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Opposite phenological responses of zooplankton to climate along a latitudinal gradient through the European Shelf

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Zooplankton phenological shifts may affect energy transfer through pelagic food web and up to fisheries, but few studies have compared zooplankton phenology across a wide latitudinal range of water temperatures. We examined the phenological variations of zooplankton at four sites along a latitudinal gradient from the Bay of Biscay [Bilbao and Urdaibai (BU)], the English Channel (Plymouth; L4), and the North Sea [Stonehaven (SH)] from 1999 to 2013. Zooplankton taxa showed interannual phenological variations that were opposite in direction between the southernmost BU and the northernmost SH sites. The East Atlantic pattern was the climate teleconnection best related to zooplankton phenological variations. Among local variables , salinity at BU was best related to phenological changes at BU as opposed to those at SH. Locally, chlorophyll *a* was most relevant at SH and temperature at L4. While we did see some imprints of temperature in causing expected directions of phenology shifts, i.e. towards earlier appearance of spring taxa and later appearance of autumn taxa in warm years, these patterns were by no means clear-cut. The dominant role of temperature in driving phenological variation suggested by some studies seems to be obscured by biotic and climatic controls acting differently along our environmental gradient.

Keywords: climate teleconnections, European shelf waters, global warming, latitudinal variations, North Atlantic, phenology, zooplankton

Introduction

Changes in phenology (the seasonal timing of annually recurring events) have been recognized as a prominent and "universal" response to climatic warming (Parmesan and Yohe, 2003; Chiba *et al.*, 2006; Parmesan, 2006). Zooplankton can be excellent indicators of such climate-induced changes because their physiology is sensitive to temperature and their short life span enables a tight coupling of their population dynamics with climate (Richardson, 2008). This group is the primary means of transfer of primary production to higher trophic levels, including commercial fish (Richardson, 2008), so changes in the phenology of zooplankton could have a big impact on marine food webs and fish production because of the potential for uncoupling of interactions between prey and predators, according to the match–mismatch hypothesis

(Cushing, 1990; Edwards and Richardson, 2004; Ji *et al.*, 2010; Mackas *et al.*, 2012).

The importance of phenology, coupled to the availability of time series data, has led to an increasing study of how phenological shifts of zooplankton relate to warming (e.g. Edwards and Richardson, 2004; Molinero *et al.*, 2005; Conversi *et al.*, 2009; Mackas *et al.*, 2012; Usov *et al.*, 2013; Atkinson *et al.*, 2015; Reygondeau *et al.*, 2015; Borkman *et al.*, 2018). In most of these studies, the best environmental predictor of the shifts was temperature, but significant relationships to teleconnection patterns such as the North Atlantic Oscillation (Molinero *et al.*, 2005), hydrodynamic conditions, and phytoplankton dynamics have also been reported (Staudinger *et al.*, 2019. However, studies have shown marked differences in the proportion of zooplankton taxa and the specific taxa displaying significant phenology changes. For example, Edwards and Richardson (2004) reported that almost all late spring-summer zooplankton from the central North Sea had significantly advanced in their seasonality over half a century of warming. Usov *et al.* (2013) concluded that, in the White Sea, the cold water *Calanus glacialis* advanced its reproduction due to warming and the associated longer phytoplankton bloom, but warm water copepods had not changed their seasonality significantly. In some studies, clear differences in the direction of phenology shift between most spring (earlier when warmer) and autumn taxa (later when warmer) have been reported (Mackas *et al.*, 2012), whereas in others only a weak tendency for earlier occurrences of spring zooplankton taxa and later ones for autumn taxa during warm years has been observed (Atkinson *et al.*, 2015). Also, the phenological response of zooplankton has been observed to be different in holoplankton and meroplankton, but again with disparity of results (Edwards and Richardson, 2004; Reygondeau *et al.*, 2015).

These contrasting results outlined here use different taxa, time-periods, sites/regions, and phenological indices, making any synthesis difficult. To achieve a better understanding, phenology needs to be studied across multiple sites over large gradients in water temperature and with consistent methods. There is some theoretical background for understanding how phenological shifts could vary across the thermal niche of a species (Beaugrand and Kirby, 2018), but despite the high concentration of time series, especially around Europe, surprisingly few empirical studies have compared phenology across large spatial scales. Perhaps the most extensive of these was by Mackas *et al.* (2012), who found that water temperature had stronger overall effects on phenological variation than effects from food. Furthermore, in most cases (but not all) they found that similarity in zooplankton phenology time series decreased with increasing distance between sites from the North Atlantic and North Pacific. As time series lengthen and become better networked (O'Brien *et al.*, 2017), we need to combine them for a better understanding of how phenological shifts operate (Mackas *et al.*, 2012).

Climatic change also varies along spatial gradients, and climate variations over the last decades have occurred at a non-homogeneous pace over time and differentially across regions (IPCC, 2014). For example, it is clear that teleconnection patterns, such as the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), and the East Atlantic (EA) pattern, are linked to differential north-to-south weather patterns in the North Atlantic (Visbeck et al., 2001; Alexander *et al.*, 2014; Bastos *et al.*, 2016). Given these large-scale climatic variations, our overall study hypothesis is that there are latitudinal differences in the directions of phenology shifts relatable to climate, which are observed coherently across the mero- and holoplankton at each of the sites. As part of this overall hypothesis, we also tested the hypothesis that temperature has a major driving influence on phenology (Richardson, 2008, Mackas *et al.*, 2012, Thackeray *et al.*, 2016), with spring taxa appearing earlier and autumn taxa appearing later in warmer years. We, therefore, examined whether there are latitudinal patterns of zooplankton phenological change in the Northeast Atlantic Shelves Province (NECS, Longhurst, 1998), and their relationship to the main large-scale teleconnection patterns with influence in the North Atlantic (NAO, AMO, and EA), and to local environmental variables measured in routine zooplankton studies (water temperature, salinity, and chlorophyll *a* concentration). To enable this, we compared variations in zooplankton phenology both within the holoplankton and the meroplankton communities, for the same time period (1999–2013), using the same taxonomic resolution and phenology index, at four sites that lie along a latitudinal gradient in NECS [Stonehaven in the northern North Sea, L4 off Plymouth in the English Channel and Bilbao 35 (B) and Urdaibai 35 (U) in the southeastern Bay of Biscay].

Material and methods

Study area and data acquisition

Time series (1999–2013) of mesozooplankton (>200 µm) abundance, water temperature, salinity, and chlorophyll *a* concentration were obtained from four sites located along a latitudinal gradient in the NECS (Longhurst, 1998). From north to south, these sites are Stonehaven (SH) in the northwestern North Sea, Plymouth L4 (L4) in the western English Channel and U and B, both located in the southeastern Bay of Biscay (Figure 1).

SH, located 5 km off Stonehaven (56°57.8′N, 02°06.2′W), with a mean water depth of ca. 50 m, is a well-mixed site due to strong tidal currents with a weak thermal stratification usually only during neap tides in summer, and where the impact of freshwater inputs of the rivers Dee and Don (outflowing at Aberdeen, 24 km north) is reduced (Bresnan *et al.*, 2015). L4 (50°15′N, 4°13′W), located 6.5 km offshore and with a mean water depth of 54 m, is a transitionally mixed site, with stratification typically spanning May to September. Hydrographically, it is influenced both by inputs of the rivers Plym and Tamar outflowing at Plymouth and by oceanic water during periods of strong south west winds (Rees *et al.*, 2009). B and U are located relatively close to each other (B at 43°20.9′N, 3°1.6′W and U at 43°24.2′N, 2°41.7′W), are nearshore (<1 km offshore) and shallow (mean water depth of 13 m at B and 4.5 m at U) sites, but, while B is a partially mixed site influenced by the estuarine plume, U is a well-mixed and marine-dominated site (Fanjul *et al.*, 2017). Taking all sites into account, the annual mean salinity ranged between 34.2 and 35.3. Further information about the characteristics of these sites has been provided in Bresnan *et al.* (2015) for SH, Southward *et al.* (2005) for L4, and Fanjul *et al.* (2017) for B and U.

At all sites, 200-µm mesh size nets were used to sample zooplankton. At SH and L4, vertical hauls (45 m to surface at SH and 50 m to surface at L4) were performed, using Bongo and WP2 nets, respectively. At B and U, horizontal tows were carried out at mid-depth, below the halocline (if present), using a ring net. Water temperature and salinity were measured *in situ* and water samples were taken for chlorophyll analysis. Surface values of these environmental variables were used for SH and L4, and

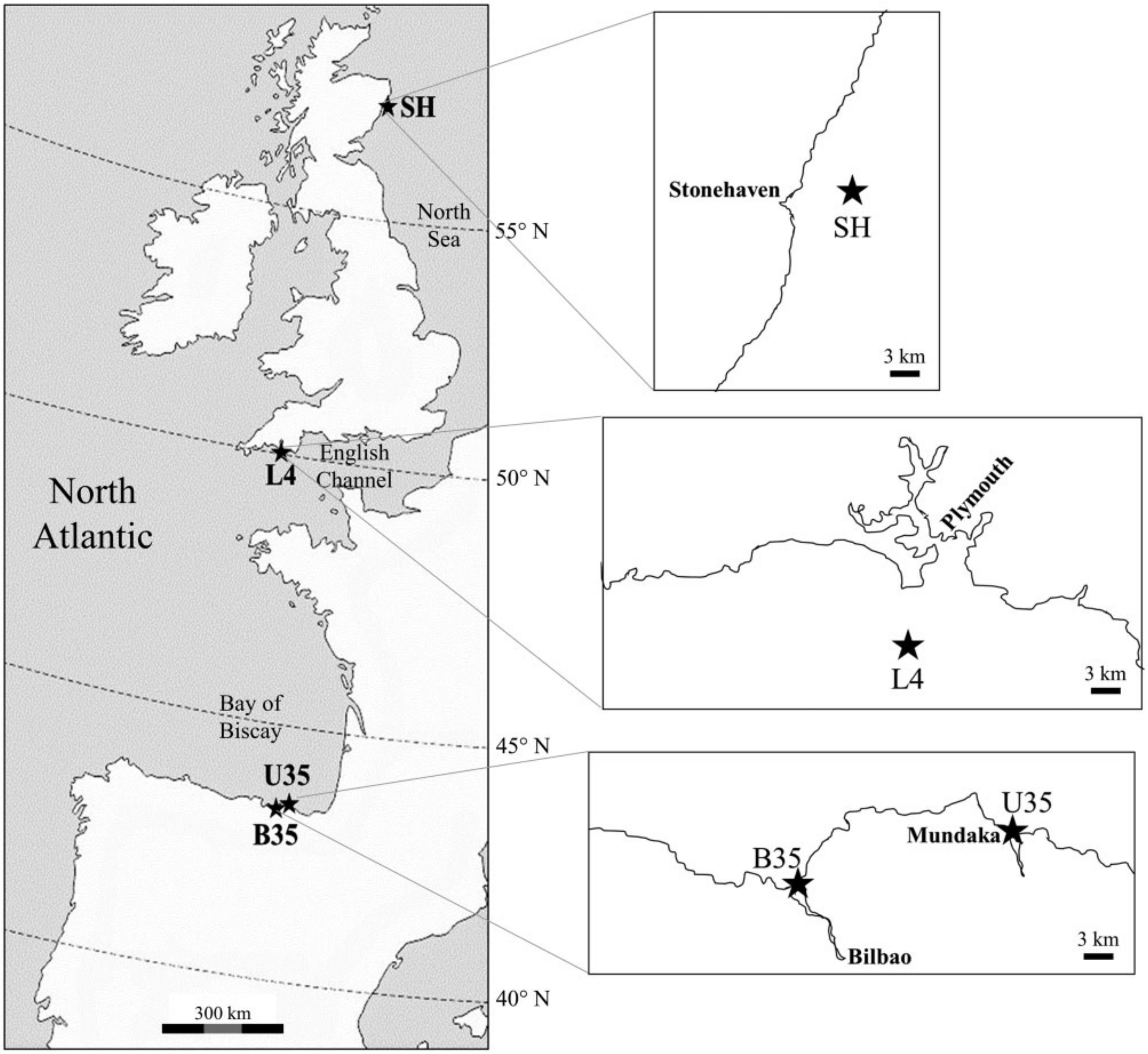

Figure 1. Map of the study area showing the location of sampling sites.

values from the sampling depth for B and U. Samplings were carried out monthly at B and U and weekly (weather permitting) at L4 and SH. Further information on sampling and analytical methods can be found in previous papers (Bresnan *et al.*, 2015; Atkinson *et al.*, 2015; Fanjul *et al.*, 2017; Fanjul *et al.*, 2018). In addition, monthly values of NAO (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii), EA (ftp://ftp.cpc.ncep.noaa.gov/wd52dg/data/indices/ea_index.tim), and AMO (https://www.esrl.noaa.gov/psd/data/timeseries/AMO/) indices were obtained from the NOAA.

Data treatment

Because of sampling frequency differences [once a month at B and U and once a week (weather permitting) at L4 and SH], to obtain the homogeneity in the data periodicity required for comparative purposes, monthly values were also used for L4 and SH by calculating the mean of all values for each month. Analogously, the day of sampling used in these latter two sites was the mean day of all sampling days for each month. Occasional missing values (fewer than 5%) in the monthly data sets were filled in by interpolation using the values of the previous and following months.

Identification of zooplankton was performed to the lowest possible taxonomic level, which depended on the expertise of the analysts involved but, when necessary, data were grouped to the lowest taxonomic level required for the between-site comparison. To examine differences in phenological patterns between holoplankton and meroplankton, data analyses were conducted separately for each group. A total of 22 taxa were analysed: (i) 13 holoplankton taxa: the cladoceran genera *Evadne* and *Podon*, the copepod genera *Acartia*, *Centropages*, *Temora*, *Oithona*, *Oncaea*, and *Corycaeus* (former genus that represents mainly the present genus *Ditrichocorycaeus* at the 4 sites), the copepod family

Calanidae (mostly represented by the genus *Calanus*), the copepod assemblage PCPC-calanus (which includes the genera *Paracalanus*, *Clausocalanus*, *Pseudocalanus*, and *Ctenocalanus*), as well as siphonophores, appendicularians, and chaetognaths, and (b) 9 meroplankton taxa: decapod, cirripede, bryozoan, gastropod, bivalve, polychaete and echinoderm larvae, fish eggs, and larvae (combined) and hydromedusae. This last taxon was included within the meroplankton because most of its abundant component taxa are meroplanktonic. We used counts for all identifiable life stages for each of the 22 taxa. We grouped the monthly values into seasons as follows: winter: January, February, and March; spring: April, May, and June; summer: July, August, and September; and autumn: October, November, and December. Annual and seasonal means, as well as the central tendencies (see below), were used for the local environmental variables and teleconnection indices when testing their relationship to zooplankton phenology changes.

The so-called "central tendency", "T index", or "centre of gravity" is a phenology index that has been widely utilized for zooplankton (Edwards & Richardson, 2004; Conversi *et al.*, 2009; McGinty *et al.*, 2011) and was chosen in the present study so that our results could be compared with those from other areas. This index was calculated for every taxon, environmental variable, and teleconnection index using the following equation:

$$T = \frac{\Sigma_{i=1}^{i=12} D_i X_i}{\Sigma_{i=1}^{i=12} X_i}$$

where T is the day of the year of the seasonal peak, i is the sampling month, D_i is the day of the year of sampling (1–365; 366 in leap years), and X_i is the abundance at the corresponding month. For further analysis, T index anomalies for each taxon were calculated as the T index value of each year minus the mean T index value for the 15-year study period. At L4 and SH, the seasonal cycles of *Corycaeus* and *Oncaea* were frequently prolonged, extending into the following year. To obtain D for those months in the following year, a value of 365 was added to the sampling day of the year, and those months were then removed from the calculations of sampling days of the subsequent year.

Multivariate ordination methods were performed using Canoco v. 4.55 (ter Braak and Šmilauer, 2002). First, preliminary PCAs (separate PCAs for holoplankton and meroplankton taxa) were carried out jointly for the four sites (SH, L4, B35, and U35). An ordination method is a technique that summarizes multivariate datasets in such a way that when they are projected onto a low dimensional space, intrinsic patterns of the data become apparent upon visual inspection (Pielou, 1984). We used the PCA as an exploratory analysis to summarize and visualize the variability in the temporal changes of the T index of zooplankton taxa from the four sites under study, and it allowed as to examine whether there were clear between-site differences/similarities in the temporal change of the T index of zooplankton taxa. Year scores obtained from this analysis (Figure 2) revealed that the major patterns of interannual variation in the zooplankton T index were very similar at the nearby B and U sites located on the southeastern Bay of Biscay, and that they were more opposite to those obtained at the SH site in the northern North Sea than to those obtained at the L4 site in the English Channel (Figure 2), following a latitudinal gradient of variation.

It was thus decided to create a composite site of the B and U sites, hereafter named Bilbao–Urdaibai (BU). A time series of the T index at BU was obtained by averaging the zooplankton T index values from the B and U sites for each year. Equally, BU values for the annual mean, seasonal mean, and T index of local environmental variables (water temperature, salinity, and chlorophyll *a* concentration) were calculated by averaging the values of the B and U sites. For the rest of data analyses, three sites were used: SH, L4, and BU.

Next, joint and separate redundancy analyses (RDAs) were performed for the three sites (SH, L4, and BU) to examine holoplankton and meroplankton phenological variability (response variables), both between sites and within sites, and their relationship with the local environmental variables and the main climatic teleconnection indices (explanatory variables). RDA can be considered a canonical (constrained) version of PCA that produces an ordination that summarizes the main patterns of variation in the response matrix, which can be explained by a matrix of explanatory variables. We used ordination biplots to visualize the relationship between the variation in the set of the response variables and the variation in the explanatory variables. Highest proximity (smaller angle) between response variables and explanatory variables indicates the best positive effect of the explanatory variable on the response variable, and lowest proximity (higher angle) between them best inverse effect. Multicollinearity between explanatory variables was checked by means of Variation Inflation Factor (VIF) analysis using vif function from the faraway R package (R version 3.5.2, 2018). Highly correlated variables ($VIF > 4$) (Hair *et al.*, 2010) were removed and not included in RDA analyses. To show more clearly the effect of explanatory variables, only those variables that showed significant conditional effects (with forward selection of variables) were depicted. In all RDAs, Monte Carlo tests were performed with 999 permutations under reduced model (ter Braak and Šmilauer, 2002).

To test separately for the relationship between explanatory variables and the patterns depicted in each of the two main modes of variability (axis 1 and axis 2) that emerged from the RDA analyses, Spearman rank correlation analyses were conducted between the year scores on each of the first two axes and all the explanatory variables under study. In addition, linear regression analyses were performed to test for unidirectional trends of T index anomalies (T index anomaly *versus* year) for each taxon.

To test for the hypothesis that in warm years spring taxa occur earlier and autumn taxa occur later (Richardson, 2008; Mackas *et al.*, 2012), we performed the following analysis. First, linear regression analyses between annual water temperature anomalies and the T index anomalies for each year were performed for each taxon. From the slope of the regression, the timing shift per 1°C increase in water temperature was estimated. Finally, the shifts in timing with warming were plotted as a function of the average phenology index for the 1999–2013 period of each taxon (which we have herein termed "average time of appearance"), which allowed us to examine whether the phenology shift direction, i.e. advance (negative values) or delay (positive values), was different for spring, summer, and autumn taxa. All correlation and regression tests were carried out using SPSS Statistics for Windows, Version 23.0 (IBM Corp., Armonk, NY).

Results

Seasonal and interannual variations of environmental variables

The seasonal and interannual patterns of variation of the environmental variables (salinity, water temperature, and chlorophyll *a*) are depicted in Figures 3 and 4, respectively. The range of monthly mean salinities was broader at BU (typically from 34.7 to 35.1) than at L4 (typically from 34.9 to 35.1) and SH (typically from 34.3 to 34.6) because BU is a site closer to shore. The monthly mean water temperatures were lowest at SH (typically from ~6°C in March to ~13°C in September), intermediate at L4 (typically from ~9°C in March to ~17°C in August), and highest at BU (typically from ~12°C in February to ~21°C in August), reflecting the latitudinal differences. Chlorophyll *a* concentration typically showed a peak in May–June at SH, whereas at L4 it showed two peaks typically in April and September and at BU a first smaller peak in March and a second larger one in August were observed. Monthly mean variations ranged from ~0.2–0.4 to ~2.3–2.8 µg l^{-1}.

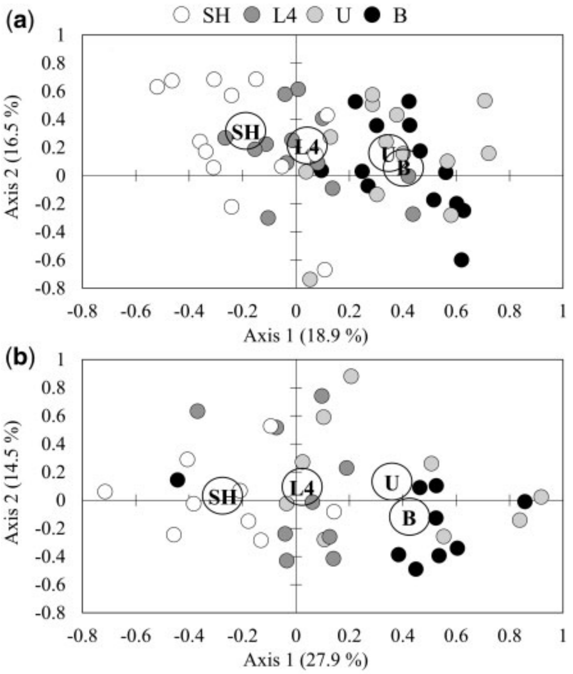

Figure 2. PCA biplots of T index anomalies of (a) holoplankton and (b) meroplankton taxa from SH, L4, U, and B sites. Large circles are the centroids of all taxa plots from each site.

The interannual variations showed no linear trend of variation in water temperature at any of the sites under study and we could only observe a slight but not significant ($r^2 = 0.234$, $p = 0.068$) tendency for an increase in salinity and a significant decrease ($r^2 = 0.378$, $p = 0.015$) in chlorophyll *a* at BU.

Between-site differences in holoplankton and meroplankton phenological changes

The first component (axis 1) of the RDA of the phenological variations at SH, L4 and BU obtained from the joint analysis for the three sites underscored the latitudinal component of the between-site differences in the interannual patterns of phenological variation for both holoplankton and meroplankton taxa (Figure 5). In general, zooplankton taxa had opposite year-to-year phenological variations at SH and BU since most holoplankton taxa and all meroplankton taxa from SH were plotted on the negative side, while most holoplankton taxa and all meroplankton taxa from BU were plotted on the positive side (Figure 5). Taxa from L4 (both holoplankton and meroplankton) showed an

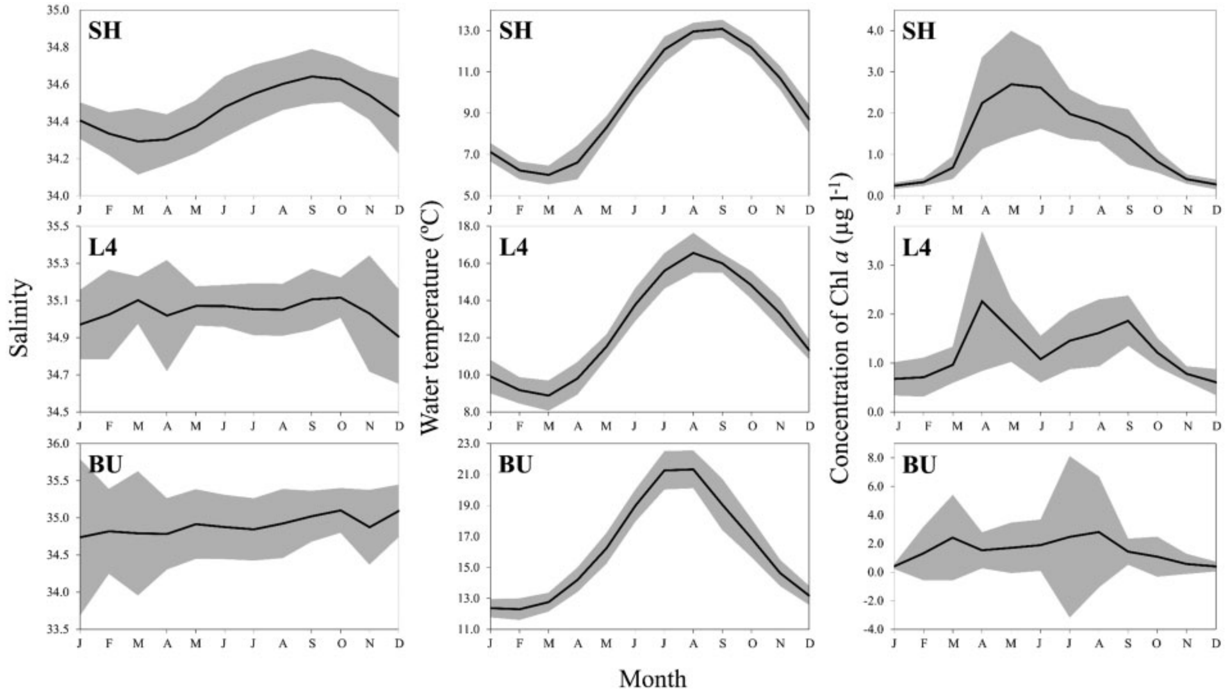

Figure 3. Monthly mean values of (and ± standard deviation in grey shade) salinity, water temperature, and chlorophyll *a* concentration at SH, L4, and BU.

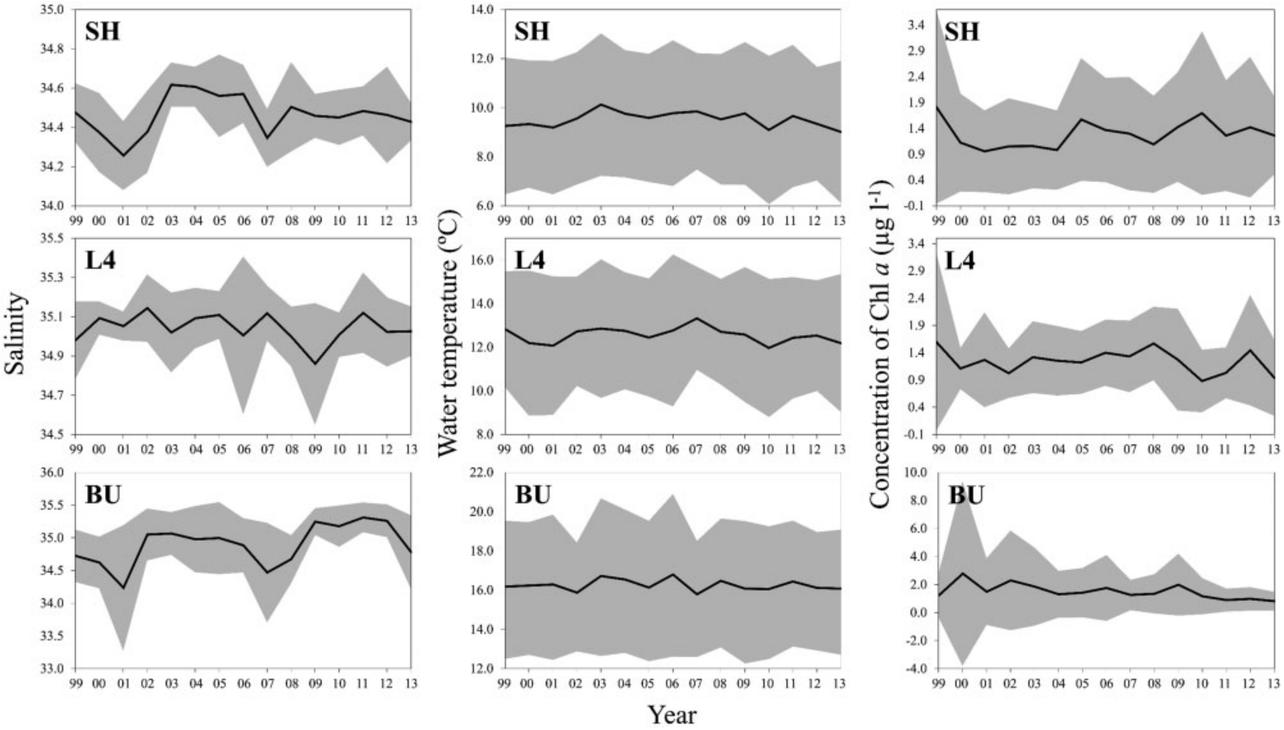

Figure 4. Annual mean values of (and ± standard deviation in grey shade) salinity, water temperature, and chlorophyll *a* concentration at SH, L4, and BU.

intermediate position but were nearer to the SH taxa in most cases. The second component of phenological variability (axis 2), however, reflected mainly phenological differences between taxa at SH among the holoplankton, and between taxa at L4 among the meroplankton. The environmental factors selected by the RDA to explain the interannual variability pattern of zooplankton phenology at the three sites under study (joint analysis for the three sites) were the annual mean salinity at BU and the EA index for holoplankton taxa, and summer salinity at BU, summer water temperature at L4 and the EA index in winter for meroplankton taxa (Figure 5a).

Correlations between environmental factors and year scores on axis 1 and axis 2 for both holoplankton and meroplankton taxa are shown in Table 1. In the case of holoplankton taxa, the first component of phenological variability (axis 1) correlated positively with salinity at BU (summer, annual, spring, and winter salinity, in decreasing order of correlation strength), summer EA, spring water temperature at BU and spring chlorophyll *a* at SH, and negatively with summer temperature at L4, spring EA and autumn water temperature at BU. The first component of phenological variability (axis 1) for meroplankton taxa correlated positively with summer salinity at BU and winter chlorophyll *a* at SH and negatively with winter water temperature at SH, summer water temperature at L4, and summer chlorophyll *a* at BU. The second component of phenological variability (axis 2) for holoplankton taxa showed highest negative correlations with the annual and the spring EA indices, and the highest positive correlation with the T index of chlorophyll *a* at BU. For meroplankton taxa, summer and winter salinities at SH and the T index of water temperature at BU were the best negatively correlated factors, and the winter EA was the best positively correlated factor.

The pattern of year-to-year changes in phenology at the three sites was similar for holoplankton and meroplankton taxa for most of the period under study (Figure 6) and the year scores on axis 1 of these taxa groups were positively correlated between them ($r = 0.683$, $p = 0.005$). The interannual variations in the best correlated environmental variables (Figure 6) showed that, after the 1999–2005 period, the spring EA index decreased within the 2006–2011 period but increased again in 2012–2013. The summer EA index showed the opposite pattern, and the most negative values of the spring EA index coincided with the most positive values of the summer EA index at the end of the 2006–2011 period. The salinity (annual mean and seasonal means) at BU showed an overall increase throughout the study period, with noticeable decreases in 2001, 2007–2008, and 2013. The spring water temperature at BU increased from 1999–2005 to 2006–2011 and decreased again in 2012–2013, while the autumn water temperature showed the opposite interannual pattern. The winter water temperature at SH increased during the first half of the study period and decreased during the second half. The summer water temperature at L4 showed higher values in the first half of the study period than in the second one. Winter and spring chlorophyll *a* concentrations at SH were lower in the first half of the study period than in the second half, while summer chlorophyll *a* at BU showed an overall decrease during the study period.

Within site differences in holoplankton and meroplankton phenological changes

RDAs (performed individually for each site) for T index anomalies of holoplankton and meroplankton taxa and the environmental factors selected by the analysis to explain them are shown in

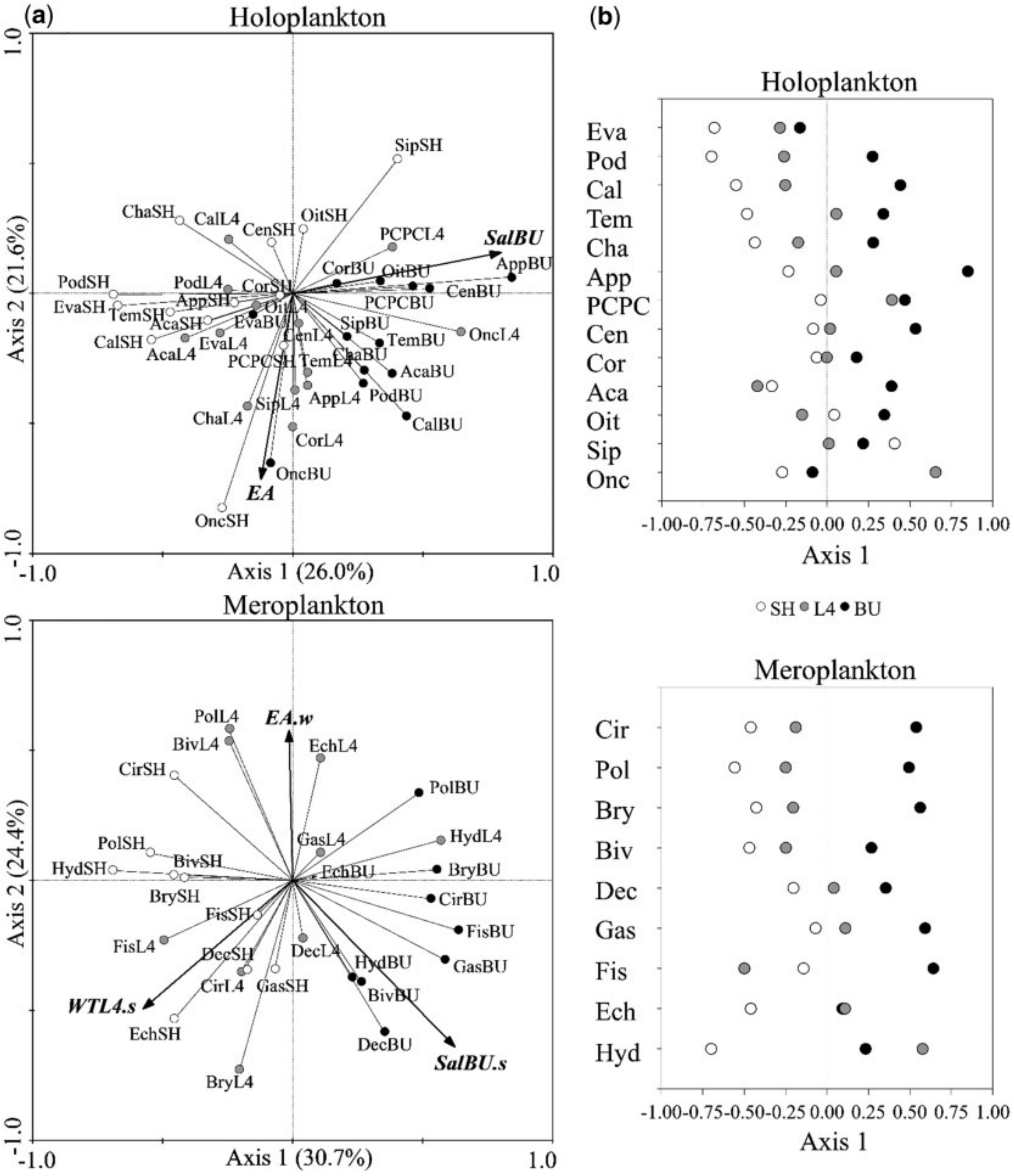

Figure 5. (a) RDA biplots of the T index anomalies of holoplankton (top panel) and meroplankton (bottom panel) taxa and the significant explanatory variables for SH (white circles), L4 (grey circles), and BU (black circles). Percentage variability explained by each axis in parenthesis. The variable abbreviation is followed by the site abbreviation. In the case of local environmental variables and teleconnection patterns, these abbreviations are followed by an additional abbreviation that represents the season (w: winter, sp: spring, s: summer, a: autumn) when they are seasonal means, or a "t" when they are T indices or by no further characters when they are annual means. (b) Plots of holoplankton (top) and meroplankton (bottom) taxa scores on axis 1 obtained from the RDAs performed jointly for SH (white circles), L4 (grey circles), and BU (black circles). Taxa abbreviations are: Aca: Acartia, App: appendicularians, Biv: bivalve larvae, Bry: bryozoan larvae, Cal: Calanidae, Cen: Centropages, Cha: chaetognaths, Cir: cirripede larvae, Cor: Corycaeus, Dec: decapod larvae, Ech: echinoderm larvae; Eva: Evadne, Fis: fish eggs and larvae, Gas: gastropod larvae, Hyd: hydromedusae, Oit: Oithona, Onc: Oncaea, PCPC: PCPC-calanus, Pod: Podon, Pol: polychaete larvae, Sip: siphonophores, and Tem: Temora. The abbreviations of local environmental variables are as follows: WT: water temperature, Sal: salinity, and Chl: chlorophyll *a* concentration.

Figure 7. The highest coherence (similar behaviour) in the inter-annual patterns of phenological change was found among holoplankton taxa at SH, where most taxa were plotted next to each other on the same side of axis 1. The EA index in spring and summer, the NAO index in summer and the T index of the concentration of chlorophyll *a* were the factors selected by the model to explain those patterns of variation. At this site, coherence decreased among meroplankton taxa, for which patterns of phenological change were mainly related to the concentration of chlorophyll *a* in winter, but also to the annual concentration of

Table 1. Environmental variables that significantly correlated (Spearman rank) with axis 1 and axis 2 year scores (RDA analyses performed jointly for the three sites under study) for holoplankton taxa and meroplankton taxa.

Holoplankton						**Meroplankton**					
Axis 1			**Axis 2**			**Axis 1**			**Axis 2**		
Variable	***R***	***p*-Value**	**Variable**	***R***	***p*-Value**	**Variable**	***R***	***p*-Value**	**Variable**	***R***	***p*-Value**
SalBU.s	**0.769**	**0.001**	ChlBU.t	0.629	0.012	SalBU.s	0.618	0.014	EA.w	0.621	0.013
EA.s	0.624	0.013	SalL4.sp	0.604	0.017	ChlSH.w	0.536	0.039	WTBU.w	0.564	0.028
SalBU	0.593	0.020	ChlBU.w	−0.514	0.050	ChlBU.s	−0.568	0.027	SalL4.a	0.524	0.045
SalBU.sp	0.579	0.024	WTSH.s	−0.518	0.048	WTL4.s	−0.636	0.011	WTBU.a	−0.546	0.035
WTBU.sp	0.546	0.035	WTL4.a	−0.600	0.018	**WTSH.w**	**−0.683**	**0.005**	EA.t	−0.550	0.034
SalBU.w	0.539	0.035	EA.sp	−0.617	0.014				SalSH	−0.581	0.023
ChlSH.sp	0.539	0.038	**EA**	**−0.722**	**0.002**				ChlSH.a	−0.608	0.016
WTBU.a	−0.561	0.030							SalSH.w	−0.630	0.012
EA.sp	**−0.697**	**0.004**							**WTBU.t**	**−0.696**	**0.004**
WTL4.s	**−0.749**	**0.001**							**SalSH.s**	**−0.742**	**0.002**

p-value < 0.01 is in bold. Dashed lines separate positive and negative correlations. Abbreviations are as in Figure 5.

chlorophyll *a*, the T index of the concentration of chlorophyll *a*, the EA index, and the AMO index in spring. The lowest coherence in patterns of phenological change among both holoplankton and meroplankton taxa was found at L4, where the ordination showed taxa scattered both along the positive and negative sides of the two principal axes of variability. At this site, winter temperature and the EA index in summer and autumn were the factors selected to explain the phenological variability of holoplankton taxa, and the EA index in winter and summer temperature to explain that of meroplankton taxa. At BU, the autumn and the annual mean EA index, in opposition to the summer NAO index and the winter AMO index, and together with winter water temperature, were selected to explain the phenological variability of holoplankton taxa. The winter AMO index was also selected to explain the phenological variability of meroplankton taxa, in opposition to the T index of chlorophyll *a*, and the concentration of chlorophyll *a* in summer and autumn.

Patterns of phenological change in individual zooplankton taxa

As seen in Figure 5b, taxa scores on axis 1 obtained from RDAs (performed jointly for the three sites) showed that, within the holoplankton, the most opposite patterns of interannual change in the phenological index between the SH and BU sites, with intermediate patterns at L4, were found for *Podon*, *Calanus*, *Temora*, chaetognaths, and appendicularians. The pattern of *Acartia* at BU was largely opposite to those at L4 and SH, and that of *Centropages* at BU also differed from those at L4 and SH. The patterns of PCPC, however, differed from SH to both L4 and BU, the latter two being quite similar, whereas the patterns of *Oncaea* were similar at BU and SH, which differed largely from that at L4. For *Evadne*, the interannual patterns of phenological change differed mainly from SH to both L4 and BU, but showing the same trend. The patterns of siphonophores were opposite to those of *Evadne* at all sites. In the meroplankton, the most opposite patterns between SH and BU were found for cirripede, polychaete, bryozoan, bivalve, and decapod larvae. Except in the last case, the interannual pattern of all these larvae at L4 showed larger differences to those at BU than at SH. The fish pattern at BU was most opposite to that at L4 and Hydromedusae showed the most opposite patterns between SH and L4. For gastropod larvae patterns, largest differences were found between SH and BU, and for echinoderm larvae, the pattern at SH differed from those at L4 and BU, being the latter two rather similar.

Positive T index anomalies mean delays in timing and negative ones signify advances. Figure 8a shows that the T index anomalies of the taxa that most contributed to the opposite phenological patterns of holoplankton at SH and BU showed delays at SH and advances at BU in the period 1999–2004, advances at SH and delays at BU in the period 2009–2011, and again delays at SH and advances at BU in 2012–2013. Similarly, the T index anomalies of the taxa that most contributed to the opposite phenological patterns of meroplankton at SH and BU showed delays at SH and advances at BU during the period 2000–2003 and advances at SH and delays at BU during the period 2009–2011. However, the delay in the timing of the annual peak during 2012–2013 at SH was not accompanied by a clear earlier timing at BU. Therefore, the phenological responses of holoplankton and meroplankton taxa were more similar at SH than at BU. In addition, these meroplankton taxa showed a clear opposite phenological behaviour between these two sites at the very beginning of the study period from 1999 to 2000. Phenological variations in these holoplankton taxa at L4 were more similar to those at SH when the entire period of study was considered, but when the analysis was performed separately for each of the two halves of the period, they were more similar to those at SH in the second half, but more similar to those at BU in the first half. Phenological variations in meroplankton taxa at L4 showed lower similarity to those at BU or SH than in the case of holoplankton taxa.

Among the environmental variables, the T index anomaly of water temperature showed a significant pattern of change ($p < 0.05$), the timing of the centre of gravity of water temperature varying from an earlier to a later occurrence along the study period at all sampling sites, while the T index of the concentration of chlorophyll *a* showed no clear interannual pattern at any study site (Figure 8b).

T index anomalies and variations in their moving averages (two consecutive years) are shown in Figures 9 and 10 for all the studied holoplankton and meroplankton taxa, respectively. Overall, tendencies over the entire study period were only weakly significant for a few taxa. In the holoplankton, weak advances in

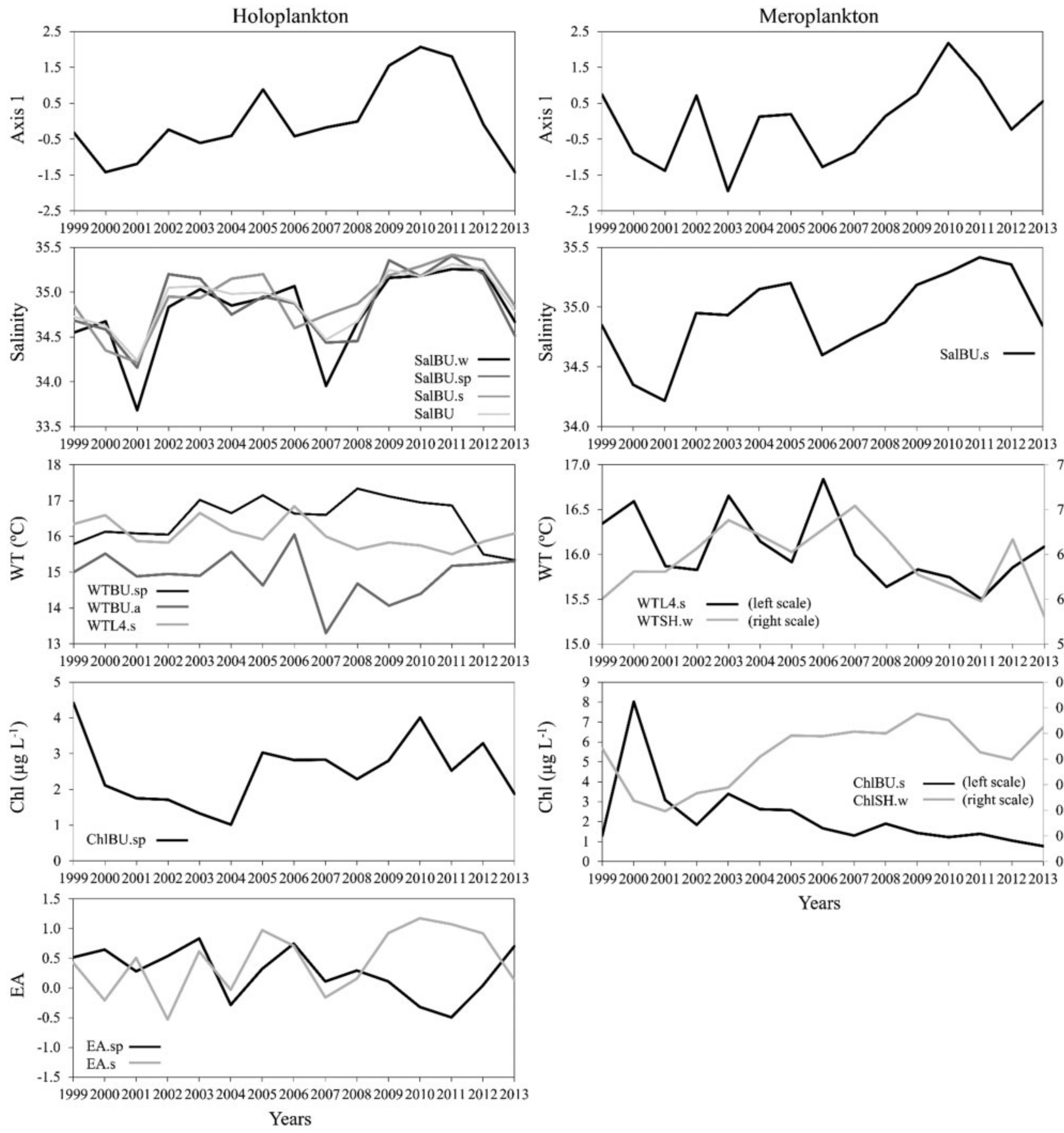

Figure 6. Interannual variations of axis 1 year scores (RDA performed jointly for the three sites under study) of holoplankton taxa and correlated variables (left panels), and meroplankton taxa and correlated variables (right panels). Abbreviations are as in Figure 5.

the timing of the annual peak were found for *Evadne* ($r^2 = 0.280$; $p = 0.043$) and *Podon* ($r^2 = 0.268$; $p = 0.048$) at SH and *Temora* ($r^2 = 0.295$; $p = 0.036$) at L4. In contrast, in the meroplankton, gastropod larvae ($r^2 = 0.309$; $p = 0.031$) at SH and gastropod ($r^2 = 0.413$; $p = 0.010$) and decapod ($r^2 = 0.362$; $p = 0.018$) larvae at BU showed delays in the timing of the annual peak over the study period.

Regarding the holoplankton (Figures 5b and 9), *Evadne* was the only taxon that showed a similar phenological tendency at the three sites during the study period, which was a pattern of phenological advance. This tendency was most marked at SH, and least marked at L4, the latter due particularly to a drastic delay of the seasonal timing in the last year of the study period. *Temora* also showed a similar tendency at the three sites for the entire period that was analysed, but in the second half of the period, it showed a clear opposite phenological behaviour at SH and BU showing leads at SH and lags at BU during 2009–2011, while showing lags at SH and leads at BU in 2012 and 2013. The clearest opposite

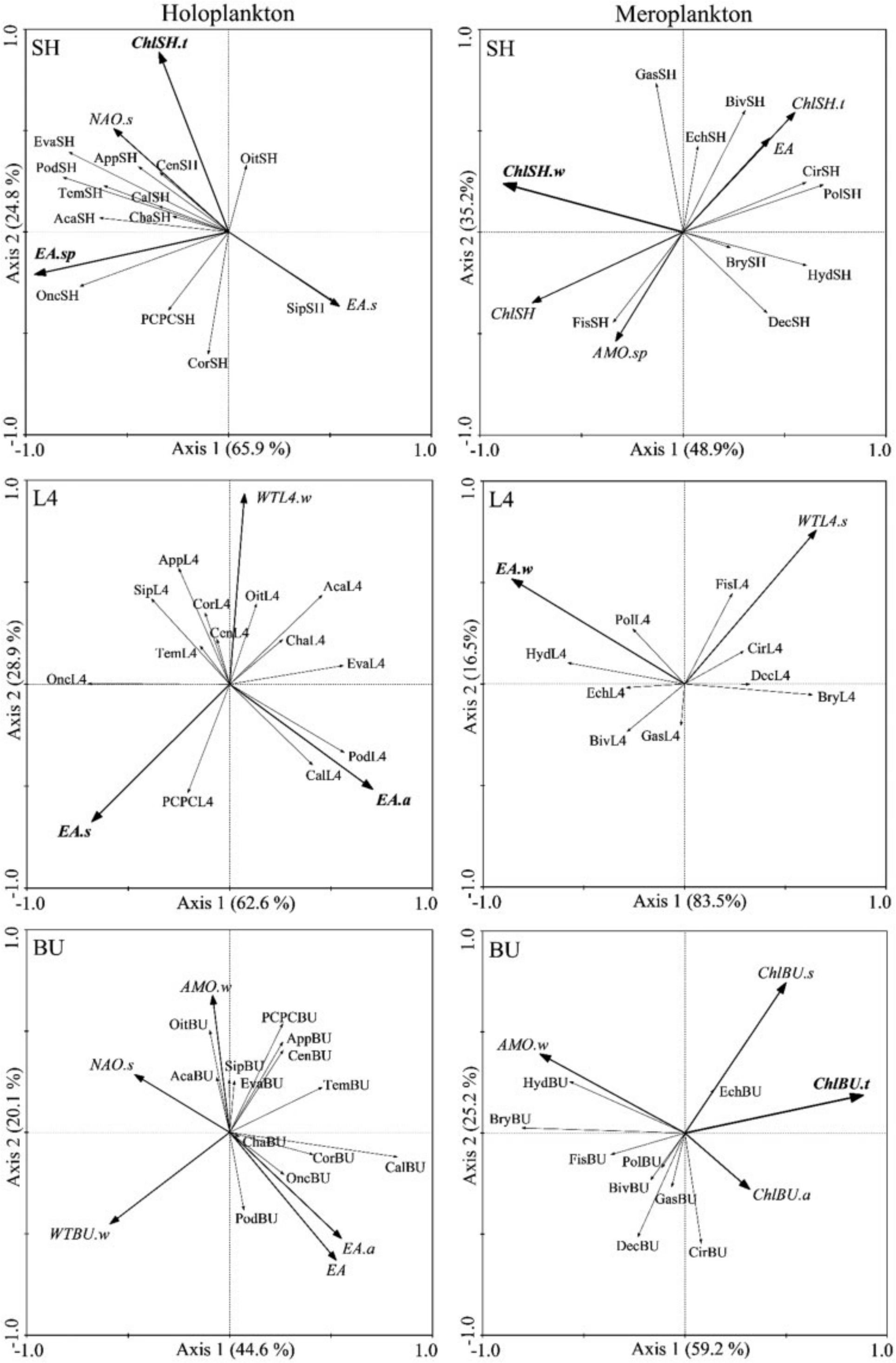

Figure 7. RDA biplots of the T index anomalies of holoplankton (left panels) and meroplankton (right panels) taxa and the explanatory variables selected in the model (significant variables in bold) for SH, L4, and BU sites. Abbreviations are as in Figure 5.

patterns during the entire period at SH and BU were observed for *Acartia*, *Podon*, Calanidae and appendicularians.

Among the meroplankton (Figures 5b and 10), clear opposite tendencies in the phenological behaviour at SH and BU were observed in cirripede and decapod larvae, which, in general, peaked later in the year in the first half of the study period and earlier in the second half at SH, while they peaked earlier in the year in the first half of the study period and later in the second half at BU. Within the meroplankton, hydromedusae showed the most differentiated phenological behaviour, with similar trends at SH and BU, which were rather opposite to that at L4. This was because hydromedusae peaked later in some years of the first half of the

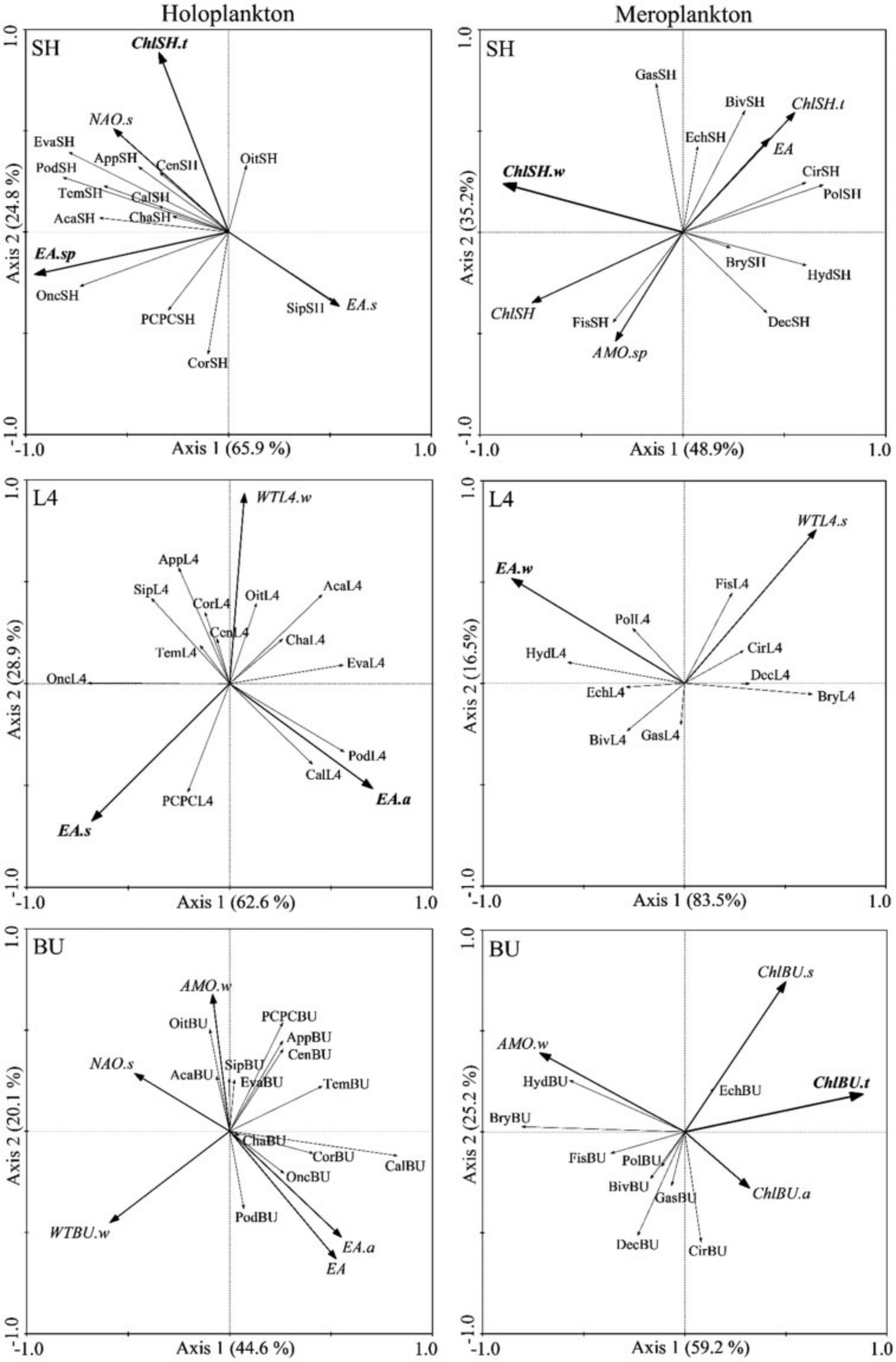

Figure 8. (a) Interannual variations of the T index anomalies (in days) of the holoplankton (left panels) and meroplankton (right panels) taxa that showed the most opposed phenological changes at SH and BU. For individual taxa values symbols and for mean values (of all taxa), lines have been used. Taxa abbreviations are as in Figure 5. (b) Interannual variations of the T index anomalies (in days) of water temperature (WT) and concentration of chlorophyll a (Chl *a*) for SH (white circles and dotted line), L4 (grey circles and line), and BU (black circles and line).

study period at SH and BU but in some years of the second half of the study period at L4. Gastropod larvae showed an overall trend towards delaying their timing at SH and BU, but the interannual phenological variations differed between sites.

Figure 11 shows the phenology shifts per 1°C for holoplankton and meroplankton taxa. The regressions of T index anomalies against temperature anomalies from which phenology shifts per 1°C temperature increase were estimated, showed R^2 values

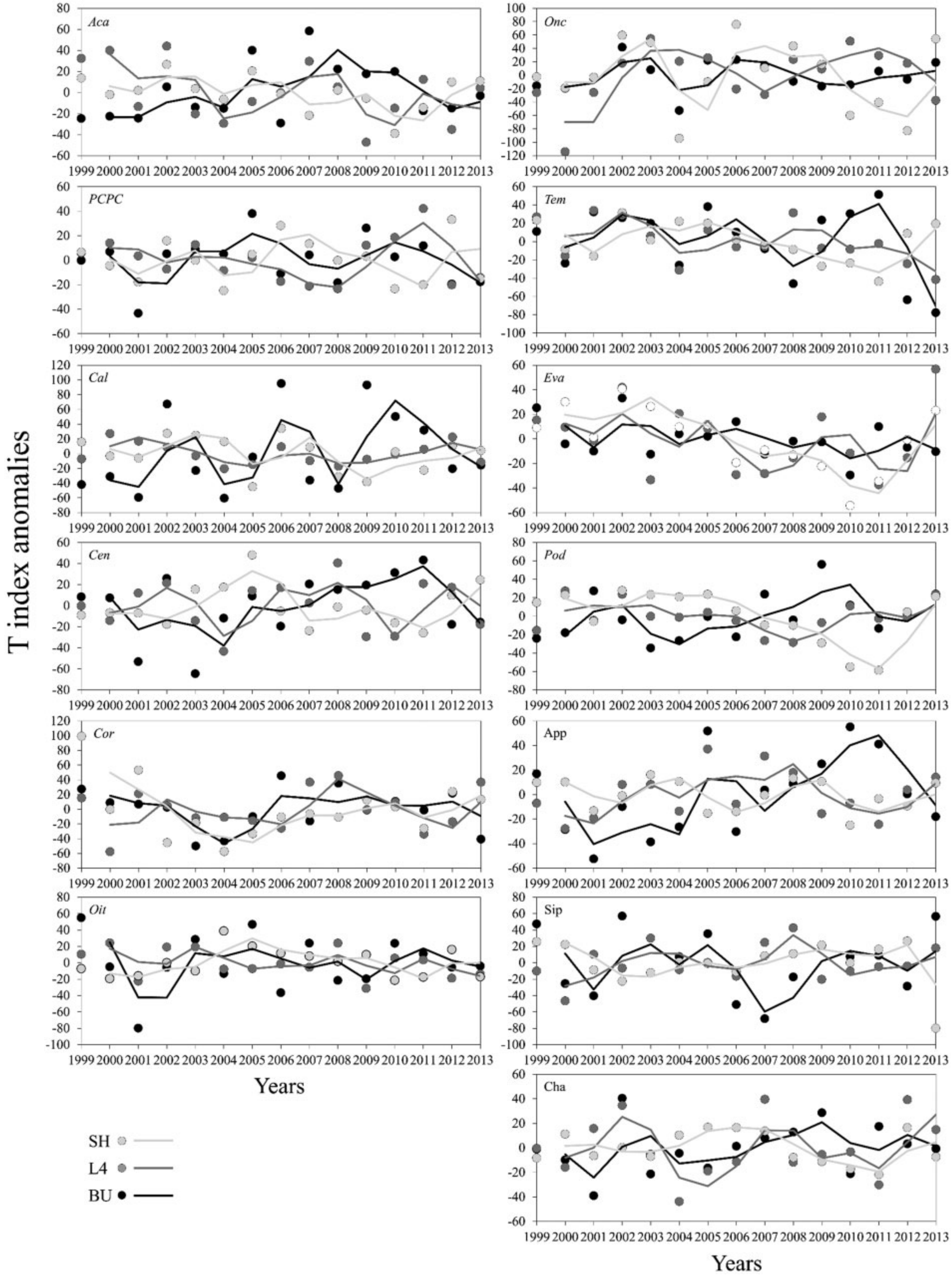

Figure 9. Interannual variations of T index anomalies (in days) for holoplankton taxa at SH, L4, and BU. Each year values are represented by symbols. Lines depict moving averages of two consecutive years. Taxa abbreviations are as in Figure 5.

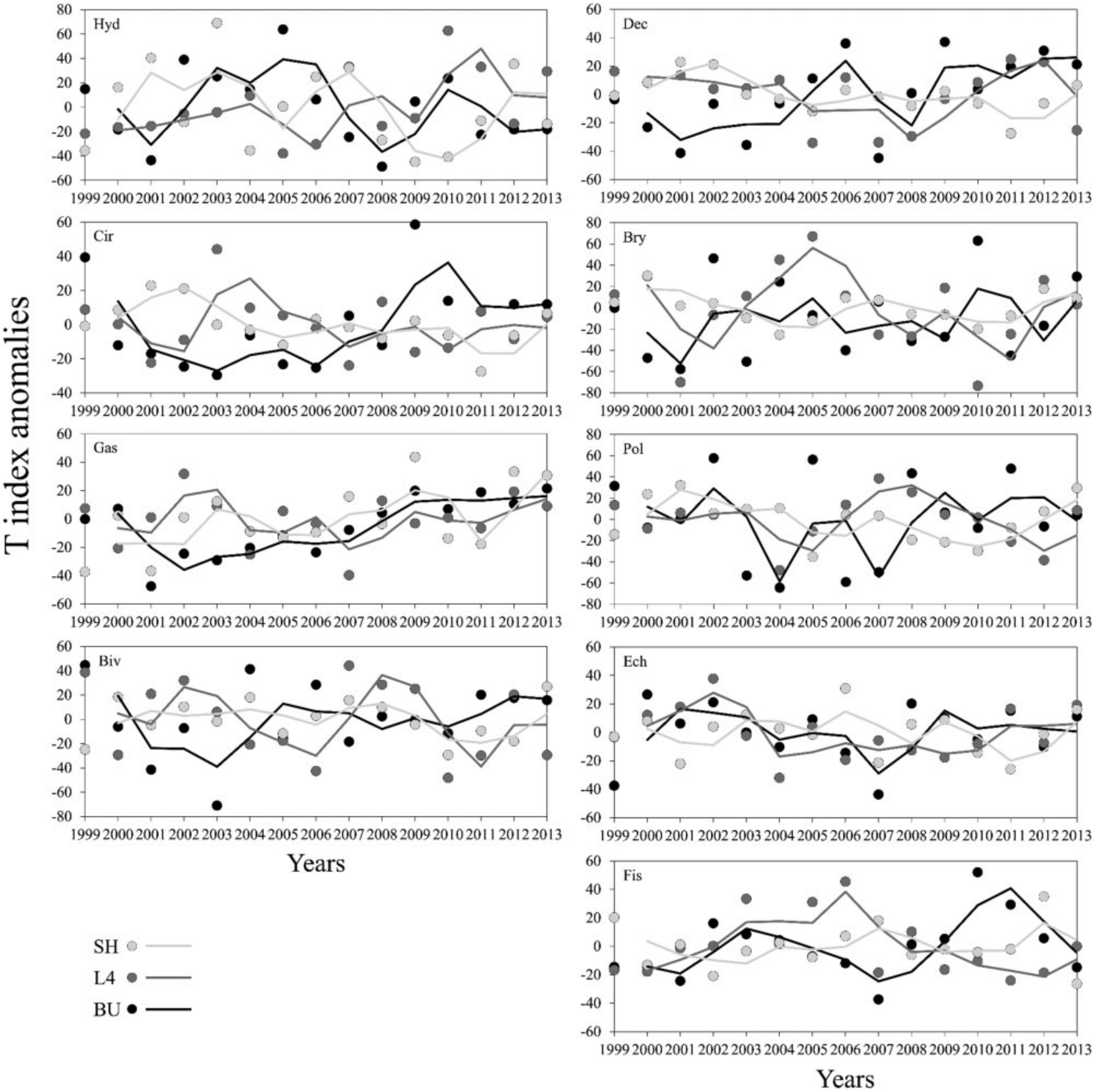

Figure 10. Interannual variations of T index anomalies (in days) for meroplankton taxa at SH, L4, and BU. Each year values are represented by symbols. Lines depict moving averages of two consecutive years. Taxa abbreviations are as in Figure 5.

>30% only in very few taxa, i.e. the cladoceran *Podon* at BU and L4 and the copepod *Acartia* at BU in the holoplankton and bivalve larvae at L4 and bryozoan larvae at BU in the meroplankton. Despite the generally weak relationship with the temperature anomalies, most holoplankton taxa tended to occur earlier when warmer at BU, while most of them tended to occur later when warmer at SH and L4. At BU and L4, positive, though non-significant ($p > 0.05$), relationships between the timing of appearance and the shift in timing per 1°C warming were found for holoplankton (explaining 27 and 18% of the variability at BU and L4, respectively). For holoplankton taxa at SH, a negative relationship was obtained, but this was driven mainly by an extremely large advance of 66 days estimated for the copepod *Corycaeus*. This is an autumn taxon whose growth period is frequently prolonged into the following year and estimating its phenology using ordinary indices may be somewhat complicated (see "Material and methods" section). When *Corycaeus* was excluded, the regression was positive but much weaker (it only explained 4% of the variability) than at L4 and BU. The positive relationships evidenced larger advances or smaller delays in taxa that occurred earlier than in those that occurred later. At L4 and SH most holoplankton taxa showed phenology shifts of <20–25 days per 1°C warming. These shifts were mainly delays at SH and both delays and advances at L4, whereas at BU for almost half of the

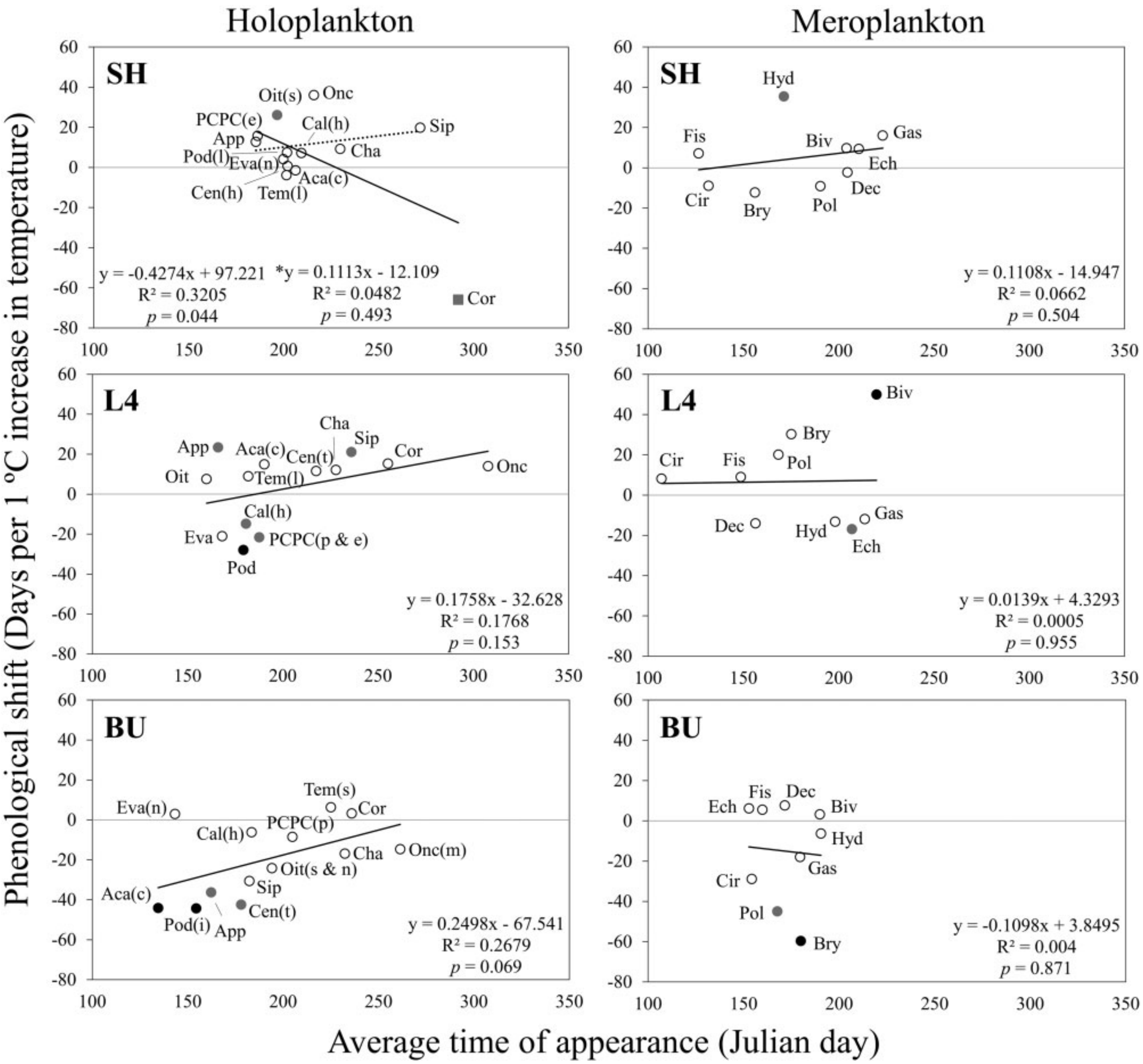

Figure 11. Relationship between phenological shifts per 1°C increase in temperature and the average time of appearance for holoplankton (left panels) and meroplankton (right panels) taxa at SH, L4, and BU. Regression lines have been depicted and regression equations, R^2 and *p*-values are also given. For holoplankton at Stonehaven the dotted line and * correspond to the regression excluding the genus Corycaeus (see text). White circles for $R^2 < 10\%$, grey circles for R^2 10–30%, and black circles for $R^2 > 30\%$. Taxa abbreviations are as in Figure 5. Letters in parentheses indicate the dominant species in a given genus or genera assemblage. A single letter denotes one dominant species (>70% of the total abundance) and two letters two dominant species with similar abundances. Aca(c): *Acartia clausi*, Cal(h): *Calanus helgolandicus*, Cen(h): *Centropages hamatus*, Cen(t): *Centropages typicus*, Eva(n): *Evadne nordmanni*, Oit(n): *Oithona nana*, Oit(s): *Oithona similis*, Onc(m): *Oncaea media*, PCPC(e): *Pseudocalanus elongatus*, PCPC(p): *Paracalanus parvus*, Pod(i): *Podon intermedius*, Pod(l): *Podon leuckartii*, Tem(l): *Temora longicornis*, and Tem(s): *Temora stylifera*.

taxa advances of between 20 and 45 days per 1°C of warming were estimated.

For meroplankton taxa (Figure 11), the relationships between the timing of appearance and the shift in timing per 1°C warming were very weak (regression lines explained only 4–6% of the variability at BU and SH and <0.1% at L4) and showed no consistency between sites (negative at BU, positive at SH and no tendency at L4). For most meroplankton taxa, the estimated shifts in timing per 1°C warming were <15–20 days at all three sites.

Discussion

Both holoplankton and meroplankton tended to show a common pattern of opposing directions of phenological change across the latitudinal range from the southeast Bay of Biscay to the northern North Sea. These opposite patterns were particularly clear for *Acartia*, *Podon*, Calanidae, and appendicularians, as well as for cirripede larvae and decapod larvae. In the English Channel, the phenological patterns were less defined and more similar to those of the North Sea, particularly in the second half of the study period. The relationship of these phenology change patterns with environmental variables was tested and among the main teleconnection patterns with effects in the North Atlantic (NAO, EA, AMO), the EA pattern was found to be significantly correlated to the observed zooplankton phenological changes along the latitudinal gradient under study. The EA pattern was suggested to be related to the intensity of upwelling, the hydrodynamic stability and the anchovy larval recruitment in the Bay of Biscay (Borja *et al.*, 2008). The EA pattern is the second mode of climate variability in the North Atlantic-European land areas and a high percentage of the multidecadal variability in winter climate is due to the combined effect of the NAO and the EA (Comas-Bru and McDermott, 2014). In southern Europe, the EA pattern is at least as important as the NAO for explaining interannual variations in climate factors such as air temperature, sea-surface temperature, precipitation and wind (see Iglesias *et al.*, 2014 and references therein) and it also has a marked influence on precipitation and likely on winds too in the British Isles (Comas-Bru and McDermott, 2014). The relationships of the EA pattern with weather factors can show opposite signs in the Iberian Peninsula and northern UK (Comas-Bru and McDermott, 2014; Bastos *et al.*, 2016), and this may be largely responsible for the opposite patterns of change in zooplankton phenology observed between the southeastern Bay of Biscay and the northern North Sea. However, it is interesting to note that the EA index was found to be much more related to holoplankton phenology changes than to meroplankton ones (for holoplankton significant correlations with the first two RDA axes and for meroplankton only with axis 2; correlations stronger for holoplankton than for meroplankton). In addition, holoplankton phenological changes were related to spring and summer EA, while winter EA was selected to account for meroplankton phenological changes. This is in agreement with the fact that meroplankton groups peak earlier in the year than holoplankton groups and cladoceran and copepod genera at all the studied sites (Fanjul *et al.*, 2017). However, the fact that the meroplankton groups we studied here are broader, i.e. contain a larger number of species, than the many genus level groups contained in the holoplankton may have also contributed since the responses of many component species may tend to cancel each other out when examining the relationships with environmental drivers.

These contrasting phenological patterns for holo- and meroplankton are interesting because over the last 50 years these two broad functional groups have shown major changes in abundance right across the NE Atlantic and NW European continental shelf (Bedford *et al.*, 2020, Schmidt *et al.*, 2020). Schmidt *et al.* (2020) invoked increasing summer food shortage due to picoplankton dominance and earlier spring blooms as contributors to the major summer decline in copepods. Meroplankton densities, by contrast, have roughly doubled over the last half century, for reasons still not fully understood (Bedford *et al.*, 2020). Based on phenology studies, holoplankton and meroplankton have been suggested to respond in different ways to common climate-related stressors in the same area (Edwards and Richardson, 2004 Reygondeau *et al.*, 2015). In this respect, our finding that holo- and meroplankton responded to climatic drivers operating at different times of year may provide clues into the changing fortunes of these contrasting groups.

Molinero *et al.* (2005) also found a significant correlation between the phenology changes of some copepod species and a teleconnection pattern in the Mediterranean Sea, although in their case it was the NAO. The lack of correlation of zooplankton phenology with the NAO index in the present study may be due to the fact that in the first decade or so of the twenty first century the NAO lost its persistence (Dippner *et al.*, 2014). Indeed, a decrease in the predictability of the NAO for forecasting benthic time series in the southern North Sea was observed (Dippner *et al.*, 2014).

We hypothesized that variations in temperature would have a dominant role in dictating phenology shifts (Richardson, 2008, Mackas *et al.*, 2012, Thackeray *et al.*, 2016, Chivers *et al.*, 2020), but this was not seen in our study. Instead, the local factors most involved in the zooplankton phenology changes varied from site to site. The concentration of chlorophyll *a* had a stronger role in explaining phenological changes at SH, temperature was the main local variable explaining phenological changes at L4 both for holoplankton and meroplankton, while chlorophyll *a* was more relevant at BU for meroplankton. This difference between sites can be due to the fact that large-scale atmospheric forcing may have different effects on regional/local hydrodynamics (Reygondeau *et al.*, 2015), and also to the fact that ecological responses and the mechanisms involved in biological changes can differ between regions, as found between the North Sea and the Baltic Sea during the North Atlantic regime shifts linked to changes in the NAO that occurred in the late 1980s (Alheit *et al.*, 2005).

The relationship to salinity at BU may be related to the fact that the EA pattern is linked to the wind patterns and the intensity of upwelling/downwelling in the Bay of Biscay (Borja *et al.*, 2008). Upwelling on the Iberian Basque coast can be considered to be weak as compared to regions located on the northwestern Iberian coast (Valencia *et al.*, 2004), however, it may still cause a noticeable dispersion of plankton off the coast (Llope *et al.*, 2006). Variations in zooplankton phenology directly related to temperature have previously been observed at L4 (Atkinson *et al.*, 2015) and elsewhere too (Edwards and Richardson, 2004; Usov *et al.*, 2013). The relationship of zooplankton seasonal timing with chlorophyll *a* at SH conforms to the paradigm that enhanced primary production contributes to advances in zooplankton phenology (Greve *et al.*, 2001). The seasonal patterns of chlorophyll *a* showed higher interannual regularity at SH than at L4 and BU (Fanjul *et al.*, 2018), and at SH it was also observed that winter (average of January, February, and March) chlorophyll *a* concentration increased ($r^2 = 0.426$; $p = 0.008$) during the study period, and that spring chlorophyll *a* concentration (data not shown) was also higher in general in the second half of the study period. In fact, the largest delay of the timing of the annual peak for many holoplankton and meroplankton taxa occurred in the period of lowest winter and spring chlorophyll *a* concentration (2000–2004) at this site, while the largest advance for the same taxa occurred during 2009–2011 with high values of chlorophyll *a* concentration both in winter and spring. Phytoplankton availability has been suggested to contribute to zooplankton phenology variations in other studies too (Usov *et al.*, 2013; Staudinger *et al.*, 2019). However, other authors have suggested no effect or at least no prominent role of the timing and magnitude of the phytoplankton bloom on zooplankton phenology for a wide range of regions including L4 (Mackas *et al.*, 2012; Atkinson *et al.*, 2015). This agrees with our results at L4, where chlorophyll *a* was not selected (neither its T index nor its seasonal mean concentrations) to account for the phenological variations in holoplankton and meroplankton assemblages. However, strong predation controls have also been found to significantly affect copepod seasonality and thereby timing indices at L4 (Maud *et al.*, 2015; Cornwell *et al.*, 2018; Atkinson *et al.*, 2018). At BU, chlorophyll *a* concentration in summer and autumn and the timing of the chlorophyll *a* concentration were related to phenological variations in the meroplankton, but such relationships had not a plausible explanation. This may reflect the fact that BU integrates two sites with noticeable differences in the magnitude and seasonal pattern of chlorophyll *a* concentration (Fanjul *et al.*, 2018).

In addition, in the present work, phenological changes in zooplankton taxa were found to be better related to seasonal mean than annual mean variations in environmental variables. It is clear that interannual variations in climate variables have been seasonally heterogeneous in the last decades (Rebetez and Reinhard, 2008; Straile *et al.*, 2015; Tabari and Willems, 2018) and it seems that the analysis of the relationship between zooplankton phenology changes and environmental factors can provide more insightful results when variations in environmental factors by seasons are considered. In fact, Chivers *et al.* (2020) found that warming, in general, but more specifically the rate of spring temperature rise was the most important environmental driver of dinoflagellate phenology in the North Sea.

Furthermore, in the present study, the season-specific relationships were, in turn, linked to the seasonality of zooplankton taxa at each site. In this regard, at SH, seasonal peaks of most holoplankton taxa occurred in summer (Fanjul *et al.*, 2017) and their phenological changes were mainly related to the spring EA index and to the T index of chlorophyll *a*, phytoplankton biomass peaking at the end of spring (Fanjul *et al.*, 2017); by contrast, most meroplankton taxa showed their maxima at the beginning of spring (Fanjul *et al.*, 2017) and their phenology changes were mainly related to winter chlorophyll *a*. Similarly, at L4 most holoplankton taxa peaked either at the beginning of spring or end of summer/autumn (Fanjul *et al.*, 2017) and the variables that explained most of their phenological variations were winter temperature and the EA index in summer and autumn, whereas most meroplankton taxa peaked in between the two peaks of holoplankton (Fanjul *et al.*, 2017) and winter EA index was the variable selected by the model to explain their phenology changes. In the case of the BU site, both holoplankton and meroplankton taxa peaked mainly in early spring or early summer (Fanjul *et al.*, 2017), but only the T index of chlorophyll *a* was selected by the model to explain meroplankton phenology changes. Zooplankton phenology has already been shown by other authors to be associated to environmental conditions usually with a 1–2-month lag (although non-lagged effects have also been reported; see Mackas *et al.*, 2012). Overall, our results suggest that in the studied area spring and summer values of environmental variables are the ones that may affect most holoplankton phenology changes, while winter values seem to be more influential in the case of meroplankton.

Within the holoplankton taxa that showed contrasting phenological changes at SH and BU, the largest changes were observed in the last years of the study period, from 2008–2010 to 2012–2013, whereas in the case of meroplankton taxa, largest changes occurred at the beginning of the study period. As for holoplankton, the change in meroplankton coincided with a strong decrease of spring water temperature at BU, but in general, it seemed to be driven by a combination of factors linked to a reversal of spring and summer EA values, in the sense that the strong divergence between the highest summer EA index values and the lowest spring EA index values, which increased during the 2009–2011 period, disappeared with the decrease of the summer EA index values and the sudden increase in the spring EA index values during the 2012–2013 period. For the meroplankton, the largest phenological changes at the beginning of the study period coincided with a strong increase of summer chlorophyll *a* concentration and a decrease of summer salinity at BU, and with a strong decrease of winter chlorophyll *a* concentration at SH. However, in general, there was no agreement between taxa about which were the years of largest changes. In accordance with this observation, during the regime shifts detected in the North Sea in the last decades, it was found that the timing of change varied between planktonic groups and species within those groups (Beaugrand, 2004; Beaugrand *et al.*, 2014).

In the context of climate change, phenological change is of great interest partly because of the potential for differing shifts between taxa phenology to alter food web interactions. Edwards and Richardson (2004) reported that most zooplankton taxa showed a trend of advance in their seasonal timing in the central North Sea from 1958 to 2002. For the same area and time period, Chivers *et al.* (2020) found 39 days advance in the timing of the peak abundance of dinoflagellates which was related to the rate of spring temperature rise. In the present work, unlike in Edwards and Richardson's (2004) study, very few zooplankton taxa showed unidirectional linear trends in seasonal timing and these were statistically rather weak. In agreement with our results, Atkinson *et al.* (2015) found no significant long-term trends in most zooplankton species' phenology variations at L4 during the 1988–2012 period, which encompassed a significant warming trend. It has to be noted that during the present study period (1999–2013), a delay trend in the central tendency (T index) of water temperature was detected at all the sites under study, but no trend of increase in water temperature was observed at any of them. In fact, during this time period, globally there were a reduction in radiative forcing and a cooling due to natural internal climate variability, as compared for example to the longer time-window from 1952 to 2012 (IPCC, 2014). Indeed, the subpolar North Atlantic decadal upper ocean and sea surface temperature trends reversed from warming during the 1994–2004 to cooling over 2005–2015 (Piecuch *et al.*, 2017). The timing of the change in pattern of zooplankton phenology variations (around 2005) observed in the present work agrees well with the timing of the reverse in surface temperature trends reported by Piecuch *et al.* (2017), although an additional reversing was detected in our phenology data during 2012–2013. This further suggests that zooplankton phenology changes might ultimately reflect large-scale atmospheric and hydrodynamic changes. In addition, it is clear that, given the uneven pace of climate change (IPCC, 2014), the time window of analysis appears critical for the observation of trends in phenology variations related to warming.

Although annual mean water temperature did not show significant trends of increase during our period of study at any of our sites, we wanted to test the hypothesis that spring taxa tend to occur earlier and autumn taxa later in warmer years (Richardson, 2008; Mackas *et al.*, 2012). As found by Atkinson *et al.* (2015) for L4 plankton, in the present study, the relationship between phenology and water temperature was only significant for very few taxa and amongst them, it is interesting to note that the cladoceran *Podon* showed significant advances at both BU and L4. Atkinson *et al.* (2015) using data from 1988 to 2012, found significant advances of *Acartia* (which is almost exclusively *A. clausi*) in warmer years, which in the present study were only observed at BU, but not at L4 or SH. Also, in accordance with findings by Atkinson *et al.* (2015) for L4 plankton, the relationship between the average timing of appearance and the shift in zooplankton phenology per 1°C warming was weak, particularly for meroplankton taxa at all sites and for holoplankton taxa at SH. However, interestingly, this relationship was positive for holoplankton at all sites, i.e. the direction of change was the expected from the general hypothesis. Holoplankton taxa at L4 were the ones that best conformed to the "earlier when warmer" for spring taxa and "later when warmer" for autumn taxa paradigm, since at BU and SH they showed smaller advances or larger delays, respectively, as the average timing of taxa occurred later in the year. This difference between L4 and the other two sites may be due to the fact that temperature played a more prominent role in driving phenology changes at L4 than at BU and SH, where other factors such as salinity at BU and chlorophyll *a* at SH were significant drivers. For meroplankton, the relationships were generally much weaker and only fitted the general hypothesis at SH. These poorer relationships may partly be an outcome of the composition of the assemblages we studied, since most meroplankton groups contained more species than holoplankton ones, which were represented by few species and usually largely dominated by only one. Thus, our results showed that exceptions to the generalised hypothesis were numerous, although there was some evidence to support the idea that the holoplankton phenology response to warming varied as a function of the average timing of taxa in the expected direction.

Data availability statement

Data are available on reasonable request to the authors.

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