



## Zooplankton seasonality across a latitudinal gradient in the Northeast Atlantic Shelves Province

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### ABSTRACT

Zooplankton seasonality and its environmental drivers were studied at four coastal sites within the Northeast Atlantic Shelves Province (Bilbao35 (B35) and Urdaibai35 (U35) in the Bay of Biscay, Plymouth L4 (L4) in the English Channel and Stonehaven (SH) in the North Sea) using time series spanning 1999–2013. Seasonal community patterns were extracted at the level of broad zooplankton groups and copepod and cladoceran genera using redundancy analysis. Temperature was generally the environmental factor that explained most of the taxa seasonal variations at the four sites. However, between-site differences related to latitude and trophic status (i.e. from oligotrophic to mesotrophic) were observed in the seasonality of zooplankton community, mainly in the pattern of taxa that peaked in spring-summer as opposed to late autumn-winter zooplankton, which were linked primarily to differences in the seasonal pattern of phytoplankton. The percentage of taxa variations explained by environmental factors increased with latitude and trophic status likely related to the increase in the co-variation of temperature and chlorophyll *a*, as well as in the increase in regularity of the seasonal patterns of both temperature and chlorophyll *a* from south to north, and of chlorophyll *a* with trophic status. Cladocerans and cirripede larvae at B35 and U35, echinoderm larvae at L4 and decapod larvae at SH made the highest contribution to shape the main mode of seasonal pattern of zooplankton community, which showed a seasonal delay with latitude, as well as with the increase in trophic status.

### 1. Introduction

Zooplankton comprise a key component of marine pelagic ecosystems, forming a major link between primary producers and upper trophic level consumers (Dam, 2013). In the marine environment the seasonal cycle of zooplankton abundance and composition, together with those of key environmental variables, are among the strongest contributors to total temporal variance (Mackas et al., 2012). Furthermore, the seasonality of zooplankton may have profound implications for the coupling or decoupling of trophic interactions (e.g. match-mismatch hypothesis, Cushing, 1990). Seasonal variations of zooplankton have been reported in the literature (e.g. Colebrook, 1984; Longhurst, 1998), but better knowledge of zooplankton seasonality is needed to understand how climate change impacts on phenology shifts (Ji et al., 2010), particularly in coastal areas where there is greater variability (Ribera d'Alcalà et al., 2004). In addition to describing temporal

patterns of variation, knowledge of the influence of environmental factors in marine plankton is also essential to understand ecological properties of pelagic ecosystems and their potential responses to a changing environment (Pepin et al., 2015).

Given the relevance for the entire food web dynamics, zooplankton seasonality is also important in the definition of marine eco-geographical units (Longhurst, 1998). Longhurst (1998) divided the sea into biomes, each one containing one or several provinces. The Northeast Atlantic Shelves Province (NECS) extends from Cape Finis-terre (NW Spain) to the edge of the Faroe Shetland channel in the north and as far east as the Baltic Sea, and is one of the largest continental shelf regions. Seasonal patterns of zooplankton have been studied in different areas within the NECS, e.g. North Sea (e.g. Greve et al., 2004; Van Ginderdeuren et al., 2014; Bresnan et al., 2015), English Channel (e.g. Eloire et al., 2010; Highfield et al., 2010) and Bay of Biscay (e.g. Huskin et al., 2006; Stenseth et al., 2006; Valdés et al., 2007). However,

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fewer attempts have been made to compare zooplankton community seasonal dynamics and their drivers between these different shelf areas. For example, using CPR data [Beaugrand et al. \(2000\)](#) compared zooplankton seasonality between the English Channel and the Bay of Biscay and [Mackas et al. \(2012\)](#) made comparisons between the North Sea (using a combination of CPR data and Helgoland Roads time-series data) and the English Channel (using Plymouth L4 time series data). However, to the best of our knowledge, comparative studies on coastal zooplankton community seasonal dynamics and their environmental drivers from these three areas (North Sea, English Channel and Bay of Biscay) using the same methodology for data analysis have not been conducted so far. Moreover, most studies of zooplankton seasonality have dealt with the seasonal timing of the abundance or biomass of individual taxa. The seasonal variations of individual zooplankton taxa, at four study sites in the NECS, located in the Bay of Biscay, the English Channel and the North Sea, have been examined by our group in a previous work ([Fanjul et al., 2017](#)), identifying different types of seasonal patterns within the main components of zooplankton communities. However, a need to extend the analysis studying the influence of environmental drivers on the seasonal patterns at the community level was identified. Multivariate ordination methods are very useful for this purpose, as they help to understand the drivers of seasonality based on a more holistic and synthetic approach ([Walker and Jackson, 2011](#)).

The aim of the present work was to compare zooplankton community seasonal patterns and their environmental drivers at four coastal sites in the NECS, located in the Bay of Biscay (Urdaibai 35 and Bilbao 35), the English Channel (Plymouth L4) and the North Sea (Stonehaven), for which comparable time-series exist, thus covering almost the entire latitudinal range within this province. In addition, the two sites located in the Bay of Biscay are at the same latitude but differ in their trophic status ([Iriarte et al., 2010](#)). Therefore, time-series from these four sites allowed us to explore the influence of latitude and anthropogenic nutrient enrichment on the seasonal dynamics of zooplankton community in the NECS. This is in line with the objectives of policy directives such as the Marine Strategy Framework Directive that seek to better understand the dynamics of coastal communities over broad geographical areas, identifying the effect of human activities.

## 2. Methods

### 2.1. Study area and data acquisition

Time-series of zooplankton ( $> 200 \mu\text{m}$ ) abundance, water temperature (WT), salinity (Sal) and chlorophyll *a* concentration (Chl *a*) from 1999 to 2013 obtained at four sites in the North East Atlantic Shelves province (NECS) were used in this study. These are, from south to north, Urdaibai 35 (U35) and Bilbao 35 (B35), both located in the inner Bay of Biscay, Plymouth L4 (L4) in the western English Channel, and Stonehaven (SH) in the northwest North Sea ([Fig. 1](#)). [Table 1](#) summarises conditions and sampling at the four sites.

#### 2.1.1. B35 and U35

B35 ( $43^{\circ}24.15'N$ ,  $3^{\circ}5.25'W$ ) is a coastal site ( $< 1 \text{ km}$  offshore) influenced by the plume of the estuary of Bilbao (high nutrient enrichment and pollution). It is partially mixed and has a mean depth of 13 m. U35 is a shallower (mean depth of 4.5 m), well-mixed coastal ( $< 1 \text{ km}$  offshore) site, that bears the influence of the Urdaibai estuary, but because of high tidal flushing, the estuarine influence is much lower than at B35. For the study period, these sites could be classified as mesotrophic (B35) and oligotrophic (U35) according to the Chl *a* concentration criteria ([Molvær et al., 1997](#); [Smith et al., 1999](#)).

At both sites samplings were performed monthly. Water temperature and salinity were measured using portable multiparameter meters and Chl *a* was determined spectrophotometrically according to the monochromatic method with acidification ([Lorenzen, 1967](#)). Water temperature, salinity and Chl *a* data used in this study correspond to

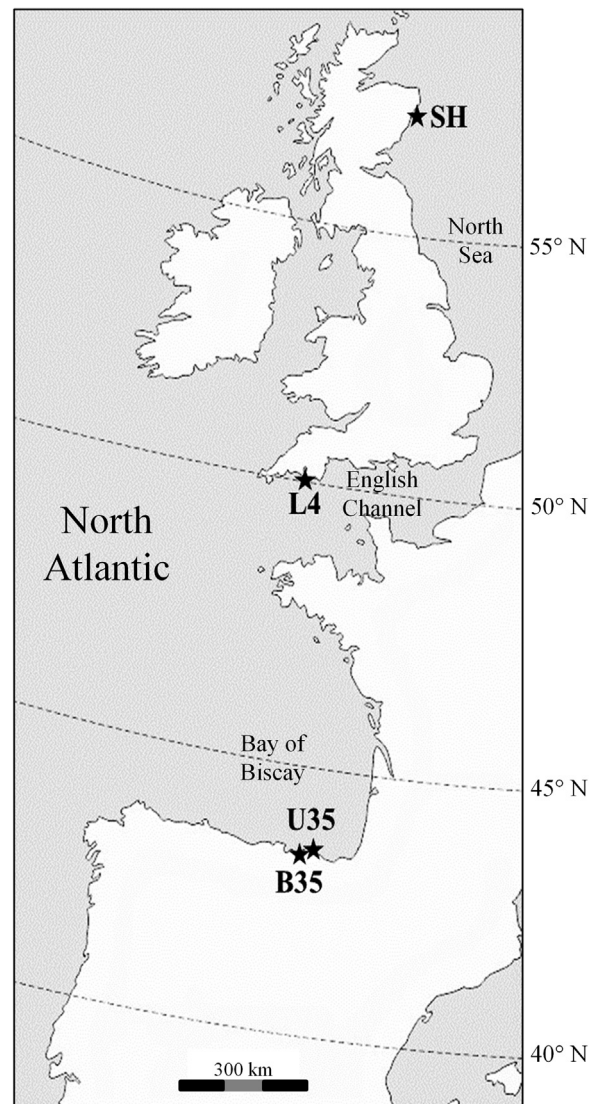


Fig. 1. Map showing the location of sampling sites.

subsurface measurements at B35 (around 4 m depth) and U35 (around 2 m depth). Zooplankton were sampled by horizontal tows at mid-depth, below the halocline (when present), of a  $200 \mu\text{m}$  mesh size ring net (mouth diameter 0.25 m) equipped with a flowmeter and preserved in 4% borax buffered formalin seawater solution. For the systematic and quantitative analysis, the original zooplankton samples were diluted in filtered sea water to a volume of 50–500 mL, depending on organism density, and sub-sampled into aliquots after gentle mixing to distribute organisms randomly. Subsamples were analyzed in Bogorov-type counting chambers under an inverted microscope ( $40\times$ – $400\times$  magnification). One or more subsamples were analyzed from each sample until 100 individuals of the most abundant taxonomic category and more than 30 individuals of the following most abundant one, or at least more than 30 individuals of the three most abundant categories were counted ([Olivar et al., 2010](#)).

#### 2.1.2. L4

L4 is a transitionally mixed site ([Southward et al., 2004](#)) with a mean depth of 54 m located about 13 km southwest of Plymouth ( $50^{\circ}15'N$ ,  $4^{\circ}13'W$ ), and 6.5 km away from the nearest land ([Litt et al., 2010](#)). It receives periodic freshwater inputs from the rivers Plym and Tamar outflowing at Plymouth and it is influenced by oceanic water during periods of strong south west winds ([Rees et al., 2009](#)). Sampling

**Table 1**  
Main characteristics of the four study sites and summary of their sampling.

| Characteristic                               |         | B35                   | U35                  | L4  | SH                                  |
|--|---------|-----------------------|----------------------|---|-------------------------------------|
| Distance offshore (km)                       |         | < 1                   | < 1                  | 6.5                                       | 5                                   |
| Water depth (m)                              | mean    | 13.0                  | 4.5                  | 54.0                                      | 48.0                                |
| Stratification/mixing                        |         | Partially mixed       | Mixed                | Transitionally mixed/stratified in summer | Mixed/weak stratification in summer |
| Salinity                                     | mean    | 34.8                  | 35.0                 | 35.0                                      | 34.5                                |
|  | (range) | (32.9-35.5)           | (30.3-35.6)          | (34.0-35.4)                               | (33.8-34.9)                         |
| Temperature (°C)                             | mean    | 16.0                  | 16.2                 | 12.6                                      | 9.5                                 |
|  | (range) | (11.3-23.7)           | (10.8-24.9)          | (7.6-19.9)                                | (4.5-13.9)                          |
| Chlorophyll <i>a</i> (µg L <sup>-1</sup> )   | mean    | 2.19                  | 0.82                 | 1.24                                      | 1.29                                |
|  | (range) | (0.08-31.33)          | (0.04-7.91)          | (0.23-6.29)                               | (0.09-5.96)                         |
| Samplings/month                              |         | 1                     | 1                    | 4   | 4                                   |
| Tows/timepoint                               |         | 1                     | 1                    | 2   | 2                                   |
| Reference of sampling and analytical methods |         | Aravena et al. (2009) | Fanjul et al. (2017) | Atkinson et al. (2015)                    | Bresnan et al. (2015)               |

is carried out weekly (weather permitting).

Water temperature was initially measured using a thermometer placed inside a stainless steel bucket and with a CTD since 2000. More details on the methodology used for data acquisition can be found in Atkinson et al. (2015). Briefly, Chl *a* was determined by using reversed-phase HPLC and we have used surface values for water temperature, salinity and Chl *a*. Two replicate vertical net hauls (WP2 net, 200 µm mesh size, 0.57 m diameter) from 50 m to the surface were used to collect zooplankton samples. These samples were stored in 5% formalin. Subsamples were taken with a stempel pipette for identifying and counting smaller organisms, whilst larger and rarer organisms were counted in subsamples, often one-half to one-eighth, taken with a Folsom splitter.

### 2.1.3. SH

SH is located 5 km offshore from Stonehaven (56°57.8'N, 02°06.2'W). It has a mean depth of ca. 48 m with reduced freshwater inputs from the rivers Dee and Don (outflowing at Aberdeen, fifteen miles north). This site remains well mixed for most of the year due to strong tidal currents, and a weak thermal stratification is usually restricted to neap tides in the summer months.

Sampling is also carried out weekly, weather permitting. Water temperature was measured using a digital reversing thermometer fitted to the Niskin sampling bottle, salinity was measured using a CTD and Chl *a* was determined fluorometrically as described in Bresnan et al. (2015). In the present study surface values were used for the latter three parameters. Zooplankton samples were taken by vertical hauls from 45 m to the surface using 200 µm mesh Bongo nets (40 cm diameter but 30 cm during January, February and March 1999) and preserved in 4% borax buffered formaldehyde. Larger zooplankton were identified and counted from the whole sample. Subsamples (of variable volume depending on density of animals, but a minimum of 2.5% of the whole sample) were taken for the identification and counting of smaller zooplankton, so that at least 100 individuals were counted. More details on the methodology used for data acquisition can be found in Bresnan et al. (2015).

## 2.2. Data preparation

As B35 and U35 were sampled monthly, usually during, or close to, the last week of the month, whereas L4 and SH were generally sampled weekly, the mean of all values for each month were calculated for L4 and SH. Occasional missing values (fewer than 5%) in the monthly data sets were filled in by linearly interpolating between the mean value of the previous month and that of the following month.

Zooplankton were identified to the lowest taxonomic level possible depending on the expertise of the analysts involved, and as a result, only copepods and cladocerans were identified to species or genera

levels at all four sites and for the entire period under study. So, based on consistency in identification throughout all time series, zooplankton data were grouped and analyzed at: (i) the herein termed *zooplankton Group level* (ZG), which included six holoplankton categories (copepods, cladocerans, appendicularians, chaetognaths, siphonophores and doliolids) and nine meroplankton categories (cirripede larvae, decapod larvae, gastropod larvae, bivalve larvae, polychaete larvae, fish eggs and larvae, bryozoan larvae, echinoderm larvae and hydromedusae) and (ii) the *copepod and cladoceran genera level* (CCGen), consisting of genera or genera-assemblages (exceptionally family) of cladocerans and copepods: *Evadne* and *Podon* genera for the cladocerans and *Acartia*, *Centropages*, *Temora*, *Oithona*, *Oncaea*, *Corycaeus* genera, the “PCPC-calanus” genera assemblage (this includes *Paracalanus*, *Clausocalanus*, *Pseudocalanus* and *Ctenocalanus*), and the family Calanidae for the copepods.

Zooplankton was expressed in units of density (individuals m<sup>-3</sup>) and prior to Redundancy Analyses (RDA), the zooplankton density data were transformed using log (x + 1) (ter Braak and Šmilauer, 2002).

## 2.3. Statistical analyses

Multivariate ordination methods were used to model the relationship between zooplankton community structure and explanatory variables using Canoco v. 4.55 (ter Braak and Šmilauer, 2002). Depending on whether the relationships between taxa and environmental variables are unimodal or linear, the use of Canonical Correspondence Analysis (CCA) or Redundancy Analysis (RDA), respectively, is advised (ter Braak and Šmilauer, 2002). To elucidate this, as a first step, Detrended Correspondence Analyses were performed, as recommended by ter Braak and Šmilauer (2002). Since the length of the longest gradient was in all cases < 2, we opted for conducting RDAs. Separate RDA analyses were performed for each of the four sites (B35, U35, L4 and SH) and each of the two taxonomic levels (ZG and CCGen) tested.

In order to extract the seasonal pattern of the zooplankton community, as well as the contribution of the different taxa to this seasonal variability, partial RDAs in which months were used as categorical explanatory variables and years as categorical covariables (thereby removing the effect of years) were performed.

In order to test the relationship between zooplankton community seasonal variations and environmental variables, preliminary partial RDAs were carried out using as explanatory variables the relevant water environment variables routinely monitored at all sites, namely, water temperature (WT), Chl *a* and salinity (Sal). Values of these variables are surface ones at L4 and SH and, although zooplankton samples were collected from surface down to 45 or 50 m, they are a valid proxy of the environmental variability that drives the seasonal variations of zooplankton. In order to obtain the final models, these partial RDAs were re-done, but using as explanatory variables only those that, in the



preliminary partial RDAs, significantly explained some of the zooplankton data variation (conditional effects, with forward selection of variables). The rest of environmental factors (i.e. the non-significant ones) were included as supplementary variables, thus not influencing the analyses.

In all RDAs Monte Carlo tests were performed with 499 permutations under reduced model (ter Braak and Šmilauer, 2002). The permutations were unrestricted and the blocks defined by the covariables.

In order to test more specifically the relationship between environmental factors and the seasonal patterns represented along the two main ordination axes obtained in RDAs, Spearman's rank correlation coefficient ( $\rho$ ) were carried out between the sample scores and environmental variables, separately for each ordination axis.

Additionally, in order to test for differences between the sites in the seasonal patterns obtained for each of the two main axes, between-site Spearman rank-order correlations of the month scores along each axis were carried out.

Finally, between-year correlation analyses were performed for temperature, Chl *a* and total zooplankton abundance (Pearson correlation for the former and Spearman rank correlation coefficient for the two latter) to assess differences between sites in the degree of year-to-year regularity of the annual cycles of those variables. These differences were determined from the frequency distribution of the correlation values for each variable at each site. These correlations were thus performed to examine how well correlated were the seasonal patterns of different years within the time series for each variable, and can be taken as indicators of the regularity or recurrence of the seasonal cycle over the time series at each site. A lower regularity would mean that the seasonal cycle shows more variations between the different years. All correlations were carried out using SPSS Statistics for Windows, Version 23.0 (IBM Corp., Armonk, NY). The use of the parametric Pearson correlation or the nonparametric Spearman rank correlation coefficient test was decided after testing for normality (Shapiro-Wilk test) and homoscedasticity (Levene test).

### 3. Results

#### 3.1. Seasonal patterns of zooplankton community and taxa contribution

The result of multivariate ordination analysis is the ordination of data along axes. The first and second axes represent the main (dominant) and second main (less dominant) modes of variability (in the present case, seasonal variability of zooplankton community), respectively. The RDA month scores along axis 1 revealed differences in the main seasonal mode of zooplankton variation from U35 to L4 and to SH, which were more evident for CCGen than for ZG (Fig. 2).

For ZG the main differences were found between U35 and both L4 and SH. The community which was most different from that of late

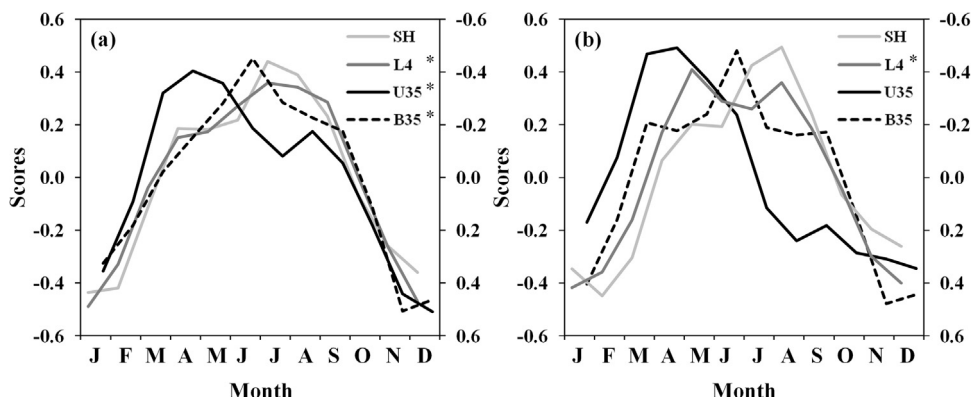
**Table 2**  
Between-site correlation (Spearman rank correlation coefficients with p-values in parentheses) of the month scores on Axis 1 for zooplankton groups (ZG) and cladoceran and copepod genera (CCGen).

|       |     | U35              | L4                 | SH                 |
|-------|-----|------------------|--------------------|--------------------|
| ZG    | B35 | 0.734<br>(0.007) | 0.867<br>(< 0.001) | 0.832<br>(0.001)   |
|       | U35 |                  | 0.559<br>(0.059)   | 0.538<br>(0.071)   |
|       | L4  |                  |                    | 0.986<br>(< 0.001) |
| CCGen | B35 | 0.755<br>(0.005) | 0.748<br>(0.005)   | 0.475<br>(0.118)   |
|       | U35 |                  | 0.329<br>(0.297)   | -0.007<br>(0.983)  |
|       | L4  |                  |                    | 0.874<br>(< 0.001) |

autumn-winter occurred in spring (March-May) at U35, and in summer (July–August) at L4 and SH. For CCGen, the differences between the patterns of the three sites were much clearer: the most differentiated community from that of late autumn-winter was found in early spring (March–April) at U35 and in summer (July–August) at SH, whilst at L4 similar levels of differentiation were found in spring (May) and summer (August). Accordingly, month scores along axis 1 from U35 showed no correlation with those obtained for L4 or SH for any of the taxonomic levels tested (Table 2).

For both levels of zooplankton grouping U35 and SH showed the strongest contrast in timing of maximum scores from spring (U35) to late summer (SH). In addition, the rather similar magnitude of the two peaks obtained for CCGen at L4 depicts an intermediate situation between those at U35 and SH. At the mesotrophic B35 site the major differences from the late autumn-winter community were found in early summer (June) for both taxonomic levels tested, but the distribution of the month scores showed two more subtle secondary peaks in early spring (March) and early autumn (September) for CCGen. Month scores along axis 1 from B35 showed weaker correlation with those from U35 than with those from L4 and SH for ZG, but no correlation with those from SH was observed for CCGen (Table 2).

Regarding the contribution of zooplankton taxa to the main mode of seasonal variation (axis 1) in each site (Fig. 3), it is clear that cladocerans made a high contribution to the seasonal pattern of ZG at B35, U35 and L4, but a lower one at SH. They showed peaks in spring-early summer at B35, U35 and L4, but in late summer at SH (Fig. 1S shown as Supplementary material). Cirripede larvae also made a high contribution at the lowest latitude sites (B35 and U35), but their contribution ranked lower at L4 and SH. Cirripedes showed maxima in spring at U35, L4 and SH, and in summer at B35 (Fig. 1S shown as Supplementary



**Fig. 2.** Month scores on Axis 1 obtained from RDAs using months as explanatory variables and years as covariables for (a) Zooplankton Groups and (b) copepod and cladoceran genera. \* On right axis.

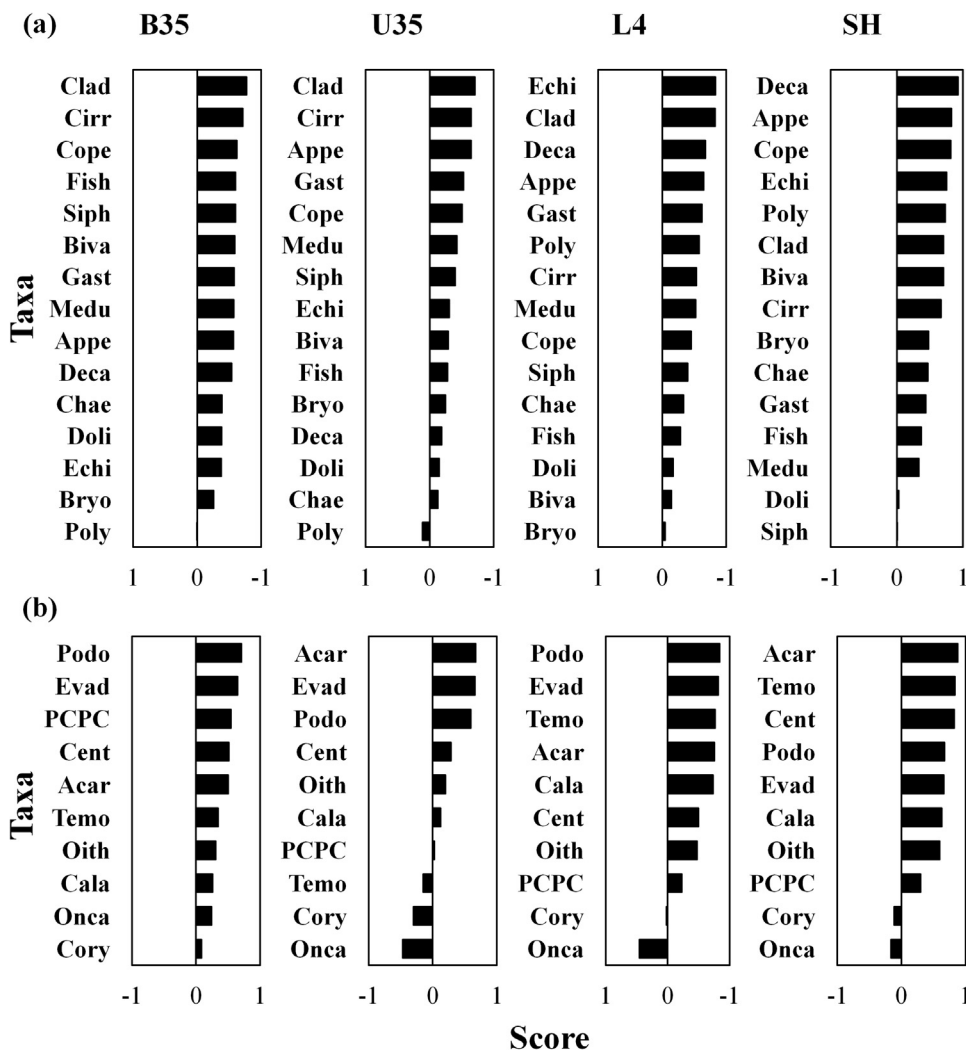


Fig. 3. Taxa scores on Axis 1 obtained from RDAs using months as explanatory variables and years as covariables for (a) zooplankton groups and (b) copepod and cladoceran genera. Acar: *Acartia*, Appe: appendicularians, Biva: bivalve larvae, Bryo: bryozoans, Cala: Calanidae, Cent: *Centropages*, Chae: chaetognaths, Cirr: cirripede larvae, Clad: cladocerans, Cope: copepods, Cory: *Corycaeus*, Deca: decapod larvae, Doli: doliolids, Echi: echinoderm larvae, Evad: *Evadne*, Fish: fish eggs and larvae, Gast: gastropod larvae, Hydr: hydromedusae, Oith: *Oithona*, Onca: *Oncaea*, PCPC: PCPC-calanus, Podo: *Podon*, Poly: polychaete larvae, Siph: siphonophores, Temo: *Temora*.

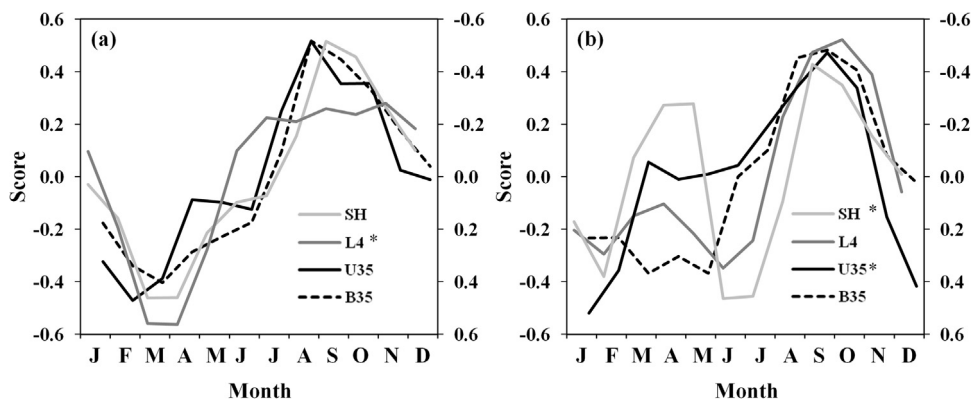


Fig. 4. Month scores on Axis 2 obtained from RDAs using months as explanatory variables and years as covariables for (a) zooplankton groups and (b) copepod and cladoceran genera. \* On right axis.

material). In contrast, decapod larvae were the group that contributed most at the highest latitude site (SH), where they showed a well-defined seasonal pattern with maxima in summer (Fig. 1S shown as Supplementary material), but their contribution decreased with decreasing latitude, particularly at U35 and B35, where they showed rather similar abundances in spring and summer. Another meroplankton group, the echinoderm larvae, was the taxon with the highest contribution at L4, where they peaked in July (Fig. 1S shown as Supplementary material), but their relevance decreased at the other

sites, particularly at the lowest latitude (B35 and U35), where they peaked earlier in the year. Appendicularians ranked high at all latitudes in oligotrophic sites (U35, L4 and SH), where they showed a latitudinal delay in their maximum densities from late winter to early summer, but not at the mesotrophic site (B35), where they peaked in late spring (Fig. 1S shown as Supplementary material). Regarding the main mode of variability (axis 1) for CCGen, *Podon* and *Evadne* were among the three taxa with the highest contribution at B35, U35 and L4, but not at SH (Fig. 3b). The occurrence of the annual maximum densities of the

**Table 3**

Between-site correlation (Spearman rank correlation coefficients with p-values in parentheses) of the month scores on Axis 2 for zooplankton groups (ZG) and cladoceran and copepod genera (CCGen).

|       |       | U35                                   | L4                                    | SH                                    |
|-------|-------|---------------------------------------|---------------------------------------|---------------------------------------|
| ZG    | B35   | <b>0.916</b><br>( <b>&lt; 0.001</b> ) | <b>0.874</b><br>( <b>&lt; 0.001</b> ) | <b>0.902</b><br>( <b>&lt; 0.001</b> ) |
|       | U35   |                                       | <b>0.720</b><br>( <b>0.008</b> )      | <b>0.741</b><br>( <b>0.006</b> )      |
|       | L4    |                                       |                                       | <b>0.916</b><br>( <b>&lt; 0.001</b> ) |
|       | CCGen |                                       |                                       | <b>0.063</b><br>( <b>0.846</b> )      |
| CCGen | B35   | <b>0.615</b><br>( <b>0.033</b> )      | 0.510<br>(0.090)                      | 0.315<br>(0.319)                      |
|       | U35   |                                       | 0.364<br>(0.245)                      | 0.755<br>( <b>0.005</b> )             |
|       | L4    |                                       |                                       |                                       |
|       |       |                                       |                                       |                                       |

latter two genera showed a delay from late winter to summer from U35 to L4 and to SH, whereas peaks were observed in spring at B35 (Fig. 2S shown as Supplementary material). *Acartia* showed the highest contribution at SH and U35, where they peaked in summer and early spring respectively, and *Temora* showed high contributions only at SH and L4, where they reached similar abundance peaks in spring and summer (Fig. 2S shown as Supplementary material).

The scores of months along axis 2 showed that the second seasonal mode of zooplankton variation had a higher between-site similarity for ZG than for CCGen (Fig. 4). The ZG responsible for this mode of variability showed the largest differences between late winter-early spring (February–April) and late summer-early autumn (August–October). L4 was an exception to this, where this second period extended through the entire second half of the year. Significant correlations of the month scores along axis 2 between all stations were found (Table 3). For CCGen the distribution of month scores was rather similar at all sites in the second half of the year (peaks in September–October) but not in the first half. Month scores along axis 2 only showed significant correlations between U35 and B35 and between L4 and SH (Table 3).

As shown in Fig. 5a, for ZG, doliolids at the lowest latitude sites (B35 and U35) and siphonophores at L4 and SH contributed most to this secondary seasonal pattern, together with chaetognaths at all sites. In contrast to the abovementioned groups, cirripede larvae and fish eggs and larvae, together with polychaete larvae at U35, also showed high contributions at all sites. Chaetognaths and doliolids at all sites and siphonophores at L4 and SH were groups characterized by peaks in late summer-early autumn, whilst cirripede larvae and fish eggs and larvae showed early annual peaks (February–April) at all latitudes in oligotrophic sites (SH, L4 and U35) and polychaete larvae had winter maxima at U35 (Fig. 1S shown as Supplementary material). For copepod and cladoceran genera there were clear between-site differences in the contribution ranking of genera, but *Oncaea*, *Corycaeus* and PCPC-calanus at all sites, *Temora* at the lowest latitude sites (B35 and U35), *Centropages* at L4 and Calanidae at SH showed high contributions. Maximum densities in *Oncaea* and *Corycaeus* or high densities in PCPC-calanus were generally observed late in the year. The annual peak of *Temora* was later at B35 and U35 than at L4 and SH; that of *Centropages* was later at L4 than at the other sites, and that of Calanidae at SH than at the other sites (Fig. 2S shown as Supplementary material).

### 3.2. Relationship between environmental factors and zooplankton seasonality

Results of the partial RDAs of zooplankton data with environmental variables as explanatory variables showed that there was a clear increase from U35 to L4 and to SH in the percentage of seasonal variation of zooplankton data explained by environmental variables at both

taxonomic levels tested (Fig. 6). It was also higher at the mesotrophic B35 site both for ZG and CCGen than at the oligotrophic U35 site.

Examination of the conditional effects of environmental variables on the seasonal zooplankton taxa variations (Table 4) showed that WT and Chl *a* were selected by the model for both taxonomic levels tested at all sites, but the largest percentage of variation was explained by WT at B35, U35 and L4, and by Chl *a* at SH. The percentage of variation explained both by WT and Chl *a* increased from south to north from U35 to SH. At the mesotrophic B35 site, WT explained a higher percentage of variance than at U35.

However, the relationship between environmental variables and each of the seasonal patterns represented by ordination along axis 1 and axis 2, respectively, was examined through the analysis of the correlations between environmental variables and sample scores along each ordination axis (Tables 5, 6). This analysis showed that Chl *a* was the factor with the highest correlation with the main mode of zooplankton community seasonal variability (sample scores along axis 1) at all stations and taxonomic levels tested (exception was at L4 where very similar correlation coefficients were obtained for Chl *a* and WT). This is in accordance with the fact that the seasonal pattern of Chl *a* (Fig. 7) showed quite a good agreement with that of monthly scores along axis 1 (Fig. 2). Conversely, WT was the environmental variable that showed the highest correlation with the second seasonal mode of zooplankton community variability (axis 2) and in most cases no significant correlation with Chl *a* was observed (Table 6).

As shown in Figs. 8 and 9, at B35 most zooplankton groups, and many copepod genera were strongly related to WT. In general, the number of zooplankton groups with high correlation with WT decreased with latitude from U35 to SH, and the relation of copepod and cladoceran genera with WT or Chl *a* also decreased with latitude from U35 to SH. At U35 a group of genera related to WT (*Corycaeus*, *Oncaea*, *Centropages*, *Temora*) was clearly distinguished from a group of genera related to Chl *a* (*Evadne*, *Podon*, *Acartia*). At SH, however, most genera showed similar relationships with WT and Chl *a*. In general, chaetognaths, doliolids and siphonophores were the zooplankton groups with the highest relationship with WT, and cirripede larvae and appendicularians the most highly related ones to Chl *a* at all sites.

### 3.3. Year-to-year regularity in the seasonal patterns of water temperature, chlorophyll *a* and total zooplankton density

Fig. 10 shows that the between-year correlation increased from B35 and U35 to L4 and to SH for WT, Chl *a* and total zooplankton abundance. This can be taken as an indication of an increase in the regularity of the annual cycle from U35 to L4 and to SH. Higher regularity would mean that the seasonal cycle varies less between years. Regularity was also higher at B35 than at U35 for Chl *a* and total zooplankton abundance.

## 4. Discussion

### 4.1. Seasonal patterns of zooplankton community

In general, our data evidenced differences between sites in the seasonal pattern that were chiefly related to the main mode of community variability (axis 1), which represented the pattern driven by taxa that peaked in the central part of the year (spring–summer) as opposed to late autumn-early winter zooplankton. On the contrary, no marked between-site differences were observed related to the second main mode of seasonal variability (axis 2) for ZG or for taxa that peaked latest in the second half of the year for CCGen. Within the oligotrophic sites a delay with latitude was apparent, since, in the southern Bay of Biscay (U35) the seasonal pattern represented by the main mode of variability of ZG was mainly accounted for by taxa that peaked in spring, whilst at the western English Channel (L4) and North Sea (SH) sites it was mainly accounted for by taxa that peaked in summer.

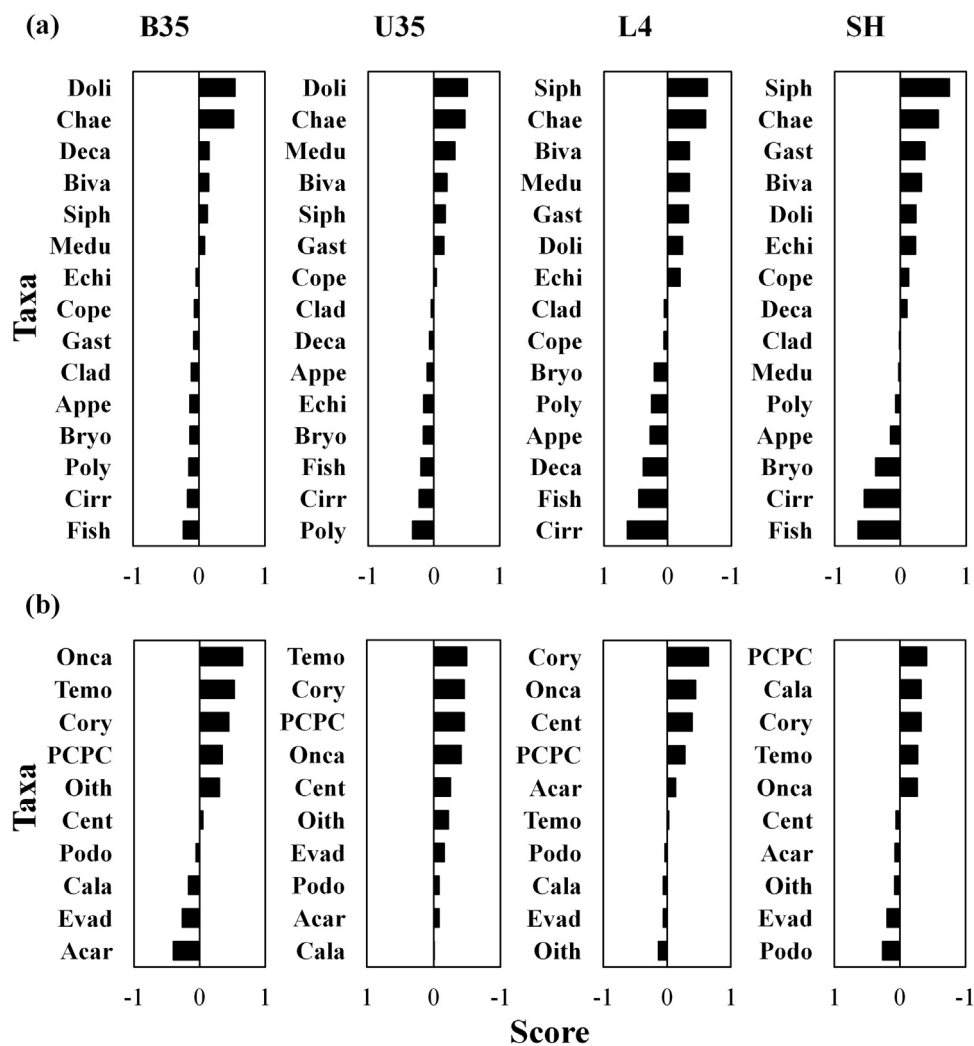


Fig. 5. Taxa scores on Axis 2 obtained from RDAs using months as explanatory variables and years as covariables for (a) zooplankton groups and (b) copepod and cladoceran genera. Abbreviations as in Fig. 3.

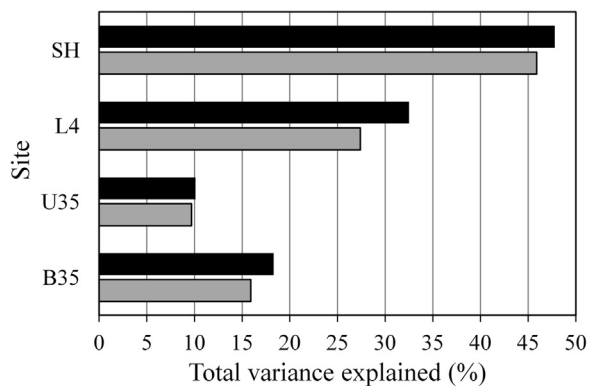


Fig. 6. Percentage of total zooplankton variance explained by environmental factors at the level of zooplankton groups (black bars) and copepod and cladoceran Genera (grey bars).

Between-site differences along the gradient from south to north were clearer at the CCGen level than at the ZG level, likely due to the fact that genera reflect better a seasonal succession of species that is masked at the group level. For instance, *Acartia* is almost exclusively *Acartia clausi* at all four sites, *Temora* is dominated by *Temora longicornis* at SH and L4 and by *Temora stylifera* at U35 and B35, and PCPC-calanus is dominated by *Pseudocalanus elongatus* at SH, *Paracalanus parvus* at B35

and U35 and the two species in similar densities at L4 (Fanjul et al., 2017). The difference in the seasonal pattern of the zooplankton community we observed between U35 and L4 agrees well with that reported by Beaugrand et al. (2000) who studied an area from the northeastern English Channel down to the southern Bay of Biscay. Similarly, Bot et al. (1996) observed a seasonal delay in the maxima of copepods from south to north in Northwest European shelves. This south to north gradient in the seasonal timing is in agreement with the general view that, for spring and summer zooplankton, the development, reproduction, and onset/termination of seasonal dormancy all shift earlier in the year where the environment is warmer (Mackas and Beaugrand, 2010; Beaugrand et al., 2014).

#### 4.2. Environmental drivers of zooplankton community seasonality

Water temperature generally explained the highest zooplankton taxa seasonal variability, as shown by RDA analyses. This agrees with the role of temperature as a primary structuring factor of the seasonality of zooplankton (Mackas et al., 2012), since it controls their rates of egg development, feeding, production, respiration and other metabolic processes (Peters and Downing, 1984; Ambler, 1985; Ikeda, 1985) and, indirectly, it can also control their food availability (Mackas et al., 2012). Despite the key role of temperature, the correlations between environmental factors and sample scores on axis 1 and axis 2 performed separately, showed clearly that the sample scores on axis 1, unlike those

**Table 4**

Conditional effects of environmental variables for zooplankton groups (ZG) and copepod and cladoceran genera (CCGen). Variables with significant effects in bold. Sal: salinity, WT: water temperature, Chl *a*: concentration of chlorophyll *a*.

|     | ZG           |             |              |              | CCGen        |             |              |              |
|-----|--------------|-------------|--------------|--------------|--------------|-------------|--------------|--------------|
|     | Variable     | Lambda A    | F            | p-value      | Variable     | Lambda A    | F            | p-value      |
| B35 | WT           | <b>0.17</b> | <b>36.58</b> | <b>0.001</b> | WT           | <b>0.14</b> | <b>29.25</b> | <b>0.001</b> |
|     | Chl <i>a</i> | <b>0.01</b> | <b>2.90</b>  | <b>0.023</b> | Chl <i>a</i> | <b>0.01</b> | <b>2.43</b>  | <b>0.041</b> |
|     | Sal          | 0.00        | 0.62         | 0.710        | Sal          | 0.01        | 1.83         | 0.096        |
| U35 | WT           | <b>0.06</b> | <b>13.06</b> | <b>0.001</b> | WT           | <b>0.07</b> | <b>13.40</b> | <b>0.001</b> |
|     | Chl <i>a</i> | <b>0.04</b> | <b>6.48</b>  | <b>0.002</b> | Chl <i>a</i> | <b>0.02</b> | <b>4.86</b>  | <b>0.004</b> |
|     | Sal          | 0.00        | 1.34         | 0.185        | Sal          | 0.01        | 1.09         | 0.318        |
| L4  | WT           | <b>0.23</b> | <b>59.09</b> | <b>0.001</b> | WT           | <b>0.18</b> | <b>42.66</b> | <b>0.001</b> |
|     | Chl <i>a</i> | <b>0.08</b> | <b>23.22</b> | <b>0.001</b> | Chl <i>a</i> | <b>0.09</b> | <b>23.81</b> | <b>0.001</b> |
|     | Sal          | <b>0.01</b> | <b>2.84</b>  | <b>0.033</b> | Sal          | 0.00        | 1.63         | 0.169        |
| SH  | Chl <i>a</i> | <b>0.31</b> | <b>79.61</b> | <b>0.001</b> | Chl <i>a</i> | <b>0.28</b> | <b>71.77</b> | <b>0.001</b> |
|     | WT           | <b>0.17</b> | <b>59.95</b> | <b>0.001</b> | WT           | <b>0.18</b> | <b>62.33</b> | <b>0.001</b> |
|     | Sal          | 0.00        | 0.74         | 0.610        | Sal          | 0.00        | 0.62         | 0.649        |

**Table 5**

Correlations between environmental factors and sample scores on axis 1 of zooplankton groups (ZG) and copepod and cladoceran genera (CCGen). Significant correlation coefficients in bold (\*\*  $p < 0.01$ ; \*  $p < 0.05$ ). Sal: salinity, WT: water temperature, Chl *a*: concentration of chlorophyll *a*.

|              | ZG                |                   |                   |                 | CCGen           |                 |                   |                 |
|--------------|-------------------|-------------------|-------------------|-----------------|-----------------|-----------------|-------------------|-----------------|
|              | B35               | U35               | L4                | SH              | B35             | U35             | L4                | SH              |
| Sal          | 0.041             | 0.070             | – <b>0.164</b> *  | <b>0.247</b> ** | – 0.011         | – 0.066         | – <b>0.160</b> *  | <b>0.333</b> ** |
| WT           | – <b>0.567</b> ** | – <b>0.313</b> ** | – <b>0.606</b> ** | <b>0.533</b> ** | <b>0.390</b> ** | – 0.124         | – <b>0.521</b> ** | <b>0.661</b> ** |
| Chl <i>a</i> | – <b>0.585</b> ** | – <b>0.359</b> ** | – <b>0.600</b> ** | <b>0.839</b> ** | <b>0.537</b> ** | <b>0.265</b> ** | – <b>0.582</b> ** | <b>0.774</b> ** |

**Table 6**

Correlations between environmental factors and sample scores on axis 2 of zooplankton groups (ZG) and copepod and cladoceran genera (CCGen). Significant correlation coefficients in bold (\*\*  $p < 0.01$ ; \*  $p < 0.05$ ). Sal: salinity, WT: water temperature, Chl *a*: concentration of chlorophyll *a*.

|              | ZG              |                 |                   |                  | CCGen           |                   |                 |         |
|--------------|-----------------|-----------------|-------------------|------------------|-----------------|-------------------|-----------------|---------|
|              | B35             | U35             | L4                | SH               | B35             | U35               | L4              | SH      |
| Sal          | 0.101           | – 0.065         | – 0.018           | <b>0.566</b> **  | 0.122           | 0.080             | <b>0.184</b> *  | – 0.079 |
| WT           | <b>0.529</b> ** | <b>0.609</b> ** | – <b>0.672</b> ** | <b>0.734</b> **  | <b>0.614</b> ** | – <b>0.525</b> ** | <b>0.445</b> ** | – 0.131 |
| Chl <i>a</i> | – 0.055         | – 0.087         | – 0.010           | – <b>0.159</b> * | 0.059           | – <b>0.206</b> ** | 0.101           | – 0.017 |

on axis 2, were generally more strongly related to Chl *a* concentration than to temperature. Therefore, since axis 1 best represented the between-site differences in the seasonal variation of the zooplankton community, we can say that it was mainly the timing of phytoplankton availability which could account for the major between-site seasonal variations of zooplankton community. The facts that (i) the phytoplankton spring bloom is delayed from U35 to L4 and to SH, and (ii) delays in phytoplankton blooms with latitude may be a general pattern within the latitudinal range at which our stations are located in the east Atlantic shelf waters (Martinez et al., 2011; Racault et al., 2012), support the view that the main differences in the zooplankton community seasonal pattern between U35, L4 and SH may be the consequence of a latitudinal effect driven by latitudinal differences in the availability of phytoplankton throughout the spring-summer period.

In addition to differences between the oligotrophic sites, our data also showed a delay in the timing of the peak in the zooplankton seasonal pattern conformed by month scores along axis 1 from the oligotrophic U35 to the mesotrophic B35. These differences in zooplankton community seasonal pattern may be related to differences between these two sites in the level of anthropogenic nutrient enrichment and in hydrographical features. The presence of an estuarine plume at B35 (Ferrer et al., 2009) results in higher nutrient concentrations at B35 than at U35 (Iriarte et al., 1997; Villate et al., 2013). It also causes B35 to have a more estuarine/enclosed coastal ecosystem type of phytoplankton seasonal cycle (*sensu* Cebrián and Valiela, 1999), with high phytoplankton biomass in spring, but higher ones in summer. In

contrast U35, where tidal flushing is high, is characterized by the typical temperate shelf water bimodal seasonal pattern found in the southern Bay of Biscay (Stenseth et al., 2006) with spring (main) and autumn (secondary) peaks, and low summer phytoplankton biomass (Iriarte et al., 2010; Villate et al., 2017). Another important finding was that for the oligotrophic sites (U35, L4, and SH), the proportion of zooplankton taxa variations explained by environmental factors increased from U35 to L4 and to SH. There was a higher seasonal covariation of water temperature and Chl *a* at SH, and this can contribute to a more similar correlation of most zooplankton taxa with these two factors. Conversely, as stated above, as we move from SH towards L4 and U35 the spring phytoplankton bloom occurs earlier in the year, and therefore, the effect of temperature and phytoplankton biomass becomes less additive. Another very influential factor can be the increase in the year-to-year regularity of the seasonal patterns of temperature and Chl *a* from U35 to SH. This causes the variation pattern of seasonal zooplankton also to be most similar between years at the northernmost site. An increase in the proportion of zooplankton community seasonal variations explained by environmental factors from the oligotrophic U35 to the mesotrophic B35 was also observed. In this case, the higher covariation between water temperature and Chl *a* could also be the most plausible explanation. In fact, the conditional effect of Chl *a* was low or not significant at B35, despite the marginal effect being significant (data not shown). It could also be affected by a higher regularity in the seasonal pattern of Chl *a* concentration. Differences in the regularity and predictability of the seasonal pattern of zooplankton can



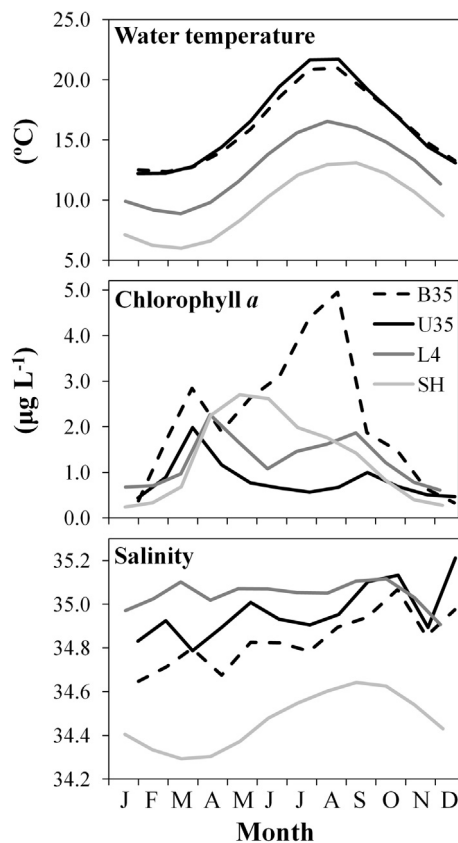


Fig. 7. Seasonal variation of monthly means of water temperature, chlorophyll *a* and salinity at B35 (dashed), U35 (black), L4 (dark grey) and SH (light grey).

have important implications for predator-prey interactions (Atkinson et al., 2015). A more regular, predictable seasonal pattern of zooplankton that we have observed northwards or under mesotrophic conditions (understanding by more regular that the seasonal cycle varies less from year to year) can increase the trophic match probability between fish larvae and their zooplankton prey (Ji et al., 2010; Mackas et al., 2012), and therefore, enhance the feeding success probability of the former, according to the match-mismatch hypothesis (Cushing, 1990; Fortier et al., 1995).

Our analysis focused on the role of environmental factors on the seasonal distribution of zooplankton, but predation controls can also be important. For instance, work at L4 on phenology of successive planktonic trophic levels reveals high inter-annual variability in timings of both predators and prey (Atkinson et al., 2015). The effects of temperature and food availability on zooplankton seasonality are also influenced strongly by simultaneous and strong top-down effects that modify the timing and amplitude of abundance peaks (Maud et al., 2015).

#### 4.3. Contribution of individual taxa to shape seasonal zooplankton community patterns and the relationship between individual taxa and environmental drivers

The differences in the main mode of seasonal variability pattern were accompanied by differences in the zooplankton taxa that contributed most to shape each pattern. At the southern Bay of Biscay sites, cladocerans made the highest contribution. Cladocerans can consume components of the microbial food web (Katechakis and Stibor, 2004), but they feed mainly on phytoplankton (Brown et al., 1997). In accordance, the timing of their seasonal peak differed from U35 to B35 (maxima in early spring and early summer, respectively) in relation to differences in the seasonal pattern of Chl *a*. At the English Channel and

North Sea sites, meroplankton groups, i.e. echinoderm larvae and decapod larvae respectively, contributed most to shape the seasonal pattern. During the present study period, echinoderm larvae have been shown to peak in July at L4, and decapod larvae in August at SH. Other works have also shown both echinoderm and decapod larvae maxima in summer in the northern North Sea (Lindley and Kirby, 2007) and western English Channel (Highfield et al., 2010). It is noteworthy that both of these meroplankton groups are known to have increased their abundances in the North Sea especially since the mid-1980s, likely due to seawater warming (Kirby et al., 2008). Meroplankton was also important at U35 and B35, since cirripede larvae, a group that peaked in early spring at U35 but in early summer at B35, ranked high in the contribution to the main mode of seasonal variability at these sites. The relevance of meroplankton groups at all sites underscores the influence of benthic communities on the seasonality of pelagic ones, and provides support for the idea that benthic-pelagic coupling has a prominent role in coastal environments (Griffith et al., 2017).

The second main mode of variability of ZG showed a high degree of coincidence between sites because it was mainly accounted for by taxa that peaked later in the year at all sites and correlated strongly with WT (i.e. chaetognaths at all sites, doliolids at B35 and U35 and siphonophores at L4 and SH), in contrast to taxa that showed highest densities earlier in the year and correlated mainly with Chl *a* (i.e. cirripede larvae and appendicularians at most sites). Highfield et al. (2010) also found cirripede larvae to be related to the timing of Chl *a* at L4 and so did Korn and Kulikova (1995) in Avacha Inlet (eastern Kamchatka coast in North Pacific). Pelagic cirripede nauplius larvae are filter-feeders that feed on phytoplankton (Moyse, 1963) and Chl *a* concentration greatly influences the release of larvae by barnacles (Starr et al., 1991). This seasonal relation of cirripede larvae with phytoplankton biomass is a standard pattern that responds to seasonal averages for multiannual periods, but timing leads or lags for individual years have been reported at L4 (Atkinson et al., 2015). Within appendicularians the availability of food (phytoplankton) has been found to be the most limiting factor for *Oikopleura dioica* in coastal waters (Tomita et al., 2003). We have no information on the species composition of appendicularians at SH, but at L4 (López-Urrutia et al., 2005), U35 and B35 (Fanjul et al., 2017) *Oikopleura* was the dominant genus and *O. dioica* the most abundant one among the *Oikopleura* identified to species level. Among the zooplankton groups that best correlated with temperature, however, we have two groups of predators, the siphonophores and the chaetognaths. Within the siphonophores, *Muggiaea* spp. were most abundant at the four stations (see Fanjul et al., 2017), and they are known to reproduce rapidly when temperature and prey densities are elevated (Blackett et al., 2014). In fact, peak periods of siphonophores coincided with high copepod densities or followed copepod peaks at our four study sites. Regarding chaetognaths, despite the dominance of different species at the different sites we studied (*Parasagitta friderici*, *Parasagitta setosa*, *Parasagitta elegans*), peak chaetognath densities were observed in late summer at all stations, at the time of highest densities of small copepods, i.e. their main prey (Falkenhaus, 1991; Tönnesson and Tiselius, 2005). The annual development of chaetognaths at the Abra Bay, where B35 is located, was found to be associated to the abundance of copepod nauplii for juvenile stages and postnaupliar cyclopoids and small calanoids for largest individuals (Villate, 1991). The high correlation of doliolids with temperature, however, may not be related to the timing of maximum food availability; instead, it may be linked to more stratified conditions being favourable for them (Menard et al., 1997).

At the finer taxonomic level among the copepods and cladocerans, various copepod genera appeared well correlated with temperature (*Corycaeus*, *Oncaea*, *Temora*, *Centropages*), but only *Corycaeus* (*Dytrichocorycaeus*) seemed to be consistently correlated with temperature across sites (less well correlated at SH). This may be because a single common species, *D. anglicus*, dominates this genus at B35, U35 and L4, a species considered to be a temperate warm water indicator (Bonnet and Frid, 2004), whereas larger differences in species

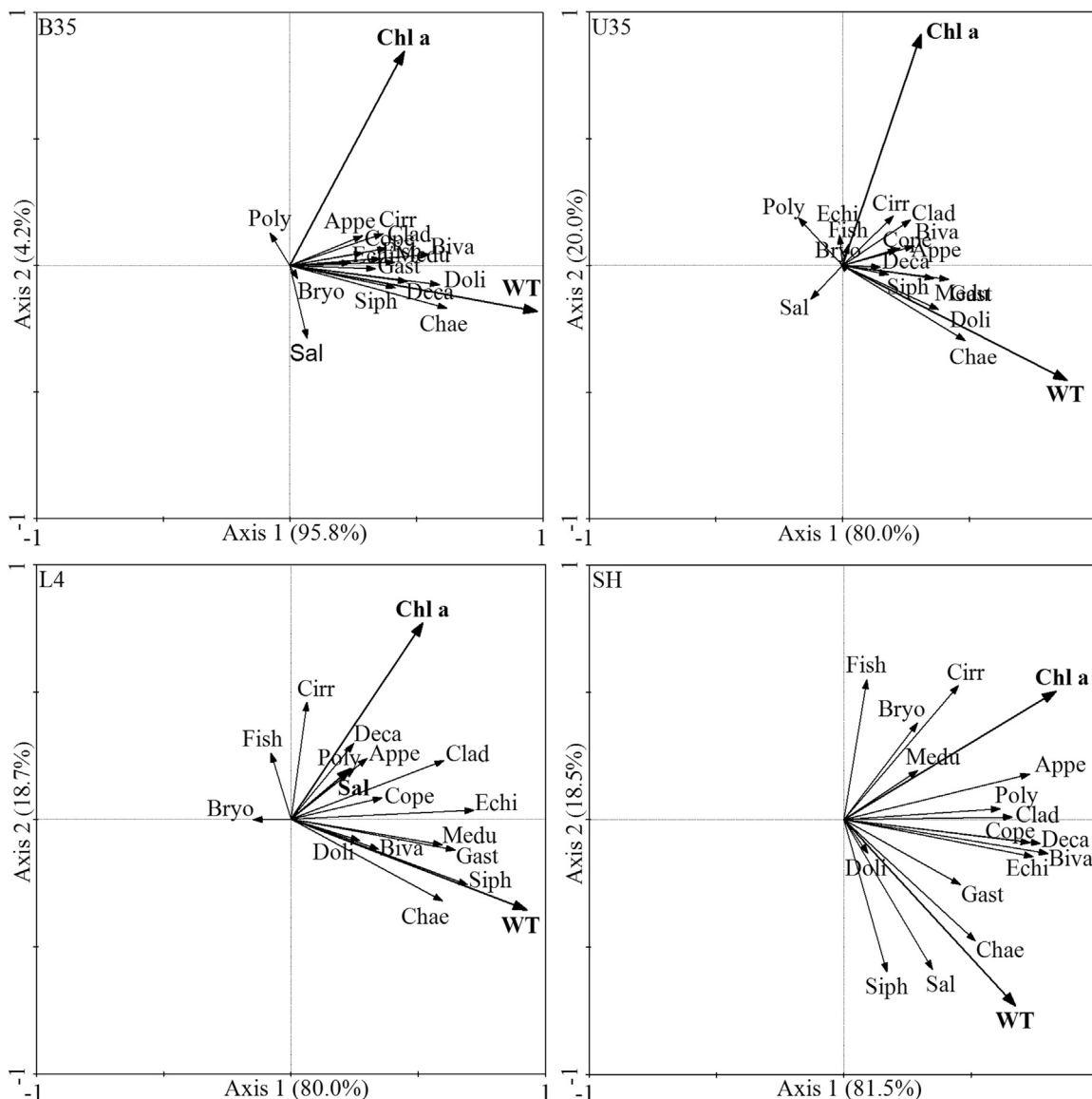


Fig. 8. RDA biplot of zooplankton group taxa (thin black arrows) and environmental variables (thick black arrows for variables with significant conditional effects and grey arrows for variables with non-significant conditional effects). In parentheses the percentage of taxa-environment relationship explained by each axis. Taxa and environmental variable abbreviations as in Fig. 3 and Table 4, respectively.

composition between sites were observed within *Temora* and *Centropages* genera, for instance.

#### 4.4. Coherence of coastal zooplankton seasonality within marine biogeographic units

In general, our results reinforce the view that coastal zooplankton community seasonal dynamics within the Northeast Atlantic Shelves Province (Longhurst, 1998) show geographical variations (Beaugrand et al., 2000; McGinty et al., 2011). Furthermore, the sites under study are located in two different provinces, i.e. the Northern European Seas province (SH and L4) and the Lusitanian province (U35 and B35) according to the classification by Spalding et al. (2007) and in three different Large Marine Ecosystems (LMEs) according to the classification by Sherman et al. (2004): the Iberian Coastal (U35 and B35), the Celtic-Biscay shelf (L4) and the North Sea (SH). However, the seasonal pattern of zooplankton community at U35 is a bimodal cycle similar to that described by Beaugrand et al. (2000) for the southern part of the Celtic Sea and the oceanic region of the Bay of Biscay, although the spring peak occurs earlier in the year at U35. Moreover, the seasonal

variability of zooplankton abundance at U35 does not seem to conform to those observed at other coastal sites located on the northwestern Iberian Peninsula (e.g. Vigo and A Coruña stations), where zooplankton maxima occur in summer/early autumn due to the influence of upwelling processes (Bode et al., 2013). Upwelling events show decreasing intensity easterly along the Cantabrian shelf, and the weakness of upwelling processes in the Basque coast (innermost Cantabrian shelf) precludes breaking of the stratification up to the surface layers (Valencia and Franco, 2004). This fact explains the decline of phytoplankton and zooplankton after the spring maxima at coastal sites that are poorly fertilized by river inputs, as is the case of U35. Therefore, a lack of homogeneity in terms of zooplankton community seasonality within the Iberian Coast LME is also evident. The division of the marine environment into coherent biogeographic units entails much complexity because of the many influencing variables (topographical, hydrographical, climatic, ecological etc.), and it is an even harder task for the more variable coastal areas where local processes usually interfere more with broader scale drivers to affect ecological phenomena. The present work provides helpful information to better delineate the boundaries between meaningful biogeographic units in the marine

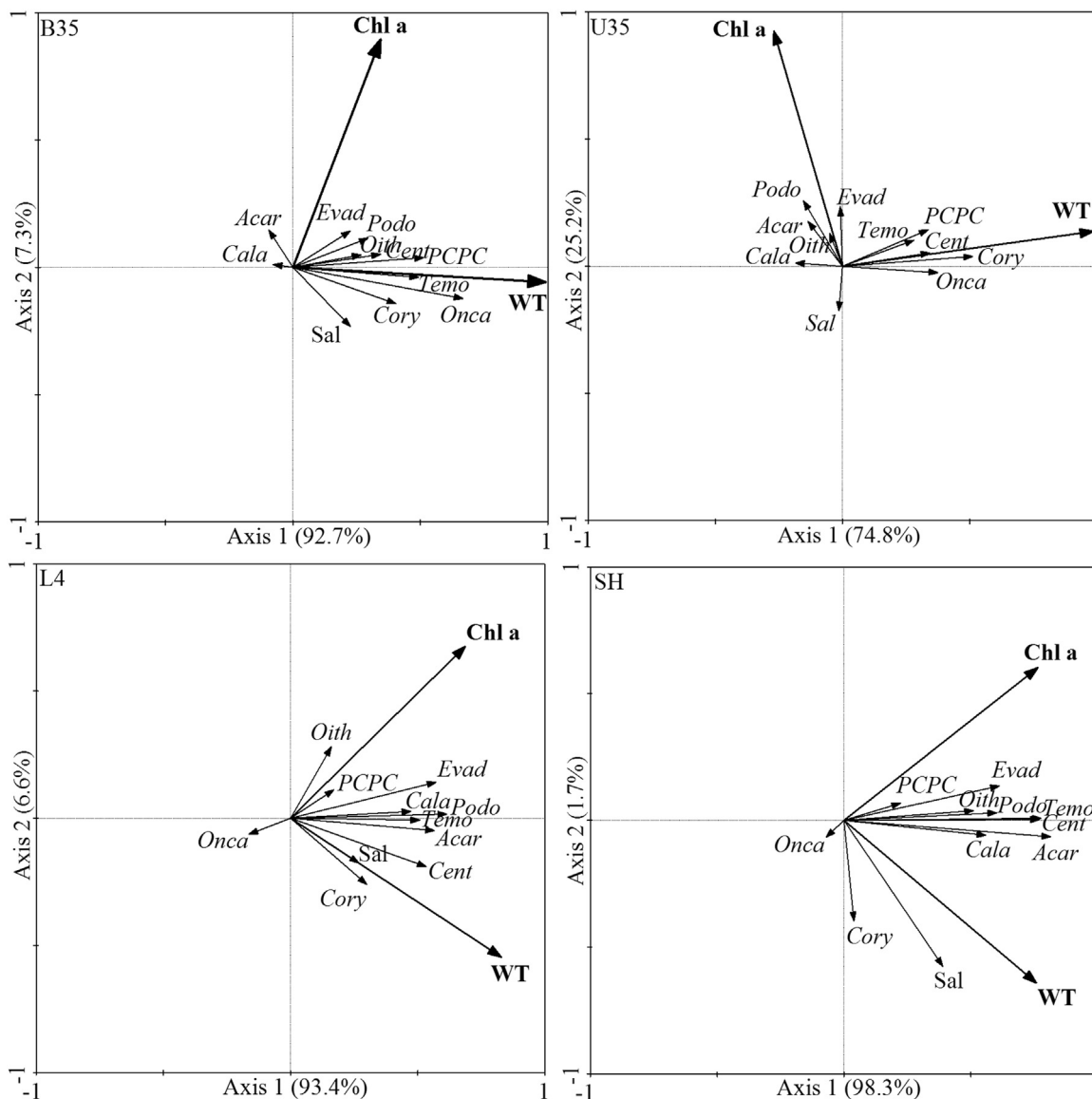


Fig. 9. RDA biplot of copepod and cladoceran genera (thin black arrows) and environmental variables (thick black arrows for variables with significant conditional effects and grey arrows for variables with non-significant conditional effects). In parentheses the percentage of taxa-environment relationship explained by each axis. Taxa and environmental variable abbreviations as in Fig. 3 and Table 4, respectively.

environment and baseline phenological data that can be useful to detect significant departures over time.

5. Conclusions

The use of multivariate ordination methods has allowed us to examine the seasonality of zooplankton at the community level, thus obtaining a more synthetic view than when dealing with seasonal patterns of individual taxa. The main mode of seasonal variability was due mainly to taxa that peaked in the central part of the year (spring-summer) and reached minima in late autumn-winter, and it was the mode of variability that showed the largest between-site differences. These differences consisted mainly in a seasonal delay (from spring to summer) with latitude as well as with the trophic status in the occurrence of the community that contrasted most with the late autumn-winter community. These delays, in turn, were primarily related to between-site differences in the seasonal pattern of phytoplankton biomass. Meroplankton taxa played a key role in shaping this main seasonal mode of variability of the zooplankton community, which highlights the influence of benthic dynamics on the pelagic ones.

Furthermore, between-site differences were observed also in the percentage variance of zooplankton explained by Chl a, water temperature and salinity, and in the regularity of the seasonal cycle of total zooplankton density, which increased with latitude and trophic status. This may be related to a higher co-variation of water temperature and chlorophyll a with the increase in latitude and trophic status, as well as to the increase in the regularity of the seasonal patterns of both water temperature and chlorophyll a from south to north, and of chlorophyll a with trophic status. It is hypothesized that differences in the regularity, and therefore predictability, of the seasonal cycle of zooplankton can have profound implications for the trophic interactions with their predators (e.g. match-mismatch hypothesis). The present data have reinforced the view that within biogeographical units such as the Northeast Atlantic Province coastal zooplankton seasonality is not uniform, suggesting that in coastal ecosystems local processes interfere more with large scale ones than in oceanic waters.

Acknowledgements

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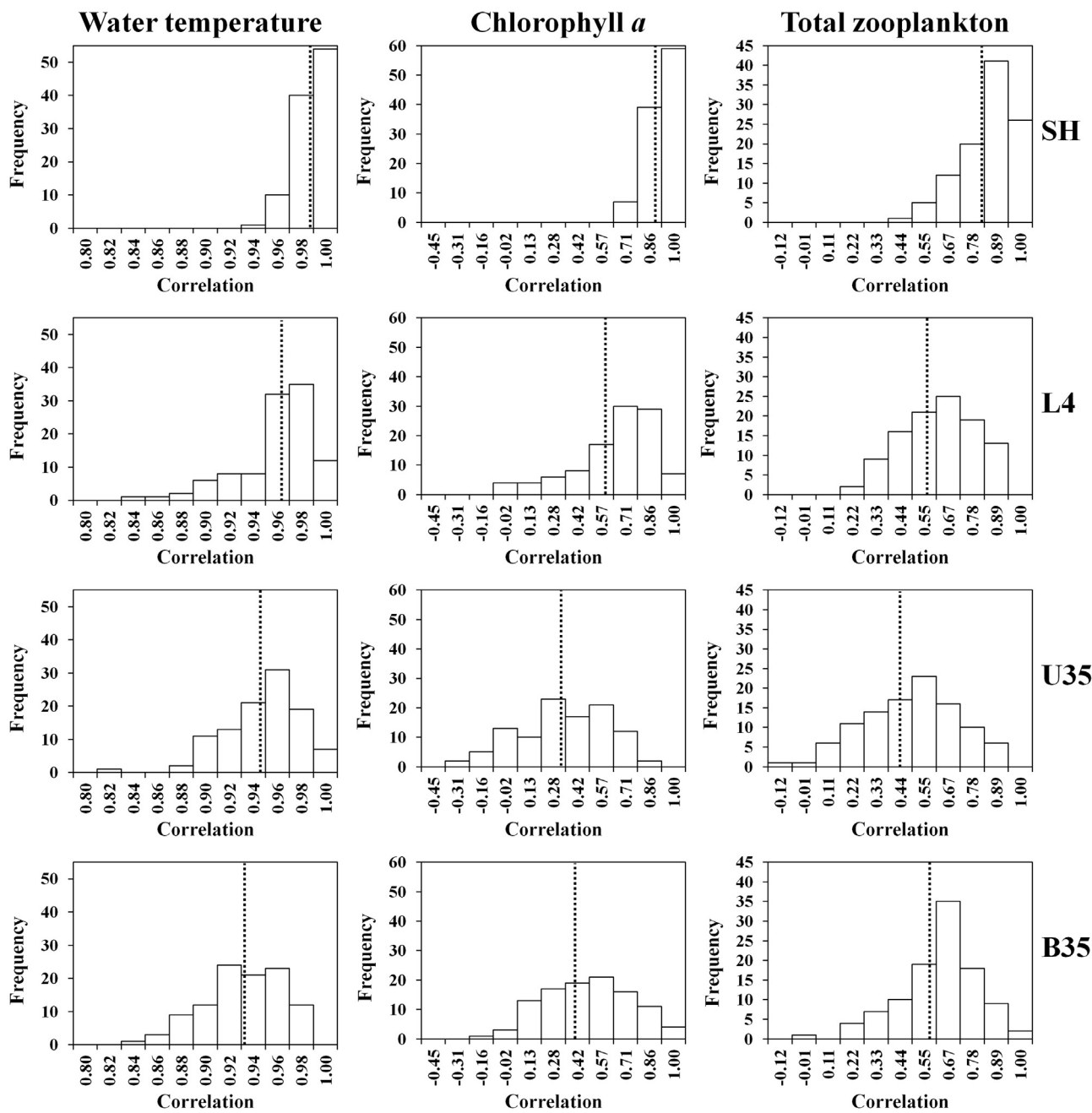


Fig. 10. Histograms of between-year correlations of annual cycles of water temperature, chlorophyll a and total zooplankton abundance. The vertical dotted line shows the mean value of the distribution.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.csr.2018.03.009>.

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