**Spring-summer transition and zooplankton phenology in the White Sea coastal zone: is the "paradox of plankton" resolved?** 

(Рабочее название)

**Introduction**

Temperature is among the primary factors (together with the solar cycle), driving seasonal cycle of high latitude marine ecosystems. Not only variations of absolute temperatures are the signs of climatic fluctuations – climate change manifests itself often through temporal shifts of seasonal temperature cycle – early/late seasonal warming or cooling (Stine et al., 2009; Dwyer et al., 2012; Mackas et al., 2012; Descamps et al., 2019). Such temporal shifts in environment inevitably leads to shifts of major phenological events in populations of marine organisms (Bertram et al., 2001; Ji et al., 2010; Mackas et al., 2012; Usov et al., 2013; Friedland et al., 2015).

Phenological changes in biological systems, which can be connected to the recent climate change, are documented all over the world, both on land and in the oceans and lakes (Parmesan, 2006; Thackeray et al., 2012; Staudinger et al., 2019; Descamps et al., 2019). Marine zooplankton is particularly sensitive to climate changes due to relatively short life cycles of planktonic organisms (Mackas, Beaugrand, 2010; Lombard et al., 2019). Phenological changes in zooplankton populations are interconnected between different trophic levels and populations of competing species (Aebischer et al., 1990; Edwards, Richardson, 2004; Miller-Rushing et al., 2010; Pau et al., 2011; Atkinson et al., 2015). The competition is one of the factors constraining diversity and species abundance in biological communities in general and in planktonic communities in particular (Hardin, 1960; DeMott, 1989; Lindegren et al., 2020). However, diversity and abundance of these communities, which inhabit relatively homogeneous medium and consist of species exploiting the same restricted resources, is surprisingly high. This was called "paradox of the plankton" (Hutchinson, 1961). One of the mechanisms of supporting such diversity is separation of temporal niches during seasonal cycle (DeMott, 1989), which is driven by changing environmental conditions during a year. This appears as differences of species phenology. Therefore, with changing phenological timing, temporal niches of competing species may overlap, causing strengthening of competition, which may have negative implications for populations and even whole ecosystems (Bertram et al., 2001; Miller-Rushing et al., 2010; Nakazawa, Doi, 2012), because of importance of the plankton as the base of aquatic trophic pyramid. Zooplankton is a key link in the trophic chain, connecting the base and the top of this pyramid, transferring energy and matter from primary producers (phytoplankton) to consumers of high levels.

The importance of problem described above demonstrates the need for thorough long-term investigations of climatic influence on the zooplankton. There are some specific requirements to such work. First, the longer is the period of observations, the greater is probability of revealing long-term patterns (e.g., cyclicity or trends) in seasonal dynamics of temperature and planktonic abundance. According to some works, observations should be 6 times as long as length of period of interest to reveal it reliably (Granger, Hatanaka, 1971)). Second, the more often we measure temperature and sample plankton, the subtler shifts in their seasonal cycles we can discern. This points out to the importance of long-term high-frequency observations of marine ecosystems. Among studies meeting these requirements is the long-term monitoring of zooplankton and environment near the White Sea Biological station Kartesh of the Zoological institute of the Russian Academy of Sciences (COPEPOD. Interactive Time-series Explorer METABASE, 2018). Present paper is based on this time series. We have already correlated significant shift of the developmental season beginning of several planktonic Copepods inhabiting the White Sea with the substantial shift of spring and summer beginning (Usov et al., 2013). However, that approach, which considered only discrete events in the seasonal temperature dynamics, did not explain how the change of the whole course of the seasonal warming/cooling may influence dynamics of planktonic animals. The latter, obviously, react to temperature continuously, not only at specific periods of life. or So, another approach may be the analysis of the seasonal temperature curve, or some parts of it, as a whole, with maximal possible resolution. Thus, one of the objectives of this study is revealing the response of copepod phenological timing to changes in the spring-summer warming curve as a whole.

It was shown that in high latitudes despite huge influence of abiotic factors at the edges of vegetation season, the role of interspecific interactions increases during warm season (Pau et al., 2011). Therefore, the phenological changes in population of any species must inevitably result in changes in populations of connected species. So, the second objective of this study is to analyze consequences of phenological changes for interactions in planktonic community.

**Materials and methods**

***Sampling site and the period of observations***. Water temperature, water salinity, and the zooplankton abundance have been monitored in Chupa Inlet (Kandalaksha Bay, the White Sea), at the standard station D-1 (depth of 65 m; 66°19′50″N; 33°40′06″E) since 1961 (Fig. 1). Data from this monitoring site are recorded in the database "White Sea Hydrology and Zooplankton Time-Series: Kartesh D1" (COPEPOD. Interactive Time-series Explorer METABASE, 2018); this dataset was used as the data source in this study. The period from 1961 to 2018 was analyzed.. We used approximating models for calculation of phenological indices, which allowed us to fill in the gaps (see below).

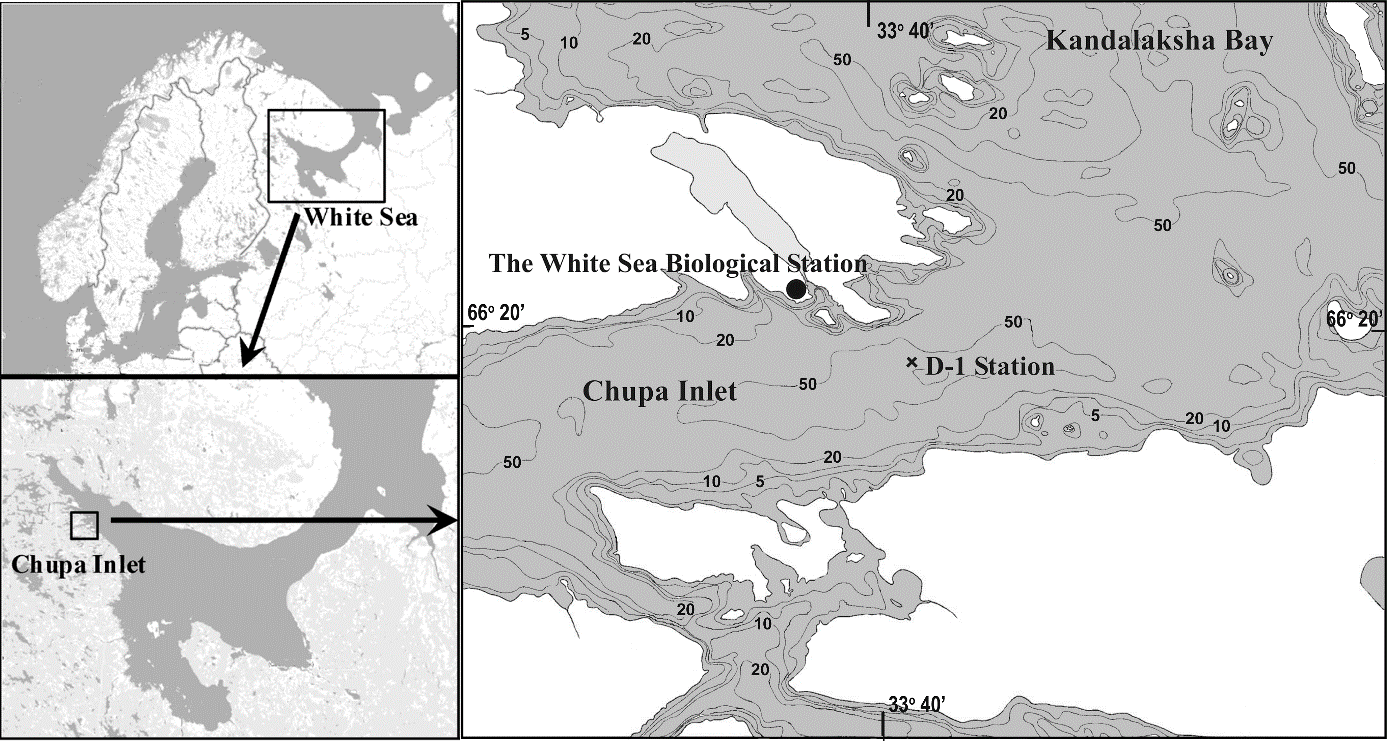


Fig. 1. Location of the study site (D-1 Station) in Chupa Inlet.

***Sampling scheme and methods***. Monitoring was conducted from research vessel during ice-free period and from the ice in winter. Zooplankton sampling was performed every ten days during the ice-free period and monthly from the ice, except for the period of 1962–1969, when the sampling was performed every ten days all the year round. The zooplankton was sampled from standard water layers (0–10 m, 10–25 m, and 25–65 m) by vertical hauls by closing Juday net (mesh size 200 μm; mouth diameter 37 cm, mouth area 0.1 m2). The samples were immediately preserved with formaldehyde (final concentration 2–4%). In total, more than 3400 samples have been collected and processed since 1961. The sample processing was performed by the standard methods (Harris et al., 2000). Briefly, the samples were concentrated to 100-mL or 200-mL volume according to the organisms' concentration assessed visually, and three 1-mL aliquots were taken using a Hensen stempel pipette from concentrated sample to count the abundant species and their stages (whose numbers in an aliquot exceeded 10 ind.); less abundant and large species were counted individually in the whole sample. The counting was performed in the Bogorov’s counting chamber. Animals were identified to the species or genus level. Developmental stages of the copepod species *Calanus glacialis* and *Pseudocalanus* spp. were determined to nauplii (all stages combined), CI–CV copepodites, and mature specimens of CVI, i.e. males and females. Copepodite stages of the other, smaller copepod species were combined at counting in a following way: nauplii (all stages combined), juveniles [CI+CII] and copepodites [CIII+CIV+CV]. The abundance was expressed as ind. m-3.

Temperature was measured in parallel to the zooplankton sampling. During the period of 1961–2006, the water temperature was measured by reversing thermometers mounted on the Nansen bottle (BM-48) at 0-, 5-, 10-, 15-, 25-, 50-m depths and near the bottom (63–65 m) or by bathythermograph GM7-III. Since 2006, the water temperature was measured by CTD probe MIDAS 500 (Valeport Ltd.) on continuous profiles from surface to bottom. Prior to active application of the new equipment, CTD was intercalibrated with reversing thermometers and bathythermograph. No significant discrepancies were found within the limits of accuracy of the previously used equipment.

***Studied species and their ecological characteristics***. The phenology of the juveniles of the 7 species/genera of planktonic Copepoda was analyzed: cold-water arctic *Calanus glacialis* Jaschnov, 1955 and boreal-arctic *Pseudocalanus* spp., warm-water boreal species *Acartia* spp., *Centropages hamatus* (Lilljeborg, 1853), and *Temora longicornis* (Müller, 1792), and ubiquitous *Oithona similis* Claus, 1866 and *Microsetella norvegica* (Boeck, 1864). Arctic *C. glacialis* reproduces at the study site in the end of winter–beginning of spring (in March–May) (Prygunkova, 1974). *Pseudocalanus* genus is presented by two species, *P. acuspes* and *P. minutus* (Markhaseva et al., 2012), which were not distinguished historically until the last years. These species are characterized by close temperature optima, according to the narrow seasonal peak of their combined abundance, the calculated temperature optimum for the pooled data is 3.5 °C (Zubakha and Usov, 2004). Boreal *C. hamatus* and *T. longicornis* have similar temperature optima at the study area: 10.3 and 9.9 °C, respectively; they produce 2–3 generations per year (Prygunkova, 1974; Pertzova, 1990). Genus *Acartia* is presented in the White Sea by two boreal species, which were not distinguished during monitoring: *A. longiremis* and *A. bifilosa*. They differ slightly by salinity and temperature preferences: *A. bifilosa* withstands freshening and inhabits estuarine regions of the White Sea with low salinity and higher temperature compared to open sea (Prudkovsky, 2003). According to our observations, this species appeared a little later during the season, than *A. longiremis*, when water became warmer. Thus, speaking about timing of appearance of these species, we mean first of all *A. longiremis*. Season of high abundance of both these species takes place in warm period of year (June-September). All the studied boreal species overwinter as the dormant eggs, which hatch in the late spring–beginning of summer (June-July; original data). Only single individuals of *Acartia* spp. are encountered during winter (December-March), while *Centropages* and *Temora* were totally absent in that period. Both *Oithona similis* and *Microsetella norvegica* are present in the plankton during the whole year and both have the same optima in the study area, about 9 °C.

***Data preprocessing***. The temperature and juvenile copepods abundance in the layer 0-25 m were used in analysis. It is the upper 25-m layer, where the major part of organic carbon is produced in the White Sea (Prygunkova, 1974; Pertsova, 1980). The reproduction and early development of the studied species also take place in this water layer (Pertsova, 1971, 1974; Prygunkova, 1974; Pertzova, Kosobokova, 2010; Martynova et al., 2011).

Several seasonal events in temperature dynamics were defined and calculated. For this purpose, the hydrological seasons in 0–25 m depth layer were defined according to methodology offered by A.I. Babkov (Babkov, 1985) with modifications. According to this scheme, the hydrological winter in a specific water layer is a season with water temperatures in this layer (0-25 m in our case) below 0 °C. Hydrological spring and autumn are the periods of the highest rate of the temperature change (increase or decrease, respectively); they correspond to the intervals between the dates of 0 °C and +5 °C thresholds. Hydrological summer is the period when the average water temperature of the layer 0-25 m exceeds +5 °C. This value corresponds also to the upper limit of the optimal temperature range of cold-water zooplankton species (Zubakha, Usov, 2004). The date when average water temperature in layer 0–25 m reached 3 °C was accepted as the beginning of hydrological spring, because period between 0 and 3 °C thresholds coincides with the period of ice melting, when the work was technically impossible neither from ice nor from boat or ship. So, the date of 3°C threshold was the first which could be detected reliably. Other thresholds analyzed are: 4, 5 and 8°C on ascending part of the seasonal curve and timing of the seasonal temperature peak (Table 1). 8°C threshold was the lowest value of the latter since the beginning of monitoring (in 1969). 6- and 7-degree thresholds were not considered, because they correlated strongly (Pearson r = 0.88), and increased unreasonably number of degrees of freedom when included in the analysis. Thus, we considered the period from the spring beginning to the temperature peak, the spring-summer transition period, when the reproduction and early development of studied species took place.

The dates throughout the paper were expressed as Julian days.

***Defining the phenological events in dynamics of juveniles.*** We analyzed juveniles of the studied species, namely: CI of *Calanus* and *Pseudocalanus* spp., combined CIII–CV of smaller *Acartia* spp., *Centropages*, *Temora*, *Oithona* and *Microsetella*. Four key dates based on the cumulative seasonal abundance (Batten, Mackas, 2009) were identified: beginning-of-season, the middle-of-season, end-of-season, which were determined in a following way. Cumulative abundances of mentioned developmental stages of each species, were calculated for each sampling date, starting from January 1 of the calendar year. These cumulative abundances were approximated using a logistic curve that described their dependence on the number of Julian days from January 1 of a given year.

The fitting of the logistic model was performed using the least squares method using the *nls()* function (Bates, Chambers, 1992) from the Stats package (R Core Team, 2019). After estimation of the logistic model parameters, we calculated three values, mentioned above:

1. Beginning-of-season: date (the number of Julian days that have passed since the beginning of the year), which accounted for 15% of the asymptote value of the logistic curve fitted for this species in a given year; or, in other words, time, when cumulative abundance of a species reached ca. 15% of the total cumulative abundance for this specific year.

2. Middle-of-season: the date at which the inflection point was observed on the logistic curve – it corresponds to 50% of the asymptote value (ca. 50% of the total cumulative abundance).

3. End-of-season: the date on which 85% of the value of the asymptote was observed (ca. 85% of the total cumulative abundance).

4. Peak: the date of direct observation (without taking into account the approximating logistic curve) of the maximum species abundance for the entire observation period in a given year.

The long-term average values of the timing of analyzed events are presented in Table 1.

In some years for some species the proposed algorithm for searching phenological events gave improbable results (the end date of the season was not reached until 365-th day, i.e., the logistic curve did not reach the plateau, so it was impossible to calculate the asymptote value of the logistic curve). It was found in *Oithona similis* and *Microsetella norvegica* dynamics (6 years and 1 year, respectively). In 1963, 1972 and 1990, the observations did not adequately describe the cumulative for *C. glacialis* (a very short period of the species presence in the plankton fell on the intervals between observations). In these cases, it was not possible to find a logistic curve. These values were considered as missing and their replacement was performed using Singular Spectral Analysis (SSA), proposed as a tool for filling gaps in time series (Golyadina, Osipov, 2007; Golyadina, Korobeynikov, 2014). For this analysis, the *gapfill()* function from the *Rssa* package was used (Golyadina, Korobeynikov, 2014).

Table 1. Average timing of spring-summer warming and phenological phases in the study region. Values are shown, which were used in analysis. In the column "Species", in brackets, the duration of developmental season (from beginning to end) is shown for each species.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Temperature** | | **Animals** | | |
| Threshold | Day ± st. error | Species | Phase | Day ± st. error |
| 3°C | 160 ± 1.4 | Calanus  (15 days) | beginning | 154 ± 1.3 |
| 4°C | 169 ± 1.8 | middle | 161 ± 1.2 |
| 5°C | 172 ± 1.9 | end | 169 ± 1.3 |
| 8°C | 191 ± 2.2 | peak | 167 ± 2 |
| t peak | 215 ± 1.9 | Pseudocalanus  (37 days) | beginning | 141 ± 2.5 |
|  |  | middle | 159 ± 2.6 |
|  |  | end | 178 ± 3.1 |
|  |  | peak | 161 ± 2.7 |
|  |  | Acartia  (67 days) | beginning | 203 ± 3.6 |
|  |  | middle | 237 ± 3.6 |
|  |  | end | 270 ± 4.8 |
|  |  | peak | 243 ± 4.1 |
|  |  | Centropages  (36 days) | beginning | 204 ± 2.1 |
|  |  | middle | 222 ± 1.7 |
|  |  | end | 240 ± 1.9 |
|  |  | peak | 229 ± 2.2 |
|  |  | Temora  (39 days) | beginning | 217 ± 1.8 |
|  |  | middle | 237 ± 1.4 |
|  |  | end | 256 ± 1.7 |
|  |  | peak | 241 ± 2.3 |
|  |  | Microsetella  (75 days) | beginning | 158 ± 3.9 |
|  |  | middle | 195 ± 3.7 |
|  |  | end | 233 ± 5.2 |
|  |  | peak | 202 ± 5.1 |
|  |  | Oithona  (122 days) | beginning | 170 ± 4.9 |
|  |  | middle | 231 ± 3.6 |
|  |  | end | 292 ± 4.7 |
|  |  | peak | 230 ± 7.3 |

***Statistical analysis***. Linear regression was used to estimate trends in the dynamics of studied parameters.

Variables had been previously standardized to zero mean and unit variance prior to analysis. During canonical correlation analysis for each year we obtained several pairs (orthogonal to each other) of canonical scores in the form of linear combinations separately of abiotic and biological variables. They were calculated in such a way as to maximize the correlation (canonical correlation) between biological and abiotic canonical variables. Only the first two pairs of canonical variables and, respectively, two first canonical correlations were significant. For visualization of results of canonical analysis, a scatterplot was built, where the first and second canonical scores of each year were indicated on x and y axes, respectively.

The signs of the first and second canonical scores indicated different gradation of two factors, which determine the shape and shift of the seasonal temperature curves. A model of ANOVA repeated measures was used to assess the significance of influence of revealed factors on the timing of thresholds 3, 4, 5 and 8°C. The estimates of the parameters of this model were used to build curves of temperature spring-summer dynamics (spring-summer transition), corresponding to contrasting types of the latter. To take into account all the data in ANOVA analysis, including incomplete ones, the ergodic method was used (Alexeyeva, 2017), which allowed us to assess model parameters without removing incomplete data and without artificial filling of missing values. Missing data causes usually a bias in parameter calculation which was estimated applying ergodic method. Then the model was centralized, and statistics were calculated on the centralized model.

Significance of the canonical correlations was assessed by Bartlett criterion. All the estimates were considered statistically significant at a critical level of significance p = 0.05. Statistical analysis was performed using R packages MASS, pracma, magic, corpcor, cancor (R Core Team, 2019).

**Results**



***Types of the spring-summer temperature dynamics.*** Canonical correlations between phenological indices of studied species and timing of the spring-summer warming are shown in the Table 2. The first and second canonical correlations exceeded 0.9. However, despite p2 = 0.072 the second canonical correlation and corresponding canonical variates reflected important patterns in temperature dynamics and species phenology (see below) and was considered in further analysis.

Canonical variables (C.V.) for temperature data characterized specific warming regimes. The latter in a specific year were expressed through the signs of canonical scores for this year. First C.V.: positive values of canonical scores indicated early spring-summer warming (negative coefficients at 4, 5 and 8°C thresholds; coefficient for 3°C is low) with late seasonal temperature peak (Fig. 2). Second C.V.: positive values of canonical scores indicated early spring beginning (negative coefficient at 3°C threshold), but slow spring warming (positive coefficient at 4°C, which means large interval between 3°C and 4°C), earlier timing of 5 and 8°C thresholds and later timing of peak (Fig. 2). In brief, first C.V. characterized shift of warming dynamics from year to year (early, when C.V.1 is positive, but late, when it is negative), the second C.V. – the rate of spring warming: slow (C.V.2 is positive) and fast (C.V.2 negative).

Thus, all the years, depending on the combination of signs of the canonical scores for the first and second canonical variables for each specific year, may be divided into four groups, which are characterized by four variants of the spring-summer transition (Fig. 2; Table 3): 1) late and fast warming; 2) late and slow warming (the variant, when the second canonical variable has positive sign, so the spring beginning (3°C) is relatively early); 3) early and fast warming; 4) early and slow warming. Definitions "slow" and "fast" refer here mostly to the part of curve between 3 and 4°C or period of spring warming. So, each year may be characterized by the form (slow – fast) and shift (early – late) of warming. These groups separate well in the space of the first two canonical axes, calculated either on the temperature or phenological data (Fig. 3). Note that the grouping is very similar in both cases (abiotic and biological data). Respective grouping of years is presented in Table 3.

Table 2. Canonical correlation results. A – significant canonical correlations and Bartlett test results (Chi-square, degrees of freedom and p-value). B – canonical coefficients for temperature threshold dates, phenological indices and abundance of studied species. C.V.1, C.V.2 – first and second canonical variates. Species are grouped according to type of response to temperature dynamics changes (see below).

|  |  |  |  |
| --- | --- | --- | --- |
| **A** | χ2 | df | p value |
| r1 = 0.96 | 221.12 | 175 | 0.010 |
| r2 = 0.95 | 160.84 | 136 | 0.072 |
| **B** |  | C.V.1 | C.V.2 |
| Temperature | 3°C | 0.044 | -0.660 |
| thresholds | 4°C | -0.266 | 0.737 |
|  | 5°C | -0.394 | -0.108 |
|  | 8°C | -0.604 | -0.093 |
|  | Peak | 0.638 | 0.026 |
| Calanus | beginning | 0.133 | 0.041 |
| Calanus | middle | -0.204 | -0.066 |
| Calanus | end | 0.125 | 0.044 |
| Calanus | peak | -0.053 | -0.019 |
| Centropages | beginning | 0.390 | 0.100 |
| Centropages | middle | -0.590 | -0.158 |
| Centropages | end | 0.350 | 0.095 |
| Centropages | peak | -0.011 | 0.001 |
| Temora | beginning | -0.003 | -0.019 |
| Temora | middle | 0.028 | 0.050 |
| Temora | end | -0.010 | -0.026 |
| Temora | peak | -0.017 | -0.008 |
| Oithona | beginning | -0.228 | -0.381 |
| Oithona | middle | 0.320 | 0.565 |
| Oithona | end | -0.214 | -0.378 |
| Oithona | peak | 0.033 | 0.008 |
| Acartia | beginning | -0.003 | -0.073 |
| Acartia | middle | -0.021 | 0.134 |
| Acartia | end | 0.033 | -0.085 |
| Acartia | peak | -0.030 | -0.003 |
| Microsetella | beginning | 0.110 | -0.070 |
| Microsetella | middle | -0.228 | 0.105 |
| Microsetella | end | 0.146 | -0.076 |
| Microsetella | peak | 0.008 | 0.011 |
| Pseudocalanus | beginning | -0.014 | 0.254 |
| Pseudocalanus | middle | 0.064 | -0.399 |
| Pseudocalanus | end | -0.042 | 0.244 |
| Pseudocalanus | peak | -0.021 | -0.010 |
| Calanus | number | 0.027 | 0.009 |
| Pseudocalanus | number | 0.003 | -0.001 |
| Acartia | number | 0.024 | 0.001 |
| Centropages | number | -0.013 | 0.001 |
| Oithona | number | -0.033 | -0.008 |
| Temora | number | 0.021 | 0.000 |
| Microsetella | number | -0.009 | -0.006 |

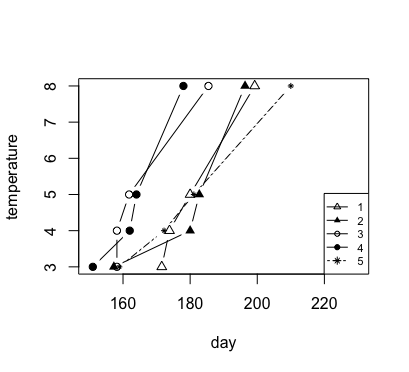


Fig. 2. Graphs of the four types of spring-summer temperature dynamics. Legend: 1 – late and fast, 2 – late and slow, 3 – early and fast, 4 – early and slow, 5 – years with incomplete data.

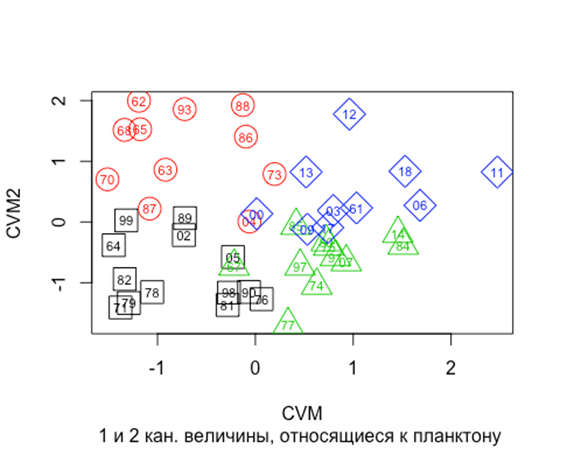
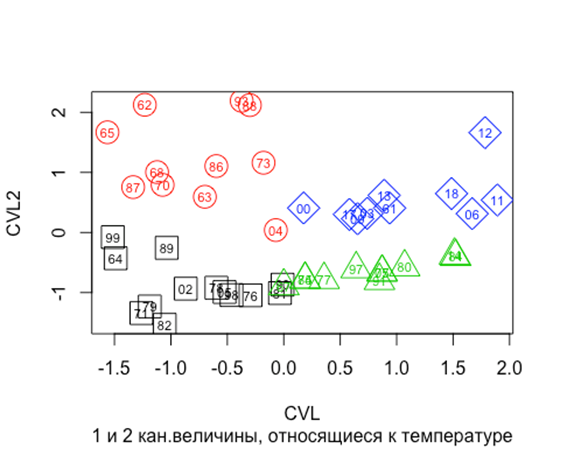


Fig. 3. Ordination of years in the space of canonical variates (axes), based on timing of the spring-summer transition (A) and phenological data (B). Numbers in figures – years (61-99 – 1961-1999; 00-18 – 2000-2018). Rectangles – late and fast, circles – late and slow, triangles – early and fast, diamonds – early and slow.

Table 3. Years with different types of spring-summer transition.

|  |  |
| --- | --- |
| Group (as on Fig. 4 and 5) | Years |
| 1 | 1964, 1971, 1976, 1978, 1979, 1981, 1982, 1989, 1990, 1998, 1999, 2002, 2005 |
| 2 | 1962, 1963, 1965, 1968, 1970, 1973, 1986, 1987, 1988, 1993, 2004 |
| 3 | 1967, 1974, 1975, 1977, 1980, 1984, 1985, 1991, 1997, 2007, 2014 |
| 4 | 1961, 2000, 2003, 2006, 2009, 2011, 2012, 2013, 2017, 2018 |
| 5 | 1966, 1969, 1983, 1992, 1994, 1995, 1996, 2001, 2008, 2010, 2015, 2016 |

**Phenological response of the abundant species to changes in spring-summer transition.** Analogous to the temperature dynamics, canonical analysis revealed two principal schemes of seasonal dynamics of the juveniles of the studied species, which could be discerned from the values of canonical coefficients for studied phenological variables. These schemes are illustrated in Figure 4. 1-st type of phenology: late beginning and end of the season with the middle of season shifted towards the beginning (signs "+" – "-" – "+" at the respective canonical coefficients for each species). 2-nd type of phenology: early beginning and end of the season with the middle of season shifted towards the end of season (signs "-" – "+" – "-" at the canonical coefficients). This pattern was broken in the case of *Acartia* spp., which demonstrated early beginning of season, early middle of season and late end of season. However, taking into account that canonical coefficient for the beginning of season was very low, dynamics of these species can be considered as the 1-st type of phenology. Specific phenology type of a species depended on the combination of the first and second canonical variables determined by the temperature ("form" and "shift" of spring-summer transition).

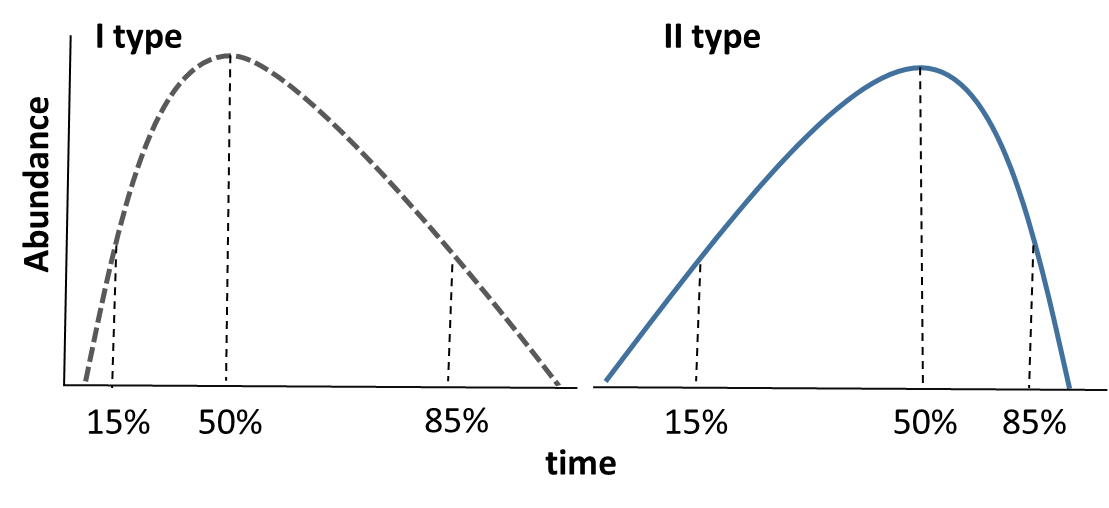


Fig. 4. Schematic view of two types of animal seasonal dynamics, described in the text. 15%, 50% and 85% - beginning, middle and end of season, respectively. Timing of the middle of season almost coincides with the timing of abundance peak (see Table 1).

Canonical coefficients at the seasonal abundance peak timing were relatively low, except *Acartia* and *Temora*, so we will not pay special attention to these phenological indices. Moreover, this timing was close to the middle of season in most cases (see Table 1).

Temperature thresholds and timing of species phenology demonstrated different contribution to the values of canonical variables and eventually to canonical correlations. The first canonical correlation was determined mostly by the "shift" of spring warming and by the phenology of two species – *Oithona similis* and *Centropages hamatus* (Table 2). *Calanus glacialis* and *Microsetella norvegica* also demonstrated significant contribution. The second correlation was determined primarily by the timing of spring and summer beginning and rate of the temperature increase from 3 to 4°С (i.e. "form" of spring-summer warming), and also by phenology of *Oithona similis* and *Pseudocalanus* spp. For all studied species the middle of season had greater weight than its beginning and end.

Two phenology schemes, described above, corresponded to four types of spring-summer temperature dynamics, revealed earlier (Table 4). For juveniles of *Calanus* and *Centropages* 1-st type of phenology (late beginning and end of the season with early middle of season) was characteristic, when the warming was early and slow, and opposite phenology (2-nd type - early beginning and end of the season with late middle of season) – when warming was late and fast. *Temora* and *Oithona* demonstrated opposite response: 1-st type of phenology, when warming was late and fast, and 2-nd type of phenology, when the warming was early and slow. *Microsetella* and *Acartia* (with admission for the latter, made above) demonstrated 1-st type of phenology, when the warming was early and fast, and 2-nd type, when that was late and slow. *Pseudocalanus*, on the contrary, demonstrated 2-nd type of phenology, when warming was early and fast, and 1-st type, when the warming was late and slow.

Abundance of juveniles responded only to the shift of spring-summer warming (coefficients for the 2-st canonical variate are very low). Abundance of *Calanus*, *Acartia* and *Temora* tended to be high, and abundance of *Oithona* и *Centropages* – low, in years with early spring-summer warming (Table 2).

Table 4. Types of the seasonal dynamics of copepod juveniles (types of phenology) at different regimes of spring-summer warming.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Type of warming  Species | Early slow | Early fast | Late slow | Late fast |
| Calanus glacialis | 1 |  |  | 2 |
| Centropages hamatus | 1 |  |  | 2 |
| Oithona similis | 2 |  |  | 1 |
| Temora longicornis | 2 |  |  | 1 |
| Acartia spp. |  | 1 | 2 |  |
| Microsetella norvegica |  | 1 | 2 |  |
| Pseudocalanus spp. |  | 2 | 1 |  |

***Trends in the long-term dynamics of the studied parameters (1961-2018).*** The years with different types of spring-summer warming demonstrated some pattern in their distribution in time (Fig. 5). General tendency was observed from late and slow towards early and slow warming. The years characterized by early slow warming were all but one (1961) concentrated after 2000.Years with fast warming were mostly concentrated in the first half of the studied period. Thus, there existed tendency towards early spring and summer and relatively prolonged spring.



Fig. 5. Temporal distribution of years with different types of spring-summer warming.

Long-term trends were revealed in the dynamics of some phenological indices, despite large interannual fluctuations (Fig. 6). *Calanus glacialis* and *Pseudocalanus* spp. demonstrated significant tendency towards earlier developmental season: R2 for different phenological phases of these species was within the range from 0.13 to 0.23 (b from -0.23 to -0.68; p < 0.05). Significant shift towards earlier time was found for *Centropages* beginning and middle of season (R2 = 0.10 and 0.12, respectively; b = -0.31 and -0.26; p = 0.01) and *Temora* beginning and middle of season (R2 = 0.23 and 0.19; b = -0.40 and -0.28; p = 0.0001 and 0.0006).

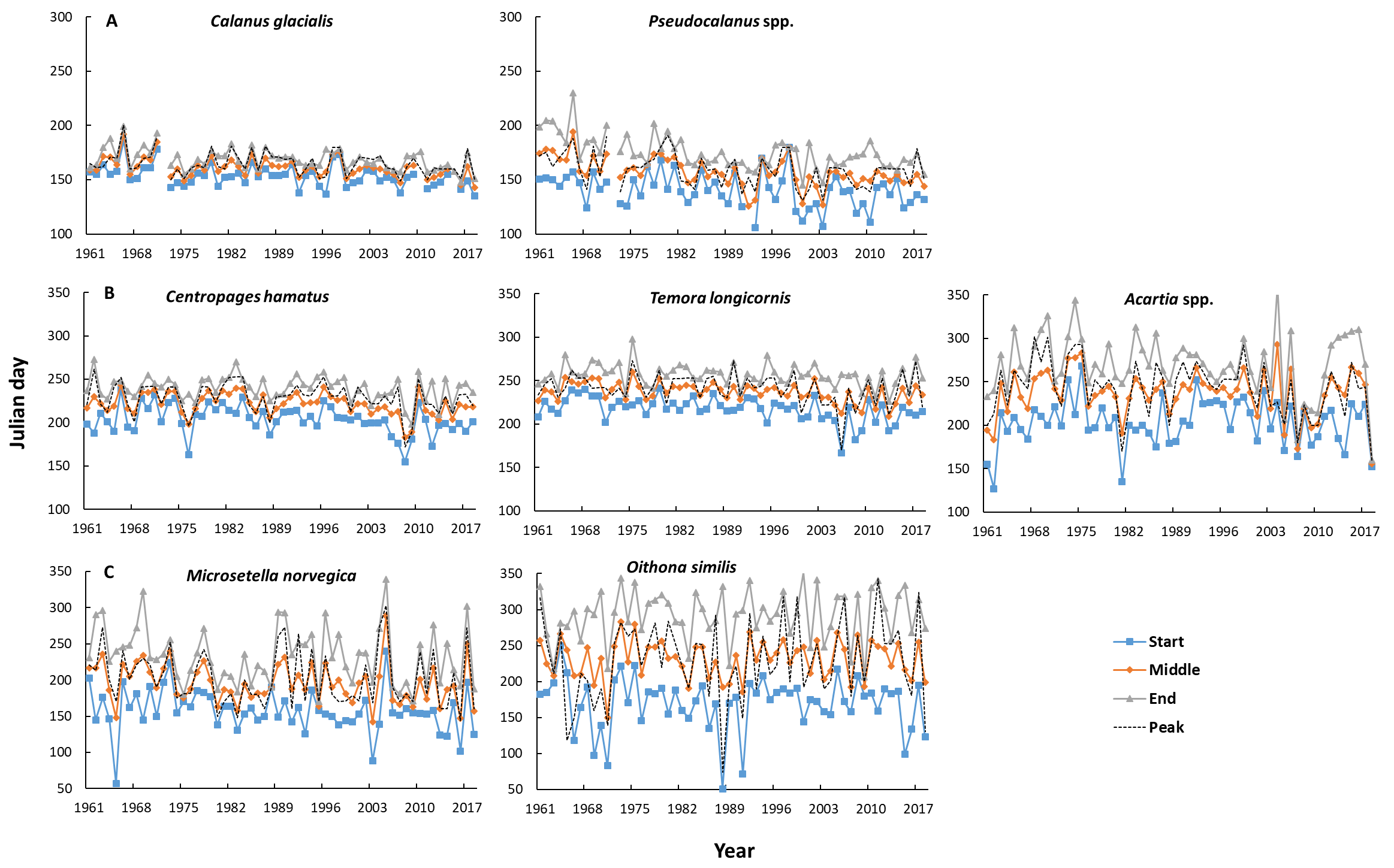


Fig. 6. Long-term dynamics of timing of the beginning, middle, end of the developmental season and abundance peak of abundant copepods. A – Arctic species, B – boreal species, C – eurybiont species.

**Discussion**

- Обсудить шире – привлечь примеры из других регионов.

Our results revealed a phenological response of copepod juveniles to the changes of timing of the spring-summer transition in the studied region of the White Sea. The response of species with different temperature preferences (Zubakha, Usov, 2004) could be similar and, on the contrary, the response of similar species could be different. For example, similar reaction of arctic cold-water *Calanus glacialis* and boreal warm-water *Centropages hamatus* was connected to the same type of spring-summer transition.

How such similarity could be explained? *Calanus* is a typical arctic species. Its middle of season, on average, coincided with the 3°С threshold, and the end of season – with the 4°С threshold. Therefore, early middle and late end of season of *Calanus* would correspond to early slow warming, and vice-versa, just what was shown in our work. This corresponds to the data, that early development of *C. glacialis* depends on water temperature – the higher the temperature, the faster development from the first naupliar stage to the first copepodite stage (Corkett et al., 1986; McLaren et al., 1988; Daase et al., 2011). *Centropages* is a warm-water boreal species with one of the highest temperature optimums in the White Sea (Zubakha, Usov, 2004). The beginning of season of *Centropages* took place just after the 8°С threshold, however negative tie was revealed between timings of those two events (opposite signs of canonical coefficients). Probably, spring warming (between 3°С and 4°С) was more important for the beginning of *Centropages* season. Indeed, fast increase of *Centropages* nauplii abundance was observed normally on the 180-th day, about 10 days after 4°С threshold (original data). Middle of season of *Centropages* was observed after seasonal peak of temperature (more, than 2 months later, than *Calanus*). The development of *Centropages* juveniles after the middle of season continued, when the water started to cool down. Hence, some factors other than temperature might influence *Centropages* and other boreal animals in that part of season (see below).

Early development of the cold-water species of the genus *Pseudocalanus* is very similar to the development of *Calanus glacialis* (Prygunkova, 1974; Usov et al., 2013). Nevertheless, response of this species to the spring-summer warming differed from the response of *Calanus* (see Table 4). It is worth noting in this regard that the first nauplii of *Pseudocalanus* spp. appeared about two months earlier than nauplii of *Calanus*, and peak of abundance of *Pseudocalanus* nauplii also was observed earlier (original data). Therefore, large part of development of *Pseudocalanus* juveniles took place under the ice, long before warming of the water above 0°С. This may be the cause that *Pseudocalanus* is less dependent on the temperature, than *Calanus*. Lower dependence of *Pseudocalanus* on the temperature in the White Sea was revealed in modelling study of Persson et al. (2012). Besides that, interpretation of the results is complicated by the existence of two species of *Pseudocalanus* in the White Sea (*P. acuspes* and *P. minutus*), which have not been distinguished since the beginning of observations (Markhaseva et al., 2012).

Phenological phases of juveniles of the boreal species *Acartia* spp. и *Temora longicornis* were very close to phenological timing of *Centropages* (Table 1). Development of all studied boreal species (*Acartia* spp., *Temora* and *Centropages*) took place after 8°С threshold and beginning of the seasonal cooling. When the peak of temperature was shifted to a later time ("early" warming), the beginning of season of *Acartia*, like in the case of *Centropages*, also was shifted forward. However, the responses of these species to the rate of warming ("slow" - "fast") were different (see Table 4). *Temora*, the most probably, was influenced by the shift of 8°С threshold: the earlier it was, the earlier development of this species began. The response of *Temora* to the rate of warming was similar to that of *Acartia* spp. Thus, despite similarity of temperature preferences of these boreal species, their responses to the dynamics of spring-summer warming differ. The development of these species (as already was mentioned regarding *Centropages* phenology) mostly took place after seasonal peak of temperature. So, the temperature must not be of primary importance for this period of the life cycle. Indeed, it was shown, that after beginning of seasonal cooling boreal species in this part of the White Sea depended mostly on the availability of food resources (Martynova, 2011).

*Oithona similis* responded to the dynamics of the seasonal warming in the same way as *Temora longicornis*, however these two species differed substantially in their biology. Despite the fact that the middle of season of *Oithona* is close to that of boreal species, *Oithona* is the most eurybiont among species inhabiting the White Sea (Prygunkova, 1974). It reproduces all the year round even in Arctic (Dvoretsky, Dvoretsky, 2009). The developmental season (defined by the appearance of the first copepodite stages) of *Oithona* in the study region began only 16 days later than season of *Calanus*, but ended later than season of any other species, after 290-th day, near mid-October. The development of *Oithona* after the middle of season, which took place after peak of temperature, like in the case of boreal species, hardly depended on the temperature.

The response of *Microsetella norvegica* to the seasonal warming was the same as *Acartia* spp., however, the developmental season of *Microsetella* passed much earlier. Therefore, juveniles of these two species was exposed to temperature fluctuations in different periods of year. Temperature optimum of *Microsetella* is negligibly lower, than optimum of *Acartia*: 8.1°С и 8.3°С, respectively (Zubakha, Usov, 2004). However, the biology of *Microsetella* differs substantially from other planktonic Copepoda. It is one of very few true planktonic Harpacticoida in the World Ocean (Boxshall, 1979; Huys, Boxshall, 1991) and the only – in the White Sea (Kornev, Chertoprud, 2008). There are data on connection of Microsetella with benthic biotopes (Zhang et al., 2004; Kornev, Chertoprud, 2008). Besides that, trophic preferences and trophic behaviour of this species distinguish *Microsetella* from other copepods found in the White Sea – in other parts of the World Ocean this species is found often on detrital aggregates and abandoned houses of Appendicularia (Green, Dagg, 1997; Koski et al., 2005; Maar et al., 2006). Abundance outbursts of *Microsetella* in the White Sea in the recent years were connected with anomalous blooms of *Phaeocystis* (original observations).

We have found that different types of spring-summer warming were distributed unevenly during the period of investigations (Fig. 5), with tendency towards early and slow warming. This trend corresponds well to the global warming trend, and explains, at least partly, tendecies in phenology towards earlier developmental season of studied species (Mackas et al., 2012; Atkinson et al., 2015). It was hypothesized earlier, that high-latitude species with early reproductive season are most sensitive to climate change (Pau et al., 2011), which is confirmed in our study by stronger trends in phenology of arctic species *Calanus* and *Pseudocalanus*. On the other hand, hatching of the resting eggs of boreal species depends to a large extent on the water temperature (Katajisto, 2003; Boyer, Bonnet, 2013; Holm et al., 2018). So, earlier beginning of season of boreal warm-water *Centropages* and *Temora*, which spend winter in the White Sea in the diapausing eggs, can be attributed to earlier summer warming (Pertzova, 1990).

Analysis of the reaction of planktonic copepods to long-term trends in seasonal temperature timing indicated that it differs from response to changes of the same sign at the year-to-year scale. E.g., *Calanus* and *Pseudocalanus* phenological response to the same seasonal warming regime differed substantially, but was similar in response to long-term shifts of the seasonal warming timing. The same can be said about boreal species. We can suppose that different factors may be of different significance at different time scales. Short-term (mostly local) fluctuations of environment and biological (competitive) interactions play important role in driving year-to-year changes of phenology. Long-term trends in dynamics of phenological variables must be determined to a larger extent by climatic, global-scale processes, expressed at the local scale through long-term changes in environment.

**Conclusion**

We have revealed the mechanism of temporal niche separation in planktonic animals with similar seasonal dynamics, e.g. boreal species characterized by close temperature preferences. Even such ecologically like species differ in their response to year-to-year changes in seasonal temperature dynamics, which leads to relative shifts of their phenological phases in time, and, therefore, to separation of their temporal niches. This separation is one of the mechanisms which facilitate competition between species, inhabiting homogeneous medium with limited resources. Owing to this temporal niche separation high abundance and production of zooplankton is supported in high latitudes, despite relatively short vegetation season. Niche separation of species with similar seasonal dynamics is enforced by separation of trophic niches. This aspect has not been considered in our work, but previous works in the White Sea pointed out at this mechanism.

Response of animals to the long-term trends in environment may differ from their reaction at the scale of year-to-year fluctuations. This, probably, arises from the different mechanisms determining dynamics at different scales: biological interactions must have more contribution at the year-to-year scale, and large-scale climatic forcing – at the scale of decades.

Of course, the mechanisms of niche separation are not limited to those mentioned in our work. Spatial dimension of multidimensional Hutchinson's niche deserves attention. It is especially important for plankton, whose habitat is three-dimensional and offer more opportunities for coexistence of ecologically similar species. This is subject for special study.

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