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ORIGINAL RESEARCH ARTICLE

Seasonal variability in the population dynamics of the main mesozooplankton species in the Gulf of Gdańsk (southern Baltic Sea): Production and mortality rates^{☆,☆☆}

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Summary This manuscript is a continuation of the results presented in the earlier work by Dzierzbicka-Głowacka et al. (2013). Major purpose of this study is to characterize population dynamics of three major Baltic calanoid copepod species (*Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp.) in the Gulf of Gdańsk during the years 2006–2007. This paper focuses mostly on biomass estimation, production and mortality rates. All three species had the highest observed biomass in summer 2007 and it was 12.62, 9.16 and 0.80 mg C m⁻³ for *Acartia* spp., *T. longicornis* and *Pseudocalanus* sp., respectively, while highest daily production rates for those species were 28.22, 18.47, 1.34 mg C m⁻², all recorded in summer 2007. Mortality rates were calculated for all copepodite stages of selected species, and in most cases highest values were observed during summer seasons.

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1. Introduction

Estimates of zooplankton production rates and mortality are a useful tool to obtain knowledge of marine productivity and quantifying transfers between food web components. Mortality is also an important process influencing behaviour, together with food availability and transport processes accounting for distribution and migration patterns (Aksnes and Ohman, 1996; Ohman and Wood, 1996). For example, mortality risk is one of the major explanatory variables used in habitat and behaviour modelling (Aksnes and Giske, 1993); therefore, there is an increasing need for empirical estimates for future application in modelling of Baltic Sea zooplankton.

The Baltic Sea is one of the largest brackish water bodies in the world; its water type and its location in the boreal climate zone determine the nature of the communities of organisms living in this sea. Consequently, zooplankton consists of brackish, marine euryhaline and freshwater species (Hernroth and Ackefors, 1979; Szulz et al., 2012; Wiktor, 1990). According to Wiktor (1990), Gulf of Gdańsk zooplankton typically consisted of euryhaline and eurythermic taxa, where for copepods these are mainly *Temora longicornis*, *Acartia* spp., and *Pseudocalanus* sp.

Recent studies indicate that a *Pseudocalanus* species from the central Baltic, hitherto named *Pseudocalanus elongatus*, might actually be *Pseudocalanus acuspes* (Bucklin et al., 2003; 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.

Data covering the seasonal and spatial variability of the investigated species have been already presented in the earlier work by Dzierzbicka-Głowacka et al. (2013). The main objective of the study is description of production and mortality rate of three major calanoid copepod species (*Acartia* spp., *T. longicornis* and *Pseudocalanus* sp.) in the southern Baltic Sea. The obtained data will be used in future numerical evaluations and for upgrading the copepod population model developed for the southern Baltic (Dzierzbicka-Głowacka, 2005; Dzierzbicka-Głowacka et al., 2006, 2010, 2011, 2013).

2. Material and methods

2.1. Sampling

The data are based on the analysis of samples collected monthly during a 2-year period (2006 and 2007). Samples were collected at six stations located in the western part of the Gulf of Gdańsk, southern Baltic Sea (Fig. 1). Five of the stations (So1 – 5 m, So2 – 10 m, So3 – 20 m, So4 – 30 m, J23 – 40 m) were located on a depth gradient transect and one station (M2 – 10 m depth) was located in Puck Bay. The zooplankton material was collected using a closing-type Copenhagen net of 0.50 m inlet diameter and 100 µm mesh size, equipped with a flowmeter. Qualitative and quantitative laboratory analyses were performed in accordance with the HELCOM guidelines included in the Combine manual Annex C-7 (www.helcom.fi), except for the nauplii, which were identified to species level. Adults of the genus *Acartia* were identified only to genus level, owing to the similarity

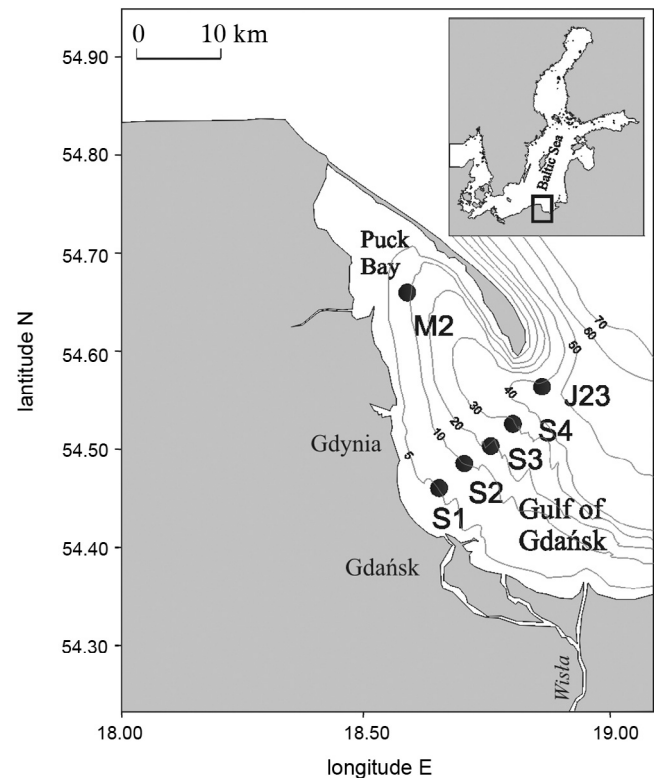


Figure 1 Location of the sampling stations in the Gulf of Gdańsk (southern Baltic Sea).

between the three *Acartia* species, these are referred to as *Acartia* spp.

2.2. Biomass

Biomass was calculated from abundance with weight standards after Hernroth (1985); afterwards, obtained values were integrated over the whole depth layer. Finally, seasonal (winter: December–March, spring: April–June, summer: July–September, autumn: October–December) biomass values were derived by averaging corresponding months (Table 1). Carbon was calculated as 5% of wet weight after Mullin (1969); this conversion rate is usually used for Baltic copepods although as showed by Tanskanen (1994) it may lead to underestimation of zooplankton biomass.

2.3. Copepod production

With assumption of non-limiting food conditions, the production of the investigated species' copepodite stages was

Table 1 Number of samples in corresponding seasons (winter: December–March, spring: April–June, summer: July–September, autumn: October–December).

Year	Winter	Spring	Summer	Autumn
2006	54	18	54	18
2007	24	36	54	30

calculated using Edmondson and Winberg's equation (Edmondson and Winberg, 1971):

$$PC_i = \frac{N_i \times \Delta W_i}{D_i}, \quad (1)$$

where PC_i represents daily potential production of stage i (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 developmental stages were computed using Belehrádek's function (Belehrádek, 1957):

$$D_i = a(T - \alpha)^{-b}, \quad (2)$$

where a is 1288, 1466, 3044, and α is -10.5 , -10.4 , -13.9 for *Acartia* spp., *T. longicornis* and *Pseudocalanus* sp. copepodite stages, respectively, and b value is 2.05, all after McLaren (1978) and McLaren et al. (1989). T was the ambient temperature ($^{\circ}\text{C}$) and was determined for each stage based on its WMD (Dzierzbicka-Głowacka et al., 2013).

2.4. Mortality rates

Estimates of zooplankton mortality were computed with the method described by Aksnes and Ohman (1996). We initially assumed that recruitment rate p_i (ind. day^{-1}) to stage i was constant over a time period corresponding to the duration of the stage α_i (days). Furthermore duration of each stage was constant for every individual, and the mortality for the period α_i can be expressed by a constant θ_i (true mortality rate of the stage i) (day^{-1}).

While estimating mortality we assumed that rate of stage i and $i + 1$ (θ) was considered for a period equal to the corresponding duration of two consecutive stages ($\alpha_i + \alpha_{i+1}$). Then, the life stages can be expressed by the equation:

$$v_{i+1} = p_{i+1} \int_{x-\alpha_{i+1}}^x \exp[-\theta(x-t)] dt, \quad (3)$$

$$v_{i+1} = p_{i+1} [1 - \exp(-\theta\alpha_{i+1})] / \theta,$$

where v_i is the number of individuals in stage i , x is a day, t is time and p_i (ind. day^{-1}) is a true recruitment rate to stage i . The ratio of the numbers of individuals in two consecutive stages is expressed as a function of the mortality and the stage durations:

$$\frac{v_i}{v_{i+1}} = \frac{\exp(\theta\alpha_i) - 1}{1 - \exp(-\theta\alpha_{i+1})}. \quad (4)$$

This equation is not applicable for adults and CV stages, therefore for those stages a different equation was used:

$$\frac{v_{q-1}}{v_q} = \exp(\theta\alpha_{q-1}) - 1, \quad (5)$$

where index q represents the adults and $q - 1$ is a juvenile stage recruiting to the adult stage.

For analyses of zooplankton dynamics, each stage duration should be computed independently (α_i denotes an estimate of α_i). Furthermore, to apply Eqs. (4) and (3) in mortality estimation, estimates of the ratio of the numbers of individuals in two consecutive stages ($r_i = n_i/n_{i+1}$) (n_i – estimate of v_i) are needed (Aksnes and Ohman, 1996). In mortality estimates it is assumed that two successive stages are taken impartially and are under the same influence of

transport processes during these stages. This lead to a mortality estimate designed in the form of the following equations (Aksnes and Ohman, 1996):

$$\frac{[\exp(m\alpha_i) - 1]}{[1 - \exp(-m\alpha_{i+1})]} = r_i \quad (\text{for two juvenile stages}), \quad (6)$$

$$m = \frac{\ln(r_{q-1} + 1)}{\alpha_{q-1}} \quad (\text{for juvenile and adult stage}), \quad (7)$$

where n_i is an estimate of abundance v_i , m is an estimate of θ (day^{-1}), index q is the adult stage and $q - 1$ is a juvenile stage recruiting to the adult stage.

Results of final Copepoda mortality estimates should be the average of several m estimates from multiple sampling.

3. Results

3.1. Biomass

Observed biomass values ranged from 0.01 mg C m^{-3} to a maximum of almost 13 mg C m^{-3} . *Acartia* spp. reached the highest biomass values in both summers (Fig. 2), although in 2007 it was almost three times higher than a year earlier. The variation of biomass between stations was very low, with the exception of So4 station in summer 2007 when visibly higher biomass was noticed, although Mann–Whitney U test showed statistically significant ($p < 0.05$) differences in copepod biomass between series of corresponding months and seasons of both investigated years in regard to each investigated species and between sampling stations. Biomass temporal variability of *T. longicornis* was very similar to *Acartia* spp., but with lower values; highest biomass was also observed in summer (highest in 2007). Although in spatial distribution *T. longicornis* reached higher biomass values at deeper stations (J23, So4, So3). For *Pseudocalanus* sp. maximum biomass was only 0.8 mg C m^{-3} , and there were no noticeable patterns in its variability depending on water temperature, although this species' biomass was clearly concentrated at the deepest stations (J23 and So4). Biomass of both *Acartia* spp. and *T. longicornis* were positively correlated with water temperature (correlation coefficient $r = 0.8$; $p < 0.05$) (except for shallowest stations M2 and So1 for *T. longicornis*), correlation was calculated for mean values for each month, as well as for each sampling station separately. Surprisingly, there was no correlation between biomass of *Pseudocalanus* sp. and temperature, probably because low number of samples belonging to this species were identified. Because of a relatively constant value of salinity observed during our research (Dzierzbicka-Głowacka et al., 2013) it had no significant impact on investigated species.

3.2. Secondary production

Production rates of analysed Copepoda species showed high variability during the research period; there were observed statistically significant differences in production rates between years 2006 and 2007, $p < 0.05$. Production of *Acartia* spp. (stages N-CV) grew from winter 2006 to summer 2006 (Table 2, Fig. 3). In 2006 the highest average production was observed in summer and amounted to 3.85 mg C m^{-2} and

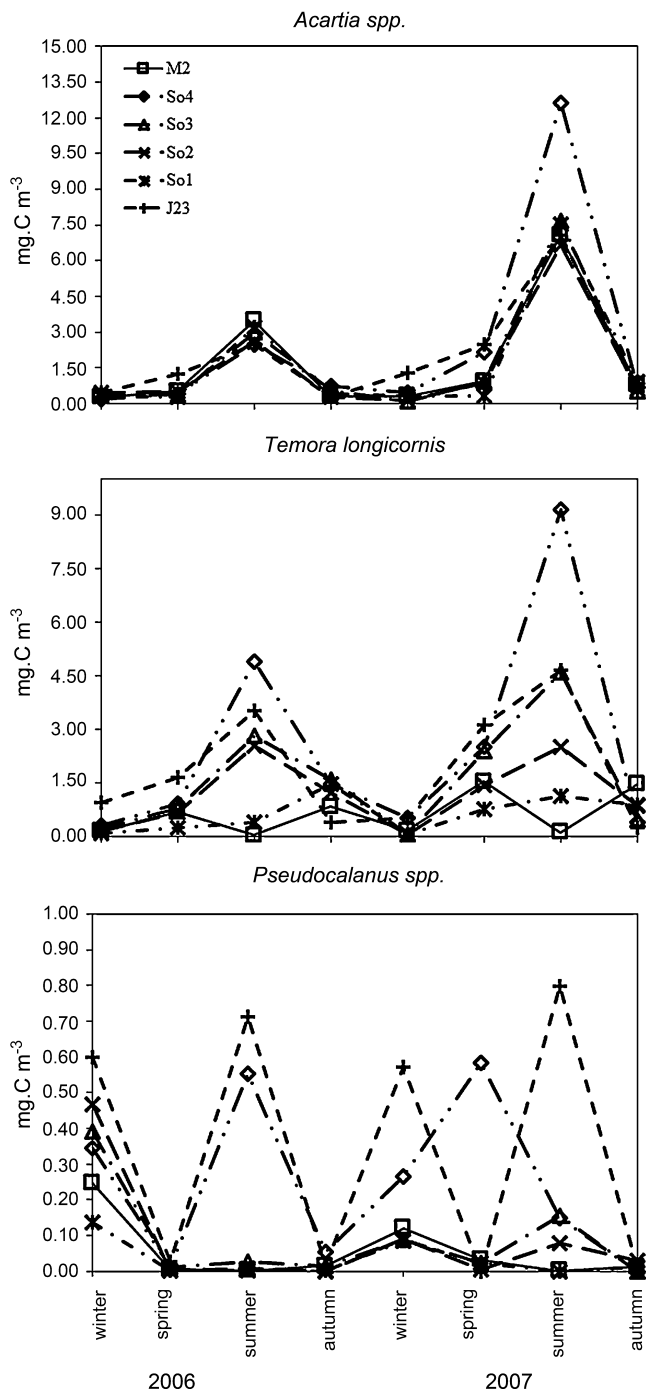


Figure 2 Biomass (mg C m^{-3}) variability of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. at different stations at Gulf of Gdańsk during eight seasons of investigation (winter 2006–autumn 2007).

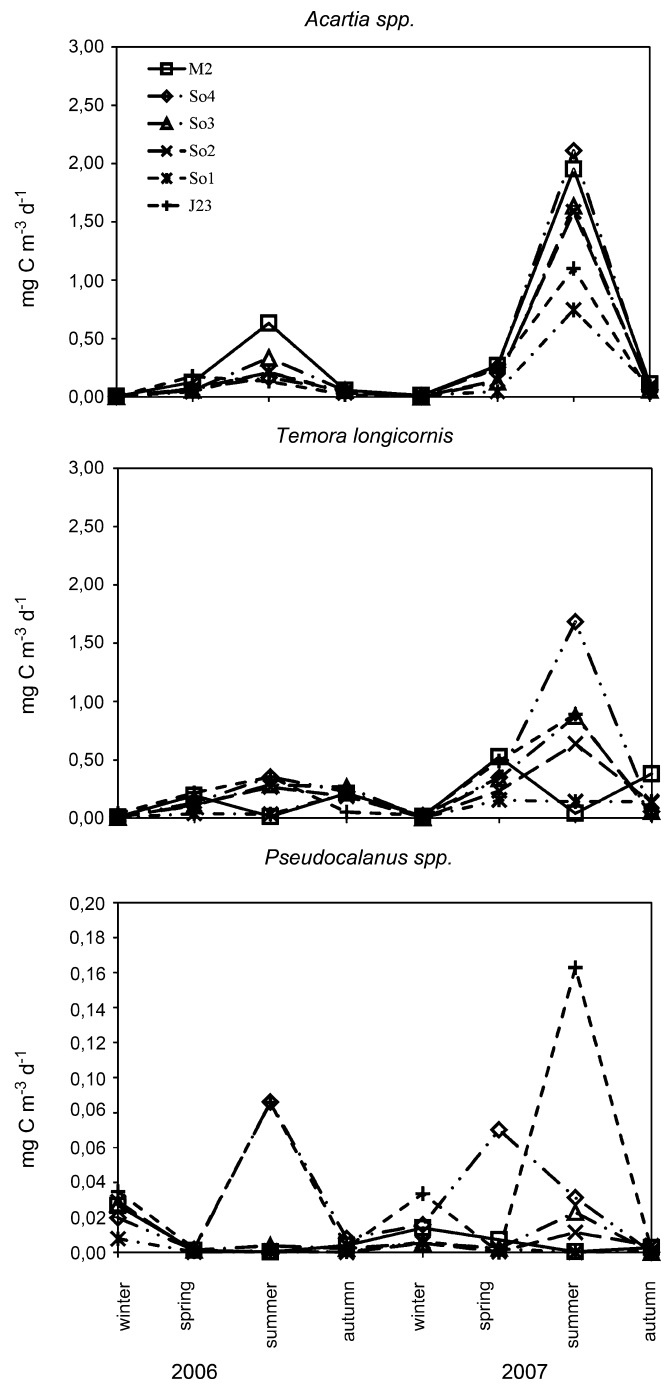


Figure 3 Secondary production of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. at different stations at Gulf of Gdańsk during eight seasons of investigation (winter 2006–autumn 2007).

slowly decreased until winter 2007. In 2007 the production of *Acartia* spp. also began to grow between winter and spring, with the highest ratio from spring to summer and amounted from 3.78 mg C m^{-2} to $28.22 \text{ mg C m}^{-2}$. In autumn 2007 average daily production values of *Acartia* spp. remained low, as in 2006.

T. longicornis (stages N-CV) showed a similar relation between production rate and seasons as it was in the case of *Acartia* spp. In the winter of 2006 and 2007, the average production rate was lowest and increased till summer of 2006. The increase in production was gradual, except 2007 when production rate of *T. longicornis* increased rapidly

Table 2 Average daily production rates ($\text{mg C m}^{-2} \text{ day}^{-1}$ and $\text{mg C m}^{-3} \text{ day}^{-1}$) of *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. life stages N-CV (winter: December–March, spring: April–June, summer: July–September, autumn: October–December).

Year	$\text{mg C m}^{-2} \text{ day}^{-1}$				$\text{mg C m}^{-3} \text{ day}^{-1}$			
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
<i>Acartia</i> spp.								
2006	0.02	1.92	3.85	0.7	0.00	0.09	0.28	0.04
2007	0.07	3.78	28.22	0.99	0.01	0.18	1.52	0.07
<i>Temora longicornis</i>								
2006	0.35	2.82	5.55	2.99	0.01	0.13	0.22	0.19
2007	0.29	7.08	18.47	1.29	0.01	0.35	0.71	0.13
<i>Pseudocalanus</i> sp.								
2006	0.50	0.03	1.02	0.07	0.02	0.00	0.03	0.00
2007	0.35	0.37	1.34	0.02	0.01	0.01	0.04	0.00

reaching a maximum average value of $18.47 \text{ mg C m}^{-2}$ (Table 2, Fig. 3).

Average daily production rates of *Pseudocalanus* sp. (N-CV) did not exceed 1.34 mg C m^{-2} during the 2-year period. The results indicate a higher production in the winter of 2006 than in spring 2006. In the summer of 2006 and 2007, the average production of *Pseudocalanus* sp. reached highest values: 1.02 mg C m^{-2} and 1.34 mg C m^{-2} in 2006 and 2007 respectively (Table 2, Fig. 3).

During the winter and spring of 2007 Copepoda daily production rates remained at a similar level of approximately 0.36 mg C m^{-2} . In autumn 2006, 2007 and winter 2006 the production rate were lowest, and did not exceed 0.07 mg C m^{-2} .

Similarly, for the biomass, there was statistically significant correlation between production values and water temperature as was observed for *Acartia* spp. and *T. longicornis* (correlation coefficient $r = 0.8$; $p < 0.05$) (except for shallowest stations M2 and So1 for *T. longicornis*). There was also no correlation observed for *Pseudocalanus* sp. Due to the way production rates were calculated correlation could only be calculated for seasons, which makes obtained results less reliable. Similarly only season series could be compared between both years, although significant differences between both series were found (Mann–Whitney U test, $p < 0.05$) for each species as well as sampling station.

3.3. Mortality rates

Acartia spp. and *T. longicornis* showed very similar pattern of mortality rates during the investigated period (Fig. 4). For *Acartia* spp., during spring 2006, increase in mortality for all stages was observed. The highest values were recorded in the range of 0.20 – 0.25 day^{-1} for CI, CII, and CIV. After autumn 2006 the mortality rate has fallen to about 0.05 for CI, CII and CIII, and low values persisted for winter 2007. For IV copepodite stage mortality gradually increased until the summer of 2007 and reached a maximum of 0.33 day^{-1} . During the summer–autumn 2007 for CII there was an inverse relation than in 2006. Daily mortality rate has increased over the period of 2007, while in 2006 it was declining (Fig. 4). For CV there was a significant increase in mortality rates between the winter and spring to 0.46 day^{-1} in 2006 and it falls in

summer to 0.18 day^{-1} . In subsequent periods, the trend also indicates a greater increase in mortality in the spring and summer, and autumn and winter daily mortality rates decline.

T. longicornis CI (Fig. 4) showed highest mortality values in winter 2006 (0.24 day^{-1}), which decreases in the autumn of the same year, and in the spring of 2007 (0.19 day^{-1}) and then decreases until the fall of 2007. Similarly, for CIII during both years mortality rate rose in the spring, and then decreased in the autumn. Between autumn 2006 and spring 2007 mortality rates for CI, CIII and CIV could not be calculated. For CV during the winter and spring of 2006 mortality of 0.05 – 0.10 day^{-1} was observed, and reached maximum value in autumn (0.34 day^{-1}). In 2007 maximum mortality rate was recorded in the spring (0.35 day^{-1}).

Due to relatively scarce data for *Pseudocalanus* sp. in many cases mortality rates could not be calculated. For example mortality rates of CI stage are marked only in the spring for both 2006 and 2007, with a similar value of about 0.20 day^{-1} . Similarly CII shows the mortality rate at 0.10 day^{-1} during the spring, summer 2006 and summer 2007. Highest mortality rates for CIV were observed in the summer of 2006 ($>0.80 \text{ day}^{-1}$), and then decreased in autumn to 0.33 day^{-1} . In 2007 mortality rate increased till summer ($>0.70 \text{ day}^{-1}$) and then again decreased in autumn to a value of approximately 0.40 day^{-1} .

Mortality rates of investigated species were significantly different between series of seasons in 2006 and 2007 (Mann–Whitney U test, $p > 0.05$); furthermore the correlation coefficient for *Acartia* spp. mortality rates and water temperature was $r = 0.7$ ($p < 0.05$), $r = 0.8$ ($p < 0.05$) for *T. longicornis* and $r = 0.8$ ($p < 0.05$) for *Pseudocalanus* sp.; however, due to calculations being made on seasonal data and overall low number of calculated mortality data results may be prone to errors.

4. Discussion

4.1. Biomass

Copepod biomass estimates may be biased by the low numbers of sampled stations, relatively long intervals between series and advective transport (Aksnes and Blindheim, 1996)

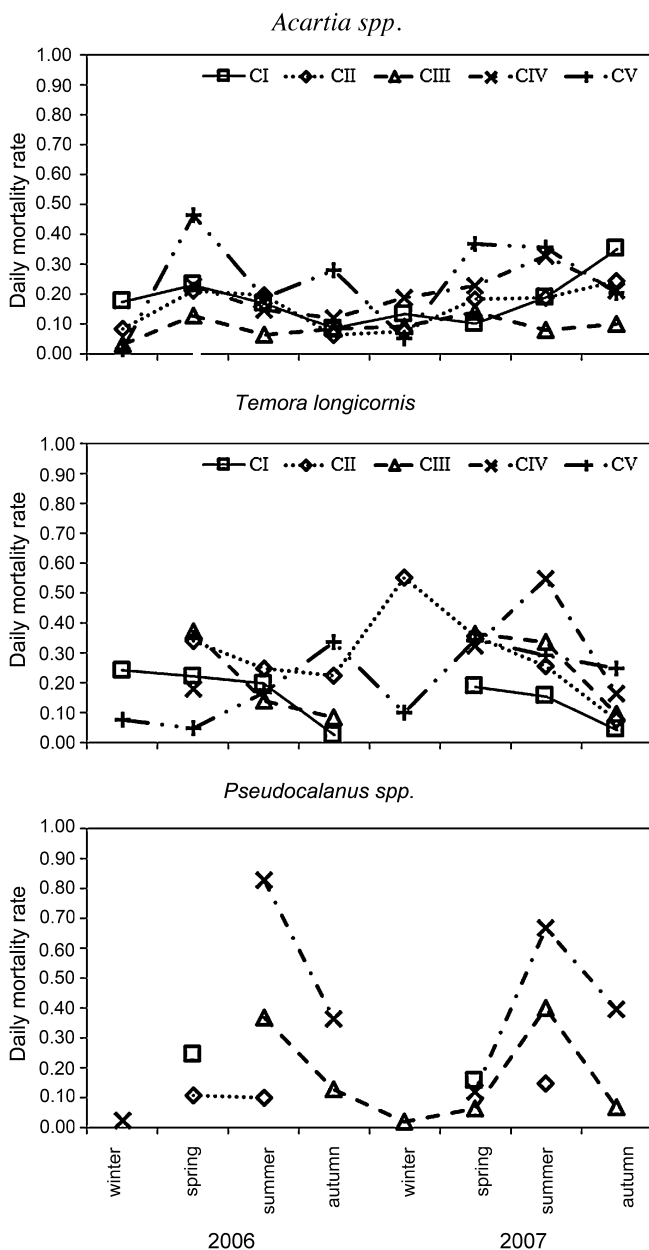


Figure 4 Daily mortality rates of copepodite stages I–V for *Acartia* spp., *Temora longicornis* and *Pseudocalanus* sp. at Gulf of Gdańsk during eight seasons of investigation (winter 2006–autumn 2007).

as well as the difference in the sampling gear used by other authors. It is also clear that a 2-year study period was too short to demonstrate long-term trends. However, analyses of the long-term biomass dynamics in Central Baltic deep basins (Dippner et al., 2000; Kornilovs et al., 2001; Möllmann and Köster, 2002; Möllmann et al., 2000) and in more coastal areas of Baltic Sea (Aleksandrov et al., 2009; Heerkloss and Schnese, 1999; Ojaveer et al., 1998; Vourinen et al., 1998) show very similar standing stocks. Main difference seems to be relatively low biomass values observed in this investigation, which may be related to adopted weight to carbon conversion rate (Tanskanen, 1994) as well as differences in used sampling gear. In conclusion we consider the

observed values as reliable and bringing valuable insight on dynamics of copepod population in Gulf of Gdańsk. *Acartia* spp. and *T. longicornis* are major copepod species in Gulf of Gdańsk (Siudziński, 1977; Szaniawska, 1977; Wiktor and Żmijewska, 1985) as well as in the central Baltic (Hansen et al., 2006). Although there are some major differences in our results and previous researches, Hansen et al. (2006) observed the highest biomass of these species in the spring, when in our research it is rather in the summer; this could indicate some delay in the population development in the coastal zone in relation to the open sea. This seems accurate in relation to other coastal Baltic regions (Ojaveer et al., 1998; Vourinen et al., 1998) where very similar biomass values were observed. Comparison of the both sampling seasons indicates the presence of similar trend but with a clear increase of biomass in 2007, which was most likely related to hydrological conditions (Dzierzbicka-Głowacka et al., 2013). Similarly increased biomass of *T. longicornis* at deeper stations was most likely associated with thermic preferences of this species. This was even more evident in the case of *Pseudocalanus* sp. which prefers deep cold waters below thermocline, which explains the relatively low biomass of this species found during our investigation (Renz and Hirche, 2006; Renz et al., 2007), as well as general declines of this species' biomass observed by other authors (Hansen et al., 2006; Möllmann et al., 2000). As for the *Acartia*, Kang and Kang (2005) described the seasonal variations in biomass and production of one of the dominant copepods from the genus *Acartia* in Ilkwang Bay (Southeastern Coast of Korea). The biomass of this species varied between 0.01 in winter and 4.55 mg C m⁻³ in summer while in our investigation total biomass of *Acartia* spp. was in the range of 0.02–3.85 mg C m⁻³. Studies conducted by Selinova and Moiseenko (2006) in a relatively shallow bay, similar to Gulf of Gdańsk, showed much higher biomass concentration of investigated *Acartia* species (*Acartia tumida*) although overall pattern was very similar and observed differences were an effect of hydrological condition as well as species characteristic.

4.2. Secondary production

During the study period *Acartia* spp. and *T. longicornis* were characterized by the highest production rates in comparison to *Pseudocalanus* sp. (Table 2, Fig. 3). Both those species reached their highest production rates in summer, while winter was the only period with higher production of *Pseudocalanus* sp. This seems to be correlated with natural population dynamics of those species in Baltic Sea (Dippner et al., 2000; Möllmann and Köster, 2002; Renz and Hirche, 2006; Szaniawska, 1977; Szulz et al., 2012; Wiktor and Żmijewska, 1985). Higher production rates of *Acartia* spp. and *T. longicornis* also fit to the trend observed by Möllmann and Köster (2002) and Renz et al. (2007) in the central Baltic. Although observed production rates were few times lower than those noticed by Hansen et al. (2006) than may be related to flaws in our methodology as well as long-term variability. The latter seems to be indicated by the production rates noticed in 2007 which were much closer in value to those observed by Hansen et al. (2006). A similar dynamics of Copepod secondary production was recorded by Kang and Kang (2005) for *Acartia steueri*. For over 2 years of research seasonal production rate for this copepod was the highest in

summer (0.47 mg C m^{-2}), while the lowest values were observed in winter. Similarly to the Gulf of Gdańsk secondary production rates does not exceed 0.1 mg C m^{-2} .

Pseudocalanus sp. is one of the key species in the Baltic Sea (Corkett and McLaren, 1978; Renz and Hirche, 2006; Renz et al., 2007), serving as a major food item for many commercially important fish species. Production rates observed for this species in Gulf of Gdańsk were low in comparison to that observed in Central Baltic (Renz et al., 2007); however this was most likely connected to relatively low depth in investigated area. Möllmann and Köster (2002) observed highest production rates of this species in Bornholm Basin in late spring and summer, with values in the range of $4\text{--}6 \text{ mg C m}^{-2}$, which is around two to three times higher than that observed in this study.

4.3. Mortality rates

In comparison of daily mortality rates of investigated species, lowest fluctuations occur in case of *Acartia* spp. Throughout the study there was a visible trend of increased mortality during spring and summer. This coincides with the observations made by Möllmann and Köster (2002), which implicates that high mortality rates of *Acartia* spp., *T. longicornis* and *Pseudocalanus* sp. in spring and summer may be related to clupeid fish predation (Köster et al., 2001).

For *T. longicornis* our results show a significant difference in mortality between different copepodite stages. In winter and autumn the highest mortality applies for stages CI/CII, and in the summer for CV. Concentrating on summer, we can compare our results of daily mortality rate with those provided by Möllmann and Köster (2002). In the summer of 2006 and 2007, the average mortality rate for CI/CII was in the range $0.10\text{--}0.25$, while in Möllmann and Köster value of mortality in the years 1978–1996 ranged from 0.0 to 0.16 , which may indicate a greater predation by fish on *T. longicornis* or deterioration of environmental conditions affecting this species in The Gulf of Gdańsk.

Pseudocalanus sp. was exposed to predation by sprat mainly in winter and spring, and by herring usually in winter and summer (Möllmann and Köster, 2002). That was not reflected in our data; during winter and spring the daily mortality rate were the lowest, while increasing from spring to summer (about 0.80). However this was most likely caused by relatively low abundance of this species, meaning that effect of predation was negligible, and other processes like advective transport were more visible.

5. Conclusion

Although the data obtained from this study are too scarce to draw any long-term conclusions, they seem to fit to the trends observed in other parts of the Baltic Sea, mostly increase in standing stocks of *Acartia* spp. and *T. longicornis* and decrease of *Pseudocalanus* sp. decline (Dippner et al., 2000; Möllmann and Köster, 2002; Möllmann et al., 2000, 2005; Renz et al., 2007). The same effect was also observed in production rates of those species, especially *Pseudocalanus* sp. which had production rates observed in bay that were several times lower than that observed in Central Baltic (Möllmann and Köster, 2002; Renz et al., 2007). Results obtained in this investigation

show higher mortality of major copepod taxa than it was observed in 1970s, 1980s and 1990s. As the growing trend in the Gulf of Gdańsk seems to be reflecting the situation in other parts of Baltic Sea this could be caused by increased predation of clupeid fish on zooplankton, and it is similar to the situation observed at the beginning of 1990s.

References

- Aksnes, D.L., Blindheim, J., 1996. Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. *Ophelia* 44, 7–28.
- Aksnes, D.L., Giske, J., 1993. A theoretical model of visual aquatic predation. *Ecol. Model.* 67, 233–250.
- Aksnes, D.L., Ohman, M.D., 1996. A vertical life table approach to zooplankton mortality estimation. *Limnol. Oceanogr.* 41, 1461–1469.
- Aleksandrov, S.V., Zhigalova, N.N., Zezera, A.S., 2009. Long-term dynamics of zooplankton in the Southeastern Baltic Sea. *Russ. J. Mar. Biol.* 35 (4), 296–304.
- Belehrádek, J., 1957. Physiological aspects of heat and cold. *Annu. Rev. Physiol.* 19, 59–82.
- Bucklin, A., Frost, B.W., Bradford-Grieve, J., Allen, L.D., Copley, N. J., 2003. Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the *Calanidae* and *Clausocalanidae*. *Mar. Biol.* 142, 333–343.
- Corkett, C.J., McLaren, I.A., 1978. The biology of *Pseudocalanus*. *Adv. Mar. Biol.* 15, 1–231.
- Dippner, J., Kornilovs, G., Sidrevics, L., 2000. Long-term variability of mesozooplankton in the Central Baltic Sea. *J. Plankton Res.* 25, 23–32.
- Dzierzbicka-Głowacka, L., 2005. A numerical investigation of phytoplankton and *Pseudocalanus elongatus* dynamics in the spring bloom time in the Gdansk Gulf. *J. Mar. Syst.* 53, 19–36.
- Dzierzbicka-Głowacka, L., Bielecka, L., Mudrak, S., 2006. Seasonal dynamics of *Pseudocalanus minutus elongatus* and *Acartia* spp. in the southern Baltic Sea (Gdansk Deep) – numerical simulations. *Biogeosciences* 3, 635–650.
- Dzierzbicka-Głowacka, L., Kalarus, M., Żmijewska, M.I., 2013. Inter-annual variability in the population dynamics of the main mesozooplankton species in the Gulf of Gdańsk (southern Baltic Sea): seasonal and spatial distribution. *Oceanologia* 55 (2), 409–434.
- Dzierzbicka-Głowacka, L., Lemieszek, A., Żmijewska, M.I., 2011. Development and growth of *Temora longicornis*: numerical simulations using laboratory culture data. *Oceanologia* 53 (1), 137–161.
- Dzierzbicka-Głowacka, L., Żmijewska, M.I., Mudrak, S., Jakacki, J., Lemieszek, A., 2010. Population modelling of *Acartia* spp. in a water column ecosystem model for the South-Eastern Baltic Sea. *Biogeosciences* 7, 2247–2259.
- Edmondson, W.T., Winberg, G.G., 1971. A manual on methods for the assessment of secondary productivity in freshwaters. *IPB Handbook*, vol. 17. 358 pp.
- Hansen, F.C., Möllmann, C., Schütz, U., Neumann, T., 2006. Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. *J. Plankton Res.* 28 (1), 39–54.
- Heerkloss, R., Schnese, W., 1999. A long-term series of zooplankton monitoring of shallow coastal water of the southern Baltic. *Limnologia* 29, 317–321.
- Hernroth, L., 1985. Recommendations on methods for marine biological studies in the Baltic Sea, *Baltic Marine Biologists*, No. 10. Institute of Marine Research, Lysekil, 32 pp.
- Hernroth, L., Ackefors, H., 1979. The Zooplankton of the Baltic Proper. *Rep. Fish. Bd. Sweden. Inst. Mar. Res.* 2, 1–60.
- Holmborn, T., Goetze, E., Pöllupüü, M., Pöllumäe, A., 2011. Genetic species identification and low genetic diversity in *Pseudocalanus acuspes* of the Baltic Sea. *J. Plankton Res.* 33 (3), 507–515.

- Kang, H.-K., Kang, Y.J., 2005. Production of *Acartia steueri* (Copepoda: Calanoida) in Ilkwang Bay, southeastern Coast of Korea. *J. Oceanogr.* 61, 327–334.
- Kornilovs, G., Sidrevics, I., Dippner, J.W., 2001. Fish and zooplankton interaction in the Central Baltic Sea. *ICES J. Mar. Sci.* 58, 579–588.
- Köster, F.W., Möllmann, C., Neuenfeldt, S., John, St., Plikshs, M.A., Voss, M.R., 2001. Developing Baltic cod recruitment models I: Resolving spatial and temporal dynamics of spawning stock and recruitment. *Can. J. Fish. Aquat. Sci.* 58, 1516–1533.
- McLaren, I.A., 1978. Generation lengths of some temperate marine copepods: estimation, prediction, and implication. *J. Fish. Res. Board Can.* 35, 1330–1342.
- McLaren, I.A., Sévigny, J.M., Corkett, G.L., 1989. Temperature dependent development in *Pseudocalanus* species. *Can. J. Zool.* 67, 559–564.
- Mullin, M.M., 1969. Production of zooplankton in the ocean: the present status and problems. *Oceanogr. Mar. Biol. Rev.* 7, 293–310.
- Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W., 2005. Climate, zooplankton, and pelagic fish growth in the Central Baltic Sea. *ICES J. Mar. Sci.* 62, 1270–1280.
- Möllmann, C., Kornilovs, G., Sidrevics, L., 2000. Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. *J. Plankton Res.* 22, 2015–2038.
- Möllmann, C., Köster, F.W., 2002. Population dynamics of Calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. *J. Plankton Res.* 24, 959–978.
- Ohman, M.D., Wood, S.N., 1996. Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. *Limnol. Oceanogr.* 41, 126–135.
- Ojaveer, E., Lumberg, A., Ojaveer, H., 1998. Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). *ICES J. Mar. Sci.* 55, 748–755.
- Renz, J., Hirche, H.J., 2006. Life cycle of *Pseudocalanus acuspes Giesbrecht* (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. *Mar. Biol.* 148, 467–580.
- Renz, J., Peters, J., Hirche, H.J., 2007. Life cycle of *Pseudocalanus acuspes Giesbrecht* (Copepoda, Calanoida) in the Central Baltic Sea: II. Reproduction, growth and secondary production. *Mar. Biol.* 151, 515–527.
- Selinova, E.N., Moiseenko, A.S., 2006. Seasonal dynamics of *Acartia tumida* Willey, 1920 (Copepoda: Calanoida) population in Near-shore Waters of Kievka Bay, Sea of Japan. *Russ. J. Mar. Biol.* 32 (3), 143–149.
- Siudziński, K., 1977. Zooplankton Zatoki Gdańskiej. *Studia i Materiały Morskiego Instytutu Rybackiego*, Gdynia 18A, 1–111.
- Szaniawska, A., 1977. Skład i sezonowe zmiany zooplanktonu Zatoki Puckiej Właściwej w 1973 i 1974 roku. *Zeszyty naukowe BiNOZ UG* 5, 79–93.
- Szulz, J., Peck, M.A., Barz, K., Schmidt, J.O., Hansen, F.C., Peters, J., Renz, J., Dickmann, M., Mohrholz, V., Dutz, J., Hirche, H.J., 2012. Spatial and temporal habitat partitioning by zooplankton in the Bornholm Basin (central Baltic Sea). *Prog. Oceanogr.* 107, 3–30.
- Tanskanen, S., 1994. Seasonal variability in the individual carbon content of the calanoid copepod *Acartia biflosa* from the northern Baltic Sea. *Hydrobiologia* 292/293, 397–403.
- Vourinen, I., Hänninen, J., Viitasaalo, M., Helminen, U., Kuosa, H., 1998. Proportion of copepod biomass declines together with decreasing salinities in the Baltic Sea. *ICES J. Mar. Sci.* 55, 767–774.
- Wiktor, K., 1990. Zooplankton. In: Majewski, A. (Ed.), *Zatoka Gdańska*. Wyd. Geologiczne, Warszawa, 100–105.
- Wiktor, K., Żmijewska, M.I., 1985. Skład i rozmieszczenie zooplanktonu przybrzeżnych wód Zatoki Gdańskiej Właściwej, SIMO nr 46. *KBM PAN Biol. Morza* 7, 70–111.