Intra-annual distribution of *Temora longicornis* biomass in the Gulf of Gdańsk (the southern Baltic Sea) – numerical simulations

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Abstract. A population model of the copepod *Temora longicornis* coupled with the ecosystem model 3D CEMBS (Coupled Ecosystem Model of the Baltic Sea) was used to determine the intra-annual distribution of the species biomass in the Gdańsk Basin (the southern Baltic Sea). The population model for *T. longicornis* consists of twelve equations for twelve state variables, six for mass and six for abundance, i.e. two state variables for each of the six model stages of the development: eggs (Egg), non-feeding stage (N1), subsequent nauplii stages (N2–N6), two copepodite stages (C1–C3 and C4–C5) and adults (C6). The empirical validation of the population model was based on in situ data collected in 2010 and 2011 in the Gdańsk Deep and the western part of the Gulf of Gdańsk. The highest values of the model biomass occurred in the period of high water temperatures – in June 2010 and July 2011 in the Gulf of Gdańsk (ca 5200 mg wet weight (w.w.) m^{-2} and 6300 mg w.w. m^{-2}), and for almost the whole summer in the Gdańsk Deep (24 500 mg w.w. m^{-2} and 27 800 mg w.w. m^{-2}). *Temora longicornis* produced 4 to 5 generations per year in the Gulf of Gdańsk and Gdańsk Deep, respectively. The population model was satisfactorily verified and the calculated results were consistent with the in situ data. Despite some differences between the field and model data, the developed population model of *T. longicornis* is the first model for this species in the Baltic Sea and, even though it needs further improvement, it can be a useful tool for determining the population dynamics of the species and ecological relationships in the environment.

Key words: Copepoda, *Temora longicornis*, population dynamics, modelling, Baltic Sea.

INTRODUCTION

The main function of zooplankton in the marine eco-system consists in transferring the energy accumulated in the process of primary production to higher trophic levels (Möllmann et al. 2000). The size and composition of zooplankton resources affect the growth and the survival rate of fish in the early stages of their development (Cushing 1995). *Temora longicornis* is the main food of the sprat (*Sprattus sprattus*) in the Baltic Sea (Möllmann & Köster 2002). The decline in the sprat population since the 1990s could have been caused by the competition between the sprat and herring as, in the absence of sufficient amounts of *Pseudocalanus minutus elongatus*, the latter incorporated to a greater extent other copepods into its diet, e.g. *Temora longicornis* (Möllmann et al. 2000).

The precise knowledge about the species composition, its abundance or biomass combined with hydrodynamic parameters (salinity, temperature) makes it possible to adequately assess changes in the ecosystem. Such knowledge, combined with numerical models, gives hypothetical predictions for the future, and predicts negative or positive effects of changes in the environment. Partial support for this study was also provided by the project 'Knowledge transfer platform FindFISH – Numerical Forecasting System for the Marine Environment of the Gulf of Gdańsk for Fisheries' funded by the European Union through the European Regional Development Fund. The FindFISH platform is a database containing historical data and current online forecasts concerning the marine environment and living resources of the Gulf of Gdańsk. It was created by means of knowledge transfer between two groups of users: scientists and fishermen.

The hydrographic regime of the Baltic Sea is highly dependent on meteorological conditions and mean atmospheric circulation patterns (Malmberg & Svanson 1982; Launiainen & Vihma 1990; Matthäus & Franck 1992; Matthäus & Schinke 1994; Möllmann et al. 2000; Fonselius & Valderrama 2003; Leppäranta & Myrberg 2009). On the other hand, changes in temperature and salinity determine the composition and abundance of mesozooplankton species, including *T. longicornis*, as described by Ojaveer et al. (1998), Vuorinen et al. (1998), Dippner et al. (2000), Hänninen et al. (2000, 2003), Dutz et al. (2010, 2012) and Otto et al. (2014). Therefore, in the face of the progressive climate change and its impact on the marine environment, efficient management is extremely important and it requires extensive research. In particular, the expected decrease in the salinity of the Baltic Sea should cause, as suggested by Hänninen et al. (2003), a decline in the abundance of the *T. longicornis* population. It is therefore essential that new and more accurate methods of environmental monitoring and prediction of the environmental response to incoming climate change be developed.

So far no population model for *Temora longicornis* has been developed. Together with *Acartia* spp. the species is a dominant pelagic copepod of the southern Baltic Sea (Line 1979, 1984; Chojnacki et al. 1984; Mudrak 2004). Being a valuable source of food for economically important fish – herring and sprat, the species plays a very important role in the ecosystem. Furthermore, together with *Pseudocalanus* sp., it is an important source of food for larval forms of codfish (Arrhenius 1996; Möllmann & Köster 2002; Dickmann et al. 2007). The frequency and number of in situ studies regarding zooplankton in the southern Baltic are largely insufficient for reliable assessment of long-term and seasonal changes in the marine environment. The only way to present reliable spatial and temporal distribution of the studied crustacean and other zooplankton species is to provide combined environmental, laboratory and modelling studies concerning the abundance and biomass at different stages of ontogenesis.

The main objective of the presented study was to determine the population dynamics of *Temora longicornis* in the Gdańsk Basin (the southern Baltic Sea) based on numerical analysis. With the use of numerical simulation we wanted to determine the dynamics of the species development, allowing for successive stages of its individual development and relationships between life processes and environmental parameters. Coupled with earlier models for *Pseudocalanus* sp. and *Acartia* spp. (Dzierzbicka-Głowacka et al. 2010, 2012), this will allow us to build a more holistic model for copepods in the Gulf of Gdańsk and the southern Baltic Sea in

general. Consequently, this should allow for more accurate predictions of the changes to occur and for better understanding of processes in the ecosystem.

This study consisted of three phases. First, the functional relationships between the physiological processes and environmental parameters were determined. Second, the population model for *T. longicornis* was developed, to describe the temporal and spatial distributions of biomass and abundance, and to be connected with the 3D CEMBS ecosystem model (Dzierzbicka-Głowacka et al. 2013a). Third, the population model was empirically validated, based on in situ data.

MATERIAL AND METHODS

Study area

The coastal region of the Gulf of Gdańsk, which belongs to the Gdańsk Basin, is wide open towards the Gdańsk Deep adjacent to the southernmost part of the Gotland Basin, the largest and deepest basin of the Baltic Sea. The life environment of pelagic animals changes with the distance from the shore and the depth of the sea. The two-layer structure of the Gulf of Gdańsk, with its almost uniform salinity but present thermal stratification, gradually morphs into a three-layer system: quasi-homogeneous surface thermocline layer, a middle halocline layer and deep waters. Even as most of the zooplankton species are identical to the species of the coastal waters, the species structure is not identical. There are more species typical for colder and more saline waters, especially in the lower layers. Among the Copepoda of the genus *Acartia* there is greater abundance of *A. longiremis*, unlike the coastal waters where the dominant species are *A. bifilosa* or *A. tonsa*, depending on the season. There is also greater abundance of *Pseudocalanus* sp. and *T. longicornis*.

The influence of North Sea water inflow events is more pronounced in the Gdańsk Deep than in the Gulf of Gdańsk. The inflows enrich the zooplankton fauna in species preferring higher salinity. The other important difference between the two basins is the structure of the population of the three water layers. The surface layer has the highest zooplankton abundance but it also features the highest variability. It is populated mostly by the youngest Copepoda forms (nauplii), and in the season of high primary production also by taxons typical for warmer waters: Cladocera, Rotatoria and meroplankton. In the middle layer, the abundance is much lower. The dominant forms are copepodite forms of *T. longicornis* and *Pseudocalanus* sp.; *Acartia* is also present, mostly *A. longiremis*. The deepest layer is populated by typical marine species such as *Oithona*

similis and *Fritillaria borealis* as well as the copepodites of developmental stages C4–C5 and adults of *Pseudocalanus* sp.

Field studies

Planktonic material which is the basis of in situ studies was collected in the southern part of the Baltic Sea from two stations: the Gdańsk Deep ($\varphi = 54^{o}50'N$, $\lambda = 19^{o}19'E$) (Fig. 1, station P1), and the western part of the Gulf of Gdańsk ($\varphi = 54^{o}32'N$, $\lambda = 18^{o}48'E$) (Fig. 1, station P2). Field data used for model calibration were collected at station P2 in the years 1991, 1999, 2000, 2006 and 2007. The data used for model validation are separate datasets for both stations P1 and P2, collected in 2010 and 2011. In the years 1991, 1999, 2000, 2006 and 2007 sampling was performed with a Copenhagen-type zooplankton sampling net and, as of 2010, a WP2-type sampling net was used (both nets had 100 μm mesh size). At station P2 sampling hauls were performed vertically in 10 m layers from a depth of 40 m. At station P1 samples were collected four times in a year. Vertical net hauls were carried out in three layers: (i) the

Fig. 1. Location of stations for which the numerical simulations were performed; P1 – the Gdańsk Deep, P2 – the Gulf of Gdańsk.

bottom–the upper limit of the halocline, (ii) the upper limit of the halocline–thermocline and (iii) the upper limit of the thermocline–the surface. Qualitative and quantitative zooplankton laboratory analysis was performed in accordance with the *Manual for Marine Monitoring in the COMBINE Programme of HELCOM* (HELCOM 2017, Annex C-7).

Temora longicornis population model

The population model defines the distribution of mass and abundance for each developmental stage of the studied copepod in order to determine the total biomass. The model was coupled with an ecosystem model – 3D CEMBS (Coupled Ecosystem Model of the Baltic Sea) (Dzierzbicka-Głowacka et al. 2013a) to simulate the annual life cycles of *T. longicornis* in a sub-basin – the Gulf of Gdańsk. Figure 2 shows a conceptual flow diagram of the 3D CEMBS model with a copepod model and a diagram of different biological processes controlling the growth and population dynamics for the species investigated in the model.

The population model consists of twelve equations for twelve state variables, six for mass W_i and six for abundance Z_i, i.e. two state variables W_i and Z_i, for each of the six model stages. The model stages were grouped as follows: eggs (Egg), non-feeding stages (N1), subsequent stages of nauplii (N2–N6), two copepodite stages – younger (C1–C3) and older (C4–C5), and adults (C6). A difference in the mass W_i of each individual, in the developmental stages from N1 to adults, is controlled by ingestion *ING* and metabolic losses (egestion *FEC*, respiration *MET*). The variable describing the abundance (Z_i) is determined by the mortality rate *MOR* and transfer *TRN*, transition from stage (i–1) to the next stage (i). Both processes, ingestion and transfer, depend on the mass of an individual at different developmental stages, using critical mass for moulting W_m. The main equations for mass W_i and abundance Z_i are as follows:

$$GROWTH_i = \partial W_i / \partial t = ING_i - FEC_i - MET_i, \quad (1)$$

$$\partial Z_i / \partial t = TRN_{i-1} - MOR_i - MIG_i - TRN_i. \quad (2)$$

For each of the model stages, biomass was calculated as a product of mass and abundance. Physiological processes that determine the growth and the dynamics of populations are presented in Table 1, whereas the parameter values for *T. longicornis* in the present model and their level of sensitivity are given in Table 2.
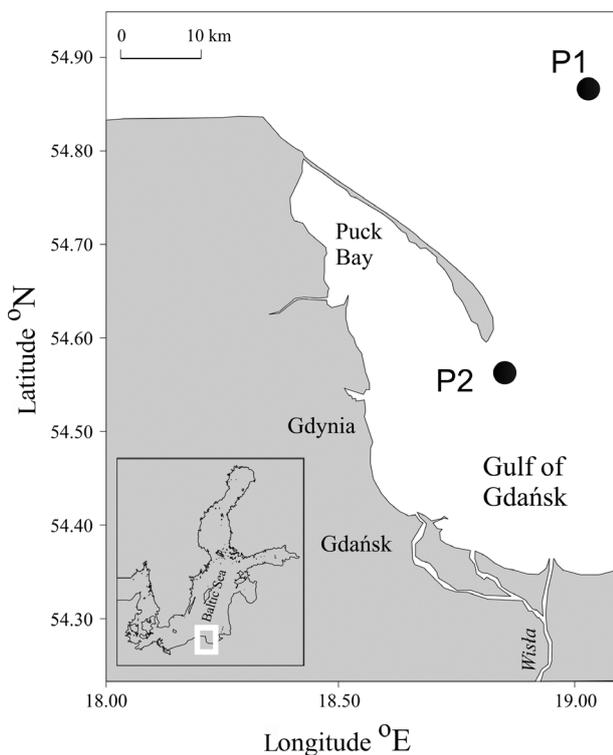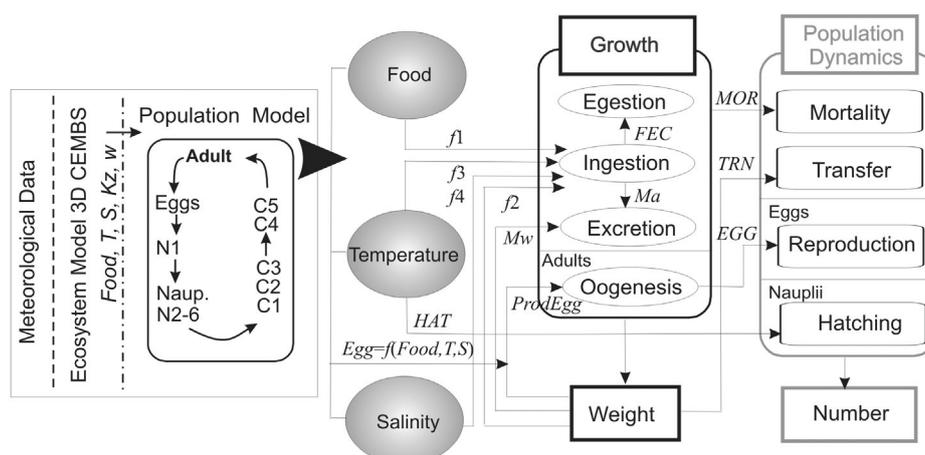
Fig. 2. Conceptual diagram of the population model combined with the 3D CEMBS model (3D Coupled Ecosystem Model of the Baltic Sea). See text for the explanation of the abbreviations.

Table 1. Mathematical relationships used in the model; i, stages; *Food*, food concentration; T, temperature; W_i, mass; W_k, critical mass, Z_i, abundance; W_{egg}, egg mass; W_{female}, female mass; N, nauplii; C, copepodites

Process	Units	Equations
Growth		
Growth N2–C5	µg C d^{-1}	$GROWTH_i = \partial W_i/\partial t = ING_i - FEC_i - MET_i$
Growth N1	µg C d^{-1}	$GROWTH_{N1} = \partial W_{N1}/\partial t = -FEC - MET$
Growth *Ad*	µg C d^{-1}	$GROWTH_{Ad} = \partial W_{Ad}/\partial t = ING_{Ad} - FEC_{Ad} - MET_{Ad} - ProdEgg$
Ingestion	µg C d^{-1}	$ING_i = f1\,f2\,f3\,f4$
		$f1 = f_{max}\{1 - \exp[-(Food - Food_0)/k_{Food}]\}$
		$f2 = 1$ dla $W_i \le 1$
		$f2 = 1 - [(W_i - W_m)/(W_k - W_m)]^2$ dla $W_i > W_m$
		$f3 = ft_1\,ft_2$
		$ft_1 = t_1 t_2^{T}$
		$ft_2 = 1$ dla $T \le T_o$
		$ft_2 = 1 - [(T - T_o)/(t_3 T_o)]^{p1}$ dla $T > T_o$
		$f4 = 1 - 0.8 \exp[-0.4(S - 2)]$
Egestion	µg C d^{-1}	$FEC_i = (1 - na)\,ING_i = nf\,ING_i$
Metabolism	µg C d^{-1}	$MET_i = Ms + Ma$
basic	µg C d^{-1}	$Ms = nw\,W_i$
active	µg C d^{-1}	$Ma = ne\,ING_i$
Production of eggs	µg C d^{-1} female^{-1}	$ProdEgg = \exp GROWTH_N - 1$
Dynamics		$\partial Z_i/\partial t = TRN_{i-1} - MOR_i - TRN_i$
Abundance		
Mortality	d^{-1}	$MOR_i = mz_i\,Z_i$
Mortality rate (i and $i+1$)	d^{-1}	$[\exp(mz_i\,D_i) - 1]/[1 - \exp(-mz_i\,D_{i+1})] = Z_i/Z_{i+1}$
Mortality rate (adults)	d^{-1}	$mz_{i-1} = \ln(Z_{i-1}/Z_{Ad} + 1)/D_{i-1}$
Transfer	d^{-1}	$TRN_i = f(W)$
		$TRN_i = (W_i - W_r)^{p2}/[(W_i - W_r)^{p2} + (W_m - W_r)^{p2}]$ dla $W_i > W_r$
Hatching	d^{-1}	$HAT = f(T)$
		$HAT = (p4\,(p5)^{T})^{-1}$
Reproduction	No. eggs female^{-1} d^{-1}	$Egg = X\,W_{female}/W_{egg}\,ProdEgg$
		$Egg = a \exp(bT)\,ft_2\,fs$
		$fs = 1 - \exp[-0.3(S - S_o)]$

Table 2. Parameter values for *Temora longicornis* in the model and their level of sensitivity (N, nauplii, C, copepodites); – no result

Parameter	Sign	Egg–N1	N2–N6	C1–C3	C4–C5	C6	Test	Sensitivity
Reference mass	W_r	0.0305	0.108	0.185	0.634	2.08	No	–
Critical moulting mass	W_m		0.131	0.317	0.894	2.69	No	–
Critical mass	W_k		0.157	0.468	1.191	3.38	No	–
Maximum ingestion rate	f_{max}		0.69	1.18	0.74	0.24	Yes	Very sensitive
Half-saturation	k_{Food}		90	140	140	140	Yes	Sensible
Minimum threshold *Food*	$Food_0$		0	0	0	0	Yes	Not sensitive
Q_{10} temperature coefficient	Q_{10}		2.274	2.274	2.274	2.274	Yes	Sensible
Maximum threshold $f3$	T_o		15	15	15	15	No	–
Temperature coefficient $f3$	t_1		0.292	0.292	0.292	0.292	No	–
Temperature coefficient	t_2		1.0856	1.0856	1.0856	1.086	No	–
Slope factor $f3$	t_3		0.6	0.6	0.6	0.6	No	–
Power coefficient $f3$	p_1		1.3	1.3	1.3	1.3	No	–
Slope factor *TRN*	p_2		4.0	4.0	4.0	4.0	No	–
Hatching rate	p_4	5.78					No	–
Slope factor *HAT*	p_5	0.94					No	–
Assimilation efficiency	na		0.7	0.65	0.65	0.65	Yes	Very sensitive
Basic metabolism	nw	0.06	0.04	0.04	0.04	0.04	Yes	Not sensitive
Active metabolism	ne		0.4	0.35	0.35	0.30	Yes	Very sensitive
Sex ratio	X					0.5	No	After data

Equations for each state variable are described by including the critical mass W_k according to the concept of Dzierzbicka-Głowacka et al. (2010), which defines a given state (i) by the mass W_i within the range of values $W_{k(i-1)} < W_i \leq W_{k(i)}$ (Carlotti & Sciandra 1989). The conversion factors of W_i (in mg wet weight (w.w.)) for each modelled stage were derived from literature (Hernroth 1985 and Mudrak 2004 – for copepodites and Ackefors 1972 – for nauplii). The content of organic carbon was used after Vinogradov & Shushkina (1987) as per g C/g w.w. = 0.064. The duration of an individual in the embryonic stage depends only on the temperature and is described by the Bělehrádek function (Table 1 – D_E) (Belehradek 1957).

Ingestion

The ingestion rate of an individual in subsequent developmental stages ING_i was determined by food concentration (*Food*) through the function $f1$, the individual critical mass in a given stage W_k and critical moulting mass W_m through the function $f2$, temperature T through the function $f3$ dependent on the temperature coefficient Q_{10}, which applies to the optimum temperature T_o ($T_o = 15\ ^\circ$C for *T. longicornis*, Dzierzbicka-Głowacka et al. 2011) and salinity S through the function $f4$ (see Table 1):

$$ING_i = f1_i f2_i f3_i f4_i . \qquad (3)$$

The transition to the next stage takes place when the critical moulting mass is reached and only a small fraction is lost in the process of moulting (Carlotti & Wolf 1998). The following parameters define the ingestion rate in relation to food concentration *Food*: f_{max} – the maximum ingestion rate, $Food_0$ – the minimum food concentration (i.e. *Food* value for which $GROWTH = 0$), k_{Food} – an approximate value of partial saturation. The model assumes that the first stage of nauplii, N1, is not capable of absorbing the food and is able to survive using the reserves supplied by eggs (Berggreen et al. 1988; Dutz et al. 2010). For every stage, $Food_0 = 0$ and $f3_i = 1$ for $T = 15\ ^\circ$C; whereas the parameter k_{Food} is a function of food concentration within the range of 90 to 140 mg C m^{-3} (Dzierzbicka-Głowacka et al. 2011).

The critical mass for the moulting process W_m is determined by the equation (Dzierzbicka-Głowacka et al. 2010, 2012)

$$W_m = (W_k + \sqrt{2} W_r) / (1 + \sqrt{2}), \qquad (4)$$

assuming that the value of half-saturation is equal to $W_h = 2W_m - W_r$ (Moll & Stegert 2007), which stipulates that the ingestion ING_i is not reduced before the transition to the next developmental stage TRN_{i+1}. The function $f2$, describing the reduction in the ingestion rate, depends on the critical mass for moulting W_m. The ingestion rate increases exponentially with temperature according to the coefficient Q_{10} assuming the value of 2.274, which applies at a temperature range from 5 to 15 °C by ft_1 term (Dzierzbicka-Głowacka et al. 2011). The temperature coefficient Q_{10} was calculated according to Klein Breteler & Gonzalez (1986). Furthermore,

the function $f3$ for temperatures above T_o is modified by ft_2 expression. Function ft_2, a parabolic threshold function (with $T_o = 15\,^{\circ}\text{C}$, $t_3 = 0.6$ and $P1 = 1.3$), reflects a reduction in the ingestion rate at higher temperatures as a result of physiological stress.

The field studies and literature data do not evidence the influence of salinity on the development of the species except for reproduction (see below). The effect of salinity on the ingestion rate was determined numerically by the function $f4$ based on our field data and experience (Table 1).

Losses

The ingestion rate *ING* is partly used for growth, while the rest is lost in the metabolic processes (such as respiration *MET* and egestion (= production of faecal matter) *FEC*), the moulting process *fm* and production of eggs and spermatophores. Respiration rates are difficult to obtain experimentally. Therefore, we assumed that the metabolic rate is represented by the excretion rate, which can be divided into two terms (Steele & Mullin 1977; Carlotti & Sciandra 1989). The first term *Ms* represents the basic metabolism and is proportional to mass; the second term *Ma* refers to the active metabolism and is proportional to the ingestion rate.

The assimilation rate *na* equal to 70% is commonly accepted for Copepoda (Steele & Mullin 1977). We accepted this value for nauplii and 65% for copepodites; thus 30% or 35% of the consumed food is egested, $nf = 30\%$ for N2−N6 stages or 35% for C1−C5 stages and adults. Juvenile stages, which do not feed (N1), lose 6% of their mass per day as a result of basic metabolism ($nw = 6\%$). The minimum respiration rate *nw* equal to 4% of the body mass per day was assigned to nauplii, copepodites and adults, plus the respiration rate equal to 40% of the ingestion rate to N2−N6, 35% to copepodites (C1−C5) and 30% to adults for active metabolism *ne*.

Reproduction

In order to determine the reproduction rate by a single female of *Temora longicornis* (Dzierzbicka-Głowacka et al. 2013b), we assumed the equivalence between the growth rate of a given development stage and production of eggs (*Egg*) per day by a single well-nourished female:

$$Egg = X\,W_{female}/W_{egg}\,ProdEgg, \qquad (5)$$

where $ProdEgg = \exp GROWTH_N - 1$ (Sekiguchi et al. 1980; McLaren & Leonard 1995). The egg production

rate was obtained, assuming the growth rate for the feeding nauplii stages. The equation describing the average number of eggs produced by a single female per day was defined for *T. longicornis*, based on the modelling results ($Egg = f(growth)$) and experimental data (Peters 2006; Holste et al. 2009), as a function of food concentration, temperature and salinity:

$$Egg = X\,W_{female}/W_{egg}\,a\,\exp(b\,T)\,ft_2\,fs, \qquad (6)$$

where coefficients a and b as a function of food concentration were determined by the following equations: $a = 0.01(0.0703\ln Food + 0.2521)\exp(0.6148\ln Food)$ and $b = -0.00003\,Food + 0.04$; ft_2 is a function of temperature and fs is a function of salinity determined by the equation $fs = 1 - \exp(-0.3\,(S - 7))$.

The parameter X in Eqs 5 and 6 was defined as efficiency, i.e. as not all females are reproductive, we considered $X = 50\%$ of adults laying eggs and 50% being males or non-productive females (Kiørboe 2006; Dzierzbicka-Głowacka et al. 2013b). We assumed 10% for non-productive females. Whereas, egg mass W_{egg} was assumed as $0.0305\,\mu\text{g C egg}^{-1}$ for *T. longicornis* (Harris & Paffenhöfer 1976).

Mortality

The mortality rate *MOR* was determined on the basis of the estimation provided by Aksnes & Ohman (1996). The average mortality rate *mz* in each developmental stage (i) depends on the duration of an individual in a given stage (D_i and D_{i+1}) and the abundance (Z_i and Z_{i+1}), and was determined by the following equations: (7) for two successive stages i and $i+1$ and (8) for adults:

$$[\exp(mz_i\,D_i) - 1]/[1 - \exp(-mz_i\,D_{i+1})] = Z_i/Z_{i+1}, \quad (7)$$

$$mz_{i-1} = \ln(Z_{i-1}/Z_{Ad} + 1)/D_{i-1}, \qquad (8)$$

which were solved numerically by applying the iterative method.

Additional calculations taking in situ data into account were also presented. They showed that the average mortality rate for C1–C2 stages was in the range of $0.10–0.25\,\text{d}^{-1}$ and $0.05–0.10\,\text{d}^{-1}$ for older stages. The values of *mz* determined numerically were in the same range and reached the maximum in summer/autumn and winter months (ca 0.23 for nauplii, 0.19 for C1–C3, 0.14 for C4–C5 and 0.08 for adults).

Transfer

The rate of transition from one stage (TRN_i) to the next one (TRN_{i+1}) is determined by the sigmoid function (see

Table 1, where p_2 is the power coefficient) that depends on W_i and W_m with a reference mass W_r as a threshold limit value, below which the transition to the next stage is not observed (after Stegert et al. 2007; Dzierzbicka-Głowacka et al. 2010). The reference W_r and critical W_k masses are defined for each model stage (see Table 2).

Migration

While considering the mass-occurring Copepoda in the southern Baltic Sea, taking all developmental stages into account, only some changes in their daily distribution within the water column have been noticed. However, it was difficult to discern classic diurnal vertical migration (Mudrak 2004). It has been observed that *Temora longicornis* adults tend to follow the normal diurnal vertical migration – to the surface at night; into the water column with the advent of dawn, while keeping there a maximum concentration during the day, only to rise up again after dusk. In this study, the migration process during the vegetation season was described in a day–night cycle according to the data given by Mudrak (2004) and Dzierzbicka-Głowacka et al. (2010).

Parameterization/calibration of the copepod model

Processes of growth and transfer were parameterized according to the data available for *Temora longicornis*. Four types of parameters were highlighted in this model: (1) parameters obtained from published studies for *T. longicornis* in the southern Baltic Sea, i.e. the mass of individuals in different developmental stages, reference and critical values as the minimum and maximum values, taken from the observed data; (2) parameters from published studies for *T. longicornis* in the southern North Sea, i.e. parameters describing the influence of temperature on the ingestion rate, taken from the experimental data; (3) parameters defining the shape functions, the values of which were taken from the literature for other Copepoda species, i.e. slope

factor; (4) parameters for which tuning was made, i.e. for the ingestion and metabolic loss processes, missing values were derived from general information on copepods. The egg production and mortality rate were defined according to the estimations given in the literature.

The numerical tests were performed to show that the model is very sensitive to changing values of parameters, such as the parameter describing active metabolism (in contrast to basic metabolism), temperature coefficient Q_{10}, the half-saturation parameter and the maximum ingestion rate. Therefore, for further tests, constants were assumed for some of them, i.e. the loss of metabolism (see Table 2) according to general information on copepods, while the Q_{10} temperature coefficient and the half-saturation parameter were obtained from a previous reference (Dzierzbicka-Głowacka et al. 2011) (Table 2).

In the next step, to determine the maximum rate of ingestion, the procedure *simulation – analysis of results – modification of the model* was repeated for as long as needed to fit the observation data, particularly, the maximum biomass in the summer (June/July), the appropriate number of generations per year and overall similarity of the numerical results to the field data. In practice, the calibration process consisted of multiple repetitions of the above-mentioned procedure until satisfactory compatibility was achieved. Changes in the model were made 'manually' by adjusting values of model parameters, after prior analysis of the results from the previous simulation. Finally, the calibration of the model, i.e. the evaluation of numerical values of parameters in the model, was performed for the set of data (1991, 1999, 2000, 2006 and 2007) for station P2 (Gulf of Gdańsk), in order to achieve the best possible compatibility between the observational and generated data. In each of these years, a regular spring/summer peak for the vertical mean total biomass, which is the algebraic sum of the vertical mean biomasses of all stages, has been observed, indicating that the model works properly (Fig. 3). The population model was
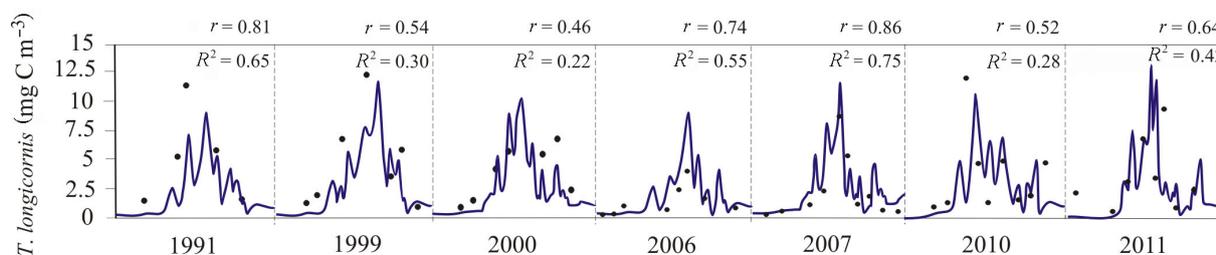
Fig. 3. The temporal distribution of the observed (circle) and modelled (line) total biomass for *Temora longicornis* as averages in the water column and Pearson's linear correlation coefficients r and coefficient of determination R^2. Data 1991, 1999, 2000, 2006 and 2007 were used for model calibration, data 2010 and 2011 for model validation.

tested mainly for a wide range of variation in the two most important parameters − temperature T and concentration of food *Food* (for data after Klein Breteler & Gonzalez 1986), which have a major impact on the zooplankton development. Simulated stage durations D are affected mostly by temperature and, to a lesser degree, by food availability. The results indicate that the effect of increasing food shortened the average time to reach each stage D at all temperatures. The decrease in stage duration was explicit at low food concentration (< 100 mg C m^{-3}) in all the model stages. Mean development time tends towards a constant value, as food concentration approaches high values (*Food* > 350 mg C m^{-3} for nauplii and younger copepodites; *Food* > 300 mg C m^{-3} for older copepodites).

Generally, the duration of all stages decreased with increasing temperature in the studied range of food concentration, thus the duration was inversely related to temperature, but only in the 5–15 °C range. The values of D were nearly equal at both 15 °C and 20 °C.

In this regard the results obtained are in accordance with the data in Klein Breteler & Gonzalez (1986) for higher food concentration except the copepodite stages (C4–C5). In these developmental stages, the critical temperature of 15 °C did not occur and the stage duration decreased with temperature rising up to 20 °C. However, there were slight differences in D at 10 °C and 15 °C.

The values of stage duration computed at each of the model stages were slightly longer (ca 20%) than the original results obtained by Klein Breteler & Gonzalez (1986) at the same range of temperature and food concentration, mainly as a result of lower salinity in the Baltic Sea but this could also be caused by differences in food sources. The differences in generation times D between modelled and experimental data were smaller at higher food concentrations, $\Delta D \approx 15$ days and $\Delta D \approx 8$ days, than at lower ones, $\Delta D \approx 22$ days and $\Delta D \approx 34$ days, at 5 °C and 20 °C, respectively. These differences were more apparent (visible) at temperatures above 15 °C, which was a result of the application of the parabolic function ft_2 in the model.

The calculations show that for the growth period from Egg to adults, when food is in excess, *T. longicornis* lives longer at lower than at higher temperatures, ca three times; however, when the population is starving, ca two times. The total stage duration Egg–adults is ca 127 days at 5 °C (*Food* = 90 mg C m^{-3}) and ca 65 days at 20 °C (*Food* = 41 mg C m^{-3}); however, it is ca 75 days at 5 °C (*Food* = 1400 mg C m^{-3}) and 23 days at 20 °C (*Food* = 370 mg C m^{-3}) as the food concentration rises to high values, at which the growth rate tends to become constant. A table of coefficients (Table 2) is presented to complete the equations describ-

ing processes occurring in the copepod model for the southern Baltic Sea (Gulf of Gdańsk).

RESULTS

Seasonal dynamics of *Temora longicornis* in the Gdańsk Basin − numerical simulations

The population model described above was used to simulate the temporal–spatial distribution of *Temora longicornis* biomass in the southern Baltic. The simulations were performed in the open sea − station P1 (Gdańsk Deep) and in the coastal zone − station P2 (in the western part of the Gulf of Gdańsk) (Fig. 1).

Seasonal dynamics of *T. longicornis* is described by average changes in the total biomass as a sum of biomass of the examined ontogenesis stages, which are the sum of the products of the mass W_i and the abundance Z_i of individual organisms at a given stage within the model. Here, values of temperature, salinity and available food concentration (*Food* = 50%*Phyt* + 25%*Zoop* + 25%*Detr*) were taken from the 3D CEMBS ecosystem model. The phytoplankton biomass as the main component of food in the Gulf of Gdańsk (station P2) was modelled as about two times higher than in the Gdańsk Deep (station P1). This situation is mainly caused by a higher concentration of nutrients near the mouth of the river into the Gulf of Gdańsk as compared to the open sea, and by higher water temperature at station P2.

For the *T. longicornis* population, *Food* was available at a concentration which considerably increases up to the value of ca 324 mg C m^{-3} at the end of March but drops to 96 mg C m^{-3} and 120 mg C m^{-3} at the end of June at stations P1 and P2, respectively. In the summer season when the temperature reached the maximum value, ca 21 °C at P2 and 18 °C at P1, the concentration of food in the upper layer remains at an almost constant level within the range of 60–120 mg C m^{-3}. The subsequent increase in food concentration was observed between late September and early October − 312 mg C m^{-3} and 182 mg C m^{-3} at stations P2 and P1, respectively.

The numerical simulation starts from the wintering population of adults (Dutz et al. 2010). The result of numerical simulation indicates five generations, from eggs to adults, per year (during 227 days) at station P1 (Gdańsk Deep) and four generations (during 235 days) at station P2 (the Gulf of Gdańsk), while the first generation G1 in both cases started between late March and early April (Fig. 4). On the basis of our results it should be noticed that the development time of *T. longicornis* is not isochronal, even at optimal food concentrations.
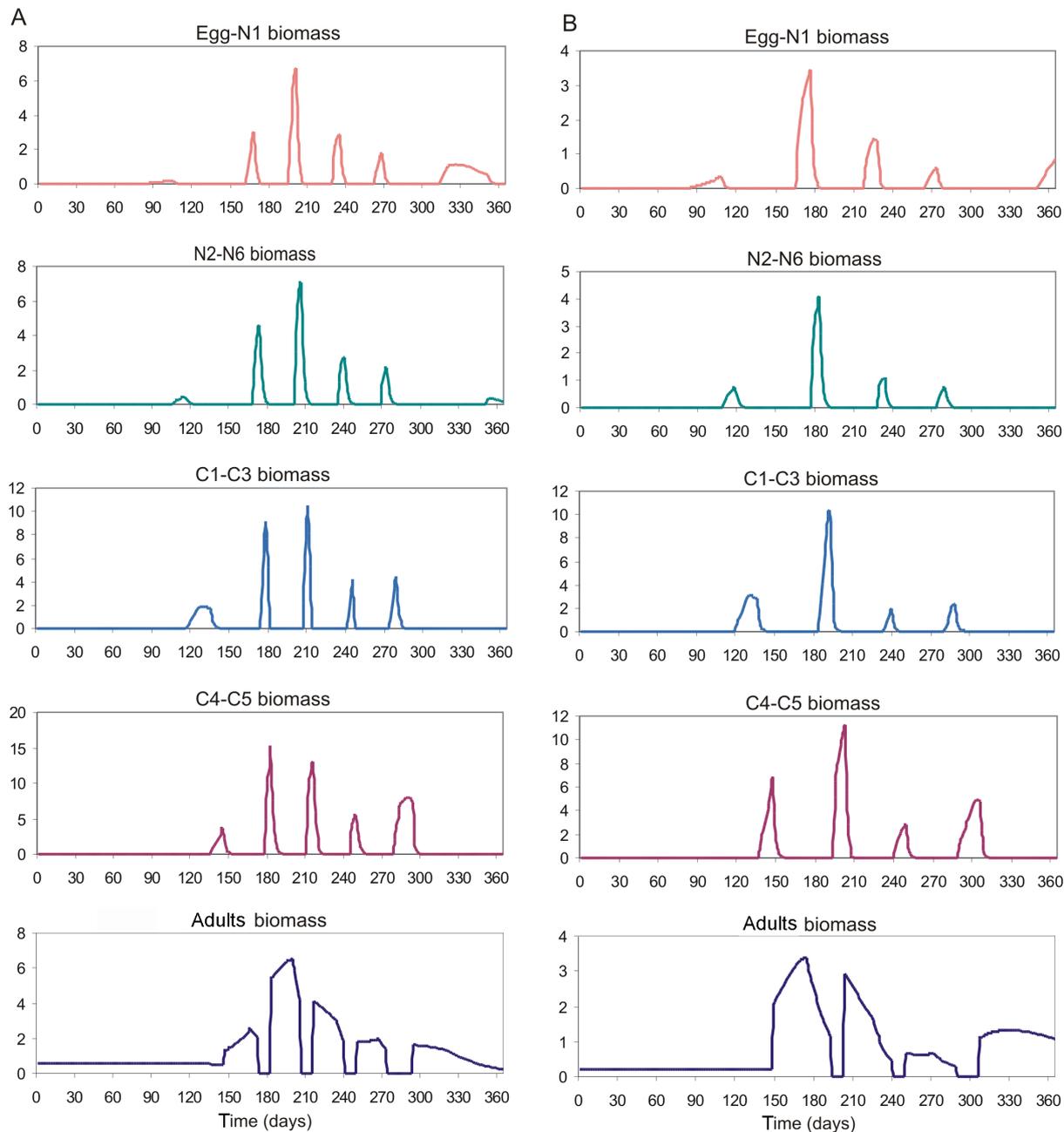
Fig. 4. Stage-specific total biomass (mg C m^{-3}) of *Temora longicornis* simulated for stations P1 – Gdańsk Deep (**A**) and P2 – Gulf of Gdańsk (**B**) for the year 2011.

The development time for subsequent generations of *T. longicornis* at stations P1 and P2 is given in Table 3. At station P1 (Gdańsk Deep) the total duration of one generation of this copepod species is shorter than in the Gulf of Gdańsk, despite the fact that station P2 is characterized by higher temperatures and concentration of food and lower salinity. This is a result of the parabolic function ft_2, which reflects a decline in the rate of the growth of the species development at a temperature above 15 °C. Basically, the temperature increase induces a faster growth of organisms and reduces the population life time. The salinity of the Gulf of Gdańsk is lower in winter than in summer. A key factor affecting the salinity of surface waters is the influence of fresh water of the Vistula River, occurring mainly in spring.

The development time of the first generation G1 at both stations differed by five days. The long duration of the spring generations was a result of low salinity caused by the inflow of the Vistula River fresh water in

Table 3. The development time (days) for subsequent generations (G1–G5) of *Temora longicornis* at stations P1 and P2

Generation	P1	P2
G1	96	101
G2	51	72
G3	44	58
G4	50	99
G5	107	–

this period. Higher temperatures of surface waters (up to 15 °C) in the summer season accelerated the growth of organisms at each stage of ontogenesis. Thus the full cycle of the second generation G2 development was 21 days longer at station P2 than at P1. The third generation G3 started in the first half of August in the Gulf of Gdańsk and one month earlier in the Gdańsk Deep. The fourth generation G4 at station P1 reached much higher biomass values than at station P2 where the development lasted till the end of the year (to the half of December), and it was the longest development time of the generation.

During the development of generations G2, G3 and G4 in the Gdańsk Deep (station P1), the temperature in the upper layer (topmost 25 m) was lower than the average by about 1−3 °C, and the food concentration was lower than at P2. The salinity in the entire water column was higher than at station P2 in the Gulf of Gdańsk.

The fifth generation G5 of *T. longicornis* (107 days) at station P1 appears in mid-September and reaches the maturity at the end of October. The individuals of G5 and the sixth generation G6 were produced by females of the previous generation in the latter half of December and November at stations P2 and P1, respectively, but they did not develop further than the model stage (Egg−N1). These organisms in their later stage of development have no chance to survive due to a significant temperature drop and insufficient food resources in winter.

Figure 5 presents the distribution of the total biomass averaged in the water column, which is an algebraic sum of vertical distributions of average biomass in all the examined development stages at two stations P2 and P1. The total biomass of *T. longicornis* in the Gdańsk Deep was higher than in the Gulf of Gdańsk. The total biomass distribution in the Gulf of Gdańsk is described by three population peaks, the highest one in July 2011 – ca 11 mg C m^{-3} and two smaller ones in May and October 2011 – 6.7 mg C m^{-3} and 4.9 mg C m^{-3}, respectively. The highest population peak results from the development of the second generation G2. All population biomass peaks result from a large biomass of copepods of mainly two simulated stages of ontogenesis: CI−CIII and CIV−CV, whereas
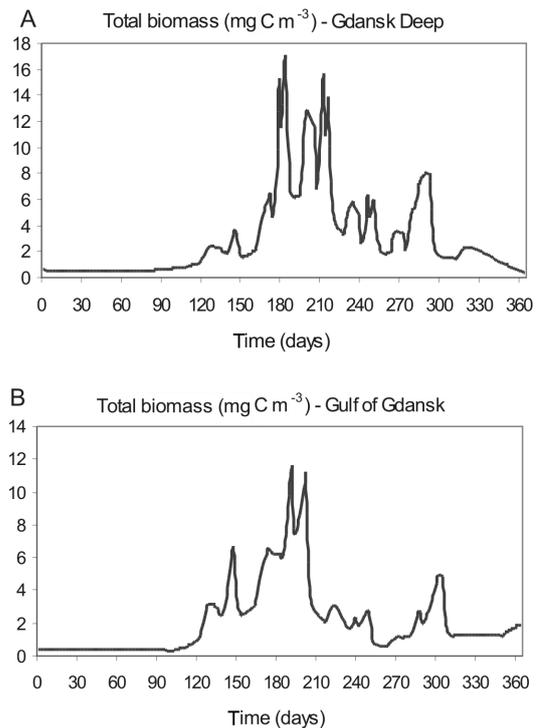
Fig. 5. The observed total biomass of *Temora longicornis*, averaged in the water column, at stations P1 – Gdańsk Deep (**A**) and P2 – Gulf of Gdańsk (**B**) in 2011.

all lower population peaks result from the production of eggs, the development of nauplii and adults. The sufficient amount of food in autumn enabled generations G4 and G5 to develop at stations P2 and P1, respectively, which consequently enabled the females of these generations to produce eggs and thus initiate the next generation in November–December.

The distribution of the total *T. longicornis* biomass in the Gdańsk Deep was characterized by one main population peak in the summer months and two smaller peaks in October (8 mg C m^{-3}) and September (6 mg C m^{-3}) in 2011. High total biomass in July and August with values ranging from 12 to 17 mg C m^{-3} resulted from a high biomass of copepods in all successive stages and especially at older copepodite stages C4−C5 of generations G2 and G3, as a result of high abundance in the previous development stages C1−C3 of these generations. High reproduction is mostly due to higher temperatures during that period. Smaller values of the population peaks (ca 6 mg C m^{-3} and 8 mg C m^{-3} in September and October, respectively) in the total biomass distribution are mainly a consequence of a high biomass of copepodite stages C1−C3 and C4−C5 of generations G4 and G5.

Distributions in Figure 6 present the vertical profiles of biomass for the model stages of the development
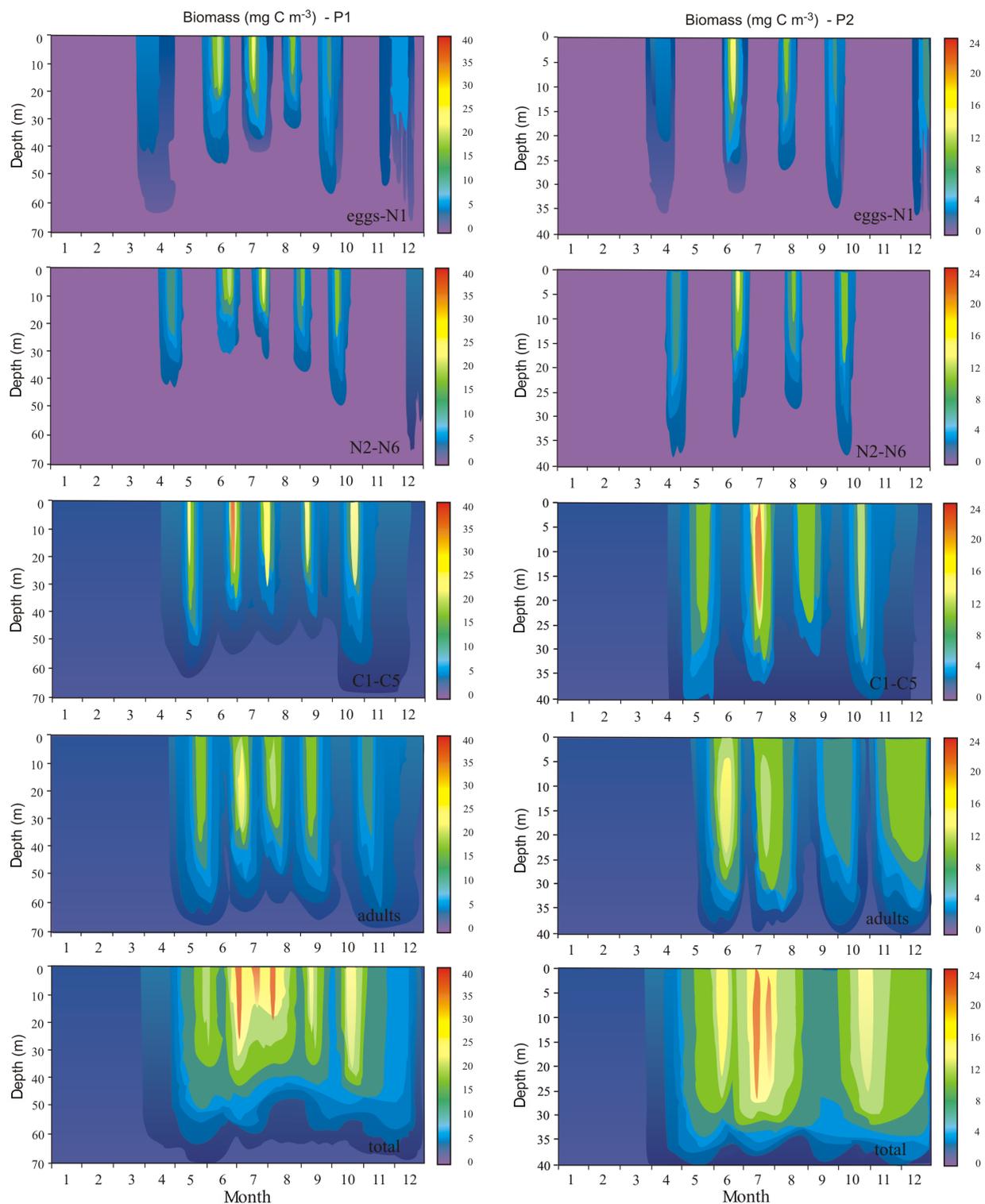
Fig. 6. Modelled vertical distributions of *Temora longicornis* development stages and the total biomass (mg C m^{-3}) at stations P1 – Gdańsk Deep and P2 – Gulf of Gdańsk in 2011.

reflecting the dynamics of *T. longicornis* in the annual cycle at stations P2 and P1. Four states of variables are presented: for Egg−N2, nauplii N3−N6, copepodites C1−C5 and adults.

The highest abundance of copepods in all development stages was located above the thermocline. In June, the thermocline occurs at a depth of ca 20−30 m at P1 and at ca 10−20 m at P2, and the temperature of the surface layer increases above 13 °C at P1 and 15 °C at P2, reaching the maximum values in August.

The highest total biomass of *T. longicornis*, determined numerically, occurred in summer in the Gdańsk Deep and ranged from 20 to 40 mg C m^{-3} in the upper water layer (30 m in June−July, 20 m in July−August). Generally it was represented by biomass of copepodites (from 15 to 37 mg C m^{-3}). Model stages of Egg−N1, older nauplii and adults, were within the range of 10−23 mg C m^{-3} each. The situation was similar in the Gulf of Gdańsk − the highest total biomass was recorded in summer, in July (from 14 to 22 mg C m^{-3} at 30 m depth) and was generally represented by biomass of copepodites (from 12 to 21 mg C m^{-3}) and Egg−N1, older nauplii and adults, within the range of 8−16 mg C m^{-3}.

Between late October and early November the thermocline begins to disappear and the development of generations G4 and G5 is terminated at stations P2 and P1, respectively. At that time most of the total *T. longicornis* biomass is observed as a sum of mostly two states of variables – adults, which produce eggs and thus initiate the next generation and organisms of this generation that do not uptake food (Egg–N1).

Model validation – comparison of the model results with the in situ data

According to field data, in late winter of 2010−2011 the average biomass of *Temora longicornis* in the Gulf of Gdańsk (P2) reached several hundred (< 1000 mg wet weight (w.w.) m^{-2}) in the water column and considerably increased in the spring−summer season. The lowest biomass was recorded in March 2010 – 480 mg w.w. m^{-2} and April 2011 – 240 mg w.w. m^{-2} (no data available for February). The maximum development occurred in spring 2010 and summer 2011, respectively, ca 6100 mg w.w. m^{-2} in May and 4500 mg w.w. m^{-2} in August (Fig. 7). The May peak of *T. longicornis* biomass in 2010 was relatively high (compared to other months), and the relatively heterogeneous structure of the population in May was probably one of the causes. This resulted in the increased values of biomass (in particular, older copepodites and adults). In the other months most of the
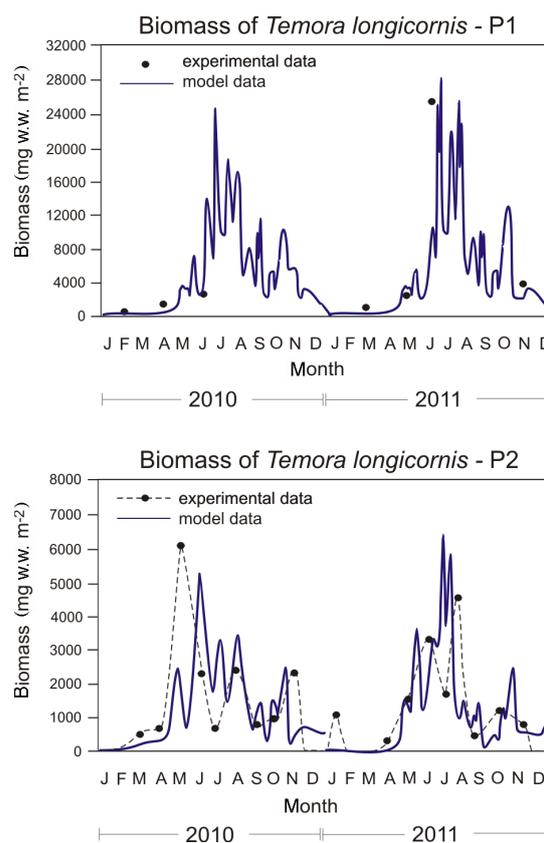
Fig. 7. The consolidated biomass of *Temora longicornis* in the water column at stations P1 – Gdańsk Deep and P2 – Gulf of Gdańsk based on in situ model data in 2010 and 2011.

observed specimens were represented by nauplii. Two smaller equivalent peaks with values of ca 2300 mg w.w. m^{-2} and 2500 mg w.w. m^{-2} were recorded in August and November. In 2011, the maximum peak was observed in June (3500 mg w.w. m^{-2}) after the spring peak in May (1800 mg w.w. m^{-2}), followed by a small biomass increase in autumn − up to the value of ca 1200 mg w.w. m^{-2}.

Due to the insufficient amount of environmental data from the Gdańsk Deep (P1), the average biomass of the studied crustacean was only estimated and it appears to be approximately four times higher than in the Gulf of Gdańsk. The results obtained from the population model are very similar but they cannot be properly compared because of the scarcity of field data. The maximum value (ca 26 400 mg w.w. m^{-2}), determined on the basis of available in situ data, was recorded in June 2011. In the other studied months, the biomass ranged from 1200 mg w.w. m^{-2} in February 2010 to 4300 mg w.w. m^{-2} in November 2011 (Fig. 7).

Figure 7 presents the observed data and also the results of numerical simulations for the total biomass of

T. longicornis (mg w.w. m^{-2}) as an integrated biomass in the water column. The highest values of the modelled *T. longicornis* biomass occurred in the period of high temperatures, i.e. in summer, in June 2010 and June–July 2011 in the Gulf of Gdańsk – at station P2, and between late June and early July, and for almost the whole summer in the Gdańsk Deep – at station P1, and amounted to respectively ca 5200 mg w.w. m^{-2} and 6300 mg w.w. m^{-2} at station P2 and 24 500 mg w.w. m^{-2} and 27 800 mg w.w. m^{-2} at station P1. Generally, the simulated biomass of *T. longicornis* was high in the Gdańsk Deep. Observation data are too scarce (seven times over two years) to verify the model for this point.

The difference in the timing of the modelled and observed peak dates of biomass is the result of inter-annual differences of the Vistula River inflows and resulting salinity values while the 3D CMBS model used inflow climatology data (although modified by the sea circulation for a given month). Validation of the model consists in the determination of the extent to which the model reflects the actual system. For this reason, the model results and field data for the total bio-mass of *T. longicornis* (mg C m^{-3}) as vertical mean values in the water column for station P2 were compared with the data available for years 2010 and 2011. Additionally, correlation coefficients were also calculated for years 1991, 1999, 2000, 2006 and 2007 for which the model calibration was made (Fig. 3).

The model results are quite consistent with the field data for station P2 having the average value of the Pearson's linear correlation coefficient $r = 0.58$ and coefficient of determination $R^2 = 0.36$ for 2010/2011 ($r = 0.68$ and $R^2 = 0.47$ for all years). The correlation coefficient of about 0.6 is a satisfactory result and it suggests that the model operates properly. Similar levels of correlation, though slightly lower ($r = 0.51$), were observed for the simulated annual distribution of the mean total abundance in the water column. When comparing the numerical results and observed data for each of the model stages within the whole of the study period, the differences were higher. This is mainly due to poorer modelled (?) results for nauplii and adults.

DISCUSSION

Factors controlling the development of *Temora longicornis*: food concentration, temperature and salinity

The significant difference in the development of *Temora longicornis* between the numerical data at stations P1 and P2 is the result of (a) temperature, which is lower at the open sea than within the Gulf of Gdańsk in spring–summer and inversely in winter, (b) salinity, which is higher at the open sea than within the Gulf of Gdańsk, (c) egg production, which is a function of food concentration, temperature and salinity. Data differences are also caused by the lack of laboratory experiments needed for a correct description of these relations in the investigated region, the Gdańsk Basin.

Among the environmental parameters influencing the development of *T. longicornis* in the Gdańsk Basin, the most important were: food concentrations *Food* with a threshold of 180 mg C m^{-3} for the development of nauplii and 280 for C1–C6; temperature T with a threshold of 15 °C and salinity in the whole range of variability in the study area. Firstly, this is so because the growth of the individual follows the exponential curve against the optimum temperature T_o (for *T. longicornis* – 15 °C), and above this value the increase in the growth rate declines following the para-bolic threshold function ft_2 as a result of physiological stress. Secondly, the growth of organisms continues only up to the maximum value g_{max} and as the food concentration reaches high values, the growth rate remains at a constant level as some Crustacea species suspend the ingestion before or during the process of moulting (Paffenhöfer 1971). Thirdly, the egg produc-tion depends on salinity in accordance with the function *fs* including a salinity threshold for egg production of 7.

The quality and quantity of food available to copepods are very important for their development. In natural conditions copepod diets are selective and diverse. Selectivity by copepods may relate to the size of the prey (Atkinson 1995), its toxicity (Huntley et al. 1986) and nutritional quality (Houde & Roman 1987). In the Bornholm Basin in the Baltic Sea the diet composition generally seems to differ from that of other habitats in a relatively moderate role of diatoms and a much larger importance of heterotrophic food compo-nents (Peters 2006; Dzierzbicka-Głowacka et al. 2011). Based on our study and literature data, we assumed in the model that the food composition includes 50% phytoplankton biomass, 25% zooplankton biomass and 25% pelagic detritus.

In our simulations the concentration of available food in spring bloom was about two times higher within the Gulf of Gdańsk than in the open sea (the Gdańsk Deep), which resulted in a higher egg production rate (G1) and consequently in higher biomass values for P2 than for P1. *Food* values above 180 mg C m^{-3} during the spring and autumn bloom events in the Gulf of Gdańsk did not influence the growth of nauplii and 280 mg C m^{-3} the growth of C1–C6. This agrees with function *f1* describing the influence of food concentra-tion on ingestion *ING* (Table 1). For those values of

Food the growth rate remains practically at a constant level. However, the egg production rate did increase, not being limited by food concentration.

Here, the impact of temperature on growth rates was defined by function *fte*, which at lower temperatures (<15 $^{\circ}$C) is described by Q_{10} and at higher ones by the parabolic threshold function ft_2. The growth rate of *T. longicornis* increases rapidly with rising temperature up to 15 $^{\circ}$C. However, during summer at temperature above 15 $^{\circ}$C and with limited food availability an increase in temperature reduces the growth of all developmental stages.

Increase in temperature above 15 $^{\circ}$C results in a reduction of the growth rate by 6% and 47% for *T* increase by, respectively, 1 $^{\circ}$C and 5 $^{\circ}$C, hampering further increase in the growth rate. A similar process reduces the increase in the egg production rate limited by function ft_2 for $T > 15$ $^{\circ}$C as a result of physiological stress.

About 85% (station P1) and 100% (station P2) of the population was distributed in the brackish-water (salinity $S < 8$) layer below 40–50 m, where mean difference in S between P1 and P2 was 0.5. Salinity at station P2 varied to a small extent, both during the year and throughout the water column. Mean values of water salinity in the western part of the Gulf of Gdańsk (P2) ranged from 6.2 in spring (May) to 7.3 in autumn–winter. The lowest salinity was observed after the inflow of Vistula flood waters. The salinity of surface waters at station P1 ranged from 6.94 to 7.85 and gradually increased along the depth gradient, reaching a maximum value of 12.05–10.84 at the bottom. An increase in salinity has a positive impact on the development of the studied species.

The effects of reduced salinity on development, represented by functions *f*4 and *fs* in the equation for ingestion and egg production, respectively (Table 1), result in (i) a drop in the growth rate (by 5% with S decrease by 0.5) which, in turn, results in an increase in stage duration, and (ii) a decrease in the number of eggs (by 12% with S decrease by 0.5). To sum up, the development of *T. longicornis* in the Gdańsk Basin depends on three main environmental parameters – availability of food and temperature (these being controlling factors), and salinity (a hampering factor).

According to our modelling results, differences in the development of *Temora longicornis* between stations P1 and P2 depend mostly on spatial and temporal 3D distribution differences in available food and temperature as well as on salinity (mostly concerning its vertical distribution). The decrease in salinity S in the coastal zone (P2) resulted in the lengthening of stage duration caused by the decreased growth rate and number of eggs produced by a female. At the same time,

increase in salinity S with depth at the deep-water station P1 resulted in increased growth rates of copepodites C1–C6, which were able to reach the depth with $S > 8$ due to migration, making the generation time shorter and increasing egg production by females. This was also the result of vertical distribution of temperature and food concentration. At depths > 25 m, those parameters were higher at station P1 than at P2 and their vertical gradient was smaller.

Our results show that conditions for the development of this species during summer and autumn were better at open sea than in the coastal area. As a result, total biomass per m^3 was ca 50% higher at P1 than at P2 (ca 17 mg C m^{-3} and 8.1 mg C m^{-3} at P1 and 11.8 mg C m^{-3} and 5 mg C m^{-3} at P2, respectively) which may be explained by higher salinity for P1 throughout the water column.

Only in the spring bloom, during the development of the first spring generation G1 with a similar stage duration at both stations (101 days – P1 and 96 days – P2), high food concentration at P2 (within the Gulf of Gdańsk) resulted in almost twice as much biomass of this species at P2 (6.9 mg C m^{-3} at P2 and 3.8 mg C m^{-3} at P1). The main reason for this feature was higher egg production.

Spatial variability

According to recent evidence (Chojnacki et al. 1984; Vuorinen et al. 1998; Hänninen et al. 2000, 2003; Mudrak 2004; Peters 2006; Holste et al. 2009; Dutz et al. 2012), the development of copepods may also depend on the area of study. Different populations may develop slightly different survival strategies to adapt to their habitat.

The comparison of the population of *Temora longicornis* in two areas of the southern Baltic Sea, the Gdańsk Basin and the Bornholm Basin, shows differences in the development of this species. Maximum biomass of the species was recorded mostly in June–July in 2010 and 2011 (model: 1.62 g C m^{-2} and 1.79 g C m^{-2}, respectively; exp: 1.64 g C m^{-2} in 2011) in the Gdańsk Basin (Gdańsk Deep), and May–June in 2002 (exp: 2.21 g C m^{-2}) in the Bornholm Basin (Dutz et al. 2010). This is caused by a high biomass of copepodites of G2 in the Gdańsk Basin and of G1 in the Bornholm Basin and coincides with the highest peak of adult organisms biomass, in July and June–July, respectively. In autumn (October), the secondary maxima in biomass were observed for both the Gdańsk (ca 0.8 g C m^{-2}) and Bornholm (ca 0.5 g C m^{-2}) basins.

Earlier spring blooms in the Bornholm Basin compared to the Gdańsk Basin due to higher food concentrations and higher values of temperature and

salinity, stimulated an earlier (ca 2 weeks) appearance of the first spring generation G1 and the occurrence of peak in abundance and biomass. Such a situation did not occur in the Gulf of Gdańsk in this period due to lower salinity caused by the inflow of the Vistula River fresh water. The peak for the Gdańsk Basin occurred in summer during the period of the second generation G2 when the temperature and salinity were higher.

Lower salinity in the Gdańsk Basin, mainly in the spring period, resulted in slower growth and reduced reproductive capacity. These are translated into characteristics that differentiate the Gdańsk Basin population from the Bornholm Basin population.

Based on our data, *T. longicornis* in the Gdańsk Basin produced four (the Gulf of Gdańsk) to five generations (the Gdańsk Deep) in 2010 and 2011. The calculated time of spring generation G1 (96 days) was two times longer than for summer generations G3 and G4 (44 and 45 days) at station P1 due to higher salinity and warm temperatures in August–September.

In the Bornholm Basin, the analysis of the life cycle by means of stage structure, copepodite length and stage duration revealed that *T. longicornis* produced 5 to 6 generations in 2002 (Dutz et al. 2010). The first spring generation G1 time was about two months and the shortest generation time was in G4 (ca 1 to 1.5 months) in September–October (Dutz et al. 2010). Figure 8 presents the *T. longicornis* scheme of life cycles for the Gdańsk Basin – the Gdańsk Deep (this study), comparing them with the previously published results for the Bornholm Basin (fig. 9 in Dutz et al. 2010).
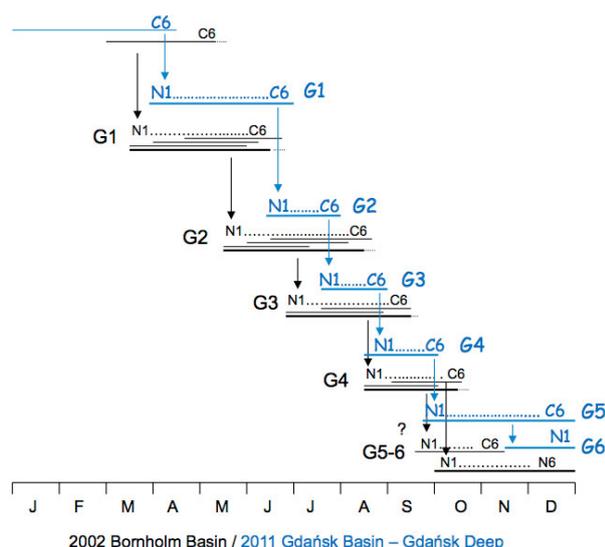
Fig. 8. Scheme of *Temora longicornis* life cycles for the Gdańsk Basin – Gdańsk Deep (this study – blue colour) and the Bornholm Basin (black colour). G1–G6, generations.

In the Baltic Sea (salinity much lower than 30), temperature as well as salinity conditions strongly impact on the rate of egg production by female *T. longicornis* (Peters 2006; Holste et al. 2009). Data on food selectivity of *T. longicornis* are controversial.

The studies in the Bornholm Basin carried out by Peters (2006: chapter III) presented the seasonal changes in the individual daily egg production rate of *T. longicornis*. Values of *Egg* reached 14 eggs per day in April and declined sharply over the summer to only 0.7 eggs per day, while a second smaller peak in reproduction occurred in October: 6 eggs per day. The value of *Egg* obtained by Holste et al. (2009) in laboratory experiments was 12 eggs produced by one female per day at salinity 14; similar values of *Egg* were obtained by Dutz et al. (2012) (i.e. from 9.8 to 12.3 eggs during spring in March 2002/May 2003 in the Bornholm Basin).

Our numerical simulations suggest that females reproduced year round in the Gdańsk Basin in 2010–2011, with maxima of 8.9 to 10.6 eggs female^{-1} d^{-1} which coincided with the spring phytoplankton bloom occurring between March and April at 4–6 ^{o}C and at salinities around 7–8. A second peak in *Egg* (ca 8.1 eggs female^{-1} d^{-1}) was obtained in September at surface water temperatures of 15–17 ^{o}C.

Individual egg production rates in the Baltic Sea (the Bornholm Basin and the Gdańsk Basin) are rather low (ca 3–5 times lower) in contrast with adjacent waters, i.e. the North Sea and the English Channel, where values are moderate or quite high and vary strongly within the investigation area, without reaching maximum values (Halsband & Hirche 2001; Arendt et al. 2005; Peters 2006: chapter 4). Therefore, the results given by Peters (2006), Holste et al. (2009), Dutz et al. (2012) and Dzierzbicka-Głowacka et al. (2013b) suggest that 'in the Baltic Sea, salinity is a masking factor' (Holste et al. 2009).

CONCLUSIONS

Simulation with the numerical model was used in this study as a method and a tool for the identification of processes describing the development of *Temora longicornis*. Our objective was to determine the dynamics of the species development, allowing for successive stages of its individual development and relationships between life processes and environmental parameters.

To this end, (i) a numerical model of the population was developed for the studied crustacean defining the mass and abundance in the model development stages in order to determine the total individual biomass and (ii)

validation of the model was performed by comparing the in situ data with the results obtained from the model.

The population model was satisfactorily verified using the field data. The results obtained from the population model are consistent with the in situ data for station P2 in the western part of the Gulf of Gdańsk. This demonstrates that the model operates properly and can be used for studies of seasonal changes in the dynamics of *T. longicornis* development in the southern Baltic Sea.

The largest deviations from the observed biomass values were related to the maximum peaks, which was especially visible in May 2010 (station P2). This relatively high peak of biomass (compared to other months) was probably caused by the relatively hetero-geneous structure of the population; this resulted in increased values of biomass (in particular, older copepodites and adults). In other months, most of the observed individuals were represented by nauplii. The other reason could be environmental factors, including transport of waters or toxic algal blooms in summer, which accounted for reduced biomass of younger copepodites.

The differences between the field data and the numerical results could be explained by a combination of several factors: (1) spatial and temporal distribution of three parameters: food concentration, temperature and salinity, (2) model 3D resolution, (3) fresh-water fluxes that can change salinity in the estuary area, (4) salinity, which is higher in the model than in the natural environment, (5) mortality which is not affected by salinity, (6) predation pressure, which in the model was treated marginally, (7) other physiological processes (i.e. egg production and growth) which are dependent on salinity through functions fs and $f4$, (8) no laboratory analysis available for the study region to describe more properly the functional relationships between the physiological processes and the environmental para-meters, (9) the insufficient amount of environmental data and (10) the field research process, i.e. sampling by different persons, the method used for sampling and data analysis.

The population model presented in this paper is a relatively good tool to describe the dynamics of *T. longicornis* populations and mechanisms of the species functioning in the marine environment. At present, it is the only population model for *T. longicornis* from the Baltic Sea.

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Temora longicornis'e biomassi jaotus aasta jooksul Gdański lahes (Läänemere lõunaosa) – modelleeritud andmed

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Ühendades aerjalgse *Temora longicornis* populatsiooni mudeli ökosüsteemi mudeliga 3D CEMBS (Coupled Ecosystem Model of the Baltic Sea), arvutati välja selle liigi aastasisene biomassi jaotus Läänemere lõunaosas paiknevas Gdański lahes. *T. longicornis*'e populatsiooni mudel koosneb kaheteistkümnest võrrandist ja kaheteistkümnest seisundimuutujast, millest kuus on massi ning kuus arvukuse kirjeldamiseks. Seega kaks seisundimuutujat iga mudelis kirjeldatud arengustaadiumi jaoks: munad (Egg), mittetoituvad vastsestaadiumid (N1), hilisemad vastsestaadiumid (N2–N6), kaks kopepodiidset staadiumi (C1–C3 ja C4–C5) ning suguküpsed täiskasvanud (C6). Populatsiooni mudeli empiiriliseks kontrolliks kasutati 2010. ja 2011. aastal Gdański lahe lääneosast ning Gdański süviku piirkonnast kogutud proovide andmeid. Mudeli kõrgeimad biomassi märgkaalu väärtused langesid kokku kõrgema veetemperatuuri perioodiga: Gdański lahes 2010. aasta juunis ja 2011. aasta juulis vastavalt 5200 mg m^{-2} ning 6300 mg m^{-2} ja Gdański süviku piirkonnas peaaegu kogu mõlema suve jooksul 24 500 mg m^{-2} ning 27 800 mg m^{-2}. *T. longicornis* esines Gdański lahes ja Gdański süvikus vastavalt 4 kuni 5 põlvkonnaga aastas. Populatsiooni mudeli arvutatud andmed olid *in situ* andmetega kooskõlas ja mudeli verifitseerimist peeti õnnestunuks. Vaatamata mõnedele erinevustele mudeli ja proovidest saadud andmete vahel, on välja töötatud *T. longicornis*'e populatsiooni mudel, mis on esimene antud liigi jaoks koostatud mudel Läänemeres, ning kuigi see vajab veel parandamist, on sellest abi populatsiooni dünaamika ja keskkonnasuhete määratlemiseks.