Decadal changes in hydrographic and ecological time-series in the Balearic Sea (western Mediterranean), identifying links between climate and zooplankton

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We investigated possible relationships between climate, hydrography, and zooplankton abundance in the Balearic Sea (BS), during a 10-year survey period spanning January 1994 to December 2003. It was demonstrated that large-scale atmospheric variability in the North Atlantic (NA) Ocean acts as a driver of regional meteorological variations and hydrographic patterns in the BS. The results also revealed that the variability of copepods, appendicularians, cladocerans, siphonophores, doliolids, and ostracods is closely related to variations in water temperature recorded during strong anomalies of the NA climate (>1 s.d.). Although the time-series that we analysed cover a period that is relatively short for investigating climate effects on marine ecosystems, the statistical results reported were consistent enough to emphasize the NA's climate effect on the BS. The cascade of links identified by these results should be considered and integrated into the assessment and modelling studies of pelagic ecosystem and biogeochemical fluxes in the western Mediterranean Sea.

Keywords: Balearic Sea, hydrography, North Atlantic climate, western Mediterranean, zooplankton.

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Introduction

During the last decades, several reports have considered global changes in long-term variations in the catches of commercially important fish species (Perry et al., 2004), shifts in the basin-scale distribution of pelagic copepods (Beaugrand et al., 2003), and anomalous outbursts of gelatinous zooplankton (Purcell, 2005). These changes may indicate modifications in the functioning of marine pelagic ecosystems. Because they occurred during a period of manifested changes in the climate pattern of the northern hemisphere, possible causal links should be considered in advance. In this framework, retrospective analyses are required to assess and understand the variability of climate and its potential effects on marine ecosystems, and to identify indicators of the state of the ecosystem. Zooplankton have been found to be useful indicators of the effects of climate change on pelagic ecosystems (Hays et al., 2005). These organisms generally have short life cycles, which favour rapid responses to environmental changes. If we consider their pivotal role linking primary producers with fish, their response could be expanded to the foodweb, thereby affecting the functioning of marine ecosystem.

The Balearic archipelago is located in the western Mediterranean (WM) between the saline, colder, and nutrient-rich waters of the North basin, and the less saline, warmer, and more oligotrophic waters of the Algerian basin. Meridional water mass exchanges between the two basins make this area suitable for investigating the dynamics of the two main surface (0–200 m) water masses that characterize the WM. Monitoring meridional exchanges may also help to identify environmental variations that may affect zooplankton communities. This is significant because the Balearic Sea (BS) encompasses important spawning areas of pelagic fish. Hence, substantial variations in the zooplankton abundance may affect the spatial distribution of fish and therefore be useful in detecting indirect climate effects on fish populations.

First, we analysed a 10-year time-series of zooplankton abundance from the BS. Although this is a relatively short period to investigate climate effects on marine ecosystems, our primary goal is to detect climate fingerprints on short time-scales (i.e. monthly) on the variability of hydrographic features of the BS. Second, we wanted to evaluate possible threshold values of climate forcing on the pelagic environmental conditions. Finally, we discuss the possible consequences that large-scale atmospheric variation may have on the abundance of zooplankton, and how changes in climate may affect the functioning of the WM pelagic ecosystem.

Methods

Hydrographic data

Sampling was performed at a monitoring station (Figure 1) located 2.5 nautical miles offshore (77-m depth) on the southern shelf of Mallorca channel (39°28′59N 2°25′63E), from January 1994 to December 2003 with the RV "Arola". The geographic
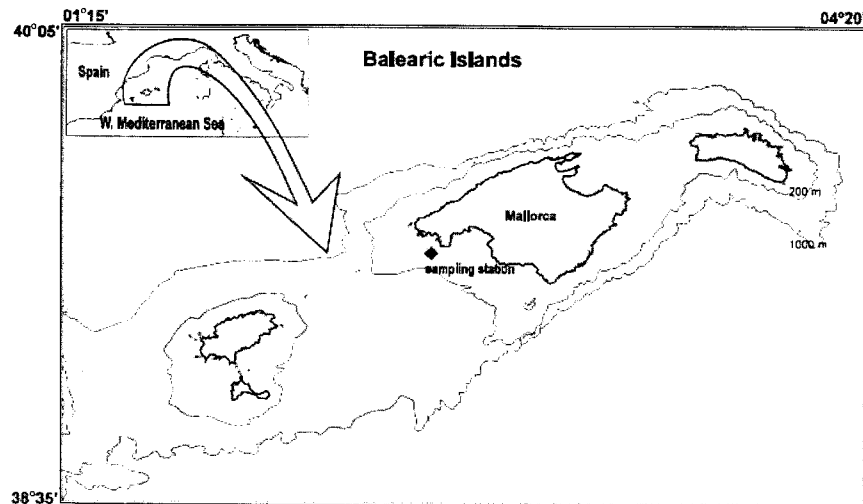
Figure 1. Map of the WM indicating the sampling area in the BS. Grey lines represent the 200 and 1000 m isobaths.

location of the Mallorca channel reflects the influence of open-sea conditions: a short island slope and its proximity to the sampling station whose depth reaches 700 m. The biweekly sampling was carried out during daylight over the 10-year period. Temperature and salinity from surface to 75-m depth were measured using a CTD. Instead of using surface water temperature and salinity, which are greatly influenced by local meteorological forcing, we used the average of the 75 m layer for analysis, which may indicate meridional water mass exchanges. Water samples for chlorophyll *a* and nutrients were taken with 5 l Niskin bottles at depths of 0, 5, 15, 25, 50, and 75 m. Nutrients samples were immediately frozen ($-20°C$) and analysed in the laboratory, according to Armstrong *et al.* (1967). Chlorophyll *a* pigment was measured by fluorometry (Holm-Hansen *et al.*, 1965) after filtering 1.5 l of seawater from the Niskin bottles (see details in Fernández de Puelles *et al.*, 2007). Nutrients and chlorophyll data were integrated over the 75 m water column, and monthly means were used for analysis.

Biological data

Zooplankton organisms were sampled with bongo nets fitted with a 250 μm mesh. In all, 364 zooplankton samples were collected 1994–2003 by oblique hauls from a depth of 75 m to the surface. Monthly mean zooplankton data were used for analysis. Details of sampling methods and analysis are given in Fernández de Puelles *et al.* (2004a).

Large-scale data

Large-scale climate patterns affecting the northwestern Mediterranean (NWM) were synthesized to build a signal that represents the continuum of North Atlantic (NA) climate forcing on the area investigated (details are given in Molinero *et al.*, 2005a; and Fernández de Puelles and Molinero, 2007). This reduces the possibility of omitting climatic signals that could be weak but ecologically important (Taylor *et al.*, 2002; Voight *et al.*, 2003). Thus, the NA climate pattern was estimated by the composition of the key modes of large-scale atmospheric circulation over the northern hemisphere [i.e. Arctic Oscillation (AO), NA Oscillation (NAO), East Atlantic Pattern (EA), Gulf Stream/Northern Current (NC) Index (GSI), EA Western Russian Pattern (EA/WRUS), and

Northern Hemisphere Temperature (NHT)]. Details can be found in Molinero *et al.* (2005a). Climate datasets for the Atlantic sector are freely available at www.cru.uea.ac.uk (NAO and NHT), www.cpc.ncep.noaa.gov/ (AO, EA, and EA/WRUS), and www.pml.ac.uk/gulfstream (GSI).

Data analysis

Prior to statistical analysis, time-series were log-transformed, then analysed in their non-dimensional form (i.e. standard deviations from the mean of the time-series). Climatic information provided by atmospheric teleconnections was condensed by applying a principal component analysis (PCA) on a matrix, Z, composed of the ensemble of climate indices (years × climate indices). This procedure integrates the large-scale climate forcing over the study area into a few mutually independent variables (the principal components). A similar approach was used by Voight *et al.* (2003) and Molinero *et al.* (2005a). Zooplankton time-series were subjected to a time delay, and the resulting matrix analysed by PCA. The procedure consists of shifting the series with a constant lag n times, which generate a $n+1$ rank matrix (month × original series + n surrogates). PCA is applied to the matrix, leading us to extract the principal modes of temporal variability of the series (Sirabella *et al.*, 2001, and references therein).

A canonical correlation analysis (CCA) was carried out using the three first-principal components of each time-series to identify correlation patterns between climate and plankton. The CCA detects and quantifies the relationships between a p-dimensional random variable X and a q-dimensional random variable Y. Therefore, we look for linear combinations $a > X$ and $b > Y$ of the original variables having maximal correlation. A similar procedure has been used previously to identify the interrelations between climate and cod recruitment (Sirabella *et al.*, 2001), and climate and zooplankton (Molinero *et al.*, 2005b). The statistically significant correlations (i.e. NAC–temp) were also tested separately by adjusting the degrees of freedom in the statistical test to account for autocorrelation. Temporal dependence between the successive observations prevents an accurate estimation of the associated probability when a correlation test was used. For this reason, an adjustment of the degrees of freedom in the statistical test is required to compensate for autocorrelation. We used the

Table 1. First canonical correlation coefficients (CCA) between principal components of NA climate, 75-m depth water temperature, salinity, and nitrate.

NA climate	Monthly		Winter	
	r	*p*	*r*	*p*
NA climate – temperature	0.59	0.0001	0.88	0.0001
NA climate – salinity	0.27	n.s.	0.88	0.0001
NA climate – nitrate	−0.41	0.01	−0.44	0.01

Correlations were calculated on the complete time-series (Monthly), and also December – March (Winter).

method proposed by Chelton (1984) and modified by Pyper and Peterman (1998). In all correlations, a conservative alpha level of 0.01 was used to avoid the likelihood of committing a type I error when identifying links between climate and biological fields.

Results

Climate and hydrographic patterns

Canonical correlations reveal a significant relationship between the NA climate pattern and the integrated average (0–75 m) water temperature at monthly scales. A significant negative relationship was also detected between the NA climate signal and nutrient variability (e.g. nitrates). However, no relationship was detected with salinity (Table 1). The same analysis demonstrated that, when considering only winter months (DJFM), canonical correlations increased substantially, and this included that of salinity, which became statistically significant (Table 1).

The monthly scale variability of NA climate revealed a close connection between hydrological patterns (i.e. water temperature) in the BS and the NA climate (Figure 2). This is illustrated by considering water temperature recorded during anomalies of NA climate higher than 1 s.d. Strong values (>1 s.d.) have been suggested as thresholds for changes in the atmospheric circulation in the NWM (Hurrell, 1995; Vignudelli et al., 1999). During strong anomalies (>1 s.d.) in the NA climate, low concentrations of nitrates appear to be associated with low salinity and high temperature, whereas high concentrations were linked to the converse conditions (Figure 3a). Chlorophyll *a* concentrations were directly correlated with nitrates (Figure 3b). Both chlorophyll and
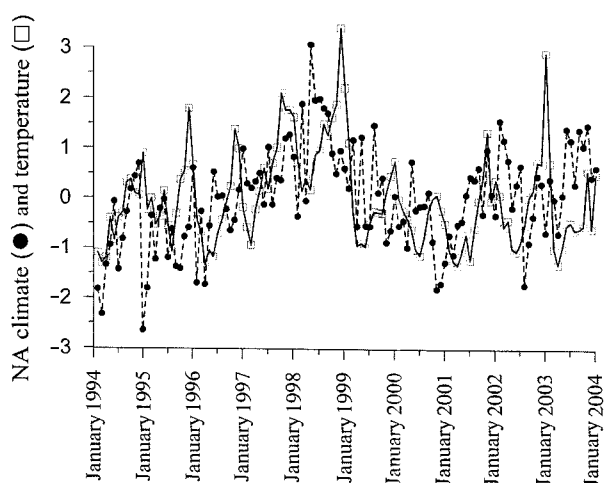
Figure 2. Monthly anomalies of the NA climate and 0–75-m-depth-averaged water temperature, 1994–2003.
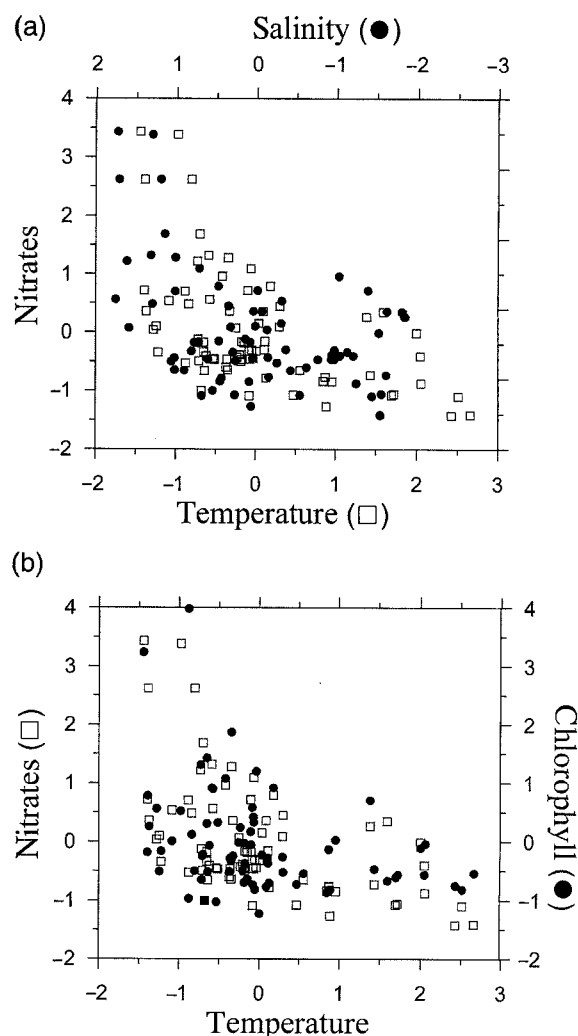
Figure 3. (a) Scatter diagrams of the relationship between temperature, salinity, and nitrate. Although a clear negative relationship is observed between nitrate and 0–75-m depth averaged water temperature ($r = -0.51; p < 0.001$), the relationship is positive between nitrate and 0–75-m depth averaged salinity ($r = 0.48; p < 0.001$). Solid symbols represent the relationship between salinity and nitrate, and empty symbols represent the relationship between temperature and nitrate; (b) scatter diagram of the relationship between nitrate, chlorophyll, and 0–75-m depth averaged water temperature. The Pearson correlation coefficient for the relationship between temperature and chlorophyll and the effective probability after correction for temporal autocorrelation are $r = -0.50$ and $p < 0.01$.

zooplankton followed a negative relationship with temperature (Figure 4). Although low chlorophyll and low zooplankton abundances were associated with high temperatures, a wide range of densities was apparent at low temperatures. Such a strong clear inverse association appears indicative of nutrient enrichment in the BS, probably linked to low anomalies of NA climate.

Zooplankton variability

A moderate zooplankton abundance was found during the study (annual mean value of 953 ind. m^{-3}, s.d. = 228) along with low
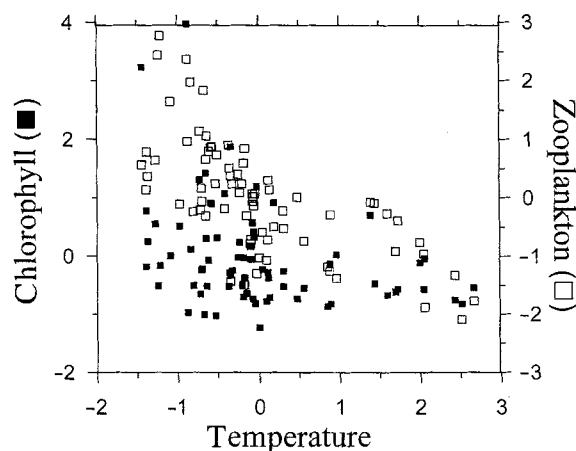
Figure 4. Scatter diagram of the relationship between chlorophyll, total zooplankton, and 0–75-m depth averaged water temperature. The Pearson correlation coefficient for the relationship between temperature and total zooplankton and the effective probability after correction for temporal autocorrelation are $r = -0.68$ and $p < 0.001$.

more abundant during high temperatures, although variability was high at low temperatures. The results show that NA climate anomalies (>1 s.d.) appear as threshold values from which the climate effect on the hydrography and zooplankton of the BS become noticeable at short time-scales.

Discussion

We have demonstrated a close connection between the NA climate and hydrographic patterns in the BS, by which the depth-averaged water temperature is linked to the expansion of the NC. This
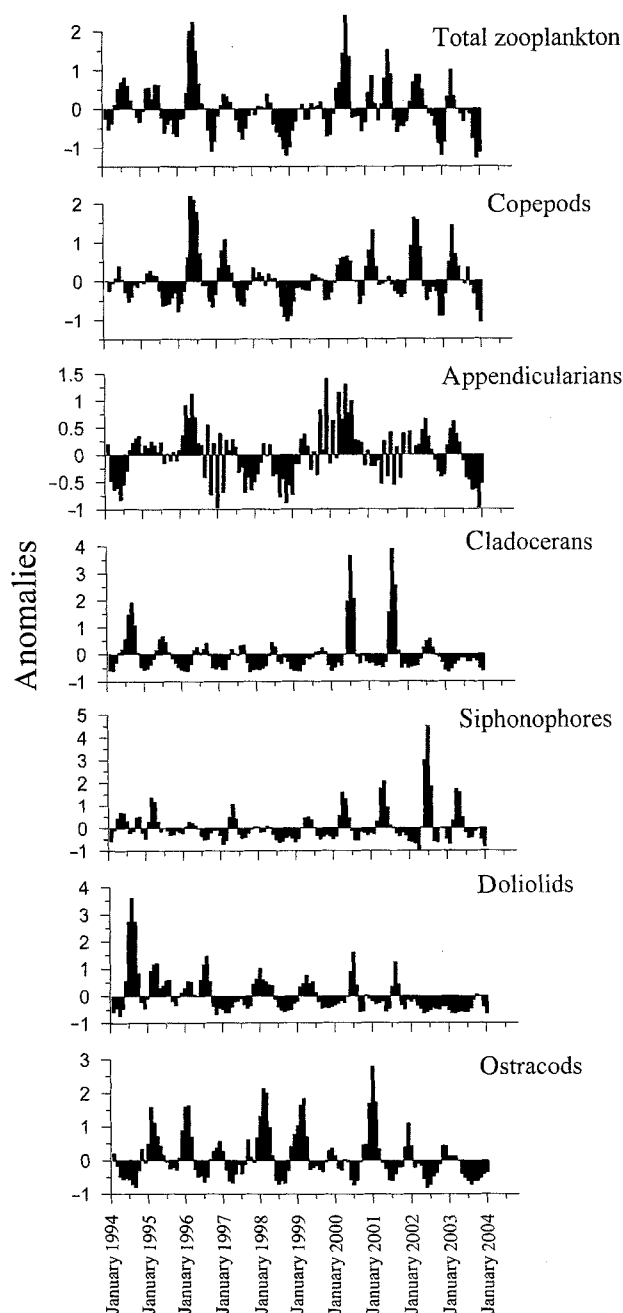
biomass (mean of 5.4 mg dry wt m^{-3}). Copepods were always the most abundant group (56% of the total), revealing a pattern similar to that of total zooplankton abundance. Other zooplankton included gelatinous species (which consisted primarily of 17% appendicularians, 5% doliolids, and 1% salps) and cladocerans (10%). During winter and spring, copepods represented 70–90% of total zooplankton. In summer, however, cladocerans became increasingly important. Other groups, such as appendicularians, were present throughout the year and demonstrated limited variability in abundance. Among the minor groups, doliolids demonstrated several peaks in abundance during the year with the greatest abundance in late spring/early summer. Siphonophores and ostracods were most abundant in winter and early spring. Overall, zooplankton biomass was greatest during the first half of the year with a maximum in spring (6.4 mg m^{-3}). Two peaks in total zooplankton abundance were clearly visible (March and May with 1200 ind. m^{-3}). During the second half of the year, zooplankton abundance remained low, although there was a slight increase after the stratification breakdown during late summer.

Over the period 1993–2004, we observed marked interannual variability in zooplankton abundance, with three major peaks in 1996, 2000, and 2001, and two lows in 1995 and 1998 (Figure 5). At the monthly time-scale, copepods were most abundant in 1996 and after 2000, and least abundant in 1998. The appendicularians showed great variability at monthly and interannual scales, with peaks in abundance in 1996 and 2000. The abundance of cladocerans and siphonophores was less variable. Cladocerans were most abundant in 2000 and 2001, whereas the numbers of siphonophores increased after 2000 and peaked in 2002. Doliolids demonstrated a marked downward trend in abundance, with the lowest abundances observed after 2002. Ostracods demonstrated great interannual variability with a peak in 2001.

Copepods, appendicularians, and cladocerans demonstrated a strong inverse correlation with temperature when the NA climate values were higher than 1 s.d. (Figure 6), whereas the pattern for siphonophores and doliolids was less evident, although it remained significant (Figure 6). The ostracods were generally

Figure 5. Monthly scale variability of total zooplankton and its main groups (copepods, appendicularians, cladocerans, siphonophores, doliolids, and ostracods), 1994–2003. Values are indicated as anomalies (standard deviations from the mean of the time-series).
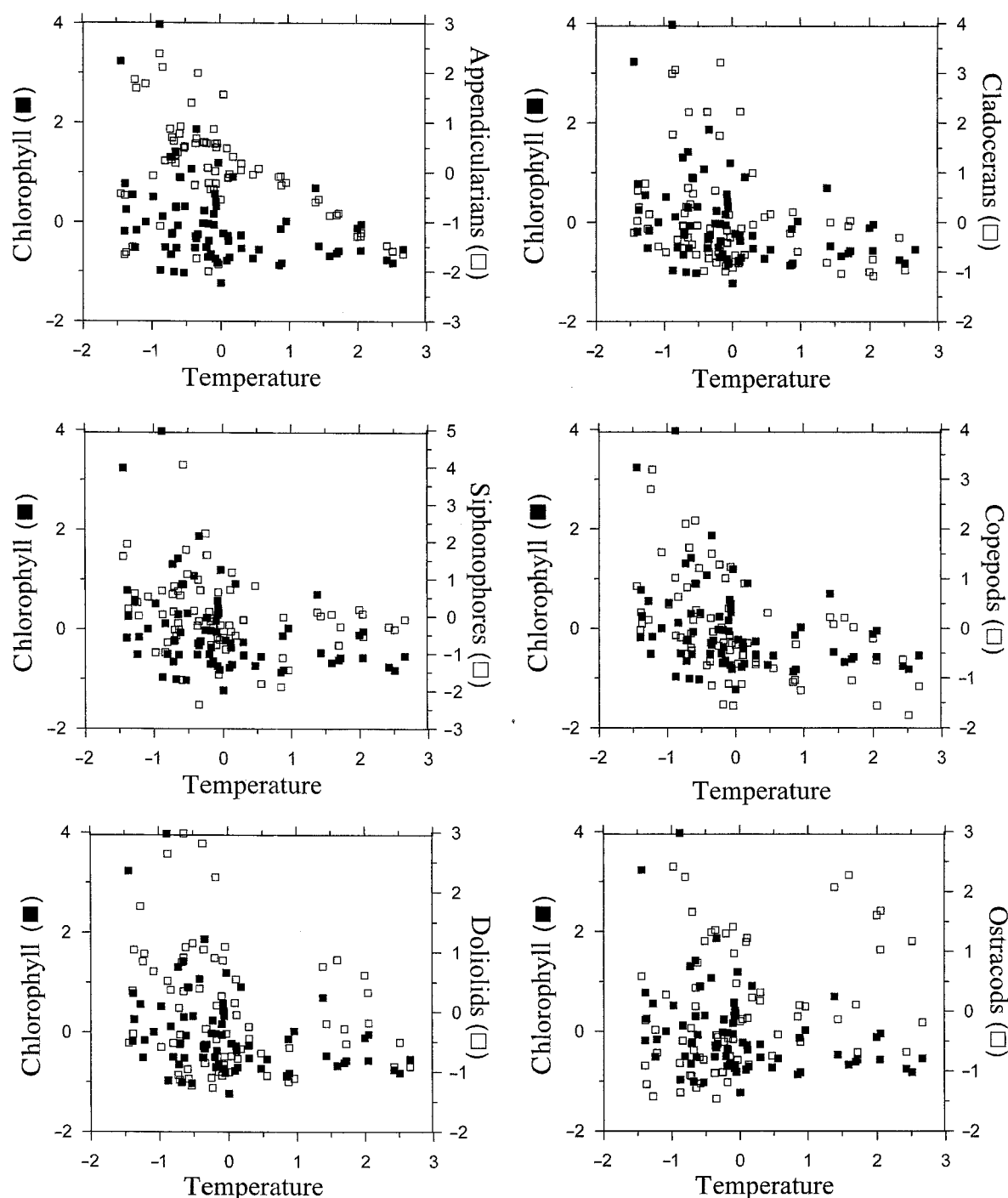
Figure 6. Scatter diagram of the relationship between chlorophyll, zooplankton groups, and 0–75-m depth averaged water temperature. The Pearson correlation coefficient and the effective probability after correction for temporal autocorrelation are shown in each panel.

current flows from the NWM through the Catalan coast and the BS in a roughly northeast–southwest direction (Font, 1986). It is associated with a shelf slope front separating the coastal and more saline open waters, which is the only permanent hydrographic structure and one of the most important features in the region. Therefore, expansion of the NC can indicate meridional water mass exchanges in the WM basin. During cool years associated with negative anomalies of the NA climate, greater productivity characterizes the Gulf of Lions (Estrada *et al.*, 1985).

That is caused partly by stronger winter mixing that reaches greater depths and partly because the formation of deep waters may spread over a larger area (MEDOC Group, 1970). We suggest that the higher production of the northern area of the WM is transported by the southern spreading of the NC, which may be reflected in the hydrographic conditions in the BS.

Our proposal that the NA climate influences the hydrographic patterns of the BS is fully consistent with recent findings of NA teleconnections effects in the sea level anomalies in the NWM

(Orfila *et al.*, 2005). This also extends our previous work on the effects of NA climate on the regional atmospheric variability in the BS (Fernández de Puelles and Molinero, 2007). The truncated monthly time-series of climate indices capture the dominant atmospheric forcing, particularly in winter, which affects the hydrographic conditions in the BS, and ultimately the abundance of zooplankton groups.

In our analyses, winter emerges as the critical time window during which a tight link between the NA climate variability and zooplankton changes is evident in the BS. This is likely because the coupled ocean–atmosphere system in the NA is most dynamic during winter and, therefore, will strongly affect the atmospheric and hydrographic conditions in the BS. Through its influence in the water column (i.e. temperature and stratification), the NA influences variations of nutrients (e.g. nitrates) and chlorophyll in the BS, leading to greater concentrations during negative anomalies of the NA. A possible ecological explanation is that negative anomalies of NA climate are associated with cold winters and stronger mixing of the water column in the NWM, which enhance the availability of nutrients for phytoplankton growth. This is supported by the close link between NA climate variability and nitrate concentration (Figure 3). We then suggest that one of the factors driving the abundance of zooplankton can be linked to food availability (i.e. phytoplankton) favoured by nutrient enrichment associated with the forcing of negative anomalies in atmospheric forcing in the NA. In accord with this, Fernández de Puelles *et al.* (2003, 2004a) demonstrated an inverse relationship between nitrate concentration and water temperature at annual scales ($p < 0.01$). When analysed at monthly scales, such a relationship remains significant ($r = -0.53$; $p < 0.001$), and it increases when only winter conditions are considered ($r = -0.60$; $p < 0.001$). This is consistent with the higher chlorophyll concentration observed in January and February in the whole water column that is associated with years of intense, cold winds and heavy storm events in the area (Fernández de Puelles *et al.*, 2007). Moreover, a marked southern spreading of a large volume of northern waters (1.3 Sv) has been noted in the BS in winter (Pinot *et al.*, 2002). The intensity of the current decreases in spring and reaches its lowest values in summer, when the transport falls to <0.05 Sv. The strength of the NC, linked to the NA climate forcing, therefore drives the spread of northern waters (colder and richer) into the BS (Pinot *et al.*, 2002). The stronger the atmospheric forcing during winter (negative anomalies of the NA climate), the more intense the water column mixing. This may reach deep waters, enhance productivity in northern areas, and favour a southern spread of rich waters (Estrada *et al.*, 1985). This can also be reflected in the increase of nutrient availability (e.g. nitrate) for primary production in the BS area. Variations in NA atmospheric forcing also affect the dynamics of the water transport in the Corsica Channel (WM) and the NC (Vignudelli *et al.*, 1999). Consequently, increased zooplankton abundance is likely favoured by both the increased productivity associated with the low NA climate anomalies and the increased advection from the NWM into the BS.

Interannual variability, based on mean annual abundance estimates of different zooplankton groups, indicated that abundance increased during cooler years. However, different relationships emerged for different zooplankton groups. For instance, the abundance of copepods, appendicularians, and siphonophores increased during cooler and more saline periods, when the NWM waters were present in the area. In contrast, other groups
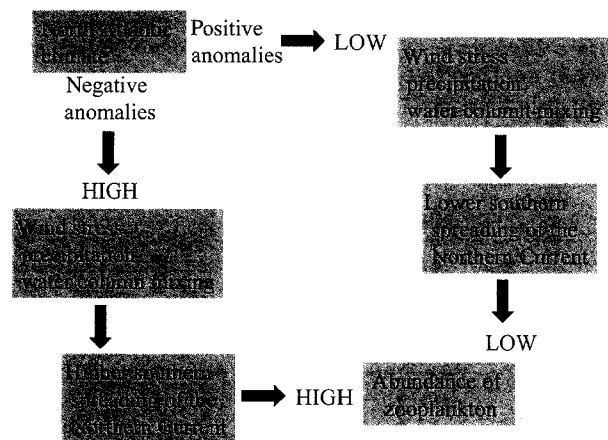

Figure 7. Mechanisms through which the NA climate may affect hydrographic patterns in the BS and ultimately the abundance of zooplankton.

such as doliolids decreased, suggesting their preference for warmer and less saline Atlantic waters (Fernández de Puelles *et al.*, 2007). Ostracods did not exhibit a clear relationship with hydrographic conditions. These differences among zooplankton groups may also be related to their seasonality, which is affected differentially by the seasonal forcing of temperature as well as by variations in the strength of the NC, which decreases substantially from winter to summer. As the NC intensity is higher during winter, it is plausible that some zooplankton groups, i.e. copepods that peak in winter/spring, may act as tracers of the meridional water mass exchanges in the WM.

The seasonal pattern of zooplankton observed in the BS was similar to that in other areas of the WM (Sabatés *et al.*, 1989; Mazzocchi and Ribera d'Alcala, 1995; Gaudy and Champalbert, 1998). However, the BS has low zooplankton biomass and abundance compared with other WM areas (Rodriguez, 1983; Razouls and Kowemberg, 1993; Seguin *et al.*, 1993; Champalbert, 1996). In the NWM, high densities of zooplankton found close to frontal systems confirm its tendency to concentrate in zones of divergence (Boucher *et al.*, 1987), where gelatinous and large zooplankton taxa are more abundant (Sabatés *et al.*, 1989; Fernández de Puelles *et al.*, 2004b).

The main processes by which large-scale climate fluctuations may affect changes in the abundance of zooplankton in waters of the BS (Figure 7) are part of a larger and long-term variability linking the pelagic dynamics in the NWM with the ocean–atmospheric system in the North Atlantic Ocean, in accord with Molinero *et al.* (2005a, b) and Fernández de Puelles and Molinero (2007). Moreover, as the abundance of zooplankton directly affects the dynamics of pelagic foodwebs, it is ecologically plausible that the NA climatic effect on zooplankton affects the vertical particle flux and carbon transfer rates between upper and lower layers. Therefore, a thorough understanding of the WM ecosystem and its temporal variability requires accurate assessment of the NA forcing effects on primary and secondary production.

Acknowledgements

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