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Phenological Response of Arctic and Boreal Copepods in the White Sea to the Climate Change --Manuscript Draft--

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Abstract:	<p>Climate change-derived temperature rise has been proved to be the most intensive in the high latitudes. However, absolute temperature increase is not the only sign of changing climate, which 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). The timing of spring warming (3-5 °C thresholds) in layer 0-25 m has shifted to an earlier time by 18-28 days since 1961. During this period, the hydrological spring duration decreased by 10 days, and summer duration increased by 30 days (from 104 to 134 days). We expect these changes to influence the timing of the phenological events in the life cycles of cold-water (<i>Calanus glacialis</i>) and warm-water (<i>Temora longicornis</i> and <i>Centropages hamatus</i>) copepod species. Indeed, the timing of the first copepodite stage appearance of all the studied copepod species has shifted to an earlier time during 1961-2015 period. Specifically, it was 22 days for <i>Calanus</i>, 33 days for <i>Centropages</i>, and 41 days for <i>Temora</i>. These changes did not have any effect on the population abundance dynamics of these organisms, which means that observed phenological changes have not caused the deterioration of trophic conditions, or the trophic mismatch, which was documented in some other regions. Our results demonstrate resilience of the zooplankton community to phenological shifts in a pelagic ecosystem of the coastal region of subarctic sea.</p>	
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Phenological Response of Arctic and Boreal Copepods in the White Sea to the Climate Change

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Abstract

Climate change-derived temperature rise has been proved to be the most intensive in the high latitudes. However, absolute temperature increase is not the only sign of changing climate, which 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). The timing of spring warming (3–5 °C thresholds) in layer 0–25 m has shifted to an earlier time by 18–28 days since 1961. During this period, the hydrological spring duration decreased by 10 days, and summer duration increased by 30 days (from 104 to 134 days). We expect these changes to influence the timing of the phenological events in the life cycles of cold-water (*Calanus glacialis*) and warm-water (*Temora longicornis* and *Centropages hamatus*) copepod species. Indeed, the timing of the first copepodite stage appearance of all the studied copepod species has shifted to an earlier time during 1961–2015 period. Specifically, it was 22 days for *Calanus*, 33 days for *Centropages*,

and 41 days for *Temora*. These changes did not have any effect on the population abundance dynamics of these organisms, which means that observed phenological changes have not caused the deterioration of trophic conditions, or the trophic mismatch, which was documented in some other regions. Our results demonstrate resilience of the zooplankton community to phenological shifts in a pelagic ecosystem of the coastal region of subarctic sea.

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

Introduction

Climate change, manifested through the temperature rise, has been proved the most intensive in high latitudes, especially in the Northern Hemisphere (Richardson, 2008; Wassmann et al., 2010). High latitudes are also characterized by the pronounced seasonality. As a result, two main factors influencing marine ecosystems can be distinguished here: the temperature itself and a timing of seasonal warming/cooling. Populations of planktonic organisms are very sensitive to climatic fluctuations because of short life cycles, when the environmental changes affect them rather quickly. Many planktonic organisms inhabit the upper water layer of the Ocean, which is the most sensitive to the climatic fluctuations. Plankton is an indispensable component of marine ecosystems, in all trophic webs, in all the seas and oceans. Therefore, any changes in zooplankton abundance or in the timing of phenological events in zooplankton may lead to changes along the entire food chain. This stresses the importance of observations of quantitative and phenological changes in plankton.

The White Sea is a semi-enclosed sub-Arctic basin, so the large-scale climatic changes in the Arctic region influence this sea directly. The White Sea has pronounced continental

features, which are the long cold winter and relatively warm summer (Berger et al., 2001; Filatov et al., 2005). The sea is covered with ice during the winter period for 4–6 months depending on the year (Babkov, 1982; original data). Consequently, the temperature is characterized by a significant variability in the upper 25-meter water layer: near shore surface waters warm up to 20 °C in summer and cool down to -1.5 °C in winter (Berger et al., 2001; Usov et al., 2013). The seasonality of the underwater irradiance and the temperature regime, pronounced greatly at these latitudes, governs the annual cycle, or timing of the phyto- and zooplankton production. Thus, one can expect that the climate change influences not only absolute values but also timing of different events during seasonal cycle.

In the present study, we focus on the abundant arctic and boreal planktonic copepods of the White Sea. Arctic copepod *Calanus glacialis* is a keystone species in the White Sea; it is a main food source for juvenile and adult herring (Troshkov and Slonova, 2000). *C. glacialis* prefers the ice algae and phytoplankton, but consumes also non-phytoplankton items (Levinsen et al., 2000). *Centropages hamatus* and *Temora longicornis* are the most abundant boreal copepods in the White Sea (Martynova et al., 2009; Martynova et al., 2011). They are omnivorous, but prefer phytoplankton, at least in the White Sea (Martynova et al., 2011). Therefore, primary production rates and timing are important for all these species.

In high latitudes, temperature may influence primary production in two ways. First, indirectly, when the temperature rise in spring causes the snow and ice melt, allowing more light penetrating through the ice and thus accelerating the production of ice and planktonic algae. Temperature influences phytoplankton production also directly after ice melts and light in upper water layers has reached saturation (Tilzer et al., 1986). Spring phytoplankton bloom is considered to be the main trigger of *C. glacialis* reproduction and its early stages recruitment (Ringuette et al., 2002); however, the algal bloom depends not only on light cycle and micronutrient concentration, but also on temperature cycle during ice-free period (Tilzer

et al., 1986). Thus, the reproduction and the early development of the arctic species *C. glacialis* depend to some extent on the timing of the spring warming. The developmental time shortens with rising temperature, which reduces the risk to be eaten by visual predators in the upper water layers (Ringuette et al., 2002). Thus, climate changes, such as faster seasonal temperature rise and earlier spring, may result in the increase of the survival rates of this species and, finally, in the increase of its abundance. This event is supposed to take place in the White Sea, where early reproduction of *C. glacialis* tends to coincide with high numbers of this species in the same years (Usov et al., 2013). However, the changes in the seasonal temperature cycle may lead also to the mismatch between *C. glacialis* physiological readiness to reproduce and phytoplankton bloom (Atkinson et al., 2015), which may cause the decrease of the species abundance, bringing to nothing the population consequences of the temperature increase.

Boreal species, which are present in the plankton communities in the White Sea predominantly in summer, depend primarily on the temperature, because their hatching from the dormant eggs here is triggered by the temperature increase (Pertzova, 1990). In addition, the abundance of the boreal species in the White Sea depends on temperature in the beginning of summer season (Martynova et al., 2011). Therefore, the timing of the water warming during the season may influence the timing of the phenological events and the average abundance of these species.

The long-term changes of the timing of water warming and phenological events in the seasonal cycles of the arctic (*Calanus glacialis*) and boreal (*Centropages hamatus* and *Temora longicornis*) copepod species in the coastal region of the White Sea have been studied for the period of 1961–2015. This dataset has also been used to search for the influence of the temperature changes on the phenology and abundance of these species, as well as to assess the effects of the long-term phenological changes on their abundance.

97

98 **Materials and methods**

99 *Sampling site and the period of observations.* Water temperature, water salinity, and
100 the zooplankton abundance have been monitored in Chupa Inlet (Kandalaksha Bay, the White
101 Sea), at the standard station D-1 (65 m depth; 66°19'50"N; 33°40'06"E) since 1957; regularly,
102 since 1961 (Fig. 1). Data from this monitoring are recorded in the database "White Sea
103 Hydrology and Zooplankton Time-Series: Kartesh D1"
104 (<https://www.st.nmfs.noaa.gov/copepod/time-series/ru-10101>); this dataset was used as the
105 data source in this study. The period from 1961 to 2015 was used for the data analyses. Some
106 gaps in the observations occurred during the periods of the ice formation and melting.

107 *Sampling scheme and methods.* Monitoring was conducted from research vessel
108 during ice-free period and from the ice in winter. Zooplankton sampling was performed every
109 ten days during the ice-free period and monthly from the ice, except for the period of 1962–
110 1969, when the sampling was performed every ten days all the year round. The zooplankton
111 was sampled from standard water layers (0–10 m, 10–25 m, and 25–65 m) using a standard
112 Juday net (mesh size 200 µm; mouth diameter 37 cm). In total, more than 3400 samples have
113 been collected and processed since 1961. The samples have been immediately preserved with
114 formaldehyde (final concentration 4%). The sample processing was performed by the
115 standard methods (Harris et al., 2000). Briefly, the samples were concentrated to 100-mL or
116 200-mL volume according to the organisms' concentration assessed visually, and the three 1-
117 mL aliquots were taken using a Hensen stempel pipette from concentrated sample to count the
118 abundant species and their stages; large and rare species were counted individually for the
119 whole sample. Animals were identified to the species or genus level, benthic species larvae
120 were determined up to the phylum, class or infraclass. Developmental stages of the copepod

species were determined to nauplii, CI–CV copepodites, and mature specimens of CVI, i.e. males and females. Copepodite stages of the small copepod species, including *Centropages hamatus* and *Temora longicornis*, were combined at counting as “juveniles” (CI–CII) and “copepodites” (CIII–CV.) The abundance was expressed as a number of individuals per one cubic meter (ind. m⁻³).

Hydrological data was collected in parallel to the zooplankton sampling. During the period of 1961–2006, the water temperature was measured by reversing thermometers mounted on a bathometer BM-48 at 0-m, 5-m, 10-m, 15-m, 25-m, 50-m depths and near the bottom (63–65 m) or by bathythermograph GM7-III. Water conductivity was measured by the conductometer GM-65M (USSR), and the water salinity was calculated according to standard method (Tenth report..., 1981). Since 2006, the water temperature and salinity have been measured by CTD probe MIDAS 500 (Valeport Ltd.) on continuous profiles from surface to bottom. In order that recently received data correspond to measurements made before we started using CTD, we averaged CTD-readings for layers 0–10, 10–25, and 25–65 m.

Hydrological seasons. The hydrological seasons were defined after Babkov (1985) for 0–25 m water layer with some modifications in compliance with peculiarities of zooplankton phenology. 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 water temperature exceeds +5 °C. This value corresponds to the upper limit of the optimal temperature range of cold-water zooplankton species (Zubakha and Usov, 2004). The duration of the hydrological seasons in each year were calculated separately according to the temperature curve. Only spring and summer periods have been considered into analysis, these are the periods when the reproduction of studied species takes place.

Studied species. Three species of planktonic Copepoda were chosen for the analysis: arctic *Calanus glacialis* Jaschnov, 1955, and two boreal species, *Centropages hamatus* (Lilljeborg, 1853) and *Temora longicornis* (Müller, 1792). Cold-water *C. glacialis* has temperature optimum at 4.1 °C with range of –0.39–4.86 °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). Warm-water *C. hamatus* and *T. longicornis* have similar temperature optimums: 10.5 and 9.5 °C, respectively; they produce 2–3 generations during a year (Prygunkova, 1974; Pertzova, 1990). These species overwinter as the dormant eggs, which hatch in the late spring–beginning of summer (June–July; original data).

Data processing. The 10-day values and seasonal averages of the water temperature and zooplankton/species/stage abundance in 0–25 m water layer were used in analysis. The reason is that this layer lies above seasonal thermocline (10–25 m), and here the major part of organic carbon is produced in the White Sea (Prygunkova, 1974; Pertsova, 1980). Zooplankton abundance in the 0–25-m layer was used in analysis, because it is the layer where the reproduction and early development of the studied species take place. Samples were not always taken exactly on each 10th day, but with 1–3 days shift, so the dates of sampling in each year referred to the nearest “standard date”. The dates were expressed as Julian days.

Several phenological indices and seasonal events were defined and calculated. Spring beginning was the date when average temperature in layer 0–25 m reached 3 °C threshold. Unfortunately, 0 °C threshold fell on the period of ice melting, when the work was technically impossible neither from ice nor from boat or ship. We defined also 4 °C threshold in each year to follow spring temperature dynamics, because duration of intervals between each threshold can change from year to year. Summer beginning corresponded to 5 °C threshold.

Spring duration, determined using Babkov method (see above), corresponded to a period between the dates of 3 °C and 5 °C thresholds. Summer duration was the period between two 5 °C thresholds (spring increase and autumn decrease of the water temperature). The timing of appearance of *Calanus glacialis* was determined as appearance of the first copepodite stage (CI), because nauplii appeared mostly during period of ice melting, the period of the most gaps in the data. The dates of disappearance of the third copepodite stage (CIII) were also considered for this species. *C. glacialis* starts to leave upper water layer at the CIII stage, as water temperature rises, and continues development to CIV stage in deep layers (beneath 25 m in this part of the White Sea). Then, at the CIV stage, this species arrests development until the next spring (Prygunkova, 1974; Kosobokova, 1999). Here, we do not include the CIV into the calculations, because it is hard to define if these specimens are of the new generation, or of the previous year. The period between CI appearance and CIII disappearance from 0–25-m water layer was considered as a season of active development for this species. Start of season for boreal species was determined as timing of appearance of CIII–CV copepodites, because these stages are caught most reliably by the net used in the sampling (200- μ mesh size). The abundance of 10 ind. m^{-3} was set as the threshold abundance, i.e. as the indicator of the start of population development, in order to avoid in the analysis the unpredictable abundance fluctuations that might take place early in the year. For the same purpose, the first and a very short seasonal peak of *C. hamatus* and *T. longicornis* abundance, which occurred in some years, was not considered. A rather long period of almost zero abundance between this peak and the main developmental season existed almost each year. The period of presence of CIII–CV of the two boreal species in pelagial was accepted as a conventional indicator of their developmental period.

Statistics. Variables' frequency distributions were not normal in all cases (Shapiro-Wilk W-test), so the Spearman rank correlation coefficient was used for analysis of variables association (Sokal and Rohlf, 1995). The effective number of independent observations was adjusted when significant autocorrelations are presented in time series using the equation:

$$n' = N / (1 + 2r_1r'_1 + 2r_2r'_2 + \dots + 2r_kr'_k),$$

where n' is the effective number of degrees of freedom; N is the total number of observations; r_i and r'_i are the lag- i temporal autocorrelation coefficient of the two series ($i = 0 \dots k$); $k = 1/5$ of total number of variants (Hays et al., 1993; Pyper and Peterman, 1998). The autocorrelations were calculated using an estimator of Box and Jenkins (1976).

A simple linear regression was used to analyze long-term trends in the environmental and zooplankton dynamics. Prior to testing the significance of the trend slope, a Durbin-Watson test was performed to detect the autocorrelation in the residuals of the regression analysis. The analyzed variable was standardized to a mean of 0 and standard deviation of 1, and the β -coefficient was used as the characteristic of a slope.

There was rather abrupt change of the atmospheric circulation over the White Sea in the beginning of 1970s (Filatov et al., 2007), which was considered here as a possible factor influencing the temperature regime and a planktonic community structure. In order to test this hypothesis, we have calculated the 10-year averages of the temperature threshold dates before the expected change and after it (Weijerman et al., 2005), starting from 1961, so the last period is 5-year long (2011–2015). Means were compared by applying non-parametric Mann-Whitney criterion.

In all cases, the significance was tested at $p = 0.05$ level. The analyses were performed using Statistica 7.1 software (StatSoft, Inc.).

Results

Temperature: seasonal and long-term dynamics

Average temperature of the upper 25-m water layer at the study site changes during year from -0.8°C in winter to 10.5°C in the beginning of August (Fig. 2). The winter lasts on average from the second 10-day period of December until the first week of May, when the temperature of this layer rises above zero, thus indicating the beginning of a spring period. The summer starts on average in the middle of June and lasts until the mid-October.

No significant trends in the dynamics of spring and summer average water temperature were detected during the fifty five years of observations (Fig. 3). Despite some increase of summer temperature in the last period (Fig. 3B) all changes between periods in question are insignificant according to Mann-Whitney U-test.

Species abundance: seasonal and long-term dynamics

The peak of *Calanus glacialis* abundance is usually observed in the end of May, which is the beginning of the spring period (Fig. 4). The nauplii are the absolute dominants in the population at this moment. *C. glacialis* are mostly absent in the upper 25-m layer by the time when the warm-water (boreal) species appear in the plankton. This occurs normally in the beginning of July (190th Julian day). The first individuals of *Centropages hamatus* appear normally in early June (160th Julian day); the maximal abundance of this species is observed usually in the end of August (240th Julian day). *Temora longicornis* develops synchronously to *Centropages*: the timing of their appearance and the abundance peaks coincide. They are first found in the plankton in the first 10 days of June; the peaks of their abundances are observed in the last 10 days of August.

The significant interannual fluctuations are the feature of the long-term dynamics of all the studied species (Fig. 5). The minimal and maximal values differ in an order of magnitude. Meantime, there are no significant long-term tendencies in the abundance dynamics of these species. The abundance of *C. glacialis* is characterized by the pronounced periods of peaks and falls. Particularly, the low abundance (comparing to the multiyear average) has been registered in the end of 1960s–mid-1970s and in late 1990s–early 2000s, and high abundance, in 1980s–mid-1990s. These quasi-cyclic fluctuations were not found for the other species' dynamics.

Speaking about the effect of the temperature, we should mention that only *Temora longicornis* abundance correlated significantly to the summer temperature of 0–25-m water layer ($r = 0.50$; $p = 0.0001$).

Phenological indices: long-term changes

Dates of spring beginning (3 °C threshold) varied during the study period between the mid-May (140th Julian day, 2012) and early July (190th Julian day, 1964). Summer began between the end of May (150th Julian day, 1984) and early August (220th Julian day, 1966). The end of summer period did not demonstrate significant long-term trends ($R^2 = 0.003$, $\beta = 0.05$, $p = 0.7$); summer duration increased owing to the shift of its beginning to earlier dates (Table 1; Fig. 6, F). In 1966, the summer was the shortest (50 days) during the period of 1961–2015. The summer in 1984 and 2011 was the longest for the 55-year study period; it lasted 150 days. Significant shift of spring beginning, according to Mann-Whitney test, took place between 2000s and 2010s ($U = 6.0$; $p < 0.05$; Fig. 6, D, F). Particularly, spring in 2011–2015 began significantly earlier than during the period of 1961–2010 (Table 1). Significant shifts of summer beginning were observed between 1960s and 1970s and between 2000s and 2010s ($U = 17.5$, $p < 0.05$ and $U = 2.5$, $p < 0.01$, respectively). Summer duration in 2011–

2015 increased significantly compared to the periods of 1961–1970 and 1971–1980 ($U = 2.5$, $p < 0.01$ and $U = 7.5$, $p < 0.05$, respectively; Fig. 6, F). As a result, the spring beginning shifted since 1960s by 18 days (from 166th Julian to 148th Julian day); and summer began earlier in 28 days (188th Julian versus 160th Julian day). Thus, spring duration decreased from 1960s to 2010s by 10 days. Meantime, the summer duration increased by 30 days (from 104 to 134 days).

The dates of appearance of *Calanus glacialis* CI also demonstrated weak but significant negative trend (Table 1; Fig. 7, A). The latest date of CI appearance was observed in 1966 (middle of July), the earliest, in 2006, 2007, and 2011 (early May). CI tended to appear 22 days earlier in the period of 2011–2015 comparing to 1961–1970 (146th Julian day against 168th). The earliest dates of appearance were observed during the 2001–2010 decade (144th Julian day on average). The dates of CIII disappearance from 0–25-m water layer were characterized by similar though less pronounced trend (Table 1; Fig. 7, A, C). The season of active *Calanus* development from CI (appearance in the plankton) to CIII (disappearing due to the downward migration) has become longer since 1960s (Table 1; Fig. 7, B, D) increasing from 31 to 38 days. The young copepodites stayed in the upper water layer the longest in 2001–2010 (46 days on average). The season of active development was the shortest in 1966 (10 days), the longest, in 2006 and 2008 (60 days).

Even more pronounced negative trend was a characteristic for timing of *Centropages hamatus* copepodites' appearance (Table 1; Fig. 8, A). As a result, the start of the developmental period shifted by 33 days, from the average 207th Julian day in 1961–1971 to the average 174th Julian day in 2011–2015. The latest appearance of copepodites was detected in 1966 (late August), the earliest, in 1988, 1992, 2006, 2007, 2012, and 2013 (early June). The developmental period duration was characterized by the pronounced year-to-year fluctuations; nevertheless, a positive trend was found in this series (Table 1; Fig. 8, B).

However, this trend was not monotonic during the observation period. 10-year means indicated that the shortest periods were in 1960s and 1970s (50 days), the longest, in 1990s (104 days). The shortest periods were observed in 1966 and 1975 (20 days), the longest, in 1992 and 2006 (130 days). In 2011–2015, the average developmental period was 73 days. There was a significant difference between the periods of 1961–1970 and 1971–1980 on the one side and 1991–2000, 2001–2010 and 2011–2015 on the other, according to Mann-Whitney test ($U = 103$; $p < 0.01$). The cause of the developmental period increase was the shift of its beginning, because timing of copepodites disappearance has not shifted significantly (Table 1; Fig. 8, A, C).

The timing of the start of developmental season of *Temora longicornis* also shifted to an earlier time during the period of observations (Table 1; Fig 9, A, C). The start of developmental period has shifted from 205th to 164th Julian day since 1960s. The latest start was observed in 1979 (mid-August), the earliest, in 1989, 2008, and in 2012–2014 (early June). According to the Mann-Whitney test the period of 1961–1980 differed significantly from the following years ($U = 15.0$, $p < 0.01$), as well as the last period of 2011–2015 differed from all the previous periods ($p < 0.05$). The shortest developmental period took place in 1966 (50 days), the longest, in 2008 (160 days). However, there was no trend found for the length of the developmental period (Table 1), comparisons of 10- and 5-year means also have not detected any significant changes (Fig. 9, A, C). No significant changes were found in dynamics of the end of developmental period (Table 1).

A significant shift of spring water warming is supposed to influence either animal abundance or the timing of the phenological events, or both (observed significant correlation coefficients are presented in the Table 2). Timing of appearance of all studied species except *Temora longicornis* is correlated to the timing of spring water warming. The timing of *Calanus glacialis* CI appearance and beginning of spring are tied by the highest significant

correlation ($r = 0.54$). Significant correlations are observed also for *Centropages* phenological indices and the spring beginning ($r = 0.49$). Thus, there is a tendency of an earlier appearance of juveniles of these two species in the years characterized by the earlier spring beginning. The cross-correlations have been calculated also to search for the possible lagged influence of temperature timing on species phenology; particularly, this was done for variables in question and the timing of seasonal temperature changes, lagged for 1 and 2 years. The correlations of *Calanus* appearance timing with spring beginning became smaller with the increasing lag and was significant only at lag 1 ($r = 0.36$). The correlations between the timing of *Centropages* appearance and spring beginning with 1-year lag was not significant – only correlations with timing of 4 °C threshold and summer start were significant ($r = 0.34$ and 0.38 , respectively). *T. longicornis* appearance, on the contrary, correlated significantly with spring beginning only at lag 1 ($r = 0.43$), correlation with timing of 4°C threshold and summer start decreased with lag ($r = 0.22$ and 0.29 , respectively). No significant correlations were observed at 2-year lag. No significant correlations were found also between abundance of studied species and timing of seasonal water warming.

Discussion

Despite the pronounced changes have been reported for many Arctic areas (ACIA, 2004; IPCC, 2012), there were no significant changes of the water temperature in the study area, though slight tendency to increase took place (Usov et al., 2013). No perceptible change of spring and summer water temperature occurred even between 1960s and 1970s, when the abrupt shift of the air circulation pattern was observed over the White Sea (Filatov et al., 2005). Westerly transport declined sharply in the end of 1960s – beginning of 1970s, after which in the middle of 1970s, it increased again (Filatov et al., 2005). This meant the

consecutive cooling and warming of climate in this region. Indeed, 1966 was the coldest year during the whole period of monitoring (Rusanova and Khlebovich, 1967). However, spring and summer average temperatures did not demonstrate any significant trend during the period of 1961—2015: $\beta = 0.22$, $p = 0.16$ (spring) and $\beta = 0.11$, $p = 0.43$ (summer). Oceanographic changes in study area during this period were expressed mostly through the changes in the timing of seasonal spring warming of water and hydrological summer beginning which demonstrated substantial shift to an earlier time.

It is spring-summer period when active reproduction and development of zooplankton species, especially copepods, take place in the cold seas (Prygunkova, 1974; Norrbin, 1991; Kwasniewski et al., 2013). Winter in the White Sea is characterized by the water temperature below zero for several months. It is the period of minimal abundance and activity of zooplankton in the upper 0–25-m water layer (Berger et al., 2001). Only when the daytime duration increases in late winter, the first signs of the zooplankton activity appear: the first nauplii of arctic-boreal *Pseudocalanus* spp. appear in March, and the nauplii of *Calanus glacialis*, in April (Usov, 2011), *Calanus glacialis* adults start feeding in March (Kosobokova et al., 2003). These animals, breeding in late winter and spring, depend on ice algae and phytoplankton (Daase et al., 2013). In turn, microalgae depend on the day length and light intensity (Eilertsen et al., 1995; Edwards and Richardson, 2004). These processes together depend on the year cycle of solar irradiation, so they are stable in time from year to year. However, in high latitudes, in seasonally freezing seas, the ice cover influences the seasonal light cycle significantly (Carton et al., 2015). The thickness of ice and snow cover and the dynamics of ice/snow melting affect the light penetration beneath ice (Zhang et al., 2015). Later in the season, as the light saturation is achieved, the water temperature may influence the photosynthesis directly: photosynthetic activity increases with rising water temperature (Tilzer et al., 1986). Therefore, the timing and intensity of spring warming is expected to

determine the period of the favorable conditions for planktonic animals' reproduction and development.

Indeed, the appearance of juveniles of *Calanus glacialis*, *Centropages hamatus*, and *Temora longicornis* shifted to an earlier dates during the study period in accordance with the shift of the seasonal water warming. It means that either reproduction of these species has shifted to an earlier time, or the developmental time has shortened, or both.

The reproduction period and its timing are among the major phenological events in the species biology. The start of *C. glacialis* reproduction, at least directly, depends more on the food availability than on the temperature (Ringuette et al., 2002). On the other hand, as it is indicated above, it is temperature that governs the ice melting and, therefore, the timing of the phytoplankton bloom, and, later in the year, its photosynthetic activity. Thus, the timing of the reproduction of *C. glacialis* depends on both food availability (directly) and temperature (indirectly). The duration of *C. glacialis* development also depends on water temperature and food availability. The developmental time of *Calanus* nauplii increases by about three days with 1°C temperature decrease (Corkett et al., 1986; McLaren et al., 1988; Daase et al., 2011). The food concentration has a similar effect, when the starvation increases the developmental time of the nauplii of this species and may even terminate it (Daase et al., 2011). The long-term shift of seasonal warming to an earlier time may have caused an earlier start of reproduction of *Calanus glacialis*, and, therefore, an earlier appearance of juvenile copepodite stages. The timing of their disappearance also has shifted to an earlier time, but by 15 days only (compared to 22 days for appearance timing). Thus, season of active development of *C. glacialis* has slightly shifted to an earlier time and increased, this change was small but significant ($R^2 = 0.09$, $\beta = -0.30$, $p = 0.03$; see Table 1). The longest seasons of the active development of *C. glacialis* juveniles were registered for the decade of 2001–2010. So, the duration of developmental season has increased during period of study. One may conclude

that with earlier warming and faster development *Calanus* must leave upper layer much earlier. Moreover, as it was indicated above, spring shifted to an earlier time, and its duration decreased by 10 days. What may explain such discrepancy? First, average temperatures of spring and summer have not changed significantly. Second, *Calanus* CIII remain in the layer 0–25 m, but stay below 10 m depth by the end of spring (our observations), thus escaping unfavorable thermal conditions. High concentrations of chlorophyll a are observed only to the depth of 10 m by this time (Usov et al., 2013). So, feeding conditions below this depth are not favorable by the time CIII leave surface layer. Thus, until *Calanus* copepodites finally leave 0–25 m layer, they experience the deficit of food. This may be the cause of observed development prolongation.

There 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). 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.

The changes of phenology of the warm-water *Centropages hamatus* and *Temora longicornis* are consistent with the changes of the seasonal cycle of temperature. Particularly, 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). Some researchers believe that this event is launched by the temperature decrease near bottom (where diapausing eggs reside) in the preceding winter, which turns on a "biological clock" (Engel, 2005; Katajisto, 2006), others find that it is the temperature increase that either induces hatching (Pertsova, 1990) or shortens egg developmental time (Katajisto et al., 1998). In the study area, the water temperature during winter is below zero for about five months from January to May (Usov et al., 2013) and is hardly responsible for turning on "biological clocks" in diapausing eggs. We suppose that it is the shift of spring warming that may influence the timing of hatching of these species in the White Sea.

All three species demonstrate the tendency to increase the period of their presence in the plankton communities, or the developmental period (we cannot speak directly about reproduction because do not have reliable data on abundance of the species in question at earlier stages): it is either the season of an active development (*Calanus*) or the reproduction season (*Centropages* and *Temora*). This prolongation occurs almost exclusively due to an earlier appearance of the juveniles, because the timing of their disappearance does not change significantly, except for the end of *Calanus* active development. The hydrological summer has become longer due to its earlier beginning. The increase of the warm season duration may cause the prolongation of period of presence of the warm-water species in the plankton (developmental period). The prolongation of the developmental period of boreal species, in turn, may lead to an increase of the generation number per season, but the latter has not changed significantly (Usov et al., 2013). According to our data, the hydrological summer has become longer but not warmer. Therefore, the development of the warm-water species could not become faster, and the generation time could not decrease. On the other hand, during a longer summer more generations could develop, but this was not observed.

Our findings indicate that the key members of zooplankton community possess, to some extent, phenological plasticity (Beaugrand and Kirby, 2018), which allows them to overcome large shifts of the seasonal temperature cycle. This also means that the temporal changes of temperature cycle have not gone beyond the limits, critical for studied species. The nature of the dynamics of total zooplankton abundance at the study site indicates that community as a whole is also resilient both to shifts in the seasonal temperature dynamics and to absolute temperature dynamics (Usov et al., 2013). Moreover, most studied species did not demonstrate any relationships with documented temperature changes.

The following conclusions can be made summarizing our work. (1) Climate change in the White Sea manifested itself through changes of seasonal temperature dynamics, not absolute temperature values. (2) Species with different temperature preferences (boreal and arctic) responded similarly to changes in temperature seasonal dynamics. This demonstrates importance of temperature as a factor, which shapes (drives) seasonal dynamics of planktonic communities despite the influence of other factors. (3) Effect of changes in temperature seasonal dynamics was more pronounced in the life cycles of boreal species – their reproductive season shifted by more than a month compared to two weeks of arctic *Calanus*. (4) Abundance of zooplankton did not change significantly, which indicates resilience of planktonic organisms to changes in environment. They simply tune in their life cycles to follow temporal changes in the environment. This point out also that trophic mismatch, possible in such cases, does not take place in the White Sea. It means that phenology of the whole plankton system (primary and secondary producers) synchronizes with temperature shifts.

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634

635 **Figure captions**

636 Figure 1. Map of the study area. D-1 Station – monitoring point.

637 Figure 2. Mean temperature of the 0–25-m water layer: seasonal dynamics. Long-term means
 638 with standard errors are presented. Number of observations varies from 3 (the last 10 day of
 639 December) to 55 (through summer period).

Figure 3. Long-term dynamics of the water temperature of the 0–25-m water layer: (A) the averages for spring (thin line) and summer periods (thick line); (B) 10-year averages (5-year mean for 2011–2015) for spring (open circles) and summer (filled circles). Vertical bars are the standard errors of mean.

Figure 4. The seasonal cycle of the abundance of the studied species in the 0–25-m water layer. Long-term means and the standard errors (vertical bars) are presented. Number of observations varies from 3 (the last 10 days of December) to 55 (through summer period). N – abundance.

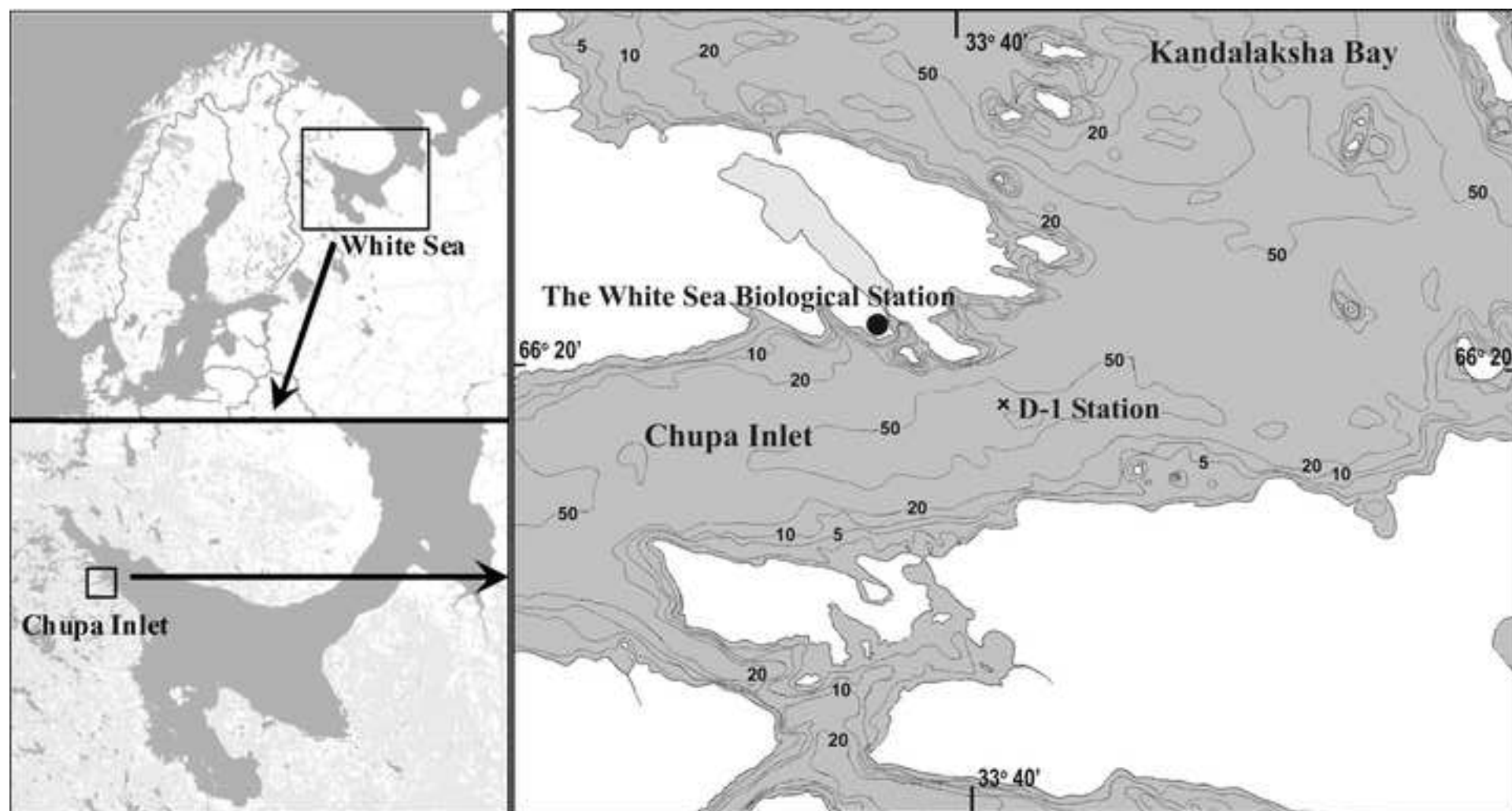
Figure 5. The long-term abundance dynamics of the studied species in the 0–25-m water layer. The average values for spring (*Calanus glacialis*, A) and summer (*Temora longicornis*, B, and *Centropages hamatus*, C) are presented. The dashed lines indicate the linear regression accompanied by the equations and the coefficients of determination.

Figure 6. Dates of main seasonal temperature thresholds: yearly data with linear trends (*left panel*) and decadal means (*right panel*) with standard errors of means. (A), (D) – beginning of spring (3°C threshold); (B), (E) – beginning of summer (5°C threshold), (C), (F) – duration of summer period. Please pay attention to the different scales of Y-axis.

Figure 7. Dates of *Calanus glacialis* CI appearance and CIII disappearance in 0–25-m water layer (A, C) and duration of the period between CI appearance and CIII disappearance ("season duration"; B and D): yearly data with linear trends (*left panel*) and decadal means with standard errors of means (*right panel*).

Figure 8. Dates of *Centropages hamatus* CIII–CV appearance and disappearance (A, C) and the duration of the developmental season (B, D): yearly data with linear trends (*left panel*) and decadal means (*right panel*) with standard errors of mean.

663 Figure 9. Dates of *Temora longicornis* CIII–CV appearance and disappearance (A, C) and the
664 duration of the developmental season (B, D): yearly data with linear trends (*left panel*) and
665 decadal means (*right panel*) with standard errors of mean.



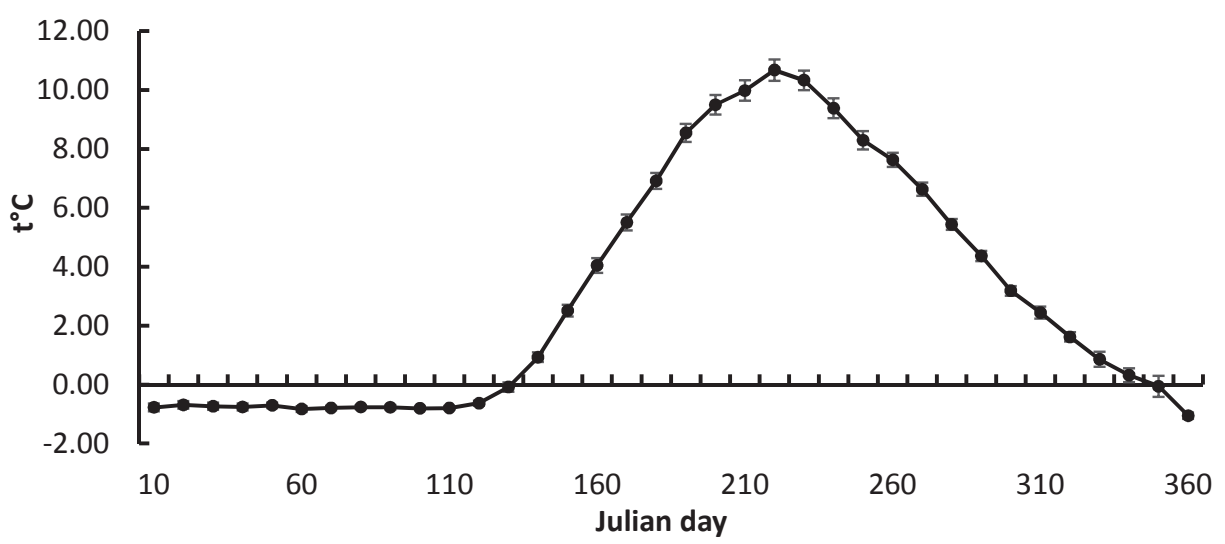


Figure3

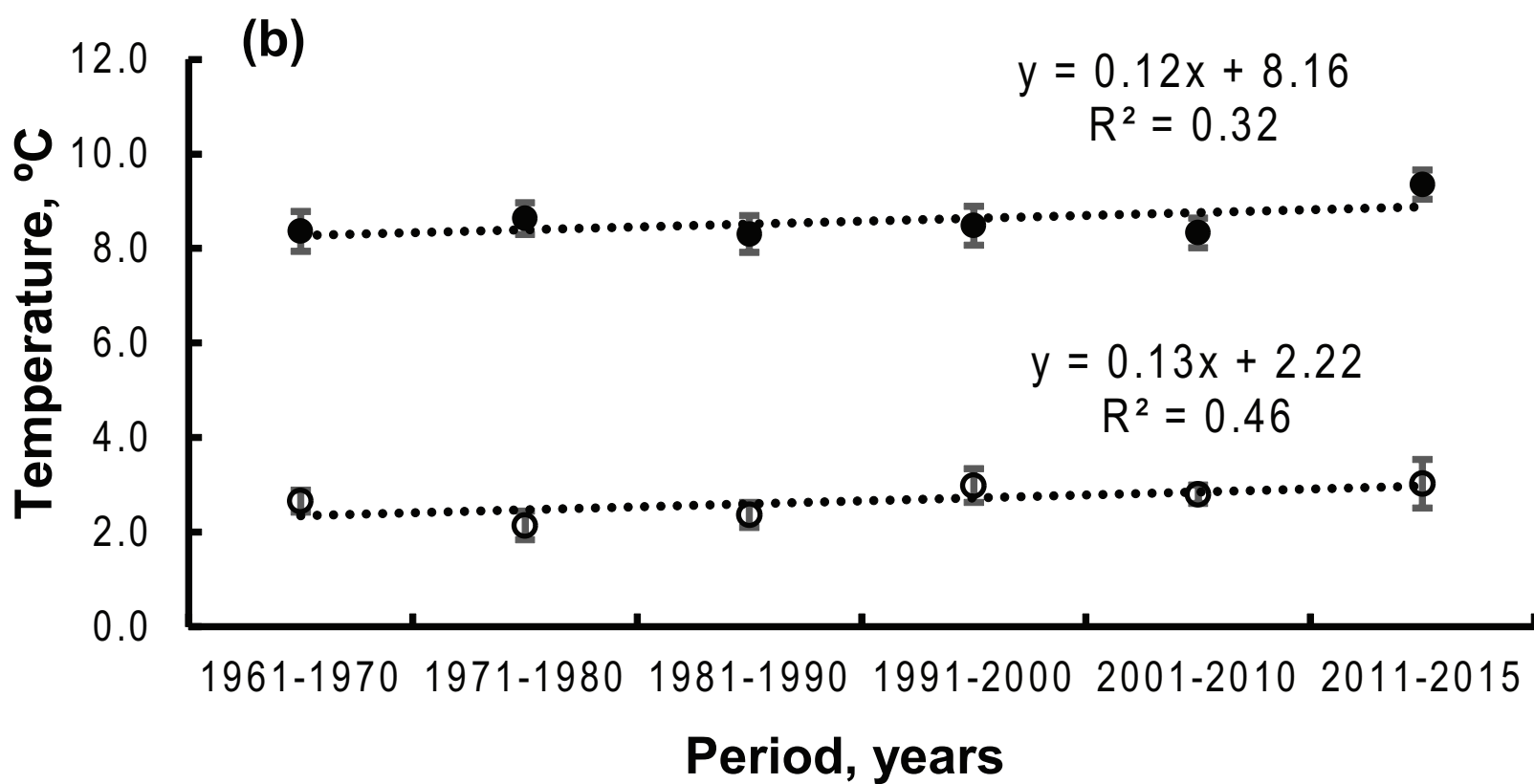
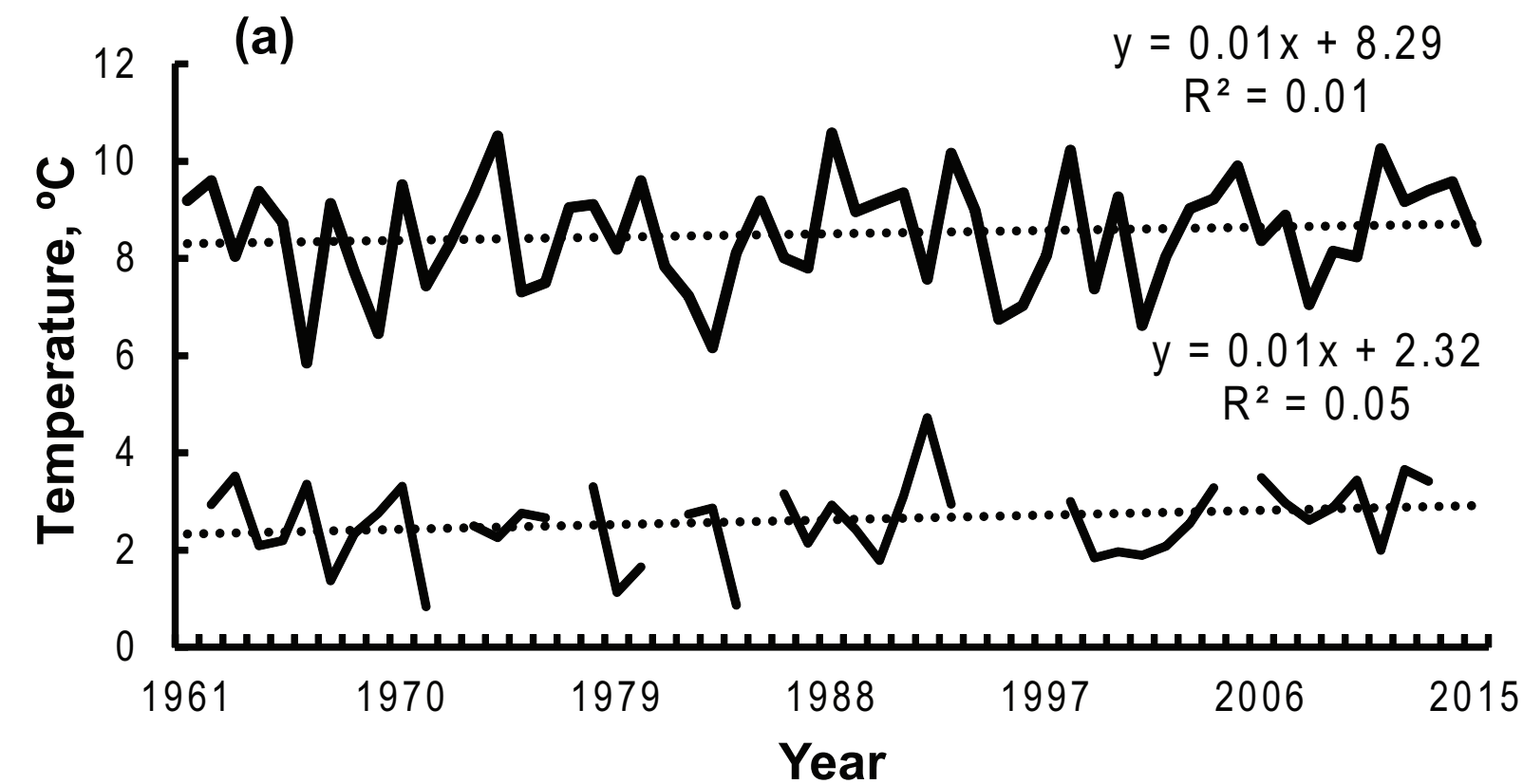
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Figure4

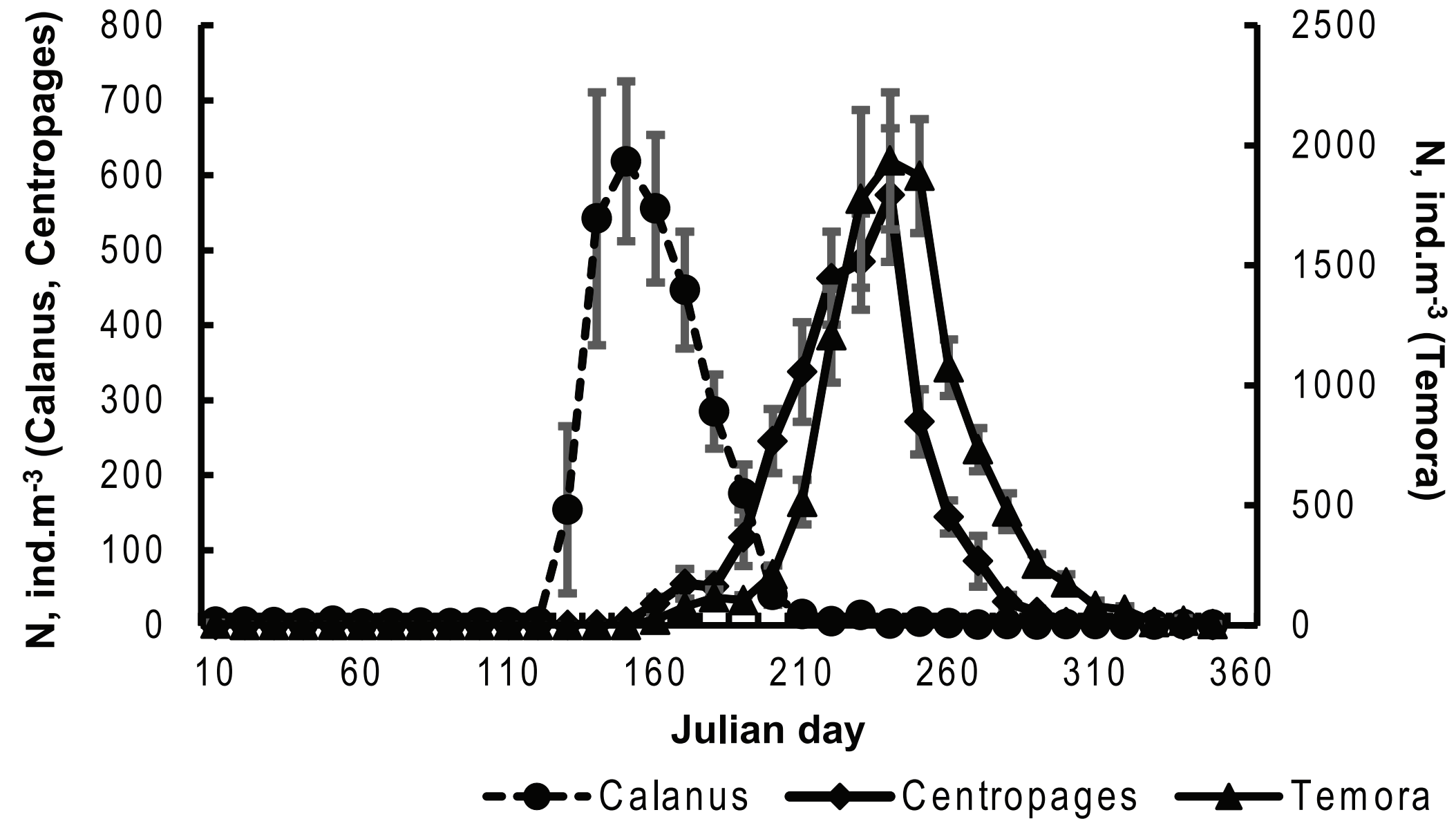
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Figure5

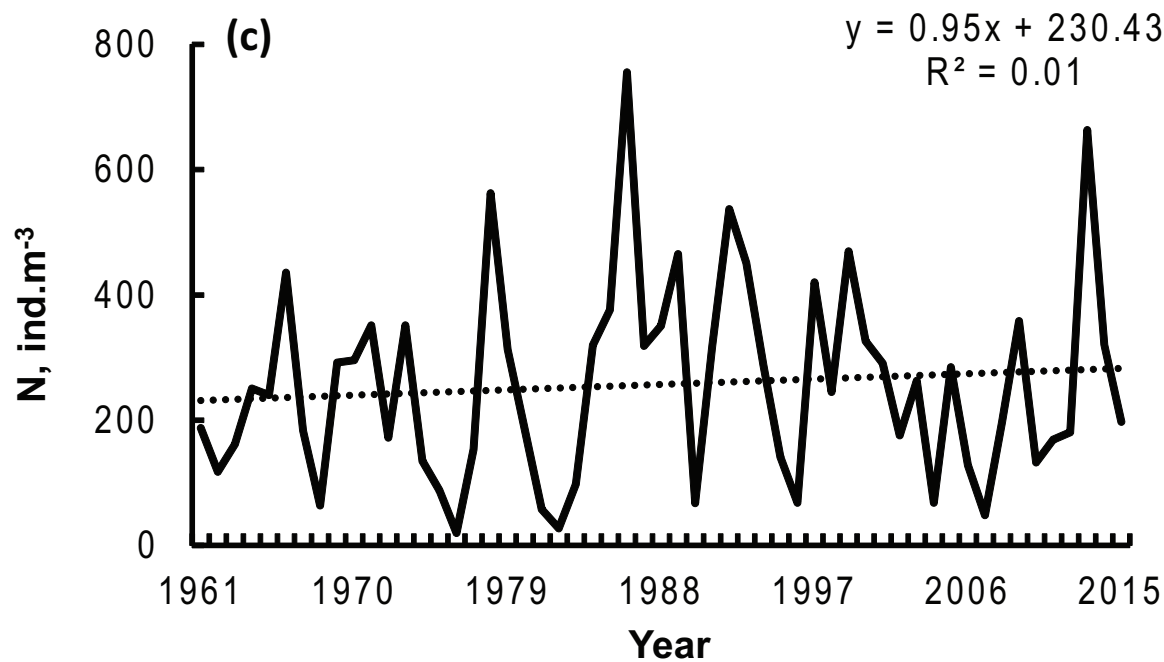
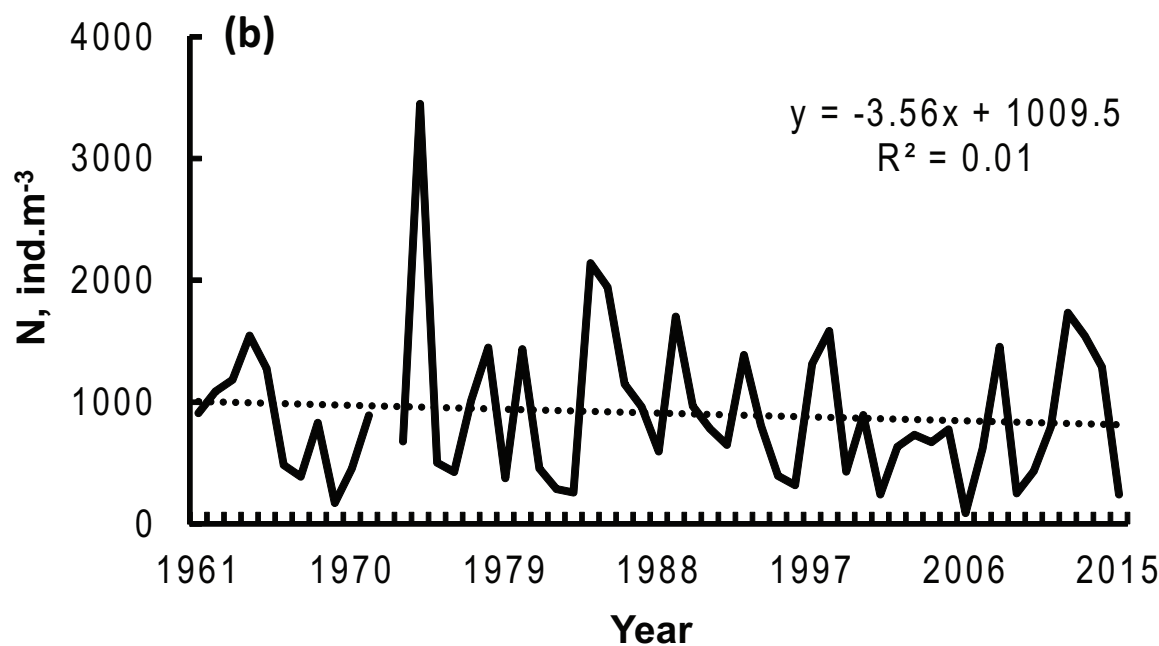
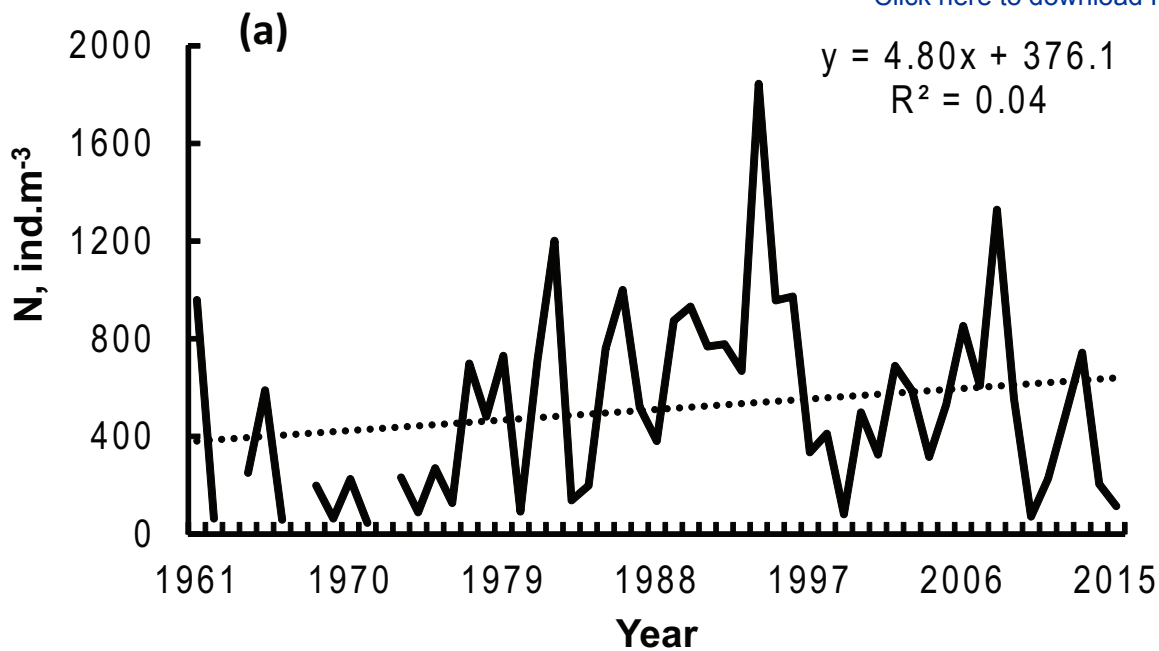


Figure6

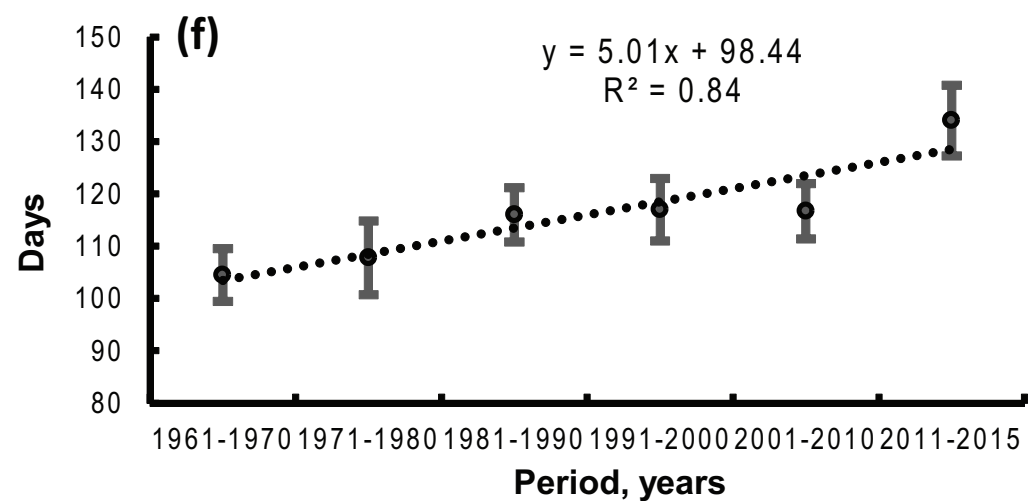
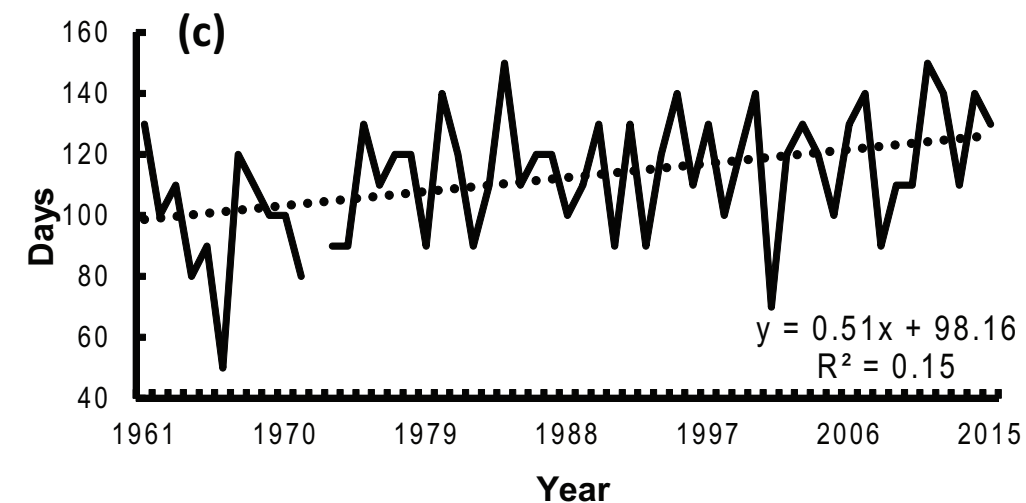
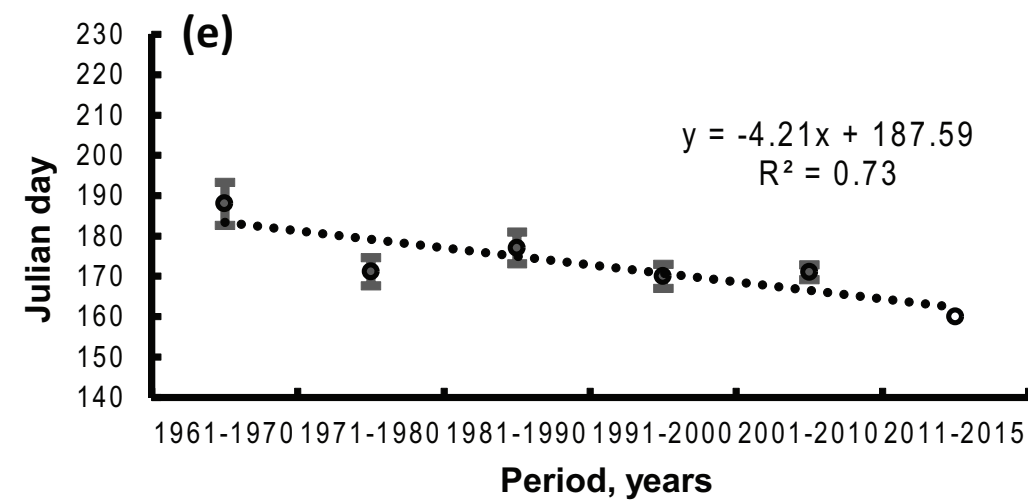
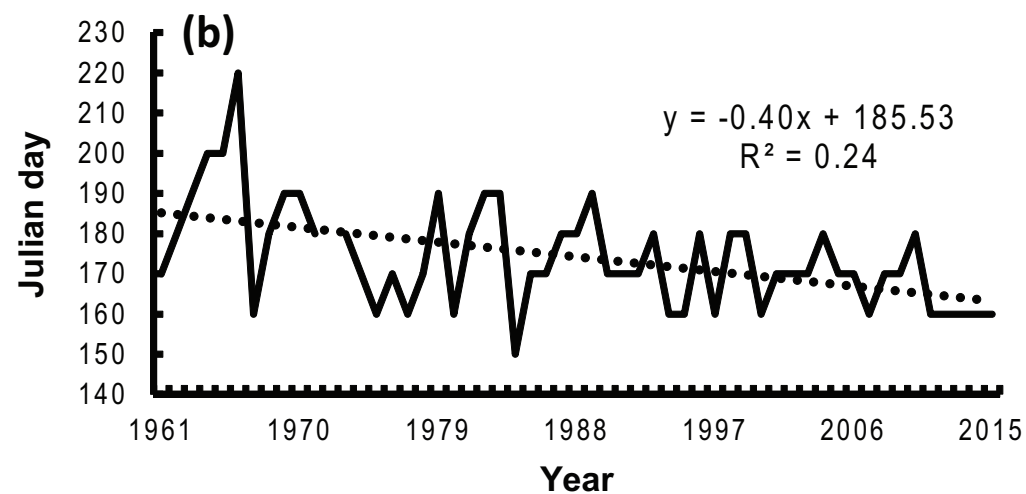
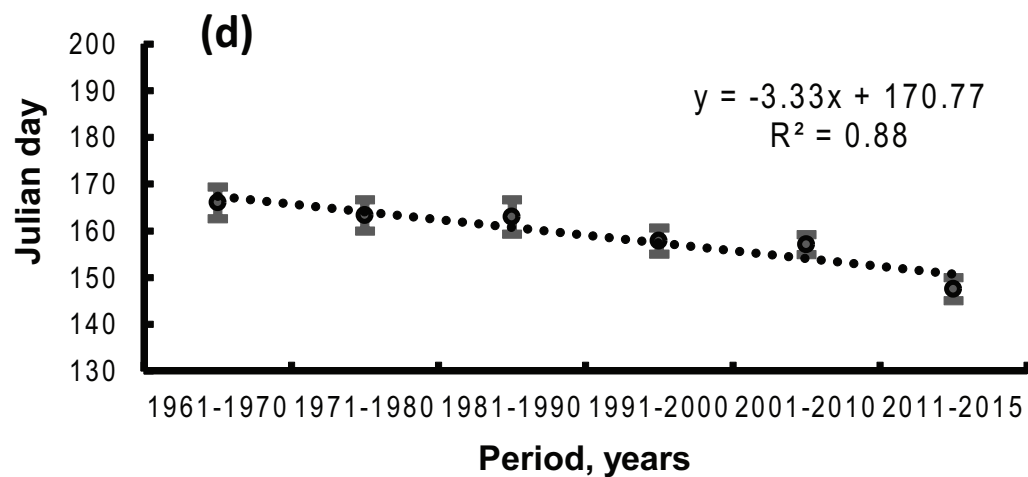
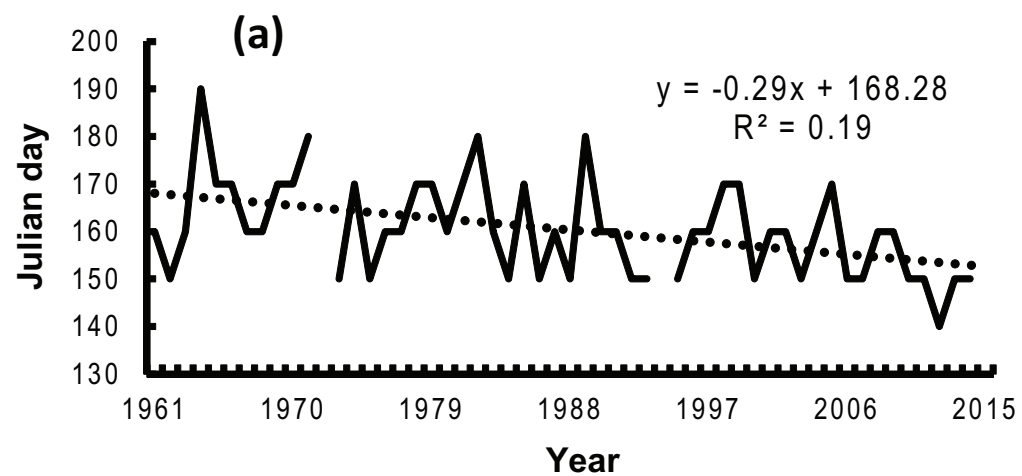
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Figure7

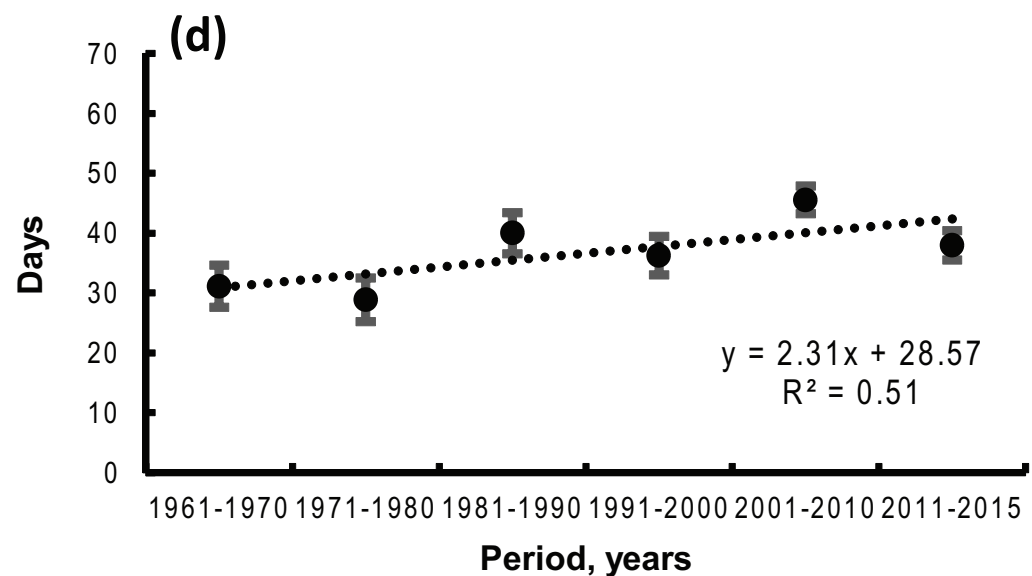
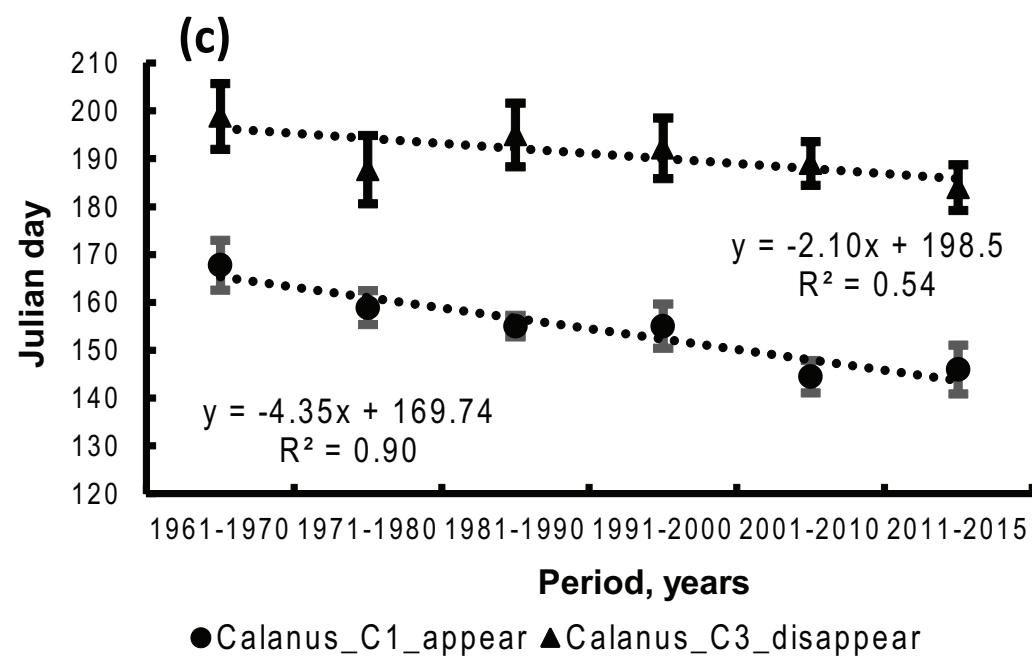
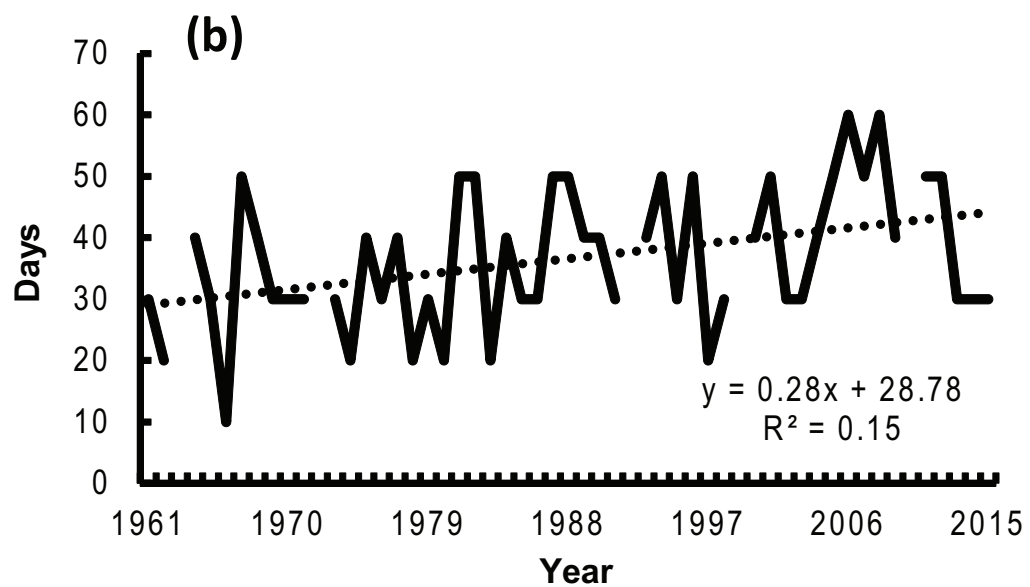
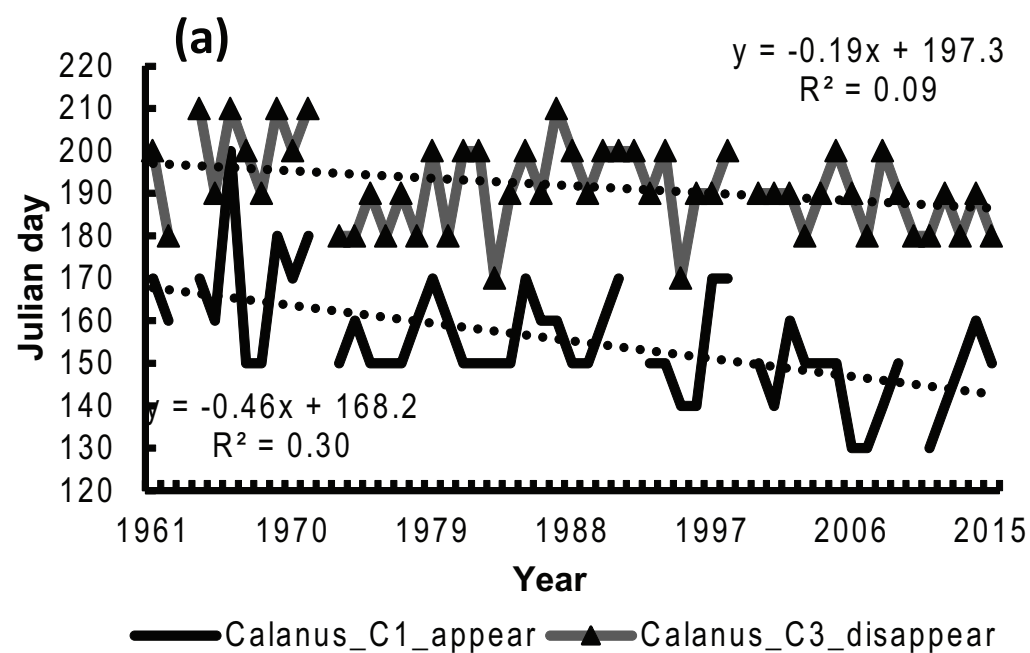
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Figure8

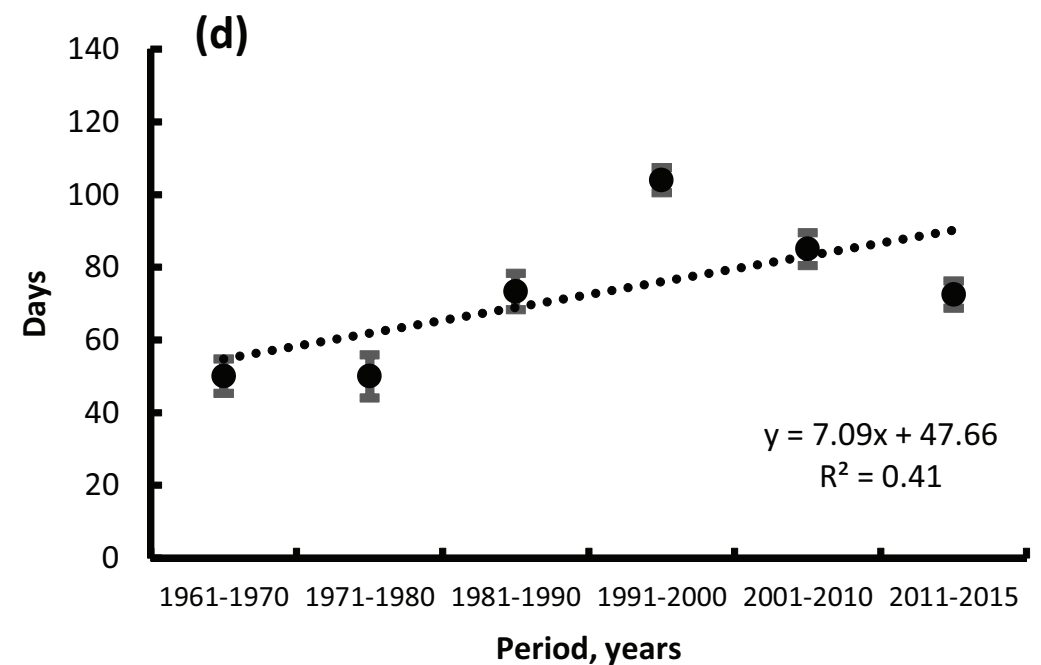
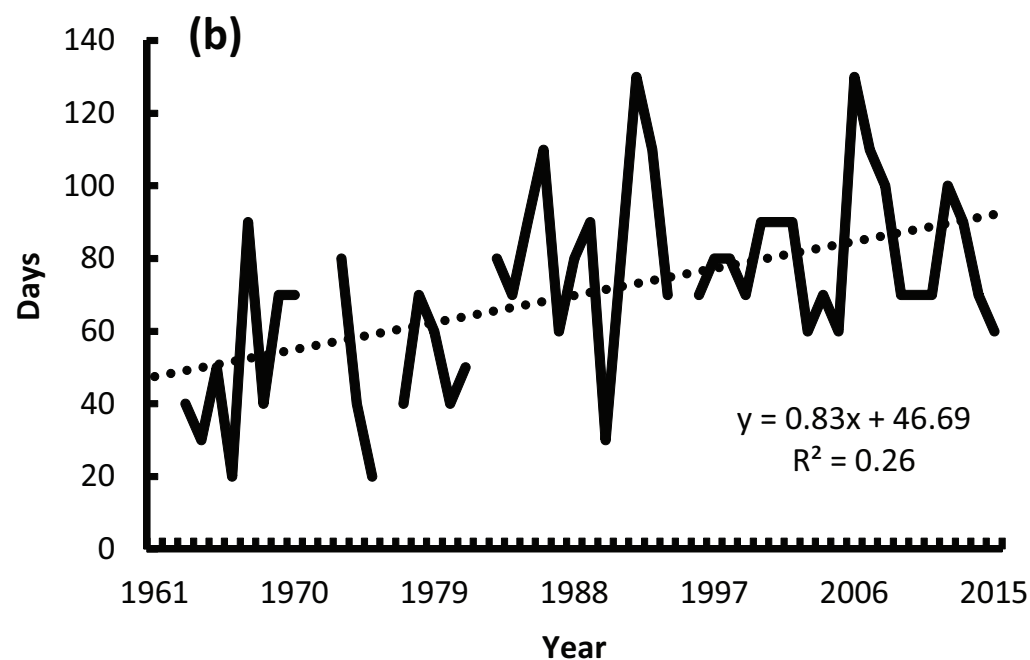
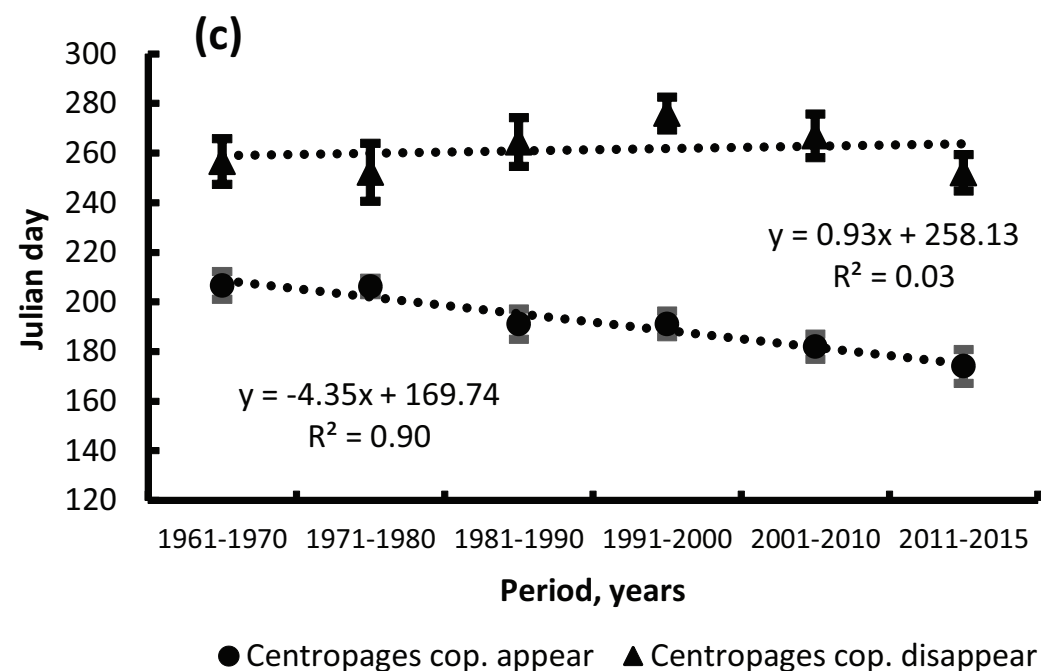
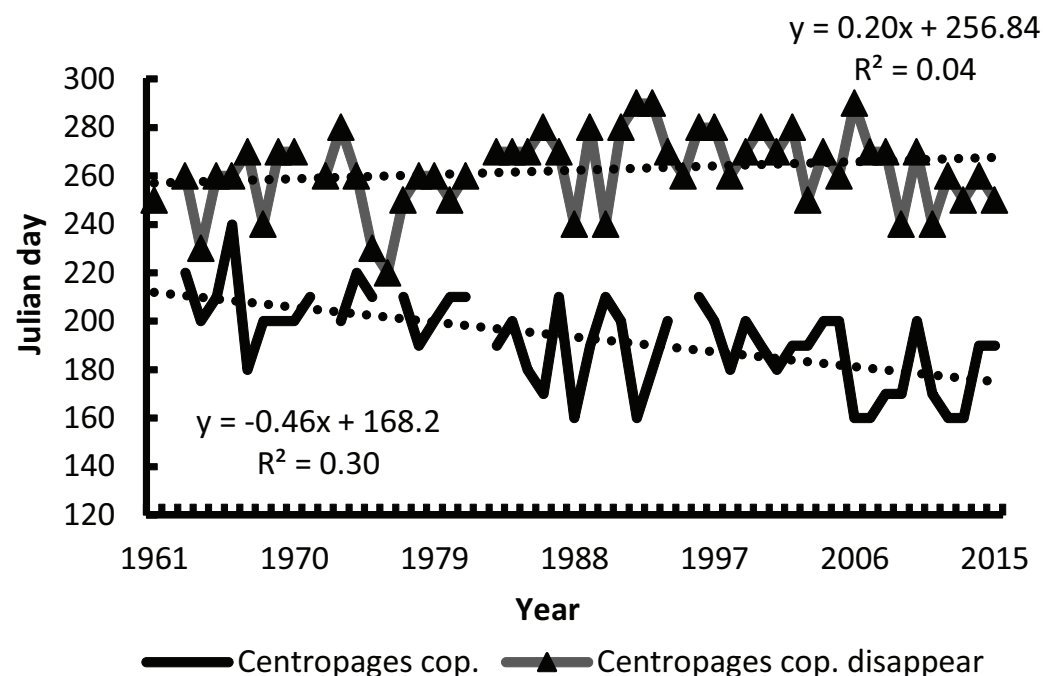
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Figure9

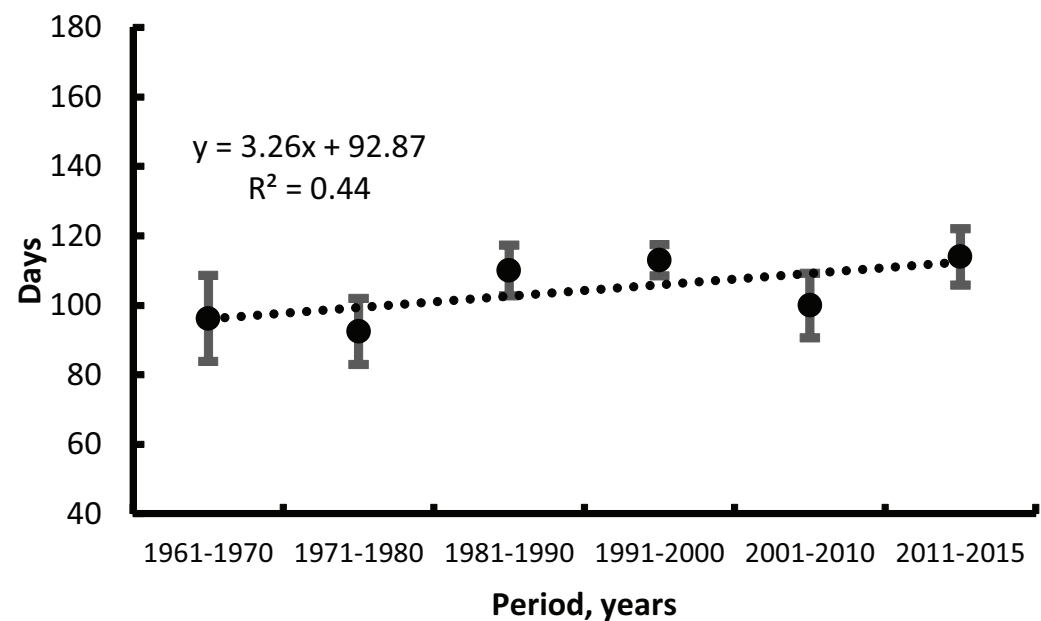
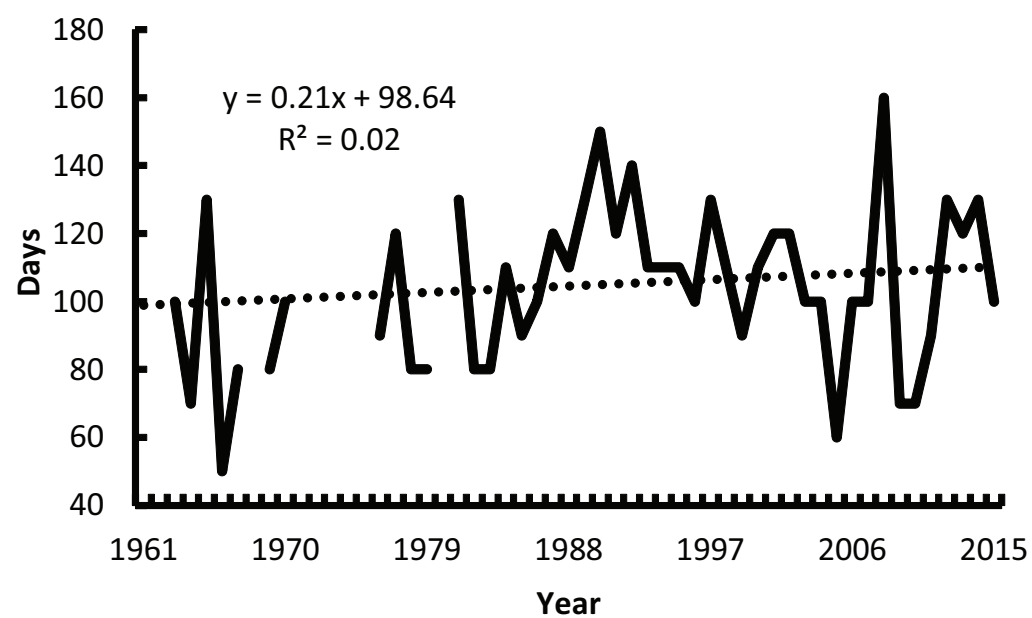
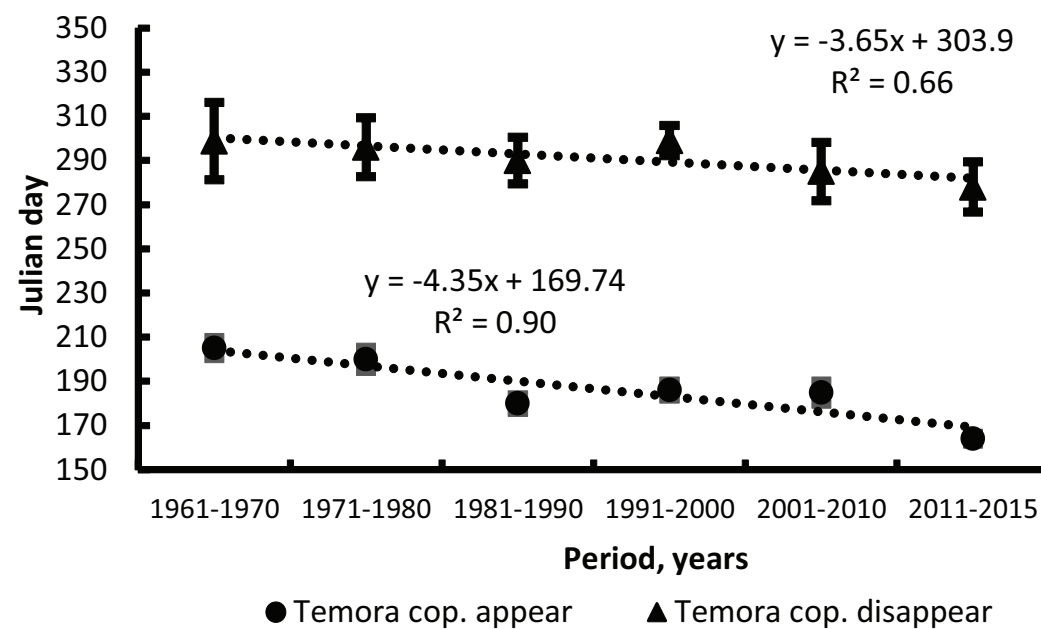
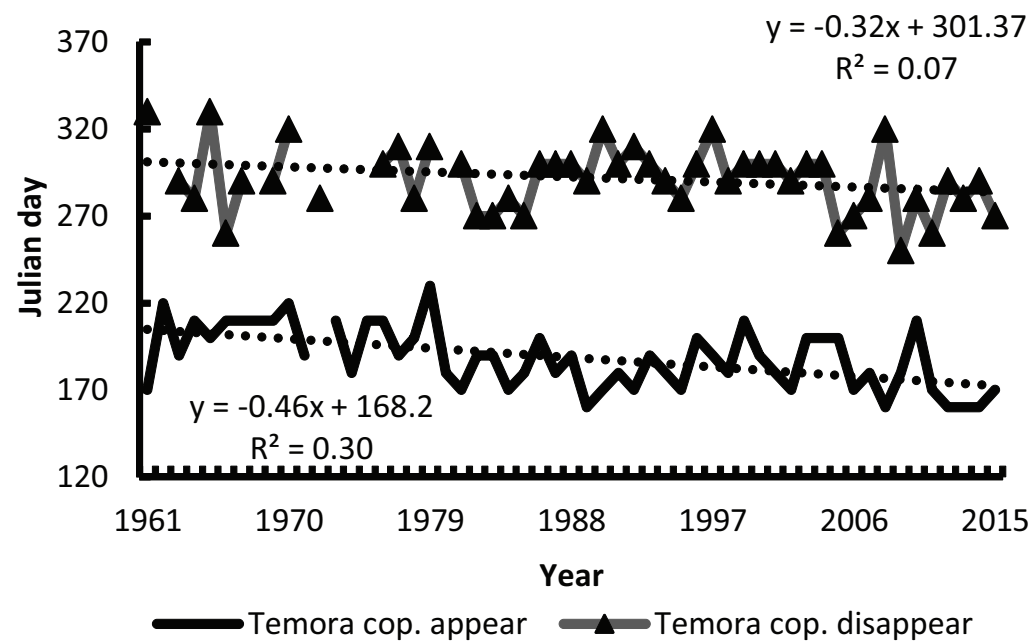
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Table 1. Parameters of the linear regression model for the phenological parameters

Timing of...	R^2	F	β	SE of β	p
T > 3 °C (Spring start)*	0.19	12.03	-0.44	0.13	< 0.01
T > 4 °C*	0.24	15.38	-0.49	0.12	< 0.01
T > 5 °C (Summer_start)*	0.24	16.38	-0.49	0.12	< 0.01
Summer duration*	0.16	9.84	0.41	0.13	< 0.01
<i>Calanus</i> _C1_appear*	0.30	20.50	-0.55	0.12	< 0.01
<i>Calanus</i> _C3_disappear*	0.09	5.02	-0.30	0.13	0.03
<i>Calanus</i> juv. season*	0.15	8.28	0.38	0.13	< 0.01
<i>Centropages</i> cop. appear*	0.34	25.07	-0.58	0.12	< 0.01
<i>Centropages</i> cop. disappear	0.04	1.97	0.19	0.14	0.167
<i>Centropages</i> cop. season*	0.28	17.86	0.52	0.12	< 0.01
<i>Temora</i> cop. appear*	0.30	22.40	-0.55	0.12	< 0.01
<i>Temora</i> cop. disappear	0.07	3.60	-0.27	0.14	0.064
<i>Temora</i> cop. season	0.02	0.81	0.13	0.15	0.374

R^2 coefficient of determination, F F-value, β regression coefficient of standardized data, SE of β standard error of β , p significance level, "Season" duration of period of appearance in zooplankton. * significant regression results (determination and regression coefficients).

Table 2. Correlations between biological and abiotic variables at study site. Only significant Spearman correlation coefficients are presented.

Correlated pair		Spearman r	Adjusted DF	r_{crit}
<i>Calanus glacialis</i> CI appearance	T > 3 °C	0.54	35	0.33
	T > 4 °C	0.40	28	0.36
	T > 5 °C	0.39	31	0.34
<i>Centropages hamatus</i> CIII-CV appearance	T > 3 °C	0.49	34	0.33
	T > 4 °C	0.36	28	0.36
	T > 5 °C	0.38	30	0.35
<i>Temora longicornis</i> CIII-CV appearance	T > 4 °C	0.47	29	0.36
	T > 5 °C	0.47	30	0.35

DF degrees of freedom, adjusted for autocorrelation, r_{crit} corrected value of critical correlation coefficient.