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## Phenological Responses of the Arctic, Ubiquitous and Boreal Copepod Species to the Long-Term Changes in the Annual Seasonality of the Water Temperature in the White Sea

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<b>Abstract:</b>	<p>Climate change-derived temperature rise has been proved the most intensive in the high latitudes. However, absolute temperature increase is not the only sign of changing climate that can manifest itself also through temporal shifts of seasonal temperature dynamics, which, in turn, causes temporal shifts of phenological processes in zooplankton. Long-term shift of the timing of seasonal water warming was registered in the north-western White Sea (Chupa Inlet, Kandalaksha Bay). Beginning of hydrological spring and summer have shifted by more than 3 weeks to an earlier timesince 1961. The shifts of about the same magnitude and even greater were detected in timing of phenological events of <i>Calanus glacialis</i>, <i>Pseudocalanus</i> spp., <i>Microsetella norvegica</i>, <i>Acartia</i> spp., and <i>Temora longicornis</i>. These shifts caused significant changes of only <i>Acartia</i> spp. abundance. No significant influence of year-to-year changes in species phenology on population abundance has been found. Several mechanisms of such resilience were proposed: 1) synchronization of changes in zooplankton and environment seasonal dynamics; 2) switching to omnivory in cases of trophic mismatch; and 3) prolongation of phytoplankton bloom with rising spring temperature, which favors cold-water spring species (<i>Calanus</i> and <i>Pseudocalanus</i>). Interspecific interactions between ubiquitous species influenced their phenology and abundance: early development of <i>Microsetella</i> caused later development of <i>Oithona</i> and higher abundance of the latter. We suggest competition for resources as one of the causes of the observed interactions, since the trophic niches of these species overlap.</p>	
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**Phenological Responses of the Arctic, Ubiquitous and Boreal Copepod Species  
to the Long-Term Changes in the Annual Seasonality of the Water Temperature  
in the White Sea**

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**Abstract**

Climate change-derived temperature rise has been proved the most intensive in the high latitudes. However, absolute temperature increase is not the only sign of changing climate that can manifest itself also through temporal shifts of seasonal temperature dynamics, which, in turn, causes temporal shifts of phenological processes in zooplankton. Long-term shift of the timing of seasonal water warming was registered in the north-western White Sea (Chupa Inlet, Kandalaksha Bay). Beginning of hydrological spring and summer have shifted by more than 3 weeks to an earlier time since 1961. The shifts of about the same magnitude and even greater were detected in timing of phenological events of *Calanus glacialis*, *Pseudocalanus* spp., *Microsetella norvegica*, *Acartia* spp., and *Temora longicornis*. These shifts caused significant changes of only *Acartia* spp. abundance. No significant influence of year-to-year changes in species phenology on population abundance has been found. Several mechanisms of such resilience were proposed: 1) synchronization of changes in zooplankton and environment seasonal dynamics; 2) switching to omnivory in cases of trophic mismatch; and 3) prolongation of phytoplankton bloom with rising spring temperature, which favors cold-water spring species (*Calanus* and *Pseudocalanus*). Interspecific interactions between ubiquitous species influenced their phenology and abundance: early development of *Microsetella* caused later development of *Oithona* and higher abundance of the latter. We suggest competition for resources as one of the causes of the observed interactions, since the trophic niches of these species overlap.

**Key words:** zooplankton, Copepoda, White Sea, phenology, long-term changes, water temperature.

## Introduction

Recent climate change, manifested through the temperature rise, has been proved the most intensive in high latitudes, especially in the Northern Hemisphere (IPCC, 2007, 2013). High latitudes are also characterized by the pronounced seasonality of solar energy supply and, as a result, seasonality of temperature, which governs the annual cycle of the phyto- and zooplankton production. Two main factors influencing marine ecosystems can be distinguished: the temperature fluctuations and the timing of seasonal warming/cooling. Thus, one can expect that the climate change influences not only absolute values of temperature and other registered environmental parameters but also timing of different events during their seasonal cycle. Populations of planktonic organisms respond rather quickly to climatic fluctuations because of short life cycles. Besides that, many planktonic organisms inhabit the upper water layer of the Ocean, which is the most sensitive to the climatic fluctuations. Indeed, climatic changes in the Arctic affect planktonic organisms significantly (Richardson, 2008; Wassmann et al., 2011). Seasonal ice retreat occurs earlier in the Arctic, which causes respective shifts of the timing of phytoplankton bloom (Ji et al., 2012). Planktonic animals respond to long-term trends and year-to-year fluctuations of environmental parameters by temporal shifts of key events in their life cycles (Edwards, Richardson, 2004; Mackas et al., 2012). For example, in the North Sea more than a half of studied species shifted their developmental season to an earlier time during period 1975–2006 (Greve et al., 2004; Mackas et al., 2012). An advance of *Calanus glacialis* development by about three weeks to an earlier time during period 1961–2010 was reported for the study area earlier (Usov et al., 2013). Large year-to-year fluctuations of *Calanus finmarchicus* CI abundance peak, spanning about 2 month, was detected in northern Norway (Mackas et al., 2012). Timing of appearance of warm-water *Acartia tonsa* in Narragansett Bay advanced by three weeks during warm period 1972–1990 (Borkman et al., 2018). The duration of *A. tonsa* presence in the water increased from 31 to 38 weeks. Timing of the biomass maximum of *Neocalanus plumchrus* in the north-eastern Pacific Ocean shifted according to the temperature dynamics in the upper mixed layer of the ocean: it was early by about 60 days in warm years than in cold ones (Mackas et al., 1998). Each species must be synchronized normally with its food, for successful reproduction and development (Post, Forchhammer, 2008). This is especially important in Arctic, where period of rich food is very short (Falk-Petersen et al., 2009; Ji et al., 2012). Temporal shifts in seasonal cycles of environmental parameters, zooplankton and trophic objects may lead to the trophic mismatch between consumers and their food, e.g. between zoo- and phytoplankton (Edwards, Richardson, 2004;

Søreide et al., 2010; Atkinson et al., 2015), because rate of phenological changes at different trophic levels may differ (Thackeray, 2012). This may negatively affect zooplankton community, which inevitably translates to the next trophic level (Edwards, Richardson, 2004; Ji et al., 2012). Planktonic organisms are indispensable component of marine trophic webs, so, any changes in phyto- and zooplankton abundance or in the timing of phenological events in plankton may lead to the changes along the entire food chain and food web. This stresses the importance of observations of quantitative and phenological changes in plankton.

In order to track the changes in communities that occur gradually over many years, it is necessary to conduct observations for a long time. An important characteristic of such observations is their continuity, since interannual fluctuations of various parameters, both biological and abiotic (environmental), are great in natural environment. In order to separate the “signal” and the “noise”, it is necessary to register the parameters of interest constantly from year to year. Due to the short life span of planktonic organisms, the frequency of sampling and measuring environmental parameters is of great importance. There are not so many time series that meet the above requirements in the world. The monitoring of the zooplankton in the White Sea performed at the White Sea Biological Station of Zoological Institute, Russian Academy of Sciences, meets most of them (COPEPOD. Interactive Time-series Explorer METABASE, 2018).

The White Sea is a semi-enclosed sub-Arctic basin, so the intensive climatic changes, observed in high latitudes of the Northern Hemisphere, influence this sea inevitably. The White Sea has pronounced continental features, which manifest themselves in the long cold winter (surface layer cools down to -1.5 °C) and short, relatively warm summer with surface temperature up to 20 °C (Berger et al., 2001; Filatov et al., 2005; Usov et al., 2013). The sea is covered with ice for 4–6 months (Babkov, 1982; original data). In this regard, the seasonality of all processes, both abiotic and biological, is pronounced in the White Sea. Therefore, any shifts in the timing of events during the year, as mentioned above, can lead to disruption of the links between trophic levels in the biocenosis. This, in turn, can have negative consequences for pelagic communities. Our data obtained over almost 60 years with a high sampling frequency theoretically allow us to track such changes in the seasonal course of both environmental parameters and quantitative characteristics of plankton communities.

The long-term changes of the temperature seasonal cycle in the White Sea has been reported earlier for the period of 1961–2010 (Usov et al., 2013). However, the detailed analysis of the phenology of the arctic (*Calanus glacialis*), boreal-arctic (*Pseudocalanus* spp.), boreal (*Acartia* spp., *Centropages hamatus* and *Temora longicornis*) and ubiquitous (*Oithona similis*,

*Microsetella norvegica*) organisms in the coastal region of the White Sea was not performed yet. Though some preliminary analysis was done in the work, mentioned above (Usov et al., 2013).

We hypothesize that the shifts in the temperature seasonal cycle may inevitably influence seasonal cycle of planktonic organisms with different temperature preferences, which, in turn, may potentially lead to the changes in the species abundance.

## 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 used for the data analysis, because in the first two years there existed gaps in the data for several species. Some gaps in the observations occurred also during the periods of the ice formation and melting, because of danger of working on the instable ice. However, they did not influence the analysis because we chose seasons less affected by these gaps – spring and summer – to calculate average abundances of animals. We used approximating models for calculation of phenological indices, which allowed us to fill in the gaps (see below).

***Sampling scheme and methods.*** Monitoring is conducted from research vessel during ice-free period and from the ice in winter. Zooplankton sampling is performed every ten days during the ice-free period and monthly from the ice, except for the period of 1962–1969, when the sampling is performed every ten days all the year round. The zooplankton is 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 m<sup>2</sup>). The samples are immediately preserved with formaldehyde (final concentration 2–4%). In total, more than 3400 samples have been collected and processed since 1961. The sample processing is performed by the standard methods (Harris et al., 2000). Briefly, the samples are concentrated to 100-mL or 200-mL volume according to the organisms' concentration assessed visually, and three 1-mL aliquots are 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 are counted individually in the whole sample. The counting is performed in the Bogorov's counting chamber. Animals are identified down to the species or genus level.

Developmental stages of the copepod species *Calanus glacialis* and *Pseudocalanus* spp. are determined to nauplii, CI–CV copepodites, and mature specimens of CVI, i.e. males and females. Copepodite stages of the other, smaller copepod species are combined at counting in a following way: juveniles [CI+CII] and copepodites [CIII+CIV+CV]. The abundance is expressed as a number of individuals per one cubic meter (ind. m<sup>-3</sup>).

Temperature is 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 is 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 six species/genera of planktonic Copepoda were 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* has temperature optimum at 3.1 °C (Zubakha, Usov, 2004) ranging from –0.39 to 4.86 °C (Prygunkova, 1974) and 2- to 3-year life cycle (Prygunkova, 1974; Kosobokova, 1999). This species reproduces at the study site in the end of winter–beginning of spring (in March–May). *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. were 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 values of water temperature and species/stage abundance in the layer 0-25 m on each sampling day were used in phenological analysis and Canonical correspondence analysis (see below). The upper 25-m layer lies above seasonal thermocline (10–25 m), and the major part of organic carbon is produced here in the White Sea (Prygunkova, 1974; Pertsova, 1980). The reproduction and early development of the studied species take place here too (Bogorov, 1941; Pertsova, 1971, 1974; Prygunkova, 1974; Pertsova, Kosobokova, 2010; Martynova et al., 2011). Average species abundance in the total water column (0-65 m) was used for analysis of influence of phenological shifts on the whole population abundance. Total water column was considered because the populations of studied species (especially older developmental stages) occupy also layers beneath 25-m isobath.

Long-term averages of each studied variable on every 10-th day of the year were calculated for analysis of seasonal dynamics. The dates here and throughout the paper were expressed as Julian days.

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 modification. According to this scheme, the hydrological winter is a season with water temperatures 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 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 temperature in layer 0–25 m reached 3 °C was accepted as the threshold of spring beginning, 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. Other thresholds used in analysis are: 4 °C, 5 °C on ascending part of the seasonal curve and 5 °C on descending part (summer end). Summer duration was the period between these two 5 °C thresholds.



Average values of temperature in spring (May and June) and summer (July-September) of each year were calculated for analysis of long-term dynamics. These periods were used because on average they correspond to hydrological spring and summer, respectively. Average total species abundances (all developmental stages) for period from May through October were used in analysis of long-term dynamics. This is the period of year which covers the reproduction and active development of all studied species. The analysis of the long-term population dynamics of *Microsetella* did not comprise the period of 1961—1964, because of uncertainties in the abundance determination of this species during this particular period.

***Defining the phenological events in populations of particular species.*** We identified four key events based on the available observations: the beginning of the species presence in plankton (Beginning-of-season), the middle of the time interval when the species is presented in plankton (Middle-of-season), the date of peak species abundance (Peak) and end date of the species in the plankton (End-of-season) (after: Batten, Mackas, 2009).

The dates of key events could fall on the intervals between observations and, therefore, were missed. In this regard, we used the following method for detection of the dates of key events. For *Calanus glacialis*, the total number of copepodites I, II and III was considered, because they for sure belong to this year generation (CIV is overwintering stage and develops in deeper layers). Besides that, each of early stages is presented in plankton for a very short time, so their combination is more representative for the developmental season of this species. Number of CI of *Pseudocalanus* was considered, because it was representative (large enough for mesh size, used in sampling). We used the abundance of late copepodites (CIII–CV) of boreal and ubiquitous species as markers of the species presence in plankton, because they are better presented in samples taken by 200 µm mesh.

A cumulative abundances of mentioned developmental stages of each species, were calculated for each sampling date, starting from January 1 in each of the calendar years. 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:

1. 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. This value was considered as the date of the beginning of the presence of the species in the plankton community (Beginning-of-season).

2. The date at which the inflection point was observed on the logistic curve. This value was considered as a characteristic of the “middle point” of the species presence in the plankton community (Middle-of-season).

3. The date on which 85% of the value of the asymptote was observed. This value was considered as a characteristic of the end of the stay of the species in the plankton (End-of-season).

4. 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, was considered as the date of the peak of the species abundance (Peak).

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 by the algorithm described below (SSA – Singular Spectral Analysis).

**Environmental parameters.** Timing of the ice disappearance (ice clearing) in Kovda estuary was used in analysis (I.O. Dumanskaya, pers. comm.). This is the nearest place (meteorological station) where ice observations have been conducted during the whole period of our observations. Climatic index of North Atlantic Oscillations (NAO) represents winter (December through March) index of the NAO based on the difference of normalized sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Hurrell, 1995; retrieved from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>). Arctic Oscillations Index (AOI) data were taken from [https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily\\_ao\\_index/ao.shtml](https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao.shtml). The latter is determined by the difference between sea-level pressure anomalies of one sign in the Arctic and anomalies of opposite sign centered at about 37–45°N.

**Abbreviations of the tested parameters.** Main phenological events mentioned above: ‘Begin’ – Beginning-of-season; ‘Middle’ – Middle-of-season; ‘Peak’ – Peak; ‘End’ – End-of-season. Species abbreviations: *Pseudocalanus* – *Pseudocalanus* spp.; *Calanus* – *Calanus glacialis*; *Microsetella* – *Microsetella norvegica*; *Oithona* – *Oithona similis*; *Acartia* – *Acartia* spp; *Temora* – *Temora longicornis*; *Centropages* – *Centropages hamatus*. The combination of

each two abbreviations is used below for indicating the phenological event for a given species (e.g. Calanus\_Peak). Species name followed by index "N" (e.g. Calanus\_N) indicates average total species abundance for period of May–October.

Environmental parameters: TPD – Julian day when temperature maximum was observed; SpSD – Julian day when hydrological spring started (water temperature reached 3 °C); SuSD – Julian day when hydrological summer started (water temperature reached 5 °C); SuFD – Julian day when hydrological summer ended (water temperature cooled down to 5 °C); SuDur – summer duration, Julian days; ICD – Julian day when ice clearing was observed; SpT – Mean spring temperature; SuT – Mean summer temperature; NAO – North Atlantic oscillation index; AOI – Arctic oscillation index. SuSDPY, SuFDPY, SuDurPY, SpTPY, NAOPY, AOIPY denote SuSD, SuFD, SuDur, SpT, NAO and AOI observed in the previous year (PY).

## Statistics

All statistical processing was carried out using the functions of the statistical programming language R 3.5.3 (R Core Team, 2019).

**Filling in missing values.** The missing values of key phenological events, animal abundance and environmental factors were reconstructed using a singular spectral analysis of time series, 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).

**Analysis of the long-term dynamics of the studied parameters.** The linear models that relate the value of a particular parameter to time (years of observation) were fitted to identify long-term linear trends in the dynamics of phenological indicators of species and their abundance, as well as environmental factors for each of them. The estimation of linear model parameters was carried out by the least squares method using the *lm()* function from the *stats* package (R Core Team, 2019).

However, due to the very high probability of the presence of temporal autocorrelations in the data, we did not use the standard estimates of the statistical significance of model parameters that require independent observations. Instead, we used the permutation assessment based on the “model matrix” approach (Clarke & Gorley, 2006; Legendre & Legendre, 2012). To do this, we calculated the matrix of pairwise Euclidean distances between years, based on a time series representing the long-term changes of a given value. The second so-called “gradient” model matrix reflected the pairwise Euclidean distances between the numbers of the

natural series from 1961 to 2018 (for *Microsetella*, model matrix was calculated for period from 1965 to 2018, see above). Next, the Mantel correlation between the two matrices was calculated. The assessment of statistical significance was carried out by the permutation method (here and in further cases of permutational significance estimates, 9999 permutations were used). Later we used the significance levels obtained in this analysis (the Mantel correlation per-se was not considered further). Since in all cases we had to deal with multiple hypotheses (several plankton species included in one analyses or several environmental parameters), all permutational  $p$ -values were adjusted in accordance with the False Discovery Rate monitoring procedure (Benjamini, Hochberg, 1995).

If the adjusted  $p$ -value was below the critical level (in all analysis, the value  $p = 0.05$  was set as the critical level), this was considered as evidence of the presence of a certain directional (upward or downward) trend in the long-term dynamics. The trend sign was estimated by the value of the slope coefficient of the fitted linear model. The magnitude of the change of the variable over the observation period was estimated by the multiplication of slope coefficient by the duration of observations (57 years, except 53 years for *Microsetella*).

**Factors, influencing phenology.** Canonical correspondence analysis (CCA) was applied to identify the factors that influence the phenological events in the seasonal dynamics of the species, (Ter Braak, 1986; Legendre, Legendre, 2012). The “phenological matrix” was used as a dependent matrix, 28 columns of which were formed by key events of each planktonic species (4 key events of 7 species), and the rows were the years of observation. The dates of key events (the numbers of Julian days) were given in the cells of the phenological matrix.

The predictor matrix was developed as follows: the rows were years and the environmental parameters were columns (see above). However, since phenological events in the life of plankton can be regulated not only by abiotic environmental parameters, but also by biotic interactions with other members of the plankton community, we also included abundance of species (total population abundance in the productive layer 0-25 m) in the predictor matrix (values were transformed using  $\log(N+1)$ ). The analysis was performed using the *cca()* function from the *vegan* package (Oksanen et al., 2019).

CCA comprised several steps. Firstly, collinear predictors with variance inflation factor exceeding 5 were rejected and were not included into the model. Secondly, the complete model, including all possible variables from the predictor matrix, was fitted. Thirdly, the permutation method was used to assess the statistical significance of both the final model as a whole, the individual constrained axes, and the predictor variables. The estimates were considered statistically significant at a critical level of significance  $p = 0.05$ . Finally, the results of CCA

were visualized by means of bi-plot combining the ordination of phenological events and predictors significant for the model.

### ***Relationship of the abundance of the species and its phenological indicators.***

It is well-known that the assessment of the correlation between population time series and external (density independent) parameters require some precautions: high correlations may appear even in the absence of any association between two time series (Royama, 1981, 1992). In this regard, more complicated approach is needed (Royama, 1992) so we used dichotomous nominal scale correlations between second derivatives (Royama, 1981, 1992) to identify the correlation between two time series.

The first stage of the analysis was to remove from abundance time series ( $\{X\} = \{\log(N+1)\}$ ) and from a series of dates of beginning-of-season ( $\{u\}$ ) their linear trends. It is necessary since the analysis require the stationarity of both time series. For this purpose we used not the raw data but the residuals from the linear models describing the relations of the values with time (see section about linear models).

The second stage is the analysis of the sign of the second derivative at each time point of the two time series. Both time series ( $\{X\}$  and  $\{u\}$ ) were divided into sliding local segments consisting of the three observation points  $X_{t-1}$ ,  $X_t$ ,  $X_{t+1}$  for a time series of abundances and  $u_{t-1}$ ,  $u_t$ ,  $u_{t+1}$  for the dates of the beginning of the season. If both segments at the points  $X_t$  and  $u_t$  were concave or both were convex (the sign of the second derivative is positive or negative, respectively), then this was considered to be a local coincidence of trends in two time series. If the signs of the second derivatives were different, then it was considered a mismatch. Next, the number of matches (p) and the number of mismatches (q) were calculated when the segments were shifted along the time axis. After that, the correlation coefficient was calculated by the following formula:

$$\delta = (p - q) / (p + q)$$

We did not evaluate statistical significance of the Royama's correlation coefficients but used these values only as indicators of the tendencies in correlations between time series.

## **Results**

### ***Seasonal dynamics: temperature and zooplankton species abundance***

Average temperature of the 0–25 m depth layer at the study site changed during year from  $-0.8^{\circ}\text{C}$  in February – April to  $10.7^{\circ}\text{C}$  in the beginning of August (Fig. 2). The winter lasted on average from the second 10-day period of December until the first week of May, when

the temperature of this layer rose above zero, thus indicating the beginning of a spring period. Timing of other events in temperature dynamics will be considered later.

The peak of *Calanus glacialis* abundance was on average observed in the end of May, in the beginning of the spring period (Fig. 2). The nauplii were the absolute dominants in the population at this moment. Juveniles of *C. glacialis* (generation of the analyzed year) peaked in the middle of June and disappeared from the 0–25 m depth layer by the end of July. Peak of *Pseudocalanus* spp. abundance was rather prolonged, with the “plateau” from the middle of May until the end of June. These species were present during the whole year. *Oithona similis* was registered year round and demonstrated several peaks in July–September. Narrow peak in the middle of June was characteristic for *Microsetella norvegica*, which was also present during the whole year. The first individuals of *Centropages hamatus* appeared normally in early June; the maximum abundance of this species was observed usually in the end of August. *Temora longicornis* developed synchronously to *Centropages*: the timing of their appearance and the abundance peaks coincided. They were first found in the plankton in the first 10 days of June; the peaks of their abundances were observed in the last 10 days of August. These two boreal species disappeared totally by the beginning of December. *Acartia* spp. had prolonged development season with several peaks in August and September, and was totally absent only in February.

Average dates of the key temperature thresholds and phenological events are present on the Fig. 3. The earliest of registered events in environment (Fig. 3B) was the timing of ice melt – it took place on average in the beginning of May (day 141). As it was mentioned before, spring normally started in the beginning of May according to temperature curve. However, the first key date in the seasonal temperature dynamics, that we could reliably register almost every year, was 3 °C threshold (arbitrary spring beginning). The latter was normally registered a month later, normally in the beginning of June (160-th day). Summer began only 2 weeks later, on 173-th day, and finished in the middle of October (day 287).

Species were ranged according to the timing of developmental season beginning. The season of *Pseudocalanus* spp. development started the earliest (middle of May, day 140). Then followed *Calanus* that had the narrowest developmental season (period between appearance of CI and disappearance of CIII from upper 25-meter layer). The latest season beginning was demonstrated by *Temora* (beginning of August, day 217). Narrow developmental seasons were characteristic for boreal species *Temora* and *Centropages* (39 and 36 days, respectively). The longest season was observed for ubiquitous *Oithona* (133 days).

### Long-term dynamics: phenology timing and species abundance

Long-term changes in phenology of the studied copepods demonstrated negative trends or were insignificant (Fig. 4). Only the end-of-season of *Oithona* tended to be later, but this trend was not significant.

Start of season of the three species has significantly shifted to earlier time: *Calanus* (by 25 days), *Temora* (23 days) and *Microsetella* (21 days). End of season of the following species significantly shifted to an earlier time *Pseudocalanus* (39 days), *Calanus* (15 days), and *Acartia* (19 days). Thus, the whole developmental season of *Calanus* shifted to an earlier time. Seasons of *Pseudocalanus* and *Acartia* have shortened, seasons of *Microsetella*, *Centropages* and *Temora* became longer.

The significant interannual fluctuations were the feature of the long-term dynamics of abundance of all the studied species (Fig. 4). The minimal and maximal values differed by an order of magnitude, which was characteristic for almost all species. However some long-term trends were noticed. Substantial increase of abundance of *Calanus* and *Microsetella* was revealed. Numbers of *Oithona* and *Acartia* decreased significantly. No significant trends were found in the abundance dynamics of *Pseudocalanus*, *Centropages* and *Temora*.

### Long-term dynamics: factors influencing phenology timing

Distinct long-term tendencies were revealed in the timing of the seasonal temperature dynamics (Fig. 5). Thus, dates of spring (SpSD) and summer beginning (SuSD) tended to shift to earlier time ( $b = -0.34$  and  $-0.45$ , respectively;  $p < 0.05$ ). This shift amounted to about 19 for spring and 27 days for summer beginning since 1961. These changes corresponded to the temporal shift of important indicator of the beginning of spring period – ice retreat (ICD,  $b = -0.39$ ), which occurred about 22 days earlier by the end of the study period. Summer end (SuFD) date has not changed significantly. However, hydrological summer duration (SuDur,  $b = 0.61$ ) increased by 35 days. Timing of the seasonal temperature peak (TPD) has not changed, in spite of pronounced fluctuations. Absolute values of temperature in spring (May-June, SpT,  $b = 0.04$ ) increased significantly during study period by about 3 °C. Increase of summer temperature (July-September, SuT) was weak and insignificant. Climatic index NAO also demonstrated significant tendency towards increase. Trend in the dynamics of AOI was not significant.

Some of the hydrological and climatic factors described above (SpT, AOI, SuDurPY, NAOPY and SpTPY) were not included in CCA since they displayed high variance inflation factor. All other environmental variables combined with abundance of species were included in the model of CCA as predictors.

The whole model was statistically significant (Table 1a) and explained 40.9% of total inertia taking into account all canonical axes. At the same time, only the first constrained axis was statistically significant (Table 1b). It accounted for 14.6% of total inertia. Only three predictors were revealed as significant: the end of summer in the previous year (SuFDPY), the abundance of *Acartia* and *Microsetella*.

The ordination of the phenological characteristics of species in the space of the first and second canonical axes is presented on Fig. 6. The date of the peak of *Microsetella* abundance (*Microsetella\_Peak*), the date of the middle-of-season of this species (*Microsetella\_Middle*), and the date of the end-of-season (*Microsetella\_End*) had maximum positive values on the first axis. Beginning-of-season, middle-of-season and date of abundance peak of *Oithona* had the highest negative values on the first axis (CCA1). Two predictors, *Microsetella* numbers and date of summer end in the previous year (SuFDPY) were correlated with the first axis. The first one correlated negatively, the second one, positively. The greater were abundance of *Microsetella*, the later tended to appear juveniles of *Oithona similis*. The earlier develops *Microsetella*, the greater was abundance of this species. Late end of summer in the previous year corresponded to later development of *Microsetella*, but earlier development of *Oithona*.

It is important to emphasize that the phenological events in *Oithona* and the phenological events in *Microsetella* occupy opposite positions along the CCA1, that is, the earlier the events in one species, the later the events in another.

We do not present here the association of phenological events with abundance of *Acartia* since the latter is correlated well only with the second canonical axis, statistical significance of which was not confirmed.

### ***Relationship of the abundance of the species and its phenological indicators***

No clearly expressed associations between species phenological events and their abundance have been found (Table 2). However, the correlation coefficients for two species (*Microsetella* and *Temora*) tended to be much higher than for all other species. The negative correlations indicate that the abundance of these species tended to be higher if the beginning of season shifted to earlier time. This tendency can also be traced in the dynamics of *Calanus*, though it was much weaker.

## **Discussion**



Significant trend in the long-term dynamics of the spring water temperature was detected at the study site, while summer temperature changed insignificantly, though slight tendency existed ( $\sim 0.03^{\circ}\text{C}$  per year). These changes correlated with the global trend towards warmer Arctic, when pronounced changes of temperature have been reported for many Arctic areas (ACIA, 2004; IPCC, 2013), and were higher than average for the Northern Hemisphere (Davy et al., 2018). Changes of the temperature may well be the consequence of the earlier seasonal spring warming of water: beginning of the spring and summer moved to an earlier time by about 3–4 weeks at the study site. It should be noted, that summer beginning shifted more (by 27 days) than start of spring (19 days), so spring duration decreased accordingly. Shift of spring beginning at the study site is confirmed by the documented shift of the ice retreat date in the adjacent areas of Kandalaksha Bay, which amounted 22 days by the end of study period. Similar trend for the timing of the ice retreat was documented in different areas over the Arctic during the last three decades (Ji et al., 2012).

Considerable change in seasonal temperature dynamics influences seasonal cycles of planktonic animals. The life-cycle events of Arctic, boreal and ubiquitous species advanced by up to a month and even more. The first copepodite stage of *Calanus glacialis* appeared 25 days earlier in the end of the study period compared to 1960s. It is reasonable to connect this shift to the advance of the seasonal water warming. However, it was shown that the start of *C. glacialis* reproduction depends more on the food availability than on the temperature (Ringuette et al., 2002). On the other hand, it is the temperature that governs the ice melting and, therefore, the timing of the phytoplankton bloom allowing more light penetrating through the ice and thus accelerating the production of ice and planktonic algae. Moreover, temperature influence phytoplankton photosynthetic activity later in the year, after light saturation of the upper water layer (Tilzer et al., 1986). Thus, the timing of the reproduction of *C. glacialis* depends on both food availability and temperature. The timing of *Calanus* juveniles' disappearance also has shifted to an earlier time, however by 15 days only (compared to 25 days for appearance timing). Thus, season of active early development of *C. glacialis* has shifted to an earlier time and increased by 10 days. One may expect that with earlier appearance and faster development *Calanus* juveniles must leave upper layer much earlier. Indeed, *Calanus* CIII stay below 10-m depth by the end of spring (our observations), thus escaping unfavorable thermal conditions, but remains in the layer 10–25 m. High concentrations of chlorophyll *a* are observed only to 10-m depth by this time (Usov et al., 2013). Therefore, the feeding conditions below this depth are not favorable by the time CIII leave surface layer, so this may cause the observed

development prolongation. It was shown that starvation increases the developmental time of *Calanus glacialis* nauplii and may even terminate it (Daase et al., 2011).

It was reported about the possible mismatch between the ice melt and *Calanus glacialis* reproduction in the Beaufort Sea and Svalbard, which may have a negative effect on the success of this species (Søreide et al., 2010; Daase et al., 2013). In high Arctic, an early ice melting and intensive warming of upper water layer may cause shortening of period between ice-algae and phytoplankton blooms (Søreide et al., 2010). The complete disappearance of ice in the study area also is registered almost a month earlier than in 1960s. It may lead to discrepancy between *Calanus* juveniles' development and the spring peak of the phytoplankton abundance, because reaching the first feeding naupliar stage (NIII) requires certain time to develop, this process may take longer than the period between the two blooms (Søreide et al., 2010). Unfortunately, we cannot either prove, or refute this for the White Sea population, since no long-term data on phytoplankton abundance are available by now. However, long-term positive trend of *Calanus glacialis* abundance points out that at least at this temporal scale there is no tendency to mismatch. Our findings are supported by the results of modeling temperature increase in Arctic (Feng et al., 2018). The authors argue that rising temperature leads to prolongation of the period of abundant phytoplankton, which leads towards increasing success of *Calanus glacialis* in Arctic Ocean. This can also be reasonable explanation of *Calanus* success in the White Sea, as well as relative success of *Pseudocalanus* populations (see below).

Time of appearance of *Pseudocalanus* spp. juveniles shifted by about 23 days. However, due to sharp fluctuations of the phenological index in the early 1970s and in the early 1990s, the changes were insignificant (Fig. 5). The end of the developmental season of *Pseudocalanus* spp. has shifted by almost six weeks (39 days), therefore, we can talk about the reduction of the season of active development of *Pseudocalanus* spp. Shrinkage of the *Pseudocalanus* spp. developmental season may be also consequence of the reduction of spring duration and early summer beginning. However, population of *Pseudocalanus* spp. demonstrated insignificant, but positive tendency. Taking into account the ecological similarity of *Pseudocalanus* spp. and *Calanus glacialis* in the White Sea and other regions (breeding dates and food preferences during the breeding season and early development; see: Lischka, Hagen, 2007; Falk-Petersen et al., 2009), the same conclusions can be drawn: a huge shift in the timing of the development of *Pseudocalanus* spp. does not lead to a noticeable trophic mismatch and population depression. Changes of temperature seasonal dynamics may be one of the drivers of the observed phenological shift and population increase. The negative shift of the center-of-gravity timing for *Pseudocalanus* species was noted in the central part of the North Sea, which

coincided with a positive trend in the dynamics of the average annual water temperature at the sea surface (Mackas et al., 2012 and references therein).

The trends of phenology of the boreal *Centropages hamatus* and *Temora longicornis* were consistent with the changes of the seasonal cycle of temperature. The latter is one of the main triggers of their hatching in the White Sea (Pertzova, 1990) and other areas, such as the northern Baltic Sea (Katajisto et al., 1998; Katajisto, 2006). The temperature increase either induces hatching (Pertzova, 1990) or shortens egg developmental time (Katajisto et al., 1998). Thus, shift of spring warming might influence the timing of hatching of these species in the White Sea. Other boreal species, *Acartia* spp., demonstrated no shifts of the beginning of the developmental season. According to our observations (Fig. 2), adults of *Acartia*<sup>1</sup> were found in the plankton all year round, and the increase in their abundance began in March, under the ice. This suggests that *Acartia* depends on temperature to a lesser extent than *Temora* and *Centropages*. Tendency for the earlier development of boreal species was observed in other areas of the World Ocean. The timing of the appearance of the thermophilic *Acartia tonsa* in Narragansett Bay (West Coast of USA) in plankton shifted to an earlier time during period from 1972 to 1990, which coincided with a significant increase in spring temperature (Borkman et al., 2018). Approximately in the same period (from 1974 to 2004), the timing of the middle of the season (time of the 50% of the annual cumulative abundance threshold) of *Temora longicornis*, *Acartia* spp., and *Temora* nauplii near the Helgoland Island in the North Sea has shifted to an earlier dates by 2.5 to 4 weeks (Mackas et al., 2012). In this case, changes in phenology coincided with an increase of average annual and summer (June-August) temperatures.

Of the two studied ubiquitous species, only the trend in dynamics of beginning-of-season of *Microsetella norvegica* was significant. The phenology of *Oithona similis* did not show significant changes. The described differences can be explained by the fact that the reproduction of *Microsetella* begins only in June (our own data), despite its presence all year round in the plankton community. At the same time, the nauplii of *Oithona* are found in plankton throughout the year. Probably, the temperature is not the main trigger of the beginning of the active development of this species. This is indirectly confirmed by its cosmopolitan distribution (OBIS, 2019). Meantime, a significant shift of the middle-of-season to an earlier dates in the seasonal dynamics of *Microsetella* spp. (15 weeks) and *Oithona* spp. (~4 weeks)

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<sup>1</sup> Most likely, this is *A. longiremis*, one of the two species inhabiting the study area, which differs by its neritic distribution from *A. bifilosa* characterized by living in the coastal and estuarine areas (Prudkovsky, 2003).

has been reported near Helgoland Island, and these changes coincided with an increase in average annual and summer temperatures (Mackas et al., 2012). The same trend to an earlier season was traced in the dynamics of *Oithona* spp. in the English Channel (Mackas et al., 2012). A similar dependence was observed in the northern part of the Pacific Ocean, where the seasonal peak of the biomass of the interzonal copepod *Neocalanus plumchrus* has shifted since the early 1970s by more than a month earlier, which coincided with an increase in spring temperature (Mackas et al., 2012). The timing of the abundance peak of *Calanus finmarchicus* CI in the Norwegian Sea was negatively associated with the temperature in April, but the long-term trend was not traced, despite its presence in the dynamics of the water temperature in April (Mackas et al., 2012). In the same study, there was a lot of evidence of the negative connection of spring temperature with the phenological events of different species in the North Atlantic and the North Pacific. As can be seen, the pattern “the warmer the earlier” was traced in different regions of the World Ocean and for species with different temperature preferences. This is consistent with the trends observed in the study area in the White Sea.

Abundance of studied species either has not changed significantly (*Pseudocalanus*, *Centropages*, and *Temora*), or increased (*Calanus* and *Microsetella*), or decreased (*Oithona* and *Acartia*) during the whole study period. Only in the case of *Acartia* spp., its abundance decrease coincided with significant reduction of developmental season duration, the same has been found for *Pseudocalanus* spp., which, however, has not affected negatively the abundance trend of the latter. No such season reduction was observed in dynamics of *Oithona similis*. When looking on the year-to-year temporal scale, significant relationship between abundance and the start-of-season timing has been revealed for *Microsetella* and *Temora*. Both correlations were negative, which indicated that the abundance of both species tended to be higher during the years characterized by early beginning of the developmental season. However, even these significant correlations were not high enough to speak about any strong cause-and-effect relationships. Thus, the majority of studied species are resilient to observed phenological changes at the long-term temporal scale.

A synchronization of the timing of the main events in the life cycles of cold-water species with changes in the environment may serve as one of the mechanisms of the resilience of the planktonic copepod populations to phenological shifts. Such synchronization was reported for phytoplankton in Arctic (Ji et al., 2012): planktonic algae developed earlier with earlier ice retreat.

Omnivory may be the alternative mechanism of resilience. Planktonic Copepoda consume heterotrophic plankton (microzooplankton) actively when suitable phytoplankton

becomes deficient, which was found in other regions, in experiments and for related species (Levinsen et al., 2000; Lischka, Hagen, 2007; Fileman et al., 2010). The ability of many animals to switch to other food objects in conditions of the food shortage, or to be potentially omnivorous, is widely reported (Saiz, Calbet, 2011; Kiørboe, 2011; Benedetti et al., 2016; Brun et al., 2017). This ability may support *Calanus* and *Pseudocalanus* population success in the changing environment of the White Sea. These hypotheses may well apply to other species, demonstrating resilience to phenological changes, which will be discussed further.

The opposite trends in dynamics of *Oithona* and *Microsetella* abundance deserve special attention, because trophic niches of these species overlap. Moreover, *Oithona* demonstrated slight tendency since 1960s to finish season later as opposed to *Microsetella*, which tended to finish season earlier. This points out to some competitive relationships between these species, and is confirmed on the year-to-year level by the results of CCA analysis. We found that the timing of events in the *Oithona* and *Microsetella* seasonal cycles changes in the opposite directions at the year-to-year scale: the earlier phenological events of one species, the later events of another. This is at least partly consistent with results of long-term trend analysis. This relationship may be explained by the fact that these two species have similar food preferences (González, Smetacek 1994; Maar et al., 2006) and may compete for food. Both species, *Oithona similis* (Cyclopoida) and *Microsetella norvegica* (Harpacticoida), are omnivorous: they feed on detritus aggregates; *O. similis* also consumes microzooplankton (Paffenhöfer, 1993; Green and Dagg, 1997; Maar et al., 2006). Normal course of seasonal succession allows co-occurring species to reduce competition by partitioning resources through time, when they occupy different *temporal* niches (Pau et al., 2011). Phenological shifts may result in temporal overlaps between species with similar trophic preferences and affect competitive relationships (Nakazawa, Doi, 2012; Borkman et al., 2018). The overlapping of the trophic niches is aggravated by the high abundances of *Microsetella* and *Oithona* in the study area and the significant intersection of the temporal niches (Fig. 3). It appears that interspecific interactions play an important role in the seasonal dynamics of these two species. It should also be noted that the timing of phenological events in the *Microsetella* seasonal cycle is negatively related to its population size in the same year. In other words, the later the developmental season of his species begins, the lower its abundance. Probably, when *Microsetella* appears late, it does not have time to achieve high abundance before the mass development of the competitor, *Oithona similis*. However, the earlier *Microsetella* appears in the plankton, the greater the abundance it reaches, gaining a competitive advantage over *Oithona*, which in such years develops later than usual. It has been found earlier that in the White Sea nearly every

zooplankton species occupies temporal niche according to its temperature preferences and this was confirmed within the present study (Figs. 2, 3; Zubakha, Usov, 2004). For sure, almost all the temporal niches overlap; however, signs of competitive relationships were found only for two ubiquitous species mentioned above. Therefore, one can conclude that some other traits of studied species help them to avoid competition. This need to be analyzed more thoroughly, although being beyond the aim of our present study.

## Conclusions

The global climate change is manifested in the White Sea through temporal shift of the seasonal temperature cycle. The spring water heating has shifted since 1961 towards an earlier time: spring beginning shifted by 23 days and summer beginning, by 29 days. This shift influences seasonal cycle of planktonic organisms. Key events of the life cycles of both cold- and warm-water copepods in the coastal area of Kandalaksha Bay of the White Sea have moved to an earlier time by up to a month. Main factors, which drive these shifts, are advance of ice melt and advance of spring water heating. For ubiquitous and boreal species, interspecific competition for resources plays an important role: in the years when the abundance of *Microsetella* is high, the key events in the *Oithona* seasonal cycle tend to occur later. The same relationship was revealed at the scale of long-term trends: end-of-season and abundance of these two species changed in the opposite directions. Period of active development of *Pseudocalanus* and *Acartia* has shortened. Revealed temporal shifts of phenological events had almost no effect on the abundance of the studied species at the scales of long-term trends and year-to-year fluctuations. Only the abundance of *Acartia* spp. demonstrated tendency to decrease with shortening of developmental season. Opposite, the abundances of both *Microsetella* and *Temora* tended to be higher in years with early beginning-of-season. This point out to the resilience of planktonic organisms to changes in seasonal cycles of environmental variables. Several mechanisms may underlie this resilience. First, organisms may synchronize key events in their life cycles with dynamics of environmental parameters. Second, to overcome temporal mismatch with feeding objects, planktonic copepods may switch their food preferences from herbivory to carnivory according to situation in plankton (presence/absence of suitable food), because the majority of Copepoda, at least at the study site, are potentially omnivorous. Third, the success of the cold-water species depends to some extent on the duration of the period of ample phytoplankton, because these species are predominantly herbivorous. These conclusions were made based on the long-term observational data, and need to be verified experimentally, where possible. Other factors, potentially important for planktonic animals but overlooked

during monitoring, and their interactions with each other should be analyzed. We suppose this to be the focus of our further scientific efforts.

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### Figure captions

Figure 1. Map of the study area. Sampling site is indicated (D-1 Station).

Figure 2. Seasonal dynamics of temperature and species abundance at the D-1 station (data for the period 1961–2018). Long-term means of total population numbers in the layer 0–25 m for each 10-day period are shown. Error bars indicate standard errors of means.

Figure 3. Seasonal succession of the key events in the environment (A) and in the life cycles of the studied species (B). ICD – ice clear date; SpSD – spring start date (the day when the water warms up to 3 °C); SuSD – summer start date (the day when the water warms up to

5 °C); TPD – date of seasonal temperature maximum; SuFD – date of summer end (the day when the water cools down to 5 °C). "Begin" – beginning-of-season; "Middle" – middle-of-season; "Peak" – peak timing; "End" – end-of-season. Horizontal line refers to median. The box margins refer to the 25th (lower) and 75th (upper) percentiles. Vertical lines refer to 1.5 IQR (inter-quartile range, or distance between the first and third quartiles).

Figure 4. Long-term changes in the timing of phenological events (beginning-of-season (A) and end-of-season (B)) and the dynamics of the total numbers of their populations in the layer 0-65 m (C). Abundance is given as ind./m<sup>3</sup>. The straight line represents the linear model connecting phenological indices and abundance with time. Numbers above the regression line are the slope coefficient of the model and the adjusted level of significance for the Mantel correlation (see Materials and Methods for details).

Figure 5. Long-term changes in the timing of seasonal events in the environment. ICD – ice clear date; SpSD – spring start date; SuSD – summer start date; TPD – date of seasonal temperature maximum; SuFD – date of summer end; SuDur – summer duration; SpT – mean spring temperature; SuT – Mean summer temperature; NAO – North Atlantic oscillation index; AOI – Arctic oscillation index. Meaning of lines and numbers – see Figure 4.

Figure 6. Ordination of phenological characteristics of species in constrained axes of CCA. Large points correspond to the phenological indicators that have absolute values on the first axis outside the 2-nd quartile. The arrows indicate the significant predictors included in the model. Microsetella\_N – Microsetella abundance, Acartia\_N – Acartia abundance, SuFDPY – end of summer in the previous year.



Figure 1

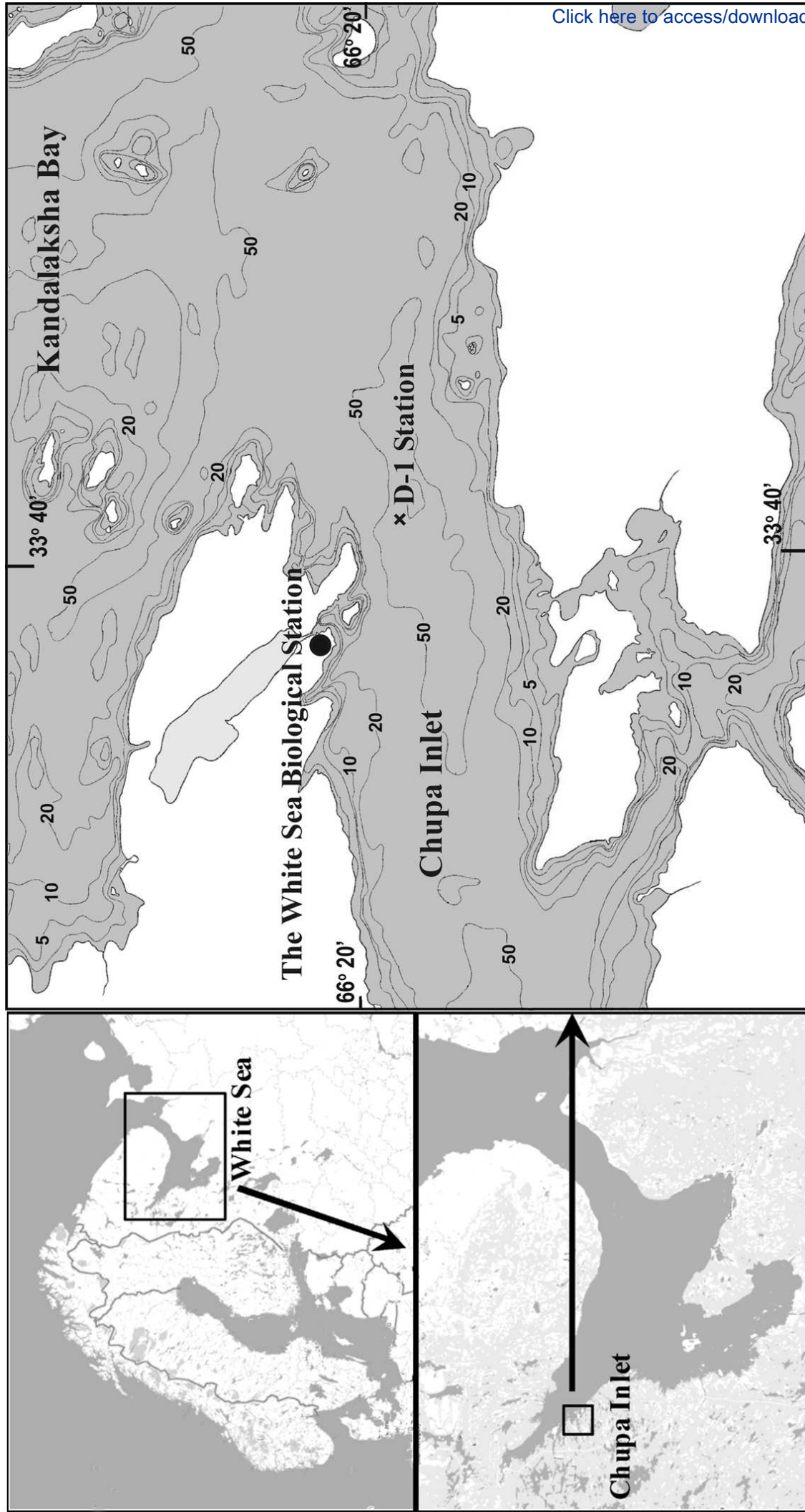
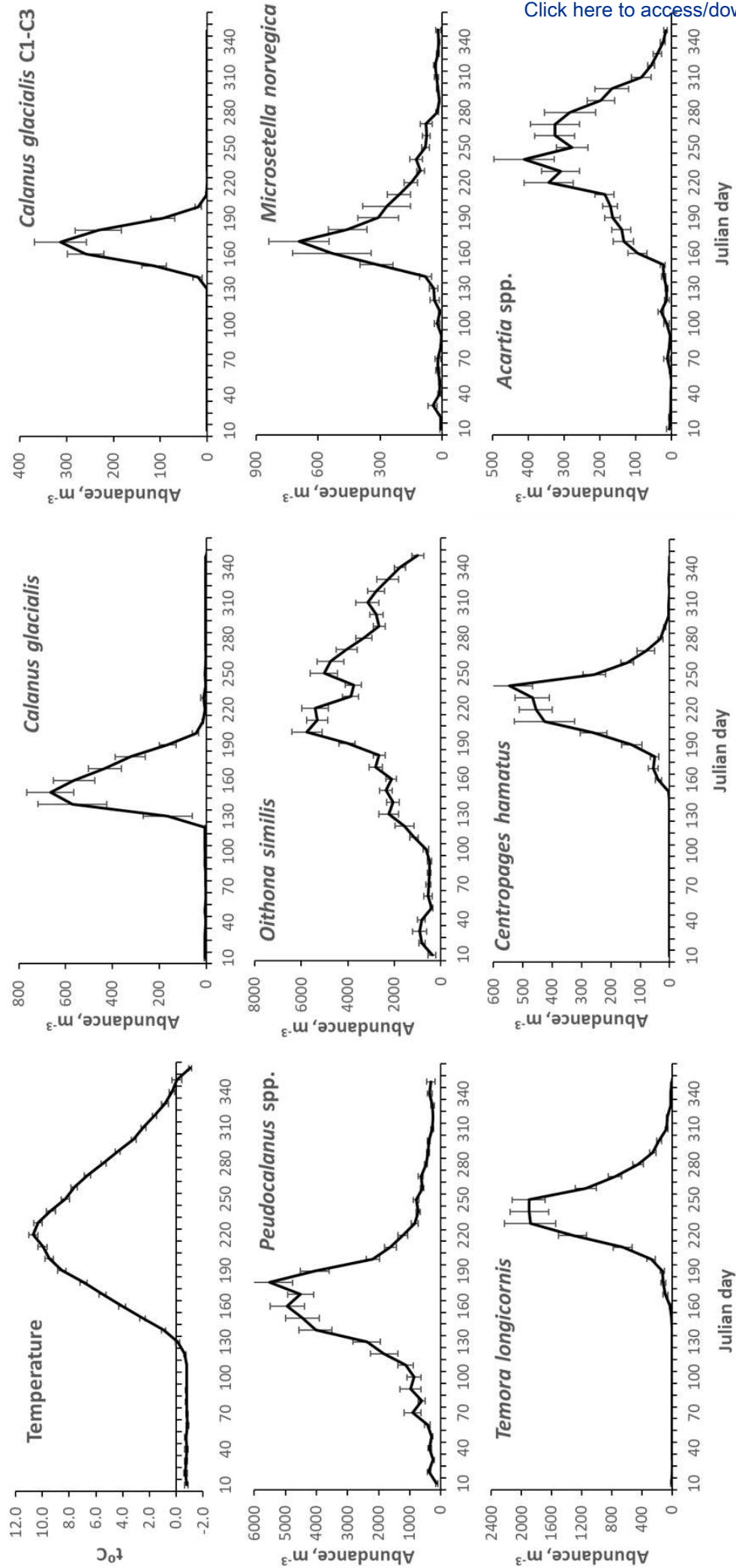


Figure 2



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Figure 3

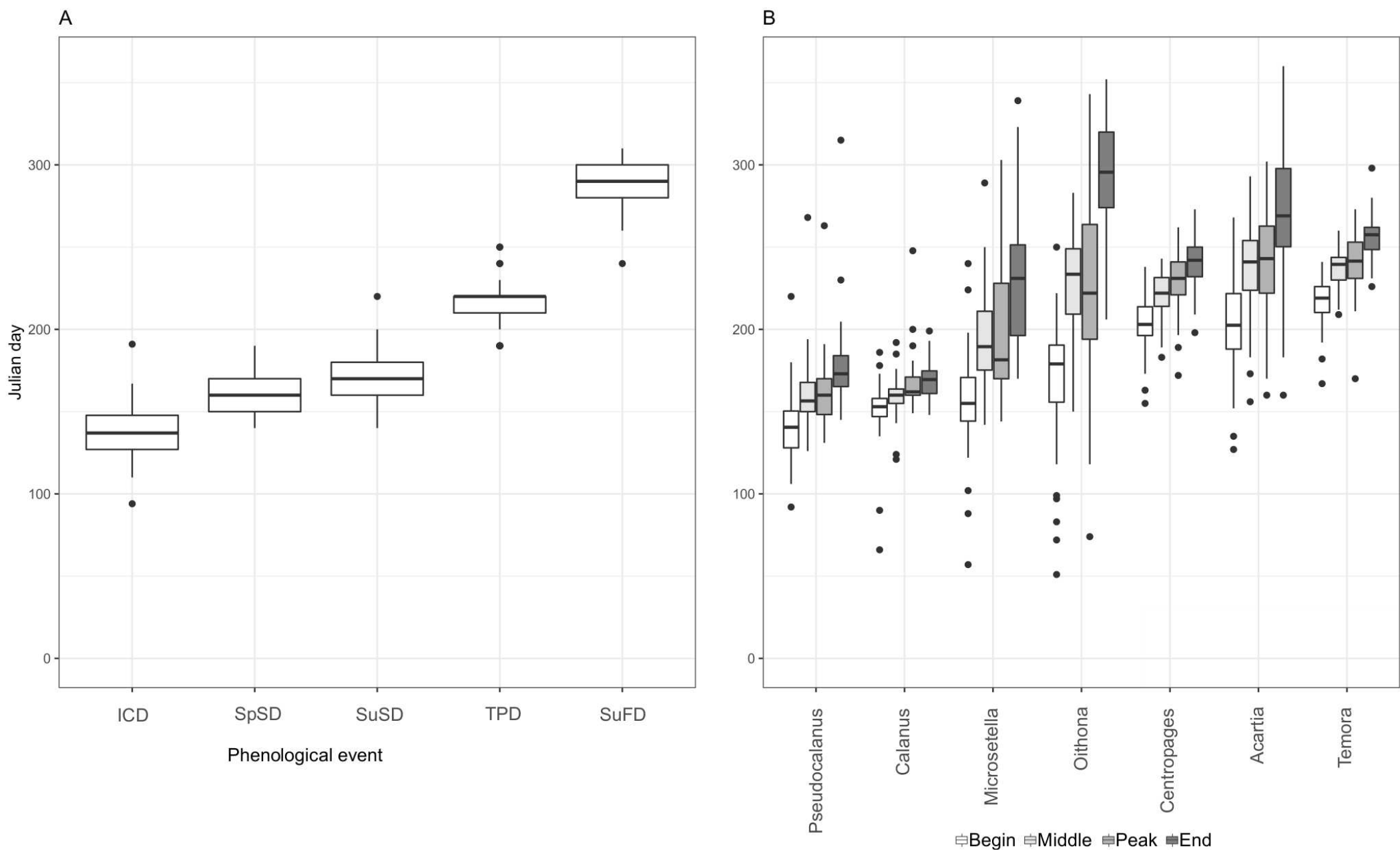


Figure 4

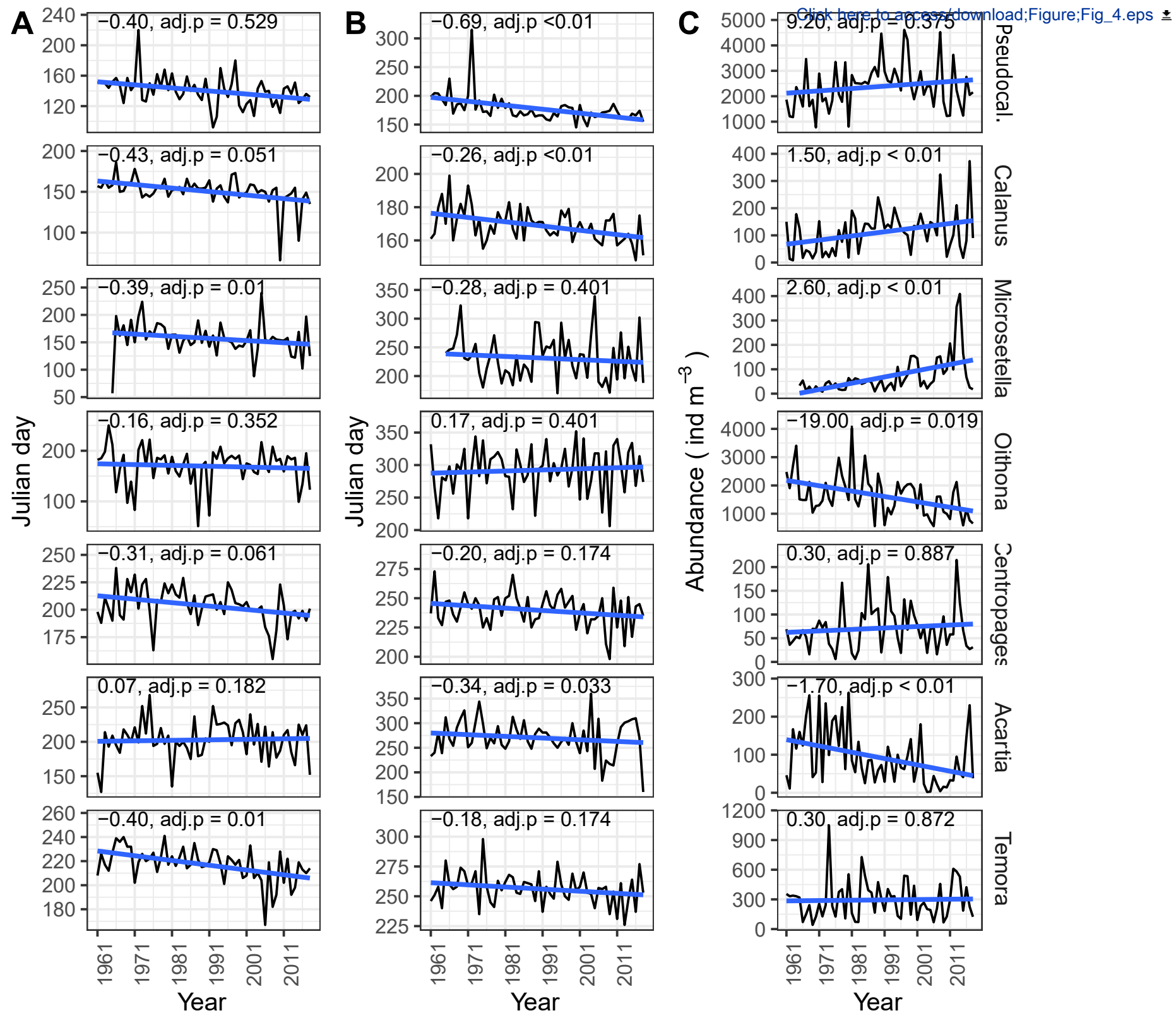


Figure 5

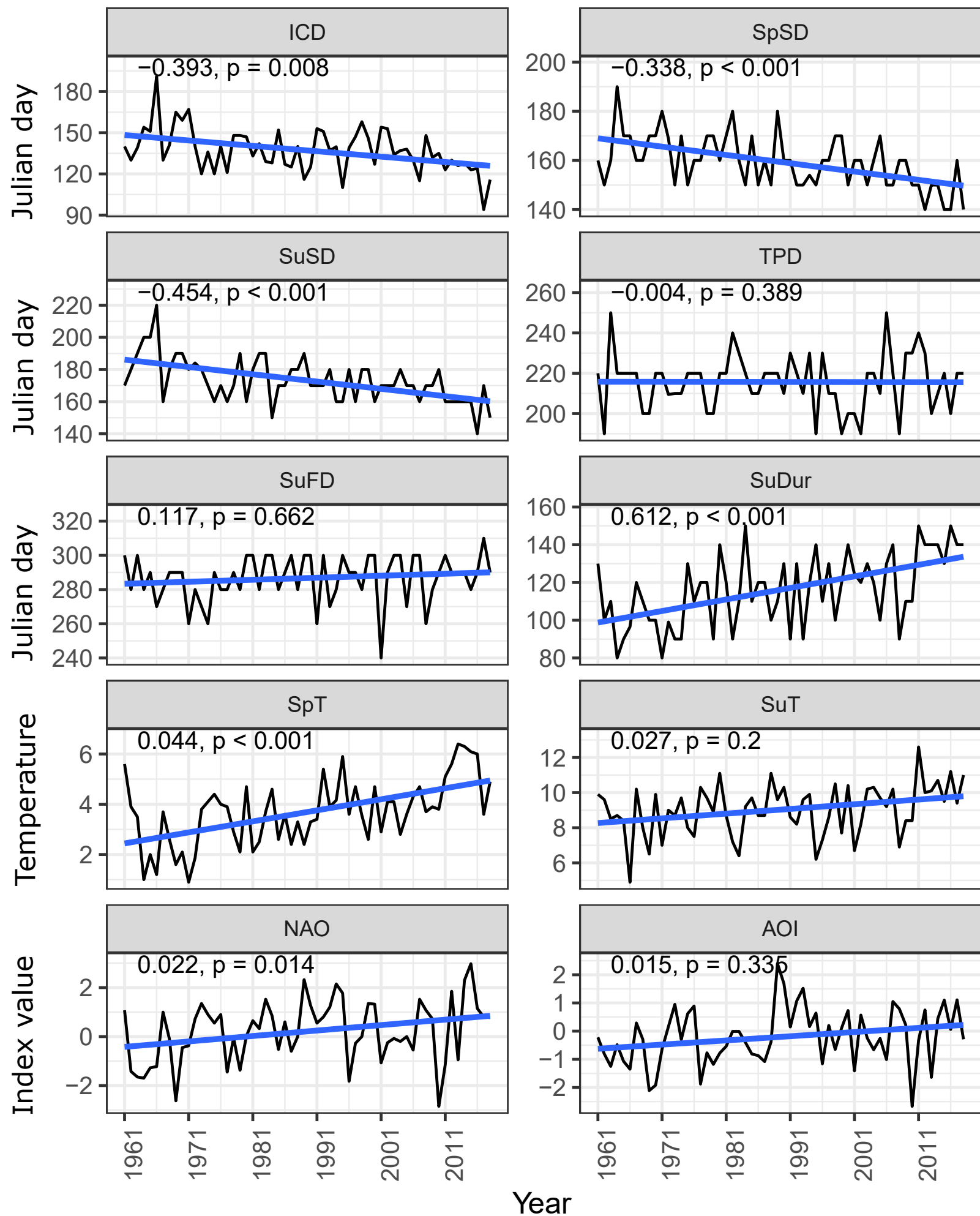
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Figure 6

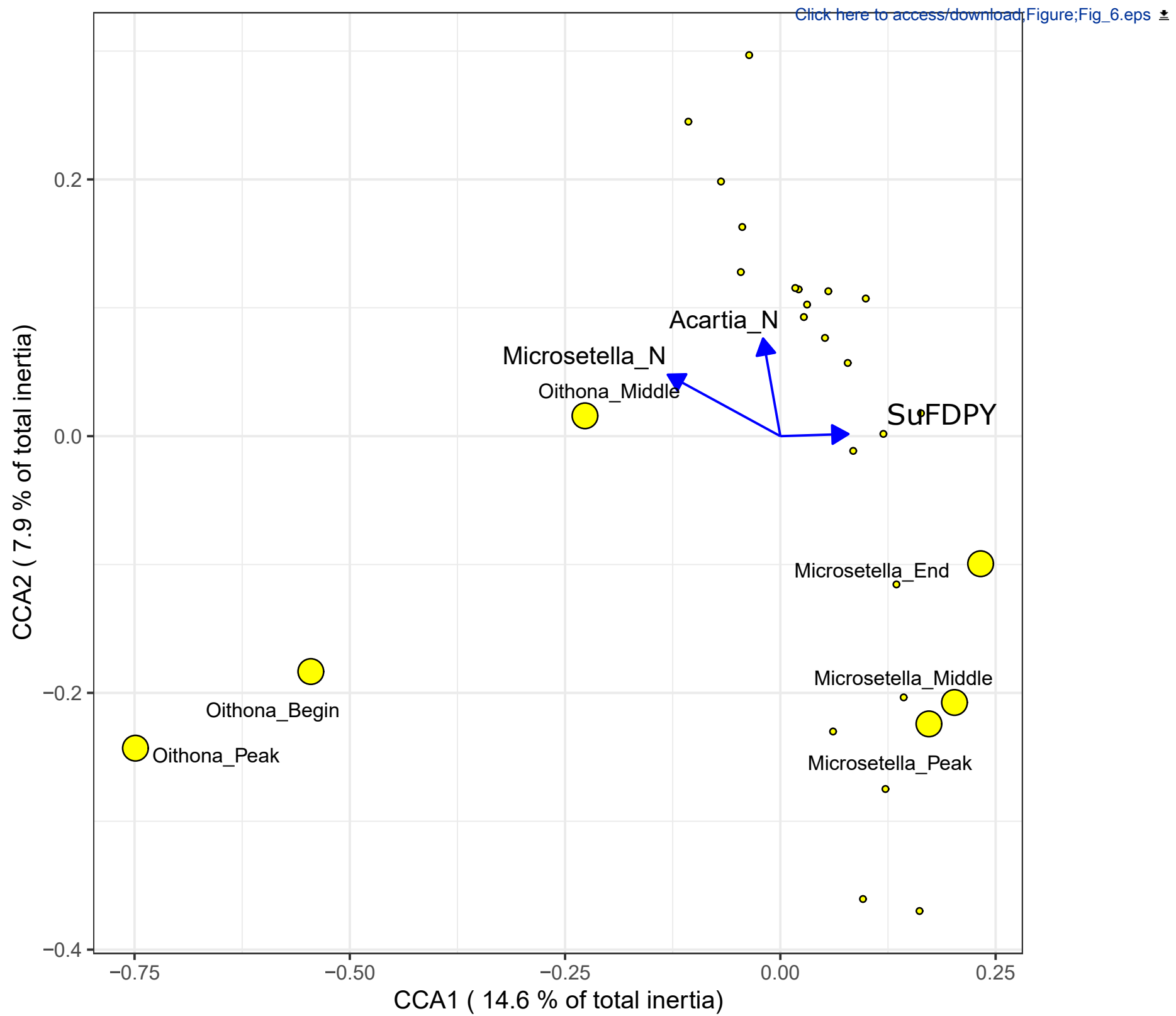


Table 1. Estimation of the significance of the CCA model. Microsetella\_N – Microsetella abundance, Acartia\_N – Acartia abundance, SuFDPY – end of summer in the previous year. Only significant results are given.

a) Permutation significance test of the final CCA model				
Term	<i>df</i>	<i>ChiSquare</i>	Statistic	<i>p</i> -value
Model	18	0.005	1.345	0.021
Residual	35	0.008		
b) Permutation significance test of CCA constrained axis				
term	<i>df</i>	<i>ChiSquare</i>	Statistic	<i>p</i> -value
CCA1	1	0.002	8.620	0.027
Residual	35	0.008		
c) Permutation significance test of terms included in the CCA model				
term	<i>df</i>	<i>ChiSquare</i>	Statistic	<i>p</i> -value
SuFDPY	1	0.0006	2.658	0.013
Acartia_N	1	0.0004	2.104	0.041
Microsetella_N	1	0.0005	2.458	0.017
Residual	35	0.0075		

Table 2. Correlations between start-of-season date and species abundance. Dichotomous nominal scale correlation coefficients are presented (for computational approach see methodological section).

Species	Correlation
<i>Pseudocalanus</i>	0.04
<i>Calanus</i>	-0.11
<i>Oithona</i>	0.04
<i>Centropages</i>	0.00
<i>Acartia</i>	0.04
<i>Temora</i>	-0.50
<i>Microsetella</i>	-0.42