



Seasonality and interannual variability of copepods in the Western English Channel, Celtic Sea, Bay of Biscay, and Cantabrian Sea with a special emphasis to *Calanus helgolandicus* and *Acartia clausi*

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A total of five mesozooplankton time series data sets were assembled to compare the seasonal and interannual patterns of abundance of calanoid copepods in the Western English Channel (Station L4), Celtic Sea, Bay of Biscay (Continuous Plankton Recorder), and the Cantabrian Sea (RADIALES time series, Santander, St-4 and St-6) from January 1992 to December 1999. A strong seasonal component in taxonomic composition was detected at the locations considered. There was also a strong latitudinal effect on diversity at each location, southernmost locations being more diverse. The seasonal dynamics and year-to-year variability of two copepod species: *Calanus helgolandicus* and *Acartia clausi* were studied in detail. A latitudinal pattern in the seasonal cycles of both copepod species was observed. The peaks of both occur earlier in spring in the warmer southern region and move northwards, consistent with the temperature regimes at each location, supporting the broad concept that species occupy a thermal niche in time as well as in space. There was a strong degree of interannual variability between sites and between species. No clear trends, but some coherent events among data sets, reveal a regional response to environmental forcing factors. Correlations suggest possible connections with environmental indices like the North Atlantic Oscillation and the Gulf Stream North Wall index. There was a positive correlation between the NAO and the abundance of *C. helgolandicus* at station L4 off Plymouth; however, the relationship in the Celtic Sea and Bay of Biscay was opposite to that expected based on previous results. Despite the differences in the sampling techniques used within each dataset, the results are comparable and coherent in terms of taxonomic composition and the seasonal and interannual patterns detected.

Keywords: *Acartia clausi*, Bay of Biscay, *Calanus helgolandicus*, Cantabrian Sea, Celtic Sea, copepods, NAO, time series analysis, Western English Channel, zooplankton.

Introduction

Long-term monitoring programmes are essential to detect and characterize changes in marine ecosystems. These programmes have been designed to describe seasonal patterns and interannual variability in marine populations and to understand their relationship with environmental factors. Although local patterns and baseline conditions can be obtained from individual monitoring programmes, distinguishing local perturbations from broader-scale phenomena can only be achieved when datasets from different locations are compared (Duarte *et al.*, 1992; Batchelder *et al.*, 2012; Mackas *et al.*, 2012a; Valdés and Lomas, 2017). Marine zooplankton populations are particularly appropriate for this comparative approach because their populations are heavily affected by large-scale environmental changes and climatic forcing (e.g. Gamble, 1994; Taylor, 1995; Fromentin and Planque, 1996; Beaugrand *et al.*, 2002a, b, 2015; Edwards and Richardson, 2004; Richardson and Schoeman, 2004; Valdés *et al.*, 2009). However, information on the degree to which these broad-scale relationships affect population dynamics at smaller regional scales and in regional seas (for instance the Celtic Sea and the

Bay of Biscay) is still scarce and dispersed (Berline *et al.*, 2012; Bode *et al.*, 2012; Fanjul *et al.*, 2017).

Several international expert groups such as the ICES Working Group on Zooplankton Ecology (WGZE), the SCOR WG125 (WG125: Working Group 125 on Global Comparisons of Zooplankton Time Series), and the International Group for Marine Ecological Time Series (IGMETS) supported by international organizations [i.e. the International Council for the Exploration of the Sea (ICES), the Scientific Committee on Oceanic Research (SCOR), and the Intergovernmental Oceanographic Commission of UNESCO (IOC-UNESCO)], have made it possible to identify, collect, and connect existing plankton time series projects. These expert groups have encouraged the interchange of data and promoted ecological analysis of plankton data at regional and global scales (Valdés *et al.*, 2006; Mackas *et al.*, 2012a; Valdés and Lomas, 2017). Within the framework of these groups, it has been relatively easy to make broad comparisons of plankton abundance and biomass, which has resulted in some comprehensive reports (e.g. Valdés *et al.*, 2006; Batchelder *et al.*, 2012; O'Brien *et al.*, 2013, 2017). It has been more compli-

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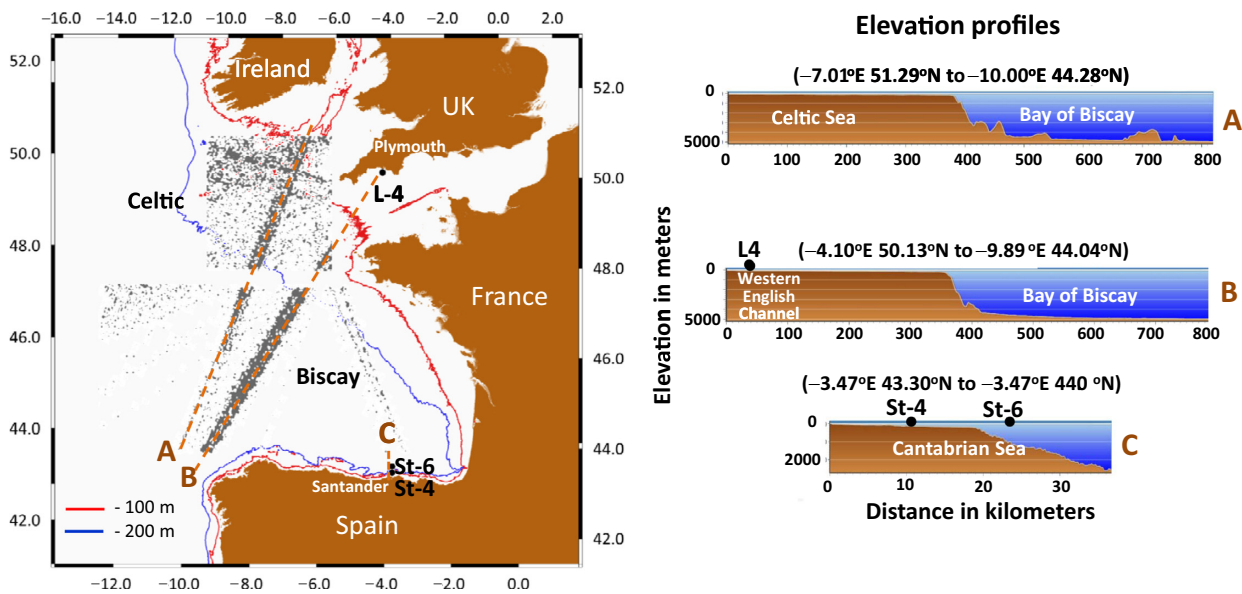


Figure 1. Left panel: map showing the sampling locations of stations L4, St-4, St-6, and the sites (grey dots) of samples taken along the CPR routes in the Celtic Sea and the Bay of Biscay. Right panel: elevation profiles corresponding to the lines indicated by the dashed lines A, B, and C in the left panel.

cated to identify and collect good and accurate mesozooplankton taxonomic datasets lasting for five or more years in the same regional seas. Even so, some good examples of international collaborative papers addressing regional species distribution, biogeography, and ecological dynamics have been published for the North Atlantic and in some European regional seas (Beaugrand *et al.*, 2000a; Berline *et al.*, 2012; Mackas *et al.*, 2012b; Bode *et al.*, 2012; Fanjul *et al.*, 2017).

In the case of the Celtic Sea, the Western English Channel, the Bay of Biscay, and the Cantabrian Sea, taxonomic mesozooplankton datasets are available since 1950 (Continuous Plankton Recorder; CPR), 1988 (Station L4, Plymouth), and 1991 (RADIALES time series, Santander), respectively. Despite the many problems that the combination of data from different zooplankton time series present (Perry *et al.*, 2004), some comparative studies from other time series suggest that the integration of data sets may be possible (Batten *et al.*, 2003; Richardson *et al.*, 2004; Fanjul *et al.*, 2017). For example, comparisons between the CPR and individual monitoring programs (Clark *et al.*, 2001; John *et al.*, 2001; Richardson *et al.*, 2004) suggest that although the absolute abundance of organisms recorded by the CPR and other zooplankton sampling gears is remarkably different, the seasonal and interannual patterns are comparable.

This study integrates data from several plankton sampling programmes and compares the seasonal and interannual patterns of abundance of calanoid copepods in the Western English Channel, Celtic Sea, Bay of Biscay, and the Cantabrian Sea, from January 1992 to December 1999 (Figure 1 and Table 1). The studied locations share common physical and ecological characteristics that make them part of a homogeneous area identified as a unique biogeochemical province: the Northeast Atlantic Shelves Province (Longhurst, 1998). The European continental shelf break and the Bay of Biscay is a region of transition from subtropical to boreal regimes, and subject to a large number of episodic mesoscale events and human activities (Beaugrand *et al.*, 2001; Valdés and Lavin, 2002; Borja *et al.*, 2019). The main objective was to compare the sampling regions according to their species composition

and to study in more detail the seasonal dynamics and year-to-year variability of two copepod species: *Calanus helgolandicus* and *Acartia clausi*. These species were selected because (i) their identification at the species level is accurate, which facilitates the comparison of their seasonality and variability among different datasets; (ii) because of their ecological importance in terms of abundance within the copepod species assemblages in the sampling programmes (John *et al.*, 2001; Bonnet *et al.*, 2005; Hirst, 2007; Maud *et al.*, 2015; Cornwell *et al.*, 2018); and (iii) because their ecology has been previously related to climatic variability (Fromentin and Planque, 1996; Taylor, 1995; Wilson *et al.*, 2016; Atkinson *et al.*, 2018; Borkman *et al.*, 2018; Villarino *et al.*, 2020), which gives additional ecological value and significance to the results and insights presented in this article.

Material and methods

Santander, RADIALES time series

Zooplankton samples were obtained on a monthly basis from January 1992 until December 1999 at two stations across the shelf off Santander (Cantabrian Sea; Figure 1 and Table 1): Station 4 (St-4), which is neritic with a bottom depth of 110 m and Station 6 (St-6), which is more oceanic with a bottom depth of 850 m. Zooplankton samples were taken with a Juday–Bogorov net (50 cm diameter and 250 μ m mesh size) equipped with a General Oceanic Flowmeter for the calculation of the volume of filtered water. A time–depth recorder was fixed onto the frame of the net to observe the trawling depth. Tows were double oblique at an approximate speed of 1–1.5 knots down to a depth of approximately 50 m. Samples were preserved in 4% buffered formaldehyde solution for subsequent analysis in the laboratory. Animals were counted and identified under a dissecting microscope. With the exception of the genus *Clausocalanus*, all calanoid copepods were identified to species level.

The list of sampling dates for stations St-4 and St-6 off Santander (RADIALES programme) is given in Supplementary Table S1. When samples are collected once a month, there

Table 1. Characteristics of the data sets used.

Monitoring programme	Western Channel Observatory	CPR	CPR	RADIALES	RADIALES
Station/data set	Plymouth L4	Celtic Sea	Bay of Biscay	Santander ST-4	Santander ST-6
Basin	Western English Channel	Celtic Sea	Bay of Biscay	Cantabrian Sea	Cantabrian Sea
Latitude (or CPR standard area name)*	50° 15'	D4	E4	43° 34'	43° 42'
Longitude	4° 13'			3° 47'	3° 47'
Station depth (m)	54	50–200	200–4 800	110	850
Frequency (number of cruises year ⁻¹)	Weekly	Approximately 12	Approximately 12	Monthly	Monthly
Gear diam ⁻¹ (cm)	WP2	CPR, aperture 1, 24 cm × 1, 24 cm	CPR, aperture 1, 24 cm × 1, 24 cm	Juday 50	Juday 50
Mesh (µm)	200	270	270	250	250
Depth of sampling (m)	50	≈6.5	≈6.5	50	50
Location of data	PML	SAHFOS database	SAHFOS database	Database SIRENO IEO	Database SIRENO IEO
Observations		Data correspond to several CPR routes and are presented here as the CPR standard areas of the North Atlantic	Data correspond to several CPR routes and are presented here as the CPR standard areas of the North Atlantic		

*For CPR standard areas map and names please see: <https://www.cprsurvey.org/data/our-data/>.

might be some temporal sampling bias. For example, if the samples are collected at the beginning of a month in one year and end of the same month in another year, the bias could be significant, especially during the month when population size fluctuates strongly (e.g. during spring population growth time). This was not the case in Santander (Supplementary Table S1), as the sampling intervals and regularity between years (from 1992 to 1999) during the spring growth season was most respected, and therefore, statistical treatment to deal with a possible bias was not necessary.

Further information on the sampling protocols followed by the programme can be obtained from the web site <http://www.seriestemporales-ieo.net> and from published literature (e.g. Valdés and Moral, 1998; Valdés *et al.*, 2002, 2007, 2021).

Plymouth, L4 time series

Zooplankton samples have been collected at station L4 (Figure 1 and Table 1), which is located at about 13 km SSW off Plymouth. Since 1988, samples are collected, on a weekly basis, by vertical net hauls using a 200-µm mesh WP-2 net (UNESCO, 1968), from 50 m (mean water depth is 54 m) to the surface and stored in 5% formalin. Much of the zooplankton analysis has been to the level of the major taxonomic groups only, but the dominant calanoid copepods are generally well discriminated to species. At L4, *C. helgolandicus* and *A. clausi* are the overwhelmingly dominant species of their respective genera. However, it is possible that a small proportion of rarer congeners, which turn up occasionally are overlooked. For example *Calanus finmarchicus* appears irregularly in winter in some years and some analysts may have overlooked them when they occur in low density (Maud *et al.*, 2015). However, because this percentage is very low, copepodite stages are not distinguished and it is assumed they are all *C. helgolandicus*. Data and further details on the programme can be obtained from its website (<https://www.westernchannelobservatory.org.uk/>) and published literature (Harris, 2010; Eloire *et al.*, 2010; Smyth *et al.*, 2015).

Because of the comparative nature of this study, samples for the period January 1992–December 1999 were selected and data averaged to produce a monthly time series comparable to that of Santander.

CPR survey

The CPR is deployed monthly on approximately 20–25 standard routes across the North Sea and North Atlantic; two of these routes cover the Celtic Sea and the Bay of Biscay (Figure 1 and Table 1). The sampling programme is based on voluntary ships of opportunity, which tow a high speed plankton recorder at an approximate depth of 6.5 m (Hays, 1994; Warner and Hays, 1994). Plankton is filtered by a slowly moving band of silk with an average mesh size of 270 µm taking samples corresponding to approximately 3 m³ of seawater filtered per sample of 18 km of tow (Hays, 1994; Jonas *et al.*, 2004). Methods of counting and data processing are described in Colebrook (1960, 1975) and Warner and Hays (1994). As at L4, much of the zooplankton analysis of CPR samples has been to the level of the major taxonomic groups, but the dominant calanoid copepods are generally well-discriminated to species, and this is the case for *C. helgolandicus*. In the case of *Acartia*, some congeners are also counted in the region, although their abundance is very low and then we assumed they are all *A. clausi*. Data from January 1992 to December 1999 were selected in this study in two target areas (Figure 1): the Celtic Sea (1910 samples) and the Bay of Biscay (1498 samples).

It must be noted that sampling by the CPR is irregular in space, as the samples follow the tracks of “ships of opportunity” (Figure 1 shows the spatial heterogeneity of CPR sampling). The size of the geographical square for the spatial regularization is fixed to circa 100 × 100 nm, and an average estimation of the abundance of a species for a geographical square was calculated when the number of 2-month time periods for which data on abundance are available was > 6 (out of a possible 12; 6 d and 6 nights). This represents the best com-

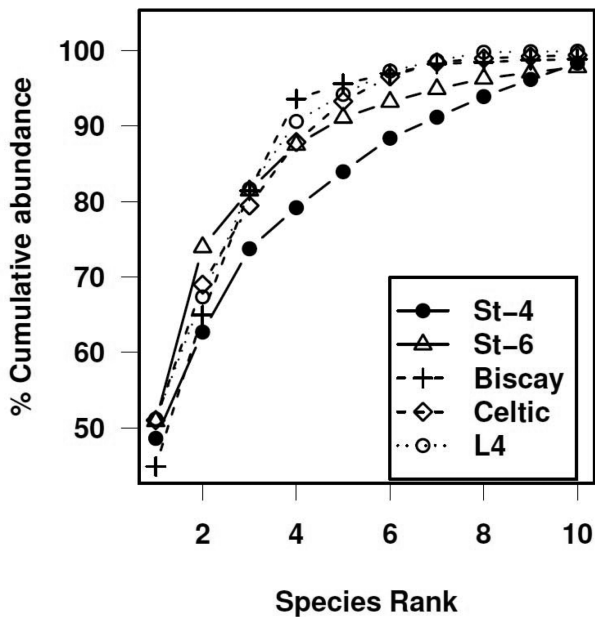


Figure 2. Percentage cumulative abundance of 10 top species for each dataset.

promise between the number of missing geographical squares and the size of the spatial resolution. No spatial interpolation was used in the biogeographical charts, therefore, the averaged data are assumed to represent any point within the standard area. This process of estimation of monthly averages is routinely used in CPR studies and detailed protocols were published by Beaugrand and Edwards (2001) and Beaugrand (2004).

Although the mesh sizes used in the plankton nets in the three sampling programmes are different (250, 270, and 200 μm , in Santander, CPR, and Plymouth, respectively), all are efficient in capturing the mesozooplankton fractions and more specifically the species *A. clausi* and *C. helgolandicus*.

Data analysis

The taxonomic and spatial coherence among collections was first investigated comparing the differences in taxonomic identification of calanoid copepods between surveys. The taxa identified by each programme were listed together and the taxonomic classification standardized to the lowest resolution by grouping several species under a single taxon name when this was done in any of the other surveys (e.g. *Clausocalanus* spp). The cumulative abundance of the main calanoid copepod species was computed and the ranking of species between surveys compared. The similarity between the data sets in their species composition and relative abundance was analyzed by cluster analysis and non-metric multidimensional scaling. This initial inspection of the taxonomic consistency between datasets was followed by a more detailed analysis of the annual cycles and interannual variations of *C. helgolandicus* and *A. clausi*. The average seasonal cycle at each location was visually compared for the mean monthly cycles. For each time series, the 10 and 90% percentiles of the recorded abundances for the 8 years (1992–1999) and for each month were calculated, and the existence of anomalous periods identified as those that surpassed the 10–90 percentile limits. The

trends in the population abundance at each location were obtained by decomposition of each time series into a seasonal, an irregular and a trend component using 'loess' as described in Cleveland *et al.* (1990) and Robert *et al.* (1990), and implemented in the R programming language (R Development Core Team, 2004). Finally, the relationship between the annual abundances at each location and hydro-climatic variability was investigated by correlation analysis against the winter North Atlantic Oscillation (NAO) index (<https://crudata.uea.ac.uk/cru/data/nao/nao.dat>; Hurrell, 2001; Osborn, 2006, 2011) and an index of the position of the North Wall of the Gulf Stream (<http://pml-gulfstream.org.uk/Gulf%20Stream%20Data%202020.pdf>; Taylor, 1995, 2011).

Results

Taxonomic coherence among collections

In the 96 samples considered for each dataset, 10 species accounted for more than 97% of the total abundance of calanoid copepods (Figure 2). Of these species *Paracalanus parvus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Clausocalanus* spp., *A. clausi*, *Centropages typicus*, and *C. helgolandicus* were also among the 10 most abundant species in each of the datasets, generally comprising more than 60% of the total copepods (Table 2). *Paracalanus parvus* was the most abundant copepod in all datasets. *Temora stylifera* was within the 10 most abundant copepods in the three southernmost datasets (St-4, St-6, and CPR Biscay). *Metridia lucens* ranked within the top 10 species at four locations (St-4, St-6, CPR Celtic Sea, and L4). Although less abundant, *Euchaeta hebes* and *Candacia armata*, were also common species identified by all data sets. Finally, *Calanoides carinatus* and *Centropages chierchiae* were within the most abundant species at the Santander stations but these species were not identified in all the data sets.

It is worth noting the remarkable coherence in the copepod species assemblages found in the samples counted in this study with the data published in studies using longer time series at the same sampling sites (Valdés *et al.*, 2007; Eloire *et al.*, 2010), which suggests that, although new species can be found in the region, the copepod taxonomic composition of the mesozooplankton fraction in these areas is reasonably well known.

There was a clear spatial trend in the increasing accumulated abundance vs. the number of species (Figure 2), as in Santander, St-4 and St-6, it took a larger number of species to achieve the same cumulative abundance. Differences in the absolute abundance of species in each dataset were remarkable (Table 2).

Spatial coherence among collections

The results outlined above suggest a strong spatial component of the taxonomic composition at the locations considered. This is reflected in the ordination of the sampling sites according to the similarity in the species composition. The dendrogram (Figure 3a) clearly illustrates the south–north position of each dataset. Also the non-metric multidimensional scaling (Figure 3b) of the sampling sites according to their species composition reflects this spatial component. In fact, Figure 3(b) shows that, the closer two stations are in the plot, the more similar they are according to their species composition. The distances are related to both the geographical

Table 2. Cumulative abundance of the calanoid species common to all data sets (units are number of individuals counted in the 96 samples considered for each dataset).

	St-4 Abund.	St-6 Abund.	Biscay Abund.	Celtic Abund.	L-4 Abund.	All stations Cum. Abund.
<i>Paracalanus parvus</i> *	56 960	33 138	11 274	21 756	26 241	149 368
<i>Clausocalanus spp.</i> *	16 491	14 997	5 040	2 303	2 226	41 057
<i>Acartia clausi</i> *	12 926	4 894	3 054	4 465	14 410	39 749
<i>Pseudocalanus elongatus</i> *	3 258	457	501	3 585	26 081	33 881
<i>Temora longicornis</i> *	5 204	899	322	808	23 101	30 335
<i>Centropages typicus</i> *	3 198	2 336	4 133	7 655	1 800	19 123
<i>Calanus helgolandicus</i> *	6 374	3 933	340	1 398	4 985	17 030
<i>Temora stylifera</i> **	5 582	1 106	61	16	3	6 768
<i>Metridia lucens</i> ***	303	339	60	214	115	1 030
<i>Euchaeta bebes</i>	385	357	15	41	4	803
<i>Candacia armata</i>	487	207	11	25	54	785
All species Cum. Abund.	111 168	62 663	24 812	42 265	99 021	

*Species included within the 10 more abundant in all data sets.

**Species included within the 10 more abundant in three data sets.

***Species included within the 10 more abundant in four data sets.

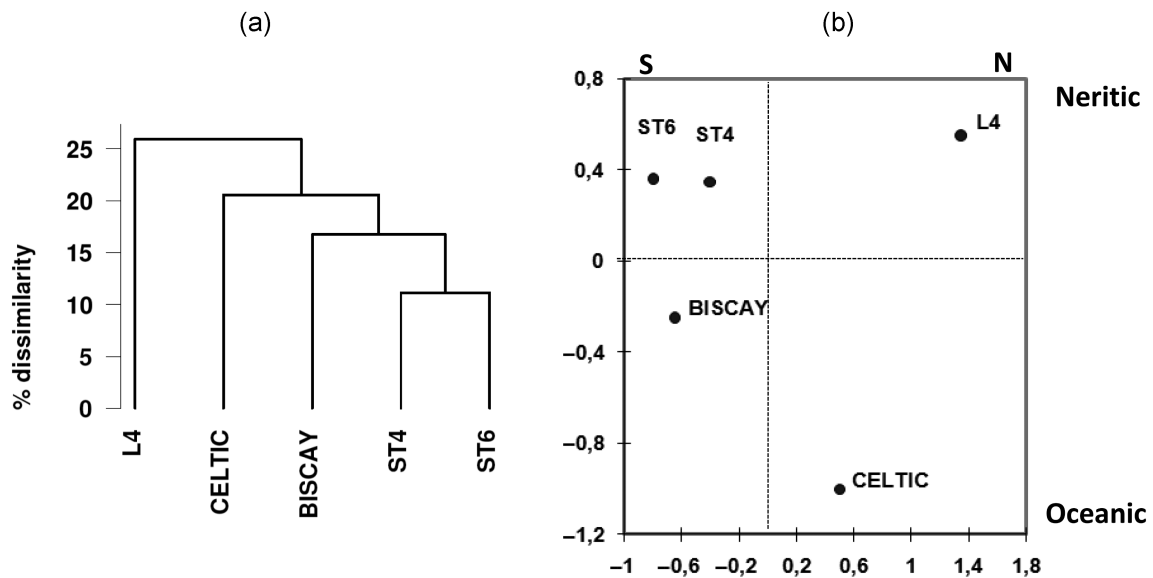


Figure 3. (a) Ordination of sampling sites according to the similarity of species and their abundances. (b) MDS plot of sampling sites according to the similarity in their species composition.

latitude (Dimension 1, X-axis) combined with a neritic-ocean component (Dimension 2, Y-axis).

Seasonal cycles of *C. helgolandicus* and *A. clausi*

The latitudinal pattern observed in the species composition is also noted when the seasonal cycles of the target copepod species, *C. helgolandicus* and *A. clausi* at each sampling site are compared (Figures 4–6). Although there are remarkable differences in the abundance at each location, there is a gradual change in the seasonal cycle with latitude, both reflected in the shape of the average seasonal cycle and in the timing of the seasonal peaks in abundance, supporting the broad concept that species occupy a thermal niche in time as well as in space (Beaugrand and Kirby, 2018). The growth season of *A. clausi* starts earlier in the southern regions (February–March on the shelf and oceanic waters off Santander) than in northern regions (May on Plymouth’ shelf; Figure 4a). The annual cycle observed from the CPR data shows that the seasonality in the Bay of Biscay is similar to that observed at the oceanic

station (St-6) off Santander, and that the annual cycle in the Celtic Sea follows the temporal pattern observed at station L4 off Plymouth. The growth period off Santander extends from February to July, and population decreases after August in the Bay of Biscay. In the Celtic Sea and Western English Channel, *A. clausi* shows a first peak in May and a second peak in August–September; afterwards, the population abundance starts to decrease in November. The absolute abundances are similar at Santander (St-4 and St-6) and Plymouth (L4), however, CPR values are much lower (Figures 4a and 5).

The average seasonal cycle of *C. helgolandicus* also shows a latitudinal pattern (Figures 4b and 6). The increase in abundance during the spring occurs earlier (March–April) in Santander (St-4 and St-6) and the Bay of Biscay than in the Celtic Sea and in the L4 off Plymouth (May). At St-4 off Santander, the growth season lasts for about 3 months (March–May), whereas at the outer station (St-6) and in the Bay of Biscay the growth period is shorter. In contrast with the southernmost locations, the Celtic Sea and station L4 off Plymouth show two different peaks, one in spring (May), and a

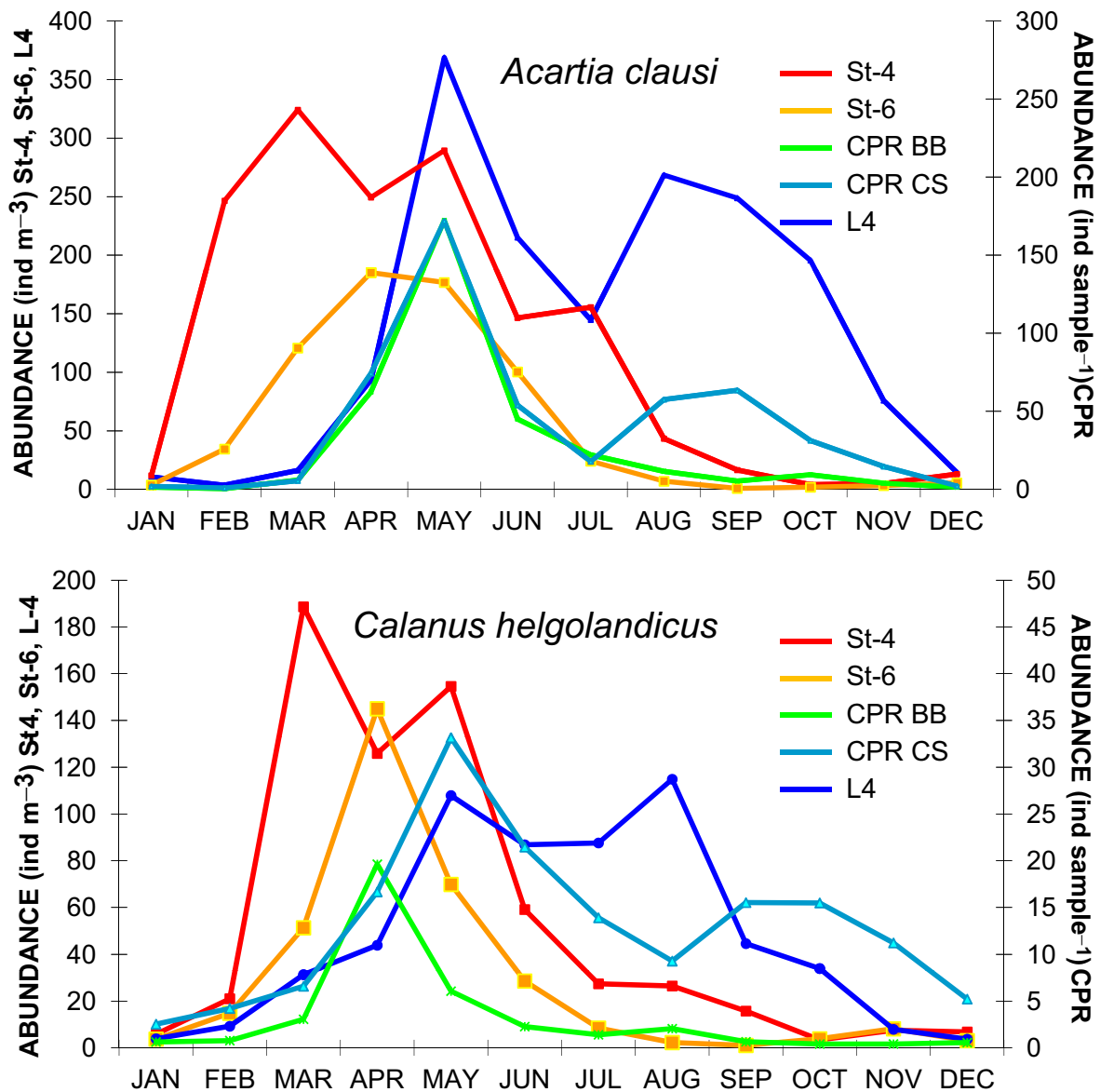


Figure 4. Mean monthly abundances (all years combined) of *A. clausi* (upper panel) and *C. helgolandicus* (lower panel). Left axis stands for abundances in Santander and Plymouth, right axis stands for abundances in the Bay of Biscay and Celtic Sea.

second in late summer–fall (August–September). Highest densities were found over the shelf at St-4 off Santander, while the overall population densities at the oceanic station St-6 off Santander and at station L4 off Plymouth were similar. The densities of *C. helgolandicus* recorded by the CPR are much lower (Figures 4b and 6).

Interannual variability of *C. helgolandicus* and *A. clausi*

The time series considered here are probably too short to evaluate any significant relationships with climatic indices or synchronies in the time series, but at least the inter-comparison of the interannual variability at each location provides some useful preliminary information. There was a stronger connection between the year-to-year variability of *A. clausi* at the different locations than that of *C. helgolandicus* (Figures 5–8).

For example, at all stations, except St-4 off Santander, the abundance of *A. clausi* was extremely low during 1996; at both sampling locations, Santander and Plymouth, 1996 was the coldest summer overall in the whole period 1992–1999 (Valdés and Lavin, 2002; Atkinson *et al.*, 2015). Nevertheless, the overall linear trend indicates a decrease in the abundance of *A. clausi* at St-4 and St-6 off Santander, while there was an increase at the northernmost locations. The autocorrelation function calculated for the extracted trend at each location (Figure 7) revealed a cycle of about 2–3 years at St-4 and St-6 off Santander. Cycles of about 2–3 years are also detected at the other locations. This cycle is more marked at the St-4, the Bay of Biscay, and L4 than in the Celtic Sea.

There was no clear similarity in the interannual variability of *C. helgolandicus* within each dataset except for some isolated cases; as for example for the St-4 off Santander, the Bay of Biscay, and the Celtic Sea when a strong peak in abundance

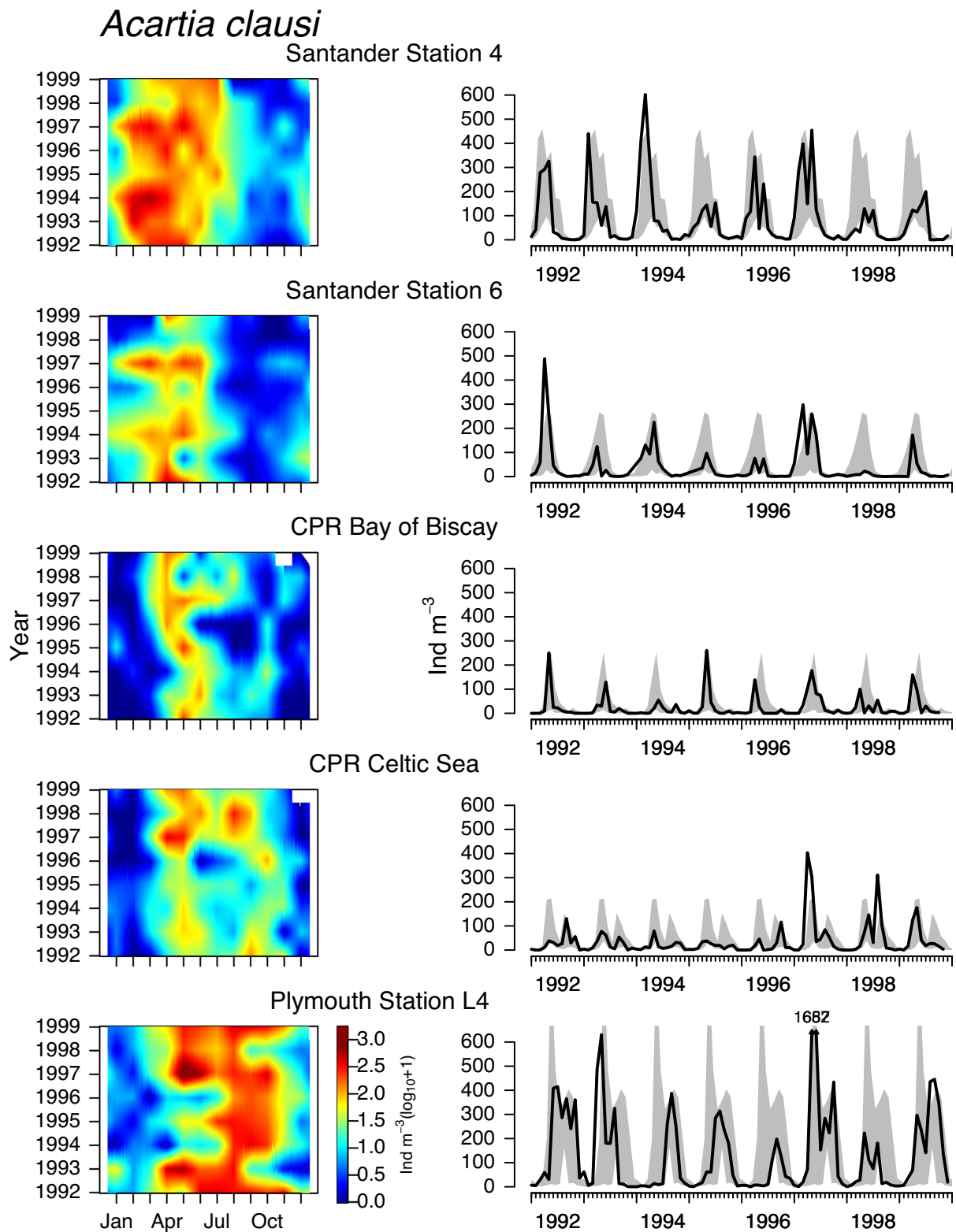


Figure 5. Left panels: density fields of *A. clausi* at each location showing the interannual changes in the seasonal cycle. Right panels: monthly abundances (solid line) of *A. clausi* superimposed on the 10 and 90% percentiles of the mean monthly values from 1992 to 1999 (shaded).

was observed in 1996 (Figure 6). Figure 8 shows a decreasing trend of *C. helgolandicus* at the Santander inner station (St-4). But, there were neither significant cycles nor trends in the interannual variability of abundances for any of the other stations as revealed by the autocorrelation functions (Figure 8).

Regarding the environmental forcing and despite the short time series considered here, there were some statistically significant correlations between the abundance of *C. helgolandicus* and the winter NAO index and between the abundance of *A. clausi* and the Gulf Stream North Wall index.

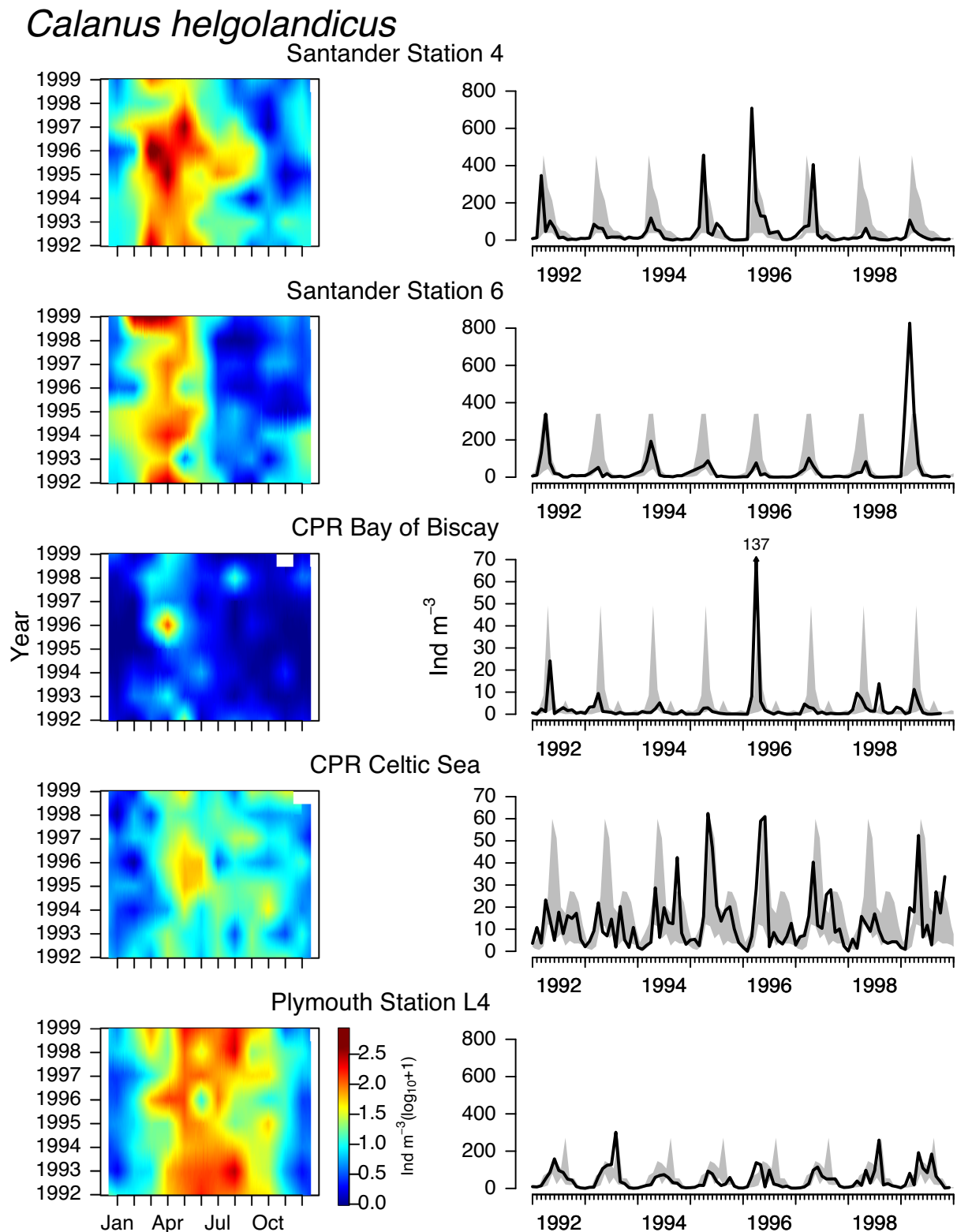


Figure 6. Left panels: density fields of *C. helgolandicus* at each location showing the interannual changes in the seasonal cycle. Right panels: monthly abundances (solid line) of *C. helgolandicus* superimposed on the 10 and 90% percentiles of the mean monthly values from 1992 to 1999 (shaded).

However, there was not any clear overall pattern; in fact, the correlation between the abundance of *C. helgolandicus* and the NAO index was negative for some locations but positive for others without any clear underlying reason (Table 3).

Discussion

Biogeography

The Western English Channel, the Celtic Sea, and the Bay of Biscay/Cantabrian Sea basins share common physical and

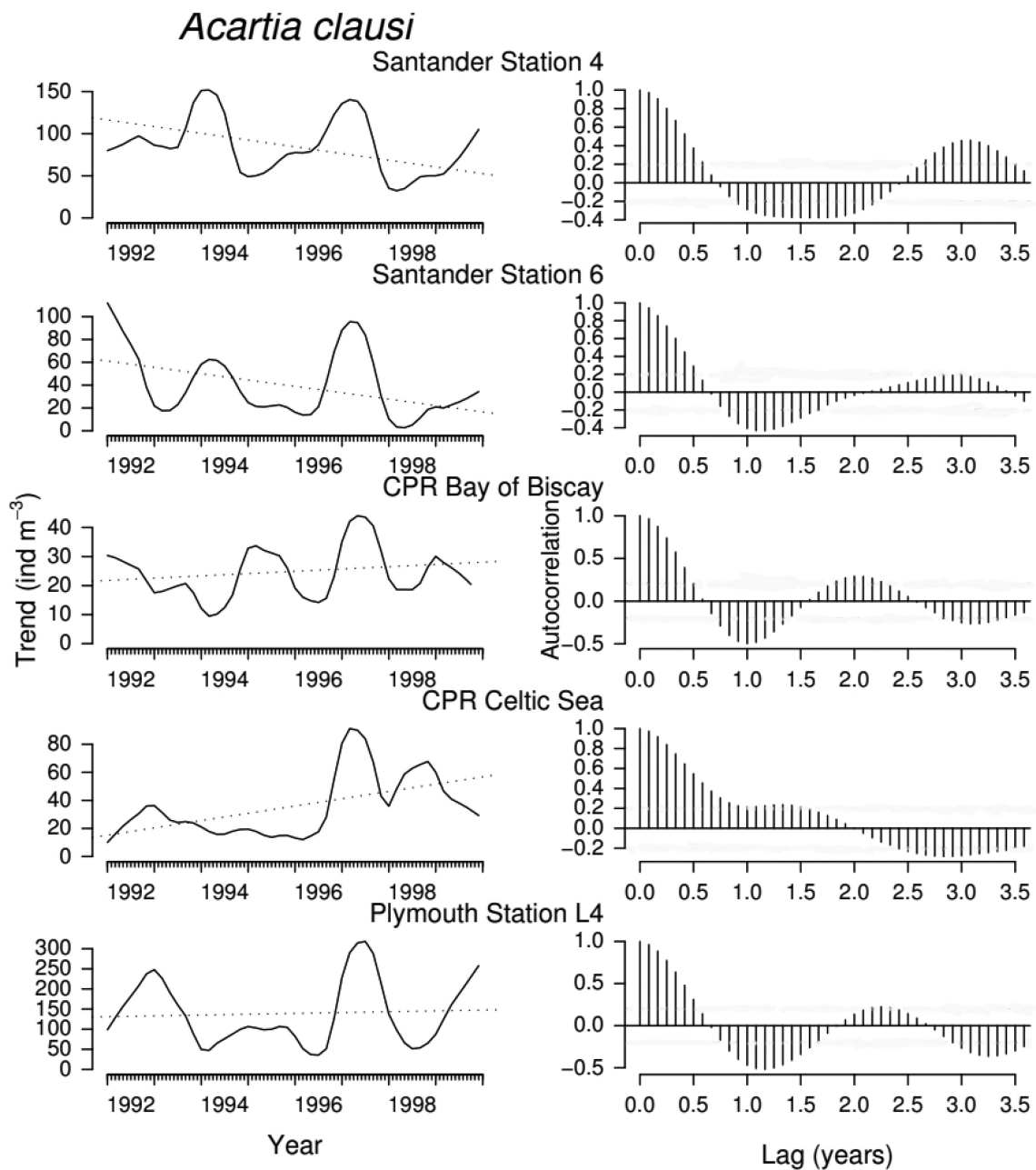


Figure 7. Left panels: interannual trend of the population abundance of *A. clausi* obtained by decomposition using 'loess' (Cleveland *et al.*, 1990). Dotted lines represent the linear trend obtained by least squares regression on the trend. Right panels: auto-correlation functions of the trends shown on the left panels.

ecological characteristics that make them part of a homogeneous area identified as a unique biogeochemical province: the Northeast Atlantic Shelves Province (*sensu*; Longhurst, 1998). On the other hand the southern European continental shelves and the Bay of Biscay represent a region of transition area from subtropical to boreal regimes and are subject to a large number of episodic mesoscale events and human activities (Beaugrand *et al.*, 2001; Valdés and Lavin, 2002; Lavin *et al.*, 2006; Borja *et al.*, 2019), with a great diversity in hydrodynamical features that affect species composition (Beaugrand *et al.*, 2019a, 2000b; Fanjul *et al.*, 2018, 2019). In accordance with this complexity, a strong gradient in species composition and seasonality of zooplankton within the region is expected. In fact, there is a strong latitudinal effect on diversity at each

location; southernmost locations were more diverse as it took a larger number of species to achieve the same cumulative abundance (Figure 2). As can be derived from the non-Metric Multidimensional Scaling (Figure 3b), there are two main factors that differentiate the locations based on their species composition, first the latitudinal geographical position and second an inshore–offshore gradient. Not only the southernmost stations were more diverse, but there was a clear differentiation in the most abundant species at each location. Some species can be used as indicators of warmer waters from southern latitudes (e.g. *T. stylifera*, *C. carinatus*, and *C. chierchiae*). In fact, Lindley and Daykin (2005) noted that *T. stylifera* and *C. chierchiae* occurred rarely in CPR samples in the Bay of Biscay, the Celtic Sea, and the English Channel before 1988, but

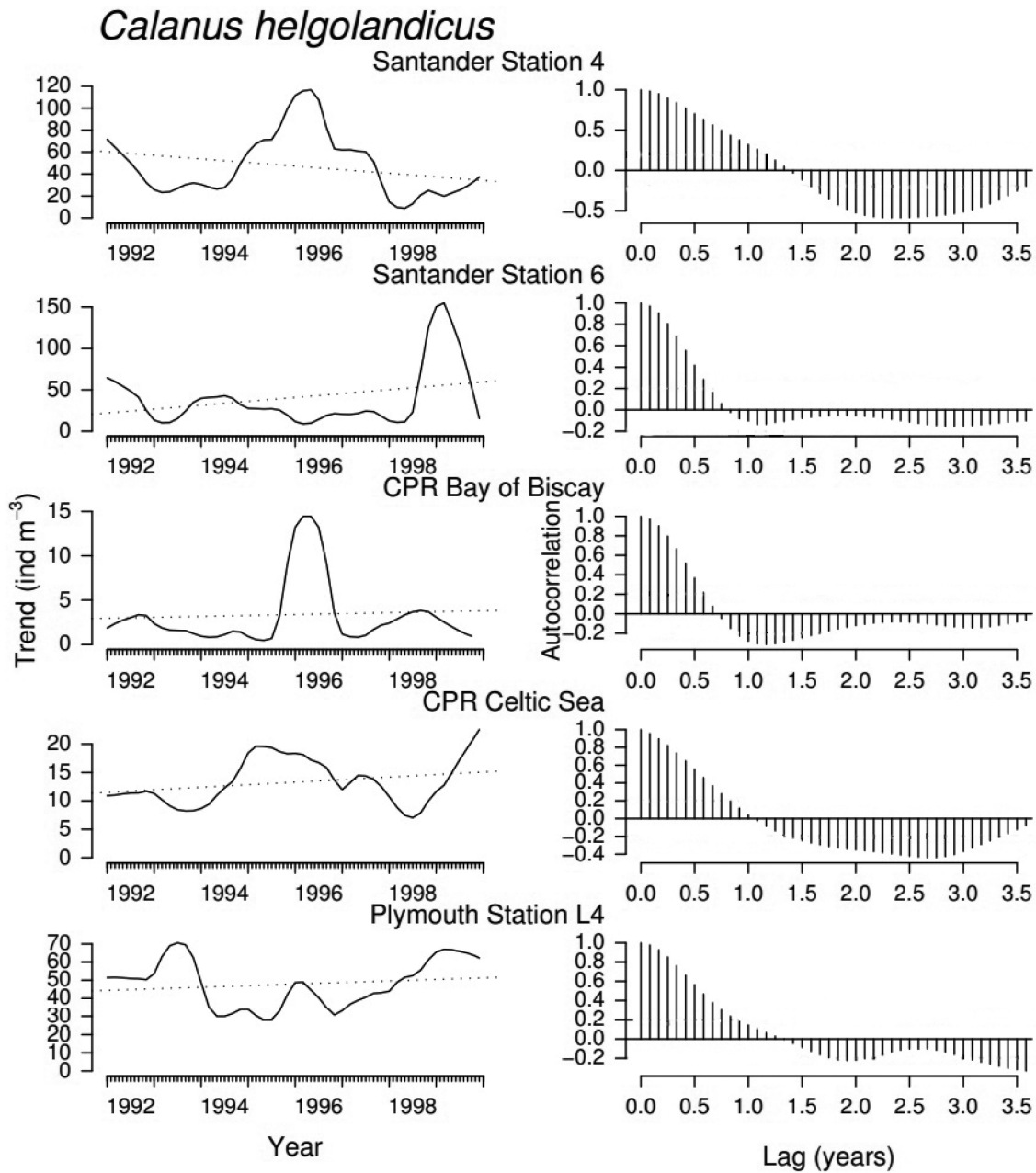


Figure 8. Left panels: interannual trend of the population abundance of *C. helgolandicus* obtained by decomposition using 'loess' (Cleveland *et al.*, 1990). Dotted lines represent the linear trend obtained by least squares regression on the trend. Right panels: auto-correlation functions of the trends shown on the left panels.

by 2000 they were found frequently and in abundance. Therefore, it could be expected that warmer water species which are at the border of their distribution ranges will be good indicators of warm water masses and long-term climate change and variability in the area (Bonnet and Frid, 2004).

Seasonal and latitudinal distribution of *A. clausi* and *C. helgolandicus*

The two selected target species, *C. helgolandicus* and *A. clausi*, are indicative of Atlantic Westerly Winds and Coastal Biomes (Beaugrand *et al.*, 2002b; Valdés *et al.*, 2007). *Acartia clausi* belongs to the temperate species association while *C. helgolandicus* is part of the European shelf edge association

(Beaugrand *et al.*, 2002b). The seasonal cycles of these species at each location agree with this classification. While *A. clausi* is more abundant at the more neritic locations (Figures 4a and 5), *C. helgolandicus* presents a more even distribution, characteristic of an oceanic-shelf edge species (Figures 4b and 6; John *et al.*, 2001; Bonnet *et al.*, 2005; Hirst, 2007; Maud *et al.*, 2015; Cornwell *et al.*, 2018).

The first step in the prediction of plankton population abundance is the characterization of the seasonal dynamics. The latitudinal pattern observed in the seasonal cycles of both copepods (Figure 4) is likely related to the temperature regimes at each location, which are linked to the seasonality and phenology of many plankton species, and supporting the broad concept that species occupy a thermal niche in time as

Table 3. Correlation coefficients (r) for all the regression lines combining *A. clausi* and *C. helgolandicus* species at a given station vs. the atmospheric indices Gulf Stream North Wall and four NAO combinations. Correlation coefficients with a significant p -value exceeding 80% are highlighted as indicated by the asterisks.

		Gulf Stream	NAO annual	NAO NDJ	NAO DJF	NAO JFM
<i>A. clausi</i>	ST-4	0.145	0.055	0.063	-0.095	0.281
	ST-6	0.190	0.167	0.095	-0.032	0.354
	CPR-BB	-0.089	-0.373	-0.315	-0.055	0.173
	CPR-CS	-0.711**	-0.122	0.141	-0.402	-0.182
	L4	-0.145	0.055	0.179	-0.045	0.292
<i>C. helgolandicus</i>	ST-4	-0.045	-0.821**	-0.731**	-0.592****	-0.532****
	ST-6	-0.045	0.509****	0.228	0.485	0.329
	CPR-BB	-0.371	-0.490	-0.318	-0.738**	-0.901*
	CPR-CS	0.313	-0.528****	-0.814**	0.148	0.114
	L4	-0.440	0.444	0.650***	0.148	0.130

* $p < 0.01$ (99%), ** $p < 0.05$ (95%), *** $p < 0.1$ (90%), and **** $p < 0.2$ (80%).

well as in space (Greve *et al.*, 2001; Edwards and Richardson, 2004; Beaugrand and Kirby, 2018; Borkman *et al.*, 2018; Samplonius *et al.*, 2020). The onset of the stratification period probably also plays an important role as it has been shown to have an impact on zooplankton dynamics (Valdés and Moral, 1998; Valdés *et al.*, 2007; Atkinson *et al.*, 2018).

At the same time in this wider NE Atlantic area, over the last half century, *Acartia* densities have very roughly halved and those of *C. helgolandicus* have doubled, while total copepod density has declined substantially during the main growth season (Schmidt *et al.*, 2020). Likewise, phenology particularly of *A. clausi* at L4 has advanced substantially with the warming of this site (Atkinson *et al.*, 2015).

Interannual variability and climatic connections

There is a strong degree of interannual variability between sites and between species. No clear trends, but some coherent events, among data sets reveal a regional response to environmental forcing factors (Figures 5–8). The year 1996 is interesting, and particularly because it showed a series of anomalies in *Acartia* abundance across multiple areas. At Santander and Plymouth, it was the coldest summer over the period 1992–1999 (Valdés and Lavín, 2002; Atkinson *et al.*, 2015).

According to the ICES Ocean Climate Status Summary 2000/2001 (Turrel and Holliday, 2002), extremely cold conditions were recorded during the year 1996 in different marine regions of the NE Atlantic, e.g. Iceland, southern and central Norwegian Sea, Helgoland, SE North Sea, and other sites. Also the temperatures in the Barents Sea dropped to values slightly below the long-term average over the whole area in 1996 (Turrel and Holliday, 2002), which is consistent with the records on snow cover on the Northern hemisphere from March to May (<https://www.ncdc.noaa.gov/snow-and-ice/extent/snow-cover/nhland/3>) and the sea ice cover in the Northern hemisphere in September 2016, which was the second major peak in sea ice extension recorded in the whole period 1979–2021 (<https://www.ncdc.noaa.gov/snow-and-ice/extent/sea-ice/N/9>).

Further analysis will be required to shed light on why one species (*A. clausi*) shows a pattern seen across multiple time series, whereas *C. helgolandicus* is presumably affected more by other local processes. Some of the species traits (e.g. resting eggs, generation time, and so on) may also shed light on their differing population dynamics.

Correlations suggest possible connections with environmental indices, but these require longer time series to be tested. However, positive and significant relationships with environmental indices have been published with time series that are equally short in time (Irigoién *et al.*, 2000; Fanjul *et al.*, 2017). The NAO can be related to interannual variability in wind, precipitation, and sea surface temperature in the North Atlantic Ocean and the North Sea (Fromentin and Planque, 1996).

This has been hypothesized as the underlying connection between the NAO and *Calanus* population dynamics. However, the Bay of Biscay is a region where there is no correlation between the NAO and precipitation, temperature, and wind, so direct biological responses to the NAO should not be expected in the Bay of Biscay (Planque *et al.*, 2003), and even for the eastern North Atlantic the correlation between the abundance of *C. helgolandicus* and the NAO is weaker than the correlation for *C. finmarchicus*. High NAO years are appropriate to maintain a higher abundance of *C. helgolandicus* in the northern parts of the European shelf with higher population levels the following year. This positive correlation between the NAO and the abundance of *C. helgolandicus* was observed at station L4 off Plymouth, although the relationship was not statistically significant (Table 3). On the other hand, the relationship in the Celtic Sea and the Bay of Biscay was significant and opposite to that expected based on previous results (Fromentin and Planque, 1996). Beaugrand *et al.* (2001) also obtained opposite relationships between variations of plankton and climate parameters for the Bay of Biscay compared to the Celtic Sea and the Western English Channel.

Clearly, the climatic connection between the NAO and *Calanus* population dynamics (Conversi *et al.*, 2001) needs further revision, especially given that even for *C. finmarchicus* the relationship has broken down for the second-half of the 1990s (Reid and Beaugrand, 2002; Beaugrand *et al.*, 2015, 2019b), and the correlations for individual copepod species have also been shown to be lower than for total copepods (Taylor, 1995). We would have expected the abundance of *A. clausi* to be related to the GSNW index since it has been previously correlated to the abundance of small copepods in part of the eastern North Atlantic and North Sea (Taylor and Stephens, 1980; Hays *et al.*, 1993; Taylor, 1995; Aravena *et al.*, 2009), but again we have not found any consistent pattern (Table 3). We lack information on whether this lack of

relationship is due to the short time series considered or to the relationship only holding for the northernmost parts of the North Atlantic (Piontkovski *et al.*, 2006).

Regional intercomparison combining different sampling programmes

This research has shown that, despite the different sampling techniques used within each dataset, they are comparable and coherent in terms of taxonomic composition and in the seasonal and interannual patterns detected. Some differences between the total recorded abundances by each programme exist. The CPR has been shown to generally underestimate the abundance of copepods when compared to other sampling techniques, although the degree seems to be species specific (Hélaouët *et al.*, 2016). Mesh size has been suggested as an important factor causing differing CPR performance, *C. helgolandicus* has been found to be twice as abundant in the North Sea and the Western English Channel stations than in the CPR for surrounding areas, while the CPR underestimates even more the abundance of *Acartia spp.* (Clark *et al.*, 2001; John *et al.*, 2001; Batten *et al.*, 2003). In this study, the abundance of *C. helgolandicus* recorded by the CPR was much lower than for the fixed locations, while for *A. clausi* these differences were not so marked and could be just due to the CPR routes sampling more oceanic regions. Richardson *et al.* (2004) also found that *A. clausi* was not underestimated by the CPR in a comparison to data collected by Longhurst Hardy Plankton Recorder (LHPR) in the North-east Atlantic (Richardson *et al.*, 2004). Moreover, these results support the conclusion reached by Batten *et al.* (2003) that although comparisons between the interannual changes recorded by the CPR and fixed stations are not as favourable as the seasonality, in general both are quite good. The patterns found in this study demonstrate that the collective value of data sets is greater than its dispersed value and that international cooperation to achieve a comparative approach to plankton time series is a feasible and pursuable objective. Through the ICES WGZE (Wiebe *et al.*, 2016), Steve Hay contributed significantly to this international collaborative approach.

Supplementary material

Supplementary material is available at the ICES/JMS online version of the manuscript.

Authors' contributions

Conceptualization: LV, RH, and GB; methodology: LV, RH, GB, ALU, and XI; software: ALU, GB, and LV; validation: LV, GB, and ALU; formal analysis: LV, RH, and GB; writing and original draft preparation: LV, RH, and GB; review and editing: LV, RH, GB, ALU, and XI; visualization: LV and ALU; supervision: LV. All the authors have read and agreed to the published version of the manuscript.

Data availability statement

The data underlying this article were provided by the monitoring project RADIALES (Instituto Español de Oceanografía), Western Channel Observatory (Plymouth Marine Laboratory) and the Continuous Plankton Recorder survey (Sir Al-

ister Hardy Foundation for Ocean Science) by permission of the respective IP. Data will be shared on request to the corresponding author with permission of the respective IP.

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