Zooplankton variability at four monitoring sites of the Northeast Atlantic Shelves differing in latitude and trophic status

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Zooplankton abundance series (1999–2013) from the coastal sites of Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH), in the Northeast Atlantic were compared to assess differences in the magnitude of seasonal, interannual and residual scales of variability, and in patterns of seasonal and interannual variation in relation to latitudinal location and trophic status. Results showed highest seasonal variability at SH consistent with its northernmost location, highest interannual variability at U35 associated to an atypical event identified in 2012 in the Bay of Biscay, and highest residual variability at U35 and B35 likely related to lower sampling frequency and higher natural and anthropogenic stress. Interannual zooplankton variations were not coherent across sites, suggesting the dominance of local influences over large scale environmental drivers. For most taxa the seasonal pattern showed coherent differences across sites, the northward delay of the annual peak being the most common feature. The between-site seasonal differences in spring–summer zooplankton taxa were related mainly to phytoplankton biomass, in turn, related to differences in latitude or anthropogenic nutrient enrichment. The northward delay in water cooling likely accounted for between-site seasonal differences in taxa that increase in the second half of the year.

KEYWORDS: zooplankton; time series; seasonality; interannual changes; latitudinal variation; trophic status; North Atlantic.

INTRODUCTION

The abundance of zooplankton may be highly variable at time scales that span from minutes to decades in response to environmental drivers and stressors operating across a wide range of temporal scales (Haury *et al.*, 1978). Relevant time scales of variance, ranging from days to years involve changes in growth, production, mortality and community function (Marine Zooplankton Colloquium 1, 1989). The seasonal cycle is a key scale because of the large physical and biotic variations (Mackas and Beaugrand, 2010; Mackas *et al.*, 2012), and the importance of phenological timing for predator-prey interactions (Sydeman and Bograd, 2009). For example, fish larvae survival and recruitment success is highly dependent on the availability of suitable zooplankton prey in synchrony with their seasonal spawning and development, according to the match-mismatch hypothesis (Cushing, 1990), and there is the potential for differential phenological shifts of predator and prey in response to environmental changes (Edwards and Richardson, 2004; Durant *et al.*, 2007).

In addition to phenological shifts, interannual variations in overall abundance of zooplankton are driven by year-to-year variations in the physical and nutritional environments, which also help to modulate the recruitment of fish populations (Liu *et al.*, 2014). Therefore, it is important to determine the extent to which the seasonal and interannual variations differ from site to site in order to build an ecological classification of pelagic ecosystems on a geographical basis (Longhurst, 1998). At a large spatial scale, latitude-dependent differences in light and temperature are the main factors responsible for the largest changes in the plankton annual cycles. The general patterns for oceanic zooplankton are (i) a large amplitude single summer peak at high-latitudes, (ii) bimodal cycles with a spring bloom and a secondary peak in autumn at middle latitudes and (iii) no clear seasonal patterns in low latitude tropical waters (Heinrich, 1962). In shallow shelf seas, however, local natural (e.g. river discharge and coastal upwelling) and anthropogenic (wastewater inputs) stressors may substantially modify the standard plankton cycles (e.g. Cloern, 1996; Jamet *et al.*, 2001; Ribera d'Alcalà *et al.*, 2004).

In the ICES area a large number of time series are available which have been obtained using comparable methodology (O'Brien *et al.*, 2013), but there have been few attempts to synthesize across multiple time series (Valdés *et al.*, 2007; Bode *et al.*, 2012; Mackas *et al.*, 2012; Castellani *et al.*, 2016). Policy directives such as the Marine Strategy Framework Directive need to assess baseline envelopes of variability and its causes, and provide a broad scale geographical context for this variability.

Many zooplankton time series in the ICES area are from sites located within the Northeast Atlantic Shelves Province (NECS), a biogeographical unit established by Longhurst (1998) for the continental shelves of western Europe that extends from northern Spain to the Faroe-Shetland Channel and the Norwegian Trench. However, this is a wide area that includes the North Sea, the Baltic Sea, the outer shelves off Britain, and the Bay of Biscay. In fact, Longhurst himself recognized that this Province can be subdivided in a way which is more sensitive to ecological differences. The classical biogeographic divisions established for the Eastern North Atlantic are also suitable to look at ecological differences within the studied area. For instance, the northern part of the North Sea is included in the Eastern Atlantic boreal region, while the English Channel and the Bay of Biscay belong to the Eastern Atlantic warm temperate region (Briggs and Bowen, 2012).

In this study, we have selected four of these ICES sites covering most of the latitudinal gradient in NECS, from the northern North Sea (1 site) to the southern Bay of Biscay (2 sites) with the western English Channel as an equidistant central part (1 site). From the two sites of the southernmost zone, one of them differs from the rest of sites in the trophic status (established on the basis of chlorophyll *a* concentration criteria (see Molvær *et al.*, 1997; Smith *et al.*, 1999). The aim was to assess between-site differences in (i) the magnitude of the temporal components of zooplankton variability (i.e. interannual, seasonal and residual components, *sensu* Cloern and Jassby, 2010), and (ii) the patterns of interannual and seasonal variation. We have tried to contribute to define zooplankton scales and patterns of variability within the NECS in relation to differences in latitude, local features and anthropogenic nutrient enrichment.

METHOD

Study area and data acquisition

Zooplankton abundance, water temperature and chlorophyll *a* (Chl*a*) data used in this study for the 15-year period of 1999–2013 were obtained from the on going monitoring programmes carried out at the Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH) sites (Fig. 1). B35 and U35 are located close to each other on the Basque coast, inner Bay of Biscay, at the southern limit of the NECS (Longhurst, 1998), but they differ substantially in their trophic status (Iriarte *et al.*, 2010). L4 is located off the southwest coast of England, in the western English Channel, at an intermediate latitude, and SH is off the eastern Scottish

coast, in the northwest North Sea, near the northern limit of the same geographical province. For the present study period, on the basis of Chl*a* criteria (Molvær *et al.*, 1997; Smith *et al.*, 1999), the B35 and U35 sites may be classified as mesotrophic and oligotrophic, respectively, the trophic status of L4 and SH being more similar to that of U35 than to that of B35. Chlorophyll *a* (Chl*a*) values and other relevant features of these sites are summarized in Table I.

Fig. 1. Map showing the zooplankton monitoring sites of Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 and Stonehaven (SH).

The B35 (43° 24.15′N, 3° 5.25′W) and U35 (43° 27.7′N, 2° 45.3′W) sites are <1 km offshore at the mouth of the estuaries of Bilbao, a once highly polluted system which is now in a rehabilitation phase (Borja *et al.*, 2010), and Urdaibai, a marine-dominated system with much lower human pressure than the estuary of Bilbao. B35 is a partially mixed site of around 13 m depth, influenced by the estuarine plume, whereas U35 is a well-mixed site with a mean water depth of 4.5 m and high rate of tidal flushing. The L4 site (50° 15′N, 4° 13′W) is located ~10 km southwest of Plymouth but 6.5 km away from the nearest land (Litt *et al.*, 2010). It is a transitionally mixed site (Southward *et al.*, 2004) with a mean water depth of 54 m, and hydrographically influenced both by inputs of riverine freshwater from the rivers Plym and Tamar outflowing at Plymouth and by oceanic water during periods of strong south west winds (Rees *et al.*, 2009). The SH site (56° 57.8′N, 02° 06.2′W), with a depth of 48 m, is located 5 km offshore from Stonehaven, where the impact of freshwater inputs of the rivers Dee and Don (outflowing at Aberdeen, 15 miles north) is reduced (Bresnan *et al.*, 2015). This is a dynamic site, well-mixed for most of the year.

Data of zooplankton abundance correspond to quantitative net (200 µm) samples obtained by horizontal tows of a ring net with flowmeter at a mid-depth, below the halocline (when present) at B35 and U35, by vertical hauls of a WP2 net from 50 m to surface at L4 and by vertical hauls of bongo nets from 45 m to surface at SH. Water temperature was measured using portable multi-parameter metres at B35 and U35, a thermometer placed inside a stainless steel bucket initially and a CTD since 2000 at L4 (Atkinson *et al.*, 2015), and a CTD at SH. Chl*a* concentration was determined spectrophotometrically according to the monochromatic method with acidification (Lorenzen, 1967) at B35 and U35, by using reversed-phase HPLC as described in Atkinson *et al.* (2015) at L4, and fluorometrically as described in Bresnan *et al.* (2015) at SH. Sampling frequency was monthly at B35 and U35, and approximately weekly, weather conditions permitting, at L4 and SH.

Table I: Main features of sampling sites and zooplankton sampling characteristics

Feature	B35	U35	L4	SH
Water depth (m) mean	13.0	4.5	54.0	48.0
Distance offshore (km)	<1	<1	6.5	5
Temperature (°C) mean (range)	16.0 (11.3–23.7)	16.2 (10.8–24.9)	12.6 (7.6–19.9)	9.5 (4.5–13.9)
Salinity mean (range)	34.8 (32.9–35.5)	35.0 (30.3–35.6)	35.0 (34.0–35.4)	34.5 (33.8–34.9)
Chlorophyll *a* (µg L^{-1}) mean (range)	2.19 (0.08–31.33)	0.82 (0.04–7.91)	1.24 (0.23–6.29)	1.29 (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)	na*	Atkinson *et al.* (2015)	Bresnan *et al.* (2015)

*na: not available.

Data pretreatment

Missing values (<5%) in the monthly data sets were filled by data interpolation using the mean values of the previous month and the following month. To ensure data consistency in zooplankton series, taxonomic homogenization was undertaken. We analysed total zooplankton and selected zooplankton taxa belonging to (i) a broad level consisting of 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, which also included the far less abundant holoplanktonic forms, such as *Liriope tetraphylla*), and (ii) a finer level consisting of ten genera or genera-assemblages of cladocerans (*Evadne* and *Podon*) and copepods (*Acartia*, *Centropages*, *Temora*, *Oithona*, *Oncaea*, *Corycaeus*, the genera assemblage herein termed "PCPC-Calanus", which includes *Paracalanus*, *Clausocalanus*, *Pseudocalanus* and *Ctenocalanus*, and the family Calanidae). The summary of the components identified and their contribution to the total in each selected taxon are shown as on line Supplementary material (Tables 1S, 2S and 3S for holoplankton groups, meroplankton groups and cladoceran-copepod genera, respectively). This information is relevant to interpret differences between sites in the seasonal pattern of zooplankton categories that include species with different seasonal optima, i.e. the copepod categories PCPC-Calanus and *Temora*. However, in some categories such as the genera *Oithona* and *Oncaea* specimens were not distinguished to species level at all sites and this issue could only be discussed in the light of available literature.

Water temperature, salinity and Chl*a* data used in this study correspond to subsurface measurements at B35 (around 4 m depth) and U35 (around 2 m depth), and to surface measurements at L4 and SH.

As the sampling at B35 and U35 was performed on a monthly scale, whereas sampling at L4 and SH was generally conducted weekly, the number of data per year was adjusted to 12, 1 per month, in all cases. For that purpose, the mean of all the values obtained within each month was calculated for L4 and SH. Mean monthly values were plotted against the mean Julian day of all samplings conducted each month. The astronomical calendar was used to define seasons.

Data treatment

The scales and patterns of variability for temperature, Chl*a*, total zooplankton and selected zooplankton taxa were extracted for each site by using the following multiplicative model described by Cloern and Jassby (2010):

$$c_{ij} = Cy_i m_j \varepsilon_{ij},$$

where c_{ij} is the value in year i ($i = 1,…,N$) and month j ($j = 1,…,12$); C is the long-term mean of the series; y_i is the annual effect in the ith year; m_j is the seasonal (monthly) effect in the jth month; and ε_{ij} is the residual.

This method decomposes time series into (i) an annual component, herein named "interannual variability", where trends, shifts and events can be detected, (ii) a seasonal component or "seasonal variability", where a standard seasonal pattern can be identified and (iii) a residual component, or "residual variability", associated with the event scale, which includes the variability that cannot be attributed to the average seasonal pattern or to fluctuations in the annual mean. In plankton time series, residual variability may reflect sampling uncertainty associated with low frequency temporal variability within months but it may also be affected by the year-to-year stability of the seasonal pattern both in terms of magnitude and phenological variations (Cloern and Jassby, 2010).

To assess the possible effect of this high frequency temporal variability on the residual variability, monthly anomalies in the time series were calculated as the difference between each single value and the series mean and divided by the standard deviation. These anomalies were calculated for five selected taxa that were abundant and showed a clear temporal segregation in the timing of the standard annual maximum at all sites (i.e. copepods, cirripede larvae, appendicularians, chaetognaths and siphonophores), as well as for total zooplankton abundance, Chl*a* concentration and water temperature. To show and compare seasonal variability between years, year vs. month diagrams of the anomalies were produced for each of the above mentioned variables at each of the four study sites.

To make the calculations of interannual and seasonal variability of all selected taxa possible, the data gap for *Centropages* in 1999 at L4 was filled by assuming the same abundance data as in 2000, and the lack of data for doliolids in some years at SH was solved by adding in such years a value of 0.01 in the month of the annual maximum obtained from the years with presence of doliolids. In addition, an unusually high value of fish eggs at L4 in March 2000 was considered erroneous, and replaced by the mean value of the month obtained from the rest of years of the series.

Paired *t*-tests were performed to determine differences between sites in the interannual, seasonal and residual

components of variability of zooplankton taxa, and differences between the three components of variability within each site. Spearman rank correlation analyses were performed to test the relationships between the year-to-year variations of total zooplankton abundance, Chl*a* concentration, water temperature and zooplankton taxa abundance at each site, and the between-site relationships of the year-to-year variations of each zooplankton taxon. Both types of analyses were performed using SPSS Statistics for Windows, Version 23.0 (IBM Corp., Armonk, NY).

Resemblance analyses were carried out by means of the Bray-–Curtis similarity index (Bray and Curtis, 1957), using the group average method, to measure the dissimilarity between all the selected zooplankton taxa, according to their patterns of variability at the four monitoring sites jointly. Dissimilarity was tested both for the interannual and the seasonal variability using the PRIMER v6 software package (Clarke and Warwick, 2001), and results were displayed in dendrograms.

RESULTS

Scales of variability

Values of interannual, seasonal and residual variability for zooplankton taxa at the four sites are depicted as box plots in Fig. 2. Interannual variability was the lowest and residual variability the highest at all sites, although the difference between seasonal and interannual variability at U35, and between residual and seasonal variability at SH were not significant (Table II). The lowest interannual, seasonal and residual variability

were obtained at L4, the highest interannual and residual variability at U35 and the highest seasonal variability at SH. Interannual variability was higher at U35 than at B35, L4 and SH, seasonal variability was higher at SH than at L4, and residual variability was higher at U35 and B35 than at L4 and SH (Table III). Due to the fact that a single value was used as a monthly estimate for B35 and U35 while within-month values (usually 4) were considered replicates and averaged for L4 and SH, a reduction by a factor of 2 of the within-month standard deviation could be expected at L4 and SH.

Figure 3 shows that the between-year differences in the timing of the annual maximum were much lower for all taxa at SH, where the range of months within which the annual maximum occurred was of 2 months for siphonophores (September–October), three for chaetognaths (July–September) and cirripede larvae (March–May), four for appendicularians (May–august) and five for copepods (May–September). For the same taxa, the

Table II: P-*value obtained from paired* t-*tests for differences between the interannual (I), seasonal (S) and residual (R) components of zooplankton taxa at Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH)*

	B35		U35		L4		SH	
	I	S	I	S	I	S	I	S
S	**0.002**		0.919		**0.044**		**0.006**	
R	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**<0.001**	0.210

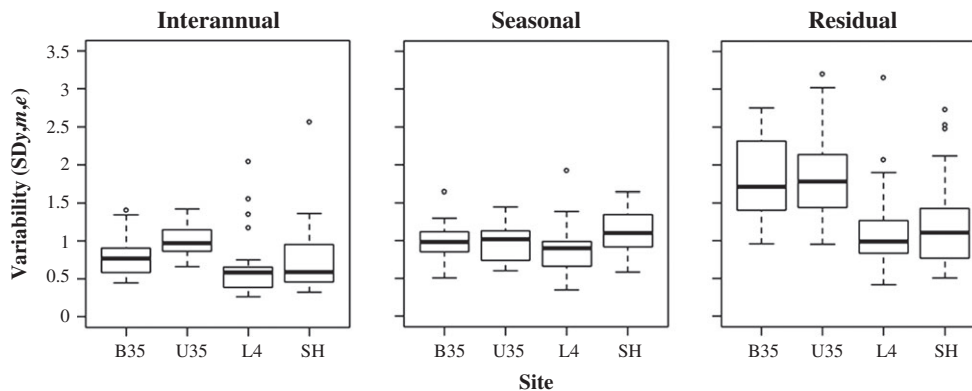In bold statistically significant differences (*P* < 0.05).

Fig. 2. Box plot of data from interannual, seasonal and residual components of zooplankton taxa variability for Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH). Box represents the interquartile (IQ) range which contains the 50% of the records. Line across the box indicates the median. Whiskers extend to the highest and lowest values which are no greater than 1.5 times the IQ range. Circles indicate outliers with values between 1.5 and 3 times the IQ range. Note that the residual variability at L4 and SH is reduced by within-month averaging (see methods).

Table III: P-values obtained from paired t-tests for differences between sites (Bilbao 35: B35, Urdaibai 35: U35, Plymouth L4: L4 and Stonehaven: SH) in the interannual, seasonal and residual components of zooplankton taxa

	Interannual			Seasonal			Residual		
	U35	L4	SH	U35	L4	SH	U35	L4	SH
B35	<0.001	0.248	0.798	0.855	0.202	0.061	0.743	<0.001	<0.001
U35		<0.001	0.023		0.078	0.060		<0.001	<0.001
L4			0.220			0.002			0.399

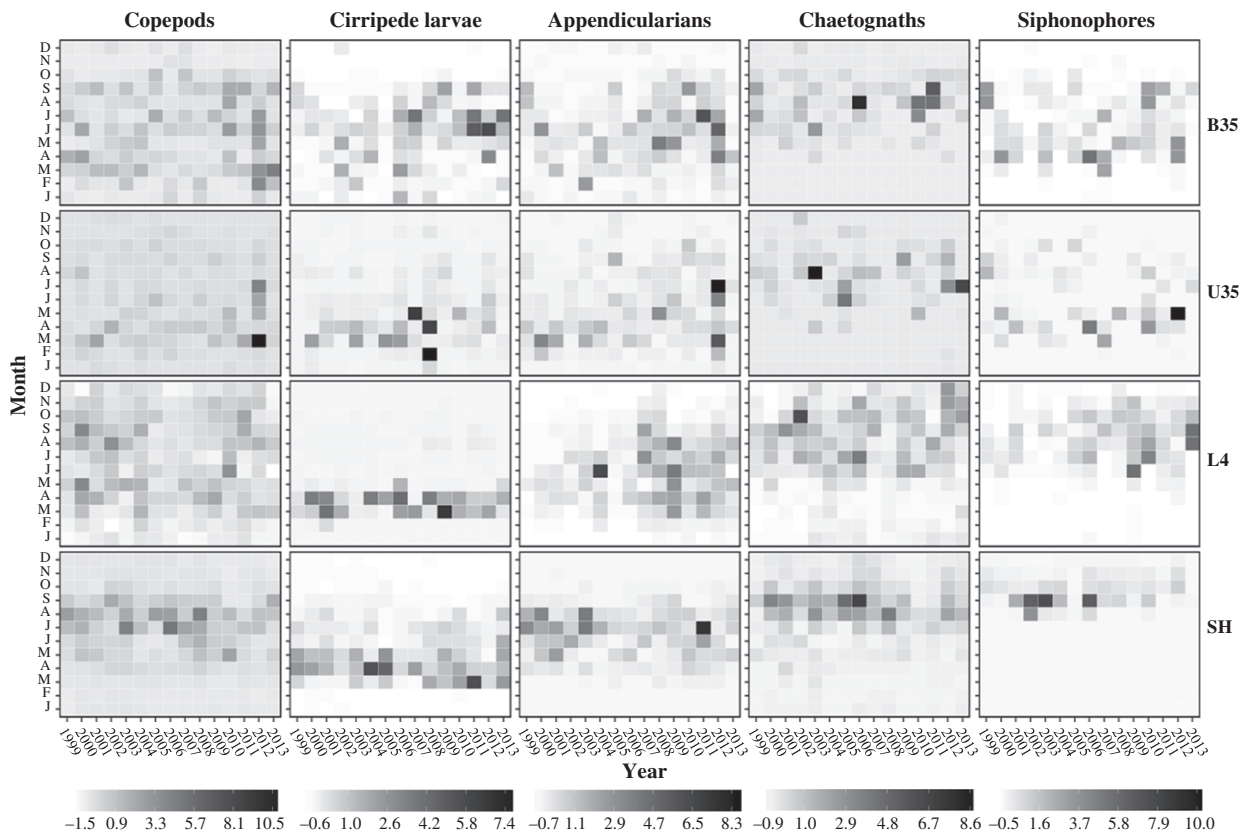In bold statistically significant differences ($P < 0.05$).

Fig. 3. Year vs. month variations of abundance (expressed as anomalies) for copepods, cirripede larvae, appendicularians, chaetognaths and siphonophores at Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH).

range of months within which the annual maximum occurred varied from two (cirripede larvae: March–April) to eight (copepods: March–October) months at L4, from five (chaetognaths: late May–September) to eight (appendicularians and siphonophores: late March–October) at U35, and from six (chaetognaths: late May–October) to nine (copepods: late February–October) at B35.

As shown in Fig. 4, the between-year differences in the timing of the annual maximum of total zooplankton abundance was also lowest at SH, with a range of

5 months (May–September), whereas the range was of 6 months at U35 (March–August), seven at L4 (March–September) and eight at B35 (February–September). The period within which Chl*a* showed annual maxima was of six months at SH and L4 (April–September), seven at B35 (late February–August) and nine at U35 (late February–October). The range for water temperature annual maxima was of 2 months at SH (August–September) and U35 (late July–August), and of 3 months at L4 (July–September) and B35 (late July–September).
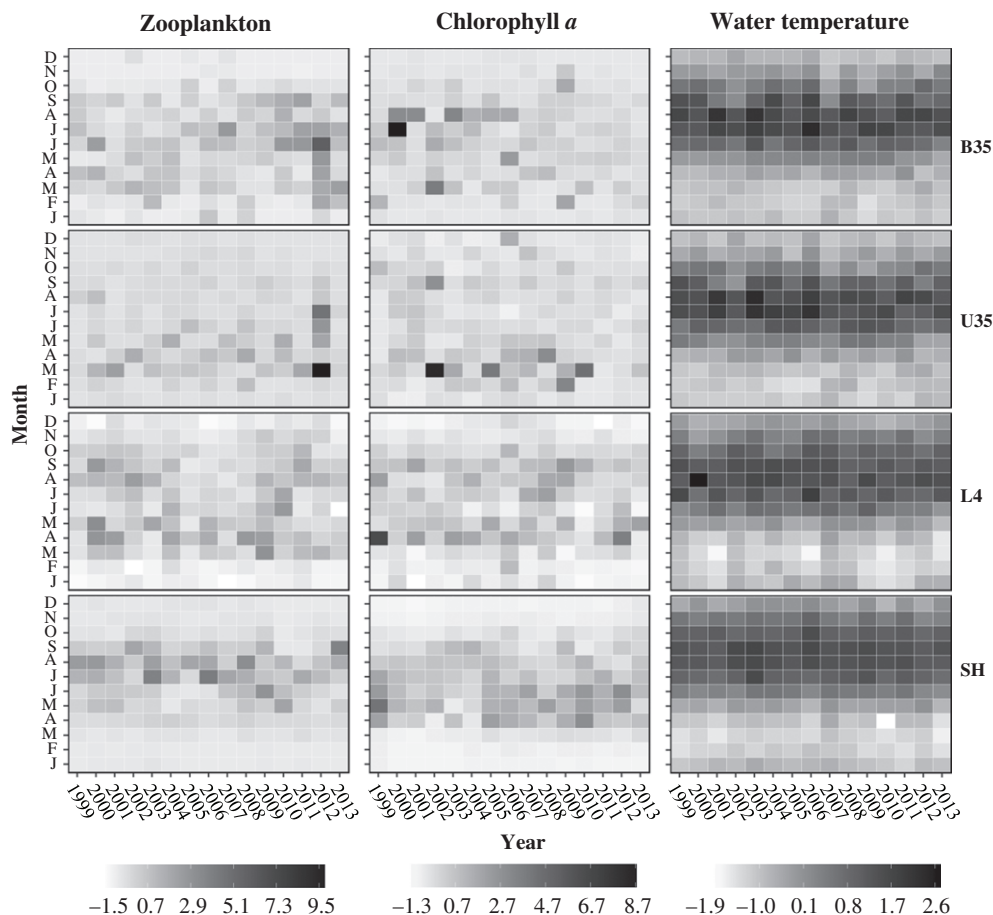
Fig. 4. Year vs. month variations of total zooplankton abundance, chlorophyll *a* concentration and water temperature (expressed as anomalies) at Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH).
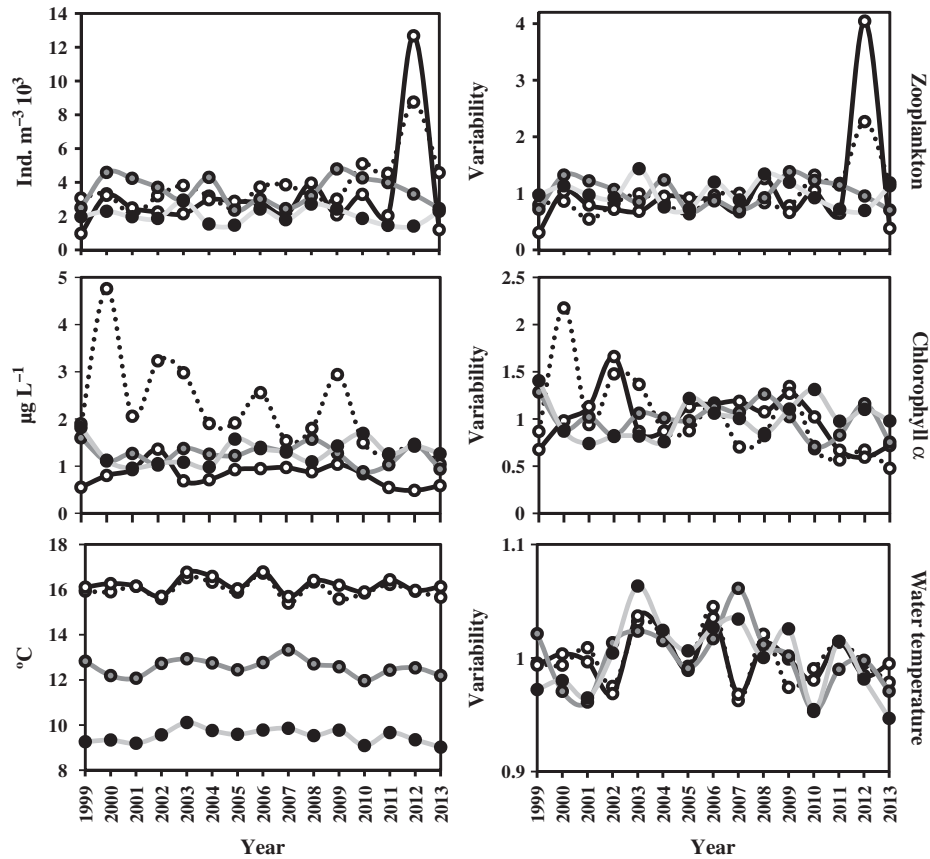
Interannual variations

Total zooplankton, chlorophyll a and temperature

The annual mean values and the interannual variability (dimensionless) of total zooplankton abundance, Chl*a* concentration and temperature are shown in Fig. 5. Zooplankton abundance fluctuated between 972 and 5097 ind. m^{-3} (all sites pooled), except in 2012 at B35 and U35, where values of 9116 and 12 866 ind. m^{-3} where obtained, respectively. Annual mean values of Chl*a* at U35, L4 and SH were similar and ranged between 0.49 and 1.81 µg L^{-1}, whereas at B35 they were higher than at the other sites ($P < 0.001$), with a maximum value of 4.76 µg L^{-1} in 2000 and a decrease over the study period. The warmest and the coldest years in the series differed between sites, although in all of them the warmest ones were recorded from 2003 to 2007 (2003 at SH, 2003 and 2006 with similar values at U35, 2006 at B35 and 2007 at L4) and the coldest ones in the second half of the series (2007 at B35 and U35, 2010 at L4 and 2013 at SH).

Zooplankton abundance and Chl*a* were not correlated between sites, whereas water temperature correlated between B35 and U35 ($P < 0.001$), and between L4 and SH ($P = 0.001$). Within sites zooplankton abundance, Chl*a* concentration and water temperature were not correlated, except for the negative correlation ($P = 0.026$) between zooplankton and Chl*a* at B35 and the positive correlation ($P = 0.024$) between Chl*a* and temperature at L4.

Zooplankton taxa

There were no defined clusters of zooplankton taxa according to their interannual variations (Fig. 6), and most zooplankton taxa showed irregular fluctuations unsynchronized between sites (Fig. 7). The most noteworthy feature of the interannual variations of zooplankton taxa was the prominent peak of some holoplankton (i.e. copepods, PCPC-Calanus, *Oithona*, *Acartia* and appendicularians) and meroplankton (i.e. bivalve larvae and echinoderm larvae) taxa in 2012 at

Fig. 5. Annual mean raw values (left) and dimensionless year-to-year variability values (right) of total zooplankton abundance, chlorophyll *a* concentration and water temperature in Bilbao 35 (white circle, dotted black line), Urdaibai 35 (white circle, black line), Plymouth L4 (dark grey circle and line) and Stonehaven (black circle, light grey line).
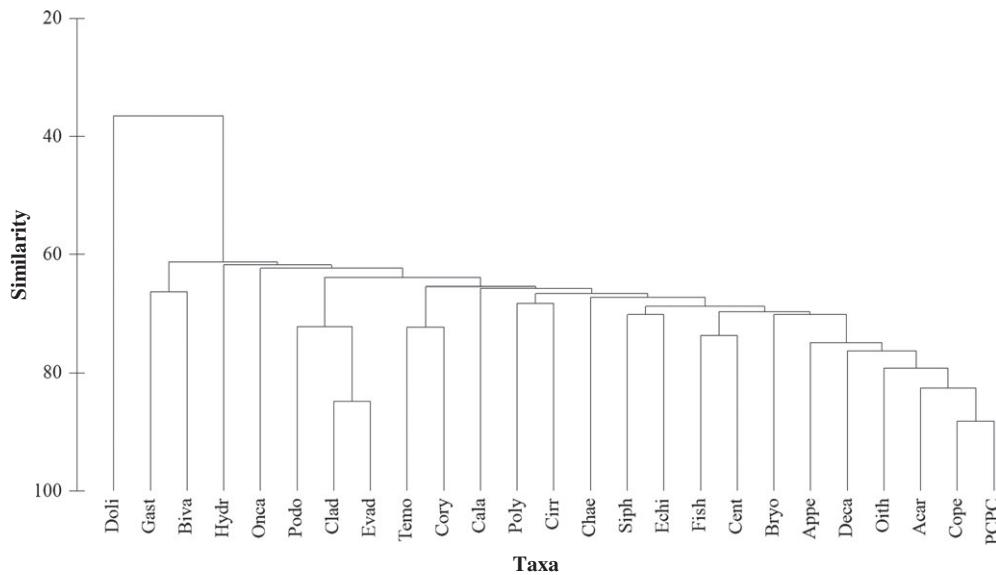
Fig. 6. Group-averaged clustering from Bray-Curtis similarities of interannual variations of zooplankton taxa (pooled for the four sites: Bilbao 35, Urdaibai 35, Plymouth L4 and Stonehaven). Acar: *Acartia*, Appe: appendicularians, Biva: bivalve larvae, Bryo: bryozoans, Cala: Calanidae, Cent: *Centropages*, 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*.
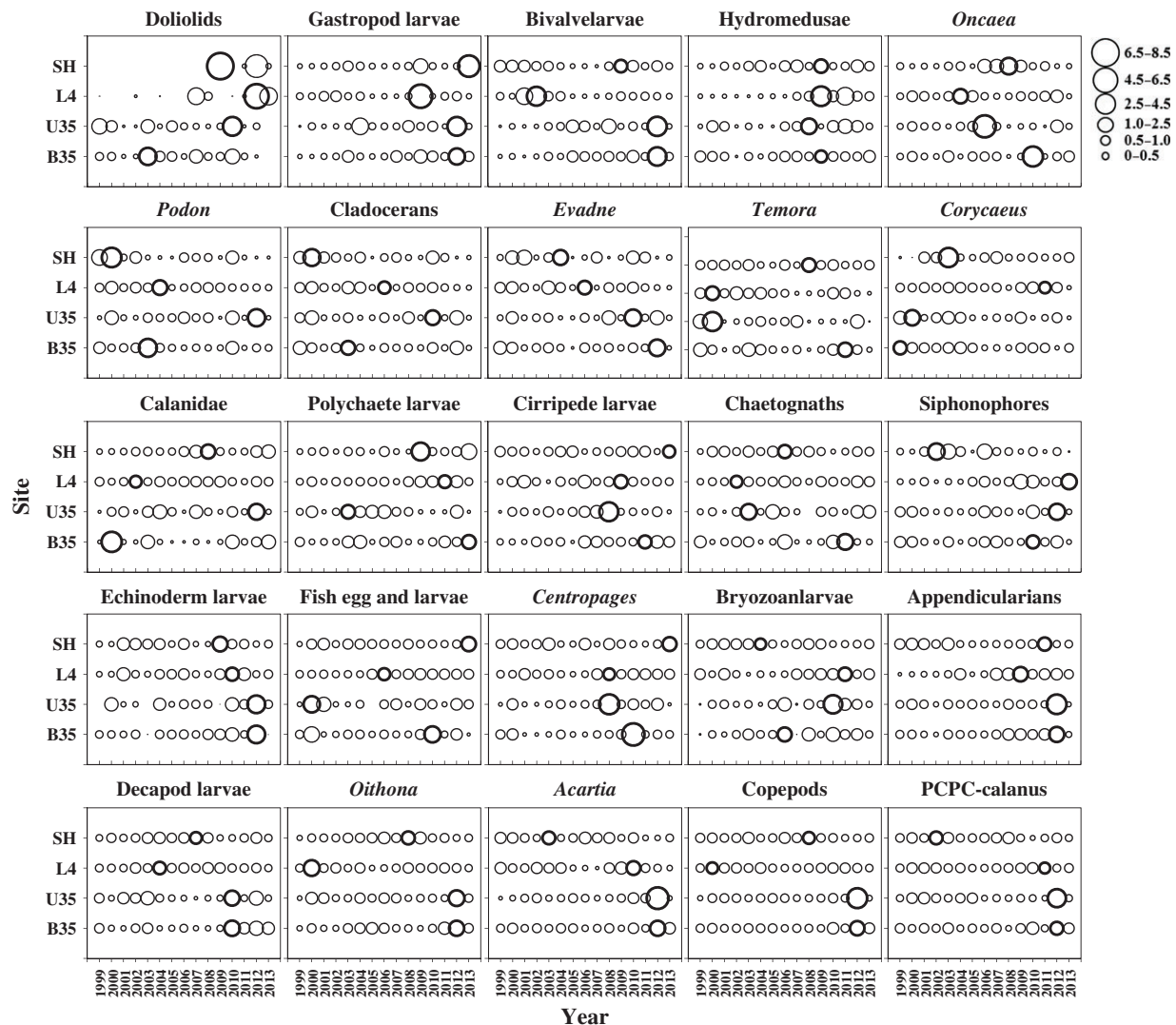
Fig. 7. Interannual dimensionless variability of zooplankton taxa at Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH) from 1999 to 2013. Thickest bubbles indicate highest values.

U35, and to a lesser extent at B35. The number of taxa that reached the highest abundance of the series in 2012 was 11 and 9 at U35 and B35, respectively, while only 4 taxa at L4 (in 2009 and 2011) and 5 at SH (in 2008) were found to reach the highest abundance in a same year of the series.

None of the taxa showed interannual synchrony between the four sites. The number of taxa that correlated ($P < 0.05$) between sites was highest between B35 and U35, with eight taxa (cladocerans, siphonophores, doliolids, bivalve larvae, bryozoan larvae, decapod larvae, *Evadne* and *Corycaeus*), and was lowest between B35 and SH and between U35 and L4, where only gastropod larvae and chaetognaths correlated, respectively. Between B35 and L4 only cladocerans, appendicularians and

bivalve larvae (this last group negatively) showed significant correlation; between U35 and SH cirripede larvae and bryozoan larvae (this last group also negatively); and between L4 and SH cladocerans, bivalve larvae and echinoderm larvae. A few significant correlations were also found between interannual variations of zooplankton taxa and environmental variables, i.e. water temperature and Chl*a*, and such correlations were unrelated between sites.

Seasonal patterns

Total zooplankton, chlorophyll a and temperature
The monthly mean values and the seasonal variability (dimensionless) of total zooplankton abundance, Chl*a*
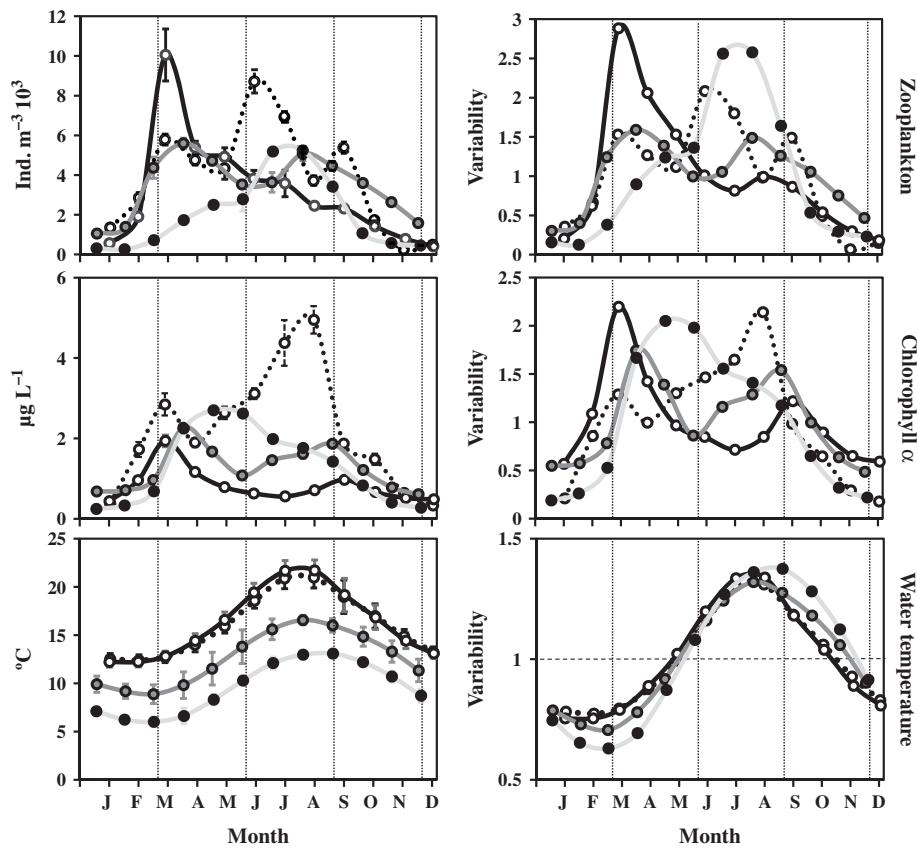
Fig. 8. Monthly mean raw values (left) and dimensionless seasonal variability values (right) of total zooplankton abundance, chlorophyll *a* concentration and water temperature in Bilbao 35 (white circle, dotted black line), Urdaibai 35 (white circle, black line), Plymouth L4 (dark grey circle and line) and Stonehaven (black circle, light grey line). Dotted lines separate seasons.

concentration and temperature are shown in Fig. 8. At U35 the zooplankton maximum was in early spring (10 494 ind. m^{-3} in late March), but the dimensionless values showed a bimodal cycle with a secondary peak in late summer. At B35 three peaks were observed in early spring (late March), early summer (maximum of 9657 ind. m^{-3} in late June) and early autumn (late September). At L4 a clear bimodal pattern with two similar peaks in spring (maximum of 5519 ind. m^{-3} in April) and summer (August) were observed. At SH, the seasonal pattern was unimodal, with a maximum of 5237 ind. m^{-3} in summer (July–August), although the stair-step shape suggests two consecutive periods for zooplankton increase in spring and summer.

Chl*a* concentration showed two peaks at B35 (a small one in early spring and the largest in summer), U35 (the major one in early spring and a secondary one in late summer) and L4 (in April and August with similar magnitudes). At SH, an extended single peak in late spring (May–June) was observed, but the stair-step shape of the decrease in August suggests masking of a secondary peak in summer. The monthly mean maximum Chl*a*

was highest at B35 (4.95 µg L^{-1}) and lowest at U35, showing a small increase from U35 (1.94 µg L^{-1}) to L4 (2.26 µg L^{-1}), and to SH (2.70 µg L^{-1}).

Monthly mean values of water temperature ranged from around 12.4°C in January–February to around 21.0°C in August at B35 and U35, from 8.9°C in March to 15.6°C in August at L4, and from 6.0°C in March to 13.1°C in September at SH. The standard dimensionless variability showed that both warming and cooling occur earliest at B35 and U35 and latest at SH.

Zooplankton taxa

The clustering of zooplankton taxa (Fig. 9) according to their patterns of seasonal variability (Fig. 10) revealed five taxa assemblages with similarity levels between 60 and 80%. Similarity was highest between cladocerans, *Evadne*, *Podon*, appendicularians and *Acartia*, which showed a seasonal progression of annual maxima northwards, from U35 in late March, to L4 in May–July and to SH in July–August. At B35 they peaked in late
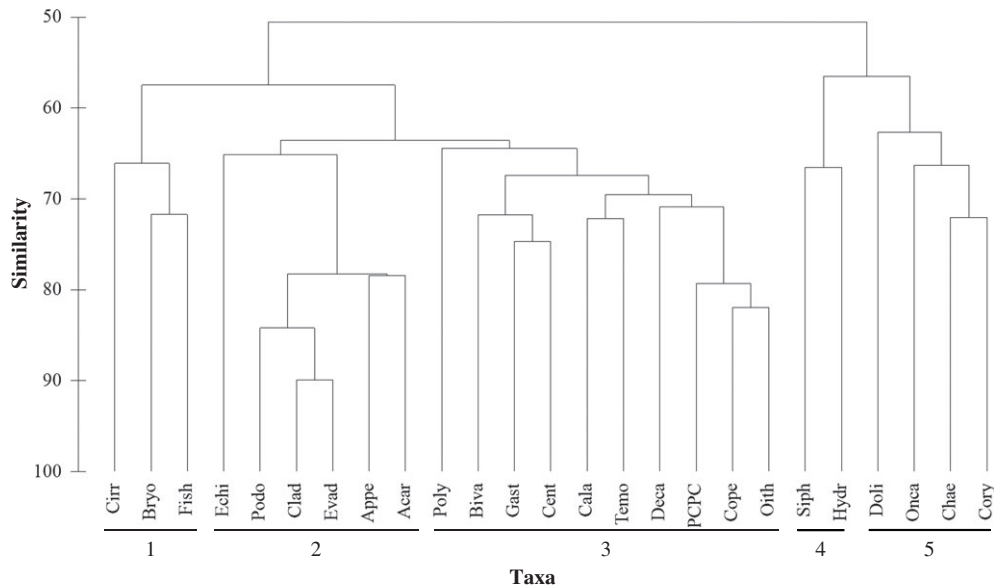
Fig. 9. Group-averaged clustering from Bray-Curtis similarities of seasonal patterns of zooplankton taxa (pooled for the four sites: Bilbao 35, Urdaibai 35, Plymouth L4 and Stonehaven). Taxa abbreviations as in Fig. 6.

May-late June, except *Acartia* (in late March). A delay of the annual maxima was also observed from spring-early summer at U35 and B35 to summer-late summer in echinoderm larvae, gastropod larvae and *Centropages*. Calanidae, *Temora*, decapod larvae, PCPC-Calanus, copepods and *Oithona* were characterized in most cases by bimodal patterns, (or trimodal patterns at B35), in which the first peak was delayed from U35 and B35 (late February–April) to SH (May), while the last one generally occurred earlier at L4 and SH (July–September) than at U35 and B35 (late August-late October). The last peak was the annual maximum for a larger number of taxa at SH (Calanidae, *Temora*, decapod larvae, copepods and *Oithona*) and B35 (*Temora*, decapod larvae, PCPC-Calanus and *Oithona*) than at U35 (*Temora*, PCPC-Calanus), where the first peak was clearly the highest one for copepods and *Oithona*. For PCPC-Calanus the importance of the first peak decreased from SH to B35. The annual maximum of polychaete larvae was delayed from U35 and B35 (late February) to L4 (June) and to SH (July). Siphonophores showed bimodal cycles at B35 and U35, with maxima in May, but unimodal cycles at L4 and SH, with maxima in September. Hydromedusae showed bimodal cycles at B35, U35 and SH, with maxima in April, but unimodal cycles at L4 with the maximum in July. Bryozoan larvae and fish eggs and larvae showed annual maxima or higher abundance earlier at L4 and SH (March–April) than at U35 and B35 (late April-late June), and cirripede larvae reached annual maxima in late March–April at SH, L4 and U35, but markedly

later (late June) at B35. Doliolids, *Oncaea*, chaetognaths and *Corycaeus* reached annual maxima in the second half of the year at all sites, with the exception of *Oncaea* at SH. Doliolids and chaetognaths showed a marked seasonality with maxima in August–September at all sites, while *Oncaea* peaked from late September to November (except at SH) and *Corycaeus* peaked in late August at U35 and B35 and in October at L4 and SH.

Figure 11 shows the number of taxa that showed their annual maximum of abundance in a given month of the year. This distribution was skewed towards spring at U35 and L4 and towards autumn at B35 and SH, with maxima in early spring at U35, early summer at B35, midsummer at L4 and late summer at SH. The extent of the period within which holoplankton groups peaked along the year showed a clear reduction from U35 (6 months, from March to August) to L4 (5 months, from May to September) and to SH (3 months, from July to September), and it was longest (7 months, from March to September) at B35. Overall, meroplankton groups peaked earlier than holoplankton groups at all sites. The largest difference was observed at SH, with most meroplankton groups peaking in April–June and most holoplankton groups in August–September, and the smallest difference at U35 and B35, with most meroplankton and holoplankton groups peaking in the same season. Most cladoceran-copepod genera peaked in spring at U35 and in summer at SH, while at L4 the number of genera peaking in spring and summer was similar, and at B35 most of them peaked in summer-early autumn.
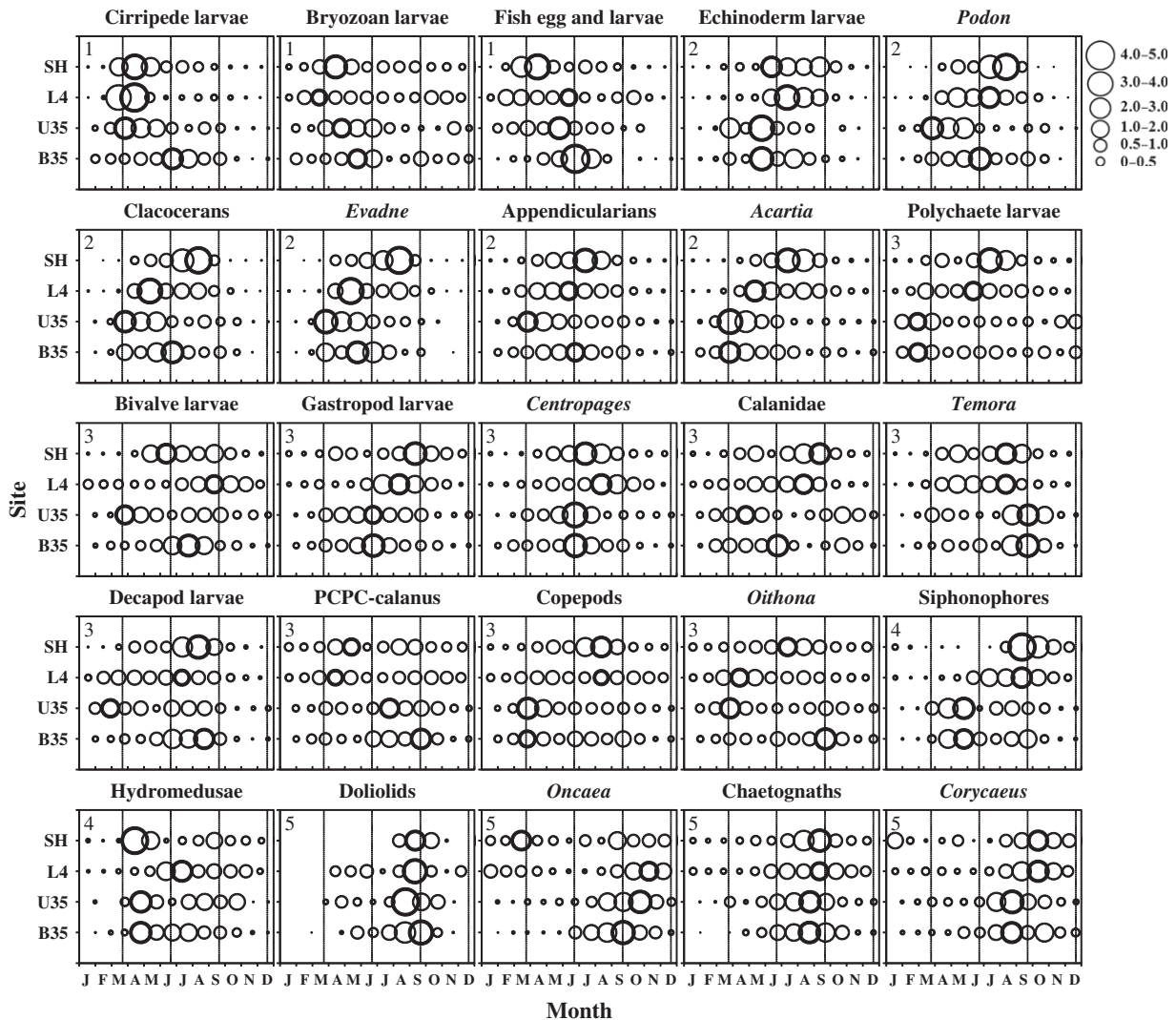
Fig. 10. Seasonal dimensionless variability of zooplankton taxa at Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH) during the 1999–2013 period. Thickest bubbles indicate highest values. Dotted lines separate seasons.

DISCUSSION

Scales of variability

The dominance of the seasonal component over the interannual, and of the residual component over the former two, that we found for zooplankton taxa abundance at all sites under study, seems to be the most common feature for coastal plankton variability (e.g. Cloern and Jassby, 2010; Zingone *et al.*, 2010; Bode *et al.*, 2013). However, the magnitude of the scales of zooplankton variability showed no clear relationship with latitude or trophic status. Latitude appears to be a key driver of the seasonal variability of phytoplankton biomass when a wide latitudinal range and many cases are considered (Cloern and Jassby, 2010). However, in our study only

the fact that the highest seasonal variability of zooplankton taxa was obtained at the northernmost site (SH) fits this assumption. The higher values of the residual component at B35 and U35 might be due to some extent to the use of single measurements as estimators of monthly mean values, instead of the weekly values used for L4 and SH, but also to the combined effect of natural and anthropogenic local factors acting at time scales shorter than the seasonal cycle and high frequency temporal changes like those related to unusual events in single years or year-to-year shifts in phenology (Cloern and Jassby, 2010). The nutrient-rich estuarine plume at B35 and the strong tidal mixing and transport at U35 have a marked influence on phytoplankton biomass and dissolved oxygen dynamics at these sites (Villate *et al.*,
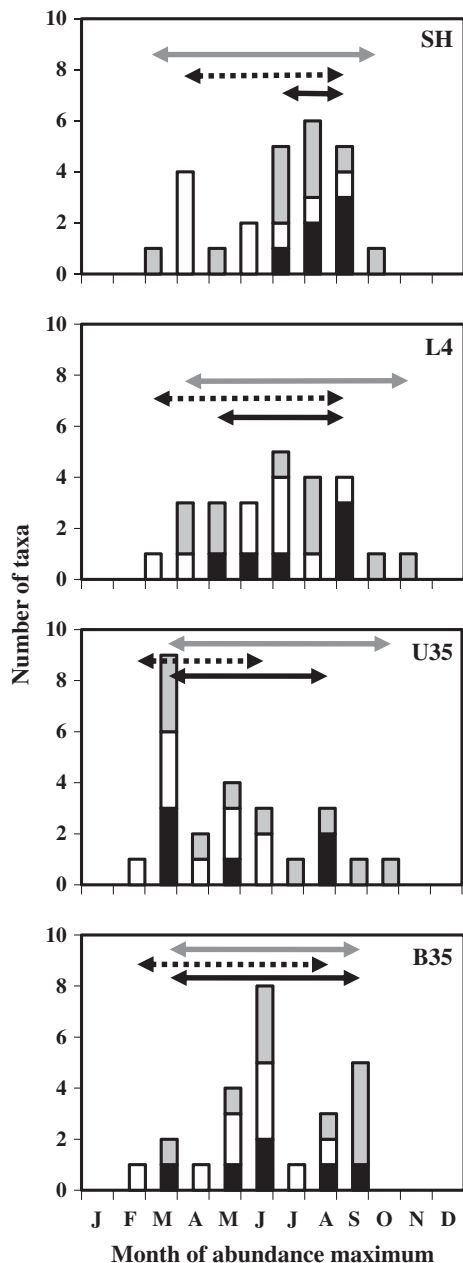
Fig. 11. Histogram of the number of taxa that showed the standard annual maximum in each month at Bilbao 35 (B35), Urdaibai 35 (U35), Plymouth L4 (L4) and Stonehaven (SH). These are cumulative bars representing the number of holoplankton groups (black bars), meroplankton groups (white bars) and copepod-cladoceran genera (grey bars). Arrows indicate the period within which annual maxima of holoplankton groups (black line), meroplankton groups (pointed line) and copepod-cladoceran genera (grey bars) occur.

2008, 2013; Iriarte *et al.*, 2010, 2015), and might enhance residual zooplankton variability as compared with further offshore and deeper sites such as L4 and SH, which can be expected to be less affected by disturbances occurring close to the coast. Strong high

frequency events like the unusual increase of some taxa in 2012 at U35, and to a lesser extent at B35, and the high variability in the timing of taxa annual maxima between years at B35, and to a lesser extent at U35, when compared to L4 and SH, very likely also contributed to increase the residual variability from L4 and SH to U35 and B35.

Interannual variations

Our results do not show the effect of strong atmospheric forcing that can lead to synchronous population fluctuations across wide areas (Goberville *et al.*, 2014; Kang and Ohman, 2014), since neither total zooplankton nor any taxa abundance correlated between all sites. The highest synchrony was observed between B35 and U35, likely due to their geographic proximity, as this enhances the probability of being affected by the same mesoscale shelf water oceanographic structures. The idea that the year-to-year changes in zooplankton might be primarily driven by a combination of forces that differ locally is reinforced by the few cases of synchrony between zooplankton taxa and temperature or phytoplankton biomass observed. Results also strengthen the hypothesis of meaningful differences within the NECS province established by Longhurst (1998), which is also supported by other biogeographical classifications that locate our sites in a variety of units. For instance, the marine ecoregions defined for coastal and shelf areas by Spalding *et al.* (2016) separate the sites of the Bay of Biscay (Lusitanian province) from those located in the English Channel and North Sea (Northern European Seas province). In addition, although all the study sites are within the north European shelf latitudinally parallel to the North Atlantic Drift ecoregion of the Westerly winds biome (Sutton *et al.*, 2017), the SH site is near to the Northwest Atlantic Subarctic ecoregion of the Polar biome, whereas U35 and B35 are in the boundary with the Central North Atlantic ecoregion of the Trade wind biome. At SH water moves generally southerly and it is a mix of coastal and oceanic Atlantic waters, with an increase of the latter in late summer-early autumn; and L4 is affected by oceanic waters coming in with the dominant southwesterly winds (Falkenhaug *et al.*, 2013). In the narrow Basque shelf, the Eastern North Atlantic Central water is the main water mass and influences coastal water (U35 and B35) (Valencia *et al.*, 2004).

The unusually high abundance of total zooplankton at U35 and B35 in 2012, mainly as a result of the marked increase of *Acartia*, PCPC-Calanus, *Oithona*, appendicularians and bivalve larvae, corroborated the importance of local or region-specific physical processes driven by meteo-climatic conditions in modifying the

range of interannual fluctuations of zooplankton abundance (Buttay *et al.*, 2015). 2012 has been reported as a peculiar year in the southern Bay of Biscay, with atypical positive values of the upwelling index for February and March (Rodriguez *et al.*, 2015) and exceptional changes in specific phytoplankton species related to climate anomalies (Díaz *et al.*, 2013).

The concurrent increase of zooplankton abundance and decrease of phytoplankton biomass at the anthropogenically enriched site of B35 excludes the bottom-up control as a plausible cause of zooplankton increase, in contrast to findings for other systems (Steinberg *et al.*, 2012). Environmental changes associated with the rehabilitation of the estuary of Bilbao might have had opposite effects on zooplankton and phytoplankton, since the phytoplankton biomass decline in the system during the period of study occurred concomitant with the decrease in anthropogenic nutrient loadings (Villate *et al.*, 2013) as observed elsewhere too (Mozetič *et al.*, 2010; Zingone *et al.*, 2010).

Seasonal patterns

Seasonal patterns of many taxa and total zooplankton abundance, as well as phytoplankton biomass, seemed to be related to latitude. This was mainly indicated by the clear delay of the early peak, and to a lesser extent by the advancement of the late peak, from the southernmost site (U35) to the northernmost one (SH), in agreement with the principle that spring processes tend to occur earlier and autumn processes later in the year with increasing temperature (Mackas and Beaugrand, 2010). However, taxa with a coincident seasonal pattern at all latitudes and taxa with a delay in the seasonal distribution at the southernmost sites were also found.

Coincident seasonal distributions at the three latitudes, such as those of cirripede larvae, chaetognaths and doliolids, could be attributable to an environmental stimulus that does not change within the latitude range we studied. No information on the species composition of cirripede larvae is available in our zooplankton series, but latitudinal differences in barnacle species distribution is supported by studies covering areas from Scotland to Portugal (Crisp *et al.*, 1981; O'Riordan *et al.*, 2004). The coincidence of a major early spawning peak of cirripedes at all sites, regardless of compositional differences, seems to be the result of a common response to the timing of phytoplankton increase from winter to spring (Starr *et al.*, 1991; Highfield *et al.*, 2010). Similarly, the coincidence of the seasonal distribution of chaetognaths, despite the dominance of different species such as *Parasagitta friderici* at U35 and B35, *P. setosa* at L4 and *P. elegans* at SH, could be attributable to them sharing the same diet, which

consists mainly of small copepods (Falkenhaug, 1991; Gibbons and Stuart, 1994; Tönnesson and Tiselius, 2005) that peak in the warmest period. The coincidence of doliolid maxima at all sites in late summer agrees with the fact that doliolid development occurs at high temperature and is favoured by stratification of the water column (Menard *et al.*, 1997).

The delay of the annual maxima of bryozoan larvae and ichthyoplankton at the southernmost sites may be related to compositional differences associated with different environmental preferences. No information is available about bryozoan species composition, but the differences in fish species distribution between sites are well known and support the observed differences in ichthyoplankton seasonality. The most abundant fish larvae off the east coast of Scotland are those of sandeel, which are almost restricted to the first half of the year and usually peak in March, whereas in the western English Channel the larvae of whiting and a mixture of clupeids (mainly sprat and sardine) are more abundant, peaking from March to June (Edwards *et al.*, 2011). In the inner Bay of Biscay fish larvae reach annual maxima around June and sardine and anchovy larvae are the most abundant, anchovy being clearly associated with warmer conditions (d'Elbée *et al.*, 2009).

The northward delay of the annual maxima across sites in cladocerans and their genera *Podon* and *Evadne* (mainly *E. nordmanni*), the copepod *Acartia* (almost exclusively *A. clausi*), and appendicularians was linked to the timing of the spring phytoplankton peak, but it may also reflect specific temperature optima. This was evident mainly for *A. clausi*, which peaked in late March, at temperatures near the annual minimum (12.4°C) at the southernmost sites, and later in the year, near the annual maximum (13°C), at the northernmost site.

Among taxa with bimodal cycles, or bimodal cycles that become unimodal at the northernmost site, latitudinal differences in timing and magnitude of peaks were related to compositional differences in some cases. For *Temora*, *T. longicornis* was responsible for the first annual peak at all sites, whereas *T. stylifera* was responsible for the second one at U35 and B35. Similarly, PCPC-Calanus is dominated by the spring peaking species *Pseudocalanus elongatus* at SH (Bresnan *et al.*, 2015) and by *Paracalanus parvus* at U35 and B35, where this species is responsible for the much higher value of the second annual peak. At L4, both species are similar in abundance, but *P. elongatus* peaks in spring and *P. parvus* in autumn (Eloire *et al.*, 2010). *Oithona similis*, accounted for the early peak of *Oithona* at U35 and the only peak of this genus at SH, whereas *O. nana* was not recorded at SH and L4 (Castellani *et al.*, 2016), but it was the main species responsible for the second peak of *Oithona* at

U35 and B35. In contrast, *Oncaea* and *Corycaeus* showed bimodal cycles at SH and unimodal ones at U35. In agreement with previous reports by Eloire *et al.* (2010), our results show a skewed distribution of *Corycaeus* and *Oncaea* towards autumn and winter at L4 and SH, which may be related to the later cooling of water as compared to U35 and B35.

A plot showing how many taxa had their annual maximum of abundance in each month of the year shows that the largest number of taxa had their peak abundances in early spring at the southernmost site (U35) but summer at the intermediate and northernmost sites (L4 and SH). This may be a response to differences in phytoplankton availability during spring–summer, since the availability decreases strongly in summer at U35 but it remains rather high at L4 and SH. At this last site, the occurrence of most meroplankton groups' maxima in spring and the later concentration of the annual maxima of all holoplankton groups and most cladoceran-copepod genera in the 3-month summer period coincide with changes in phytoplankton availability (higher in spring than in summer), but also with the succession of the late spring diatom bloom by the annual maximum of dinoflagellates in summer at SH (Bresnan *et al.*, 2015). The wider seasonal distribution of the annual maxima for meroplankton groups than for holoplankton groups at all sites also suggests that the spawning behaviour of different benthic populations does not only depend on phytoplankton abundance, but also on phytoplankton composition or physical factors such as temperature (Starr *et al.*, 1992, 1993; Highfield *et al.*, 2010).

The effect of the trophic status was mainly shown by the delay in the annual maximum of many taxa and the transformation of the bimodal cycles of total zooplankton and some taxa at the oligotrophic site into trimodal cycles at the mesotrophic site. Because no significant differences in temperature occur between U35 and B35, the modification of the phytoplankton biomass cycle and composition at the mesotrophic site by man-made eutrophication (Garmendia *et al.*, 2013) seems the main factor responsible for such differences. At U35, Chl*a* showed the classical summer decrease related to nutrient-limitation, as in other nearby continental shelf areas of the southern Bay of Biscay (Stenseth *et al.*, 2006), whereas at B35 summer Chl*a* values exceeded those of spring. The seasonal delay of most holoplankton taxa at B35 revealed that the same species were able to reach higher densities later than at U35 due to the maintenance of high phytoplankton biomass until autumn. In *Oithona*, however, seasonal differences were mainly related to between-site differences in species dominance. The spring species *O. similis*, which may be limited by high (>20°C) temperatures (Castellani *et al.*, 2016),

dominated at U35, whereas the summer-autumn species *O. nana*, which is associated with high temperature and Chl*a*, and to eutrophicated/polluted conditions (Arfi *et al.*, 1981; Villate, 1991; Jamet *et al.*, 2001), dominated at B35. In spite of their location, the between-site differences in the seasonal patterns of phytoplankton and zooplankton at U35 and B35 were larger than those reported by Bresnan *et al.* (2015) between SH and Loch Ewe. The latter are also located around the same latitude but Loch Ewe is on the west Scottish coast and is more influenced by river discharges. In this case, although both phytoplankton and zooplankton showed earlier increases at Loch Ewe than at Stonehaven, the seasonal maxima occurred only 1 month earlier in spring at the former site for phytoplankton and in the same month in summer at both sites for zooplankton (Bresnan *et al.*, 2015).

The comparison of our results with those obtained at L4 and sites of the Cantabrian coast (Valdés *et al.*, 2007; Bode *et al.*, 2012) near U35 and B35 in previous decades corroborates seasonal differences from the English Channel to the southern Bay of Biscay, but it also suggests that phenological changes could be occurring in some taxa. This is the case for *Centropages* (almost exclusively *C. typicus* at L4, U35 and B35), which in our study was found to have the standard annual maximum in August at L4 and in late June at U35 and B35, but in other studies where previous decades were considered, maxima were observed in September at L4 and July at the coastal site of Santander (around 100 km from B35 and U35) (Bonnet *et al.*, 2007). *Centropages typicus* is a typical temperate neritic-coastal species of the North Atlantic which responds to temperature increases and changes in the structure and timing of occurrence of phytoplankton (Beaugrand *et al.*, 2007). The seasonal advance experienced by this species may be related to the warming of the northwest European shelf region (Smith *et al.*, 2010). Similarly, the timing of the annual maximum in September observed in this study for Calanidae (mainly *C. helgolandicus*) at SH can be interpreted in the context of the replacement in the dominance of *Calanus finmarchicus* (subarctic spring peaking Calanidae) by *C. helgolandicus* (temperate species) in the North Sea from the late 80 s as a result of warming, since temperature has been identified as the main environmental variable that has influenced the abundance of both species (Beaugrand *et al.*, 2002, 2009; Bonnet *et al.*, 2005; Helaouët and Beaugrand, 2007). However, the differences in the seasonal pattern of *C. helgolandicus* at U35 and B35 suggest a response of population dynamics to the trophic status that was not observed for *C. typicus*. Expanding our study in the future to include more updated information would be interesting to follow the

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evolution of these and other zooplankton components in contrasting areas within the NECS province, and to be able to detect significant local effects.

CONCLUSIONS

The present study shows that in the four coastal sites of the Northeast Atlantic Shelves Province of the ICES area, during the 1999–2013 period, the magnitude of zooplankton interannual, seasonal and residual components of variability did not show a clear relationship with the latitudinal gradient, and the interannual zooplankton variations were not coherent across sites, this suggesting the dominance of local forces over wider scale climatic drivers. Seasonal patterns, however, differed across sites in such a way that allowed north–south trends to be identified. The most recurrent one was the delay of the early seasonal peak of many spring–summer taxa northwards, together with the earlier occurrence of the late peak in taxa showing bimodal cycles during the spring–summer period. In addition, taxa with coincident seasonal patterns at all sites, taxa peaking earlier with increasing latitude over the first half of the year or taxa peaking later with increasing latitude over the second half were also observed. Phenological differences in zooplankton from sites at the same latitude but with different trophic status allowed us to distinguish the effect of climatic variability from the effect of man-induced perturbations, which is one of the priorities stated by the Marine Strategy Framework Directive (MSFD). In addition, envelopes of zooplankton variability that can be used as reference baselines to detect anomalous years have been defined, and helped to establish that 2012 was an anomalous year at our southern Bay of Biscay sites.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plankton Research* online.

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