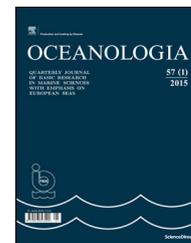




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ORIGINAL RESEARCH ARTICLE

Influence of environmental factors on the population dynamics of key zooplankton species in the Gulf of Gdańsk (Southern Baltic Sea)

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Summary We studied the influence of abiotic environmental factors on the seasonal population dynamics of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. in the southern Baltic Sea in the period of 2006–2007 and 2010–2012. Zooplankton samples were being collected monthly at 6 stations located in the western part of the Gulf of Gdańsk with a WP2 net (100 µm mesh sizes) and then analyzed according to the HELCOM guidelines. Although the sampling stations did not significantly differ from each other in the terms of variability of abiotic environmental factors, the biomass of copepods developmental stages differed between them, apart from the shallow stations in both, Gulf of Gdańsk and in its inner part – Puck Bay. According to redundancy analysis, 26.1% of the total variability observed in the biomass of the copepod species has been explained by water temperature, salinity, air temperature, cloudiness, wind speed and direction and station's depth, with the first variable having the greatest power, alone explaining 13.7%. ANOSIM revealed that sampling stations in the Gulf of Gdańsk were significantly different from one another in terms of copepods' biomasses. Generalized Additive Models fitted for water temperature and salinity were significant for all ontogenetic stages of *Acartia* spp. and *Temora longicornis* and for the majority of stages of *Pseudocalanus* sp. (apart from the C1 for both and the males for salinity). © 2018 Institute of Oceanology of the Polish Academy of Sciences. Production and hosting by Elsevier Sp. z o.o. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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1. Introduction

At present, the Baltic Sea ecosystem raises a major concern in the fishery sector of the Polish economy.

Over the last hundred years, this ecosystem has been subject to various transformations resulting from both, the climate fluctuations and the anthropogenic pressure (BACC II). So far the observed climate-driven changes in the Baltic Sea environmental conditions included *inter alia*: the increase in both, the sea surface temperature and in the atmospheric precipitation, as well as river discharge (causing a significant drop in a seawater salinity), and a reduction of the seasonal ice cover. Despite the fact that the biggest warming has been recorded in the northern Baltic Sea, the ecosystem of its southern part – more productive and diverse – is much more susceptible to the negative effects of the climate change.

The latest computer simulations indicated that the Baltic Sea warming will continue (Meier et al., 2012), therefore investigating the reactions of marine organisms to the ongoing transformation of the environment is a particularly important task. The Baltic Sea is relatively sensitive to changes in the environmental conditions, due to its inland location, a large catchment area and a limited exchange of sea waters with the Atlantic Ocean.

Zooplankton are bioindicators of the climate change for many reasons (Richardson, 2008). Their physiological processes such as ingestion, respiration and reproductive development are highly sensitive to temperature (Mauchline, 1998). Additionally, most zooplankton species have a short life cycle and a fast reproduction rate so they are highly associated with both climate and population dynamics (Hays et al., 2005).

In terms of biomass and abundance, the key zooplankton taxa of the southern part of the Baltic Sea are copepods such as *Acartia* spp., *Pseudocalanus* sp. and *Temora longicornis*, then Rotifera, mainly *Synchaeta* spp. and *Keratella quadrata*, and amid Cladocera, which are dominated by *Evadne nordmanni*, *Eubosmina maritima* and *Pleopis polyphemoides*. The less important are euryhaline freshwater and typical freshwater species, found mainly in estuaries (*Eurytemora* sp.) (Lemieszek, 2013).

Copepods are part of the pelagic trophic chain and therefore they play an important role in the transfer of energy between producers and consumers from higher levels, acting as a food source for much pelagic fish (Dippner et al., 2000; Möllmann et al., 2000; Vuorinen et al., 1998). Being the organisms feeding on phytoplankton, copepods indirectly indicate changes in the trophic status of the water body, such as eutrophication, reflecting changes in the structure of phytoplankton. They also indicate climate changes, predation, contamination with synthetic compounds and the impact of alien species (Richardson, 2008).

The most important copepods species in the Gulf of Gdańsk, such as *Acartia* spp. (i.e. *A. bifilosa*, *A. longiremis* and *A. tonsa*), *Temora longicornis* and *Pseudocalanus* sp. are the main food components of commercial fish, like, *Clupea harengus* and *Sprattus sprattus* (Möllmann et al., 2003), hence any anomalies in the copepod biomass negatively affect fish populations (Dzierzbicka-Głowacka et al., 2013). In the Baltic Sea, *Pseudocalanus* sp. is the food for

large larvae of cod (*Gadus morhua*) (Hinrichsen et al., 2002; Möllmann et al., 2003) and for the adult pelagic fish such as sprat (*Sprattus sprattus*) or herring (*Clupea harengus*) (Flinkman et al., 1992; Möllmann and Köster 1999, 2002). *Temora longicornis* is primarily the food for sprat (*Sprattus sprattus*) which abundance in the Baltic Sea has begun to decrease since the 1990s (Möllmann and Köster, 1999). *Acartia* spp. is a brackish species, adapted to lower salinity and common in the Baltic Sea (Ackefors, 1969; Fransz et al., 1991). It occurs in the upper part of the water column where, due to the food availability, growth conditions are presumably better compared to the ones in the deeper regions. The same may hold for the neritic, euryhaline species *Temora longicornis*, which can be found in the waters spanning over a wide salinity range but which is less strongly confined to shallow water than *Acartia* spp. Both copepods are described as thermophilic species (Chojnacki and Antończak, 2008; Hansen et al., 2006; Möllmann et al., 2000, 2003). In contrast, *Pseudocalanus* sp. prefers lower temperatures and higher salinities (Hansen et al., 2006).

Although sampled regularly during monitoring programs, the detailed knowledge on the copepod seasonal distribution and production patterns in the coastal area of the southern Baltic Sea is still insufficient. The Baltic Monitoring Programme (HELCOM) provided zooplankton data mostly with a very low spatiotemporal resolution. Apart from these studies, data on the copepod distribution in the southern Baltic Sea are available only sporadically or from the coastal areas (Bielecka et al., 2000; Chojnacki et al., 1975; Chojnacki and Drzycimski, 1976; Józefczuk et al., 2003; Mudrak and Żmijewska, 2006; Otto et al., 2014).

The aim of this study was to investigate how seasonal changes in abiotic environmental conditions such as hydrographic water properties as well as wind speed and direction or cloudiness, influence population dynamics and distribution of the copepods, important to fisheries. Another goal was to describe an average monthly distribution of the key copepod species observed in the southern Baltic Sea during the following research periods: 2006–2007 and 2010–2012.

2. Material and methods

2.1. The study area

The Study area covers the Gulf of Gdańsk and its inner basin – Puck Bay, located in the southern Baltic Sea. The Gulf of Gdańsk is a system of estuaries in which there is a mix of brackish and marine waters that is typical for this type of a basin. All zooplankton samples were being collected at six stations, out of which five (S1, S2, S3, S4, J23) were located along a depth gradient in the Gulf of Gdańsk and one (M2) was located in Puck Bay (Fig. 1) (Table 1). Puck Bay is a semi-enclosed area, isolated from the rest of the Gulf of Gdańsk by the presence of the shoal.

2.2. Sampling

Zooplankton was sampled monthly in the periods from January 2006 to December 2007 and from March 2010 to December 2012 with a WP2 net (100 µm mesh size), equipped with

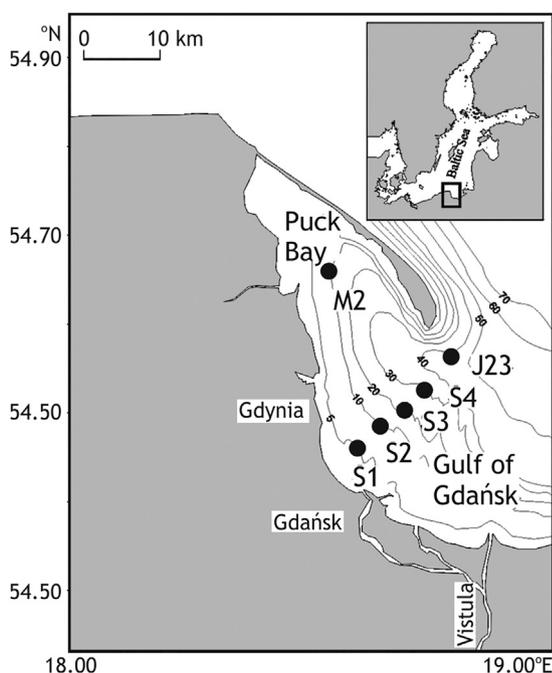


Figure 1 Study area and location of the sampling stations.

Table 1 Location of the sampling stations in the western part of the Gulf of Gdańsk.

| Station | Lat. | Long. | Depth [m] |
|---------|------------|------------|-----------|
| M2 | N 54°39'0" | E 18°33'8" | 10 |
| J23 | N 54°32'0" | E 18°48'2" | 40 |
| S4 | N 54°30'7" | E 18°46'0" | 30 |
| S3 | N 54°29'7" | E 18°43'7" | 20 |
| S2 | N 54°27'7" | E 18°36'7" | 10 |
| S1 | N 54°27'0" | E 18°34'8" | 5 |

Hydro-Bios Mechanical Flow Meter. At the shallow stations, S1, S2, M2, vertical hauls were conducted from the bottom to the surface. At deeper stations, J23, S4, S3 (>10 m), samples were collected from the water column every 10 m. All samples were collected during the daytime (mainly between 11 am and 2 pm) so the diurnal vertical migrations were not taken into account. Water salinity and temperature were measured each time after collecting zooplankton samples, with a handheld WTW Cond 3110. In addition, the air temperature, cloudiness, wind speed and direction were also being noted. Qualitative and quantitative zooplankton laboratory analysis was performed in accordance with the Manual for Marine Monitoring in the COMBINE (Cooperative Monitoring in the Baltic Marine Environment) Programme of HELCOM (Helsinki Commission) (Annex C-7) (HELCOM, 2015).

2.3. Statistical analyses

Statistical analyses were run on the square root transformed biomass data of copepods' development stages for sampling layers integrated at the stations [mg C m^{-3}]. To reveal differences between particular sampling locations for the

biomasses of the main copepod taxa, significance tests for differences between ordered groups of samples were performed using one-way Analysis of Similarities (ANOSIM). Similarly, ANOSIM has been used to reveal differences between sampling stations – in terms of biotic environmental factors such as water temperature, salinity, air temperature, cloudiness, wind speed and direction, which were normalized prior to the analysis. Above analyses were performed in PRIMER version 7 (Plymouth Marine Laboratory, Plymouth, UK) (Clarke and Warwick, 1994).

To study the relationship between environmental variables (water temperature, salinity, air temperature, cloudiness, wind speed and direction, station depth) and biomasses of developmental stages of the studied calanoid copepods, redundancy analysis (RDA) was performed in CANOCO 5 (Ter Braak and Šmilauer, 2012). The environmental variables were ranked, according to their quantitative importance, by manual selection based on the Monte Carlo permutation test adjusted for temporal autocorrelation (Ter Braak and Šmilauer, 2012). Then, Generalized Additive Model (GAM, Poisson distribution, 4 df) was used to examine responses of individual developmental stages separately against water temperature and salinity, hence to illustrate non-parametric relationships between copepods' life stages and significant environmental variables.

3. Results

3.1. Hydrology

The temperature was characterized by a very similar distribution throughout the study period (Fig. 2). In the period of 2006–2007 the average water temperature ranged from 1°C in March 2006 to 17°C in July 2007. From June to September 2007, the average temperature was above 15°C. In the period of 2010–2012 the average temperature fluctuated between 1°C in March 2010 and 18°C in August 2010. Temperature above 10°C has been observed from June to September 2010, June–October 2011 and 2012. Differences in salinity were even less distinguished, with the annual variations between 5.8 and 7.6.

Interestingly, according to ANOSIM test for differences, the sampling stations did not differ significantly, in the terms of biotic environmental factors such as water temperature, salinity, air temperature, cloudiness, and neither of wind speed nor of its direction ($p = 0.999$, global $R = -0.017$).

3.2. Seasonal changes in biomass

The average biomass of investigated copepods showed a seasonal variability for each species. The highest biomass in the water column for *Acartia* spp. and *Temora longicornis* has been recorded during the summer months, while the highest biomass for *Pseudocalanus* sp. has been noted in winter. The minimal average biomass has been observed for *Acartia* spp. in December (2.05 mg C m^{-3}) and for *Temora longicornis* in January (4.33 mg C m^{-3}). The minimal biomass values for *Pseudocalanus* sp. have been observed in the spring and in the autumn months (Fig. 3).

During the study period, a bimodal biomass of Copepoda distribution has been observed. For *Acartia* spp., the first

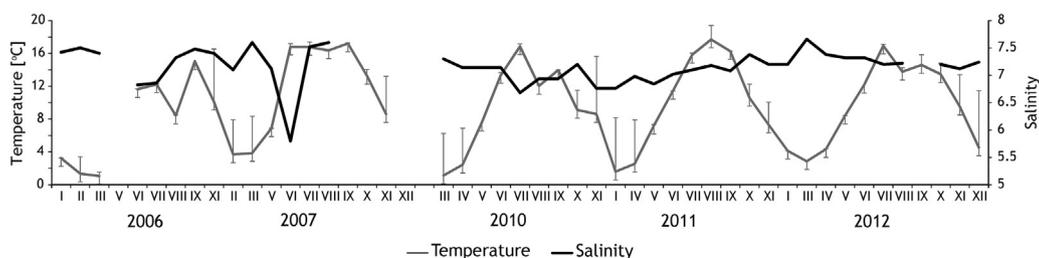


Figure 2 Water temperature with SD and salinity in the Gulf of Gdańsk.

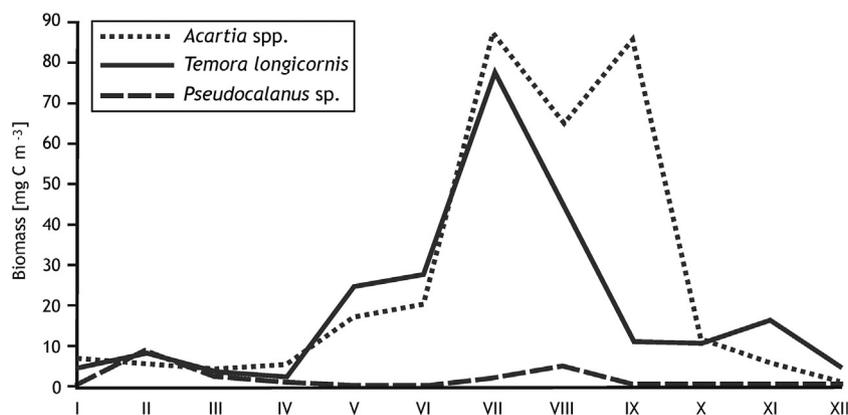


Figure 3 The average value of biomass in the Gulf of Gdańsk in 2006–2007 and 2010–2012.

biomass peak was recorded in July with the value of $86.45 \text{ mg C m}^{-3}$, then in September – $85.80 \text{ mg C m}^{-3}$. In July, the first biomass peak for *Temora longicornis* ($76.95 \text{ mg C m}^{-3}$) was also observed, while the second, much lower, was recorded in November ($16.11 \text{ mg C m}^{-3}$). *Pseudocalanus* sp. was characterized by the first, higher biomass peak in February with the value of 7.61 mg C m^{-3} , and the second peak in August – 4.19 mg C m^{-3} .

ANOSIM revealed that the sampling stations in the Gulf of Gdańsk were significantly different from one another in terms of copepods' biomasses ($p = 0.001$, global $R = 0.056$). According to the following pairwise tests, no similarities have been noted between the S2 and M2 stations, the S1 and M2 stations, and also not between S1–S4 stations. The highest similarity has been noted between the S4 and S3 stations (over 84%). The analysis also showed the lower similarity between the S3 and S2 (24%), S4 and S2 (18%) stations. The shallower stations S2, S1 and M2 were similar to each other in ca. 12%.

3.3. Influence of environmental factors on copepods

The model based on the species-environment relationships in RDA ($p = 0.001$, pseudo- $F = 7.6$) explained 26.1% of the total variability observed in the population composition and biomass of the three copepod species in the Gulf of Gdańsk during the study period. The environmental variable with the greatest explanatory power was water temperature, which explained 13.7% of the total variability. The air temperature (3.2%), cloudiness (2.5%), station depth (2.4%), and salinity

(2.2%) were of secondary importance. The wind speed and direction were responsible for 1.2% and 0.8%, respectively (Table 2).

The RDA analysis revealed that the higher biomass of *Acartia* spp. corresponded with the higher water and air temperatures (Fig. 4). The older stages of *Pseudocalanus* sp. and the females of *Temora longicornis* were strongly correlated with the wind direction in the southern part of the Baltic Sea. The presence of nauplii and the females of both *Acartia* spp. and *Temora longicornis* as well as young copepodids of *Pseudocalanus* sp. was correlated with both salinity and cloudiness.

Generalized Additive Models fitted for the water temperature and salinity were significant for all ontogenetic stages of *Acartia* spp. and *Temora longicornis* ($p \leq 0.00001$), and for the majority of stages of *Pseudocalanus* sp., apart from C1 for both (temperature $p = 0.84325$, salinity $p = 0.60031$) and the males for salinity ($p = 0.3372$) (Fig. 5). For the first two mentioned species, the nauplii responded strongly to the temperature around $16\text{--}17^\circ\text{C}$, with the remaining stages peaking in slightly lower temperatures in case of *Acartia* spp., or in higher temperatures for *Temora longicornis*. However, the latter species mentioned, show a bi-modal distribution with the less intense, primary peak around 10°C for most of its stages. The females, C4 and C5 of *Pseudocalanus* sp. peaked in the lowest temperatures, while C2, C3 and nauplii have also shown a bi-modal biomass distribution, with the second peak in similar temperatures as in case of the species mentioned before. In case of salinity, all copepods clearly preferred the highest measured values, peaking above 7.5.

Table 2 Environmental variables that best explained the variability of biomasses of ontogenetic stages of the three dominant Baltic calanoid copepods. These variables are significant, according to the Monte Carlo permutation test applied during forward selection in the redundancy analysis (RDA).

| Variable | Explains [%] | Contribution [%] | pseudo-F | p |
|-----------------|--------------|------------------|----------|-------|
| Temperature | 13.7 | 47.7 | 34.5 | 0.001 |
| Air temperature | 3.2 | 11.2 | 8.3 | 0.001 |
| Cloudiness | 2.5 | 8.6 | 6.6 | 0.001 |
| Station depth | 2.4 | 8.4 | 6.6 | 0.001 |
| Salinity | 2.2 | 7.5 | 6.1 | 0.001 |
| Wind speed | 1.2 | 4.3 | 3.5 | 0.005 |
| Wind direction | 0.8 | 2.9 | 2.3 | 0.042 |

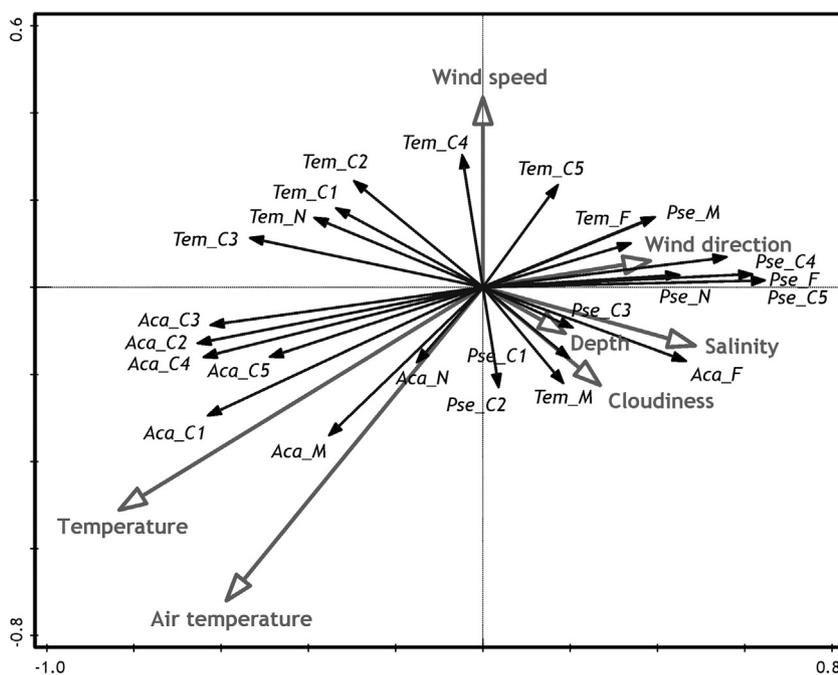


Figure 4 Ordination plot from redundancy analysis (RDA) on biomasses of development stages of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. (N – nauplii, F – females, M – males, C1 – C5 copepodids of respective stage) monthly sampled in the Gulf of Gdańsk (black arrows) and their relation to abiotic environmental variables (grey arrows).

4. Discussion

Our studies indicate that the Gulf of Gdańsk is a specific reservoir of brackish water where temperature determines the occurrence of copepods. The Generalized Additive Models (GAM) were used to determine the relationship between temperature and biomass of the studied copepods. Similarly to Möllmann et al. (2000), the GAM results obtained for *Acartia* spp. reflect a positive correlation between the biomass and temperature. This confirms the fact that *Acartia* spp. is classified as a thermophilic organism and also that the increase in biomass of this copepod follows the increase of temperature (Möllmann et al., 2000). The sudden increase in the biomass of this taxon began when the water temperature exceeded the level of 10°C, and the maximum for all stages was observed at the temperature level of 17–18°C. According to Dzierzbicka-Głowacka et al., 2010 and the parabolic function of temperature, a decrease occurs at the level of above 18°C as a result of physiological depression. The results

obtained for *Temora longicornis* also indicate the correlation between temperature and biomass. The rapid growth of biomass began at the temperature of 13°C, and the optimum temperature for this species was 18°C. This result is consistent with the results obtained by Mudrak (2004). Based on all the data obtained, we can conclude that the temperature in the Gulf of Gdańsk determines the biological processes, affects variability, including distribution, abundance and biomass of Copepoda. Therefore, any temperature anomalies may have a direct effect on phenology, community structure or on trophic interactions in the Baltic ecosystem.

The gradual increase in water temperature related to the global warming may, on one hand, accelerate copepods metabolism and life cycle, thus reducing the total time of transition from the stage of nauplii into the stage of adult forms (Weydmann et al., 2015; Weydmann et al., 2018), but on the other hand, may have a negative impact on psychrophilic species such as *Pseudocalanus* sp. The research conducted by Holste in the Baltic Sea (Holste et al., 2008) has

research conducted by Möllmann et al. (2000). Möllmann et al. (2000) showed that the biomass of the main species in the Baltic Sea in 1959–1997 was partly determined by the hydrography of the water body. The strongest correlation has been obtained for *Pseudocalanus elongatus*, which shows the strong affinity with higher salinity at low temperature (Möllmann et al., 2000). The discrepancy in the results and the lack of correlation between salinity and biomass of *Pseudocalanus sp.* may result from the small depth of the Gulf of Gdańsk and the rarity of this taxon in the region. *Pseudocalanus sp.* prefers salinity of about 12 and, therefore, it occurs in small numbers in the coastal waters such as the Gulf of Gdańsk. Due to a small amount of data available for this taxon, our analysis does not provide a clear answer on whether a complete generation of *Pseudocalanus sp.* develops in the Gulf of Gdańsk. However, the species is common in the Gdańsk Deep where the life cycle of this taxon includes only one generation per year (Mudrak, 2004). In the North Sea, due to a high water temperature during summer, higher salinity and sufficient concentration of food in months between March and August, three or four generations of *Pseudocalanus elongatus* have been observed in the German South Bay (Dippner et al., 2000) during the annual cycle and three generations have been noted in its northern part (Bossicart, 1980). Evans (1977) has described four to six generations of *Pseudocalanus elongatus* in the coastal waters of Northumberland (the North Sea) (Renz and Hirche, 2005).

The variability of copepods in the Gulf of Gdańsk is also affected by meteorological factors. The air temperature is connected with seasonality what in a temperate climate has a considerable impact on the variability of zooplankton species, thereby directly affecting the water temperature in the sea area. According to the RDA analysis, the cloud cover accounts for 2.5% of the variation in copepods and appears to affect the vertical migrations in the water column, as well as the occurrence of the studied organisms – in the areas being closer to the water surface during cloudy days. Copepods are planktonic organisms, passively floating in the pelagic zone and are not capable to resist the sea currents. Therefore, the wind direction and velocity affect the variability, carrying these organisms along with the water masses. The wave displaces water organisms within the water column and influences the local communities of mesozooplankton, which are additionally affected by the tidal range and currents. The topography of the shallow coastal waters affects the water circulation and relevant water properties (temperature, oxygen, turbidity), and thus can be mainly responsible for the space-time variation of mesozooplankton (Pineda, 2000).

The obtained results confirm that zooplankton of the Baltic Sea is subject to the seasonal biomass changes. The seasonality is a pronounced reason for a structural variability in plankton communities of temperate regions like the Baltic Sea. It is associated with the species demands' for food availability and specified temperature levels. Literature data often indicate that seasonality of zooplankton is directly related to seasonality and productivity of phytoplankton, development of which is being primarily regulated by the lighting cycle (Chiba et al., 2008). However, studies conducted in the offshore waters of the Baltic Sea indicate that the composition and abundance structure of zooplankton were not related to the occurrence and abundance of phytoplankton (Lennuk et al., 2016). So the seasonal dynamics of

copepods is probably caused mainly by the temperature, in our research area. In the area of the temperate waters of the Baltic Sea, the structural variability of the plankton communities is also observed (Józefczuk et al., 2003; Mudrak and Żmijewska, 2006). Copepoda were recorded in the Baltic zooplankton samples throughout the year, and according to Lemieszek, they are the main component of zooplankton in the water column for the most months (Lemieszek, 2013), while Rotifera and Cladocera are being observed in the highest abundances, particularly in the summer time (Mudrak and Żmijewska, 2006). Rotifera typically dominate in May (*Synchaeta* spp.) and in August (*Keratella* spp.) when their parthenogenetic reproduction mode allows utilizing the optimal food conditions within a short period.

We have noticed that the biomass of *Pseudocalanus sp.* in the Gulf of Gdańsk, in comparison with the research conducted on the Gdańsk Deep in 2010, was very low. *Pseudocalanus sp.* has been accounted for over 50% of the share as a component of zooplankton in the spring and autumn seasons. This difference may be the result of a small tolerance to low salinity, which limits the occurrence of this copepod in the Gulf of Gdańsk. The species is a stenohaline organism, which is the main component of plankton in deeper waters and is one of the most important zooplankton taxa in the Baltic Sea (Ojaveer et al., 2000). Analyzing the seasonal biomass distribution, we can conclude that *Acartia* spp. dominated in terms of biomass, and *Temora longicornis* was a subdominant species in the Gulf of Gdańsk. In addition to the investigated copepods species in the southern Baltic *Centropages hamatus* also appears, with its largest share in biomass is being recorded in the summer season with the maximum average biomass in July (7 mg C m^{-3}) and in the autumn season (about 2 mg C m^{-3}) (Mudrak, 2004). *Eurytemora* species is present rather rarely but with a negligible share in biomass (Lemieszek, 2013).

The quantity and taxonomic composition of zooplankton resources have an influence on growth and survival of fish in early development stages (Cushing, 1995). According to Sparholt (1994), reduction of *Pseudocalanus sp.* biomass in the Baltic Sea, as the main component of food, has undoubtedly contributed to the herring population decline (*Clupea harengus*) since the early 1980s. Möllmann et al. (2003) showed that condition of the herring population (*Clupea harengus*) depends on the amount of *Pseudocalanus sp.* biomass, in the central Baltic. Another species of Baltic fish, which population has been declining since the 1990s, was sprat (*Sprattus sprattus*). The food of this pelagic fish is primarily *Temora longicornis* (Möllmann and Köster, 1999). The decrease of *Sprattus sprattus* population may be caused by the competition between *Sprattus sprattus* and *Clupea harengus*, and which, with the absence of a sufficient amount of *Pseudocalanus sp.*, had to include other copepods species, such as *Temora longicornis*, in their diet.

5. Conclusions

The environmental variable in the Gulf of Gdańsk, with the greatest explanatory power of the total variability in the copepods population composition and biomass, was the water temperature. Therefore, we contend that it is the controlling factor in the Gulf of Gdańsk.

Generalized Additive Models fitted for water temperature and salinity were significant for all ontogenetic stages of the *Acartia* spp. and *Temora longicornis* and also for most stages of *Pseudocalanus* sp., apart from the C1 for both and the males – for salinity.

ANOSIM has revealed that the sampling stations in the Gulf of Gdańsk were significantly different from one another in the terms of copepods' biomasses.

Copepoda taxa composition has changed seasonally in the Gulf of Gdańsk. *Acartia* spp. and has reached the highest values in the summer months, while, *Temora longicornis* dominated in biomass in the spring and autumn seasons. The maximum value of biomass for *Pseudocalanus* sp. has been observed in the winter time.

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