Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling

DAMIEN ELOIRE[1,2]*, PAUL J. SOMERFIELD[1], DAVID V. P. CONWAY[3], CLAUDIA HALSBAND-LENK[1], ROGER HARRIS[1] AND DELPHINE BONNET[2]

[1]PLYMOUTH MARINE LABORATORY, PROSPECT PLACE, THE HOE, PLYMOUTH, DEVON PL1 3DH, UK, [2]LABORATOIRE ECOSYSTÈME LAGUNAIRE, UMR 5119, CNRS − UNIVERSITÉ MONTPELLIER II − IRD −IFREMER, CC093, PLACE EUGÈNE BATAILLON, 34095 MONTPELLIER CEDEX 05, FRANCE AND [3]MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM, CITADEL HILL, THE HOE, PLYMOUTH, DEVON PL1 2PB, UK

*CORRESPONDING AUTHOR: dmelo@pml.ac.uk

Zooplankton community composition and diversity have been analysed for the period 1988−2007 at the coastal station L4 off Plymouth in the Western Channel. The seasonal cycle of the total zooplankton was characterized by two peaks. The total zooplankton abundance did not show any long-term trend and its interannual variations were not directly related to changes in environmental conditions. However, different periods of change in total zooplankton abundance were observed that appeared to be consistently related to changes in sea surface temperature (SST) and wind. The number of taxa (22) contributing 80−90% of the total zooplankton abundance was consistent over the 20 years and their cumulative contribution to the community showed only small interannual variations. A significant long-term increase in species richness of the copepod community was detected and its maximum annual value was significantly related to annual average SST. There was evidence of long-term changes: numbers of *Oncaea* spp., Cirripede larvae, *Calanus helgolandicus* and Chaetognaths have increased, whereas numbers of *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi*, *Evadne nordmanni*, Appendicularians, *Podon* spp. and *Ctenocalanus vanus* have decreased. The use of indicator species to monitor hydroclimatic changes in the Western Channel is discussed.

KEYWORDS: zooplankton; community structure; long-term series; L4; Western Channel

INTRODUCTION

The importance of zooplankton for marine ecosystem functioning is widely recognized and zooplankton long-term series (>10 years) provide crucial information to better understand ecosystem dynamics and make global comparisons in order to tackle key issues such as climate change (Perry *et al.*, 2004; Richardson, 2008). Since 1988, a plankton time series has been maintained at the monitoring station L4 in the Western Channel off Plymouth (UK), a region with both cold temperate and warm temperate species and where a large number of historical studies have been carried out (Southward

et al., 2005). Station L4, with an average depth of 55 m, is affected by highly variable meteorological conditions and dominating wind from the south-west (Smyth *et al.*, 2010). The station is continually affected by the tide (Pingree, 1980) and is influenced by estuarine outflow from Plymouth Sound and by oceanic waters from the south-west. The water column is weakly stratified from mid-April to September and mixed during the winter (Pingree *et al.*, 1976, 1978; Holligan and Harbour, 1977; Holligan *et al.*, 1984). The minimum surface temperature is observed in March (9.1°C), the maximum in August (16.4°C) and a warming of around 0.6°C per decade has been seen over the last two decades (Smyth *et al.*, 2010). Spring diatom and autumn dinoflagellate blooms are the main features in the seasonal cycle of the phytoplankton community (Harvey *et al.*, 1935; Widdicombe *et al.*, 2010).

Published studies on zooplankton at L4 have focused on particular species or groups, especially calanoid copepods (Bautista and Harris, 1992), *Calanus helgolandicus* (Pond *et al.*, 1996; Irigoien and Harris, 2003; Bonnet *et al.*, 2005; Hirst *et al.*, 2007), *Centropages typicus* (Bonnet *et al.*, 2007), but also Appendicularians (Acuna *et al.*, 1995) and Chaetognaths (Russell, 1935; Bonnet *et al.*, 2010), while the seasonal variation and parallel changes occurring in the whole plankton community have been described from October 1992 to January 1994 (Rodríguez *et al.*, 2000).

In many studies, the North Atlantic Oscillation (NAO) has been suggested to be a main driver of changes in the plankton community of the eastern North Atlantic Ocean and adjacent shelf-seas (Fromentin and Planque, 1996; Edwards *et al.*, 2002; Piontkovski *et al.*, 2006), by influencing meteorological conditions and affecting plankton populations directly and/or indirectly (Beaugrand *et al.*, 2000). Previous studies have suggested that the NAO (Irigoien *et al.*, 2000; Irigoien and Harris, 2003), changes in the wind regime (Irigoien *et al.*, 2000) and also advection (Russell, 1935; Irigoien and Harris, 2003) can affect the plankton community at L4. In addition, several studies have demonstrated how key species can be used to monitor changes in plankton communities at L4 and in surrounding regions (Russell, 1935; Southward, 1984; Villate *et al.*, 1997; Beaugrand *et al.*, 2002; Bonnet and Frid, 2004), for example indicating the influence of different water masses.

While previous investigations have described the temporal variability of some species and groups at L4, for the first time in this paper we look in detail at seasonal, interannual and long-term variations in overall mesozooplankton community structure and diversity over the 20 years, 1988–2007, and link these variations to environmental descriptors. The purpose of this study is to identify (i) long-term changes in zooplankton community structure and (ii) environmental factors and key species that might have a major role in controlling the zooplankton dynamics.

METHOD

Zooplankton sampling

Station L4 (50°15′N, 4°13′W) is located in coastal waters 7.5 nautical miles (∼13.9 km) south-west off Plymouth. Since March 1988, zooplankton samples have been collected weekly, weather permitting, by vertical net hauls from the sea floor to the surface using a WP2 net with a mesh-size of 200 μm and a mouth area of 0.25 m^2 (UNESCO, 1968). Two hauls are successively taken at approximately mid-morning and the samples are preserved and stored in 5% formalin. Zooplankton are later sub-sampled, counted and identified under a microscope in the laboratory. Subsamples are extracted using a Folsom splitter and a Stempel pipette, to identify separately large and small organisms. Subsamples contain around 200–400 individuals. Abundances in the two hauls taken on each sampling date are averaged to reduce the variability related to the sampling. Abundance is expressed as numbers of organisms per cubic meter (N m^{-3}).

The entire set of zooplankton samples is stored at the Plymouth Marine Laboratory and available for further taxonomic analysis. The complete zooplankton abundance data set, as well as graphical displays of the temporal variations of the different species and groups identified, are available on the Western Channel Observatory website: http://www.westernchannel observatory.org.uk/. Zooplankton identification is to the lowest taxonomic level possible, but some groups, meroplankton in particular, are only identified to major taxonomic groups. The dominant copepods are generally well discriminated to genus or species levels and to life-history stages for species of particular interest, such as *Calanus helgolandicus*.

Additional data

Other environmental and biological measurements are taken simultaneously with the zooplankton sampling. Sea surface temperature (SST in °C) has been measured since the beginning of the time series using a mercury-in-glass thermometer immersed in a stainless steel bucket of surface water.

Since 1992, sea surface water samples (10 m depth) collected with a Niskin bottle have been used to determine abundance and biomass of phytoplankton and microzooplankton (Widdicombe *et al.*, 2010), as well as chlorophyll concentrations.

Atmospheric data used in this study, wind speed (in m s^{-1}) and direction from West to East (W/E) and South to North (S/N), are part of the ECMWF ERA-40 Re-Analysis data available from http://badc .nerc.ac.uk/data/ecmwf-e40/ and were provided by the European Centre for Medium-Range Weather Forecasts (ECMWF 1995) through the British Atmospheric Data Centre. Raw data for the NAO index were obtained from the Climatic Research Unit website (http://www. cru.uea.ac.uk/). The index is based on the difference between the normalized sea level pressure over Gibraltar and that over Southwest Iceland. The winter NAO index is calculated by averaging the values of the NAO index from December to March (Hurrell, 1995; Beaugrand and Reid, 2003). Data for the Gulf Stream North Wall (GSNW) position index were obtained from Arnold Taylor's website hosted by Plymouth Marine Laboratory (http://web.pml.ac.uk/gulfstream/). The index is the first principal component of the monthly mean position of the North Wall of the Gulf Stream (Taylor and Stephens, 1980).

Data manipulation

The level of taxonomic analysis has generally been consistent over the 20 years, owing to the restricted number of analysts who have counted the L4 samples. Only for copepods and cladocerans has identification to genus or species level been consistent, and all the other zooplankton species have been recorded as broad taxonomic groups. Nevertheless, a taxonomic homogenization of the data set was undertaken to ensure data consistency. A taxonomic list of the 243 species and groups identified since the beginning of the time series was created, with information on 19 taxonomic levels, from kingdom to life-history stages (e.g. male, female, adult, juvenile and larval stages). The aim of the homogenization was to keep as much detail as possible, while respecting the consistency of the taxonomy. Data on certain groups such as copepod nauplii were removed, as they were too small to be accurately sampled. For each species or group, the minimum taxonomic level of identification that was consistent from January 1988 to December 2007 was determined. Some species and groups were rare and/or underestimated due to the sampling method used and the expertise of the analysts, so these were pooled to higher taxonomic levels. Following these procedures, 59 distinct categories at different taxonomic levels were

retained for the analysis, of which 32 were found on ≤ 20% of the sampling dates over the entire time series. Here we use the terms "taxon" and "taxa" not in the strict sense, but to refer to these categories which include species and specific groups of organisms.

Numerical and statistical analysis

Total zooplankton abundances were determined for each month between January 1988 and December 2007. Gaps occurred in January and February 1988, which were interpolated with the average abundance for that month over the rest of the time series, and August 2000 which was interpolated using the average of the previous and following month. The average seasonal cycle of each time series was determined using monthly averages over sampled years. Annual anomalies were obtained by averaging monthly anomalies, which in turn were calculated using monthly abundances. Monthly abundance anomalies of each month of the time series were obtained by subtracting the overall average over the entire time series for a given month from the observed monthly value, using the formula:

$$x'_{m,y} = \frac{x_{m,y} - \bar{x}_m}{\sigma(x_m)}$$

where m is the month (m: 1 = January, 2 = February, ..., 12 = December) and y the year; $x'_{m,y}$ is the monthly anomaly of month m in year y; $x_{m,y}$ is the monthly average abundance of month m in year y; $\bar{x}_m$ is the average abundance and $\sigma(x_m)$ the standard deviation, of month m over the entire time series. Thus, a positive anomaly means that the observed value was higher than the overall average for that month, and vice versa. The ranking of total monthly zooplankton abundances was obtained by sorting the monthly averages over the entire time series rather than within each year, meaning that each month was ranked without reference to the year in which it occurred.

Variations in zooplankton community abundances were analysed using a non-parametric multivariate method. Abundances of each taxon were averaged within each month of each year. Inter-sample similarities were calculated using the Bray−Curtis coefficient and visualized using non-metric multidimensional scaling (NMDS) ordination. This technique produces a plot in a predefined number of dimensions (in our study two) in which samples are represented by points, and distances between points preserve the rank order of similarities between samples in the similarity matrix (Clarke and Warwick, 2001).

The average abundance of each taxon over the entire time series (1988–2007) was obtained using monthly averages. Their relative contribution to the total zooplankton was calculated and then used to determine the ranking of each taxon and the cumulative sum of the percentage of the total zooplankton abundance at each rank. Trends for the monthly anomalies and averages were obtained by applying a type I linear model. Prior to testing the significance of the trend slope, a Durbin–Watson test to detect autocorrelation in the residuals of the regression analysis was performed (MacKenzie and Köster, 2004). When autocorrelation was present, the effective number of independent values used in the significance testing was adjusted using the formula:

$$n_{\text{eff}} \approx n_{\text{t}} \frac{1 - r_1}{1 + r_1}$$

where n_{eff} is the effective number of independent observations; n_{t} is the total number of observations and r_1 is the lag-1 temporal autocorrelation coefficient (Quenouille, 1952; Pyper and Peterman, 1998; Santer et al., 2000). Finally, a Student's t-test was used to determine whether the slope of the linear model was significantly different from 0. For each significant trend ($P \leq 0.05$), the overall change over the 20-year period was estimated and then compared to the overall average, using the slope from the regression analysis of the monthly averages.

Correlation between time series was investigated using the Spearman rank correlation coefficient ρ, again adjusted to account for autocorrelation. The effective number of independent observations was adjusted when necessary using the formula:

$$n_{\text{eff}} \approx n_{\text{t}}(1 + 2r_1 r_1' + 2r_2 r_2' + \cdots)$$

where n_{eff} is the effective number of independent observations; n_{t} is the total number of observations; r_1 and r_1' are the lag-1 temporal autocorrelation coefficient of the two series, r_2 and r_2' are the lag-2 autocorrelations of the two series, and so on (Quenouille, 1952; Hays et al., 1993; Pyper and Peterman, 1998).

The dominance structure of the zooplankton community was described using k-dominance curves, where the cumulative percentage of each taxon is plotted against its respective rank (Lambshead et al., 1983; Clarke, 1990). A cluster analysis, using the group average linkage method, was applied to a matrix of differences between dominance curves. The most dominant taxa were defined as those that appeared at least once in the top 10 of the monthly relative contribution

ranking. Using this definition, the 22 most dominant taxa were selected and their relative contributions to the total zooplankton community were calculated for each month and year. Ranking of the monthly abundances was achieved by sorting the time series of monthly averages of the abundances of each dominant taxon.

Two diversity indices, species richness and Simpson's dominance index, referred to here as richness index and Simpson index, respectively, were calculated using abundances of the species or genera of copepods. We used this restricted group because including wide taxonomic categories (e.g. Appendicularians and Chaetognaths) will not represent the complexity of the community and may bias the estimation of diversity indices. The two indices were calculated for each sample date using the following equations:

Richness index:

$$S = \sum_{i=1}^{S} n_i^0$$

Simpson index:

$$\lambda = \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{S(S - 1)}$$

where n_i is the number of individuals found in the i-th taxon and S is the total number of taxa in the sample. The average seasonal cycle, the monthly ranking, annual anomalies and trends were estimated for each diversity index.

The cumulative sums technique was used to detect local changes in the annual average of each biological and environmental factor. This simple method also allows an assessment of the intensity and duration of these changes (Ibañez et al., 1993, Beaugrand et al., 2003, Conversi et al., 2009). A reference value, here the overall average of the time series, is subtracted from each value in the original time series to produce a new time series of residuals. These are then progressively pooled, each element being summed to the previous, to calculate the cumulative sum.

RESULTS

Total zooplankton abundance

The monthly averages of total zooplankton abundance were highly variable between 1988 and 2007 (Fig. 1A). Temporal variations did not show any clear long-term pattern; however, a seasonal signal of a 1-year period was discernable. The overall average abundance was
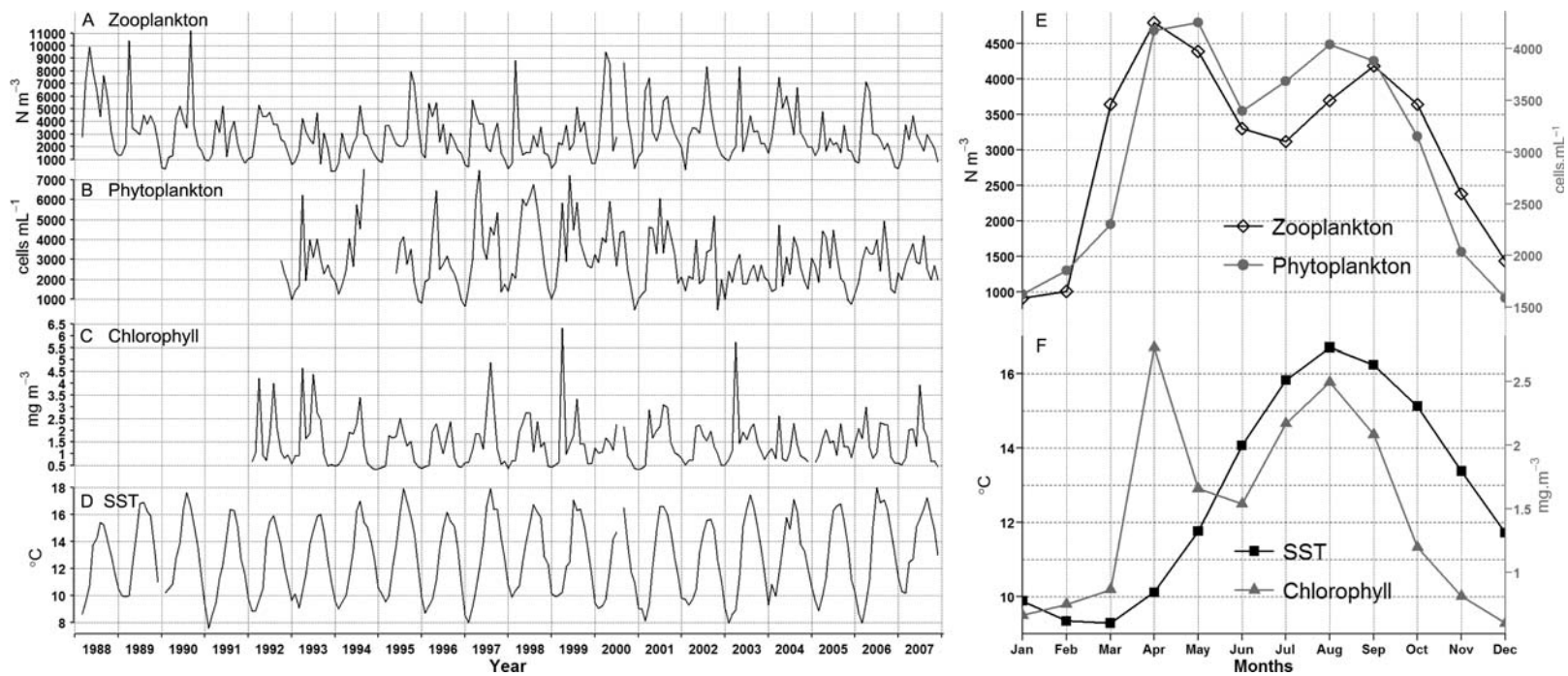
Fig. 1. Monthly average time series (**A**–**D**) and seasonal cycle (**E** and **F**) of total zooplankton, total phytoplankton, chlorophyll and SST.

3054.36 ± 2146.19 N m^{-3} (Table I). Results from regression analysis showed that there was no significant long-term trend in either monthly averages ($P = 0.375$) or anomalies ($P = 0.525$) of the total zooplankton abundance (Table I).

Between 1988 and 2007, the average seasonal cycle of total zooplankton abundance at L4 was characterized by two peaks (Fig. 1E). The first and main peak ($\sim$4800 N m^{-3}) generally occurred in April (early spring), and the second ($\sim$4200 N m^{-3}) in September (beginning of autumn). Between these periods abundances were higher than during the winter ($\sim$1000 N m^{-3}). Phytoplankton abundance and chlorophyll concentration also had similar average seasonal cycles with two peaks, the main one occurring in spring (Fig. 1E and F). The SST seasonal cycle was characterized by a clear sinusoidal signal (Fig. 1F) with the lowest temperatures ($\sim$9°C) in late winter (February–March) and the highest ($\sim$17°C) in late summer (August).

Periods dominated by negative anomalies (1990–1999 and 2005–2007) corresponded to years with low abundances (Fig. 2A). Some unusual years showed either an abrupt change (e.g. between 1999 and 2000), or episodic anomalies (e.g. in 1995 and 2003). Monthly averages of total zooplankton abundance varied within the range 21.8–11 200 N m^{-3} (Fig. 2B). The autumn and winter of 1995–1996 were very unusual, with a high and long-lived autumn peak in abundance, causing the positive anomaly observed for 1995. Looking at the overall pattern displayed by the monthly averages, seasonal variations are greater than interannual variability over the 20 years, even if the latter was discernable for some periods (Fig. 2B).

Ordination by NMDS (Fig. 3) shows tight clustering of the different months and the clear and continuous change in composition throughout the seasonal cycle. Changes between the winter (December–February) and spring (March–May) communities were marked. The summer (June–August) community appeared to be more stable, as a consequence of higher abundances of a range of taxa. Changes in community composition were greatest within years, and community structure was relatively stable among years.

Community composition and dominant taxa

Out of 59 taxa, the 10 most abundant represented $\geq$80% of the total zooplankton abundance, and the 20 most abundant $\geq$95% (Table II). Only 17 taxa contributed $\geq$1% of the total zooplankton abundance and 25 contributed $\geq$0.1%. Copepods represented 60–90% of the total abundance with higher contributions relative to other taxa in autumn-winter than in spring-summer, and 62.02% on average throughout the entire time series (Table I). These results were corroborated by the k-dominance curves showing that the 10 most abundant taxa made a more or less even contribution (Fig. 4A) and together contributed between 82% (2003) and 92% (2000) of the total abundance. The general pattern was of little variability in community structure with significant variations only within the first five ranks separating the two main groups of the cluster analysis, although 4 years (1996, 1997, 1998 and 2000) appeared to be more highly dominated than the others. The winter, spring and autumn communities appeared to be dominated by a smaller number of taxa compared with the summer which had a larger number of taxa contributing evenly to the total zooplankton community (Fig. 4B).

Table I: *Average and corresponding standard deviation obtained for the abundance (N m^{-3}) and diversity at L4 over the 20-year period*

Time series (1988–2007)	Average (N m^{-3})	SD (N m^{-3})	Contrib. (%)	Change (%)	Change (%)	Monthly averages Trend P-value	Trend slope	Trend	Monthly anomalies Trend P-value	Trend slope	Trend
Total zooplankton	3064.31	2109.46	–			0.209	−2.5047	n.s.	0.249	−0.0010	n.s.
Total copepods	1900.61	1327.06	62.02			0.122	−1.9382	n.s.	0.178	−0.0012	n.s.
Calanoid copepods	1145.73	896.20	37.39	−602.48	−52.6	0.003	−2.5208		0.003	−0.0027	
Poecilostomatoid copepods	357.59	481.84	11.67			0.514[a]	0.6664	n.s.	0.046	0.0018	
Cyclopoid copepods	348.17	407.18	11.36			0.974	0.0126	n.s.	0.873	−0.0001	n.s.
Harpacticoid copepod	39.49	62.94	1.29			0.473	0.0428	n.s.	0.676	−0.0004	n.s.
Species richness index	11.07	1.76	–	0.58	5.3	0.003	0.0049		0.004	0.0026	
Simpson's dominance index	0.27	0.08	–			0.535	<0.0001	n.s.	0.814	−0.0002	n.s.

Relative contribution to the total zooplankton abundance was calculated for different copepod groups. Trend P-value and slope come from the regression analysis (superscript 'a' indicates a significant autocorrelation in which case the effective number of independent observations has been adjusted and n.s. indicates non-significant trends with P-value > 0.05). Change in abundance or diversity over the 20 years was calculated for significant trends using the slope from the regression analysis of the monthly averages, and this value was compared with the overall average to determine the percentage of change.
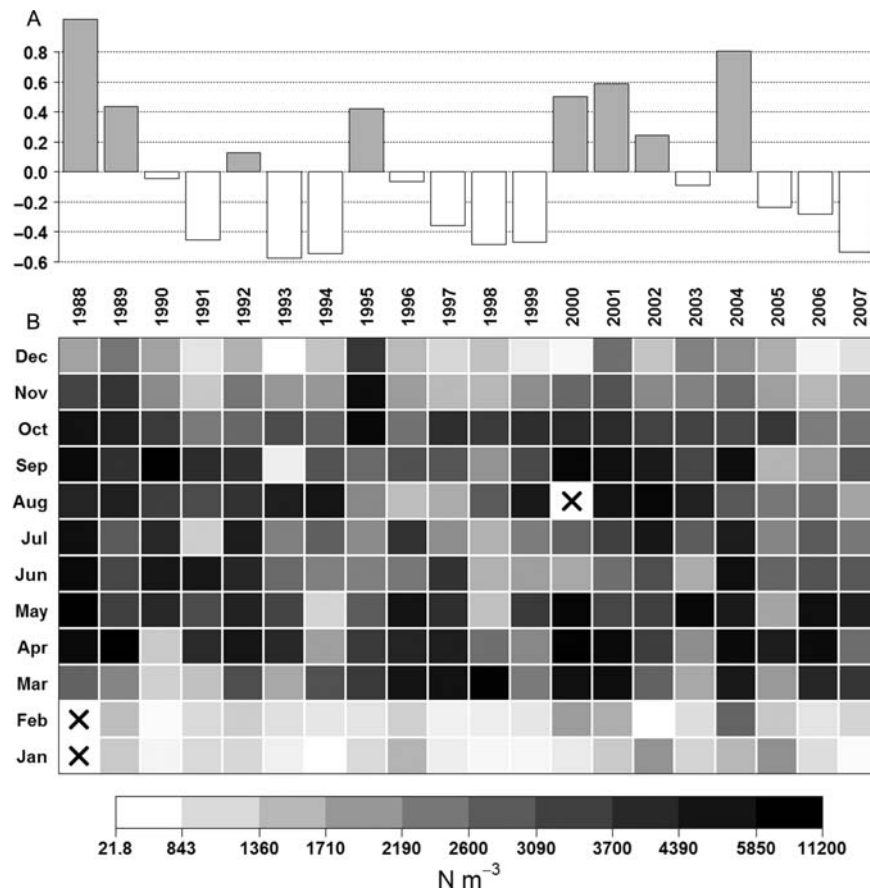
Fig. 2. (**A**) Annual anomalies of the total zooplankton abundance (positive and negative anomalies: grey and white bars, respectively) and (**B**) ranking of the monthly average of the total zooplankton abundance (where black squares represents the highest values, white squares the lowest and a cross indicates missing data for the given month).
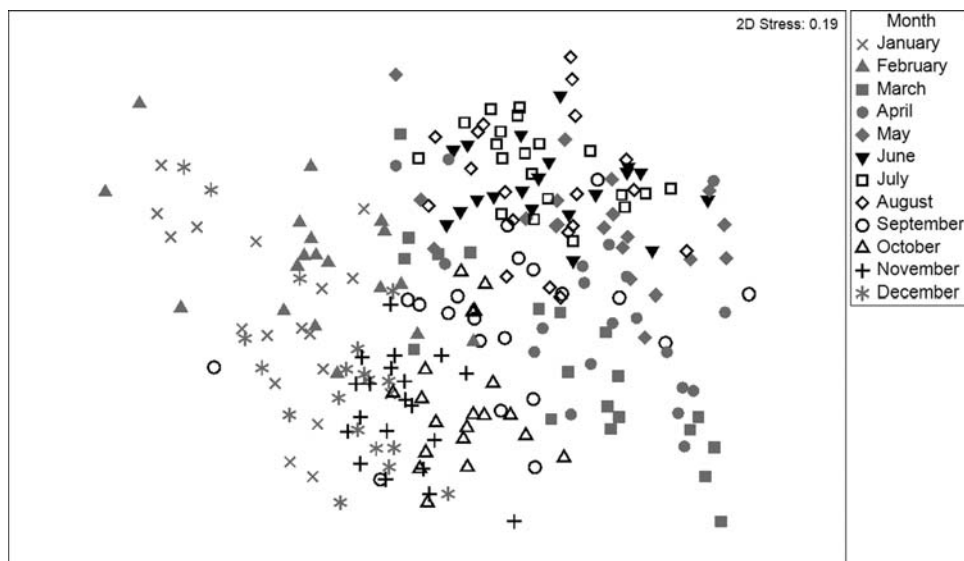

Fig. 3. Non-metric multidimensional scaling ordination plot based on Bray–Curtis similarities calculated from untransformed monthly average abundances of the 59 zooplankton taxa identified at L4 for the period 1988–2007.

Table II: *Ranking, average abundance (N m⁻³) and corresponding standard deviation, the relative contribution to the total zooplankton abundance and cumulative sum of the percentage obtained for each one of the 59 taxa identified at L4 over the 20-year period*

Rank	Taxon time series (1988–2007)	Average (N m⁻³)	SD (N m⁻³)	Contrib. (%)	Cum. Contrib. (%)	Change (N m⁻³)	Change (%)	Monthly averages Trend P-value	Monthly averages Trend slope	Trend	Monthly anomalies Trend P-value	Monthly anomalies Trend slope	Trend
1	*Pseudocalanus elongatus*	391.77	447.88	12.83	12.83	−255.85	−65.3	0.011	−1.0705		0.026	−0.0020	
2	*Oncaea* spp.	357.59	481.84	11.71	24.55			0.514[a]	0.6664	n.s.	0.046	0.0018	
3	*Oithona* spp.	348.17	407.18	11.41	35.95			0.974	0.0126	n.s.	0.873	−0.0001	n.s.
4	*Paracalanus parvus*	341.66	372.02	11.19	47.15			0.305[a]	−0.6034	n.s.	0.123	−0.0014	n.s.
5	Cirripede larvae	301.12	879.78	9.86	57.01			0.190	1.0907	n.s.	0.006	0.0025	
6	*Temora longicornis*	266.31	418.87	8.72	65.74			0.057	−0.7534	n.s.	0.001	−0.0030	
7	*Evadne nordmanni*	163.60	373.94	5.36	71.09			0.051	−0.6890	n.s.	0.003	−0.0027	
8	*Acartia clausi*	161.63	310.92	5.29	76.39	−288.10	−178.3	<0.001	−1.2054		<0.001	−0.0054	
9	*Ditrichocorycaeus anglicus*	82.72	115.40	2.71	79.10			0.517[a]	0.1185	n.s.	0.795	0.0002	n.s.
10	Appendicularians	77.61	119.68	2.54	81.64			0.136	−0.1689	n.s.	0.007	−0.0024	
11	Echinoderm larvae	76.23	228.90	2.50	84.14			0.239	0.2550	n.s.	0.622	0.0004	n.s.
12	*Calanus helgolandicus*	71.00	88.95	2.33	86.47	41.53	58.5	0.038	0.1738		<0.001	0.0037	
13	*Podon* spp.	54.88	109.76	1.80	88.26	−57.18	−104.2	0.021	−0.2392		0.014	−0.0022	
14	Bivalve larvae	52.35	124.71	1.71	89.98			0.567[a]	0.1393	n.s.	0.408	0.0007	n.s.
15	Siphonophores	50.41	77.50	1.65	91.63			0.823	−0.0165	n.s.	0.427	0.0007	n.s.
16	Gastropods	41.88	98.44	1.37	93.00			0.266	−0.1036	n.s.	0.469	−0.0007	n.s.
17	*Euterpina acutifrons*	36.20	61.13	1.19	94.19			0.814	0.0136	n.s.	0.108	−0.0015	n.s.
18	Chaetognaths	30.36	43.16	0.99	95.18	23.18	76.4	0.017	0.0970		0.001	0.0029	
19	Polychaetes	29.08	31.63	0.95	96.13			0.953	0.0017	n.s.	0.482	−0.0006	n.s.
20	*Clausocalanus* spp.	25.77	61.62	0.84	96.98			0.734	0.0198	n.s.	0.951	−0.0001	n.s.
21	*Ctenocalanus vanus*	17.80	47.68	0.58	97.56	−62.80	−352.8	<0.001	−0.2628		<0.001	−0.0065	
22	*Centropages typicus*	17.77	39.52	0.58	98.14			0.334	−0.0362	n.s.	0.039	−0.0019	
23	Hydromedusae	17.63	31.97	0.58	98.72	−24.36	−138.2	0.001	−0.1019		0.038	−0.0019	
24	Decapod larvae	14.75	13.56	0.48	99.20			0.241	0.0151	n.s.	0.157	0.0013	n.s.
25	Fish eggs and larvae	10.06	60.70	0.33	99.53			0.891	−0.0079	n.s.	0.208	0.0011	n.s.
26	Amphipods	2.48	4.84	0.08	99.61			0.800	−0.0012	n.s.	0.680	0.0004	n.s.
27	*Metridia lucens*	2.46	10.19	0.08	99.70			0.236[a]	−0.0222	n.s.	0.679	−0.0004	n.s.
28	*Clytemnestra* spp.	1.94	6.40	0.06	99.76	4.68	241.2	0.001	0.0196		<0.001	0.0040	
29	*Subeucalanus crassus*	1.64	4.87	0.05	99.81	3.05	186.4	0.005	0.0128		<0.001	0.0035	
30	Euphausiids	1.09	2.82	0.04	99.85	1.47	134.1	0.021	0.0061		0.010	0.0023	
31	Doliolids	0.82	9.82	0.03	99.88			0.094	0.0155	n.s.	0.012	0.0020	
32	Cephalopods	0.78	5.93	0.03	99.90			0.064	0.0104	n.s.	0.016	0.0018	
33	*Microsetella* spp.	0.73	2.21	0.02	99.93			0.975	0.0012	n.s.	0.757	0.0003	n.s.
34	*Candacia armata*	0.71	1.98	0.02	99.95	1.02	143.0	0.022	0.0043		0.010	0.0023	
35	*Centropages chierchiae*	0.35	2.59	0.01	99.96			0.79[a]	0.0012	n.s.	0.427	0.0005	n.s.
36	*Temora stylifera*	0.21	2.97	0.01	99.97			0.429	0.0022	n.s.	0.047	0.0012	
37	*Centropages hamatus*	0.16	0.96	0.01	99.97			0.797	0.0002	n.s.	0.502	0.0005	n.s.
38	*Paraeuchaeta hebes*	0.16	1.04	0.01	99.98	0.68	425.0	0.004	0.0028		<0.001	0.0037	
39	Hemichordates	0.10	0.59	<0.01	99.98	−0.33	−312.6	0.014	−0.0014		0.085	−0.0011	n.s.
40	*Isias clavipes*	0.09	0.47	<0.01	99.98	−0.33	−383.5	0.002	−0.0014		<0.001	−0.0023	
41	*Microcalanus pygmaeus*	0.08	0.82	<0.01	99.99			0.590	−0.0004	n.s.	0.440	0.0005	n.s.
42	Isopods	0.05	0.25	<0.01	99.99	0.22	408.6	<0.001	0.0009		<0.001	0.0050	
43	*Anomalocera pattersoni*	0.05	0.29	<0.01	99.99			0.301	−0.0003	n.s.	0.733	0.0003	n.s.

44	*Calocalanus* spp.	0.04	0.51	<0.01	99.99			0.085	0.0008	n.s.	0.002	0.0016	
45	Cephalochordates	0.04	0.28	<0.01	99.99	0.17	454.6	0.006	0.0007	n.s.	0.001	0.0023	
46	*Parapontella brevicornis*	0.04	0.31	<0.01	99.99			0.160	−0.0004	n.s.	0.575	0.0003	n.s.
47	Mysids	0.03	0.14	<0.01	99.99			0.578	0.0001	n.s.	0.011	0.0020	
48	*Calanoides carinatus*	0.03	0.42	<0.01	99.99			0.240	0.0005	n.s.	0.023	0.0016	
49	Ctenophores	0.03	0.27	<0.01	99.99			0.468	−0.0002	n.s.	0.026[a]	0.0032	
50	*Scolecithricella minor*	0.03	0.29	<0.01	99.99	−0.13	−483.9	0.038	−0.0006		0.024	−0.0014	
51	Trachymedusae	0.03	0.25	<0.01	99.99	−0.12	−457.1	0.035	−0.0005		0.007	−0.0014	
52	*Solmaris corona*	0.01	0.21	<0.01	99.99			0.172	−0.0003	n.s.	0.708	−0.0001	n.s.
53	Siphonostomatoids	0.01	0.14	<0.01	99.99			0.487	0.0001	n.s.	0.206	0.0007	n.s.
54	*Ischnocalanus* spp.	0.01	0.10	<0.01	99.99	−0.06	−558.7	0.006	−0.0003		0.004	−0.0013	
55	Cumacea	0.01	0.13	<0.01	99.99			0.545	0.0001	n.s.	0.721	0.0002	n.s.
56	*Diaixis hibernica*	0.01	0.06	<0.01	99.99			0.887	<0.0001	n.s.	0.418	0.0004	n.s.
57	Nematodes	<0.01	0.03	<0.01	99.99			0.791	<0.0001	n.s.	0.794	0.0001	n.s.
58	*Labidocera wollastoni*	<0.01	0.01	<0.01	99.99	0.01	388.2	0.019	<0.0001		0.007	0.0014	
59	Ascidians	<0.01	<0.01	<0.01	100.00			0.950	<0.0001	n.s.	0.930	<0.0001	n.s.

Taxa highlighted in light grey are the rare and/or underestimated taxa due to the sampling methods used and the expertise of the analysts: these taxa appear on less than 20% of the L4 sample dates over the entire time series. Trend P-value and slope come from the regression analysis (superscript 'a' indicates a significant autocorrelation in which case the effective number of independent observations has been adjusted and n.s. indicates non-significant trends with P-value > 0.05). Change in abundance over the 20 years was calculated for significant trends using the slope from the regression analysis of the monthly averages, and this value was compared with the overall average to determine the percentage of change.
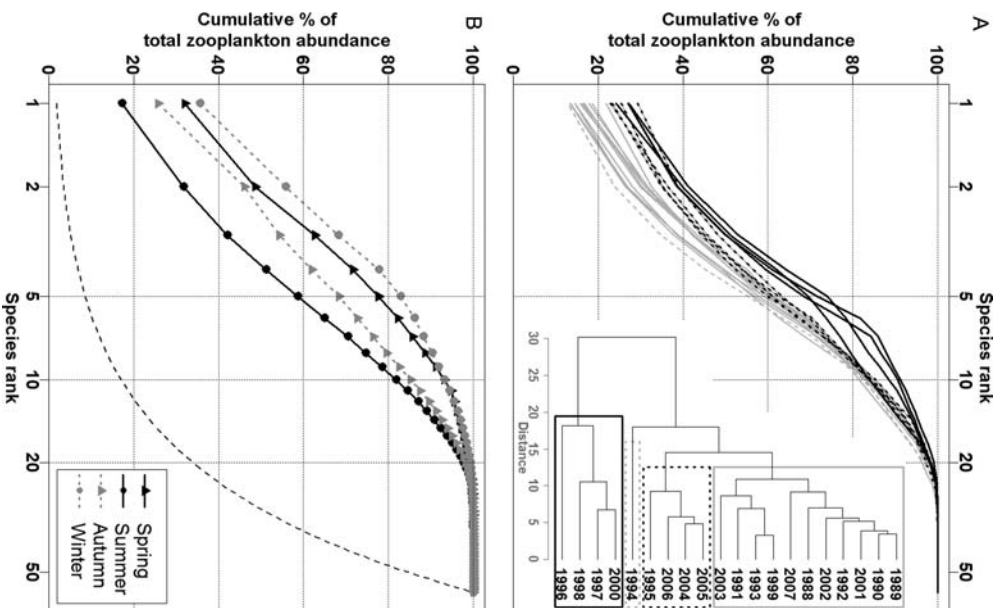
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Fig. 4. The k-dominance curves of the zooplankton community structure: (**A**) interannual variation and corresponding dendrogram (each curve is represented with the colour and line type of the group it comes from), and (**B**) the seasonal variation for each season where winter is from December to February, spring is from March to May, summer is from June to August and autumn is from September to November, and the k-dominance curve for a community with an even structure is also displayed (black dashed curve).

Only 22 taxa appeared among the 10 most abundant taxa in any month throughout the time series, representing together ≥95% on average of the total community, and their joint contribution over the year remained fairly stable (Fig. 4A and B). The majority of these taxa contributed ≥0.1% of the total zooplankton abundance (Table II). These taxa were mainly copepods, but also included a number of meroplanktonic organisms (e.g. Cirripede larvae, Echinoderm larvae and Bivalve larvae) which were abundant in spring, summer and autumn, respectively (Fig. 5). The temporal variations and seasonal succession of the meroplankton at L4 are described in more detail by Highfield *et al.* (Highfield *et al.*, 2010). The winter community was mainly
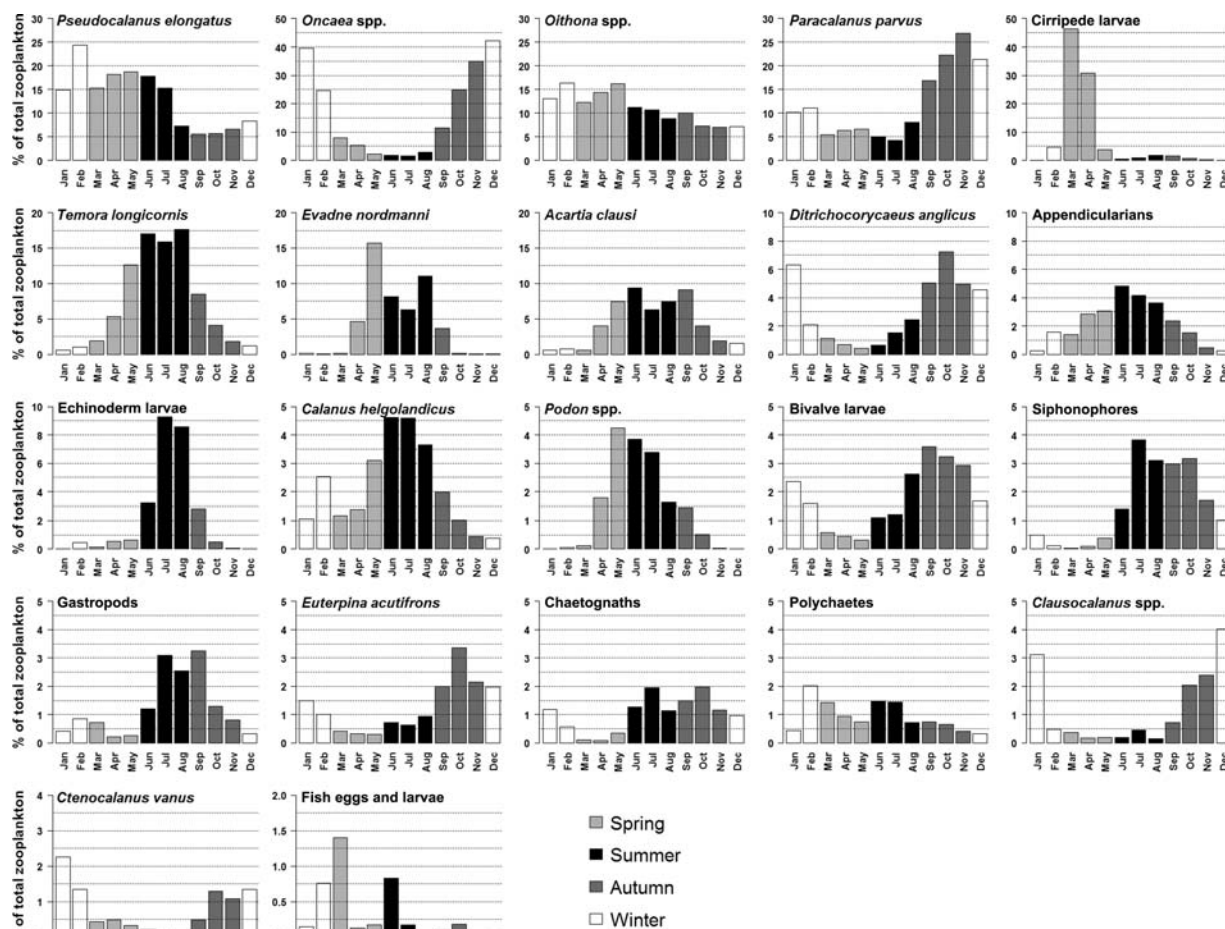
Fig. 5. Seasonal variation of the relative contribution of the dominant taxa: the relative contribution of each taxon to the total zooplankton abundance is represented for each month considering the entire time series.

dominated by a relatively small number of taxa (Fig. 5) such as *Oncaea* spp. (∼36%) and *Paracalanus parvus* (∼22%), whereas in spring Cirripede larvae (∼27%), *Pseudocalanus elongatus* (∼17%) and *Oithona* spp. (∼14%) were the dominant taxa. During the summer, a larger number of taxa contributed evenly to the zooplankton community, including *Pseudocalanus elongatus* (∼13%), *Temora longicornis* (∼17%), *Oithona* spp. (∼10%), *Evadne nordmanni* (∼9%) and *Acartia clausi* (∼8%).

In terms of their average annual contribution to the community over the 20-year period, only 8 taxa (e.g. *Pseudocalanus elongatus*, *Oncaea* spp., *Oithona* spp., *Paracalanus parvus*, Cirripede larvae, *Temora longicornis*, *Acartia clausi* and *Evadne nordmanni*) contributed significantly each year to the total abundance (Fig. 6). Taxa, such as *Pseudocalanus elongatus*, *Oncaea* spp., *Oithona* spp. and *Paracalanus parvus*, generally remained stable with small interannual variations; apart from some unusual years such as 1995–1996 and 2000 (Fig. 6). In some

years, certain taxa were very abundant compared with the others, for instance in 1995, 2004 and 2005 *Oncaea* spp. contributed 20–30% of the total zooplankton abundance; in 1988 and 1996 *Pseudocalanus elongatus* contributed >20%; in 1997, 1998 and 2006, Cirripede larvae contributed >25%; and in 2000 *Oithona* spp. contributed >25% of the total zooplankton abundance.

The seasonal patterns of the abundance of the 22 dominant taxa highlighted seasonal successions among them (Fig. 7). Within the copepods, *Pseudocalanus elongatus* and *Oithona* spp. were abundant from spring to summer, then *Temora longicornis*, *Acartia clausi* and *Calanus helgolandicus* from mid-spring to mid-autumn. *Paracalanus parvus* and *Ditrichocorycaeus anglicus* were restricted to autumn and *Oncaea* spp. to winter. Considering the other groups, Cirripede larvae appeared first in spring, followed by *Evadne nordmanni* and *Podon* spp. from spring to summer, accompanied by Appendicularians throughout spring to mid-autumn, whereas Echinoderm larvae and
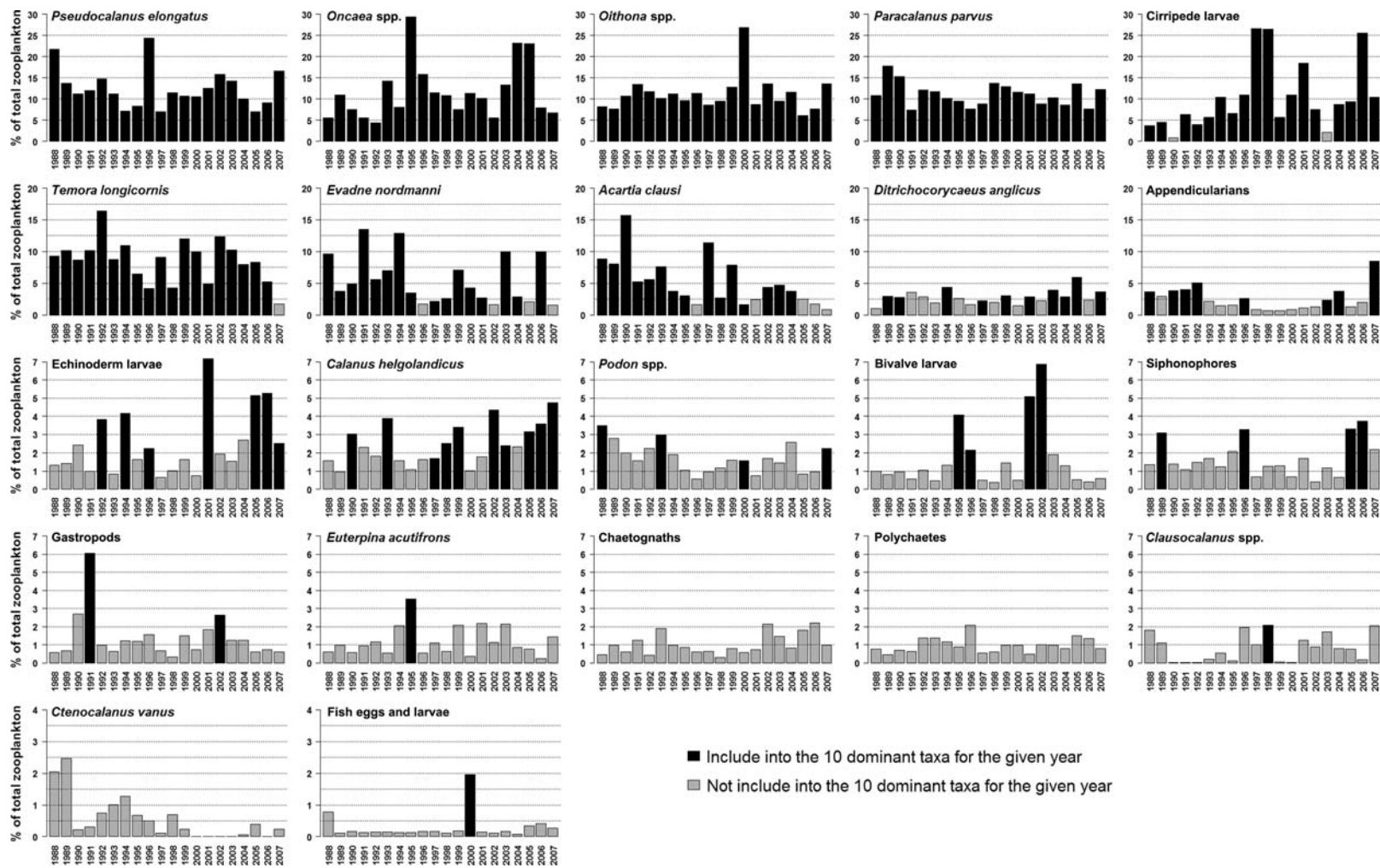
Fig. 6. Interannual variation of the relative contribution of the dominant taxa: the relative contribution of each taxon to the total zooplankton abundance is represented for each year of the time series (black bars represent years when the taxon was part of the 10 dominant taxa and grey bars represent when it was not).
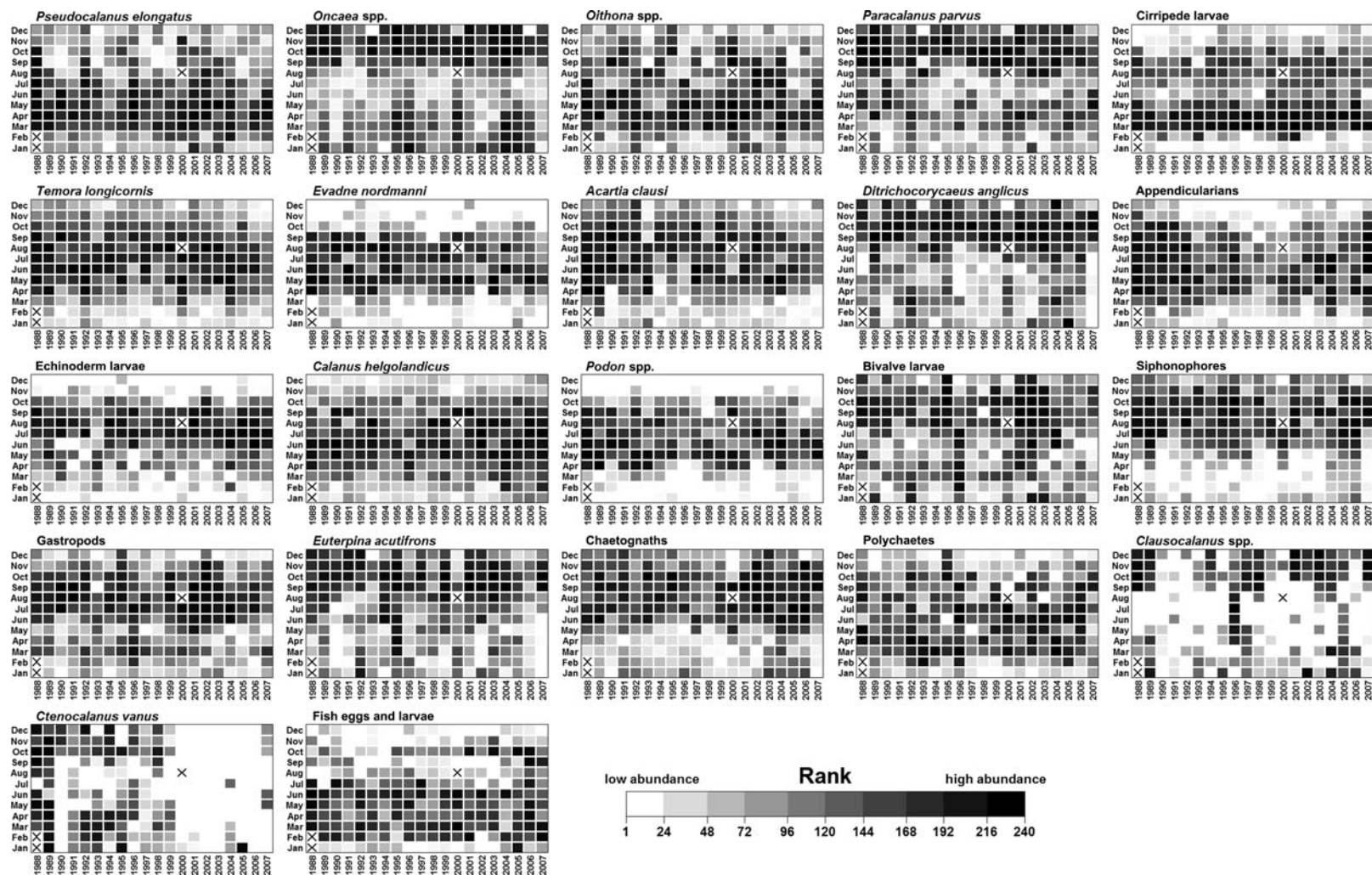
Fig. 7. Ranking of the monthly average of the dominant taxa abundance (where black squares represent the highest values, white squares the lowest and a cross indicates missing data for the given month).

Table III: Long-term trend of the 22 dominant taxa obtained from the regression analysis using the monthly anomalies over the period 1988–2007

	Positive trend	Negative trend
P-value ≤ 0.001	*Calanus helgolandicus*[a]; Chaetognaths[a]	*Temora longicornis*; *Acartia clausi*[a]; *Ctenocalanus vanus*[a]
P-value ≤ 0.01	Cirripede larvae	*Evadne nordmanni*; Appendicularians
P-value ≤ 0.05	*Oncaea* spp.	*Pseudocalanus elongatus*[a]; *Podon* spp.[a]
non-significant trend	*Oithona* spp.; *Paracalanus parvus*; *Ditrichocorycaeus anglicus*; Echinoderm larvae; Bivalve larvae; Siphonophores; Gastropods; *Euterpina acutifrons*; Polychaetes; *Clausocalanus* spp.; Fish eggs and larvae	

The categories are based on the trend sign, positive or negative, and the associated *P*-value.
[a]Indicates that the trend displayed by the monthly average abundances was also significant for this taxon, with a *P*-value ≤ 0.05.

Chaetognaths occurred from summer to autumn and Bivalve larvae arrived only in autumn.

There was also evidence of long-term changes in abundance of some of the dominant taxa (Table III). For instance, results of the regression analysis based on the monthly anomalies (Table II), suggested that *Calanus helgolandicus*, Chaetognaths, Cirripede larvae and *Oncaea* spp. increased in abundance, whereas *Acartia clausi*, *Ctenocalanus vanus*, *Temora longicornis*, *Evadne nordmanni*, Appendicularians, *Pseudocalanus elongatus* and *Podon* spp. decreased over the 20-year period. For some of these taxa (i.e. *Acartia clausi*, *Calanus helgolandicus*, Chaetognaths, *Ctenocalanus vanus*, *Pseudocalanus elongatus* and *Podon* spp.), the trend displayed by the monthly averages was also significant; thus, we were able to estimate the magnitude of these changes (Table II).

Diversity

The average seasonal cycle of the richness index for the copepod community showed only small variations with the highest values (∼12.5) in autumn and the lowest (∼10.2) in summer (Fig. 8A). The annual anomalies showed years with high positive (e.g. 1998, 1999 and 2007) or negative (e.g. 1990, 1996, 2000, 2002 and 2003) anomalies (Fig. 8B). The ranking of the monthly averages varied little without any clear seasonal or long-term pattern and only some unusual periods of low values in 1996, 2000 and 2002–2003, and high values in 1997–1999, 2004 and 2006–2007 (Fig. 8C). However, a significant positive long-term trend (slope = 0.0049, $P = 0.003$) was estimated for the richness of the copepod community (Table I).

The Simpson index for the copepod community was lower (∼0.23) in autumn and higher (∼0.32) in winter (Fig. 8D). The annual anomalies for the copepod community showed a long period (1995–2002) of positive anomalies and 2 years with a high positive anomaly (e.g. 1990 and 2004) (Fig. 8E). Several years had high negative anomalies (e.g. 1991, 1992, 1994 and 2007). The ranking of the monthly averages showed a very heterogeneous pattern (Fig. 8F), but generally most of the highest values were in winter and the lowest in autumn, except for 2 years (1991 and 1992) when the lowest values were during the winter period. The long-term trend for the Simpson index was not significant ($P = 0.535$) (Table I).

Cumulative sums

The cumulative sums of the zooplankton abundance (Fig. 9) indicate four periods delimited by three major changes, which occurred in 1990/1991, 1999/2000 and 2004/2005, and four minor changes (i.e. 1994/1995, 1995/1996, 2002/2003 and 2003/2004). As expected, the results of the cumulative sums for the total copepods abundance were very similar to those for the total zooplankton. Considering the cumulative sums of the other biological and environmental parameters, a number of similarities appeared between the timing of changes for these parameters and those described previously for the total zooplankton abundances (Table IV).

Changes were seen in some variables that were not shown by the cumulative sums of the total zooplankton. For instance, in 1991/1992 *Temora longicornis*, Gastropods and Polychaetes exhibited a change in their cumulative sums, whereas changes occurred in 1996/1997 for the Cirripede larvae and the richness index. In 2000/2001, *Ditrichocorycaeus anglicus*, Bivalve larvae, Gastropods, *Euterpina acutifrons* and *Clausocalanus* spp., as well as the W/E wind, the NAO index and winter NAO index, showed a change. In 2001/2002, *Calanus helgolandicus*, Chaetognaths and Cirripede larvae exhibited a change in their cumulative sums. Finally, another change was also noticeable in 2005/2006 for *Oncaea* spp., *Paracalanus parvus*, *Ditrichocorycaeus anglicus* and the GSNW position index. Another noticeable result from the cumulative sums was the similarity in the timing and duration of changes for *Calanus helgolandicus* and Chaetognaths.
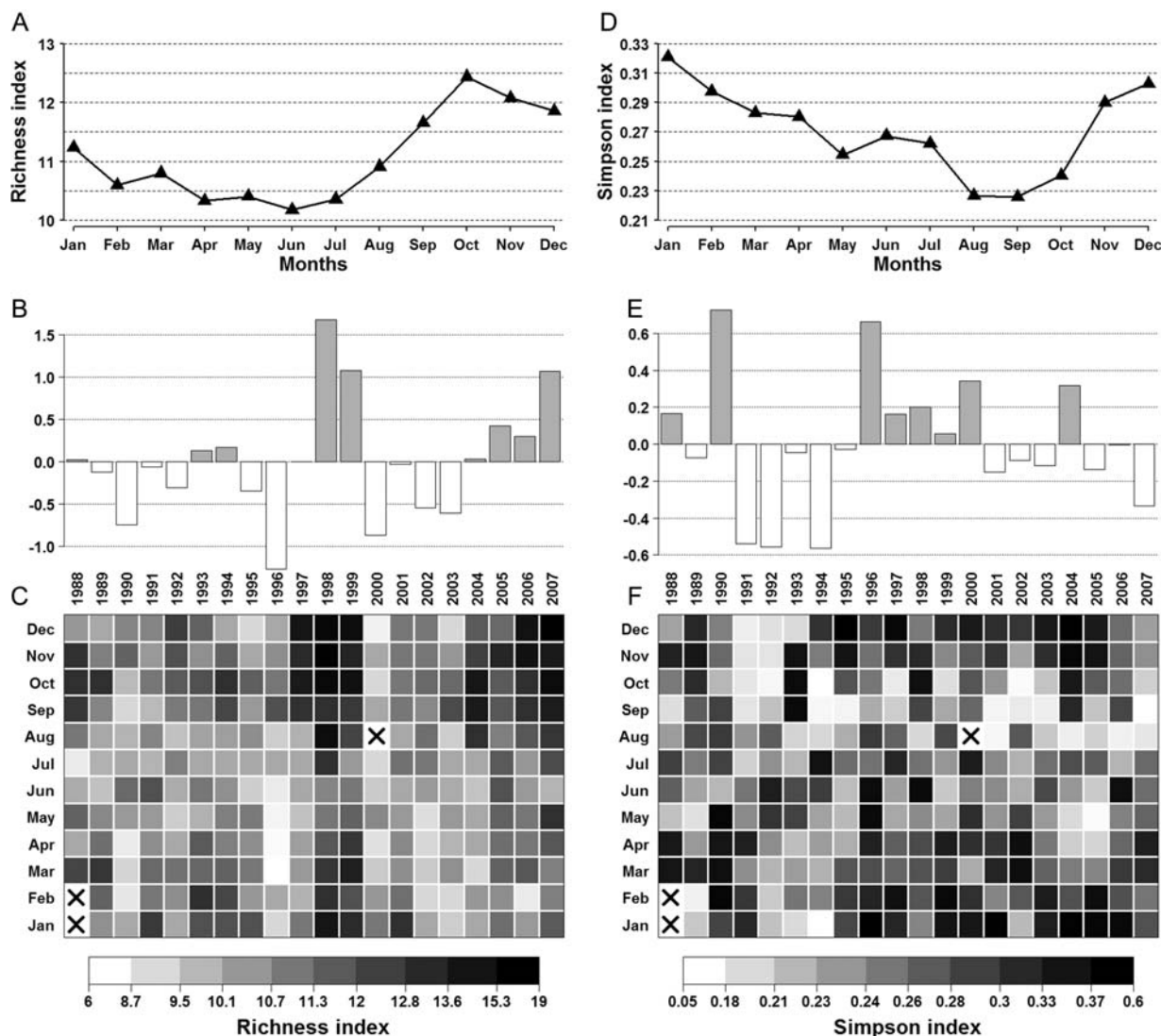
Fig. 8. Monthly seasonal cycle, annual anomalies and ranking of the monthly average time series of the richness index (**A**–**C**) and Simpson index (**D**–**F**) obtained for the copepod community [on panels (B) and (E), grey and white bars represent positive and negative anomalies, respectively; on panels (C) and (F), black squares represent the highest values, white squares the lowest and a cross indicates missing data for the given month].

DISCUSSION

Temporal variation in total zooplankton abundance

The total zooplankton abundance at L4 had a clear seasonal signal over the 20 years studied, with two peaks (Fig. 1E) similar to previous observations made by Harvey *et al.* in 1934 (Harvey *et al.*, 1935). The authors described a comparable timing for the appearance of the two peaks, but it appeared that the autumn peak was more intense than the spring one. These differences could be explained by a different sampling method used and/or because the seasonal cycle exhibited in 1934 was

peculiar and therefore not representative of the average seasonal cycle for that time of the century. This seasonal pattern also shows similarities with the coastal stations of Stonehaven in the Northwest North Sea and Santander in the Southern Bay of Biscay (O'Brien *et al.*, 2008). These two peaks are related to the phytoplankton seasonal cycle. The first peak of zooplankton abundance corresponds to the phytoplankton spring bloom dominated by diatoms and the second peak follows the dinoflagellates bloom occurring at the beginning of the autumn (Harvey *et al.*, 1935; Widdicombe *et al.*, 2010).

There was no evidence that the intensity of the spring peak of zooplankton abundance has increased
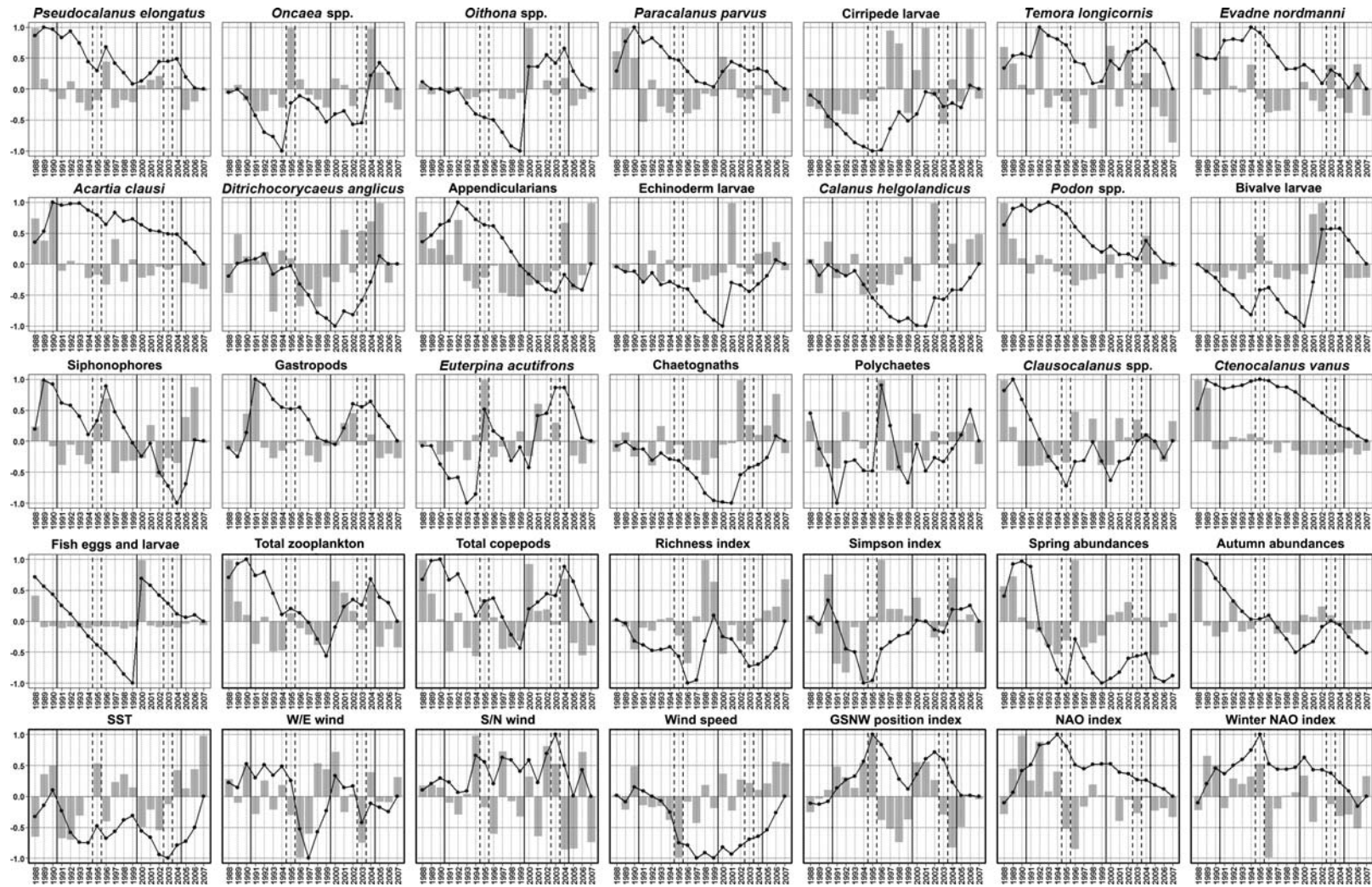
Fig. 9. Cumulative sums and corresponding residuals of each biological and environmental factor (vertical solid lines separate periods of change in total zooplankton abundance, and vertical dashed lines indicate other possible changes occurring in the plankton community). The spring and autumn abundances represent the yearly average of the total zooplankton abundances from March to May and from August to October, respectively.

Table IV: Summary of results obtained from the analysis of the cumulative sums of each biological and environmental parameter

	1990/1991	94/95	95/96	1999/2000	02/03	03/04	2004/2005
Total zooplankton	×	×	×	×	×	×	×
Total copepods	×	×	×	×	×	×	×
Richness index				×		×	
Simpson index		×					×
Spring abundances	×			×	×		
Autumn abundances				×		×	
SST	×	×		×		×	
W/E wind		×					
S/N wind						×	
Wind speed	×			×			
GSNW position index			×	×	×		
NAO index		×					
Winter NAO index			×				
Pseudocalanus elongatus			×	×	×		×
Oncaea spp.		×				×	
Oithona spp.				×			×
Paracalanus parvus	×			×			
Cirripede larvae							
Temora longicornis				×			×
Acartia clausi	×						
Evadne nordmanni		×					
Ditrichocorycaeus anglicus			×				
Appendicularians						×	
Echinoderm larvae							
Calanus helgolandicus							
Podon spp.							
Bivalve larvae		×			×		×
Siphonophores		×					×
Gastropods					×		×
Euterpina acutifrons			×				×
Chaetognaths							
Polychaetes			×	×			
Clausocalanus spp.			×				×
Ctenocalanus vanus							
Fish eggs and larvae							

Periods of change were defined for the total zooplankton and included three main changes (bold crosses) and four minor changes. Similar changes occurring in the cumulative sums of others factors were indicated.

significantly over the 20-year time series. However, the correlation between the total zooplankton and the diatoms abundance in March over the 20 years was negative and significant ($\rho = -0.62$, $P = 0.02$), suggesting either the existence of a close relationship between the two plankton communities and/or different ways of responding to a common factor. More than 45% of the total zooplankton abundance in March was composed of Cirripede larvae (Fig. 5) and this group showed a significant positive long-term trend in its monthly anomalies (Tables II and III). An increase of the zooplankton population in spring, such as Cirripede larvae, could have a top-down effect on the phytoplankton by increased grazing (Harvey *et al.*, 1935). There is little information available regarding Cirripede larvae and their ecology, especially on the impact this group could have on the plankton community. Nevertheless, a study investigating the size of particles selected by copepods and Cirripede larvae suggested that the two

grazers can compete because of their similarity in food selection (Barlow and Monteiro, 1979). However, zooplankton grazing is not the only reason for the observed decrease of the phytoplankton spring bloom intensity, changes in water column conditions and nutrients have also a significant impact on the phytoplankton community structure (Widdicombe *et al.*, 2010).

In contrast, the pattern observed in the cumulative sums of the autumn abundances (Fig. 9) suggests that the intensity of the autumn peak decreased over the two periods 1988–1999 and 2004–2007, probably driven by the decreases among some dominant taxa (e.g. *Temora longicornis*, *Acartia clausi*, *Evadne nordmanni* and Appendicularians), which are usually abundant during this time of the year (Table III, Figs 5 and 7). The maximum autumn abundance of the total zooplankton was negatively and significantly ($\rho = -0.47$, $P = 0.04$) correlated to the average autumn SST over the 20 years. The long-term trend of the monthly anomalies of

SST was positive and significant (slope $= 0.0002$, $P = 0.003$), especially in September (slope $= 0.08$, $P = 0.02$). The key environmental factor allowing the start of autumn phytoplankton production is the breakdown of summer stratification, resulting in the redistribution of nutrients in the water column close to the surface (Smyth *et al.*, 2010). With increasing temperatures, stratification might be maintained longer and the autumn phytoplankton bloom may be limited by nutrient depletion and in turn be delayed and less intense.

The analysis of the current time series revealed that the seasonal cycle of the total zooplankton abundance was generally consistent from 1 year to another and this variability was typically greater than interannual variations. In addition, the 20-year time series did not display any significant long-term trend, but this result could have been the sum of compensatory long-term changes occurring in the community. The use of monthly averages also removes changes that occur at a smaller temporal scale, but we chose this temporal frequency to reduce the number of gaps in our time series. It may be that 20 years of data may still not be sufficient to detect a significant change at L4 and a number of years of additional sampling might allow one to be detected.

Temporal variation in diversity and community composition

It is clear that the composition and structure of the community varied through the year with a more diverse and evenly distributed community in summer and one strongly dominated by just a few species during winter (Figs 4, 5 and 8). However, the community at L4 appeared relatively stable over the 20 years except for few atypical years, and only variations in the rank of the most dominant taxa and small changes in composition of the less dominant taxa were visible. This was consistent with what has been already described at L4 in the past (Digby, 1950). The species richness displayed heterogeneous and small variations in both seasonal and interannual pattern, but showed a significant positive long-term trend, indicating a small increase in the number of copepod taxa identified at L4. This latter result, even if significant, has to be interpreted with care as it could be due to the improvement of the taxonomic expertise over the 20-year period. Unfortunately, we did not have enough information to test and verify this hypothesis. In contrast, the Simpson index, which gives information on the dominance of the community, did not show any significant long-term trend. Its seasonal variation was in general, but not always, more important than its interannual variability due to the abrupt change of the index between autumn and winter.

The most abundant taxa at L4 (Table II) were also found to be the most abundant at different locations in the coastal waters of the North Atlantic region (O'Brien *et al.*, 2008). At five long-term stations (Gulf of St Lawrence, Iceland, Northern Skagerrak, Northwest North Sea, Northwest Iberian Peninsula), *Pseudocalanus* spp. and *Oithona* spp. appeared among the 10 most dominant taxa at all of them, *Acartia* spp. at four, *Temora longicornis* and Appendicularians at three and *Oncaea* spp. and Cirripede larvae at two (O'Brien *et al.*, 2008). The proportion of the dominant copepods *Acartia* spp., *Oithona* spp., *Oncaea* spp., *Paracalanus parvus*, *Clausocalanus* spp. and *Pseudocalanus elongatus* also showed similarities with a recent study in the Gulf of Trieste (Conversi *et al.*, 2009). However, these authors observed a shift towards smaller copepod species in the community during the period 1970−2005. Such a shift has not been observed at L4.

There was evidence for long-term changes in the numbers of some of the dominant taxa. *Oncaea* spp., Cirripede larvae, *Calanus helgolandicus* and Chaetognaths have increased whereas *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi*, *Evadne nordmanni*, Appendicularians, *Podon* spp. and *Ctenocalanus vanus* have decreased over the 20-year period (Tables II and III). Similar patterns have been observed for some of these species and groups elsewhere, such as increases in abundance of *Calanus helgolandicus* in the North Atlantic and North Sea (Planque and Fromentin, 1996; Beaugrand, 2003) and declines in *Temora longicornis* in the Northeast Atlantic (Kane and Prezioso, 2008).

Of the 22 dominant taxa, 4 increased significantly in abundance and 7 decreased (Tables II and III). Those taxa which increased showed a range of seasonal cycles: *Oncaea* spp. was abundant in autumn and winter, Cirripede larvae in March and April, *Calanus helgolandicus* in spring and summer and Chaetognaths in summer and autumn. Consequently, different factors may influence their increase. On the other hand, taxa showing a negative trend had similar seasonal patterns. *Temora longicornis*, *Acartia clausi*, *Evadne nordmanni*, *Podon* spp. and Appendicularians are all abundant from spring to the end of the summer, and thus they may be affected by the same factor(s) and/or competition for similar resources. However, no relationship was found between these taxa and any of the environmental parameters measured.

Some taxa, such as Cirripede larvae or *Oncaea* spp., contributed significantly to the community during short periods of the year (spring and winter, respectively; Fig. 5). Others, such as *Pseudocalanus elongatus* or *Oithona* spp. contributed evenly all year round. These observations have already been well documented at L4, for

the same taxa in 1933 (Harvey *et al.*, 1935) and for the copepod species only in 1947 (Digby, 1950), although over periods of a year only. Their results were similar to those from the 20-year period in this study, suggesting that the contributions of these taxa to the seasonal succession may not have changed significantly in the past 70 years.

Cirripede larvae are an important group since they are very abundant at L4 during the spring period (Figs 5 and 7) and their increasing abundance could have an impact on the community by increasing competition for food and the grazing pressure during the spring bloom, as suggested in a previous study in Southampton water (Barlow and Monteiro, 1979). Likewise, the increasing abundance of the winter dominant species *Oncaea* spp. may have a strong impact on the small number of other winter taxa, as diversity reaches its lowest value during winter. The increasing abundances of both taxa might have an effect on the diversity of the zooplankton community if these changes in dominance persist.

Possible relations between zooplankton at L4 and environmental conditions

Although the NAO index and SST have already been used in other studies to demonstrate the linkages between the long-term changes in the plankton community and the North Atlantic and Western Channel climate (Southward *et al.*, 1995; Fromentin and Planque, 1996; Beaugrand *et al.*, 2000; Irigoien *et al.*, 2000), at L4 total zooplankton abundance did not show such a relationship whereas phytoplankton did, at least during the period 1993–1999 (Irigoien *et al.*, 2000). Zooplankton have a more complicated linkage with climate, since the possible pathways by which the NAO may affect ecological processes vary and affect the environment and biology at different levels (Ottersen *et al.*, 2001). Since L4 is a spatially confined coastal station subject to a variety of influences such as fresh water input from the estuary and anthropogenic influences such as fishing (Smyth *et al.*, 2010), links with climate indices may be weak compared those further offshore, where climate and currents are likely to be the only environmental parameters affecting the zooplankton community. Linkages between the NAO, SST and diversity (Table V) may be explained by the fact that a high NAO pattern will increase air temperature and westerly wind stress, which in turn will increase the SST and flow of water coming from the west (Fromentin and Planque, 1996; Irigoien *et al.*, 2000; Irigoien and Harris, 2003), favouring an increase in zooplankton community

Table V: Correlation coefficient between the winter NAO index, annual average SST, annual average abundances of four zooplankton taxa and annual maximum of the species richness calculated for the period 1988 to 2007, using the Spearman rank correlation (P-values ≤ 0.05)

Spearman rank correlation coefficient	winter NAO index	SST
Temora longicornis		−0.45
Cirripede larvae	−0.45	
Podon spp.	0.47	
Clausocalanus spp.	−0.45	
Subeucalanus crassus	−0.49	
Maximum richness index		0.46

diversity due to the increase of the number of species advected into the region.

Results from the cumulative sums provide evidence supporting hypotheses as regards the existence of links between zooplankton and the environment. Different periods of change in the total zooplankton were related to changes occurring in some of the dominant taxa and in environmental conditions (Table IV, Fig. 9). Each main change visible in the total zooplankton over the 20 years occurred at the same time as a change in the SST and wind. For the most obvious change, between 1999 and 2000, the majority of the dominant taxa and environmental factors were affected. In contrast, minor changes occurring between 1994 and 1996 affected only a few dominant taxa (e.g. *Pseudocalanus elongatus* and *Oncaea* spp.). These were related to changes in the NAO, but no changes were visible in total zooplankton. Therefore, changes in the abundance of some of the dominant taxa, in response to changes in the environmental conditions, did not necessarily correspond to changes in total zooplankton. In addition, changes in total zooplankton were not consistently related to changes in the same dominant taxa. Thus, it is difficult to relate changes in total zooplankton to changes in one environmental parameter or one of the dominant taxa, as each taxon may respond differently to change in environmental conditions with different degrees of response.

The environmental conditions, SST and wind, as well as the food resources, for instance the phytoplankton, must play major roles in controlling directly or indirectly the total zooplankton abundance at L4, but more evidence is needed to investigate linkages and mechanisms. We did not find any direct relationship between the NAO and the zooplankton, but other studies have provided evidence of a link between the phytoplankton and the NAO (Irigoien *et al.*, 2000) or

the SST and the NAO (Fromentin and Planque, 1996). The NAO may indirectly affect zooplankton abundance by influencing the winter conditions and thus perhaps the preconditioning of the spring population and its response to the spring bloom. This was suggested by the positive and significant ($\rho = 0.47$, $P = 0.04$) correlation we found between the winter NAO index and the spring temperature at L4. Nevertheless, pathways by which hydroclimatic factors control zooplankton abundance and community composition are complex and numerous, as are the interactions between the parameters. Furthermore, mixing, river runoff and tide might also play an important role in controlling the plankton community at L4.

Zooplankton indicators at L4

The concept of indicator species has many applications. It has been used in the Western Channel and North Sea to characterize species indicative of particular water masses (Russell, 1935; Southward, 1963, 1984; Bonnet and Frid, 2004), whereas in the Bay of Biscay it was used for rare/unusual species appearing occasionally or consistently, depending on the hydroclimatic conditions (Villate *et al.*, 1997; Lindley and Daykin, 2005; Valdés *et al.*, 2007). In past studies, it has already been suggested that copepod species such as *Temora stylifera* and *Acartia clausi* could be key species for monitoring climate changes affecting the Bay of Biscay and the north-eastern Atlantic Ocean (Villate *et al.*, 1997; Lindley and Daykin, 2005; Valdés *et al.*, 2007). The increase in abundance of these copepod species was related to temperature, but also to the hydrological characteristics of the region. Of these species, only *Acartia clausi* was abundant at L4. Its abundance declined significantly over time (Tables II and III) but its abundance did not show a significant correlation with the environmental factors used in our analysis. *Temora stylifera* showed a significant increase over the 20 years studied (Table II), although this result can be criticized as the species was one of the taxa that may have been underestimated by the analysts. However, its congeneric species, *Temora longicornis*, was abundant at L4 and showed both a significant decrease over time (Tables II and III) and a significant negative correlation with the SST (Table V), a pattern which has also been observed in the Northeast Atlantic (Kane and Prezioso, 2008). *Temora longicornis* is a boreal species (Halsband-Lenk *et al.*, 2002, 2004) and the increase in temperature at L4, 0.6°C per decade (Smyth *et al.*, 2010), may not favour it.

The NAO index exhibited a significant negative trend (slope $= -0.004$, $P = 0.02$) in its monthly values over the 20-year period. Cirripede larvae, *Podon* spp. and *Subeucalanus crassus* were significantly correlated to the winter NAO index (Table V) and all displayed a significant trend in their monthly anomalies (Table II) suggesting that the NAO may be an indicator of factors controlling their abundance, such as the degree of climate driven influx of waters coming from the south and west. However, it is difficult to explain such a relationship. Previous studies have already tried to address this issue, but their conclusions were ambivalent. For instance, the abundance of *Centropages typicus* was positively related to the NAO in the eastern North Sea and negatively in the Celtic Sea and Bay of Biscay (Reid and Planque, 2000). It is likely that uncertainties in interpretation reflect the complex interactions among species life cycles, variability in local productivity and food availability, and changes in seasonal patterns of advection.

A number of taxa present at L4 showing significant variability may also be considered as indicators. Past studies have shown that patterns in abundance of specific taxa, such as *Calanus helgolandicus*, Chaetognaths and Echinoderm larvae, were related to hydroclimatic changes in seas surrounding the Western Channel. In the present study, *Calanus helgolandicus* showed a significant positive trend with a marked increase in abundance since 1994 (Table II, Fig. 6). This species has been intensively studied during recent years, especially with respect to its link with its congener *Calanus finmarchicus* and climate change over the North Atlantic (Fromentin and Planque, 1996; Planque and Fromentin, 1996; Beaugrand, 2003; Bonnet *et al.*, 2005; Helaouët and Beaugrand, 2007). In contrast to two other studies that link the increase in abundance of *Calanus helgolandicus* with changes in the hydroclimatic environment (Fromentin and Planque, 1996; Beaugrand, 2003), no relationship was found with SST or the winter NAO index at L4, supporting the idea that it may be advection, stratification of the water column and/or mortality that are the main factors controlling the population, as has been previously suggested for *Calanus helgolandicus* at L4 (Irigoien and Harris, 2003; Bonnet *et al.*, 2010).

Chaetognaths are planktonic predators and can have an important impact on the plankton community through top-down control, especially on copepods (Williams and Collins, 1985; Roff *et al.*, 1988; Nicholas and Frid, 1999). They have been observed in the laboratory feeding on *Acartia clausi* (Frid *et al.*, 1994) or *in situ* on *Calanus helgolandicus* (Bonnet *et al.*, 2010). The importance of Chaetognaths as indicators has been highlighted in past studies. For example, Russell (Russell, 1935) determined that the presence of each of two species of *Sagitta* in the Western Channel indicated

water bodies with different origins. *Sagitta setosa* occurs in waters in the Channel, whereas *Sagitta elegans* is a more oceanic species and its presence indicates water with a western, or oceanic, origin. Their temporal variations were used to explain changes in the plankton community observed in the Western Channel during the last century (Russell, 1935; Southward, 1963, 1984; Øresland, 1986). At L4, most Chaetognaths were *Sagitta setosa* over the 20-year time series, and we did not observe any change in the species composition. Chaetognaths were abundant throughout the summer and autumn (Fig. 5) and exhibited a positive significant trend over the time series (Tables II and III). Because of their abundance, Chaetognaths may have a role in the control of copepod population numbers during the summer/autumn, as has been suggested for *Calanus helgolandicus* (Bonnet *et al.*, 2010). Enhanced predation by Chaetognaths could be a factor explaining the decrease in the autumn peak of total zooplankton abundance. The factors influencing the abundance of Chaetognaths could be diverse: advection and temperature have already been used to explain interannual variations and autumn densities and thus predation impact (Nicholas and Frid, 1999). However, we have not found any correlation between the abundance of this taxon and SST, and do not have sufficient information on advection at L4.

A temporal link has already been observed between the SST, the NAO index and the abundance of Echinoderm larvae in the North Sea CPR samples (Kirby *et al.*, 2007, 2008), but we did not find such a relationship at L4. Echinoderm larvae did not show a significant trend in monthly average abundances over the time series (Table II), but they have significantly increased during summer. Average abundances in June showed a significant positive trend (slope = 17.2, $P = 0.02$). This was the time of the year that they were most abundant, representing 10–40% of the total zooplankton abundance depending on the year. This coincided with the timing of the most significant temperature increase over the 20 years, since June was the month with the highest significant positive trend in SST (slope = 0.08, $P = 0.02$). For meroplankton larvae, time spent in the plankton is a period of high mortality and an increase in temperature can improve larval survival by reducing this time through increased development rates (Kirby *et al.*, 2007).

Rare species are also important indicators, but because they are rare we cannot analyse their data with the same accuracy and confidence as for the dominant species. In this category at L4, *Temora stylifera*, *Centropages chierchiae* or *Penilia avirostris* could be considered potentially important indicator species in future studies.

Penilia avirostris was recorded in the L4 samples for the first time in September 2008. This species has not been recorded in the Western Channel before, but is commonly found in the Bay of Biscay, southern North Sea and Baltic Sea. The presence of the species could be related to a change in the climate conditions during this year. Increased autumn SSTs were found to be favourable for *Penilia avirostris* in the North Sea and Baltic Sea (Johns *et al.*, 2005), warmer conditions contributing to the survival success of its resting eggs, and facilitating its spread. The NAO index was negative for six consecutive months in 2008, from April to September, with an average index of −1.8 for that period. This led to less westerly winds and a relatively mild autumn in 2008. A change in the dominant wind could have affected the origin of the waters at L4 and favoured the presence of waters coming from the eastern part of the Channel, which are influenced by the southern North Sea where this species has become more and more abundant (Johns *et al.*, 2005).

SUMMARY

The data and results presented in this study provide information on the zooplankton community at L4 over the period 1988–2007:

(i) The seasonal cycle did not show a significant difference to that described at L4 in the past, but we observed variability and potential changes in the intensity of peaks during the spring and the autumn periods.
(ii) The total zooplankton abundance did not show any long-term trend, but this might change in the future if the decreasing tendency observed for the last years of the time series continues, thus we need to maintain sampling to extend our time series.
(iii) The community structure remained stable without radical changes in the composition of the dominant taxa, but long-term trends were highlighted over the 20-year period as well as changes in diversity related to changes in environmental conditions.
(iv) It was unclear which environmental parameter was driving zooplankton abundance over the 20-year period, but SST, wind and/or the NAO were related to temporal variations of some dominant taxa and diversity measures.
(v) Plankton indicator species will be key factors in monitoring future changes in the plankton ecosystem of the Western Channel in relation to environmental and climate variations.

The analysis of the current time series showed that the seasonal pattern was generally, but not always, consistent from 1 year to another. Interannual variation in total zooplankton, community composition and diversity were typically of a lesser magnitude than variability related to seasonal changes in environmental conditions. Compared to oceanic waters, where communities might only respond to variations due to climate changes, coastal waters are influenced by many factors, especially factors induced by human activities, that can alter plankton community in different ways. The extension of the long-term plankton time series at L4 is important for monitoring the plankton ecosystem in the Western Channel and further analyses on the data set are in progress. We also need to extend the range of *in situ* data collected, and perhaps to increase the frequency of the sampling, to better understand processes taking place in the plankton community and relate their temporal variations to changes in environmental conditions.

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