Interannual variability of copepod abundance in the Balearic region (Western Mediterranean) as indicator of basin scale hydrological changes

Mª Luz Fernández de Puelles[1*], Ana Morillas[1], Angel Lopez-Urrutia[2] and Juan Carlos Molinero[3]

[1] Centro Oceanográfico de Baleares. Instituto Español de Oceanografía. Muelle de Poniente s/n 07015- Palma de Mallorca, Baleares. Spain.

[2] Centro Oceanográfico de Gijón. Instituto Español de Oceanografía. Avda. Principe de Asturias 70 bis. 33212-Gijón, Asturias. Spain.

[3] Ecosystem Complexity Research Group, Station Marine, Université des Sciences et Technologies de Lille. CNRS - UMR 8013 ELICO, 28 avenue Foch, BP 80, F-62930 Wimereux, France.

Key words: *Copepods, hydrography, interannual-changes, Balearic Sea, Western Mediterranean, North Atlantic Oscillation.*

* *Corresponding author*

e-mail address: mluz.fernandez@ba.ieo.es

Abstract

We have analyzed yearly changes of the copepod community during the period 1994-1999 in relation to the environmental variability in the Balearic Sea, Western Mediterranean. There were marked hydrological changes which in turn appeared as main drivers of the interannual variability of the copepod community in this Balearic region. Moreover, the synchronous variations of copepods and hydrography strongly suggest a rapid response of copepods to environmental changes, i.e. inputs of different water masses coming through the study area. We suggest that changes in temperature and salinity are linked to large-scale processes, likely occurring at a basin scale, which is reflected in the Western Mediterranean by the differential effect of water masses from distinct origin. These results highlight NAO effects in a boundary area for meridional exchanges of water masses, and therefore stress on changes in copepods community as potential tracers of the functioning of western Mediterranean pelagic ecosystem.

INTRODUCTION

The Mediterranean Sea is a mid-latitude semi-enclosed sea connected with the Atlantic Ocean via the Gibraltar strait. Its geographical location means this area is exposed to the major processes acting upon the global climate system, and consequently to be one of the most sensitive areas to future climate change previsions (IPCC 2001). In the Western Mediterranean, the Balearic Sea is a hydrographical transition area that separates two sub-basins where different water masses come trough: the Gulf of Lion and the Alborán basin. The former is characterized by cool and salty waters, whereas the latter shows fresher waters of Atlantic origin and milder weather conditions (Font *et al.* , 1988; Pinot *et al.*, 2002). The geographic location of the Balearic islands (39-40º N; 1-4º30' E) led this region to be influenced by a combined effect of atmospheric forces and mesoscale circulation governing the Western Mediterranean (Pinot *et al.* 1995; Schneider *et al.* , 2005). In turn, the ocean-atmosphere coupled system may favour in this area a complex geographical barrier between different water masses, which may also vary seasonally (Garcia *et al.*, 1994). Therefore, the Balearic Sea appears as an ideal site to investigate the variability of the two main water masses characterizing the western basin, and therefore their influence on the dynamics of the pelagic ecosystem.

Zooplankton, and particularly copepods, cab be good indicators of water masses flows (Edwards *et al.*, 2002; Hwang and Wong, 2005; Peterson *et al.*, 2001). Indeed, particular assemblages are related to specific water masses, which could be useful to detect through the long-term changes of copepods anomalous variations in hydrographic regimes. Furthermore, copepods link primary producers with top predators (i.e. copepods constitute a key food item for fish larvae), and therefore they may be used as an integrative measure of biological productivity in marine ecosystems.

2

The interannual variability of plankton is high in relation to the environment, and time-series are strongly recommended to investigate functional changes in the marine ecosystem (Colebrook, 1978, 1985). So far, such kind of studies are scarce in low latitudes, such as the case of the Balearic Islands, although they are fundamental to assess environmental health in the Mediterranean marine ecosystem. Indeed, biological time-series, combined with meteorologicaland oceanographic information are fundamental tools to understand long-term changes in marine ecosystemsa (CIESM, 2003).

In the Mediterranean basin, previous works have investigated the interannual variability of copepods in different sites, such as the Gulf of Lyon (Razouls and Kouwenberg, 1993), Marseille (Gaudy, 1985), Ligurian Sea (Licandro and Ibanez, 2000; Molinero *et al.*, 2005), the Saronikos Gulf (Christou, 1998), the Balearic region (Fernández de Puelles *et al.*, 2003b), Gulf of Naples (Mazzocchi and Ribera d'Alcala, 1995), and the Adriatic Sea (Baranovic *et al.*, 1993; Cataletto *et al.*, 1995), however most of these studies were carried out in coastal waters while time series from offshore waters are very scarce. Furthermore, although global atmospheric forcing strongly drives the dynamics of the Mediterranean basin (Hurrel, 1995; Redaway and Bigg, 1996) only few studies have investigated the response of copepods to large-scale atmospheric oscillations (Fernández de Puelles *et al.*, 2004a; Molinero *et al.,* 2005a,b).

In this work we have investigated the seasonal and interannual variability of the copepod community in the Mallorca channel over a transect across the shelf. This region has very freshwater inputs from rivers or chemical industries . The stations sampled are under strong influence of open-ocean circulation and located in the boundary area between the southern and northern Western Mediterranean. Our aim is to assess the response of copepods to hydrographic conditions governing the Balearic Islands, understand the role of copepods as indicators of the water mass dynamics in the study region and therefore study the potential link of these findings with the North Atlantic climate forcing.

METHOD

Physical and chemical data.- From January 1994 to December 1999 three stations at 75, 100 and 200 m depth (St. 1, 2 and 3 respectively), located along a transect reaching the shelf-break over the southern shelf of Mallorca, were visited monthly at the same time each day (9:30 am to 12:00 pm; Fig. 1). Water for nutrient analysis and hydrography were collected at depths of 0, 5, 15, 25, 50, 75, 100, 125 and 200 m (if bottom depth was not shallower) with 5 L niskin bottles. Nutrient samples were frozen (-20ºC) and analysed following Armstrong *et al.* (1967). CTD data were recorded monthly with a Seabird 19 probe. Air temperature data was obtained from a coastal station located 20 Km apart from the neritic station (data provided by the Spanish Meteorological Institute).

3

Biological information- Zooplankton was sampled with a Bongo Plankton net, fitted with a mesh with 250 µm pore size, by means of oblique hauls from 100 m to the surface (from 75 m at St. 1). Samples were fixed in 4% neutralised formaldehyde buffered with borax. The subsamples analysed were obtained using a Folsom Plankton splitter. At least two subsamples were analyzed and the data given as ind. m^{-3} (for details see Fernández de Puelles *et al.*, 2003a).

Statistical analysis.- Time series were log-transformed previous to statistical analysis. The studied environmental variables, temperature, salinity and nitrates were grouped together in a cluster analysis of monthly values in order to identify hydrological similarities between years. The method used for the hierarchical classification was the Bray-Curtis similarity index after squared root data transformation. The hierarchical classifications were carried out using the PRIMER program (Plymouth Marine Laboratory, UK).

To summarize the information available on the spatio temporal variability of species abundance we determined groups of species with similar patterns in the interannual, seasonal and coastal-ocean gradients. We excluded from our analysis rare species that appeared in less than 10% of the samples. We centered the data to zero mean to normalise the effect of species that appear in low densities (e.g. large copepods) to those that are generally very abundant (e.g. small copepods). We then calculated a k-means cluster on the monthly log (x+1) transformed data following Hartigan and Wong (1979). The four cluster encompassed 38 species which represent most of the total abundance of copepods. To investigate the differences amongst the four species clusters obtained we calculated the average abundance (centered and log transformed as explained above) of the species densities within each group. The seasonal, interannual and spatial differences amongst groups were then inspected graphically. To determine the differences in the interannual variation in abundance of each species cluster we calculated the annual means of the times series average for each group and regressed them against environmental variables. To further assess the temporal variability of the groups identified by the clustering analysis Principal Component Analysis (PCA) was applied on a matrix, Z, composed by the ensemble of species belonging to each group (month x species). Thereafter, we investigated the influence of environmental conditions on the temporal variability of different copepods assemblages by means of Pearson product moment correlation. Correlation tests were modified (i.e. re-estimation of the number of degrees of freedom) in order to account for autocorrelation (Pyper and Peterman, 1998).

RESULTS

Hydrography.- A seasonal cycle in temperature was the most obvious signal detectable in the upper waters of the study area, characterized by winter cooling and summer warming as a typical thermic regime of these temperate latitudes. Strong stratification develops between May and October from 50

4

to 75 m depth and a well mixed water column occurs during winter months (see St. 3 representing the area, Fig. 2 upper panel). During the six-year study the Sea Surface temperature (SST) has ranged from 13.1ºC in January (1994, 1996 and 1997) to 27.4ºC in August 1998. A sinking of the thermocline was observed during 1997 and 1998 (specially clear at 75 m depth). Conversely, salinity did not shown a well defined seasonality probably due to the influence of different water masses in the area (St. 3 ; Fig 2 bottom panel). Higher values were usually observed during winter (38.3 PSU) and lower iduring autumn (37 PSU). Monthly fluctuations dominated the signal particularly evident in the upper 50 m.

The average temperature for each year evidence a marked interannual variability, with an annual mean in 1998 which exceeded the mean of all 6 years by more than 0.7ºC. A warming trend was noticeable during the study period, although the years 1996 and 1998 were anomalous, as will be discussed later (Fig. 3a). The annual means of salinity are indicative of the interannual signal modulating the mesoscale hydrographic fluctuations in the study region (Fig 3b). The lowest values of 1995 and 1998 suggest that these fresher water masses originate from the south, at the same time these waters are warmer, what contributed to the warming trend described previously. The annual concentration of nitrates exhibited a strong depletion during the warming period and during those years with low salinity (Fig. 3c). The cluster output reflects the interannual variation of hydrological properties during the study period (Fig. 4). For example, the years 1994 and 1996 showed similar environmental conditions, that is, high salinity and nutrient concentrations, and low temperatures, suggesting the influence of the northern waters. The year 1998 was particularly warm with low salinities and nitrate concentrations, indicative of more recent Atlantic waters, while the other years, 1995, 1997 and 1999, were considered as transitional, as the more typical situation in the Balearic Sea.

Variability of the copepods community.- Copepods were dominant in the zooplankton assemblage at the three stations (54%) and between 10 to 15 species (68 to 80% of total copepods) determined the bulk of the copepod abundances. Accounting the 95% of the copepods, 15 genera were found and a total of 83 species identified. *Oithona* and *Clausocalanus* (*C. furcatus, C. arcuicornis, C. pergens* and *C. paululus*) were the most abundant copepods (52% of total copepods) but *Ctenocalanus vanus, Paracalanus parvus, Centropages typicus, Acartia clausi* and *Diaixis hibernica* were also very abundant (>2%; Fig. 5).

Total copepod abundance showed a cross-shelf gradient being lowest at the more oceanic station. (Fig. 6). Two peaks in total abundace ocurring in spring (high) and end-summer (low) characterized the seasonal variability with the spring peak being usually larger.

[ELIMINA ESTE PARRAFO Y LA FIGURA 7] Interannual variability was observed in the temporal distribution of some of the species analyzed. For instance, *Centropages typicus* more abundant during spring was more abundant during the last years of the series. *Acartia clausi* was more abundant during the summer preference and more coastal presence, being particularly abundant during the warmer years. *Temora stylifera*, abundant at the three stations showed highest abundance during the autumn but without any clearinterannual variability (Fig. 7). The most abundant copepods such as *Clausocalanus furcatus, Ctenocalanus vanus* and *Paracalanus parvus* more abundant during the cooler months did not show clear interannual differences during the study period. On the contrary, the less abundant *Calanus helgolandicus*, only present during the winter of the first three years completely vanished from the study area(Fig. 7). *Nannocalanus minor* exhibited a hig**her** abundance during the autumn and *Neocalanus gracilis* a higher presence during the winter, but they both exhibited similar interanual variability. Some other few species seem to bemore abundant at the end of the time-series, such as *Acartia danae* (Fig. 7) and *Centropages bradyi,* present in late summer and autumn respectively.

The most abundant copepods were grouped into four copepod assemblages by theK-means cluster analysis (Fig. 8). The first group was composed by *Calanus helgolandicus, Clausocalanus arcuicornis, C. pergens + C. paululus, Ctenocalanus vanus, Ischnocalanus tenuis, Pleuromamma gracilis* and *Candacia* spp. They were generally present at the three stations during the cold months, from winter to early spring. There was a significant correlation between the abundance of this copepod group and salinity (r=0.73; p<0.05) and an inverse correlation was observed with temperature (r=-0.91, p<0.01).

As a member of thesecond assemblage was the most abundant species *Clausocalanus furcatus,* that exhibited highest abundances at themore coastal locations (St1>St2>St3; p<0.05) with *Paracalanus parvus, Centropages typicus, Acartia clausi, Isias clavipes* and *Diaixis hibernica* being more abundant during warm months, from late spring to summer. This group also showed positive correlation with salinity, but only the coastal station was significant (St. 1; r= 0.53; p<0.05) and a negative correlation with temperature (St. 1; r= -0.64; p<0.05).

The third group consisted of more oceanic species with *Neocalanus gracilis, Nannocalanus minor*, *Mecynocera clausi*, *Pleuromamma abdominalis*, *Lucicutia flavicornis* and *Farranula rostrata,* as the most representative species. They were more abundant when temperature was low (St. 3; r=-0.77; p<0.05) while low correlation was observed with salinity. Only the coastal station showed negative correlation when the salinity was increasing (St. 1; r=-0.70; p<0.05) indicating their preference for less saline, oceanic waters.

The 4th group was dominated by *Oithona* that was present at the three stations,with a peak in abundance during the autumn, together with *Calocalanus pavo, Calocalanus styliremis, Ischnocalanus plumulosus, Temora stylifera, Centropages bradyi* and *Acartia danae.* This group did

6

not show differences amongst stations. Nevertheless these species were the only assemblage that was generally more abundant when the temperature was high (r= 0.53; p<0.05).

Regarding the temporal variability of the copepods assemblages obtained from the Principal Components analysis,for each group we found that most of the variability is contained in the PC1 (mean 43% of the total variance). The investigation of the relationship between PC1s and hydrographic parameters (e.g. temperature and salinity) showed again significant relationship between group 1 and both salinity and temperature (r=0.64; p<0.001, and r=-0.66; p<0.001, respectively), and group 2 and salinity (r=0.70; p<0.001). The observed synchronous changes on their temporal variability strongly suggest these groups, but particularly group 1, may act as indicators of hydrographic changes in the Balearic Sea, as represented in Fig. 9. This was supported by the tight link between the interannual variability of group 1 (PC1) and the North Atlantic Oscillation, which summarizes a major large-scale climatic forcing on the dynamics of water masses in the western Mediterranean. Therefore, these results strongly highlight that group 1 integrates the variability of mesoscale hydrographic features, which are ultimately linked to the forcing of large-scale climate on the Western Mediterranean.

DISCUSSION

We have analyzed yearly changes of the copepod community during the period 1994-1999 in relation to the environmental variability in a boundary area of the Western Mediterranean. Our results highlight the strong hydrological changes that the area experiences, i.e. saltier and cooler waters noticed in 1996, and a warmer trend observed during 1998-1999. These changes appeared to be importantdrivers of the interannual and seasonal variability of the copepod community in the Balearic region. Moreover, the synchronous variations of copepods and hydrography strongly suggest a rapid response of copepods to the environmental changes, i.e. inputs of different water masses coming through the study area. This result suggest the importance of copepods as indicators of hydrological regimes, as has also been reported in the Northeast Atlantic (Edwards *et al.* , 2002; Beaugrand *et al.*, 2002; Beaugrand, 2003), the California current (Peterson *et al.* , 2001; Rebstock 2002), the China current (Hwang and Wong, 2005), and the North Pacific (Mackas *et al.* , 2001)

Hydrography is likely to have substantial influence on the overall zooplankton distribution at coarse and mesoscales (Boucher, 1984; Longhurst, 1967; Peterson *et al.*, 1979), and is in turn tightly linked to atmospheric forcing. A clear cross-shelf gradient was observed in the copepod abundance as in other areas of the Western Mediterranean Sea (Estrada *et al.*, 1985). Such trend is particularly evident in the Balearic Sea where the shelf is very short compared to other coastal areas of the Iberian mainland. The copepod data collected during the 6 year study showed moderate abundance comparable to that observed in the Thyrrenian Sea (Mazzocchi *et al.*, 1997), between poor areas of

7

the eastern Mediterranean (Siokou-Frangou, 1996; Christou, 1998) and richer areas of the Western Mediterranean, such as the Alborán Sea (Rodriguez, 1983; Seguin *et al.*, 1993), the Catalán Sea (Sabatés *et al.*, 1989; Calbet *et al.*, 2001) or the Ligurian Sea (Champalbert, 1996; Licandro and Ibanez, 2000).

The four copepod species assemblages identified seem to indicate preference for different seasons and water masses. The characterisation of the communiy assemblages is the first step needed to understant the response of marine communites to hygrological forcing as they represent groups of species with similar environmental preferences. Indeed, the first group represented by the abundant *Clausocalanus arcuicornis, C. pergens, C. paululus, Ctenocalanus vanus* and the minor dominant as *Calanus helgolandicus*, showed a wide bathymetric distribution, and was generally more abundant during the winter. It is worth noting that the abundance of these species was enhanced when salinity increased, what suggests intrusions of northern Mediterranean waters, saltier and cooler than those water masses from the Alboran basin and the Balearic ones (Hopkins, 1985; Pinot *et al.*, 2002). In contrast, the species belonging to group 4, such as *Oithona* and *Temora stylifera*, showed higher abundances during warmer months. The only group with positive relation to enhanced temperature and no relation with salinity suggests their increased abundance during the warmer years.

The group conformed by *Paracalanus parvus, C. furcatus, C. typicus, A. clausi* and *D. hibernica* is characterized by higher abundance in the coastal region during spring-summer. On the contrary, the group consisting of *Nannocalanus minor, Neocalanus gracilis, Pleuromamma abdominalis* and *Mecynocera clausi* was characterized by higher prevalence in the oceanic stations during the autumn. Thewith fact that they are more abundant when salinity is lowest might indicate that they are characteristic of Atlantic water masses. The above species represent the 85% of the total copepod community, and therefore are indicative of the coupling between the abundance of dominant copepod species and the governing hydrographic conditions in the Balearic area. Although information on coastal species has been extensively documented in many areas of the Mediterranean (Mazzochi *et al.*, 1995; Siokou-Frangou,1996; Christou,1998; Vives,1966), less information exists for oceanic species, particularly in relation to hydrography (Mazzocchi *et al.*, 1997) or in deeper waters (Scotto di Carlo and Ianora, 1983). In this sense, our work provides information on the temporal variability of pelagic copepods associated with mesoscale hydrographic patterns. Indeed, some species exhibited higher abundances during the cooler period, as it was the case for *C. helgolandicus*, or warming period, as it was the case for *N. minor* and *N. gracilis*. In fact, the presence of *C. helgolandicus* during the first three years and its absence in the subsequent years, which were characterized by warmer conditions, indicate the affinity of this species for the colder and nutrient-rich waters from the North of the western basin. Conversely, *Nanocalanus minor* and *Neocalanus gracilis* showed a preference for southern waters of more recent Atlantic origin. A seminal review has

8

been done on the biology and ecology of *C. helgolandicus* in European waters (Bonet *et al.*, 2005), in which the effect of the water temperature on the fecundity on the species was highlighted, but also on its distributional area. Accordingly, in the Balearic Sea, *C. helgolandicus* may be an indicator of the northern water masses intrusions in the study site.

The geographical location of the Mallorca channel in the fluctuating boundary region between southern and northern waters determines the hydrographic features of the area characterized by the Balearic front and neighboring features, such as eddys, gyres and filaments (Jansá *et al.*,1998; Pinot *et al.*, 2002). The character of hydrological boundary area of the Baleares channels and their biological implications have been previously mentioned (Pinot *et al.*, 1995; Pinot and Jansá, 2001). In cold springs the water mass exchange is more intense in the Mallorca channel and clear segregations appear in the species of copepods (Fernández de Puelles *et al.*, 2004b). During the whole 1996 and particularly during winter and spring of 1997 the highest salinity records indicated the influence of northern waters. On the other hand, in 1998 the lowest salinity values suggest the influence of fresher waters of Atlantic origin. It is worth noting that the higher values of salinity registered during late 1996 and 1997, seem to be linked to a strong negative phase of the NAO, that increases westerlies and brings moist air to the Mediterranean region. An increased abundance of copepods was observed during these years in a coastal area of the Mallorca island in relation to hydrography and climatic anomalies (Fernández de Puelles *et al.*, 2004a). The low salinity was associated with mild winter atmospheric conditions (1995 and 1998), while high salinity with more severe winters (1994 and 1996). This strongly suggest that cold stormy weather in the Western Mediterranean favour the southward spread of northern waters while milder winter conditions allow for the northward spread of waters of recent Atlantic origin.

The study area is characterized by low concentrations of nutrients (Jansá *et al.*, 1998) and copepod abundance, and overall a low productivity (Fernández de Puelles *et al.*, 2003b). However, it is also characterized by a high diversity of copepods that likely results from the boundary position of the Balearic zone in the Western Mediterranean in which the intrusions of southern and northern water masses favour a mosaic of species from different water masses. The seasonal cycle constitutes the most important periodic oscillation in the copepod abundance. Maximum abundances were registered in the first months of the year when the waters are well mixed, whereas low abundances were observed during the stratified and warmer season, with abundance values closer to other oligothrophic areas of the Mediterranean sea (Siokou-Frangou, 1996; Christou, 1998).

The high monthly variability in the abundance of the main species of copepods suggests the complex interactions between them, mainly linked not only to the timing but also to the variability of the water masses they inhabit, as in other frontal areas of the Mediterranean sea (Boucher *et al.*, 1987; Gowen *et al.*, 1998; Thibault *et al.*, 1994; Zagami *et al.*, 1996). These results also showed a decrease

9

in the abundance of copepods during the study period. The positive correlation obtained between the yearly averages of temperature and copepod abundance strongly suggests that the progressive depletion could be a response to the warming trend. Such change has been also noticed in other zooplankton groups, and also appeared to be linked to the warming trend and nutrient depletion, when fresher water of Atlantic origin northward reached the area (Fernández de Puelles *et al.*, 2003b; Pinot *et al.*, 2002). The opposite relationship between zooplankton and temperature highlights the importance of a longer duration in the stratification of the water column in limiting the input of nutrients to surface waters and the limitation of phyto and zooplankton growth, a similar phenomena has been reported in waters of the Bay of Biscay during 90`s (Valdés and Morales, 1998).

In other areas of the Mediterranean the link with temperature was not always so clear since during 80's, a zooplankton decline was also observed with not relationship with environmental water conditions (Mazzocchi and Ribera d'Alcala, 1995). However in early 90's the increase in the abundance of copepods observed in the Aegean Sea seems to be related to an increase in salinity that was the reflect of water masses changes in the area, i.e. the intrusion of more saline open waters in the Saronikos gulf (Christou, 1998). Similar results were reported in the northern Western Mediterranean where the salinity was the more important variable in relation to the higher abundance of *Clausocalanus* spp. (Kowenberg and Razouls, 1990).

The observed warming trend during the study period was mainly linked to winter climate conditions milder each year from 1994 to 1998. In turn, the milder winter conditions may reduce cooling by local mixing in winter and also the spread of warm southern waters into the Mallorca channel (Fernández de Puelles *et al.*, 2004a). With regard to hydrography we have found that different waters reach the Mallorca channel (Pinot el al., 2002) and during the period of inflow of Atlantic waters, persistent eddies lying to the south of the Baleares. These structures are characterized by stratification and less nutrients than waters from the north, what suggest that southern waters could severely limit primary and secondary productions, and in turn strongly modify the structure of the copepod community in the Balearic Sea (Fernández de Puelles *et al.*, 2004b). Therefore, we suggest that temperature and salinity changes are linked to a large-scale process, likely occurring at a basin scale, which in turn are indicative of the water masses response to the North Atlantic forcing, as indexed by the NAO. Indeed, recent investigations have shown a strong effect of the North Atlantic climate on zooplankton populations in the Northwestern Mediterranean (Molinero *et al.* 2005a,b). Accordingly, the recognition of large scale dependence on the physical environment (Mackas, 1984; Sabatés *et al.*, 1989) is a fundamental step to understand zooplankton distribution at a yet finer level. In the Balearic Sea although the abundance of copepods seems lower than other Mediterranean regions in the western basin, these results led us to speculate that the variability observed is linked to mechanisms acting over a larger spatial scale in the western basin and likely related to atmospheric

10

oscillations, as they mainly drive the hydrodynamic conditions in the Mediterranean basin. These results have several implications in the functioning of the pelagic ecosystem of the Western Mediterranean. Indeed, they showed a rapid response of the main group of zooplankton to hydrographic variability, they also highlighted the effects of such changes on the productivity of the pelagic ecosystems, and finally, these results showed that such hydrographic changes are ultimately driven by meso- and large-scale processes linking the North Atlantic atmospheric forcing with the Western Mediterranean. Future work should focus on the identified indicator species and other zooplankton groups at different time-scales, in order to assess the ecological mechanisms through which planktonic functional groups response to hydrographic regimes driven by climate. In turn, this could facilitate the development of models of pelagic ecosystem in the Balearic region and else will improve our ability to forecast future changes in the Western Mediterranean.

ACKNOWLEDGEMENTS

This research has been carried out in the framework of project 1007 "Time-series of oceanographic observations in the Balearic Islands", supported by the Instituto Español de Oceanografía. Our thanks go to the crew of R/V "Odón de Buén" and to all those who contributed to the cruises and laboratory work: M. Serra, D. Oñate, MC. Iglesias and in particular to B. Amengual for the nutrient analysis and L. Vicente for the total copepod estimations.

REFERENCES

Armstrong, F. A. J., Sterns, R. C. and Strickland, J. D. H. (1967) The measurements of upwelling and subsequent biological processes by means of technicon autoanalyzer and associated equipment. *Deep-Sea Res*., **14**, 381-389.

Baranovic, A., Solic, M., Vucetic, T. and Krustulovic, N. (1993) Temporal fluctuations of zooplankton and bacteria in the middle Adriatic Sea. *Mar. Ecol. Progr. Ser*., **92**, 65-75.

Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A. and Edwards, M. (2002) Reorganization of noratlantic marine copepod biodiversity and climate. *Science*, **296**, 1692-1694.

Beaugrand, G. (2003) Long term changes in copepod abundance and diversity in the north east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fish. Oceanogr.,* **12,** 4-5, 270-283.

Bonet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., Ceballos, S., Dickman, R., Lopez-Urrutia, A., Valdes, L., Carlotti, F., Molinero, J. C., Weikert, H., Greve, W., Lucic, D., Albaina, A., Daly Yahia, N., Fonda-Umani, S., Miranda, A., Dos Santos, A., Cook, K., Robinson, S. and Fernández de Puelles, M. L. (2005) An overview of *Calanus helgolandicus* ecology in European waters. *Prog. Oceanogr.*, **65**, 1-53.

11

Boucher, J. (1984) Localization of zooplankton populations in the Ligurian marine front role of ontogenic migration. *Deep-Sea Res.*, **31** (5), 469-484.

Boucher, M. J., Ibañez F. and Prieur, L. (1987) Daily and seasonal variation in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front. *J. Mar. Res.*, **45**, 133-173.

Calbet, A., Garrido, S., Sainz, E., Alcaraz, M. and Duarte, C. (2000) Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *J. Plankton Res.*, **23**, 3, 319-331.

Cataletto, B., Feoli, E., Fonda-Umani, S. and Cheng-Yong, S. (1995) Eleven years of time-series analysis on the net-zooplankton community in the Gulf of Trieste. *ICES J. Mar. Sci.*, **52**, 669-678.

Champalbet, G. (1996) Characteristics of zooplankton standing stock and communities in the Western Mediterranean :relation to hydrology. *Sci. Mar.*, **60,** 2, 97-113.

Christou, E. D. (1998) Interannual variability of copepods in a Mediterranean coastal area (Aegean Sea). *J. Mar. Syst.*, **15**, 523-532.

CIESM. (2003) Mediterranean Biological Time Series. CIESM Workshop Monographs No. **22**, 142 pp. Monaco.

Colebrook, J. M. (1978) Continuous plankton records: zooplankton and environment, north-east Atlantic and North Sea, 1948-1975. *Oceanol. Acta*, **1**, 9-23.

Colebrook, J. M. (1985) Sea surface temperature and zooplankton, North Sea, 1948 to 1983. *J. Cons. Perm. Int. Explor. Mer.*, **42**, 179-185.

Edwards, M., Beaugrand, G., Reid, C., Rowden, A. and Jones M. (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar. Ecol. Prog. Series*, **239,** 1-10.

Estrada, M., Vives, F. and Alcaraz, M. (1985) Life and production in the open sea. In Margalef, R. (ed), *The Western Mediterranean*, Pergamon Press, London, pp. 150-200.

Fernández de Puelles, M. L., Gras, D. and Hernandez de Leon, S. (2003a) Annual cycle of zooplankton. Biomass, abundance and species composition in the neritic areas of the Balearic sea, Western Mediterranean. *P.S.Z.N. Mar. Ecol.*, **24** (2), 123-129.

Fernández de Puelles, M. L., Jansá, J., Gomis, C., Gras, D. and Amengual, B. (1997) Variación anual de los principales parámetros oceanográficos y planctónicos en el Mar Balear. *Bol. Inst. Esp. Oceanogr.*, **13**, 1, 12-26.

Fernández de Puelles, M. L., Pinot, J. M. and Valencia, J. (2003b) Seasonal and interannual variability of zooplankton community in waters off Mallorca island: 1994-1999. *Oceanol. Acta*, **26,** 673-686.

12

Fernández de Puelles, M. L., Valencia, J., Jansá, J. and Morillas, A. (2004a) Hydrographical characteristics and zooplankton distribution in the Mallorca channel (WM). *ICES J. Mar. Sci.*, **61**, 654-666.

Fernández de Puelles, M. L. Valencia, J. and Vicente, L. (2004b) Zooplankton variability and climatic anomalies from 1994 to 2001 in the Balearic Sea (WM). *ICES J. Mar. Sci.*, **61,** 492-500.

Font, J., Salat, J. and Tintoré, J. (1988) Permanent features of the circulation in the Catalan sea. In Minas, H. J. and Nival, P., (eds), *Oceanography Pelagic Mediterranean*, *Oceanol. Acta*, **9**, 51-57.

Fromentin, J. M. and Planque, B. (1996) Calanus and environment in the eastern north atlantic II Influence of the north Atlantic oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.*, **134**, 101-109.

García, E., Tintoré, J., Pinot, J. M., Font, J. and Manriquez, M. (1994) Surface circulation and dynamic of the Balearic Sea. Seasonal and interannual variability of the Western Mediterranean Sea. *Coastal and Estuarine Studies*, **46**, 73-91.

Gaudy, R. (1985) Features and peculiarities of the zooplankton community from the western Mediterranean. In Moraitou Apostolopoulou M. and Kiartsis, V. (eds), *Mediterranean Marine Ecosystems*, Plenum Press, New York, USA, pp. 279-302.

Gaudy, R. and Champalbert, G. (1998) Space and time variations in zooplankton distribution south of Marseilles. *Oceanol. Acta*, **21**, 6, 793-802.

Gowen, R. J., Cullough, M., Dickey-Collas, M. and Kleppel, G. S. (1998) Copepod abundance in the Western Irish Sea: relation to physical regime, phytoplankton production and standing stock. *J. Plankton Res.*, **20**, 2, 315-330.

Halsband-Lenk., C., Carlotti, F. and Greeve, W. (2004) Life strategies of calanoid congeners in two different climatic regimes: a comparison. *ICES J. Mar. Sci.*, **61**, 709-720.

Hopkins, T. S. (1985) Physics of the sea. In Margalef, R. (ed), *The Western Mediterranean*, Pergamon Press, Oxford, pp. 100-125.

Hartigan, J. A. and Wong M. A. (1979) A k-means clustering algorithm. *Applied Statistics,* **28**, 100-108.

Hurrell, J. W. (1995) Decadal Trends in the North Atlantic Oscillation: Regional Temperature and Precipitation. *Science,* **269**, 676-679.

Hwang, J-S. and Wong, K. (2005) The China Coastal Current as a driving force for transporting *Calanus sinicus* (Copepoda: Calanoida) from its population centers to waters of Taiwan and Hong Kong during the winter northeast monsoon period. *J. Plankton Res.,* **27**, 205-210.

13

ICES Working group on zooplankton ecology (2002) Zooplankton monitoring results in ICES area. Summary status report 2001/2002, 21pp.

IPCC, 2001. Climate change 2001. The scientific basis. Cambridge University Press, Cambridge.

Jansá, J., López-Jurado, J. L., Morillas, A. and Amengual, B. (1998) Seasonal and mesoscale variability of biological and chemical parameters related to the hydrodynamics of the Ibiza Channel. *Bol. Inst. Esp. Oceanogr.*, **14**, 1 and 2, 31-47.

Kouwemberg, J. and Razouls, C. (1990) The incidence of environmental factors on the evolution of copepod populations in the Gulf of Lion during the period 1986-1988 in comparison with the period 1957-1964. *Bull. Soc. Zool.*, **115**, 23-36.

Licandro, P. and Ibanez, F. (2000) Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, WM) from 1985 to 1995. Influence of hydroclimatic factors. *J. Plankton Res.*, **22,** 12, 2225-2253.

Mackas, D. L. (1984) Spatial autocorrelation of plankton community in a continental shelf ecosystem. *Limnol. Oceanog.*, **29**, 451-471.

Mackas, D.L, Thomsom, R.E., and Galbraith, M. (2001) Changes in the zooplankton community of the British Columbia continental margin, 1985-1999, and their covariation with oceanographic conditions. *Can. J. Fish. Aquat. Sci.*, **58**, 685-702.

Mazzocchi, M. G. and Ribera d'Alcalá, M. (1995) Recurrent patterns in zooplankton structure and succession in a variable coastal environment. *ICES J. Mar. Sci.*, **52**, 679-691.

Mazzocchi, M. G., Christou, E., Fragopoulu, N. and Siokou-Frangou, I. (1997) Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): General aspects. *Oceanol. Acta*, **20**, 3, 521-535.

Molinero, J. C., Ibanez, F., Nival, P., Buecher, E., Souissi S. (2005a) The North Atlantic climate and the Northwestern Mediterranean plankton variability. *Limnol. Oceanogr.*, **50**, 1213-1220.

Molinero, J. C., Ibanez, F., Soussi, S., Chifflet, M. and Nival, P. (2005b) Phenological changes in the Northwestern Mediterranean Copepods *Centropages typicus* and *Temora stylifera* linked to climate forcing. *Oecologia*, **145**, 640-649.

Peterson, W. T., Miller, C. B. and Huchinson, A. (1979) Zonation and maintenance of copepod population in the Oregon upwelling zone. *Deep-Sea Res.*, **26**, 467-494.

Peterson, W. T., Keister, J. E., and Pinnix, W. D. (2001) The 1998/1999 Regime Shift in the northern Californian Current: what are the copepods telling us? *PICES 10th Annual Meeting,* British Columbia, Canada.

14

Pinot, J. M. and Jansá, J. (2001) Time variability of acoustic backscatter from zooplankton in the Ibiza Channel (western Mediterranean). *Deep-Sea Res. I*, **48**, 1651-1670.

Pinot, J. M., López-Jurado, J. L. and Riera R. (2002) The CANALES experiment (1996-1998). Interannual, seasonal and mesoscale variability of the circulation in the Balearic Channels. *Progr. Oceanogr.*, **55**, 3-4, 335-370.

Pinot, J. M., Tintoré, J., López-Jurado, J. L., Fernández de Puelles, M. L., and Jansá, J. (1995) Three-dimensional circulation of a mesoescale eddy/front system and its biological implications. *Oceanol. Acta*, **18**, 4, 389-399.

Pyper BJ, Peterman RM (1998). Comparison of methods to account for autocorrelation in correlation analysis of fish data. *Can. J. Fish. Aquat. Sci.*, **55**, 2127-2140.

Razouls, C. and Kouwenberg, J. (1993) Spatial distribution and seasonal variation of mesozooplankton biomass in the Gulf of Lions. *Oceanol. Acta,* **16**, 4, 393-401.

Rebstock, G. A. (2002) Climatic regime shifts and decadal-scale variability in calanoid copepod populations off southern California. *Global Change Biology*, **8,** 71-89.

Reddaway, J. and Bigg, G. (1996) Climatic change over the Mediterranean and links to the more general atmospheric circulation. *Int. J. Climatol.*, **16**, 651-661.

Richardson, A. J. and Soechman, D. S. (2004) Climate impact on plankton ecosystems in the Northest Atlantic. *Science*, **305**, 5690, 1609-1612.

Rodríguez, J. (1983) Estudio de la comunidad planctónica nerítica en el mar de Alboran: II Ciclo de zooplancton. *Bol. Inst. Esp. Oceanogr*., **1**, 19-44.

Roemmich, D. and Mc Gowan, J. (1995) Climatic warming and the decline of zooplankton in the California Current. Science, **267**, 1324-1326.

Sabates, A., Gili, J. and Pages, F. (1989) Relationship between zooplankton distribution, geographic characteristic an hydrographic patterns off the Catalan Coast. *Mar. Biol.*, **103**, 153-159.

Scotto di Carlo, B. and Ianora, A. (1983) Standing stocks and species composition of Mediterranean zooplankton. *UNESCO Rep. Mar. Sci*., **20**, 59-69.

Seguin, G., Gaudy, R., Errhif, A. and Thibault, D. (1993) Observations sur l'abondance, la composition taxonomique et les affinités écologiques des copépodes pélagiques récoltés dans la région du front Almeria-Oran. *Mar. Life*, **3**, 1-2, 19-29.

Siokou-Frangou, I. (1996) Zooplankton annual cycle in a Mediterranean coastal area. *J. Plankton Res.*, **18**, 2803-2823.

15

Schneider, J., Fernández, V. and Hernandez-Garcia, E. (2005) Leaking method approach to surface transport in the Mediterranean Sea from a numerical ocean model. *J. Mar. Syst.*, **57**, 1-2, 111-126.

Thibault, D., Gaudy, R. and Le Fevre, J. (1994) Zooplankton biomass, feeding and metabolism in a geostrophic frontal area (Almeria-Oran Front; Western Mediterranean). Significance to pelagic food webs. *J. Mar. Syst.*, **5**, 297-311.

Valdés, L. and Morales, M. (1998) Time-series analysis of copepod diversity and species richness in the southern bay of Biscay and their relationship with environmental conditions. *ICES J. Mar Sci.,* **55**, 783-792.

Vives, F. (1966) Zooplancton nerítico de las aguas de Castellón Mediterráneo Occidental. *Inv. Pesq*., **30**, 49-166.

Zagami, G., Badalamanti, F., Guglielmo, L. and Manganero, A. (1996) Short-term variations of the zooplankton community near the straits of Messina: Relationships with the hydrodynamics regime. *Est. Coast. Shelf Sci.***,** **42**, 5, 667-681.

16

FIGURE LEGENDS

Figure 1: Map of the Western Mediterranean indicating the location of the sampling stations at the south-west of Mallorca (Balearic Sea).

Figure 2: monthly time-series of temperature (ºC, upper panel) and salinity (PSU, bottom panel) in the upper 200 m depth at station 3.

Figure 3: Mean annual values of a) sea water temperature (ºC), b) salinity (PSU) and c) nitrates (µM) at 75m depth (modified from Fernández de Puelles *et al.*, 2003b).

Figure 4: Hierarchical classification of environmental conditions during the study period. Dendrogram considers water temperature, salinity and nitrates concentrations at the three stations, based on the Bray-Curtis similarity matrix and squared root data transformation (taken from Fernández de Puelles *et al.*, 2003b).

Figure 5: Top abundant copepod species collected at the three stations (relative abundance >1%).

Figure 6: Seasonal and interannual abundance of copepods (as ind m^{-3}) during the study at the three stations.

Figure 7: Interannual and seasonal distribution pattern of *Centropages typicus, Acartia clausi, Temora stylifera, Calanus helgolandicus* and *Acartia danae.*

Figure 8: Interannual and seasonal changes on the four copepod assemblages of identified by the k-means cluster analysis.

Figure 9: Interannual variability of the patterns of salinity and copepods assemblages. In top panel, salinity and group 1. In bottom panel, salinity and group 2.

Figure 10: Interannual variability of the winter North Atlantic Oscillation and the pattern of variability of the group 1 of copepods.

17

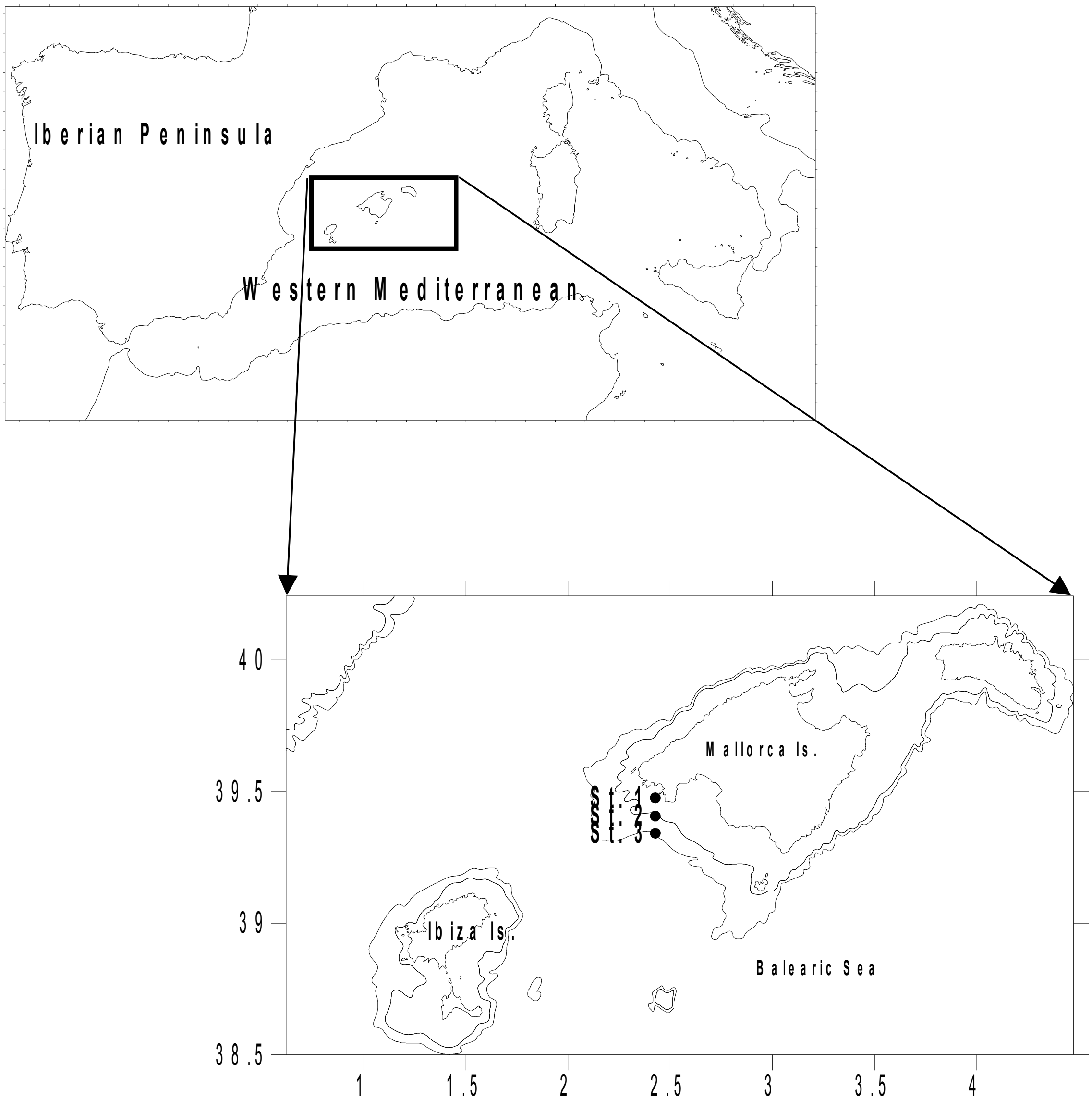

Iberian Peninsula
Western Mediterranean
Mallorca Is.
St. 1
St. 2
St. 3
Ibiza Is.
Balearic Sea
40
39.5
39
38.5
1
1.5
2
2.5
3
3.5
4

Fig. 1

18

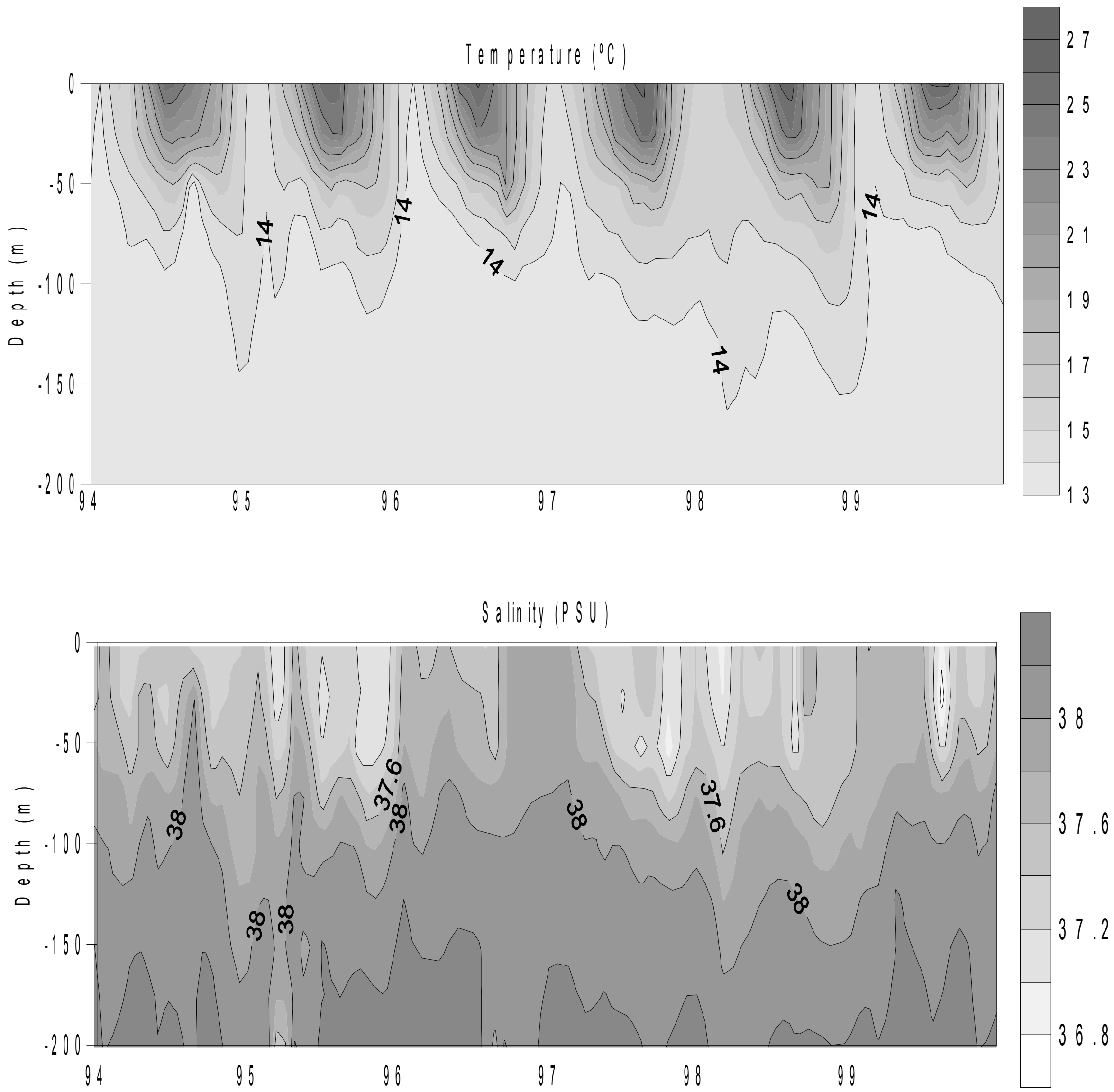

Temperature (°C)
Depth (m)
0
-50
-100
-150
-200
94
95
96
97
98
99
14
27
25
23
21
19
17
15
13
Salinity (PSU)
Depth (m)
0
-50
-100
-150
-200
94
95
96
97
98
99
38
37.6
38
37.2
36.8

Fig. 2

19

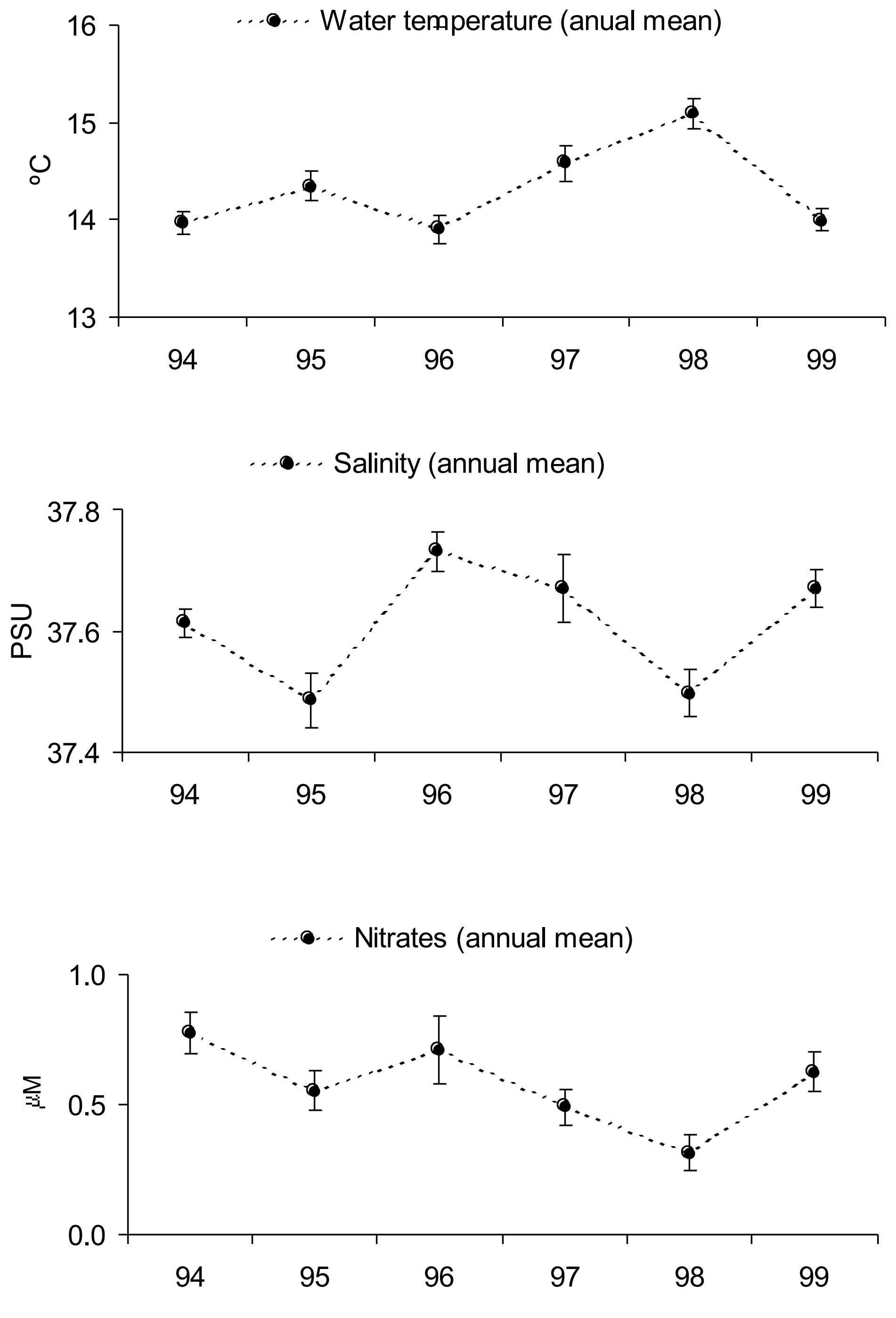

Water temperature (anual mean)
°C
16
15
14
13
94
95
96
97
98
99
Salinity (annual mean)
PSU
37.8
37.6
37.4
94
95
96
97
98
99
Nitrates (annual mean)
μM
1.0
0.5
0.0
94
95
96
97
98
99

Fig. 3

20

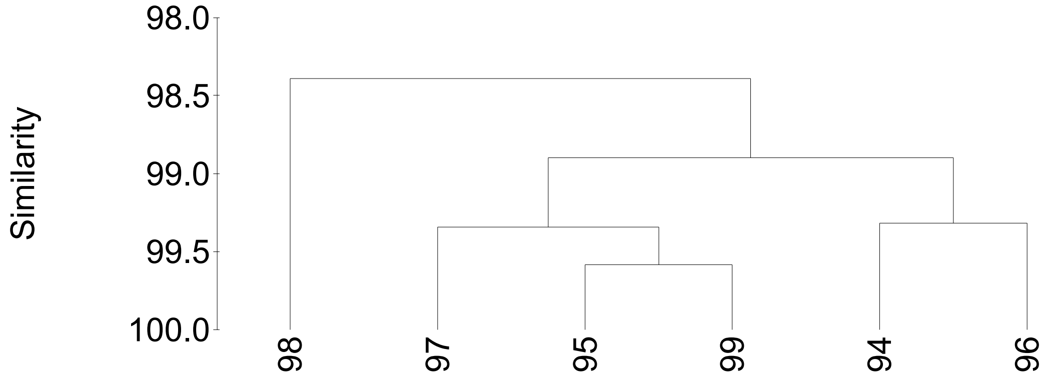


Fig. 4

21

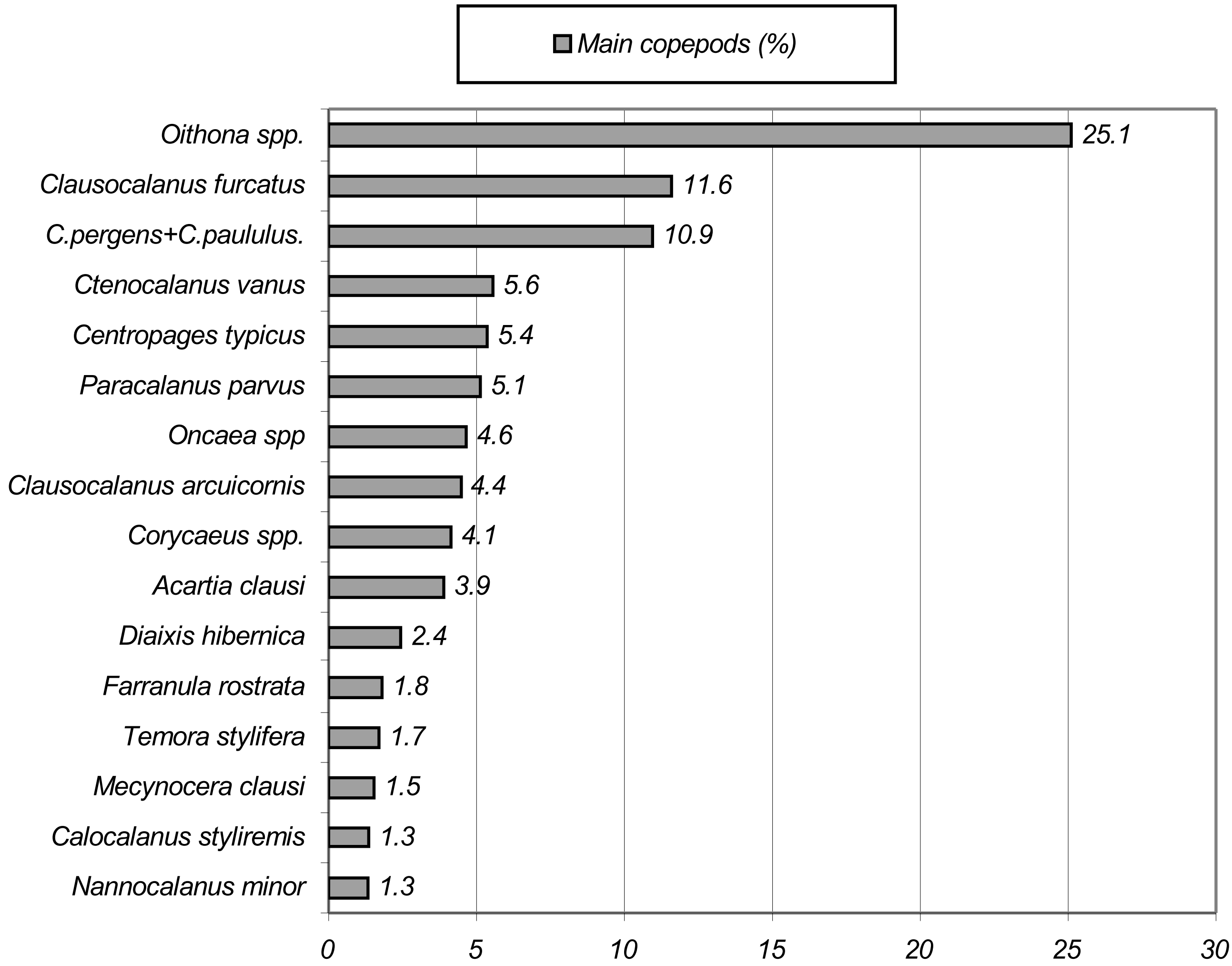
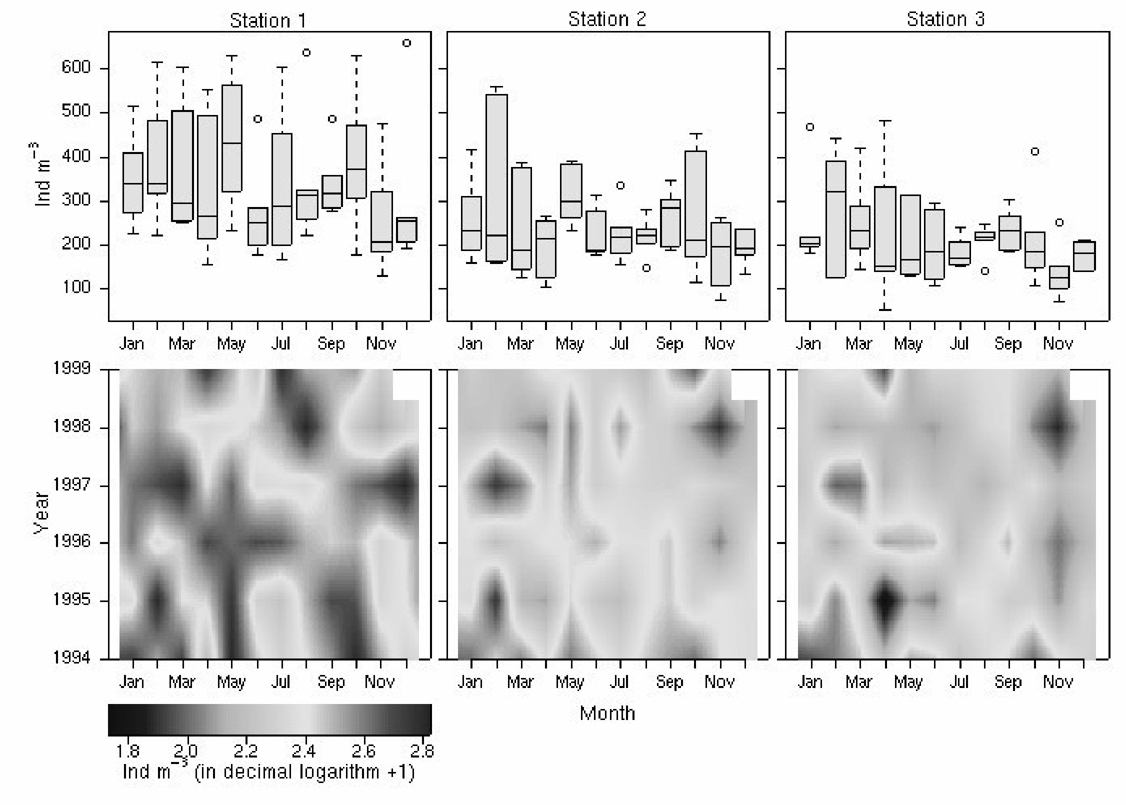
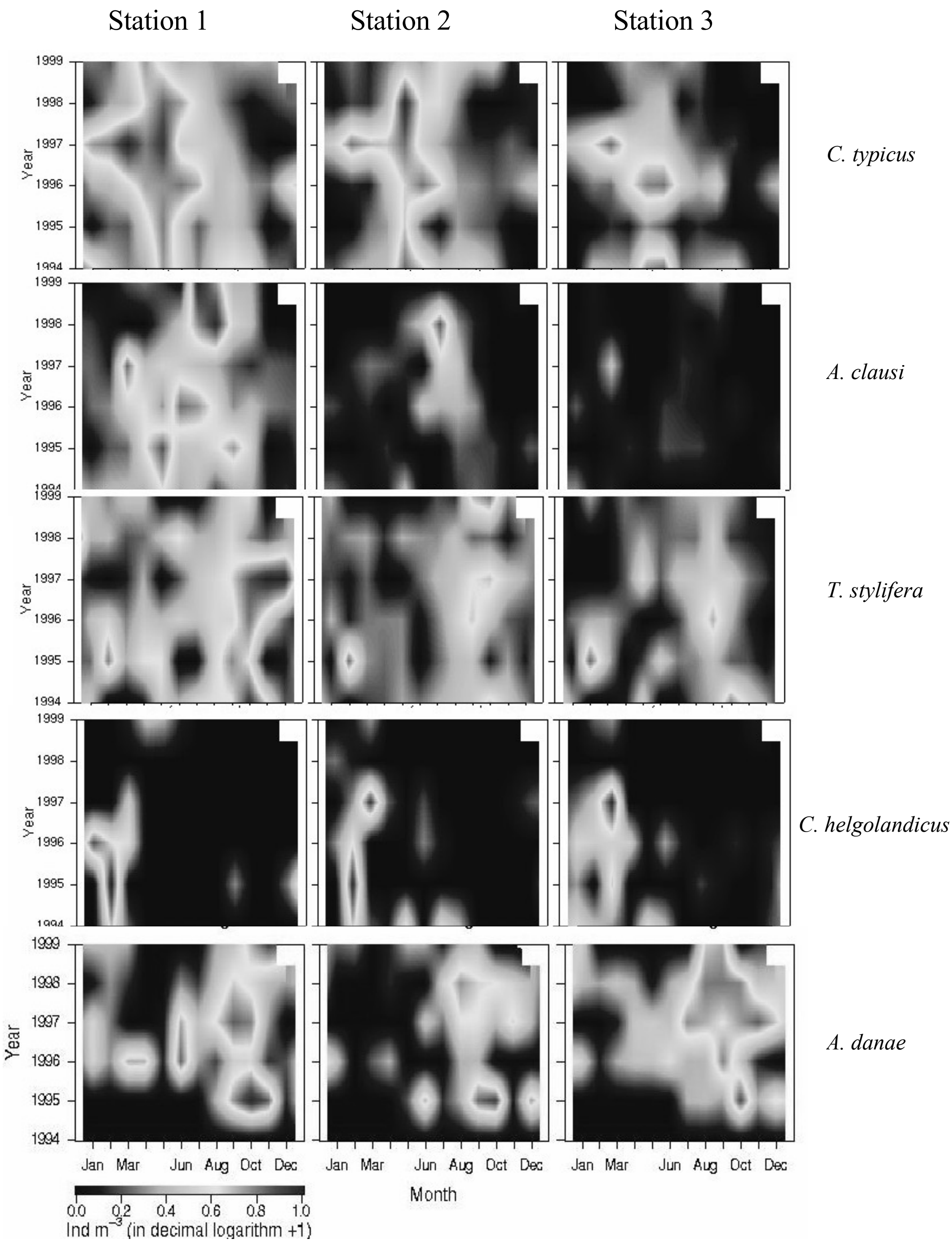

Main copepods (%)
Oithona spp.
Clausocalanus furcatus
C.pergens+C.paululus.
Ctenocalanus vanus
Centropages typicus
Paracalanus parvus
Oncaea spp
Clausocalanus arcuicornis
Corycaeus spp.
Acartia clausi
Diaixis hibernica
Farranula rostrata
Temora stylifera
Mecynocera clausi
Calocalanus styliremis
Nannocalanus minor
25.1
11.6
10.9
5.6
5.4
5.1
4.6
4.4
4.1
3.9
2.4
1.8
1.7
1.5
1.3
1.3
0
5
10
15
20
25
30

Fig. 5

22


Station 1
Station 2
Station 3
Ind m^{-3}
600
500
400
300
200
100
Jan
Mar
May
Jul
Sep
Nov
Year
1999
1998
1997
1996
1995
1994
Month
1.8
2.0
2.2
2.4
2.6
2.8
Ind m^{-3} (in decimal logarithm +1)

552 Fig. 6



Station 1
Station 2
Station 3
C. typicus
A. clausi
T. stylifera
C. helgolandicus
A. danae
Year
1999
1998
1997
1996
1995
1994
Jan Mar Jun Aug Oct Dec
Month
0.0 0.2 0.4 0.6 0.8 1.0
Ind m-3 (in decimal logarithm +1)

Fig. 7

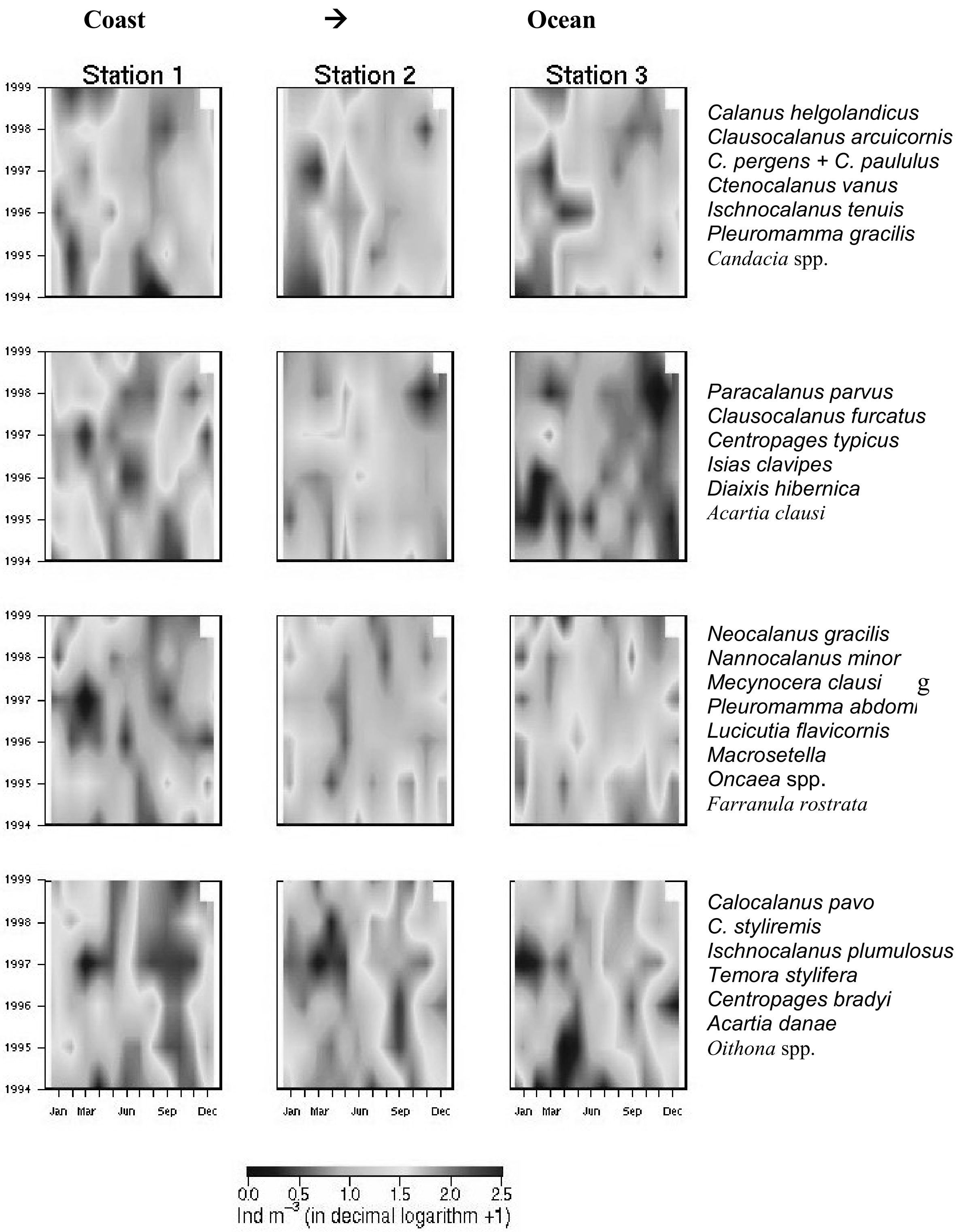

Coast
Ocean
Station 1
Station 2
Station 3
1999
1998
1997
1996
1995
1994
Calanus helgolandicus
Clausocalanus arcuicornis
C. pergens + C. paululus
Ctenocalanus vanus
Ischnocalanus tenuis
Pleuromamma gracilis
Candacia spp.
Paracalanus parvus
Clausocalanus furcatus
Centropages typicus
Isias clavipes
Diaixis hibernica
Acartia clausi
Neocalanus gracilis
Nannocalanus minor
Mecynocera clausi g
Pleuromamma abdomi
Lucicutia flavicornis
Macrosetella
Oncaea spp.
Farranula rostrata
Calocalanus pavo
C. styliremis
Ischnocalanus plumulosus
Temora stylifera
Centropages bradyi
Acartia danae
Oithona spp.
Jan Mar Jun Sep Dec
0.0 0.5 1.0 1.5 2.0 2.5
Ind m^{-3} (in decimal logarithm +1)

Fig. 8

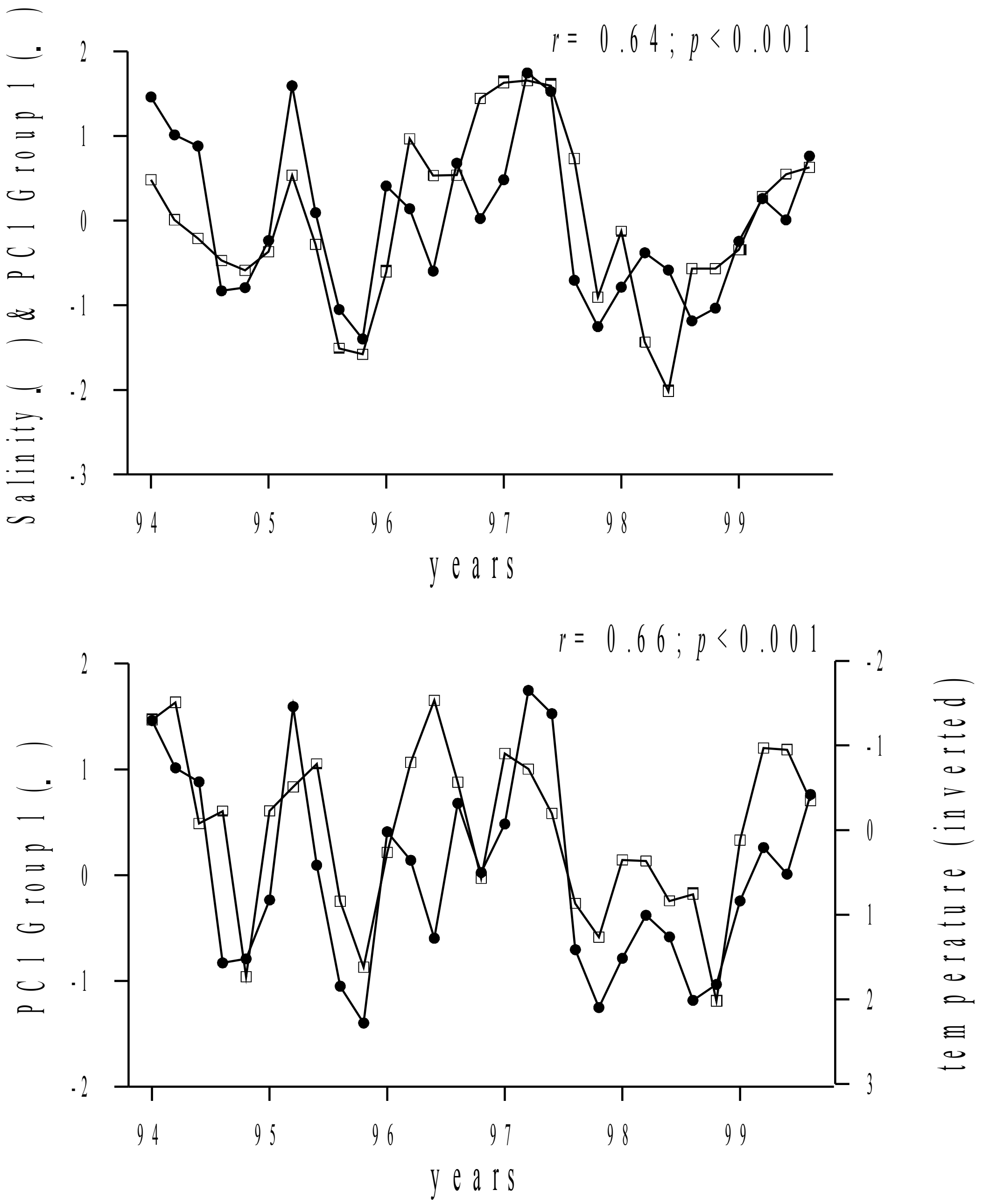

r = 0.64; p < 0.001
Salinity ( ) & PC1 Group1 ( )
2
1
0
-1
-2
-3
94
95
96
97
98
99
years
r = 0.66; p < 0.001
PC1 Group1 ( )
temperature (inverted)
2
1
0
-1
-2
-2
-1
0
1
2
3
94
95
96
97
98
99
years

Fig. 9

26

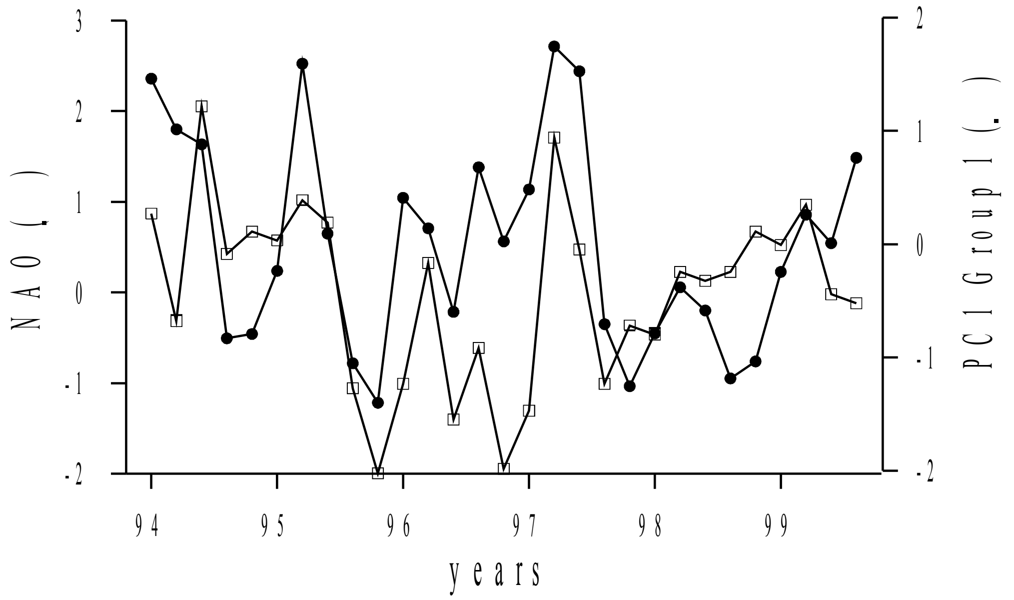


Fig. 10