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Interannual variability in the population dynamics of the main mesozooplankton species in the Gulf of Gdańsk (southern Baltic Sea): Seasonal and spatial distribution*

KEYWORDS
Acartia spp.
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Abstract

The paper characterizes the population dynamics of the major Baltic calanoid copepod species (*Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp.) in the Gulf of Gdańsk (southern Baltic Sea) from January 2006 to December 2007. The data were collected at six stations (M2, S1, S2, S3, S4, J23) located in the western part of the Gulf of Gdańsk. The objective of this research was to describe and compare the seasonal and spatial distributions of these three major copepod species. Their distributions in the study area are largely similar, although there are some exceptions regarding *Pseudocalanus* sp. Copepoda development in the Gulf was at its most intense from May to September, peaking in July. The abundance of these

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species was the least at the shallowest stations. Based on these results, the weighted mean depth WMD per developmental stage was calculated for *Pseudocalanus* sp., *Acartia* spp. and *T. longicornis*. The paper also compares the abundance (in indiv. m^{-2}) of the copepodite stages of these species in two regions of the Baltic Sea (the Gulf of Gdańsk and the Gotland Basin). Except for *Pseudocalanus* sp., the abundance of these copepodite stages ($\sum$CII–CVI) in the Gulf of Gdańsk in 2006 was similar to that in the Gotland Basin in the mid-1990s; in spring/summer 2007, however, their abundances were significantly higher (ca 2–4 times) in the former region.

1. Introduction

The Baltic Sea is one of the largest brackish water bodies in the world. This type of water and its location in the boreal climate zone determine the nature of the communities of organisms living in this sea. The zooplankton consists of marine euryhaline, brackish and freshwater species.

Being exposed to a variety of environmental conditions, the zooplankton is subject to considerable seasonal changes, in terms of both taxonomic structure and the dominance of individual species (Hernroth & Ackefors 1979, Wiktor 1990, Schulz et al. 2012). Wiktor (1990) reported that because of the considerable spatial and seasonal variability in salinity and temperature, the Baltic zooplankton typically consisted of euryhaline and eurythermic taxa such as *Temora longicornis*, *Centropages hamatus*, *Acartia* spp., *Bosmina coregoni maritima*, *Evadne nordmanni* and *Pleopsis polyphemoides*, as well as representatives of the genera *Podon* and *Synchaeta*. Some of them, like *T. longicornis*, prefer colder water when available. Species preferring lower temperatures, e.g. *Acartia longiremis*, *Pseudocalanus* sp. and *Fritillaria borealis*, are the most abundant during the cooler seasons and in colder, deeper waters in the warmer seasons.

Recent studies indicate that a *Pseudocalanus* species from the central Baltic, hitherto named *P. elongatus*, might actually be *P. acuspes* (Bucklin et al. 2002, Holmborn et al. 2011). Although *P. elongatus* may also be present in the southern Baltic, the designation *Pseudocalanus* sp. (after Möllmann et al. 2005) seems to be more appropriate for the present work.

Numerical investigations of the population dynamics of *Pseudocalanus* sp. and *Acartia* spp. in the southern Baltic Sea were first conducted by Dzierzbicka-Głowacka (2005a,b and 2006), and Dzierzbicka-Głowacka et al. (2006, 2010, 2012, 2013). That work also included quantitative descriptions of the effects of food concentration and temperature on stage duration, growth rate and egg production rate (Dzierzbicka-Głowacka 2004a,b, Dzierzbicka-Głowacka et al. 2009a,b, 2011). The present study will be used to upgrade earlier models.

The main objective of the study is to describe the seasonal and spatial distribution of the major Baltic calanoid copepod species (*Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp.) in the southern Baltic Sea. The data obtained will be used as a background for future numerical evaluations. The WMD (copepod weighted mean depth in relation to estimated numbers of particular stages) for these species in the Gdańsk Basin has not been established before.

2. Material and methods

2.1. Sampling

The data are based on the analysis of samples collected almost every month during a two-year period (2006 and 2007); a few months were missed when meteorological or technical problems were encountered (April, October, December 2006 and January and April 2007). Samples were collected at six stations located in the western part of the Gulf of Gdańsk, southern Baltic Sea (Figure 1; Table 1). Five stations (S1, S2, S3,

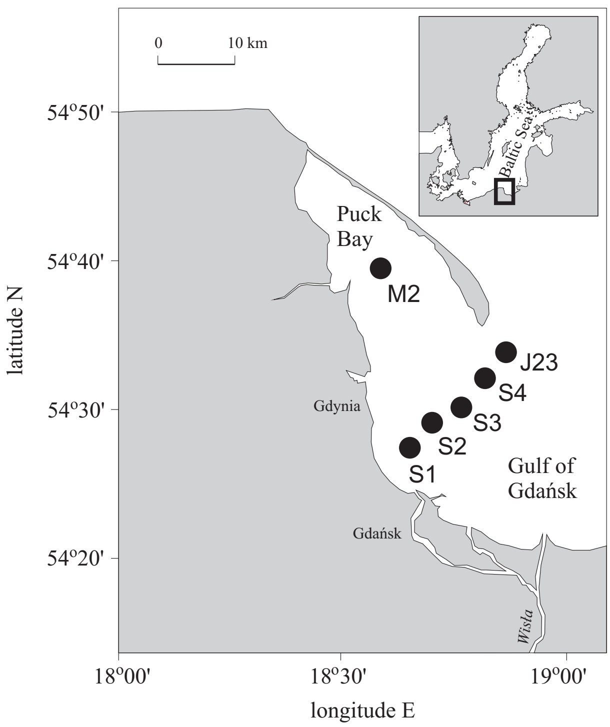

Figure 1. Location of the sampling stations in the Gulf of Gdańsk (southern Baltic Sea)

Table 1. Positions and maximum sampling depths of the stations investigated

Station	Longitude N	Latitude E	Depth [m]
M2	18°33.8′	54°39.0′	10
J23	18°48.2′	54°32.0′	40
S4	18°46.0′	54°30.7′	30
S3	18°43.7′	54°29.7′	20
S2	18°36.7′	54°27.7′	10
S1	18°34.8′	54°27.0′	5

S4, J23) were located on a depth gradient transect representative of the Gulf. One station (M2) was located in Puck Bay, the hydrological conditions of which differ from those the Gulf proper. The zooplankton material was collected using a closing-type Copenhagen net of 0.50 m inlet diameter and 100 μm mesh size. At shallower stations (≤ 10 m), vertical hauls were carried out from the bottom to the surface, whereas at deeper stations water layers at 10 m intervals were sampled separately. In this latter case, water temperature and salinity were measured at the same time as the plankton was sampled. Qualitative and quantitative laboratory analyses were performed in accordance with the HELCOM guidelines included in the Combine manual Annex C-7 (www.helcom.fi/groups/monas/CombineManual/AnnexesC/en_GB/annex7/), except for the nauplii, which were identified to species level. Adults of the genus *Acartia* were identified only to generic level, owing to the similarity between the three *Acartia* species: these are referred to as *Acartia* spp. Later in the article most of results will refer to station J23, as this was the deepest stations and the most representative of the Gulf proper.

2.2. Weighted mean depth WMD

The vertical distribution of stages of the copepods was described by computing the weighted mean depths WMD (Bollens & Frost 1989, Renz & Hirche 2006) per month and per year:

$$\mathrm{WMD} = \frac{\sum n_i d_i}{n_i}, \tag{1}$$

where n_i is the abundance [indiv. m^{-3}] at each depth layer with midpoint d_i. The calculations were made for seven stages: nauplii, copepodites (C1, C2, C3, C4, C5) and adults. Nauplii were included, as reporting them is advised by the HELCOM guidelines and gives more comprehensive insight into the vertical distribution of the stages. The diurnal vertical migrations of copepods could not be investigated because the samples for this study were taken only during daylight (mainly between 10:00 and 13:00 hrs).

3. Results

3.1. Hydrography

In our study region (Gulf of Gdańsk, station J23), the water is well mixed throughout the column in winter (Figures 2, 3). At station J23 during this season, the temperature was ca 1.5°C in February 2006 and 3.6°C in February 2007, and ca 10°C in November 2006 and 8.5°C in November 2007. In June 2006 and May 2007 the thermocline developed at 15–20 m depth; the surface temperature increased from 15°C in June 2006 and 17°C in June 2007 to 23°C in July 2006 and 19°C in July 2007, and to 19°C in August 2006 and 2007. Thereafter it fell to 10°C in November 2006 and 9°C in November 2007. The thermocline depth shifted to 30 m in September 2006, but in 2007 it was still at 15 m in August – unfortunately there are no data for September. The thermocline disappeared in mid-October of both years. The salinity was ca 7.5 PSU throughout the water column, except in summer, when the surface water salinity decreased to 5.4 PSU (2006) and 5.8 PSU (2007) in June (and to 5.8 PSU in July 2006 and 6 PSU in July 2007, and to 6.4 PSU in August 2006 and 7 PSU in August 2007) following intensive inflows of water from the River Vistula during that period. Temperatures at the other stations were similar to those at J23, but because they were shallower, vertical changes were less evident. The only difference was at the end of summer, when the water temperature decreased faster in the coastal region. The salinity at the other stations was similar to that at J23, and the inflow of freshwater from June to August was recorded to an equal extent at all the stations.

Abundances and stage structures were very similar at all the stations, the only exception being *Pseudocalanus* sp., which was less abundant at the shallower stations and whose population structure was shifted in favour of nauplii. The analysis of the results will therefore relate to station J23, which is the most representative and exhibits the most distinctive variations in spatial and temporal distributions.

3.2. Abundance, stage-structure and horizontal distribution

The stocks of the three copepod species varied considerably in time during the study period (Figures 4, 5). *Acartia* spp. reached their highest concentrations in July–September, *Temora longicornis* was most abundant from June to August, and *Pseudocalanus* sp. in March, July and August. The abundance of nauplii in the study area varied from 7×10^3 to

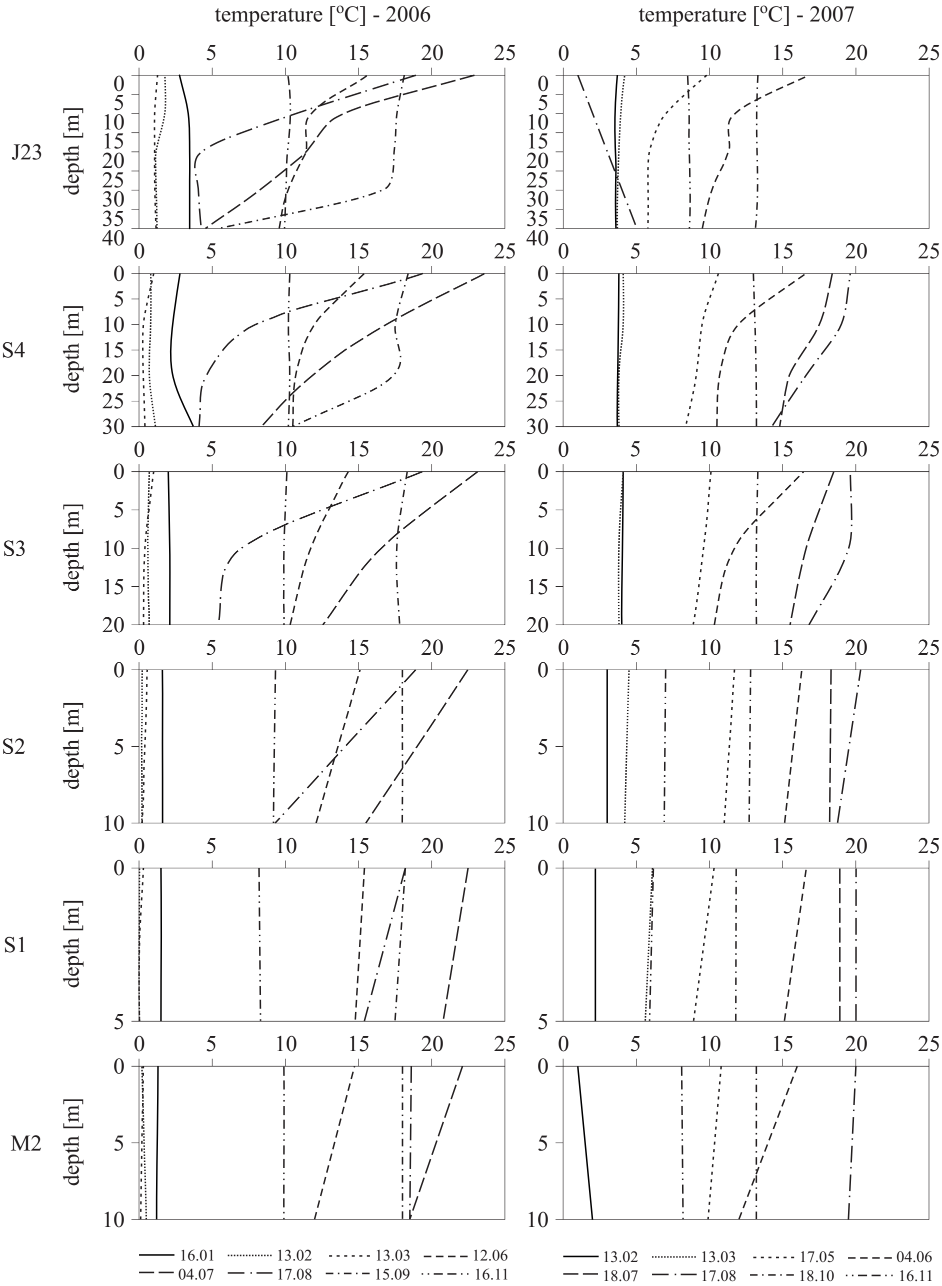

Figure 2. Vertical profiles of temperature [°C] at the stations in 2006–2007

339×10^3 indiv. m^{-2} (*Acartia* spp.), from 610 to 540×10^3 indiv. m^{-2} (*T. longicornis*), and from 0 to 32×10^3 indiv. m^{-2} (*Pseudocalanus* sp.). All three abundance maxima were recorded in July 2007. The abundances

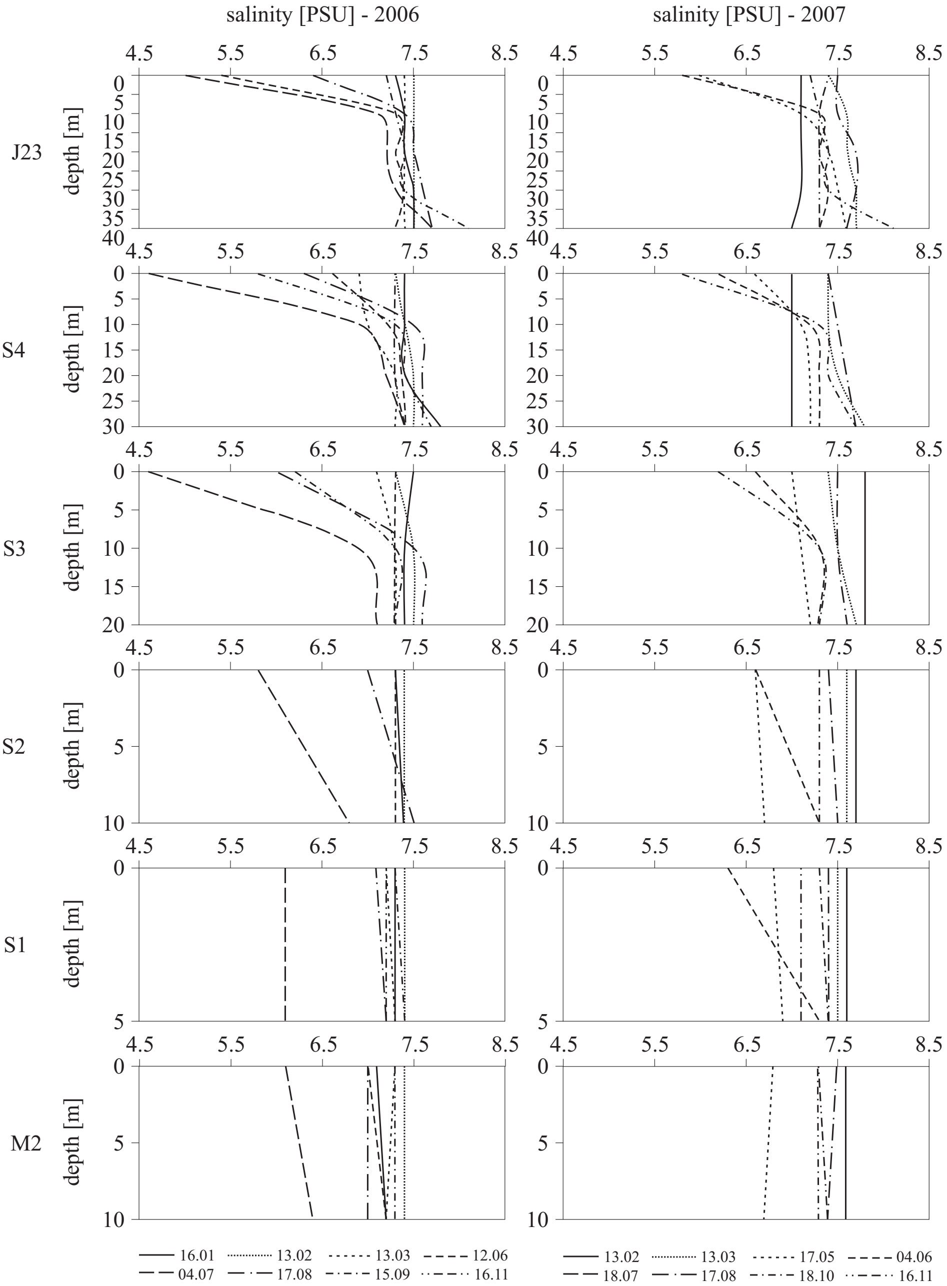

Figure 3. Vertical profiles of salinity [PSU] at the stations in 2006–2007

of copepodite stages were: 3×10^3 – 608×10^3 indiv. m^{-2} (*Acartia* spp. – July 2007), 970–352×10^3 indiv. m^{-2} (*T. longicornis* – July 2007), and 0–24×10^3 indiv. m^{-2} (*Pseudocalanus* sp. – August 2006).

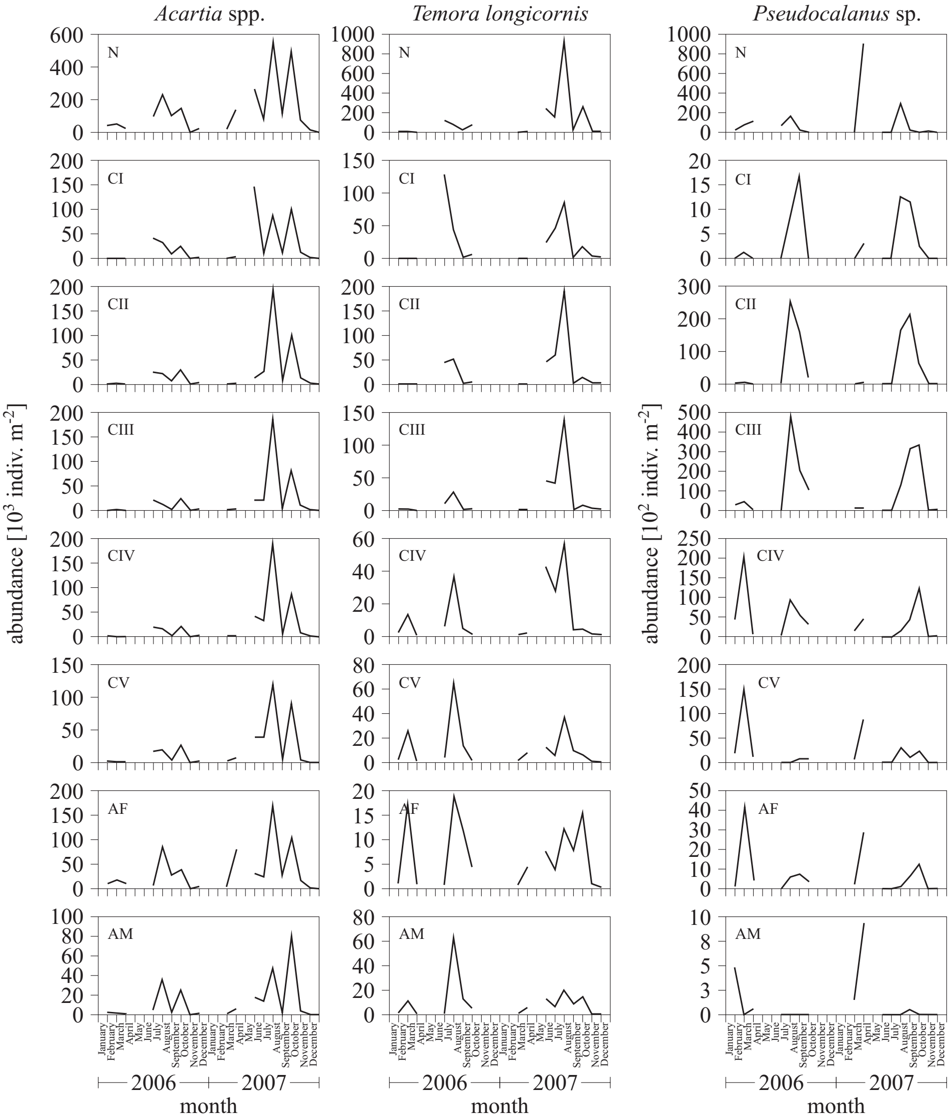

Figure 4. Abundance [indiv. m^{-2}] of developmental stages of *Acartia* spp., *Temora longicornis*, *Pseudocalanus* sp. at station J23 in the Gulf of Gdańsk in 2006–2007

At station J23 all the developmental stages of the three taxa were present throughout both years of the study. Nauplii constituted the most abundant stage of *Acartia* spp., with two peaks: one in July and the other in September. Likewise, the most abundant stage of *T. longicornis* consisted of nauplii, but with just one clear peak in July 2007; in 2006 they were very much less abundant. Copepodite abundance peaked in June 2006 and

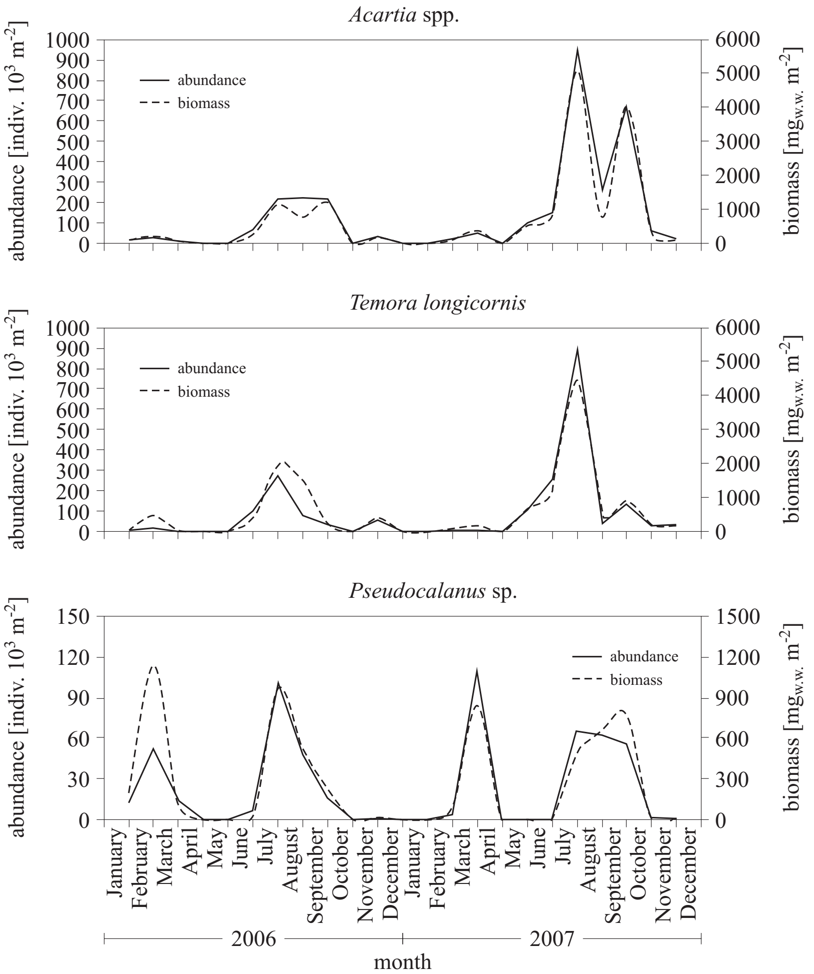

Figure 5. Abundance [indiv. m^{-2}] and wet weight [$mg_{w.w.}$ m^{-2}] of *Acartia* spp., *Temora longicornis*, *Pseudocalanus* sp. at station J23 in the Gulf of Gdańsk in 2006–2007

July 2007 (stage CI), and in July 2006 and July 2007 (stages CII–V). Both males and females were similarly abundant in both years, except in July 2006 when males were around three times more abundant than females. *Pseudocalanus* sp. nauplii peaked in July 2006 and July 2007; there was also a very high peak in March 2007, which was almost four times higher than the other maxima. The highest abundances of younger copepodites (CI–CIII) were noted in July and August; CIV peaked in February 2006, but this maximum was not in evidence the following year. Stage CV and adults peaked in February 2006 and March 2007; adult females were clearly much more abundant than males.

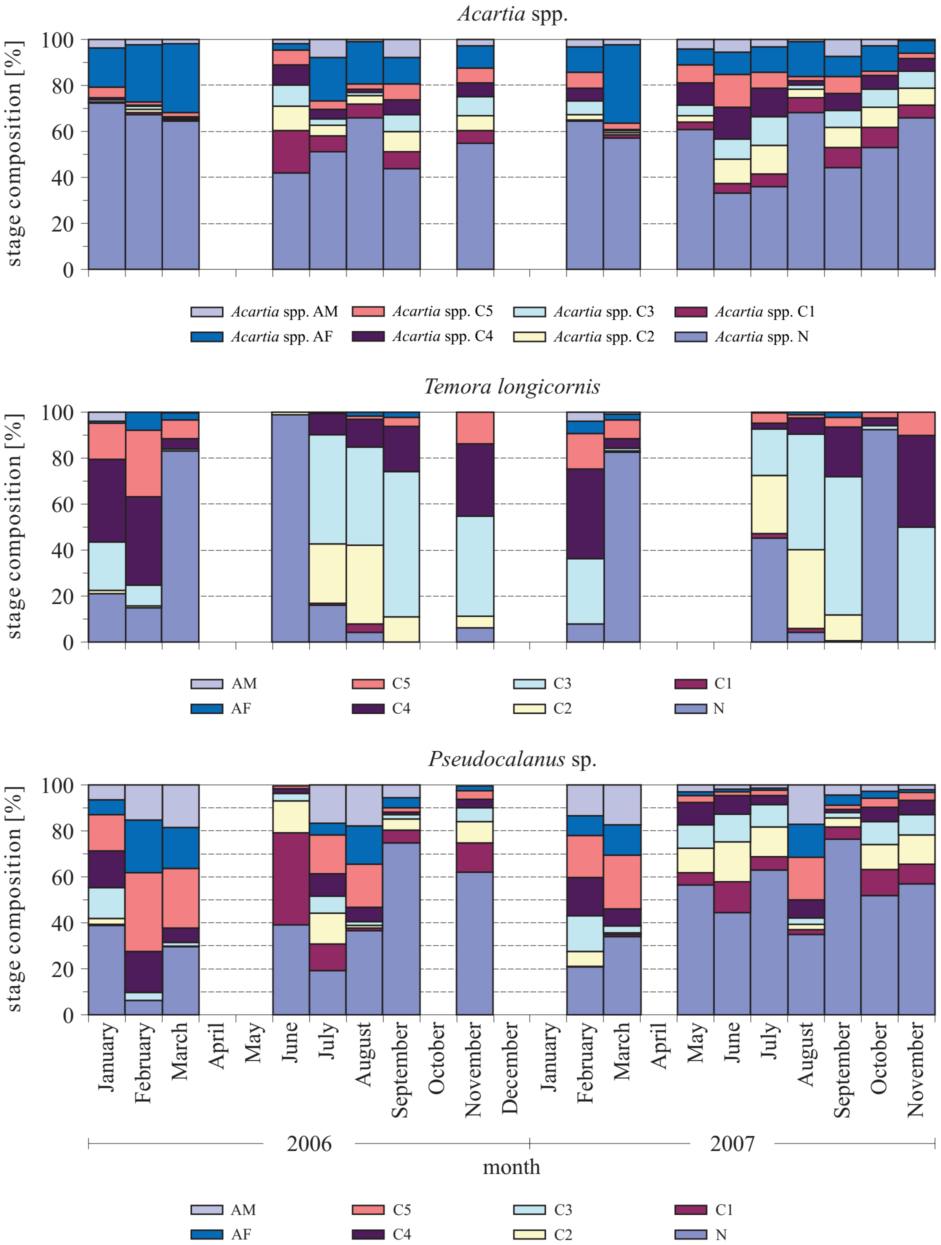

Figure 6. Stage structure of *Acartia* spp., *Temora longicornis*, *Pseudocalanus* sp. at station J23 in the Gulf of Gdańsk in 2006–2007 (the months without data have been omitted)

The wet weights of Copepoda stock were calculated from the specific wet weights taken from Hernroth (1985) (Figure 5). In two of the taxa, temporal variabilities closely resembled abundances: the maximum biomass of *Acartia* spp. was approximately 5×10^6 μg m^{-2} and that of *T. longicornis* was 4.5×10^6 μg m^{-2}. This was not the case, however, with *Pseudocalanus* sp., whose wet weight peaked in February (1×10^6 μg m^{-2}) in a population consisting mainly of adults.

Nauplii were evidently dominant in the relative composition of *Acartia* spp. (Figure 6) during both years (from 40% in January to ca 70% in August). In *T. longicornis* there was a visible shift in the proportion of nauplii from 10% in February to almost 80% in September 2006, but this change was not so clear-cut the following year. The stage shift pattern in *Pseudocalanus* sp. was more distinctive: nauplii made up $>80\%$ in March and June 2006, and March and October 2007; these proportions declined in the subsequent months, reaching minimum values in February

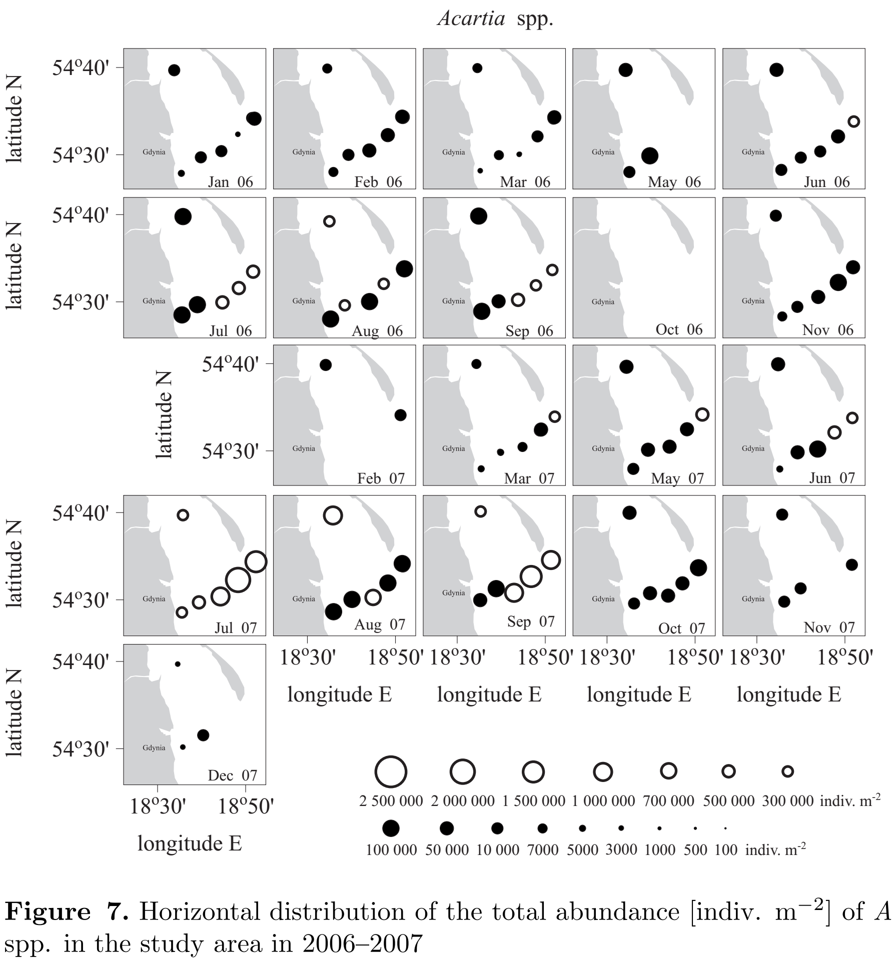

Figure 7. Horizontal distribution of the total abundance [indiv. m^{-2}] of *Acartia* spp. in the study area in 2006–2007

and September of both years. Surprisingly, CI never made up a conspicuous proportion of the population; the greatest proportion of CII was recorded in August, that of CIV in October and November, and that of CV in February; moreover, the proportion of adults was the highest in February (8% in 2006).

During the sampling seasons, the lowest concentrations of the three species were recorded at shallow stations (M1, S1, S2) (Figures 7–9). The horizontal distribution revealed the highest concentrations (indiv. m^{-2}) at the deepest stations, mainly S4 and J23. This pattern was most in evidence for *Pseudocalanus* sp., the abundance of which at these two stations was as much as twenty times greater than at the other stations in 2006 and two-five times greater in 2007. However, peak abundances of *Acartia* spp. and *T. longicornis* were respectively five and seven times higher at stations more distant from the coast (S4, J23).

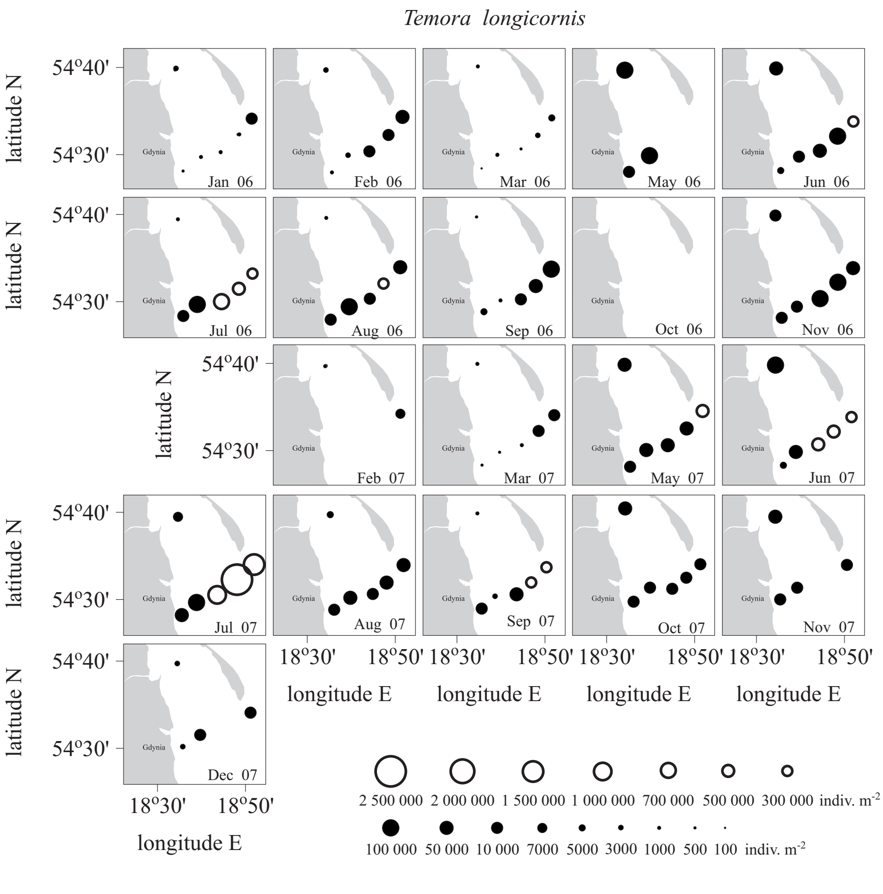

Figure 8. Horizontal distribution of the total abundance [indiv. m^{-2}] of *Temora longicornis* in the study area in 2006–2007

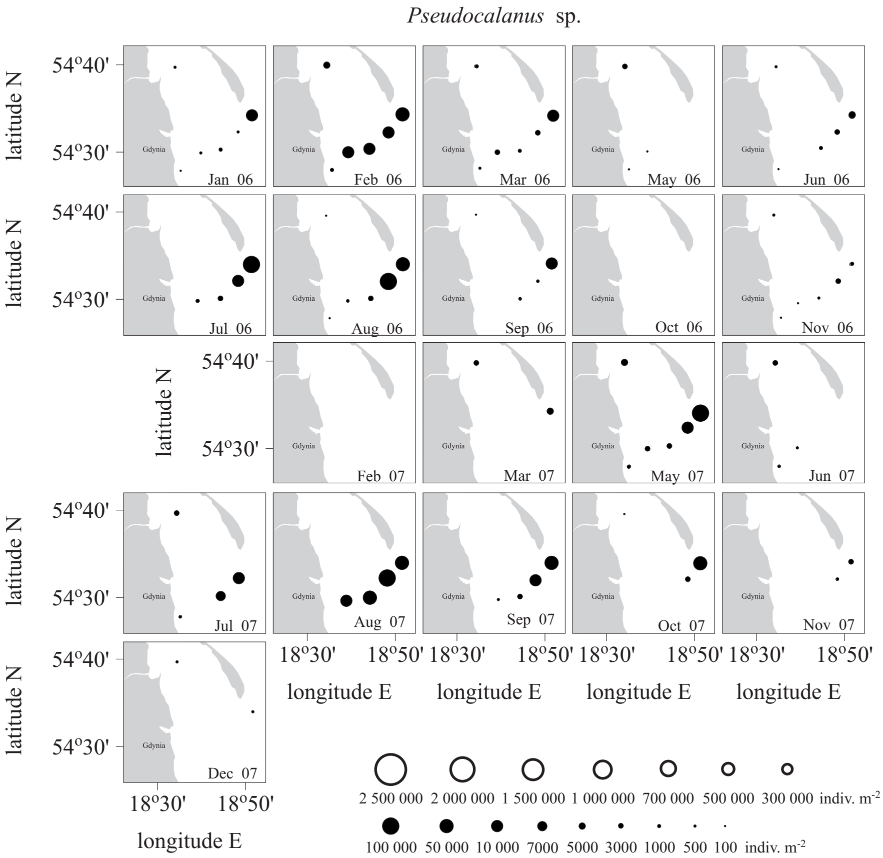

Figure 9. Horizontal distribution of the total abundance [indiv. m^{-2}] of *Pseudocalanus* sp. in the study area in 2006–2007

3.3. Vertical distribution

Figures 10–12 show the vertical distributions of all the developmental stages of *Acartia* spp., *T. longicornis* and *Pseudocalanus* sp. at station J23 (40 m).

3.3.1. *Acartia* spp.

In January 2006, all stages were concentrated in the upper 20 m. In February 2006, abundance was the highest exclusively in the 20–10 m layer. In February 2007 the younger stages (N, C1, C2) were concentrated in the 20–10 m layer, while the rest of the population was distributed evenly, though with a slight preference for the deepest layer (40–30 m). During March 2006 C1 were still concentrated in the 20–10 m layer, C2 and C3 were scattered between the layers at 40–30 m and 10–0 m, while the remaining stages were distributed more or less evenly. In 2007, however, the distribution of the *Acartia* population was completely different: all the stages were concentrated in the deepest layer of 40–30 m; a similar situation was observed in May 2007. In June 2006 C2 and adults preferred the deepest layer; in June 2007, however, nauplii and copepodites preferred the surface layer whereas most of the females were found in the deepest part of the water column. In July 2006 copepodites from C1 to C3 were found mostly in the 20–10 m layer, while older stages preferred deeper water (especially adults). In 2007 most of the individuals inhabited the 30–0 m depth range. Nauplii, C1–C4 and adult males in April 2006 were found mostly in the upper 10–0 m layer; adult females were concentrated in the 30–20 m layer. In 2007 the distribution of stages was quite different – nauplii and copepodites were scattered throughout the 10–0 m and 40–30 m layers, whereas adult females were concentrated primarily at 40–30 m and males mostly at the surface. In September the distribution of stages became more homogeneous.

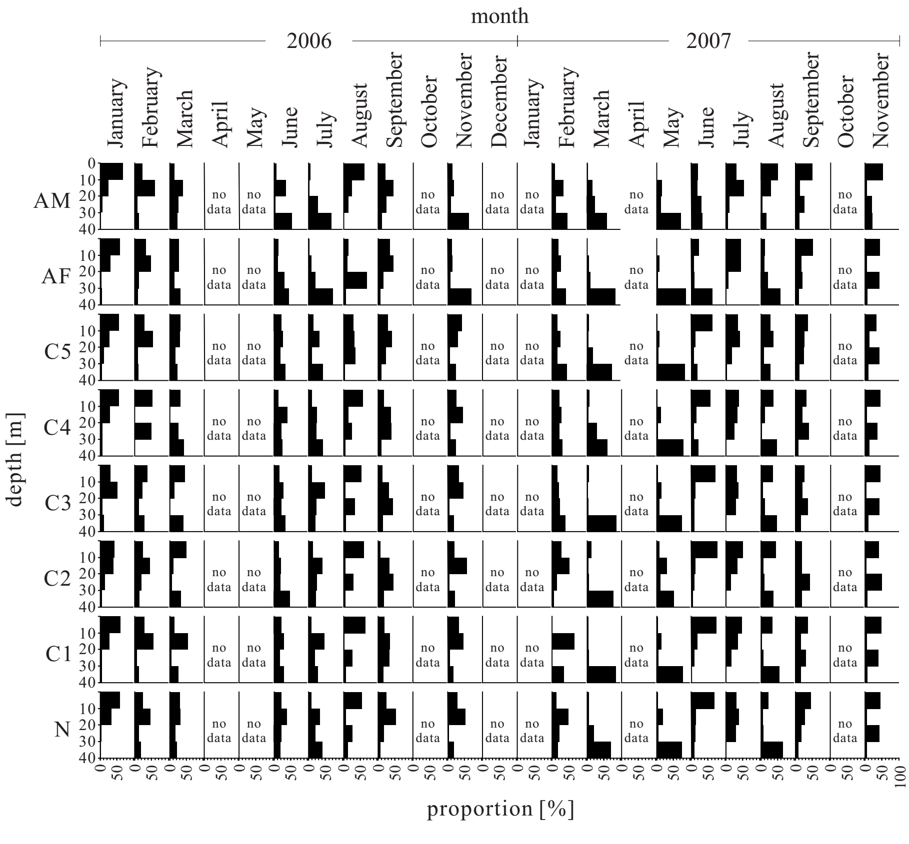

Figure 10. Vertical distribution [%] of nauplii, C1 to C5 and adults (M and F) of *Acartia* spp. at station J23

In November 2006 nauplii and copepodites inhabited mostly the 20–10 m layer, and adults were usually found near the bottom; in 2007 all stages were found primarily in the 30–20 m and 10–0 m layers.

3.3.2. *Temora longicornis*

In January 2006 the developmental stages of *T. longicornis* were concentrated mostly in surface waters from 20–0 m. In February most of the population extended over two depth layers, 10–20 m and 40–30 m; stages C1 and C2 were not observed. In March 2006 the stages were spread evenly throughout the water column, except for C2 (only in the 30–20 m layer) and C3 (only in the 20–10 m layer). In summer 2006 most of the stages appeared to avoid surface waters, their preference for deeper layers apparently increasing with age – up to 90% of adult males were found in the 40–30 m layer. In 2007, however, the 30–20 m layer was the preferred depth of all stages, which seemed to avoid the near-bottom layer. In September

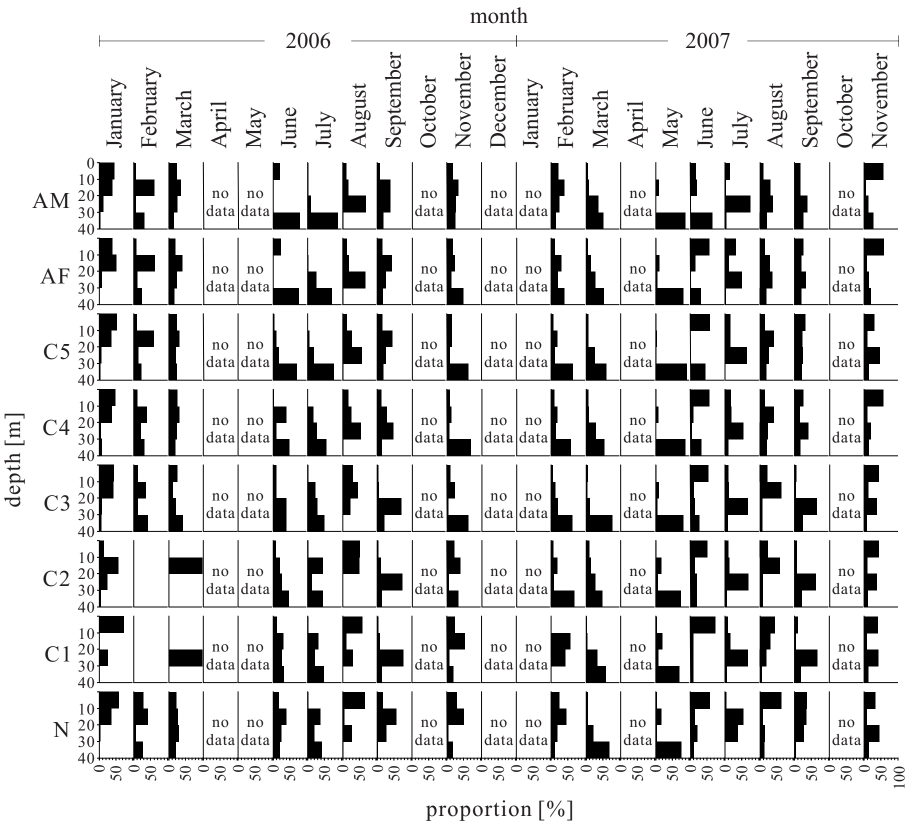

Figure 11. Vertical distribution [%] of nauplii, C1 to C5 and adults (M and F) of *Temora longicornis* at station J23

2006 young copepodites C1–C3 were concentrated in the 30–20 m layer (up to 80%), whereas the other stages were spread evenly; the following year the distribution of stages was very similar. In November 2006 up to 50% of nauplii and CI were found in the 20–10 m layer, whereas older copepodites and adult females preferred the deepest layer. In 2007 most of the stages were distributed evenly in the 30–20 m and 10–0 m layers; CIV and adults exhibited a clear preference for surface waters.

3.3.3. *Pseudocalanus* sp.

In January 2006 all of the developmental stages except C1 (found near the bottom) were concentrated in the surface layer (up to 90% of adult males). In February 2006 most of the *Pseudocalanus* sp. stages preferred the 20–10 m and surface water layers, although no adult males were found there. In the same month in 2007 all the stages inhabited the deepest layer, except the nauplii, which were spread rather more evenly in the water column. In

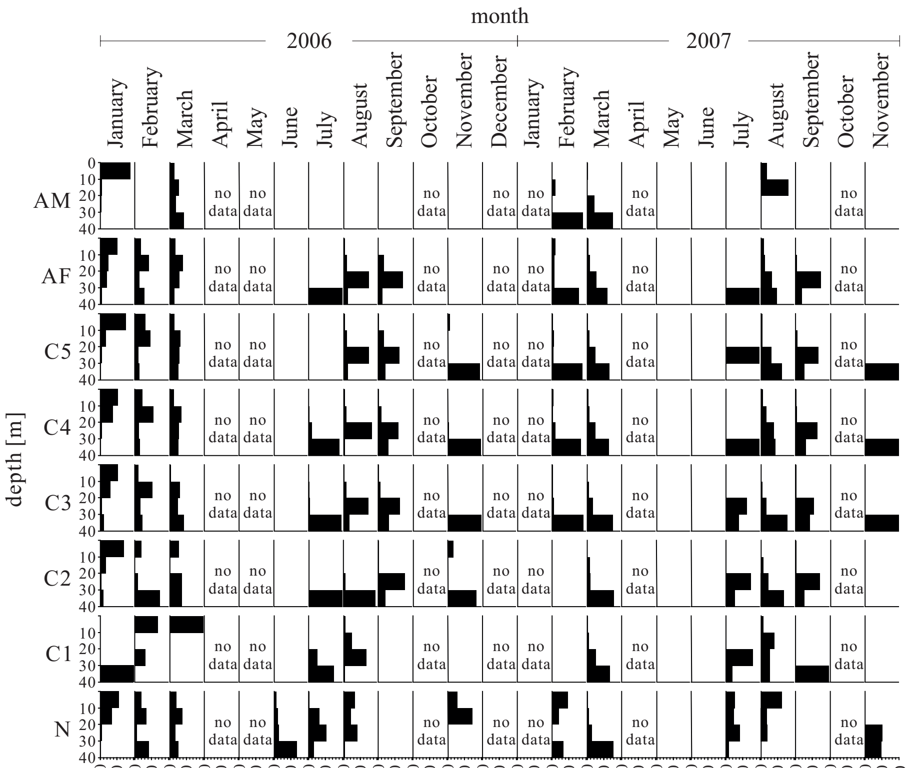

Figure 12. Vertical distribution [%] of nauplii, C1 to C5 and adults (M and F) of *Pseudocalanus* sp. at station J23

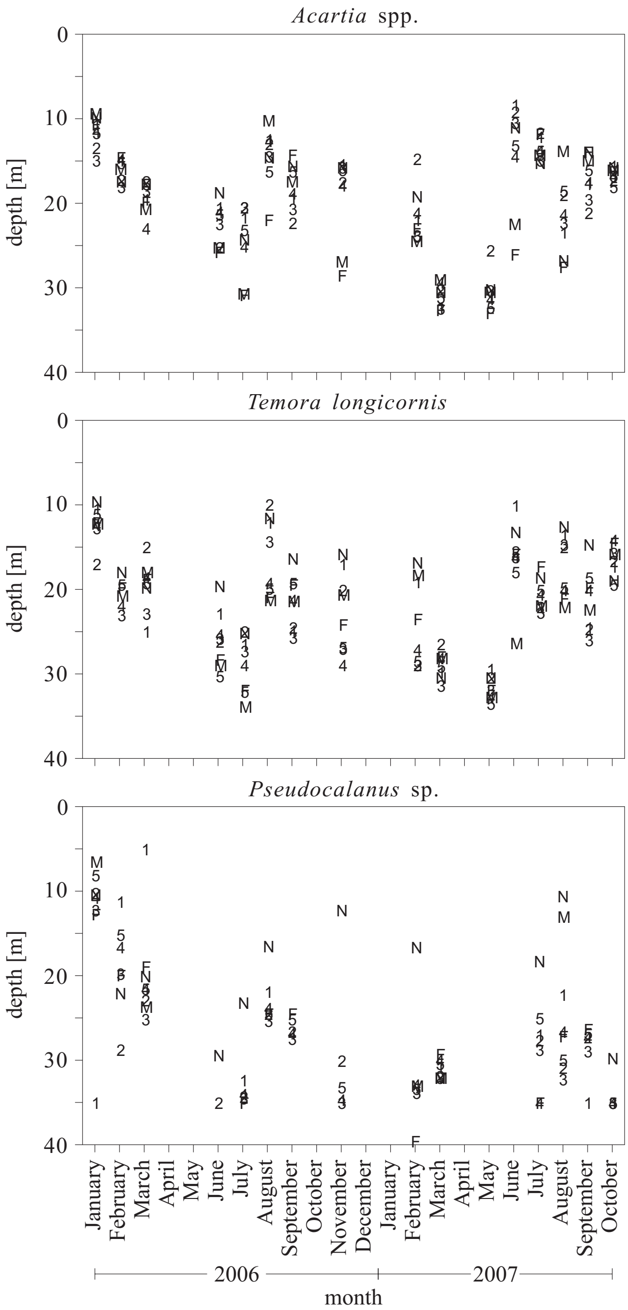

Figure 13. Weighted mean depth WMD of nauplii (N), copepodites (C1–3, C4–5) and adult (F, M) stages of *Acartia* spp., *Temora longicornis*, *Pseudocalanus* sp. at station J23 in the Gulf of Gdańsk

March 2006 the stages were evenly distributed throughout the water column; in 2007, however, all the stages displayed a preference for the deepest layer. In May and June 2007 no individuals of *Pseudocalanus* sp. were observed at station J23, although in June 2006 some nauplii were noted there, mostly in the bottom layer. In July 2006 the stages were concentrated in the 40–30 m layer. In July 2007 nauplii were evenly distributed, whilst the other stages and females preferred the deepest part of the water column. In August and September 2006 all the stages were concentrated at 30–20 m depth. In August 2007 nauplii were found primarily in the surface layer, whereas the other stages were more widely distributed, though tending to prefer the deepest layer. Adult males were an exception, being found mostly in the 20–10 m layer. In September 2007, most stages preferred the 30–20 m layer; only C1 were mostly found near the bottom. In November 2006 nauplii were concentrated in the top two layers, but a year later in the two deepest layers; the copepodite stages were concentrated in the 40–30 m layer in both years.

3.4. Weighted mean depth

Figure 13 presents the weighted mean depth WMD of seven developmental stages of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp., i.e. nauplii and copepodites C1–C6, as well as adults (M and F). All the developmental stages of *Acartia* spp. lived very close to each other throughout the study period. There are no clear patterns in the distribution of stages, and the difference in the mean annual WMD was around 20 m. The stages of *T. longicornis* also seemed to live close to one another, but nauplii were found near the surface and adults preferred the deepest waters, especially from June to September. Differences in the mean WMD during the investigation period were around 25 m for this species. It seems that older stages rather than younger ones of *Pseudocalanus* sp. prefer greater depths: this was especially noticeable among the nauplii in November 2006. Mean WMDs were also more scattered, with a difference of 30 m during the whole investigation period.

4. Discussion

Because of the small number of stations and relatively long intervals between sampling, the data may be biased and not show the full variation.

4.1. Comparison of species in the Gulf of Gdańsk

In 2006 and 2007, the years when the research was conducted, Copepoda were the dominant component of zooplankton in the western part of the Gulf of Gdańsk (except for June and July 2006, and May 2007); in addition, Rotifera made a substantial contribution during the spring and summer. Of the other components of the zooplankton, only meroplankton was present in any significant number (September 2006 – 10%; July 2007 – 24%). This is the typical pattern of seasonal variation in the zooplankton in this region; it resembles the patterns recorded by other authors (Szaniawska 1977, Wiktor & Żmijewska 1985, Mudrak 2004). The small numbers of Cladocera in 2006/2007 were an evident exception; in previous reports this was an important component of the spring and summer zooplankton, quite often the dominant one. Although in 2006/2007 their numbers were insignificant, even they were large in comparison to other shallow areas of the Baltic Sea like the Neva Estuary (Telesh 2004) and the Gulf of Riga (Ikauniece 2001).

Quite a unique situation was observed in August 2007 at all the deep stations. An exceptionally small number of Copepoda was recorded, comparable to that in autumn (October), whereas in September the density of copepods was relatively high, which is characteristic of late summer. It is difficult to determine the reason for this situation, since the average temperatures during this period were very similar.

Wiktor et al. (1982) recorded two peaks in the abundance of copepods during the year: the first in May and another, higher one in August. Mudrak (2004) also recorded a maximum count of Copepoda in August. Rakowski (1997) observed an increase in the abundance of copepods in May and July. Gaj (1999) recorded an increase in the density of copepods in the coastal zone in June and a second (lower) one in September. Guzera (2002) also noted two peaks, but in March and at the end of August.

The minimal impact of the hydrological conditions on vertical distribution, which was statistically insignificant with respect to all three taxa studied, was striking. In the case of *Pseudocalanus* sp. certain trends were discernible, such as the accumulation of older stages and adults at greater depths and of nauplii closer to the surface. This was probably due to the relatively homogeneous hydrological conditions in the bay, and the relatively short-lived stratification, especially at the shallower stations. Conspicuous changes in the distribution and biomass appear to correspond to those observed by other researchers (Renz & Hirche 2006, Renz et al. 2007).

Analysis of the variation in Copepoda taxonomic structure indicates that during both winter and summer (August and September 2006, and from July to September 2007), *Acartia* spp. dominated the Copepoda composition.

Among adult individuals of *Acartia*, *A. bifilosa* occurred in the smallest numbers. During this research period, the species was present from March to November, with a significant increase in abundance in July. But these results are completely different from those reported by Siudziński (1977), Szaniawska (1977), Wiktor et al. (1982), Wiktor & Żmijewska (1985), Rakowski (1997), where *A. bifilosa* was the most abundant *Acartia* species. In subsequent years, however, Guzera (2002, the coastal zone) and Mudrak (2004) recorded a reduction in the numbers of this species, which was probably replaced by another species – *Acartia tonsa*. *A. tonsa* was the second most abundant *Acartia* taxon, recorded from June to November 2006 and from July to September 2007, and peaking in September (ca 95% in 2006 and 90% in 2007 of all *Acartia* adults). The most abundant species was *A. longiremis*, which is very unusual for the southern Baltic, as it is a species characteristic of winter and autumn, and occurs in deeper water layers (Siudziński 1977). This uncommon situation also contrasts with that observed, for example, in the Darss-Zingst Bodden Chain (Heerkloss & Schnese 1999). On the other hand, it may be one of the reasons for the strong similarity observed between the vertical distribution of *Acartia* and *A. longicornis*.

The presence of *A. longiremis* in the shallow coastal zone in the summer season was reported only by Gaj (1999); interestingly, this author did not confirm the presence of *A. tonsa*. Large numbers of *A. longiremis* (a species that usually prefers deeper and cooler waters), peaking in July in the surface layer and in the coastal area in spring and summer, could be related to upwelling in Puck Bay, a phenomenon that involves the upward movement of waters from deeper layers towards the surface (Nowicki et al. 2009). The structure of the *Acartia* spp. population was dominated mostly by nauplii and younger copepodites. This could have been due to the overlapping of the reproductive cycles of individual species: monthly intervals between sampling were too long to capture possible breaks between cycles.

Temora longicornis was the second most abundant copepod, with a population structure, like that of *Acartia*, dominated by younger stages, although in winter their contribution was significantly smaller than that of older copepodite stages. Siudziński (1977) observed two peaks in abundance – in June and November. Szaniawska (1977) reported the largest number of individuals in June and July, and in September and October. Rakowski (1997) recorded a maximum count of *T. longicornis* in May, and Mudrak (2004) did likewise in June and July. In the coastal zone, Gaj (1999) recorded peak numbers of this taxon in August, and Guzera (2002) in June.

Pseudocalanus sp. is a typical representative of the winter zooplankton; outside the winter season this taxon is present mostly in cooler, deeper water layers in the Gulf of Gdańsk (Siudziński 1977). This occurrence pattern has been confirmed by many authors (Wiktor & Żmijewska 1985, Gaj 1999, Guzera 2002, Mudrak 2004, Renz & Hirche 2006, Renz et al.

2007, Dzierzbicka-Głowacka et al. 2006, 2010, 2012). During our research period, this taxon was most abundant in winter and, unusually, also in July and August. Outside the winter season it was mainly nauplii and younger copepodite stages of *Pseudocalanus* sp. that were found. This pattern of seasonal variation in the abundance of this species was reported by Rakowski (1997).

4.2. Abundance: comparison with other data

The population dynamics of the major Baltic calanoid copepod species in the Gotland Basin for the period 1977–1996 was characterized by a decline in *Pseudocalanus* sp. associated with diminishing salinity and an increase in *Temora longicornis* and *Acartia* spp., possibly as a result of warmer conditions (Möllmann & Köster 2002). Generally, the abundance of the copepodite stages ($\sum$C2–C6) of these species, except *Pseudocalanus* sp., in the Gulf of Gdańsk in 2006 was similar to that in the Gotland Basin in the mid-1990s: *Acartia* spp. in all seasons, and *T. longicornis* in all seasons but spring, when the abundance was four times higher in the Gulf of Gdańsk. In spring and autumn, the abundance of *Pseudocalanus* sp. was low compared to the Gotland Basin owing to a decrease in salinity in the Gulf of Gdańsk. In spring/summer 2007, the abundance of *Acartia* spp. and *T. longicornis* in the Gulf of Gdańsk was significantly higher (ca 2–4 times) compared to the Gotland Basin (see Table 2). In spring and autumn 2006/2007, our results could have been over- and/or underestimated because of data missing from every months in this period.

Table 2. Seasonal abundance (in indiv. m^{-3}) of copepodite stages $\sum$(C2–C6) of *Acartia* spp., *Pseudocalanus* sp. and *Temora longicornis*; the total seasonal abundance is given in parentheses; the values in bold denote data from the Gotland Basin in the mid-1990s (Möllmann & Köster 2002)

	Winter	Spring	Summer	Autumn
Acartia spp.	**ca 40**	**ca 300**	**ca 550**	**ca 250**
2006	71 (172)	373 (703)	546 (971)	65 (122)
2007	224 (412)	638 (1055)	2033 (2935)	153 (327)
Temora longicornis	**ca 20**	**ca 80**	**ca 250**	**ca 210**
2006	36 (37)	321 (981)	234 (772)	204 (401)
2007	27 (31)	451 (763)	598 (1719)	120 (276)
Pseudocalanus sp.	**ca 30**	**ca 120**	**ca 280**	**ca 190**
2006	78 (81)	20 (85)	199 (171)	3 (3)
2007	46 (177)	0 (0)	194 (191)	4 (6)

4.3. Interactions between copepods and fish

Research into the long-term taxonomic changes of zooplankton is particularly important for augmenting knowledge about how marine ecosystems function. As planktonic organisms respond relatively quickly to changes in their environment, they can be very good indicators of the state of a particular ecosystem.

Zooplankton in general and copepods in particular play a very important function in the trophic chain, constituting as they do a link between phytoplankton, microzooplankton and higher trophic levels, including fish, and being a source of food for many of them.

Furthermore, they can be used in the assessment of water quality in hydrophysical, hydrochemical, hydrological and biological terms (Telesh 2004). When writing about the effects of eutrophication on fish resources in the Baltic Sea, Winkler (2002) demonstrated a correlation between their occurrence and zooplankton. This correlation was found in the Darss-Zingst Bodden Chain, Germany (a string of shallow lagoons bordering the Baltic Sea), at the end of summer and particularly in fish in the early development stages (Telesh 2004).

The reduction in biomass of *Pseudocalanus* sp., the main food component of the herring (*Clupea harengus*) in the Baltic Sea, certainly contributed to the diminishing population of this fish since the early 1980s (Sparholt 1994). The size and the composition of zooplankton resources affect the growth and survival rate of fish in the early stages of their development (Cushing 1995). The sprat (*Sprattus sprattus*) is another species of Baltic fish whose population size has been diminishing since the 1990s. *T. longicornis* is the main food of this pelagic fish (Möllmann & Köster 1999). The decline in the sprat population may have been caused by competition between sprat and herring; in the absence of sufficient quantities of *Pseudocalanus* sp., the latter to a greater extent incorporated other copepods in its diet, e.g. *T. longicornis* (Möllmann et al. 2005). The biomass of *Pseudocalanus* sp. is closely connected with the salinity, and its value affects the herring population. Many studies have demonstrated that this copepod species is of paramount importance for the diet of the Baltic herring (Davidyuk et al. 1992, Möllmann et al. 2005). Möllmann et al. (2003) showed that the condition of the herring population is determined by the size of this copepod population in the central Baltic. Witek (1995), on the other hand, discussed the percentage contribution of individual species of Baltic copepods in the diet of herring and sprat. Moreover, the results of the latter author indicate that *Pseudocalanus* sp. is the main food of herring, which also feeds on *T. longicornis*, although to a lesser extent. Other copepods make up only a very small percentage of the herring's diet. *T. longicornis* is the main food of sprat, followed by *Pseudocalanus* sp. The contribution of other copepods in the diet of the Baltic sprat is much higher compared to herring (Möllmann et al. 2005).

Accurate knowledge of the species composition, the dominance of particular taxa, density and biomass in combination with abiotic parameters (salinity, temperature, pressure etc.) facilitates the evaluation of changes taking place in an ecosystem. In conjunction with simulation models, such knowledge provides hypothetical forecasts for the future, leading to predictions of the positive or negative effects of environment changes.

5. Conclusion

Although the population dynamics of calanoid copepods in the central Baltic are governed mainly by hydrographic conditions, it seems that in such a relatively shallow and homogeneous region as the Gulf of Gdańsk they do not affect the distribution of these species, apart from seasonal shifts. Of course, it is impossible to draw definitive conclusions owing to the insufficient data available.

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