



Patterns of bathymetric distribution among deep-sea fauna at local spatial scale: comparison of mainland vs. insular areas

Joan E. Cartes ^{a,*}, Francesc Maynou ^a, Joan Moranta ^b, Enric Massutí ^c,
Domènec Lloris ^a, Beatriz Morales-Nin ^b

^a Institut de Ciències del Mar, Centre Mediterrani d'Investigacions Marines i ambientals, CSIC. Pg. Marítim de La Barceloneta, 37-49, 08003 Barcelona, Spain

^b Institut Mediterrani d'Estudis Avançats (IMEDEA, CSICUIB). Miquel Marqués 21, 07190 Esporles, Illes Balears, Spain

^c I.E.O. Centre Oceanogràfic de les Balears. P.O. Box 291, 07080 Palma de Mallorca, Illes Balears, Spain

Abstract

We have compared the distribution of mesopelagic, benthopelagic and benthic fauna between two areas: one on the continental side of the Catalan Sea (cCS: northwestern Mediterranean) and one to the SW of the Balearic Islands (SWB: southwestern Mediterranean) at depths between 147 and 2266 m. Based on 88 bathyal fish and crustaceans (Decapoda and Peracarida) dominant in these communities, we compared the maximum depth of occurrence (MDO) of (upper) middle-slope species and the minimum depth of occurrence (mDO) of lower-slope dwelling species. Mid-slope fish, decapods, peracarids and, within the latter, amphipods and cumaceans had a deeper MDO in the cCS than in the SWB. Depth differences between MDO of species were significant for all taxa, except isopods. In the same way, lower slope fish and decapods had a shallower mDO in the SWB than in the cCS. Within peracarids, the dominant taxon (amphipods) also followed this trend. Depth differences in mDO of species between the areas were significant for decapods and for amphipods (not for fish, nor all peracarids nor cumaceans). In summary, most taxa showed a deeper depth distribution of middle-slope species in the cCS, and a shallower depth distribution of lower-slope dwelling species in the SWB. This suggests that the whole community, from small detritus-feeders (peracarids) to top predators (fish) have a similar response to a common signal. Much basic information on the biology and possible environmental factors affecting deep-sea species distribution is not available, so causes of the trends demonstrated here cannot be fully evaluated. In spite of these obvious limitations, we have shown that (1) mesopelagic decapods (e.g., *Gennadas elegans* and *Sergia robusta*), with a higher dependence upon primary sources of food close to the surface primary production, showed greater differences in their mDO between the areas than benthopelagic (e.g., *Acanthephyra eximia*, *Nematocarcinus exilis*) and benthic (e.g., *Stereomastis sculpta*, *Munida tenuimana*, *Geryon longipes*) species, and (2) fish at lower trophic levels, deduced from fractional trophic levels, showed higher differences in the MDO than fish at higher trophic levels. Trophic position of species in food webs seems the most important factor affecting the distributional differences between contrasting areas.
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* Corresponding author. Tel.: +34-9323-09500; fax: +34-9323-09-555.
E-mail address: jcartes@icm.csic.es (J.E. Cartes).

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1. Introduction

The study of the distribution of species along environmental gradients has traditionally been important to characterizing the organisation of animal communities, both in terrestrial and aquatic systems (e.g., Therborg, 1970; Wenner & Boesch, 1979). As depth is considered the major environmental gradient in the sea, depth-related patterns are important in the study of deep-sea fauna (Gage & Tyler, 1991; Haedrich, Rowe, & Polloni, 1980; Merrett & Haedrich, 1997; Stefanescu, Rucabado, & Lloris, 1992).

In marine environments, species and communities often exhibit greater changes as a function of increasing depth than along horizontal gradients (Gage & Tyler, 1991). This greater change in the distribution of species with depth suggested the idea of depth bands of high faunal homogeneity separated by boundaries of faunal renewal, a zonation, that has been proposed in many deep-sea studies, from small macrobenthic invertebrates (e.g., gastropods: Rex, 1977; polychaetes, or cumaceans: Grassle, Sanders, & Smith, 1979) to megabenthic fish (Day & Percy, 1968; Haedrich, Rowe, & Polloni, 1975; Haedrich et al., 1980; Merrett & Haedrich, 1997; Stefanescu, Lloris, & Rucabado, 1993 and references cited therein) and crustaceans (Cartes & Sarda, 1993; Wenner & Boesch, 1979).

The distribution of species depends on a number of environmental variables, such as temperature or food availability, which can affect both the maximum density attained and the extreme limits of their distribution. The distribution range of species is wider or narrower as a function of physical changes and biotic interactions (Therborg, 1970). Depth has been often argued as the major structuring gradient in marine communities, though marine organisms may respond, in reality, to a combination of factors including food availability, light, temperature and pressure.

Species are usually distributed in patches on a two-dimensional scale, but have a bell-shaped abundance curve as a one-dimensional function of depth, as occurs with diversity (Gage & Tyler, 1991; Rex, Etter, & Stuart, 1997). Species are distributed along environmental gradients (see e.g., ter Braak & Prentice, 1988 for a review), and indices such as the *habitat amplitude* or the *center of gravity* (in Stefanescu et al., 1992 adopted from terrestrial studies by Daget, 1977, and Blondel, 1986) have been applied to summarize the characteristics of species habitat in a single and comparative value. Along the depth gradient, species have minimal and maximal depths of occurrence, with an intermediate depth, the *optimal abundance depth*, where their populations most often reach their highest densities. The concept of center of gravity has been used to define this (Moranta, Stefanescu, Massuti, Morales-Nin, & Lloris, 1998; Stefanescu et al., 1992). Species may find better living conditions, for example better feeding conditions, near their *optimal abundance depth*. This is where their adaptive success is greatest. In deep-Mediterranean Sea fish assemblages, for instance, most species show an increase in their trophic diversity (H') associated with their *optimal abundance depth* (Carrassón & Cartes, 2002).

Parameters related to the distribution of species may vary with time and space. Marine species, particularly benthopelagic fish or crustaceans having swimming capacity, can perform daily or seasonal migrations upward or downward along the slope, presumably to feed, or related to their reproductive cycle (e.g., the shrimp *Aristeus antennatus* in the western Mediterranean: Cartes, Company, & Maynou, 1994; the fish *Thyrsites atun* off southern New Zealand: Jacob, McClatchie, Probert, & Hurst, 1998; *Halargyrens johnsonii* in Rockall Trough: Gordon & Duncan, 1985). Such movements have been suggested, and sometimes relatively well documented, on the upper part of the continental slope (Wenner & Read, 1982). In the same way, species distributed across wide geographical areas may also exhibit variations in their depths of occurrence at different localities. Horizontal variability in the form of patchiness can originate from local phenomena (hydrography or geomorphology: Maynou, Conan, Cartes, Company, & Sardà, 1996). However, for deep-sea fauna, information on such changes are scarce (Maynou & Cartes, 2000; Wenner & Read, 1982). This can be, at least partially, a consequence of the survey design adopted. Non-simultaneous sampling performed in contrasting areas, or sampling at different locations along the studied coenocline (see Wenner & Boesch, 1979) in the same area can easily mask temporal changes in the species distribution.

Since 1989, surveys designed to study suprabenthos and megafauna have been performed in the Catalano-Balearic Basin (northwestern Mediterranean) and to the southwest of the Balearic Islands (northern Algerian basin; southwestern Mediterranean). These are two neighbouring areas, separated by ca. 350 km, have a priori some contrasting features regarding primary production, sediment granulometry, and other factors. The area SW of the Balearic Islands is open, far from the mainland in comparison to the Catalano-Balearic Basin, situated close to the influence of continental processes. Previous work was performed in the deep Mediterranean at mid and shallow depths, covering sampling areas subject to distinct regimes of *mainland influence* (Carpine, 1970; Ledoyer, 1987; Maurin, 1965; Maynou & Cartes, 2000), though differences in the distributional limits and abundance of species and the possible causes of these differences were rarely discussed (Maynou & Cartes, 2000). Our objective in the present work is to compare in geographically close areas the distribution patterns of the most representative species, comprising different trophic levels from megafauna (fish and decapod crustaceans as the widely dominant taxa) to macrofauna (swimming suprafauuna: peracarid crustaceans).

2. Material and methods

2.1. Study area

We compared two study areas: one continental in the western part of the Balearic Basin (between the Catalan coasts and the Valencia channel), the other to the southwest of the Balearic Islands (mainly in the

Algerian Basin; Fig. 1). The Balearic Basin is also known as the Catalan Sea, the name we will use to avoid confusion with the SW Balearic Islands site. Comparisons were made based on selected species pertaining to different taxa of crustacea and fish.

2.2. Dataset

We compare samplings made in both areas between 1989 and 1998, excluding old, rather rare citations of the selected species. The sampling effort in each area is quite comparable. The maximum depth of occurrence (MDO), the depth of the deepest appearance of middle (or upper) slope species, and the minimum depth of occurrence (mDO), depth of first appearance of lower-slope species, have been recorded in both the continental Catalan Sea and in the SW Balearic Islands for characteristic target species. We do not compare abundances (e.g., centers of gravity or whole distribution curves), because different sampling gear was used. Thus, we must analyse the data qualitatively, not quantitatively (see e.g., Moranta et al., 1998).

Concerning megafauna (fish and decapod crustaceans), samples in the continental Catalan Sea pertain to the cruises Bathos III, IV, and V (June–July 1989), while samples southwest of the Balearic Islands were made during October 1996 and May 1998 (*Deep-Sea Fisheries* project: FAIR-CT95-0655, 0371/II) on 2 oceanographic cruises (Q1, and Q2). In addition, during the cruise Zonap1 (May 1992), 26 trawls were collected in the continental side of the Catalan Sea and 14 in the NE of Eivissa (south-west of Balearic Islands). Samples from Bathos/Zonap cruises were performed using an OTSB-14 bottom trawl, a standard system to catch deep-sea megafauna (Merrett & Marshall, 1981), whereas samples on Q1, and Q2 cruises were collected using an MTS bottom trawl, with characteristics similar to the OTSB-14 (Cartes et al., 1994). Trawl characteristics that can bias the qualitative species composition of samples, such as cod-end mesh size (6 mm) and trawling speed (around 2.5 knots) were the same in all cases. Trawls were conducted following isobaths, trying to minimize the depth range covered within each haul. The present comparison is based on a total of 65 bottom trawls performed in the Catalan Sea (continental side) and 59 southwest of the Balearic Islands. Sampling covered depths in the Catalan Sea between 147 and 2266 m and in the SW Balearic

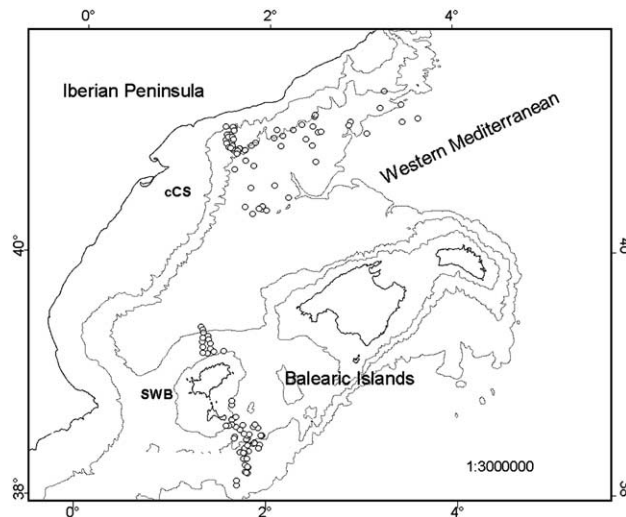


Fig. 1. The two study areas and the sites sampled for the depth of occurrences of mid and low-bathyal species in the western Mediterranean: the continental (western) part of the Catalano-Balearic Sea (cCS) and the SW of the Balearic Islands (SWB). Isobaths shown are at 500, 1000 and 2000 m.

Table 1

List of selected species distributed on the middle (upper) slope, with their maximum depth of occurrence (MDO) in the Catalan Sea (continental side) and the SW Balearic Islands

| | MDO | |
|--------------------------------------|-------------|---------------------|
| | Catalan Sea | SW Balearic Islands |
| Fish | | |
| <i>Nezumia aequalis</i> | 1212 | 1407 |
| <i>Notacanthus bonapartei</i> | 1862 | 1513 |
| <i>Trachyrhynchus trachyrhynchus</i> | 1589 | 816 |
| <i>Symphurus ligulatus</i> | 1049 | 898 |
| <i>Phycis blennoides</i> | 1308 | 1032 |
| <i>Etmopterus spinax</i> | 1488 | 1416 |
| <i>Nettastoma melanurum</i> | 1078 | 1416 |
| <i>Lepidorhombus boscii</i> | 984 | 595 |
| <i>Merluccius merluccius</i> | 1075 | 802 |
| <i>Antonogadus megalokinodon</i> | 1212 | 802 |
| <i>Galeus melastomus</i> | 1739 | 1713 |
| <i>Epigonus denticulatus</i> | 970 | 816 |
| <i>Conger conger</i> | 960 | 816 |
| Decapod crustaceans | | |
| <i>Sergestes henseni</i> | 1224 | 1624 |
| <i>Plesionika acanthonotus</i> | 1680 | 1323 |
| <i>Pontocaris lacazei</i> | 1041 | 538 |
| <i>Calocaris macandreae</i> | 1675 | 720 |
| <i>Polycheles typhlops</i> | 1927 | 1426 |
| <i>Munida tenuimana</i> | 1899 | 1714 |
| <i>Paromola cuvieri</i> | 1165 | 1148 |
| <i>Macropodia longipes</i> | 1249 | 546 |
| <i>Dorhynchus thomsoni</i> | 2211 | 1049 |
| <i>Macropipus tuberculatus</i> | 1041 | 420 |
| <i>Geryon longipes</i> | 1895 | 1709 |
| <i>Monodaeus couchi</i> | 1120 | 900 |
| Peracarid crustaceans | | |
| Mysidacea | | |
| <i>Erythrope neapolitana</i> | 1355 | 603 |
| <i>Paramblyops rostrata</i> | 1859 | 1594 |
| <i>Parapseudomma callophura</i> | 1355 | 1204 |
| Amphipoda | | |
| <i>Rhachotropis grimaldii</i> | 1280 | 1204 |
| <i>Leucothoe lilljeborgi</i> | 1263 | 402 |
| <i>Idunella pirata</i> | 1263 | 1204 |
| <i>Orchomenella nana</i> | 1263 | 1204 |
| <i>Scopelocheirus hopei</i> | 1263 | 804 |
| <i>Tmetonyx similis</i> | 1284 | 1204 |
| <i>Tryphosites alleni</i> | 1808 | 900 |
| <i>Bathymedon banyulsensis</i> | 1284 | 1204 |
| <i>Oediceropsis brevicornis</i> | 1355 | 1594 |
| <i>Synchelidium maculatum</i> | 1355 | 804 |
| <i>Nicippe tumida</i> | 1263 | 603 |
| <i>Harpinia dellavallei</i> | 1355 | 804 |
| <i>Harpinia pectinata</i> | 1255 | 1049 |
| <i>Syrrhoites pusilla</i> | 1279 | 900 |

Table 1 (continued)

| | MDO | |
|--------------------------------|-------------|---------------------|
| | Catalan Sea | SW Balearic Islands |
| Cumacea | | |
| <i>Eudorella truncatula</i> | 1263 | 402 |
| <i>Leucon affinis</i> | 1263 | 900 |
| <i>Cumella gracillima</i> | 1275 | 1024 |
| Isopoda | | |
| <i>Chelator chelatus</i> | 1808 | 1594 |
| <i>Natatolana borealis</i> | 1260 | 1204 |
| <i>Desmosoma lineare</i> | 1355 | 804 |
| <i>Disconectes phallangium</i> | 1260 | 1594 |
| <i>Eugerdia filipes</i> | 1355 | 900 |
| <i>Eurycopidae</i> sp. A | 1355 | 1594 |
| <i>Eurydice grimaldii</i> | 1263 | 1624 |
| <i>Ilyarachna longicornis</i> | 1355 | 1594 |
| <i>Ischnomesus bispinosus</i> | 1355 | 1594 |

Islands between 183 and 1714 m. No wide sampling gaps appeared in either area. Differences between the two trawl models (see Cartes et al., 1994; Moranta et al., 1998) should affect only quantitative biomass or density estimates, not the level of our qualitative comparison based on the occurrence of species. Inter-annual variability in the qualitative composition of fauna sampled is assumed to have been trivial during the period sampled (9 years).

Concerning peracarids, 24 suprabenthos samples, 6 with the Macer-GIROQ sledge and 18 with plankton nets, were taken in the SW Balearic Islands during Q1 and Q2 cruises at depths ranging from 249 to 1622 m. Some sampling gaps (hardly exceeding 100 m depth) remained in this sampling, which covered depth the intervals 249–268, 384–402, 543–694, 802–1049, 1200–1204, and 1503–1622 m. Twenty-six hauls performed in the Catalan Sea were selected for comparison to those of the SW Balearic Islands. Hauls from two seasons (spring and autumn) comparable to the periods (May and October) sampled in the SW Balears were chosen: SP89-P89 (16, 20-21/10/89: 5 plankton net samples); P90 (5/11/90: 3 plankton net samples); R1 (25/04/91: 3 sledge samples); R2 (9/12/91: 5 sledge samples); BT1 (22/03/94, 1 sledge at 1859 m), Pr96 (13, 28/10/96: 4 sledge samples); and BBC2 (23/09/98; 5 sledge samples). Sampling depths ranged from 208 to 1859 m and, as in the previous case, some sampling gaps remained. The sampling covered the depth intervals 208–214, 402–644, 862–989, 1250–1355, 1478–1645 and 1772–1859 m.

2.3. Selection of target species

Criteria adopted to select the target species for comparisons of the maximum (MDO) and minimum (mDO) depth of occurrence of species were as follows:

2.3.1. MDO

We selected species whose center of gravity or *optimal abundance depth* was situated above ~1000 m. These are species characteristic of the middle (or upper) slope communities of the western Mediterranean (Cartes & Sarda, 1993; Cartes & Sorbe, 1993, 1997; Moranta et al., 1998; Pérès, 1985). The most eurybathic species, distributed along all the bathymetric range comprising the entire mid- and low-bathyal communities (below depths of ~400 m), were excluded a priori from this analysis. Thus, for instance, we eliminated the shrimp *Pasiphaea multidentata* and the Myctophid *Lampanyctus crocodilus*. Some rare species, only occurring a few times (<5% of trawls), were also excluded (e.g., *Paraliparis leptochirus*).

2.3.2. *mDO*

We selected species whose center of gravity or *optimal abundance depth* was below ~1000 m (deduced from Cartes & Sarda, 1993; Pérès, 1985; Stefanescu et al., 1993), reaching in most cases the maximum depth sampled. These are species characteristic of the lower slope communities of the western Mediterranean. As in the previous case, eurybathic species (e.g., the shrimp *A. antennatus*) and rare species (e.g.,

Table 2

List of selected species selected distributed on the lower slope, with their minimum depth of occurrence (mDO) in the Catalan Sea (continental side) and the SW Balearic Islands

| | mDO | |
|-----------------------------------|-------------|---------------------|
| | Catalan Sea | SW Balearic Islands |
| Fish | | |
| <i>Centroscymnus coelolepis</i> | 1419 | 1012 |
| <i>Alepocephalus rostratus</i> | 711 | 700 |
| <i>Bathypterois mediterraneus</i> | 986 | 744 |
| <i>Polyacanthonotus rissoanus</i> | 711 | 694 |
| <i>Chalinura mediterranea</i> | 1308 | 1094 |
| <i>Coelorhynchus labiatus</i> | 1049 | 1012 |
| <i>Coryphanoides guentheri</i> | 1308 | 1418 |
| <i>Lepidion lepidion</i> | 711 | 708 |
| <i>Mora moro</i> | 427 | 694 |
| <i>Cataetyx alleni</i> | 519 | 700 |
| Decapod crustaceans | | |
| <i>Gennadas elegans</i> | 546 | 469 |
| <i>AcanthePHYra eximia</i> | 969 | 816 |
| <i>AcanthePHYra pelagica</i> | 994 | 613 |
| <i>Nematocarcinus exilis</i> | 1267 | 1075 |
| <i>Pontophilus norvegicus</i> | 662 | 694 |
| <i>Sergia robusta</i> | 861 | 470 |
| <i>Stereomastis sculpta</i> | 861 | 800 |
| Peracarid crustaceans | | |
| Mysidacea | | |
| <i>Calyptomma puritani</i> | 604 | 601 |
| Amphipoda | | |
| <i>Lepechinella manco</i> | 1250 | 1015 |
| <i>Rhachotropis gracilis</i> | 1250 | 802 |
| <i>Bathymedon longirostris</i> | 593 | 398 |
| <i>Oediceroides pilosus</i> | 1250 | 1015 |
| <i>Ilerastroe ilergetes</i> | 549 | 601 |
| <i>Pseudotiron bouvieri</i> | 1250 | 617 |
| Cumacea | | |
| <i>Bathycuma brevirostre</i> | 524 | 802 |
| <i>Cyclaspis longicaudata</i> | 862 | 617 |
| <i>Platysympus typicus</i> | 1253 | 802 |
| <i>Diastylis jonesi</i> | 1275 | 1586 |
| <i>Makrokyllindrus longipes</i> | 524 | 1024 |
| <i>Campylaspis horridoides</i> | 1253 | 1024 |
| Isopoda | | |
| <i>Ilyarachna sekhari</i> | 1253 | 802 |
| <i>Ilyarachna calidus</i> | 1263 | 1204 |
| <i>Janirella</i> spp. | 862 | 802 |

Chaceon mediterraneus and *Munidopsis tridentata* among decapods and *Cataetyx laticeps* and *Lepidion guentheri* among fish) were excluded a priori from the analysis. The lists of species selected are shown in Tables 1 and 2.

The comparisons MDO and mDO values for the Catalan Sea (continental side) and in the SW of Balearic Islands were tested only for those taxa (e.g., for mDO fish, decapod and peracarid crustaceans, amphipods and cumaceans) accumulating at least 6 species for comparisons in each area. Therefore, mysids and cumaceans (3 species) were not considered to test their MDO, while mysids (1 species) and Isopods (3 species) were not considered to test their mDO.

The ratio was calculated between the number of species reaching their maximum (or minimum) depth of occurrence in the Catalan Sea (continental side) and in the SW of Balearic Islands. Then, a likelihood-ratio *G*-test (Sokal & Rohlf, 1981) was performed to compare the deviation of these ratios in relation to the theoretical 1:1 ratio expected in the absence of differences of the MDO and mDO between the areas. Further, a Wilcoxon signed-rank test was used to evaluate departures from the null hypothesis that differences in the median MDO or mDO are zero.

3. Results

3.1. Maximum depth of occurrence of mid-slope species

3.1.1. Fish

The MDO ratio between the areas differed significantly from 1:1 (*G* test; $p < 0.001$). All but 2 of the 13 species of dominant fish distributed in both areas had a deeper MDO in the continental Catalan Sea than in the Balearic Islands (Fig. 2(a); $V = 76$, $p = 0.033$; Table 3). The exceptions were *Nezumia aequalis* and *Nettastoma melanurum*.

3.1.2. Decapod crustaceans

Among dominant decapods, 11 of 12 species present in both areas had a deeper MDO in the continental Catalan Sea, with only the exception of *Sergestes henseni* (Fig. 2(a)). The MDO ratio between both areas differed significantly from 1:1 (*G* test; $p < 0.001$). The maximum depth of occurrence was clearly deeper in the Catalan sea than in the Balearic sea ($V = 72$, $p = 0.007$; Table 3).

3.1.3. Peracarid crustaceans

Results are shown by taxon. Amphipods had a deeper MDO in the continental Catalan Sea than in the SW Balearic Islands, with 13 of the 14 species selected (with only the exception of *Oediceropsis brevicornis*) fitting this trend (Fig. 2(b)). Isopods, however, exhibited an inverse trend (or no significant difference) with 5 of the 9 selected species from the middle slope having a deeper MDO in the Balearic Islands than in the continental Catalan Sea (Fig. 2(b)). All mid-slope dwelling mysids and cumaceans (only 3 species) selected had also deeper MDOs in the continental Catalan Sea than in the SW Balearic Islands. The MDO ratio between both areas differed significantly from 1:1 (*G* test; $p < 0.001$) for all taxa except isopods. The results of the Wilcoxon test yielded significant for amphipods ($V = 113$, $p = 0.003$; Table 3), and for all peracarids taken together ($V = 474$, $p = 0.001$), due to the predominance of amphipods in the samples.

3.2. Minimum depth of occurrence by lower-slope dwelling species

3.2.1. Fish

Among 11 species of dominant fish distributed in both areas, 7 (*Centroscymnus coelolepis*, *Alepocephalus rostratus*, *Bathypterois mediterraneus*, *Polyacanthonotus rissoanus*, *Chalinura mediterranea*, and *Coel-*

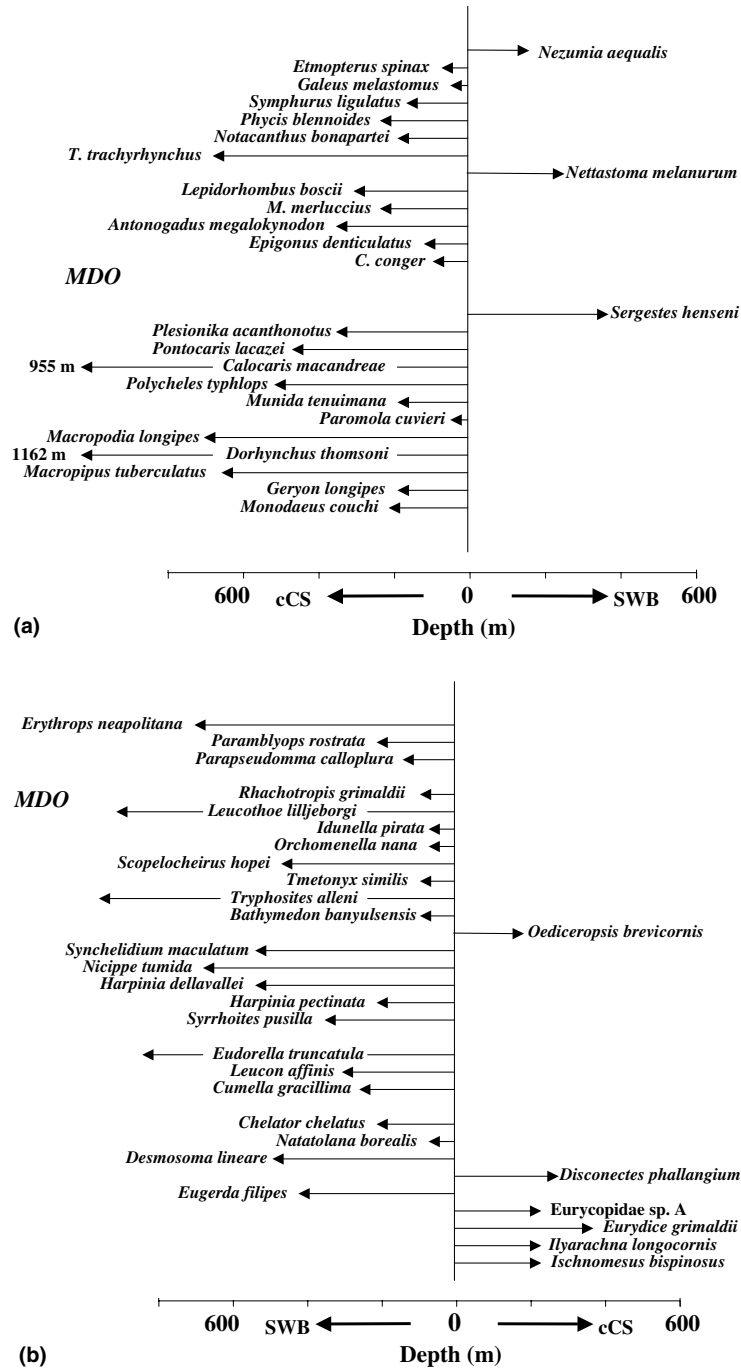


Fig. 2. Differences in the maximum depth of occurrence (MDO) between dominant species inhabiting the continental side of the Catalano-Balearic Basin and the south-west of the Balearic Islands; A, megafauna (fish and decapod crustaceans); B, macrofauna (peracarid crustaceans). Arrows in X-axis indicate shallower distribution in cCS or in SWB.

Table 3

Results of the G test and the Wilcoxon signed-rank test (V) on the differences on the mDO and MDO between the Catalan Sea and Balearic Islands

| Taxon | n | G | V | p |
|--|-----|--------------------|-----|-------|
| <i>Minimum depth of occurrence (mDO)</i> | | | | |
| Fish | 11 | 7.54* | 41 | 0.520 |
| Decapods | 7 | 56.59** | 27 | 0.031 |
| Peracarids | 16 | 11.79** | 149 | 0.465 |
| Amphipods | 6 | 47.45** | 20 | 0.048 |
| Cumaceans | 6 | 1.97 ^{ns} | 17 | 0.570 |
| <i>Maximum depth of occurrence (MDO)</i> | | | | |
| Fish | 13 | 48.51** | 76 | 0.033 |
| Decapods | 12 | 81.32** | 72 | 0.007 |
| Peracarids | 29 | 38.55** | 474 | 0.001 |
| Amphipods | 14 | 87.90** | 113 | 0.003 |
| Isopods | 9 | 1.24 ^{ns} | 20 | 0.812 |

G test: * $p < 0.01$; ** $p < 0.001$; (ns), non significant; p is indicated for V test.

orhynchus labiatus) had a shallower mDO in the Balearic Islands than in the continental Catalan Sea. By contrast, 4 species (the macrourid *Coryphaenoides guentheri*, *Lepidion lepidion*, *Mora moro*, and *Cataetyx alleni*) occurred shallower in the Catalan Sea Basin (Fig. 3). The 7 species with shallower mDO around the Balearic Islands were distributed between 3 and 407 m shallower than in the Catalan Sea Basin. The major part, however, occurred only slightly shallower (3–37 m). The mDO ratio between the Catalan Sea and the Balearic Islands differed significantly from 1:1 (G test; $p < 0.01$) in fish. The Wilcoxon test did not show significant differences in mDO for this taxon ($V = 41$, $p = 0.520$; Table 3). This means that differences in mDO of species between the areas are not significant.

3.2.2. Decapod crustaceans

From 7 species of dominant decapods distributed in both areas, 6 (*Gennadas elegans*, *Acantheephyra eximia*, *Acantheephyra pelagica*, *Nematocarcinus exilis*, *Sergia robusta*, and *Stereomastis sculpta*) had the shallower mDO in the Balearic Islands. The only lower-slope species whose mDO was shallower in the continental Catalan Sea was *Pontophilus norvegicus* (Fig. 3). The species in the Balearic Islands were distributed between 61 and 391 m shallower than in the continental Catalan Sea. The mDO ratio of decapods between the Catalan Sea and the Balearic Islands differed significantly from 1:1 (G test; $p < 0.001$). The Wilcoxon test also showed significant differences in mDO for this taxon ($V = 27$, $p = 0.031$; Table 3).

3.2.3. Peracarid crustaceans

Results in this group must be interpreted with caution due to the occurrence of gaps exceeding 100 m in the depth interval sampled. From the 16 selected species (Fig. 3), 11 (the amphipods *Lepechinella manco*, *Rhachotropis (gracilis)*, *Bathymedon longirostris*, *Oediceroides pilosus*, and *Pseudotiron bowieri*, the cumaceans *Cyclaspis longicaudata*, *Platysympus typicus* and *Campylaspis horridoides* and the isopods *Ilyarachna sekhari*, *Ilyarachna calidus* and *Janirella* spp.) had their shallowest mDO around the Balearic Islands. The exceptions to this trend were mainly among cumaceans (3 species: *Bathycuma brevirostre*, *Diastylis jonesi* and *Makrokyllindrus longipes*). Species whose mDO was shallower around the Balearic Islands were distributed between 59 and 451 m shallower than on the continental side of the Catalan Sea. The mDO ratio between the areas differed significantly from 1:1 (G test; $p < 0.001$) in all taxa except for cumaceans, and the Wilcoxon test was significant for amphipods ($V = 20$, $p = 0.058$; Table 3), but was not for cumaceans. Peracarids as a whole were not significant.

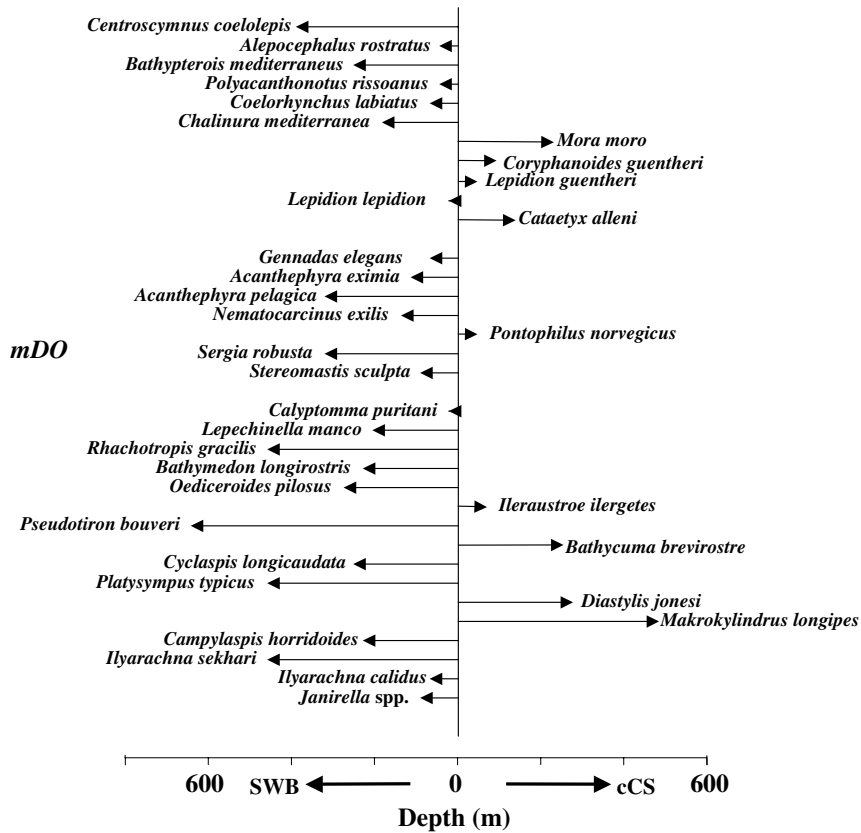


Fig. 3. Differences in the minimum depth of occurrence (mDO) between dominant species inhabiting the continental side of the Catalano-Balearic Sea (cCS) and the SW of the Balearic Islands (SWB). Arrows in X-axis indicate shallower distribution in cCS or in SWB.

4. Discussion

We have demonstrated two parallel trends: (1) a deeper distribution (greater MDO) by middle-slope dwelling species in the continental Catalan Sea (in comparison to the SW Balearic Islands), and (2) a shallower depth distribution (low mDO) by lower-slope dwelling species in the SW Balearic Islands. Most taxa exhibited both trends, suggesting that the whole community, from small detritus-feeding fauna (peracarids) to top predators (fish and decapods) have a similar response to a common signal. However, when the significance of the differences was tested, we found some taxa not following one of the two aspects compared. That was the case for fish and cumaceans in respect to their mDO. In the case of mDO, however, we found some limitations in our data set, specifically in the low number of species inhabiting the lower slope assemblage. This number is low in part because of the high number of eurybathic species in the deep bathyal Mediterranean, an important feature of the fauna dwelling in this area (Carpine, 1970; Pérès, 1985).

The comparatively shallow depths occupied by the characteristic decapod species of the lower slope in the SW Balearic Islands are related to the shallower location of the main faunal boundary of this taxon in this area than in the Catalan Sea (Maynou & Cartes, 2000). However, changes in the distributional patterns of species can be more problematic when the evidence is evaluated by multivariate analyses, because differences by cruise in the allocation of samplings along the studied coenocline (Wenner & Boesch, 1979) can

bias the estimated centers of gravity of species and the apparent boundaries of faunal renewal (Wenner & Read, 1982).

Changes in the depth of occurrence of bathyal species distributed over wide geographical areas can also be masked by temporal changes. For instance, there are possible seasonal downward movements among benthopelagic fauna on the upper and middle slope (e.g., in the deep-western Mediterranean for the red shrimp *A. antennatus* to 800 m: Cartes et al., 1994). This possible bias, however, does not seem to occur in our study because our comparisons of depths of species occurrences were always made on distributional limits situated around or below 1000 m. Moreover, no seasonal differences have been found in deep-sea fish assemblages, either at a community or at a species level (Moranta, Massutí, & Morales-Nin,; Stefanescu, Morales-Nin, & Massutí, 1994). Seasonal changes in the distribution of upper slope decapod crustaceans have been reported from the South Atlantic Bight off North America (Wenner & Read, 1982), with the upper slope assemblage located shallower in summer (August–September) and spring (April). Seasonal changes in that area were attributable to changes in the temperature, hydrographic regime and also to biogeographic aspects (boreal vs. tropical origin of decapod fauna).

The deep Mediterranean fauna, by contrast, inhabit an environment stable thermally and in salinity below 200 m (Hopkins, 1985). This fauna has a high resemblance to that of the boreal Atlantic, with differences in the depth distribution of common species (e.g., *Campylaspis glabra* and *Calocaris macandreae*) attributable, particularly, to thermal stability (Carpine, 1970). Temperature, however, is not the only variable affecting the distribution of Mediterranean species, because deep-Mediterranean species show differences under isothermal conditions in the lower limits of their depth distribution. Thus, burrowing decapods such as *Nephrops norvegicus* and *Calocaris macandreae* were more abundant in the Catalano-Balearic Basin than in the SW Balearic Islands probably related to more suitable sediments (terrigenous mud) for burrowing, (Cartes, Maynou, Morales-Nin, Massutí, & Moranta, 2001; Maynou & Cartes, 2000).

Though these trends in abundance can also be somewhat biased by using different bottom trawl models (see Moranta et al., 1998), we obtained similar trends for suprabenthos using the same sampling gear (a Macer-GIROQ sledge) in both study areas. In the same fashion, the feeding guilds of upper-slope dwelling peracarids also showed important differences in both study areas, with a higher proportion of deposit feeders in the Catalan Sea than in the Balearic Islands (Cartes, Jaume, & Madurell, 2003). These trends probably reflect the absence of terrigenous muddy bottoms off the SW Balearic Islands, where detrital material dominates in inshore areas and hemipelagic material of biogenic origin dominates offshore (Emelyanov, 1972). Hydrodynamic conditions are the most important factor controlling grain size of sediments (Etcheber et al., 1999), and lower proportion of mud is expected occur in more hydrodynamic areas. Eddies periodically occur around the Balearic Islands (Garcia-Ladona, Castellón, Font, & Tintoré, 1996). Though the absence of terrigenous muddy bottoms in the SWB can be favoured by these oceanographic features, this absence seems ultimately due to the lack of river discharges occurring in that area of the Balearic Islands.

4.1. Possible explanatory factors

Changes in diversity of upper slope fish communities off New Zealand have been suggested to be associated with regional changes in primary production (McClatchie et al., 1997). In a thermally stable environment such as the deep Mediterranean, trophic causes have also been suggested as the most plausible explanation for patterns in species distribution and zonation (Cartes, 1998; Cartes & Sarda, 1993). At assemblage level, the depth of first appearance of deep living decapod crustaceans seems to shoal eastward in the Mediterranean, which has also been suggested to be related to a parallel increase in oligotrophy eastward (Maynou & Cartes, 2000). The boundary between the upper (middle) and lower slope, regularly situated at around 1000–1400 m, was related in the deep Mediterranean to the decreasing influence of some key prey taxa in the environment and in the diet of decapods and fish (Cartes, 1998; Cartes & Sarda, 1993;

Stefanescu et al., 1993). These taxa, having a more direct relation with sources of primary production and detrital fluxes, also had a shallower distribution (e.g., *C. macandreae*) in the more oligotrophic area (SW Balearic Islands: see phytoplankton pigment concentration data in *seawifs.gsfc.nasa.gov*) in our present, comparative study, supporting the hypothesis that the eutrophic–oligotrophic gradient must be the main factor explaining the trend in the distribution of bathyal species demonstrated by our data.

In addition, we found some, more general, trends in the position of species in trophic webs. Comparing the distribution of species between and within taxa in both areas, mesopelagic decapods (e.g., *G. elegans* and *S. robusta*) showed greater differences in their minimum depth of occurrence than bathypelagic (e.g., *A. eximia*, *N. exilis*) and benthic (e.g., *S. sculpta*, *Munida tenuimana*, *Geryon longipes*) species (Fig. 4). This is also related to the lower trophic level (see Cartes & Carrassón, 2004) of mesopelagic species with higher dependence towards primary sources of food (surface primary production). Similar trends were found among fish, as significant differences were found regarding differences of MDO between both areas. Fish with lower trophic levels (using data in Stergiou & Karpouzi, 2002) showed higher differences in the MDO than species in higher trophic levels (Fig. 5(a)). The lowest TL among deep-sea fish occurred among benthos feeders, while large Macrouridae and sharks tend to show the highest TL (Polunin et al., 2001). Further, the trophic guild occupied by each species (Fig. 5(b), from data in Cartes et al., 2002) followed the same trend as TL of fish, with species feeding on nektobenthos-suprabenthos (NS) and infauna (Inf) showing higher differences in their maximum depth than species feeding on macroplankton (nmM). Higher MDO imply a much shallower distribution in the SW Balearic Islands than in the Catalan Sea among benthos feeders. The mainland influence in the Catalan Sea (advective flux by river discharges) may favour higher increase of organic carbon (orgC) below 1000 m (between 1169 and 634 m: Cartes et al., 2002), attributable to a canyon effect. Higher organic matter (OM) in sediments (food available for benthos) at increasing depths may favour the deeper distribution of benthos feeders in the Catalan Sea. Although no similar detailed OM data are available in the SW Balearic area, indirect evidence for the lesser downward

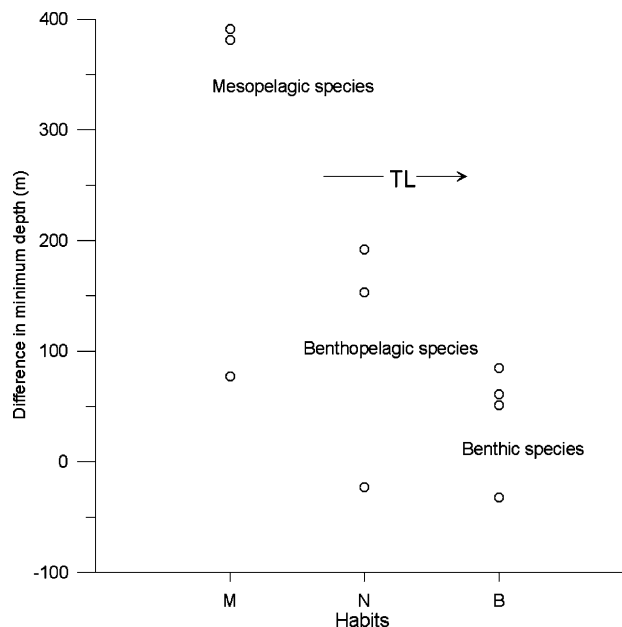


Fig. 4. Differences in minimum depth between the Catalano-Balearic Basin and the south-west of the Balearic Islands for target species of crustacean decapods as a function of habits (Cartes & Sarda, 1993). Arrow indicates increasing trophic level.

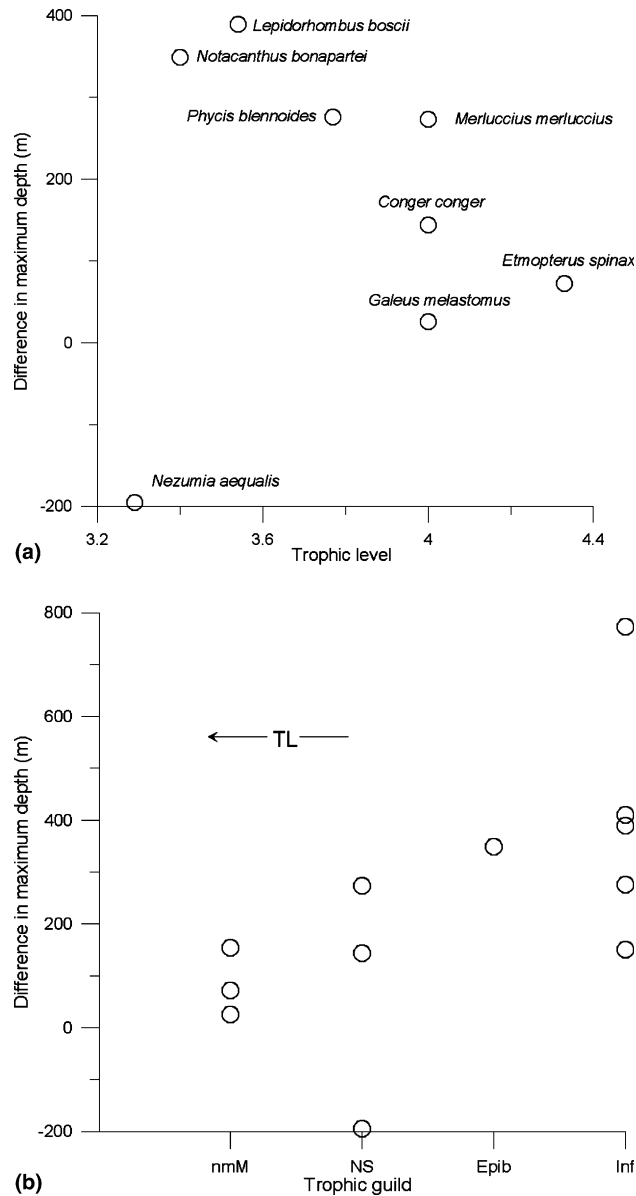


Fig. 5. Differences in maximum depth (MDO) of fishes as a function of. (a) their trophic level (fractional TL values obtained from Stergiou & Karpouzi, 2002). Higher MDO indicates deeper distribution in the Catalan sea than in the SW Balearic Islands; (b) their trophic guild. Trophic guilds are defined following Cartes, Grémare, Maynou, Villora-Moreno, and Dinet (2002): nmM, non-migrator macroplankton feeders; NS, Nektobenthos-Suprabenthos feeders; Epib, Epibenthos feeders; Inf, Infauna feeders. Arrow indicates increasing trophic level.

extent of organic enrichment is again the shallower distribution of key prey-species among the infauna (e.g., *C. macandreae*) in this area.

Among taxa, peracarids showed a greater difference in their MDO between the two areas than did decapods and fish (Wilcoxon-test results). Again, taxa showing lower TL have increasing differences in their

comparative distributions between the areas. However, in the case of peracarids this result should be interpreted with caution due to the occurrence of sampling gaps.

Apart from trophic variables, the organization of deep-marine communities may also depend on biological factors such as the dispersal capabilities of early developmental stages (Grassle et al., 1979). The development of embryos among peracarid crustaceans takes place exclusively in the marsupium of oostegal females, which may result in lower dispersal capabilities than those of decapods and fish with predominantly free larval stages. Among fish (Fig. 4(a)), two ovoviviparous chondrichthians (*Galeus melastomus* and *Etmopterus spinax*) showed lower differences in their MDO (suggesting lower dispersal capabilities) than osteichthyes which often have free larval stages. More work on biological aspects of deep-sea species (e.g., egg size, fecundity) is needed before we can fully understand their influence of these variables on species distribution.

In conclusion, we found in this comparative study, both within and between taxa, that differences in the local distribution of species pertaining to the same community are consistently stronger among species situated at the lowest trophic levels. This is probably a consequence of a higher sensitivity to changes in the quality of primary sources of food (both primary production and detritus) at the lowest trophic levels compared to top predators.

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References

- Blondel, J. (1986). *Biogéographie évolutive*. Paris: Mason, p. 221.
- Carpine, C. (1970). Ecologie de l'étage bathyal dans la Méditerranée occidentale. *Memoires de l'Institut Océanographique de Monaco*, 2, 1–146.
- Carrassón, M., & Cartes, J. E. (2002). Trophic relationships in a Mediterranean deep-sea fish community: Partition of food resources, dietary overlap and connections with the Benthic Boundary Layer. *Marine Ecology Progress Series*, 241, 41–55.
- Cartes, J. E. (1998). Dynamics of the bathyal benthic boundary layer in the northwestern Mediterranean: Depth and temporal variations in macrofaunal–megafaunal communities and their possible connections within deep-sea trophic webs. *Progress in Oceanography*, 41, 111–139.
- Cartes, J. E., & Sarda, F. (1993). Zonation of the deep-sea decapod fauna in the Catalan Sea (Western Mediterranean). *Marine Ecology Progress Series*, 94, 27–34.
- Cartes, J. E., & Sorbe, J. C. (1993). Les communautés suprabenthiques de la Mer Catalane (Méditerranée occidentale): données préliminaires sur la repartition bathymétrique et l'abondance des crustacés pécararides. *Crustaceana*, 64(2), 155–171.
- Cartes, J. E., & Sorbe, J. C. (1997). Bathyal Cumaceans of the Catalan Sea (north-western Mediterranean): Faunistic composition, diversity and near bottom distribution along the slope (between 389 and 1859 m). *Journal of Natural History*, 31, 1041–1054.
- Cartes, J. E., & Carrassón, M. (2004). The influence of trophic variables in the depth-range distribution and zonation rates of deep-sea megafauna: The case of the Western Mediterranean assemblages. *Deep Sea Research*, 51(2), 263–279.
- Cartes, J. E., Company, J. B., & Maynou, F. (1994). Deep-water decapod crustaceans communities in the Northwestern Mediterranean: Influence of submarine canyons and season. *Marine Biology*, 120, 221–230.
- Cartes, J. E., Maynou, F., Morales-Nin, B., Massutí, E., & Moranta, J. (2001). Trophic structure of a bathyal-Benthopelagic boundary layer community off the south of the Balearic Islands (Southwestern Mediterranean). *Marine Ecology Progress Series*, 215, 23–35.
- Cartes, J. E., Grémare, A., Maynou, F., Villora-Moreno, S., & Dinet, A. (2002). Benthic boundary layer response to fluxes of labile particulate organic matter in the bathyal environment of the Catalan Sea (northwestern Mediterranean). *Progress in Oceanography*, 53, 29–56.

- Cartes, J. E., Jaume, D., & Madurell, T. (2003). Local changes in the composition and community structure of suprabenthic peracarid crustaceans on the deep-bathyal Mediterranean: Influence of environmental variables. *Marine Biology*, *143*, 745–758.
- Daget, Ph. (1977). Espèces indicatrices et leur valeur caractérisante vis-a-vis du milieu. *Naturalia monspeliense, série Botanique*, *27*, 93–107.
- Day, D. S., & Pearcy, W. G. (1968). Species associations of benthic fish on the continental shelf and slope off Oregon. *Journal of Fisheries Research Board of Canada*, *25*, 2665–2675.
- Emelyanov, E. M. (1972). In D. J. Stanley (Ed.), *The mediterranean sea: A natural sedimentation laboratory, Principal types of recent bottom sediments in the Mediterranean Sea: Their mineralogy and geochemistry* (pp. 355–386). Stroudsburg: Dowden Hutchinson and Ross.
- Etcheber, H., Relaxans, J. C., Beliard, M., Weber, O., Buscail, R., & Heussner, S. (1999). Distribution and quality of sedimentary organic matter on the Aquitanian margin (bay of Biscay). *Deep Sea Research II*, *46*, 2249–2288.
- Gage, J. D., & Tyler, P. A. (1991). *Deep sea biology: A natural history of organisms at the deep-sea floor*. Cambridge: Cambridge University Press, p. 504.
- Garcia-Ladona, E., Castellón, A., Font, J., & Tintoré, J. (1996). The Balearic current and volume transports in the Balearic Basin. *Oceanologica Acta*, *19*, 489–497.
- Gordon, J. D. M., & Duncan, J. A. R. (1985). The biology of fish of the family Moridae in the deep-water of the Rockall Trough. *Journal of the Marine Biological Association of the United Kingdom*, *65*, 475–485.
- Grassle, J. F., Sanders, H. L., & Smith, V. (1979). Faunal changes with depth in the deep-sea benthos. *Ambio Special Report*, *6*, 47–50.
- Haedrich, R. L., Rowe, G. T., & Polloni, P. T. (1975). Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *Journal of Marine Research*, *33*, 191–212.
- Haedrich, R. L., Rowe, G. T., & Polloni, P. T. (1980). The megabenthic fauna in the deep sea south of New England, USA. *Marine Biology*, *57*, 165–179.
- Hopkins, T. S. (1985). Physics of the sea. In R. Margalef (Ed.), *Western mediterranean*. Oxford: Pergamon Press.
- Jacob, W., McClatchie, S., Probert, P. K., & Hurst, R. J. (1998). Demersal fish assemblages off southern New Zealand in relation to depth and temperature. *Deep Sea Research*, *45*, 2119–2155.
- Ledoyer, M. (1987). Les Cumacés Méditerranéens profonds (Crustacea) des Campagnes Bioméde I et II et Balgim. Synthèse de la distribution bathyale du groupe en Méditerranée occidentale. *Mésogée*, *57*, 49–70.
- McClatchie, S., Millar, R. B., Webster, F., Lester, P. J., Hurst, R., & Bagley, N. (1997). Demersal fish community diversity off New Zealand: Is it related to depth, latitude and regional surface phytoplankton? *Deep Sea Research I*, *44*, 647–667.
- Maurin, C. (1965). Répartition des crevettes profondes au large des côtes de Sardaigne et de Corse. *Rapports Commite internationale de la Mer Méditerranée*, *18*, 175–178.
- Maynou, F., & Cartes, J. E. (2000). Community structure of bathyal decapod crustacean assemblages off the Balearic Islands (South-western Mediterranean): Seasonal changes and regional patterns in zonation. *Journal of the Marine Biological Association of the United Kingdom*, *80*, 789–798.
- Maynou, F., Conan, G. Y., Cartes, J. E., Company, J. B., & Sardà, F. (1996). Spatial structure and seasonality of decapod crustacean populations on the Northwestern Mediterranean slope. *Limnology and Oceanography*, *41*(1), 113–125.
- Merrett, N. R., & Marshall, N. B. (1981). Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08–27°N). *Progress in Oceanography*, *9*, 185–244.
- Merrett, N. R., & Haedrich, R. L. (1997). *Deep sea demersal fish and fisheries*. London: Chapman & Hall, p. 282.
- Moranta, J., Stefanescu, C., Massuti, E., Morales-Nin, B., & Lloris, D. (1998). Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean). *Marine Ecology Progress Series*, *171*, 247–259.
- Moranta, J., Massuti, E., & Morales-Nin, B. (In press). Spatio-temporal variations in fish community structure and body size on the continental slope of the Balearic Islands (western Mediterranean). *Scientia Marina*.
- Pérès, J. M. (1985). In R. Margalef (Ed.), *Key environments: Western mediterranean, History of the mediterranean biota and the colonization of the depths* (pp. 198–232). New York: Pergamon Press.
- Polunin, N. V. C., Morales-Nin, B., Herod, W., Cartes, J. E., Pinnegar, J. K., & Moranta, J. (2001). Feeding relationships in Mediterranean bathyal assemblages elucidated by carbon and nitrogen stable-isotope data. *Marine Ecology Progress Series*, *220*, 13–23.
- Rex, M. A. (1977). Zonation in deep-sea gastropods: The importance of biological interactions to rates of zonation. In B. F. Keenan, P. O. Ceidigh, & P. J. S. Boaden, *Biology of benthic organisms. 11th European Symposium on Marine Biology, Galway* (pp. 521–529).
- Rex, M. A., Etter, R. J., & Stuart, C. T. (1997). In R. F. G. Ormond, J. D. Gage, & M. V. Angel (Eds.), *Marine biodiversity: Patterns and processes, Large-scale patterns of species diversity in the deep-sea benthos* (pp. 94–121). Cambridge: Cambridge University Press.
- Sokal, R. R., & Rohlf, F. J. (1981). *Biometria. Principios y métodos estadísticos en la investigación biológica*. Madrid: H. Blume ediciones, p. 832.
- Stefanescu, C., Lloris, D., & Rucabado, J. (1993). Deep-sea fish assemblages in the Catalan Sea (western Mediterranean) below a depth of 1000 m. *Deep Sea Research*, *40*, 695–707.

- Stefanescu, C., Morales-Nin, B., & Massutí, E. (1994). Fish assemblages on the slope in the Catalan Sea (western Mediterranean): Influence of a submarine canyon. *Journal of the Marine Biological Association of the United Kingdom*, *74*, 499–512.
- Stefanescu, C., Rucabado, J., & Lloris, D. (1992). Depth-size trends in Western Mediterranean demersal deep-sea fish. *Marine Ecology Progress Series*, *81*, 205–213.
- Stergiou, K. I., & Karpouzi, V. S. (2002). Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries*, 1–38.
- ter Braak, C. J. F., & Prentice, I. C. (1988). A theory of gradient analysis. *Advances in Ecological Research*, *18*, 271–317.
- Therborg, J. (1970). Distribution on environmental gradients: Theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Perú. *Ecology*, *52*, 23–40.
- Wenner, E. L., & Boesch, D. F. (1979). Distribution patterns of epibenthic decapod Crustacea along the shelf-slope coenocline, middle Atlantic Bight, USA. *Bulletin of the Biological Society of Washington*, *3*, 106–133.
- Wenner, E. L., & Read, T. H. (1982). Seasonal composition and abundance of decapod crustacean assemblages from the South Atlantic Bight, USA. *Bulletin of Marine Science*, *32*, 181–206.