

Zooplankton time-series in the Balearic Sea (Western Mediterranean): Variability during the decade 1994–2003

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Abstract

Studies of plankton time-series from the Balearic islands waters are presented for the past decade, with main emphasis on the variability of zooplankton and how it relates to the environment. The seasonal and interannual patterns of temperature, salinity, nutrients, chlorophyll concentration and zooplankton abundance are described with data obtained between 1994 and 2003. Samples were collected every 10 days at a monitoring station in the Mallorca channel, an area with marked hydrographic variability in the Western Mediterranean. Mesoscale variability was also assessed using data from monthly sampling survey carried out between 1994 and 1999 in a three station transect located in the same study area. The copepods were the most abundant group with three higher peaks (March, May and September) distinguished during the annual cycle and a clear coastal-offshore decreasing gradient. Analysis of the zooplankton community revealed two distinct periods: the mixing period during winter and early spring, where copepods, siphonophores and ostracods were most abundant and, the stratified period characterised by an increase of cladocerans and meroplankton abundances. Remarkable interannual zooplankton variability was observed in relation to hydrographic regime with higher abundances of main groups during cool years, when northern Mediterranean waters prevailed in the area. The warmer years showed the lowest zooplankton abundances, associated with the inflow of less saline and nutrient-depleted Atlantic Waters. Moreover, the correlation found between copepod abundance and large scale climatic factors (e.g., NAO) suggested that they act as main driver of the zooplankton variability. Therefore, the seasonal but particularly the interannual variation observed in plankton abundance and structure patterns of the Balearic Sea seems to be highly modulated by large-scale forcing and can be considered an ideal place where to investigate potential consequences of global climate change.

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1. Introduction

1.1. Study area: the role of the Balearic islands in the hydrography of the Western Mediterranean

The general surface circulation in the Western Mediterranean follows a cyclonic pattern, with two well known permanent surface currents: the Algerian current in the south and the Northern Mediterranean current in the north. The Algerian current flows along the African coast and carries waters of Atlantic origin which reach the Balearic islands by anticyclonic eddies that detach from the main current body. The Northern current from the Ligurian Sea carrying Mediterranean waters along the continental slope to the Balearic channels. However, high resolution data highlighted that the circulation in the Western Mediterranean is characterized by important mesoscale activity that distorts the main circulation pattern of along-slope currents (García et al., 1994; Pinot et al., 1994). Some of those hydrographic structures, such as divergence fronts and eddies (Font et al., 1988; La Violette et al., 1990), can be very important in the nutrient supply to the photic layer in a highly oligotrophic region (Margalef, 1985), producing a remarkable spatial and temporal heterogeneity (Estrada et al., 1985).

The Balearic islands constitute a topographical barrier aligned in a SW–NE direction between the north Balearic Sea and the Algerian Basin. Satellite and *in situ* observations have suggested complex interactions between surface mesoscale eddies and topography, with strong effects on seasonal exchange dynamics through the Balearic channels (Pinot et al., 1995; López-Jurado et al., 1996). These authors highlighted the role played by these channels in controlling the meridional mass transport and fluxes of heat, salt and other properties. It is through the Mallorca channel where the distribution of the planktonic communities are strongly influenced by the inflow/outflow of different water masses (Fernández de Puellas et al., 2003b, 2004b).

The seasonal variability of the hydrographic regime in the Mallorca and Ibiza channels is well known (Pinot et al., 2002). Overall, the annual circulation pattern consists of cool, south flowing waters of northern origin during the first part of the year, changing to warm northward flowing waters of Atlantic origin in the second part. However, the circulation within the region becomes very complex due to the permanent mesoscale activity (López-Jurado et al., 2001). Depending on these structures influence we can observe mixing of the two water masses, or incursions of either of them forming frontal systems or eddies what drives the planktonic community (Fernández de Puellas, 1996; Alemany et al., 2006). Furthermore, remarkable interannual variability of surface water masses around the Balearic islands has been observed (López-Jurado, 2002). Not surprisingly, severe winters are associated with an increased inflow of northern waters, whereas milder winters result in a higher northward flow of recent Atlantic water through the Mallorca channel (Pinot et al., 2002). Thus, a direct correlation between the thermohaline circulation regime and climate variability is suggested. Monitoring studies since 1994 have found that hydrographic changes are reflected in the planktonic distribution and linked to large atmospheric factors (Fernández de Puellas et al., 2004a,b). Moreover, due to the proximity of the Atlantic, the Mallorca channel has been proposed as a suitable place for a long-term time-series to observe zooplankton changes in relation to large-scale climatic fluctuations (Fernández de Puellas et al., 2004a; Fernández de Puellas and Molinero, 2007). As in other areas in the North Atlantic, zooplankton communities could be good indicators of water mass history (Edwards et al., 2002; Peterson et al., 2001) and linked to large atmospheric oscillations (Richardson and Soechman, 2004; Beaugrand, 2003). Due to the special geographic situation, the oligotrophic waters of the Mallorca channel are sensitive to hydrographic regime variation and, in consequence, a good area where to detect changes at both regional and global scales (e.g., global warming).

1.2. Zooplankton time-series in the Western Mediterranean Sea

Seasonal and interannual zooplankton dynamics and the driving mechanisms of their variability are at present a central issue of oceanographic investigation (ICES, 2002; CIESM, 2002, 2003). Identification of qualitative and quantitative biological changes in relation to long-term trends in the ocean is a strategy used to monitor the influence of global change on marine communities, and a way to find important groups or species that act as indicators of the health of ecosystems (Colebrook, 1978; Colebrook, 1985). In high and tem-

perate latitudes this task is relatively simple due to the predominance of a few well studied species (e.g., *Calanus finmarchicus*, Fromentin and Planque, 1996; Beaugrand et al., 2002), but at low latitudes and oligotrophic areas information about short- and long-term variability of zooplankton species is harder to obtain due to higher diversities and low abundances. Consequently time-series of zooplankton community in the Western Mediterranean are scarce (Mazzocchi et al., 2007). Stochastic fluctuations in plankton communities occurring over short time-scales can be important (Underwood, 1989), particularly in oligotrophic seas in which changes in environmental conditions and planktonic abundance occur both rapidly and irregularly over short time periods (Bustillos-Guzmán et al., 1995). Therefore, depending on the community under study, temporal studies based on regular sampling at even monthly intervals can miss important changes. The issue may be further complicated as global atmospheric forces seem to drive the dynamics of the Mediterranean basin (Hurrell, 1995; Redaway and Bigg, 1996) where very few studies have investigated the response of zooplankton to large-scale atmospheric oscillations (Molinero et al., 2005a,b).

The relevant interannual variability observed in the environmental conditions of the Western Mediterranean (Fuda et al., 2002; Vargas-Yañez et al., 2005) highlights the need for large biological time-series, as has been done in several areas of the Mediterranean (Mazzocchi and Ribera d'Alcala, 1995; Cataletto et al., 1995; Licandro and Ibanez, 2000; Ribera D'Alcala et al., 2004) to detect trends and irregularities which could reflect large-scale processes.

The purpose of this paper is to review the complete time-series of zooplankton data gathered in the Mallorca channel (a highly dynamic oceanographic area) during the period 1994–2003, examining the relationship between the temporal variation of main zooplankton groups with environmental variables and its relation to some large-scale climatic indices, such as the winter NAO.

2. Data sets and sampling methodologies

To achieve the aforementioned objectives, two main zooplankton time series from the Mallorca channel were analysed. The first time-series was carried out at a neritic station which was sampled every 10 days from January 1994 to December 2003 and provided a high resolution time series of zooplankton community variability. The second time-series was carried out at three stations along a cross-shelf transect, monthly from January 1994 to December 1999, and was designed to acquire information about mesoscale spatial variability of zooplankton communities in the same area.

Details of the sampling methodology are presented in the following section:

2.1. Ten years of time-series at a neritic station

Between January 1994 and December 2003 a fixed station 5 km offshore (78 m depth) to the southwest of Mallorca island (St. 1, Fig. 1) was sampled every 10 days from the small research vessel “Arola”. The station was always visited between 9:00 and 12:00 h local time. Water samples for physical–chemical and biological data were collected at depths of 5, 15, 25, 50 and 75 m using 5 L Niskin bottles. CTD data were recorded with a Seabird 19 probe, which was calibrated every 2 years. Also, monthly mean air temperature values were gathered from the Spanish Meteorological Institute which were registered at a coastal station located 20 km from St. 1.

Nutrient samples from the 5 L Niskin bottles were immediately frozen to -20°C for laboratory analysis of nitrates, nitrites, silicates and orthophosphates (Armstrong et al., 1967). Chlorophyll *a* pigment was measured by fluorometry (Holm-Hansen et al., 1966), filtering 1.5 L of water from Niskin bottles through GF/C Whatman filters that were kept frozen at -20°C for later analysis. Zooplankton was sampled by means of oblique hauls from 75 m depth to surface at a vessel speed of two knots with a Bongo-20 Plankton net fitted with 250 μm and 100 μm meshes. A General Oceanics flowmeter was fitted to each net to estimate the volume of water filtered. Immediately after collection, the zooplankton samples were split into subsamples for biomass and taxonomic analysis with a Folsom plankton splitter. Subsamples for taxonomic studies were preserved with 4% neutralised formaldehyde buffered with borax. Representative aliquots from both subsamples for taxonomic analysis were analyzed and the organisms identified to the level of main taxonomic groups, except for copepods and cladocerans, which were identified to the lowest possible taxonomic level. Subsamples for

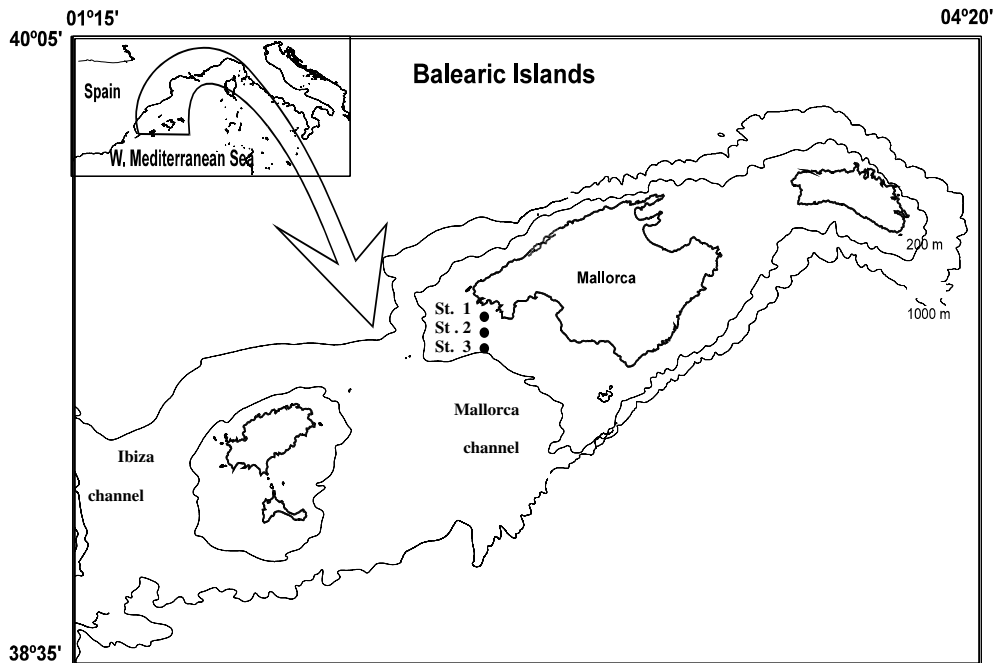


Fig. 1. Location of the monitoring station (St. 1) during the period 1994–2003 and deeper stations (St. 2 and St. 3) sampled from 1994 to 1999 in the Balearic Sea (Western Mediterranean).

biomass were frozen ($-20\text{ }^{\circ}\text{C}$) for subsequent estimation of the biomass as dry weight (Fernández de Puelles et al., 1997). All the data presented here are derived from the $250\text{ }\mu\text{m}$ mesh.

2.2. Six years of time-series in a cross-shelf transect

A cross-shelf transect of three stations was also sampled monthly over a 6-year period, from 1994 to 1999. The neritic station was the same fixed station over the 75 m isobath mentioned above (St. 1), whereas the other two, St. 2 and 3, were located over the 100 and 200 m depth, respectively (Fig. 1). The sampling methodology in these stations was the same as for St. 1., except that water samples were also collected at 100 m depth at St. 2 and at 100 , 125 , 150 and 200 m depth at St. 3. Zooplankton oblique hauls were conducted from 100 m depth to surface at the two deeper stations. Furthermore, the ichthyoplankton community was sampled by a complementary haul at the three stations and at the same depths as the zooplankton hauls, using the same Bongo-20 net equipped with $333\text{ }\mu\text{m}$ mesh. Later in the lab, all the fish larvae from the two replicates were sorted and identified to the lowest taxonomic level possible.

2.3. Statistical analyses

Simple linear regression was used to quantify the relationship between biomass and zooplankton abundance for the different groups, and ANOVA was used to test differences among data series. The relationship between environmental variables and zooplankton groups were also similarly explored. Multidimensional scaling ordination and cluster analysis were carried out both with environmental (temperature–salinity and nutrients) and biological data (zooplankton groups and species abundances ($\ln(x + 1)$)) using the Bray–Curtis similarity index, applying squared root data transformation). Ordination analyses were performed using the PRIMER program (Plymouth Marine Laboratory).

3. Plankton variability in relation to environment

3.1. Hydrography

Temperature. Data from 10 years of study at Station 1 showed a clear seasonal cycles (Fig. 2a) with a mixing period during colder months and a stratification period during more than 5 months, from June to October (Fig. 2b). During this 10-year period the mean surface water temperature had a range of almost 14 °C, with the

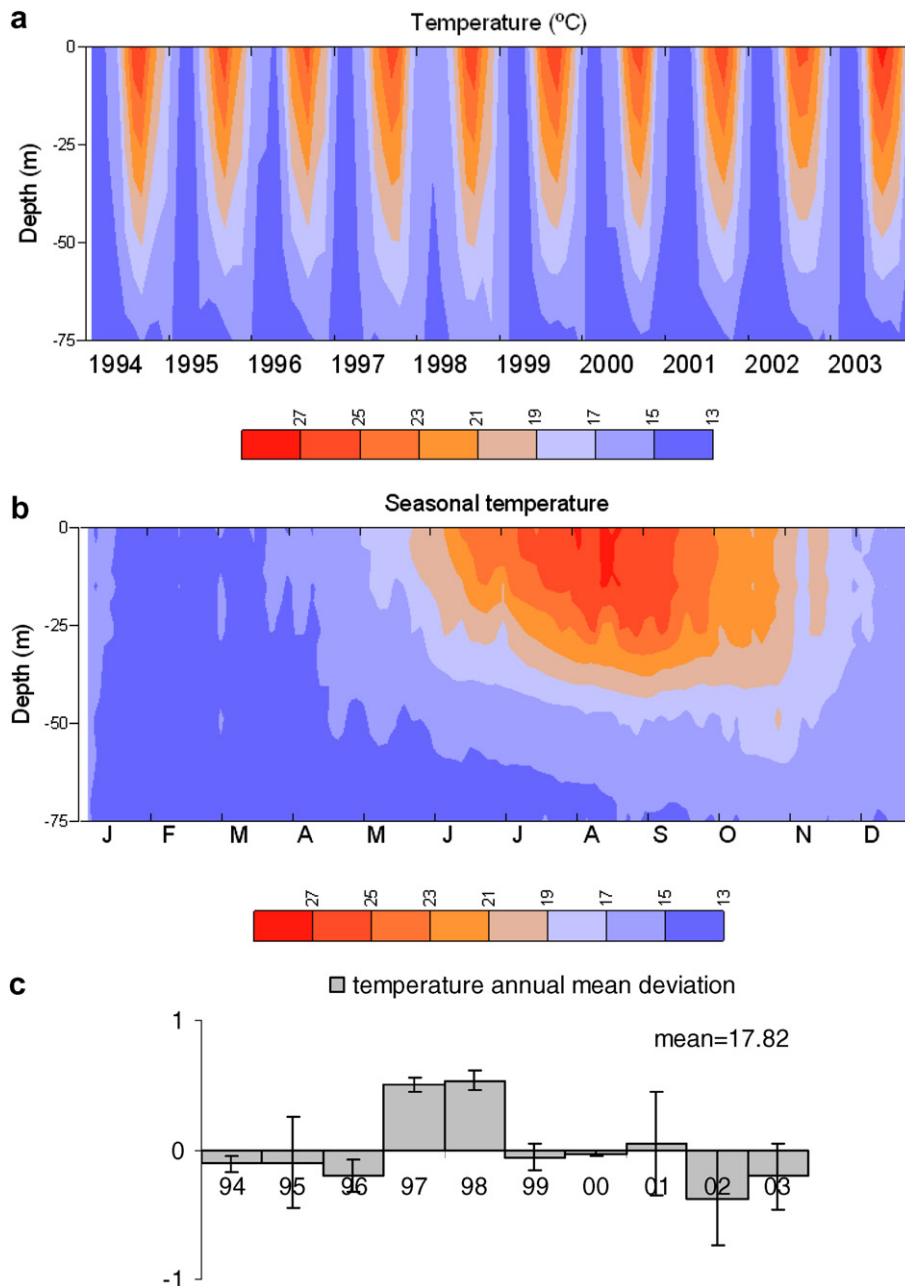


Fig. 2. (a) interannual variability of temperature pattern (°C) from 1994 to 2003 in the neritic station (St. 1). (b) Seasonal pattern of temperature (monthly average) from 1994 to 2003. (c) Annual mean values of temperature and its year standard deviations (SD).

minimum in late winter (13.5 °C) and the maximum in late summer (27.2 °C), whereas at 75 m depth the difference was only from 13 °C (in March) to 16 °C (in October). Minimum single readings were registered at 75 m depth in March of 1994 and 1996 (13 °C), while a maximum record of 30 °C was registered at the surface in August 2003, followed by 1998 (27.5 °C).

Remarkable interannual variability was observed during the whole period with a mean value of 17.82 °C (SD = 2.91; Fig. 2c). The year 2002 had the minimum temperature (17.5 °C), which was followed by year 1996. The highest value was reached in 1998 (18.36 °C), followed by 1997. Mean temperature values were higher during 1997 and 1998, but generally lower than the mean after year 1999. Because of that, we did not observe any increasing pattern in the total studied period. Interannual variability was particularly high during 1995 and after year 2000, what indicates the irregular fluctuations of temperature in the Balearic Sea.

The analysis based on the first 6 years of the time-series showed clear correlations between mean monthly air temperature and seawater temperature ($R^2 = 0.63$; $P < 0.05$; Fernández de Puelles et al., 2003b). During this study, it was found that interannual temperature variability was mainly controlled by winter mixing conditions. Summer heating played a secondary role because it varied little from year to year and only affecting the upper water column.

Salinity. Unlike temperature, which is strongly driven by the local ocean–atmosphere interaction, salinity is a good indicator of the origin of the water mass present in the area, allowing us to accurately define thermohaline circulation. Decadal time-series of salinity at the monitoring station are presented in Fig. 3a, showing evident variability. Several years could be observed in which more saline waters dominated the entire water column (1996–1997 and after 2000), whereas in other years, less saline waters were prevalent (1995 and 1998). The highest and lowest salinity records were registered during the winters of 1996 and 2001 (38.2 psu) and during autumn of 1995 and 1998 (37.0 psu), respectively. Although no clear seasonality was seen, monthly averaged values for the 10-year period (Fig. 3b) indicated that the highest salinities (>38 psu) were recorded during winter and spring, while the lowest values (37 psu) were observed during summer and autumn. The interannual variability based on mean annual values indicated that the lowest values were found in 1995 and 1998 (37.43 and 37.46 psu respectively) and besides 1996, the highest values were observed at the end of the period (total mean value of 37.62 psu; SD = 0.16; Fig. 3c). Contrary to temperature, an evident increase of salinity was observed during the last 4 years of the time-series.

The variability and complex patterns recorded may be the result of a climate-driven mesoscale oscillation in the area, which is influenced by the location of the Mallorca channel. Accordingly, fluctuations in this boundary region lead to low salinity values associated with mild winter atmospheric conditions, and saltier years associated with severe winters in the north Western Mediterranean.

Nutrients. In general, very low nutrient concentrations were measured (nitrate, nitrite, orthophosphate and silicates) throughout the annual cycle during the 10-year time-series from the fixed station. Interannual differences based on mean year values of the analyzed nutrients could be observed during the whole period where particularly nitrates and silicates exhibited important fluctuations (Fig. 4). In fact, nitrites and orthophosphates had very low values (<0.1 µM). Nevertheless, silicates showed higher concentrations during years 1996 and 2001 and nitrates after 2000, when cool and saltier water penetrated in the area. Seasonally, these nutrients were practically undetectable in surface layers (data not presented) and in the surface during the summer months (e.g., concentrations < 0.1 µM). However, higher values were recorded during the mixing winter period (e.g., concentrations > 2.5 µM). During the stratified period the highest concentrations were recorded at 75 m depth (e.g., concentrations > 4.5 µM).

There was a significant correlation between salinity and nitrates, ($p < 0.01$) as well as between temperature and salinity ($p < 0.05$). Taking into account all the environmental variables analyzed, temperature, salinity and nutrients together during the 10-year study, a cluster analysis indicated how the years were grouped by conditions of the water masses. One group, years 2000–2002, was characterized by higher nutrient concentrations, saltier and cooler waters. A second group was formed by the warmer years (1998, 1997 and 2003), which showed lower nutrient concentrations. The remaining years, showing high water mass variability, constituted the third group (Fig. 5). This pattern confirmed the previous results observed during the shorter period 1994–1999, when 1997 and particularly 1998 were related to warmer, less saline and nutrient poor recent Atlantic waters (Fernández de Puelles et al., 2003b).

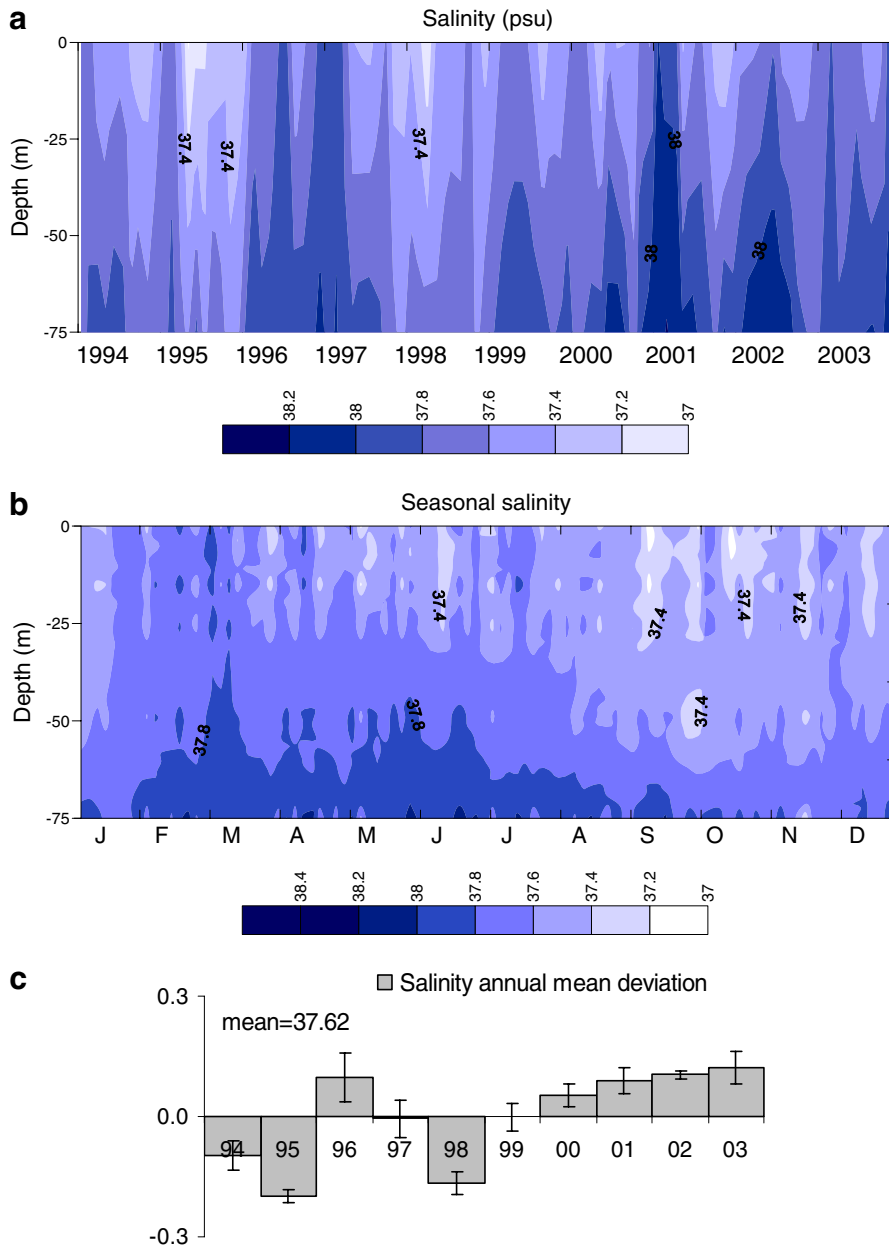


Fig. 3. (a) Interannual variability of salinity (psu) from 1994 to 2003 at the St. 1. (b) Seasonal pattern of salinity (monthly averages) from 1994 to 2003. (c) Annual mean values of salinity and its SD.

3.2. Phytoplankton

Chlorophyll *a* 10-year data from the Station 1 revealed an evident seasonal cycle in which maxima appear regularly in the upper water column at the beginning of the year and closer to the bottom in spring (Fig. 6a). This seasonal pattern is clearly observed when the 10-year monthly averaged values were considered (Fig. 6b). Such results indicate a higher chlorophyll concentration during January–February in the surface 25 m depth and close to the bottom in May. The movement of the observed chlorophyll maxima into deeper water from winter to summer is a characteristic of this area (Duran and Jansá, 1986) and is consid-

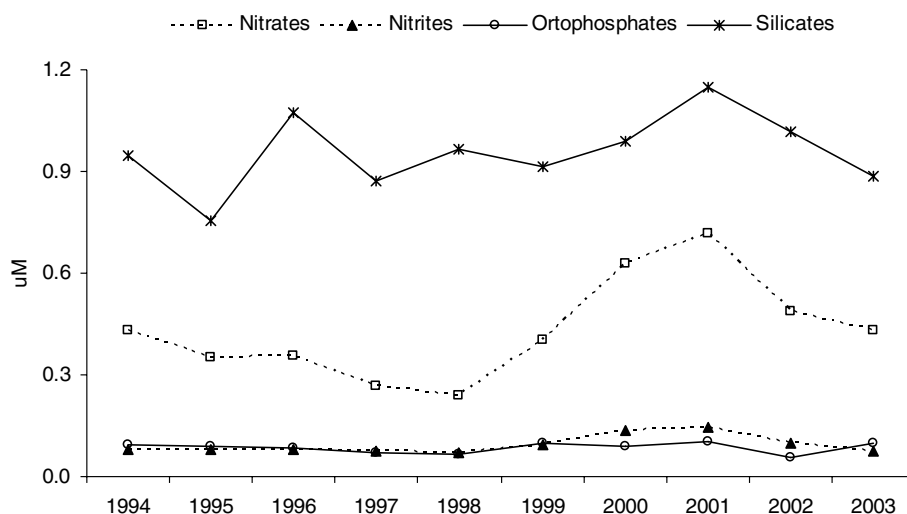


Fig. 4. Mean annual values of nitrates, nitrites, orthophosphates and silicates analyzed from 1994 to 2003 (μM) at the St. 1.

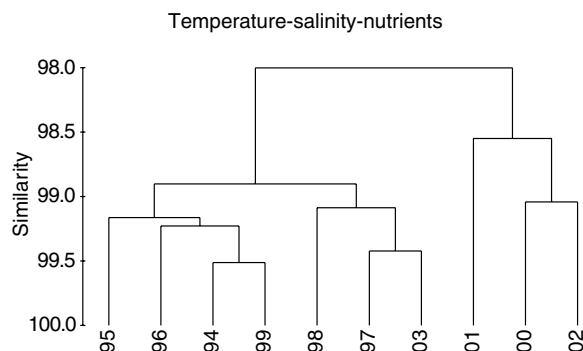


Fig. 5. Dendrogram for hierarchical clustering of samples during the 10 year period, considering temperature, salinity and nutrients, based on the Bray–Curtis similarity matrix and squared root data transformation.

ered a typical feature of the Western Mediterranean Sea (Estrada and Salat, 1989; Estrada et al., 1993). During the study, chlorophyll concentrations at deeper layers usually did not exceed $1.5 \mu\text{g l}^{-1}$, though higher values during spring 1999 ($3.9 \mu\text{g l}^{-1}$) and values over $2.5 \mu\text{g l}^{-1}$ were recorded during 2000 and 2001. Furthermore, we should mention the lower importance of the autumn peak in our study area in comparison with those detected in other coastal areas of the western Mediterranean (Estrada et al., 1985). This seasonal pattern is obviously closely related to the development of the thermocline that acts as a barrier to the supply of nutrients to the photic layer. Except in 2000 and 2001, the winter peaks were of moderate intensity and presented low interannual variation (range = $0.2\text{--}0.3 \mu\text{g l}^{-1}$), whereas spring peaks (range = $0.2\text{--}3.8 \mu\text{g l}^{-1}$) were generally a bit more intense and varied over a wider range. However, very low values were commonly recorded (total annual mean = $0.28 \mu\text{g l}^{-1}$), as is expected in this oligotrophic area (Margalef, 1984; Estrada et al., 1985).

The highest chlorophyll concentration was registered during January 2000 and 2001 ($>1.1 \mu\text{g l}^{-1}$), probably due to the intense cold winds and heavy storms events that occurred in the area these years which favoured the mixing of the water column and the entrance of nutrient-rich northern waters in the Mallorca channel. Such winter phytoplankton blooms can take place during short stable periods associated with anticyclonic meteorological events immediately after convective mixing (Duarte et al., 1999). During the stratified season the surface chlorophyll values were barely detectable ($<0.2 \mu\text{g l}^{-1}$), which is a characteristic feature of this temperate latitude (Estrada et al., 1985). Accordingly, the interannual variability based on mean annual values was

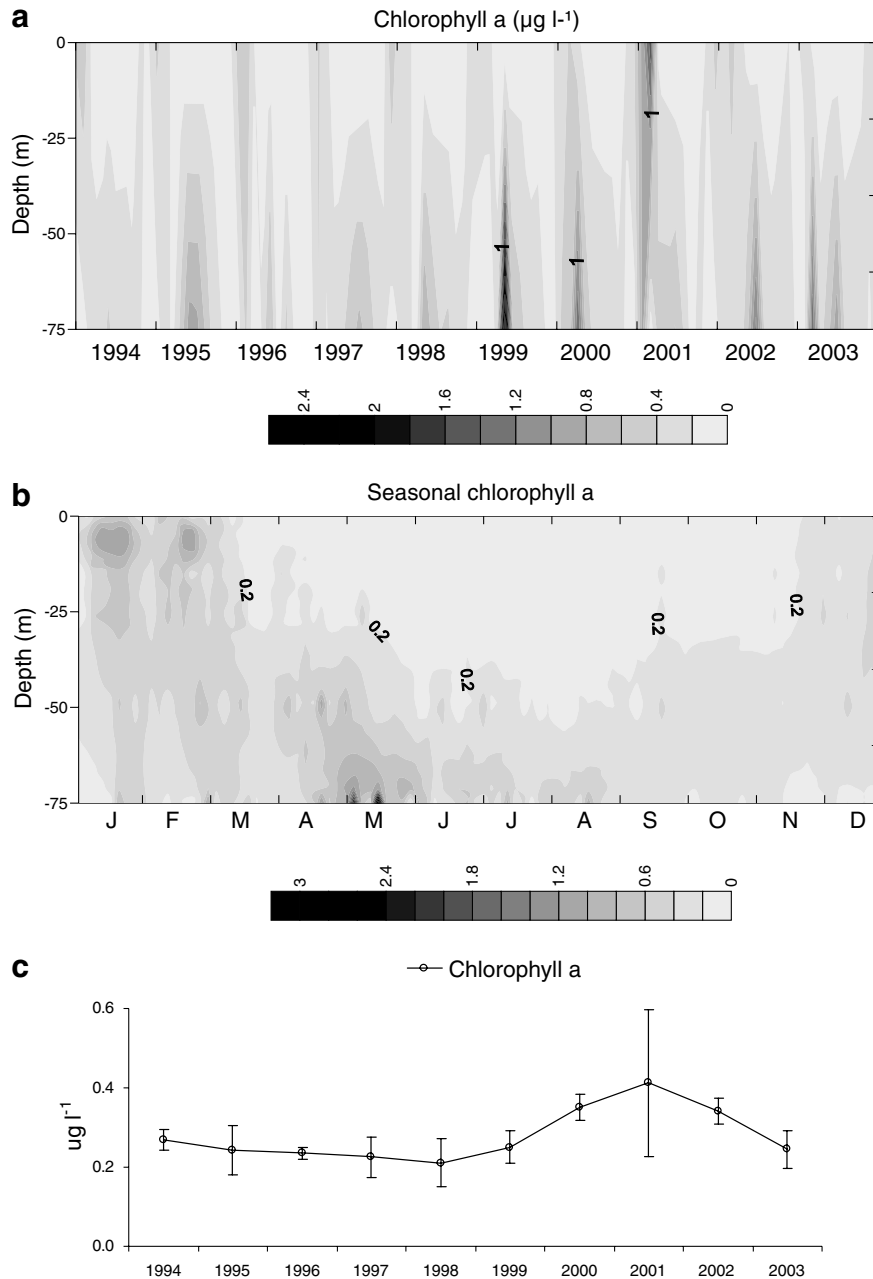


Fig. 6. (a) Interannual variability pattern of chlorophyll *a* ($\mu\text{g l}^{-1}$) from 1994 to 2003 at the St. 1. (b) Seasonal pattern of chlorophyll *a* ($\mu\text{g l}^{-1}$) from 1994 to 2003. (c) Mean annual values of chlorophyll ($\mu\text{g l}^{-1}$) and its standard error (monthly average).

remarkable, with the highest concentration during 2001 (Fig. 6c). The lowest annual values were recorded during the warmest and less saline years, related to the presence of southern Atlantic water. Therefore interannual changes observed in chlorophyll seems to be strongly influenced by the mesoscale patchiness that characterizes the whole Balearic area (Pinot et al., 1994).

It is worth stressing the importance of the plankton $<20 \mu\text{m}$ (nanodinoflagellates, coccolithophorids and other tiny groups of difficult identification) in the study area (Valencia, unpublished data), a characteristic that has been observed before at different areas of the Mallorca island (Puigserver, 2003; Fernández de Puelles et al., 1997) as well as in other coastal areas of the Western Mediterranean (Catalan coast, Estrada, 1980;

French Coast, Bustillos-Guzmán et al., 1995). The presence of small plankton is also associated with conditions of stratified waters and oligotrophy, which lead to the formation of a microbial web, contrasting with more efficient food webs like the ‘herbivorous web’ (Legendre and Rassoulzadegan, 1995). On the other hand, the microplankton (mostly represented by diatoms) blooms mainly in short, winter or spring, episodes (Valencia, unpublished data), is a pattern that in most cases can be attributed to important events of vertical mixing and nutrient enrichment that particularly favour the development of diatoms (Margalef, 1978).

3.3. Zooplankton

3.3.1. Population structure, abundance and biomass at the seasonal scales

Data from the 250 µm mesh size zooplankton samples, taken at the monitoring station (St. 1), showed that copepods were the most abundant and perennial group (56% of the total). Other important zooplankton groups were the gelatinous (23%, which consisted primarily of 17% appendicularians, 5% doliolids and 1% salps), cladocerans (10%) and meroplankton (4%). Siphonophores (3%), chaetognaths (2%), ostracods (1%) and pteropods (1%) were also found in the area. Monthly averaged abundances of the main zooplankton groups are presented in Table 1.

More than 80 copepod species were identified during the entire study period, but only 10 species accounted for 62% of total copepods. The group of *Clausocalanus* was the most abundant (*C. arcuicornis*, *C. furcatus*, *C. pergens* and *C. paululus*, 27%), followed by *Oithona* spp. (25%). Species such as *Paracalanus parvus* (8%) never disappear completely from the studied area but others such as *Centropages typicus* (6%) had a limited seasonal occurrence. *Ctenocalanus vanus* (5%) and *Diaixis hibernica* (5%) were mostly present in early spring and *Acartia clausi* (7%) was more abundant during summer. In autumn, *Temora stylifera* (4%), *Farranula rostrata* (3%) and *Oithona plumifera* (3%) exhibited higher abundances. Some species presented very low abundances during short periods, such as *Calanus helgolandicus* in winter, or *Acartia danae* in late summer.

The well known *Clausocalanus* and *Oithona*, dominant in all oceans, were by far the most abundant genera in the study area, being considered the most stable fraction of the total zooplankton, as occur in other neritic areas of the Mediterranean (Mazzocchi and Ribera d’Alcala, 1995; Christou, 1998). *P. parvus*, *C. vanus*, *C. typicus* and *A. clausi* have been also highlighted as important species in the Balearic Sea (Fernández de Puelles et al., 2003a). The importance of *C. typicus* as a candidate to provide useful information about evolution of the Mediterranean ecosystem has been recently indicated (Mazzocchi et al., 2007). Furthermore, *A. clausi* and *T. stylifera* may also be other key species as they have been proposed in northern Western Mediterranean (Molinero et al., 2005a). Although less abundant, *C. helgolandicus* would be another suitable species related to environmental changes in the Western Mediterranean, as has been mentioned for the North Atlantic (Bonet et al., 2005). All these species can collectively be considered as main species to depict the copepod community, being good indicators of the hydrographic regime in the Balearic Sea (Fernández de Puelles et al., 2004b). It is important to consider that the more abundant copepod species previously mentioned are the same as those observed in other Mediterranean areas during previous years (Mazzocchi and Ribera d’Alcala, 1995; Christou, 1998). This suggests that, at least in the last decades, the environmental changes which have been taking place in neritic waters of the Balearic Sea did not strongly affect the structure of the copepod community.

Among the cladocerans, *Penilia avirostris* was the most abundant (42%) particularly in summer. *Evadne spinifera* (23%), *Podon intermedius* (22%) and *E. tergestina* (10%) followed in abundance with their higher peaks in late spring. The meroplankton was well represented by gasteropods and bivalve larvae in early summer. During winter the appendicularia *Fritillaria pellucida* and the ostracod *Conchoecia* were abundant. The Siphonophores were represented by species of *Mugilaea*, *Lensia*, *Eudoxia* and *Abylopsis* year-around. Similarly for *Doliolum nationalis* which was the dominant species among the doliolids. Pteropods were mainly represented in autumn by *Creseis acicula* and within the chaetognaths, *Sagitta* was always the main genera (the chaetognaths usually found were immature). Salps peaked in spring and were mainly represented by *Thalia democratica*, *Salpa maxima* and *S. fusiformis*, but *Isias zonaria*, *Pegea confederata* and *Ihleia punctata* were also relatively abundant.

The hierarchical classification of the first 20 taxa, in a rank order of abundance, based on monthly averaged data from the total period, can summarize the above mentioned (Fig. 7). Those species can depict the zooplankton community and their main assemblages in the Balearic Sea. One large group is constituted by species

Table 1
Monthly mean abundances (ind. m⁻³) of main zooplankton groups and their standard deviations (SD) during the period study (1994–2003)

1994–2003	Total abundance	Copepoda		Appendicularia		Cladocera		Doliolida		Meroplankton		Chaetognatha		Siphonophora		Pteropoda		Ostracoda	
Mean	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³
J	806	135	486	123	175	54	10	47	38	17	13	16	12	14	7	6	6	17	10
F	958	301	662	271	151	84	20	18	37	41	15	9	15	26	22	2	3	11	10
M	1168	307	723	318	184	64	40	21	56	58	16	10	19	15	52	28	1	10	6
A	1072	457	606	374	192	90	94	44	34	25	33	23	22	17	47	23	2	5	4
M	1254	249	718	172	180	66	141	63	46	40	54	36	15	8	36	14	3	5	4
J	1215	466	587	215	171	72	198	248	84	88	72	55	24	16	41	59	11	22	3
J	1136	441	491	199	154	83	262	293	91	99	64	42	31	18	20	12	7	6	2
A	903	224	461	136	115	32	171	150	49	76	61	38	20	12	11	6	6	4	6
S	853	212	466	119	173	66	99	60	22	24	30	15	12	5	21	11	10	9	5
O	780	194	435	118	144	55	70	44	44	36	22	13	20	8	24	7	8	4	4
N	621	193	347	97	148	117	17	10	26	16	15	10	24	9	15	7	7	6	7
D	666	258	430	178	111	45	15	22	37	45	11	8	18	17	16	10	6	6	14

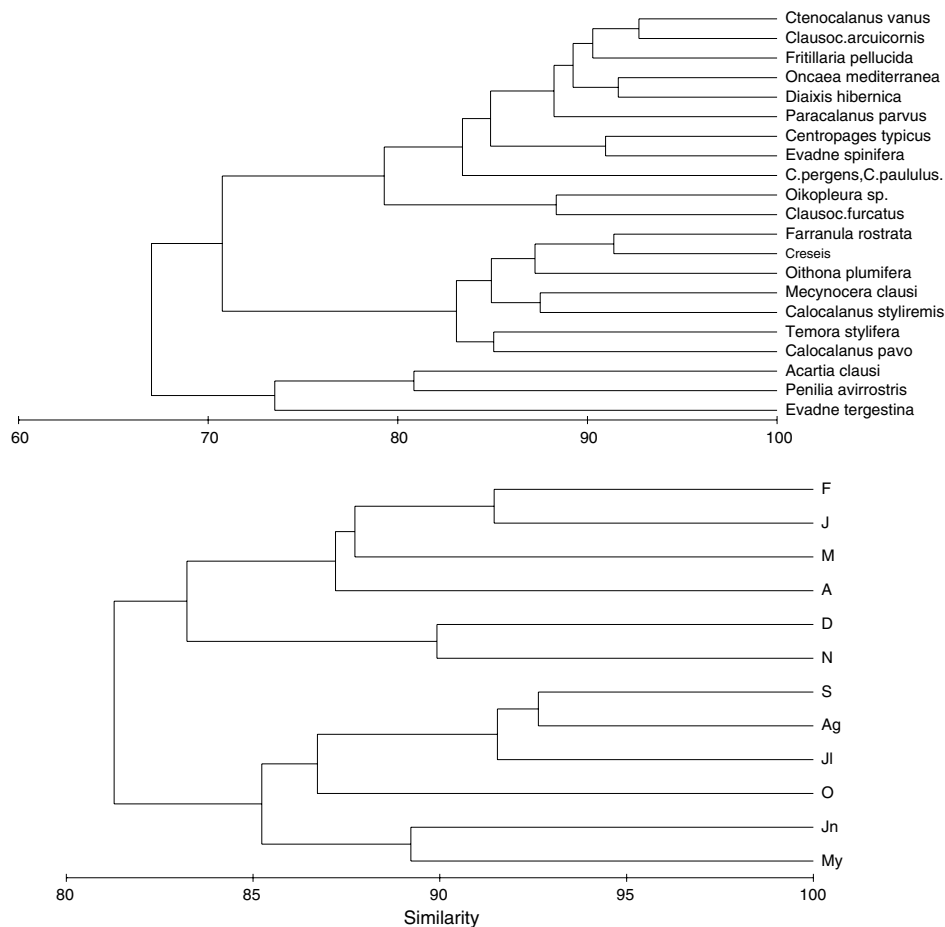


Fig. 7. Dendrogram using group average linking on Bray–Curtis similarity of the main species (variables) and months (samples) found from 1994 to 2003 based on the Bray–Curtis similarity matrix.

showing a higher presence during a cooler period. Among these, *C. arcuicornis*, *C. vanus*, *D. hibernica*, *P. parvus* and *F. pellucida* are the most abundant in early spring, whereas in late spring *C. typicus*, small *Clausocalanus* and *E. spinifera* are more important. Another large group includes the species *C. furcatus*, *F. rostrata*, *M. clausi*, *T. stylifera*, *O. plumifera* and the pteropod *Creseis*, which showed their dominance during autumn. Finally, a group constituted by *Acartia clausi*, *P. avirrostris* and *E. tergestina* was more abundant during summer months.

The cluster analysis of the mean monthly abundance of selected zooplankton taxa (considering samples) showed the two main assemblages previously cited, coinciding temporally with the main annual environmental situations. Very similar results were obtained during the first period of the time-series (Fernández de Puelles et al., 2003a) where two evident periods emerged, with a short transition periods between them: a well stratified water period from July to October and thoroughly mixed water period from December to April.

Regarding the fish larvae studied community from 1994 to 1999 a total of 64 species were identified, giving a good picture of the ichthyoplankton composition in the area. However, the diversity found was lower than values previously reported from other ichthyoplankton surveys from the same (Alemany, 1997) or nearby areas (Sabatés, 1988). The most abundant species were *Sardina pilchardus*, with 50 larvae and 278 eggs 10 m^{-3} respectively, representing 18% of larvae and 55% of eggs. It was followed by larvae of *Hygophum* sp. (10%), *Sardinella aurita* (8%), *Cyclothone braueri* (7%) and *Boops boops* (6%), whereas the rest represented less than 5%. *Ceratoscopelus maderensis*, *Lampanyctus pusillus*, *Spicara smarís*, *Trachurus mediterraneus*, *Centracanthus cirrus* were the most abundant of these scarcer species.

The mean annual cycle of mesozooplankton biomass obtained from the neritic station during the 10-year study (annual mean of $5.4 \text{ mg dry weight m}^{-3}$) showed a clear seasonal pattern with a higher mean biomass corresponding to the first semester (maximum in April, 6.4 mg m^{-3}) and lower values detected in the second half of the year (minimum in August, 4 mg m^{-3}). However, in September, a smaller peak of biomass was observed (5 mg m^{-3}), and might be attributed to the slightly increase of several groups after the high stratification period (Fig. 8a). This peak was not so evident when zooplankton abundance was calculated. Two higher peaks were clearly distinguished in the abundance of the main zooplankton group, the copepods, in March and end of May. The moderate total zooplankton abundance (mean annual value of 963 ind. m^{-3}) found and the low biomass indicated that the Balearic area was characterized by the presence of relatively small organisms. Moreover, large gelatinous zooplankton did not appear in great quantities in the samples.

During winter and spring the contribution of copepods to the total abundance ranged from 94 to 72%, but during summer, characterized by stratified waters, cladocerans and meroplankton larvae were more numerous, and the proportion of copepods decreased to 38%. The cladocerans seasonal oscillation was well defined from March to October, reaching its highest peak in July, whereas the meroplankton (4%) were more abundant during a shorter period (June–August). Abundance of appendicularians varied little throughout the year, although a slight decrease was observed during summer. Some minor zooplankton groups, such as doliolids, were more abundant during the stratified months (Fig. 8b). Siphonophores were more abundant in late winter and early spring, with a closer pattern to the ostracods. During autumn however, almost all groups slightly increased. Added to this, a large number of protozoa (mainly radiolarians) were observed in summer. Although they were considered for biomass estimates, they were excluded from the estimations of total abundance.

In the analysis of the ichthyoplankton community, the 6-year sampling scheme allowed us to describe the spawning period of the most abundant species in detail (Figs. 8c and 8d). The three most abundant species, *C. braueri*, *Hygophum* sp. and *C. maderensis*, exhibited a wide and overlapped spawning period, almost all year round, but peaking in the warm months. The only difference among them was that *C. braueri* showed two spawning peaks, May and September, whereas the others showed a unimodal spawning peak centred in July. Conversely, the six more abundant coastal species exhibited narrower non-overlapping spawning periods: *S. pilchardus* peaks in winter, *B. boops* in March, *S. smaris* in May, *T. mediterraneus* in July, *S. aurita* in August and *C. cirrus* in October. It is plausible that this temporal variability results from an adaptive strategy to avoid competition for resources of this oligotrophic area.

Overall, the maximum values of zooplankton abundance were generally centered on the first months of the year, just after the convective mixing period. However, a few groups increased in abundance when the waters were well stratified, such as the doliolids, cladocerans and meroplankton larvae. Spring time was the most representative season for the most populous groups, the copepods and gelatinous species. The seasonal cycle constitutes the most important periodic oscillation in the recorded zooplankton abundance and explains much of the variance in time fluctuations (Fernández de Puelles et al., 2004a).

Seasonal distribution is likely to be related to the different hydrological scenarios observed in the Western Mediterranean basin. The zooplankton peak in March was related to the period of vertical mixing when the cold, dense, nutrient-rich waters reach the surface, which is a widespread event in the Mediterranean. This early spring maximum seems to occur yearly in response to the previous winter phytoplankton bloom (Margalef, 1984). However, the late spring and particularly the autumn peaks, although reported in other areas of the Mediterranean (Rodríguez, 1983; Fonda-Umani, 1992; Mazzocchi and Ribera d'Alcala, 1995; Siokou-Frangou, 1996), do not seem to have such a clear connection between phytoplankton and mesozooplankton abundance. During spring, when the thermocline is developing, the inputs of offshore waters and the proximity of frontal systems usually enhance the zooplankton abundance. Intermittent fertilization pulses due to hydrographic perturbations may explain the presence of significant growth of the phytoplankton populations at the DCM layer (Estrada, 1985), which can be considered a characteristic of this period in the north Western Mediterranean (Alcaraz, 1988; Latasa et al., 1992). In our study, the predominant Atlantic water observed during the second part of the year had influence on the presence of some zooplankton groups, such as doliolids and chaetognaths, as has also been described for other mid Western Mediterranean areas (Vives, 1966; Scotto di Carlo et al., 1985). The higher peaks in copepod abundance could be related to autotrophic food potentially available in previous weeks, as in the Tyrrhenian Sea (Mazzocchi and Ribera d'Alcala, 1995). However,

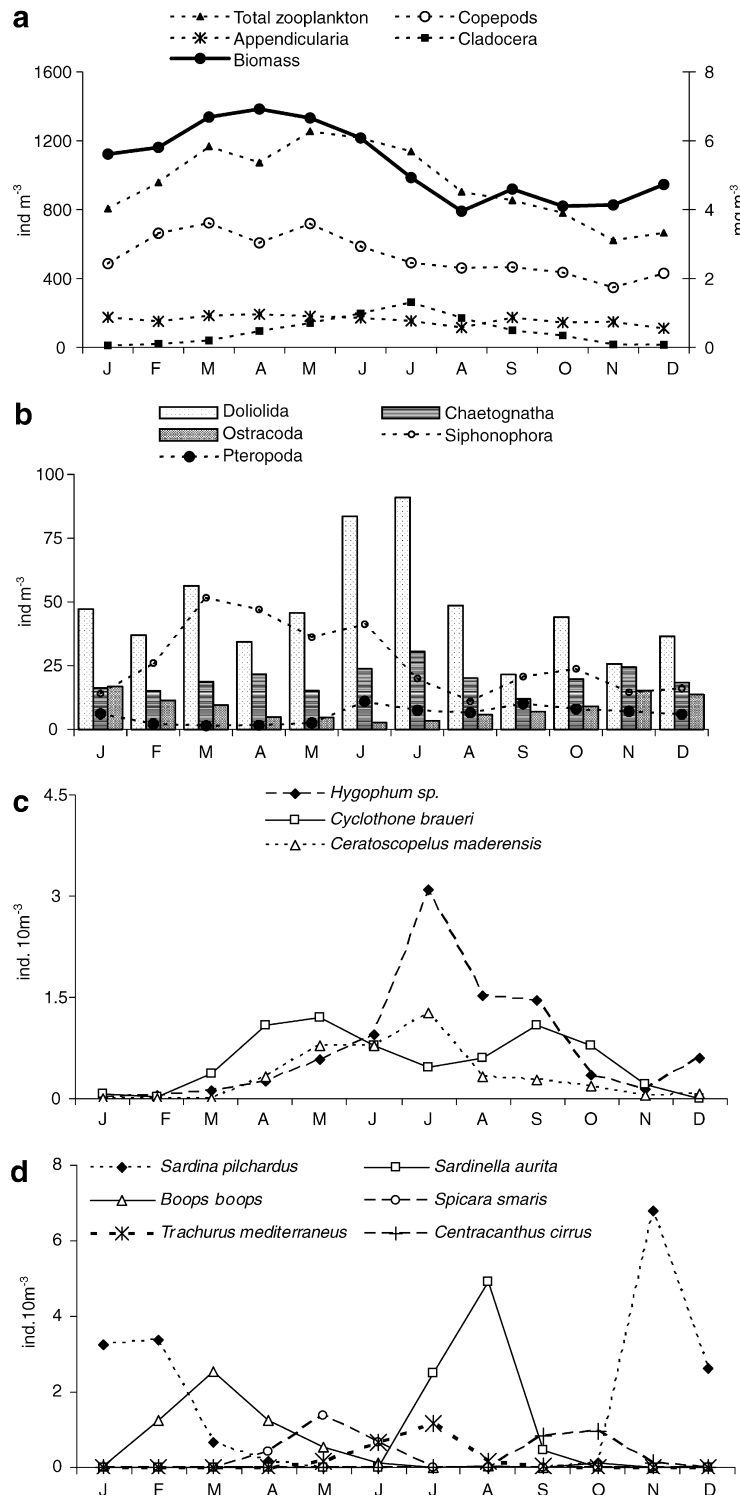


Fig. 8. (a) Seasonal pattern (monthly average), based on the 10-year data-series of zooplankton biomass (mg m^{-3}) and total abundance, copepods, appendicularians and cladocerans (ind. m^{-3}) at the St. 1. (b) Seasonal abundance (monthly average) of minor groups, doliolids, chaetognaths, siphonophors, ostracods and pteropods (ind. m^{-3}). (c) Main ichthyoplankton species found during the period 1994–1999. (d) Minor species of ichthyoplankton found during the period 1994–1999.

during the well stratified period when the autotrophic food is rather limited and below the thermocline, the main copepods might maintain their biomass by having preferences for food other than phytoplankton. There is a large body of literature suggesting that microzooplankton can be a major component in the diet of copepods in oligotrophic waters (Dam et al., 1993; Roman and Gauzens, 1997; Hernández-León et al., 2002, among others). In fact, microzooplankton is responsible for most of the control of primary production in warm waters (Dam et al., 1995). Thus, during the stratified period, the trophic web based on the microbial loop could assume greater importance (Turner et al., 1988; Urban et al., 1992), indicating a close relationship to small zooplankton. In this context, the importance of the smaller zooplankton has been pointed out in North Western Mediterranean coastal waters by Calbet et al. (2001) and also at the beginning of the time-series in the Balearic Sea (Fernández de Puelles et al., 2003a). During that year the smaller zooplankton fraction analysed (100–250 µm) was found correlated to chlorophyll *a*. However, this pigment proved to be significantly correlated with large organisms on very few occasions. No correlations were found during the total period between mesozooplankton abundance and chlorophyll *a* pigment. On this sense, smaller zooplankton communities should be taken into account during larger period in order to find out possible relationship between phytoplankton and zooplankton communities.

Seasonal variations are significant throughout the oceans, but it is in oligotrophic waters where the patchiness found in short time intervals and/or small spatial scales may assume greater importance. However, during the mixing period, the strong and persistent physical forces maintain the homogeneity of the water column. Nonetheless, though a direct and important relationship emerges between the distribution of the plankton and hydrographic features (Sabatés et al., 1989; Mazzocchi et al., 1997; Siokou-Frangou et al., 1997), the dynamic aspects alone seem to be insufficient to explain all the variation observed (Taupier-Letage et al., 1988; Thibault et al., 1994), since a quite complex interaction exists between the magnitude and persistence of hydrographic features and the phenology of planktonic communities.

3.3.2. Interannual variability

During the 10-year sampling at St. 1, important interannual variability emerged when the total zooplankton abundance was considered (Fig. 9a). These overall fluctuations were always shaped by the most abundant group, the copepods. Monthly zooplankton abundance data indicated that the highest peaks were found during the first part of cool years (1996, 2000 and 2001), and the lowest values during the period 1997–1999. The annual values based on monthly averaged zooplankton abundance showed higher abundances during the cool years and vice-versa (Table 2). The appendicularians, the second group in abundance exhibited a similar pattern to copepods. They were followed by the cladocerans. It is noteworthy that during late spring and early summer of years 2000 and 2001 a considerable increase in the abundance of cladocerans was observed, mainly due to *Penilia avirostris* increasing (Fig. 9a). The highest values of copepod abundance that occurred during the springs of 1996 and after year 2001, were not observed the other years. Among this irregular pattern, seasonal cycles were always evident. Siphonophores, showed an increased abundance during the last years of the studied period (Fig. 9c). On the other hand, chaetognaths and doliolids decreased from the beginning of the study to the end of the time-series. However, pteropods and ostracods did not show any particular pattern (Fig. 9d).

Interannual variability based on mean annual values of main zooplankton groups indicated that the highest increases of zooplankton, in both total abundance and biomass, occurred during 1996 and 2000 (Fig. 10a). The lowest abundance however, was observed during the warmest year 1998 but also at the end of the time-series. The decrease observed during the last years was not followed by the group of copepods, appendicularians or siphonophores. On the contrary, the group of doliolids and chaetognaths almost disappeared in the area from the beginning of the time-series (Fig. 10b). It seems that a clear but different relationship emerged among the zooplankton groups and the physical conditions of the water masses (Table 3). In relation to that, significant correlations between temperature and salinity and zooplankton abundance of the main groups were found ($p < 0.05$). Copepods, siphonophores and ostracods showed a decrease when the temperature increased. On the contrary, cladocerans, chaetognaths and pteropods increased with a higher temperature. When salinity was considered, different biological responses were found among the abundance of the main zooplankton groups. Positive correlation was found with copepods and siphonophores, while negative correlations were found for doliolids, chaetognaths, pteropods and ostracods. This indicates the preference of

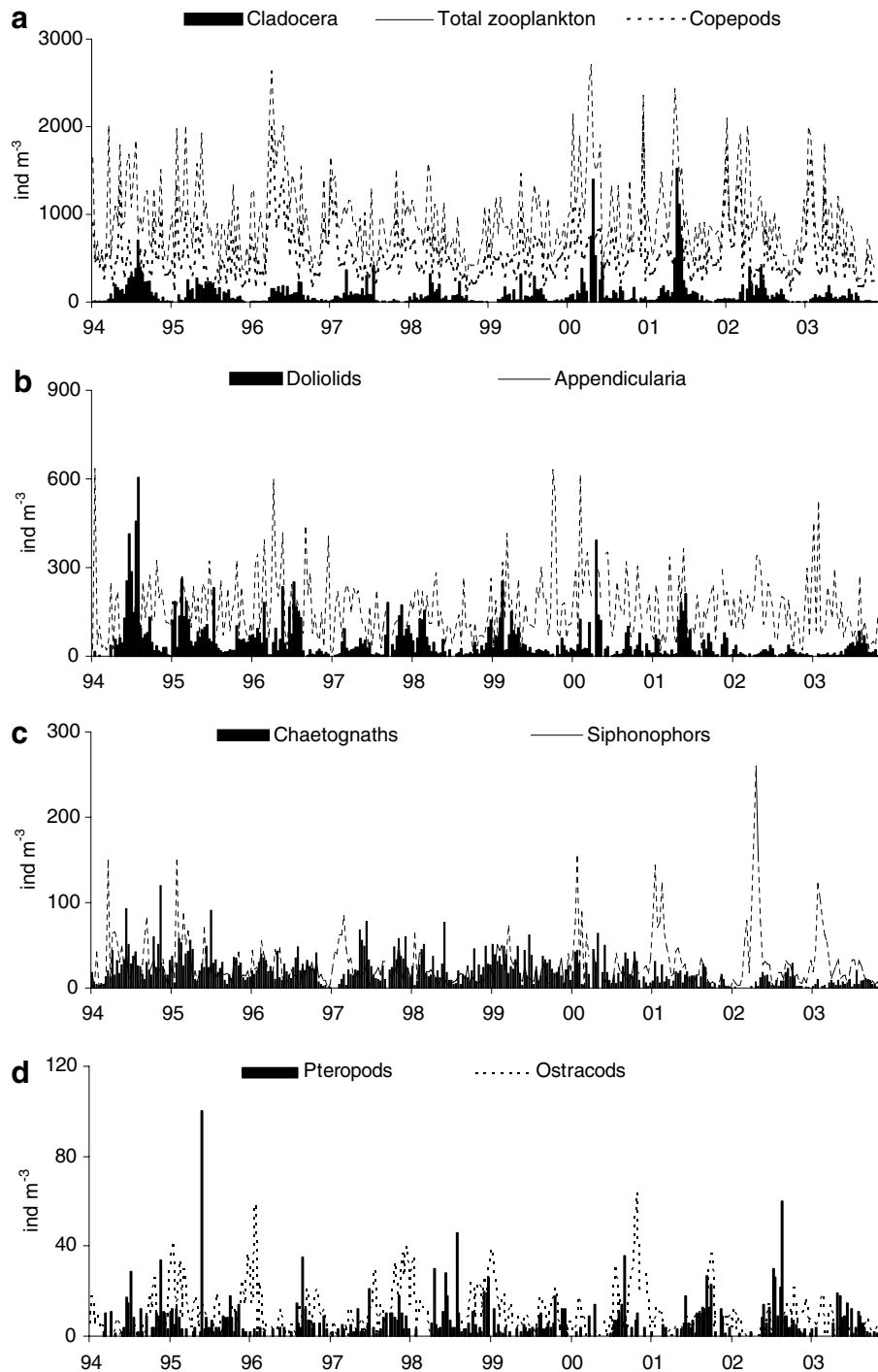


Fig. 9. (a) Interannual variability of zooplankton abundance, copepods and cladocerans from 1994 to 2003 (ind. m^{-3}) at the St. 1. (b) Interannual variability of doliolids and appendicularians (ind. m^{-3}). (c) Interannual variability of chaetognaths and siphonophores (ind. m^{-3}) at the St. 1. (d) Interannual variability of pteropods and ostracods (ind. m^{-3}) at the St. 1.

the former groups for different properties of the water masses when they were prevalent in the area. Main zooplankton group assemblages emerged when hierarchical classification was done during the whole period of study (Fig. 11). Copepods, siphonophores and appendicularians were found correlated, exhibiting higher

Table 2
Annual mean abundances (ind. m⁻³) of the main zooplankton groups and their standard deviations (SD) in the studied period (1994–2003)

1994–2003	Total abundance	Copepoda		Appendicularia		Cladocera		Doliolida		Meroplankton		Chaetognatha		Siphonophora		Pteropoda		Ostracoda	
		ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD	ind. m ⁻³	SD
94	1008	232	163	141	64	139	145	90	112	46	39	27	16	29	14	6	6	5	4
95	917	243	159	158	57	89	145	73	109	45	38	27	15	29	13	11	6	12	7
96	1113	211	174	191	54	71	142	64	105	52	37	23	14	22	19	4	6	9	8
97	890	221	176	134	55	65	139	42	102	33	36	20	13	25	20	5	6	8	8
98	781	218	171	119	55	59	140	38	101	30	35	23	13	15	19	7	6	12	8
99	880	213	122	182	39	65	142	50	100	28	38	29	14	22	20	5	6	11	8
00	1113	226	120	211	31	168	142	47	89	28	42	23	13	28	20	5	19	10	8
01	1044	226	148	143	36	165	132	40	66	29	30	12	14	33	20	5	19	9	8
02	940	242	151	162	37	83	81	16	46	28	29	7	14	37	20	7	19	6	7
03	839	250	151	143	37	44	72	17	48	21	29	5	14	29	20	4	19	4	7

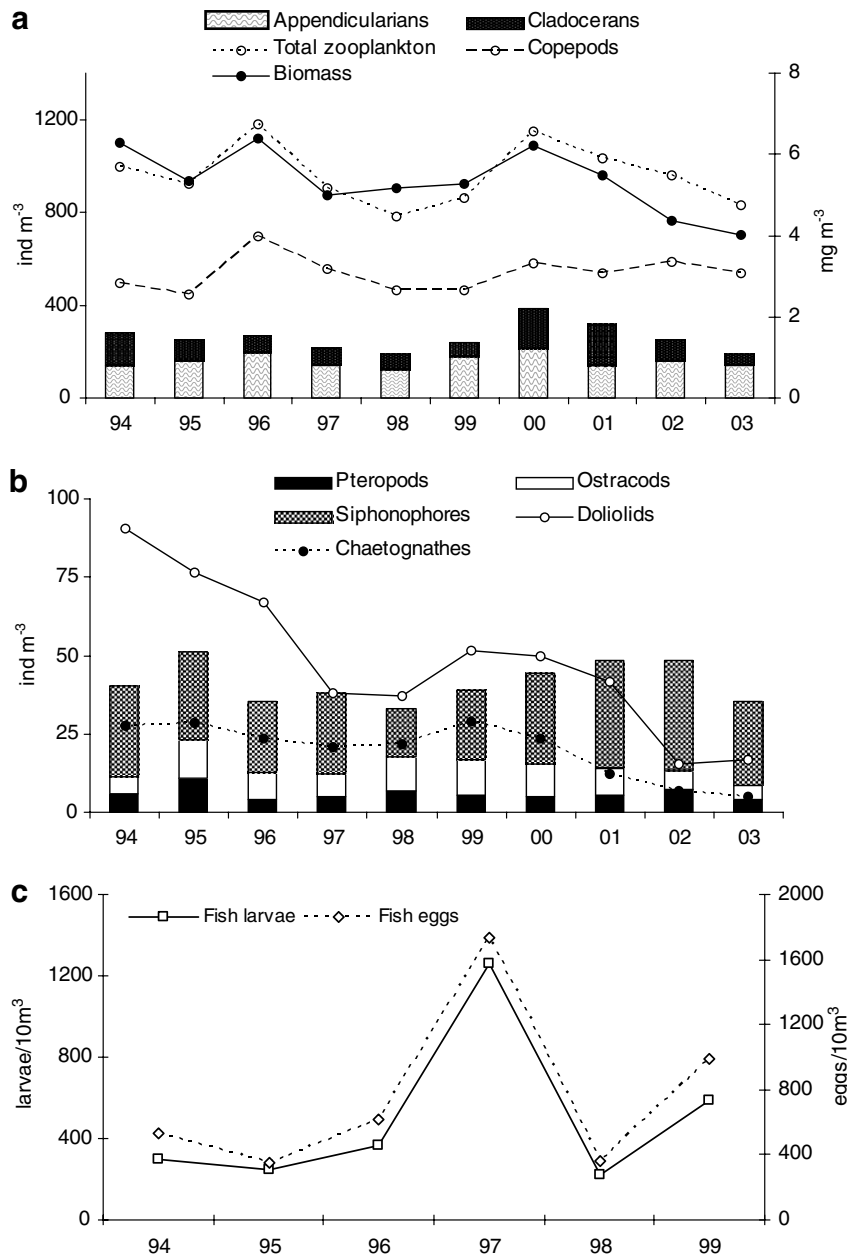


Fig. 10. Mean annual values of zooplanktonic abundance in the St. 1 (ind. m⁻³) of (a) Total organisms and biomass, copepods, appendicularians and cladocerans; (b) Siphonophores, doliolids, chaetognaths, ostracods and pteropods and (c) Interannual variability of ichthyoplankton from 1994 to 1999.

abundances when cool and saltier water conditions were in the Balearic area. However, doliolids, chaetognaths and also pteropods exhibited higher abundances when warm and low salinity waters were in the area. Ostracods present in autumn and winter liked low salinity waters. Furthermore, meroplankton present in the summer have a preference for low salinity waters. Cladocerans however, did exhibit clear salinity pattern.

During the 6-year ichthyoplankton study, high interannual variability was also found. Both egg and larval abundances follow exactly the same pattern, peaking in 1997 with another smooth maximum in 1999 (Fig. 10c). In this last year, the high annual larval and egg abundances were a result of the high quantities

Table 3

Relationship between main zooplankton groups ($\ln(x + 1)$), temperature (0–75 m) and salinity (0–75 m) given as correlation coefficient values ($n = 343$, * $P < 0.05$, ** $P < 0.001$)

	Temperature	Salinity
Total	−0.05 ns	0.09 ns
Copepoda	−0.19**	0.19**
Appendicularia	−0.05 ns	−0.05 ns
Cladocera	0.41**	−0.025 ns
Doliolida	0.05 ns	−0.22**
Chaetognatha	0.19**	−0.4**
Siphonophora	−0.18**	0.14*
Pteropoda	0.39**	−0.29**
Ostracoda	−0.22**	−0.24**
Meroplankton	0.34**	−0.14*

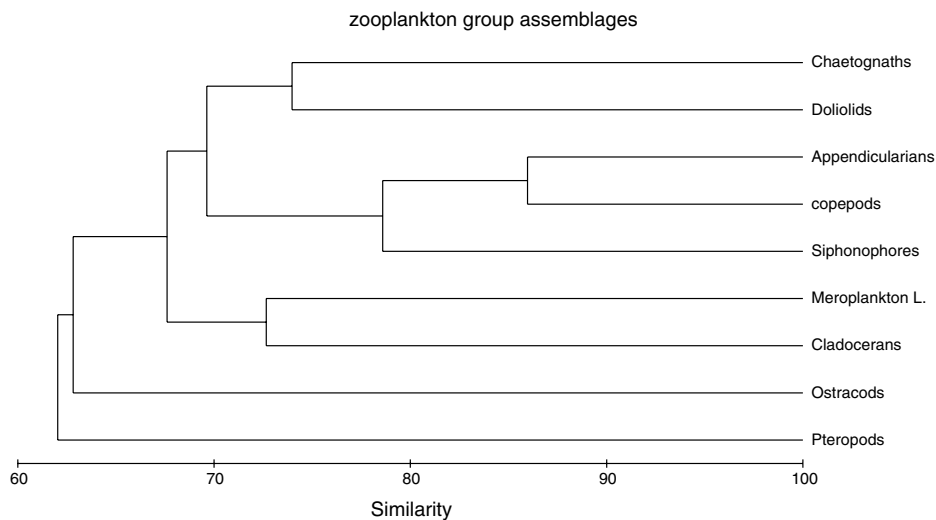


Fig. 11. Dendrogram for hierarchical clustering using group average linking on Bray–Curtis similarity of main zooplankton groups during the whole period from 1994 to 2003.

of sardine eggs and larvae sampled, whereas the maximum peak of 1997 was attributable to the presence of mesopelagic species, such as *C. braueri*, *C. pygmaea* and *Hygophum* sp., as well as there being high abundances of *C. cirrus* larvae, whose eggs were also the most abundant this year. It was interesting to observe that the highest abundance of this community was just after the cold 1996, in which an important inflow of saltier surface waters from the northern basin over the study area which lasted until May 1997, took place. It is possible that the high abundances of mesopelagic species larvae at the neritic station are the result of inflow of offshore waters over the shelf. A similar situation has been described for nearby areas by [Alemán et al. \(2006\)](#). However, the cause of the increased overall abundance of mesopelagic fish larvae in 1997 over other years remains unclear. It could be suggested that it is a result of the higher zooplankton abundances in the previous cold years, which would have produced an increase in the populations of these zooplanktivorous species. In order to understand the functioning of the pelagic Mediterranean ecosystem, additional and longer time-series should be focused on the ichthyoplankton community, particularly in the Balearic sea.

Overall, the low biomasses and moderate abundances found in the present study were comparable to oligotrophic areas of the Eastern Mediterranean ([Siokou-Frangou, 1996](#); [Christou, 1998](#)), although they were lower, compared to other areas of the Western Mediterranean ([Seguin, 1973](#); [Rodríguez, 1983](#); [Boucher et al., 1987](#); [Seguin et al., 1993](#); [Mazzocchi and Ribera d'Alcalá, 1995](#); [Champalbert, 1996](#); [Gaudy and Champalbert, 1998](#)). These authors suggest that a general “poverty” is evident from the low concentrations

of nutrients and plankton biomass. However, this may not always apply to the abundance of zooplankton (predominantly small organism size) whose seasonal distribution may vary irregularly in relation to changes in the circulation of the Balearic Sea (Pinot et al., 2002). According to other authors (Razouls and Kowenberg, 1993), oceanic areas in the northern Mediterranean Sea might have noticeable concentrations of small zooplankton that could vary year by year. Very complex interactions occur in the zooplankton abundance pattern, which seem to be related to changes in the proportion of the water masses they inhabit. Moreover, the range of zooplankton biomass and abundance, whether from neritic or oceanic western Mediterranean waters, is not always well defined (Gaudy, 1985) and their seasonal distribution can be very irregular (Furnestin, 1968; Razouls and Kowenberg, 1993). Furthermore, it is worth mentioning that comparative data should be used with caution, since an enormous variety of sampling methods and different net meshes have been used in Mediterranean zooplankton studies (Gaudy, 1985).

In the Western Mediterranean, cold years tend to be more productive, partly because winter mixing may reach greater depth, and in part because the formation of deep water in the Gulf of Lion may occur over a larger area (Estrada et al., 1985). This enhanced production during cool winters and spring also gives rise to an increase in zooplankton production, as was observed in our data during the cool years. The increase in 1996 and year 2000, was related to northern Mediterranean Waters and could be caused by a higher influence from the northwestern Mediterranean, whose fertility is higher in relation to the rest of the basin (Flos, 1985; López-Jurado, 2002). Contrary to this, a high influence of recent Atlantic Water was observed during 1998 (Pinot et al., 2002), and the lowest zooplankton abundance during this period could be a clear response to warming, when the waters were more stratified and poorer in nutrients. During the period 1994–1999, an overall decrease of zooplankton was clearly observed in relation to the warming of coastal waters (Fernández de Puelles et al., 2003b). However, due to the cold temperature registered during the last years no significant zooplankton nor copepod trends were found during the 10-year time-series. The observed decline in abundance in relation to increased water temperature observed for late 1990s might be a response to the global warming, as was found during 30 years observation of the California current (Roemmich and Mc Gowan, 1995) and during the 10-year series in the Bay of Biscay (Valdés and Morales, 1998). In other Mediterranean areas, a zooplankton decline was observed during the 1970s (Cataletto et al., 1995) and also during the 1980s (Mazzocchi and Ribera d'Alcala, 1995). However, in the Eastern Mediterranean and in the early 1990s an increase of the copepod abundance was found in relation to a higher salinity of the Aegean Sea (Christou, 1998).

In the present study, during the entire period no significant zooplankton decrease was observed but the correlation of copepods with temperature (negative) and salinity (positive) indicated their direct relation to the presence of the different surface water masses; when colder and saltier Mediterranean Waters prevailed in the area higher zooplankton biomass values were observed. This phenomenon has been detected previously in the Balearic Sea (Fernández de Puelles et al., 2003b), and in northern areas of the Western Mediterranean (Razouls and Kowenberg, 1993). This could explain the higher copepod preference for cooler and more saline waters, which characterize the northern Mediterranean Water. We realize that factors other than temperature and salinity could contribute to the plankton pattern observed, but the recognition of large-scale dependence on the physical environment (Mackas, 1984; Sabatés et al., 1989) is a first and necessary step to understanding zooplankton distribution in the Western Mediterranean.

3.3.3. Zooplankton mesoscale spatial variability

During the period 1994 to 1999 a significant decrease in zooplankton abundance was observed as one moved offshore from coastal to ocean stations (33%). However, no clear differences in biomass were found (ANOVA, $p > 0.05$; Fernández de Puelles et al., 2003b). The onshore increase in abundance was due to the higher numbers of the main zooplankton groups at the neritic station. All of them exhibit a steeply decreasing trend in their abundances (33%, 34% and 40%, copepods, appendicularians, cladocerans and meroplankton larvae grouped together, respectively) as one goes from the neritic to deeper stations. Copepods continued dominating the zooplankton assemblages with a high decrease further offshore (St. 3) particularly relevant during the late spring peak. Such a decrease was observed in almost all copepod species but no differences were observed for some copepods, such as *C. vanus* and *C. helgolandicus*. Other copepods such as *Nannocalanus minor*, *Neocalanus gracilis*, *M. clausi* and *F. rostrata* were even more abundant at deeper stations (Fernández

de Puelles et al., submitted for publication). Minor groups, such as doliolids, siphonophores, chaetognaths and pteropods, did not exhibit a cross-shelf gradient during the study. Meanwhile the ostracods were more abundant offshore. Meroplankton however, exhibited higher abundance at the neritic station, while the cladocerans did not show differences all along the shelf (Fernández de Puelles et al., 2003b).

Ichthyoplankton species also differed significantly among the cross-shelf stations. In the neritic station, shelf species larvae represented 87% of total, 59% in the intermediate station, whereas in the outer station, oceanic species were predominant, representing 63% of larvae. In St. 1 the six most abundant taxa of larvae belonged to coastal species (mainly clupeids as *S. pilchardus* and *S. aurita*), but also to other small pelagic or demersal species (such as *B. boops*, *T. mediterraneus* and *S. smaris*). At deeper stations the most abundant larvae were also those of the above mentioned Clupeidae, with around 10% each one, but also larvae of meso-pelagic species (such as *Hygophum* spp., *C. braueri* and *C. maderensis*). Just offshore, the latter species clearly predominated. The only well represented coastal species was *S. pilchardus*, representing 10% of the total. All these species can be included among the more abundant in the study area, as previous data on ichthyoplankton (Alemany, 1997) and fishing fleet landings and discards suggest. The total abundance of fish larvae presented a decreasing trend from the coast offshore, with a mean of 114 larvae per 10 m³ captured by year at St. 1, 88 at St. 2 and 83 at St. 3. The egg abundances showed the same trend, with a more drastic decrease, from 2565 at St. 1 to 353 at St. 2 and only 110 in St. 3, as could be expected due to the fact that most of sampled eggs belonged to neritic species with coastal spawning areas.

Overall, in the Mediterranean Sea two peaks of zooplankton abundance are typically described (late winter or spring and autumn; Scotto di Carlo and Ianora, 1983; Siokou-Frangou, 1996). Whereas in coastal areas the spring peak stands out (Mazzocchi and Ribera d'Alcala, 1995), in open sea areas the earlier peak is the most important (Gaudy and Champalbert, 1998). In the Balearic area, despite the spatial sampling scale being relatively small, two spring peaks always occurred, with a decreasing coast-open sea gradient. Late spring peak was rather important in the coastal station than earlier spring peak, which was more important offshore (Fernández de Puelles et al., 2003b). However, the total zooplankton abundance did not vary much among them. The three analyzed stations presented maximum values in spring and a minimum values in summer, closer to other oligotrophic areas of the Mediterranean Sea (Siokou-Frangou, 1996).

3.3.4. Zooplankton variability linked to large-scale processes

Climate plays a key role in the oceanographic regime and consequently directly influences the plankton community production. Therefore, during the last decades, an interest in the effects of climate variability on biological processes has emerged where they showed that climate interacts with population densities (Molinero et al., 2005; Chiba et al., 2006). In many tropical and subtropical regions it has been observed that increased global temperatures cause stronger stratification and lower zooplankton production (Williamson, 2000). The relationship between zooplankton variability and long-term climatic indicators such as the North Atlantic Oscillation (NAO) has been established in the North Atlantic (Fromentin and Planque, 1996). It is the state of this index of interannual variability in the north Atlantic (NAO) that influences the speed and direction of westerly winds across the north Atlantic as far as Europe, as well as winter temperature (Taylor et al., 1992). The persistence of an exceptionally strong positive NAO is the source of recent temperature anomalies and changes in the atmospheric moisture transport (Hurrell, 1995). Although the long-term sea surface temperature and circulation in the Western Mediterranean Sea has been related to the NAO (Vignudelly et al., 1999; Bolle, 2002), very little is known about the relationship between the zooplankton and the causal mechanisms involved.

An attempt was made to explore the relationship between long-term atmospheric North Atlantic indicators and the main zooplankton group, the copepods. A significant correlation between copepods abundance and the winter NAO index during the period from 1994 to year 2000 was found (Fernández de Puelles et al., 2004a) and similar results when the 10 years were considered ($R^2 = 0.50$; $P < 0.05$). Taking into account that other than 1996 (−2.86), only 2001 had a negative winter NAO value (−1.05). The highest copepod abundance of the time-series coincided with the lowest winter NAO value (−2.86) in 1996, when conditions changed dramatically from previously high positive anomalies turned into a strong negative anomaly. However, our work reveals an interesting relation between the winter NAO index and copepods abundance. It seems that a negative NAO index (<1) produces a strong effect in the northern Western Mediterranean, since it may bring cold

air to northern Europe and moist air into the Mediterranean producing cooler winters (Vignudelly et al., 1999), suggesting a possible link between atmospheric forcing and copepod abundance in the Balearic Sea. On the other hand, a positive winter NAO does not exhibit such a clear relationship with zooplankton (Turrel and Holliday, 2003). If cold winters (negative winter NAO) favor rich northern Mediterranean waters, then higher amounts of zooplankton, and particularly copepods, could be expected in the Balearic Sea. The lack of westerly winds in western Europe, which are characteristic of a negative NAO, would favor the input of northern winds (Turrel and Holliday, 2003) and northern upper waters in the Balearic area. During a positive index of winter NAO, the westerly winds reaching the Iberian mainland would favor the input of Atlantic water into the Mediterranean. As a consequence, this water could reach the Balearic Sea and a warmer temperature would prevail in the area. In the North Atlantic, the abundance of plankton has been clearly related to the NAO index (Fromentin and Planque, 1996; Irigoien et al., 2000), but was not always the same for all planktonic groups.

The synchronous variation found between the main zooplankton groups and the hydrographic changes in the Balearic Sea may suggest strong links to mechanisms acting over large spatial scales. Likely related are atmospheric oscillations, as the main drivers of the hydrodynamics on the scale of the western Mediterranean basin. We know that 10 years of data are not enough to draw any final conclusions, but an overall pattern has emerged, particularly from the group of copepods. The effect of the NAO on hydrographic variability and the copepod abundance in the area are even remarkable at monthly scale (Fernández de Puelles and Molinero, 2007). More investigations should be conducted, especially to further determine the relationship between NAO oscillations and other groups of zooplankton, and a much longer time series would be desirable, particularly in the Mediterranean where research is at a fairly advanced stage. All this information may help to better comprehend the zooplankton variability in transitional and oligotrophic areas at other temperate latitudes.

4. Concluding remarks

Overall, the data presented here provides important information of the zooplankton community from the Balearic Sea over a 10-year period, and its relationship with local environmental conditions. For the first time, the physico-chemical parameters, phytoplankton and zooplankton were analyzed together in this hydrographic boundary area. Furthermore, based on the time-series analysis, the seasonal cycle of the different zooplankton groups (ichthyoplankton included) is assessed. A progressive decrease in zooplankton abundance was detected from 1995 to 1998, with subsequent recovery after the year 2000 when colder years were more prevalent in the area. The increase in zooplankton and predominance of copepods during more saline springs can be related to incursions of northern MW whose fertility is higher in relation to the southern nutrient-poor waters. In this sense, the lower zooplankton levels found during warmer years were in turn related to increased inflow of Atlantic water into the study area. Parallel atmospheric warming trends, and the associated depletion in nutrients, appear to be likely candidates to explain this pattern, and may be related to the global warming of the marine ecosystem. We conclude that the dominant physical factor governing zooplankton abundance at a large scale was winter air temperature, a proxy for winter climatic conditions which influenced the water temperature by local mixing and by driving oceanic advection into the Mallorca channel. So, in colder years the southward spread of northern MW would be higher, whereas when milder winters occur in the region, the northward spread of southern surface waters of recent Atlantic origin increases. At smaller scales, the meso-scale hydrographic features, as fronts or eddies, resulting from the interaction between both surface water masses, condition the abundance and the structure of planktonic communities in the Balearic channels.

Because of the high variability observed in the area, larger scale investigations should be conducted to further determine the interactions with atmospheric oscillations and the main zooplankton groups. Indeed, the key species' variability in relation to hydrography changes highlighted their indicator character and their response to climatic change. This may help us better understand the zooplankton pattern variability in temperate latitudes, and in particular to improve our knowledge of the Mediterranean pelagic ecosystem. Future work should focus on the identified indicator species and other zooplankton groups at different time-scales, in order to assess ecological mechanisms through which planktonic functional groups respond to hydrographic regimes driven by climate. In turn in response to a warming climate, this will improve our ability to forecast

future changes in the abundance and distribution of the zooplankton community in the Western Mediterranean.

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References

- Alcaraz, M., 1988. Summer zooplankton metabolism and its relation to primary production in the Western Mediterranean. *Oceanologica Acta* 55, 185–191.
- Aleman, F., 1997. Ictioplancton del Mar Balear. Ph.D. Thesis, Univ. Illes Balears, Palma de Mallorca, 608 pp.
- Aleman, F., Deudero, S., Morales-Nin, B., López-Jurado, J.L., Jansá, J., Palmer, M., Palomera, I., 2006. Influence of physical environmental factors on the composition and horizontal distribution of summer larval fish assemblages off Mallorca island (Balearic archipelago, Western Mediterranean). *Journal of Plankton Research* 28 (2), 1–15.
- Armstrong, F.A.J., Sterns, R.C., Strickland, J.D.H., 1967. The measurements of upwelling and subsequent biological processes by The Technicon autoanalyzer and associated equipment. *Deep-Sea Research* 14, 381–389.
- Beaugrand, G., 2003. Long term changes in copepod abundance and diversity in the north east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fisheries & Oceanography* 12 (4–5), 270–283.
- Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of north Atlantic marine copepod biodiversity and climate. *Science* 296, 1692–1694.
- Bolle, H.-J. (Ed.), 2002. *Mediterranean Climate: Variability and Trend*. Springer-Verlag, Berlin, 450pp.
- Bonet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., Ceballos, S., Dickman, R., Lopez-Urrutia, A., Valdes, L., Carloti, 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., Fernández de Puelles, M.L., 2005. An overview of *Calanus helgolandicus* ecology in European waters. *Progress in Oceanography* 65, 1–53.
- Boucher, M.J., Ibanez, F., 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. *Journal Marine Research* 45, 133–173.
- Bustillos-Guzmán, J., Claustre, H., Marty, J.C., 1995. Specific phytoplankton signatures and their relationship to hydrographic conditions in the coastal north-western Mediterranean Sea. *Marine Ecology Progress Series* 124, 247–258.
- Calbet, A., Garrido, S., Sainz, E., Alcaraz, M., Duarte, C., 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *Journal of Plankton Research* 23 (3), 319–331.
- Cataletto, B., Feoli, E., Fonda-Umani, S., Cheng-Yong, S., 1995. Eleven years of time-series analysis on the net-zooplankton community in the Gulf of Trieste. *ICES Journal Marine Science* 52, 669–678.
- Champalbert, G., 1996. Characteristics of zooplankton standing stock and communities in the Western Mediterranean: relation to hydrology. *Scientia Marina* 60, 97–113.
- Chiba, S., Tadokoro, K., Sugisakis, H., Saino, T., 2006. Effects of decadal climate change on zooplankton over the last 50 years in the western subarctic North Pacific. *Global Change Biology* 12, 907–920. doi:10.1111/j.1365-2486.2006.01136.
- Christou, E.D., 1998. Interannual variability of copepods in a Mediterranean coastal area (Aegean Sea). *Journal Marine System* 15, 523–532.
- CIESM, 2002. Long term sustained observing system for climatic variability studies in the Meditterane. In: Paper presented at the Third EuroGOOS Conference. Athens.
- CIESM, 2003. *Mediterranean Biological Time Series*. CIESM Workshop Monographs No. 22, Mónaco, 142 pp.
- Colebrook, J.M., 1978. Continuous plankton records: zooplankton and environment, north-east Atlantic and North Sea, 1948–1975. *Oceanologica Acta* 1, 9–23.
- Colebrook, J.M., 1985. Sea surface temperature and zooplankton, North Sea, 1948 to 1983. *Journal Conseil Permanent International Exploration Mer* 42, 179–185.
- Dam, H.G., Roman, M.R., Younblot, M.J., 1995. Downward export of respiratory carbon and dissolved inorganic nitrogen by diel-migrant mesozooplankton at the JGOFS Bermuda time-series station. *Deep-Sea Research II* 42, 1187–1197.
- Dam, H.G., Zhang, X., Butler, M., Roman, M.R., 1993. Mesozooplankton grazing and metabolism at the equator in the central Pacific: implications for carbon and nitrogen fluxes. *Deep-Sea Research II* 42, 735–756.

- Duarte, C.M., Agusti, S., Kennedy, H., Vaque, D., 1999. The Mediterranean climate as a template for Mediterranean marine ecosystems: the example of the northeast Spanish littoral. *Progress in Oceanography* 44, 245–270.
- Duran, M., Jansá, J., 1986. Distribution vertical des chlorophylles planctoniques dans les eaux voisines de l'île de Majorque. *CIESM Rapports et Procès Verbaux des Réunions*, 30, 2, 184pp.
- Edwards, M., Beaugrand, G., Reid, C., Rowden, A., Jones, M., 2002. Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series* 239, 1–10.
- Estrada, M., 1980. Composición taxonómica del fitoplancton en una zona próxima a la desembocadura del río Besós (Barcelona), de octubre de 1978 a marzo de 1979. *Investigaciones pesqueras* 44 (2), 275–289.
- Estrada, M., 1985. Deep phytoplankton and chlorophyll maxima in the Western Mediterranean. In: Moraitou-Apostolopoulou, M., Kiortsis, V. (Eds.), *Mediterranean Marine Ecosystems*. Plenum Press, New York, pp. 247–276.
- Estrada, M., Marrasé, C., Latasa, M., Berdalet, E., Delgado, M., Riera, T., 1993. Variability of deep chlorophyll maximum characteristics in the North-western Mediterranean. *Marine Ecology Progress Series* 92, 289–300.
- Estrada, M., Salat, J., 1989. Phytoplankton assemblages of deep and surface water layers in a Mediterranean frontal zone. In: Ros, J., (Eds.), *Topics in marine biology*. *Scientia Marina*, vol. 53 (2–3), 203–214.
- Estrada, M., Vives, F., 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 Puellas, M.L., 1996. Plankton dynamics in relation to physical structures around the Ibiza Channel. In: Briand, F., (Ed.), *Dynamics of Mediterranean straits and channels*. *CIESM Science Series* 2, Mónaco. *Bulletin Institute Oceanography*, vol. 17, pp. 65–80.
- Fernández de Puellas, M.L., Gras, D., Hernández de León, 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. Marine Ecology* 24 (2), 123–129.
- Fernández de Puellas, M.L., Jansá, J., Gomis, C., Gras, D., Amengual, B., 1997. Variación anual de los principales parámetros oceanográficos y planctónicos en el Mar Balear. *Boletín Instituto Español Oceanografía* 13 (1), 12–26.
- Fernández de Puellas, M.L., Molinero, J.C., 2007. North Atlantic climate control on plankton variability in the Balearic sea (Western Mediterranean). *Geophysical Research Letters* 34, L04608. doi:10.1029/2006GL028354.
- Fernández de Puellas, M.L., Morillas, A., López-Urrutia, A., Molinero, J.C., submitted for publication. Seasonal and interannual variability of copepod abundance in the Balearic region (Western Mediterranean) as indicator of basin scale hydrological changes. *Hydrobiologia*.
- Fernández de Puellas, M.L., Pinot, J.M., Valencia, J., 2003b. Seasonal and interannual variability of zooplankton community in waters off Mallorca island: 1994–1999. *Oceanologica Acta* 26, 673–686.
- Fernández de Puellas, M.L., Valencia, J., Vicente, L., 2004a. Zooplankton variability and climatic anomalies from 1994 to 2001 in the Balearic Sea (Western Mediterranean). *ICES Journal Marine Science* 61, 492–500.
- Fernández de Puellas, M.L., Valencia, J., Jansá, J., Morillas, A., 2004b. Hydrographical characteristics and zooplankton distribution in the Mallorca channel (Western Mediterranean). *ICES Journal Marine Science* 61, 654–666.
- Flos, J., 1985. The driven machine. In: Margalef, R. (Ed.), *Western Mediterranean*. Pergamon Press, Oxford, pp. 60–99.
- Fonda-Umani, S., 1992. Successione fitoplanctonica, micro e mesozooplanctonica nell 'Alto Adriatico. In: Marchetti, R., Cotta-Ramussino, M., (Eds.), *Atti V Congresso SITE*, pp. 221–246.
- Font, J., Salat, J., Tintoré, J., 1988. Permanent features of the circulation in the Catalan sea. In: Minas, H.J., and Nival, P., (Eds.), *Oceanography Pelagic Mediterranean*. *Oceanologica Acta*, vol. 9, pp. 51–57.
- Fromentin, J.M., Planque, B., 1996. *Calanus* and environment in the eastern north Atlantic. II Influence of the north Atlantic oscillation on *C. finmarchicus* and *C. it helgolandicus*. *Marine Ecology Progress Series* 134, 101–109.
- Fuda, J.L., Etiope, G., Millot, C., Favali, P., Calcara, M., Smriglio, G., Boschi, E., 2002. Warming, salting and origin of the Tyrrhenian deep water. *Geophysical Research Letters* 29 (19), 1898. doi:10.1029/2001GL014072.
- Furnestin, M.L., 1968. Le zooplancton de la Méditerranée (Bassin occidental). *Essai de synthèse*. *Journal Conseil International Exploration Mer* 32, 29–69.
- García, E., Tintoré, J., Pinot, J.M., Font, J., 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., Kiortsis, V. (Eds.), *Mediterranean Marine Ecosystems*. Plenum Press, New York, pp. 279–302.
- Gaudy, R., Champalbert, G., 1998. Space and time variations in zooplankton distribution south of Marseilles. *Oceanologica Acta* 21 (6), 793–802.
- Hernández-León, S., Almeida, C., Portillo-Hanhfeld, A., Gómez, M., Rodríguez, J.M., Aristegui, J., 2002. Zooplankton biomass and indices of feeding and metabolism in relation to an upwelling filament off Northwest Africa. *Journal Marine Research* 60, 327–346.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1966. Fluorometry determination of chlorophyll. *ICES Journal du Conseil* 30, 3–15.
- Hurrell, J.W., 1995. Decadal trend in the North Atlantic oscillation. *Regional temperatures and precipitation*. *Science* 269, 676–679.
- ICES Working group on zooplankton ecology, 2002. Zooplankton monitoring results in ICES area. Summary status report 2001/2002, 21pp.
- Irigoin, X., Harris, R., Head, R., Harbour, D., 2000. North Atlantic Oscillation and spring bloom phytoplankton composition in the English Channel. *Journal of Plankton Research* 22, 2367–2371.
- La Violette, P.E., Tintoré, J., Font, J., 1990. The surface circulation of the Balearic Sea. *Journal Geophysics Research* 95, 1559–1568.

- Latasa, M., Estrada, M., Delgado, M., 1992. Plankton pigment relationships in the north-western Mediterranean during stratification. *Marine Ecology Progress Series* 88, 61–73.
- Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in marine waters. *Ophelia* 41, 153–172.
- Licandro, P., Ibanez, F., 2000. Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. *Journal Plankton Research* 22 (12), 2225–2253.
- López-Jurado, J.L., 2002. Interannual variability in waters of the Balearic islands. In: Briand, F., (Ed.), Tracking long-term hydrological change in the Mediterranean Sea. CIESM Workshop series. vol. 16, pp. 33–36.
- López-Jurado, J.L., García-La fuente, J., Pinot J.M., Álvarez, A., 1996. Water exchanges in the Balearic channels. In: Briand, F., Dynamics of Mediterranean Straits and Channels. CIESM Science Series 2, Mónaco. *Bulletin Institute Oceanography* 17, 41–63.
- López-Jurado, J.L., Pinot, J.M., González Pola, C., Jansá, J., Fernández de Puellas, M.L., 2001. Interannual variability of the circulation in the Balearic Channels (1996–2000). *Rapport Commission International mer Méditerranée* 36, 74.
- Mackas, D.L., 1984. Spatial autocorrelation of plankton community in a continental shelf ecosystem. *Limnology Oceanography* 29, 451–471.
- Margalef, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1 (4), 493–509.
- Margalef, R., 1984. Le plankton de la Méditerranée. *La Recherche* 158, 1082–1094, Paris.
- Margalef, R., 1985. Environmental control of the mesoscale distribution of primary producers and its bearing to primary production in the Western Mediterranean. In: Moraitou-Apostolopoulou, M., Kiartsis, V. (Eds.), *Mediterranean Marine Ecosystem*. Plenum Press, New York, pp. 213–229.
- Mazzocchi, M.G., Christou, E., Di Capua, I., Fernández de Puellas, M.L., Fonda-Umani, S., Molinero, J.C., Siokou-Frangou, I., 2007. Temporal variability of *Centropages typicus* in the Mediterranean sea: from seasonal to decadal scale. *Progress in Oceanography* 72, 214–232.
- Mazzocchi, M.G., Ribera d'Alcala, M., 1995. Recurrent patterns in zooplankton structure and succession in a variable coastal environment. *ICES Journal Marine Science* 52, 679–691.
- Mazzocchi, M.G., Christou, E., Frangopoulos, N., Siokou-Frangou, I., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): general aspects. *Oceanologica Acta* 20 (3), 521–535.
- Molinero, J.C., Ibanez, F., Nival, P., Boucher, E., Souissi, S., 2005a. The North Atlantic climate and the North-western Mediterranean plankton variability. *Limnology Oceanography* 50, 1213–1220.
- Molinero, J.C., Ibanez, F., Souissi, S., Chifflet, M., Nival, P., 2005b. Phenological changes in the North-western Mediterranean Copepods *Centropages typicus* and *Temora stylifera* linked to climate forcing. *Oecologia* 145, 640–649.
- Peterson, W.T., Keister, J.E., 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.
- Pinot, J.M., López-Jurado, J.L., Riera, R., 2002. The CANALES experiment (1996–1998). Interannual, seasonal and mesoscale variability of the circulation in the Balearic Channels. *Progress in Oceanography* 55 (3–4), 335–370.
- Pinot, J.M., Tintoré, J., Gomis, D., 1994. Quasy-synoptic mesoscale variability in the Balearic Sea. *Deep Sea Research* 41 (5–6), 897–914.
- Pinot, J.M., Tintoré, J., López-Jurado, J.L., Fernández de Puellas, M.L., Jansá, J., 1995. Three-dimensional circulation of a mesoscale eddy/front and its biological implications. *Oceanologica Acta* 18 (4), 389–399.
- Puigserver, M., 2003. Aspectes ecològics i taxonòmics del fitoplàncton a zones costaneres de la Mediterrània. Ph.D. Thesis, Universitat de les Illes Balears.
- Razouls, C., Kowemberg, J., 1993. Spatial distribution and seasonal variation of mesozooplankton biomass in the Gulf of Lions. *Oceanologica Acta* 16 (4), 393–401.
- Redaway, J., Bigg, G., 1996. Climatic change over the Mediterranean and links to the more general atmospheric circulation. *International Journal Climatology* 16, 651–661.
- Ribera D'Alcala, M.R., Conversano, F., Corato, F., Lisandro, P., Mangoni, O., Marino, D., Mazzocchi, M.G., Modigh, M., Montresor, M., Nardella, M., Saggiomo, V., Sarno, D., Zingone, A., 2004. Seasonal patterns in plankton communities in a plurianual time-series at a coastal Mediterranean site (Gulf of Naples) an attempt to discern recurrences and trends. *Scientia Marina* 68 (1), 65–83.
- Richardson, A.J., Soechman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305, 1609–1612.
- Rodríguez, J., 1983. Estudio de la comunidad planctónica nerítica en el mar de Alboran: II Ciclo de zooplancton. *Boletín Instituto Español Oceanografía* 1, 19–44.
- Roemmich, D., Mc Gowan, J., 1995. Climatic warming and the decline of zooplankton in the California Current. *Science* 267, 1324–1326.
- Roman, M.R., Gauzens, A.L., 1997. Copepod grazing in the Equatorial Pacific. *Limnology & Oceanography* 42, 623–634.
- Sabatés, A., 1988. Sistemática y distribución espacio-temporal del Ictioplankton en la costa catalana. Ph.D. Thesis, Univ. de Barcelona, Barcelona.
- Sabatés, A., Gili, J., Pages, F., 1989. Relationship between zooplankton distribution, geographic characteristic an hydrographic patterns off the Catalan Coast. *Marine Biology* 103, 153–159.
- Scotto di Carlo, B., Ianora, A., 1983. Standing stocks and species composition of Mediterranean zooplankton. *UNESCO Report Marine Science* 20, 59–69.
- Scotto di Carlo, B., Tomas, C.R., Ianora, A., Marino, D., Mazzocchi, M.G., Modigh, M., Montresor, M., Petrillo, L., Ribera d'Alcala, M., Saggiomo, V., Zingone, A., 1985. Uno studio integrato dell' ecosistema pelágico costero del Golfo di Napoli. *Nova Thalassia* 7, 99–128.
- Seguin, G., 1973. Sur la présence, dans les eaux d'Alger de Copépodes considérés comme d'origine atlantique. *Bulletin Société Histoire Natural Afrique Nord* 63, 25–32.

- Seguin, G., Gaudy, R., Errhif, A., 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. *Marine Life* 3 (1–2), 19–29.
- Siokou-Frangou, I., 1996. Zooplankton annual cycle in a Mediterranean coastal area. *Journal Plankton Research* 18, 2803–2823.
- Siokou-Frangou, I., Christou, E.D., Frangopoulos, N., Mazzocchi, M.G., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean). II. Copepod assemblages. *Oceanologica Acta* 20, 537–548.
- Taupier-Letage, I., Rainbault, P., Millot, C., 1988. Biological consequences of the Algerian Current mesoscale activity. *Journal Geophysic Research Special Issue* 10, 180–195.
- Taylor, A.H., Colebrook, J.M., Stephens, J.A., Baker, N.G., 1992. Latitudinal displacements of the Gulf Stream and the abundance of plankton in the north-east Atlantic. *Journal of the Marine Biological Association of United Kingdom* 72, 919–921.
- Thibault, D., Gaudy, R., Le Fevre, J., 1994. Zooplankton biomass, feeding and metabolism in a geostrophic frontal area (Almeria-Oran Front; Western Mediterranean). Significance to pelagic food webs. *Journal Marine System* 5, 297–311.
- Turner, J.T., Tester, P.A., Ferguson, R.L., 1988. The marine cladoceran *Penilia avirostris* and the microbial loop of pelagic food webs. *Limnology Oceanography* 33, 245–255.
- Turrel, W.R., Holliday, N.P., 2003. The ICES Annual Ocean Climate Status Summary: 2000/2001. *ICES Marine Science Symposia* 219, 309–310.
- Underwood, A.J., 1989. The analysis of stress in natural population. *Biology Journal Limnology Society* 37, 51–78.
- Urban, J., Mackenzie, C., Deibel, D., 1992. Seasonal differences in the content of *Oikopleura vanhoeffeni* and *Calanus finmarchicus* faecal pellets. Illustrations of zooplankton food webs in coastal Newfoundland waters. *Marine Ecology Progress Series* 84, 255–264.
- Valdés, L., 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 Journal Marine Science* 55, 783–792.
- Vargas-Yañez, M., Salat, J., Fernández de Puellas, M.L., López-Jurado, J.L., Pascual, J., Ramírez, T., Cortes, D., Franco, I., 2005. Trends and time variability in the northern continental shelf of the Western Mediterranean. *Journal of Geophysical Research* 110, C10019. doi:10.1029/2004JC002799.
- Vignudelly, S., Gasparini, G.P., Astraldi, M., Schiano, M.E., 1999. A possible influence of the North Atlantic Oscillation on the circulation of the Western Mediterranean. *Geophysic Research Letters* 26 (5), 623–626.
- Vives, F., 1966. Zooplankton nerítico de las aguas de Castellón Mediterráneo Occidental. *Investigación Pesquera* 30, 49–166.
- Williamson, P., 2000. Community interactions amongst zooplankton and researchers. *Ocean Challenge* 11 (2), 15–18.