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Article

Response of the Black Sea Zooplankton to the Marine Heat Wave 2010: Case of the Sevastopol Bay

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Abstract: Global warming is increasing the frequency and severity of the marine heat waves, which poses a serious threat to the marine ecosystem. This study analyzes seasonal and interannual dynamics in the abundance and structure of the mesozooplankton community in Sevastopol Bay based on bi-monthly routine observations over 2003–2014. The focus is on the impact of the summer 2010 marine heat wave (MHW2010) on crustaceans belonging to different ecological groups. As a response to the MHW2010, three warm-water species (*O. davisae, A. tonsa* and *P. avirostris*) exhibiting the maximum seasonal density in latter summer showed a sharp increase in the annual abundance and their share in the mesozooplankton community. The increase in the annual abundance in 2010 of the eurythermal species *P. parvus* and *P. polyphemoides* exhibiting seasonal peaks in spring and autumn is not related to the MHW2010 but can be explained by a rise of temperature in the first part of the year. *O. davisae* and *A. tonsa* showed the most pronounced response among the species to the MHW2010, confirming that non-native species exhibited great flexibility as an adaptive response to environmental changes, especially in the case of climate warming. Among crustaceans observed in this study, *O. davisae* can be considered as an indicator of the environmental conditions associated with the warming of the Black Sea and the Mediterranean basin as a whole.

Keywords: marine heat waves; mesozooplankton; copepod; crustacean; Sevastopol Bay; Black Sea

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1. Introduction

Marine heat waves (MHWs) are extreme warm oceanic events that persist for days to months and can have devastating impacts on marine ecosystem often with ecological and socioeconomic consequences. Over the last decades, the MHWs have been increasing in frequency, intensity and duration worldwide, and these trends are projected to continue in the future as a consequence of anthropogenic climate change [1,2]. The Black Sea is an example of semi-closed sea experiencing a rapid warming, which is considered an amplified precursor of the changes to expect in the greater oceans [3]. The increasing warming rate of the Sea Surface Temperature (SST) in the Black Sea in the two last decades with respect to the previous two decades was associated with an increasing rate in MHWs frequency: the annual mean SST trends was 0.4 °C/decade in 1982–2000 and 0.7 °C/decade in 2001–2020, and the corresponding average frequencies of MHW were estimated as about 0.6 events/year and about 3 events/year, respectively [4]. Among the most intense and prolonged MHWs is the summer 2010 event associated with the extreme atmospheric heat wave that hit western Russia as result of the strong atmospheric blocking [5]. Given that MHW are expected to rise in magnitude, frequency and duration in the future, it is important to evaluate the response of pelagic communities to extreme MHWs, especially in shallow coastal areas which are more sensitive to temperature variations than open seas [6].

Marine mesozooplankton is a suitable candidate for investigation of the ecosystem response to climate variability and extremes, and multi-year mesozooplankton time series provide useful information about climate–ecosystem interactions [7,8]. Indeed, mesozooplankton plays a pivotal role in marine ecosystems, providing a link between primary producers and secondary consumers in food webs. Therefore, all changes in the food chain, from the bottom to the top, are reflected in the mesozooplankton. Mesozooplankton comprises poikilothermic animals, sensitive to temperature changes, which is one of the most important factors, driving its temporal and spatial distribution. Mesozooplankton species have a short lifespan, six to nine generations of copepods per year in the Black Sea, and can provide an early signal of environmental changes [9,10].

Despite its major role in marine ecosystems, only a few studies have investigated the response of coastal populations of zooplankton species to MHWs. Rhian Evans and co-authors demonstrated that the 2015–2016 Tasman MHW caused a shift in the abundance and compositions of the zooplankton community resulting in an increase (decrease) in warm- (cold-) water species of copepods [11]. Similarly, Caitlin A.E. Mckinstry and co-authors showed an elevated abundance of warm waters copepods in response to the 2014–2015 MHW in the low Cook Inlet, Alaska [12].

A specific feature of the Black Sea is its low biodiversity. In general, it is 3.5–4 times poorer than that in the Mediterranean Sea, where the copepod species are generally functionally redundant [13]. This redundancy should compensate for the loss of ecosystem functions of the Mediterranean zooplankton communities caused by climate change [14]. In the Black Sea, there are currently 12 species of marine planktonic copepods, three of which are invasive, namely *Acartia tonsa*, *Oithona davisae*, and *Pseudadiaptomus marinus* [15,16]. In this regard, changes in environment caused by climate impact or anthropogenic pressure lead to noticeable effects in the zooplankton community and the ecosystem of the Black Sea as a whole. Thus, the Black Sea, and in particular Sevastopol Bay, is a suitable model for assessing the environmental impacts of climate change on marine biodiversity.

Zooplankton of the Black Sea include species of various origins and, hence, they are different in ecology and biology [17,18]. Cold-water assemblage copepods are considered boreal-Atlantic relics that inhabited the Black Sea during the past cooling period. They dwell in a deep layer of the open sea in summer and appear in surface waters and coastal areas during the cold season. Thermophilic species colonized the Black Sea as it warmed in the last stages of the Quaternary. They survive the cold season at the dormancy stage, rapidly increase in abundance in the warm season and peak in abundance from late July to October. Individual representatives of this group (namely ctenophores *Mnemiopsis leidyi*, *Beroe ovata* and copepods *Acartia tonsa*, *Oithona davisae*) were established in the Black Sea quite recently, during the last 50 years. Finally, some copepods belong to the eurythermal assemblage and are quite numerous in the plankton all year round [10,15].

Our goal in this paper is to assess the response of the crustacean mesozooplankton populations in the Sevastopol Bay (northern Black Sea) to the 2010 summer MHW, which was one of the most intense and longest MHWs observed in the region. Based on long-term (2003–2014) routine observations of zooplankton, we aim at identifying species sensitive to extreme warm temperature anomalies observed during summer 2010 and documenting corresponding changes in composition, abundance, structure and seasonal variations.

2. Materials and Methods

2.1. Area of Investigation

Sevastopol Bay is located in the northern part of the Black Sea at the southwestern tip of the Crimean Peninsula (Figure 1). It is about 7 km long and 1 km wide at its widest point, and it has an average depth of 12 m. It is a semi-enclosed estuarine-type bay having a restricted water exchange with the open sea because of its large length and the mole built at the entrance.

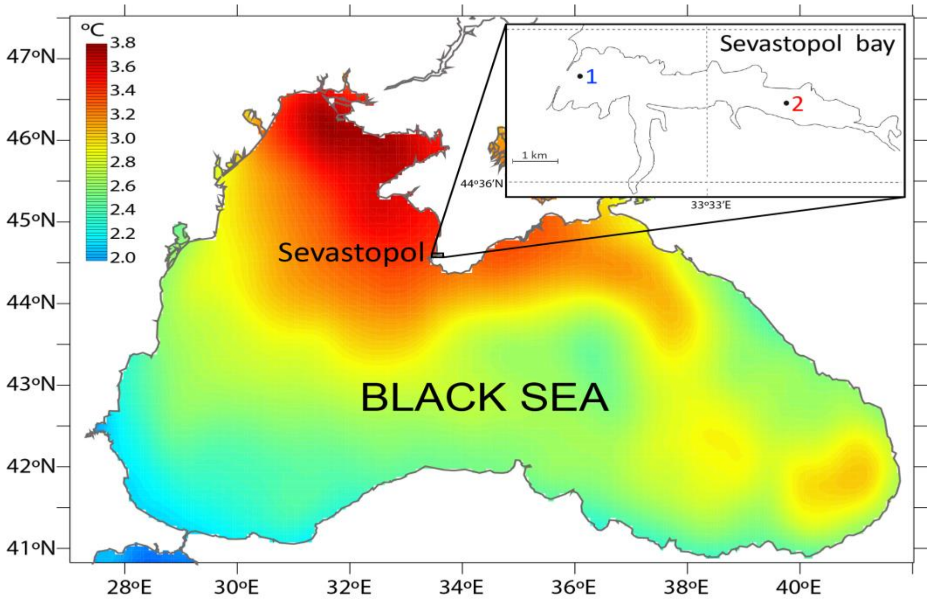

Figure 1. Sampling stations in Sevastopol Bay and spatial pattern of the monthly average sea surface temperature (SST, °C) anomalies in the Black Sea in August 2010 with respect to the 1985–2014 monthly climatology.

The salinity ranges within 14–17.5 ppt and is largely controlled by freshwater input from the Chernaya River that flows into the head of the bay [19]. The bay is suffering from a heavy anthropogenic pressure associated with discharges of industrial and domestic wastewaters as well as stormwater runoff. Based on the eutrophication E-TRIX-index assessments made in 2011–2012, the trophic level in the Sevastopol Bay was characterized as a transitional from medium to high [20]. Both pollution and trophic levels gradually decrease from the head of the bay to its mouth [21]. Being a port area, Sevastopol Bay is also heavily affected by maritime traffic, which contributes to invasions of alien species.

2.2. SST Data

SST in Sevastopol Bay is investigated based on a long-term series of continuous 6 h measurements from 1950 to 2014 provided by the Sevastopol Hydrometeorological Station. Additionally, the SST product from the OSTIA archive (Operational Sea Surface Temperature and Sea Ice Analysis) with a spatial resolution of 0.054° (about 5 km) was used to analyze the spatial distribution of the summer 2010 warm anomaly in the Black sea. The archive includes daily fields averaged using optimal interpolation and is based on satellite data from sensors AVHRR, AMSRE, AATSR, SEVERI and TMI, as well as on data received from drifting and moored buoys [22].

2.3. Sampling and Zooplankton Processing

The analysis of the mesozooplankton community is based on a long-term data set collected between 2003 and 2014 at two stations (Figure 1), one located in the mouth of Sevastopol Bay (station 1) and the other one in the middle of the bay (station 2). Throughout the entire period, sampling and samples processing were made according to the same methods, allowing a reliable assessment of seasonal and interannual changes.

Zooplankton samples were taken twice per month in the morning using a Juday plankton net (with a mouth area of 0.1 m^2 and a mesh size of 150 mm) from the whole water column: 10–0 m at station 1, and 9–0 m at station 2. Samples were fixed with formaldehyde solution (4% final conc.) and processed in the laboratory using the standard methodology for zooplankton. The sample was homogenized before taking aliquot. A calibrated 1 mL Stempel pipette was used for sub-sampling. Quantitative and qualitative processing was carried out in Bogorov's chamber under a stereomicroscope. At least 2 aliquots were calculated for each sample. In the sub-sample(s), all crustaceans were counted until each of the three dominant species reached 100 individuals. The entire specimen was examined for rare species [23,24].

2.4. Data Analysis

2.4.1. SST Data

The monthly seasonal cycle of SST (or monthly mean climatology) was calculated based on observed mean monthly data averaged for each calendar month over the 30-year period from 1985 to 2014. The monthly SST anomalies were then calculated by subtracting the monthly seasonal cycle from the observed monthly means. In order to obtain the monthly mean climatology on a daily basis, the monthly climatology was interpolated from 12 calendar months to 365 calendar days using a spline interpolation.

To describe the summer 2010 MHW characteristics, we used the MHW definition from [25]: the mean daily SST exceeds a seasonally varying threshold (95th percentile) for at least 5 consecutive days; successive heatwaves with gaps of 2 days or less are considered part of the same event. The seasonally varying 95th percentile was calculated as monthly 95th percentile climatology for each calendar month over the period 1985–2014 and then interpolated to 365 calendar days using a spline interpolation.

2.4.2. Zooplankton

Based on the long-term observation dataset described in Section 2.3, seasonal and interannual variability in zooplankton abundance was analyzed at both stations for 12 species of crustacean zooplankton representing different ecological groups (warm-water, cold-water and eurythermal).

The seasonal variability of zooplankton species abundance was analyzed based on normalized average monthly values calculated as:

$$N_{ij}^{\sigma} = \left(\overline{N_{ij}} - \overline{\overline{N_j}}\right) / \sigma\overline{\overline{N_j}} \tag{1}$$

where $\overline{N_{ij}}$—average monthly values of the abundance for each i-th month and j-th species; $\overline{\overline{N_j}}$ and $\sigma\overline{\overline{N_j}}$ the average long-term value of the abundance and its standard deviation for the j-th species, respectively.

Interannual abundance variability was estimated as the deviation of the numbers of each zooplankton species (N_{ij}) from the corresponding average monthly values (for each i-th month and j-th species) according to:

$$\delta N_{ij} = N_{ij} - \overline{N_{ij}} \tag{2}$$

Furthermore, the values of abundance anomalies relative to the annual variation (δN_{ij}) were averaged over the 2003 to 2014 ($\overline{\delta N_{ij}}$), and the standard deviation $\sigma(\overline{\delta N_{ij}})$ of the obtained time series were calculated. The average annual values of abundance anomalies relative to the annual variation normalized to this value (${}^{\sigma}_{\delta}\overline{N}_{ij}$) were used to characterize the interannual variability of particular zooplankton species and to assess the significance of differences in their abundance among years.

Hereafter, the normalized average annual values of abundance anomalies relative to the annual variation ${}^{\sigma}_{\delta}\overline{N}$ will be referred to as the indicator of interannual variability.

3. Results

3.1. SST Variability and the Summer 2010 MHW

The SST of Sevastopol Bay has a marked seasonal cycle with a cold season from January to March and a warm season occurring form June to September (Figure 2a, blue line). The minimum and maximum are observed in February (6.6 °C) and August (24.8 °C), respectively. During the study period, SST shows a clear warming trend from 2003 to 2010, the latter year being the hottest one (Figure 2b). The month-to-month variability was rather low between 2003 and 2010. The period 2011–2014 exhibits stronger variability, which is associated in particular with two cold events (February 2012 and October 2013) when the monthly anomalies fell below −2 °C and the hottest event in May 2013 when the monthly anomaly reached 3.4 °C. The minimum and maximum are observed in February (6.6 °C) and August (24.8 °C), respectively.

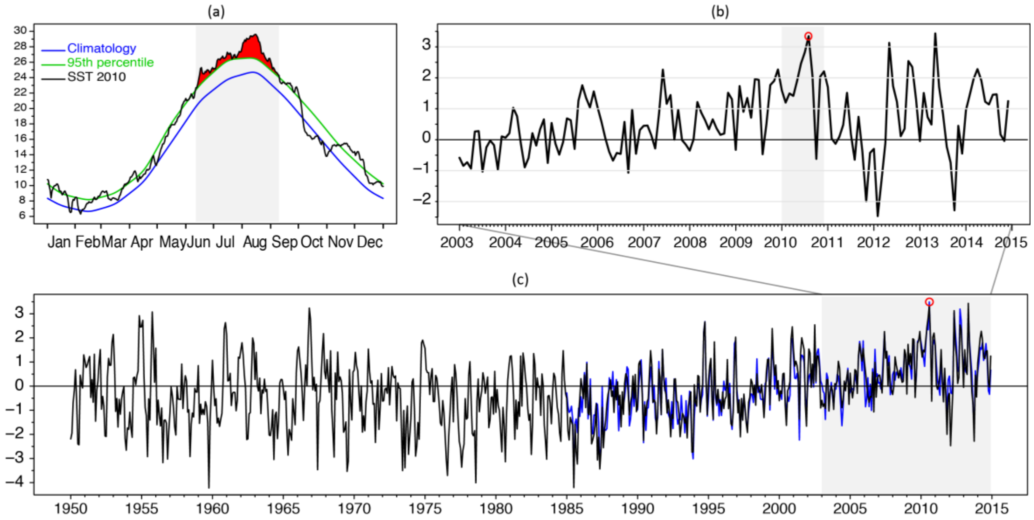

Figure 2. SST series in Sevastopol Bay (°C): (**a**) The climatology (blue), 95th percentile marine heat wave (MHW) threshold (green) and time series (black) for 2010. The red filled area indicates the period of time associated with the MHW; (**b**) Monthly averaged anomalies over the study period 2003–2014 with respect to the 1985–2014 monthly climatology as recorded by in situ observations; (**c**) As in (**b**) but over the period 1950–2014. Black and blue lines in (**c**) show the in situ and satellite observations, respectively.

During the study period (Figure 2b), SST shows a clear warming trend from 2003 to 2010, the latter year being the hottest one. The month-to-month variability was rather low between 2003 and 2010. The period 2011–2014 exhibits stronger variability, which is associated in particular with two cold events (February 2012 and October 2013) when the monthly anomalies fell below −2 °C and the hottest event in May 2013 when the monthly anomaly reached 3.4 °C. Figure 2c further evidences that the study period (2003–2014) corresponds to the warmest duodecad and 2010 is the warmest year since at least 1950 when began regular SST observations in Sevastopol Bay.

We now focus on the summer 2010 MHW event. Figure 2a shows that during almost all of 2010, the daily SST anomalies were above the climatological values. The summer MHW event starts on June 11th and ends on 9th September, lasting in total 3 months. The peak of the event was observed from 1 August to 19 August, when the daily SST anomalies exceeded 4 °C and reached 5 °C on 15 August. Figure 1 shows that in August 2010, abnormally high SSTs were recorded throughout the entire Black Sea area. The mean monthly anomalies ranged from about 2 °C in the Bosphorus region to almost 3.8 °C near the Dnieper-Bug Estuary in the northwestern shelf. Crimea's southwestern coast was marked by extremely high values (more than 3 °C), which closely matched the in situ observations in Sevastopol Bay (Figure 2).

3.2. *Species Composition and Ecological Groups of Zooplankton*

During the study period, 12 species of crustaceans representing three different ecological groups (thermophilic, eurythermal and cold-water) were found in Sevastopol Bay. Table 1 summarizes the annual average abundance of each species. Copepods *Acartia tonsa*, *Centropages ponticus*, *Oithona davisae* and cladocerans *Penilia avirostris*, *Pseudevadne tergestina*, *Evadne spinifera* are representatives of a thermophilic assemblage. Among them, *A. tonsa* and *O. davisae* are non-indigenous species, which appeared in the Black Sea in 1970s and

2005, respectively. *Pseudevadne tergestina* and *Evadne spinifera* were not numerous and were not considered here.

Table 1. Interannual variations in abundance of the numerous crustaceans (ind. m^{-3} ± standart error) at the mouth of Sevastopol Bay (station 1) and in the middle of the bay (station 2).

Station 1.												
Year	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**
Samples Number	21	21	19	24	21	24	23	23	22	22	21	22
Penilia avirostris	238 ± 117	433 ± 268	2391 ± 1596	792 ± 630	272 ± 166	334 ± 198	590 ± 370	1164 ± 597	825 ± 477	483 ± 284	518 ± 421	378 ± 241
Pleopis polyphemoides	227 ± 151	526 ± 246	741 ± 506	360 ± 114	383 ± 142	799 ± 513	372 ± 136	865 ± 374	795 ± 426	362 ± 219	376 ± 226	202 ± 97
Acartia clausi	582 ± 194	263 ± 56	232 ± 51	203 ± 52	142 ± 44	922 ± 408	198 ± 53	362 ± 162	389 ± 87	125 ± 35	573 ± 126	238 ± 42
Acartia tonsa	129 ± 47	480 ± 246	116 ± 53	99 ± 42	52 ± 26	62 ± 24	8 ± 7	72 ± 35	3 ± 1	13 ± 6	38 ± 18	13 ± 7
Centropages ponticus	62 ± 25	92 ± 54	37 ± 15	171 ± 50	346 ± 174	72 ± 31	321 ± 104	268 ± 109	177 ± 64	310 ± 174	471 ± 159	248 ± 57
Oithona davisae	NA *	NA *	22 ± 14	1892 ± 1056	2344 ± 1717	3256 ± 1349	5770 ± 1763	17,236 ± 5400	5043 ± 1384	4678 ± 2729	4211 ± 1159	7140 ± 3107
Oithona similis	30 ± 10	58 ± 20	23 ± 9	31 ± 7	63 ± 22	24 ± 8	160 ± 46	43 ± 10	122 ± 35	156 ± 57	127 ± 33	87 ± 21
Paracalanus parvus	173 ± 57	178 ± 41	377 ± 176	564 ± 169	524 ± 146	638 ± 207	1786 ± 354	1830 ± 567	1280 ± 249	474 ± 125	1261 ± 386	839 ± 165
Pseudocalanus elongatus	204 ± 74	193 ± 68	121 ± 44	120 ± 37	234 ± 102	55 ± 21	189 ± 61	64 ± 25	325 ± 141	118 ± 43	224 ± 67	180 ± 72
Station 2.												
Year	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**
Samples number	18	20	15	21	21	22	22	22	22	16	21	21
Penilia avirostris	284 ± 117	133 ± 100	1265 ± 1170	75 ± 29	73 ± 45	80 ± 62	664 ± 369	1202 ± 749	258 ± 221	348 ± 168	215 ± 144	2362 ± 2151
Pleopis polyphemoides	1051 ± 612	966 ± 475	959 ± 641	1636 ± 845	1401 ± 678	912 ± 501	688 ± 398	1056 ± 511	2027 ± 1086	1662 ± 820	1060 ± 777	617 ± 295
Acartia clausi	338 ± 162	308 ± 71	159 ± 50	372 ± 157	137 ± 45	472 ± 131	198 ± 43	232 ± 62	270 ± 63	83 ± 17	485 ± 117	375 ± 106
Acartia tonsa	1777 ± 1245	690 ± 361	599 ± 264	366 ± 215	292 ± 162	261 ± 152	30 ± 17	883 ± 609	73 ± 25	197 ± 110	483 ± 237	189 ± 130
Centropages ponticus	61 ± 36	40 ± 20	25 ± 10	36 ± 15	196 ± 98	32 ± 14	184 ± 63	79 ± 28	284 ± 130	183 ± 85	186 ± 53	122 ± 32
Oithona davisae	NA *	NA *	301 ± 168	4849 ± 2224	6867 ± 3128	16,312 ± 5456	22,069 ± 4345	41,754 ± 12,337	25,059 ± 6520	13,174 ± 6807	8946 ± 2017	18,131 ± 7869
Oithona similis	69 ± 50	120 ± 60	20 ± 7	49 ± 19	111 ± 36	22 ± 7	151 ± 60	36 ± 15	115 ± 37	247 ± 146	177 ± 67	193 ± 76
Paracalanus parvus	61 ± 17	85 ± 28	174 ± 60	364 ± 113	295 ± 65	484 ± 211	674 ± 160	731 ± 192	686 ± 137	214 ± 59	474 ± 91	548 ± 102
Pseudocalanus elongatus	324 ± 195	305 ± 118	224 ± 87	303 ± 145	262 ± 84	130 ± 40	598 ± 228	152 ± 64	370 ± 126	254 ± 115	241 ± 128	426 ± 184

* NA—not available.

The seasonal pattern dynamics of warm-water species are shown in Figure 3. All these species survived in the cold season in the Black Sea at a dormant stage. Most of them produced resting eggs in response to low temperatures, and *O. davisae* maintained in plankton at the stage of fertilized females. The populations of warm-water species began to grow rapidly in late May (at a temperature of 16–18 °C) and peaked in August–October (Figure 3A–C).

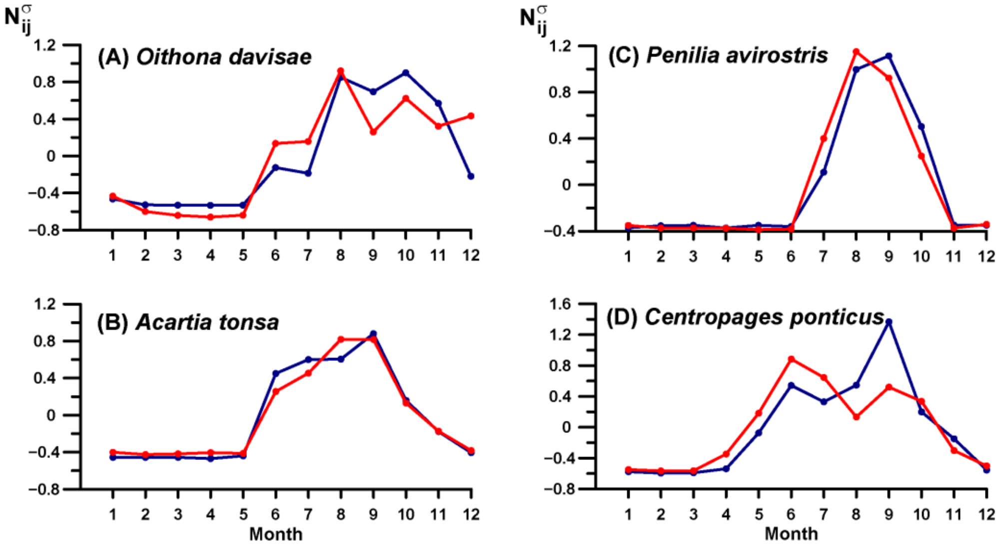

Figure 3. The patterns of seasonal dynamics of warm-water crustaceans in Sevastopol Bay at station 1 (blue) and station 2 (red) presented as normalized average monthly values (see details of the method in Section 2.4): (**A**)—*Oithona davisae*; (**B**)—*Acartia tonsa*; (**C**)—*Centropages ponticus*; (**D**)—*Penilia avirostris*.

Such seasonal pattern was typical for all the above-mentioned species with the exception of *C. ponticus* (Figure 3D). The first peak of *C. ponticus* abundance occurred in June, which was followed by a slight decline in the hottest months of July and August. The more pronounced peak took place in September (Figure 3D). So, despite the fact that centropages is typically a warm-water species, it preferred temperatures not higher than 23 °C.

The eurythermal assemblage of crustaceans was represented by copepods *A. clausi*, *P. parvus* and cladocera *P. polyphemoides*. All these species are numerous in the Sevastopol Bay plankton community all year round. Seasonal pattern of *A. clausi* demonstrated two pronounced picks, in early spring (March) and autumn (September–November), respectively (Figure 4A). *P. parvus* peaked in November–December (Figure 4B). For both species, there was a summertime decline in abundance. (Figure 4A,B). *P. polyphemoides* showed strong picks only in May–June (Figure 4C).

Copepods *P. elongatus, O. similis, C. euxinus* belong to a cold-water assemblage. Two of them, *P. elongatus* and *O. similis,* are important components of the zooplankton of Sevastopol Bay in cold seasons. *C. euxinus*, an inhabitant of the open Black Sea, was found in small amounts in the bay, usually during winter. It was not taken under consideration in the present analysis. *P. elongatus* and *O. similis* were abundant in Sevastopol Bay during January–April and November–December, whereas in June–October, their density was the lowest (Figure 5A,B).

3.3. Interannual Variation in Abundance

For the study period 2003–2014, the maximum abundance of crustaceans was recorded in 2010: 22,000 ind. m^{-3} at the mouth of the bay (station 1) and 46,000 ind. m^{-3} in its middle (station 2), which is nearly three times the long-term average values for the whole period (about 7000 ind. m^{-3} and about 17,000 ind. m^{-3}, respectively). At both stations, the crustaceans were numerically dominated by warm water species in 2010 (Table 1; Figure 6a). They amounted more than 19,000 ind. m^{-3} at station 1 and about 44,000 ± ind. m^{-3} at station 2 (85% and 95% of the total crustacean abundance, respectively). The warm-water assemblage prevailed not only among crustaceans but also in the mesozooplankton community as a whole, both by season (in the summer–autumn months) and by year (on average per year). Warm-water species abundance increased year after year from 2006 to 2010. This was attributable to the introduction and rapid growth of the *O. davisae* population, which is a new copepod species discovered in the Black Sea in 2005. Note also that a general positive trend in warm-water species abundance over 2003–2010 coincides with a strong warming SST trend in this period (Figure 2c).

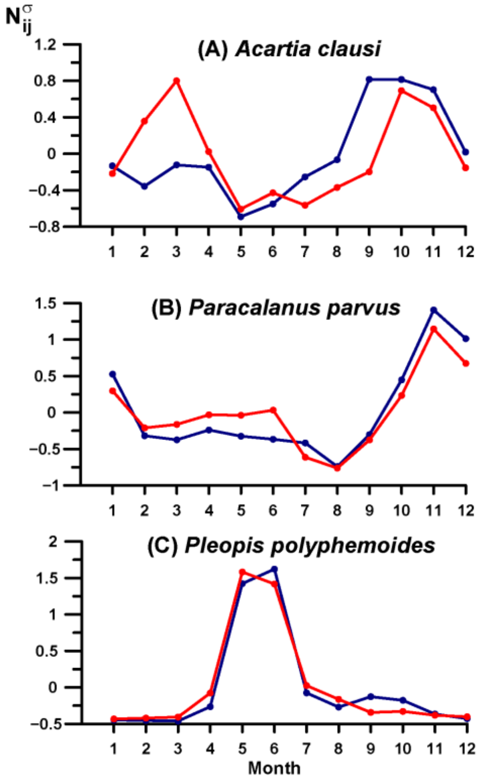

Figure 4. The patterns of seasonal dynamics of eurythermalcrustaceansin Sevastopol Bay at station 1 (blue) and station 2 (red) presented as normalized average monthly values (see details of the method in Section 2.4): (**A**)—*Acartia clausi*; (**B**)—*Paracalanus parvus*; (**C**)—*Pleopis polyphemoides*.

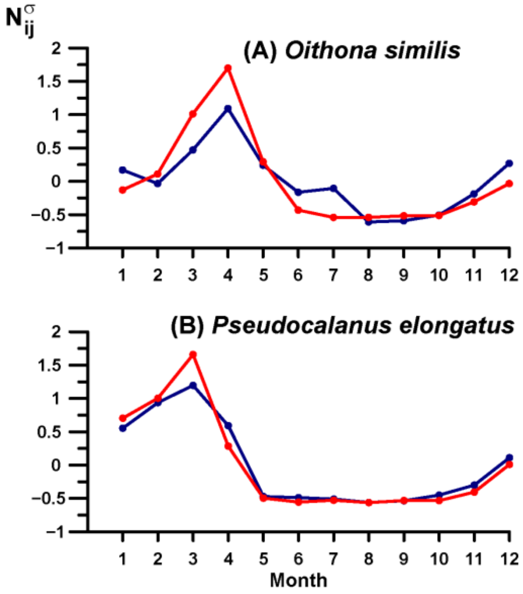

Figure 5. The patterns of seasonal dynamics of cold-water crustaceans in Sevastopol Bay at station 1 (blue) and station 2 (red) presented as normalized average monthly values (see details of the method in Section 2.4): (**A**)—*Oithona similis*; (**B**)—*Pseudocalanus elongatus*.

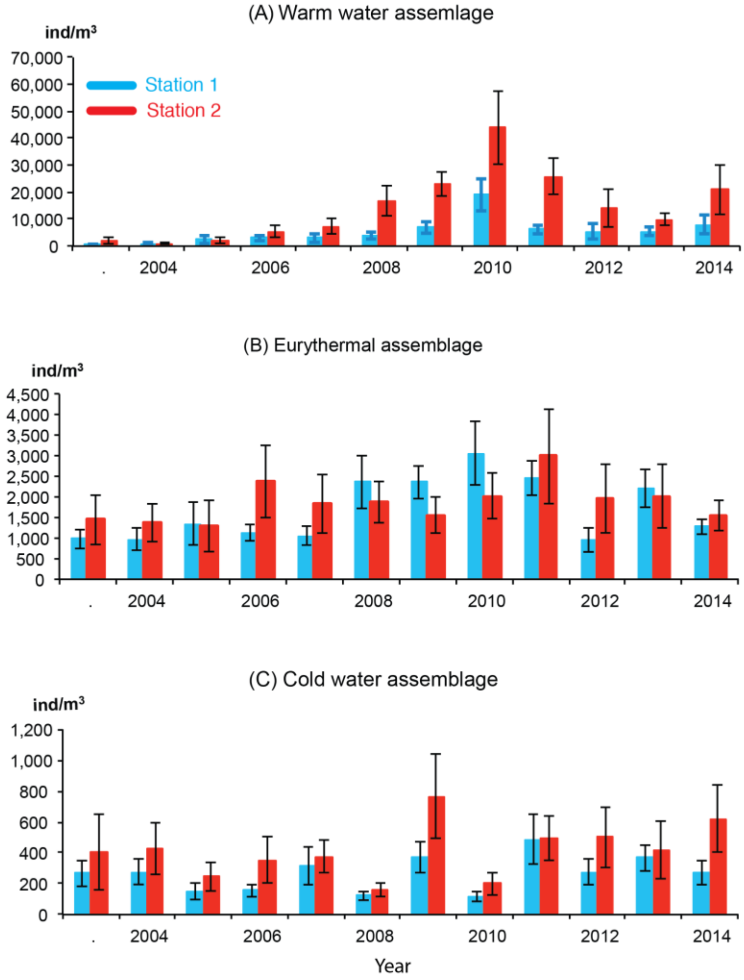

Figure 6. Interannual variability of annual average abundance of the: (**A**)—warm-water crustacean assemblage, (**B**)—euthermal crustacean assemblage; (**C**)—cold-water crustacean assemblage in Sevastopol Bay at station 1 (blue bars) and station 2 (red bars).

The density of eurythermal and cold-water species varied slightly during the study period (Figure 6B,C). The eurythermal crustacean abundance ranged from 960 to 3057 ind. m^{-3} at station 1 and from 1292 to 2983 ind. m^{-3} at station 2, whereas the abundance of cold-water crustacean ranged from 119 to 487 ind. m^{-3} at station 1 and from 162 to 767 ind. m^{-3} at station 2. A minor rise in the abundance of eurythermal species was observed in 2010, notably at the mouth of the bay (Figure 6B). In the middle of the bay (station 2), the abundance of eurythermal species reached the highest values in 2011. On the contrary, the density of cold-water crustaceans was the lowest in 2010: 119 ind. m^{-3} at station 1 and 199 ind. m^{-3} at station 2 (Figure 6C).

3.4. Key Species Variability

Warm-water assemblages of crustaceans in Sevastopol Bay were represented by four key species: *O. davisae*, *A. tonsa*, *C. ponticus* and *P. avirostris*. Non-indigenous copepod *O. davisae* was detected in the Black Sea at the end of 2005 and contributed the most to the total abundance of crustaceans in Sevastopol Bay during the following years. Since 2006, its abundance increased annually by about 1.5 times and reached 5770 ± 1763 ind. m^{-3} at station 1 and 22,069 ± 4345 ind. m^{-3} at station 2 in 2009 (Table 1). The population explosion occurred in 2010 (17,236 ± 5400 ind. m^{-3} at station 1 and 41,754 ± 12,337 ind. m^{-3} at station 2), and since 2011, species density stabilized near the values of 2009 (Table 1). At both stations, the indicator of interannual variability of abundance (${}^{\sigma}_{\delta}\overline{N}$) reached 3σ in 2010 (Figure 7A).

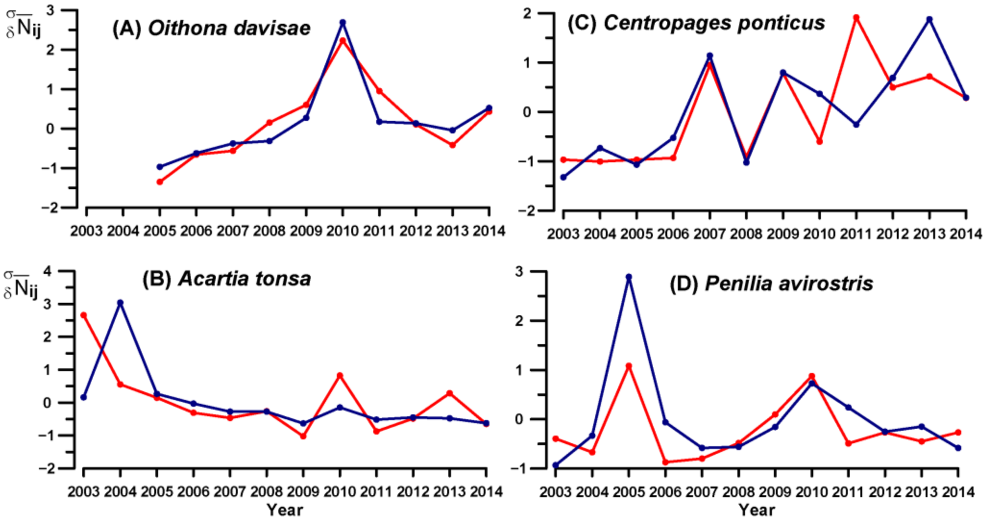

Figure 7. Pattern of interannual variability of abundance of the warm-water crustaceans in Sevastopol Bay at station 1 (blue) and station 2 (red) presented as normalized annual anomalies (see details of the method in Section 2.4): (**A**)—*Oithona davisae*; (**B**)—*Acartia tonsa*; (**C**)—*Centropages ponticus*; (**D**)—*Penilia avirostris*.

Positive anomalies in the abundance of *O. davisae* in Sevastopol Bay were observed throughout the entire breeding season of 2010 (Figure 8A). The largest abundance of *O. davisae* was recorded at both stations (86,000 ind. m^{-3} at station 1 and 145,000 ind. m^{-3} at station 2) in August 2010 during the peak of the summer MHW when the highest daily SST reached 29.6 °C. Moreover, *O. davisae* contributed hugely to the total abundance of crustaceans in August 2010: 78% at the mouth and 90% in the middle of the bay.

Another warm-water species *A. tonsa* was more abundant in 2003–2005, before the introduction of *O. davisae* (Figure 7B), showing the annual average density between 116 and 480 ind. m^{-3} at station 1 and between 599 and 1777 ind. m^{-3} at station 2. Since 2006, the density of *A. tonsa* decreased steadily, dropping to 52–99 (261–366) ind. m^{-3} at station 1 (station 2) in 2006–2008, and further to 3–38 (30–483) ind. m^{-3} at station 1 (station 2) in 2009 and 2011–2014 (Table 1). However, in 2010, the average annual abundance of *A. tonsa* increased sharply with respect to the previous years (up to 72 ± 35 ind. m^{-3} at station 1 and 883 ± 609 ind. m^{-3} at station 2). The maximum abundance was observed in July–August during the peak of the MHW (Figure 8B): 563 ind. m^{-3} and 12,000 ind. m^{-3} at the mouth and in the middle of the bay, respectively.

The warm-water species *P. avirostris* exhibited two pronounced peaks in its density in 2005 and 2010 (Table 1, Figure 7D). The peak of 2005 at the mouth of the bay (station 1) was the most significant and showed the indicator of interannual variability above 3σ. The average abundance in 2010 amounted to 1164 ind. m^{-3} ± 374 at station 1 and to 1202 ind. m^{-3} ± 749 at station 2. *P. avirostris* density reached the maximum in July–August (Figure 8D): the abundance was 7000–8000 ind. m^{-3} in July and 3000–4000 ind. m^{-3} in August (Table 1). The indicator of interannual variability reached 1σ for these peaks (Figure 7D).

Unlike the three warm-water species described above, the pattern of interannual fluctuations in *C. ponticus* abundance was more heterogenous, showing different behaviors at two stations (Figure 7C). The annual average density of *C. ponticus* reached its maximum in 2013 at station 1 (471 ± 159 ind. m^{-3}) and 2011 at station 2 (284 ± 130 ind. m^{-3}) (Table 1). Both stations did not experience a density peak in 2010 showing the values of 268 ± 109 ind. m^{-3} and 79 ± 28 ind. m^{-3} at station 1 and station 2, respectively. In August 2010, negative anomalies of *C. ponticus* abundance were observed at both stations (Figure 8D).

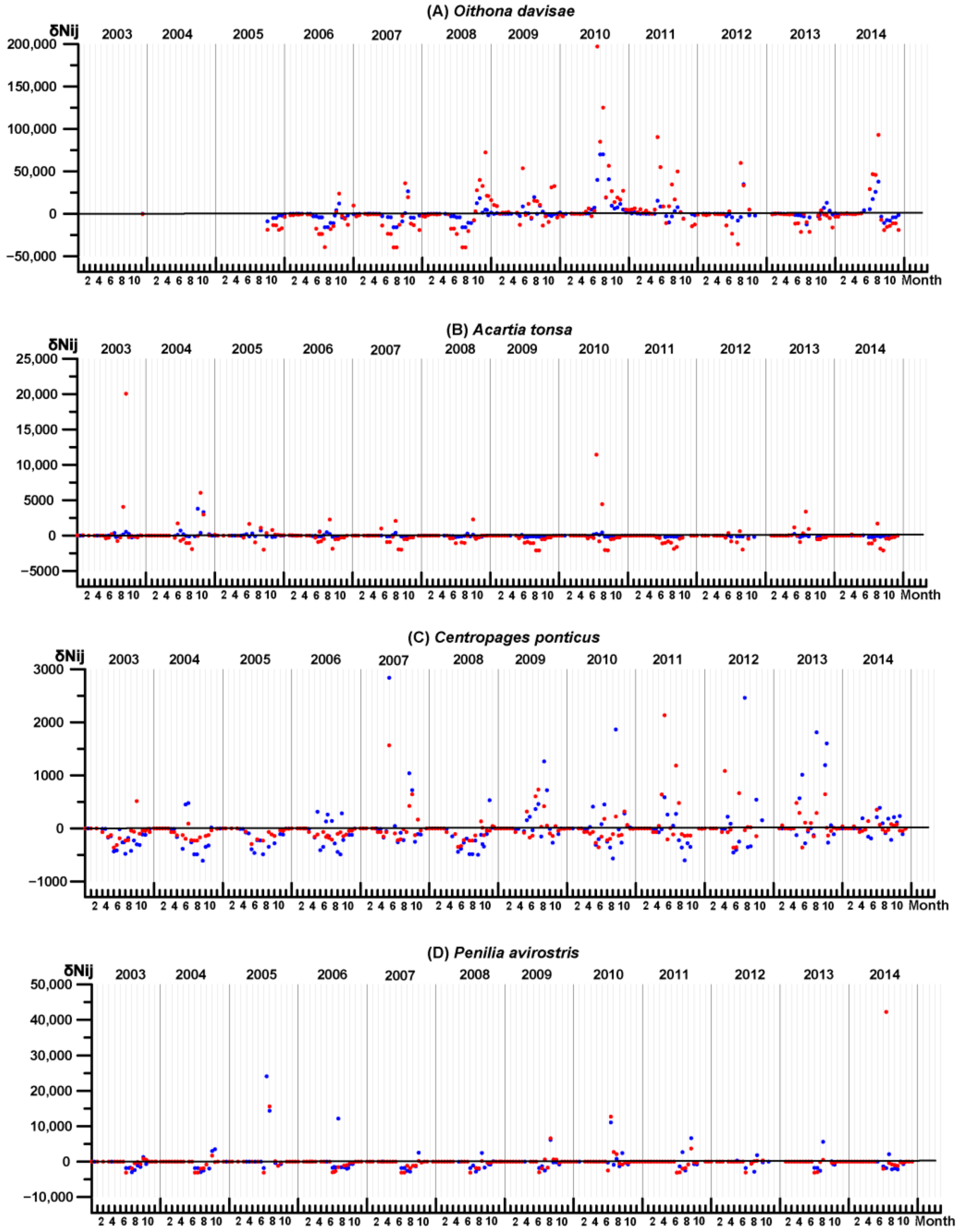

Figure 8. Long-term fluctuations in anomalies of warm-water crustaceans abundance relative to the annual variation (see details of the method in Section 2.4) in Sevastopol Bay at station 1 (blue) and station 2 (red): (**A**)—*Oithona davisae*; (**B**)—*Acartia tonsa*; (**C**)—*Centropages ponticus*; (**D**)—*Penilia avirostris*.

Eurythermal crustacean assemblages were represented by *A. clausi*, *P. parvus* and *P. polyphemoides*. The pattern of interannual variability of *A. clausi* showed a significant increase in population in 2008 and 2013 (Figure 9A) associated with seasonal picks in its abundance in spring and autumn (Figure 10A).

The annual average abundance of *A. clausi* ranged within 125 ± 35 ind. m^{-3} and 922 ± 408 ind. m^{-3} at station 1 and within 83 ± 17 ind. m^{-3} and 485 ± 117 ind. m^{-3} at station 2 (Table 1). In 2010, the abundance was close to the average value (362 ± 162 and 232 ± 62 ind. m^{-3} at stations 1 and 2, respectively). The annual average abundances of *P. parvus* increased at both stations in period 2009–2011 (Figure 9B), with the maximum density in 2010 (1830 ± 567 ind. m^{-3} at station 1 and 731 ± 192 ind. m^{-3} at station 2) (Table 1). The highest abundance of *P. parvus* occurred in November 2010 at the mouth of the bay (9100 ind. m^{-3}). The abundance was also high in April–May and in October–December in 2010.

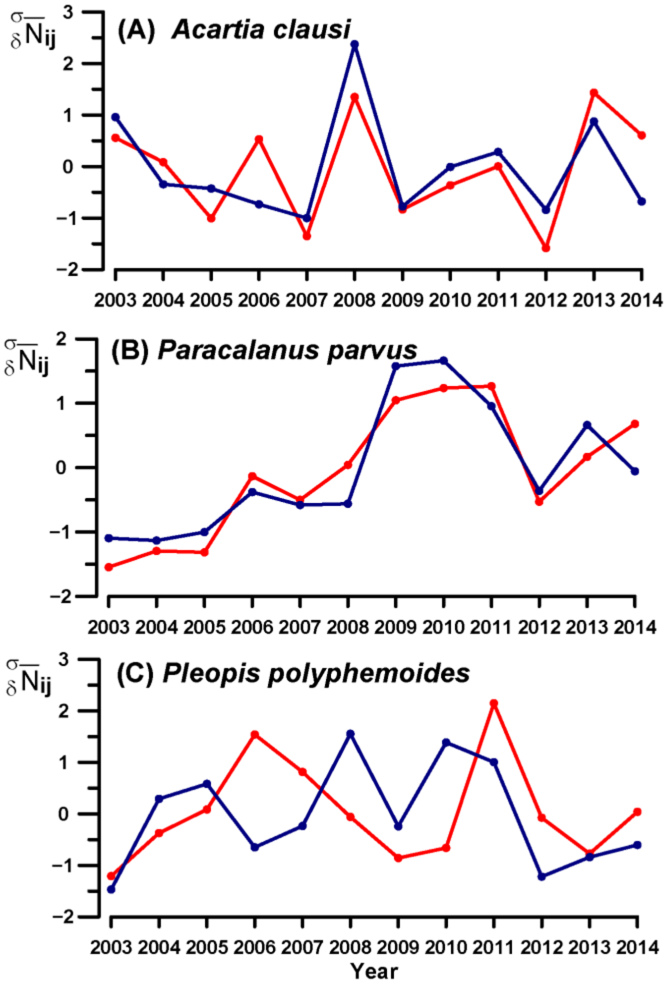

Figure 9. Pattern of interannual variability of abundance of eurythermal crustaceans in Sevastopol Bay at station 1 (blue) and station 2 (red) presented as normalized annual anomalies (see details of the method in Section 2.4): (**A**)—*Acartia clausi*; (**B**)—*Paracalanus parvus*; (**C**)—*Pleopis polyphemoides*.

Positive anomalies of *P. parvus* were observed from January to May 2010 and from October 2010 to February 2011 (Figure 10B). The abundance of *P. parvus* was significantly higher at the mouth of the bay over the study period.

Unlike other species, the extremes of the interannual variability in the abundance of *P. poliphemoides* did not coincide at two stations (Figure 9C). At the mouth of the bay, the maximum of annual average density was in 2010 (865 ± 374 ind. m^{-3}) followed by 2008 (799 ± 513 ind. m^{-3}) and 2011 (795 ± 426 ind. m^{-3}). In the middle of the bay, the most abundant year was 2011 (2027 ± 1086 ind. m^{-3}), although 2010 was also abundant (1056 ± 511 ind. m^{-3}) (Table 1). These interannual extremes were largely contributed by strong positive anomalies in abundance observed in May–June at both stations (Figure 10C).

The density of cold-water species *P. elongatus* and O. *similis* was low throughout the study period (Table 1). Their annual average abundance fluctuated from year to year, and the long-term variability of its anomalies had an irregular pattern (Figure 11A,B). A common feature of the long-term variability curves for both species was an increase in the density in 2009 and a decline in 2008 and 2010. (Figure 11A,B). Negative anomalies in the seasonal dynamics of *P. elongatus* and O. *similis* were observed from January to April in 2008 and 2010 (Figure 12A,B).

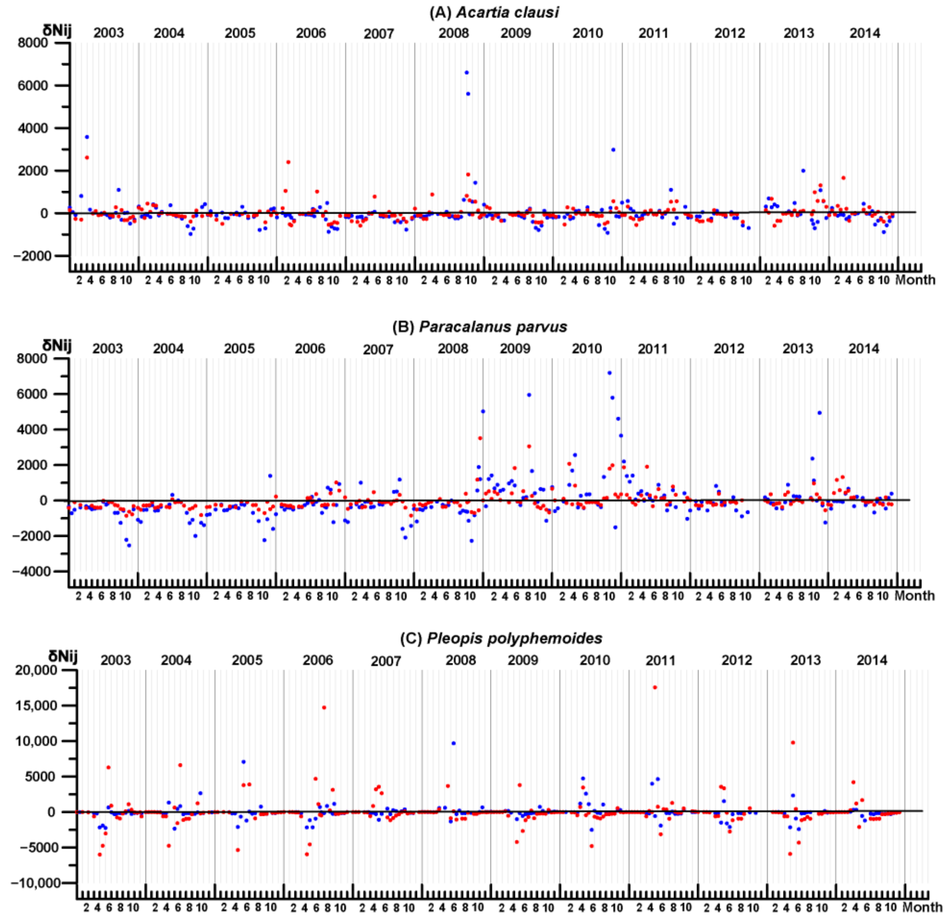

Figure 10. Long-term fluctuations in anomalies of eurythermal crustaceans abundance relative to the annual variation (see details of the method in Section 2.4) in Sevastopol Bay at station 1 (blue) and station 2 (red): (**A**)—*Acartia clausi*; (**B**)—*Paracalanus parvus*; (**C**)—*Pleopis polyphemoides*.

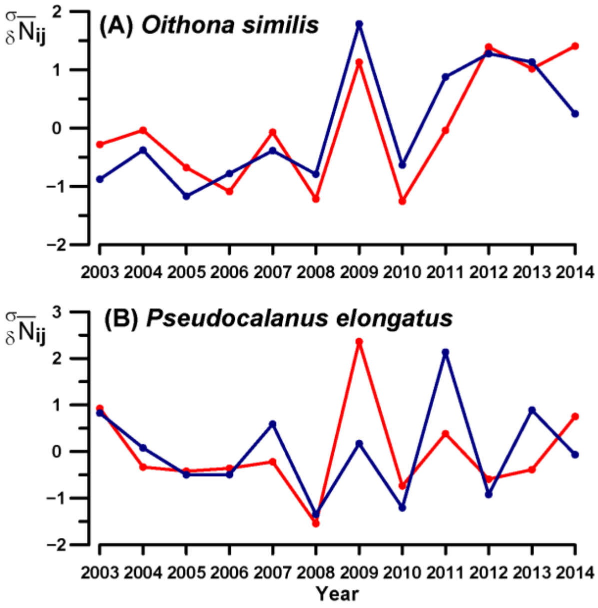

Figure 11. Pattern of interannual variability of abundance of cold-water crustaceans in Sevastopol Bay at station 1 (blue) and station 2 (red) presented as normalized annual anomalies (see details of the method in Section 2.4): (**A**)—*Oithona similis*; (**B**)—*Pseudocalanus elongatus*.

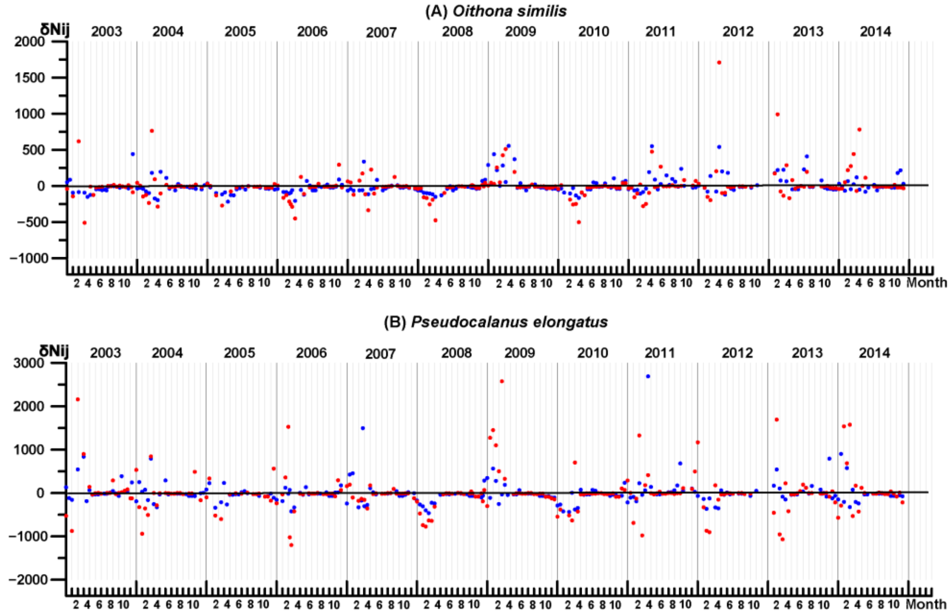

Figure 12. Long-term fluctuations in anomalies of cold-water crustaceans abundance relative to the annual variation (see details of the method in Section 2.4) in Sevastopol Bay at station 1 (blue) and station 2 (red): (**A**)—*Oithona similis*; (**B**)—*Pseudocalanus elongates*.

The annual average abundance of *P. elongatus* ranged between 55 ± 21 ind. m^{-3} and 352 ± 141 ind. m^{-3} at station 1 and 130 ± 40 ind. m^{-3} and 598 ± 228 ind. m^{-3} at station 2. The maximum seasonal abundance of *P. elongatus* occurred in February and March, the strongest peak being observed in March 2009 (about 4000 ind. m^{-3}). The density of *O. similis* varied from 23 ± 9 ind. m^{-3} to 160 ± 46 ind. m^{-3} at station 1 and from 20 ± 7 ind. m^{-3} to 247 ± 151 ind. m^{-3} at station 2. The maximum seasonal abundance of *O. similis* was observed in February and April, the highest value of about 1500 ind. m^{-3} being found in April 2014.

4. Discussion

As a distinct signature of contemporary global warming, the MHWs are increasing in frequency, duration and magnitudes, posing a serious threat for the marine ecosystem. The Black Sea is an example of semi-closed sea experiencing a rapid warming, which is considered an amplified precursor of the changes to expect in the greater oceans [3]. Recent studies have shown that the frequency of MHW in the Black Sea has increased by a factor of five in the last two decades compared with the two previous decades [4].

In this study, we assessed the response of the zooplankton in Sevastopol Bay to the summer 2010 event, which was among the most persistent and intense MHW recorded in the Black Sea. In order to interpret the changes observed in 2010, the patterns of seasonal dynamics and interannual variability in the abundance of crustacean species were analyzed based on a dataset of zooplankton samples collected twice per month between 2003 and 2014.

The analysis of the SST in Sevastopol Bay showed that the study period was the warmest duodecad since at least 1950. Within this period, the SST showed a strong increasing trend between 2003 and 2010. 2010 was the warmest year since 1950 and exhibited positive SST anomalies almost all year round. The summer 2010 MHW starts at the beginning of June and lasts for 3 months, reaching the maximum amplitudes (daily SST anomaly > 4 °C) between the end of July and mid-August. Extreme positive SST anomalies in 2010 led to a sharp increase in the abundance of three warm-water species of crustaceans, namely *O. davisae, A. tonsa and P. avirostris,* and their share in the mesozooplankton community of Sevastopol Bay. An increase in the annual abundance in 2010 was also observed for two eurythermal species *P. parvus* and *P. poliphemoides*, although it is not related to the

MHW event but can be rather explained by warm SST anomalies during the first part of the year. We now discuss in detail the response of each species to the MHV 2010 depending on unique peculiarities of its biology, seasonal dynamics and sensitivity to high temperature.

4.1. Warm-Water Assemblages

The largest contribution to the total abundance of crustaceans in 2010 was made by a non-indigenous species (NIS) of warm-water copepod *Oithona davisae*. This species was discovered in the Black Sea for the first time in October 2005 (it was initially misidentified as *Oithona brevicornis*) [26,27]. Its abundance rapidly increased, and already in 2006, *Oithona davisae* outnumbered other copepods in summer–autumn and on average per year [28]. A logarithmic acceleration phase such as a phase of NIS invasion pattern was observed in 2006–2008, when abundance raised sharply [29,30]. Afterwards, the growth was limited, and density remained at the same level as in 2009–2014, with the exception of 2010. In 2010, the abundance of *O. davisae* was extremely high with a maximum in July–August during the peak of the summer MHW 2010. A general positive trend in *O. davisae* abundance over 2003–2010 coincides with a strong warming SST trend in this period. We suggest that the increase in temperature during this period promoted the rapid growth in the population of *O. davisae*.

The other non-indigenous warm-water copepod *A. tonsa* appeared in the Black Sea in the 1970s [31,32]. It dominated the Sevastopol Bay in summer–autumn to 2006 before colonization of the bay by *O. davisae*. A considerable and statistically significant decline in *A. tonsa* abundance occurred from 2006 to 2014 due to competitive interactions between the two non-indigenous copepods [30]. It is worth noting that the negative effect of the non-indigenous *O. davisae* on populations of *Acartia omori, Micosetelle norvegica* and *P. parvus* have been also found in Tokyo Bay [33]. A sharp rise of the *A. tonsa* population in Sevastopol Bay was observed in July and August 2010 as a response to the MHW. The positive correlation of *O. davisae* and *A. tonsa* abundance with temperature was revealed in other areas of the world ocean [34–36].

At a seasonal scale, *P. avirostris* occurred in Sevastopol Bay in May–November and had one pronounced peak in August–September. The same seasonal dynamics was observed in the Mediterranean Vigo and Trieste regions, while in the subtropical highly productive waters of the Arabian Sea (Gulf of Oman), its population persisted all the year round. A regional link between the abundance of this species and temperature was also reflected in Gulf of Oman [37]. In Sevastopol Bay, the *P. avirostris* population was most abundant in 2005 and 2010 when strong positive SST anomalies were reported in August and September. A similar link between the average long-term abundance of *P. avirostris* and SST in August was reported for the coastal waters near Sevastopol [10].

Calanoid copepod *C. ponticus* is endemic to the Mediterranean and Black Sea [38,39]. It is a typical warm-water species that appears in plankton only during the warm season. However, unlike the warm-water species described above, *O. davisae* and *A. tonsa*, its peaks occurred in June and September at 22–23 °C. In July and August, when SST reached its maximum value, *C. ponticus* density declines. The annual average density of *C. ponticus* was relatively low in 2010 in Sevastopol Bay.

4.2. Eurythermal Assemblages

The native eurythermal *Acartia clausi* is one of the most common and numerous copepod in the World Ocean and also in the coastal area of the Black Sea [15,40–42]. In Sevastopol Bay, it was present year-round and reproduced throughout the year. According to long-term routine observations of zooplankton in the coastal area near Sevastopol in 1961–1969, a high abundance of *A. clausi* was observed in the years with negative temperature anomalies [10]. This is rather in line with our data: at the mouth of the bay, *A. clausi* exhibits the positive anomalies in its annual average density in the years when the SST anomalies in the bay was lower than 0.6 °C (2003, 2004, 2006, 2008, 2011 and 2013). In 2010, the annual population of *A. clausi* was close to its long-term average value, showing a seasonal peak in November, when the seasonal temperature drops. Thus, this eurythermal-type species did not show any response to the 2010 MHW.

Our results further suggested that the warm anomalies 2010 affected populations of eurythermal copepods *P. parvus* and *P. polyphemoides*. The highest average annual abundance of these species was reported in 2010 in Sevastopol Bay. The rise in *P. parvus* density was observed from February to June and in September-November 2010. The average annual abundance of *P. polyphemoides* in 2010 was higher than in other years, with positive abundance anomalies in spring and autumn, while in July and August, its abundance was low. Overall, the increase in annual abundance in 2010 of these eurythermal species can be explained by the rise of temperature in the first part of 2010, and it is not related to the summer MHW. Indeed, although both species occurred in the plankton of the bay all year round, their seasonal peaks occur in the spring and autumn and not in July–August when the 2010 MHW occurred. Interestingly, V.N. Grese with co-authors documented a significant summertime abundance of *P. parvus* in the coastal arear near Sevastopol in 1961–1969 [10]. The discrepancy in the seasonal patterns with their study could possibly be explained by the fact that the optimal temperature range for the *P. parvus* population development was reported between 10 and 20 °C, while over the study period, the late summer SST in Sevastopol Bay was near 26 °C, which led to a seasonal population decline.

4.3. Cold-Water Assemblage

Cold-water crustaceans were represented by copepods *P. elongatus* and *O. similis*. *P. elongatus* is common in the temperate eastern North Atlantic Ocean, including the Black Sea and some localities in Mediterranean Sea [43,44]. *O. similis* is cosmopolitan, distributed from tropical to polar waters [36,45]. In the summer, both species stay in the open Black Sea under a thermocline and appear in the surface waters and coastal areas in the cold season. In Sevastopol Bay, these copepods reached their greatest abundance in the first half of the year and were not found in summer. The year 2010 was one of the years characterized by the lowest annual average abundance of the cold-water species within the study period.

4.4. Concluding Remarks

Among all considered species, the most pronounced response to the summer 2010 MHW was observed in the population of non-native warm-water copepods *O. davisae* and *A. tonsa* at both seasonal and interannual scales. These species showed the ability of rapid population growth with rising temperatures. A large number of previous laboratory studies have indicated that increasing temperatures accelerate the development times of eggs and larval stages (nauplii and copepodids) of copepods [46,47]. Apparently, the extreme temperature in 2010 led to a reduction in the generation time of the warm-water species *O. davisae* and *A. tonsa*, resulting in a sharp increase in their abundance.

These NIS have a number of competitive advantages over native species. Their specific biological features ensured its rapid spread across the world ocean, establishment in new habitats, and successful competition with native species [30,48]. Non-native species also exhibit great flexibility as an adaptive response to environmental changes, especially in the case of climate warming.

The current climate changes significantly reduce the resistance of marine ecosystems to disturbance effects, which greatly facilitates the introduction of alien species into new ecosystems, especially into coastal areas [49]. The number of alien species and their abundance has increased in the Black Sea in recent decades. In addition to the described above *A. tonsa* and *O. davisae*, a new non-indigenous copepod *P. marinus* was reported in Sevastopol Bay in September 2016 [16,50]. All these new species are members of the warm-water mesozooplankton assemblage. Observations in other estuaries have also indicated that non-indigenous zooplankton species usually prevail in summer and autumn [34,36,50,51].

Studies of the climate warming impact on the marine ecosystems may be facilitated by the description of the indicator species. Following Reed Noss, the indicator should be (1) sensitive enough to warn of changes in a timely manner; (2) distributed over a wide geographic area or otherwise widely applicable; and (3) able to provide continuous assessment over a wide range of stresses [52]. Our results suggest that future warming may lead to an increase in *O. davisae* dominance in the mesozooplankton community of the Black Sea coastal area and that among crustaceans observed in this study, this species can be considered as an indicator of the environmental conditions associated with the warming of the Black Sea and the Mediterranean basin as a whole.

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