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Long-term changes in the total development time of Copepoda species occurring in large numbers in the Southern Baltic Sea - numerical calculations

by

Mariusz Figiela[1,*], Maja Musialik-Koszarowska[2], Artur Nowicki[1], Anna Lemieszek[3], Marcin Kalarus[2], Czesław Druet[1]

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[1]Institute of Oceanology of the Polish Academy of Sciences, ul. Powstańców Warszawy 55, 81-712 Sopot, Poland

[2]University of Gdańsk, Faculty of Oceanography and Geography, Al. M. Piłsudskiego 46, 81-378 Gdynia, Poland

[3]Maritime Institute, ul. Długi Targ 41/42, 80-830 Gdańsk, Poland

* Corresponding author: *mariusz.figiela@gmail.com*

Abstract

The study presents changes in the total development time of Copepoda species, i.e. *Pseudocalanus* sp., *Temora longicornis* and *Acartia* spp. occurring in large numbers in the Southern Baltic Sea. The following factors were taken into account: temperature, salinity and concentration of food. The presented research involved simulations with greenhouse gas emissions scenarios A1B and B1. The analysis was performed for naupliar and copepodid stages combined together, and the results present the total development time of organisms from the naupliar stage to the adult form. The calculations were carried out using numerical methods based on the experimental data available in the literature.

Key words: Baltic Sea, Copepoda, development time, food concentration, temperature, salinity

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Introduction

Copepoda are the most abundant group of zooplankton in the seas and oceans. They represent one of the most important elements of the trophic chain in the world's ocean and they are the main nutritional component of many organisms from plankton to fish (Dzierzbicka-Glowacka 2004; 2009; Holste et al. 2011; Bucklin et al. 2003). For this reason, it is important to know how the hydrodynamic and biogeochemical parameters of the environment may affect the development of the populations of different copepod species, which will also help to determine changes in the trophic chain in the study area. Long-term analysis of the abundance and biomass of individual species in the monitored environment and within a specific time help to eliminate the impact of less important factors on their development. The detailed knowledge about the effect of marine environmental parameters on Copepoda is invaluable for the prediction of biological changes observed in the Baltic ecosystem.

The research presented in this paper was carried out based on numerical calculations and show the impact of climate change on the development of Copepoda. Organisms occurring in large numbers in the Southern Baltic were taken into account in the study: *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. The effect of three environmental parameters, e.g. temperature, salinity and concentration of food, on the development time of the studied Copepoda species was determined in the selected region of the Baltic Sea (Gdańsk Deep) on the basis of accepted assumptions (scenarios). The calculations were based on mathematical relationships that describe the duration of ontogenesis stages (nauplius and copepodid) as well as the total generation time of the studied species as a function of three variables, i.e. temperature, salinity and concentration of food.

Publications on the copepod *Pseudocalanus* occurring in the central Baltic show that the dispute over what species occurs in this environment is not entirely solved (Bucklin et al. 2003; Holmborn et al. 2011). Since it is likely that the two species, i.e. *Pseudocalanus acuspes* and *Pseudocalanus minutus elongatus* occur together, the authors believe that the name *Pseudocalanus* sp. from the Baltic, as proposed by Möllmann et al. (2005), is the most appropriate.

Materials and methods

Klein Breteler et al. determined in laboratory conditions the development time of *Pseudocalanus elongatus* (Klein Breteler et al. 1995), *Acartia clausi* (Klein Breteler & Schogt 1994) and *Temora longicornis* (Klein Breteler & Gonzalez 1986) as a function of temperature at four different levels of food concentration.

The studies described in the literature (Paffenhöfer & Harris 1976; Harris & Paffenhöfer 1976a,b; Thompson 1982; Klein Breteler et al. 1995; Vidal 1980a,b) as well as the hitherto published work by Dzierzbicka-Głowacka, Dzierzbicka-Głowacka (2004) and Dzierzbicka-Głowacka et al. (2009; 2011) show that the reduction in the development time *D* at various stages of ontogenesis follows an increase in temperature up to the optimum value T_o (19°C for *Acartia* spp., 15°C for *Temora longicornis* and 14°C for *Pseudocalanus* sp.). In the summer season, however, further increase in the temperature above the T_o value results in the prolonged *D* time.

In the Baltic Sea, the development time of many species largely depends on salinity and increases with its decreasing values. According to the studies by Mudrak (2004) and other laboratory analysis (unpublished results), the best conditions for the development of Copepoda prevail in the south-western part of the Baltic Sea where salinity is above 17 PSU. Therefore, the development time of the species studied in our project is also dependent on the salinity through the function *fs*. Our observations and literature data do not show a significant effect of salinity on the development of *Acartia* spp. and *Temora longicornis*, except for reproduction of *T. longicornis* (Peters 2006; Holste et al. 2009; Dzierzbicka-Glowacka et al. 2013). On the other hand, the development of *Pseudocalanus* sp. is determined not only by temperature and concentration of food, but also, to a large extent, by salinity, which in the Baltic Sea acts as a factor masking (concealing) the growth (Holste et al. 2009; Dzierzbicka-Glowacka et al. 2013).

Mathematical relationships

With regard to the above data, the development time at two stages of ontogenesis (nauplius and copepodid) as well as the total generation time of the studied species were described by mathematical relationships taking into account the effect of marine environmental parameters: temperature T, salinity S, and concentration of food $Food$. The effect of temperature on the development time was described by the ft function (eq(1) for *Acartia* spp., eq(6) for *Temora longicornis* and eq(11) for *Pseudocalanus* sp.), as a parabolic threshold function where the development time increases at a temperature above the optimum value ($T > T_0$), as a result of physiological stress. The development time D of the studied species, as a function of three variables: concentration of food $Food$, temperature T and salinity S, allowing for the minimum development time D_{min} was described by the equation:

$$D = (D_{\min} + R) \times ft \times fs$$

where D_{min} is the minimum value of the development time, for which the growth rate of an individual is not limited by food availability, i.e. $Food$=max$Food$. It has been assumed that $D_{\min} = f(T)$ is a function of temperature defined at salinity of 35 PSU. The value of R is an additional time required for the development in the conditions below the optimum, i.e. $Food$<max$Food$ and is defined as a function of temperature and concentration of food $R = f(T, Food)$. The functions ft and fs (i.e. temperature and salinity, respectively) were defined arbitrarily, based on the available data, as functions determining and reducing the development of the studied species.

The following quantitative expressions were used for numerical calculations to describe the effect of the aforementioned environmental parameters ($Food$, T and S) on the development time of the studied species at the nauplius and copepodid stage as well as the total generation time:

Acartia spp.

$$ft = \begin{cases} 1 & for\ T \le 19^o C \\ 0.9957 e^{0.0181(T\text{-}19)} & for\ T \ge 19^o C \end{cases} \quad (1)$$

$$fs = 2 - (1 - \exp(-0.9(S - 0.001))) \quad (2)$$

for the naupliar stage:

$$D_N = 31.34 e^{-0.092T} + 4921.7 Food^{-1.7462} e^{-(0.1805 Food^{-0.1061})T}) ft \times fs \quad (3)$$

for the copepodid stage:

$$D_C = (40.956 e^{-0.0849T} + 1178.5 Food^{-1.0486} e^{-(0.0739 Food^{0.1059})T}) ft \times fs \quad (4)$$

for the total generation:

$$D_T = (94.62 e^{-0.0949T} + 1997.6 Food^{-0.9856} e^{-(0.0917 Food^{0.0646})T}) ft \times fs \quad (5)$$

Temora longicornis

$$ft = \begin{cases} 1 & for\ T \le 15^o C \\ 0.9972 e^{0.0269(T\text{-}15)} & for\ T \ge 15^o C \end{cases} \quad (6)$$

$$fs = 2 - (1 - \exp(-0.5(S - 2))) \quad (7)$$

for the naupliar stage:

$$D_N = (39.565 e^{-0.0964T} + 61 e^{-0.0081 Food} e^{-(0.0006 Food + 0.0588)T}) ft \times fs \quad (8)$$

for the copepodid stage:

$$D_C = (38.693 e^{-0.0809T} + 57.438 e^{-0.0037 Food} e^{-(0.0007 Food + 0.0517)T}) ft \times fs \quad (9)$$

for the total generation:

$$D_T = (79.656 e^{-0.0884T} + 154.66 e^{-0.0083 Food} e^{-(0.0005 Food + 0.0711)T}) ft \times fs \quad (10)$$

Pseudocalanus sp.

$$ft = \begin{cases} 1 & for\ T \le 14^o C \\ 0.9993 e^{0.0377(T\text{-}14)} & for\ T \ge 14^o C \end{cases} \quad (11)$$

$$fs = 3 - (2 - \exp(-0.25(S - 9))) \quad (12)$$

for the naupliar stage:

$$D_N = (41.342 e^{-0.069T} + 2.679 T^{1.0988} e^{(0.0209 \ln T - 0.0829) Food}) ft \times fs \quad (13)$$

for the copepodid stage:

$$D_C = (34.888 e^{-0.0781T} + 1.786 e^{1.0988 \ln T} e^{(-0.0559 e^{-0.0486T}) Food}) ft \times fs \quad (14)$$

for the total generation :

$$D_T = (83.773 e^{-0.0745T} + 4.465 e^{2.53 \log T} e^{(-0.1696 T^{-0.6908}) Food}) ft \times fs \quad (15)$$

Respectively 91%, 83% and 86% of the D values for *Acartia* spp, *Temora longicornis* and *Pseudocalanus* sp, calculated from the equations (eq. 3, 4, 5 for

Acartia spp., eq. 8, 9, 10 for *Temora longicornis*, eq. 13, 14, 15 for *Pseudocalanus* sp.) and being a function of food concentration and temperature at 30 PSU, are within the range of values reported by Klein Breteler et al. (1995), Klein Breteler and Gonzalez (1986) and Klein Breteler and Schogt (1994). On the basis of data from the papers by Ciszewski and Witek (1977) and Witek (1995) for *Acartia bifilosa* and *Pseudocalanus elongatus*, the calculated value of the development time *D* is in the range of 81-93% (detailed description of equations will be presented in another paper).

Assumptions of the scenarios

Numerical simulations were performed on the basis of the assumptions of the scenarios regarding the climate changes "Greenhouse Gas Emission" for the years 2000-2100 (Hollweg et al. 2008). Scenarios A1B and B1 were taken into account in the calculations for S1 and S2 based on the study by Neumannn (2010).

Assumptions for numerical simulations:

S1:

a) S1a:
- temperature *T* rise from by 2.2°C (autumn, winter) and 4°C (summer)
- salinity *S* decrease by 2 PSU
- concentration of food *Food* unchanged

b) S1b (A1B):
- temperature *T* rise by 2.2°C (autumn, winter) and 4°C (summer)
- salinity *S* decrease by 2 units
- increase in the concentration of food *Food* by 5% and spring algal blooms are likely to occur a week earlier

S2:

c) S2a:
- temperature *T* rise by 0.2°C (autumn, winter) and 2°C (summer)
- salinity *S* decrease by 1.6 PSU
- concentration of food *Food* unchanged

d) S2b (B1):
- temperature *T* rise by 0.2°C (autumn, winter) and 2°C (summer),
- salinity *S* decrease by 1.6 PSU
- increase in the concentration of food *Food* by 5% and spring algal blooms are likely to occur a week earlier

Results of numerical simulations

Annual distributions of environmental parameters, i.e. temperature *T*, salinity *S* and food concentration *Food* were used as input data to determine the duration of ontogenetic stages (nauplius and copepodid) as well as the total generation time of the studied Copepoda species

Variables *T*, *S* and *Food* (as *Food* = *Phyt* + *Zoop* + *DetrP*) (Fig. 1). were derived from the 3D CEMBS ecosystem model for station P1 (Gdańsk Deep) in the Southern Baltic for 2010 (Dzierzbicka-Glowacka et al. 2012, 2013a,b; website www.cembs.pl).

The structure (i.e. shape and character) of the obtained curves presenting the variability in the annual cycle of the minimum D_{min} and the total development time *DT* (from eggs to adult individuals) of the studied species *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp., divided into stages (nauplii N_{min} and *NT*, copepodid C_{min} and *CT*) and the total generation time D_{min} and *DT*, is similar in all the examined cases. Differences occur only in the values.

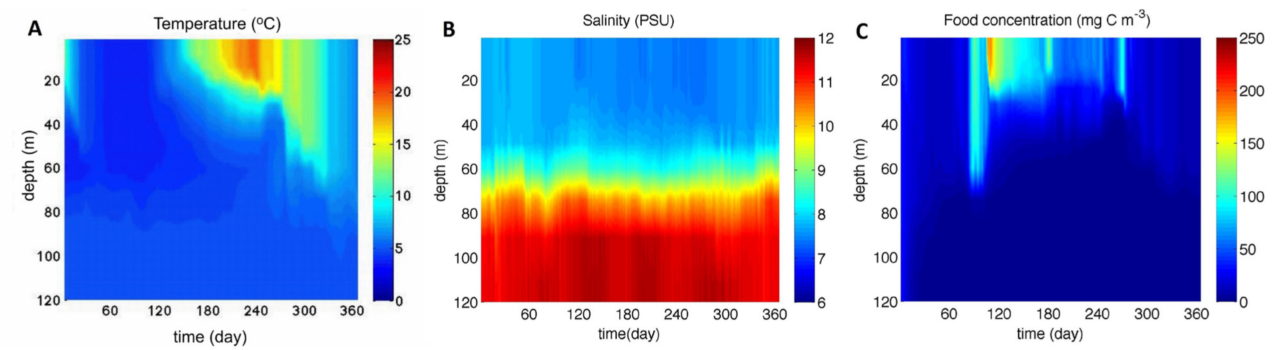

Figure 1

Mean annual changes in temperature (A), salinity (B) and concentration of food (C) in Gdańsk Deep

Acartia spp.

It appears from the performed calculations that environmental conditions for the development of *Acartia* spp. were much better in both examined cases compared to the initial condition (in terms of food concentration *Food* and temperature *T*), and they were more suitable in the case of scenario A1B than in B1.

In the case of scenario A1B, the temperature increase is greater than in B1 by ca. 2°C, which gives effective results in the calculations. In all the examined stages (nauplii *NT*, copepodid *CT* and the total development *DT*), it is clear that the minimum development time D_{min} for the nauplius, expressed as a function of temperature at the maximum concentration of food, is shorter by ~ 8 days in A1B (~ 5 days in B1) in the winter/spring season, and by ~ 3 days in A1B (~ 1.5 days w B1) in summer, as compared to the initial state. Graphs for the copepodid show similar values. For the total generation time, the reduction in the D_{min} value is twice as large compared to the nauplii stage and is ~ 17 days in A1B (~ 10 days in B1) in winter (Fig. 2).

Considering the total development time, in both cases (A1B and B1), a shorter duration of ontogenetic stages was observed in scenario A1B compared to B1. The differences are significant in relation to initial values, especially in winter: ~ 35 days – *NT*, 50 days – *CT* and 105 days for *DT* in A1B (S1b), and for scenario B1 (S2b): 30, 50 and 90 days, respectively (Fig. 2).

As evidenced by the obtained results, the temperature and concentration of food have a major influence on the development of *Acartia* spp. at all stages of ontogenesis and they determine the development of this species. Large differences in the development of this species are observed in winter and early spring when an increase in temperature and the amount of food has a significant influence on the development of a given individual, as well as in summer when the temperature is the main determining factor. The obtained numerical results indicate that the number of *Acartia* spp. populations will increase in the studied region by at least one or two populations, and the growth rate at each ontogenetic stage will be higher and the first population may be observed in the earlier period of the year.

Temora longicornis

The calculations performed suggest that in most cases, environmental conditions for the development of *Temora longicornis* were slightly better in scenario A1B compared to B1.

At different stages of *Temora longicornis* ontogeny (nauplius *NT*, copepodid *CT*, and the total development time *DT*), the minimum development time D_{min} is shorter compared to the initial state, only in scenario A1B. Both for the nauplius and copepodid, it is shorter by ~ 5 days in the winter-spring season, and by ~ 1-2 days in summer. In the case of the total development time *DT*, a decrease in D_{min} values is doubled compared to D_{min} at the nauplius stage (Fig. 3).

In both cases (A1B and B1), the total development time *DT of Temora longicornis* is shorter in relation to the initial values, and the values are lower in

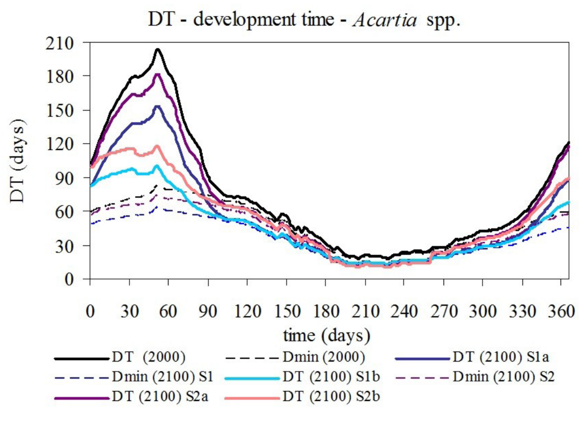

Figure 2

The total development time of *Acartia* spp. in the considered scenarios

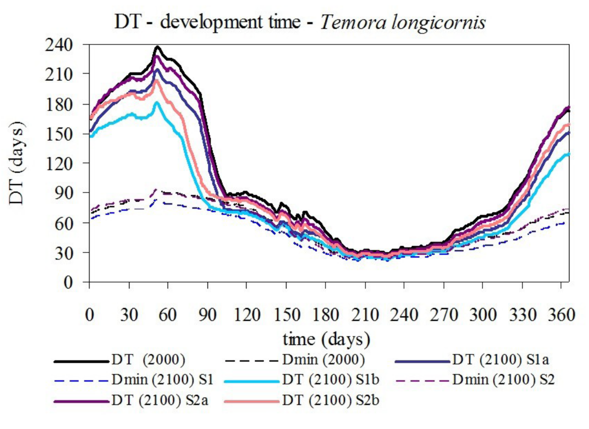

Figure 3

The total development time of *Temora longicornis* in the considered scenarios scenario A1B compared to B1. These differences in winter are ~ 25 days – *NT*, 15 days – *CT* and 60 days for *DT* in A1B, and for scenario B1 (S2b): 10, 5 and 35 days, respectively. In summer, a decrease in the duration of individual stages is insignificant (Fig. 3).

It appears from the results that (as in the case of *Acartia* spp.) temperature and food concentration are factors determining the development of *Temora longicornis* at all stages of ontogenesis. In accordance with the accepted function *fs*, salinity significantly affects the development of *Temora longicornis* and slightly reduces the effect of temperature. The differences in the development of the examined individual are observed in winter and early spring when an increase in temperature and the amount of food are of crucial importance. According to the obtained numerical results, the number of *Temora longicornis* populations may increase in the studied region by half or one population. The development of individuals representing this species will be faster in the winter-spring season and the first population in a given year may occur earlier.

Pseudocalanus sp.

Based on the obtained results, it appears that worse environmental conditions for the development of *Pseudocalanus* sp. individuals occurred in both examined cases, and they were less favorable in scenario A1B compared to scenario B1, except for spring.

At different stages of *Pseudocalanus* sp. ontogeny (nauplius *NT*, copepodid *CT* and the total generation time *DT*), the minimum development time D_{min} is longer in both cases compared to the initial state. These values for the copepodid are ~ 10 days – in A1B and ~ 15 days – in B1 in the winter-spring season, and ~ 7 days – A1B and 4 days – B1 in summer. For the total generation time, D_{min} values increased two times in relation to the copepodid stage. It should be noted, however, that the conditions for the development of *Pseudocalanus* sp. in summer are less favorable in A1B than in B1. This is due to a greater temperature rise in the case of A1B (Fig. 4).

There are considerable differences in the total development time *D* in relation to the initial values, especially in winter and summer. They are on average ~ 10 days – *CT* and 30 days – *DT* in A1B and B1 in winter; and in summer: 7 days – *CT* and 20 days – *DT* in B1 and 35 days – *CT* and 80 days – *DT* in A1B, respectively. In summer, an increase in the development time *D* for scenario A1B is significant

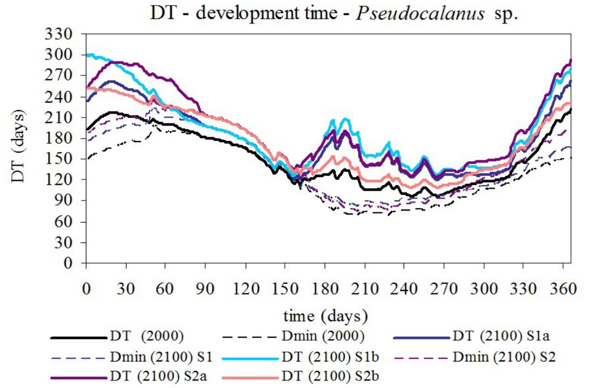

Figure 4

The total development time of *Pseudocalanus* sp. in the considered scenarios

and almost twofold in relation to the initial values (Fig. 4).

On the basis of the obtained results, we can conclude that the temperature and salinity are parameters that significantly affect the development of *Pseudocalanus* sp. at all stages of ontogenesis. Salinity, as a masking factor according to the adopted function *fs*, has the major influence on the development of the studied species in winter, and intensifies the effect of temperature in summer. Significant differences are observed in winter and spring when despite an increased temperature compared to the initial state, ontogeny is inhibited due to reduced salinity. This leads to an increased duration of subsequent stages of ontogenesis in both scenarios. Numerical simulations also show that salinity has a greater effect on the ontogeny during this period than temperature. In summer, both salinity and temperature reduce the development of this species, causing an increase in the duration of different ontogeny stages. This situation is induced by i) a decrease in salinity which has a significant effect on the development of *Pseudocalanus* sp. causing a reduction in the growth rate, as well as by ii) an increase in temperature above the optimum value T_o, which in this period has a negative impact (like salinity) on the development of this species.

The presented results of calculations evidence that in the Bay of Gdańsk i) the number of *Pseudocalanus* sp. populations will decline, ii) the development of individuals representing this species will be inhibited, iii) the total development time may last for more than one year and iv) the first population will be observed at a later date. Numerical analysis shows that the species will develop only in the open sea, mainly in the Southern Baltic, far from the coastal zone and in deeper layers of the studied basin, below the halocline.

Discussion

Studies presented in this paper are particularly important, because they offer the possibility of determining long-term changes in secondary production in the seas and oceans. For many years, various changes have been observed in the Baltic Sea, both of natural – reflected in temperature and salinity (Fonselius & Valderrama 2003), as well as of anthropogenic origin – reflected in the concentration of food. The numerical simulations show that the development time of the studied species depends on changing environmental conditions, which may also affect the whole population. Forecasts for the Baltic Sea reveal a decrease in salinity with a simultaneous increase in temperature.

The level of salinity in this basin is determined mainly by inflows of saline water from the North Sea. The analysis shows that their frequency has drastically decreased in the 1980s (Elken & Matthäus 2008). Furthermore, it appears from LME (Large Marine Ecosystems) data that the temperature in the Baltic Sea is growing faster compared to the whole ocean (Belkin 2009). The growing evaporation is likely to increase the amount of precipitation within a decade, which will finally increase the amount of fresh water supplied to the sea by rivers. It appears from the obtained results that changes in the environmental parameters, described in scenarios A1B and B1, will result in the reduced development time and an increased number of *Acartia* spp. and *Temora longicornis* populations throughout the year. The results of the calculations evidence that *Pseudocalanus* sp. is particularly sensitive to changes in the environment. The ongoing changes in the studied region will likely result in a prolonged development time of each stage of the ontogeny as well as in the reduced number of the species' populations.

Changes in biomass

Based on the obtained results, it was possible to determine certain forecasts of changes in the population of selected Copepoda species. If climate changes will follow according to scenarios A1B and B1, some major changes in the distribution of the studied organisms are likely to occur. It has been shown that the population of *Acartia* spp. and *Temora longicornis* will grow, while the population of *Pseudocalanus* sp. will become extinct or will reduce its area of distribution. The above-mentioned organisms are the dominant species of Copepoda in the Baltic Sea. The biomass of *Pseudocalanus* sp. ranges throughout the year from a few to several percent, and from January to March – up to 10% of the total biomass of Copepoda (Dzierzbicka-Głowacka et al. 2010). Reduction in the number of populations of this species or its extinction in some regions of the Southern Baltic, together with the growing number of *Acartia* spp. and *Temora longicornis* populations, will significantly affect the quantitative and qualitative structure of Copepoda in the Baltic Sea. At this stage of research it is difficult to foresee the extent of changes in the total biomass of Copepoda. The authors believe that the decline in *Pseudocalanus* sp. biomass in the total biomass of Copepoda may be offset by an increase in the biomass of *Acartia* spp. and *Temora longicornis.* On the other hand, an increase in the abundance of the latter two species, mainly *Acartia* spp., will considerably exceed the expected decline in the species *Pseudocalanus* sp.

Trophic interactions with ichthyofauna

In the Baltic Sea, zooplankton is the main component of the diet of two fish species caught commercially, i.e. herring (*Clupea harrengus*) and sprat (*Sprattus sprattus*). Analysis of the stomach content of these fishes showed that Copepoda are their main food component, and *Temora longicornis* was the dominant taxon (Casini et al. 2004). *Pseudocalanus elongatus minutus* dominated in the diet of sprat in winter, while the stomach content of herring (during the same period) was dominated by amphipods, *Mysis mixta* and polychaetes. Further research conducted by Michelle Casini et al. (2006), covering the period from 1986 to 2004, show a close trophic relationship between herring and the copepod *Pseudocalanus elongatus minutus.* These studies established a correlation between the absence of this species in the stomach content of herring and the deterioration of the condition of these fishes. One can also find some information in the literature that a decline in the growth of herring, observed in the early 1990s, was mainly caused by a decrease in the amount of food available in the preferred size in the Baltic Proper (Flinkman et al. 1998). Studies conducted by Möllmann et al. (2003; 2004) also show that the deterioration of herring's condition follows a decrease in the number of *Pseudocalanus* sp. There are many contradictory reports on the deteriorated condition of planktivorous fish in the Baltic Sea, but most of them predict that a quantitative reduction or removal of *Pseudocalanus* sp. from the ecosystem may negatively affect the ecosystem functioning and the condition of fish caught commercially.

The conducted analysis can be particularly useful for predicting trophic changes in the seas and oceans. The ongoing changes in the marine environment will directly affect the zooplankton which is one of the main links in the trophic chain, and its availability will affect the associated organisms. Compared to organisms developing in the ocean salinity, those from the Baltic Sea are affected by pauperization. Typical marine organisms, the ontogenetic development of which occurs in the lower salinity, consume greater amounts of energy to maintain the osmotic equilibrium, rather than the growth. Consistent with the forecasts, the future salinity in the Baltic Sea will decrease, which will affect the biomass of a single organism, and consequently the condition of the whole population.

Conclusions

Mathematical models through numerical simulations can be used to predict long-term changes in the ecosystem for a long time before they occur. Such models allow for reconstruction of the ongoing changes in the marine environment and calculations in the conditions other than those currently prevailing, or in the case when it is not possible to directly determine how environmental parameters will affect the development of biological life in the ecosystem.

The presented results of our studies enabled us to determine the effect of three main parameters of the marine environmental: temperature, salinity and concentration of food, on the development time of Copepoda species occurring in large numbers in the Southern Baltic. Copepoda, as the basis of the second link in the food chain, play a very important role in trophic relations across the oceans.

Studies of this type are particularly important, because physicochemical properties of the Baltic Sea are constantly changing. In this case, the determination of their effect on changes in the populations of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. is very important (Christensen & Walters 2004). The conducted studies demonstrate that changes occurring in the marine environment described in the guidelines "Green House Gas Emission" will likely lead to changes in the number and abundance of the analyzed Copepoda species. These organisms play a key role in the transformation of organic matter (Martynova et al. 2011). Quick determination of the direction of these inevitable changes is of great scientific importance, because it provides new information on the ecosystem functioning and economy based on the exploitation of the marine environment.

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