

Time-series analysis of copepod diversity and species richness in the southern Bay of Biscay off Santander, Spain, in relation to environmental conditions

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Changes in the copepod species composition and their relative abundances at two stations on a cross-shelf section off Santander (Spain) in the southern Bay of Biscay are described by means of species richness, Shannon-Weaver diversity, and similarity coefficients. The seasonal and inter-annual variability in these indices is compared with changes observed in thermal stratification indices from monthly collected data over 5 years (June 1991 to June 1996). Copepods represent the main taxonomic group in the zooplankton assemblage in terms of abundance and persistence. Ordination of the samples by their similarity coefficients has a clear temporal meaning, and the clusters formed are linked to seasonal characteristics of the water column. Autocorrelation and spectral analysis of species richness and diversity show a 12-month periodic cycle throughout the time series, with a less important peak every 30 months. The long-term trends between these indices and the standard deviation of water column temperature (as an index of thermal stratification) are of opposite sign. The significant negative correlation between the pairs suggests a strong relationship between the maintenance of copepod diversity and environmental conditions.

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Key words: Bay of Biscay, copepods, temporal variability, time series.

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Introduction

The dynamics of zooplankton populations show large fluctuations over a wide variety of time scales (e.g. seasonal, inter-annual, and decadal), which strongly limits attempts to make predictions of how changes in the environment will affect abundance, diversity, production, and other properties of the assemblage. In addition, the high variability limits our ability to differentiate between anthropogenic and naturally occurring effects. It has been with the purpose of overcoming these bottlenecks in mind that long-term observation programmes have been encouraged by international agencies, and that national projects have been established within the framework of IGBP initiatives (e.g. GOOS, JGOFS, GLOBEC, etc.). The developing time series of oceanographic and planktonic data allow studies of the magnitude of variation in some structural parameters of the zooplankton community. For example, data on seasonal and inter-annual variations in mesozooplankton abundance and biomass off the Spanish coast in the

Bay of Biscay have been described by Valdés (1993) and Moral (1994). Valdés *et al.* (in press) reported that the range of variation of mesozooplankton biomass in this region is as wide as 1–70 mg DW m⁻³ in coastal areas. Similar ranges have been reported by several authors in other coastal and neritic waters of the Bay of Biscay (Arbault and Lacroix-Boutin, 1973; Le Corre and Treger, 1976; Boucher, 1985; d’Elbée and Castel, 1991; Valdés *et al.*, 1991; Poulet *et al.*, 1996).

The wide range of variation makes the comparison of data from different locations and years difficult. Therefore, many authors have advocated searching for trends within time series as the best procedure by which to compare and identify common patterns in the variation among different data sets (Legendre and Demers, 1984; Peters, 1986; Paffenhöfer, 1989; Valdés *et al.*, in press). This approach allows a closer investigation of the links between environmental conditions and plankton dynamics.

This study, based on a time series of 5 years and covering observations made during different seasons and water column conditions at the shelf edge in the southern Bay of

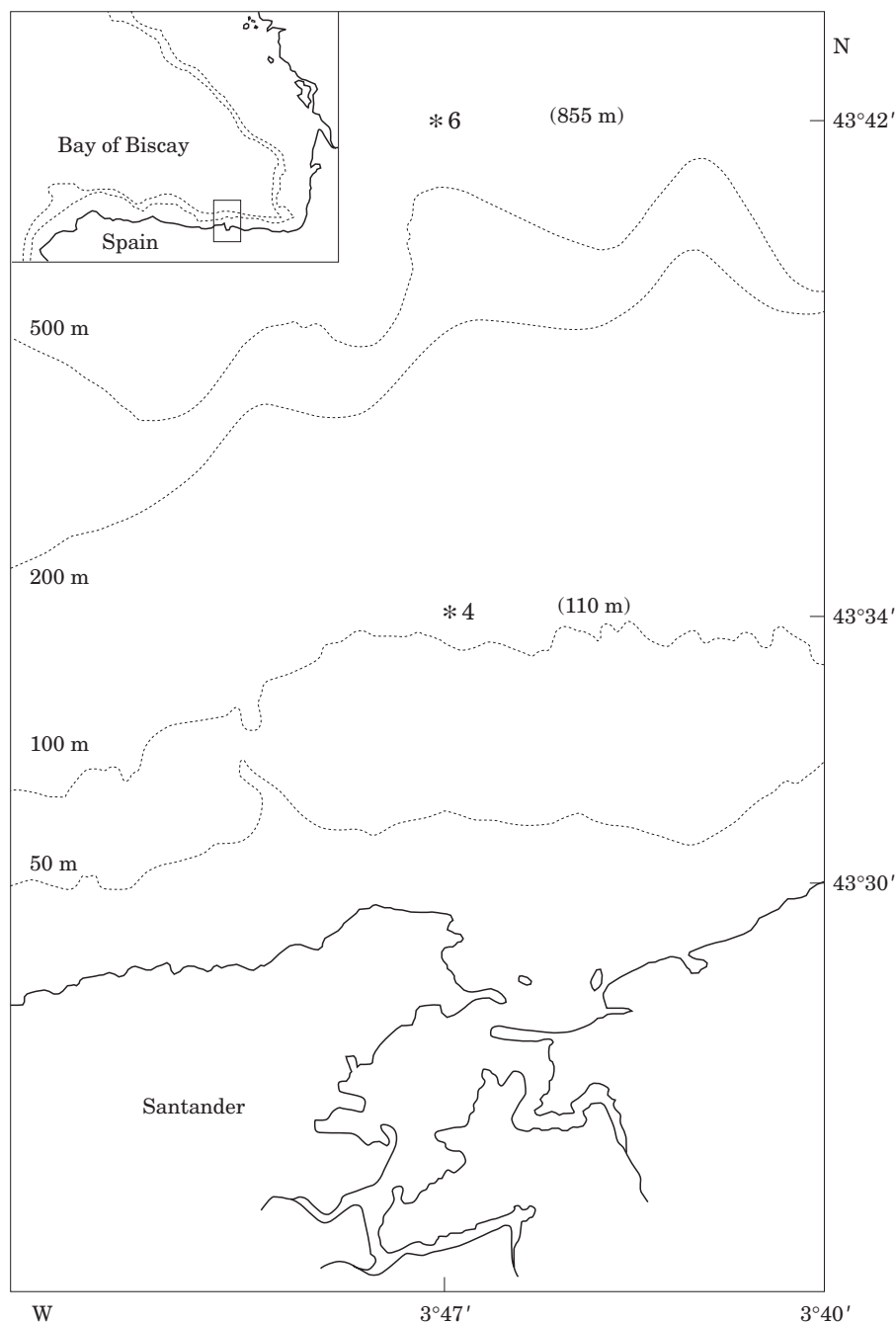


Figure 1. Location of the neritic (*4) and oceanic (*6) sampling stations.

Biscay, examines (i) the possible existence of periodic cycles, (ii) temporal trends in certain synthetic parameters (copepod species richness and Shannon-Weaver diversity index) which offer more integrated information than mere structural parameters, such as abundance or biomass (Margalef, 1978; Magurran, 1989), and (iii) the linkages between main trends in zooplankton indices and patterns

shown in environmental variables. Copepods are the main taxonomic group in the zooplankton assemblages of the Bay of Biscay, and so these were selected to characterize the zooplankton in terms of abundance and persistence.

Studies on seasonal and inter-annual variability in the physical properties of surface water, and cross-shelf trends in abundance and biomass of mesozooplankton

in the same area, have been published elsewhere (Lavín *et al.*, in press; Valdés *et al.*, in press).

Materials and methods

The samples were obtained in a cross-shelf section located at 3°47'W off Santander (Fig. 1). Hydrographic parameters and plankton communities were sampled monthly (68 occasions) in the period from June 1991 to June 1996 in the two outer stations characterizing neritic (no. 4) and oceanic conditions (no. 6) at depths of 110 and 850 m, respectively.

Hydrographic measurements of temperature and salinity were carried out using a CTD SBE 19 (Sea Bird Instruments) from the beginning of the time series to December 1994, and a CTD SBE 25 thereafter. Standard deviation of temperature over the water column from 0 to 100 m was used as a simple index of thermal stratification.

Zooplankton was sampled with a Juday–Bogorov net of 50 cm diameter and 250 µm mesh size equipped with a General Oceanic Flowmeter. A depth recorder was fixed to the net frame to observe the maximum haul depth. Double oblique tows were made at a speed of 1–1.5 knots up to a depth of 50 m. In order to avoid acidification of the sample and to minimize damage to the zooplankters, samples were preserved in 4% buffered formaldehyde solution for subsequent analysis in the laboratory.

For calculating total abundance, at least three subsamples were counted. To this end, the original sample was diluted to a volume of 500 ml from which three to five subsamples were taken by means of a 5 ml Stempel pipette. Each subsample was counted separately and the results were expressed in numbers per cubic metre. The mean CV between subsamples was $7.5 \pm 5.3\%$. For taxonomic identification, the rarefaction method described by Sanders (1968) and modified by Heck *et al.* (1975) was followed to ensure that species in the sample were counted properly, and to be able to compute the number of species corresponding to samples of a given number of organisms per unit volume. All copepods were identified to species level, with the exception of the genus *Clausocalanus*.

Shannon–Weaver diversity indices were calculated and cluster analysis was based on Bray–Curtis similarity indices. Statistical time-series analysis, including autocorrelation, spectral analysis, and moving averages, was carried out using the statistical packages SPSS and STATISTICA. Since time-series analysis requires a set of observations spaced equally over time, and since the original series did not meet this requirement – for a variety of logistical reasons common to work at sea – the series was completed by interpolating missing values. Subsequently, the raw data were fitted by a cubic spline

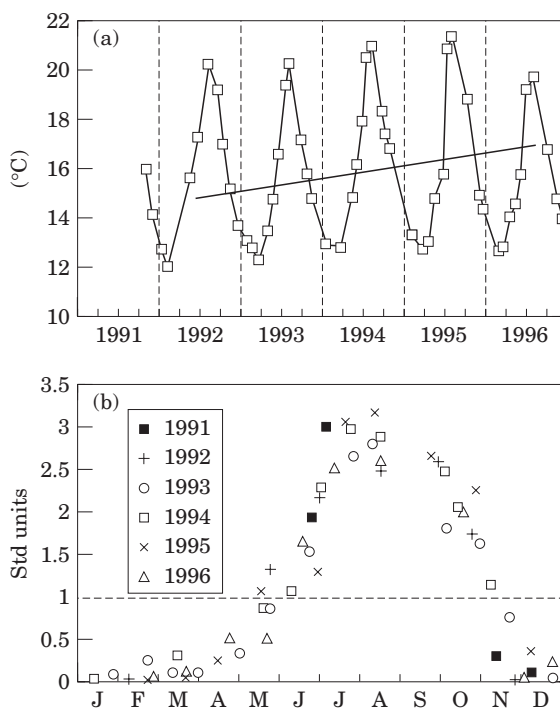


Figure 2. Temperature data for the neritic station (*4). (a) Monthly temperature (°C) at 10 m depth. The line represents the estimated trend based on the 12-month moving averages; (b) Index of thermal stratification by month and year based on the standard deviation of temperature over 0–100 m. One unit of std (dashed line) is equivalent to 2.5°C of thermal difference in the water column.

to obtain a new data series reflecting a sampling scheme at regular intervals.

Results

The annual sequence of temperature and salinity values shows the usual seasonal cycle of temperate seas. Thus, temperature follows the expected warming and cooling pattern which is determined by alternating processes of stratification and mixing of the water column (Fig. 2a, b). The stratification period occurs annually between May and October, when a thermocline builds up at about 50 m depth from the neritic station up to and beyond the shelf-break. In the period between November and April, the water column is mixed.

Zooplankton biomass shows a periodic annual cycle over the 5-year time series, with marked seasonal variations in both parameters (Fig. 3). The main differences between the neritic and the oceanic station lie in the maximum densities observed during the growth season and in the duration of the period of high abundance. Essentially, the annual cycle of zooplankton at the neritic station fits the classical model for neritic areas

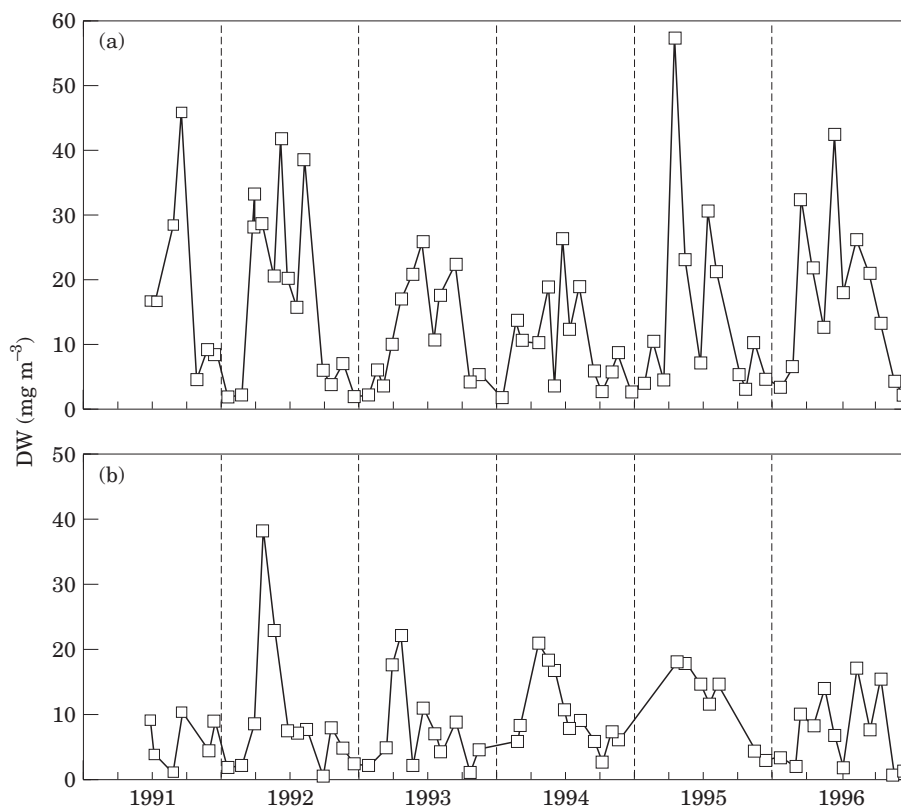


Figure 3. Monthly zooplankton biomass (in mg DW m⁻³). (a) Neritic station (*4); (b) Oceanic station (*6).

at this latitude, with maximum values in late spring extending into summer, a secondary peak of high biomass in autumn, and minimum values in winter. At the oceanic station, there is either no autumn peak or it is very weak, and summer values too are generally low. This pattern of a single annual peak in April is characteristic of oligotrophic areas.

Copepods were present in all samples and accounted for 68% of the total zooplankton abundance at the neritic station, and up to 83% at the oceanic station. They constitute the major taxonomic group within the zooplankton assemblage and are largely responsible for the seasonal pattern in total biomass described above. Taking the two stations together, 33 species of copepods were identified, 24 of them present only in low numbers. The other nine species accounting for more than 90% of total copepod abundance include: *Paracalanus parvus* (Claus 1863), *Clausocalanus* spp., *Acartia clausi* Giesbrecht 1889, *Calanus helgolandicus* (Claus 1863), *Oithona plumifera* Baird 1843, *Temora longicornis* (Muller 1785), *T. stylifera* (Dana 1848), *Centropages typicus* Kroyer 1849, and *C. chierchiae* Giesbrecht 1889.

Regular patterns in species richness and related indices are determined by biological cycles and are therefore

assumed to reflect periodic changes in the ecosystem more accurately than copepod abundance, which often reflects the numerical response of one or two dominant species to local events. Examples of seasonal changes, autocorrelation coefficients, and moving averages in species richness at the neritic station and in the Shannon–Weaver diversity index at the oceanic station are given in Figs 4 and 5, respectively. The alternative results are not reproduced here, because they exhibit essentially the same patterns. In all cases, these indices show a clear sinusoidal oscillation, indicating that there is a strong annual periodic component. In fact, both the spectral analyses and the autocorrelations of species richness and diversity gave maximum correlation values at 12 months for both stations. At the oceanic station, there was a second significant peak at 30 months. Thus, the seasonal model is determined by a time-lag of 12 months, a value which has been used to calculate the moving average to show the trend in the time series. At both stations, species richness and diversity show a decreasing trend throughout the time series. It is noteworthy that there is evidence of the second periodic component at the oceanic station, which reaches a maximum every 30 months (Fig. 5).

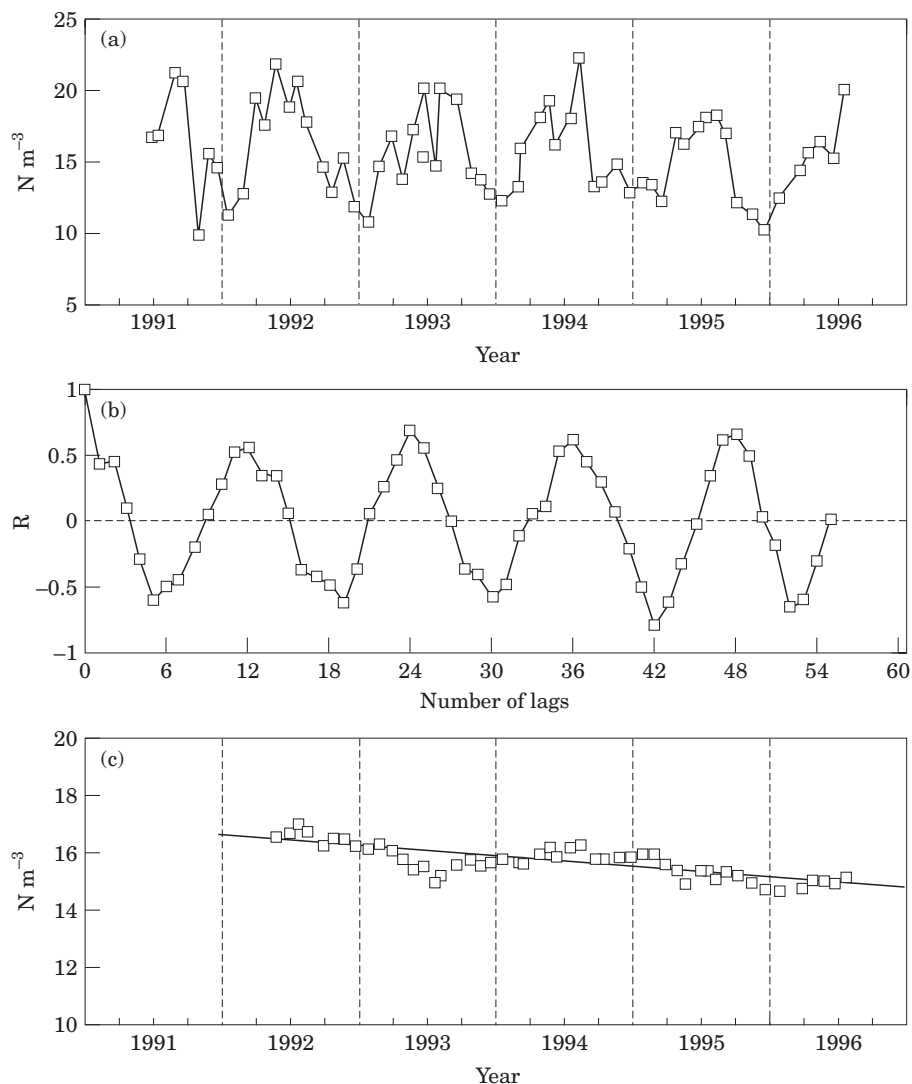


Figure 4. Copepod species richness at the neritic station (*4). (a) Time series of the number of species observed by month corrected for sampling volume ($N\ m^{-3}$); (b) Autocorrelation coefficients of the time series; (c) De-seasonalized series (12-month moving average) and trend.

Although the two indices share the same sinusoidal shape, they are not synchronized. The observed phase difference may be related to their ecological significance. For species richness, the maximum of the curve coincides with the growth season (2nd and 3rd quarters) and the minimum with the 4th and 1st quarters (Fig. 4). By contrast, the community gains diversity when the species counted in a sample tend to be equally represented, which occurs mainly during the 1st and at the beginning of the 2nd quarter (Fig. 5), and loses diversity when a few species become dominant. This occurs progressively throughout the growth season until the end of the 3rd and beginning of the 4th quarters, when diversity is at its lowest. This pattern

was consistent throughout the time series at both stations.

The seasonality of copepod dynamics was also observed in the ordination of the samples with the Bray–Curtis similarity index (example shown for the neritic station in Fig. 6). The samples could be divided into two groups: one branch corresponding to the spring–summer period, the other to the autumn–winter period.

Discussion

In addition to the response of planktonic communities to episodic events and local environmental

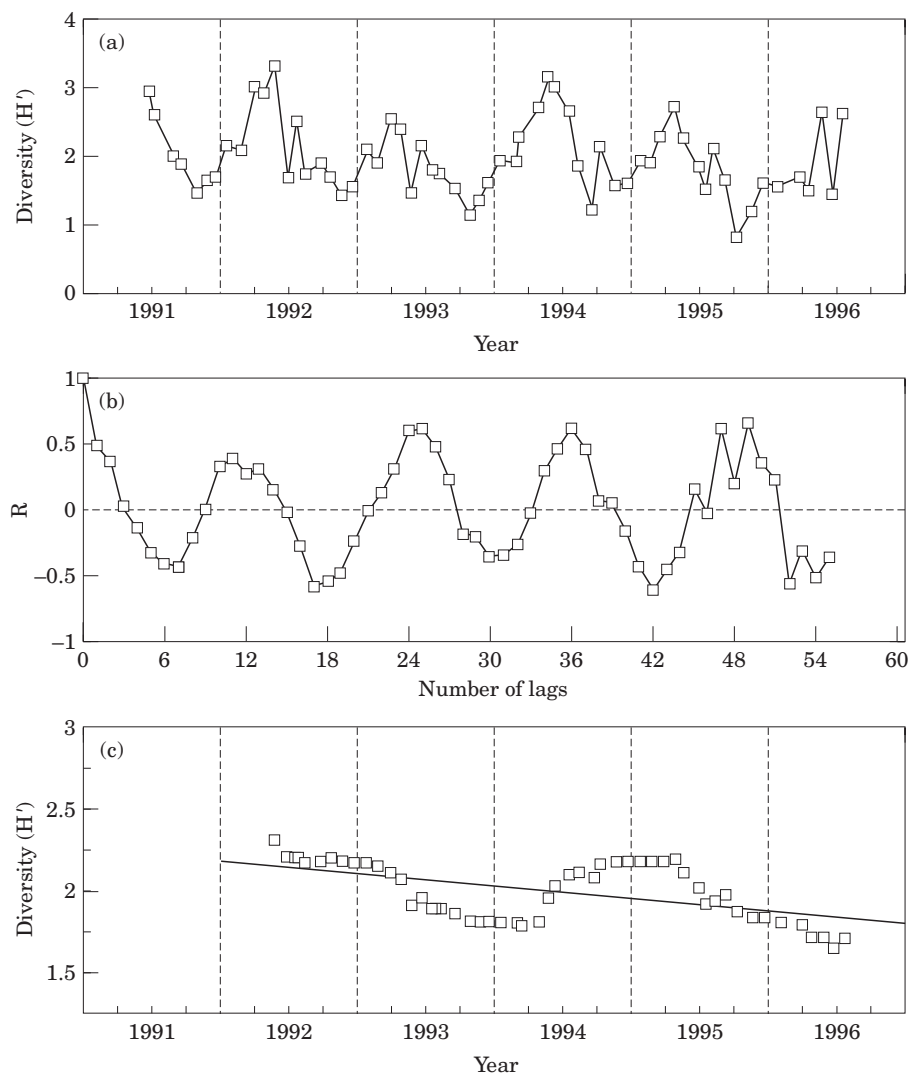


Figure 5. Copepod Shannon-Weaver diversity index at the oceanic station (*6). (a) Time series of the index by month; (b) Autocorrelation coefficients of the time series; (c) De-seasonalized series (12-month moving average) and trend.

perturbations, which represent two non-periodic sources of variability in the hydrographic and biological descriptors, a significant part of the temporal variability is caused by the effect of periodic cycles that underlie the biology of the species. These periodic cycles have different amplitudes. Those with periods of 12 months and their harmonics (2, 3, 6 months) are related to seasonal variability, and those with periods over 12 months to inter-annual variability. Apart from the non-periodic or random behaviour of the variable and periodic cycles, a last component of any time series is given by the trend.

During spring and summer, low salinities were observed in surface waters due to continental runoff and advection from oceanic waters, whereas in late autumn and winter the salinity pattern is governed

by an influx of salty water associated with the Warm Winter Poleward Current (Frouin *et al.*, 1990). According to Lavín *et al.* (in press), the inter-annual variability of temperature suggests a warming trend in the upper layers up to 75 m depth. In contrast, there was a decreasing trend in salinity throughout the water column which corresponds to the relaxation of the high salinity anomaly detected in the North Atlantic at the beginning of the 1990s. The neritic and the oceanic station show a coherent picture in respect of these two trends.

The environmental data obtained in the cross-shelf section show that the temperature and salinity deviations from the seasonal pattern are related to non-periodic events, such as upwelling (June 1995),

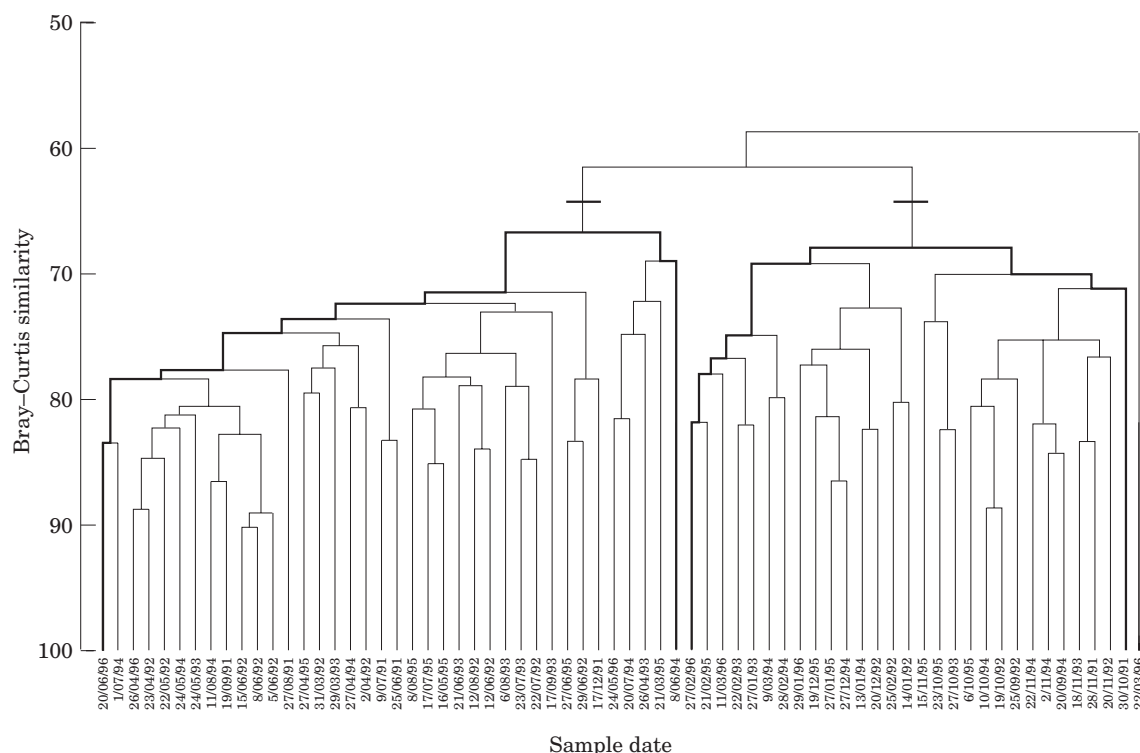


Figure 6. Dendrogram for hierarchical clustering by date of the Bray-Curtis similarity coefficients of the samples taken at the neritic station (*4).

continental runoff (autumn 1992, summer 1994, winter 1995) and other non-periodic singularities (Lavin *et al.*, in press). These singularities are closely related to changes in the abundance of zooplankton and to the presence of indicator species. For example, runoff events coincide with low biomass values and *T. stylifera* is associated with the intrusion of saline and warm oceanic water. Other biological descriptors (primary production, grazing rate, etc.) may also be affected. The non-periodic anomalies, which are governed by factors external to the general ocean dynamics (e.g. mesoscale features, turbulence due to wind stress, storms, etc.) may also explain some of the deviations from the overall seasonal pattern observed in species richness and diversity.

The clear distinction between a summer and a winter zooplankton assemblage appears to be common to temperate latitudes (Valdés, 1993) and is closely related to the environmental changes that occur regularly in the water column, such as surface heating and cooling, stratification and mixing, phytoplankton blooms, and other central ecological processes.

Evidence of inter-annual periodicity in the data set is given by a peak at 30 months in the spectral analysis of the copepod data for the oceanic station, the oscillation cycle of which is also seen in the de-seasonalized series

(Fig. 5). Causes of large fluctuations in planktonic communities have been related to the North-Atlantic Oscillation (NAO; 5–6 year signal) by Dickson *et al.* (1988), Planque and Fromentin (1996) and Fromentin and Planque (1996), and to the Quasi Biennial Oscillation (QBO; 28–32 month signal). Evidence for the latter has been reported for zooplankton biomass in the Gulf of Alaska (Hameed and Conversi, 1995; Conversi and Hameed, in press), for sea level in the Mediterranean sea (Vilibic and Leder, 1996), for atmospheric pressure and precipitation in the Bay of Biscay (Fromentin and Ibanez, 1994), and recently for hydro-climatic parameters and zooplankton abundance in the North Sea (Le Fevre-Lehoerff *et al.*, 1995). Although the time series is too short to provide real evidence of any periodicity longer than 12 months, the data obtained so far would clearly fit a QBO causality.

The force causing the QBO seems to be related to the quasi-periodic reversal of tropical stratospheric winds (Reed *et al.*, 1961). However, the transmission mechanism from its climatic origin to the oceanographic processes and planktonic communities remains unclear. An intriguing feature of our data is why the 30-months signal in the oceanic station is stronger than the 3- and 2-month harmonics of the seasonal cycle observed at the neritic station. This suggests that in neritic waters local

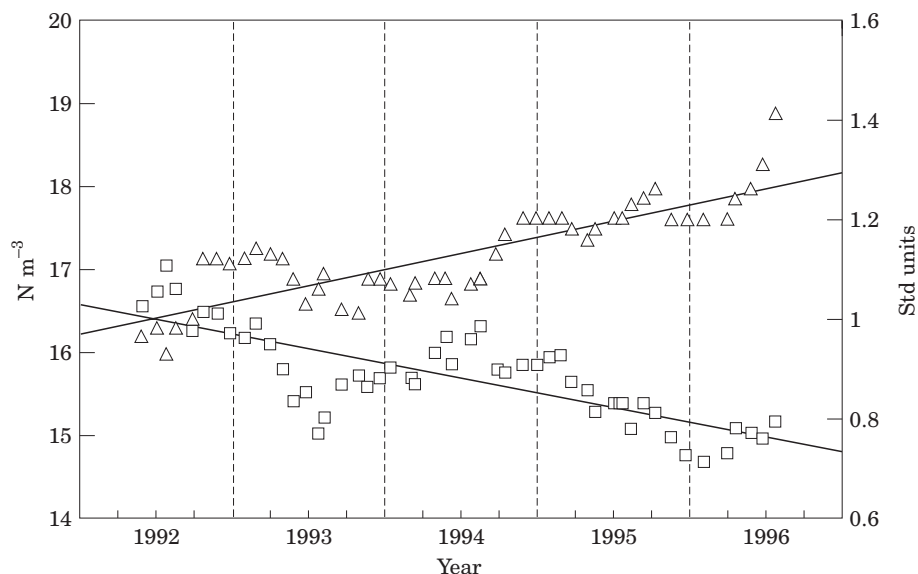


Figure 7. De-seasonalized series (12-month moving average) and trends of species richness (\square ; $N\ m^{-3}$), and thermal stratification index (\triangle ; std units) at the neritic station (*4).

atmospheric characteristics are immediately translated in water column conditions, which may then determine seasonal oceanographic and biological oscillations. In oceanic waters, local atmospheric characteristics may be less important, and the main circulation pattern, or other forces of larger amplitude and low frequency oscillation, may govern periodic patterns in the presence/absence of species.

An interesting feature is the long-term upward trend in the thermal stratification index, and the downward trend in species richness (Fig. 7) and diversity for the neritic station, which was confirmed statistically by the significant negative correlation between the de-seasonalized series of the two descriptors (Table 1). Approximately 40% of the variance in species richness at the neritic station was explained by the correlation (Fig. 8). At the oceanic station the correlations were not significant. However, cross-correlations on the detrended series were significant for both stations when a 6 months' time-lag was introduced (Table 1). However, the reasons for the time-lag effects remain obscure.

A negative relationship between stratification and zooplankton biomass has been reported for the Californian coast by Roemmich and McGowan (1995). They suggested that a longer stratification period, as well as stronger stratification, might hamper the interchange of nutrients from deeper to surface waters and consequently limit phytoplankton growth and thus food for zooplankton. According to our data, not just biomass but also the species richness and diversity might be affected by the different processes involved.

Table 1. Linear correlations between species richness and diversity at the two stations and the de-seasonalized thermal stratification index. Results are given for a time-lag of 0 and 6 months (number of observations in parentheses).

	Species	Diversity
Neritic station (no. 4)		
Lag=0 (n=50)	$y = 19.96 - 3.73x$ $r = 0.63$ $p < 0.001$	$y = 2.65 - 0.41x$ $r = 0.38$ $p < 0.005$
Lag=6 (n=44)	$y = 21.29 - 5.10x$ $r = 0.87$ $p < 0.001$	$y = 2.81 - 0.58x$ $r = 0.51$ $p < 0.001$
Oceanic station (no. 6)		
Lag=0 (n=50)	$y = 13.23 - 0.12x$ $r = 0.02$ n.s.	$y = 2.05 - 0.04x$ $r = 0.05$ n.s.
Lag=6 (n=44)	$y = 16.08 - 2.59x$ $r = 0.42$ $p < 0.005$	$y = 2.60 - 0.51x$ $r = 0.45$ $p < 0.005$

Time-series analysis is a valuable approach by which to split the high temporal variability observed in zooplankton communities into several components with different time amplitudes, because each component can then be compared with potential environmental forcing events on appropriate time scales. With the time series available, some patterns of variation have been identified but the potential to establish causes and effects of periodic inter-annual variability with an amplitude longer than 2 years remains severely limited.

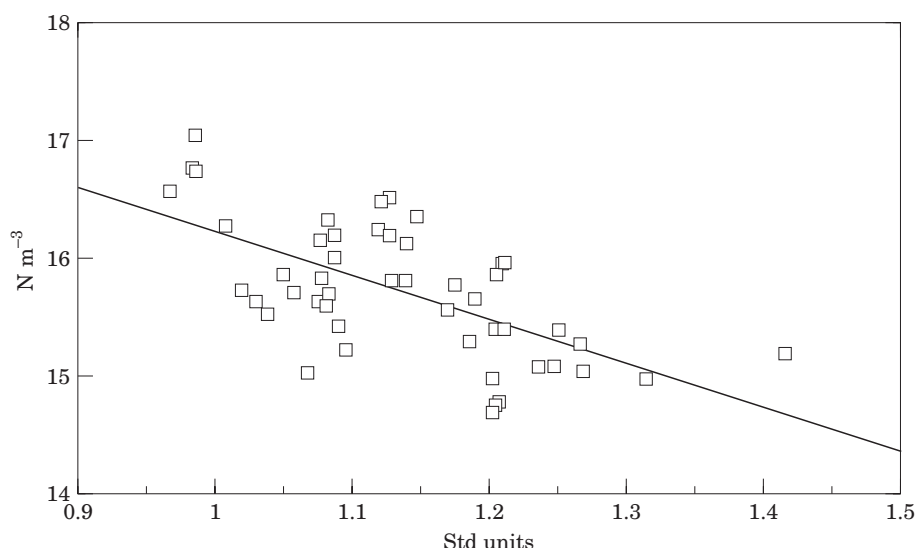


Figure 8. Correlation between thermal stratification index and species richness at the neritic station (*4), based on 12-month moving averages. Line represents fitted equation ($y = 19.96 - 3.73x$; $n = 50$; $r = 0.63$).

Among the different forcing factors, we suggest that seasonal variability is closely related to environmental variability in water column characteristics and to phytoplankton dynamics, and that non-periodic oscillations could be governed by factors external to the general ocean dynamic, such as mesoscale anomalies, wind-induced turbulence, storms, etc. Inter-annual variability appears to be related to forces of large amplitude and low frequency, such as atmospheric oscillations and displacements in the general circulation. Evidence for this stems from boreal waters in the Northeast Atlantic, where latitudinal displacements of the Gulf Stream have been related to changes in plankton abundance (Taylor *et al.*, 1992; Taylor, 1995). Even part of the inter-annual variation in the average summer biomass of zooplankton in a freshwater lake has been explained by variations in the Gulf Stream (George and Taylor, 1995). Although other large-scale forcing factors (e.g. NAO) have also been successfully applied to explain part of the variability in ecological parameters (Planque and Fromentin, 1996; Fromentin and Planque, 1996), more time-series observations of relevant variables at representative sites and with sufficient time resolution are required before they can be generalized at the ocean basin level and before the time-lags involved in their translation in possible effects at different locations can be evaluated.

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