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A decade of sampling in the Bay of Biscay: What are the zooplankton time series telling us?

Luis Valdés [a,*], A. López-Urrutia [a], J. Cabal [a], M. Alvarez-Ossorio [b], A. Bode [b], A. Miranda [c], M. Cabanas [c], I. Huskin [d], R. Anadón [e], F. Alvarez-Marqués [e], M. Llope [e], N. Rodríguez [e]

[a] *Instituto Español de Oceanografía, Centro Oceanográfico de Gijón, Avda. Príncipe de Asturias 70bis, 33212 Gijón, Spain*
[b] *Instituto Español de Oceanografía, Centro Oceanográfico de A Coruña, Apdo. 130, 15080 A Coruña, Spain*
[c] *Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Apdo. 1552, 36280 Vigo, Spain*
[d] *Instituto Español de Oceanografía, Centro Oceanográfico de Santander, Promontorio de San Martín s/n, 39004 Santander, Spain*
[e] *Universidad de Oviedo, Dep. Biol. Organismos y Sistemas, 33071 Oviedo, Spain*

Abstract

The project "Studies on time series of oceanographic data" was established as a pilot project by the Instituto Español de Oceanografía (I.E.O.) in 1991. After more than a decade, the project has grown to encompass a network of 19 sampling stations in five different transects along the North and Northwest coast of Spain: Vigo, Coruña, Cudillero, Gijón and Santander beginning in 1987, 1988, 1993, 2001, 1991, respectively. At each location a coastal-ocean gradient is sampled monthly for hydrography, nutrients and planktonic communities. We have used these data to set with statistical significance the range of variability of several environmental variables and biological communities and determined the rates and trends of warming due to climate change as well as to describe some direct and indirect effects of the increase in water temperature on the pelagic ecology. The project had substantially contributed to get a deeper knowledge on planktonic communities and species and to produce baselines, climatologies and reference levels for the North coast of Spain, which allow us to do accurate evaluations on the effects of environmental perturbations on the ecosystem and forecast the expected recovery time. These changes both in the physical structure of the water column and in the trophic level that drives ecosystem production and functioning are likely to also modify the structure, production and organization of higher trophic levels like zooplankton. Our analysis shows that only through sustained and repeated time series sampling it is feasible to detect these changes. Indeed, the annual cycle of zooplankton biomass seems to be restricted in time, with the annual decrease in zooplankton biomass matching the onset of stratification. The observed patterns in the seasonal occurrence of incoming species like *Temora stylifera* are related to those observed in the water column stratification, which is reinforced by the warming trend.
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* Corresponding author.
E-mail address: luis.valdes@gi.ieo.es (L. Valdés).

1. Introduction

Variability in marine ecosystems occurs on a wide range of space and time scales and is inherent to the ecosystem's functioning. The ecosystem's variability over time, particularly in plankton communities, is manifested through its seasonal, inter-annual, decadal and multidecadal cycles. Spatial variability is associated with the vertical and horizontal movements of water. Biological processes also introduce variability, such as competition for limited resources, predation, vertical migration and heterogeneous distributions of species and populations. We must also consider human impacts on the ecosystem (e.g. fishing and pollution) and the largely unknown impacts of global warming on the ecosystem and its species.

These cycles and sources of variability (i) produce fluctuations in species abundance, which are not always easy to explain and make it very difficult to determine equilibrium states; and (ii) limits our ability to discriminate the natural and anthropogenically-caused ecosystem perturbations. These cycles limit our capacity to accurately predict the dynamic of the ecosystem from a set of initial conditions.

Such limitation is particularly severe when studying plankton communities (Paffenhöfer et al., 1989; Gamble and Hunt, 1992; Perry and McKinnell, 2005) calling for observational programmes of adequate temporal and spatial resolution to characterise variability in zooplankton populations.

Recognising the necessity to include mesozooplankton in time series of oceanographic data, and within the frameworks of international initiatives such as IGBP, IOC, GLOBEC, GOOS, OSPAR, etc. (related with global warming, ocean observation and ecosystem protection), the Instituto Español de Oceanografía (IEO) has established a core strategic programme to obtain and analyse long-time series data. A sampling programme of systematic observations of ocean properties and biological communities was established in 1987 (Valdés et al., 2002) along the Spanish coast of the Bay of Biscay (Cantabrian Sea) and Galicia. It has now been extended to include transects off Santander, Gijón, Cudillero, Coruña and Vigo. The temporal resolution of this ongoing project allows the study and resolution of seasonal to inter-annual plankton dynamics, and allows for comparisons to be made among areas. Such studies on physical properties of surface water, and cross-shelf trends in phytoplankton and mesozooplankton abundance and biomass in the same area have been published elsewhere (Valdés et al., 1991; Varela, 1996; Poulet et al., 1996; Valdés and Lavín, 2002; Blanco-Bercial et al., 2006). Biological variables measured include structural parameters such as abundance, biomass, species composition, body sizes and physiological rates such as production, respiration and consumption.

The main objective of this study is to understand how zooplankton respond to environmental conditions, such as water column stratification and upwelling events, and to distinguish broad-scale perturbations from local phenomena. The biogeography of the region is also analysed as well as abundance changes in particular species.

2. Materials and methods

The project Radiales[1] (Valdés et al., 2002) was established by the Instituto Español de Oceanografía (IEO) in 1991. Since 2001, the project comprises a network of 19 sampling stations in five different transects along the N and NW coast of Spain (Fig. 1). Here, we use data from the four transects that have been sampled for a longer period of time, namely Vigo, Coruña, Cudillero and Santander. Each transect consists of at least three sampling stations, generally covering coastal, shelf and oceanic conditions.

Each station is sampled monthly, following standard protocols for hydrography, nutrients and plankton. A detailed description of hydrographic sampling methods is given by González-Pola et al. (2005). The upwelling index at each location was obtained using the Pacific Fisheries Environmental Laboratory Global Upwelling Index (http://las.pfeg.noaa.gov/las6_5/servlets/constrain?var=81).

Zooplankton was sampled at 13 stations using 40-cm diameter WP-2 plankton nets with 200 μm mesh size (Vigo, Coruña, Cudillero) or in Santander the Juday-Bogorov net of 50 cm diameter and 250 μm. Nets were equipped with General Oceanic Flowmeters for the calculation of water filtered and depth recorders. Tows were vertical (WP-2) or double oblique (Juday-Bogorov) from 5 m from the bottom or from 100 m depth
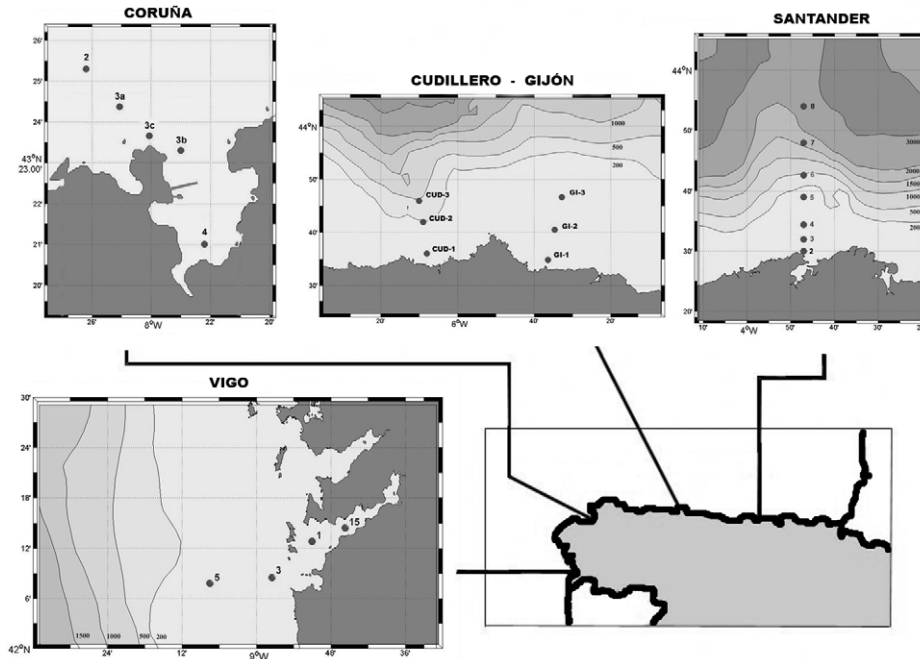
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[1] www.seriestemporales-ieo.net.

Fig. 1. Location of sampling stations in north and northwest Spain.

at deeper stations, except in Santander where only the upper 50 m is sampled. Samples were preserved in 2–4% sodium borate-buffered formaldehyde. Sub-samples were taken to estimate total zooplankton abundances (ind m^{-3}), and biomass (mg DW m^{-3}). No correction for shrinkage was used, but measurements were performed after 8 weeks of collection, when the sample weight stabilizes, to ensure that biomass underestimation was the same for all samples. At least 1000 organisms per sample were counted and classified. Copepods and Cladocera were identified at genera or species level.

The Santander transect, the most consistent and prolonged zooplankton time series, with sufficient taxonomical resolution, was used to determine groups of species with similar patterns in their inter-annual, seasonal and coast-ocean gradients. A k-means cluster on the monthly log $(x + 1)$ was computed with data transformed to an N $(0, 1)$ function. For each group we then calculated the average abundance (centred and log transformed) to graphically inspect the characteristics of the group.

Both hydrographic and zooplankton results are reported annually to the ICES and summarised together with other time series from Europe, Canada and USA in the annual ICES Climate (e.g., Hughes and Lavín, 2004) and Zooplankton Status Report (e.g., Valdés et al., 2005).

3. Environmental setting

As expected, the annual sequence of temperature and salinity values in this region is characterised by a temperate seasonal cycle. This is particularly apparent in the Cantabrian Sea, while off the Galician coast, upwelling events mix the water column during the summer (Fig. 2). This leads to a smoother seasonal temperature cycle in the Cantabrian Sea, but with a wider range of variation that off the Galician coast (Fig. 2).

Upwelling events and the Iberian Poleward Current (IPC, also known as *Navidad*) are the most common and important hydrographic events in Galicia and the Cantabrian Sea, both showing high seasonal and inter-annual variability (Koutsikopoulos and Le Cann, 1996). Coastal upwelling on the Spanish continental margin, extends from Galicia to the Cantabrian Sea (Molina, 1972; Estrada, 1982; Botas et al., 1990; Ríos et al., 1992; Lavín et al., 1998), and is particularly intense to the west of Cape Peñas and Ortegal up to Finisterre. This generates spatial variability between the western and eastern zones of the Cantabrian Sea, and between the
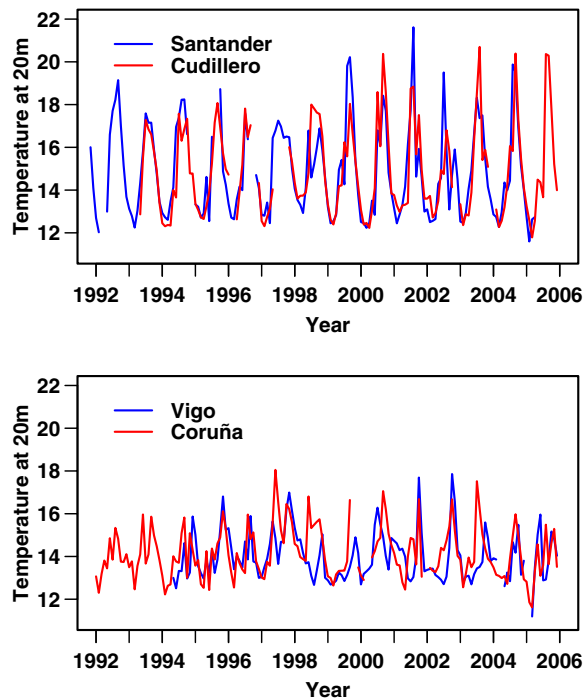
Fig. 2. Temperature at 20 m for the shelf-break stations in the Cantabrian Sea (Upper panel) and in the Galician coast (Lower Panel).

coastal mixed waters and the neighbouring stratified oceanic areas. Upwelling events are highly variable in intensity and frequency and show significant inter-annual variability (Fig. 3). Cabanas et al. (2003) showed that a notable shift in the winds has occurred during the last two decades, resulting in a reduction in the spring–summer upwelling off the northwest of the Iberian Peninsula (Fig. 3). Lavín et al. (1998) noted that the water column off Santander is now more stratified and remains so for longer than at the start of the monitoring programme. The same pattern is now observed for the other transects, although this is less pronounced in Coruña and Vigo (Fig. 3).

The warm and salty *Navidad* current flows in winter from the central Atlantic and runs from west to east along the slope of Spain's northern coast, then flowing northward along the French continental slope (Frouin et al., 1990; Pingree, 1994). Mean velocities of 30 cm s^{-1} were recorded at the shelf break in the central Cantabrian Sea during late December 1995 and January 1996 (Díaz del Río et al., 1996). The *Navidad*'s biological influence has been extensively studied (Botas et al., 1988; Fernandez et al., 1993; Sanchez and Gil, 2000; Huskin et al., 2003; González-Quirós et al., 2004; Isla et al., 2004). Although the extent of the intrusion is not a well-studied phenomenon, it seems to be more intense in the western zone of the Cantabrian Sea. These saline intrusions have high space-time variability (Pingree and Le Cann, 1990; Varela et al., 1995; Garcia-Soto et al., 2002; Llope et al., 2006), and they are of great importance in the transport of drifting particles.

Accurate records of sea surface temperature in the Bay of Biscay are available for the whole 20th century and the data show an oscillating pattern. It increased about half a degree during the period 1920–1960, reversed into a cooling phase subsequently, and entered a warming period in 1981 (Southward et al., 1995) that continues to the present. Koutsikopoulos et al. (1998) determined a mean increase of 1.4 °C in the surface waters of the southeast Bay of Biscay for the period 1972–1993 (0.6 °C per decade), which was slightly higher in winter than in summer. Over the last century, Planque et al. (2003) showed an increase in the mean annual SST of 1.03 °C, which occurred mainly in the last two decades.

Starting in 1991, the Radiales project has provided good hydrographical data for the southern Bay of Biscay. Using these series, Cabanas et al. (2003) calculated a warming trend of +0.02–0.05 °C yr^{-1} in surface layers over the shelf off Santander. This warming is currently detected in the intermediate waters from the mixed layer down to 1000 m depth in the oceanic waters off Santander (González-Pola et al., 2005). The trend has an
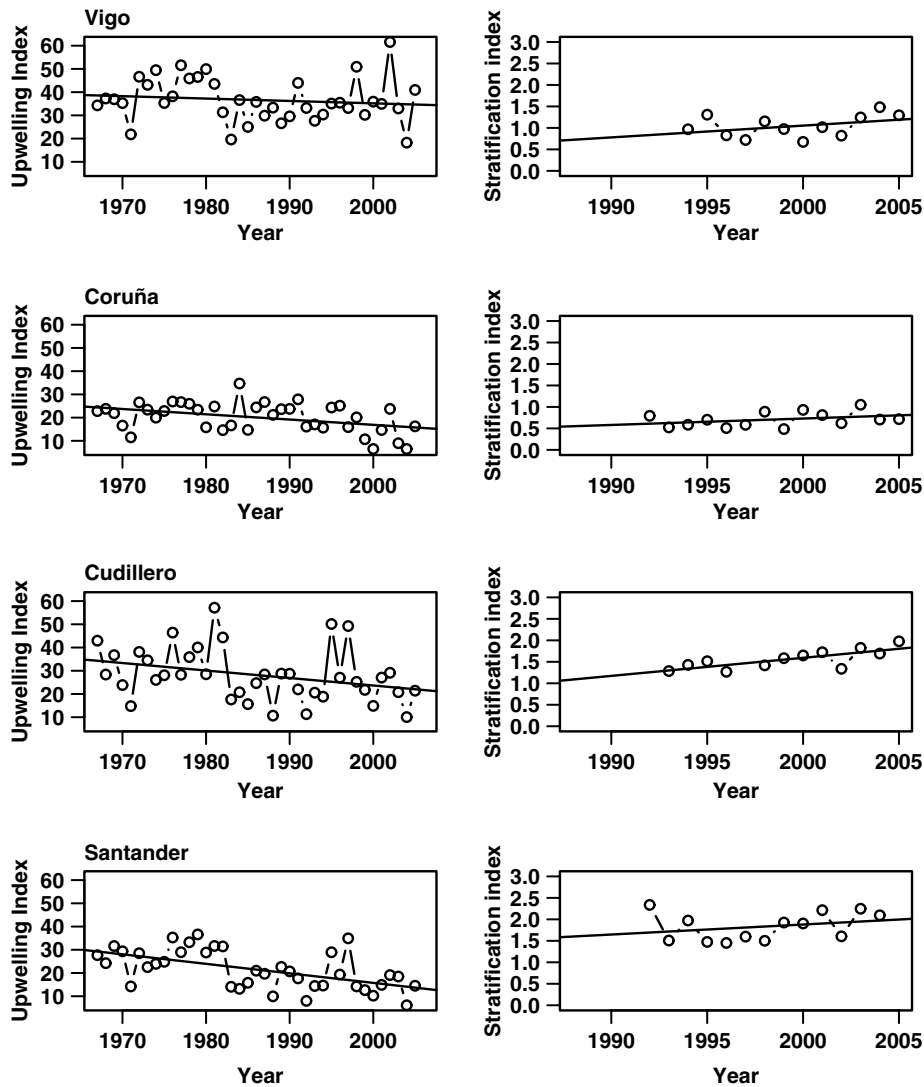
Fig. 3. Time series of mean April–September yearly upwelling index calculated for each of the transects from the Pacific Fisheries Environmental Laboratory Global Upwelling Index (left panel) and stratification index calculated as the standard deviation of water column temperature (right panel).

average annual rate of +0.032 °C yr^{-1} (González-Pola et al., 2005), which is two to six times greater than was reported for the North Atlantic during the last half century (e.g. Levitus et al., 2000; Arbic and Owens, 2001). Fig. 2 shows the differences in the patterns of surface temperature over shelf stations off Galicia (Coruña and Vigo sections) and in the Cantabrian Sea (Cudillero and Santander sections). The warming trend in surface waters, however, varies geographically, being positive in the Cantabrian Sea, but is less evident off Galicia. Maximum temperatures off Galicia, as a consequence of seasonal upwelling, do not reach the values observed in the Cantabrian Sea either. Particularly evident over last 5 years is the increased amplitude of surface temperature in the Cantabrian Sea with warmer summers and colder winters (Fig. 2).

4. Results

Understanding of plankton ecology requires a good knowledge on species composition, abundance and distribution. Currently we have over 10 years of mesozooplankton taxonomic identifications and counts at group

and/or species level, for the Vigo, Coruña, Cudillero and Santander transects, aimed mainly at biodiversity and distribution studies.

Zooplankton assemblages in the southern European continental margin comprise more than 20 taxonomic groups, copepods being the most important. A copepod species check list is maintained and rarely requires the addition of new species (Table 1). In Galicia and Bay of Biscay copepod species account for 60–95% of the abundance of marine zooplankton and makes the bulk of the mesozoolankton biomass (Valdés, 1993; Cabal, 1993). The region is very diverse, including up to 83 copepod taxa from Vigo, Coruña, Cudillero and Santander (Table 1), increasing to ∼200 species when the whole Ibero-Atlantic margin is considered.

Table 1
Mesozooplankton taxa recorded in the Galicia and north Spain time series project

Foraminifera
Radiolaria
Acantharia
Tintinnina
Hydromedusae
Ctenophora
Siphonophora
Polychaeta
Pteropoda
Cladocera
Penilia avirostris Dana, 1849
Evadne nordmanni Loven, 1835
Evadne spinifera Muller 1868
Podon intermedius Lilljeborg, 1853
Podon poliphemoides (Leuckart, 1859)
Ostracoda
Copepoda
Calanoides carinatus (Kröyer, 1848)
Calanus helgolandicus (Claus, 1863)
Mesocalanus tenuicornis (Dana, 1849) (=*Calanus tenuicornis*)
Nannocalanus minor (Claus, 1863)
Neocalanus gracilis (Dana, 1849) (=*Calanus gracilis*)
Eucalanus elongatus (Dana, 1849)
Rhincalanus cornutus (Dana, 1849)
Rhincalanus nasutus (Giesbrecht, 1888)
Subeucalanus crassus (Giesbrecht, 1888) (=*Eucalanus crassus*)
Subeucalanus monachus (Giesbrecht, 1888) (=*Eucalanus monachus*)
Paracalanus parvus (Claus, 1863)
Calocalanus contractus (Farran, 1926)
Calocalanus pavo (Dana, 1849)
Calocalanus styliremis (Giesbrecht, 1888)
Ischnocalanus tenuis (Farran, 1926)
Mecynocera clausi (I.C. Thompson, 1888)
Clausocalanus arcuicornis (Dana, 1849)
Clausocalanus farrani (Sewell, 1929)
Clausocalanus furcatus (Brady, 1883)
Clausocalanus jobei (Frost & Fleminger, 1968)
Clausocalanus lividus (Frost & Fleminger, 1968)
Clausocalanus paululus (Farran, 1926)
Clausocalanus pergens (Farran, 1926)
Ctenocalanus vanus (Giesbrecht, 1888)
Microcalanus pusillus (Sars, 1903)
Pseudocalanus elongatus (Boeck, 1865)
Aetideus armatus (Boeck, 1872)
Undinopsis sp.
Euchirella rostrata (Claus,1866)
Gaetanus minor (Farran, 1905)
Euchaeta acuta (Giesbrecht, 1892)

Table 1 (*continued*)

Paraeuchaeta hebes (Giesbrecht, 1888) (=*Euchaeta hebes*)
Paraeuchaeta norvegica (Boeck, 1872)
Paraeuchaeta tonsa (Giesbrecht, 1895) (=*Euchaeta tonsa*)
Amallothrix sp.
Scaphocalanus echinatus (Farran, 1905)
Scolecithricella dentata (Giesbrecht, 1892)
Scolecithricella ovata (Farran, 1905)
Scolecithrix bradyi Giesbrecht, 1888 (=*Scolecithricella bradyi*)
Scolecithrix danae (Lubbock, 1856)
Diaixis durani (Corral, 1972)
Diaixis hibernica (A. Scott, 1896)
Diaixis pygmaea (T. Scott, 1899)
Tharybis macrophthalma (Sars, 1902)
Temora longicornis (Müller, 1792)
Temora stylifera (Dana, 1849)
Temoropia mayumbaensis (T. Scott, 1894)
Metridia lucens (Boeck, 1864)
Pleuromamma gracilis (Claus, 1863)
Centropages chierchiae (Giesbrecht, 1889)
Centropages hamatus (Lilljeborg, 1853)
Centropages typicus (Kröyer, 1849)
Centropages kröyeri (Giesbrescht, 1892)
Isias clavipes (Boeck, 1864)
Lucicutia flavicornis (Claus, 1863)
Heterorhabdus papilliger (Claus, 1863)
Candacia armata (Boeck, 1872)
Anomalocera patersoni (Templeton, 1837)
Parapontella brevicornis (Lubbock,1857)
Acartia clausi (Giesbrecht, 1889)
Acartia danae (Giesbrecht, 1889)
Acartia discaudata (Giesbrecht, 1881)
Acartia longiremis (Lilljeborg, 1853)
Acartia margalefi (Alcaraz, 1976)
Oithona nana (Giesbrecht, 1892) (=*O. minuta*)
Oithona plumifera (Baird,1843)
Oithona similis (Claus, 1866) (=*O. helgolandica*)
Euterpina acutifrons (Dana, 1852)
Microsetella rosea (Dana, 1852)
Clytemnestra rostrata (Brady, 1883)
Clytemnestra scutellata (Dana, 1852)
Oncaea media (Giesbrecht, 1891)
Oncaea mediterranea (Claus, 1863)
Oncaea subtilis (Giesbrecht, 1892)
Agetus flaccus (Giesbrecht, 1891) (=*Corycaeus flaccus*)
Ditrichocorycaeus anglicus (Lubbock, 1855) (=*Corycaeus anglicus*)
Ditrichocorycaeus brehmi (Steuer, 1910) (=*Corycaeus brehmi*)
Onychocorycaeus latus (Dana, 1849) (=*Corycaeus latus*)
Onychocorycaeus ovalis (Claus, 1863) (*Corycaeus ovalis*)
Urocorycaeus furcifer (Claus, 1863) (=*Corycaeus furcifer*)
Shapphirina angusta (Dana, 1849)
Monstrilla spp.
Tisbe sp.
Anphipoda
Mysidacea
Euphausiacea
Chaetognata
Appendicularia
Doliolida
Salpida
Gastropoda
Bibalvia

Table 1 (*continued*)

Cirripedia
Isopoda
Stomatopoda
Natantia
Anomura
Brachiura
Bryozoa
Echinodermata
Teleostei

Cladocera and Copepod species are ordered accordingly to Families.

This number of copepod species is within the average of the region from the Celtic Sea to the Gulf of Cádiz. When the number of species and assemblages are considered, the groups from Galicia, Asturias and the Bay of Biscay fall within the same cluster (Fig. 4), named the Subtropical-Boreal transition zone. Within the same cluster at a higher hierarchical level the region is part of the Lusitanic Subtropical Province. The analyses of similarity comparing 24 collections from Cape Blanc (20°N) up to the Celtic Sea (50°N), i.e. covering 30° of latitude (a third of the northern hemisphere), shows the entire region is divided into the Northern Subtropical and the Lusitanic provinces. The division between these is located in the Atlantic waters of southern Iberia.

The frequency of species occurrence in the samples and their abundance at two locations (Coruña and Santander, where more years of taxonomic details are available) were summarized by abundance:number of samples diagrams by Williams (1964, Fig. 5). In these plots four main groups of species can be seen, dominant species that appear in most samples with high abundances (upper right corner of the figures), species that appear during restricted periods both seasonally or interannually (located in the middle of the chart), rare species, usually in low abundance and found in a small number of the samples collected (left part of chart) and very rare species that appear in approximately less than 10 samples with an abundance of less than 10 individuals per cubic meter. The copepod fauna is dominated by small-sized, widely distributed species like *Oncaea media*, *Paracalanus parvus*, *Clausocalanus* spp., *Oithona* spp., *Pseudocalanus elongatus* and *Temora* spp. (Fig. 5). The sum of these species populations' abundances plays a fundamental role in establishing the changes in mesozooplankton abundances in these pelagic ecosystems. In both areas the dominant species are similar except for *O. media* and *T. stylifera*.

The spatial distribution, seasonal and interannual variability of copepods species can be combined to discriminate groups of species co-occurring in similar environmental conditions. There are five k-mean clusters observed for the Santander transect (period 1992–2000) (Fig. 6). A first cluster of species predominate in the coastal region during late winter and spring. A second cluster consists of coastal and shelf species with density maxima occurring later, during spring and summer. A third cluster is composed by shelf and oceanic species
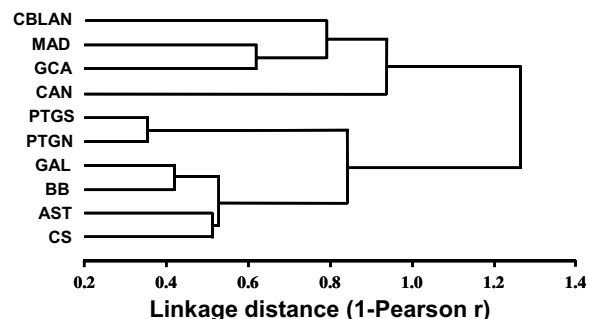

Fig. 4. Ordination of copepod collections at different sampling sites. Cabo Blanco (CBLAN), Madeiria Islands (MAD), Gulf of Cadiz (GCA), Canary Islands (CAN), South of Portugal (PTGS), North of Portugal (PTGN), Galicia (GAL), Asturias (AST), Bay of Biscay (BB) and the Celtic Sea (CS). Data source (Cabal, J. et al., in press).
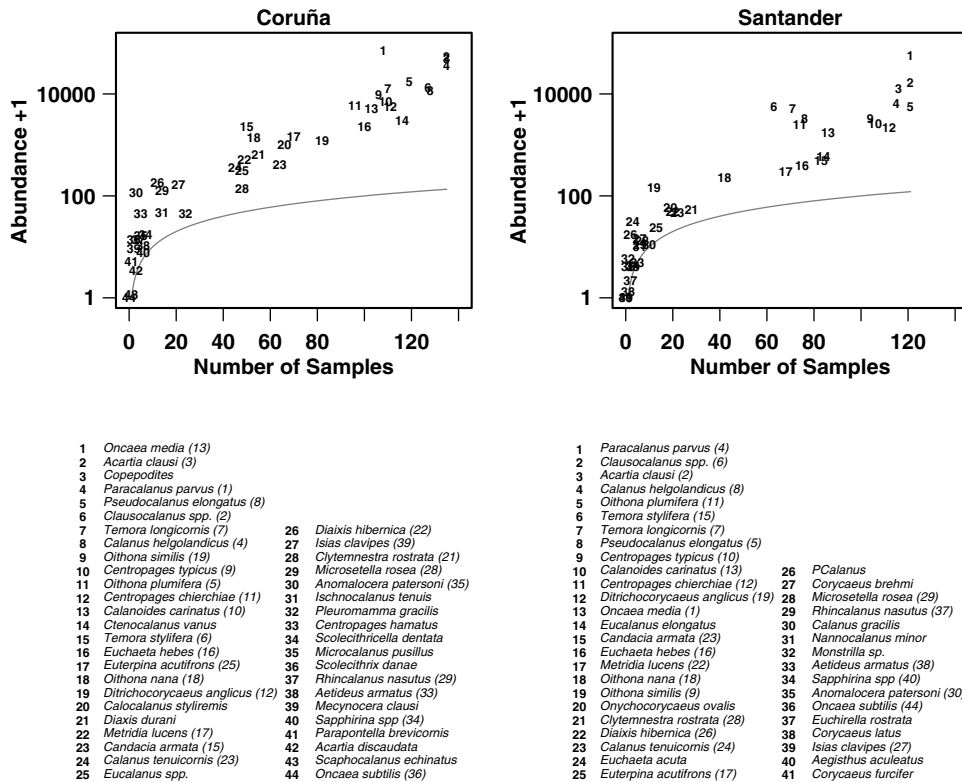
Fig. 5. Frequency of occurrence of species in the samples analysed and their respective abundance at two locations of the N-NW Iberian coast summarized by abundance:number of samples diagrams. Solid line represents the reference 1:1 line, i.e., no data can fall bellow that line.

appearing in spring, whereas the fourth cluster consists of species also appearing in spring but more restricted to oceanic conditions. Finally there is a cluster of summer–autumn species composed of *T. stylifera*, *Onychocorycaeus ovalis* and *Sapphirina* spp. The former two species are characteristic of subtropical and Mediterranean areas (Razouls, 1995, 1996), and were more abundant during the last years of the time series when they also exhibited an extended seasonal persistence, from two months in the early 90s to five months (summer and fall) during the late 90s (Fig. 6).

The case of *T. stylifera* is especially interesting as it was not recorded in the N-NW Iberian Peninsula before 1978 (Lakkis, 1967; Sphor and Corral, 1976; Alvarez-Ossorio, 1977, 1984; Corral and Alvarez-Ossorio, 1978; Vives, 1980). It was observed for first time in the Cantabrian Sea by Alvarez-Marqués (1980) as a rare species always occurring at low densities (Fig. 7). Over ensuing years it has been recorded often (Valdés et al., 1991; Valdés, 1993; Cabal, 1993; Villate et al., 1997; Valdés and Moral, 1998; Bode et al., 2003; D'Elbee and Castel, 1991, 1995; D'Elbee, 1998, 2001; Villate et al., 2004), and has been cited as an example of distributional change driven by global warming (Villate et al., 1997).

The above patterns are confirmed in this study from the transects off Vigo, Coruña and particularly Santander since the mid 1990s (Fig. 8). There is also an increase in *T. stylifera* abundance from west to east. The patterns of water column stratification are similar in the three location (Figs. 3 and 9), though with much stronger water column stratification in Santander, particularly in recent years. We hypothesize that the observed seasonal, spatial and temporal patterns in occurrence of *T. stylifera* are related to those in the water column stratification, reinforced by the warming trend.

There were no clear inter-annual changes in the zooplankton biomass at any of the transects sampled (Fig. 9). There is, however, a strong regional gradient in the seasonal extension of the mesozooplankton biomass peak, driven by differences in water column stratification at each study site. In contrast to Cudillero and
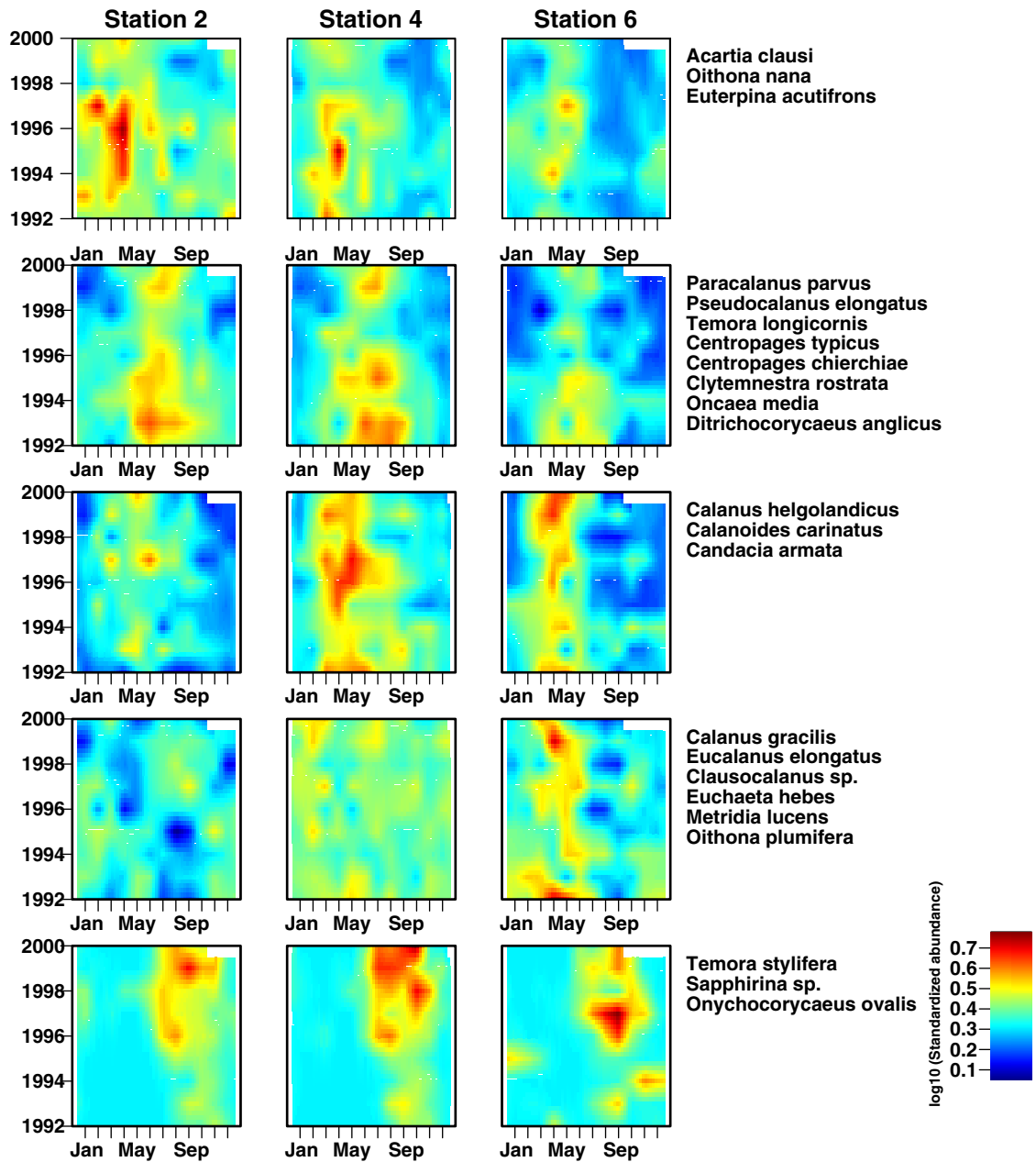
Fig. 6. Species associations in the Santander transect as depicted from the *k*-mean cluster. Each cluster represents the centered and log transformed average abundance.

Santander, and in particular at the most oceanic Station 6 where water column stratification is much stronger, the Vigo and Coruña transects are in an area where frequent upwelling events break up the water column during the summer months (Figs. 2, 3 and 9). This seems to be correlated to the seasonal decrease in zooplankton abundance. Those locations where stratification is more intense have much lower zooplankton biomass during the stratified period; hence the peak in biomass is restricted to the spring period before the onset of surface warming.
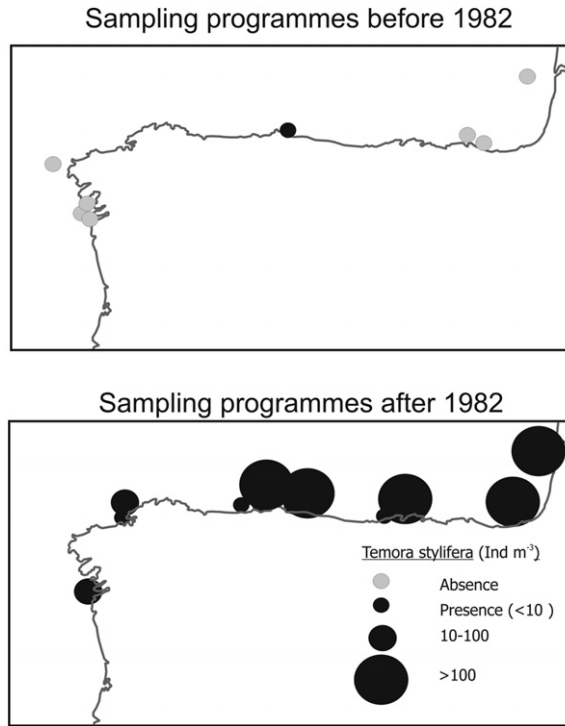
Fig. 7. Records of *Temora stylifera* in studies before and after 1982 (i.e 1967–1982 and 1982–1998).
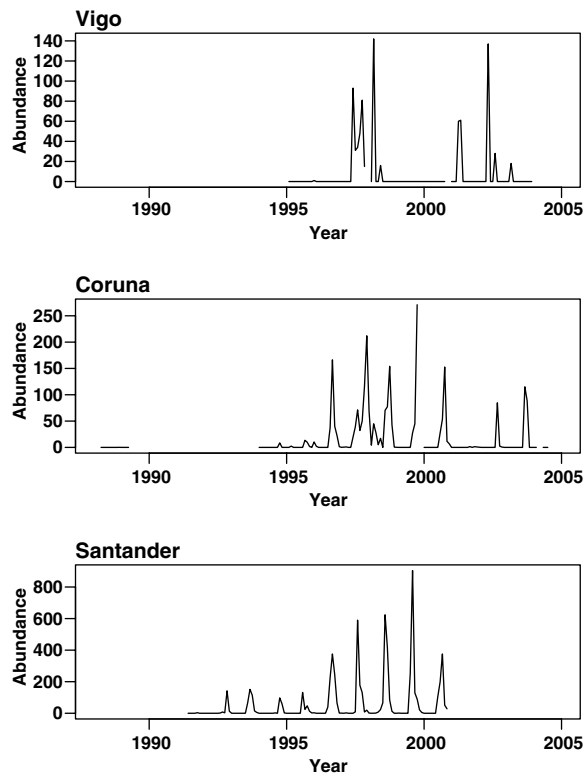

Fig. 8. Time series of *Temora stylifera* abundance off Vigo, Coruña and Santander.
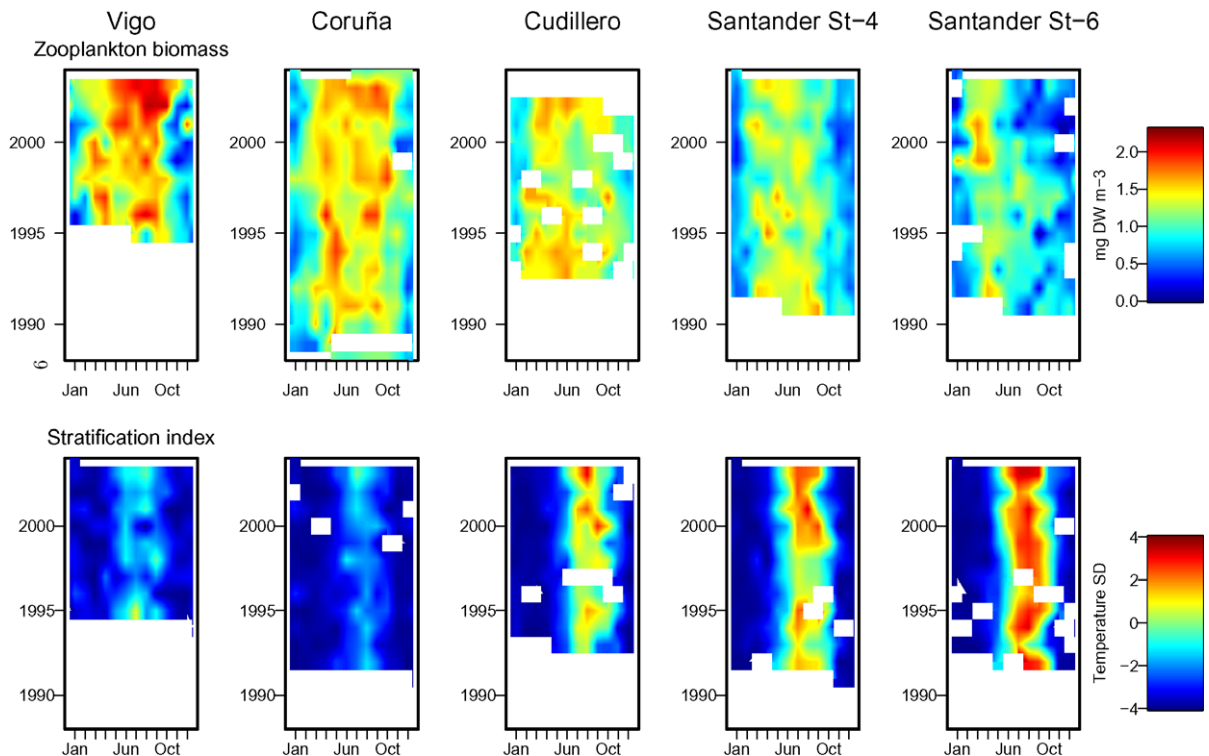
Fig. 9. Zooplankton biomass (upper panels) and the stratification index (lower panels) for each of the shelf-break stations in each transect and for the most oceanic station off Santander.

5. Discussion

5.1. Living in an increasingly stratified ocean

Stratification plays a crucial role in structuring marine communities as it largely controls the input of nutrients into the upper photic layers. Global change is predicted to increase the degree and duration of the stratification phase (Roemmich and McGowan, 1995; Sarmiento et al., 2004). As the stratification reaches deeper waters and the nutrient depletion in photic layers is extended in time, consequences are expected in seasonal and annual phytoplankton dynamics resulting in increased oligotrophy. This predicted change is already occurring and is observed in the increased stratification in the Radiales transects (Figs. 2, 3 and 7). Both, increase in stratification and decreases in upwelling intensity combine to reduce phytoplankton growth. We hypothesize that the inner Bay of Biscay will be less productive in the future, as already observed. Such a response is evident in a shelf-break station off Cudillero, where primary production decreased significantly in the period 1993–2003 (Fig. 10a). Off Coruña, where upwelling is intense and stratification remains unchanged (Figs. 3 and 9), an opposite trend in primary production was noted (Fig. 10b). These changes in the physical structure of the water column and in the subsequent functioning of lower trophic levels that drive ecosystem production, are likely to modify the structure, production and organization of higher trophic levels from zooplankton to fish. We already observed that the annual zooplankton biomass decreases consistent with the onset of stratification (Fig. 9). Our analysis shows that only through prolonged and regularly repeated time series sampling can these changes be detected.

Higher water column stratification and less nutrient enrichment will lead to more oligotrophic conditions (Valdés and Moral, 1998), potentially reinforcing the microbial loop, causing a decrease in mesozooplankton biomass and a drop in the number of species per unit of volume. This scenario may be extended throughout
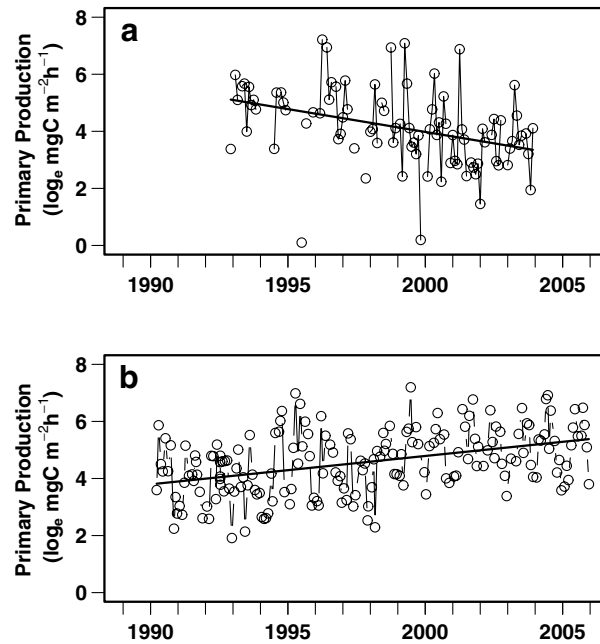
Fig. 10. Variation in primary production 1993–2003 at the shelf-break station of the transect Cudillero (panel a) and off Coruña (panel b).

the Bay of Biscay since changes in wind force and surface heating are geographically consistent, with potentially devastating biological impacts (sensu Roemmich and McGowan, 1995) in temperate regions.

The seasonal timing of zooplankton populations has been observed to change with temperature (Greve et al., 1996; Edwards and Richardson, 2004). We observed here the correlation between temperature and zooplankton biomass when we analysed the seasonal cycles at each location in relation to the water column stratification (Fig. 9).

Climate change influences zooplankton species distributions (Southward et al., 1995). Beaugrand et al. (2002) observed a northward displacement of copepod populations characteristic of warmer southern conditions as registered on the Continuous Plankton Recorder Surveys. Thermophilic and opportunistic species (such as *T. stylifera*, *O. media* and *Ditrichocorycaeus anglicus*) gain an advantage if the environment changes towards warmer conditions, whereas other species characteristic of colder waters and blooms of phytoplankton formed by large sized cells are clearly disadvantaged if such temperature changes occur. Ecosystem changes due to immigration of new species and the loss of species no longer able to exist in future warmer years can best be appreciated in time series comparisons of present and the future data with the documented past.

T. stylifera and *Centropages chierchiae* are found to increase in abundance in relation to temperature (Lindley and Daykin, 2005), and these observed dynamics are linked to oceanic climate forcing (Molinero et al., 2005). Villate et al. (1997) indicate that *T. stylifera* is a good descriptor of the year-to-year changes in shelf-water properties, especially of the warmest environmental situation. This species becomes a more important constituent of the copepod assemblages in the Cantabrian Sea in late summer–autumn during 1990–2000 (Figs. 6 and 8) corresponding with a period when water column stratification is stronger (Fig. 3). However, in the Galicia area, influenced by upwelling processes, this species usually appears at lower densities (Figs. 5 and 8).

5.2. Time series programmes: capturing the ocean variability

In a system in constant motion in three dimensions, it is difficult to interpret trends without knowledge of system variability at different scales. To capture this variability, merely collecting data at a single point is completely inadequate. Collecting data at sparse locations with discontinuities in time, as in data archaeology, is a valid approach to reconstruct past time series (Southward et al., 1995; Levitus et al., 2000), but the establish-

ment of a network of time series stations for repeated physical, biological and chemical measurements is the proper method for ecosystem surveillance. This sampling strategy is essential if we are to record and understand complex oceanic and biological processes and adopt an ecosystem approach to marine resource management. This was recognized when the IEO Radiales project was planned and its extended time series observations was established: an appropriate time scale was determined, sampling sites were located as representative of the region to characterize not only the local conditions, but with strategically located stations to avoid undesired variability caused by continental effects.

The importance of obtaining taxonomic species data in time series programmes is beyond doubt. This is no easy task however, and the difficulties in intercomparison of time series analysed by different people with different degrees of taxonomic expertise and objectives has been recognised (Perry et al., 2004). Even within the Radiales programme maintained by a single institution some difficulties have been inevitable. The list of species and stages counted at each transect varied over time with taxonomic changes in the plankton community and with changing professional expertise. This implied that in order to compare composition between samples from different transects collected over several years we need to reduce the information obtained to the lowest taxonomic level common in all transects losing information in some of the local transect. For example, this implied that we presented only data from Coruña and Santander in our Abundance-Number of samples diagrams (Fig. 5) because it is at those transects were taxonomic analysis has been carried in more detail. In the future it is necessary to obtain a consensus among the taxonomists involved in the determination of zooplankton samples as to the level of taxonomic analysis that is both practical to maintain in order to analyse the high number of samples. Such consensus has also to minimise any possible differences in taxonomic expertise between the people in charge of each individual transect.

Given an adequate ocean observing system and given continued advances in our understanding of ocean processes, the next step is to use these observations to drive and update models from an "initial value" input in a predictive mode (Stenseth et al., 2006). The basis of these assimilation models is the continued sampling in time as the modelling effort requires constant validation of the predictions with real-world data. These needs for continued sampling are also evident when we face unexpected events such as an oil-spill (e.g. Prestige, Figueras et al., 2005); when we need to compare the situation after the event with that monitored immediately before (Varela et al., 2006).

6. Conclusions

Long-term research programmes based on systematic observations have rendered significant results to the earth's sciences in general and to the oceanography in particular. The Spanish IEO project Radiales has allowed us to set statistically significant ranges for the variability of several environmental variables and biological communities. We have determined the rates and trends of warming due to the climate change as well as describing some direct and indirect effects in the water column and effects on pelagic ecology. The project has contributed substantially to gaining a deeper knowledge of planktonic communities and species and to production of baselines, climatologies and reference levels for the north coast of Spain. These allow accurate evaluations of the effects of environmental perturbations on the ecosystem, enabling forecast of expected recovery times from perturbations and monitoring of the ecosystem for reversion to the previous states.

We remark that time series programmes are extraordinarily difficult to maintain and few survive for periods longer than a decade (Duarte et al., 1992). In this sense the Radiales project has been a pioneer and successful Spanish initiative. It represents a significant contribution to the understanding of an important regional marine environment and is a good example of the importance of the basic research as an essential instrument for a responsible management of natural resources.

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