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

Alvaro Fanjul[a,□], Arantza Iriarte[b], Fernando Villate[a], Ibon Uriarte[b], Angus Atkinson[c], Kathryn Cook[d,1]

[a] Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), PO Box 644, 48080 Bilbao, Spain
[b] Department of Plant Biology and Ecology, Faculty of Pharmacy, University of the Basque Country (UPV/EHU), Paseo de la Universidad 7, 01006 Gasteiz, Spain
[c] Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL13DH, United Kingdom
[d] Marine Laboratory, Marine Scotland Science, Scottish Government, 375 Victoria Road, Aberdeen AB11 9DB, United Kingdom

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 temperatura 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.

Keywords: zooplankton, multivariate ordination, seasonal changes, trophic status, latitudinal variation, North Atlantic.

Introduction

Zooplankton comprise a key component of marine pelagic ecosystems, forming the link between primary producers and upper trophic level consumers (Dam, 2013). In the marine environment, the seasonal cycle of zooplankton abundance and composition, together those of key environmental variables are among the strongest contributors to total temporal variance (Mackas et al., 2012). Furthermore, the study of the seasonality of zooplankton is critical, since it may have profound implications for the couplingdecoupling of food webs (e.g. match-mismatch hypothesis, Cushing, 1990). Seasonal variations of zooplankton have been reported in the literature (e.g. Colebrook, 1984; Longhurst, 1998), but a need for a broader understanding of zooplankton seasonality has been identified, in order to better quantify and monitor future plankton phenology shifts induced by climate change (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 an important aspect to be taken into account when delimiting marine eco-geographical units (Longhurst, 1998). Regarding these, Longhurst (1998) divided the sea into biomes, each one containing one or several provinces, but as he stated, the coastal/shelf provinces could rationally be subdivided almost infinitely. The Northeast Atlantic Shelves Province (NECS) extends from Cape Finisterre (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.

The aim of the present work was to compare zooplankton community seasonal variability and its environmental drivers at four coastal sites in the NECS, located in the Bay of Biscay (Urdaibai35 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.

Studies on the seasonal patterns of zooplankton have been conducted in each of these coastal areas: North Sea (e.g. Greve et al., 2001; 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., 2002; Stenseth et al., 2006; Valdes et al 2007), but 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, but the approach used in the present work has been the assessment of the seasonal pattern of zooplankton at the community level using multivariate ordination methods, which help to understand complex data (Walker and Jackson, 2011) and provide a more holistic and synthetic information.

Methods

Study area and data acquisition

Time-series of zooplankton (< 200 μm) abundance, water temperature, salinity and chlorophyll *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).

B35 and U35

B35 (43° 24.15’N, 3º 5.25’W) is a coastal site (< 1 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 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 chlorophyll *a* concentration criteria (Molvaer *et al.*, 1997; Smith *et al.*, 1999).

At both sites samplings were performed monthly. Zooplankton were sampled by horizontal tows at mid-depth, below the halocline (when present), of a 200 µm mesh size ring net (mouth diameter 0.25 m) equipped with a flowmeter. More details on the methodology used for data acquisition can be found in Fanjul et al. (submitted).

L4

L4 is a transitionally mixed site (Southward et al., 2004) with a mean depth of 54 m located at about 13 km southwest of Plymouth (50° 15'N, 4° 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). Samplings were carried out weekly (weather permitting). 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. More details on the methodology used for data acquisition can be found in Atkinson et al. (2015).

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. Samplings were carried out weekly, weather conditions permitting. Zooplankton samples were taken by vertical hauls from 45 m to the surface using 200 µm mesh Bongo nets (40 cm diameter (30 cm during January, February and March 1999). More details on the methodology used for data acquisition can be found in Bresnan et al. (2015).

Additionally, 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 pretreatment

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 data were grouped and analysed 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 cladoceran and copepod 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.

Prior to RDA analyses, the zooplankton abundance data were transformed using log (x + 1) (ter Braak and Smilauer, 2002).

Data treatment

Multivariate ordination methods were used to model the relationship between zooplankton community structure and explanatory variables using Canoco v. 4.55 (ter Braak and Smilauer, 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. To elucidate this, as a first step, Detrended Correspondence Analyses were performed, as recommended by ter Braak and Smilauer (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, surface water temperature (WT), Chlorophyll *a* (Chla) and salinity (Sal), plus the following climate indices that can be influential in the North Atlantic: NAO (Northern Atlantic Oscillation), EA (Eastern Atlantic) and AMO (Atlantic Multidecadal Oscillation), with years as covariables (thereby removing the effect of years). 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 Smilauer, 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, correlations (Spearman rank) were carried out between the sample scores along each axis and environmental variables. 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 correlations of the month scores along each axis were carried out. Finally, between-year correlation analyses were performed for temperature, chlorophyll *a* concentration and total zooplankton abundance (Pearson correlation for the former and Spearman rank correlation for the two latter). This allowed us to assess differences between sites in the degree of year-to-year regularity of the annual cycles of those variables. All correlations were carried out using SPSS Statistics for Windows, Version 23.0 (IBM Corp., Armonk, NY).

Results

The RDA monthly 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 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). In accordance, 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 1). The bimodal or stepped seasonal patterns observed at U35 and SH for both taxonomic levels tested reinforced the differences between them, because from the two peaks of the month scores distribution the smallest one was the latest one (August or September) at U35 and the earliest one (April or May) at 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 1).

The contribution of zooplankton taxa to the main mode of seasonal variation (axis 1) in each site (Fig. 3) showed that cladocerans made a high contribution to the seasonal pattern of ZG at B35, U35 and L4, but their contribution decreased at SH. Cirripede larvae also made a high contribution at the lowest latitude sites (B35 and U35), but their contribution ranked lower at L4 and SH. In contrast, decapod larvae were the group that contributed most at the highest latitude site (SH), but their contribution decreased with decreasing latitude, particularly at U35 and B35. Another meroplankton group, the echinoderm larvae, was the taxon with the highest contribution at L4, but their relevance decreased at the other sites, particularly at the lowest latitude (B35 and U35). Appendicularians ranked high at all latitudes in oligotrophic sites (U35, L4 and SH), but not at the mesotrophic site (B35). 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. *Acartia* showed the highest contribution at SH and U35, and *Temora* showed high contributions only at SH and L4.

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 2). 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 2). As shown in Fig. 5, 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 above mentioned groups, cirripede larvae and fish eggs and larvae at all sites, together with polychaete larvae at U35, also showed high contributions. For cladoceran and copepod 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.

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 3) showed that WT and Chl *a* were selected by the model for both taxonomic levels tested at U35, L4 and SH, but the largest percentage of variation was explained by WT at U35 and L4, and by Chl *a* at SH. The percentage of variation explained both by WT and Chla increased from south to north from U35 to SH. AMO was selected in third place to explain the variability of zooplankton groups at L4 and to explain the variability at both zooplankton levels at SH, although the increase in the percentage of variance explained was very small. At the mesotrophic B35 site, WT explained a higher percentage of variance than at U35, and the contribution of Chla was smaller for ZG and non significant for CCGen.

However, correlations between sample scores along each ordination axis and environmental variables (Tables 4 and 5) showed that Chla 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 Chla and WT). 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 Chla was observed (Table 5).

Fig. 7 shows that there was also an increasing pattern in the degree of between-year correlation in WT, Chla and total zooplankton abundance from The two Spanish sites to L4 and to SH, showing an increase in the regularity of the annual cycle from U35 to L4 and to SH. Regularity was also higher at B35 than at U35 for Chla and total zooplankton abundance.

As shown in Figs. 8 and 9, at B35 most zooplankton groups, but only some copepod genera such as *Corycaeus*, *Oncaea* and *Temora* 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 cladoceran and copepod genera with WT or Chla 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 Chla (*Evadne*, *Podon*, *Acartia*). At SH, however, most groups showed similar relationships with WT and Chla. 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 Chla at all sites.

Discussion

Zooplankton communities contain developmentally, physiologically and behaviourally diverse organisms that can show a relatively wide range of annual cycles of abundance (e.g. Colebrook, 1984; Highfield et al., 2010). However, the analysis of the seasonal pattern at the community level by using multivariate ordination techniques (Beaugrand et al., 2000) helps the understanding of complex data through a process of dimension reduction (Walker and Jackson, 2011), and has allowed us to assess differences in zooplankton seasonality in a more synthetic way. In general, our data evidenced differences between sites in the seasonal pattern that were related chiefly 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, 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. 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. The difference in 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).

These 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 chlorophyll *a* (see Fanjul et al., submitted). At the English Channel and North Sea sites, meroplankton groups, i.e. echinoderm larvae and decapod larvae respectively, contributed most. During the present study period, echinoderm larvae have been shown to peak in July at L4, and decapod larvae in August at SH (Fanjul et al., submitted). Other works have also shown both echinoderm and decapod larvae maxima in summer in the northern North Sea (Lindly 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 since the 1990s, 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 (Fanjul et al., submitted), 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 by significantly affecting energy transfer in food webs (Griffith et al., 2017).

Water temperature generally explained the highest zooplankton taxa variability, and 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 et al., 1985; Ikeda, 1985) and, indirectly, it can also control their food availability (Mackas et al., 2012). However, the correlations between environmental factors and sample scores on axis 1 and axis 2 performed separately, showed clearly that the between-site differences in the main mode of zooplankton seasonal variability (axis 1) was more strongly related to chlorophyll *a* concentration than to temperature and, therefore, 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 (Fanjul et al., submitted), and (ii) delays in phytoplankton blooms with latitude may be a generalized 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 seasonal zooplankton community 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 eutrophic 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, whereas 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).

It is also interesting to note that for the oligotrophic sites the proportion of zooplankton taxa variations explained by environmental factors increased from U35 to L4 and to SH. It is clear that there was a higher seasonal covariation of water temperature and chlorophyll *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 towards lower latitudes (L4 and U35) the spring phytoplankton bloom occurs earlier in the year, and as a consequence, the effect of temperature and phytoplankton biomass becomes less additive. Another influential factor can be the increase in the year-to-year regularity of the seasonal patterns of temperature and chlorophyll *a* with latitude from U35 to SH. This causes the year-to-year variation pattern of seasonal zooplankton also to be most regular at the northernmost site. We also observed an increase in the proportion of zooplankton community seasonal variations explained by environmental factors from the oligotrophic U35 to the mesotrophic B35. In this case, the higher covariation between water temperature and chlorophyll *a* could also be the most plausible explanation. In fact, the conditional effect of chlorophyll *a* was low or not significant at B35, despite the marginal effect was significant (data not shown). A higher regularity in the seasonal pattern of chlorophyll *a* concentration can also be influential. Differences in the regularity and predictability of the seasonal pattern of zooplankton can 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 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 focusses 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).

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 opposition to taxa that peaked earlier in the year and correlated mainly with chlorophyll *a* (i.e. cirripede larvae, appendicularians). Highfield et al. (2010) also found cirripede larvae to be related to the timing of chlorophyll *a* at L4 and so did Korn and Kulikova (1995) in Avacha Inlet. Pelagic cirripede nauplius larvae are filter-feeders that feed on phytoplankton (Moyse, 1963) and chlorophyll concentration greatly influences the release of larvae by barnacles (Starr et al., 1991). Within appendicularians food (phytoplankton) availability 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 L4 and SH, but at U35 and B35 *Oikopleura* was the dominant genus and *O. dioica* the most abundant one among the *Oikopleura* identified to species level (Fanjul et al., submitted). Among the zooplankton groups that best correlated with temperature, however, we have two groups of predators, the siphonophores and the chaetognaths. Within the siphonophores, individuals of the *Muggiaea* genus were the most abundant ones at the four stations (see Fanjul et al., submitted), 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 at our four study sites (Fanjul et al., submitted). 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 (Fanjul et al., submitted), i.e. their main prey (Falkenhaug, 1991; Tönnesson and Tiselius, 2005). The high correlation of doliolids with temperature, however, does not seem to be related to the timing of maximum food availability; instead, it may be related 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* (*Dytrichocoricaeus*) 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 composition between sites were observed within *Temora* and *Centropages* genera, for instance.

Regarding the effect of climate indices, AMO was the one that showed the highest correlation with seasonal variations of zooplankton community (although no correlation was observed in the oligotrophic site of the Bay of Biscay for the seasonal variability reflected by ordination along axis 1). AMO has been suggestedto exert significant effects variations of the marine biota of the North Atlantic at multidecadal scales (Edwards et al., 2013; Alheit et al., 2014), however, in the present study of seasonal variations correlations were markedly smaller than with direct driving factors, such as temperature and chlorophyll *a*.

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 three different Large Marine Ecosystems (LMEs): the Iberian Coastal (U35 and B35), the Celtic-Biscay shelf (L4) and the North Sea (SH) (Sherman et al., 2004). 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 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 environment and baseline phenological data that can be useful to detect significant departures over time.

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Figure Captions

Figure 1. Map showing the location of sampling sites.

Figure 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.

Figure 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*.

Figure 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.

Figure 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.

Figure 6. Percentage of total zooplankton variance explained by environmental factors at the level of (a) zooplankton groups and (b) copepod and cladoceran genera.

Figure 7. Histograms of between-year correlations of annual cycles of temperature, chlorophyll *a* and total zooplankton abundance

Figure 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 3, respectively.

Figure 9. RDA biplot of Cladoceran and Copepod 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 3, respectively.

Tables

Table 1. 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)

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

Table 2. Between-site correlation (Spearman rank correlation coefficients with p-values in parentheses) of the month scores on Axis 2 for Zooplankton groups and Cladoceran and Copepod genera.

	Zooplankton groups (ZG)			*Copepod and cladoceran genera (CCGen)*		
	U35	L4	SH	U35	L4	SH
B35	**0.916 (<0.001)**	**0.874(<0.001)**	**0.902 (<0.001)**	**0.615 (0.033)**	0.510 (0.090)	0.063 (0.846)
U35		**0.720 (0.008)**	**0.741 (0.006)**		0.364 (0.245)	0.315 (0.319)
L4			**0.916 (<0.001)**			**0.755 (0.005)**

Table 3. Conditional effects of environmental variables for Zooplankton groups (ZG) and Cladoceran and Copepod genera (CCGen). Variables with significant effects in bold. Sal: salinity, WT: water temperature, Chl*a*: concentration of chlorophyll *a*, NAO: North Atlantic Oscillation index, EA: East Atlantic index, AMO: Atlantic Multidecadal Oscillation index.

	Zooplankton groups (ZG)				*Cladoceran and Copepod genera (CCGen)*			
	Variable	LambdaA	F	p-value	Variable	LambdaA	F	p-value
B35	**WT**	**0.17**	**36.58**	**0.002**	**WT**	**0.14**	**29.25**	**0.002**
	Chl *a*	**0.01**	**2.90**	**0.028**	Chl *a*	0.01	2.43	0.060
	AMO	0.00	0.88	0.472	Sal	0.01	1.83	0.092
	NAO	0.01	0.85	0.522	AMO	0.01	1.55	0.166
	Sal	0.00	0.61	0.738	NAO	0.00	0.81	0.470
	EA	0.00	0.30	0.974	EA	0.00	0.56	0.726
U35	**WT**	**0.06**	**13.06**	**0.002**	**WT**	**0.07**	**13.4**	**0.002**
	Chl *a*	**0.04**	**6.48**	**0.002**	**Chl *a***	**0.02**	**4.86**	**0.002**
	Sal	0.00	1.34	0.184	AMO	0.01	2.39	0.058
	AMO	0.01	1.41	0.208	Sal	0.01	1.00	0.400
	NAO	0.00	0.67	0.676	NAO	0.00	0.45	0.862
	EA	0.00	0.40	0.938	EA	0.00	0.45	0.874
L4	**WT**	**0.23**	**59.09**	**0.002**	**WT**	**0.18**	**42.66**	**0.002**
	Chl *a*	**0.08**	**23.22**	**0.002**	**Chl *a***	**0.09**	**23.81**	**0.002**
	AMO	**0.02**	**3.04**	**0.014**	Sal	0.00	1.63	0.170
	Sal	0.00	2.74	0.056	AMO	0.01	1.54	0.158
	EA	0.01	0.75	0.564	EA	0.00	0.78	0.474
	NAO	0.00	0.54	0.776	NAO	0.00	0.47	0.760
SH	**Chl *a***	**0.31**	**79.61**	**0.002**	**Chl *a***	**0.28**	**71.77**	**0.002**
	WT	**0.17**	**58.95**	**0.002**	**WT**	**0.18**	**62.33**	**0.002**
	AMO	0.00	2.23	0.050	**AMO**	**0.00**	**2.64**	**0.022**
	EA	0.01	1.32	0.248	EA	0.01	1.69	0.148
	NAO	0.00	1.08	0.324	NAO	0.00	1.18	0.294
	Sal	0.00	0.60	0.726	Sal	0.00	0.51	0.772

Table 4. Correlations between environmental factors and sample scores on axis 1 of Zooplankton groups (ZG) and Cladoceran and Copepod genera (CCGen). Significant correlation coefficients in bold (** p<0.01; * p<0.05). Abbreviations as in Table 3.

	ZG				CCGen			
	B35	U35	L4	SH	B35	U35	L4	SH
Sal	0.041	0.070	__-0.164*__	__0.247**__	-0.011	-0.066	__-0.160 *__	__0.333 **__
WT	__-0.567 **__	__-0.313 **__	__-0.606 **__	__0.533 **__	__0.390 **__	-0.124	__-0.521 **__	__0.661 **__
Chl*a*	__-0.585 **__	__-0.359 **__	__-0.600 **__	__0.839 **__	__0.537 **__	__0.265 **__	__-0.582 **__	__0.774 **__
NAO	0.108	0.024	__0.149 *__	__-0.176 *__	-0.054	0.081	0.107	__-0.221**__
EA	-0.093	-0.043	-0.131	__0.097__	0.071	-0.065	-0.096	0.112
AMO	__-0.230 **__	-0.109	__-0.347 **__	__0.384 **__	__0.156 *__	-0.131	__-0.264 **__	__0.382 **__

Table 5. Correlations between environmental factors and sample scores on axis 2 of Zooplankton groups (ZG) and Cladoceran and Copepod genera (CCGen). Significant correlation coefficients in bold (** p<0.01; * p<0.05). Abbreviations as in Table 3.

	ZG				CCGen			
	B35	U35	L4	SH	B35	U35	L4	SH
Sal	0.101	-0.065	-0.018	__0.566 **__	0.122	0.080	__0.184 *__	-0.079
WT	__0.529 **__	__0.609 **__	__-0.672 **__	__0.734 **__	__0.614 **__	__-0.525 **__	__0.445 **__	-0.131
Chl*a*	-0.055	-0.087	-0.010	__-0.159 *__	0.059	__-0.206 **__	0.101	-0.017
NAO	__-0.191 *__	__-0.194**__	0.099	-0.109	-0.145	__0.187 *__	-0.021	0.020
EA	0.095	0.109	0.005	-0.025	0.049	-0.059	-0.054	-0.094
AMO	__0.240 **__	__0.302 **__	__-0.274 **__	__0.227 **__	__0.294 **__	__-0.260 **__	__0.159 *__	-0.038

Figure 1.

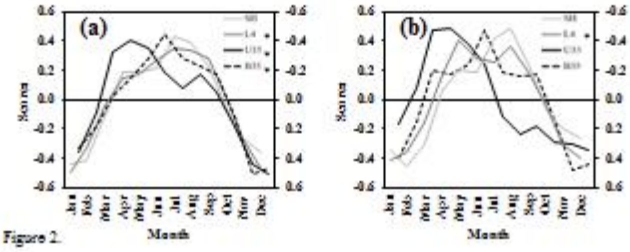

Figure 2.

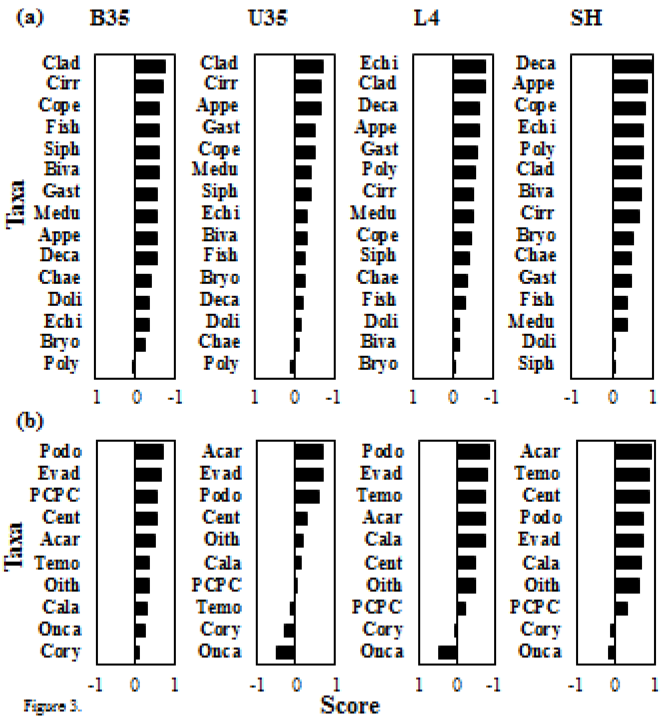

Figure 3.

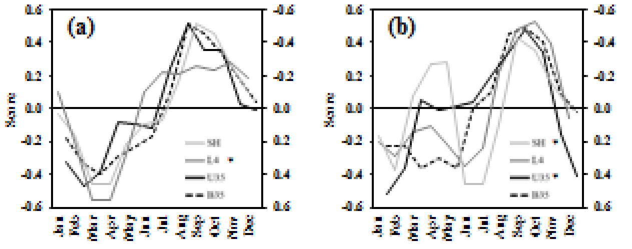

Figure 4.

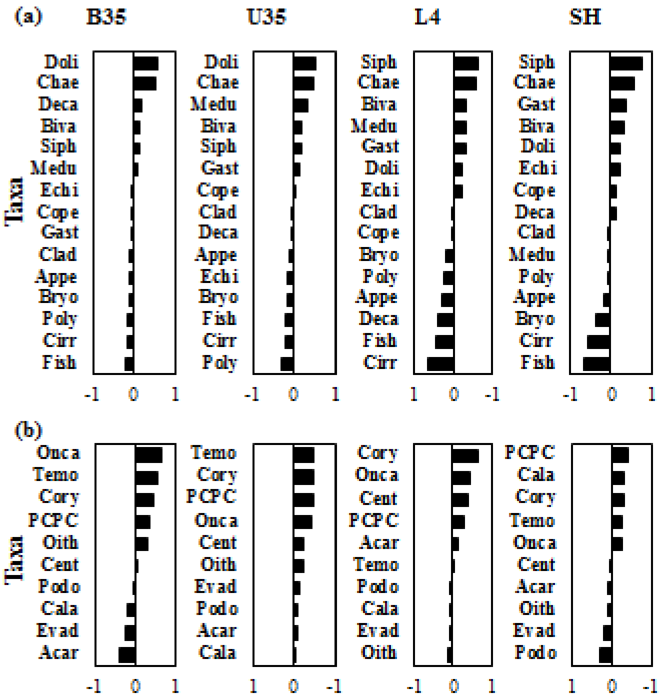
(a)
B35
U35
L4
SH
Taxa
Doli
Chae
Deca
Biva
Siph
Medu
Echi
Cope
Gast
Clad
Appe
Bryo
Poly
Cirr
Fish
Doli
Chae
Medu
Biva
Siph
Gast
Cope
Clad
Deca
Appe
Echi
Bryo
Fish
Cirr
Poly
Siph
Chae
Biva
Medu
Gast
Doli
Echi
Clad
Cope
Bryo
Poly
Appe
Deca
Fish
Cirr
Siph
Chae
Gast
Biva
Doli
Echi
Cope
Deca
Clad
Medu
Poly
Appe
Bryo
Cirr
Fish
-1 0 1
-1 0 1
1 0 -1
-1 0 1
(b)
Taxa
Onca
Temo
Cory
PCPC
Oith
Cent
Podo
Cala
Evad
Acar
Temo
Cory
PCPC
Onca
Cent
Oith
Evad
Podo
Acar
Cala
Cory
Onca
Cent
PCPC
Acar
Temo
Podo
Cala
Evad
Oith
PCPC
Cala
Cory
Temo
Onca
Cent
Acar
Oith
Evad
Podo
-1 0 1
1 0 -1
-1 0 1
1 0 -1
Score

Figure 5.

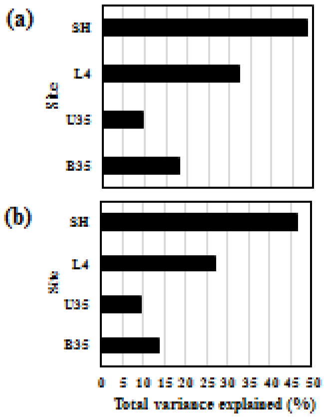
(a)
(b)
Site
SH
L4
U35
B35
0
5
10
15
20
25
30
35
40
45
50
Total variance explained (%)

Figure 6.

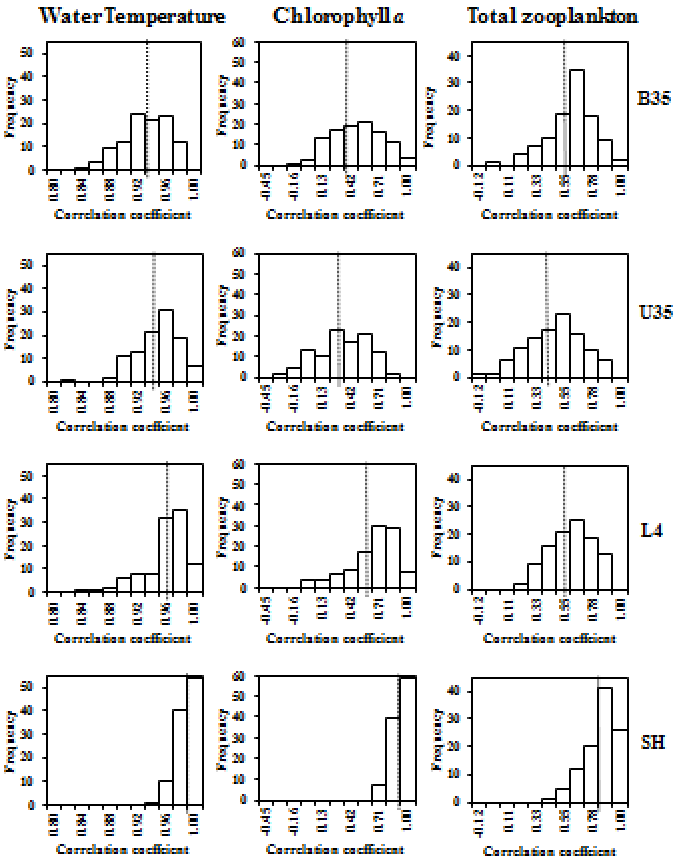
Water Temperature
Chlorophyll *a*
Total zooplankton
B35
U35
L4
SH
Frequency
Correlation coefficient
0
10
20
30
40
50
60
0.80
0.84
0.88
0.92
0.96
1.00
-0.45
-0.16
0.13
0.42
0.71
1.00
-0.12
0.11
0.33
0.55
0.78
1.00

Figure 7.

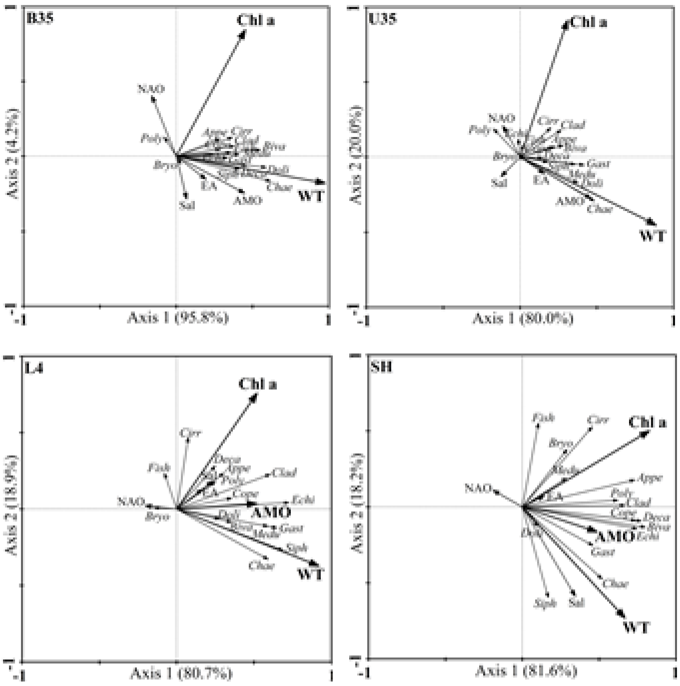
B35
Chl a
NAO
Poly
Appe
Cirr
Clad
Biva
Bryo
Doli
Chae
WT
EA
AMO
Sal
Axis 2 (4.2%)
Axis 1 (95.8%)
-1
1
U35
Chl a
NAO
Poly
Echi
Cirr
Clad
Appe
Biva
Bryo
Deca
Gast
Medu
Doli
Sal
EA
AMO
Chae
WT
Axis 2 (20.0%)
Axis 1 (80.0%)
-1
1
L4
Chl a
Cirr
Deca
Appe
Fish
Poly
Clad
EA
Cope
Echi
NAO
Bryo
AMO
Doli
Biva
Gast
Medu
Siph
Chae
WT
Axis 2 (18.9%)
Axis 1 (80.7%)
-1
1
SH
Fish
Cirr
Chl a
Bryo
Medu
Appe
NAO
EA
Poly
Clad
Cope
Deca
Biva
AMO
Echi
Doli
Gast
Chae
Siph
Sal
WT
Axis 2 (18.2%)
Axis 1 (81.6%)
-1
1

Figure 8.

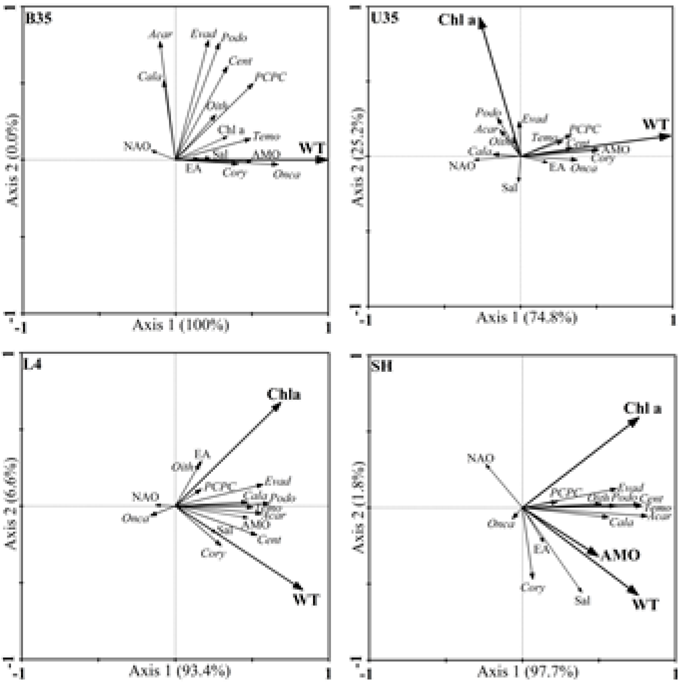
B35
Acar
Evad
Podo
Cala
Cent
PCPC
Oith
Chl a
Temo
NAO
WT
Sal
AMO
EA
Cory
Onca
Axis 2 (0.0%)
Axis 1 (100%)
U35
Chl a
Podo
Evad
Acar
Oith
Temo
PCPC
WT
Cala
Cent
AMO
Cory
NAO
EA
Onca
Sal
Axis 2 (25.2%)
Axis 1 (74.8%)
L4
Chla
EA
Oith
PCPC
Evad
NAO
Cala
Podo
Temo
Acar
Onca
AMO
Sal
Cent
Cory
WT
Axis 2 (6.6%)
Axis 1 (93.4%)
SH
Chl a
NAO
PCPC
Evad
Oith
Podo
Cent
Temo
Acar
Cala
Onca
EA
AMO
Cory
Sal
WT
Axis 2 (1.8%)
Axis 1 (97.7%)
1
-1
1
-1
1
-1
1
-1
1
-1
1
-1
1
-1
1
-1

Figure 9.