in an available food concentration that rises to 235 mgC m^{-3} at the beginning of April, but falls to c. 80 mgC m^{-3} by the end of June. The comparatively high food level is sustained during summer. When the temperature reaches its maximum,

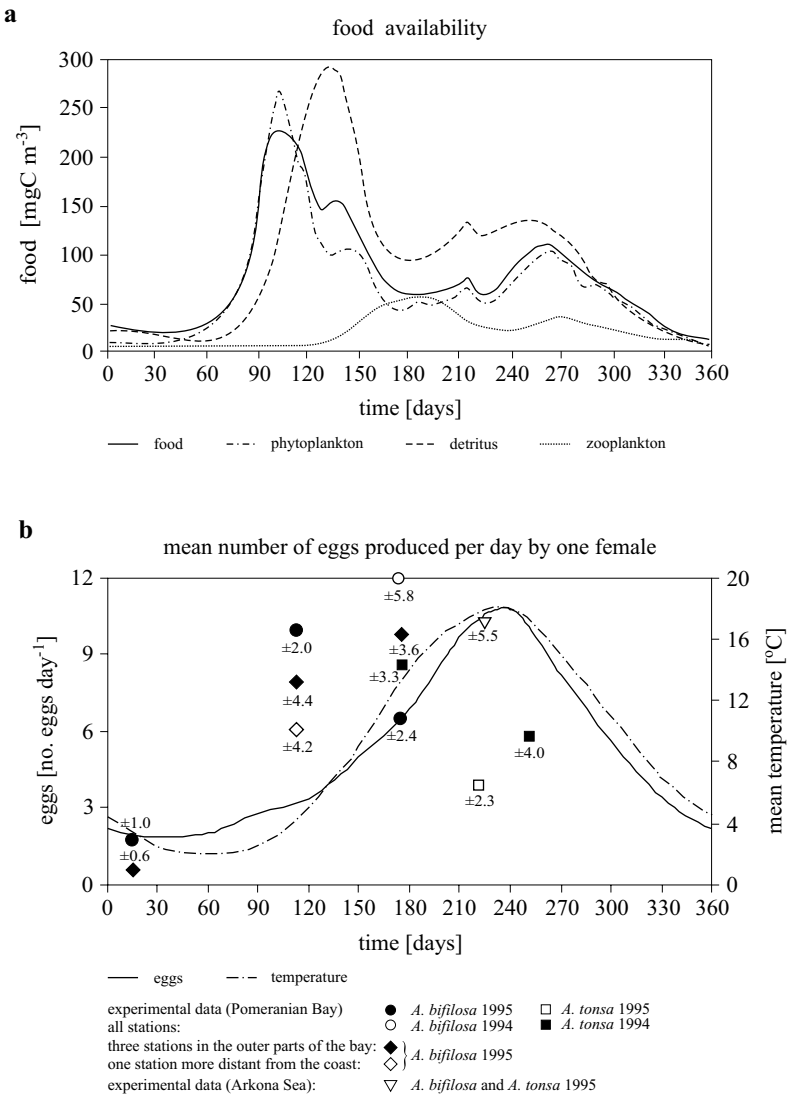

Figure 5. Simulated forcing and egg production of *Acartia* spp. for the annual cycle in the Gdańsk Deep; mean food availability (a), mean number of eggs produced per day by one female (b)

the food concentration reaches c. 135 mgC m^{-3} by the end of August (Figure 5a).

The influence of temperature and food concentration on the number of eggs was described earlier. The annual cycle of the reproductive rate is related to the above parameters, but mainly temperature: *Acartia* spp. produces more eggs at higher than at lower temperatures. When the

population is starving, the number of eggs produced per day by one female is ~ 2 at temperatures from 4.5 to 2°C at the beginning of year (January and February). However, *Egg* increases to ~ 3.8 eggs at 4.5°C when the food concentration rises to a high value, at which the growth rate tends to become constant during the spring bloom. Hence, at low temperatures and food concentrations, the female produces only about 1.8 eggs per day or about 72 eggs during the period of egg production; this period for *Acartia bifilosa* from the southern Baltic Sea is assumed to last about 40 days.

This is the situation in the winter (February). However, at high temperatures and sufficiently high food concentrations (August – $T = 18$°C, $Food = 135$ mgC m^{-3}), individuals can achieve maturity after just 20 days and females produce about 10 eggs per day or c. 140 eggs during the egg production period, assumed to be around 2 weeks. Hence, in summer, females produce about five times more eggs per day and twice as many during the whole reproductive period than in winter.

4. Discussion

An interaction of broad biological and ecological significance was obtained in the present study. An attempt was made to formulate one general statement about the population dynamics of *Acartia* spp. in the southern Baltic Sea by integrating the experimental data in Ciszewski & Witek (1977) with those in other papers in order to calculate the growth rate of *Acartia* spp. (see Part 1 – Dzierzbicka-Głowacka et al. 2009 – this issue).

An important interaction is the one resulting from the effects of temperature and food concentration on egg production. The number of eggs produced by one female per day as a function of growth rate for the naupliar stage – N3–N6 (second model stage) was obtained in this study. The modelled results were compared with experimental data from other localities taken from the literature, because data for *Acartia* spp. from the Gdańsk Deep were lacking. The mean egg production rates of *A. bifilosa* and *A. tonsa* obtained on the basis of experimental data from all the stations (30 stations) in the Pomeranian Bay and from three stations in the outer parts of that bay are cited in Figure 5b after Schmidt et al. (1998). Table 1 gives the measurements made in August, but only at stations near the outlets of the lagoon and in adjacent areas of the southern Baltic (Mecklenburg Bay [MB] at 25 m depth, the Arkona Sea [AS] at 22 and 46 m and in Bornholms Gatt [BG] at 65 m): the mean reproductive rates are 10 ± 5.5 eggs female^{-1} d^{-1} [AS], 18 ± 7.5 eggs female^{-1} d^{-1} [MB] and 23.6 ± 8.2 eggs female^{-1}d^{-1} [BG]. The spatial variability in egg production rates was high. During summer and autumn, Schmidt et al. (1998) recorded

both high and very low egg production rates in the Pomeranian Bay for both species. Analysis of the phytoplankton composition in summer suggests that a high proportion of dinoflagellates was beneficial to egg production, whereas high proportions of cyanobacterial colonies and filaments had negative effects.

The change in the mean number of eggs produced per day by one female computed here is similar to that emerging from the Pomeranian Bay field data given by Schmidt et al. (1998); the latter includes only data from stations farther offshore and data from all stations except for April 1995 (*A. bifilosa*) and August 1995 (*A. tonsa*). Generally good agreement between the measured and modelled reproductive rate was obtained for January and June/July in two cases (see Figure 5b). In April, egg production rates in the Pomeranian Bay were 10.5 eggs female^{-1} d^{-1} (data from all stations), 8.2 eggs female^{-1} d^{-1} (data from stations in the outer parts of the bay) and 6.4 eggs female^{-1} d^{-1} (data from a station farther offshore). Hence, based on the results of Schmidt et al. (1998), egg production in April decreases rapidly with increasing distance from the coast. The experimental data from the offshore station are c. 2.6 eggs female^{-1} d^{-1} higher than the modelled values. Presumably, the egg production rate in the open sea is slower. Hence, the difference between the experimental data and the model results will be small. The low egg production rates in the Pomeranian Bay in summer were due to the large numbers of phytoplankton. Hence, the Pomeranian Bay is not very favourable to copepod egg production in summer. In August 1995, egg production rates of *Acartia* were significantly higher in other areas of the southern Baltic Sea (Mecklenburg Bay, Arkona Sea, Bornholms Gatt) than in the Pomeranian Bay, although the chlorophyll *a* concentration was distinctly lower there (see Table 1). The egg production rate of *Acartia* spp. from the Gdańsk Deep computed in this paper as a function of growth rate for August (10.5 eggs female^{-1} d^{-1}) is also significantly higher than that emerging from the Pomeranian Bay data, but is in agreement with those from the Arkona Sea (10 ± 5.5 eggs female^{-1} d^{-1} [AS]) (Schmidt et al. 1998).

The differences in *Egg* between the modelled and mean values reported from the stations in the Pomeranian Bay depend on the environmental parameters for which the calculations and measurements were made. The three main characteristics of the Pomeranian Bay are: (1) heterogeneous mixing of nutrient-rich river water with open Baltic Sea water, causing strong temporal and spatial variations in phytoplankton abundance and species composition, (2) the weak salinity gradient from the river mouths to the outer parts of the bay, the open Baltic Sea itself being mesohaline, and (3) the shallow water (maximum depth 20 m) and forcing winds keep the water column almost permanently mixed (Schmidt et al. 1998). It

should be borne in mind that the proportion of cyanobacteria in the total phytoplankton biomass is significantly lower in the open sea water than in the estuaries. In this study, the phytoplankton was modelled with the aid of only one state variable, and the food composition was constant during the seasons, which could also have had a certain influence on the determination of egg production rates.

For comparison, egg production rates for geographically separate populations of *Acartia* spp. are given below.

Egg production by *Acartia hudsonica* (5°C) and *A. tonsa* (10°C) from Narragansett Bay, USA, was measured in the laboratory by Verity & Smayda (1989). *A. hudsonica* fed with 10^4 cells cm^{-3} of *Skeletonema costatum* produced c. 9 to 10 eggs female^{-1} d^{-1}, compared to c. 1 egg female^{-1} d^{-1} by copepods fed with equivalent concentrations of *Phaeocystis pouchetii*. Females in mixtures of colonies produced eggs at daily rates (7 to 9 eggs female^{-1}) that were not significantly correlated with the abundance of *P. pouchetii* colonies. *A. tonsa* fed with unialgal cultures of *P. pouchetii* and *S. costatum* at 10°C exhibited responses similar to those of *A. hudsonica*. Egg production also increased with *S. costatum* concentration up to a maximum of 19 eggs female^{-1} d^{-1}. The maximum egg production calculated for *Acartia* spp. from the Gdańsk Deep was 2.6 (5°C) and 3.2 (10°C) times lower than the values given by Verity & Smayda (1989) for *A. hudsonica* (5°C) and *A. tonsa* (10°C) from Narragansett Bay, USA.

In a study conducted in the inner Los Angeles Harbor, Kleppel (1992) considered the response of *A. tonsa* to quasi-natural environmental variability. The author applied a correlative approach to determine how temperature and food concentration affect feeding (see Part 1 – Dzierzbicka-Głowacka et al. 2009 – this issue) and egg production. Multiple-regression analysis revealed that ingestion rate was dependent on both temperature and food availability, but that below 21°C, egg production depended more on temperature than on food concentration. Above 21°C, ingestion and egg production rates appeared to be independent of temperature. The production rate of egg matter by *Acartia* spp. females from the Gdańsk Deep obtained in the present study was from 0.05 to 0.39 μg μg^{-1} female C day^{-1} at temperatures between 3 and 18°C; moreover, *ProdEgg* was from 0.04 to 0.37 μg μg^{-1} female C day^{-1} for *A. tonsa* from southern California, where water temperatures ranged from 14.6 to 21.5°C (Kleppel 1992). The values of *ProdEgg* for two geographically separate populations of *Acartia* over different temperature ranges are thus similar. Kleppel (1992) showed that egg production was not food-dependent over much of the temperature range; his results largely mirror those obtained in this study.

5. Conclusions

The present work discusses the idea of determining the combined effect of temperature and food concentration on the egg production of *Acartia* spp. from the Gdańsk Deep (southern Baltic Sea). It is important to investigate and identify the critical factors in mathematical models of pelagic communities with a copepod module since zooplankton, a top-down regulator, may play a significant role in marine ecosystems.

Based on literature data, the present analysis applies the hypothesis that food-saturated production of egg matter is equivalent to the maximum specific growth rate in copepods (Sekiguchi et al. 1980). In this paper, a quantitative expression is presented, describing the effects of the above parameters on the egg production rate of *Acartia* spp. from the Gdańsk Deep. Another result was the annual cycle of the reproductive rate for the modelled temperature and available food concentration, the food comprising phytoplankton, microzooplankton and pelagic detritus. The calculations suggest that the mean egg production rate during summer (8.2 eggs female^{-1} d^{-1}) is c. 1.6 times higher than the average for the entire study (5.1 eggs female^{-1} d^{-1}).

Our numerical study showed that egg production in *Acartia* spp. from the Gdańsk Deep is determined primarily by temperature, because it is mainly this factor that explains the observed differences within each period. The effect of food concentration appears to be secondary; this may have been due to the use in the model of the phytoplankton concentration as the only variable, since both the abundance of taxonomic groups of phytoplankton and the proportion of cyanobacteria in the total phytoplankton biomass are significantly lower in the open sea than in coastal waters. Our assumptions and approximations appear to offer quite a good prediction of the temperature- food concentration-dependent daily rates of egg production of *Acartia* spp. from the Gdańsk Deep (southern Baltic Sea). We suggest that they can be used in ecosystem models coupled with population models of a dominant species.

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