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Seasonal changes in the abundance and biomass of copepod in the southwestern Baltic Sea in 2010 and 2011

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Background. Copepods are the major secondary producers in the World Ocean. They represent an important link between phytoplankton, microzooplankton and higher trophic levels such as fish. They are an important source of food for many fish species, but also a significant producer of detritus. In terms of their role in the marine food web, it is important to know how the environmental variability affects the population of Copepoda.

Methods. The study of the zooplankton community in the south-western Baltic Sea conducted during a 24-month survey (January 2010 to November 2011) resulted in 24 invertebrate species identified (10copepods, 7cladocerans, 4rotifers, 1ctenophore, *Fritillaria borealis* and *Hyperia galba*). Data were collected at two stations located on the open-sea deep-water station – the Gdańsk Deep (54°50'φN, 19°19'λE) and in the western, inner part of the Gulf of Gdańsk (54°32' φN, 18°48.2 'λE). Vertical hauls were carried out using two nets: a Copenhagen net with an inlet diameter of 50 cm and a mesh diameter of 100 μm (in 2010) and WP-2 net from KC Denmark with an inlet diameter of 57 cm and a mesh diameter of 100 μm (in 2011).

Results. The paper describes seasonal changes in the abundance and biomass of Copepoda, taking into account the main Baltic calanoid copepod taxa (*Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp.). They usually represented the main component of zooplankton. The average number of Copepoda at station P1 during the study period of 2010 was 3913 ind.m^{-3} (SD 2572) and their number ranged from 1184 ind. m^{-3} (in winter) to 6293 ind.m^{-3} (in spring). One year later, the average count of copepods was higher, i.e. 11 723 ind. m^{-3} (SD 6980) and ranged from 2351 ind. m^{-3} (in winter) to 18 307 ind.m^{-3} (in summer). Their average count at station P2 in 2010 was 29 141 ind. m^{-3} ranging from 3330 ind.m^{-3} (in March) to 67 789 ind. m^{-3} (in May). The average count of copepods in 2011 was much lower – 17 883 ind./m^3 and ranged from 1360 ind./m^3 (in April) to 39 559 ind./m^3 (in May).

Discussion. The environment of pelagic animals changes with the distance from the shore and with the sea depth. Although the qualitative structure of zooplankton is almost identical with that of the coastal waters, the quantitative structure changes quite significantly. The maximum values of zooplankton abundance and biomass were observed in the summer season, both in the Gdańsk Deep and the inner part of the Gulf of Gdańsk. Copepoda dominated in the composition of zooplankton for almost the entire duration of the research.. Quantitative taxonomic composition of Copepoda at station P1 (the Gdańsk Deep) was different compared to station P2 (the western, inner part of the Gulf of Gdańsk) due to a high percentage of a crustacean preferring waters with lower temperature and higher salinity – *Pseudocalanus* sp.

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Abstract

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Results. The paper describes seasonal changes in the abundance and biomass of Copepod, taking into account the main Baltic calanoid copepod taxa (*Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp.). They usually represented the main component of zooplankton.

The average number of Copepod at station P1 during the study period of 2010 was 3913 ind. m^{-3} (SD 2572) and their number ranged from 1184 ind. m^{-3} (in winter) to 6293 ind. m^{-3} (in spring).

One year later, the average count of copepods was higher, i.e. 11 723 ind. m^{-3} (SD 6980) and ranged from 2351 ind. m^{-3} (in winter) to 18 307 ind. m^{-3} (in summer).

Their average count at station P2 in 2010 was 29 141 ind. m^{-3} ranging from 3330 ind. m^{-3} (in March) to 67 789 ind. m^{-3} (in May). The average count of copepods in 2011 was much lower – 17 883 ind./m^3 and ranged from 1360 ind./m^3 (in April) to 39 559 ind./m^3 (in May).

Discussion. The environment of pelagic animals changes with the distance from the shore and with the sea depth. Although the qualitative structure of zooplankton is almost identical with that of the coastal waters, the quantitative structure changes quite significantly. The maximum values of zooplankton abundance and biomass were observed in the summer season, both in the Gdańsk Deep and the inner part of the Gulf of Gdańsk. Copepod dominated in the composition of zooplankton for almost the entire duration of the research.. Quantitative taxonomic composition of Copepod at station P1 (the Gdańsk Deep) was different compared to station P2 (the western,

inner part of the Gulf of Gdańsk) due to a high percentage of a crustacean preferring waters with lower temperature and higher salinity – *Pseudocalanus* sp.

Main article text

Introduction

The Baltic is a shallow, shelf sea from the group of internal (intracontinental) seas. It is the youngest European sea and one of the youngest seas of the Atlantic Ocean. It covers an area of ca. 415 000 km². It is connected with the North Sea through a number of straits: the Danish Straits (Sund, Little Belt and Great Belt), Kattegat and Skagerrak. The generally accepted division of the Baltic Sea, based on the seabed topography, enables the identification of regions with clearly defined hydrographic parameters (Fonselius, 1969; Omstedt, 1990), i.e. the Gulf of Bothnia, the Bothnian Sea, the Gulf of Finland, the Gulf of Riga, the Baltic Proper (the southern Baltic), the Danish Straits and Kattegat.

The Baltic waters are characterized by fluctuations in salinity resulting from, inter alia, irregular inflows of fresh waters and inflows from the North Sea. This phenomenon occurs mainly in the Danish Straits and estuaries, and contributes to the two-layer structure of the Baltic waters (Matthäus & Franck, 1992; Fonselius & Valderrama, 2003; Leppärant & Myrberg, 2009). The upper layer consists of lighter waters with salinity ranging from 20 PSU in the Kattegat to 2-3 PSU at the northern end of the Gulf of Bothnia and the eastern end of the Gulf of Finland, and 8 PSU in the Baltic Proper. Surface waters are well mixed and oxygenated, and their temperature varies depending on the season from 0°C to 20°C. The lower, deepwater zone is characterized by basically constant temperature of 4-6°C and higher salinity ranging from 12 to 20 PSU depending on the region. Stability between these zones is attributed to the halocline, which separates the surface waters from the deepwater layer preventing mixing of the waters, in particular at the open sea. The Southern Baltic is an area of particular importance to the entire Baltic Sea. Saline waters from the North Sea are passing through this region of the Baltic. The direction of the near-bottom flows is affected by the seabed topography. The Słupsk Furrow, with the maximum depth of 92 m and the width of 40 km, is a gateway through which inflow waters move eastwards from the North Sea. Water inflows from the North Sea raises the Baltic water salinity. The oxygen content and the dynamics of temperature are determined by the seasons. Although the Gdańsk Deep is located off the inflow-water transit axis, it plays an important role in this process (Osiński, 2009).

Zooplankton of the Baltic Sea consists of both unicellular (protozooplankton) and multicellular organisms of the complex structure (metazooplankton). Mesozooplankton is the dominant group of organisms in the Baltic Sea in terms of biomass (Möllmann, Kornilovs & Sidrevics, 2000; Dzierzbicka-Glowacka, Bielecka & Mudrak, 2006; Dzierzbicka-Glowacka at al., 2012; Dzierzbicka-Glowacka, Kalarus & Żmijewska, 2013). As reported by the studies conducted in the western part of the Gulf of Gdańsk in 1980 (Wiktor, 1990), it may represent up to 76% of the average annual carbon weight. In terms of biomass and production, Copepod are the most important taxa of zooplankton in the Baltic Sea, e.g. *Pseudocalanus* sp., *Temora longicornis* and *Acartia* spp., while Rotatoria are mainly represented by *Synchaeta* spp. and Cladocera with the dominance of *Evadne nordmanni* (Dzierzbicka-Glowacka at al., 2015). The species *Pleurobrachia pileus* belonging to Ctenophora, the copepod *Eurytemora affinis* and rotifers *Keratella* spp. are the least important taxa in the biomass and production of zooplankton (Wiktor, 1990; Wiktor & Żmijewska, 1996; Mudrak & Żmijewska, 2007). Between the dominant species and those from the end of the scale, there are intermediate species living in the Baltic Sea and characterized by very similar biomass values, e.g. *Flitilaria borealis* (Appendicularia), larvae of Polycheata and Bivalvia, cladocerans *Bosmina* spp. and *Podon* spp. as well as the copepod *Centropages hamatus* (Andrulewicz et al., 2008).

Spatial variation in the species composition of mesozooplankton results primarily from the salinity of the Baltic Sea. The smallest number of species (13-20) occurs in the central region of the Baltic Proper and it increases in marine and freshwater regions. The largest number of species (ca. 28-32) is encountered in the south-western part of the Baltic Proper, which is strongly affected by the North Sea (Andrulewicz et al., 2008).

Copepods are one of the most important links in the food web. They play an important role in the transmission of energy between producers and consumers of higher orders, being i.a. food for many pelagic, planktivorous fishes. Copepod are also characterized by varying tolerance to salinity and consequently the presence or absence of specific species enables the determination of physicochemical properties of the environment.

The main objective of the study was to describe the seasonal changes in the abundance and biomass of the major Baltic copepod species (*Acartia* spp., *Temora longicornis* and

Pseudocalanus sp.) in the Gdańsk Basin (the southwestern Baltic Sea) based on the research conducted in 2010-2011 in the Gdańsk Deep and in the western part of Gulf of Gdańsk. The data obtained will be used as a background for future numerical evaluations.

Material and methods

Planktonic material, which is the basis of *in situ* studies, was collected in the southern part of the Baltic Sea from two stations: the Gdańsk Deep and the western part of the Gulf of Gdańsk. The first series consists of biological material collected aboard the ship of the Institute of Oceanology of the Polish Academy of Sciences − r/v "Oceans" − during 7 cruises in the area of Gdańsk Deep (54°50'φN, 19°19'λE) (Fig. 1, station P1), in the period from February 2010 to November 2011. The maximum depth of this site is ca. 100 m.

Vertical hauls were carried out using two nets: a Copenhagen net with an inlet diameter of 50 cm and a mesh diameter of 100 µm (in 2010) and WP-2 net from KC Denmark with an inlet diameter of 57 cm and a mesh diameter of 100 µm (in 2011).

The plankton net mesh size was selected so as to collect the mesozooplankton together with the younger developmental stages of Copepod, i.e. the main object of the study. A flow meter was placed at 1/3 of the diameter of the net inlet to determine the amount of water filtered.

The material was collected in accordance with the HELCOM guidelines (Manual for Marine Monitoring in the COMBINE Programme of HELCOM, Annex C-7). Vertical net hauls were carried out in three layers: the bottom – the upper limit of the halocline (with no halocline present – 75 m), the upper limit of the halocline – thermocline (with no thermocline present – 25 m), the upper limit of the thermocline – the surface. A total of 21 samples were collected, both during the day and night.

Table S1 presents a list of material at P1 station. The division into seasons used in Table S1 and in the following part of the study was adopted on the basis of water temperature.

The analyzed material from the Gdańsk Deep was used to determine the composition and seasonal changes in the abundance and biomass related to time and space.

The second series of the study material consisted of monthly zooplankton samples collected in the western part of the Gulf of Gdańsk (54°32' φN, 18°48.2 'λE) (Fig. 1, station P2) in the period from 11 February 2010 to 29 November 2011, from aboard the ship of the Institute of Oceanography of the University of Gdańsk – kh "Oceanograf 2". The site of biological material collection was characterized by a depth of 40 m and was located 9.5 Mm away from the shore. Vertical net hauls were carried out along the water column divided into 10 m thick layers, from the bottom up to the water surface. The exception was the 27th of July 2011 when samples were collected from the following layers: 20-0, 30-20 and 40-30 m, due to equipment failure. In total, 71 samples were collected in this series.

Table S2 presents a list of material at P2 station.

Net hauls were carried out only during the day, using (like in Gdańsk Deep in 2011) a WP-2 closing net with an inlet diameter of 57 cm and mesh size of 100 µm. The flow meter was placed at 1/3 of the net inlet diameter to determine the amount of water filtered. The collected material was immediately moved into plastic bottles and treated with 4% solution of formaldehyde to preserve animals for subsequent analysis. A total of 92 samples were analyzed. Biomass was calculated from abundance with weight standards after Hernroth (1985).

Results

Environmental conditions during the study period

Measurements of hydrometeorological conditions, taken during the biological material sampling (from January 2010 to November 2011), represent an environmental description within a specific time and space frame (Data S1).

Environmental data for Gdańsk Deep (P1), water temperature and salinity were measured in the whole water column using the STD probe. Measurements were performed during seven cruises aboard the vessel r/v "Oceania" prior to the biological material collection.

In February 2010, the water temperature in the surface layer was 1.83°C and it gradually increases with increasing depth, reaching the maximum value of 9.08°C at the bottom. The upper limit of the thermocline was determined at a depth of approximately 60 m. In June 2010, the water temperature was measured only to a depth of 60 m and it ranged from 10.7°C on the surface to ca. 13°C in the deepest layer.

The temperature of surface waters in March 2011 was much lower compared to February 2010, i.e. 1.39°C and remained constant to a depth of ca. 65 m, i.e. the upper limit of the thermocline. Below this depth, the temperature significantly increases, reaching the value of 6.19°C at the bottom. In June 2011, the water temperature was measured only to a depth of ca. 50 m. The temperature drops with increasing depth, from 15.18°C at the surface to 6.38°C at a depth of

50 m. November 2011 was characterized by a high temperature of surface water, i.e. 11.45^{o}C, which remained relatively constant up to a depth of ca. 40 m and rapidly dropped at greater depths. Due to strong waves and surface-water cooling, the thermocline was at a depth of ca. 40-50 m. The water temperature at the bottom was 5.17^{o}C.

Salinity of surface waters at station P1 ranged from 7.45 to 6.94 PSU and gradually increased along the depth gradient, reaching the maximum value of 12.55-10.84 PSU at the bottom. In June 2010, the salinity was measured only to a depth of 60 m; it ranged from 7.3 PSU at the surface to 6.2 PSU in the deepest layer. Such a large decline in salinity was probably caused by the inflow of flash flood waves into the Gulf of Gdańsk after a disastrous spring inundation in the Vistula drainage basin. A likely increase followed along with the increasing depth, which is attributed to the impact of oceanic water inflows from the North Sea.

Temperature of surface water and salinity measured in 2010 and 2011 at station P1 (based on the example of June) significantly varied during those two years. The runoff of flood waters in May 2010 disturbed the thermohaline system in Gdańsk Deep, which was reflected in a warmer layer of less saline water.

The environmental data on the western, inner part of the Gulf of Gdańsk (P2) came from direct measurements carried out on board k/h "Oceanograf-2" (16 trips) and "Hestia" (2 trips).

Water temperature at station P2 in the western part of the Gulf of Gdańsk was slightly higher for 2010 compared to 2011.

From January to March, the surface-water temperature (ca. 1^{o}C) was lower than at the bottom. It gradually increased starting from April and eventually was higher at the surface than at the bottom. However, the differences in both cases were below 1^{o}C. This situation lasted until October 2010 and from July 2011 the water temperature began to level off and uniformly fluctuated till the end of the year. In November 2010 and 2011, basically a constant temperature was observed throughout the water column, on average 8.6^{o}C and 7.3^{o}C, respectively. The warmest month in 2010 and 2011 was August (19.4^{o}C and 18^{o}C), whereas the coldest one – January and March (from 1 to 2.1^{o}C).

Salinity at station P2 (depth of 40 m) varied to a small extent, both during the year and throughout the water column. Mean values of water salinity in the western part of the Gulf of Gdańsk ranged from 6.68 PSU (in July 2010) to 7.38 PSU (in October 2011). The lowest salinity was recorded in July 2010 (6.4 PSU), which probably resulted from the inflow of Vistula flood waters.

Copepod abundance

At stations P1

Copepods occurred both in 2010 and 2011; at stations P1 they occurred throughout the study period. They were usually the main component of zooplankton (Data S2).

Due to the limited possibility of monthly collections of biological material for the analysis, data collected for selected seasons were interpreted. Nevertheless, they provide a general picture of the situation prevailing at a given time in the pelagic zone.

The average number of Copepod during the study period of 2010 was 3913 ind. m^{-3} (SD 2572) and their number ranged from 1184 ind. m^{-3} (in winter) to 6293 ind. m^{-3} (in spring). One year later, the average count of copepods was higher, i.e. 11 723 ind. m^{-3} (SD 6980) and ranged from 2351 ind. m^{-3} (in winter) to 18 307 ind. m^{-3} (in summer) (Fig. 2) (Data S2).

The maximum number of Copepod in spring 2010 in the surface layer (25-0 m) was 12 545 ind. m^{-3}, while in spring 2011 the count of Copepod in the same layer was 2.5 times higher. In the other months, the highest values of the Copepod count were also recorded in the layer between the upper limit of the thermocline to the surface (Data S2).

Quantitative taxonomic composition of Copepod at station P1, based on the quantitative contribution of species, was different compared to station P2, which was attributed to the high percentage of a crustacean preferring waters with lower temperature and higher salinity – *Pseudocalanus elongates.*

The species was the main component of Copepod in the winter-spring season of 2010 (ca. 50%), while replaced by *Acartia* spp. (40.26%) and *Temora longicornis* (33.31%) in the summer. During this period, *Centropages hamatus* accounted for several percent of Copepod, while *Eurytemora* sp. was insignificant.

In 2011, the situation was similar, i.e. *Pseudocalanus* was the main component of Copepod in the winter-spring season (over 50%), while in the summer-autumn season its contribution dropped and was similar to that of *Temora longicornis* – 40% in summer and 35% in autumn. The percentage of the genus *Acartia* in the described seasons ranged from 10 to 30%. The presence of *Centropages hamatus* in this region ranged from a few to several percent, while the count of *Eurytemora* sp. (similarly to the previous year) was insignificant (Fig. 3).

At stations P2

At station P2, copepods occurred throughout the study period, both in 2010 and 2011. They usually represented the main component of zooplankton. Their average count in 2010 was 29 141 ind. m^{-3} (SD 23315), and ranged from 3330 ind. m^{-3} (in March) to 67 789 ind. m^{-3} (in May). The average count of copepods in 2011 was much lower – 17 883 ind./m^3 (SD 11407), and ranged from 1360 ind./m^3 (in April) to 39 558 ind./m^3 (in May) (Fig.4) (Data S3).

The maximum count of Copepod in May 2010 was determined in the 10-0 m layer – 161 150 ind. m^{-3}, while in September 2011 the Copepod abundance in the same layer was over two times lower (70 314 ind. m^{-3}) (Data S5).

The analysis of seasonal changes in 2010 revealed two peaks in Copepod abundance: the first one in May and the second one in September with abundance of 67 789 ind. m^{-3} and 57 822 ind. m^{-3}, respectively. In 2011, there were also two abundance peaks, the smaller one in June-July (22 155 ind./m^3) and the larger one in September (39 559 ind./m^3) (Fig. 4).

It appears that the distribution of Copepod in the water column is determined by the preferences of a species dominant at a given time and its developmental stage.

In March and June 2010, the largest number of Copepod was observed in the layer of 30-20 m, while in April – in the 20-10 m layer. During the rest of the year, copepods occurred mainly in the surface layer (10-0 m) (Fig. S1). In 2011, the situation was slightly different. In the early spring and autumn, the largest numbers of Copepod were observed in the layer of up to 20 m. Whereas in the summer, they definitely preferred deeper waters (Fig. S2) (Data S5).

In 2010, the genus *Acartia* was the main component of Copepod from March to September (ranging from 26.23 to 89.38%), while in October and November – 32% (Fig. 5). (Data S3).

Temora longicornis was the second most abundant Copepod species – from 6.85% (in July) to 44.90% (in November). In October and November, *Temora longicornis* dominated and in May its abundance was only slightly lower compared to *Acartia* spp.

The contribution of *Pseudocalanus elongatus* was also relatively significant and ranged from 21.16% in March and 29.16% in April. During the rest of the year, it ranged from only 0.07 (in June) to 6.43% (in November).

The abundance of *Centropages hamatus*, similarly to *Pseudocalanus*, was higher in spring and autumn and ranged from 11.38% in March to 16-17% in October and November.

On the other hand, the contribution of *Eurytemora* sp. did not exceed 1% throughout the study period, except for October 2010 when it reached ca. 7%.

In 2011, the genus *Acartia* accounted for the largest contribution in the abundance of Copepod (except for May and June) and it ranged from 15.81% (in May) to 85.25% (in August) (Fig. 6)(Data S3).

Temora longicornis was the dominant species among Copepod in May (77.19%) and June (58.42%). Its contribution in July, October and November was approximately 30%, and in the other months – just several percent.

Similarly to the previous year, *Pseudocalanus elongatus* was the most abundant Copepod species in April (23.45%), while in the other months – it accounted for up to 7%.

Centropages hamatus was a significant component of Copepod, in October (15.16%) and November (16.33%), the same as in the autumn 2010. Its contribution was insignificant for most of the year, ranging from 0.65 (in May) to 5.34% (in September).

In 2011, *Eurytemora* sp. was only an accompanying, supplementary species, accounting for up to 1.63% (July) of the total count of Copepod.

Copepod biomass

At stations P1

The average biomass of Copepod in the zooplankton in 2010 at station P1 was about 116.68 mg m^{-3} (SD 37.49) and it ranged from 92.19 mg m^{-3} (in summer) to 159.84 mg m^{-3} (in spring), while in 2011 – the average value was 321.26 mg m^{-3} (SD 247.418) and ranged from 103.67 mg m^{-3} (in winter) to 676.20 mg m^{-3} (in summer)(Fig.7) (Data S4).

The maximum biomass of copepods in spring 2010 was recorded in the surface layer (up to a depth of 25 m) – 83.59 mg m^{-3}, and in summer 2011 in the intermediate layer (from the upper limit of the halocline to the upper limit of the thermocline, i.e. 70-25 m) – 467.07 mg/m^3 (Data S4).

Considering the contribution of individual Copepod taxa in the zooplankton biomass at station P1, one can observe a clear dominance of *Psedocalanus elongatus*, which accounted for about 50% of the total Copepod biomass in the winter-spring season of 2010, while in summer 2010 its abundance dropped in favor of *Temora longicornis* and *Acartia* spp. (ca. 40%). The abundance of *Centropages hamatus* also increased in the spring season up to 23.64%.

In the winter-spring season of 2011, *Psedocalanus* sp. represented approximately 60% of the Copepod biomass, while in the summer its contribution dropped to 22.88% and again increased to 47.97% in the autumn. *Temora longicornis* (65.05%) was the main component of the Copepod biomass in the summer. The contribution of other species was negligible: *Acartia* spp. from 8.80 to 13.33% and *Centropages hamatus* from 3.22 to 10.24% (Fig. 8) (Data S4).

At stations P2

The average biomass of Copepod at station P2 in 2010 was 151.46 mg m^{-3} (SD 115) and ranged from 33.87 mg m^{-3} (in March) to 390.12 mg m^{-3} (in May). In 2011, the average Copepod biomass was 95.47 mg m^{-3} (SD 52) and ranged from 12.40 mg m^{-3} (in April) to 164.82 mg m^{-3} (in September) (Fig. 9)(Data S3).

The maximum biomass of copepods in May 2010 was recorded in the 10-0 m layer – 692.12 mg m^{-3} and 403.98 mg m^{-3} in September 2011.

When looking into seasonal changes in the Copepod biomass in 2010, it appears that a significant peak occurred in May – 390.12 mg m^{-3} and two smaller peaks in September (186.73 mg m^{-3}) and November (114.36 mg m^{-3}). In 2011, there were two, basically equivalent biomass peaks: in June (143.27 mg m^{-3}) and September (164.82 mg m^{-3}) (Fig. 9).

As in the case of the Copepod count, the distribution of Copepod biomass in the water column is determined by the preferences of a species dominant at a given time and its development stage.

In March and June 2010, the largest number of Copepod was observed in the 30-20 m layer, while in April 2010 – in the 20-10 m layer. In the other months, the highest values of biomass were determined in the surface layer (10-0 m) (Fig. S3) (Data S5).

In 2011, the biomass values had a similar pattern, except for January and October when the values were slightly higher at the bottom (40-30 m) (Fig. S4) (Data S5).

Species from the genus *Acartia* spp. dominated in the biomass of Copepod at station P2 for most of the 2010 season. Their contribution ranged from 18.92% in November to 89.38% in September. In March, April and November, they were replaced by *Temora longicornis*. In October, the biomass of both taxa was at a similar level – ca. 37%.

Temora longicornis was a subdominant in the biomass of Copepod. Its contribution ranged from 9.65% (in September) to 55.69% (in November).

As in the case of abundance, a significant percentage of *Pseudocalanus elongatus* in the biomass of copepods was observed only in March (19.63%) and April (15%), while in the remaining months it ranged from only 0.10% (July) to 7.04% (November).

Centropages hamatus was a constant component of the Copepod biomass, with the highest values recorded in March (20.74%), April (13.49%), June (13.55%), October (16.12%) and November (17.98%). The percentage of *Eurytemora* sp. in the Copepod biomass was usually up to 1%, except for October – 7.05% (Fig. 10) (Data S3).

In 2011, the genus *Acartia* represented a significant component of the Copepod biomass with the contribution ranging from 12.87% (in May) to 88.16% (in August).

Temora longicornis, being an important and constant component in the biomass of copepods, was observed from April to June, and then in November, ranging from 8.05% (in August) to 79.87% (in May). In January and November, the biomass values of *Acartia* spp. and *Temora longicornis* were similar.

The maximum biomass of *Pseudocalanus elongatus* was determined in April – 14.94%, while for the rest of the year the biomass values were small. In 2011, the crustacean *Centropages hamatus* was much more important in the biomass of copepods – over 10% in January, July, October and November, and from 0.89% in May to 7.23% in April. *Eurytemora* sp. were of minor significance in the biomass of Copepod, the same way as in the previous year (Fig. 11) (Data S3).

Discussion

In terms of biomass and abundance, Copepod are the most important zooplankton taxa in the southern Baltic, and they are mainly represented by e.g. *Acartia* spp., *Pseudocalanus elongatus* and *Temora longicornis*, Rotatoria: *Synchaeta* spp. and *Keratella quadrata*, *Cladocera: Evadne nordmanni*, *Eubosmina maritima* and *Pleopis polyphaemoides.* Euryhaline freshwater and typically freshwater species are of lesser importance; they occur mainly at the river mouths (e.g. *Eurytemora* sp.).

Copepods represent one of the largest groups of secondary producers in the global ocean. They are an important link between phytoplankton, microzooplankton and higher trophic levels such as fish (Longhurst, 1981; Longhurst & Harrison, 1989; Kleppel, Holliday & Pieper, 1991; Kleppel, 1992; Dzierzbicka-Glowacka et al., 2011). They are an important source of food for many fish species, but also a significant producer of detritus. One individual organism can produce 200 portions of fecal 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.

The study presents an analysis of 92 zooplankton samples from Gdańsk Deep (Gdańsk Basin) and from the western part of the Gulf of Gdańsk in terms of composition, abundance and biomass of zooplankton, with particular emphasis on Copepod, as well as the structure of populations of species occurring in large numbers in the southern Baltic, i.e. *Pseudocalanus* sp., *Acartia* spp. *Temora longicorni* (which will be described in a separate paper) in 2010 and 2011.

Description of the study area

The environment of Gdańsk Basin is determined by a varying volume of river runoff, easy exchange of water with the Baltic Sea, including periodical inflows (infusions) of seawater, and highly variable morphometric conditions.

Seasonal temperature changes occurring in the upper water layer result from seasonal variability in meteorological elements. They are affected mainly by vertical processes, in particular the convection and wind mixing as well as the Vistula water inflows into the Gulf of Gdańsk, which raise the water temperature in the spring-summer season and lower it in the autumn-winter season (Cyberski, 1995). The water temperature in the layer above 80 m gradually increases up to the maximum value at the bottom. Due to lack of contact with the atmosphere, deep waters do not exhibit seasonal changes typical of the upper layer, and their temperature depends on temperatures of inflow waters (Majewski, 1990).

Distribution of salinity throughout the year in the surface layer of Gdańsk Basin is affected by a varying volume of river waters reaching the Basin and affecting the anemobaric conditions. Salinity shows a clear seasonal variability in the shallow littoral zone. Differences in the vertical stratification of salinity result from interactions between the Vistula waters – reducing the salinity and deep waters – increasing the salinity (Majewski, 1990). Salinity of benthic waters (above 80 m) also depends on the inflows of saline waters from the North Sea.

Taxonomic composition of zooplankton

According to our environmental studies conducted in 2010/2011, zooplankton was represented mainly by organisms that occur in the pelagic zone (holoplankton) – copepods, cladocerans, rotifers and the only representative of Appendicularia occurring in the Baltic Sea – *Fritillaria borealis*. Furthermore, eggs and juveniles of unidentified Ctenophora, a few specimens of the species *Hyperia galba*, larvae of the benthic fauna (meroplankton) as well as eggs and fish spawn (ichthyoplankton) were found. The percentage of individual taxa as well as their horizontal and vertical distribution were determined by meteorological and hydrological conditions prevailing at a given time.

A total of 24 taxa were identified in the analyzed material, including: 10 Copepod, 4 Rotifera, 7 Cladocera, Ctenophora, *Fritillaria borealis* and *Hyperia galba*. In addition, larvae of the benthic fauna were counted (Polychaeta, Bivalvia, Gastropoda and Cirripedia). They were not identified to the species level, but generally defined as meroplankton. Ichthyoplankton was not analyzed in detail.

The research showed that the taxonomic composition of holoplankton in the Gulf of Gdańsk was similar to that observed in this region for many years. The exceptions are two invasive species of Cladocera, which occurred in summer 2010 in the shallow part of the Gulf of Gdańsk – *Cercopagis pengoi* and *Evadne anonyx*. Copepod dominated except for only a few short periods.

The maximum values of zooplankton abundance and biomass were observed in the summer season, both in the Gdańsk Deep and the inner part of the Gulf of Gdańsk. Copepod dominated in the composition of zooplankton for almost the entire duration of the research. Rotifers occurred in larger numbers only in summer 2010 in Gdańsk Deep and in May and July 2010 in the western part of the Gulf of Gdańsk, and meroplankton – in April 2011. This is a typical pattern of seasonal changes in the zooplankton in this region. In the study season of 2006/2007, Copepod also dominated in the zooplankton in the western part of the Gulf of Gdańsk (except for June and July 2006, and May 2007) and Rotifera had a significant contribution during the spring and summer season. Of the other components, only meroplankton had a considerable contribution in the zooplankton (September 2006 – 10%; July – 24%) (Dzierzbicka-Głowacka, Kalarus &Żmijewska, 2013).

Changes in the abundance and biomass of zooplankton

Taxa occurring in the samples occasionally or in small numbers (*Hyperia galba*, *Oithona similis*, Ctenophora, freshwater Cyclopoida, Harpacticoida) were not included in the determination of zooplankton abundance and biomass.

The average count of zooplankton in Gdańsk Deep (station P1) during the conducted studies was 10685 ind. per m^{-3} (SD 12027), whereas in 2011 – 14 607 ind. per. m^{-3} (SD 9565). The highest mean values of abundance in the water column were recorded in the summer season of 2010 and 2011, i.e. 24238 ind. m^{-3} and 23659 ind. m^{-3}, respectively. Minimum values were observed in the winter-spring season (1283 ind. m^{-3} and 2807 ind. m^{-3}) (Fig. 12) (Data S2).

The average count of zooplankton in the western part of the Gulf of Gdańsk (at station P2) in 2010 was 87 122 ind. m^{-3} (SD 104836), and in 2011 – 31 649 ind. m^{-3} (SD 20487). In 2010, the maximum average count of zooplankton in the water column was recorded in July, whereas in 2011 – in September, i.e. 28 2166 ind. m^{-3} and 56 657 ind. m^{-3}, respectively. The minimum values were recorded in March 2010 (3617 ind. m^{-3}) and April 2011 (7249 ind. m^{-3}) (Fig. 13) (Data S3).

Zooplankton at station P1 varied depending on the seasons, although not as much as in the shallow regions of the Gulf of Gdańsk. In the two-year cycle of scientific studies, Copepod were the main component of zooplankton, representing from 69% of the total zooplankton in spring 2011 to 96% in spring 2010 (except for summer 2010, ca. 18%) (Data S2).

In 2010 and 2011, Copepod occurred at station P2 throughout the study period and for most of the months they were the main component of zooplankton, with the contribution ranging from ca. 67% (in September) to 92% (in March) in 2010 and from 47% (in June) to 93% (in January) in 2011, except for May (24%) and July (over 9%), when rotifers dominated in the zooplankton. In August, the contribution of Copepod was similar to Cladocera and Rotifera and amounted to ca. 40%. In 2011, the exceptions were April and July when pelagic fauna was dominated by meroplankton – mainly veligers of bivalves (Data S3).

Copepod were the main component of the zooplankton biomass at station P1 for the whole duration of the study, with the contribution ranging from 55.3% in summer 2010 to 99.2% in winter 2010.

The situation was different at station P2. In March, April and June as well as in September, October and November 2010, Copepod accounted for the main part of the zooplankton biomass, i.e. from 67.6% in October to ca. 94.6% in March. In May, July and August, as a result of seasonal zooplankton components occurring during these months (e.g. Cladocera), the proportion of Copepod significantly decreased and ranged from 24.2 to 36.7%. In 2011, copepods dominated at station P2, and their contribution in the total biomass ranged from 31.7% (in April) to 96.7% (in January). In April, juvenile stages of the benthic fauna dominated in the zooplankton biomass – 64.35%, while in the following months their contribution dropped to 7.03%, and then increased again in July – 34.95% (Lemieszek, 2013).

Changes in the abundance and biomass of Copepod

The coastal region of the Gulf of Gdańsk is wide open towards the Gdańsk Deep, which is part of the Gdańsk Basin, the southernmost part of the Gotland Basin, i.e. the largest and the deepest basin of the Baltic Sea.

The vertical profile of waters in the Gulf of Gdańsk can be divided into two layers. The surface layer in the coastal area reaches the bottom. In the deeper part, it is separated from the lower layer by intermediate waters up to 60-80m depth. The surface layer is subject to seasonal changes in temperature, caused by meteorological factors, convection, wind mixing and the impact of the Vistula River water, which causes warming in spring and summer and cooling in autumn and winter. The impact of the Vistula River has a different range during the year, in spring and summer it covers almost the entire gulf, while in November – it is limited to estuaries. This is due to the force and direction of winds. There is a difference in the vertical distribution between coastal and deep-sea regions. The coastal areas have higher temperatures in summer compared to the surrounding waters, while in winter they are cooler. The annual report shows that the salinity in the Gulf of Gdańsk is lower in winter than in summer. A key factor affecting the salinity of surface waters are fresh waters from the Vistula River.

The environment of pelagic animals changes with the distance from the shore and with the sea depth. Although the qualitative structure of zooplankton is almost identical with that of the coastal waters, the quantitative structure changes quite significantly. There are more species typical of colder and more saline waters, especially in the lower water layers. The abundance of *A. longiremis* from the genus *Acartia* is higher compared to the coastal waters where *A. bifilosa* and *A. tonsa* are the dominant species. Also the concentration of *Pseudocalanus* sp. and *T. longicornis* is higher (Dzierzbicka-Głowacka at el., 2013; 2015).

Taxonomic composition of Copepod during the research conducted in the Gulf of Gdańsk at station P1 (open sea), based on the quantitative contribution in the biomass, was different compared to station P2 (the inner part of Gdańsk Gulf), which was attributed to a high percentage of a crustacean that prefers waters with lower temperature and higher salinity – *Pseudocalanus* sp.

In 2010 and 2011, *Pseudocalanus* sp. was the main component of Copepod at station P1 in the winter-spring season (ca. 50% and 60% of the abundance and biomass, respectively), and in the summer-autumn season its contribution dropped and was similar to that of *Temora longicornis*:

ca. 40% in summer and 35% in autumn. The percentage of the genus *Acartia* in these seasons ranged from 10% to 30%.

Analysis of the variation in the Copepod taxonomic structure in the inner part of the Gulf of Gdańsk at station P2 indicates that *Acartia* spp. dominated in the Copepod composition. Its contribution in 2010 ranged from 26% (in March) to 89% (in September), and in 2011 – from 16% (in May) to 85% (in August), while in October and November – ca. 32%.

Temora longicornis was a sub-dominant species in terms of abundance and biomass of Copepod in the Gulf of Gdańsk. Its maximum contribution in the total abundance at station P2 was ca. 45% (in November 2010) and 77% (in May 2011) and ca. 56% (in November 2010) and 80% (in May 2011) in biomass.

Abundance, comparison with the other data

Taking into account the two periods – 2006/2007 (Kalarus, 2010; Dzierzbicka-Glowacka, Kalarus & Żmijewska, 2013) and 2010/2011, the total count of Copepod in the Gdańsk Basin (at station P2) was characterized by a significant increase (three- and twofold) in the maximum abundance within the 10-0 m layer in May 2010 (161 150 ind. m^{-3}) and within the 20-10 m layer in July 2007 (127 000 ind. m^{-3}), as well as in the average value in the water column, i.e. 67 790 ind. in May 2010 and 83 500 ind. in July 2007, compared to 2006 and 2011. In Lithuanian Baltic Sea, at the coastal stations (B1-B4) and open sea stations (B5-B9) in 2014 (Data S6), the average abundances of Copepod in surface layer (i.e. 36 320 and 21 327 ind. m^{-3}) were similar to values from 2011 and 2006 for the Gulf of Gdańsk and about two and four times lower than for 2011 and 2010, respectively. (Table 1).

In general, the maximum contribution (%) of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. in the abundance of Copepod at station P2 in the western part of Gdańsk Gulf was similar in the two periods – 2006/2007 and 2010/2011 (Table 2). The population dynamics of the main Baltic calanoid copepod species in the Gdańk Basin in the two study periods was characterized by an increase in the maximum percentage contribution of *Acartia* spp. (up to 90%) and *Pseudocalanus* sp. (up to 29%) and a decline of *Temora longicornis* (to 45%) in the abundance of Copepod in 2010 and a major growth (up to 77%) of *T. longicornis* in 2011, as well as a decline of *Acartia* spp. and *Pseudocalanus* sp. in 2011 to the level from 2006/2007. In the other cases, the percentage of individual taxa was at a similar level throughout the study period.

The taxon *Acartia* spp. had the highest percentage contribution (ca. 82-90%) in all the studied years, particularly in the summer (June-September). *Temora longicornis* accounted for ca. 45-57% (i.e. almost half the *Acartia* abundance) of the total Copepod abundance in the studied period (2006/2007 and 2010/2011; except for 2011 – 77%), i.e. late spring/summer (May/June) or autumn (November) when soon after or before these periods *Acartia* spp. reached the first of the second peak in the abundance, respectively. On the other hand, the highest contribution of *Pseudocalanus* sp., the third most abundant Copepod species in the inner part of the Gulf of Gdańsk, was observed in early spring (March/April – ca. 23-29%), except for 2006 (in February – 25%). *Pseudocalanus* sp. is a typical representative of the winter zooplankton. Outside the winter season, the taxon is present mostly in cooler, deepwater layers in the Gulf of Gdańsk (Siudziński, 1977).

At station P1 (Gdańsk Deep) in 2010 and 2011, the maximum contribution (%) of *Acartia* spp.(40-33%) was similar to that for *Temora longicornis* (33-45%) and two times lower than at station P2. However, *Pseudocalanus* sp., had the highest percentage contribution (ca. 53-62%), particularly in the spring (April).

The percentage contribution observed for this species in Gulf of Gdańsk (P1) was similar in comparison to that observed in Lithuanian Baltic Sea on the open sea stations (B5-B9): for *Acartia* spp. and *Temora longicornis* for the average values (in ( )), in turn for *Pseudocalanus* sp. for maximum value (in [ ]) (Table 2).

Conclusion

Taxonomic composition of the zooplankton in the Gulf of Gdańsk appears to be stable. An additional difficulty in comparing the data from different years results from different sampling methods, especially the mesh size. It appears that contrary to the Gulf of Bothnia, the Gulf of Finland and the Gulf of Riga, characterized by specific biocenoses (Ojaveer and Alken 1997), the Gulf of Gdańsk is not isolated from the open-sea impact, which is evidenced by the high similarity of zooplankton composition between the Gdańsk Deep and the coastal waters of the Gulf of Gdańsk, and consequently the gulf represents the unique coastal ecosystem of the Baltic Proper (Dzierzbicka-Głowacka at el., 2012).

Thorough knowledge of the species composition, the dominance of particular taxa, density and biomass in combination with abiotic makes it easier to assess changes taking place in an ecosystem. In combination with simulation models, such knowledge provides hypothetical forecasts for the future, leading to anticipating the positive or negative effects of environmental changes.

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Figure 1

Location of the sampling stations (P1 and P2) in the southern Baltic Sea in 2010-2011.

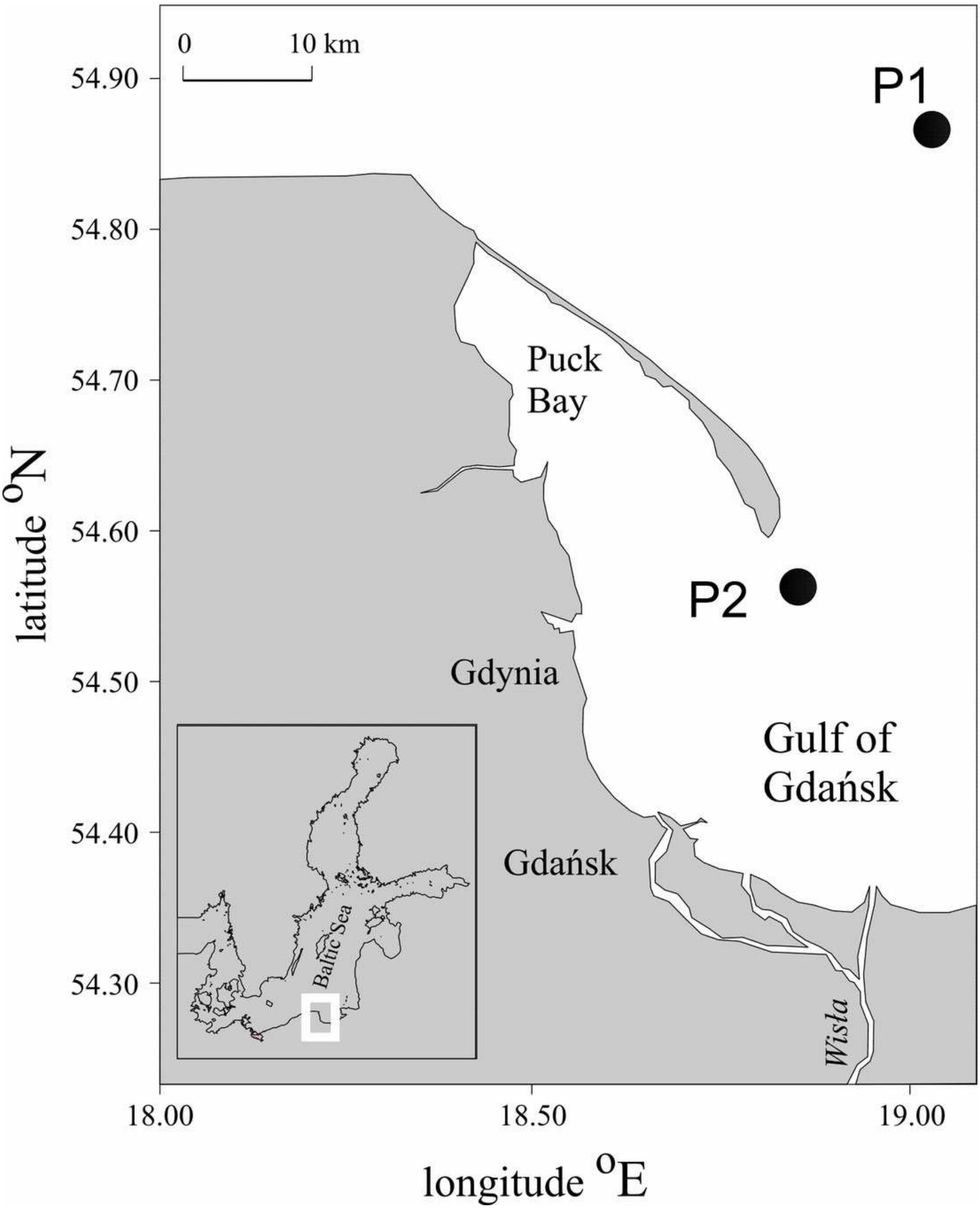
0
10 km
54.90
54.80
54.70
54.60
54.50
54.40
54.30
latitude oN
P1
P2
Puck
Bay
Gdynia
Gulf of
Gdańsk
Gdańsk
Baltic Sea
Wisła
18.00
18.50
19.00
longitude oE

Figure 2

Abundance of Copepoda at P1 station (the southern Baltic Sea – the Gdańsk Deep: 54ᵒ50'φN, 19ᵒ19'λE) in 2010-2011.

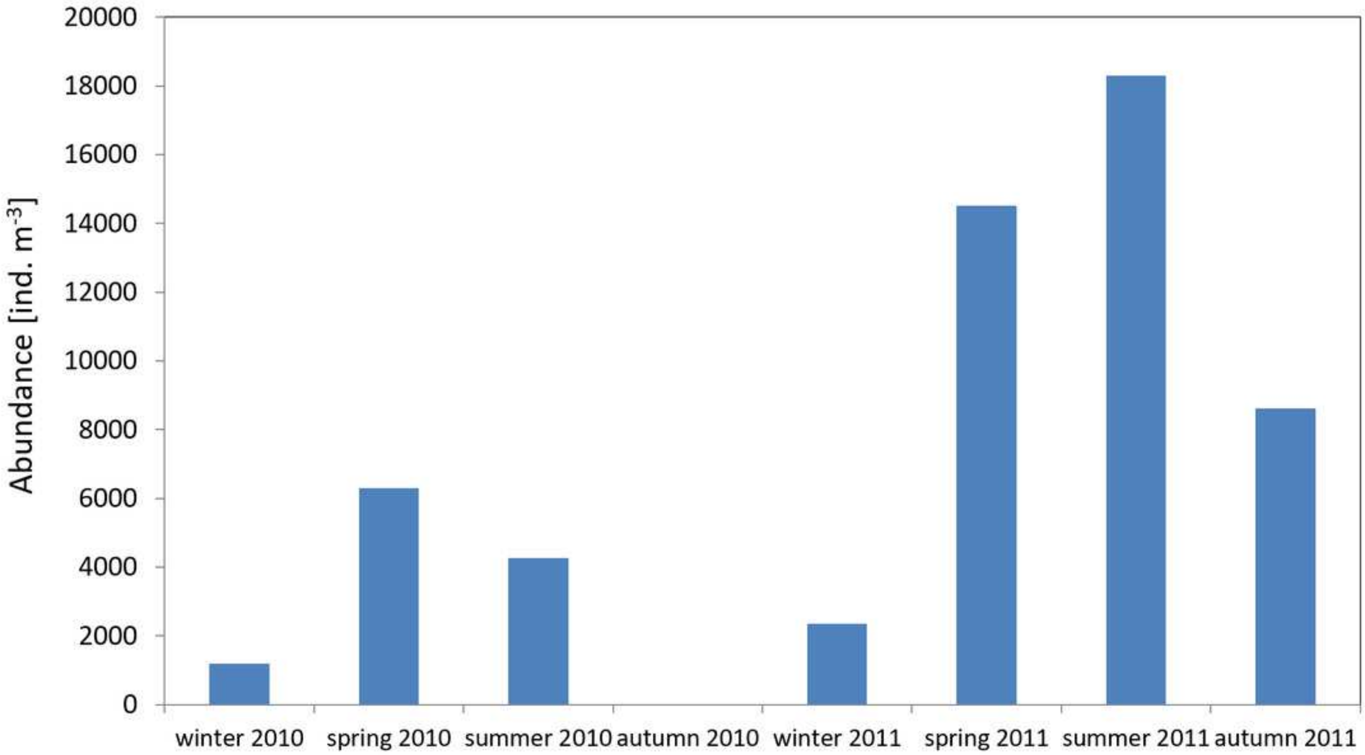

Figure 3

Taxonomic community structure of Copepod abundance at P1 station (the southern Baltic Sea – the Gdańsk Deep: 54°50’φN, 19°19’λE) in 2010-2011.

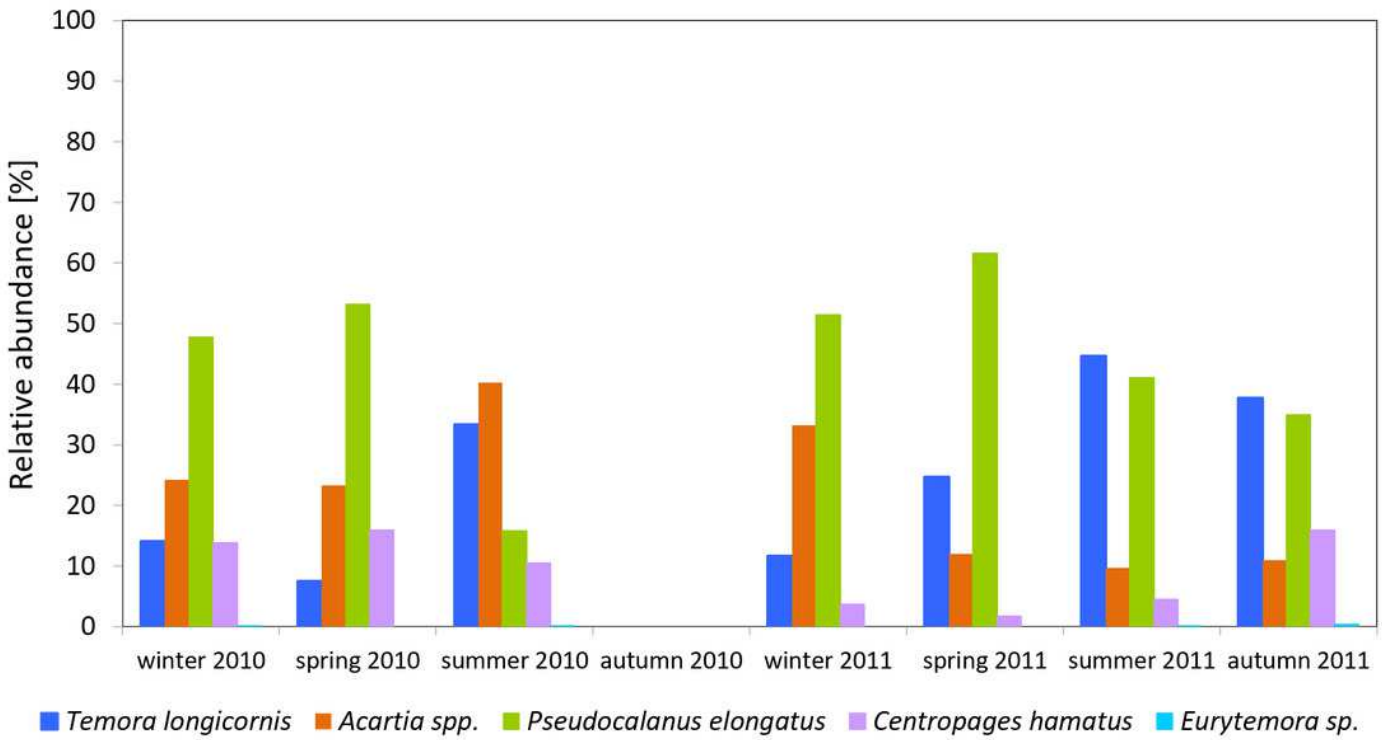

Figure 4

Abundance of Copepoda at P2 station (the southern Baltic Sea – the western, inner part of the Gulf of Gdańsk: 54°32' φN, 18°48.2 'λE) in 2010-2011.

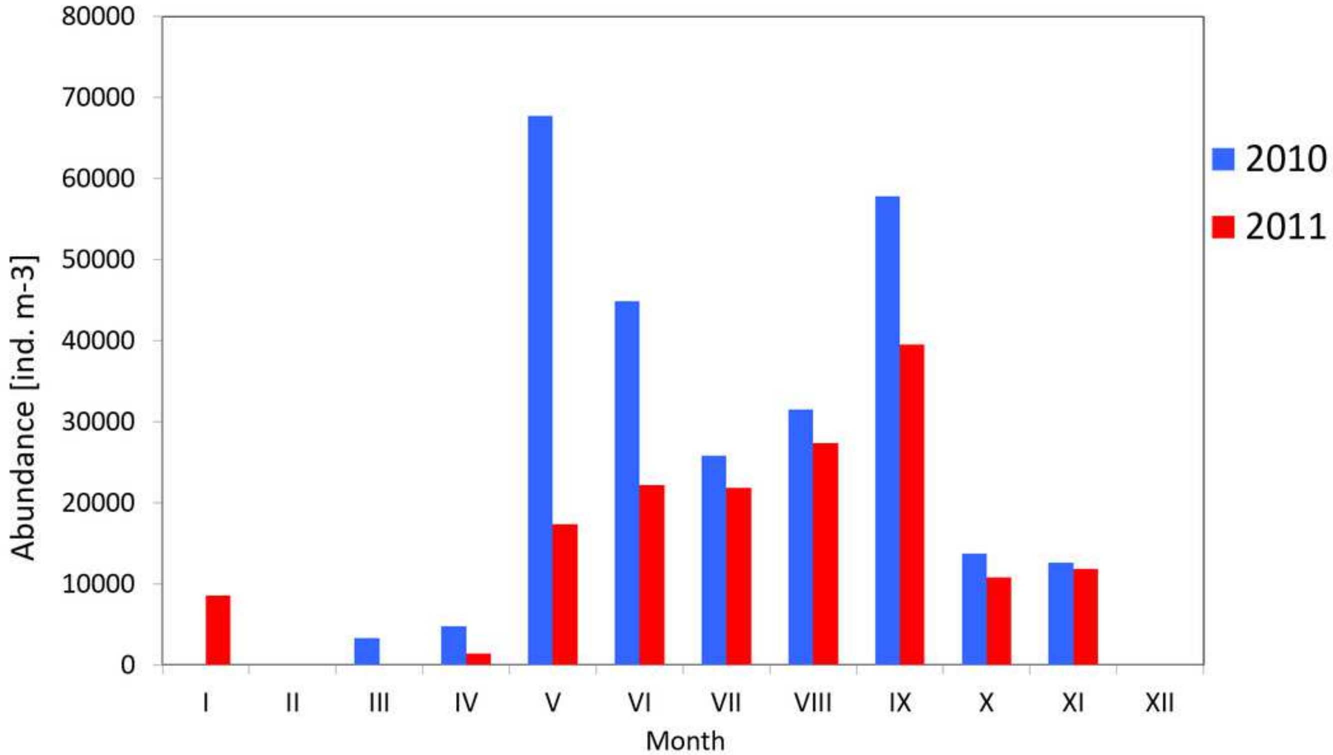

Figure 5

Taxonomic community structure of Copepod abundance at P2 station (the southern Baltic Sea – the western, inner part of the Gulf of Gdańsk: 54°32’ φN, 18°48.2 ’λE) in 2010.

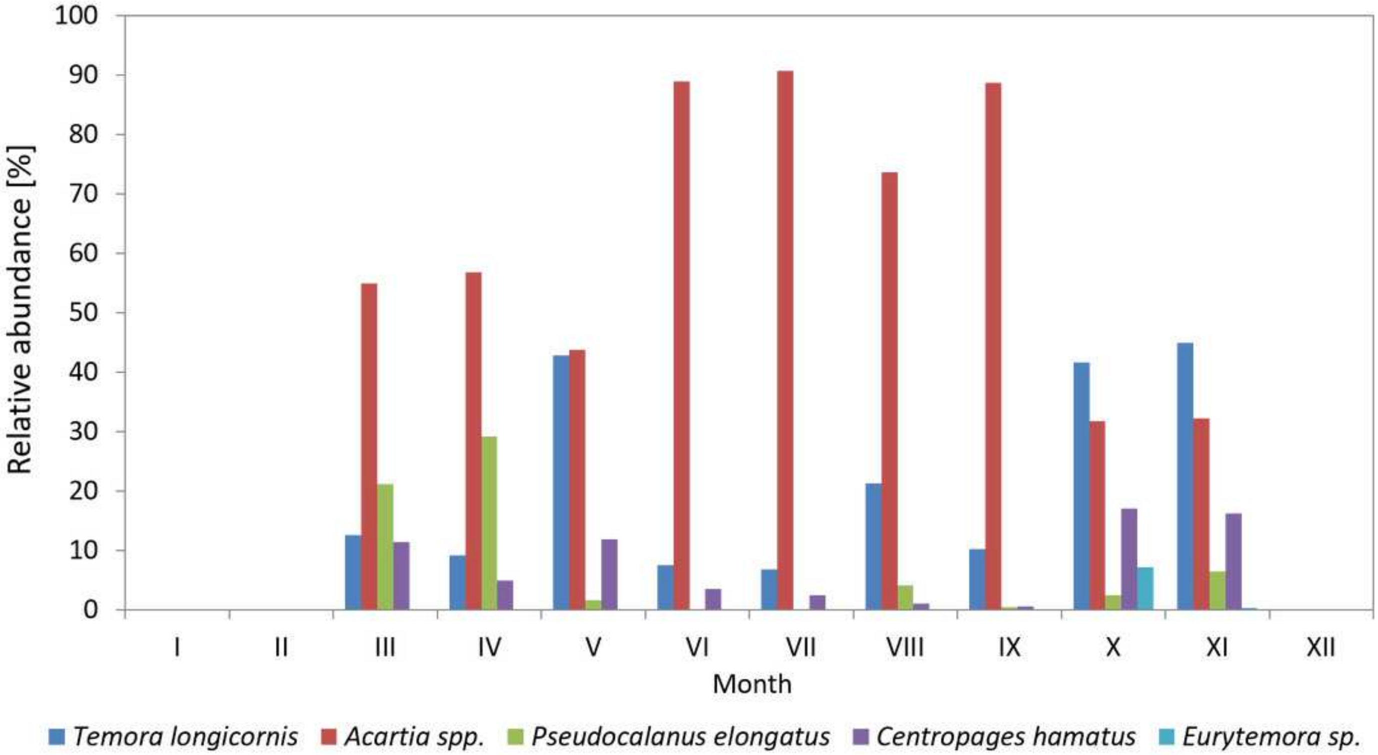

Figure 6

Taxonomic community structure of Copepod abundance at P2 station (the southern Baltic Sea – the western, inner part of the Gulf of Gdańsk: 54°32' φN, 18°48.2 'λE) in 2011.

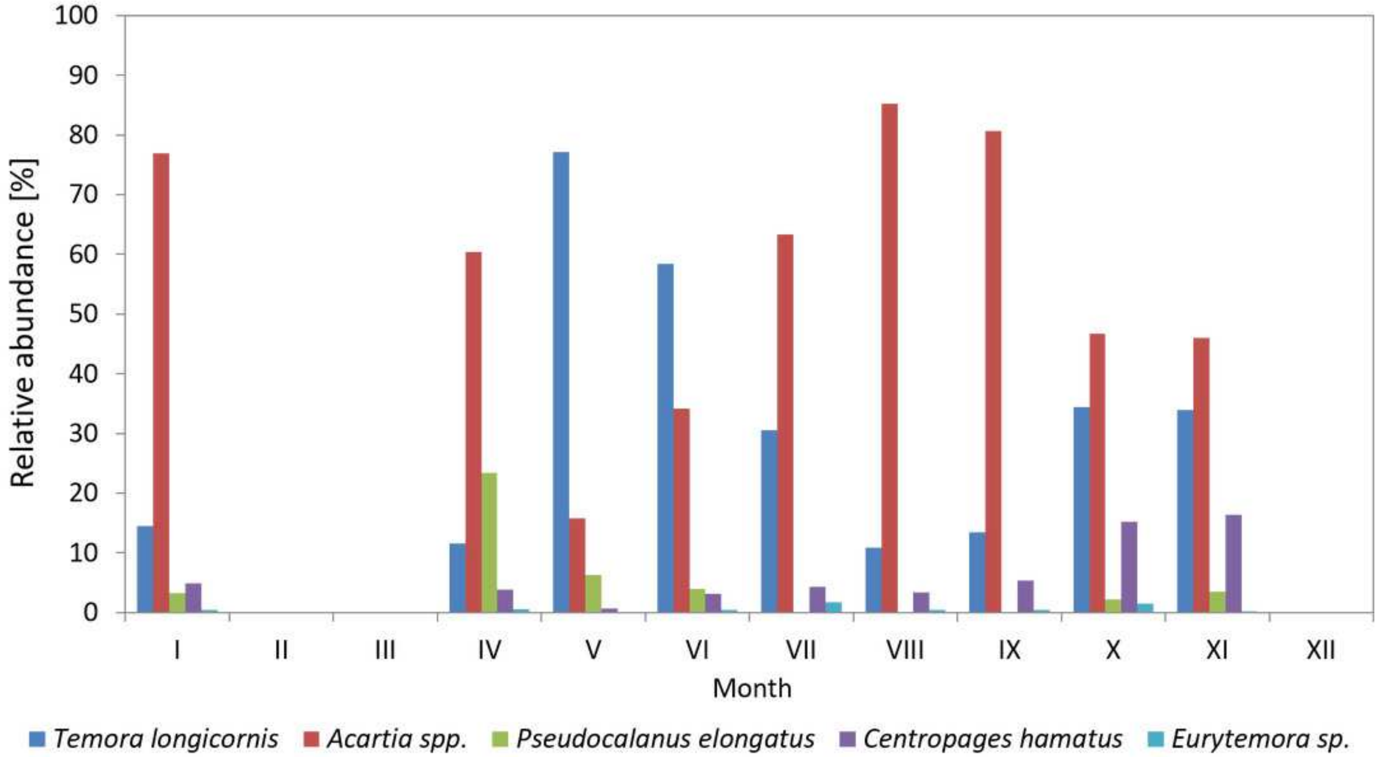

Figure 7

Biomass of Copepod at P1 station (the southern Baltic Sea – the Gdańsk Deep: 54°50'φN, 19°19'λE) in 2010-2011.

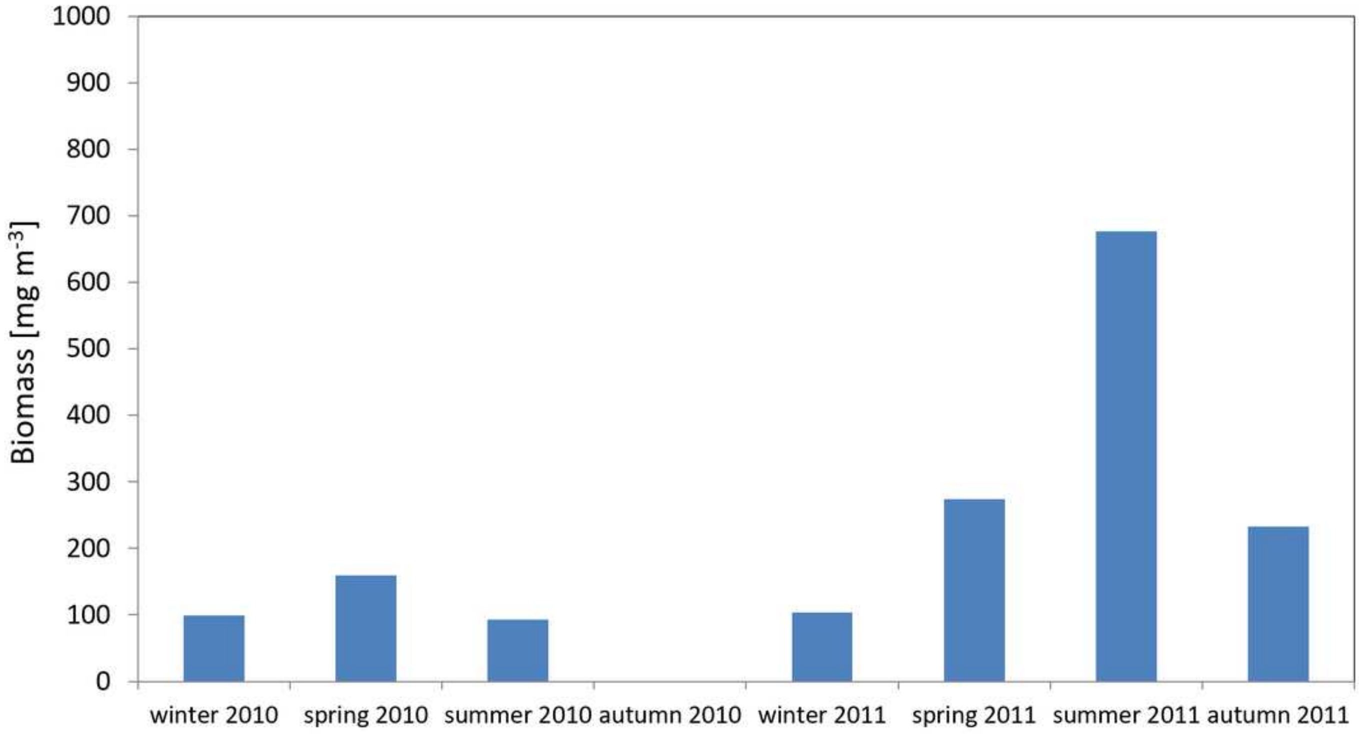

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Figure 8

Taxonomic community structure of Copepod biomass at P1 station (the southern Baltic Sea – the Gdańsk Deep: 54°50'φN, 19°19'λE) in 2010-2011.

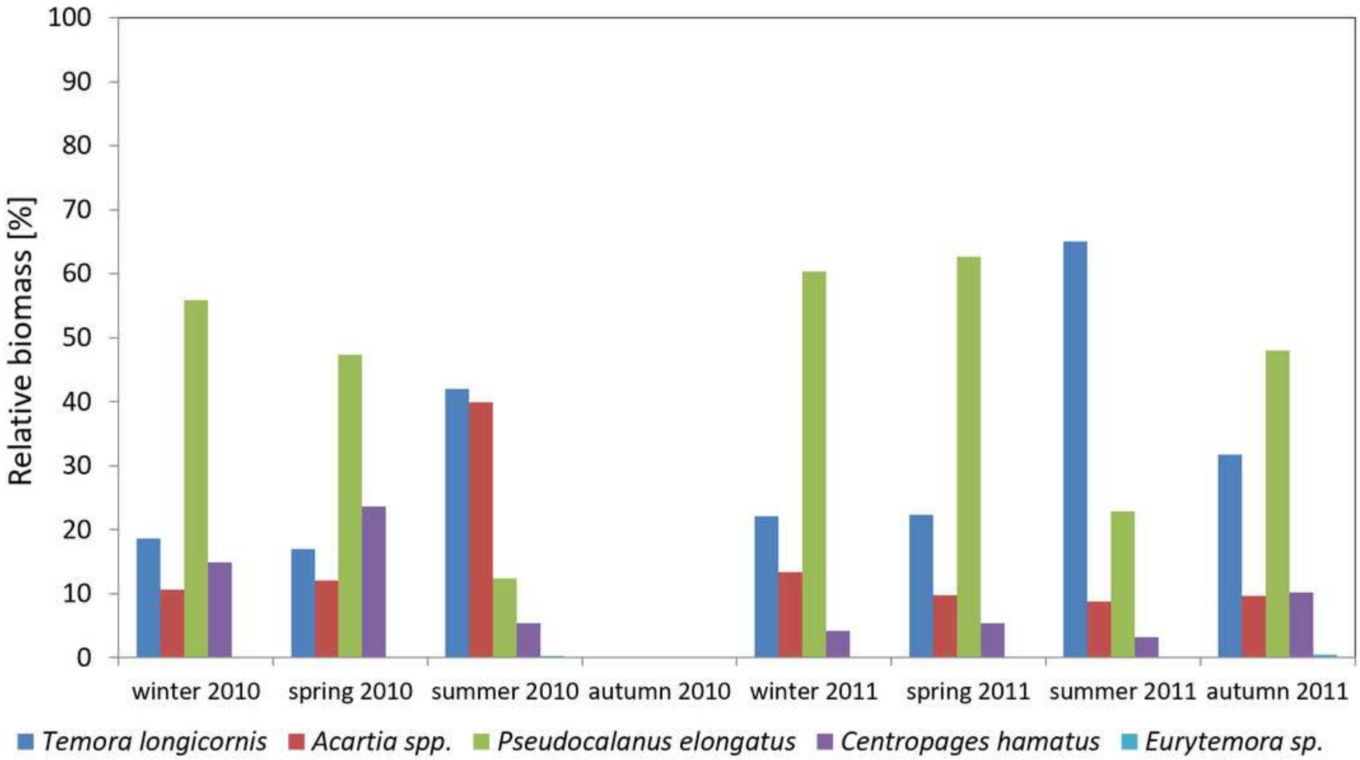

Figure 9

Biomass of Copepod at P2 station (the southern Baltic Sea – the western, inner part of the Gulf of Gdańsk: 54°32' φN, 18°48.2 'λE) in 2010-2011

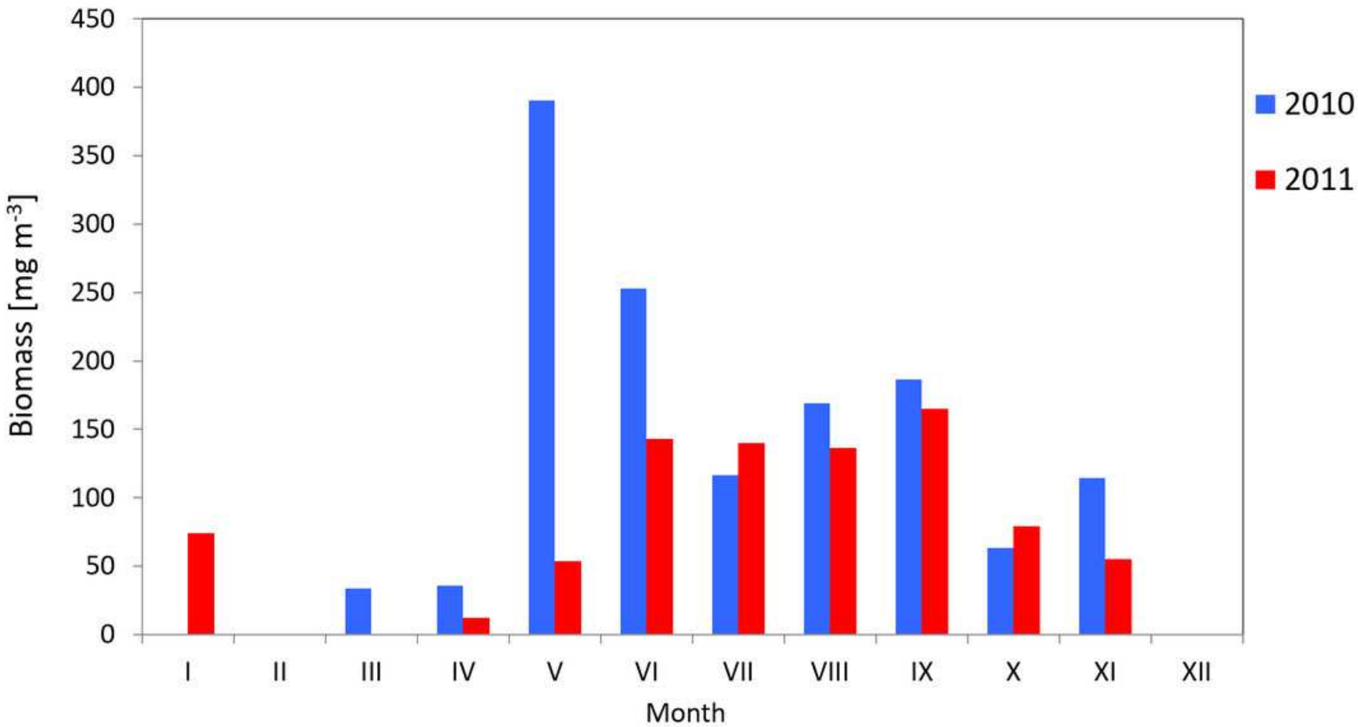

Figure 10

Taxonomic community structure of Copepod biomass at station P2 (the southern Baltic Sea – the western, inner part of the Gulf of Gdańsk: 54°32’ φN, 18°48.2 ’λE) in 2010.

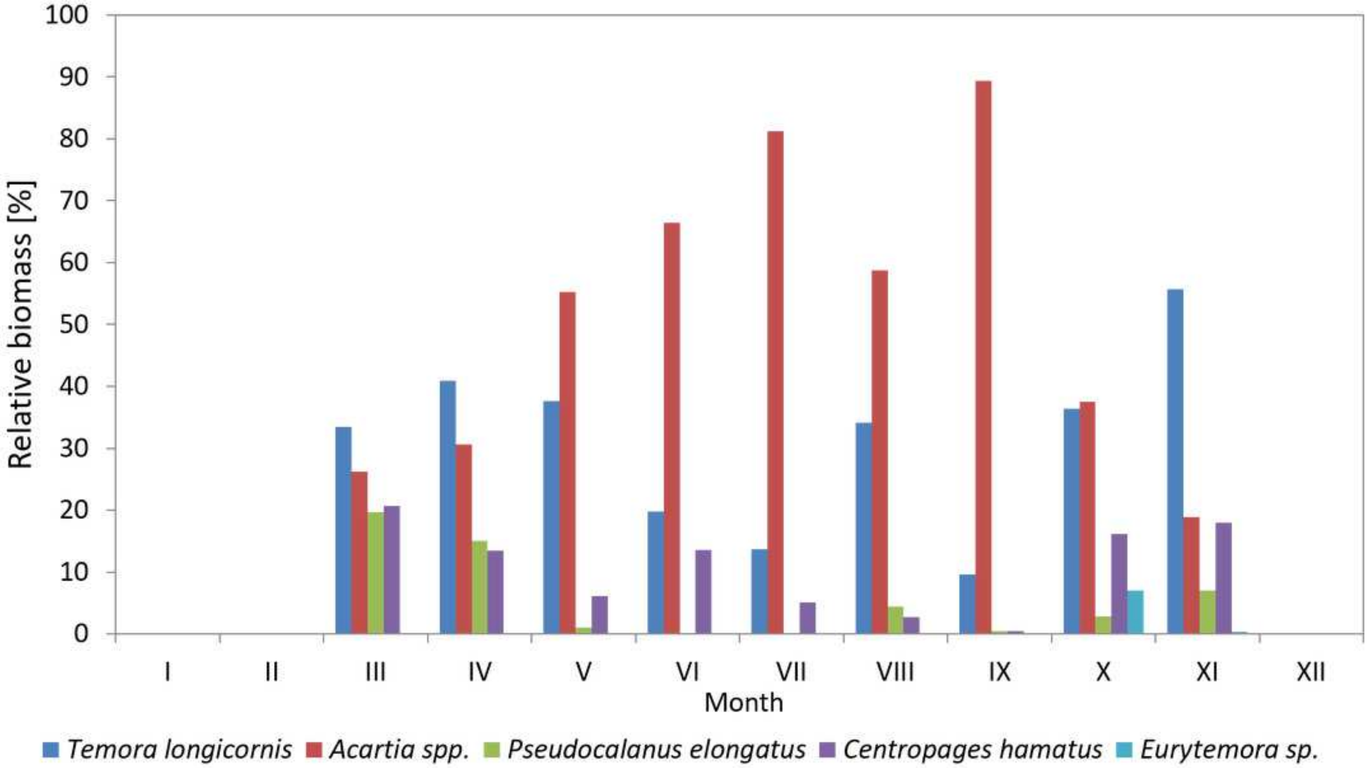

Figure 11

Taxonomic community structure of Copepod biomass at P2 station P2 (the southern Baltic Sea – the western, inner part of the Gulf of Gdańsk: 54°32’ φN, 18°48.2 ’λE) in 2011.

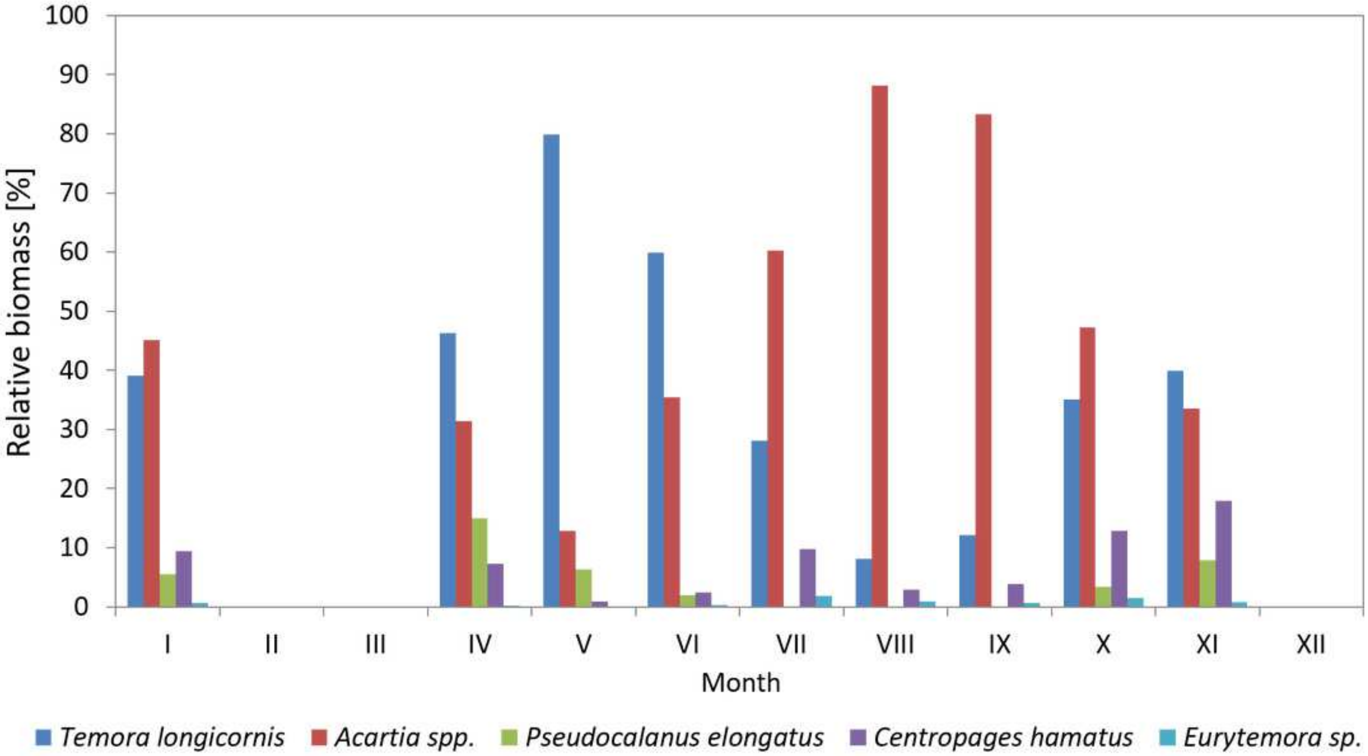

Figure 12

Zooplankton abundance at P1 station (the southern Baltic Sea – the western, inner part of the Gulf of Gdańsk: 54◦32’ φN, 18◦48.2 ’λE) in 2010-2011

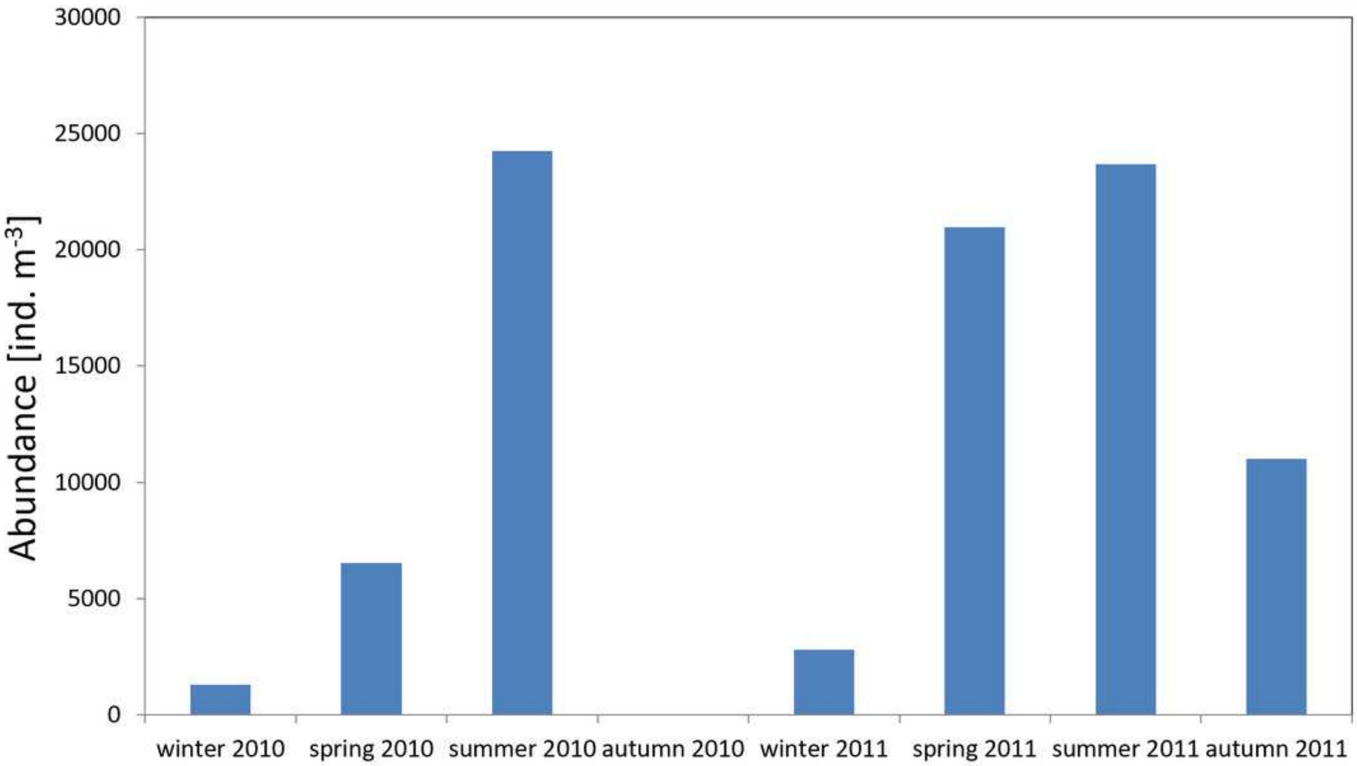

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Figure 13

Zooplankton abundance at P2 station (the southern Baltic Sea – the Gdańsk Deep: 54°50’φN, 19°19’λE) in 2010-2011

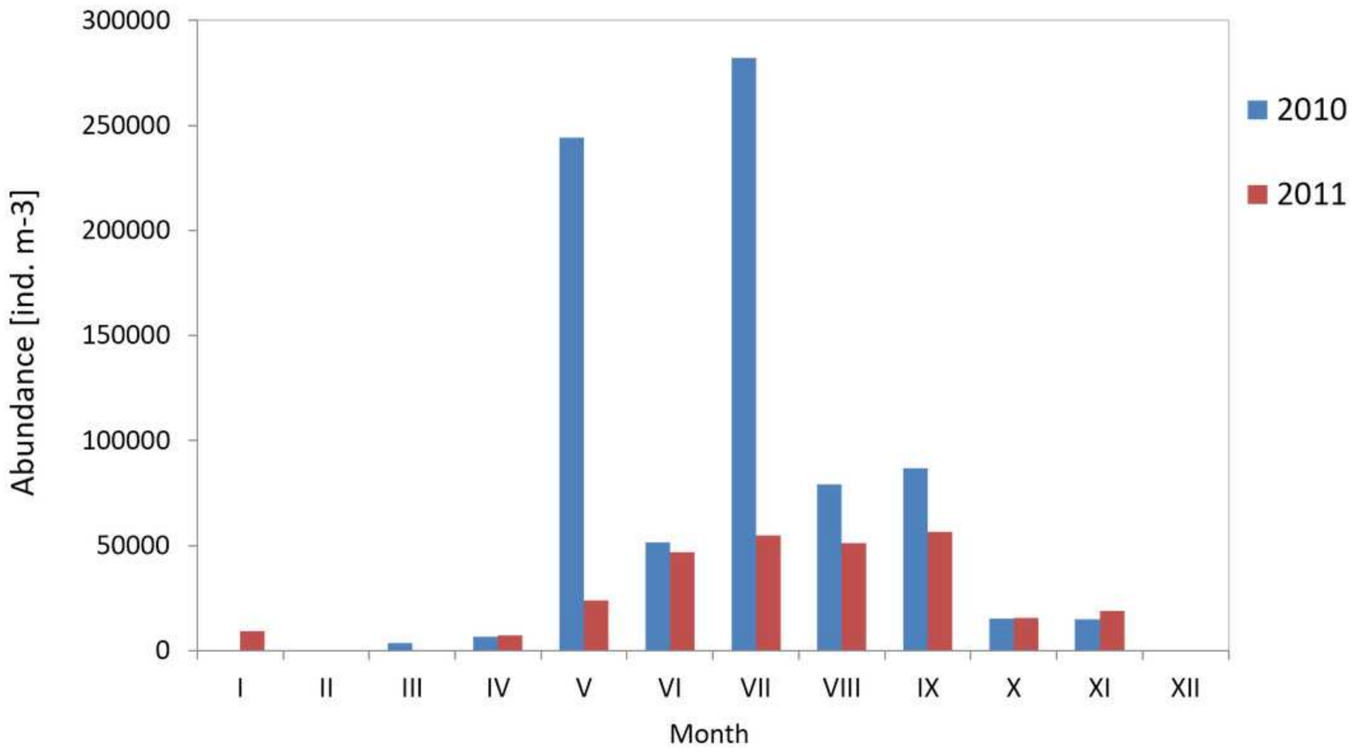

Table 1 (on next page)

Abundance (ind. m^{-3}) – max (left column) and mean (right column) of *Acartia* spp., *Temora longicornis, Pseudocalanus* sp. at station P2 in the Gulf of Gdańsk and at stations B1-B4 and B5-B9 in Lithuanian Baltic Sea.

Data from the Gulf of Gdańsk for 2006 and 2007 (Kalarus, 2010), 2010 and 2011 (Lemieszek, 2013) – unpublished data. Data from Lithuanian Baltic Sea coastal stations (B1-B4)* and open sea stations (B5-B9)** for 2014 – unpublished data.

year	max ind. m^{-3} (month and layer)	average ind. m^{-3} (month)
2006	57 500 (July in 40-30 m)	25 600 (June)
2007	127 000 (July in 20-10 m)	83 500 (July)
2010	161 150 (May in 10-0 m)	67 790 (May)
2011	70 300 (Sept. in 10-0 m)	39 560 (Sept.)
2014*	40 317 (July in 25-0 m)	36 320 (July)
2014**	43 912 (July in 25-0 m)	21 327 (July)

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Table 2 (on next page)

Maximum contribution (in %) of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. to the total abundance of Copepoda at stations P1 and P2 in the Gulf of Gdańsk and at stations B1-B4 and B5-B9 in Lithuanian Baltic Sea.

Data from the Gulf of Gdańsk for 2006 and 2007 (Kalarus, 2010), 2010 and 2011 (Lemieszek, 2013) – unpublished data. Data from Lithuanian Baltic Sea coastal stations (B1-B4)* and open sea stations (B5-B9)** for 2014 – unpublished data. [ ] - Max % in separate station from stations B1-B4 and B5-B9; ( ) - Averaged per stations B1-B4 and B5-B9.

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	Acartia spp.	*Temora longicornis*	*Pseudocalanus* sp.
2006 (P2)	86 (Sept.)	57 (Nov.)	25 (Feb.)
2007 (P2)	82 (Aug. and Sept.)	51 (June)	25 (March)
2010 (P2)	90 (June, July and Sept.)	45 (Nov.)	29 (April)
2011 (P2)	85 (Aug.)	77 (May)	23 (April)
2010 (P1)	40 (June)	33 (June)	53 (April)
2011 (P1)	33 (March)	45 (June)	62 (May)
2014*	[57](43) (July)	[66] (47) (July)	[39] (13) (April)
2014**	[59] (39) (April)	[71] (56) (July)	[69] (37) (April)

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