

Zonation of deep-sea decapod fauna in the Catalan Sea (Western Mediterranean)

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ABSTRACT: Zonation of deep-sea decapod crustacean fauna was established in the Catalan Sea (Western Mediterranean) based on a total of 66 bottom trawls carried out between 552 and 2261 m depth. An OTSB-14 bottom trawl was used as sampling gear. The main boundaries were located at 1200 to 1300 m and around 1900 to 2000 m. The 1200 to 1300 m boundary separates the decapod communities dwelling on the middle and lower slopes. The most important causes of decapod zonation in the Mediterranean are more closely linked to trophic factors, in view of the fact that basic hydrographic parameters (temperature, salinity) remain constant along the entire slope. In the Catalan Sea impoverishment of the organic matter content in the bottom sediment with depth and resuspension associated with the steeper portions of the slope (i.e. submarine canyons) are probably the most important factors responsible for the changes recorded. These factors may be directly responsible for the near absence of a variety of organisms that are highly abundant components of the endofauna on the middle slope but disappear below 1200 m. The limits of influence of different macroplanktonic groups (euphausiids, mesopelagic fishes) in the diet of benthic decapods also coincided with the observed boundaries between decapod communities.

INTRODUCTION

Deep-sea decapod crustacean communities have been little studied. Work on this group has traditionally been carried out from a systematic or faunistic perspective. Aspects of a more ecological nature, such as biomass and diversity distribution patterns and faunal zonation, traditional lines of deep-sea research on fish (Rowe & Menzies 1969, Smith & Hamilton 1983, Sulak 1984, Lampitt et al. 1986) or on the megafauna in general (Haedrich et al. 1975, 1980, Hecker 1990, etc.), have received little attention in the case of decapod crustaceans. One possible reason might be that decapods are a secondary group in the megabenthic communities in the study areas (deep-sea regions of the North Atlantic and North Pacific) (Haedrich et al. 1975, 1980, Lampitt et al. 1986). Nevertheless, few such studies have been carried out in tropical or subtropical oceanic zones, where decapod crustaceans form a highly diversified group (Crosnier & Forest 1973, Abele 1982, Gore 1983, 1984, 1985, Domanski 1986).

Decapod communities on the continental slope have mainly been studied on the upper and middle sub-

zones on the slope (Abelló et al. 1988, Markle et al. 1988, Macpherson 1991), whereas studies on the lower slope and in abyssal zones are still more limited (Haedrich et al. 1975, 1980, Wenner & Boesch 1979).

The general boundaries between megabenthic communities on the different zones of the slope have been established in different works. The limit between the upper slope and the middle slope is variable, ranging between depths of 285 and 653 m (Day & Pearcy 1968, Haedrich et al. 1975, 1980, Musick 1976). In the Western Mediterranean this boundary ranges between 400 and 500 m depth (Pérès & Picard 1964, Abelló et al. 1988).

The boundary between the middle and the lower slope is more uniform and is located at depths between 1000 and 1400 m (Day & Pearcy 1968, Rowe & Menzies 1969, Haedrich et al. 1975, 1980, Musick 1976, Lagardère 1977a, Wenner & Boesch 1979, Hecker 1990). However, boundaries between the depth zones separating different communities are affected by local conditions. Geographic factors are important (Hecker 1990). Even so, the existence of boundaries is a regular phenomenon, though it is not always distinctly observ-

able (Merrett & Marshall 1981, Sulak 1984, Snelgrove & Haedrich 1985), and the boundaries for faunal succession appear to be more pronounced when there is adequate sampling coverage over all depth intervals in a given zone.

Both physical and biological factors have been discussed as causes responsible for faunal zonation with depth. Hydrographic conditions, the steepness of the continental slope, and sedimentation rates are among the major physical factors considered. Resource availability, predator-prey relationships, and interspecific competition are the most important biological factors cited (Rex 1977).

In the Western Mediterranean environmental parameters (temperature, salinity) are fairly constant along the slope below 200 m (Hopkins 1985). Dissolved oxygen presented minima between 200 and 1000 m in the water column, where seasonal changes were reported (Jacobsen 1912). Muddy sediments predominate on the slope, although in the upper part of the Balearic Basin sediments are terrigenous, whereas in the deeper part biogenic deposits are more important (Emelyanov 1972). The upper and middle slope is heavily incised by numerous submarine canyons (Monaco et al. 1990). Decapod crustaceans are a dominant group in terms of abundance at depths between 600 and 2200 m in the Catalan Sea (Western Mediterranean) (Cartes 1991, Cartes & Sardà 1992). In view of the extremely important role of decapods in the study area, the object of the present study was to determine the structure of communities and zonation in relation to depth for the deep-sea decapod taxocenosis in the Catalan Sea. Possible causes of the zonation pattern observed for these communities are also discussed.

MATERIAL AND METHODS

A total of 61 bottom trawls were carried out at depths of 862 to 2261 m in the period 1985 to 1989 in the Catalan Sea between Catalonia and the Balearic Islands (Fig. 1). Sampling locations have been described elsewhere (Cartes 1993). Maximum depth in the study area is around 2300 m. Sampling at depths below 862 m was uniform and continuous (Table 1). A further 6 bottom trawls were carried out on the middle slope at depths between 552 and 669 m for purposes of comparison.

An OTSB-14 bottom trawl equipped with 2 doors and a single bridle (Merrett & Marshall 1981, Sulak 1984) was used as the sampling gear. The size of the OTSB-14 trawl at a towing speed of 2.5 knots was estimated as 1.5 m for the vertical opening and 7 m for the distance between the wings. These measurements were

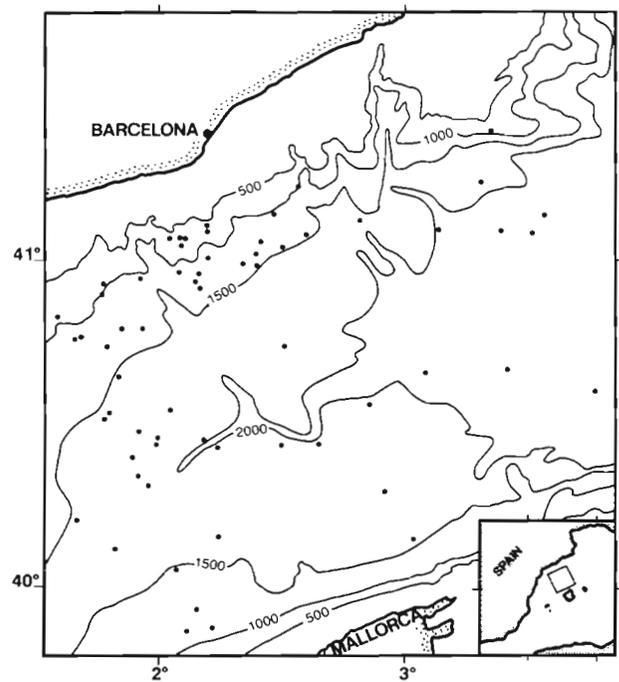


Fig. 1. Location of bottom trawls carried out in the Catalan Sea

verified with the aid of a remote acoustic sensing system attached to the gear (unpubl. data) and were approximately the same as those reported by Sulak (1984). The end of the net was equipped with a 6 mm mesh inside codend liner. All the samples were collected on board the RV 'García del Cid'.

Species abundance was calculated for each sample after standardization of the results to a 1 h tow. Analysis of the sampling data was carried out by cluster analysis applied to all hauls and all species com-

Table 1. Distribution of trawls carried out in this study by 100 m depth interval

Depth (m)	No. of samples
600	6
1000	9
1100	5
1200	3
1300	6
1400	3
1500	4
1600	5
1700	8
1800	2
2000	2
2100	1
2200	4
Total	67

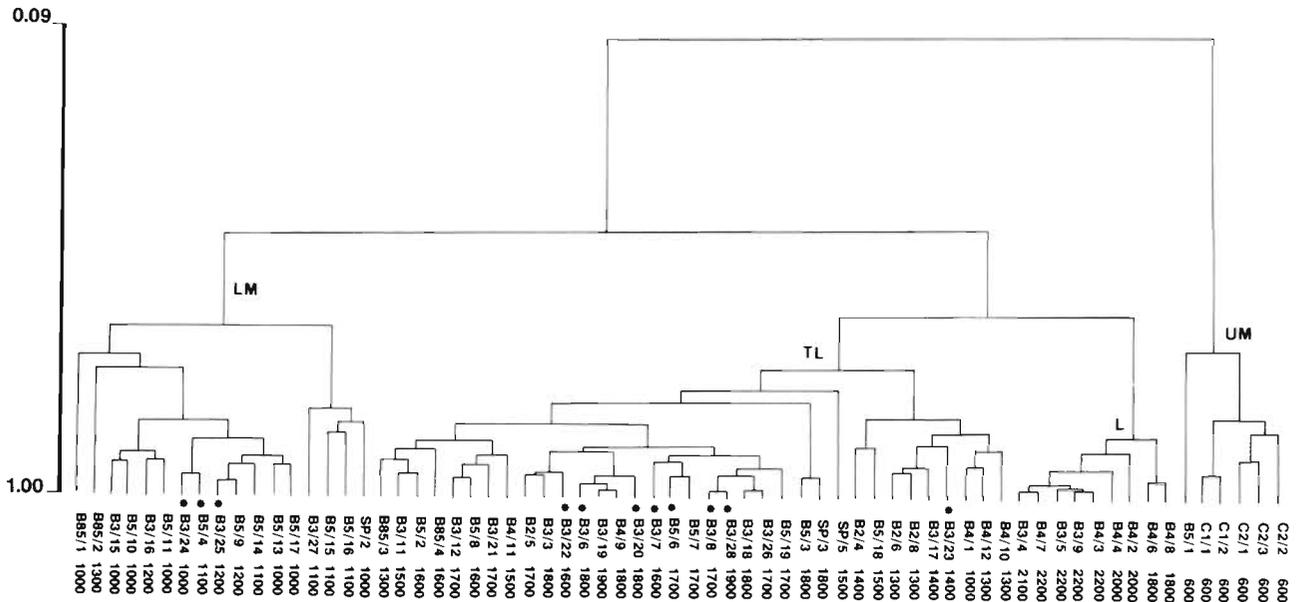


Fig. 2. Cluster analysis of all trawls performed on the deep-sea slope in the Catalan Sea. The mean depth of each sampling station, rounded to the nearest 100 m isobath, is also indicated. (*): Samples carried out on the eastern slope in the Balearic Islands (see Fig. 1). UM: upper-middle slope; LM: lower-middle slope; TL: transitional lower slope; L: lower slope

binéd as well as by reciprocal averaging analysis following log transformation [$\ln(x + 1)$] of the abundance and biomass data. Previously uncommon species that occurred only 1 time in the samples were removed from the data matrix. The cluster analysis performed used linear correlation as a measure of similarity and UPGMA as the aggregation algorithm (Leonart & Roel 1984). Reciprocal averaging analysis was applied to the same data matrix, but only for hauls carried out at depths below 862 m.

Biomass values were calculated for the different depth strata taking as the centre point for each depth interval (600 to 2200 m) the multiple of 100 m nearest to the centre. Cluster analysis based on linear correlation-UPGMA was also applied to these data.

RESULTS

Analysis of the trawl results yielded groupings of samples according to trawl depth (Fig. 2). The first of the identifiable groups consisted of 6 samples taken around the 600 m isobath (552 to 669 m) on the upper-middle slope (UM). The samples collected at depths greater than 862 m presented a number of groups. The approximate depth boundaries of the first group were 862 and 1200 m. This grouping has been associated with the communities on the lower-middle slope (LM). The separation between the clusters for the samples on the upper-middle and lower-middle slopes was the result of the lack of continuity in sampling between

669 and 862 m. Nevertheless, the dominant species in these 2 zones are common to both (Pérès & Picard 1964, Pérès 1985, Abelló et al. 1988, Cartes & Sardà 1992). Bathyal decapod communities on the middle slope in the Catalan Sea dwell at depths between 500 and 1300 m. Certain species, like *Calocaris macandreae*, *Plesionika martia*, and *Acantheephyra eximia*, underwent major changes in density over the middle slope, and in fact this zone should be subdivided into a further 2 subzones (upper and lower) according to the results reported for other regions (Musick 1976, Haedrich et al. 1980). At depths below 1300 m there was a homogeneous group that consisted of the hauls carried out on the deep lower slope below 2000 m (L), although this group also included 2 hauls carried out at shallower depths. This group was separate from the samples taken on the transition zone on the lower slope (TL) between 1300 and 1900 m. Both these groups together made up the lower-slope decapod communities. The most typically characteristic lower-slope communities dwelled at depths below 2000 m.

The species analysis disregarded those species recorded only in a single haul and produced coherent groups (Fig. 3). The first group comprised the bathyal community on the deep lower slope, including abundant species like *Acantheephyra eximia*, *Stereomastis sculpta* and *Nematocarcinus exilis*, together with rarer species like *Chaceon mediterraneus* and the unidentified Axiid (cf. Cartes & Sardà 1992). Lastly, certain bathypelagic species like *Acantheephyra pelagica* and *Sergia robusta* were also included in this group.

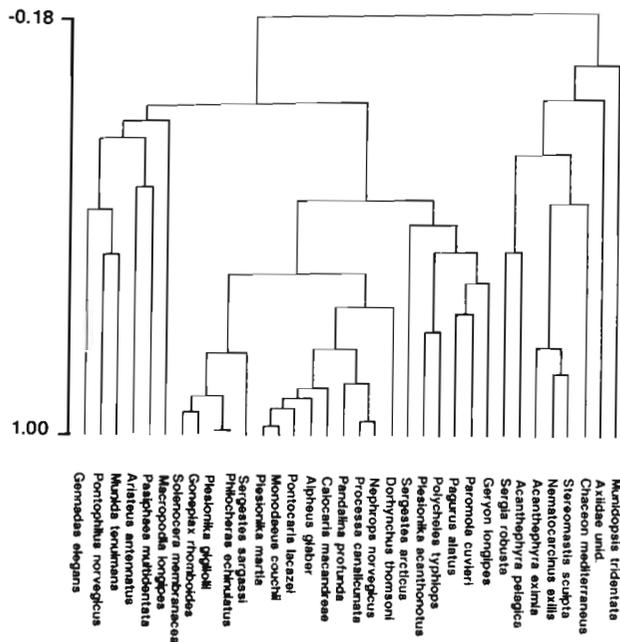


Fig. 3. Cluster analysis of species

The next group comprised the species that were most abundant in the hauls carried out on the transition zone (TL), on the lower-middle slope (LM), and on the upper-middle slope (UM). However, the results of species analysis must be viewed with caution due to the sampling discontinuity in the 669 to 862 m depth range. Furthermore, the entire depth distribution

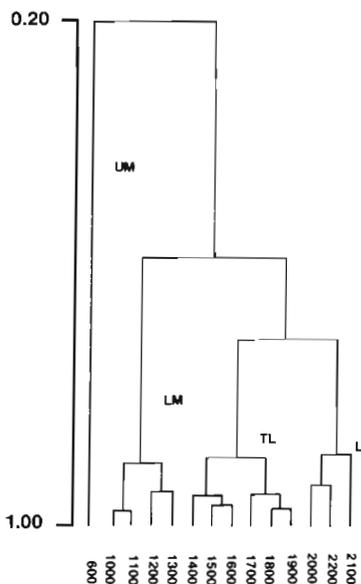


Fig. 4. Cluster analysis of biomass (biomass results calculated per 100 m depth interval). UM: upper-middle slope; LM: lower-middle slope; TL: transitional lower slope; L: lower slope

range of these species was not fully covered. Thus, such species as *Aristeus antennatus*, *Pontophilus norvegicus*, and *Munida tenuimana* appeared to be characteristic of the bathyal communities on the middle slope. These species were cited by Abelló et al. (1988) as typical on the slope at depths between 500 and 800 m.

The results of biomass analysis also yielded structured groups according to depth (Fig. 4). The groups corresponded to the depth intervals of 600 m (UM), 1000 to 1300 m (LM), 1400 to 1900 m (TL), and 2000 to 2200 m (L). These groups conformed nearly exactly to those from the analysis of species abundance in the hauls (Fig. 2).

The results of reciprocal averaging analysis for the hauls and the species identified are given in Fig. 5, relating the mean depth of each sample to the values of the first axis. The first axis is distinctly related to depth. The eigenvalue of the first axis is 0.529 and accounted for 40.0 % of the analysis variance. The cumulative variance of the first 3 axes was 61.7 %. The resulting point distribution indicated 2 inflection points at depths of from 1200 to 1300 m and from 1900 to 2000 m. These inflection points reflected the increased rate of faunal change over comparable changes in depth (Wenner & Boesch 1979).

Species were plotted according to their position in the different depth strata. On the whole, the results were similar to those for the cluster analysis by species.

DISCUSSION

All the analyses carried out have pointed to a zonation pattern for the decapod crustacean taxocenosis in the Catalan Sea. The main boundary was located at 1200 to 1300 m (1300 to 1400 m for the biomass results), with a secondary boundary located at around 1900 to 2000 m in depth. Based on the species composition (Cartes & Sardà 1992) and on the structure of the communities reported earlier for the Western Mediterranean (Péres 1985, Abelló et al. 1988), the first boundary (1200 to 1300 m) separates the decapod communities dwelling on the middle and lower slopes. Predominance of *Acantheephyra eximia*, *Nematocarcinus exilis* and *Stereomastix sculpta* in terms of both abundance and biomass (Cartes & Sardà 1992) was characteristic of the lower slope, which is equivalent to the lower subzone defined by Péres (1985). The most typical lower-slope communities dwelled at depths below 2000 m.

Local geographic conditions are responsible for the location of depth boundaries between communities (Hecker 1990). This effect was observed in the associations among the hauls carried out on the lower slope

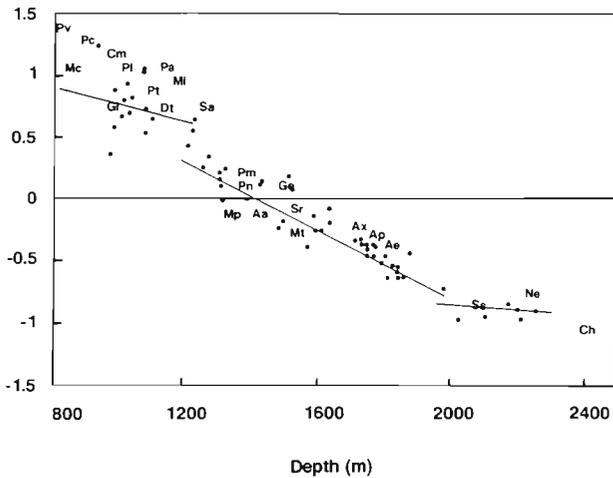


Fig. 5. Reciprocal averaging analysis (distribution of species and trawls along the first axis versus the mean depth of each trawl). Aa: *Aristeus antennatus*; Ae: *Acantheephyra eximia*; Ap: *Acantheephyra pelagica*; Ax: Axiidae unidentified; Ch: *Chaceon mediterraneus*; Cm: *Calocaris macandreae*; Dt: *Dorhynchus thomsoni*; Ge: *Gennadas elegans*; Gl: *Geryon longipes*; Mc: *Monodaeus couchii*; Mi: *Macropodia longipes*; Mp: *Munida tenuimana*; Mt: *Munidopsis tridentata*; Ne: *Nematocarcinus exilis*; Pa: *Plesionika acanthonotus*; Pc: *Paromola cuvieri*; Pl: *Plesionika martia*; Pm: *Pasiphaea multidentata*; Pn: *Pontophilus norvegicus*; Pt: *Polycheles typhlops*; Pv: *Pagurus alatus*; Sa: *Sergestes arcticus*; Sr: *Sergia robusta*; Ss: *Stereomastis sculpta*

around the Balearic Islands, which formed certain separate aggregation in the clusters. A low level of geographical homogeneity in samples may prove a problem in delimiting the boundaries between communities, because a given boundary determined by a given set of factors may be located at differing depths depending on local conditions.

The boundary between the middle and lower slopes is distinctly variable in location (Day & Pearcy 1968, Rowe & Menzies 1969, Haedrich et al. 1975, 1980, Musick 1976, Lagardère 1977a, Wenner & Boesch 1979, Hecker 1990). These studies have been carried out on different megafaunal communities, as well as on different taxocenoses (fish, decapods). Also, trophic factors exert an influence on species zonation through competitive interactions (Rex 1977), which are stronger between groups at higher trophic levels. Therefore, the boundaries between megabenthic communities in general, or between fish, decapod, and echinoderm communities, may not coincide because of the different trophic strategies employed by each group (Haedrich et al. 1980). This same phenomenon occurred in the Catalan Sea when comparing the zonation of decapod crustaceans and fish (Stefanescu et al. in press), which only partially shared the main boundary around 1300 m. This may have been the result of the different feeding habits and prey selection (mainly

due to prey size) of these 2 megafaunal groups. The diet of fish on the lower slope is more heavily slanted towards the capture of mobile benthopelagic prey (Gordon & Mauchline 1990), whereas the diet of decapod crustaceans is based more on the capture of epibenthic and endobenthic prey (Cartes & Sardà 1989, Cartes 1991, Cartes & Abelló 1992).

Hydrographic conditions would appear to be another cause of change in environmental conditions at the boundary between the upper and middle slope (Haedrich et al. 1975, Abelló et al. 1988). Intermediate Mediterranean water, submitted to certain seasonal hydrographic changes (Jacobsen 1912), is present above the upper slope in the Catalan Sea and may be responsible for the boundary (around 400 to 500 m) between the upper and middle slopes (Abelló et al. 1988). The 1200 m boundary is not linked to such conditions, because of the high hydrological (temperature, salinity, dissolved oxygen) stability of the deep-water masses in the Mediterranean Sea (Jacobsen 1912, Hopkins 1985). Changes in the degradation of organic matter with depth are also important, both as concerns the vertical downward drift through the water column (Wishner 1980) and the organic matter content on the slope (Carpine 1970, Drake et al. 1978, Rowe et al. 1982). The high constant temperature in the deep-sea Mediterranean are conducive to a rapid degradation of organic matter during the sedimentation process in which it drifts down to the lower slope, as postulated previously for the Red Sea (Wishner 1980) and the Mediterranean (Stefanescu et al. in press).

The most important causes of decapod zonation in the Mediterranean are probably more closely linked to trophic factors. The middle slope, particularly the upper subzone, is characterized by relatively eutrophic conditions, because of the local influence of the submarine canyons. The trophic group composed by deposit feeders is always well represented in eutrophic zones (Sokolova 1972), and in the Catalan Sea a number of endobenthic species are important on the middle slope, including *Calocaris macandreae* (Cartes 1991), which is a sedimentivorous species (Carpine 1970), echinoderms (e.g. *Molpadia musculus*, *Brissopsis lyrifera*) and the bivalve *Abra longicallus*. The lower limit to the distribution range of all these species is 1000 m (Carpine 1970). These species are not present below 1200 m, nor are they replaced by similar species (Carpine 1970, Cartes 1991, Cartes & Sardà 1992). In contrast, oligotrophic conditions in the lower subzone seem pronounced, giving rise to the presence of suspension feeders like sponges (Uriz & Rosell 1990), polyps of medusae *Stephanoscyphus* spp., cirripeds *Scalpellum* sp., and the asteroid *Brisingella coronata* (Fredj & Laubier 1985, Alvà 1987), which are more typical of oligotrophic oceanic regions (Sokolova

1972). A decrease in the concentration of organic matter in the bottom sediment from 700 m has been reported in the Northwestern Mediterranean (Carpine 1970). The nature of the recently deposited upper layer of bottom sediment also changes. On the outlying edges of the Catalan Sea the sediment is terrigenous and continental in origin. In contrast, the sediment in the deeper central part of the Catalan-Balearic Basin consists of biogenic deposits originating from globigerina and pteropods (Emelyanov 1972, Fredj & Laubier 1985). The upper and middle slopes would also benefit from the presence of submarine canyons where resuspension of organic matter is important because of the existence of periodical up- and down-canyon bottom currents (cf. Shepard et al. 1974, Monaco et al. 1990).

The macrobenthos is the chief source of available resources for decapod crustaceans. Different authors have reported a general tendency for the benthos biomass (Sanders & Hessler 1969), macrobenthos (Rowe 1983), and meiobenthos (Thiel 1983) to decrease markedly with depth, and data have been provided for the deep-sea Mediterranean macrofauna (Jumars & Gallagher 1982, Pérès 1985). There is also a generalized decrease in macrofaunal size with depth (Jumars & Gallagher 1982, Sokolova 1990) that also occurs in the deep-sea Mediterranean (Chardy et al. 1973, Pérès 1985). Decrease in the size of available resources is probably related to the decrease in the mean weight of decapod crustaceans with depth in the Catalan Sea (Sardà & Cartes 1993).

Another important trophic factor that must affect the existing zonation of decapod crustaceans in the Catalan Sea at around 1200 to 1300 m is a possible reduction in the density of the benthic boundary layer (BBL) parallel to that reported in the NE Atlantic (Hargreaves 1984, Hargreaves et al. 1984) and probably related to the lack of resuspended organic matter (Angel 1990) due to turbidity currents and sediment slides (Sedberry & Musick 1978, Tyler 1988). Based on our own data the limits of influence of different macroplanktonic groups in the diet of benthic decapods were detected in the Catalan Sea (Cartes 1991). The lower limit for mesopelagic fish and euphausiids *Meganyctiphanes norvegica* is located at around 1200 to 1300 m and for siphonophores and hyperids at around 2000 m (Cartes 1991) coinciding with the boundaries observed for decapod communities and, in part, for fish communities as well (Stefanescu et al. in press). The 1200 m boundary approximately coincides with the commonly accepted limit to the influence of the mesopelagic fauna on benthic slope species (around 1000 m) generally (Lagardère 1977a, Sedberry & Musick 1978) as well as in the Mediterranean (Bernard 1958, Pérès 1958, Goodyear et al. 1972). The existence of a benthopelagic fauna close to the bathyal bottoms

(Marshall & Merrett 1977, Wishner 1980, Hargreaves 1984) was linked to resuspension phenomenon (Angel 1990). The low level of resuspended organic matter might account for the disappearance of macroplanktonic components such as the euphausiid *M. norvegica*, an omnivorous species (Mauchline 1980). Resuspension would be particularly important in the Catalan Sea down to 1000 m, because of the multiplicity of submarine canyons in this area (Reyss 1971).

In summary, zonation of the Mediterranean deep-sea decapods is probably the result of a set of physical and biological factors which are difficult to quantify. However and in our opinion, in the Catalan Sea, in view of the fact that environmental parameters such as temperature and salinity remain constant, resuspension associated with canyons and the steeper portions of the slope and the impoverishment of the organic matter content in the bottom sediments with depth are probably the most important factors responsible for the changes in bathyal biocenoses recorded with depth. These factors exert a direct influence on biological aspects like the near absence below 1200 m of organisms that are highly abundant components of the endofauna on the middle slope (Carpine 1970, Cartes & Sardà 1992), and the limits of influence on the diet of benthic decapods established by various macroplanktonic groups, which coincided with the observed boundaries in decapod communities. The last phenomenon was probably also related to the boundary between 1000 and 1300 m in other oceanic areas (Lagardère 1977b, Mauchline & Gordon 1991).

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