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Spring to summer transition timing influences zooplankton phenology and temporal niche partitioning in the coastal zone of the White Sea

N.V. Usov[1]*, V.M. Khaitov[2, 3], D.M. Martynova[1] and N.P. Alexeyeva[4]

[1] *White Sea Biological Station, Zoological Institute, Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: nikolay.usov@zin.ru*

[2] *Saint Petersburg State University, Department of Invertebrate Zoology, Universitetskaya Emb. 7/9, 199034 Saint Petersburg, Russia; e-mail: polydora@rambler.ru*

[3] *Kandalaksha State Nature Reserve, Lineynaya Str. 35, 184042 Kandalaksha, Russia*

[4] *Saint Petersburg State University, Department of Statistical Modeling, Universitetskiy Pr. 28, 198504 Stary Peterhof, Saint Petersburg, Russia; e-mail: aninap4@gmail.com*

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ABSTRACT

Climatic changes are manifested through temporal shifts of seasonal events in environment, which may be critical for planktonic organisms. Temporal shift of seasonal warming curve in high latitudes affects phenology of aquatic organisms. Significant correlation between timing of phenological events in the life cycles of planktonic copepods and spring-summer temperature transition dates was revealed by canonical correlation analysis. We analyzed the long-term zooplankton and temperature time series (1961–2018) from the White Sea (66°19'50"N; 33°40'06"E, near the White Sea Biological Station of the Zoological Institute of the Russian Academy of Sciences). Two types of seasonal abundance dynamics of copepod juveniles and four types of the spring to summer transition were revealed. Each species demonstrated specific dynamics in response to each type of spring to summer transition. Species with similar ecological traits differed in their phenological response to the changes in the temperature dynamics. This phenomenon was explained, at least partly, by niche partitioning, when temporal niches of ecologically similar species were separated as a result of shifting the phenological events in time. The latter, in turn, was the result of organisms' response to changes of spring to summer transition dynamics from year to year. We hypothesize that such separation may be one of the solutions of the "Paradox of the plankton", favouring success of species-rich planktonic communities in high-latitude ecosystems, characterized by relative paucity of food resources and short productive season.

Key words: competition, phenological shifts, seasonal cycle, temperature, temporal niche, White Sea, zooplankton

Хронология весеннего прогрева влияет на фенологию зоопланктона и разделение временных ниш в прибрежье Белого моря

Н.В. Усов[1]*, В.М. Хайтов[2, 3], Д.М. Мартынова[1] и Н.П. Алексеева[4]

[1] *Зоологический институт Российской академии наук, Беломорская биологическая станция, Университетская наб. 1, 199034 Санкт-Петербург, Россия; e-mail: nikolay.usov@zin.ru*

[2] *Санкт-Петербургский государственный университет, Кафедра зоологии беспозвоночных, Университетская наб. 7/9, 199034 Санкт-Петербург, Россия; e-mail: polydora@rambler.ru*

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* Corresponding author / Автор-корреспондент

[3] Кандалакшский государственный природный заповедник, Линейная ул. 35, 184042 Кандалакша, Россия

[4] Санкт-Петербургский государственный университет, Кафедра статистического моделирования, Университетский пр. 28. 198504 Старый Петергоф, Санкт-Петербург, Россия; e-mail: aninap4@gmail.com

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РЕЗЮМЕ

Климатические изменения проявляются через сдвиги во времени сезонных явлений в природе, что может быть критически важно для планктонных организмов. Временной сдвиг кривой сезонного прогрева воды в высоких широтах определяет фенологию водных организмов. Значительная корреляция между сроками фенологических событий в жизненных циклах планктонных Copepoda и сроками весеннего прогрева водной толщи была выявлена с помощью канонического корреляционного анализа. Мы анализировали многолетний ряд наблюдений за зоопланктоном и температурой (1961–2018) из Белого моря (66°19'50" с.ш.; 33°40'06" в.д., рядом с Беломорской биологической станцией Зоологического института Российской Академии Наук). Было выявлено два типа сезонной динамики численности молоди копепод и четыре типа динамики перехода от весны к лету. Каждый вид демонстрировал специфическую динамику численности в ответ на каждый тип весенне-летнего перехода. Виды со сходными экологическими свойствами различались фенологическими реакциями на изменения динамики температуры. Этот феномен определялся, по крайней мере частично, разделением ниш: временные ниши экологически близких видов разделялись в результате сдвига фенологических событий во времени. Последнее является результатом реакции организмов на изменения динамики весенне-летнего прогрева от года к году. Мы предполагаем, что такое разделение ниш – это одно из решений «Парадокса планктона», которое благоприятствует процветанию многовидовых сообществ в высокоширотных экосистемах, характеризующихся относительной бедностью пищевых ресурсов и коротким продуктивным сезоном.

Ключевые слова: конкуренция, фенологические сдвиги, сезонный цикл, температура, временная ниша, Белое море, зоопланктон

INTRODUCTION

Temperature is one of the primary environmental factors, driving seasonal cycle of high latitude marine ecosystems, together with the solar cycle. In addition to the variations of absolute temperatures, climate change often manifests itself through temporal shifts of seasonal temperature cycle, i.e. 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 lead to shifts of major phenological events in the populations of marine organisms (Bertram et al. 2001; Ji et al. 2010; Mackas et al. 2012; Usov et al. 2013; Usov et al. 2021).

Phenological changes in biological systems, which can be connected to recent climate change, are documented worldwide, both in terrestrial and aquatic realms (Parmesan 2006; Thackeray et al. 2016; Descamps et al. 2019; Staudinger et al. 2019). Marine zooplankton is particularly sensitive to climate changes due to the relatively short life cycles of most species (Mackas and Beaugrand 2010). Phenology of planktonic organisms is susceptible to climatic fluctuations: some organisms cannot match their life-cycle events to phenological shifts in environment, while others adapt to climatic changes shifting main events in their life cycles (Mackas et al. 1998; Edwards and Richardson 2004; Feng et al. 2016). Phenological changes in zooplankton populations are closely connected in populations of competing species so that shifts of phenology of any species influence seasonal dynamics of competing species (Aebischer et al. 1990; Edwards and Richardson 2004; Miller-Rushing et al. 2010). On the other hand, ecological competition is one of the factors constraining diversity and species abundance in biological communities in general and in planktonic communities in particular (Hardin 1960; Hutchinson 1961; DeMott 1989; Lindegren et al. 2020). However, the diversity and abundance of these communities, inhabiting a relatively homogeneous environment and comprising species exploiting the same restricted resources, is surprisingly high. This phenomenon was called “the

Paradox of the plankton" (Hutchinson 1961). This concept was developed for phytoplankton, however, with certain degree of approximation, it may be applied to zooplankton, due to the same environment, high diversity and short life cycles of planktonic animals. Decoupling of temporal niches during seasonal cycle is one of the mechanisms maintaining diversity (DeMott 1989), which is driven by changing environmental conditions through a year, that results in different species-specific phenology. Therefore, as phenological timing changes, the temporal niches of competing species may overlap, increasing a possibility of competition that may have a negative impact on certain planktonic populations and even for entire ecosystem, since zooplankton forms the base of aquatic trophic pyramid (Bertram et al. 2001; Miller-Rushing et al. 2010; Nakazawa and Doi 2012).

The analysis of phenological changes and their influence on the ecosystem demands thorough long-term investigations of climatic influence on zooplankton. Firstly, the longer the observation period, the greater the probability of finding long-term patterns (e.g., cyclicity or trends) in seasonal dynamics of temperature and plankton abundance. According to some authors, observations should exceed the period of fluctuations by a factor of six to reveal such trends and cyclicity reliably (Granger and Hatanaka 1964). Secondly, high observation frequency helps to reveal even smaller shifts in the seasonal cycle and shorter life-cycle phases of plankton. The long-term monitoring of zooplankton and environment near the White Sea Biological Station of the Zoological Institute of the Russian Academy of Sciences (Cape Kartesh) meets these requirements (COPEPOD 2018).

In the present study, we performed detailed analysis of the long-term phenological changes of several abundant Copepoda species, belonging to different biogeographical groups: cold-water arctic *Calanus glacialis* Jaschnov, 1955, boreal-arctic *Pseudocalanus* spp., warm-water boreal *Acartia* spp., *Centropages hamatus* (Lilljeborg, 1853), and *Temora longicornis* (Müller, 1792), ubiquitous *Oithona similis* Claus, 1866 and *Microsetella norvegica* (Boeck, 1864). *C. glacialis* prefers low temperatures from −0.39 to 4.86 °C (Prygunkova 1974; Zubakha and Usov 2004), its life span lasts for 2 or 3 years (Prygunkova 1974; Kosobokova 1999). The genus *Pseudocalanus* is represented by two species, *P. acuspes* (Giesbrecht, 1881) and *P. minutus* (Krøyer, 1845) (Markhaseva et al. 2012), which have not been distinguished historically until the last years. These species are quite close in their biogeographic distribution (Frost 1989), though their combined abundance demonstrated several seasonal peaks in the study area. In the White Sea, *Calanus* and *Pseudocalanus* reproduce in the end of winter – beginning of spring (March–May). Boreal *C. hamatus* and *T. longicornis* have similar temperature optima in the study area, 10.3 °C and 9.9 °C, respectively (Zubakha and Usov 2004), and they produce 2–3 generations per year (Prygunkova 1974; Pertzova 1990). The genus *Acartia* is presented in the White Sea by two boreal species, *A. longiremis* (Lilljeborg, 1853) and *A. bifilosa* (Giesbrecht, 1881), which have not been distinguished historically. They differ slightly by salinity and temperature preferences: *A. bifilosa* withstands freshening and inhabits estuarine areas of the White Sea with lower salinity and higher temperature compared to the open sea (Prudkovsky 2003). According to our observations, this species appears a little later during the season than *A. longiremis*, when water becomes warmer. Peaks of abundance of both species coincide with warm period of year (June–September). All the studied boreal species overwinter as dormant eggs, which hatch in the late spring–beginning of summer (June–July, original data). Only single specimens of *Acartia* spp. are found from time to time during winter (December–March), while *Centropages* and *Temora* are totally absent from November to May. Both *Oithona similis* and *Microsetella norvegica* are present in the plankton during the entire year and both have the same optima in the study area, about 9 °C (Zubakha and Usov 2004). Thus, the listed species represent well the ecological and biogeographical spectra of the local zooplankton. Moreover, *Calanus glacialis*, *Pseudocalanus* spp. and *Oithona similis* are among the most abundant species in the study area and in the North Atlantic and Arctic oceans (Weydmann et al. 2013; Cornils et al. 2017). They make up, respectively, 1.4, 32 and 43% of the total number and 4.2, 36 and 7.9% of biomass of the zooplankton community in the study area.

Inclusion of the species of *Acartia* and *Pseudocalanus* in analysis may be questionable because of the differences in their seasonal dynamics. However, we decided to consider these taxa, because the whole model loses its power and significance without them. However, any conclusions on the results concerning these taxa should be drawn with caution.

The correlation between a significant shift of the beginning of developmental season with the substantial shift of spring and summer seasons to an earlier time has been previously reported for several planktonic Copepoda inhabiting the White Sea (Usov et al. 2013; Usov et al. 2021). In these publications, we considered temporal shifts of specific events in the seasonal temperature dynamics, it was shown that it was temperature shift that drove phenological shifts of studied organisms. So that we decided to concentrate on this factor in the present work. Salinity is a factor which also change during transition from winter to summer, however the most perceptible changes are constrained by the thin surface layer (not more than 1–2 m in the study area; original observation). Moreover, planktonic species in the White Sea seems to have rather wide salinity optima, because they feed actively under the ice in the late winter despite the most intensive freshening in this time (Melnikov et al. 2005). Feeding success during the period of reproduction and early development seems to be more important than salinity stress for these animals. Therefore, any correlations of biological parameters with salinity may well be spurious and should be interpreted with caution. So that we did not consider this factor in the present work and left it for the future research.

It should be noted, that plankton responds to continuous seasonal water temperature changes, not to discrete temperature values. For example, early start of summer but slow summer warming, or late summer beginning but quick temperature increase during summer may theoretically have different consequences for planktonic animals. The analysis of the seasonal temperature curve, or parts of it, with maximal possible resolution therefore may become another approach to study an influence of phenological shifts in environment on plankton life-cycles. As it was stated above, phenological changes in populations of competing species are interconnected (Aebischer et al. 1990; Edwards and Richardson 2004; Miller-Rushing et al. 2010). Therefore, the phenological changes in population of any species must inevitably result in changes in the populations of interacting species. Thus, the first objective of this study is to reveal response of copepod phenology to the changes in temperature dynamics (the shape of the seasonal warming curve) during the spring to summer transition. The second objective is to evaluate consequences of phenological changes for interspecific interactions in plankton community.

MATERIAL AND METHODS

Sampling site and the period of observations

Water temperature and the zooplankton abundance have been monitored in the Chupa Inlet (the Kandalaksha Bay, the White Sea), at the monitoring 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 2018), this dataset for the period of 1961–2018 has been used as the data source in this study.

Sampling scheme and methods

Sampling was performed from a research vessel during the ice-free period and from the ice in winter. Zooplankton was sampled 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. Zooplankton was sampled from standard water layers (0–10 m, 10–25 m, and 25–65 m) by vertical tows with a Juday plankton net (mesh size 200 µm, mouth diameter 37 cm, mouth area 0.1 m^2). 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 using standard methods (Harris et al. 2000). Developmental stages of *Calanus glacialis* and *Pseudocalanus* spp. were determined to nauplii, immature copepodites CI–CV (each stage separately), and mature specimens CVI (males and females separately). Copepodite stages of smaller species were combined at counting as juvenile copepodites [“juveniles”, CI+CII+CIII] and immature copepodites [“copepodites”, CIV+CV]. The abundance was expressed as the number of specimens per one cubic meter (ind./m^3).

Temperature was measured simultaneously with 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 has been measured by CTD probe MIDAS 500 (Valeport Ltd.) as continuous profiles from surface to bottom. Prior to active use of new equipment, the CTD was intercalibrated with reversing thermometers and bathythermograph. No significant discrepancies were

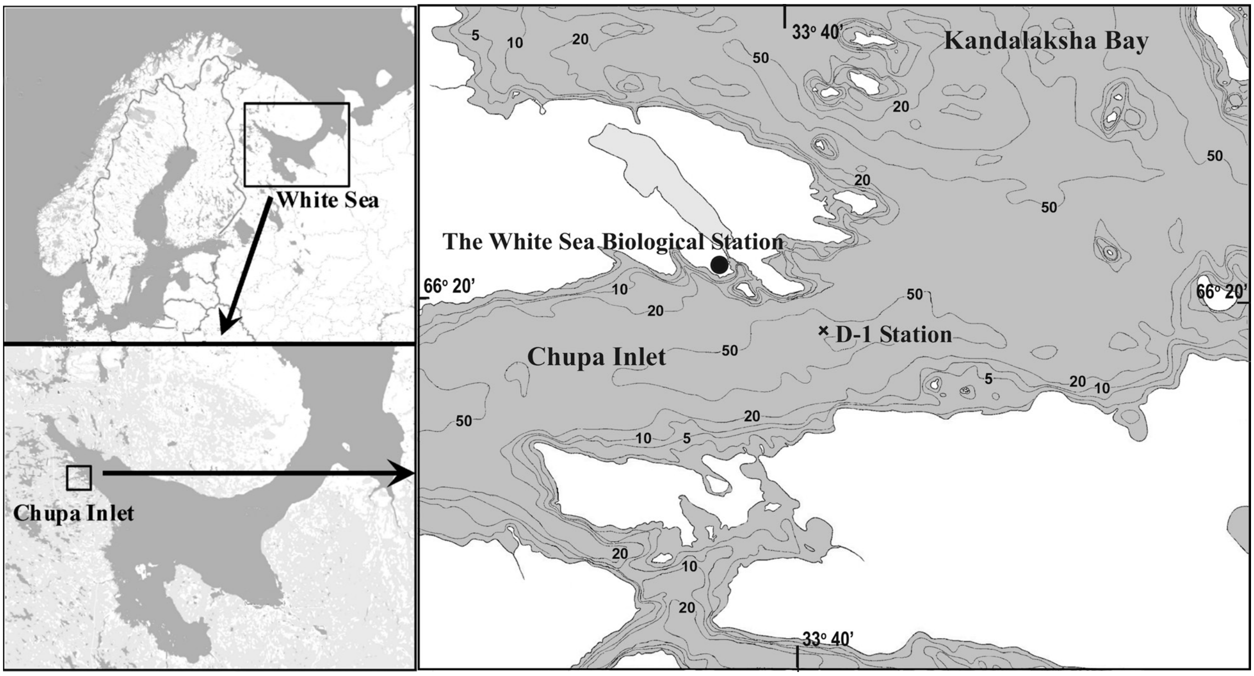


Fig. 1. Location of the study site (D-1 Station) in Chupa Inlet.

found within the limits of accuracy of the previously used equipment.

The water temperature and abundance of copepod juveniles have been analyzed in the most productive 0–25 m layer.

Defining the phenological events

The seasonal dynamics of juveniles of the studied species were analyzed. For each species, the earliest possible stage(s) that could be reliably sampled by 200 μm mesh was (were) analyzed, these stages were considered as indicating the reproductive season of the species. Copepodites of the first stage (CI) of *Calanus* and *Pseudocalanus* spp., and combined CIII–CV of smaller species (*Acartia* spp., *Centropages*, *Temora*, *Oithona* and *Microsetella*) were considered. Four key phenological dates based on the cumulative seasonal abundance were identified: (1) beginning-of-season, (2) middle-of-season, (3) end-of-season, and (4) timing of peak abundance (Batten and Mackas 2009, with modifications). They were determined through cumulative abundances of the CI/CIII–CV of each species at 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 method of calculation of these dates was described in details in Usov et al. (2021), see also supplement to that paper: ES 1.1.

1. Julian day which corresponded to 15% of the asymptote value of the logistic curve fitted for this species' abundance in a given year. This value was considered as "the Beginning-of-season" (*BS*).
2. Julian day at which the inflection point was observed on the logistic curve ("Middle-of-season", *MS*).
3. Julian day which corresponded to 85% of the asymptote value ("End-of-season", *ES*).
4. The date of direct observation of the maximum species abundance for the given year was considered as the date of the peak of the species abundance (*Peak*).

The "forward" temporal shift of any event means its later beginning. Long-term average dates of phenological events are present in Table 1.

Water temperature

Several seasonal events in temperature dynamics were defined and calculated in accordance to the hydrological seasons suggested by A.I. Babkov (Babkov 1985) with modifications. According to this scheme,

Table 1. Average timing of phenological phases in the study area, calculated for the period of 1961–2018. *BS* – beginning of developmental season; *MS* – middle of season; *ES* – end of season; *SE* – standard error of mean. *BS* to *ES* – the duration of developmental season.

Species and stage(s)	*BS* to *ES*	*BS*	*MS*	*ES*	*Peak*
	days	Julian day ± *SE*			
Calanus CI	15	154 ± 1.3	161 ± 1.2	169 ± 1.3	167 ± 2.0
Pseudocalanus CI	37	141 ± 2.5	159 ± 2.6	178 ± 3.1	161 ± 2.7
Acartia CIII–CV	67	203 ± 3.6	237 ± 3.6	270 ± 4.8	243 ± 4.1
Centropages CIII–CV	36	204 ± 2.1	222 ± 1.7	240 ± 1.9	229 ± 2.2
Temora CIII–CV	39	217 ± 1.8	237 ± 1.4	256 ± 1.7	241 ± 2.3
Microsetella CIII–CV	75	158 ± 3.9	195 ± 3.7	233 ± 5.2	202 ± 5.1
Oithona CIII–CV	122	170 ± 4.9	231 ± 3.6	292 ± 4.7	230 ± 7.3

the hydrological winter is a season, when the water temperature is below 0°C in a specific water layer. Hydrological spring and autumn are the periods of the highest rate of temperature change (increase or decrease, respectively), they correspond to the intervals between the dates of 0°C and +5°C thresholds in the upper 25 m layer. Hydrological summer is the period when the average water temperature of the layer exceeds +5°C. This value corresponds also to the upper limit of the optimal temperature range of cold-water zooplankton species in the White Sea (Zubakha and Usov 2004). The date when average water temperature in the 0–25 m layer reaches 3°C has been considered as the beginning of hydrological spring, because the period between 0 °C and 3°C thresholds coincides with the period of ice melting. At this time, work is technically impossible either from ice or from boat or ship. Thus, the date of 3°C threshold was the first date that could be detected reliably. Other analyzed thresholds were 4°C, 5°C, and 8°C on the ascending part of the seasonal curve, and the timing of the seasonal temperature peak (Table 2). The 6°C and 7°C thresholds were not considered, because they correlated strongly (Pearson $r = 0.88$), as well as they raised unreasonably the number of degrees of freedom, when included in the canonical correlation analysis (CCA). This allowed also to avoid the effect of multicollinearity, when predictors masked the effects of each other. Therefore, we considered the period from the spring beginning to the temperature peak as the "spring to summer transition period", when the reproduction and early development of studied species took place.

Table 2. Average timing of spring to summer transition, calculated for the period of 1961–2018. *SE* – standard error.

Water temperature	
Threshold	Julian day ± *SE*
3°C	160 ± 1.4
4°C	169 ± 1.8
5°C	172 ± 1.9
8°C	191 ± 2.2
t_{peak}	215 ± 1.9

Statistical analysis

Two arrays of data were used in analysis: (1) dataset of biological parameters (timing of phenological events in the seasonal dynamics of studied species and species abundance) and (2) dataset of abiotic parameters (timing of temperature thresholds). Prior to analysis, variables were standardized to zero mean and unit variance. Several pairs of canonical scores (orthogonal to each other) in the form of linear combinations of abiotic and biological variables were obtained for each year by canonical correlation analysis. They were calculated in such a way as to maximize the correlation (canonical correlation) between biological and abiotic canonical variables (C.V.). Only the first two pairs of canonical variables (C.V.1 and C.V.2) and, respectively, two first canonical correlations were significant. Significance of the canonical correlations was assessed by Bartlett criterion (Kendall and Stuart 1966). A scatterplot was built for visualization of results of canonical analysis, where the first and second canonical scores of each year were indicated as X and Y axes, respectively. Calculations were made in R (R Core Team 2019), using the package *CCA* (González and Déjean 2012).

The signs of the first and second canonical scores indicated different gradation of two factors, which determine the shift and shape of the seasonal tempera-

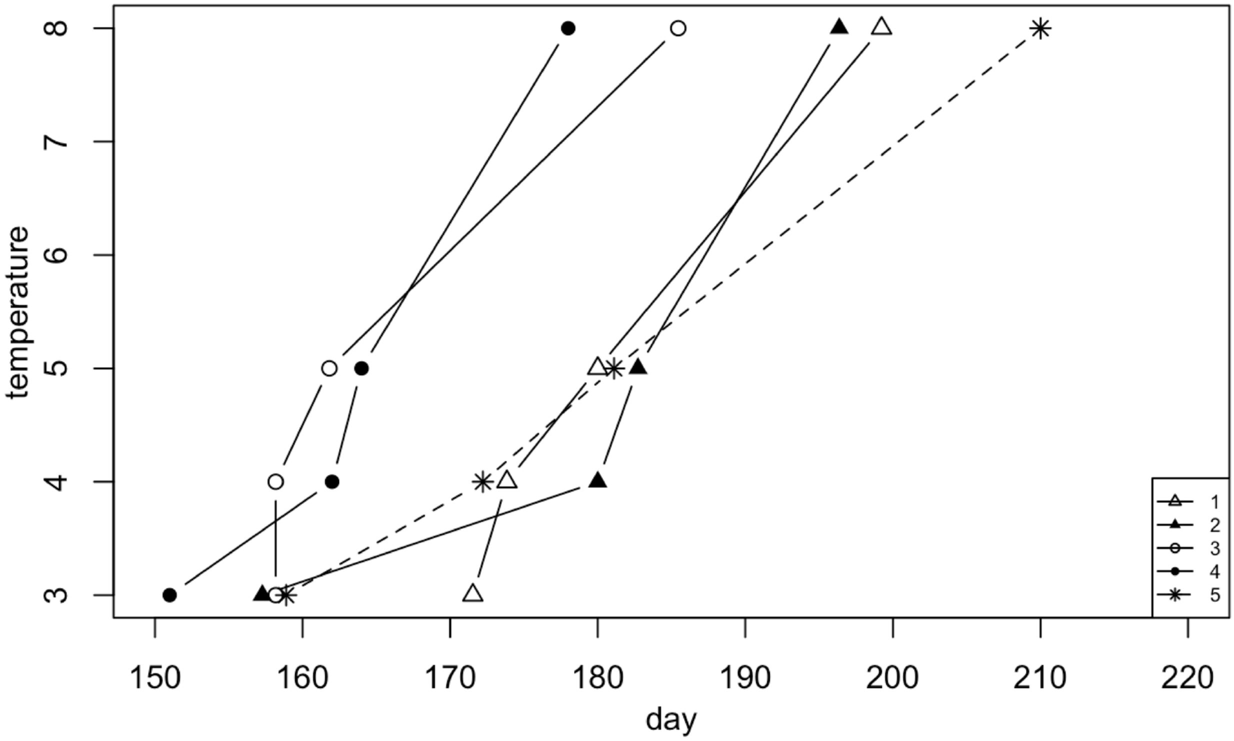


Fig. 2. Four types of the water temperature dynamics in 0–25 m layer in Chupa Inlet during spring to summer transition: 1 – late and fast, 2 – late and slow, 3 – early and fast, 4 – early and slow, 5 – years with incomplete data (according to the data for period 1961–2018).

ture curves, respectively. The ANOVA repeated measures analysis was used to assess the significance of influence of revealed factors on the timing of thresholds 3°C, 4°C, 5°C, and 8°C. The estimates of the parameters of this model were used to build curves of temperature spring-summer dynamics (spring to summer transition), corresponding to contrasting types of the latter. The ergodic method was applied to take into account all the data in ANOVA Repeated Measures, including incomplete ones (Alexeyeva 2017). This allowed assessing model parameters without omitting incomplete data and without model-based filling of missing values. In the ANOVA Repeated Measures model, the missing data leads to a bias that may be estimated using the ergodic method, so an appropriate correction was applied to the data, and then statistics were calculated from the already centralized model. Following R packages were used for ANOVA Repeated Measures: *MASS* (Ripley et al. 2020), *pracma* (Borchers 2019), *magic* (Hankin 2018) and *corpcor* (Schafer et al. 2017).

The significance level in all analyses was set as $p = 0.05$.

RESULTS

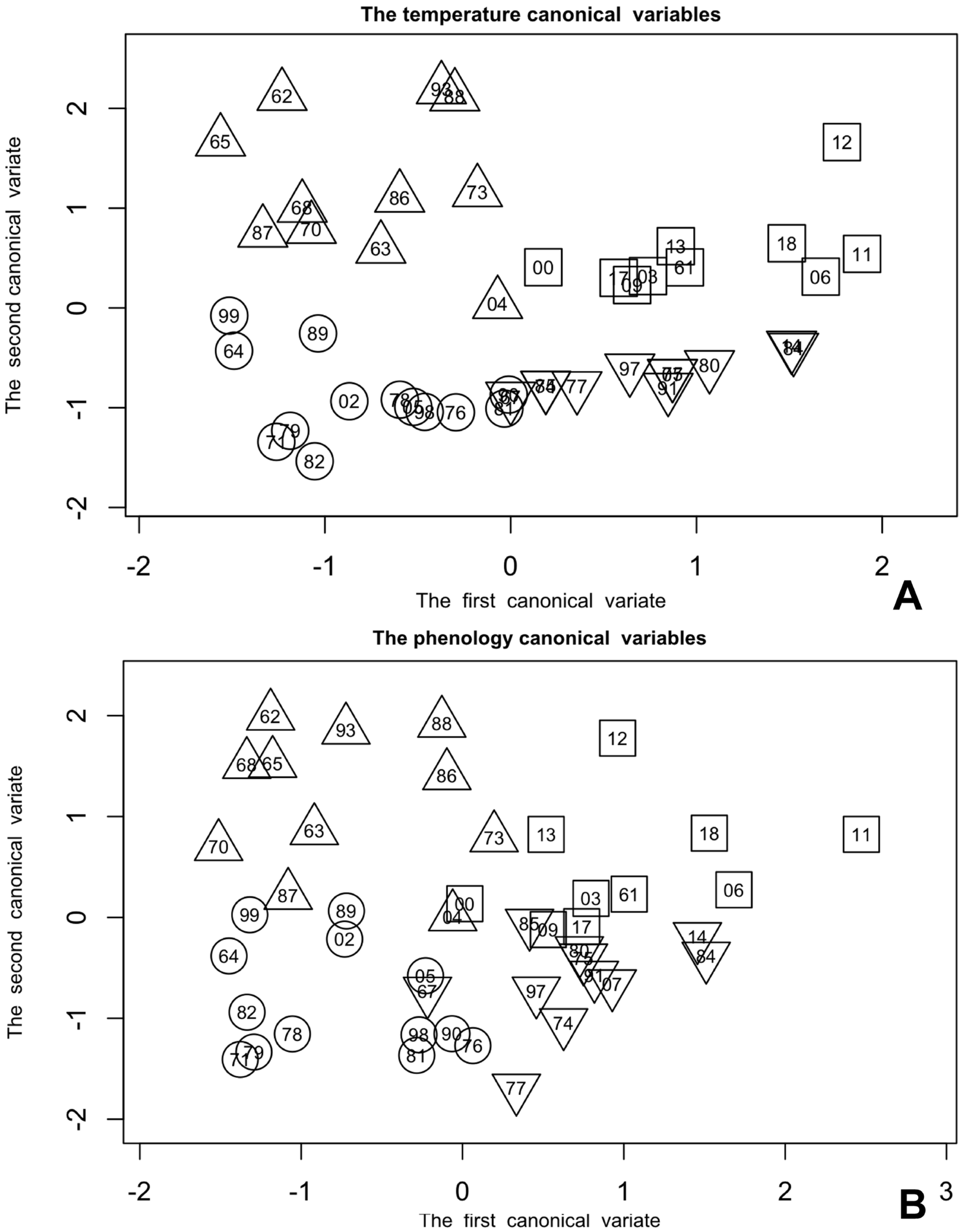
Types of the spring to summer transition

The seasonal and long-term dynamics of the water temperature was considered in detail in the previous works (Usov et al. 2013; Usov et al. 2021), so that we will not concentrate on these questions in the present work.

The first and second canonical correlations between phenological indices of studied species and timing of the spring to summer transition exceeded 0.9 (Table 3). Despite the second canonical correlation was insignificant ($p_2 = 0.072$), this correlation and corresponding canonical variates reflected important patterns in temperature dynamics and

Table 3. Canonical correlation results. Significant canonical correlations and Bartlett test results (Chi-square, degrees of freedom, and *p*-value).

A Correlations	χ^2	*df*	*p*
$r_1 = 0.96$	221.12	175	0.010
$r_2 = 0.95$	160.84	136	0.072


The temperature canonical variables

The phenology canonical variables

Fig. 3. Ordination of years in the space of canonical variates (axes), based on timing of the spring to summer transition (A) and phenological data (B). Numbers in figures are years: "61"–"99" – 1961–1999, "00"–"18" – 2000–2018. Circles – late and fast, triangles – late and slow, diamonds – early and fast, rectangles – early and slow transition. The years with the incomplete data are not presented.

Table 4. Canonical correlation results. Canonical coefficients for temperature threshold dates. C.V.1, C.V.2 – first and second canonical variables.

Temperature threshold	C.V.1	C.V.2
3°C	0.044	−0.660
4°C	−0.266	0.737
5°C	−0.394	−0.108
8°C	−0.604	−0.093
t_{peak}	0.638	0.026

Table 5. Years with different types of spring to summer transition.

Type	Years
Late and fast	1964, 1971, 1976, 1978, 1979, 1981, 1982, 1989, 1990, 1998, 1999, 2002, 2005
Late and slow	1962, 1963, 1965, 1968, 1970, 1973, 1986, 1987, 1988, 1993, 2004
Early and fast	1967, 1974, 1975, 1977, 1980, 1984, 1985, 1991, 1997, 2007, 2014
Early and slow	1961, 2000, 2003, 2006, 2009, 2011, 2012, 2013, 2017, 2018
Incomplete data	1966, 1969, 1983, 1992, 1994, 1995, 1996, 2001, 2008, 2010, 2015, 2016

species phenology (see below) and thus were considered for further analysis.

Canonical variables for temperature data characterized specific transition regimes. The latter in a specific year were expressed through the signs of canonical scores for this year, which depended on the combination of canonical coefficients for each C.V. in specific year (Table 4). The first C.V. (C.V.1): positive values of canonical scores indicated early spring to summer transition with late seasonal temperature peak (Fig. 2, negative coefficients at 4°C, 5°C, and 8°C thresholds, coefficient for 3°C threshold was low). C.V.2: positive values of canonical scores indicated early spring beginning (negative coefficient at 3°C threshold), but slow spring transition (positive coefficient at 4°C, which meant large time interval between 3°C and 4°C), earlier timing of 5°C and 8°C thresholds and later timing of peak (Fig. 2). Briefly, C.V.1 characterized shift of transition from year to year (early, when C.V.1 was positive, late, when negative), C.V.2 characterized the rate of spring transition: slow (C.V.2 positive) and fast (C.V.2 negative).

Thus, all the considered years may be divided into four groups in regard to the combination of signs of the canonical scores for the first and second canonical variables, i.e. the type of the spring to summer transition: (1) late and fast transition, (2) late and slow, (3) early and fast, and (4) early and slow transition (Fig. 2, Table 5). Definitions "slow" and "fast" refer here to the time needed for warming from 3°C to 4°C, or duration of spring transition. Therefore, each year may be characterized by the transition rate (slow or fast) and shift (early or late). These groups separate well in the space of the first two canonical axes, calculated either on the temperature or phenological data (Fig. 3). The grouping is very similar when considering abiotic and biological data.

The years with different types of spring to summer transition had a pronounced temporal pattern, when general tendency is observed from late and slow towards early and slow transition (Fig. 4). The years characterized by early and slow transition were 1961 and all the years after 2000. Years with fast transition were observed mostly until 1999. There was a tendency towards early spring and summer and relatively long spring after 2000.

Phenological response of the abundant species to changes in spring to summer transition

Similarly to the temperature dynamics, canonical analysis revealed two principal schemes of seasonal dynamics (phenological events) of the juveniles of the

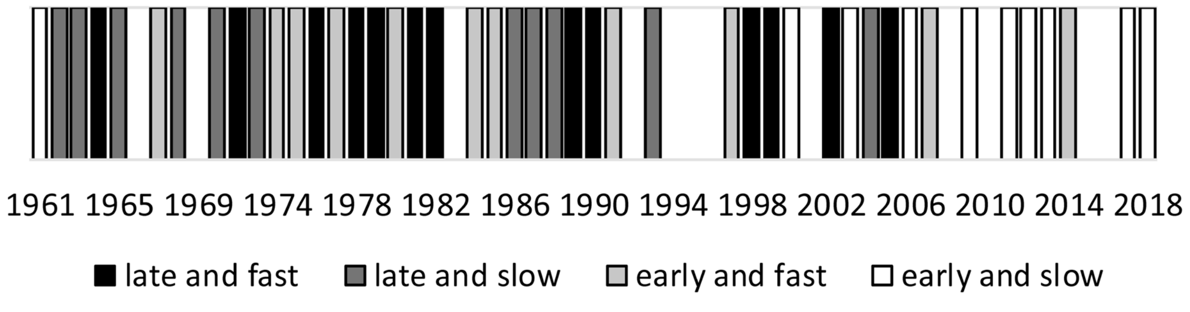


Fig. 4. Distribution of years with different types of spring to summer transition in Chupa Inlet.

Table 6. Canonical correlation results. Canonical coefficients for phenological indices and abundance of studied species. C.V.1, C.V.2 – first and second canonical variables. N – abundance. Other acronyms – see legend to Table 1.

Species	C.V.1					C.V.2				
	BS	*MS*	*ES*	*Peak*	N	*BS*	*MS*	*ES*	*Peak*	N
Calanus	0.133	−0.204	0.125	−0.053	0.027	0.041	−0.066	0.044	−0.019	0.009
Centropages	0.390	−0.590	0.350	−0.011	0.003	0.100	−0.158	0.095	0.001	−0.001
Temora	−0.003	0.028	−0.010	−0.017	0.024	−0.019	0.050	−0.026	−0.008	0.001
Oithona	−0.228	0.320	−0.214	0.033	−0.013	−0.381	0.565	−0.378	0.008	0.001
Acartia	−0.003	−0.021	0.033	−0.030	−0.033	−0.073	0.134	−0.085	−0.003	−0.008
Microsetella	0.110	−0.228	0.146	0.008	0.021	−0.070	0.105	−0.076	0.011	0.000
Pseudocalanus	−0.014	0.064	−0.042	−0.021	−0.009	0.254	−0.399	0.244	−0.010	−0.006

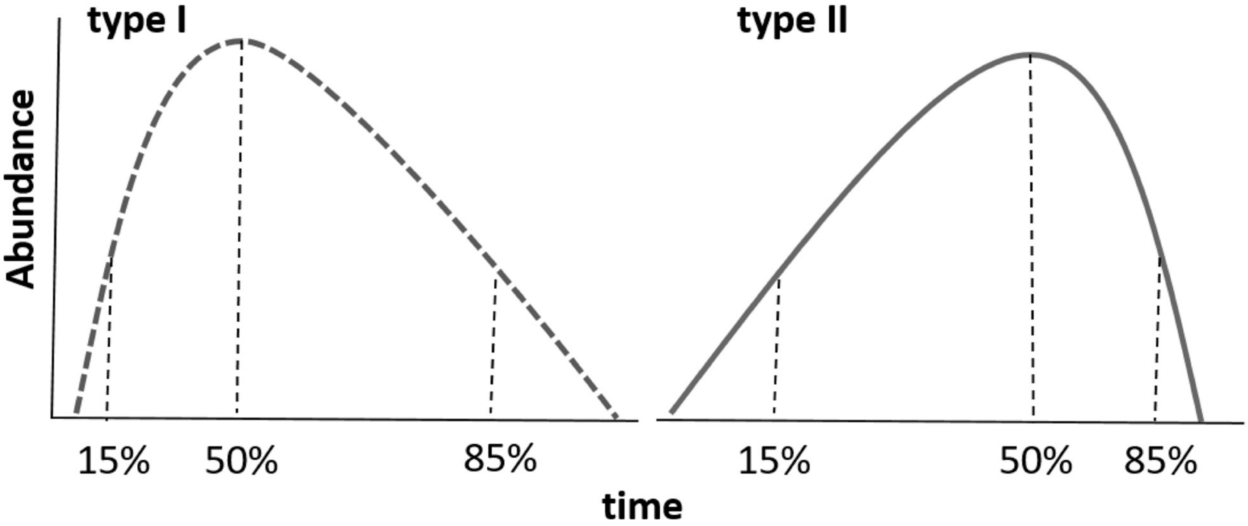


Fig. 5. Schematic view of the two types of copepod seasonal dynamics. “15%”, “50%”, and “85%” denote timing when percentiles of the cumulative abundance (beginning, middle and end of season, respectively) are expected in respective dynamics type. Timing of the middle of season (*MS*) almost coincides with the timing of the abundance peak (Table 1).

studied species, based on the combination of canonical coefficients (Table 6; Fig. 5). Phenology type I: late *BS*, early *MS* and late *ES*; phenology type II: early *BS*, late *MS*, early *ES* (Table 7). The only exception was *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 *BS* was very low, dynamics of these species could be considered as the phenology type I. Two phenology types, described above, corresponded to four types of the spring to summer temperature transition (Table 7).

Canonical coefficients at the seasonal abundance peak timing (*Peak*) were relatively low, except for *Acartia* and *Temora*, and the *Peak* timing was close to the middle of season (*MS*) in most cases (Table 1), so no special attention was paid to this phenological index.

Timing of temperature thresholds and 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 transition and by the phenology of two species, *Oithona similis* and *Centropages hamatus*, which was indicated by the values of canonical coefficients (Table 6). *Calanus glacialis* and *Microsetella norvegica* also contributed significantly. The second canonical correlation

Table 7. Phenology types (seasonal dynamics) of copepod juveniles at different types of spring to summer transition: I – late *BS*, early *MS*, late *ES*, II – early *BS*, late *MS*, early *ES*.

Species	Type of spring to summer transition			
	Early and slow	Early and fast	Late and slow	Late and fast
Calanus glacialis	I			II
Centropages hamatus	I			II
Oithona similis	II			I
Temora longicornis	II			I
Acartia spp.		I	II	
Microsetella norvegica		I	II	
Pseudocalanus spp.		II	I	

was primarily preconditioned by the timing of spring and summer beginning and the rate of the temperature increase from 3°C to 4°C (as a spring to summer transition), as well as by phenology of *Oithona similis* and *Pseudocalanus* spp. In all studied species, *MS* had greater impact than *BS* and *ES*.

DISCUSSION

The juveniles of seven copepod species responded to the changes of timing of the spring to summer transition in the studied area of the White Sea. The similar response of species with similar temperature preferences (Zubakha and Usov 2004) was expected to the same changes in temperature dynamics. However, our results provide evidence of the opposite pattern, where some species with different temperature preferences responded similarly in years with the same transition types, but the responses of ecologically similar species differed in the same years. For example, a similar response of arctic cold-water *Calanus glacialis* and boreal warm-water *Centropages hamatus* was observed to the same type of spring to summer transition. This phenomenon requires explanation.

Calanus glacialis is a typical arctic species (Walter and Boxshall 2021), on average, the middle of the season for this species coincided with the 3°C threshold, the end of season, with 4°C. Therefore, early middle and late end of season in *Calanus* phenology would correspond to early and slow transition, and vice versa, and this became clear under the applied analyses. These results fit nicely the assumption that early development of *C. glacialis* depends on water temperature, i.e., the higher the temperature the faster the development from the first naupliar stage to the first copepodite stage (Corkett et al. 1986; McLaren et al. 1988; Daase et al. 2011). A shift of the beginning of season of this species to earlier timing was documented at the study site in previous works (Usov et al. 2013; Usov et al. 2021). Opposite to *C. glacialis*, *Centropages* is a warm-water boreal species, characterized by one of the highest temperature optima in the White Sea (Zubakha and Usov 2004). The beginning of the season of *Centropages* starts only after the 8°C threshold has been reached, however, the timing of these two events relate negatively (opposite signs of canonical coefficients have been obtained). It is probable that the spring to summer transition (period between 3°C and 4°C) is more important for the beginning of the season of *Centropages*. A rapid increase of *Centropages* nauplii abundance is observed normally at the 180th Julian day (end of June), which is about 10 days after 4°C threshold, which is confirmed by the data on the 100 µm net, sampled since 1998 (original data). One of the explanations is that hatching of *Centropages*, which like other local boreal species overwinters as dormant eggs (Pertzova 1990), is triggered by temperature dynamics (Katajisto et al. 1998; Katajisto 2003, 2006; Engel 2005). The middle of season of *Centropages* is always observed after the seasonal peak of temperature, i.e., more than two months later than that of *Calanus*. Therefore, similarity of response of these two species to temperature shifts do not lead to any competition between these species due to the difference of their life history strategies. The development of *Centropages* juveniles after the middle of season of this species continues, when the water starts to cool down in late summer. Hence, some factors other than water temperature might influence *Centropages* and other boreal species during this period.

The phenological phases of juveniles of other boreal species, *Acartia* spp. and *Temora longicornis,* are very close by time to those of *Centropages* (Table 1). The development of all studied boreal species (*Acartia* spp., *Temora* and *Centropages*) takes place mainly after 8°C threshold, during the beginning of the water cooling in late summer. When the temperature maximum shifted to a later time, the beginning of season of *Acartia* also shifts forward, like that in *Centropages.* However, the responses of these species to the rate of transition ("slow"–"fast") are remarkably different (Table 7). However, we cannot conclude, which species of *Acartia* is responsible for that changes. We may only suppose that the beginning of season moves most probably due to changes in phenology of *A. longiremis*, because this species always appears first during a season, according to our recent observations. However, the shift of the middle and end of season to a later time may well be due to substitution of *A. longiremis* by *A. bifilosa.* Anyway, this question needs further clarification. *Temora*, most probably, is influenced by the 8°C shift, i.e. the earlier this threshold, the earlier is the start of the development of this species. The response of *Temora* to the transition rate is similar to that of *Acartia* spp. Therefore, despite similarity of temperature preferences of these boreal species, their responses to the dynamics of spring to summer transition differ, which promotes their successful coexistence. The absolute water temperature is probably not as important factor as the timing of temperature dynamics in particular year. After the water cooling begins, boreal species in the White Sea depend mostly on the availability of food resources, not the absolute water temperature (Martynova et al. 2011). Additional mechanisms of niche separation of the boreal species *Acartia*, *Centropages,* and *Temora*, may be the documented differences in the food preferences of these species (Martynova et al. 2011). Low competition between boreal copepods and *Oithona similis*, which have seasonal peaks that are close in time, is provided by substantially wider trophic spectra of the latter (Marshall and Orr 1966; Kattner et al. 2003). Indeed, *Oithona* is known to feed not only on phytoplankton and microzooplankton, but also use detritus and fecal pellets as food source.

Early development of the cold-water species of the genus *Pseudocalanus* spp. is very similar to that of *Calanus glacialis* (Prygunkova 1974; Usov et al. 2021). Nevertheless, the response of *Pseudocalanus* spp. to the spring to summer transition differs from that of *Calanus* (Table 7). Regard must be paid to the fact that the first nauplii of *Pseudocalanus* spp. appear about two months earlier than the nauplii of *Calanus*, and peak of abundance of *Pseudocalanus* nauplii is also observed earlier (unpubl.). Therefore, a large part of the development of *Pseudocalanus* juveniles takes place under the ice, long before the water temperature warms above 0°C. This may explain why *Pseudocalanus* depends on water temperature less than *Calanus* does (Persson et al. 2012). However, the interpretation of the obtained results is complicated and requires specific attention, since the *Pseudocalanus* genus in the study area has been shown to be represented by two species (*P. acuspes* and *P. minutus*), which have not been distinguished since the beginning of observations (Markhaseva et al. 2012). So the question is left unresolved: which of the two species (*P. minutus* or *P. acuspes*) responds to phenology changes, or both of them? Here we cannot even hypothesize, which species is responsible for shift of the beginning, middle and end of season, because no data exist on the biology of each species in the White Sea.

Oithona similis responded to the dynamics of the spring to summer transition in the same way as *Temora longicornis* did. However, these two species differ substantially in their biology. *Oithona* is the species with the broadest temperature niche in the White Sea (Prygunkova 1974). It reproduces all the year round even in the Arctic (Dvoretsky and Dvoretsky 2009). Despite the fact that the middle of season of *Oithona* is close to that of boreal species, the developmental season of this species, marked by the appearance of the first copepodite stages, begins only 16 days later than that of *Calanus*, but ends later than the season of any other species (after 290th Julian day, in mid-October). The development of *Oithona* after the middle of season, which took place after the water temperature maximum, hardly depends on the absolute temperature. Other factors, mainly trophic, probably govern the life of *Oithona* after the temperature peak, as the development of boreal species.

The response of *Microsetella norvegica* to the changes of seasonal transition resembled that of *Acartia* spp., but the developmental season of *Microsetella* occurs much earlier. Therefore, juveniles of these two species are affected by fluctuations of water temperature in different periods of the year. Temperature optima of *Microsetella* and *Acartia* are almost the same, 8.1°C and 8.3°C, respectively (Zubakha and Usov 2004). However, the biology of *Microsetella* differs substantially from other planktonic Copepoda. It is one of a very few true planktonic Harpacticoida in the World Ocean (Boxshall 1979; Huys and Boxshall 1991) and the only one in the White Sea (Kornev and Chertoprud 2008), although some authors report its interstitial nature (Zhang et al. 2004). In addition, the food spectrum and trophic features of *Microsetella* distinguish it from other copepods found in the White Sea, since this species is often found on detrital aggregates and abandoned houses of Appendicularia in other parts of the World Ocean (Green and Dagg 1997; Koski et al. 2005; Maar et al. 2006). In the White Sea, it is a constant and abundant component of the plankton communities (Usov et al. 2013; Usov et al. 2021), exhibiting population outbursts in association with anomalous blooms of *Phaeocystis* spp. in the White Sea in recent years (unpubl. data).

We found that different types of spring to summer transition prevail in certain periods of the study (Fig. 4), with a tendency towards early transition. This trend corresponds well to the global warming trend (Mackas et al. 2012; Atkinson et al. 2015). Though some regional specific existed – transition between 3 and 4°C during the last 20 years in years with early spring beginning was relatively slow. However, in all years with early spring-summer transition summer began almost at the same time. It has been hypothesized that high-latitude species with early reproductive season are most sensitive to climate change (Pau et al. 2011), which was confirmed by strong trends towards earlier developmental season in the phenology of the arctic species *Calanus* and *Pseudocalanus* spp. found in our previous study (Usov et al. 2021). And, again, it is left unclear, which of the two species of *Pseudocalanus* is responsible for this. However, it is clear, that conditions have become favourable for earlier reproduction and development of Arctic and boreal-arctic copepod species in the White Sea because of climate change. On the other hand, the hatching of the resting eggs of boreal species depends to a large extent on the dynamics of the water temperature (Katajisto 2003; Boyer and Bonnet 2013; Holm et al. 2018). Therefore, earlier beginning of developmental season of boreal warm-water *Centropages* and *Temora* (Usov et al. 2021), which overwinter as latent eggs in the White Sea (Pertzova 1990), may be attributed to earlier summer warming.

There is the difference between the response of planktonic copepods to long-term changes of temperature seasonal dynamics and to such changes at the year-to-year scale (short-term). Responses of *Calanus* to year-to-year changes of transition regime (early vs. late) and to long-term trends of this parameter are opposite (Usov et al. 2021). We suppose that various factors may be of different significance at different time scales. Short-term (mostly local) fluctuations of environment and biological interactions must play an important role in driving year-to-year changes of phenology. Long-term trends in dynamics of phenological variables are probably determined to a larger extent by climatic, global-scale processes, expressed at the local scale through long-term changes in environment. Such time-space dependencies, where larger-scale processes correspond to longer time-scale, are well known (Haury et al. 1978; Benway et al. 2019).

The phenology of a certain species is a result of combined effect of environmental factors and competitive interactions between the community elements (Pau et al. 2011). This is especially apparent in plankton, where high competition for the same resource is observed in relatively homogeneous 3D environment, where competing species cannot be fully separated in space. Despite that, relatively high diversity is maintained in planktonic communities, this phenomenon has been called “the Paradox of plankton” (Hutchinson 1961). One of the explanations of it is that temporal change of environmental conditions and accessibility of resources lead to change in competitive abilities of species (Hutchinson 1961; DeMott 1989). As a result, in a seasonal climate in each specific period of year, the species get advantage, which are the most adapted to these conditions. Basically, it is expressed in the difference of the seasonal dynamics of various species. This helps to separate in time key events in life cycles of different community members, or, in other words, separate their temporal niches (Gotelli and Graves 1996). Nevertheless, the seasonal dynamics of some species are very close to each other, and the boreal species in the White Sea are an example of this. This inevitably leads toward higher competitive pressure between these species. In such situation, differences in phenological responses to specific temperature dynamics allow separating temporal, and, therefore, trophic niches of these species. Thus, in years with different temperature dynamics various species may take advantage, which is the solution of the "paradox of plankton" at the year-to-year level. Of course, this is not the only mechanism of niche separation and even is not the most important one, however, it worth paying attention to it and this phenomenon needs further analysis.

CONCLUSION

We have found, that one of the mechanisms of temporal niche separation of planktonic species with close temperature preferences may be the differentiation of their response to phenological changes in environment. In the White Sea, year-to-year temporal shifts of phenology of planktonic copepods are connected to the changes in the dynamics of the water temperature during the transition from spring to summer. Several types of seasonal temperature dynamics have been revealed with different time of spring beginning (early and late) and rate of seasonal warming (fast and slow). Several types of seasonal dynamics of copepod juveniles have also been found: with various timing of beginning, middle and end of developmental season. Each species demonstrated specific type of seasonal dynamics in response to certain type of temperature dynamics. As a rule, species with similar temperature preferences had different responses to the same changes in temperature dynamics. These differences allow separation of the temporal niches of ecologically similar organisms, which may be one of the mechanisms that reduce competition between species, characterized by close food spectra and temperature preferences and inhabiting a homogeneous medium with limited resources. Such temporal niche decoupling supports high abundance and production of zooplankton in high latitudes despite paucity of food resources and very short productive season.

Besides distinct interannual phenology fluctuations, there exists the tendency towards early and slow spring-summer transition. This trend coincides with strong tendencies towards early developmental season of Arctic species *Calanus glacialis* and *Pseudocalanus* spp. and boreal species *Centropages hamatus* and *Temora longicornis*. This means that climatic changes influences species with contrasting temperature preferences, therefore its effect is important for the whole community.

The mechanisms of niche decoupling undoubtedly are not limited to those mentioned in our study. Factors other than temperature, such as food availability and predation pressure must play important role in this process. Spatial dimension of multidimensional Hutchinson's niche also deserves attention. It is especially important for planktonic animals, whose habitat is three-dimensional and thus must offer opportunities for successful coexistence of ecologically similar species, despite the productive layer in high latitudes being very thin. This is subject for further studies.

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