

Population dynamics of the main copepod species in the Gulf of Gdańsk (the southern Baltic Sea): abundance, biomass and production rates

by

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Abstract

The aim of this study was to describe the production biomass and abundance dynamics of the major Baltic calanoid copepods (*Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp.) in the Gulf of Gdańsk (the southern Baltic Sea) during a three-year period from March 2010 to December 2012. The data were collected at six stations located in the western part of the gulf. *Acartia* spp. was the most abundant taxon throughout the study period. The observed differences in the weighted mean depth for the investigated species were >2 m between nauplii and adults of *Acartia* spp., >5 m between nauplii and adults of *Temora longicornis* and 3 m between nauplii and younger copepodites of *Pseudocalanus* sp. The highest values of the secondary production rates were determined for *Acartia* spp. – almost 17.55 mg C m⁻² d⁻¹ (summer 2011), while *Temora longicornis* reached 3.80 mg C m⁻² d⁻¹ in spring 2010 and *Pseudocalanus* sp. had the highest secondary production values in summer 2011 – about 1.28 mg C m⁻² d⁻¹.

Key words: Copepoda, biomass, abundance, production rates, population dynamics, Gulf of Gdańsk

Introduction

Being exposed to a variety of environmental conditions, zooplankton is subject to considerable seasonal changes, both in terms of taxonomic structure and the dominance of individual species (Hernroth, Ackefors 1979; Wiktor 1990; Schulz et. al. 2012). Due to the considerable spatial and seasonal variability in salinity and temperature, the Baltic zooplankton typically consisted of euryhaline and eurythermic taxa (Wiktor 1990) such as copepods: *Temora longicornis*, *Centropages hamatus*, *Acartia* spp., cladocerans: *Bosmina coregoni maritima*, *Evadne nordmanni* and *Pleosis polyphaemoides*, as well as representatives of the *Podon* genera. Species that prefer lower temperatures, e.g. *Acartia longiremis*, *Pseudocalanus* sp. and *Fritillaria borealis*, are usually most abundant during the cooler seasons and in colder, deeper waters.

Recent studies indicate that a *Pseudocalanus* species from the central Baltic, hitherto named *P. elongatus*, is actually *P. acuspes* (Bucklin et al. 2003; Holmborn 2011). However, since *P. elongatus* may also be present in the southern Baltic, we decided that the designation of *Pseudocalanus* sp. (Möllmann 2005) seems to be more appropriate for the present work.

The main objective of the study is to describe the seasonal and spatial distribution, as well as biomass and production rates of the major calanoid copepod species (*Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp.) in the southern Baltic Sea.

Estimates of zooplankton production and mortality rates are very useful for the determination of marine productivity and the quantification of transfers between food web components.

Materials and methods

Sampling

Samples used in this study were collected monthly during a three-year period between March 2010 and December 2012, at six stations located in the western part of the Gulf of Gdańsk (the southern Baltic Sea) (Fig. 1). Five of the sampling stations (S1, S2, S3, S4, J23) were located on a depth gradient transect (depth from 5 to 40 m) and one station (M2 - 10 m deep). Station M2 is located in the western part of the Gulf of Gdańsk. It is a semi-enclosed area, isolated from the rest of the

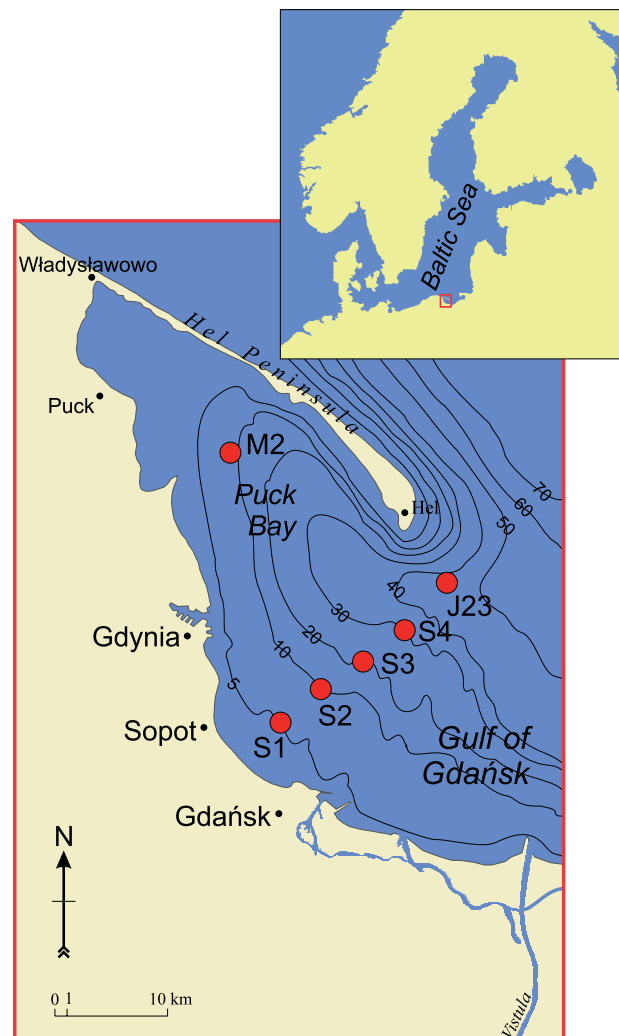


Figure 1

Location of the sampling stations in the Gulf of Gdańsk

Gulf of Gdańsk by the presence of a shoal. Due to the hydrological dissimilarity of the region from the rest of the bay, we found it advisable to include this station in our study area. The Sopot profile and the M2 station are part of the monitoring stations' network, which are used for zooplankton monitoring since the 1970s. This provides a complete picture of this part of the bay. The zooplankton material was collected with a WP2 zooplankton sampling net (100 µm mesh size). Sampling at specific stations was performed in 10 layers. All samples were collected during daytime (mainly between 10 am and 2 pm) so the diurnal vertical migrations were not taken into account. Qualitative and quantitative laboratory analyses were performed in accordance with the Manual for Marine Monitoring in the COMBINE Programme of Helcom (Annex C-7).

Weighted mean depth WMD

The vertical distribution of copepod development stages was determined by computing weighted mean depths (WMD) (Bollens, Frost 1989, Renz, Hirche 2004) for the three studied species:

$$WMD = \frac{\sum n_i d_i}{n_i} \quad (1)$$

where n_i is the abundance (individuals m^{-3}) at each depth layer with the midpoint d_i . The calculations were made for four stages: nauplii (N), copepodites CI-CIII, copepodites CIV-CV and adults.

Copepod secondary production

Biomass was calculated from the abundance using weight standards after Hernroth (1985), and the obtained values were integrated for the whole water column. Finally, seasonal biomass values were derived by averaging the corresponding months. Carbon was calculated as 5% of the wet weight according to Mullin (1969). This conversion rate is usually used for the Baltic copepods, although as illustrated by Tanskanen (1994), it may lead to the underestimation of the zooplankton biomass.

Production of the copepodite stages of the studied species was calculated using Edmondson and Winberg' equation (Edmondson, Winberg 1971) with the assumption that there were non-limiting food conditions:

$$PC_i = \frac{N_i \times \Delta W_i}{D_i} \quad (2)$$

where PC_i represents daily potential production of stage i (g wet weight); N_i is the abundance of the corresponding development stage i ; D_i is the development time of stage i (day^{-1}), and ΔW_i is the difference in wet weight of stage i . D_i of the developmental stages were calculated using Belehrádek's function (Belehrádek 1957):

$$D_i = a(T - \alpha)^{-b} \quad (3)$$

where a and α for copepodite stages are 1 288 and -10.5 for *Acartia* spp., 1 466 and -10.4 for *T. longicornis*, 3044 and -13.9 for *Pseudocalanus* sp., respectively, and b is 2.05 for all taxa according to McLaren (1978, 1989). T was the ambient temperature ($^{\circ}C$) and was determined for each stage on the basis of its WMD.

Results and discussion

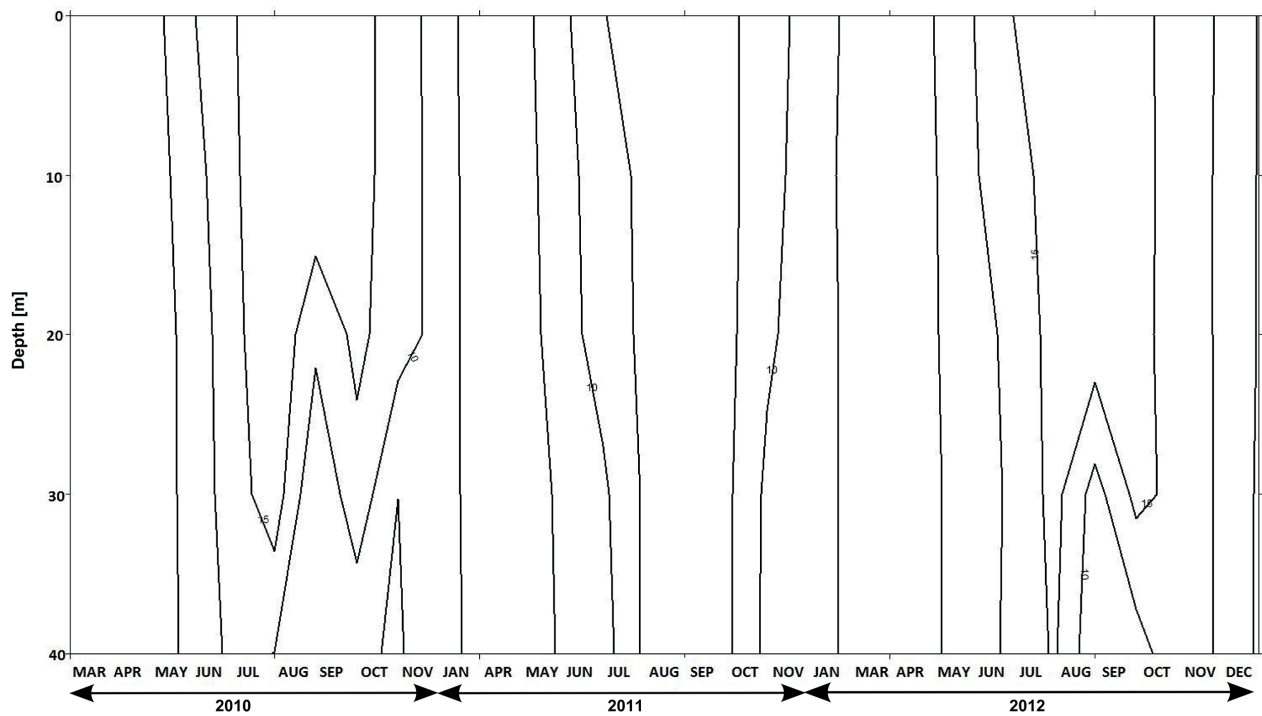
Hydrology

The temperature fluctuated throughout the study period between 15 to 20 $^{\circ}C$ in June – September (Fig. 2). For the other months, the temperature was about 10 $^{\circ}C$ and below. The thermocline was observed in 2010 from July to October, and in 2012 between August and October. Salinity oscillated throughout the study period around 7, which is typical of the Gulf of Gdańsk (Fig. 3). The lowest value of salinity (6.6) for the study period was recorded in the surface water layer at the turn of July and August 2010.

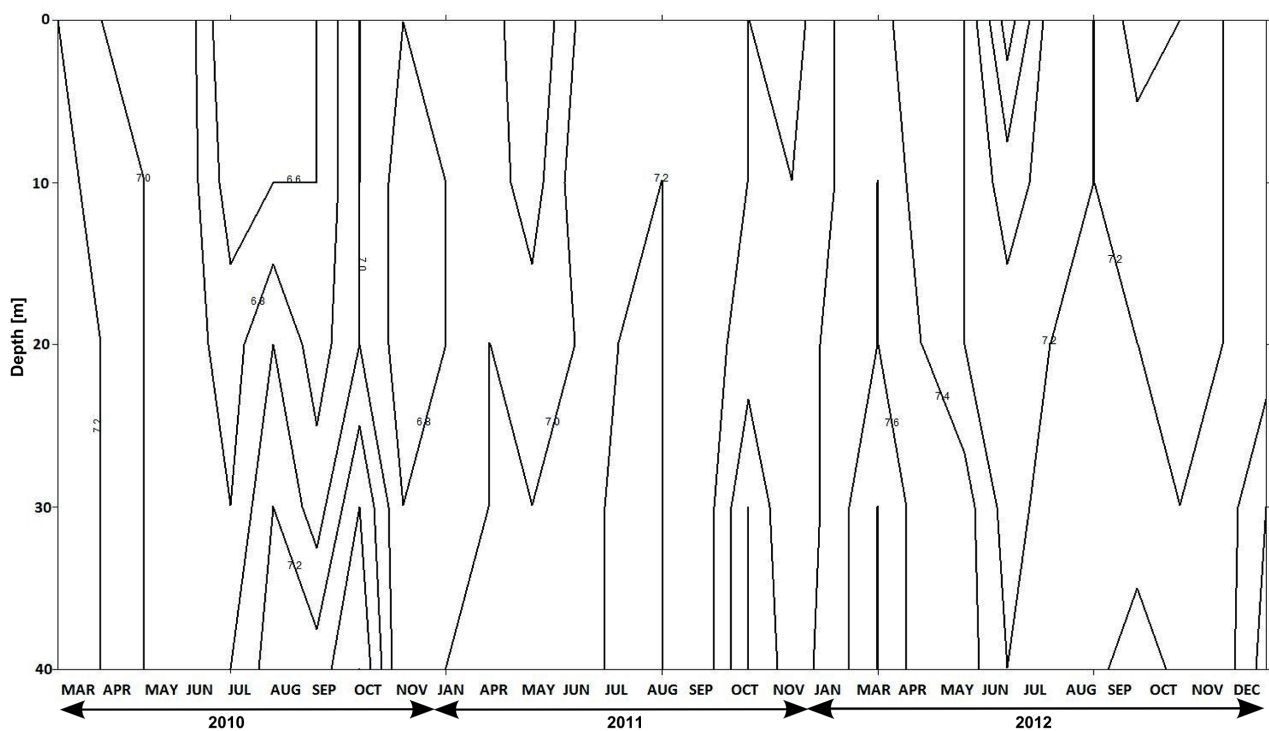
Abundance and biomass

During the three-year study period, the average copepod abundance reached the highest value between July and August. In 2010, the maximum abundance was observed in July (25 101 ind. m^{-3}) (Fig. 4), while in August the value was slightly lower and reached 24 570 ind. m^{-3} . The highest three-year value of copepod abundance was recorded in August 2011, i.e. 26 448 ind. m^{-3} . A significant decline in copepod abundance in 2010-2012 was observed from September to December. In September, the values ranged from 17778 ind. m^{-3} (2011) to 16323 ind. m^{-3} (2012). The years 2011-2012 were characterized by a similar distribution of abundance from January to June. From January to April, the average abundance of copepods in the Gulf of Gdańsk gradually decreased below 736 ind. m^{-3} . In May, the concentration of copepods increased rapidly and was similar in both years (~7000 ind. m^{-3}) (Fig. 4).

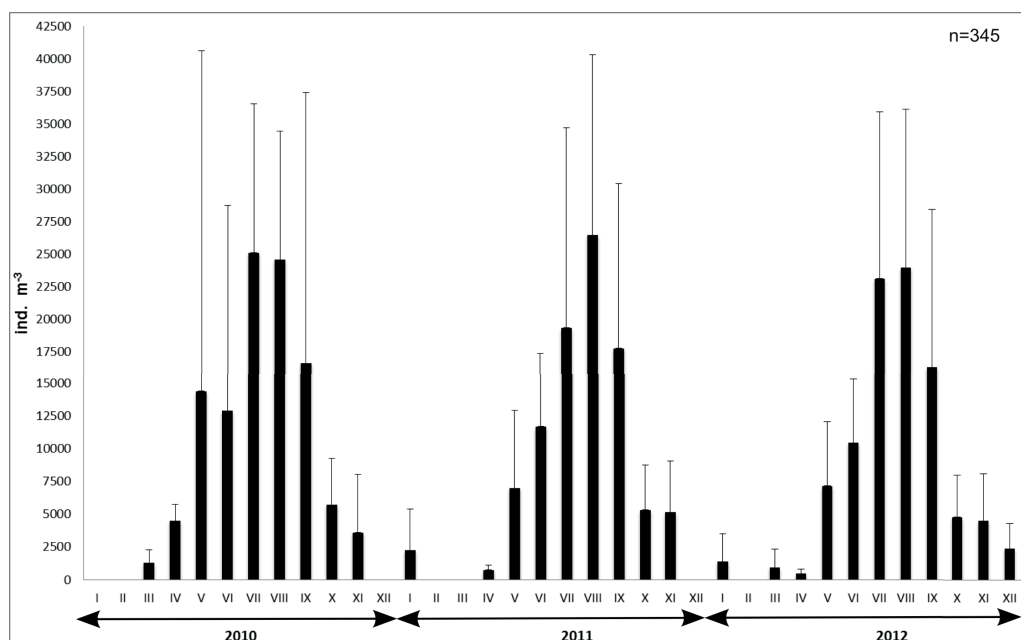
The distribution of biomass throughout the years 2010-2012 showed a similar trend as the abundance. The lowest values in both 2011 and 2012 were observed in April (6.64 mg C m^{-3} - 2011, 4.47 mg C m^{-3} - 2012). The biomass of these crustaceans increased steadily in late summer and spring reaching the maximum values in August

**Figure 2**

Water temperature at station J23 in 2010-2012

**Figure 3**

Water salinity at station J23 in 2010-2012

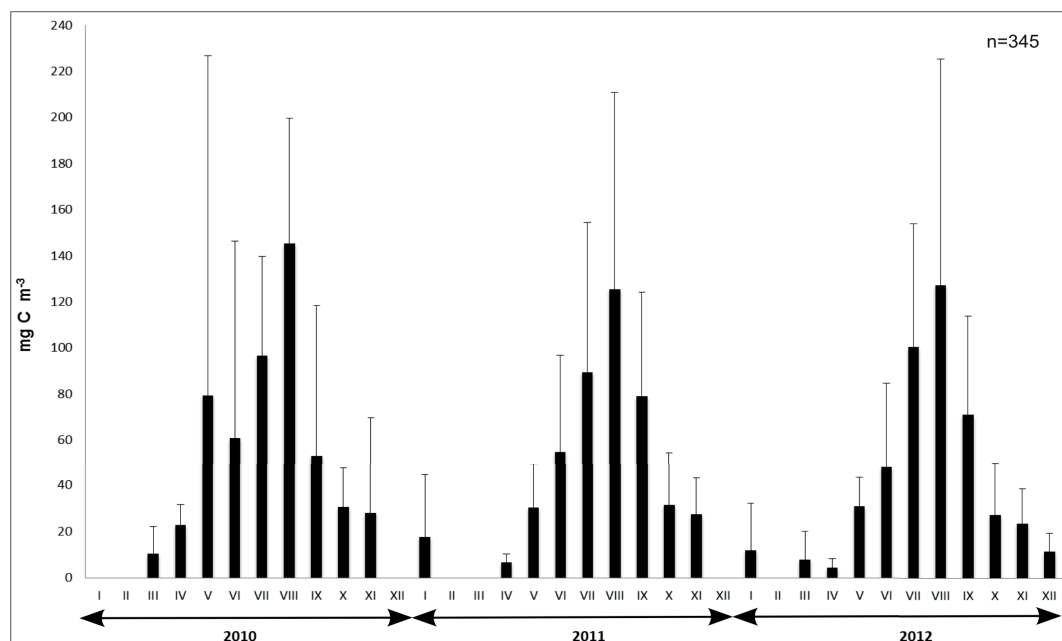
**Figure 4**

Abundance variability with SD for Copepoda in 2010-2012

2010 ($145.30 \text{ mg C m}^{-3}$), 2011 ($125.46 \text{ mg C m}^{-3}$) and 2012 ($127.07 \text{ mg C m}^{-3}$). Through the rest of the year, the biomass values dropped to less than 80 mg C m^{-3} in September and less than 30 mg C m^{-3} in October and November (Fig. 5).

The biomass concentration of *Acartia* spp. was the highest among the studied taxa. The

distribution of biomass values of *Acartia* spp. in 2011 and 2012 had a similar trend, with an increase between June and July and the maximum in September – $70.60 \text{ mg C m}^{-3}$ in 2011 and $63.57 \text{ mg C m}^{-3}$ in 2012 (Fig. 6). In 2010, the rapid growth observed between April and May was followed by a slight decrease in June. The maximum biomass

**Figure 5**

Biomass variability with SD for Copepoda in 2010-2012

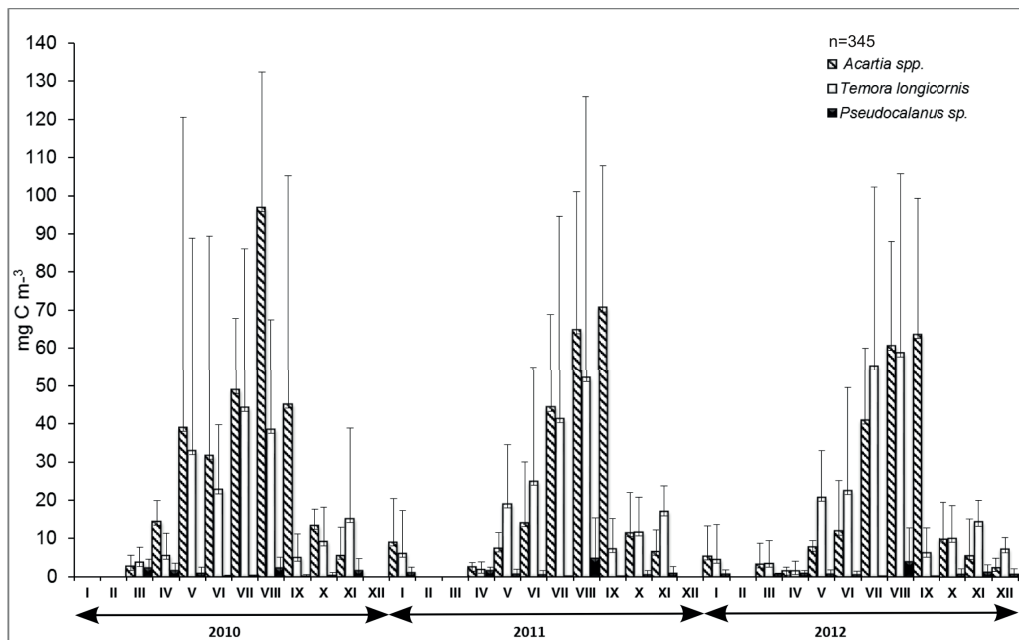


Figure 6

Biomass variability with SD for *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. in 2010-2012

in 2010 was noticed in August ($96.85 \text{ mg C m}^{-3}$). During the cold months, the value of *Acartia* spp. biomass did not exceed 15 mg C m^{-3} (Fig. 6).

The abundant occurrence of species from the genus *Acartia* during summer is typical of the Gulf of Gdańsk (Dzierzbicka-Głowacka et al. 2012) and the Baltic Proper (Holste 2010). According to Mudrak (2004), maximum abundance values of this copepod occur also in mid-summer. Abundance of this taxa was clearly correlated with water temperature (Table 1). Similar to the results obtained by Möllmann et al. (2000), who described the long-term trends in the biomass of the main mesozooplankton taxa in the central Baltic Sea, the fluctuations in the biomass of *Acartia* spp. and *T. longicornis* observed during our study were positively correlated with temperature. Due to its thermophilic nature, *Acartia* spp. tends to concentrate in the upper water layers since mid-spring was observed (Fig. 7). The optimum

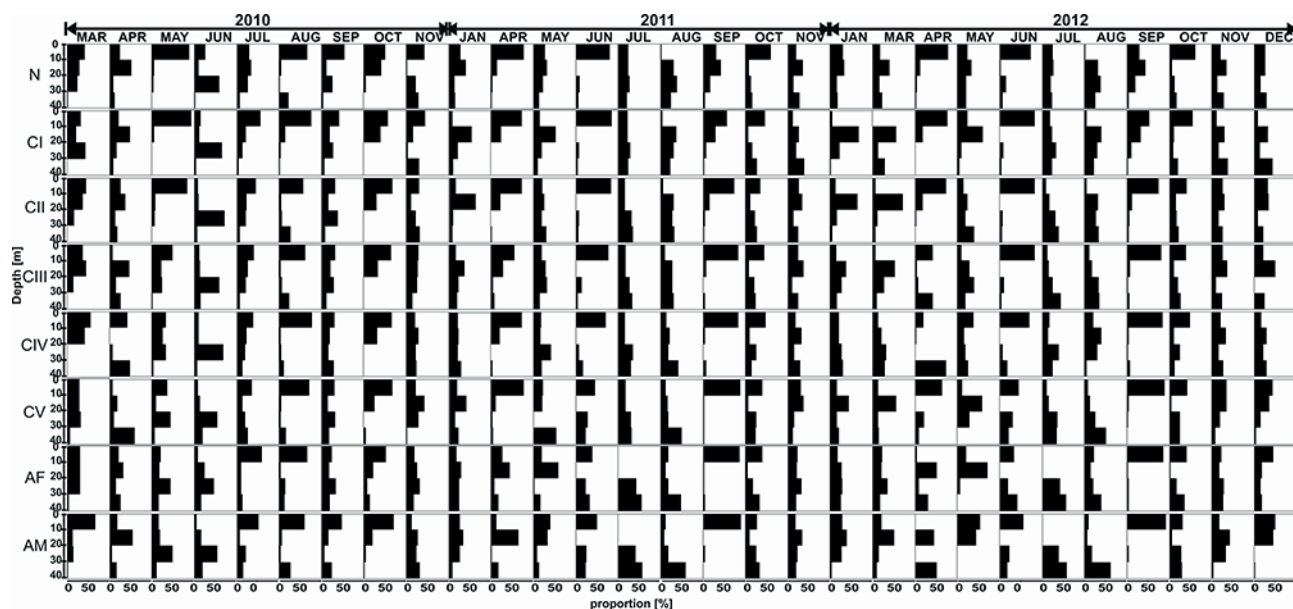
temperature for *Acartia* spp. ranges from 3 to 16°C , with the preferred temperatures above 10°C (Mudrak 2004). The lack of these copepods in the surface waters during summer might be caused by too high light intensity (Speckmann et al. 2000). Through the rest of the year, the population of *Acartia* spp. was dispersed in the whole water column.

The biomass of *T. longicornis* showed a similar distribution in particular months. In cold months of 2010-2012, the biomass values did not exceed 10 mg C m^{-3} (Fig. 6). A significant growth of biomass was observed only in May (about 20 mg C m^{-3}). The upward trend continued until August where it reached its maximum. In 2010, the rapid growth of biomass began in May, like in the case of *Acartia* spp. June 2010 was the month when biomass reached minimum values (about 10 mg C m^{-3}), and this year's maximum was recorded in July. *T. longicornis* had the second, smaller peak of biomass

Table 1

Values of the Pearson correlation coefficient for the temperature and abundance of the development stages of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. (***bold** – $p < 0.05$)

	N	CI	CII	CIII	CIV	CV	Female	Male
<i>Acartia</i> spp.	0.38*	0.36*	0.23*	0.18*	0.16*	0.14	0.25*	0.23*
<i>Temora longicornis</i>	0.20*	0.05	-0.02	-0.03	-0.02	0.10	0.13	0.18*
<i>Pseudocalanus</i> sp.	-0.35	-0.30	-0.45*	-0.52*	-0.48*	-0.37	-0.35	-0.46*

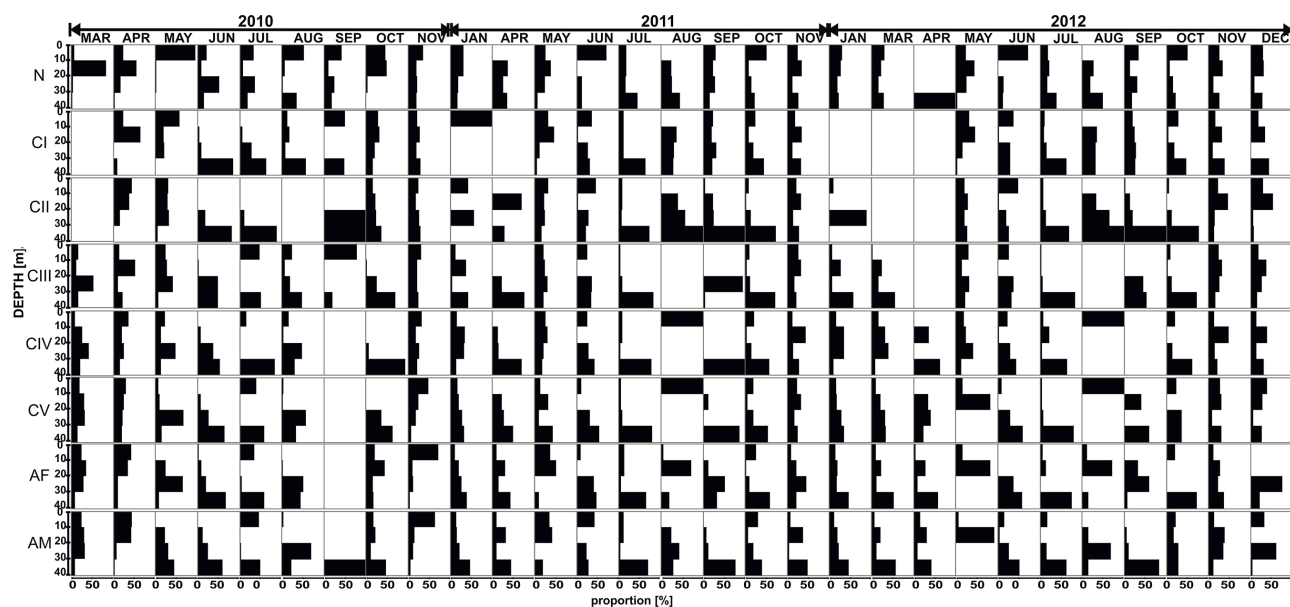
**Figure 7**

Proportion of respective developmental stages of *Acartia* spp. at station J23 in 2010-2012

in autumn with the maximum in November. During this period, mean biomass values ranged from $14.36 \text{ mg C m}^{-3}$ in 2012 to $16.98 \text{ mg C m}^{-3}$ in 2011. This species had its highest concentrations in the summer when water temperature ranged from 15 mg C m^{-3} to 18 mg C m^{-3} (Fig. 6). Mudrak (2004) showed that *T. longicornis* occurs in the Gulf of Gdańsk throughout the year, with the largest concentration in the summer months and autumn. The previous studies (Witek 1995) showed that June

was the month with the maximum abundance, and July – the maximum biomass.

Between January and April, *T. longicornis* was present in the entire water column (Fig. 8). In May, the population moved to the upper water layers. In June, nauplii and stages CI and CII concentrated in the upper water masses, and stages CIII and CIV were found in the lower layers. Through the rest of the summer, this copepod preferred the lower water masses.

**Figure 8**

Proportion of respective developmental stages of *Temora longicornis* at station J23 in 2010-2012

Pseudocalanus sp. had the lowest contribution to the copepod biomass in the Gulf of Gdańsk during the study period. There was no clear pattern in the biomass of this species, as the highest values were recorded in different months. In August 2012, *Pseudocalanus* sp. biomass had the maximum value (4.60 mg C m^{-3}) (Fig. 6). In the remaining months of this year, the biomass did not exceed 1.5 mg C m^{-3} . In 2010, *Pseudocalanus* sp. had the lowest contribution to the biomass of Copepoda, as compared to the rest of the three-year period. The maximum of this year was recorded in March – only 2.24 mg C m^{-3} and August – 2.21 mg C m^{-3} (Fig. 6).

The abundance of *Pseudocalanus* sp. is mostly dependent on salinity (Carter 1965), however, our research was conducted in a relatively shallow area with no clear halocline, which may be a reason for so low and chaotic distribution of this species. Unfortunately, due to the relatively low abundance there was no clear correlation between abundance and temperature (Table 1). From June, the highest abundance of *Pseudocalanus* sp. was observed in the bottom water layers (Fig. 9) due to the preference for colder water for the growth and development (Dzierzbicka-Głowacka 2004). Through the rest of the year, *Pseudocalanus* sp. was dispersed in the whole water column due to relatively low water temperature, not exceeding 10°C .

WMD

Figure 10 presents the weighted mean depths (WMD) of four established ranges of developmental stages (nauplii N, copepodites CI–CIII, copepodites CIV–CV and adults) of *Acartia* spp., *T. longicornis* and *Pseudocalanus* sp. at the deepest sampling station J23.

There are no clear patterns in the distribution of stages. The observed differences in the three-year mean WMD were $>2 \text{ m}$ between nauplii and adults of *Acartia* spp., $>5 \text{ m}$ between nauplii and adults of *T. longicornis* and 3 m between nauplii and copepodites CI–CIII of *Pseudocalanus* sp.

The differences in the mean annual WMD were: $>3 \text{ m}$ in 2010 and 2011 and $>2 \text{ m}$ in 2012 between nauplii and *Acartia* spp. adults; $>6 \text{ m}$ in 2010 and $>4 \text{ m}$ in 2011 and 2012 between nauplii and *T. longicornis* adults; $>10 \text{ m}$ in 2010 between copepodites CI–CIII and adults of *Pseudocalanus* sp.; $>4 \text{ m}$ in 2011 between copepodites CIV–CV and adults, and $>8 \text{ m}$ in 2012 between nauplii and copepodites CI–CIII of *Pseudocalanus* sp.

Acartia spp. individuals were primarily concentrated within the upper 17 m of the water column. After 3 years of the studies, it could be noticed that WMD of different developmental stages of *Acartia* spp. in the successive seasons did not change significantly, in contrast to *T. longicornis*. The maximum values of WMD for *T. longicornis* were observed in late summer. In September 2010 and 2011, WMD for adults of *T. longicornis* were 35 m and 28.5 m, respectively,

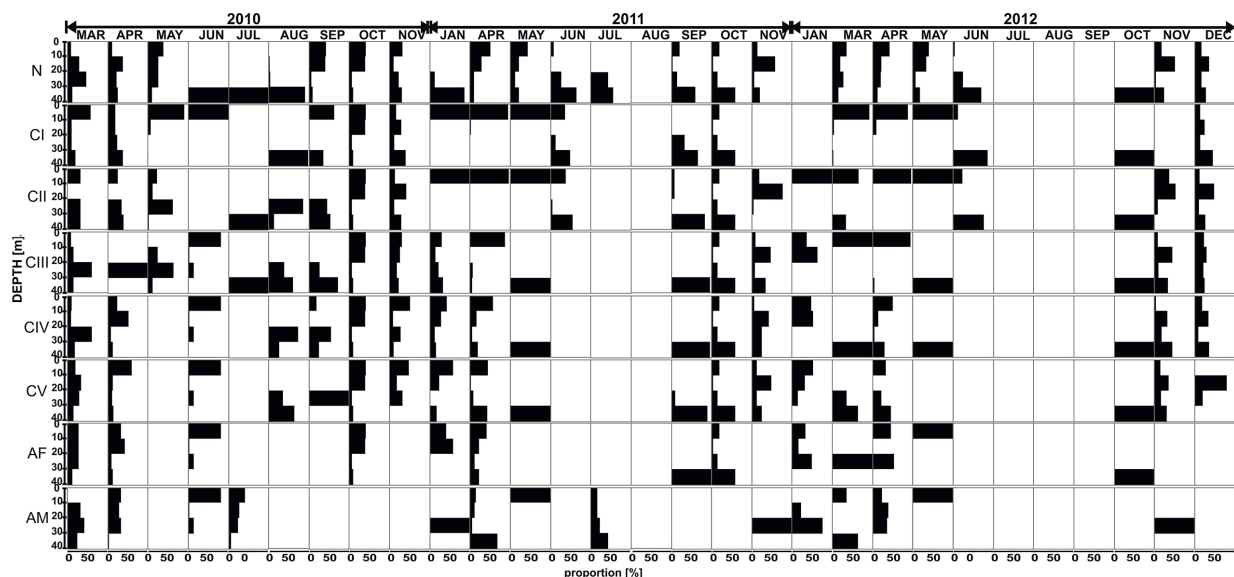
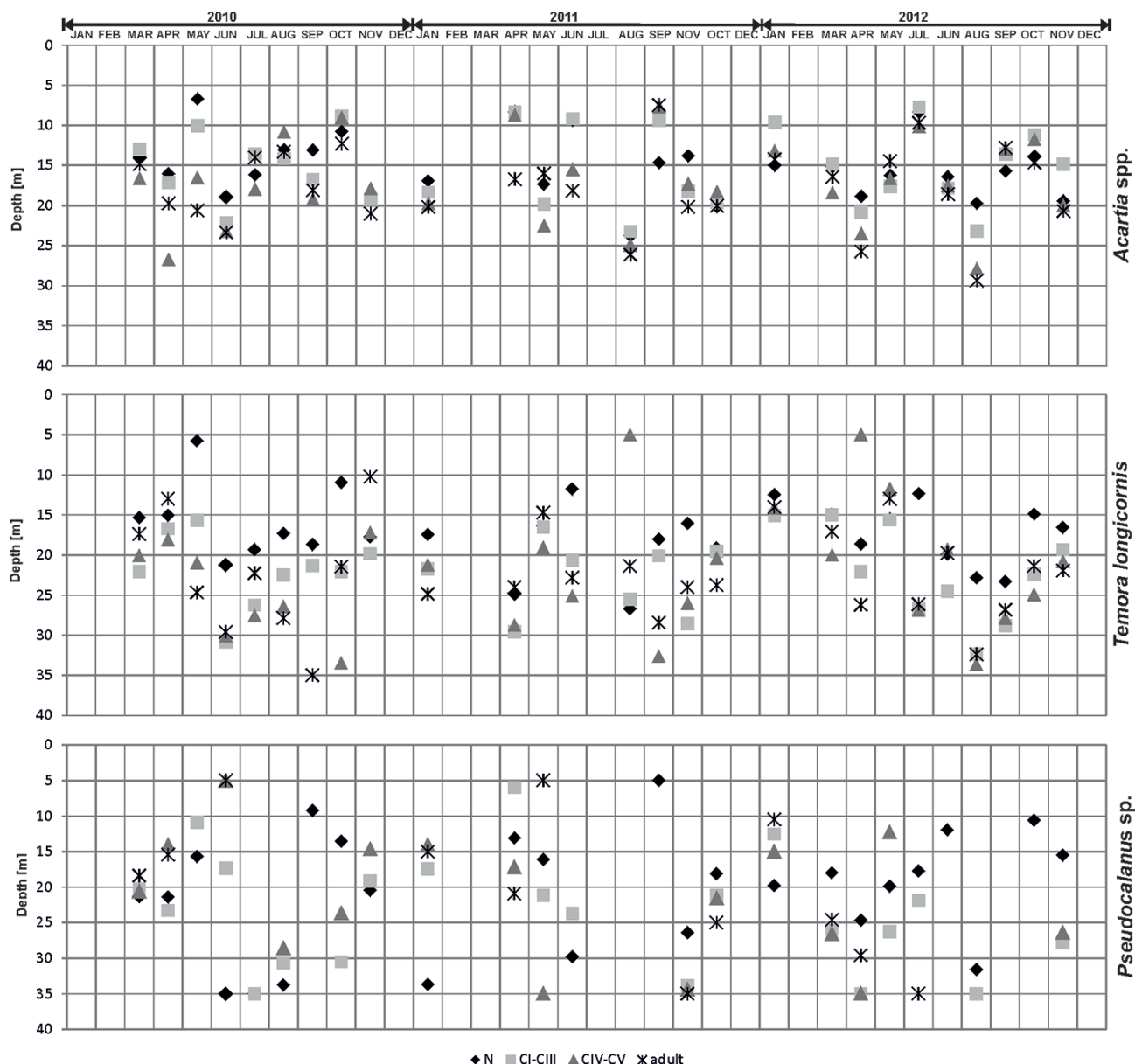


Figure 9

Proportion of respective developmental stages of *Pseudocalanus* sp. at station J23 in 2010–2012

**Figure 10**

WMD values of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. in 2010-2012

and in August 2012 – 32.4 m. *Pseudocalanus* sp. individuals were not observed during summer and WMD in the remaining months was between 5 and 35 m for different developmental stages.

The results obtained in our studies are similar to those presented by Dzierzbicka-Głowacka et al. (2013) for the same area in 2006 and 2007. The authors observed all developmental stages of *Acartia* spp. remaining very close to each other, but the observed difference in the mean annual WMD was much lower. We have noticed that the stages of *T. longicornis* also seem to stay close to one another, but nauplii were found near the surface

and adults preferred the deepest waters. The same conclusions were drawn by Dzierzbicka-Głowacka et al. (2013). As for *Acartia* spp., the difference in the mean annual WMD for *T. longicornis* was much lower in this study compared to that obtained by Dzierzbicka-Głowacka et al. In the case of *Pseudocalanus* sp., older stages (rather than younger ones) preferred greater depths. The differences in the mean annual WMD were the same as those obtained by Dzierzbicka-Głowacka et al. (2013) – approximately 30 m. Also, similarly to our study, Möllmann and Köster (2002) observed no significant relationship between the

vertical distribution of different developmental stages and the depth for *Acartia* spp. and *Temora longicornis*. Renz and Hirche (2005) studied vertical distribution patterns as WMD for each stage of *Pseudocalanus acuspes* and concluded that it was stage specific. Similar results were obtained in our studies.

Production

Over the three-year study period, a significant increase in the production of copepods was observed in the Gulf of Gdańsk. The highest production rates were noted for *Acartia* spp., followed by *T. longicornis*, and the lowest amount was recorded for *Pseudocalanus* sp. Among those species, only *Acartia* spp. showed a clear correlation between temperature and production rates (Table 2). In the case of *T. longicornis*, there were probably other factors involved, like grazing having a stronger impact on the production rates, and in the case of *Pseudocalanus* sp., it was most likely the effect of data scarcity.

Table 2

Values of the Pearson correlation coefficient for the temperature and production rates of the development stages of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. (***bold** – $p < 0.05$)

	N	CI	CII	CIII	CIV	CV
<i>Acartia</i> spp.	-0.76*	0.84*	0.80*	0.84*	0.78*	0.81*
<i>Temora longicornis</i>	-0.87*	0.34	0.10	0.14	0.23	0.29
<i>Pseudocalanus</i> sp.	-0.22	0.18	0.71	0.70	0.30	-0.56

In the winter-spring periods of 2010-2012, the production rates for *Acartia* spp. and *T. longicornis* increased steadily and the observed values were similar for both taxa. In the spring of 2010, the production rate was approximately $4 \text{ mg C m}^{-2} \text{ d}^{-1}$, while in 2011 and 2012, this value was $2 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Fig. 11). The production for *Acartia* spp. and *T. longicornis* reached a peak in the summer. The exception is 2010, when the maximum production for *T. longicornis* occurred in spring. The estimated value of production in the summer was significantly higher for *Acartia* spp. than for *T. longicornis* and ranged from $12 \text{ mg C m}^{-2} \text{ d}^{-1}$ (2010) to $18 \text{ mg C m}^{-2} \text{ d}^{-1}$ (2011), while the production rate for *T. longicornis* did not exceed $3 \text{ mg C m}^{-2} \text{ d}^{-1}$ in

the summer period (Fig. 11).

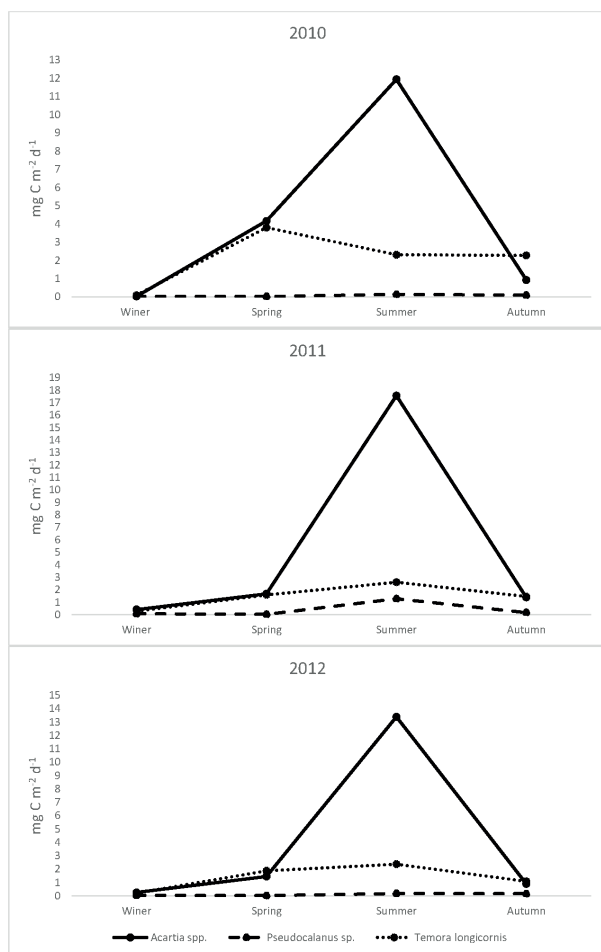
The average daily production of *Pseudocalanus* sp. did not exceed $0.8 \text{ mg C m}^{-2} \text{ d}^{-1}$ over the three years. The results show the highest production in the summer of 2011 ($0.77 \text{ mg C m}^{-2} \text{ d}^{-1}$). In 2010, the average daily production ranged from $0.02 \text{ mg C m}^{-2} \text{ d}^{-1}$ in winter and spring to $0.10 \text{ mg C m}^{-2} \text{ d}^{-1}$ in summer, while in 2012 the average daily production ranged from $0.02 \text{ mg C m}^{-2} \text{ d}^{-1}$ in spring to $0.17 \text{ mg C m}^{-2} \text{ d}^{-1}$ in summer (Fig. 11).

The estimation of copepod secondary production is one of the most important objectives in marine ecology, because it explains and predicts the amount of energy transferred within communities and ecosystems to higher trophic levels (Renz et al. 2012).

During the study period, *Acartia* spp. and *T. longicornis* were characterized by higher rates of production in comparison with *Pseudocalanus* sp. Taxa were recorded in all studies, but the maximum value of production was reported in the summer. This seems to correlate with natural population dynamics of those species in the Baltic Sea (Wiktor 1985), (Dippner et al. 2000; Renz, Hirche 2005; Schulz et al. 2012). Higher production rates of *Acartia* spp. and *T. longicornis* correspond also with the trend observed by Möllmann and Köster (2002) and Renz et al. (2007) in the central Baltic.

When comparing the results with the literature from 2006 and 2007, we notice a significant decrease in the average daily production of *T. longicornis* in the Gulf of Gdańsk. The 2010-2012 results for *Acartia* spp. compared with the previous research conducted in the Gulf of Gdańsk indicate a slight production growth in the winter, and a production decrease in spring. A significant change occurred for *Pseudocalanus* sp.: the previous studies showed the maximum value of production for this taxon in the winter, while the present results show the highest production in the summer.

In 2004, the research on the secondary production was conducted in the southern North Sea. The results showed the lowest values in October ($0.04 \text{ mg C m}^{-2} \text{ d}^{-1}$) and February ($0.07 \text{ mg C m}^{-2} \text{ d}^{-1}$), while the maximum was recorded in May and June ($136 \text{ mg C m}^{-2} \text{ d}^{-1}$ and $124 \text{ mg C m}^{-2} \text{ d}^{-1}$, respectively). Such large differences in the value of production for *Pseudocalanus* sp. may be caused mainly by the life strategy and metabolic processes of the organisms. The *Pseudocalanus* sp. population of the North Sea is in fact about 3 times larger than in the Baltic Sea. The North Sea population also develops 3-5 times faster, which may cause the

**Figure 11**

Secondary production of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. in 2010-2012

secondary production of this taxon to be 10 times higher (Renz, Hirche 2005; Renz et al. 2007).

Values of secondary mesozooplankton production in the Bornholm Basin described by Dahmen (1999) significantly exceed our results in the Gulf of Gdańsk. Dahmen (1999) observed the highest values of secondary production for all species in July 1991, (CI-adult stages). The largest part in the secondary production of Copepoda was contributed by *T. longicornis* – about 200 mg C m⁻² d⁻¹, followed by *Acartia* spp. – about 170 mg C m⁻² d⁻¹ and *Pseudocalanus minutus* – about 80 mg C m⁻² d⁻¹. More than two times lower production were obtained in October 1988 (CI-adult stages) for *Acartia* spp. and *Pseudocalanus minutus*, while the secondary production for *T. longicornis* remained high at about 165 mg C m⁻² d⁻¹. Such a large discrepancy compared to our results was most likely caused by differences in the calculation

method as well as specific characteristics of the study areas, mainly the sampling depth.

In 1977, Ciszewski and Witek published the results on the secondary production of two copepod species: *Acartia biflosa* and *Pseudocalanus elongatus* in Gdańsk Basin. In these studies, growth rates were determined from a lab culture. Additional secondary production values were calculated as annual production rates: 16.75 for *Acartia biflosa*, and 12.42 for *Pseudocalanus elongatus* which makes them difficult to compare.

Conclusion

The data obtained in this study, especially the increase in the standing stocks of *Acartia* spp. and *T. longicornis* and the decrease in the production rates of *Pseudocalanus* sp., seem to be consistent with the trends observed in other parts of the Baltic Sea, and with those observed previously in the bay (Dippner et al. 2000; Möllmann et al. 2000; Möllmann, Köster 2002; Renz et al. 2007; Dzierzbicka-Głowacka et al. 2015). Similar trends were also observed in the production rates of those species, especially *Pseudocalanus* sp. whose production rates in the bay were several times lower than those in the central Baltic (Möllmann, Köster 2002; Renz et al. 2007). The mortality rates obtained in this study show higher values than those observed for the taxa in the 1970s, the 1980s and the 1990s. This growing trend in the bay seems to be similar to the situation in other parts of the Baltic Sea and is most likely caused by the increased predation of clupeid fish, which resembles the situation observed at the beginning of the 1990s.

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