Recent changes in the pelagic ecosystem of the Iberian Atlantic in the context of multidecadal variability

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Abstract

Trends in ecosystem variables of the Eastern North Atlantic shelf near the Iberian Peninsula were analysed in relation to regional climate and oceanographic variability. In addition, detailed changes in oceanographic properties (surface temperature, upwelling and poleward current activity) and biological components (plankton and pelagic consumers) in the period 1989-2005 were compared with the main trends and multidecadal periods observed in time series dating back to 1950. In contrast to previous studies, the North Atlantic Oscillation did not appear as the main influence in the climate of the North Iberian region, while East-West and subtropical gradients were the dominant modes. Climatic oscillations at decadal scales were paralleled by similar oscillations in oceanographic and biological variables, but the latter appeared weakly related to climate. Time-lags of up to 5 years in the biological response may partly explain these relationships. The main planktivorous fish species (sardine and anchovy) alternate in periods of 10-15 years of relative dominance, in synchrony with equivalent species around the world. In contrast, plankton cycles appear greatly modified after 1990 in coincidence with shifts in climatic and oceanographic variables. Subregional variability indicated divergent trends in biological variables, particularly the zooplankton increase off A Coruña and the decrease in the Bay of Biscay since 1990. Such divergences are related to direct and indirect effects of global changes in this transitional upwelling region.

Keywords: plankton, fish, interannual variability, climate, NAO, upwelling, continental shelf, NE Atlantic

Introduction

Climate fluctuations over the Northern Hemisphere were recognised as one of the major sources of variability in the North Atlantic (Visbeck et al., 2003; Hurrell and Dickson, 2004). Changes in the ocean temperature, circulation and stratification, among others, were primarily driven by alterations in atmospheric pressure fields over large regions. The effects were transmitted to marine ecosystems in the form of changes in the species distribution and abundance patterns, notably from plankton receiving effects of climate at the base of the food web (Southward et al., 1995; Beaugrand, 2004; Leterme et al., 2005; Molinero et al., 2005). Some of the changes, even at local or subregional scales, were directly related to single climatic components, as the North Atlantic Oscillation (Beaugrand, 2004; Molinero et al., 2005). In other cases, as in the Southern Bay of Biscay, the influence of a single component appears to be variable, even at the oceanographic level (Pérez et al., 2000; Planque et al., 2003).

Planktivorous fish populations, notably clupeids, are a good indicator of the ecosystems responses to climate fluctuations, because they closely track alterations in climate and plankton composition through both direct and indirect effects (Chavez et al., 2003). In addition they are the objective of one of the most productive fisheries in the world and there are historical records of landings which can be taken as a proxy for the actual variations in their populations. For instance, increase in upwelling intensity is associated to an increased input of nutrients to phytoplankton and the subsequent increase in primary production and planktivorous fish. At the same time, upwelling may negatively affect fish recruitment by dispersing eggs during the spawning season (Guisande et al., 2004). Changes of low-frequency and high-amplitude in oceanic conditions that reflect in biological variables and propagate through the food web, termed 'regime shifts', have received considerable attention in recent years (Lluch-Belda et al., 1989; Reid et al., 1998; Chavez et al., 2003; Beaugrand, 2004; Collie et al., 2004; Leterme et al., 2005).

Despite its interest as the northern limit of an eastern boundary current ecosystem, studies of the effects of climate in the Eastern North Atlantic surrounding the Iberian Peninsula were generally limited to the assessment of direct effects of climate on water mass characteristics and circulation (Lavin et al., 1998; Pérez et al., 2000; Alvarez-Salgado et al., 2003; Cabanas et al., 2003; Planque et al., 2003). Only few studies considered climatic influences on plankton (Valdés and Moral, 1998) and clupeid fish (Borja et al., 1998; Borges et al., 2003; Guisande et al., 2004). To date, however, there is no a comprehensive study of long-term changes in climate and ecosystem properties in the region.

The objectives of the present study are 1) to analyse long-term multidecadal variability in climatic, oceanographic and biological indices at a regional scale in the Iberian Atlantic and 2) to compare long-term trends with recent changes at local scales.

Methods

Climate variables

Climatic indices for the Atlantic region were represented from the key modes of large-scale atmospheric circulation over the Northern Hemisphere (Barnston and Livezey, 1987). Six indices were selected: North Atlantic Oscillation (NAO), East Atlantic Pattern (EA), East Atlantic/Western Russia pattern (EA/WR), Scandinavia pattern (SCA), Tropical/Northern

Hemisphere pattern (TNH) and Polar/Eurasia pattern (POL). The data, covering the period 1950-2005, were obtained from the US NOAA Climate Prediction Center (CPC, http://www.cpc.ncep.noaa.gov/).

Oceanographic variables

Sea surface temperatures (SST) in the region were represented by mean values at a 2ºx2º cell centred at 42º N, 10º W, and were obtained from reprocessed historical data at the International Comprehensive Ocean-Atmosphere Data Set (ICOADS, http://icoads.noaa.gov/). The main oceanographic circulation over the shelf was represented by coastal upwelling during spring and summer (Varela and Rosón, 2005) and poleward currents during autumn and winter (Alvarez-Salgado et al., 2003). An Upwelling Index (UI) was computed from geostrophic winds at a 2ºx2º cell centred at 42º 30' N, 12º 30' W by the Pacific Environmental Laboratory (PFEL, http://www.pfeg.noaa.gov/). Monthly UI values were averaged between March and October (upwelling season) for each year during the period 1966-2004. Similarly, a Poleward Index (POLE) was computed from geostrophic winds at a 2ºx2º cell centred at 43º N, 11º W (Cabanas, 1999). Annual means of POLE were values averaged between October and December of the previous year. In addition, monthly observations of SST were recorded at A Coruña (43º 25' N, 8º 26' W) in the period 1990-2005 as part of the oceanographic time-series RADIALES programme (http://www.seriestemporales-ieo.net/).

Biological variables

Long-term plankton observations were obtained from the Continuous Plankton Recorder (CPR) survey (http://www.sahfos.org/). Data were averaged over the CPR grid E4 covering most of the Bay of Biscay between 1958 and 2004. Phytoplankton biomass was estimated from the Phytoplankton Colour Index (PCI), whereas zooplankton abundance was represented by total copepod abundance (COP). In addition plankton abundance and biomass were analysed in detail in monthly samples at A Coruña including chlorophyll-a (CHL), abundance of diatoms (DIAT), dinoflagellates (DINO), microflagellates (FLAG) and ciliates (CIL) and zooplankton carbon biomass (ZOO). Sampling and analytical details for these variables can be found in Casas et al. (1997) and Bode et al. (1998). The abundance of planktivorous fish in the region was estimated from landings of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the ICES Areas VIII (VIIIc for sardine) and IXa (ICES, 2005).

Data analysis

First, linear regression was performed on all series of annual mean values to study temporal trends. Second, detrended series of climate variables were analysed by principal component analysis to extract the main patterns of variability. Subsequently, climatic variability was represented by the first three principal components. Oceanographic and biological variables were projected on the climatic factorial space to identify the possible relationships between data sets. Finally, several indices were computed using biological variables to summarize changes at ecosystem level. Plankton variables were combined in a Phytoplankton-Zooplankton Index (PZI), representing the relative dominance of phytoplankton over zooplankton, and a Diatom – Dinoflagellate Index (DDI), representing the relative dominance of diatoms over dinoflagellates. These indices were computed by difference of the detrended, normalised and standardised values of phytoplankton abundance (PCI and CHL) and zooplankton (COP and ZOO), in the case of PZI, or DIAT and DINO, in the case of DDI.

Fish landings were also transformed to obtain an index of relative dominance of each species, Relative Indicator Series (RIS), similar to that described by Lluch-Cota et al. (1997). The original landing values for each species were detrended, normalised and standardised before computing RIS as the difference of the sardine and anchovy landings.

Results and discussion

Long-term trends

All time-series showed ample variations since 1950 (Fig. 2). Climatic index values (as exemplified by NAO) increased markedly after 1970, in parallel with SST and some biological variables as PCI. Most series (except anchovy data) displayed significant linear trends with time considering the whole study period (Table 1) but multidecadal oscillations were apparent. For instance, NAO decreased in the last 10-15 years to values similar to those observed before 1970, while SST, after reaching the maximum value of the series in 1997, decreased to values characteristic of late 1980s. Biological variables also showed periods of increase and decrease but contrasting trends. Phytoplankton increased significantly over the Bay of Biscay, but particularly after 1985, with maximum PCI values observed in 1995 and decreasing thereafter (Fig. 2c). In contrast, zooplanktonic copepods showed maximum values in 1975 but then decreased to historical minimum values in 2004. Fish landing series indicated the characteristic fluctuation of planktivorous fish populations, with decades of historical abundance, as the sardine in the 1960s and 1980s, alternating with periods of low biomass (Fig. 2d). In the overall, however, there was a significant decrease of the size of the sardine population over the region, reaching a historical minimum value in 2000. The size of the anchovy population also fluctuated in multidecadal periods, sometimes in apparent phase with sardine (as in the 1960s) but often out of phase.

Climatic variability

Three principal components were extracted from the climatic indices (Fig. 3) accounting for up to 63.8% of total variance. The first two components (CLI1 and CLI2) accounted for only 22.3 and 22.1% of variance, however, indicating that none of the climatic indices clearly prevailed. Indeed the NAO index, generally associated to dominant climatic conditions over Western Europe (Hurrell and Dickson, 2004), only displayed relatively high contributions on CLI2, whereas POL and EA/WR were the main contributors to CLI1 (Fig. 3a). The Scandinavian pattern (SCA) was the dominant index in CLI3. Interestingly, EA index was negatively correlated to all three principal components. The East Atlantic (EA) pattern is the second prominent mode of low-frequency variability over the North Atlantic, and appears as a leading mode in all months (Barnston and Livezey, 1987). The EA pattern is structurally similar to the NAO, and consists of a north-south dipole of anomaly centres spanning the North Atlantic from east to west but it differs from the NAO by a strong subtropical link in association with modulations in the subtropical ridge intensity and location. This EA/WR pattern consists of four main anomaly centres. The positive phase is associated with positive anomalies of atmospheric pressure located over Europe and northern China, and negative anomalies located over the central North Atlantic and north of the Caspian Sea (Barnston and Livezey, 1987).

Apparently there were no strong relationships between climate and oceanographic or biological variables, as the latter were located in central positions in the factorial space of climate (Fig. 3). The largest correlations (indicated by low angles with the components) were

negative and occurred between the poleward current index (POLE) and either CLI1 or CLI3 components. Also negative correlations were found between PZI and CLI2. The upwelling index and SST were weakly related to climatic components, although they formed relatively low angles (i.e. high correlations) with EA and NAO. These results contrast with the generally high correlations found between climatic indices, notably NAO, and oceanographic or biological variables in other studies. In this way, changes in SST are generally associated to changes in the surface wind and air-sea heat exchanges associated with NAO (Hurrell and Dickson, 2004). Similarly, plankton species composition over the North Atlantic (Beaugrand, 2003) and the Western Mediterranean (Molinero et al., 2005) were shown to vary according to changes in stratification and/or temperature related to general NAO anomalies. Our results, however, point to a lower importance of NAO compared to other climatic indices in the regulation of the ocean and biology in the Atlantic Iberian shelf, and particularly considering the Bay of Biscay, as suggested by other studies in the region (Planque et al., 2003). In this case, the use of combined climatic indices, as the principal components in this study, may be more appropriate to include the main sources of regional climate variability. This approach also is consistent with the recognised teleconnection patterns in the Northern Hemisphere (Barnston and Livezey, 1987). In addition, it must be taken into account that the ocean response to climatic forcing is partly local and rapid but also partly delayed and non-local (Visbeck et al., 2003), the latter greatly affecting the interpretation of changes in ocean properties.

Multidecadal periods

Besides the described trends, all time-series exhibited alternating periods of positive or negative anomalies compared to the series mean (Fig. 4). For instance the first climatic component displayed positive anomalies between 1963 and 1980, and between 1990 and 1999. The other climatic components (not shown in Fig. 4) had similar variations. The changes in the plankton PZI index over the Bay of Biscay also displayed periods of positive and negative anomalies but in this case positive anomalies were of short duration (<5 y) before 1993, when an exceptional period of positive anomaly established and remained until present days. This pattern is due to the increasing dominance of phytoplankton (PCI) over zooplankton (COP) already described (Fig. 2c) and is consistent with the analysis of CPR data in the whole North Atlantic (Richardson and Schoeman, 2004), indicating an increase of phytoplankton in cooler regions. The large change in the duration of the phytoplankton dominance periods in the 1990s, however, suggests the existence of one major shift in the ecosystem in recent years. Similar regime shifts were also described in other areas of the Atlantic (Reid et al., 1998; Beaugrand, 2004; Leterme et al., 2005). Furthermore, the contrasting changes in phyto- and zooplankton abundance in the NW Iberian region suggest larger changes in the trophic control of the food web.

The increase in phytoplankton can be attributed to an increase in water column stratification driven primarily by higher SST, which favours the use of nutrients near the surface (Richardson and Schoeman, 2004). The nutrients would never get exhausted for long periods because the existence of upwelling events. In contrast, intense stratification coupled with a decrease in the intensity of upwelling was related to the decrease in zooplankton in other regions (e.g. Roemmich and McGowan, 1995) and particularly in the Southern Bay of Biscay (Valdés and Moral, 1998). While in most North Atlantic regions the positive association between changes in phyto- and zooplankton was interpreted as an indicator of bottom-up control of the pelagic food web (Richardson and Schoeman, 2004), in our case the negative association of trends suggest a marked change in the food web due to the growing inability of

zooplankton in controlling phytoplankton blooms, at least in the Bay of Biscay. This would imply an increase in the bottom-up control and would ultimately lead to an increase of eutrophication. Data collected at other localities in the study region, however, showed different results (see *Short term variability*). In any case, the causes of the copepod decline in the CPR records of the Bay of Biscay will require further study.

Periodic cycles were also shown by alternating maxima of sardines and anchovies measured with the RIS index (Fig. 4c). Similar periods were described for populations of equivalent fish species in other ocean areas (Lluch-Belda et al., 1989; Lluch-Cota et al., 1997; Chavez et al., 2003) as they seem to react in apparent synchrony. These species respond generally well to changes in climatic and oceanic conditions over large spatial scales. Their replacement was explained by different feeding capabilities and strategies to exploit favourable environmental conditions near upwelling regions. For instance, sardines are generally more adapted to phytoplankton bloom conditions because of their higher efficiency in filtering abundant food particles in the water compared to anchovies (Plounevez and Champalbert, 1999; Bode et al., 2004). Also, relatively cold conditions would favour anchovies over sardines (Chavez et al., 2003). Some changes, however, remain unexplained because they lack one or more of the required links. Recent studies point to the existence of subregional characteristics (or 'loopholes') within a certain set of climatic and oceanographic conditions which may modify the expected patterns at larger spatial or temporal scales (Bakun and Broad, 2003; Bertrand et al., 2004). The relatively stable pattern of change from positive RIS values ('sardine phase') to negative values ('anchovy phase') observed in our study contrasts with the pattern observed in the plankton of the Bay of Biscay (Fig. 4b). It also contrasts with the recognised decreasing trend in both populations, particularly at subregional level (Junquera, 1984; Borges et al., 2003; Carrera and Porteiro, 2003; ICES, 2005). The repeated pattern, however, supports the estimations of the optimal environmental conditions for the recruitment of sardine (Guisande et al., 2004), which remained stable for more than 100 y. Environmental 'loopholes', as the local increase in upwelling favouring anchovy recruitment in the Southern Bay of Biscay (Borja et al., 1998) or the reduced upwelling off Southern Galicia for sardine recruitment (Guisande et al., 2004) have been invoked to explain interannual variations within the region.

Since the biological response to climatic forcing may be delayed, we examined the cross-correlations between the first climate component and biological indices (Fig. 5). Due to the periodic nature of the cycles, significance was found at both positive and negative lags, although we were interested in correlations at positive lags indicating changes in climate leading changes in the biological variables. The PZI index was not significantly correlated with CLI1 (i.e. correlation values not exceeding the 95% confidence limits) when values of the same year were compared, but significance was found at lags >2 y (Fig. 5a). Maximum correlations were found when PZI values were compared with CLI1 values from 5 years ago. Positive values of CLI1, indicating a relative dominance of POL and EA/WR patterns, were associated with increases in PZI (and therefore in phytoplankton abundance). The correlations between CLI1 and RIS, however, were significant at zero lags (i.e. values measured in the same year) although maximum values were reached when RIS values were compared with CLI1 values measured 3 years ago. In this case the sign of the correlation was negative, indicating a relative decrease in sardines (or an increase in anchovies) when CLI1 increased. These relationships between biological indices and climate can be described by linear regression (Fig. 6) and could be applied in further research and forecasting of ecosystem changes at large temporal and spatial scales.

Short term variability

The changes observed since 1989 at A Coruña in SST (Fig. 7a) showed a general agreement with the increasing trend observed over the region (Lavin et al., 1998; Valdés and Moral, 1998; Pérez et al., 2000; Cabanas et al., 2003). In our case, however, the oscillations lead to a mean decrease in recent years, after maximum values in 1997-1998, with values in 2005 comparable to those observed in early 1990s. The waters off A Coruña, although affected by a general decreasing trend in upwelling intensity observed in the region since the 1970s (Lavin et al., 1991, 2000), still do not display the large increases in temperature at all depths and surface stratification observed in the Southern Bay of Biscay (Lavin et al., 1998; Valdés and Moral, 1998), suggesting differential effects of similar climatic forcing at local scales. This is further supported by the lack of significance of the linear trend of SST at A Coruña (Table 2).

Variations in plankton biomass after 1989 (Fig. 7b) also differed from the large-scale trend observed in the Bay of Biscay (Fig. 2c). First, phytoplankton biomass (CHL) displayed a general decrease until 1997 and increased with large amplitude oscillations thereafter. Because of these variations, the overall trend between 1989 and 2005 was not significant (Table 2). Second, and in contrast with the pattern in the Bay of Biscay, zooplankton biomass (ZOO) increased steadily to maximum values after 2000. In this way, phyto- and zooplankton biomass displayed similar trends since late 1990s off A Coruña thus in agreement with the observations in cooler regions of the North Atlantic (Richardson and Schoeman, 2004) while zooplankton decreased in the Southern Bay of Biscay (Valdés and Moral, 1998) as observed in warmer regions. Our data also indicated a general decrease of diatoms and an increase in dinoflagellates (Fig. 7c), both with significant linear trends (Table 2). In this case the data off A Coruña follow the same general trends found with CPR observations in the whole Southeast Atlantic (Leterme et al., 2005) which were related to an increase in water-column stratification. Diatoms, more adapted to turbulent conditions, would decrease in favour of dinoflagellates (and flagellates in general) if stratified conditions become more frequent (Margalef, 1997). The change from a diatom-dominated community, typical of upwelling ecosystems, to flagellate-dominated communities, typical of stratified ecosystems seemed not complete, as we observed a first decrease in microflagellates and ciliates but abundance of both groups remained stable since mid 1990s. This suggests that the change towards a microbial-loop food web has not progressed in the western Iberian shelf likely because the influence of upwelling. In this way, our results are consistent with previous work showing the importance of shifts in the turbulence regime of the upper water column for phytoplankton assemblages (Rodríguez et al., 2001) and the apparent global increase in dinoflagellate-caused harmful algal blooms (Hallegraef, 1993).

Finally, we analysed the coupling between large-scale and local trends in the last decades using biological indices. Phytoplankton-zooplankton indices in the Bay of Biscay and off A Coruña were not significantly correlated (Fig. 8a), but a distinct sequence could be traced between values from early 1990s and later years. This lack of significance confirms the existence of different patterns in plankton at subregional scales (Leterme et al., 2005). Significant correlations, however, were found between the diatom-dinoflagellate index and either PZI in the Bay of Biscay or RIS (Fig. 8b, c). In the first case the relationship was negative, due to the marked decrease in diatoms off A Coruña in early 1990s. In the case of RIS there was a positive relationship with DDI, thus confirming the importance of diatoms in periods of sardine dominance (RIS>0).

Conclusions

This study showed significant linear trends in climatic, oceanographic and biological time-series in the period 1950-2005 but multidecadal oscillations were also apparent. Climate, described as a combination of several indices, was related to changes in key oceanographic variables, as SST, upwelling and poleward flow. In contrast to previous studies, NAO did not appear as the main influence in the climate of the North Iberian region, while east-west and subtropical gradients were the dominant modes. Climatic oscillations at decadal scales were paralleled by similar oscillations in biological indices. The succession of sardine and anchovy phases of 10-15 y contrasts with periods of phytoplankton abundance in the Bay of Biscay, as the latter greatly increased in the 1990s. Biological indices showed responses to changes in climate which were delayed up to 5 y, suggesting the existence of both short and long-term effects. The examination of recent changes off A Coruña, indicated large divergences at subregional scales, particularly in biological variables. Local changes, however, were related to changes at larger spatial scales during regime shifts periods, as illustrated by the decrease in diatoms after 1990.

Acknowledgements

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Table 1. Linear trend (slope) of selected climatic, ocean and biological variables in the region between 1950 and 2005 (Fig. 2). r: Pearson correlation coefficient. Significance is indicated by asterisks: *: P<0.05, **: P<0.01; ***: P<0.001; ns: P>0.05.

Variable	slope	r	
NAO	0.020	0.327	*
SST	0.034	0.547	***
PCI	0.042	0.582	***
COP	-0.027	0.365	**
Sardine	-0.027	0.429	*
Anchovy	0.004	0.184	ns

Table 2. . Linear trend (slope) of selected ocean and biological variables off A Coruña between 1989 and 2005 (Fig. 7). r: Pearson correlation coefficient. Significance is indicated by asterisks: *: P<0.05, **: P<0.01; ***: P<0.001; ns: P>0.05.

Variable	slope	r	
SST	0.013	0.066	ns
CHL	0.034	0.172	ns
ZOO	0.186	0.830	***
DIAT	-0.118	0.527	*
DINO	0.117	0.523	*
FLAG	-0.170	0.762	**
CIL	-0.054	0.239	ns
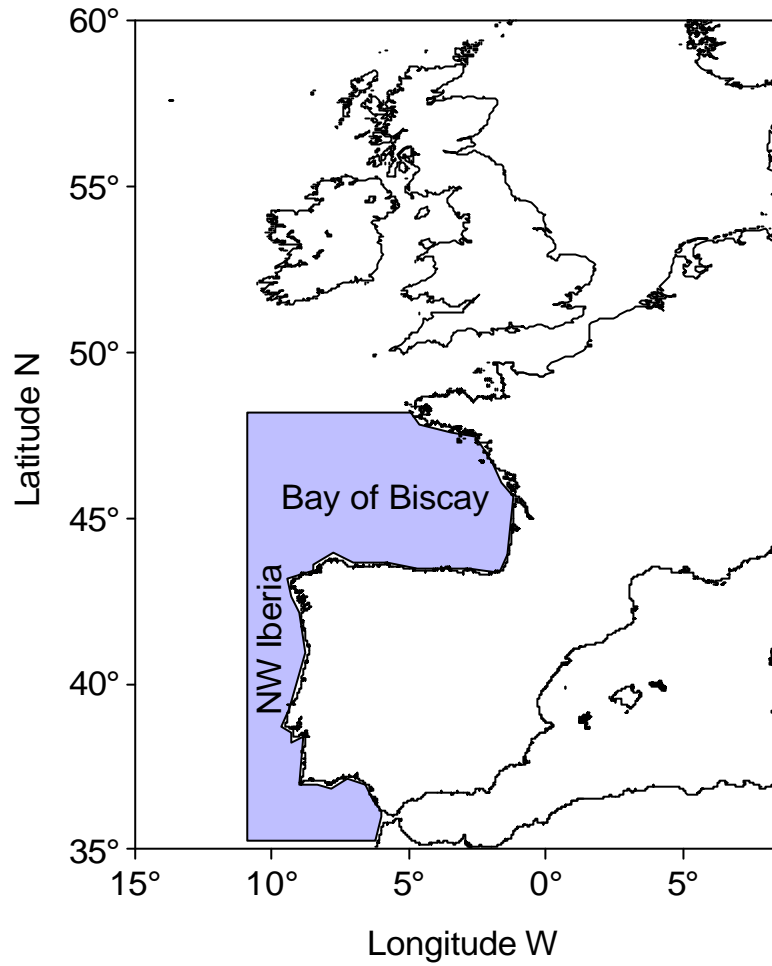
Fig. 1. Map of study region (shaded) including the NW Iberian shelf and the Bay of Biscay.
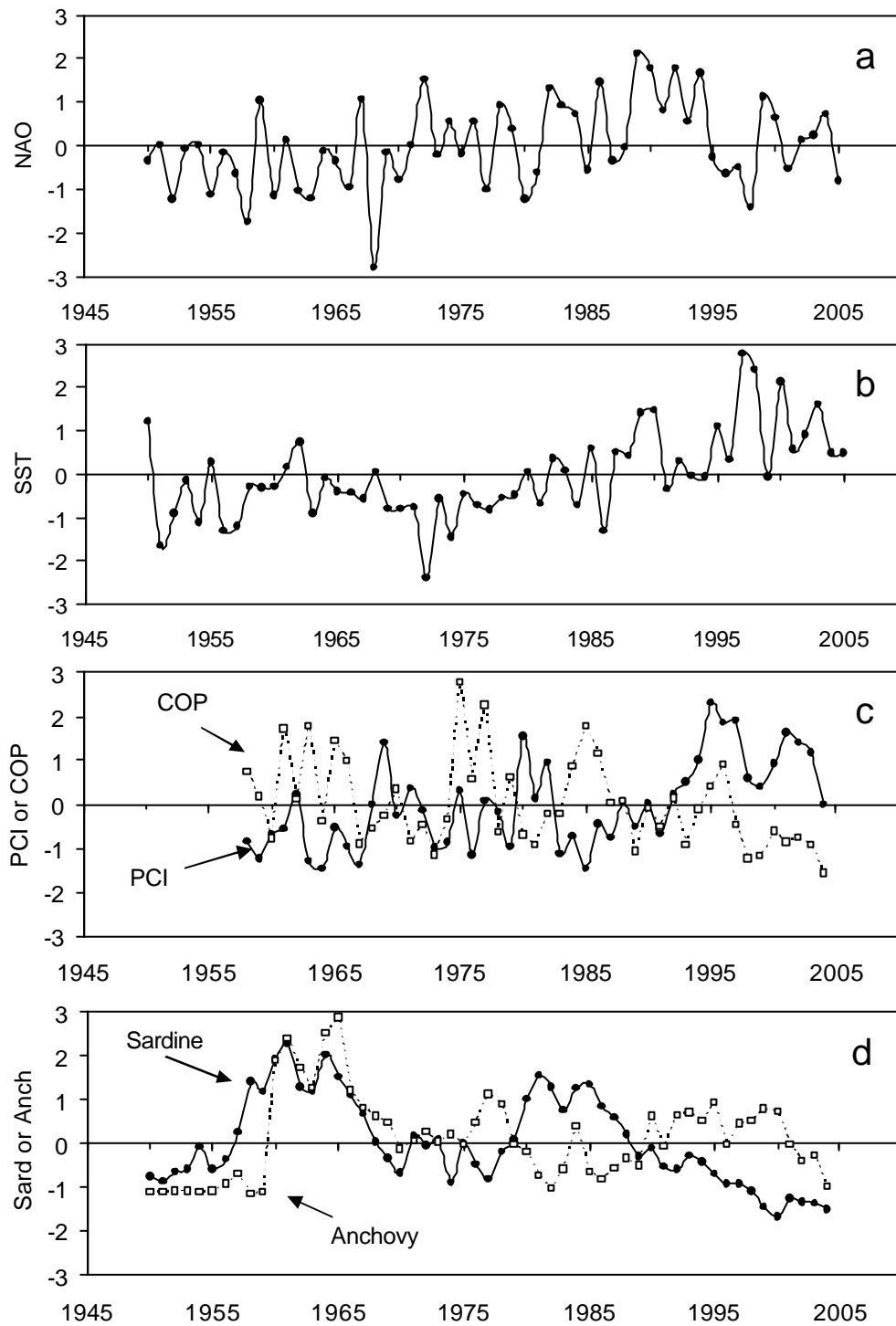
Fig. 2. Time-series of (a) North Atlantic Oscillation (NAO), (b) sea surface temperature (SST), (c) Phytoplankton Colour Index (PCI) and copepod abundance (COP), and (d) sardine (Sard) and anchovy (Anch) landings. All series normalised and standardised. Trends and significance appear in Table 1.
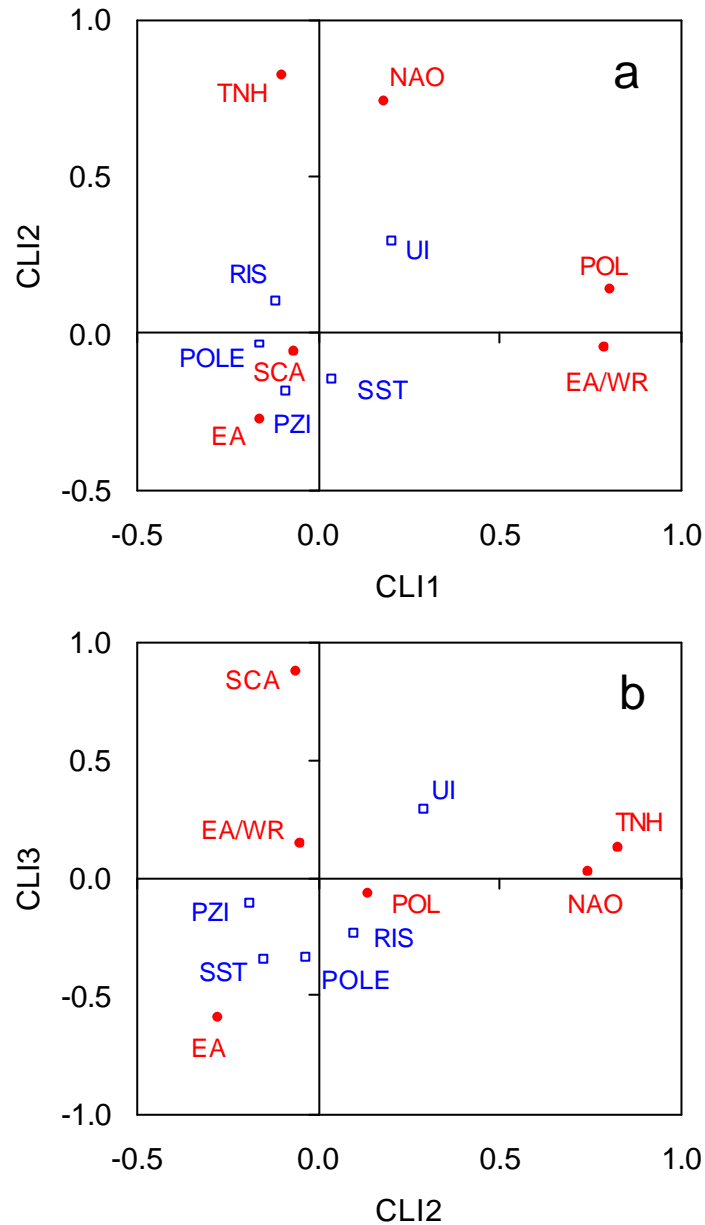
Fig. 3. Projection of climatic indices (see Methods) in the factorial space of (a) the first (CLI1) and second (CLI2) principal components, and (b) in the factorial space of the second and third (CLI3) principal components of climate. Oceanographic (SST, UI and POLE) and biological variables (RIS and PZI), not used in the principal component analysis, were also projected in each space.
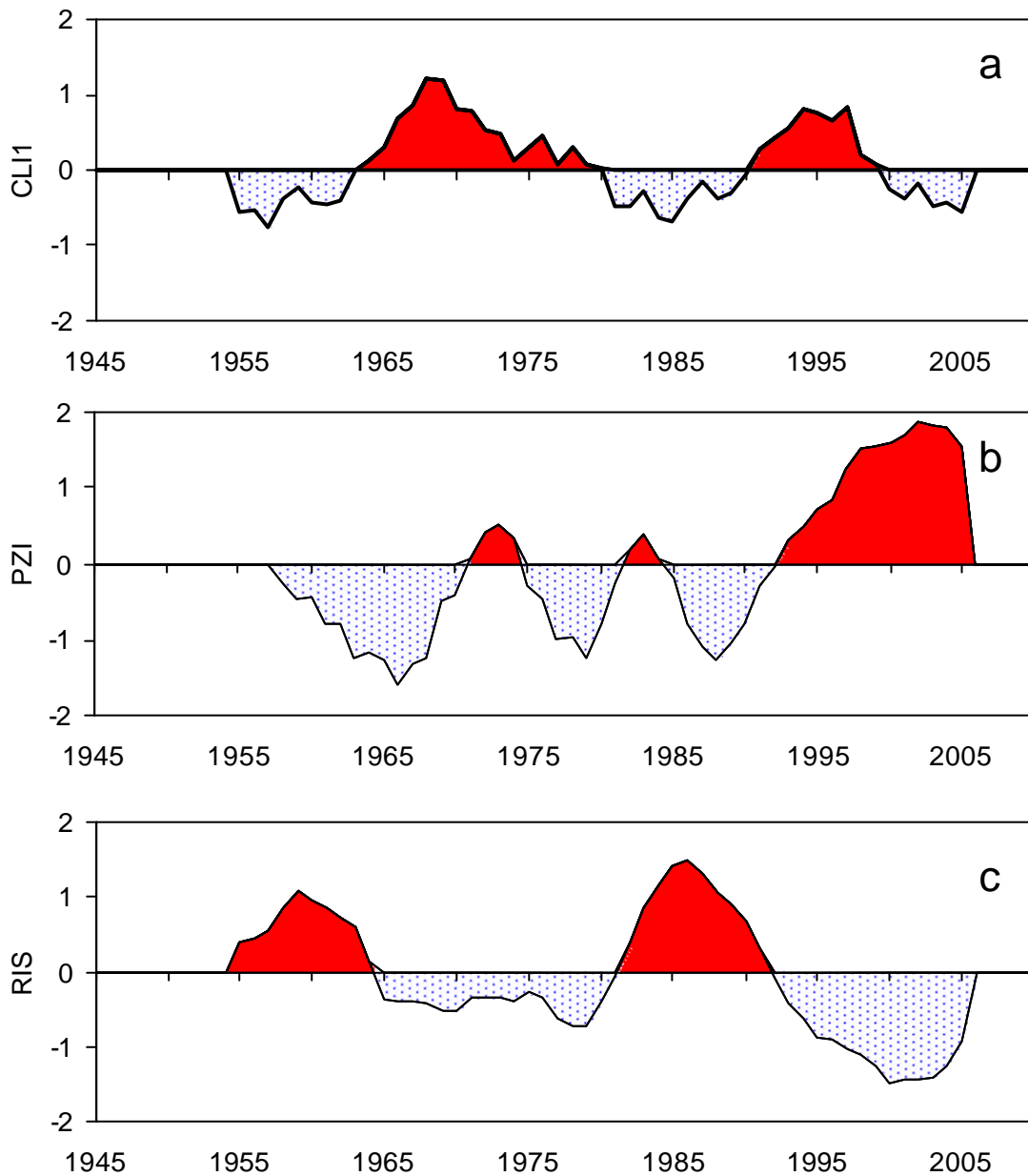
Fig. 4. Succession of multidecadal periods of relative maxima and minima in (a) climate (exemplified by CLI1 component), and biological indices (b) phytoplankton – zooplankton index (PZI), and (c) relative indicator series (RIS). Values were detrended, normalised, standardised, and smoothed with a moving average of 5 y.
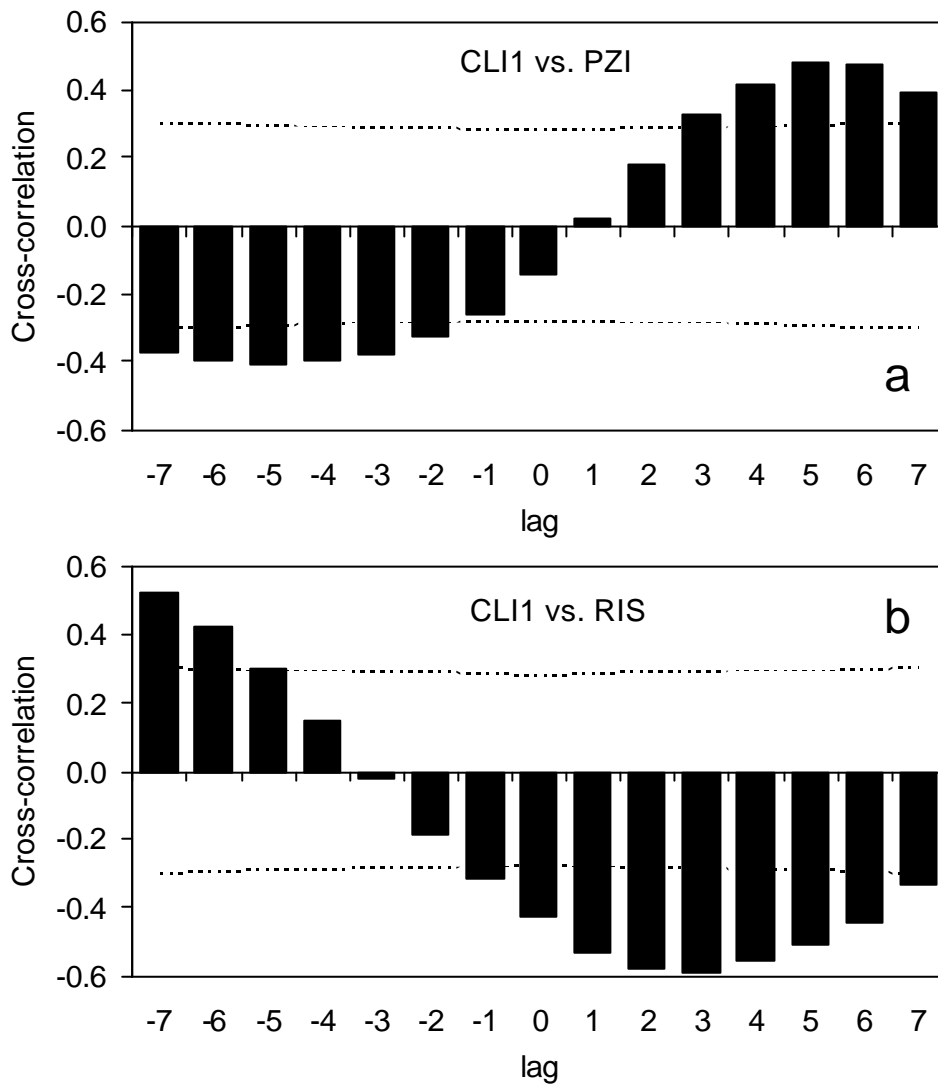
Fig. 5. Cross-correlations of the first climate component (CLI1) with (a) PZI and (b) RIS indices. The dotted lines indicate the 95% confidence limits.
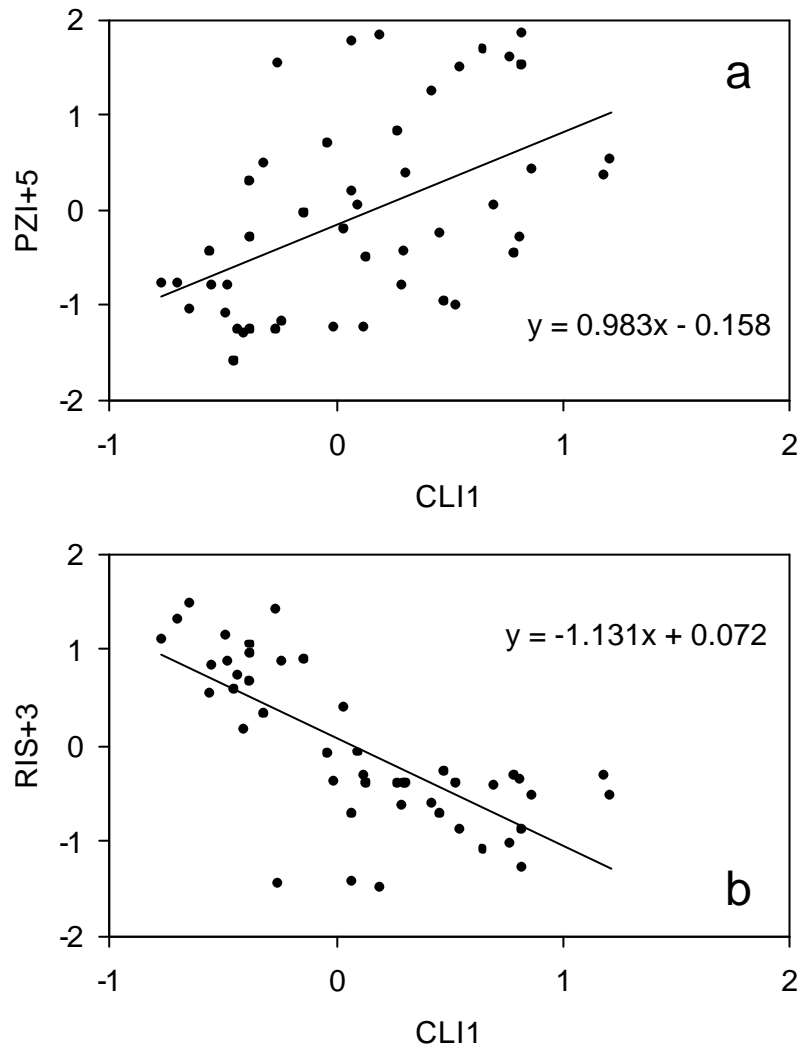
Fig. 6. Plot of (a) FZI with a time-lag of 5 y and (b) RIS with a time-lag of 3 y versus the first climate component (CLI1). The regression lines and equations are also indicated.
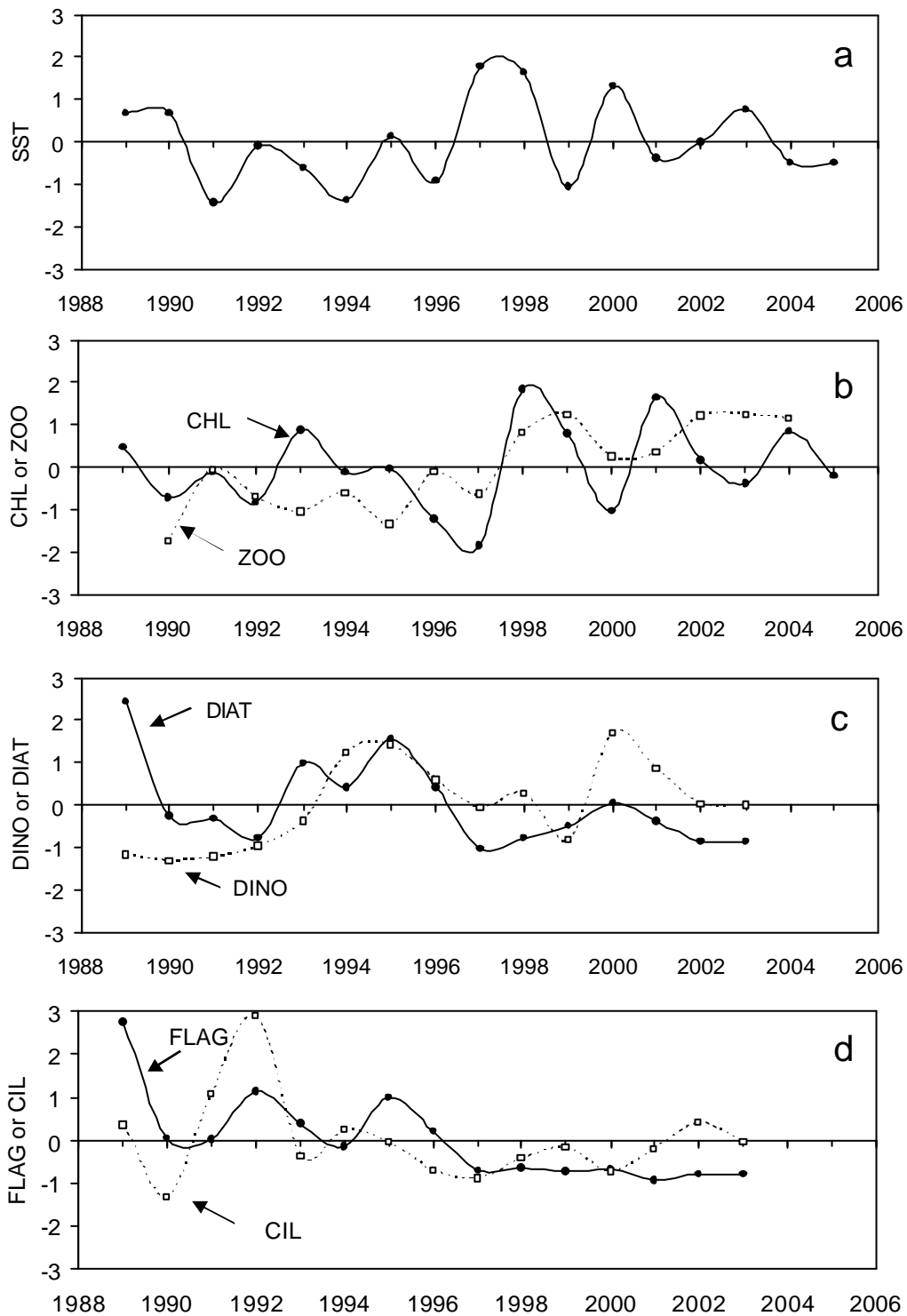
Fig. 7. Time-series of (a) sea surface temperature (SST), (b) water-column integrated chlorophyll-a (CHL) and zooplankton carbon biomass (ZOO), (c) diatom (DIAT) and dinoflagellate (DINO) abundance, and (d) microflagellate (FLAG) and ciliate (CIL) abundance observed at A Coruña. All series normalised and standardised. Trends and significance appear in Table 1.
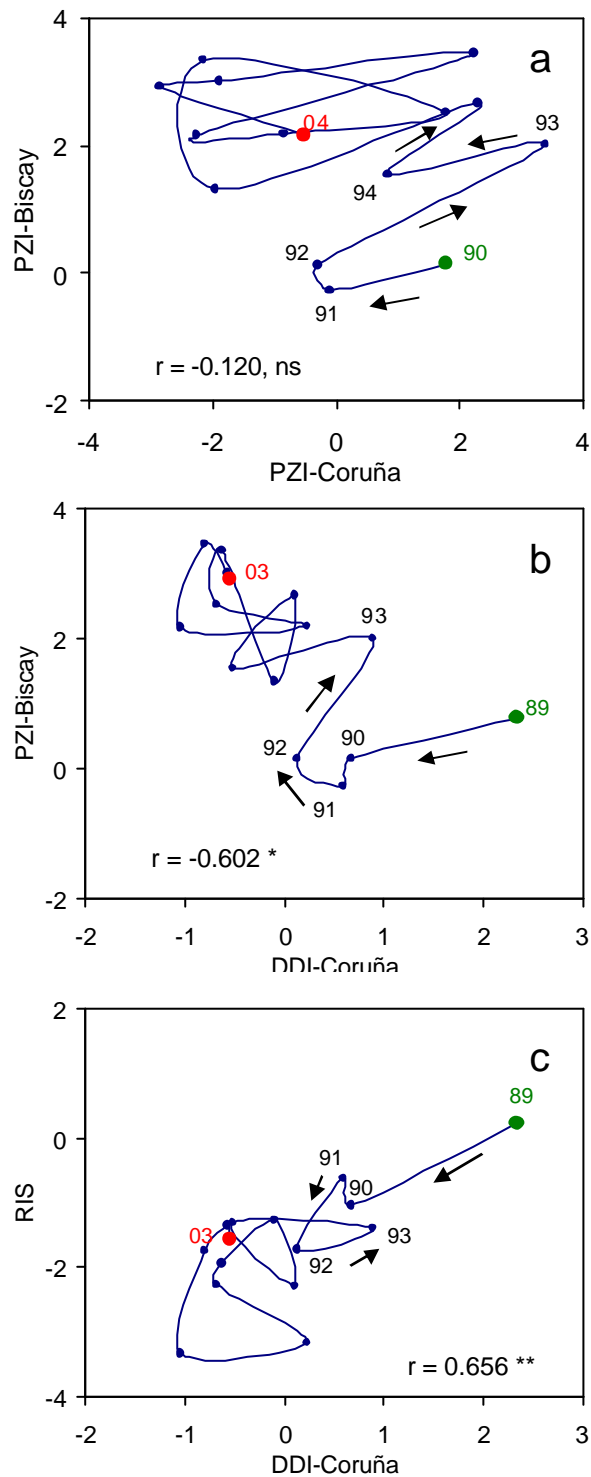
Fig. 8. Plots of (a) PZI of the Bay of Biscay versus PZI of A Coruña or (b) versus the diatom – dinoflagellate index of A Coruña (DDI); (c) plot of RIS versus DDI. Points are linked according to the temporal sequence (indicated also by the arrows and years). Numbers indicate selected years. The Pearson correlation coefficient (r) and its significance are also indicated in each panel. *: P<0.05; **: P<0.01; ns: not significant.