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Modelling the population dynamics of *Temora longicornis* in the Basin Gdańsk (southern Baltic Sea)

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Abstract

The ecosystem model 3-D CEMBS connected with the population model, described in this paper, was used to determine the temporal distributions of *T. longicornis* in the Gdańsk Basin (the southern Baltic Sea) divided into the coastal zone P2 (the Gulf of Gdańsk) and the open sea P1 (Gdańsk Deep). The population model for *T. longicornis* consists of twelve equations for twelve states of variables, six for the mass W_i and six for the abundance Z_i, i.e. two states of variables W_i and Z_i, for each of the six model stages of the development; the stages were grouped as follows: eggs – Egg, stages not taking food – NI–NII, subsequent stages of nauplii – NIII–NVI, two copepodid stages – CI–CIII and CIV–CV and the last stage of adult organisms – CVI. 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.

The empirical verification of the population model based on in situ data obtained from the analysis of biological material collected in 2010–2011 in the region of Gdańsk Deep (P1) and in the western part of Gdańsk Bay (P2), and in 2006–2007 – only in Gdańsk Bay (P2). The highest values of the modelled *T. longicornis* biomass occurred in the period of high temperatures, i.e. in summer, in June 2010 and July 2011 in the Bay of Gdańsk – at station P2, and between late June and early July, and for almost the whole summer in 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. In 2006 and 2007 at station P2 the highest numerical values were recorded between late July and early August, exactly at the same time as environmental data, and amounted to 4300 $mg_{w.w.}\,m^{-2}$ and 5800 $mg_{w.w.}\,m^{-2}$, respectively. The results determined from the model are 0.25–2 times higher compared to in situ data. The most similar values were obtained for 2007.

1 Introduction

Over the last century, the Baltic ecosystem has been exposed to miscellaneous transformations as a result of global climate change and broadly defined human impact (anthropopressure). This has a very negative impact on the marine life. Therefore, the efficient management of the marine environment is extremely important and requires extensive research with the main objective to develop new and more accurate methods of environmental monitoring and prediction of environmental response to different economic activities and global climate change.

In ecosystem models, zooplankton is usually treated as a group of individuals rather than as biomass. Due to this distinction, zooplankton should be considered as organisms with specific forms of growth, propagation and mortality. The research on this subject was conducted i.a. by: Carlotti (Carlotti and Radach, 1996; Carlotti and Wolf, 1998), Fennel (Fennel, 2001; Fennel and Neumann, 2003) or Stengert (Stengert et al., 2007; Moll and Stengert, 2007) and focused on modelling of *Calanus finmarchicus* and *Pseudocalanus* spp. dynamics. In Poland, studies of the population modelling were presented by Dzierzbicka-Glowacka (Dzierzbicka-Glowacka, 2004, 2006; Dzierzbicka-Glowacka et al., 2009, 2010, 2012, 2013) and they were related to *Pseudocalanus* sp. and *Acartia* spp. from the Baltic Sea.

So far, no population model has been presented for *Temora longicornis*, which is a subdominant zooplankton (Copedoda) species from the southern Baltic. The species plays a very important role in the ecosystem as it constitutes a valuable source of food for economically important fish – herring and sprat. Furthermore, together with *Pseudocalanus* sp., it is a food source for larval forms of codfish. Planktonic organisms respond relatively quickly to changes occurring in the surrounding environment, therefore they can be good indicators of the ecological status of a given ecosystem. Frequency and the number of performed in situ studies are insufficient for reliable assessment of the ongoing long-term and seasonal changes in the marine environment. Only combined environmental, laboratory and modelling studies may give the reliable picture of

the spatial and temporal distribution of the studied crustacean and other zooplankton species, in terms of abundance and biomass at different stages of ontogenesis.

Therefore, the main objective of the presented study was to determine the dynamics of the *Temora longicornis* population in Gdańsk Basin (the southern Baltic) based on the numerical analysis.

The research consisted of the following phases: (i) determination of the functional relationships between the physiological processes and environmental parameters – mathematical description of these processes is necessary to model the mesozooplankton dynamics in population terms; (ii) determination of the population model for *Temora longicornis*, which defined temporal and spatial distributions of weights and abundance, and was connected with the ecosystem model 3-D CEMBS (Dzierzbicka-Glowacka et al.2013c, d); (iii) empirical verification of the population model based on in situ data obtained from the analysis of biological material collected in 2010–2011 in the region of Gdańsk Deep (Gdańsk Basin) and in the western part of Gdańsk Bay, and in 2006–2007 – only in Gdańsk Bay.

2 Baltic Ecosystem Model – 3-D CEMBS

The 3-D CEMBS Baltic Ecosystem Model is based on the global model for the world ocean – CCSM4.0/CESM1.0 (Community Climate System Model/Community Earth System Model), which was adapted to the Baltic region (Dzierzbicka-Glowacka et al., 2013c, d). The ocean model (POP, version 2.1) and the ice model (CICE, version 4.0) operate in the active mode; they are forced by the atmospheric data model (DATM7). The main task of datm7 consists in interpolation of atmospheric data on the domain of the model. External forces (= atmospheric data) – input data for the model – come from the re-analysis ECMWF (ERA-40) and from the UM model of the Interdisciplinary Centre for Mathematical and Computational Modelling, the University of Warsaw (ICM UW). At present, 48 h weather forecasts are used in the operational system, supplied by the UM model of ICM UW. The 3-D CEMBS model has also the biogeochemical

module, which is executed by the active ocean model and is located inside the source code of the ocean model (http://deep.iopan.gda.pl/CEMBaltic/new_lay/index.php).

The biogeochemical module consists of 14 equations for the main pelagic variables: the biomass of small phytoplankton and large phytoplankton such as diatoms and cyanobacteria, the biomass of microzooplankton, deposits of dissolved pelagic detritus, dissolved oxygen concentrations, and concentrations of nutrients: nitrates, ammonia, phosphates and silicates (Dzierzbicka-Glowacka et al., 2013d).

The results presented below and on the website illustrate the correct performance of the model. Figure 1 presents the results from the model for hydrodynamic (temperature, salinity, water currents and the water level) and biogeochemical variables (chlorophyll *a* concentration, the biomass of phytoplankton and zooplankton, concentration of nutrients: NO_3, NH_4, PO_4, SiO_4 and dissolved oxygen concentration) for 2 May 2012 (Dzierzbicka-Glowacka et al., 2013d, http://deep.iopan.gda.pl/CEMBaltic/new_lay/index.php).

3 *Temora longicornis* population model

This chapter presents parametrization of the Copepoda population model for *Temora longicornis*. The model defines the distributions of mass and abundance at each stage of the individual development of the studied copepod in order to determine the total biomass.

The population model combined with the 3-DCEMBS ecosystem model consists of twelve equations for twelve states of variables, six for the mass W_i and six for the abundance Z_i, i.e. two states of variables W_i and Z_i, for each of the six model stages of the development; the stages were grouped as follows: eggs – Egg, stages not taking food – N1–N2, subsequent stages of nauplii – N3–N6, two copepodid stages – C1–C3 and C4–C5 and the last stage of adult organisms – C6 (Fig. 2). A change in the individual mass W_i of each specimen, in the developmental stages from N1 to adult organisms, is controlled by ingestion ING and metabolic losses (FEC, MET). Whereas

a variable describing the abundance Z_i is determined by the mortality rate MOR and transfer TRN, transition from stage $(i-1)$ to next stage (i). Both processes, ingestion and transfer, depend on the individual mass of specimens at different stages of their development, using critical mass for moulting W_m (Dzierzbicka-Glowacka et al., 2010). The main equations for weights W_i and abundance Z_i are as follows:

$$\frac{\partial W_i}{\partial t} = \mathrm{ING}_i - \mathrm{FEC}_i - \mathrm{MET}_i \tag{1}$$

$$\frac{\partial Z_i}{\partial t} = \mathrm{TRN}_{i-1} - \mathrm{MOR}_i - \mathrm{TRN}_i \tag{2}$$

The total biomass BT for each individual was defined as a sum of its biomass B_i in the subsequent development stages (six stages in this case), which are the sum of the products of the mass W_i and the abundance Z_i:

$$\mathrm{BT} = \sum_{i=1}^{i=6} B_i \quad \text{where } B_i = \sum_{i=1}^{i=6} W_i Z_i \quad \text{and } \frac{\partial B_i}{\partial t} = \sum_{i=1}^{i=6} \left(W_i \frac{\partial Z_i}{\partial t} + Z_i \frac{\partial W_i}{\partial t} \right) \tag{3}$$

Physiological processes that determine the growth and dynamics of populations are presented in Table 1 and in Fig. 3, whereas the list of abbreviations is presented in Table 2.

Equations for each state of variables are described by including the critical mass W_k according to the concept of Dzierzbicka-Glowacka et al. (2010), which defines a given state (i) by the mass W_i inside the range of values $W_{k(i-1)} < W_i \leq W_{k(i)}$. Duration of each model development stage as a function of environmental parameters, concentration of food and temperature, is determined by relationships presented in Dzierzbicka-Glowacka et al. (2009); whereas, duration of a given individual in the embryonic stage depends only on the temperature and is described by the function of Bělehrádek (Table 1 – D_E).

The ingestion rate by an individual organism in subsequent development stages ING_i is determined by the concentration of food Food through the function $f1$, the individual

critical mass in a given development stage W_k and critical mass of exuviae W_m through the function $f2$ and temperature T through the function $f3$ dependent on the temperature coefficient Q_{10}, which applies to the optimum temperature T_o(T_o = 15 °C for *Temora longicornis*, see Dzierzbicka-Glowacka et al., 2009) and individual mass W_i in a given development stage through the function $f4$. The transition to the next stage takes place when the critical mass of exuviae is reached and only a small fraction of the mass is lost in the process of moulting (Carlotti and Wolf, 1998). There are following parameters defining the rate of ingestion in relation to food concentration Food: f_{max} – the maximum rate of ingestion, $Food_o$ – 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 two stages of nauplii, N1 and N2, are not capable of absorbing the food and are able to survive using the reserves supplied by eggs (Berggreen et al., 1988). For every stage, $Food_o = 0$ and $f3_i = 1$ for T = 15 °C; whereas the parameter k_{Food} is a function of food concentration, which ranges from 90 to 140 mg C m^{-3} and is described by Dzierzbicka-Glowacka et al. (2009).

The weight of exuviae W_m i.e. critical mass for the moulting process, is determined by the equation $W_m = \left(W_k + \sqrt{2}W_r\right) / \left(1 + \sqrt{2}\right)$ defined by Dzierzbicka-Glowacka et al. (2010, 2012) assuming that the value of half saturation is equal to $W_h = 2W_m - W_r$, (Moll and Stegert, 2007), which stipulates that the process of ingestion ING_i is not reduced before the transition to the next development stage TRN_{i+1}. The function $f2$ describing the reduction in the ingestion rate depends on the weight of exuviae W_m (see Fig. 3). Some Crustacea species suspend the ingestion before or during the process of moulting (Paffenhöfer, 1971). During the experimental research, Paffenhöfer and Harris (1976) observed the inhibition of ingestion in *Temora longicornis* before moulting to stage C1 and before the final moulting to the adult stage. Presumably, the ingestion rate is reduced when the individual body weight reaches the weight of exuviae, because the growth is limited by the external skeleton – cuticle. It was assumed that ingestion by an individual in the subsequent stage of development depends on the negative parabolic function $f2_i$, when the weight of exuviae exceeds the critical value

of W_m in the stage (i). Such an assumption does not occur in the adult stage, in which the process of egg production reduces the weight gain (Carlotti and Sciandra, 1989).

The rate of ingestion increases exponentially with the temperature according to the coefficient Q_{10} assuming the value of 2.274, which applies to the range of temperatures 5–15 °C by term ft_1 (Dzierzbicka-Glowacka et al., 2009). The temperature coefficient Q_{10} was calculated based on the data of Klein Breteler and Gonzalez (1986). Furthermore, the function $f3$ for temperatures (see Fig. 3) above T_o is modified by term ft_2. Function ft_2, a parabolic threshold function (with T_o = 15 °C, t_3 = 0.6 and $P1$ = 1.3), reflects reduction in the ingestion rate at higher temperatures as a result of physiological stress.

The ingestion ING is partly used for the growth, while the remaining part is lost in the metabolic processes, i.e. respiration MET and egestion (= production of faecal matter) FEC, additionally by moulting fm and production of eggs by a female Egg. The assimilation rate na equal to 70 % is commonly accepted for Copepoda (Steele, 1977); thus 30 % of the consumed food is egested (production of faeces), nf = 30 %. Juvenile stages N1 and N2, which do not feed, lose 20 % of their mass per day as a result of basic metabolism, nw = 20 %. The minimum respiration rate, i.e. 4 % of the body mass per day plus the respiration rate equal to 30 % of the ingestion rate for active metabolism ne, was assigned to nauplii N3–N6, copepodids and adult organisms.

As in the case of *Acartia* spp. and *Pseudocalanus* sp. (Dzierzbicka-Glowacka et al., 2006, 2010, 2012 and 2013), in order to determine the reproduction rate by a single female of *Temora longicornis*, a hypothesis was accepted about the equivalence between the growth rate of a given development stage and production of eggs Egg per day by a single well-nourished female (Sekiguchi et al., 1980; McLaren and Leonard, 1995). Taking into account the above aspects, the equation for the average number of eggs produced by a single female per day was defined for *Temora 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 (Dzierzbicka-

Glowacka et al., 2013e):

$$\mathrm{Egg} = a\exp(bT)\mathrm{ft}_2\mathrm{fs} \quad (4)$$

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

The parameter X in the equation for EGG (see Table 1) defining the efficiency, i.e. a percentage of females among adult specimens was assumed as $X = 50\,\%$.

Whereas, egg weight W_{egg} was assumed as: $0.03\,\mu\mathrm{g\,C\,egg}^{-1}$ for *Temora longicornis* (Harris and Paffenhöfer, 1976). Wet biomass of the studied species for every modelled stage of development was calculated in accordance with the recommendation of HELCOM-u (Hernroth (ed.), 1985) and the content of organic carbon as per $\mathrm{g\,C\,(g\,w.w.)}^{-1} = 0.064$ presented by Vinogradov and Shushkina (1987).

The mortality rate MOR was determined based on the estimation provided by Aksnes and Ohman (1996). Using the equations presented by the aforementioned Authors, the average rate of mortality mz in each development stage (i), dependent on the duration of a given stage for a given individual D_i and D_{i+1}, and the abundance Z_i and Z_{i+1}, was determined based on the following equations:

$$[\exp(\mathrm{mz}_i D_i) - 1]/[1 - \exp(-\mathrm{mz}_i D_{i+1})] = Z_i/Z_{i+1} \text{ (for two successive stages } i \text{ and } i+1)$$
$$\mathrm{mz}_{i-1} = \ln(Z_{i-1}/Z_{\mathrm{Ad}} + 1)/D_{i-1} (i = \text{Ad. for the adult stage}) \quad (5)$$

The above equations were solved numerically applying the iterative method.

Whereas, the rate of transition from stage (i) to next stage ($i+1$) TRN_i is determined by the sigmoid function that depends on W_i and W_{m} with the reference weight W_{r} as a threshold value, below which the transition to the next stage does not take place (Dzierzbicka-Glowacka et al., 2010).

3.1 Calibration and validation of the model

Calibration is the most time-consuming stage in the development of simulation models and it consists in fitting the results of simulation to real experimental data. It is very difficult to obtain satisfactory compatibility of the model with real data and it requires a large number (tens) of simulations.

In practice, the calibration process consists in multiple repetition of the procedure: *simulation – analysis of results – modification of the model* until satisfactory compatibility is achieved, and changes in the model are made "manually" by altering the value of coefficients in the model in terms of their occurrence, after prior analysis of the results from the previous simulation.

The population model for *T. longicornis* was tested mainly for a wide range of variation in the two most important parameters – temperature T and concentration of food *Food*, which have a major impact on the zooplankton development. Finally, the calibration of the model, i.e. evaluation of numerical values of coefficients in the model was performed for 2006 and 2007 in order to achieve the best possible compatibility between the observational data and data generated by the model.

Values of these coefficients were selected so as to obtain the results of the model for the total biomass of the studied species most similar to the observed average monthly values. For this purpose, the experimental data were used, which were made available by the Department of Marine Plankton Research, the Institute of Oceanography, the University of Gdańsk. Measurements taken at station P2 in the Bay of Gdańsk were used during the calibration and validation of the model.

Validation of the model, i.e. the quality control of the model, consists in determining the degree to which the model is an accurate reflection of the actual system. The results from the model and experimental data for the total biomass of *T. longicornis* for station P2 in the Bay of Gdańsk were compared for the years of 1991, 1999–2000 and 2006–2007. In each of these years, a regular spring/summer biomass increase was observed, which means that the model works properly.

Pearson's linear correlation coefficient was used to compare the numerical simulations with experimental data for the total biomass of the studied species as monthly mean values in the water column. The model results are quite consistent with the observations for five years, with the average correlation coefficient of 0.53.

Temporal and spatial variability of zooplankton is usually so high that each model presenting the results different from the measured data by an order of magnitude is within the range of experimental data.

4 Seasonal dynamics of *Temora longicornis* in Gdańsk Basin – numerical simulations

The 3-D CEMBS ecosystem model (http://deep.iopan.gda.pl/CEMBaltic/new_lay/index.php) connected with the population model described in Sect. 2 was used to determine the temporal-spatial distributions of *T. longicornis* in the southern Baltic divided into the coastal zone P2 (the Bay of Gdańsk) and the open sea P1 (Gdańsk Deep) (Fig. 4).

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.

Temperature (Fig. 5), salinity and concentration of available food (Food = 50 %Phyt + 25 %Zoop + 25 %Detr) (Fig. 6) – a mixture of phytoplankton, microzooplankton and pelagic detritus used in the population model as the input data for the model, are values from the 3-D CEMBS ecosystem model. The phytoplankton biomass as the main component of food in the Bay of Gdańsk (station P2) is about two times higher than in the Gdańsk Deep (station P1). This situation is mainly caused by the concentration of nutrients, which was higher in the Bay of Gdańsk near the mouth of the river compared to the open sea, and by the water temperature – higher at station P2 compared to station P1.

For the population of *T. longicornis, Food* is available at a concentration which considerably increases up to the value of ca. 27 mmol C m^{-3} at the end of March and up to 15 mmol C m^{-3} in the first half of April, but drops to 8 mmol C m^{-3} and 10 mmol C m^{-3} at the end of June at stations P2 and P1, respectively (Figure). In the summer season when the temperature reached the maximum value, ca. 21 °C at P2 and 18 °C at P1, the concentration of available food in the upper layer remains at an almost constant level within the range of 5–10 mmol C m^{-3}. The subsequent increase in the food concentration is observed in early autumn, between late September and early October – up to the value of ca. 26 mmol C m^{-3} and 11 mmol C m^{-3} at stations P2 and P1, respectively.

The distribution of *T. longicornis* biomass reflects the presence of 3–5 generations per year in the Basin of Gdańsk. Figure 7 presents the simulated biomass distributions in the modelled development stages, which are an algebraic sum of products of the mass W_i and abundance Z_i of individual organisms at a given stage, as a mean value in the water column, at two stations P1 and P2 in the Southern Baltic (Gdańsk Deep and Gdańsk Bay). The numerical simulation starts from the wintering population of adult specimens. The result of numerical simulation indicates five generations per year, from eggs to adults, at station P1 (Gdańsk Deep) and four generations at station P2 (Gdańsk Bay), while the first generation in both cases started between late March and early April.

The maxima in individual biomass distributions in stage Eggs–N2 result from the oviposition by females, which increases their number. A strong increase in the concentration of available food, mostly phytoplankton biomass during the spring algal bloom, and the temperature increase initiate the production of eggs.

At station P1 (open sea), the total duration of one generation of this copepod species is shorter compared to Gdańsk Bay, despite the fact that station P2 is characterised by higher temperatures and higher concentration of food. This is a result of parabolic function ft_2, which reflects a decline in the growth of the species development at a temperature above 15 °C. Basically, the temperature increase induces faster growth of organisms and reduces the population life time.

The residence time of individual organisms at different development stages was determined from equations presented by Dzierzbicka-Glowacka et al. (2009), which allow for parabolic threshold function ft_2 describing a decline in the individual growth at a temperature above 15 °C. The development time of the first generation at both stations differed by two weeks (13 days), at station P2 – 102 days, at station P1 – 92 days. Higher temperatures of surface waters (up to 15 °C) in the summer season accelerated the growth of organisms at each stage of ontogenesis during the development of next generations. And thus, the full cycle of the second generation development at stations P2 and P1 lasted for 72 and 46 days, respectively. The third generation started in the first half of August in Gdańsk Bay and one month earlier in Gdańsk Deep, and lasted for 58 and 44 days. The fourth generation, which appeared at station P1 lasted for ca. 45 days and reached much higher biomass values compared to station P2, where the development time was the longest and lasted till the end of the year. During the development of generations 2, 3 and 4 in the region of Gdańsk Deep P1, the temperature was lower on average by 1–3 °C, and the concentration of available food was lower compared to station P2 in the Bay of Gdańsk. Higher values of these two parameters, temperature (above 15 °C) and food concentration (above 200 mg C m^{-3}), were of little importance for the development of *T. longicornis*, because (i) the growth of individual organisms follows the exponential curve against the optimum temperature T_o, for *T. longicornis* – 15 °C, and the growth declines above this value following the parabolic threshold function ft_2 as a result of physiological stress, (ii) 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, and (iii) an increase in salinity has a positive impact on the development of the studied species. The fifth generation of *T. longicornis* (107 days) at station P1 appears in mid-September and reaches the maturity at the end of October. Whereas individuals of the fifth and the sixth generations 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 (eggs-N2). 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 8 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. They mostly reflect the impact of food concentration, temperature and salinity.

The total biomass of *T. longicornis* in Gdańsk Deep was higher compared to Gdańsk Bay (Fig. 8). The total biomass distribution in Gdańsk Bay is described by three population peaks, the main 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 main population peak results from the development of the second generation. All population peaks in the total biomass distribution result from large biomass of individual organisms of mainly two simulated stages of ontogenesis: CI–CIII and CIV–CV. Whereas all lower population peaks result from production of eggs, the development of nauplii and adults. The sufficient amount of food in autumn enabled the fourth and the fifth generations 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.

High biomass for each modelled development stage of all generations produced per year at stations P1 results from the fact that the production of eggs by females of the previous generations was two times higher compared to station P2. On the other hand, higher reproduction results mostly from higher salinity in the open sea compared to the coastal zone. Whereas, the size of nauplii future generations affects the size of the total biomass in the early stage of growth.

The distribution of the total *T. longicornis* biomass in the Gdańsk Deep was characterised 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 biomass in July and August with values ranging from 12 to 17 mg C m^{-3} results from high biomass of individual organisms in all successional stages and especially in older copepodid stages

C4–C5 of the second and third generations as a result of high abundance in the previous development stage C1–C3 of this generation. High reproduction results mostly from 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 high biomass of copepodid stages C1–C3 and C4–C5 of the fourth and the fifth generations.

Higher biomass of each modelled development stage at station P1 compared to station P2 results from higher salinity of waters in the open sea compared to the Bay, coastal regions and the mouth of the river where food concentration and temperatures are higher.

Distributions in Fig. 9 present the vertical profiles of biomass for the model stages of the development reflecting the dynamics of *T. longicornis* in the annual cycle at station P2 – the western region of the Bay and P1 – the open sea. Four states of variables are presented: for eggs–N2, nauplii N3–N6, copepodids C1–C5 and adults. Production of eggs starts late March with the beginning of spring phytoplankton bloom and a temperature increase.

Several generation peaks in the biomass distribution of the analysed states of variables can be observed during the development of *T. longicornis* throughout the year. The development of *T. longicornis* concentrates mainly in the euphotic layer where temperature reaches the maximum values and food – mixture of phytoplankton, microzooplankton and pelagic detritus – is available, but also goes beyond the thermocline because of the food taken in the form of dead organic matter.

In spring and summer, the development of four generations occurs at station P1 during 227 days and three generations at station P2 during 235 days, starting at the end of March.

The largest contribution of individuals in all development stages is located above the thermocline. In June, the thermocline occurs at a depth of ca. 20–30 m at station P1 (Gdańsk Deep) and at ca. 10–20 m at station P2 (Gdańsk Bay), and the temperature of

the surface layer increases above 13 °C at P1 and 15 °C at P2 reaching the maximum values in August, before it gets colder (Fig. 4).

The highest total biomass of *T. Longicornis*, determined numerically, occurred in summer in, and in the Gdańsk Deep ranged from 20–40 mg C m^{-3} in the upper water layer, to 30 m in June/July and 20 m in July/August, as a sum of mostly copepodid biomass (from 15 to 37 mg C m^{-3}) and other biomass of the analysed model stages for nauplii, eggs-N2 and adults, respectively, within the range of 10–23 mg C m^{-3} each. The situation was similar in the Bay of Gdańsk – the highest total biomass of *T. longicornis*was recorded in summer, although only in July and ranged from 14 to 22 mg C m^{-3} to a depth of 30 m, also as a sum of mostly copepodid biomass (from 12 to 21 mg C m^{-3}) and other biomass of nauplii, eggs-N2 and adults, respectively, 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 the fourth and the fifth generations 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 not take food (eggs-N2).

5 Comparison of the model results with in situ data

Analysis of variation in the Copepoda taxonomic structure in 2010 and 2011 showed that, similarly to the previous years, *Temora longicornis* was the second most important taxon (Dzierzbicka-Glowacka et al., 2013a,b).

In the late-winter season of 2010–2011, the average biomass of *T. longicornis* in the Bay of Gdańsk reached several hundred (< 1000) mg w.w. in the water column and still considerably increased in the spring-summer season. The smallest biomass was recorded in March – 480 mg$_{w.w.}$ m^{-2} in 2010 and in April – 240 mg$_{w.w.}$ m^{-2} in 2011 (no data available for February). The maximum development of this crustacean occurred in spring and summer of 2010 and 2011, respectively – ca. 6100 mg$_{w.w.}$ m^{-2} in May

and 4500 $mg_{w.w.}\,m^{-2}$ in August (SD) (Fig. 10). The May peak of *T. longicornis* biomass in 2010 was relatively high (compared to other months) and 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 copepodids and adults). In the other months, most of the observed specimens were represented by nauplii. The May biomass peak occurred at station P2 and could also be caused by environmental factors, including transport of waters or toxic algal blooms in summer, which accounted for reduced biomass of crustaceans. In Gdańsk Bay, 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 an insufficient amount of environmental data on the Gdańsk Deep, the average biomass of the studied crustacean was only estimated and it appears to be approximately four times higher than in the Bay of Gdańsk; similar results were obtained from the population model. The maximum value (ca. 26 400 $mg_{w.w.}\,m^{-2}$), determined based on the available in situ data, was recorded in June 2011. In the other studied months, the value of biomass ranged from 1200 $mg_{w.w.}\,m^{-2}$ in February 2010 to 4300 $mg_{w.w.}\,m^{-2}$ in November 2011.

The corresponding values of abundance during those months did not differ significantly, which could be related to the fact that the *Temora* population consisted mainly of older organisms (copepodids) whose individual weight is much greater compared to younger forms.

Figure 10 presents the results of numerical simulation and the observed data for the total biomass of *T. longicornis* (in $mg\,m.m.\,m^{-2}$) consolidated in the water column as mean monthly values in the Bay of Gdańsk – P2 and Gdańsk Deep – P1.

The highest values of the modelled *T. longicornis* biomass occurred in the period of high temperatures, i.e. in summer, in June 2010 and July 2011 in the Bay of Gdańsk – at station P2, and between late June and early July, and for almost the whole summer

in 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. One can assume that higher values in Gdańsk Deep compared to Gdańsk Bay probably resulted from higher salinity, which significantly affected the production of eggs.

During all months, the average observed values are within the range similar to the values obtained from the model, but in May 2010 at station P2 in the Bay of Gdańsk, the in situ data are most distant from the numerical results. Taking into account the average values determined from the model for Gdańsk Bay and Gdańsk Deep, it can be concluded that numerical results are similar to the observational data.

Similar studies in the Bay of Gdańsk were conducted in 2006 and 2007. The observational data of the previous studies are presented in two papers (Dzierzbicka-Glowacka et al., 2013b).

Temora longicornis dominated in May and June, as well as in November and December 2006 and 2007 in the Bay of Gdańsk. During those years, the maximum abundance was recorded in July. In this region, Siudziński (1977) observed two population peaks in June and November. Szaniawska (1977) reported that the largest number of individuals occurred in June and July, and in September and October. Rakowski (1997) recorded the maximum count of *T*. longicornis in May, whereas Mudrak (2004) – in June and July. In the coastal zone, the population peak of this taxon was recorded in August – Gaj (1999), and in June – Guzera (2002). During the research conducted in 2007, the structure of the *T. longicornis* population in February and March was dominated by older copepodids. The contribution of younger copepodids significantly decreased from February to March. Between May and July, as well as in September and October, nauplii and younger copepodids (CI–CIII) dominated, while in August – older copepodid stages and adults, particularly in deeper layers of the water column. It can be therefore assumed that there were at least two breeding seasons – in late spring and summer. In June 2006, nauplii and younger copepodid stages occurred; their contribution dropped by September in favour of older copepodid stages. Rakowski (1997)

reported that the contribution of younger *T. longicornis* forms increased from April to May, and in September. Mudrak (2004) reported that the largest contribution of nauplii and younger copepodid stages of this species occurred in April and July.

In general, the total biomass of *T. longicornis* integrated in the water column at station P2 in the Bay of Gdańsk, determined based on the in situ studies, had one main peak of ca. 2000 $mg_{w.w.}\,m^{-2}$ in 2006 and another one, two times higher – 4600 $mg_{w.w.}\,m^{-2}$ in 2007 (Fig. 11). It is interesting that also the corresponding counts during those months had the maximum values (Dzierzbicka-Glowacka et al., 2013). The modelling studies support the hypothesis that model stage C4–C5 had a major influence on the total biomass of the studied species. The highest numerical values of the total *T. longicornis* biomass were recorded in the period of high temperatures, i.e. in the summer between late July and early August, exactly at the same time as environmental data, and amounted to 4300 $mg_{w.w.}\,m^{-2}$ and 5800 $mg_{w.w.}\,m^{-2}$ in 2006 and 2007, respectively. The results determined from the model are 0.25–2 times higher compared to in situ data. The most similar values were obtained for 2007 (Fig. 11).

6 Discussion

The main function of zooplankton in the marine ecosystem consists in transferring the energy accumulated in the process of primary production to higher trophic levels (Möllmann et al., 2000). These organisms are important food for fish, throughout their entire life cycle, or in the first period of their growth (Mańkowski, 1978; Cury et al., 2008). In terms of biomass and production, Copepoda are the most important taxa of the Baltic zooplankton, including *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp., from Rotatoria – mostly *Synchaeta* spp. and *Cladocera* with the dominance of *Evadne nordmanni. Pleurobrachia pileus* from Ctenophora, the copepod *Eurytemora affinis* and rotifers *Keratella* spp. are the least important in the zooplankton biomass and production.

Copepods are among the most abundant secondary producers of the world ocean. They are an important link between phytoplankton, microzooplankton and higher trophic levels, such as fish (Longhurst and Harrison, 1989; Longhurst, 2007; Kleppel, 1992). With regard to their importance in the food chain, it is necessary to know how environmental parameters affect their population. They are a very important source of food for many fish species, but also a significant producer of detritus. One individual organism can produce 200 portions of faecal matter per day, which is an important source of food for detritivores and is very important in the processes of sedimentation and circulation of biogenic substances (Rybak and Błędzki, 2005).

The research focused on the selected aspects related to the development of *Temora longicornis. T. longicornis* is a relatively common crustacean species in the southern Baltic.

Simulation with the numerical model was used in this study as a method and a tool for identification of processes describing the development of *Temora longicornis*.

The study determined 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 weight and abundance in the model development stages in order to determine the total individual biomass, and (ii) calibration and verification 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 environmental data from the Department of Marine Plankton Research, the Institute of Oceanography, the University of Gdańsk. The results obtained from the population model are consistent with the in situ data for station P2 in the western part of Gdańsk Bay. Pearson's linear correlation coefficient of 0.53 for five years proves 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.

The differences between the observational data and the numerical results are a product of several factors: (1) the impact of salinity on the development of Crustaceans, which in this case was included only to describe the process of reproduction, (2) no laboratory analysis available for the study region to describe more properly the functional relationships between the physiological processes and the environmental parameters, (3) the insufficient amount of environmental data and (4) field research, sampling by different persons, the method used for sampling and data analysis. This means that not only the modelling results are burdened with error, but also the obtained environmental data as a result of analyses performed by man. This was also caused by the structure of the population model, in which the description of physiological processes is not entirely correct, i.e. typical of this species from the southern Baltic. Furthermore, the error in the population model consists of both – the error in the ecosystem model and the error in the meteorological data as input data for the model.

Due to the fact that very dynamic changes may occur in the environment, studies aiming at the determination of temporal and spatial distributions of abundance and biomass at different stages of ontogenesis should be performed not only by extended and long-term in situ measurements, but also by experimental studies in strictly defined conditions in order to have better understanding and description of physiological processes of copepods.

Each model is just a simplified picture of reality and the total compatibility can never be expected. It is worth noting that errors and inaccuracies arise not only in the course of work on the model, but also in the field or laboratory research.

This is frequently evidenced by mathematical models.

The population model presented in this paper is a relatively good tool to describe the dynamics of *Temora 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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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 weight; W_{female}: female weight.

Process	Units	Equations
Growth	$\mu g\,C\,d^{-1}$	$GROWTH_i = ING_i - FEC_i - MET_i$
Growth $i = 2$	$\mu g\,C\,d^{-1}$	GROWTH = – FEC – MET
Growth $i = 6$	$\mu g\,C\,d^{-1}$	$GROWTH_{Ad} = ING_{Ad} - FEC_{Ad} - MET_{Ad} - ProdEgg$
Ingestion	$\mu g\,C\,d^{-1}$	$ING_i = f1_i f2_i f3 f4_i$
Egestion	$\mu g\,C\,d^{-1}$	$FEC_i = (1 - na)ING_i = nf\ ING_i$
Metabolism	$\mu g\,C\,d^{-1}$	$MET_i = Ms + Ma$
basic		$Ms = nw\ W_i$
active		$Ma = ne\ ING_i$
Production of egg matter	$\mu g\,C\,d^{-1}\,female^{-1}$	$ProdEgg = expGROWTH_{nauplii} - 1$
Dynamics		
Mortality	d^{-1}	$MOR_i = mz\ Z_i$
Transfer	d^{-1}	$TRN_i = f(W)$
Hatching	d^{-1}	$HAT = f(T)$
Reproduction	no. eggs $female^{-1}\,d^{-1}$	$EGG = X Z_{Ad} \int_J Egg$;
where		$Egg = \frac{W_{female}}{W_{egg}} ProdEgg = f(Food, T, S)$

Table 2. The list of abbreviations used in the population model.

Parameters	Units	Definitions
ING	$\mu g C d^{-1}$	ingestion
f_{max}	d^{-1}	maximal ingestion rate
Food	$\mu g C m^{-3}$	food concentration
$Food_o$	$\mu g C m^{-3}$	minimal threshold food concentration
k_{Phyt}	$\mu g C m^{-3}$	half-saturation constant
t_1	wd	temperature coefficient
t_2	wd	temperature coefficient
t_3	wd	temperature coefficient
P1	wd	temperature coefficient
P3	wd	exponent of allometric relation
W_i	$\mu g C$	weight
W_k	$\mu g C$	critical weight
FEC	$\mu g C d^{-1}$	egestion
na	wd	assimilation efficiency
nf	wd	percentage of ingestion egested as fecal material
MET	$\mu g C d^{-1}$	metabolism
ne	wd	coefficient of proportionality
nw	d^{-1}	routine excretion rate
Prod Egg	$\mu g C d^{-1}$ female^{-1}	production of egg matter
Egg	no. eggs female^{-1} d^{-1}	reproduction
D_e	d	duration of embryonic stage
α_e	wd	temperature coefficient
a	wd	population specific constant
b	wd	slope of the line D_e, $b = -2.05$
J	d	time span of egg production
X	wd	sex ratio
MOR	$no.m^{-3} d^{-1}$	mortality
mz	d^{-1}	mortality rate
Z_i	$no.m^{-3}$	abundance
W_{female}	$\mu g C$	weight of female
W_{egg}	$\mu g C$	weight of egg
Z_{Ad}	$no.m^{-3}$	abundance of adults
TRN	d^{-1}	transfer
P2	wd	exponent
HAT	d^{-1}	hatching
P4	d^{-1}	hatching rate at 20 °C
P5	wd	shape factor of HAT

wd: without dimension.

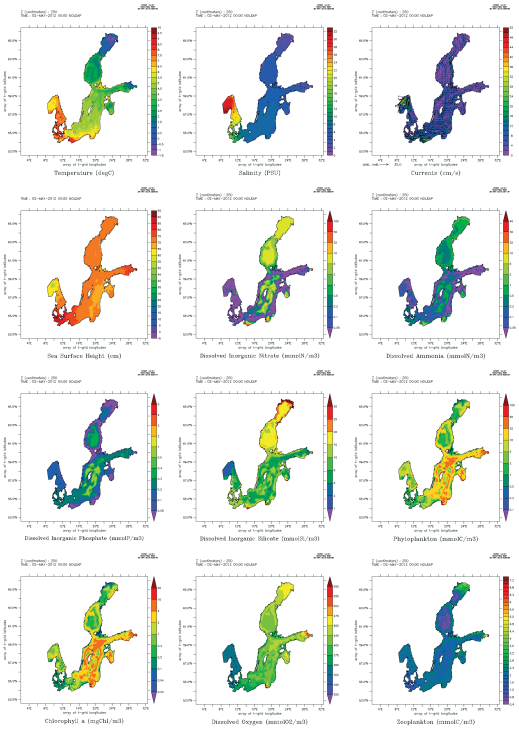

Fig. 1. Sample results for hydrodynamic and biogeochemical variables derived from the 3-D CEMBS model for the whole Baltic Sea as of 2 May 2012 (Dzierzbicka-Glowacka et al., 2013c).

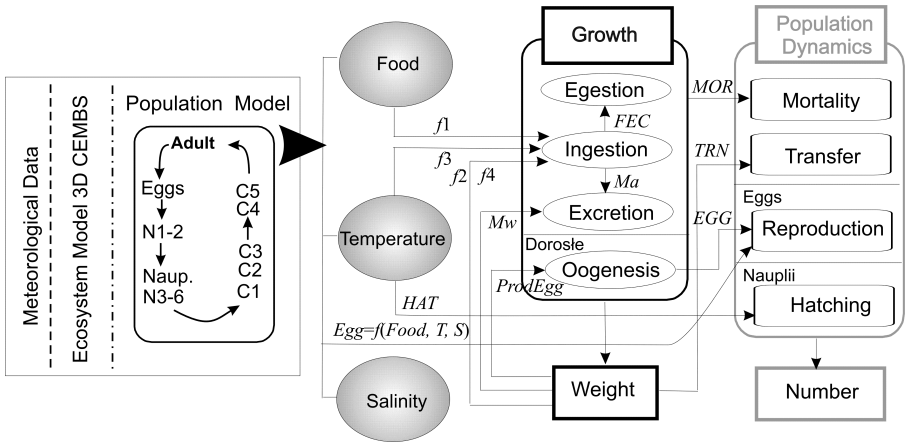

Fig. 2. Conceptual diagram of the population model combined with the 3-D CEMBS model.

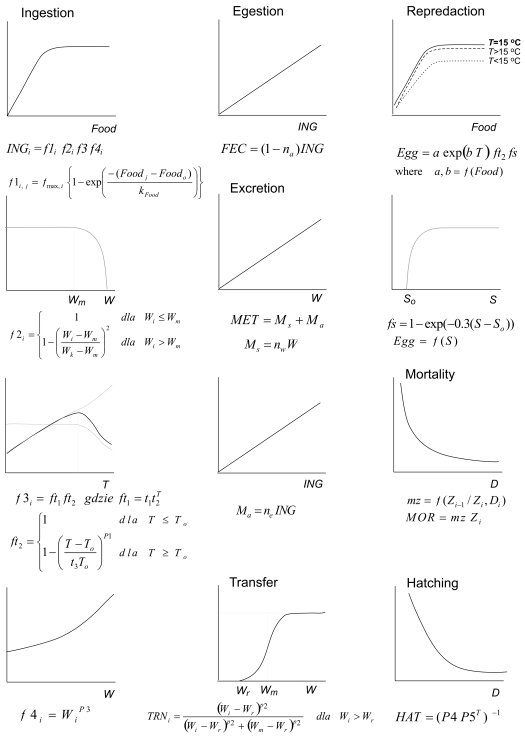

Fig. 3. Mathematical curves and formula describing the physiological processes and population dynamics used in the model.

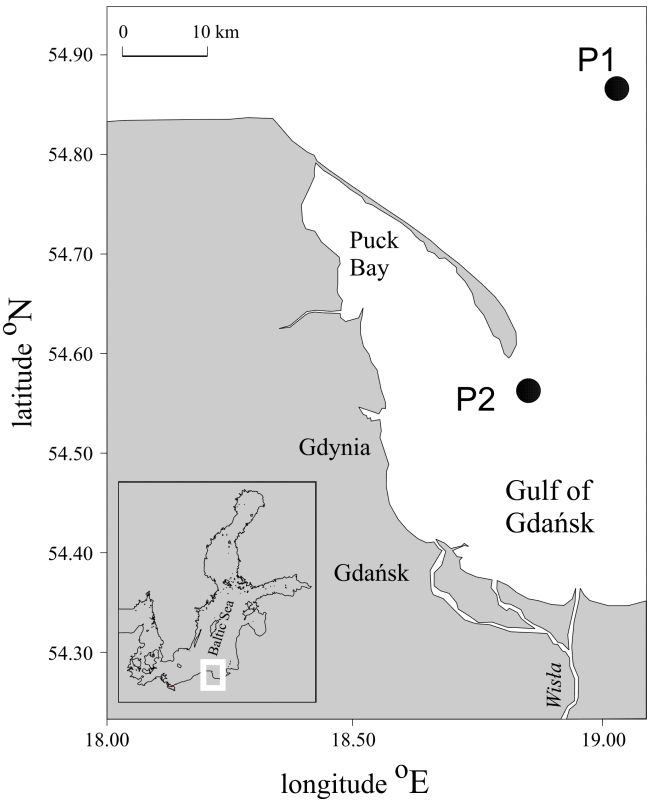

Fig. 4. Location of stations for which numerical simulations were performed; P1 – Gdańsk Deep, P2 – Gdańsk Bay.

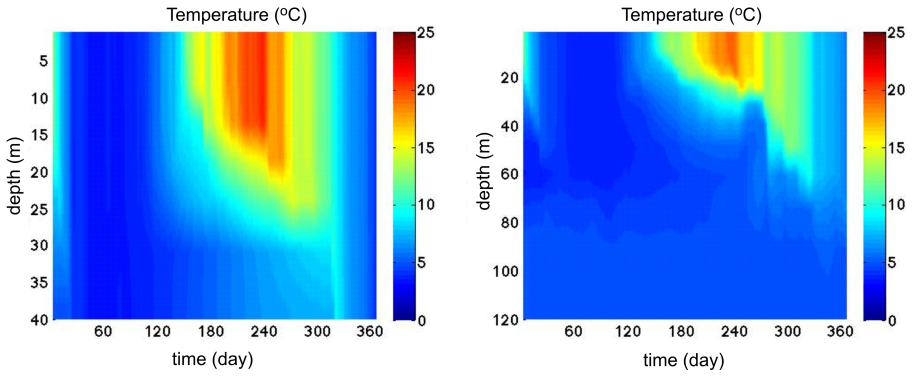

Fig. 5. Temperature distribution (°C) at stations P2 (Gdańsk Bay) (left column) and P1 (Gdańsk Deep) (right column).

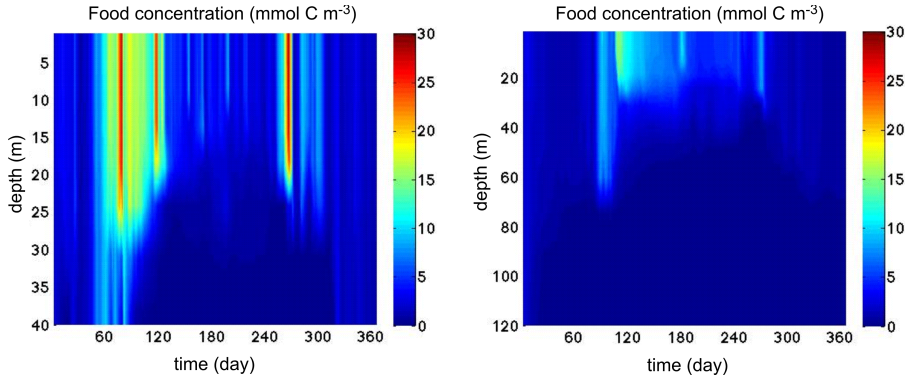

Fig. 6. The annual cycle of food contrentration distribution (Food = Phyt 50 % + Zoop 50 % + Detr 25 %) (mmol C m^{-3}) at station P2 (Gdańsk Bay) (left column) and P1 (Gdańsk Deep) (right column).

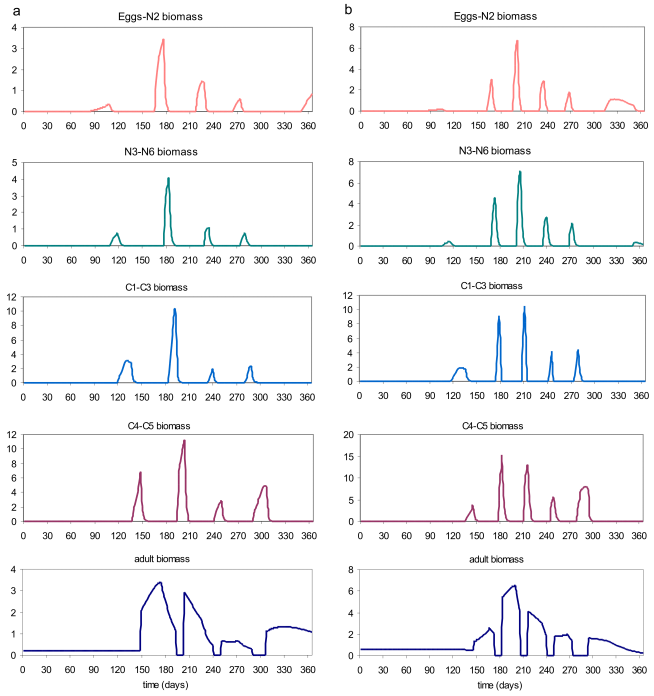

Fig. 7. Simulated generations of *T. longicornis* at two stations – in the Bay of Gdańsk **(a)** and in the Gdańsk Deep **(b)** in 2011; the average biomass (mg C m^{-3}) of organisms not taking food (eggs–NII), nauplii (NIII–NVI), younger copepodids (CI–CIII), older copepodids (CIV–CV) and adults.

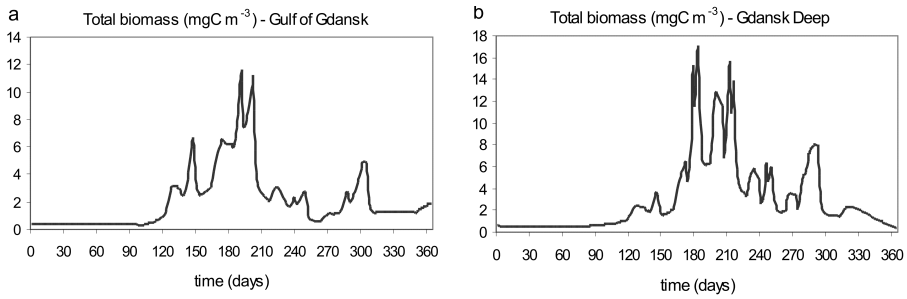

Fig. 8. The total biomass of *T. longicornis* (mg C m^{-3}), averaged in the water column, at two stations, in the Bay of Gdańsk P2 **(a)** and the Gdańsk Deep P1 **(b)** in 2011.

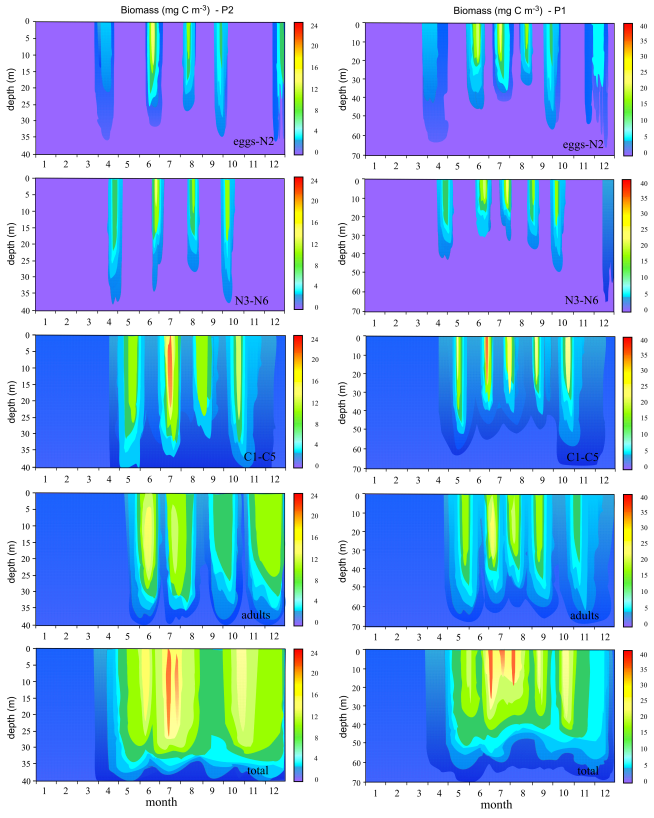

Fig. 9. Vertical distributions of *T. longicornis* biomass in the model development stages (mg C m^{-3}) and the total biomass at station P2 – Gdańsk Bay and P1 – Gdańsk Deep in 2011.

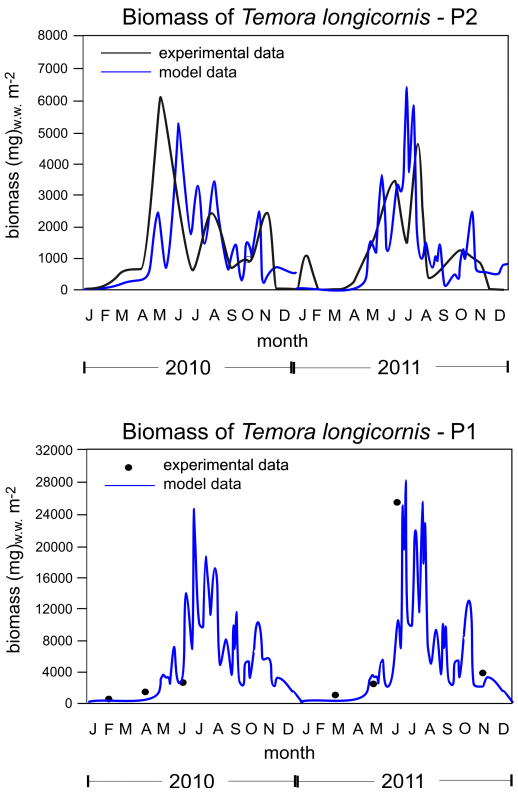

Fig. 10. The consolidated biomass of *Temora* in the water column at station P2 – Gdańsk Bay and P1 – Gdańsk Deep based on in situ data and the model results in 2010 and 2011.

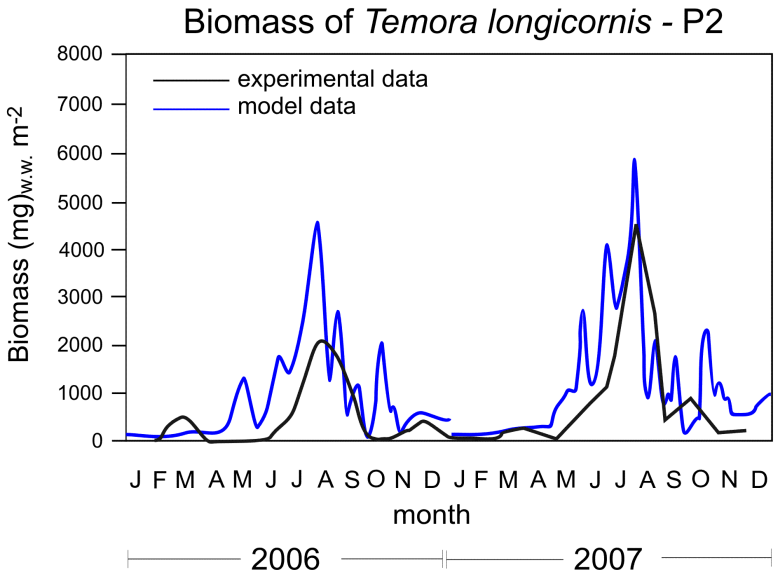

Fig. 11. Consolidated biomass of *Temora longicornis*in the water column at station P2 in the Bay of Gdańsk according to in situ data and the model results for 2006 and 2007.