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Relationship between zooplankton distribution, geographic characteristics and hydrographic patterns off the Catalan coast (Western Mediterranean)

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Abstract

We studied the distribution patterns of ten zooplankton taxa of the Catalan coast (Western Mediterranean) using data collected in six research cruises along the continental shelf from April to July and September to October 1983. Zooplankton biomass ranged from 0.2–0.4 mg m^{-3} to 48–60 mg m^{-3}, the greatest values being recorded between April and May, when gelatinous zooplankton concentrations were consistently present along the edge of the continental shelf. We identified the main factors contributing to the observed pattern of zooplankton distribution as the high degree of environmental fluctuation close to the coast (thermal gradient from north to south), the structural heterogeneity inherent to the continental shelf, and the persistence of a hydrographical front along the margin of the shelf.

Introduction

The distribution of zooplankton depends largely upon the physical and dynamic characteristics of the water masses they inhabit, and is reflected in the adaptation of various animal taxa to relatively narrow temperature and salinity ranges. However, Margalef (1984) argued that adaptations to particular temperatures or other environmental conditions are of secondary importance to conditions favouring the growth and reproduction of organisms, which involve a larger set of environmental conditions than just temperature or salinity and would include a sufficient supply of external energy (i.e., food), and depend upon other environmental characteristics such as currents, turbulence or divergence areas, and wind patterns.

Along the Catalan shelf-break, there is a permanent shelf/slope front separating coastal waters from the more saline waters of the open sea (Salat and Font 1987, Font et al. 1988). The associated circulation pattern is dominated by a current flowing in a roughly NE–SW direction, almost parallel to the shoreline (Font 1986). This is the only permanent hydrographical structure in the study area, and one of the most important features in the north-west Mediterranean Sea.

The influx of low-salinity waters from the Gulf of Lions, which originate from the River Rhône, intensifies the horizontal density gradient, and thus the front, in the northern part of the study area. At the southern end of the area, the influx from the River Ebro has a similar effect. The bottom topography includes three main canyons, and therefore exerts great influence on the dynamics of the water currents.

The hydrographical dynamics associated with the shelf/slope front are very complicated. If this front is assumed to be a continuation of that of the Ligurian Sea with a similar hydrographic structure, then, according to Boucher et al. (1987), very small-scale cells of covergence/divergence are involved. The position of the front is variable and, although always present, it is sometimes unstable, being subject to the influx of surface waters which enter surface layers during the season of stratified water masses (Wang et al. 1988).

We hypothesize that the distribution of zooplankton reflects the hydrographic structure of the study area and should, therefore, exhibit heterogeneous distribution in both space and time. The hydrographic characteristics considered in this study (main currents, hydrographic front, etc.) should also allow large-scale studies of the distributional patterns of zooplankton organisms (Mackas et al. 1985).

The zooplankton of the Catalan coast has received little attention in comparison to neighbouring areas, such as Castellón (Vives 1966) and Banyuls-sur-mer (Razouls and Thiriot 1968). A few studies, however, do deal with particular aspects of the zooplankton communities of the port of Barcelona (Alcaraz 1980), and other, more general studies, with some aspects of the distribution of zooplankton biomass (Alcaraz 1981, Vives 1986, Gili et al. 1988).

Materials and methods

The data used in this analysis were collected during six research cruises from April to July and September to Octo-

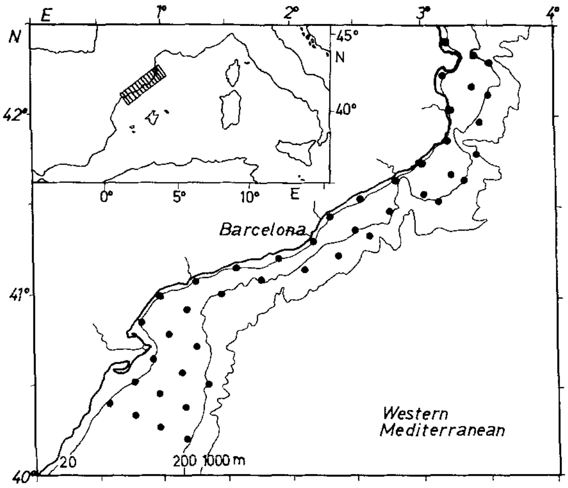

Fig. 1. Geographical location of study area (hatched) and distribution of 44 sampling stations along Catalan coast, north-east Spain

ber 1983. The sampling stations were located along a series of regularly spaced (ca. 10 nautical miles) transects perpendicular to the coast, and were 10 miles apart along each transect up to the edge of the continental shelf (ca. 200 m depth, Fig. 1). At each station, zooplankton samples were collected with a 40 cm diam Bongo net fitted with a 300 μm-mesh net, towed from the bottom to the surface at stations shallower than 200 m, and from 200 m to the surface at the other stations. In addition, we measured temperature and salinity with a Neilbrown conductivity-temperature-depth probe for the first three cruises, and from water samples collected with 5-liter Niskin bottles at standard depths during the following three cruises.

Because of the difficulties inherent in comparing numbers of individuals across the wide range of zooplankton taxa studied, we estimated the abundance of organisms for each taxon by means of a relative scale ranging from 1 (≤ 10 individuals) to 5 (very abundant, $>10\,000$ individuals m^{-3}), corresponding to logarithmic increases in zooplankton density. Similar abundance scales have proved highly efficient for statistical analyses in similar studies (Frontier and Ibanez 1974, Ibanez 1974). The taxa studied were: Cnidaria, Salpida, ichthyoplankton, Copepoda, Amphipoda, Chaetognatha, Doliolida, decapod larvae, Mollusca, and Euphausiacea.

The hydrological and physical characteristics that, according to our hypothesis, would explain the distributional patterns of the above taxa, were (1) Depth: maximum sampling depth in m. (2) Geographic distance (a distance in kilometres assigned to each station, with the smallest values in the northern and the largest values in the southern stations). (3) Distance from the coast, i.e., minimum distance from each station to the coast, in nautical miles. (4) Hydrographic characteristics, i.e., temperature, salinity, and density (σ_t); to maximize comparability between stations, we used the values recorded at 20 m, since these should reflect the dominant conditions within the sampling-depth range more truly than the more variable surface values. (5) Displacement volume (cm^3 100 m^{-3}), measured in accordance with Omori and Ikeda (1984); these values were transformed to biomass, assuming 1 ml displacement volume to be 0.12 mg m^{-3} (Cushing et al. 1958).

The relationship between zooplankton distribution and these environmental characteristics was investigated by combining two principal-components analyses: an analysis of the physical variables (1), and of the estimated abundances of the different zooplankton groups (2). The analyses used average values per station in order to offset seasonal influences. The validity of such analysis for describing zooplankton distribution has been discussed by, e.g., Ibanez (1976), and Gauch et al. (1977). To test the interaction between environmental and biological properties, we also performed a canonical correlation analysis (Jeffers 1978), which demonstrates the correlation between physical properties and the structure of zooplankton communities. To better appraise the spatial distribution of the patterns observed, we plotted the coordinates of the first two factors obtained in each analysis.

Results

Zooplankton distribution

Gelatinous zooplankton were very abundant from April to May. Salpida were most abundant in the stations furthest from the coast; they achieved peak abundance in April at the northern stations, and in May at the southern stations. Cnidaria were present throughout the whole study area, although their abundance was greatest in the northern two-thirds of the area. In contrast to Salpida, their frequency was similar throughout the sampling period, this temporal uniformity being particularly evident for the Siphonophora. Among the gelatinous zooplankton, the Doliolida were abundant throughout the area, but were especially abundant in the north in July.

Euphausiacea were common throughout the sampling period, peaking in abundance in April and June. They were predominantly found in the stations furthest from the coast. Copepoda were the dominant group, both in time and space, with abundance maxima in April, June and July. The greatest concentrations of copepods were consistently recorded in the coastal zone of the southern part of the area.

Chaetognatha were abundant in September and October; their concentration increased off-shore. Other groups, such as decapod larvae and Mollusca were highly seasonal and localized. In particular, decapod larvae were most abundant in July and September, especially at the northern coastal stations.

Together with zooplankton, the highest concentrations of phytoplankton and detrital aggregates were recorded between June and September, and tended to be greatest at the coastal stations.

Biomass was greatest from April to May, with values as high as 4 to 5 ml m^{-3} displacement volume (i.e., 48 to 60 mg m^{-3}). The largest biomasses within the area were consistently at stations furthest from the coast (Fig. 2).

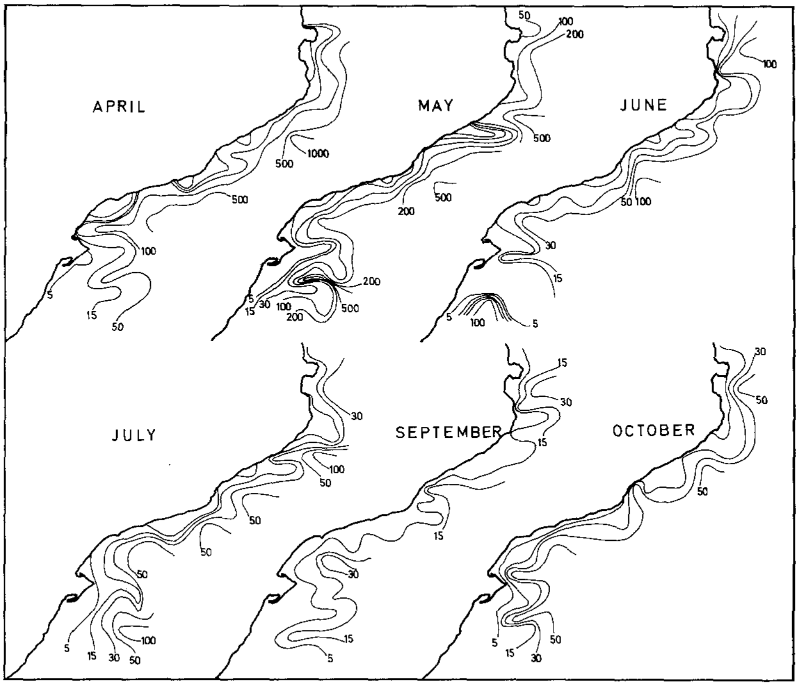

Fig. 2. Biomass (= displacement volume, ml 100 m^{-3}) of all zooplankton groups along Catalan coast, for the 6 mo studied

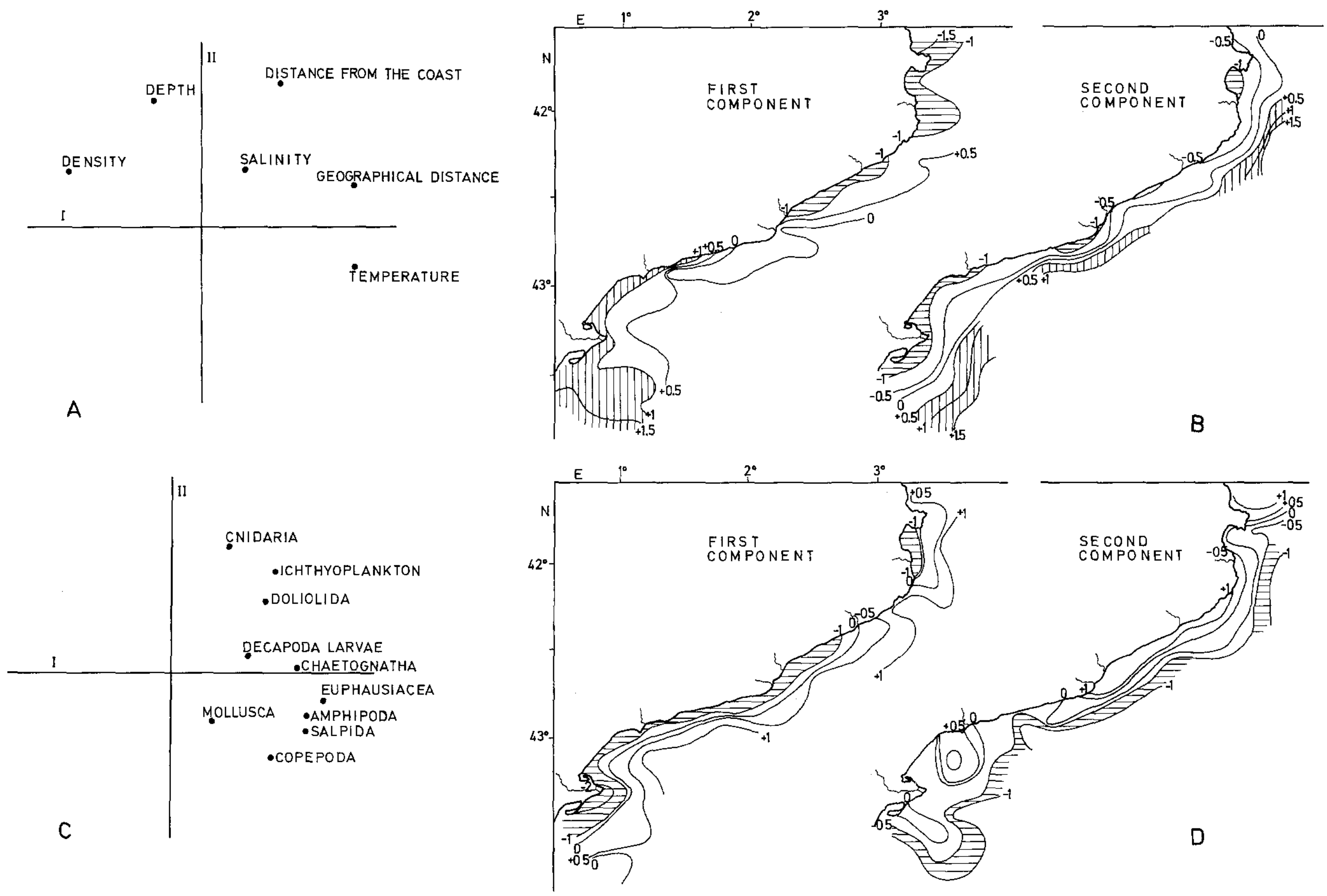

Fig. 3. Principal-components analysis (Axes I and II) of environmental variables (A) and biological variables (= zooplankton taxa) (C) along Catalan coast. Factor scores for first two axes of principal-component analyses are shown along contour lines following coastline for environmental variables (B) and biological variables (D); hatching indicates most negative and positive factor scores

Biomass had declined to 0.9 to 1.0 ml m^{-3} (10.8 to 12 mg m^{-3}) by June and July, although the spatial pattern was maintained. The lowest biomasses were recorded in September, maximum values in this month being only 0.3 to 0.38 ml m^{-3} (3.1 to 4.5 mg m^{-3}); this had increased to 0.5 to 0.8 ml m^{-3} (6.1 to 9.8 mg m^{-3}) by October. The lowest biomass measured per cruise was similar among cruises (0.12 to 0.36 mg m^{-3}), as was the trend to increased biomass with increasing distance from shore.

In general, maximum zooplankton abundance was in spring, at the stations furthest from the coast in the northern part of the area. Later, in summer, highest values were recorded along the whole edge of the continental shelf in association with the hydrographic front that runs parallel to the coast along the shelf slope. Zooplankton abundance was more uniformly distributed in the fall, although some of the stations furthest from shore still displayed relatively high zooplankton abundances in comparison with nearshore stations.

Statistical analyses

The first three axes of the principal-components analysis (PCA) of the environmental variables explain 79.6% of the variance. Geographic distance and water temperature are diametrically opposite to density along the first axis (Fig. 3A). The contours calculated using the factor-score values for the first component reveal positive values in the southern half and negative values in the northern half (Fig. 3B) of the study area. This spatial distribution of the factor scores reflects the presence of warmer waters in the south and less dense waters in the north. Depth and distance from shore exhibit the most positive values on the second axis (Fig. 3A), which explains the spatial pattern observed for the factor scores of the second axis in Fig. 3B; i.e., negative values inshore, positive values further seawards.

The first three axes of the PCA of the biological variables (zooplankton taxa) explains 57.8% of the variance in the data. All groups are positively correlated with the first axis (Fig. 3C). The spatial distribution of the factor scores of this axis (Fig. 3D) reveals that the most positive values are associated with the deeper stations located along the shelf break. Cnidaria and ichthyoplankton have positive correlations with the second axis, whereas Copepoda, Salpida, Amphipoda and Euphausiacea display the most negative values. The spatial distribution of the factor scores of this second component reveals highest positive values inshore, and negative values for the more seaward stations. The taxa with positive values are, therefore, associated with the coast and tend to occupy the northern half of the area, whereas taxa displaying negative values have a more oceanic distribution.

Table 1 shows the canonic correlation coefficients. Temperature is the variable displaying the highest coefficients for all factors except Factor 2. With the exception of Cnidaria, decapod larvae, and Mollusca, all zooplankton groups correlated well with at least one of the factors that show high correlations with temperature. The physical variables best correlated with the Factor 2 are depth and salinity. The highest correlation coefficients between biological properties and Factor 2 were obtained for Chaetognatha and Salpida, which both displayed a pronounced seasonality, such that their average abundance were lower than those of the other groups.

Distance from the coast also emerged as an important environmental characteristic, being well correlated with the canonical correlation factors, as were most zooplankton groups.

Table 1. Scaled vectors for canonical correlation of geographical and hydrographical variables and of biological variables (zooplankton groups)

Variables	Scaled vectors for canonical correlation of Factors:					
	1	2	3	4	5	6
Geographical and hydrographical variables						
Depth	−0.072	0.525	0.655	−0.074	−0.926	0.023
Geographical distance	−0.145	−0.257	0.262	0.843	−1.000	−0.435
Distance from the coast	0.098	0.427	−0.027	−0.084	1.432	−0.249
Temperature	0.996	−0.001	0.893	1.753	0.674	2.799
Salinity	0.026	0.627	−0.878	−0.159	−0.281	−0.381
Density	−0.007	0.119	0.733	1.865	0.664	2.850
Biological variables (zooplankton)						
Cnidaria	−0.365	−0.071	−0.314	−0.670	−0.578	0.212
Copepoda	−0.172	0.383	−0.484	0.595	0.229	−0.006
Amphipoda	0.111	0.256	−0.019	−0.176	0.408	−0.134
Euphausiacea	−0.107	0.190	0.968	0.001	0.927	−0.034
Decapod larvae	0.018	0.040	−0.180	−0.013	0.238	0.081
Mollusca	−0.012	−0.035	−0.023	0.160	0.054	−0.373
Chaetognatha	0.549	0.621	−0.344	−0.568	0.077	0.304
Doliolida	0.159	−0.083	0.225	−0.482	0.538	0.850
Salpida	−0.352	0.509	−0.063	−0.227	0.580	0.416
Ichthyoplankton	−0.074	−0.044	−0.005	−0.360	0.424	−0.813

Discussion

The results demonstrate that most taxonomic groups are most abundant along the shelf-slope interface. This pattern is similar to that indicated by the spatial distribution of the first two axes in the principal-components analysis for zooplankton taxa (Fig. 3D), where all groups were correlated with station depth. In contrast, the stations closest to the coast, which experience the greatest environmental variability, support the lowest zooplankton biomasses. The only abundant taxa at these coastal stations are those that develop a benthic habit later in their ontogeny (i.e., Cnidaria and decapod larvae). In particular, the abundance of Cnidaria in the coastal zone is largely attributable to the dominance of a single euryhaline species (*Muggiaea atlantica;* Gili et al. 1987). The more unstable conditions characteristic of the littoral zone are reflected in the increasing north-to-south gradient revealed by the principal-components analysis of the environmental variables. This is due to a permanent north-south thermal increase that results in higher water densities in the northern stations of the study area.

Comparison of the factor scores for the spatial distributions of the principal-comonents analyses of environmental and biological variables indicates some similarity between the second axis of the physical analysis and the first axis of the zooplankton-taxa analysis. The greater zooplankton abundance at the deeper stations is related, therefore, to the presence of a permanent hydrographic front, which is less variable than that of coastal areas. In addition, the spatial distribution of the factor scores for the first factor of the physical variables (Fig. 3B) is somewhat similar to that of the factor scores for the second factor of the biological variables (Fig. 3D).

The relatively large zooplankton biomass observed at the stations furthest from the coast was partially related to the greater abundance of these taxa with a more oceanic distribution. Chaetognatha and Euphausiacea, although represented by only a few species in the western Mediterranean Sea (Furnestin 1968), tend to achieve their greatest concentrations in warmer waters and open-sea areas (Tokioka 1969). Similarly, Amphipoda are more abundant further from shore, and are associated with large masses of gelatinous zooplankton (Laval 1980) such as Salpida, which are occasionally abundant at the stations furthest from shore.

Number and biomass of all zooplankton taxa varied greatly between spring-summer and fall, in response to seasonal fluctuations in temperature, which regulates the life history of all species (Deevey 1960, Razouls 1972), and to variations in salinity which affect the passive transport of the water masses harbouring these organisms. However, while fluctuations in temperature were correlated with variations in abundance for all zooplankton taxa, changes in salinity were correlated only with changes in abundance of those taxa associated with offshore stations.

Although areas of maximum abundance and population density can be determined for a local zooplankton population, the pattern of specific components and their relative abundance corresponds to a process of serial replacement of species along a geographic gradient (Deevey 1960). This is particularly evident for some groups such as Copepoda, which usually comprise >50% of the organisms in a zooplankton population (Longhurst 1985). Recent studies which focused on the distribution of particular taxa such as Cnidaria (Gili et al. 1988) or the ichthyoplankton (Sabatès 1988), agree with the patterns described here for the same taxa, but reveal that this distribution pattern may differ for some extremely seasonal species.

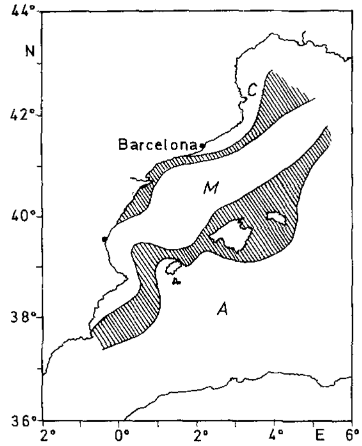

Fig. 4. Distribution of surface water masses in Catalan Sea. C: continental waters; M: Mediterranean waters; A: Atlantic waters. Hatching indicates transitional areas throughout the year (redrawn from Salat and Cruzado 1981, their Fig. 1)

The patterns of zooplankton distribution described herein parallel the distribution patterns of surface-water masses described by Salat and Cruzado (1981) (see present Fig. 4). These authors distinguished a northern (colder) water mass near the coast, which sometimes approached the coast in the southern part of the area. Zooplankton distribution is also related to the dominant local current which, in our study area, is a north-south current flowing along the edge of the Catalan shelf (present Fig. 5; see also Allain 1960, Font 1987). The importance of this current (believed to originate from the River Rhône influx), in the stimulation of secondary production in the Catalan Sea has been discussed by Furnestin (1968). Also, increased zooplankton abundance near Sardinia has been attributed to the influence of oceanic water (Ehrhardt 1967).

The distributional pattern of zooplankton observed in the present study is similar to that described by Carrada et al. (1980) for the Gulf of Naples, where the highest zooplankton biomasses were recoreded at stations furthest from shore, in association with the higher phytoplankton production at these stations. High densities of zooplankton associated with a zone of hydrographic divergence have also been observed in the Alboran Sea (Rodríguez et al. 1982).

The range of zooplankton biomass recorded in the present study is similar to that previously reported for the northwestern Mediterranean Sea (Gaudy 1985), and the biomass peak in spring which we observed is also consistent with the

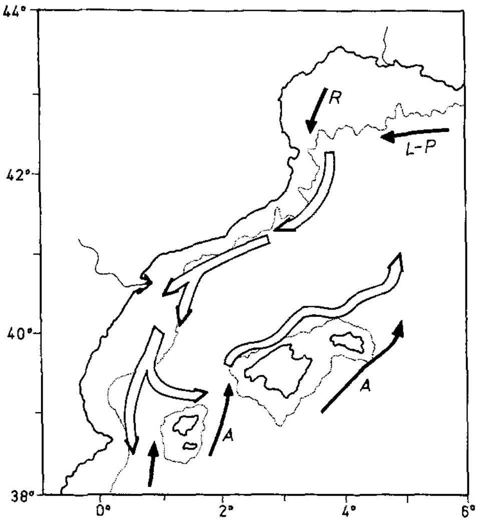

Fig. 5. General surface-water circulation in Catalan Sea. L-P: Liguro-Provençal Current; R: Rhône waters; A: Atlantic waters (redrawn from Font 1987, his Fig. 3)

pattern described elsewhere for the western Mediterranean (Nival et al. 1975). The high densities of zooplankton in the proximity of the hydrographic front confirm the tendency of zooplankton to concentrate in divergence zones (Olson and Backus 1985, Boucher et al. 1987). The zooplankton communities of such areas of maximum concentration are comprised of the largest zooplankton taxa (e.g. Euphausiacea and Salpida).

In summary, our results demonstrate the close link between zooplankton distribution and physical features of their environment such as hydrographic heterogeneity, geomorphology of the continental shelf, and the presence of a hydrographic front along the shelf slope of the Catalan coast. However, the most important feature is the increased abundance of zooplankton in connection with a permanent hydrographic shelf-slope front. This seaward area appears to be hydrographically more stable than more coastal waters; therefore, the increased zooplankton abundance recorded along the shelf-slope front may be the result of zooplankton survial strategy. The large-scale environmental factors are further complicated by smaller, more local, heterogeneity (e.g. Denman and Powell 1984). The recognition of large-scale dependence of zooplankton biomass on the physical environment (e.g. Mackas 1984) is a first, but necessary, step to understanding zooplankton distribution at a yet finer level.

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