

1 Article

2 **The interannual changes in the secondary production and mortality rate of main copepod species**  
3 **in the Gulf of Gdańsk (the southern Baltic Sea)**

4 Lidia Dzierzbicka-Głowacka <sup>1\*</sup>, Maja Musialik-Koszarowska <sup>1</sup>, Marcin Kalarus <sup>2</sup>, Anna  
5 Lemieszek <sup>2</sup>, Paula Prątnicka <sup>3</sup>, Maciej Janecki <sup>1</sup> and Maria Iwona Żmijewska <sup>3</sup>

6 <sup>1</sup> Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot,  
7 Poland; dzierzb@iopan.pl; m.musialik@ug.edu.pl; mjanecki@iopan.pl

8 <sup>2</sup> Maritime Institute of Gdańsk, Długi Targ 41/42, 80-830 Gdańsk, Poland;  
9 Anna.Lemieszek@im.gda.pl; Marcin.Kalarus@im.gda.pl

10 <sup>3</sup> Institute of Oceanography, University of Gdańsk, Av. Marszałka Piłsudskiego 46, 81-378 Gdynia,  
11 Poland; paula.kacprzak@phdstud.ug.edu.pl; maria.iwona.zmijewska@ug.edu.pl

12 Correspondence: dzierzb@iopan.pl; Tel.: (+48 58 731 19 15)

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14 **Abstract:** The main objective of this paper was description of seasonal and interannual trends in  
15 secondary production and mortality rates of the three most important Copepoda taxa in the Gulf of  
16 Gdańsk (southern Baltic Sea). Samples were collected monthly from 6 stations located in the  
17 western part of the Gulf of Gdańsk during three research periods: 1998-2000, 2006-2007 and  
18 2010-2012. Production was computed basing on copepod biomass and mortality rates estimated  
19 according to vertical life table approach. Redundancy analysis was used to investigate relationship  
20 between secondary production and environmental conditions. Considering the entire research  
21 period there was significant interannual and seasonal variability of secondary production,  
22 mortality rate as well as abundance and biomass anomalies. Conducted analysis revealed  
23 correlation between increasing temperature and production of *Acartia* spp. and *T.longicornis*  
24 developmental stages, while older copepodites of *P.acuspes* showed almost negative correlation  
25 with temperature. The mortality rate estimations obtained for *Acartia* spp. Were highest in summer,  
26 while for *T.longicornis* peak was usually noted in spring-summer period. Lowest mortality rate  
27 estimations were noted in autumn and winter for almost all stages of investigated taxa.

28 **Keywords:** Copepoda; Secondary production; Mortality rates; Baltic Sea; Gulf of Gdańsk

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30 **1. Introduction**

31 The Baltic Sea is a unique ecosystem, and due to its inland character, large drainage area and  
32 limited exchange of sea water with the Atlantic it is very sensitive to the ongoing natural and  
33 anthropogenic (climate change, pollution, eutrophication, overfishing) changes. The coastal zone is  
34 especially vulnerable, and in similarity to other regions of the Baltic Sea, exhibits little variety in the  
35 number of animal species, which is the result of eutrophication and the degradation of the  
36 environment. Despite this, it is considered among the marine habitats with the highest biological  
37 productivity. It plays an important ecological role by offering a variety of habitat types for many  
38 species, giving shelter to animals, and functioning as nursery areas and feeding grounds for many  
39 marine fishes and crustaceans.

40 In marine pelagic food webs, zooplankton plays a key role as an important link in energy  
41 transfer between primary producers and higher tier consumers, strongly influencing fish  
42 production. Zooplankton of the Gulf of Gdańsk typically consists of euryhaline and eurythermic  
43 taxa, among copepods mainly species from genera *Acartia* and *Temora longicornis*, as well as the less  
44 abundant but ecologically important *Pseudocalanus acuspes*. They are preferred prey items for  
45 commercially important fishes like sprat and herring as well as larval cod.

46 In order to properly assess the role of zooplankton in the marine food web, zooplankton  
47 secondary production and mortality rates need to be estimated. It is a useful tool to obtain

48 knowledge of marine productivity, quantifying, behavior, distribution, migration patterns, and  
49 transfers between food web components [1-3]. Many studies have focused on vital rates of copepods  
50 in the laboratory [4-10], yet only few studies exist on its population dynamics in the field [11-17].

51 The aim of this study was to describe the secondary production and mortality rates of three  
52 dominant calanoid copepod species *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* in the  
53 southern Baltic Sea with relation to hydrographic water conditions. The data will be used for  
54 upgrading the copepod population model for the Baltic Sea [18-22].

## 55 2. Materials and Methods

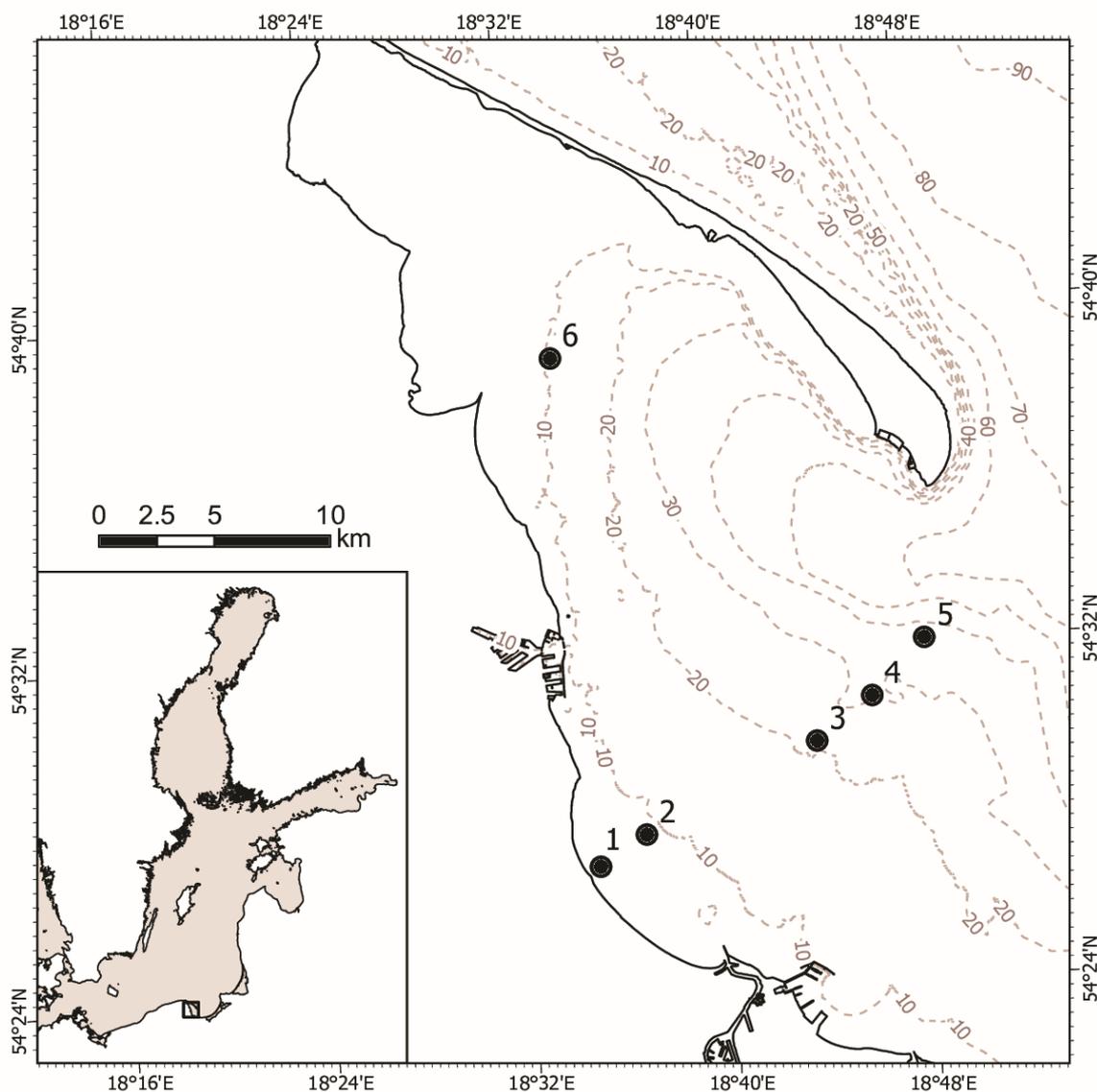
### 56 2.1. Study area

57 The Gulf of Gdańsk is a widely open gulf located in the southern part of the Baltic Sea, between  
58 Poland and Russia. The western part of the bay can be separated into a shallow part known as Puck  
59 Bay and further to the west the semi-enclosed Puck Lagoon. The bay is strongly influenced by river  
60 waters, especially by its largest river, the Vistula, which on average brings  $1\,080\text{ m}^3\text{ s}^{-1}$  of fresh water.  
61 The average depth of the gulf is about 50 m, with the maximum depth (Gdańsk Deep) of 118 m. Water  
62 temperature ranges from over 20 °C at the surface during summer, with the maximum usually in  
63 August, to around 2 °C in February. Water stratification is frequent during the warmer months,  
64 leading to the occurrence of seasonal thermocline, while during the winter gulf waters become  
65 well-mixed. Due to the brackish character the Baltic Sea, gulf water salinity stays within the range of  
66 7-8. Surface waters, especially in the coastal region, can be less saline due to river discharge. Halocline  
67 is present in the deepest part of the gulf, mainly in the region of Gdańsk Deep. Due to high  
68 eutrophication and frequent algal bloom, water transparency varies highly depending on the season,  
69 from a few meters to even 16 m.

70 Hydrology of the gulf is heavily impacted by the Vistula River, which is the largest river flowing  
71 into the bay, bringing fresh water and nutrients. The gulf is also the location of the largest Polish ports:  
72 Gdańsk and Gdynia, which have a significant impact on its environment due to pollution, sea  
73 transport and fishing.

### 74 2.2. Sampling

75 Sampling stations were located at a depth gradient in the central part of the bay (stations 1-5);  
76 one station was also located in the shallower, semi-enclosed Puck Bay (6) (Figure 1).



77

78 **Figure 1.** Study area and location of the sampling stations in the Gulf of Gdańsk (southern  
79 Baltic Sea).

80 Conducted research included: investigation of spatial and temporal variations of hydrological  
81 conditions (temperature and salinity) as well as investigations of the qualitative and quantitative  
82 structure of three main copepod taxa (*Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes*).  
83 Sampling was conducted during three separate projects spanning almost 14 years, from 1998 to 2012.  
84 the first sampling period lasted from August 1998 to September 2000, the second took place in  
85 2006-2007, and the last one in 2010-2012. During the sampling campaigns zooplankton samples were  
86 collected with almost monthly coverage. Two types of sampling nets were used: from 1998 to 2007  
87 samples were collected with a Copenhagen type net, and since 2010 the WP-2 type net was utilized.  
88 Both types of nets were of 100  $\mu$ m mesh size. Samples were collected with vertical hauls; at stations  
89 shallower (1, 2, 6) haul was conducted from the bottom to the surface, while at deeper stations (3, 4,  
90 5) the water column was divided into 10 m layers. All samples were collected during the daytime  
91 (mainly between 11 am and 2 pm) so the diurnal vertical migrations were not accounted for. Along  
92 with the collection of biological material water, physicochemical conditions (T, S) were measured.  
93

## 94 2.3. Model data

95 The source of the numerical results used in the manuscript is the “Baltic Sea Biogeochemical  
96 Reanalysis” product which provides a 24 years biogeochemical reanalysis for the Baltic Sea  
97 (1993-2016) using the ice-ocean model NEMO-Nordic (based on NEMO-3.6, Nucleus for European  
98 Modelling of the Ocean) coupled with the biogeochemical model SCOBI (Swedish Coastal and  
99 Ocean Biogeochemical model) together with LSEIK data assimilation. Values for all the presented  
100 variables (dissolved oxygen and chlorophyll *a*) have been derived from the daily means. Direct files  
101 have been accessed and downloaded upon registration via a Copernicus Marine Environment  
102 Monitoring Service’s (CMEMS) and choosing the BALTICSEA\_REANALYSIS\_BIO\_003\_012  
103 product. Detailed description of the product is available as an online resource in the documentation  
104 section. In particular, a Product User Manual [23] that covers detailed Production Subsystem  
105 Description as well as Quality Report of the product [24] which provides an estimated accuracy  
106 numbers for each variable summarized in the table below (Table 1).

107 **Table 1.** Estimated accuracy of the numerical model data according to quality information  
108 document.

| RMS error                                  | 0-5 m | 5-30 m | 30-80 m |
|--|-------|--------|---------|
| Dissolved oxygen (mmol m <sup>-3</sup> )   | 19    | 38     | 51      |
| Chlorophyll <i>a</i> (mg m <sup>-3</sup> ) | 5     | 3      | 0.9     |

109

110 Each in-situ station has been paired with the closest grid cell in the product’s model domain  
111 estimating the minimal distance between station and each grid cell using longitude and latitude  
112 meta information. Vertical means were calculated for the related timeseries.

## 113 2.4. Biomass and abundance

114 Collected zooplankton samples were analyzed in terms of qualitative and quantitative  
115 descriptions of three copepod taxa, key for southern Baltic mesozooplankton populations: *Acartia* spp.  
116 (including *A. bifilosa*, *A. longiremis* and *A. tonsa*), *Temora longicornis* and *Pseudocalanus acuspes*. All analysis  
117 was performed in accordance with the HELCOM COMBINE methodology [25]. Obtained abundances  
118 were then used to calculate the numbers of individuals per m<sup>2</sup> and m<sup>3</sup>. Finally, standard weights [26]  
119 were used to estimate the biomass values (mg C) of each of the taxa per m<sup>3</sup>.

120 Obtained biological data were normalized by transforming to natural logarithms (ln(x+1)).  
121 Copepod abundances and biomasses were averaged over stations and the seasonal cycle was removed  
122 subtracting long-term monthly means from annual monthly means.

123 Abundance values (ind. m<sup>-2</sup>) were next used to calculate secondary production rates and  
124 mortality rates of the abovementioned copepod taxa.

## 125 2.5. Secondary production

126 Production rates of the investigated species were calculated with the Edmondson and Winberg  
127 equation [27]. Calculations were carried out for each of the copepodite stages with assumption of  
128 non-limiting food conditions:

$$PC_i = N_i * \Delta W_i / D_{\min i} \quad (1)$$

129 where  $PC_i$  is daily potential production of stage  $i$  (wet weight),  $i$  is the development stage,  $D_{\min i}$  is  
130 the development time of stage  $i$  (day<sup>-1</sup>),  $\Delta W_i$  is the weight increase of stage  $i$  and  $N_i$  is the abundance  
131 of stage  $i$  (ind. m<sup>-2</sup>).  $D_{\min}$  of developmental stages were computed using the function provided by  
132 Figiela et al. [28]:

$$D_{\min} = f(T), \quad (2)$$

133 where  $D_{\min}$  is the minimum value of the development time, for which the growth rate of an  
 134 individual is not limited by food availability. The wet weights of the copepodite stages and adults  
 135 were accepted after Hernroth [26]. The conversion factor of 0.05 after Mullin [29] was used to  
 136 transform the wet weight to carbon content.

137 The development time  $D$  is a function of three variables: concentration of food  $Food$  (food  
 138 availability varying depending on season [22]), temperature  $T$ , and salinity  $S$ .  $D_{\min}$  was described for  
 139 each species at the nauplius and I to V copepodid developmental stages, by the equations described by  
 140 Figiela [28].

141 For *Acartia* spp.:

$$ft = \begin{cases} 1 & \text{for } T \leq 19 \text{ }^{\circ}\text{C}, \\ 0.9957 e^{0.0181 (T - 19)} & \text{for } T \geq 19 \text{ }^{\circ}\text{C}, \end{cases} \quad (3)$$

$$fs = 2 - (1 - \exp(-0.9 (S - 0.001))), \quad (4)$$

142 *Acartia* spp. nauplii:

$$D_N = [31.34 e^{-0.092 T} + 4921.7 Food^{-1.7462} e^{-(0.1805 Food^{-0.1061}) T}] ft fs, \quad (5)$$

143 *Acartia* spp. copepodite:

$$D_C = [40.956 e^{-0.0849 T} + 1178.5 Food^{-1.0486} e^{-(0.0739 Food^{0.1059}) T}] ft fs, \quad (6)$$

144 For *Temora longicornis*:

$$ft = \begin{cases} 1 & \text{for } T \leq 15 \text{ }^{\circ}\text{C}, \\ 0.9972 e^{0.0269 (T - 15)} & \text{for } T \geq 15 \text{ }^{\circ}\text{C}, \end{cases} \quad (7)$$

$$fs = 2 - (1 - \exp(-0.5 (S - 2))), \quad (8)$$

145 *Temora longicornis* nauplii:

$$D_N = [39.565 e^{-0.0964 T} + 61 e^{-0.0081 Food} e^{-(0.0006 Food + 0.0588) T}] ft fs, \quad (9)$$

146 *Temora longicornis* copepodite:

$$D_C = [38.693 e^{-0.0809 T} + 57.438 Food^{-0.0037} e^{-(0.0007 Food + 0.0517) T}] ft fs, \quad (10)$$

147 For *Pseudocalanus acuspes*:

$$ft = \begin{cases} 1 & \text{for } T \leq 14 \text{ }^{\circ}\text{C}, \\ 0.9993 e^{0.0377 (T - 14)} & \text{for } T \geq 14 \text{ }^{\circ}\text{C}, \end{cases} \quad (11)$$

$$fs = 3 - (2 - \exp(-0.25 (S - 9))), \quad (12)$$

148 *Pseudocalanus acuspes* nauplii:

$$D_N = [41.342 e^{-0.069 T} + 2.679 T^{1.0988} e^{(0.0209 \ln T - 0.0829) Food}] ft fs, \quad (13)$$

149 *Pseudocalanus acuspes* copepodite:

$$D_C = [34.888 e^{-0.0781 T} + 1.786 e^{1.0988 \ln T} e^{-(0.0559 e^{-0.0486 T}) Food}] ft fs, \quad (14)$$

150 2.6. Mortality rate

151 Mortality rates of the three investigated taxa were computed with Aksnes and Ohman [1]  
 152 method, which is based on the abundances at different developmental stages.

153 While estimating mortality rate of stage  $i$  and  $i+1$  ( $\theta$ ) stage duration was considered for a period  
 154 equal to the corresponding duration of two consecutive stages ( $\alpha_i + \alpha_{i+1}$ ) and it is assumed that the two  
 155 successive stages are taken impartially and are under the same influence of transport processes during  
 156 these stages. This led to the following formula of mortality estimates [1]:

157 For nauplii and copepodite stages CI to CIV:

$$(e^{mD_i} - 1) / (1 - e^{-mD_{i+1}}) = Z_i / Z_{i+1} \quad (15)$$

158 For copepodite stage CV (since the stage duration of adults is infinite):

$$m = [\ln(Z_i / Z_{adult}) + 1] / D_i \quad (16)$$

159 where  $Z_i$  is the abundance of the developmental stage  $i$ ,  $Z_{adult}$  is the abundance of adults,  $Z_{i+1}$  is the  
 160 abundance of next stage ( $i+1$ ),  $m_i$  is instantaneous mortality rate of stage  $i$  ( $d^{-1}$ ),  $D$  followed by  
 161 subscripts are stage durations of copepodite stages  $i$  and  $i+1$ .

## 162 2.7. Statistical analyses

163 The obtained biomass of copepods developmental stages was square root transformed prior to  
 164 analysis. Similarities between samples were examined using the Euclidean distance index, depicted as  
 165 a non-metric multidimensional scaling (nMDS) [31], which illustrated similarities between analyzed  
 166 seasons. One-way Analyses of Similarities (ANOSIM) were performed in order to test the significance  
 167 between sampling seasons, years and stations. The association between temperature and each  
 168 developmental stage of all investigated copepod species was fitted using generalized linear models  
 169 (GLMs) with normal distribution. Additionally, means plots were carried out to illustrate the  
 170 production and mortality of different developmental stages of copepods according to analyzed  
 171 seasons. All analyses were performed in PRIMER version 7 [31] and CANOCO version 5 [32].

## 172 3. Results

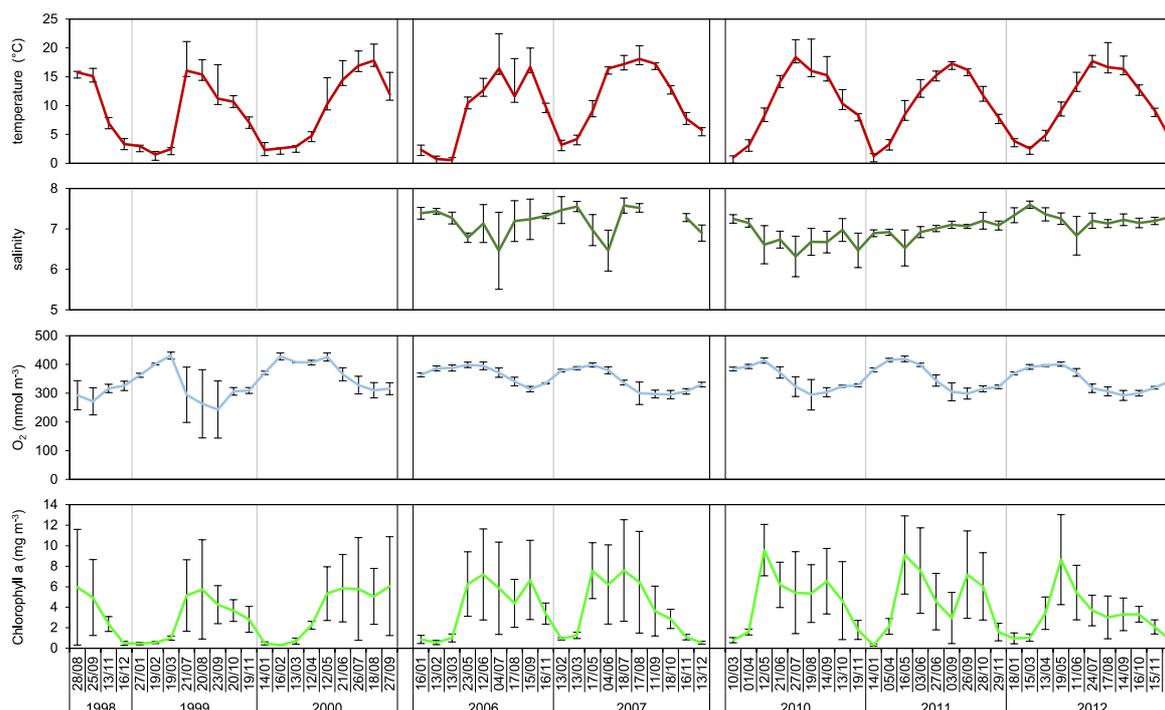
### 173 3.1. Hydrology

174 The water temperature was characterized by a very similar distribution throughout the whole  
 175 study period, with summer to winter fluctuations typical for the temperate climate region. Mean  
 176 values of water temperature noted at the investigated region ranged from  $0.57 \pm 0.43$  °C in March  
 177 2006 to  $18.42 \pm 3.03$  °C in August 2010 (Figure 2).

178 Due to technical reasons, salinity values were not recorded during the first sampling campaign.  
 179 Recorded salinity fluctuations were minimal, and did not exceed 1; mean values ranged from  
 180  $6.32 \pm 0.50$  in July 2010 to  $7.60 \pm 0.09$  in March 2012 (Figure 2).

181 The mean oxygen concentration during the study was also relatively constant. The maximum  
 182 values were observed in the spring (about  $400 \text{ mmol O}_2 \cdot \text{m}^{-3}$ ) and the minimum in August/September  
 183 (about  $300 \text{ mmol O}_2 \cdot \text{m}^{-3}$ ) (Figure 2). The oxygen concentration was at the same level at all sampling  
 184 stations except stations shallower than 10 m (1, 2, 6), where it was generally slightly lower.

185 The highest mean values of chlorophyll  $a$  concentration was reached in May of 2010, 2011 and  
 186 2012 with average value about  $9 \text{ mg m}^{-3}$ . In the spring/summer period the values were generally  
 187 over  $5 \text{ mg m}^{-3}$ . The minimum chlorophyll  $a$  concentration was always noted in the winter. In the  
 188 annual cycle, usually two different peaks in chlorophyll  $a$  concentration was observed, in May and  
 189 September (Figure 2). The highest values of chlorophyll  $a$  concentration was noted at shallow  
 190 stations (1, 2, 6) and the lowest at the deepest sampling station (5).



191

192 **Figure 2.** Water temperature, salinity, dissolved oxygen and chlorophyll *a* ( $\pm$  standard  
 193 deviation) in the Gulf of Gdańsk.

### 194 3.2. Abundance and biomass anomalies

195 Both abundance and biomass of the considered taxa were highly seasonal. After a decrease at  
 196 the beginning of the year, mainly in February, peak abundances and biomasses were found in  
 197 summer. In the case of *Acartia* spp. highest abundance was observed in August while biomass  
 198 peaked in July; for *T.longicornis* both abundance and biomass peaks were found in July; while  
 199 *P.acuspes* had its abundance peak in May, for biomass it was in August. The seasonal development,  
 200 with maximum abundance and biomass in summer, is confirmed by monthly long-term means  
 201 (Table 2, Table 3).

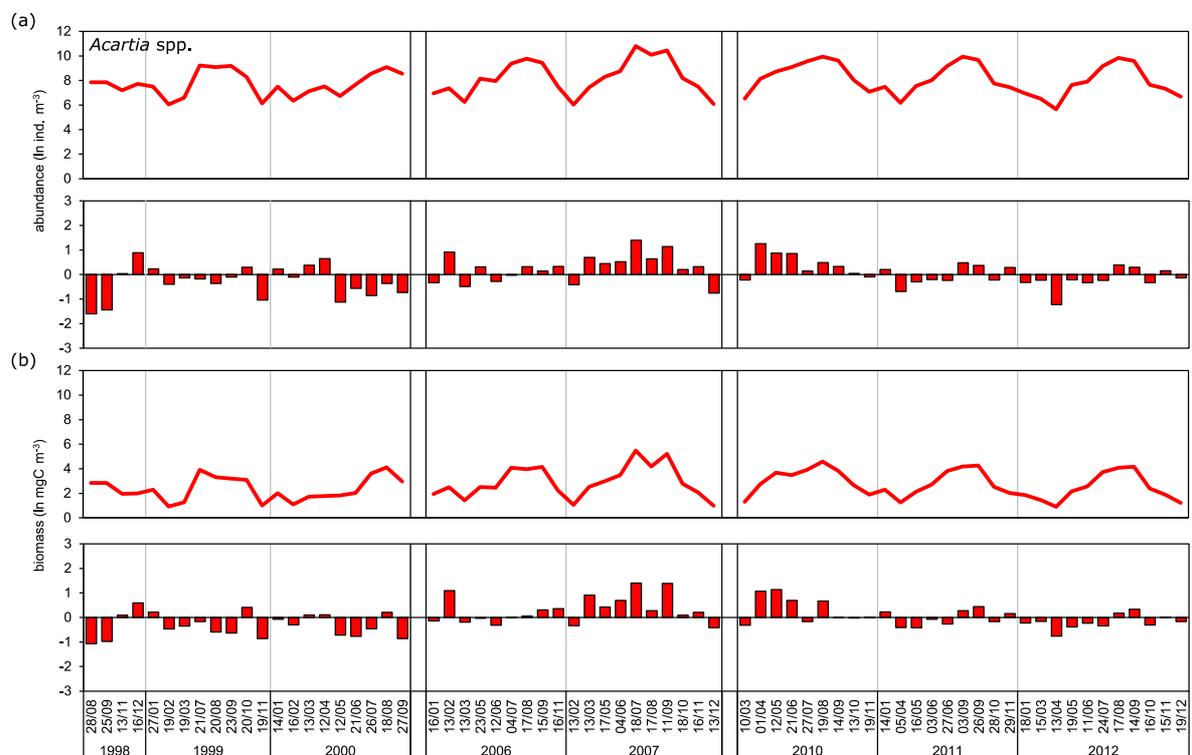
202 **Table 2.** Long-term monthly means ( $\pm$  standard deviation) for abundance (ln ind.  $m^{-3}$ ) of  
 203 three copepod taxa.

| Month     | <i>Acartia</i> spp. | <i>T.longicornis</i> | <i>P.acuspes</i> |
|-----------|---------------------|----------------------|------------------|
| January   | 7.28 $\pm$ 0.30     | 5.26 $\pm$ 0.63      | 4.27 $\pm$ 0.43  |
| February  | 6.45 $\pm$ 0.63     | 4.62 $\pm$ 1.26      | 4.34 $\pm$ 1.60  |
| March     | 6.74 $\pm$ 0.44     | 4.87 $\pm$ 0.62      | 5.21 $\pm$ 0.71  |
| April     | 6.88 $\pm$ 1.15     | 5.09 $\pm$ 1.11      | 4.86 $\pm$ 0.83  |
| May       | 7.85 $\pm$ 0.70     | 8.19 $\pm$ 1.04      | 4.95 $\pm$ 0.52  |
| June      | 8.23 $\pm$ 0.56     | 8.49 $\pm$ 0.41      | 4.38 $\pm$ 0.76  |
| July      | 9.41 $\pm$ 0.69     | 9.10 $\pm$ 0.87      | 4.04 $\pm$ 2.34  |
| August    | 9.46 $\pm$ 0.75     | 7.58 $\pm$ 0.93      | 4.38 $\pm$ 2.83  |
| September | 9.30 $\pm$ 0.78     | 6.94 $\pm$ 1.14      | 3.02 $\pm$ 2.10  |
| October   | 7.98 $\pm$ 0.27     | 7.41 $\pm$ 0.15      | 3.29 $\pm$ 0.92  |
| November  | 7.18 $\pm$ 0.49     | 7.46 $\pm$ 0.66      | 4.04 $\pm$ 0.78  |
| December  | 6.83 $\pm$ 0.83     | 6.39 $\pm$ 0.69      | 2.78 $\pm$ 2.42  |

204 **Table 3.** Long-term monthly means ( $\pm$  standard deviation) for biomass (ln mgC  $m^{-3}$ ) of  
 205 three copepod taxa.

| Month     | <i>Acartia</i> spp. | <i>T.longicornis</i> | <i>P.acuspes</i> |
|-----------|---------------------|----------------------|------------------|
| January   | 2.08 ± 0.21         | 1.54 ± 0.48          | 0.69 ± 0.24      |
| February  | 1.39 ± 0.74         | 1.29 ± 0.98          | 1.01 ± 1.17      |
| March     | 1.62 ± 0.47         | 1.26 ± 0.44          | 1.01 ± 0.52      |
| April     | 1.67 ± 0.80         | 1.13 ± 0.53          | 0.67 ± 0.33      |
| May       | 2.55 ± 0.68         | 2.94 ± 0.69          | 0.41 ± 0.20      |
| June      | 2.79 ± 0.59         | 3.21 ± 0.38          | 0.29 ± 0.12      |
| July      | 4.08 ± 0.64         | 3.85 ± 0.77          | 0.62 ± 0.85      |
| August    | 3.91 ± 0.56         | 3.01 ± 1.13          | 1.07 ± 0.80      |
| September | 3.83 ± 0.80         | 1.92 ± 0.80          | 0.40 ± 0.49      |
| October   | 2.69 ± 0.27         | 2.45 ± 0.21          | 0.25 ± 0.21      |
| November  | 1.87 ± 0.40         | 2.50 ± 0.58          | 0.47 ± 0.30      |
| December  | 1.40 ± 0.53         | 1.52 ± 0.53          | 0.30 ± 0.28      |

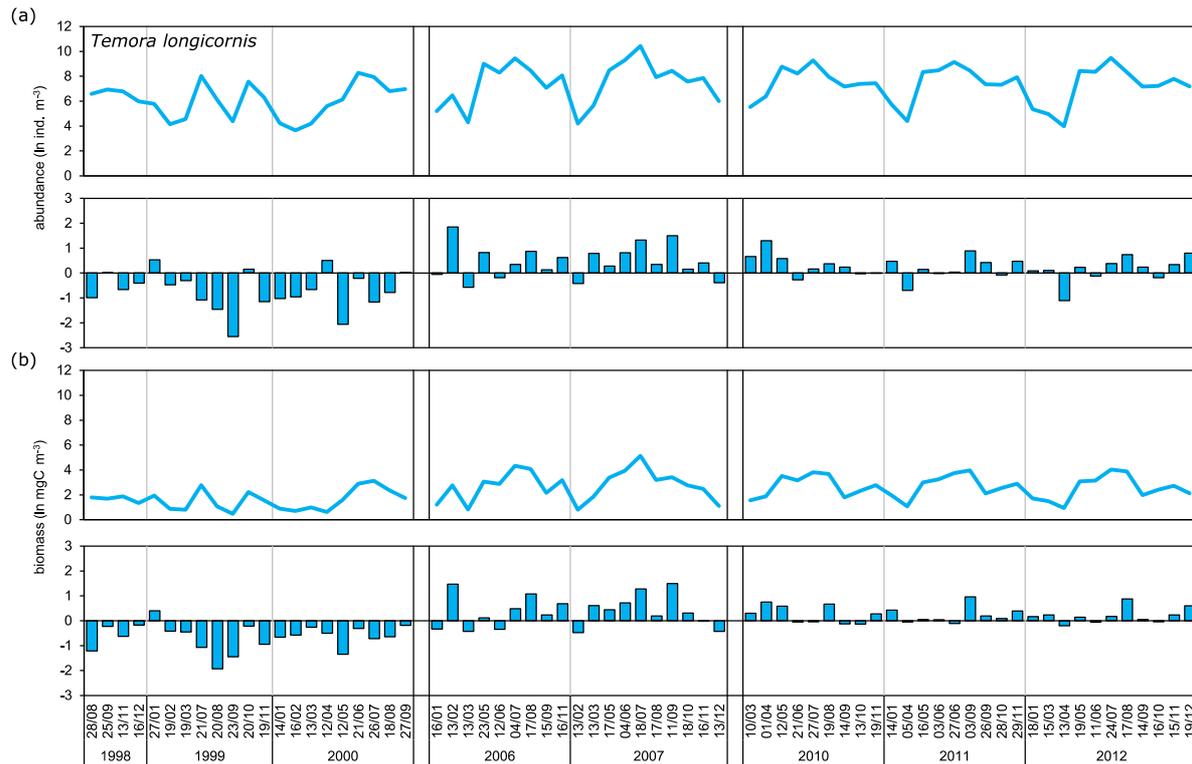
206 The abundance and biomass of *Acartia* spp. (Figure 3) showed negative non-seasonal anomalies  
 207 during the first research period (1998-2000); it became positive during the second research period  
 208 (2007) and at the beginning of the third period (2010) to later become mostly negative (2011-2012).  
 209 The second of the investigated copepods, *T.longicornis*, also showed negative non-seasonal  
 210 anomalies during the period from 1998 to 2000, while in the second research period (2006-2007)  
 211 observed anomalies were mostly positive. This was also true for the beginning of 2010; later it came  
 212 closer to 0, and again positive at the end of 2011 (Figure 4). Anomalies for *P.acuspes* showed a similar  
 213 trend, with negative anomaly during the first research period, especially during 1998 and 1999.  
 214 During the second research period observed anomalies for that species were mostly positive, with a  
 215 drop at the end of 2007. In the third research period anomalies were mostly positive, especially in  
 216 2010, with occasional negative values in 2011 and 2012 (Figure 5).



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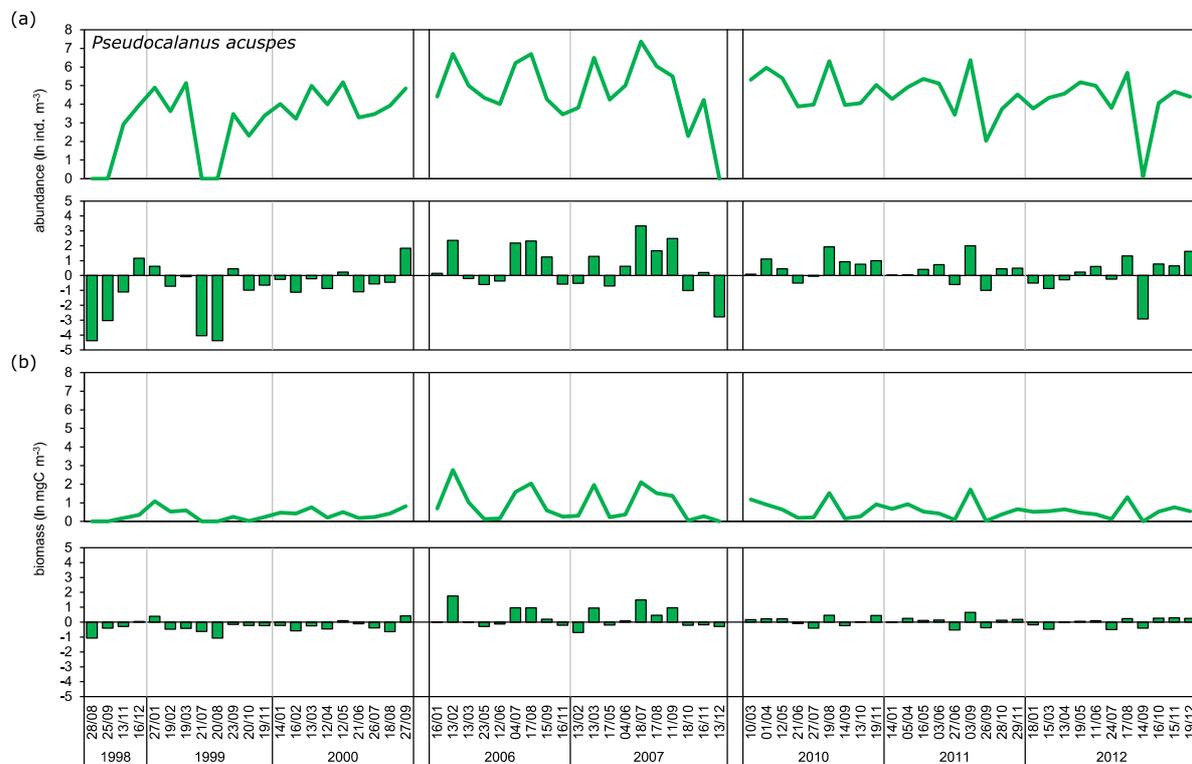
Figure 3. Interannual (a) abundance and (b) biomass monthly mean and anomaly of *Acartia* spp..



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**Figure 4.** Interannual (a) abundance and (b) biomass monthly mean and anomaly of *Temora longicornis*.



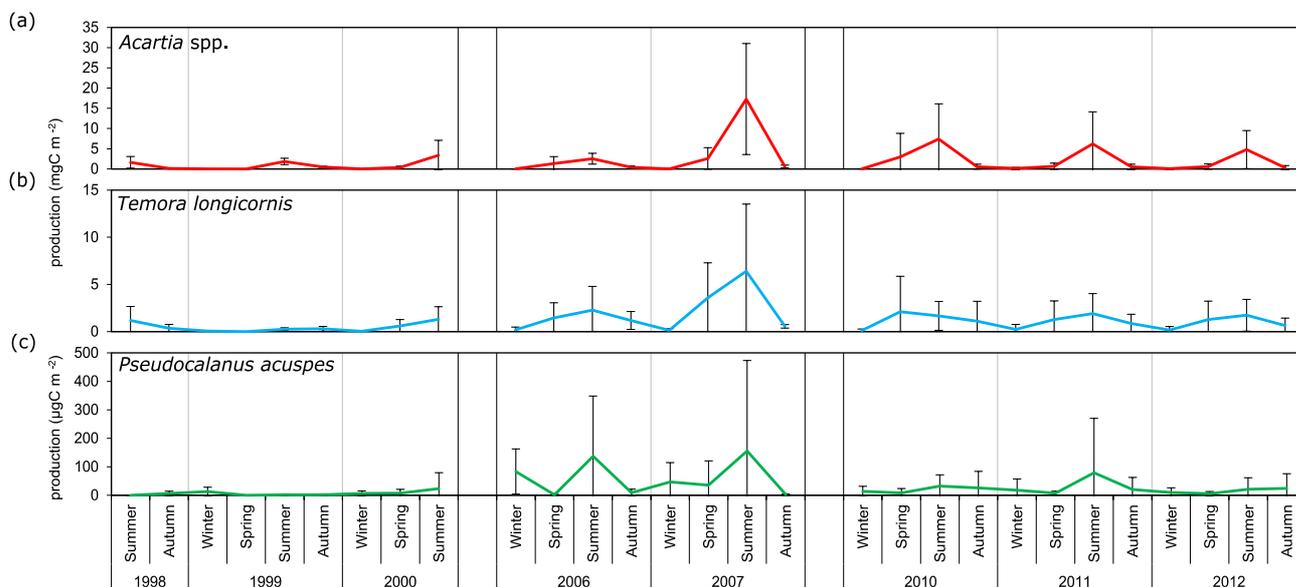
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**Figure 5.** Interannual (a) abundance and (b) biomass monthly mean and anomaly of *Pseudocalanus acuspes*.

## 225 3.3. Secondary production

226 Considering the entire research period, inter-annual and seasonal variability of secondary  
 227 production of *Acartia* spp., *T.longicornis* and *P.acuspes* was visible. Obtained results showed that the  
 228 highest average secondary production was recorded during 2006 and 2007, while the lowest values  
 229 were observed from 1998 to 2000. During each of the years, the summer season was characterized by  
 230 the highest values of production rates (Figure 6).



231

232 **Figure 6.** Mean secondary production rates ( $\pm$  standard deviation) of for (a) *Acartia* spp., (b) *Temora*  
 233 *longicornis* and (c) *Pseudocalanus acuspes* in the Gulf of Gdańsk during particular seasons.

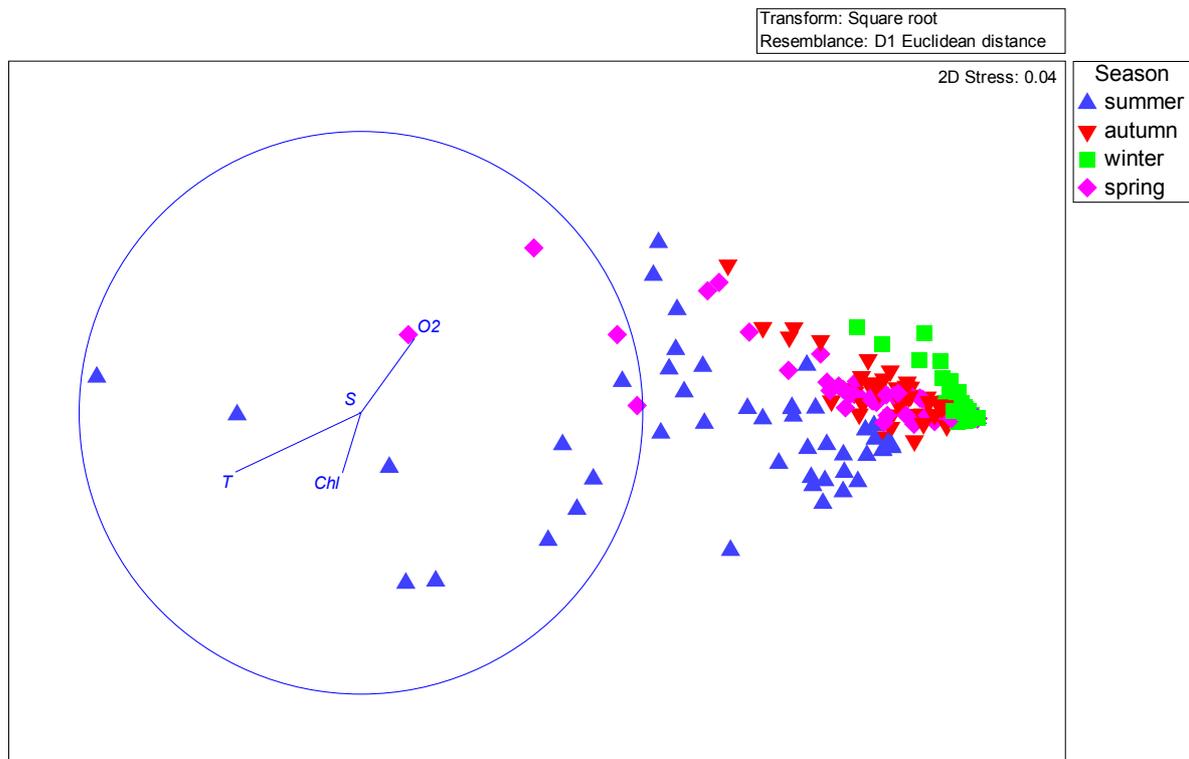
234 During the first research period, the average production rate for *Acartia* spp. reached the  
 235 highest value in the summer of 2000, almost 4 mg C m<sup>-2</sup>. In the second study period (2006-2007),  
 236 there was a large variation in the production rate. In summer 2007 it was more than 4 times higher  
 237 (about 16 mg C m<sup>-2</sup>) than recorded in the previous year. In the last years of research, a downward  
 238 tendency in production was observed, from about 8 mg C m<sup>-2</sup> in the summer of 2010, to about 6 mg C  
 239 m<sup>-2</sup> the following year, and finally about 4 mg C m<sup>-2</sup> in summer 2012 (Figure 6).

240 The secondary production of *T.longicornis* was lower than for *Acartia* spp.. In the first years of  
 241 the study, from 1998 to 2000, the average maximum value in the summer fluctuated around 1 mg C  
 242 m<sup>-2</sup>. During the second time interval, similarly to *Acartia* spp., significant variations in production  
 243 values were observed, reaching around 2 mg C m<sup>-2</sup> in summer 2006, and around 6 mg C m<sup>-2</sup> a year  
 244 later. In following years of research, the highest average production rates were observed in  
 245 spring-summer periods. In 2010 it fluctuated between 2 mg C m<sup>-2</sup> in spring to 1.8 mg C m<sup>-2</sup> in  
 246 summer, while in 2011 and 2012, noted values were 1.7 mg C m<sup>-2</sup> in spring and 2 mg C m<sup>-2</sup> in  
 247 summer [Figure 6].

248 Among the investigated copepods, *P.acuspes* was characterized by the lowest secondary  
 249 production values. In the 1998-2000 period the average values of production rates of the species did  
 250 not exceed 25  $\mu$ g C m<sup>-2</sup> (summer 2000). During the second period of our research, two production  
 251 peaks were observed during each year. In 2006 the first was recorded in the summer with an average  
 252 value of around 175  $\mu$ g C m<sup>-2</sup>, and the second one in the autumn – around 80  $\mu$ g C m<sup>-2</sup>. In 2007 these  
 253 values were similar: in the summer the average production was 150  $\mu$ g C m<sup>-2</sup> and in autumn it  
 254 reached approximately 50  $\mu$ g C m<sup>-2</sup>. During the last research period even lower production rate  
 255 values were observed. In 2010 and 2012 the average values did not exceed 50  $\mu$ g C m<sup>-2</sup>, and the  
 256 maximum was observed in the summer of 2011, reaching 70  $\mu$ g C m<sup>-2</sup> (Figure 6).

257 Obtained production values show significant differences between each designated season  
 258 (winter, spring, summer, autumn) (ANOSIM,  $p=0.001$ , global  $R=0.454$ ), which is quite clearly visible

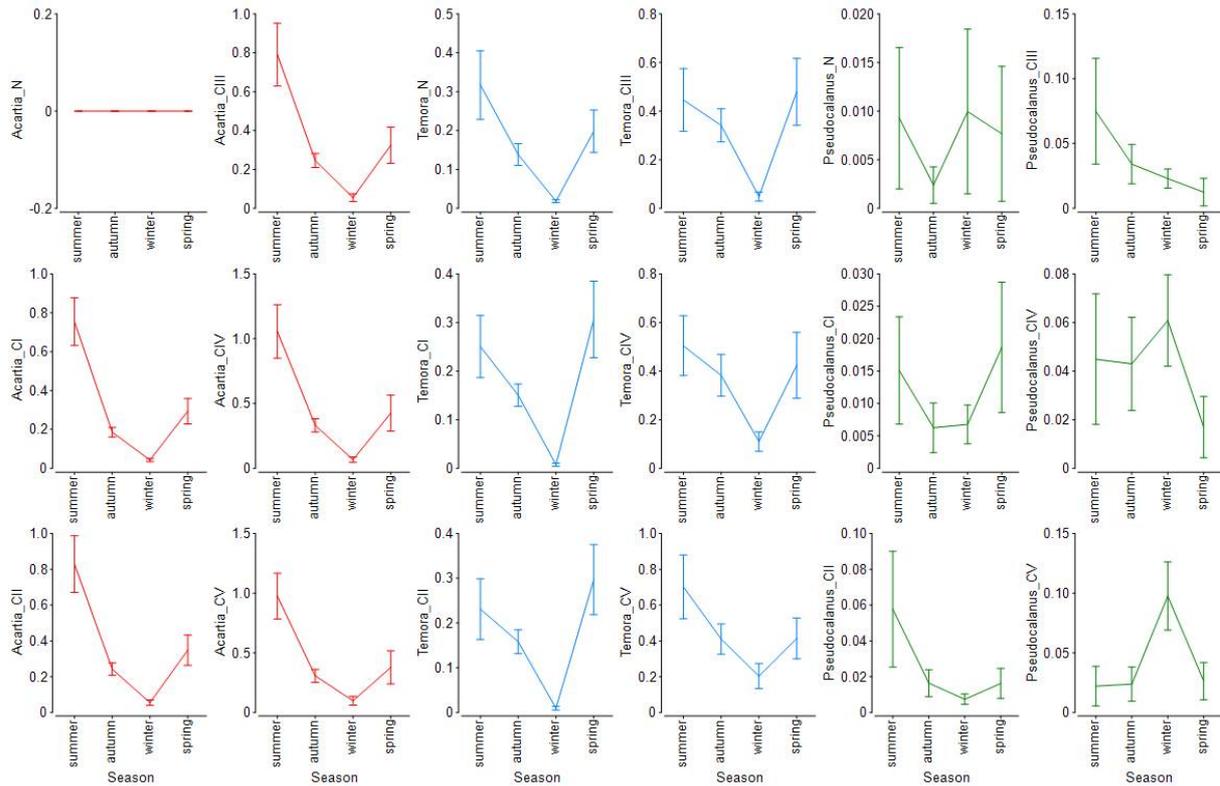
259 on the nMDS plot (Figure 7). There is, however, a visible connection between spring and autumn  
 260 groups, which overlap partially ( $p=0.001$ , global  $R=0.089$ ). The largest differences in production rates  
 261 were recorded between summer and winter ( $p=0.01$ , global  $R=0.841$ ).



262

263 **Figure 7.** nMDS plot illustrating the samples ordination according to production rates based on the  
 264 seasons factor.

265 Generally, production rates of *Acartia* spp. for all stages were the highest in summer season  
 266 (Figure 8). Also, the range of production rates was highest in case of this taxon. *T.longicornis* showed  
 267 a similar trend, but during spring, production values were even higher than in summer, especially  
 268 for the youngest copepodites (CI-CIII). What is more, *T.longicornis* production values were generally  
 269 lower than for *Acartia* spp. (Figure 8). There was no visible tendency for production distribution of  
 270 *P.acuspes* stages. Nauplii production was the lowest in autumn, but during all seasons there were  
 271 very high discrepancies in production ranges. Copepodites CII and CIII production values were the  
 272 highest during the summer season, while the production rates of older CIV and CV increased in  
 273 winter (Figure 8).



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**Figure 8.** Means plot illustrating production distribution of *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* developmental stages in relation to seasons.

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GLM analysis revealed that, with increasing temperature, the production of *Acartia* spp. and *T.longicornis* developmental stages increased, while stage CV of *P.acuspes* indicated almost neutral correlation with temperature. The most intensive production rise with increasing temperature demonstrated *Acartia* spp. stages (Table 4, Figure 9).

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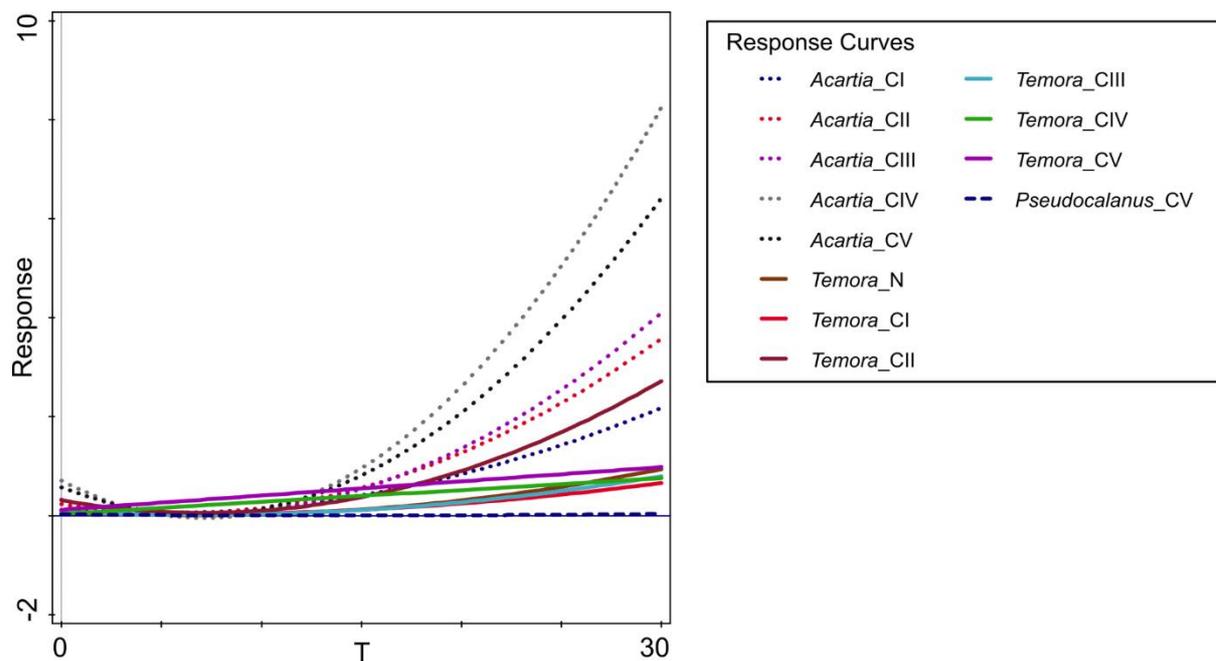
**Table 4.** Response of copepods developmental stages production to temperature (GLM model).

| Predictors    | T        |
|---------------|----------|
| Distribution  | normal   |
| Link function | identity |

GLM fitted for 12 response variables:

| Developmental stages             | Type      | R2[%] | F    | p        |
|----------------------------------|-----------|-------|------|----------|
| <i>Acartia</i> spp._CI           | quadratic | 18.4  | 18.4 | <0.00001 |
| <i>Acartia</i> spp._CII          | quadratic | 1.0   | 17.4 | <0.00001 |
| <i>Acartia</i> spp._CIII         | quadratic | 20.5  | 21.0 | <0.00001 |
| <i>Acartia</i> spp._CIV          | quadratic | 24.6  | 26.6 | <0.00001 |
| <i>Acartia</i> spp._CV           | quadratic | 20.9  | 21.5 | <0.00001 |
| <i>Temora longicornis</i> _N     | quadratic | 19.5  | 19.8 | <0.00001 |
| <i>Temora longicornis</i> _CI    | quadratic | 12.2  | 11.3 | 0.00002  |
| <i>Temora longicornis</i> _CII   | quadratic | 15.0  | 14.3 | <0.00001 |
| <i>Temora longicornis</i> _CIII  | quadratic | 14.0  | 13.3 | <0.00001 |
| <i>Temora longicornis</i> _CIV   | linear    | 5.5   | 9.6  | 0.00229  |
| <i>Temora longicornis</i> _CV    | linear    | 4.3   | 7.4  | 0.00732  |
| <i>Pseudocalanus acuspes</i> _CV | quadratic | 8.3   | 7.4  | 0.00086  |

283



284

285 **Figure 9.** Relationship of *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes*  
 286 developmental stages with temperature from the generalized linear models (GLM).

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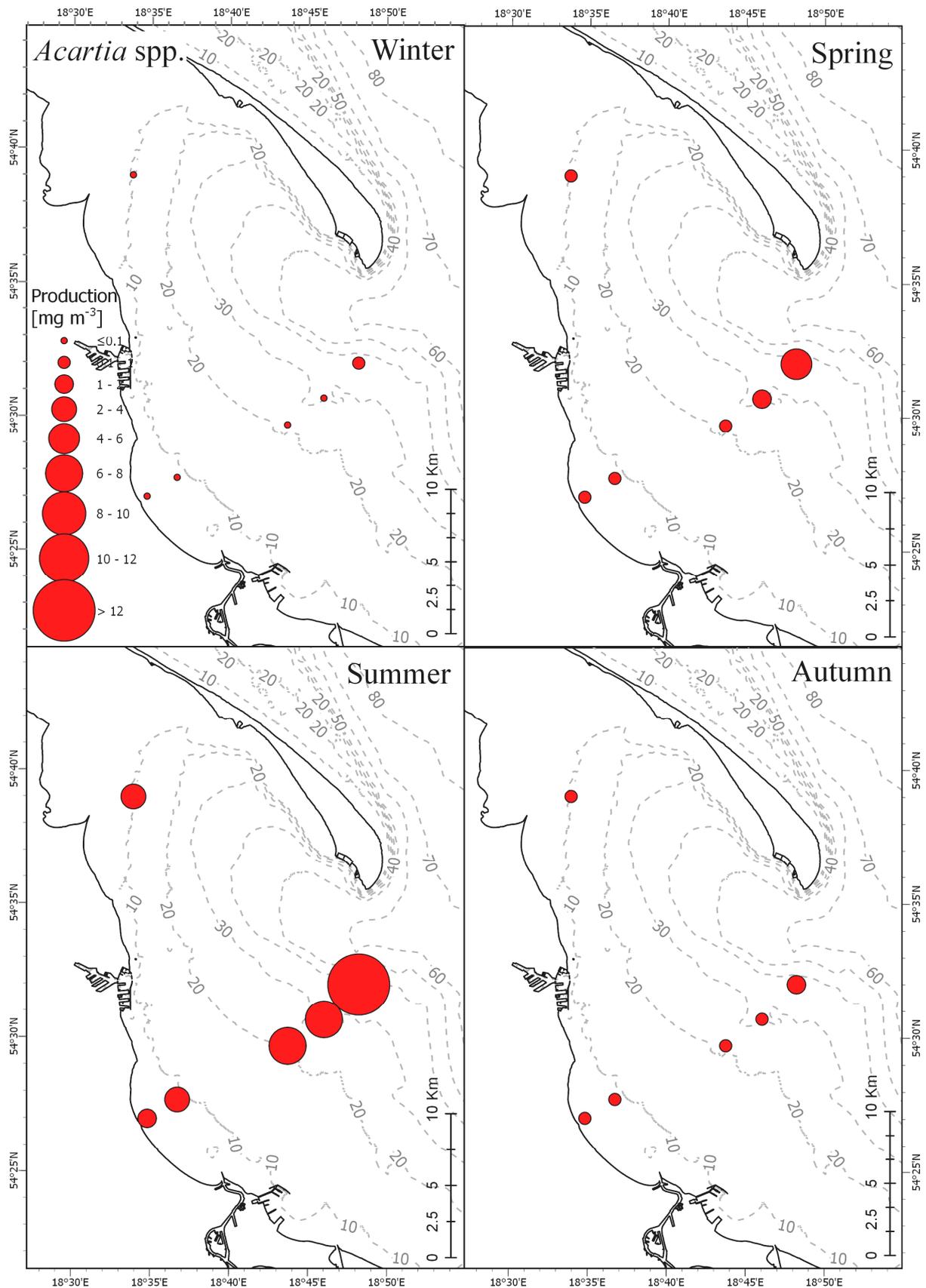
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Horizontal distribution showed that the lowest average production rates of the three species in the Gulf of Gdańsk were recorded at the shallow stations (1, 2, 6), while the deeper stations, mainly 4 and 5, were characterized by the highest production. The difference between production values between the stations was particularly visible in the spring and summer seasons. Horizontal distribution of secondary production of *Acartia* spp. showed the highest values for all six stations in the summer (Figure 10). In the case of *T.longicornis* the highest production was observed in spring at station 5, while in the summer the maximum production was recorded at station 4 (Figure 11). For *P.acuspes* the highest production was noted in summer at station 5, while the lowest values were observed at shallow stations 1 and 6 thorough all seasons (Figure 12).

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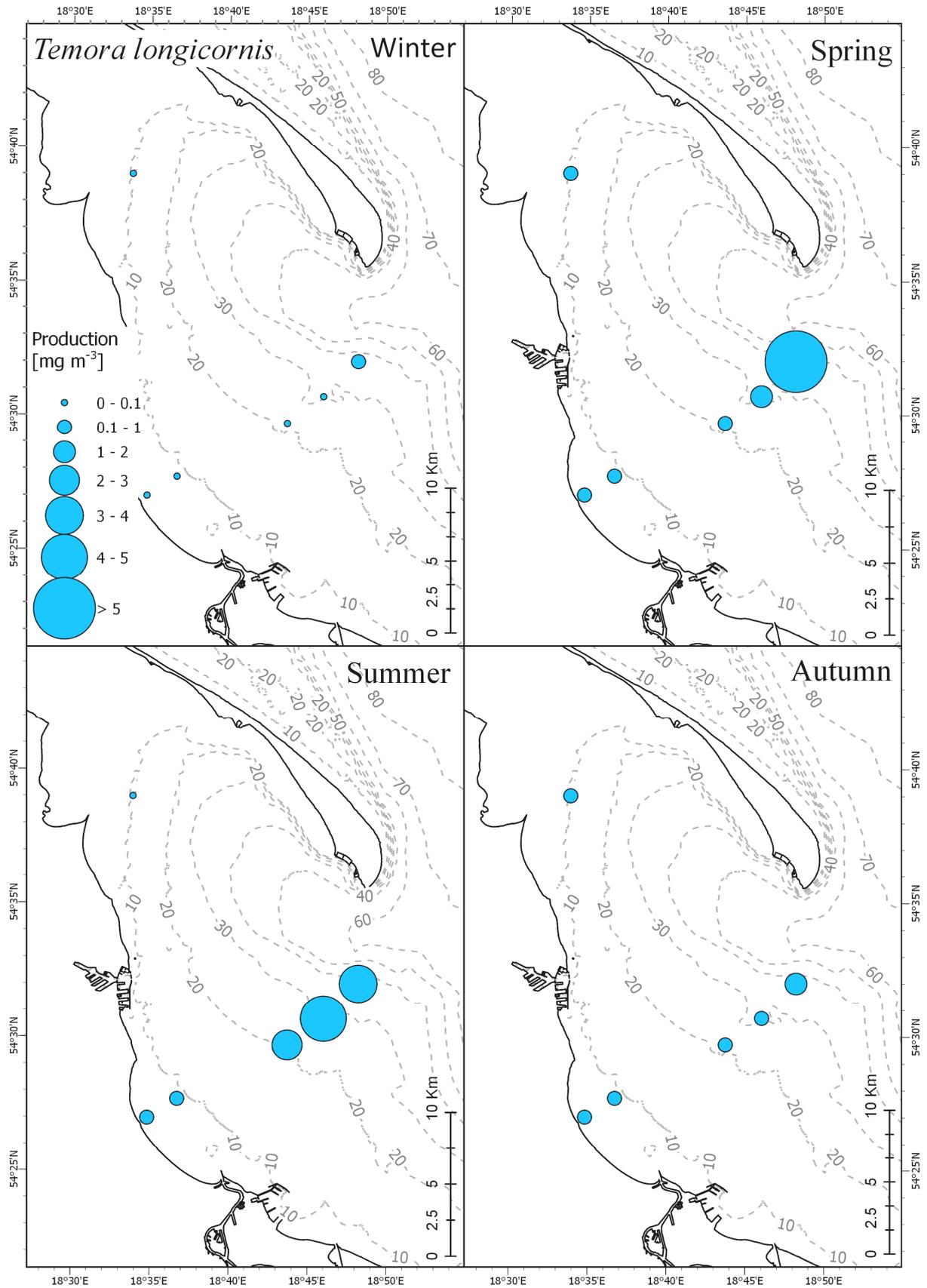


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**Figure 10.** Horizontal distribution of average secondary production rates of *Acartia* spp. in the Gulf of Gdańsk.

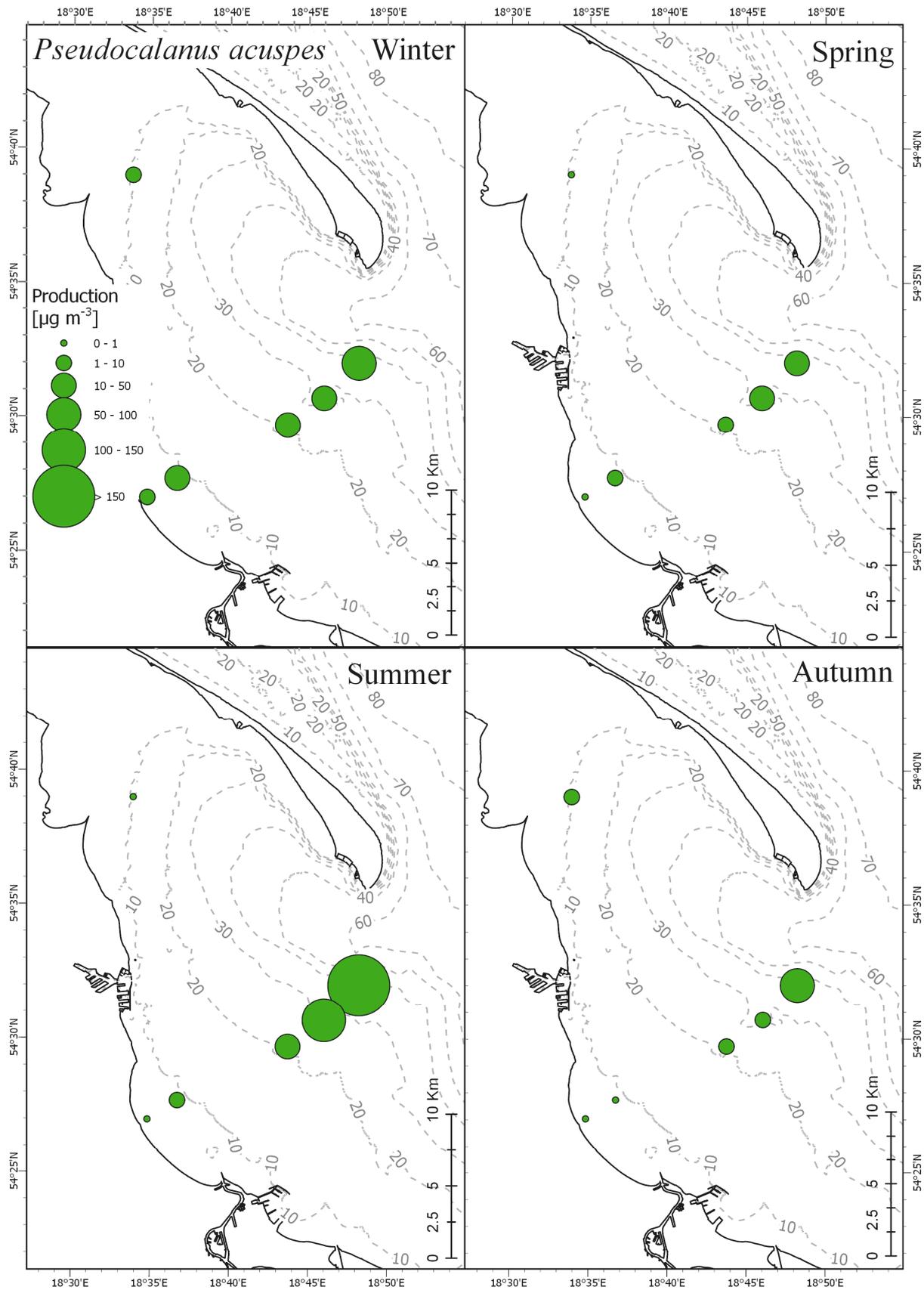


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**Figure 11.** Horizontal distribution of average secondary production rates of *Temora longicornis* in the Gulf of Gdańsk.



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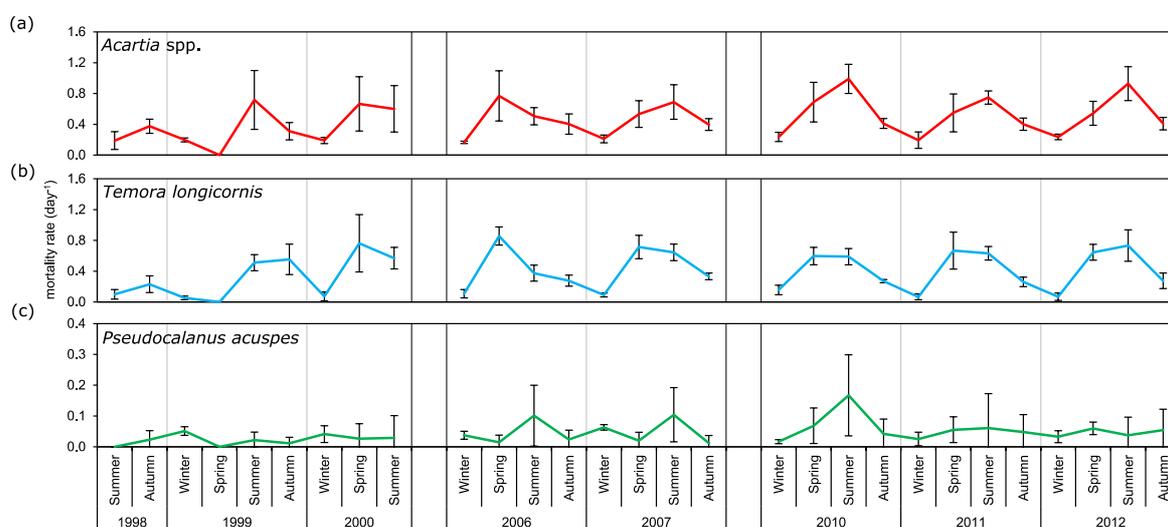
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**Figure 12.** Horizontal distribution of average secondary production rates of *Pseudocalanus acuspes* in the Gulf of Gdańsk.

306

### 3.3. Mortality rate

307 Mortality rates of the investigated species were diverse thorough the research period. The result  
 308 obtained for *Acartia* spp. showed the highest mortality rates mainly in summer, although in the  
 309 initial years of research a different trend was observed. In 1998 the highest mortality rate was  
 310 recorded in autumn ( $0.4 \text{ day}^{-1}$ ), while in 2000 and 2006 the peak mortality rate was recorded in  
 311 spring. The highest rate of mortality of *Acartia* spp. was obtained in summer 2010, with a value of  $0.8$   
 312  $\text{day}^{-1}$ . Winter was characterized by lowest mortality, remaining during all years of research at a  
 313 similar level: about  $0.2 \text{ day}^{-1}$ . Increased mortality rates of *T.longicornis* were usually noted for two  
 314 seasons, in summer-autumn 1999, spring-summer 2007, and spring-summer 2010-2012. These values  
 315 fluctuated between  $0.5 \text{ day}^{-1}$  to  $0.7 \text{ day}^{-1}$ . However, the highest mortality rate of *T.longicornis* was  
 316 observed in spring 2006, reaching over  $0.8 \text{ day}^{-1}$ . In winter mortality remained low, not exceeding  $0.2$   
 317  $\text{day}^{-1}$ . The mortality rates of *P.acuspes* showed a very irregular distribution throughout the study  
 318 period. In 1999 and 2007, two peaks were recorded, in winter and in summer. During 2006 and 2010  
 319 increased mortality of this species was observed during the summer season. Mortality rates in 2011  
 320 and 2012 remained at a similar level in all seasons (Figure 13).



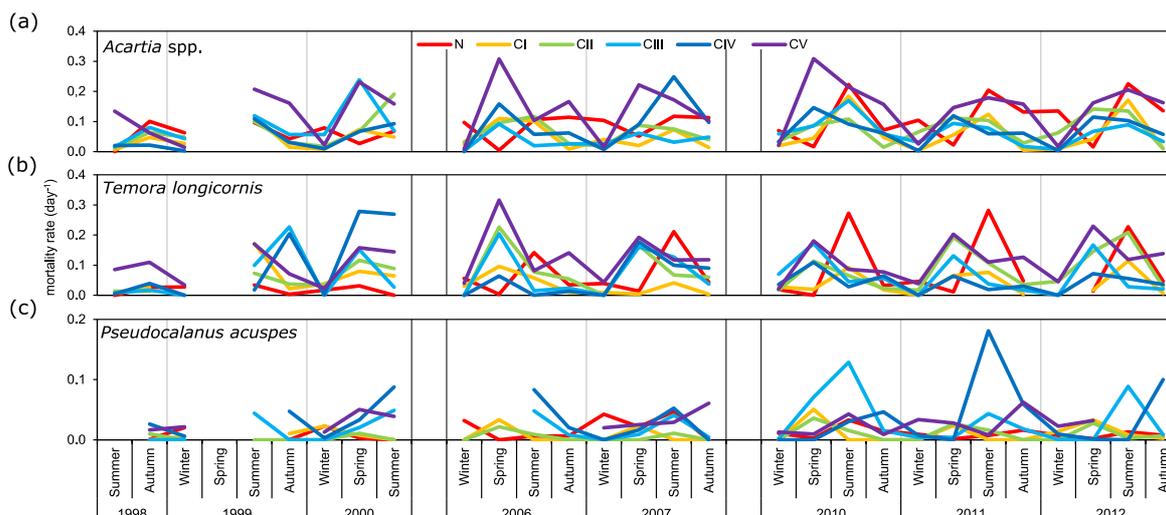
321

322 **Figure 13.** Mean daily mortality rates ( $\pm$  standard deviation) for (a) *Acartia* spp., (b) *Temora longicornis*  
 323 and (c) *Pseudocalanus acuspes* in the Gulf of Gdańsk during seasons of investigation.

324 In context of mortality of individual development stages for *Acartia* spp. (N-CV) the highest  
 325 mortality was noted in the spring-summer period, and it concerned mainly the fifth copepodite  
 326 stage (CV). Maximum values were noted in spring 2006 and 2010, about  $0.3 \text{ day}^{-1}$ , while in spring  
 327 2000 a high mortality rate was noted for CIII. In the second research period there was an increase in  
 328 mortality of nauplii, persisting from summer 2006 to winter 2007 (oscillating around  $0.1 \text{ day}^{-1}$ ), in  
 329 summer 2007 a high mortality rate of CIV ( $0.24 \text{ day}^{-1}$ ) was also observed. The third time interval was  
 330 characterized by high mortality mainly among nauplii – about  $0.2 \text{ day}^{-1}$  and CV mortality, between  
 331 spring and autumn 2011 and 2012 (Figure 14a).

332 Considering mortality rates of *T.longicornis* stages during the first study period, the highest  
 333 values were observed for CIII, CIV and CV, ranging from  $0.15 \text{ day}^{-1}$  to  $0.28 \text{ day}^{-1}$ . The lowest  
 334 mortality rate during that period was recorded for nauplii. In 2006-2007 and 2010-2012, the highest  
 335 mortality was observed for stages CII, CIII, CIV in spring and for nauplii in the summer, while for  
 336 CV two mortality peaks were noted, the first in spring and the second one in the autumn (Figure  
 337 14b).

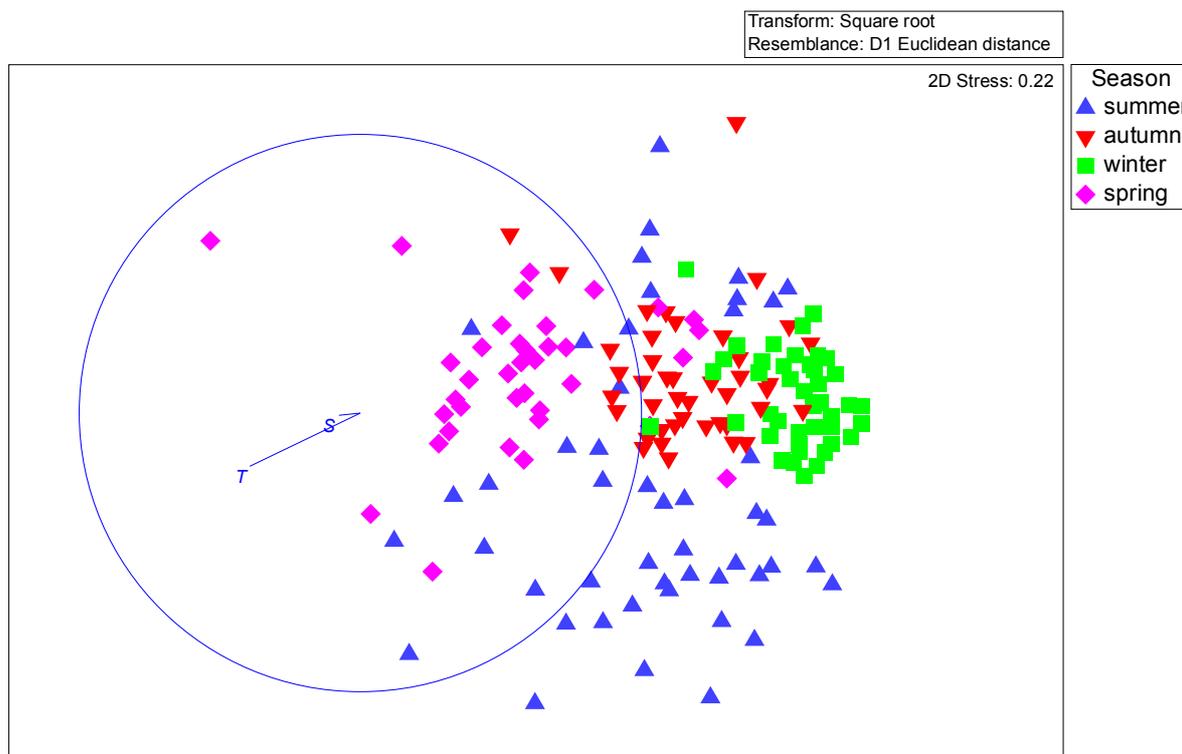
338 For *P.acuspes* chaotic distribution of mortality of all stages was noted, which may have been  
 339 caused by a relatively low abundance of that species. High mortality rates for CIII in winter of 2010  
 340 and 2012 and for CIV in winter 2011 were noticeable (Figure 14c).



341

342 **Figure 14.** Daily mortality rates of Copepoda stages N-CV for *Acartia* spp., *Temora longicornis* and  
 343 *Pseudocalanus acuspes* in the Gulf of Gdańsk during seasons of investigation.

344 When considering mortality rates in relation to seasons, significant differences were observed  
 345 ( $p=0.001$ , global  $R=0.355$ ). The most visible differences in mortality rates were noted between winter  
 346 and spring seasons ( $p=0.001$ , global  $R=0.584$ ) as well as between autumn and winter ( $p=0.001$ , global  
 347  $R=0.539$ ) (Figure 15).

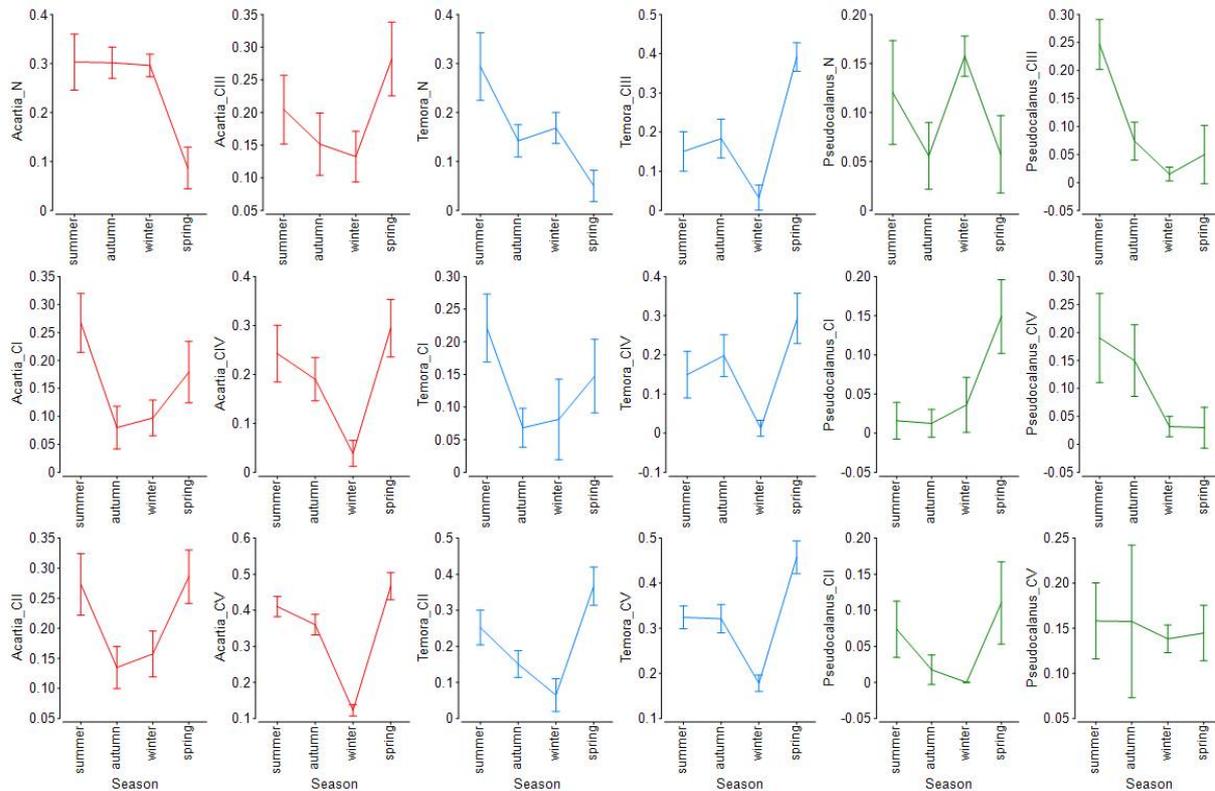


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349 **Figure 15.** nMDS plot illustrating the samples ordination according to mortality rates based on the  
 350 seasons factor.

351 Mortality of *Acartia* spp. and *T.longicornis* was the lowest in autumn and winter for almost  
 352 all stages, with the exception of nauplii of both species, which achieved the lowest values of  
 353 mortality during spring. *P.acuspes* mortality distribution, as in the case of production analysis,

354 was unspecified. However, nauplii demonstrated the highest mortality in summer and winter,  
 355 but CI and CII in spring. CIII and CIV in turn indicated the highest mortality in summer.  
 356 *P.acuspes* CV presented almost equal mortality for all seasons, but during autumn, the range of  
 357 values was the widest (Figure 16).



358

359 **Figure 16.** Means plot illustrating mortality distribution of *Acartia* spp., *Temora longicornis* and  
 360 *Pseudocalanus acuspes* developmental stages in relation to seasons.

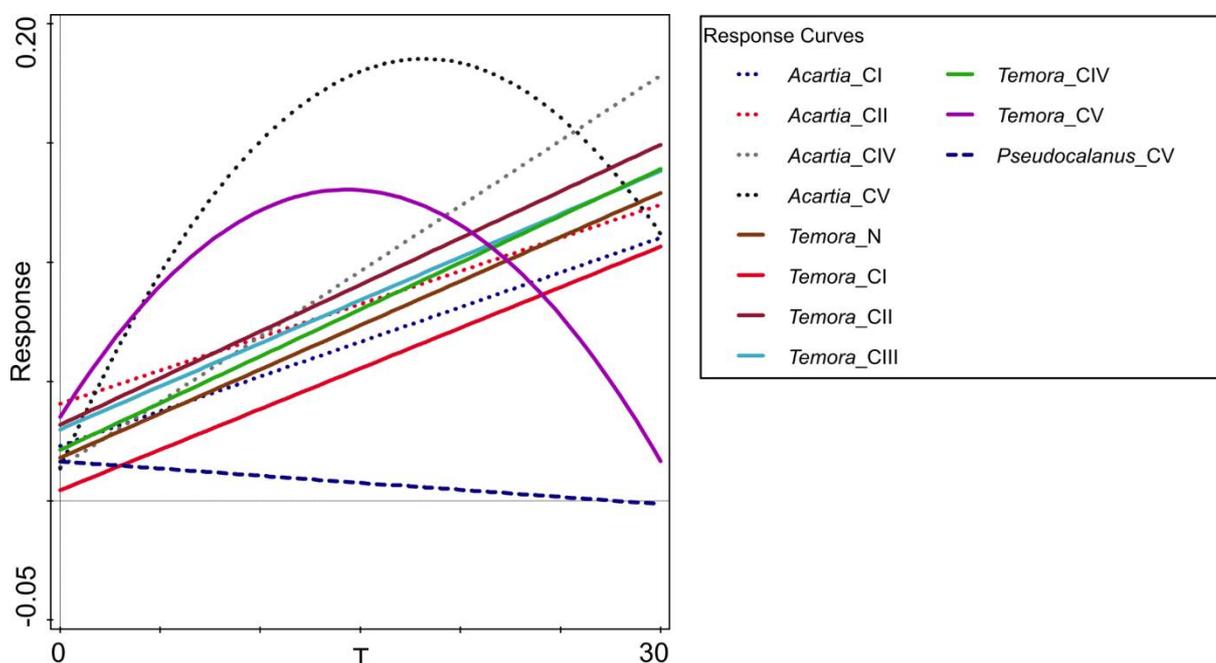
361 Considering mortality rates, GLM plots showed positive, linear relationship between  
 362 *T.longicornis* stages (from N to CIV), *Acartia* spp. (CI, CII, CIV) and temperature. Both *Acartia* spp.  
 363 CV and *T.longicornis* CV demonstrated unimodal response along the temperature gradient, while  
 364 *P.acuspes* CV showed a negative relationship with temperature factor (Table 5, Figure 17).

365 **Table 5.** Response of copepods developmental stages mortality to temperature (GLM model).

| Predictors                            | T         |       |      |          |
|---------------------------------------|-----------|-------|------|----------|
| Distribution                          | normal    |       |      |          |
| Link function                         | identity  |       |      |          |
| GLM fitted for 11 response variables: |           |       |      |          |
| Developmental stages                  | Type      | R2[%] | F    | p        |
| <i>Acartia</i> spp._CI                | linear    | 5.1   | 8.9  | 0.00331  |
| <i>Acartia</i> spp._CII               | linear    | 4.1   | 7.1  | 0.00868  |
| <i>Acartia</i> spp._CIV               | linear    | 11.5  | 21.3 | <0.00001 |
| <i>Acartia</i> spp._CV                | quadratic | 20.3  | 20.7 | <0.00001 |
| <i>Temora longicornis</i> _N          | linear    | 5.4   | 9.3  | 0.00266  |
| <i>Temora longicornis</i> _CI         | linear    | 8.6   | 15.5 | 0.00012  |
| <i>Temora longicornis</i> _CII        | linear    | 5.6   | 9.8  | 0.00206  |
| <i>Temora longicornis</i> _CIII       | linear    | 4.5   | 7.7  | 0.00617  |

|                                  |           |     |     |         |
|----------------------------------|-----------|-----|-----|---------|
| <i>Temora longicornis</i> _CIV   | linear    | 4.0 | 6.9 | 0.00946 |
| <i>Temora longicornis</i> _CV    | quadratic | 8.6 | 7.7 | 0.00064 |
| <i>Pseudocalanus acuspes</i> _CV | linear    | 4.8 | 8.2 | 0.00478 |

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**Figure 17.** Relationship of *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* developmental stages with temperature from the generalized linear models (GLM).

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Horizontal mortality distribution of *Acartia* spp. showed the highest mortality rate at the shallow station 6 in spring and at stations 6, 1, 2 (> 0.68) in summer. In the autumn mortality rate of *Acartia* spp. was within the same range at all stations (0.34 - 0.68). The lowest mortality was recorded at station 6 in winter (0 - 0.17) (Figure 18).

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The results for *T.longicornis* showed the highest mortality rates at stations 6 and 2 as well as at station 3 in spring (> 0.64). In the summer season, at all stations the mortality rate was in the same range (0.32 - 0.64). The lowest values were recorded in the winter at stations 6, 4 and 5 (0 - 0.08) (Figure 19).

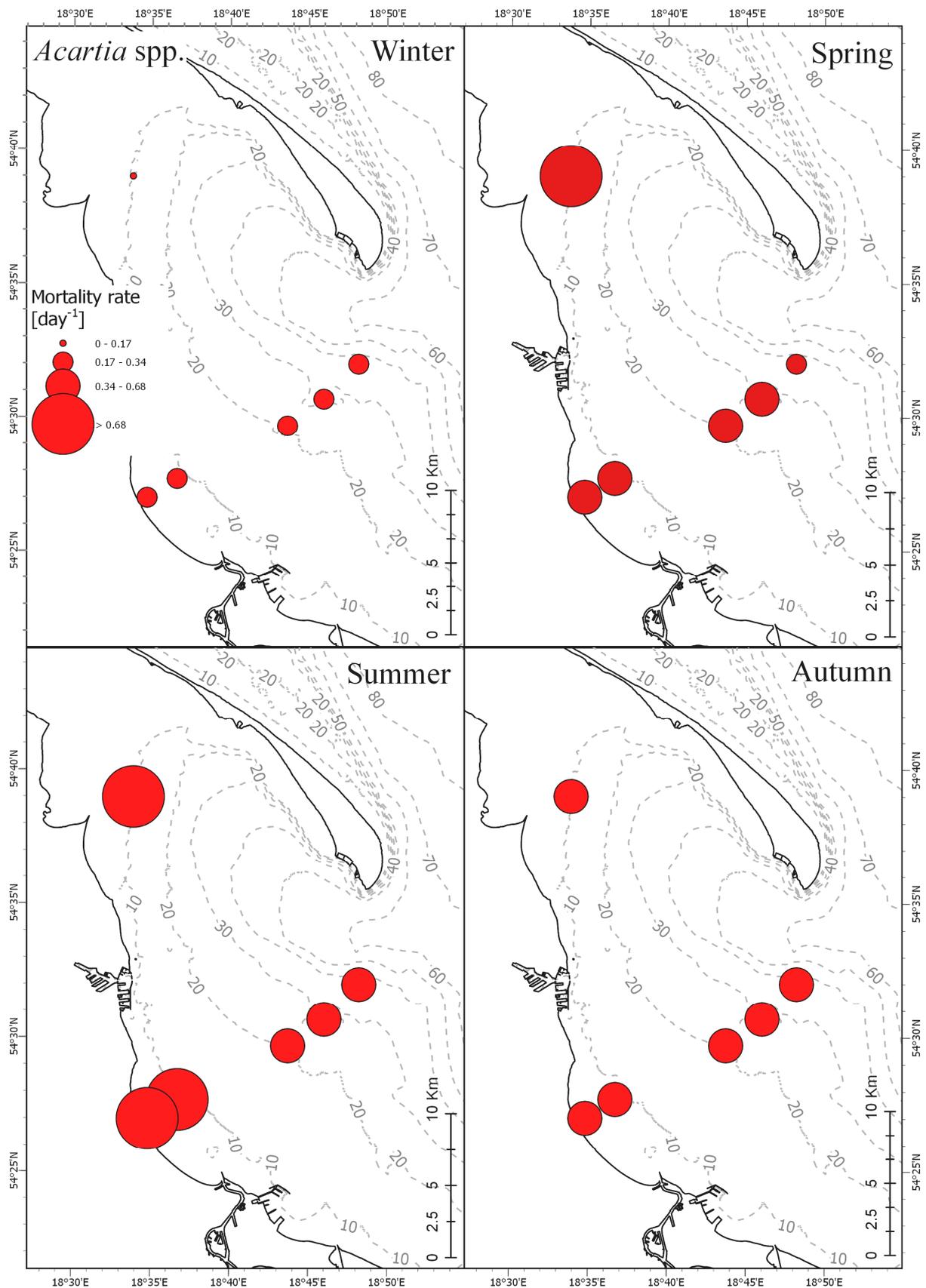
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For *P.acuspes*, the horizontal mortality distribution showed the highest mortality at deep stations 3 and 4 in the summer season (> 0.08). However, the lowest mortality was recorded at shallow stations 1 and 6, also in summer, and at stations 1 and 2 in autumn (Figure 20).

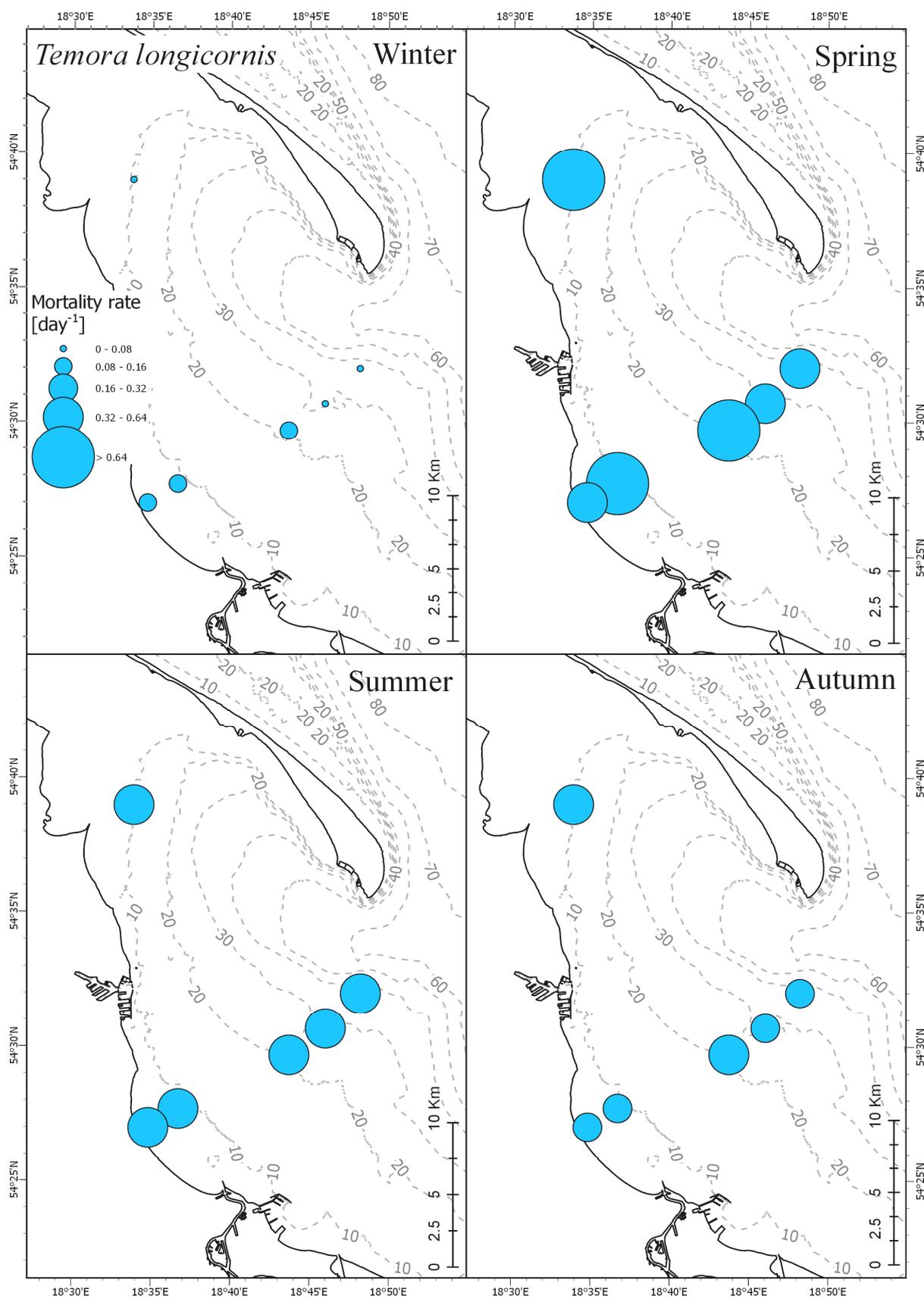
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Figure 18. Horizontal distribution of average mortality rates of *Acartia* spp. in the Gulf of Gdańsk.

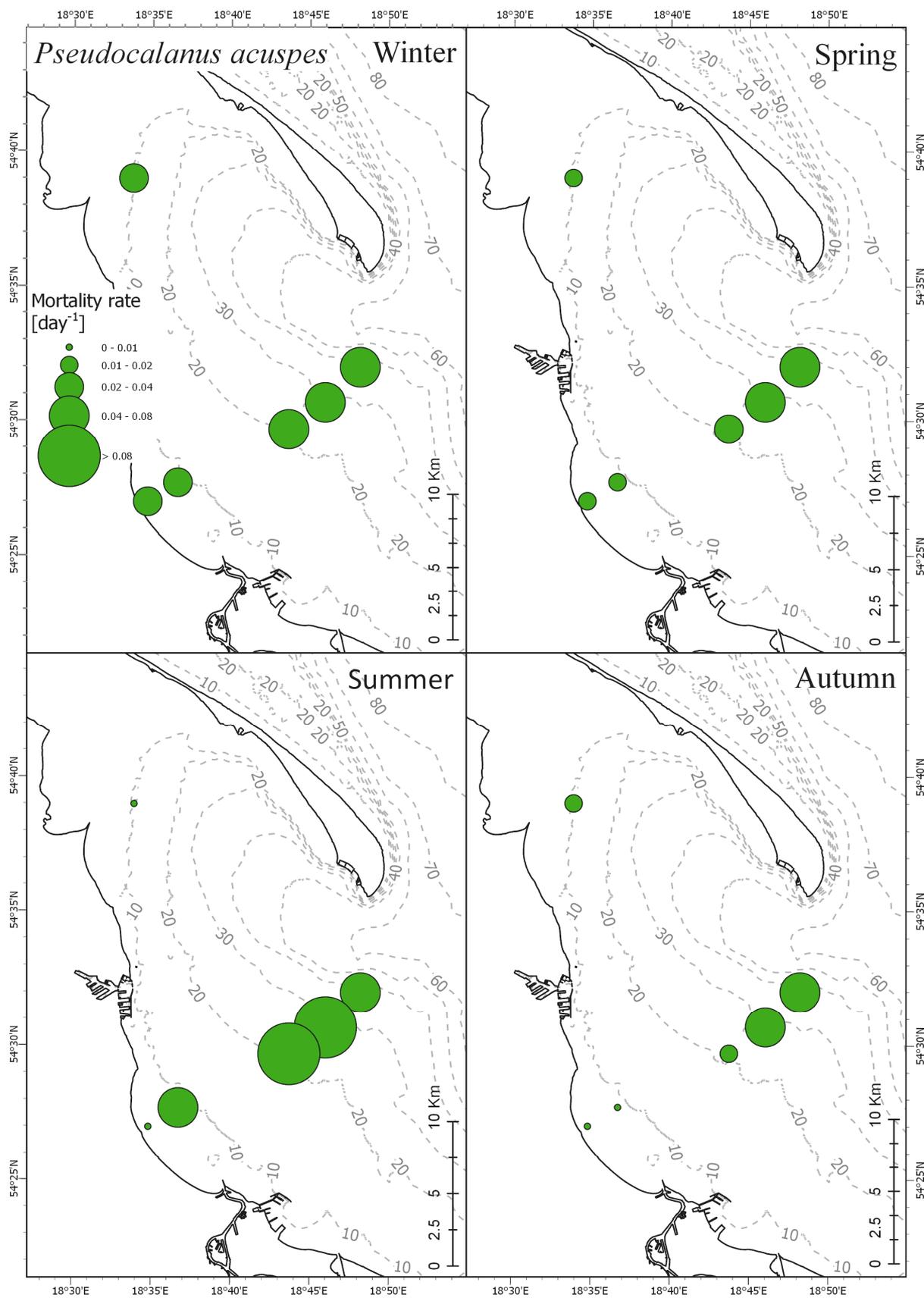


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**Figure 19.** Horizontal distribution of average mortality rates of *Temora longicornis* in the Gulf of Gdańsk.



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**Figure 20.** Horizontal distribution of average mortality rates of *Pseudocalanus acuspis* in the gulf of Gdańsk.

391 **4. Discussion**

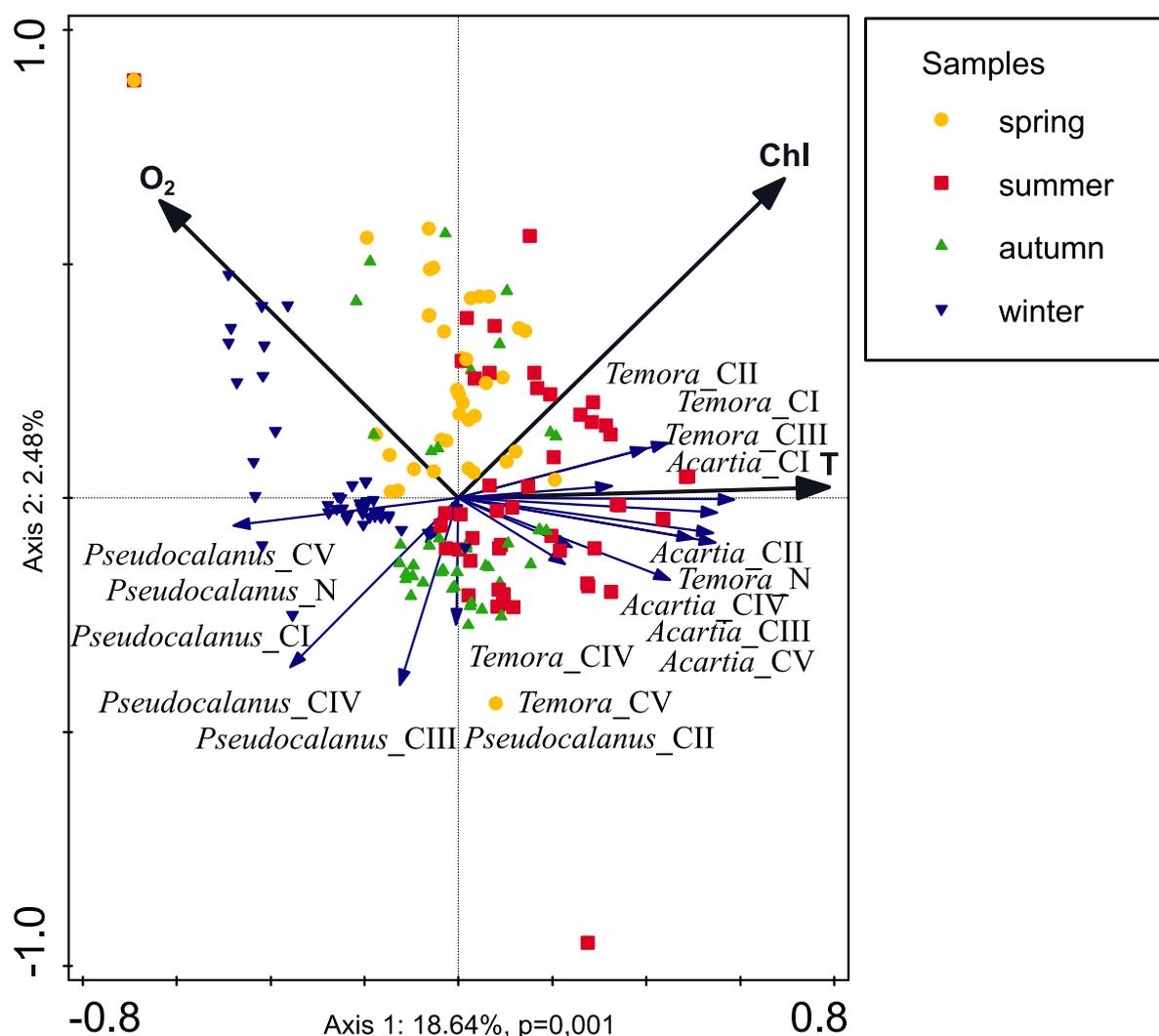
392 The aim of our study was a description of seasonal and interannual patterns of secondary  
 393 production and mortality rates for the main southern Baltic copepods. The main factors determining  
 394 zooplankton production are temperature and food availability [33]. Therefore we decided to  
 395 investigate seasonal and interannual fluctuations of secondary production of three copepod taxa:  
 396 *Acartia* spp., *T.longicornis* and *P.acuspes* in the southern Baltic. This is even more important in context  
 397 of increasing water temperatures observed in the Baltic related to global warming [34]. Higher water  
 398 temperature leads to shorter generation time and smaller body size of copepods, also causing  
 399 individuals to reach reproductive age quicker, and causing rapid increases in density [35]. However,  
 400 different copepod species have their individual temperature optimums, at which their development  
 401 is most optimal [21]. Therefore, when estimating the rate of secondary production of these copepods,  
 402 we used the *Di* function that takes into account the individual temperature optimums. We are also  
 403 aware that accurate estimates, most approximate to the natural state, of the secondary production  
 404 based on mathematical expressions require a method that combines a variety of factors. Because of  
 405 that our estimations do not fully reflect actual, real as in the natural environment, secondary  
 406 production values. However, they allow for an approximation of these values and enable  
 407 recognition of trends or anomalies occurring in the studied ecosystem.

408 Results obtained in our research showed clear correlation between seasonal production  
 409 fluctuations in the Gulf of Gdańsk and the hydrological conditions, mainly water temperature  
 410 (Figure 21). The highest correlation was recorded during summer, mainly for the young copepodite  
 411 stages of *Acartia* spp. as well as nauplii and copepodites of *T.longicornis*. This is consistent with  
 412 research carried out by Koski et al. [36] in the North Sea, which also indicates that the production  
 413 coefficient is significantly positively correlated with the average water temperature. However,  
 414 research from the Western Scheldt Estuary [37], showed that neither the biomass nor the secondary  
 415 copepod production was associated with chlorophyll concentration, and the temperature seemed to  
 416 have a significant impact only on the predominance of certain copepods. In contrary to those two  
 417 taxa, *P.acuspes* showed mostly negative correlation of secondary production with temperature. This  
 418 species in the central Baltic is associated with the deeper, more saline and also colder water layer  
 419 [38-40]. This was visible in high mean values of secondary production of nauplii and older  
 420 copepodites (CIV, CV) noted during winter seasons (Figure 8). We can therefore clearly state that,  
 421 similarly to other water basins, water temperature is one of the main factors controlling not only  
 422 biomass and abundance [17, 41] but also secondary production of main copepod taxa in the Gulf of  
 423 Gdańsk. Temperature was responsible for 11.8% of variability observed in RDA. In addition to  
 424 temperature, variability of secondary production was also to some extent explained by the  
 425 concentration of dissolved oxygen (5%) and chlorophyll *a* (4.5%) (Table 6).

426 **Table 6.** Explained variability and p values of particular environmental variables for redundancy  
 427 analysis (RDA).

| Name                               | Explains % | pseudo-F | p     |
|------------------------------------|------------|----------|-------|
| Temperature (T)                    | 11.8       | 15.6     | 0.001 |
| Dissolved oxygen (O <sub>2</sub> ) | 5.0        | 7.0      | 0.002 |
| Chlorophyll <i>a</i>               | 4.5        | 6.6      | 0.005 |
| Salinity (S)                       | 0.5        | 0.8      | 0.442 |

428



429

430 **Figure 21.** Ordination plot from redundancy analysis (RDA) on secondary production of  
 431 development stages of *Acartia* spp., *Temora longicornis* and *Pseudocalanus acuspes* (N – nauplii, CI-CV  
 432 copepodids of respective stage) and their relation to chlorophyll *a* and dissolved oxygen.

433 Comparison of the estimated values of secondary production of crustaceans from other regions  
 434 shows that that copepod production in the Gulf of Gdańsk is relatively low. The maximum  
 435 estimated average value of *P.acuspes* was (from the table) in the summer of 2007, while Renz [42]  
 436 described it as 26.2 mg C m<sup>-2</sup> day<sup>-1</sup> in June. Such a large difference in the obtained values is probably  
 437 due to differences in hydrological factors leading to differences in metabolic rates [40]. Renz and  
 438 Hirche [40] have shown that the rate of North Sea *P.elongatus* population development is about 3-5  
 439 times higher and the growth rate is up to 10 times higher than the *P.acuspes* population from the  
 440 Baltic Sea, which translates directly into the higher production of *P.elongatus*. Results reported by  
 441 Frasz [43] from the North Sea show that the secondary production of *T.longicornis* and *Acartia clausi*  
 442 fluctuated between 22-16 mgC m<sup>-2</sup> between May and September. In the brackish waters of the  
 443 Western Scheldt Estuary, estimated maximum average secondary production of *Acartia tonsa*  
 444 oscillated around 25 mgC m<sup>-3</sup> in August and the second peak was recorded in September with the  
 445 value of 8 mgC m<sup>-3</sup>. The presence of maxima of secondary production in these months is consistent  
 446 with the seasonality of production observed for these species from genus *Acartia* in the Gulf of  
 447 Gdańsk. Production values, as in the case of *P.acuspes*, were, however, lower than those recorded in  
 448 the North Sea. Differences in the value of secondary production can also be caused by the use of

449 different calculation methods and wet mass converters for the copepod from various sources of  
450 literature.

451 In the perspective of the observed progressing warming of the Baltic Sea, which is particularly  
452 noticeable in its northern region (the air temperature in the spring increased by about 1.5 °C in the  
453 period 1871-2011 [44]. The ecosystem of the southern Baltic – much more productive and biodiverse  
454 – is more susceptible to the negative effects of such changes. Due to the currently observed  
455 restructuring of unicellular plankton and the shift of phenological phases [45]. Further  
456 comprehensive research on biological production in ecosystems is needed, combining the research  
457 on primary phytoplankton production and the production of zooplankton. Observed progressing  
458 delaying of the maximum of secondary production in relation to spring bloom of phytoplankton  
459 may lead to serious consequences for the whole organic production and higher trophic levels in the  
460 ecosystem [46].

461 Zooplankton mortality estimates are still not a well-developed parameter in determining  
462 population dynamics. Therefore, selecting a proper methodology to describe this phenomenon can  
463 be challenging, and the main uncertainty results from inherent difficulties in measuring this process  
464 in the natural environment [47].

465 It is widely accepted that the daily copepod mortality decreases with consecutive  
466 developmental stages or with an increase in size [48, 49]. Based on these assumptions we wanted to  
467 describe mortality rates of main copepod taxa from the Gulf of Gdańsk at particular seasons of the  
468 year. The results obtained for *Acartia* spp. and *T.longicornis*, however, show differences in mortality  
469 for particular stages from that described by the above-mentioned authors. The highest mortality rate  
470 for *Acartia* spp. was observed for the oldest copepodites (CV) with maximum values noted in spring:  
471 about 0.3 day<sup>-1</sup>. For *T.longicornis* high rates were observed for CIII, CIV and CV, within a range from  
472 0.15 day<sup>-1</sup> to 0.28 day. High variability in mortality estimates between copepod species and  
473 developmental stages in both spatial and seasonal distribution were also observed by other authors  
474 [15, 50, 51].

475 In our research we observed cyclical changes in mortality, with the peak falling in the spring  
476 and summer season. Maud et al. [52], on the other hand, recorded the highest mortality rates in  
477 summer and autumn, with the lowest – as in our research – in winter. Differences in seasonality of  
478 mortality in different regions may result from differences in the main cause of mortality. Mortality of  
479 copepods can be caused by predatory (consumptive) or physicochemical and biological factors as  
480 factors causing non-consumptive mortality. Consumptive mortality may be associated with the  
481 abundance of predators [53] and is described in the literature as usually occurring in the autumn  
482 season, when the abundance of predators is the highest. This type of mortality described for *Calanus*  
483 *helgolandicus* constituted an average of 89% of the total mortality for this species [52]. In the Baltic  
484 Sea, copepods are a valuable source of food for the commercially important fish species sprat and  
485 herring, but jellyfish can also have a significant predatory impact. The gelatinous zooplankton was  
486 the main cause of mortality variability observed in deep coastal sampling station located near  
487 south-west of Plymouth, UK [54]. Non-consumer mortality may result from death caused by age  
488 [55], diseases and parasitism [56], exposure to environmental pollution [57], and physiological stress  
489 [58]. Field and laboratory studies show that non-consumptive factors can account for 25 to 33% of  
490 the total death rate among adult copepods [59].

491 The species from genus *Acartia* had the highest abundance and biomass among the three  
492 investigated taxa, while *P.acuspes* was far less abundant than the other two taxa. Such proportions  
493 between those taxa is quite typical for the coastal region of the southern Baltic. *P.acuspes* tends to  
494 dominate offshore areas of the Baltic Sea, is much less abundant in the coastal zones, and it is rarely  
495 present above the thermocline, especially during the warm season [60, 61].

496 Observed long-term biomass means for *Acartia* spp. were in a similar range as those reported  
497 for this region by Möllmann [34], while for *T.longicornis* and especially *P.acuspes* they were much  
498 lower. This was probably due to our sampling stations being located mostly in the inner, coastal part  
499 of the Gulf of Gdańsk. Möllmann [34] also showed mostly negative anomalies for both *T.longicornis*  
500 and *P.acuspes* as well as the mostly neutral anomaly of *Acartia* spp. during the later 1990s. This is

501 consistent with our findings, which also showed strong positive anomalies for those taxa during the  
502 first decade of the 2000s.

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505 and Anna Lemieszek; Methodology, Maja Musialik-Koszarowska, Anna Lemieszek, Paula Prątnicka and Maciej  
506 Janecki; Project administration, Lidia Dzierzbicka-Głowacka; Supervision, Maria Iwona Żmijewska;  
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