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Community structure of bathyal decapod crustaceans off south-west Balearic Islands (western Mediterranean): seasonality and regional patterns in zonation

Francesc Maynou* and Joan E. Cartes

Institut de Ciències del Mar, CSIC, Pg Joan de Borbó s/n, 08039-Barcelona, Spain. *E-mail: maynouf@icm.csic.es

The community structure of decapod crustacean assemblages was established and analysed from two experimental trawl samplings. The data were taken in the south-west Balearic Islands (Algerian Basin, western Mediterranean Sea) at depths ranging from ~200 to 1800 m. The results of multivariate analysis indicate that the community structure remained constant between samplings. The analysis also revealed that there exist differences between bathyal decapod communities at a regional level (<1000 km) when compared with well-studied nearby areas. The differences relate mainly to the relative contribution of different species and feeding guilds, not to the taxonomic composition of the assemblages studied. It is proposed that these differences result from contrasting surface production regimes (coastal vs open sea) and food web organization (relative dependence on mesopelagic or infaunal prey).

INTRODUCTION

During the last decades, the organization of deep-sea megafaunal communities has been intensively studied (Rowe & Menzies, 1969; Haedrich et al., 1975, 1980; Smith & Hamilton, 1983; Abelló et al., 1988; Markle et al., 1988; Cartes & Sardà, 1993; Stefanescu et al., 1992). Fish were the focus of most of these studies, probably due to their dominance in terms of biomass in deep-sea communities from mid latitudes and because they are subject to a growing interest related to the development of new fisheries and fishing grounds (Merrett & Haedrich, 1997). The results of these studies have permitted the establishment of the biomass and diversity distribution patterns and the boundaries between communities (zonation).

Trophic arguments have variously been used to explain community organization at different spatial and temporal scales (Dayton & Hessler, 1972; Gage & Tyler, 1991), and to explain changes in megafaunal/macrofaunal community structure, although only a few studies relate changes in megafaunal/macrofaunal community structure with changes in food supply (from superficial phytoplankton pigment concentration to faunal diets; Watts et al., 1992). At a coarse scale, seasonally averaged phytoplankton pigment concentration can be a useful index of the magnitude or organic vertical flux and food supply for demersal megafauna (Rex et al., 1993).

A limited number of studies on decapod crustacean assemblages exist (Wenner & Boesch, 1979; Abelló et al., 1988; Cartes & Sardà, 1993), although this taxon is less well documented than fish. Decapod crustaceans are a dominant or subdominant faunal component in subtemperate to subtropical assemblages, such as the Mediterranean Sea, and are a key taxon linking lower and higher trophic levels (Cartes, 1998). Therefore, studies on the organization of dominant megafaunal taxa other than fish, with different trophic requirements, can offer a new approach to the study of megafaunal community structure and function.

More or less clearly separated communities have been described for megafaunal assemblages at bathyal and abyssal depths, but somewhat conflicting conclusions can be drawn from these results: first, although the geographic variation is important, most results point to a recurring boundary between the upper and middle slope assemblages, located at 300–700 m (Day & Pearcy, 1968; Haedrich et al., 1975, 1980). In the deep Mediterranean Sea, this boundary was established at comparable depths (between 350 and 500 m) by Abelló et al. (1988) and Cartes et al. (1994) for decapods of the Catalan Sea. The boundary between the middle and the lower slope assemblages was established at depths ranging between 1000–1400 m (Day & Pearcy, 1968; Haedrich et al., 1975; 1980; Wenner & Boesch, 1979; Hecker, 1990), with little variation between fish and decapod crustaceans in the deep western Mediterranean (Cartes & Sardà, 1993; Stefanescu et al., 1992; Moranta et al., 1998).

On the other hand, the boundaries between communities seem to be weaker at low latitudes (Gage & Tyler, 1991) and, in many cases, zonation seems to be more of a regional than a general phenomenon, of only local significance. As pointed out by Haedrich & Merrett (1990) for Atlantic deep-sea fish assemblages, it is problematic to extrapolate a locally observed trend to wider geographic areas. These seemingly conflicting views (existence of boundaries at recurring depth zones and local significance of deep-sea assemblages) can perhaps be reconciled by looking into the abiotic and biotic factors governing species distributions and biogeographic aspects but also considering the differences in practical and methodological aspects (such as sampling intensity).

The objectives of the present work are to present new results on community organization of deep-water decapods in the south-west Balearic Islands, to compare the

results with the well-studied Catalan Sea (located ~300 km to the north of the Balearic Islands) and, drawing from this comparison, to investigate the underlying factors structuring local communities of deep-water megafauna. We discuss the relevance of ecological (especially, trophic and environmental factors) and biogeographical aspects in structuring deep-water communities. We especially invoke trophic arguments to explain some patterns, bearing in mind the particular environmental conditions of the deep Mediterranean, with thermal and saline stability, below 200 m (Fredj & Laubier, 1985).

MATERIALS AND METHODS

Data source

Two oceanographic cruises were conducted in 1996 (Q1, October) and 1998 (Q2, May), in the Algerian Basin south-west of the Balearic Islands (western Mediterranean; Figure 1) to study the bottom-living community on the continental slope, for two contrasting oceanographic conditions. The megafaunal assemblage (comprising mostly fish and decapod crustaceans) was sampled by means of an experimental trawl MST, equipped with two doors, a single trawl warp, and a 25-m long bridle. The general size and structure of the trawl is close to the OTSB-14 commonly used in deep sea megafaunal studies (Merrett & Marshall, 1981). Forty-five valid bottom trawls were performed (31 during Q1 and 14 during Q2; Table 1). The trawl hauls lasted for 0.5 h (effective trawling time) and were monitored by means of an acoustic device (SCANMAR). Megafaunal species were determined to specific level (in Table 2 the list of decapods collected is included), counted and weighed (g wet weight). The exact area swept by the trawl was quantified with the SCANMAR readings, and was used to compute the abundance (number and weight) of the catch 10,000 m^{-2}. A CTD probe was used to determine the environmental characteristics of the water column (temperature, salinity and fluorescence). The CTD casts were performed along a transect for each oceanographic cruise, using a Seabird 25 probe with an attached Seatech flurometer.

Statistical analyses

The data on megafaunal abundance were plotted over a depth axis to display the trends with depth of the standardized abundance indices (N 10,000 m^{-2} and g 10,000 m^{-2}) for decapods and total megafauna. The identification of the main decapod crustacean assemblages was performed by multidimensional scaling (MDS) on the correlation matrix of the standardized abundance (N 10,000 m^{-2}) for each trawl haul and for each sampling cruise. Species appearing less than three times on each cruise were not taken into consideration for further analysis. The similarity index used in MDS ordination was Pearson's product moment correlation (r). The decapod assemblages (*sensu* Paine, 1994, table 1) identified were characterized by the following descriptors: mean density of the species comprising 95% of the abundance, species richness (S), expected species number (ES(n); Hurlbert, 1971), relative contribution of feeding guilds (*sensu* Paine, 1994, table 1) and relative location in the water column. Following the feeding studies of Cartes (1998) for the same species in the nearby Catalan Sea, the decapod species studied were classified as migrator macroplankton-feeders (MMF), non-migrator macroplankton-feeders (NMF), macroplankton-feeders and scavengers (MSF), epifauna-feeders (EPI), infauna-feeders (INF) and deposit-feeders (DEF). Regarding their relative location in the water column, decapod crustaceans can be classified as mesopelagic species (undertaking day/night migrations in the water column), nektobenthic species (swimming or hovering above the sea bottom) and benthic species (living on or in the sea bottom, mostly corresponding to reptantian decapods). The ecological

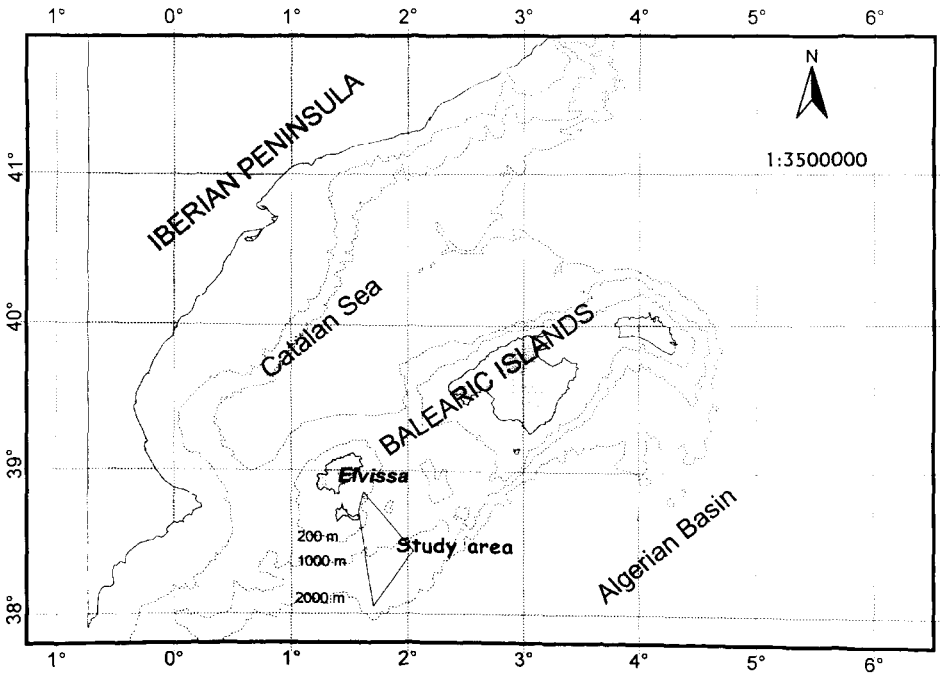

Figure 1. Location of the study area in the western Mediterranean Sea.

Table 1. *Depth distribution of trawl hauls. Cruise Q1, October 1996; cruise Q2, May 1998.*

Depth range (m)	Cruise Q1	Cruise Q2
0–200	0	1
200–400	5	1
400–600	4	2
600–800	3	2
800–1000	4	2
1000–1200	4	2
1200–1400	3	1
1400–1600	6	2
1600–1800	2	1
Total	31	14

descriptors were analysed by season, comparing our two cruises and also, to enlarge the comparative value of the present study, we draw from published results (Cartes & Sardà, 1993; Cartes et al., 1994) and own data from the well-studied, nearby area of the Catalan Sea, standardizing density values per unit area of 10,000 m^2. Comparisons between the Catalan Sea and the south-west Balearic Islands were made at the levels of abundance/biomass for the entire assemblage and for selected (indicator) species, faunal composition, and trophic groups (or guilds).

RESULTS

Environmental features

The thermal and saline stability reported for the deep Mediterranean Sea (Fredj & Laubier, 1985) was confirmed by the CTD casts. Temperature varied between 13.0 and 13.5°C and salinity between 38.3 and 38.5 psu, from 200 m to the bottom at all localities sampled. On the continental slope, the muddy sediment comprises biogenic material (such as the foraminiferan *Orbulina universa*) of planktonic origin (Emelyanov, 1972). This type of sediment is indicative of oligotrophic conditions (Sokolova, 1972). The hydrological data recorded in the October 1996 cruise showed that the water masses were still structured as in the summer period, with a surface temperature of 21°C and a strong gradient between 50 and 100 m depth to ~13.0°C. During May 1998, the surface temperature was 17.5°C and thermal stability was reached at around 200 m depth, with a less pronounced temperature gradient between 0 and 150 m. This hydrological situation is indicative of early spring oceanographic conditions, with an incipient thermocline.

Depth profiles

In both cruises, a general decrease in crustacean decapod abundance (in number) was observed from 200 to 800 m (Figure 2, left), from over 100 ind 10,000 m^{-2} to about 20 ind 10,000 m^{-2}. Their abundance slightly increased again beyond 1400 m, to ~70 ind 10,000 m^{-2}. Decapod abundance (in weight; Figure 2, middle) peaked to 1,000 g 10,000 m^{-2} between 600 and 800 m in both cruises, and decreased progressively afterwards. The megafaunal abundance depth profile (Figure 2, left) was markedly influenced by fish biomass, decreasing very rapidly from 1,000 ind 10,000 m^{-2} at 200 m (shelf break) to about 100 ind 10,000 m^{-2} at 800 m. The megafaunal depth profile stabilized below this depth at ~60 ind 10,000 m^{-2}, with a secondary peak higher than 100 ind 10,000 m^{-2} at 1400–1600 m depth. This secondary peak in abundance resulted from the high abundance of the

Table 2. *Bathyal decapod crustaceans collected during cruises Q1 (October 1996) and Q2 (May 1998) off south-west Balearic Islands (Algerian Basin, western Mediterranean) in 44 valid trawl hauls from ~200–1800 m depth.*

Family	Species	Occurrences	Frequency (%)
Aristeidae	*Aristaeomorpha foliacea*	3	6.82
	Aristeus antennatus	36	81.82
	Gennadas elegans	20	45.45
Penaeidae	*Parapenaeus longirostris*	8	18.18
	Funchalia woodwardii	2	4.55
Solenoceridae	*Solenocera membranacea*	9	20.45
	Hymenopenaeus debilis	1	2.27
Sergestidae	*Sergestes arcticus*	19	43.18
	Sergestes henseni	6	13.64
	Sergia robusta	33	75.00
Stenopodidae	*Richardina fredericii*	5	11.36
Oplophoridae	*Acanthephyra eximia*	23	52.27
	Acanthephyra pelagica	24	54.55
Pasiphaeidae	*Pasiphaea multidentata*	19	43.18
	Pasiphaea sivado	5	11.36
Nematocarcinidae	*Nematocarcinus exilis*	16	36.36
Alpheidae	*Alpheus glaber*	5	11.36
Hippolitidae	*Ligur ensiferus*	1	2.27
Processidae	*Processa canaliculata*	7	15.91
	Processa nouveli	8	18.18
Pandalidae	*Chlorotocus crassicornis*	6	13.64
	Pandalina profunda	4	9.09
	Plesionika acanthonotus	24	54.55
	Plesionika antigai	5	11.36
	Plesionika edwardsi	5	11.36
	Plesionika gigliolii	8	18.18
	Plesionika heterocarpus	12	27.27
	Plesionika martia	13	29.55
	Plesionika narval	2	4.55
Crangonidae	*Philocheras echinulatus*	3	6.82
	Pontocaris lacazei	5	11.36
	Pontophilus norvegicus	12	27.27
Nephropidae	*Nephrops norvegicus*	7	15.91
Axiidae	*Calocaris macandreae*	9	20.45
Polychelidae	*Polycheles typhlops*	24	54.55
	Stereomastis sculpta	17	38.64
Diogenidae	*Dardanus arrosor*	1	2.27
Galatheidae	*Munida intermedia*	4	9.09
	Munida iris	7	15.91
	Munida tenuimana	27	61.36
Homolidae	*Paromola cuvieri*	12	27.27
Majidae	*Dorhynchus thomsoni*	3	6.82
	Macropodia longipes	7	15.91
Geryonidae	*Geryon longipes*	25	56.82
Portunidae	*Macropipus tuberculatus*	8	18.18
	Bathynectes maravigna	1	2.27
Goneplacidae	*Goneplax rhomboides*	4	9.09
Xanthidae	*Monodaeus couchi*	4	9.09

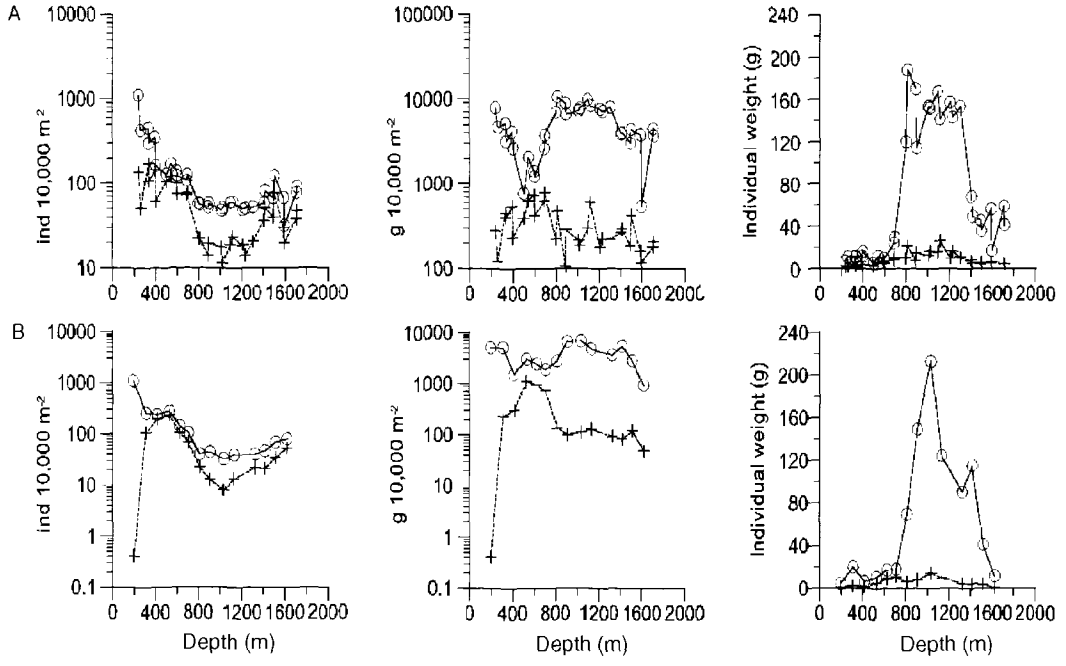

Figure 2. Distribution by depth of the abundance (number and weight 10,000 m^{-2}) and individual weight of decapod crustaceans (crosses and hatched lines) and total megafauna (circles and solid lines). (A) Cruise Q1 (October 1996); (B) cruise Q2 (May 1998).

deep-sea fish *Alepocephalus rostratus* (cf. Moranta et al., 1998). In terms of biomass (Figure 2, middle), the pattern changed completely: megafaunal biomass decreased rapidly from 10,000 g 10,000 m^{-2} at 200 m to 1,000 g 10,000 m^{-2} at 400 m, but increased again rapidly to reach values of ~10,000 g 10,000 m^{-2} between 800 and 1200 m. These high megafaunal densities were comparable to the biomass densities at the shelf break. This secondary peak in megafaunal biomass (at 800–1200 m) has been previously reported for fishes in the Mediterranean (Stefanescu et al., 1992) and can be attributed to high individual weight for fish, and to a lesser extent decapod crustaceans, at these depths (Figure 2, right). It is interesting to note that decapod crustaceans accounted for a large share of the megafaunal abundance at ~400–800 m, for both cruises, totalling 70 and 40% of the megafaunal density in number and weight, respectively. To a lesser extent, decapods again became important, but only in number below 1400 m.

Results of MDS analysis

The results of the multidimensional scaling analysis are shown in Figure 3. Three clearly differentiated groups emerged in the first cruise: a shelf break/upper slope assemblage (SST/US) comprising trawl hauls between 230 and 404 m depth, a shallow middle-slope assemblage (MS1, 544–602 m depth) and a deep middle-slope to lower slope assemblage (MS2, 687–1714 m). In the second cruise, the same three groups were found although at slightly different depths. The SST/US assemblage comprised hauls from 195 to 312 m, the MS1 assemblage from 415 to 529 m and the MS2 assemblage from 626 to 1622 m. The first two dimensions of the MDS were plotted against depth and species richness (Figure 4). The first dimension of the MDS ordination was explained by the depth gradient at least down to 800 m (corresponding approximately to the SST/US and MS1 assemblages), while the second dimension was correlated with species richness, for both surveys.

Community characteristics

The summary features of the decapod assemblages studied are reported in Table 3. In Q1, species richness was higher than in Q2 but this is probably an artefact resulting from the paucity of samples in the second survey and the area-diversity relationship. High abundance (more than 100 ind 10,000 m^{-2}) of crustacean decapods was found on the SST/US and the MS1 assemblages, for both surveys. The abundance then diminished deeper, on the MS2 assemblage (below 600 m), to 36 ind 10,000 m^{-2}. On the other hand, the abundance in weight showed values of more than 500 g 10,000 m^{-2} on the MS1 assemblage, while decapod biomass was half this value both in shallower and deeper waters. No marked seasonal differences were recorded between Q1 (October 1996) and Q2 (May 1998) in abundance or biomass for each assemblage (Table 3). Only in the MS1 assemblage an increase in density (in number as well as biomass) can be detected, from ~100 ind 10,000 m^{-2} in Q1 to over 200 ind 10,000 m^{-2} in Q2, and a slight increase in biomass, from 550 g 10,000 m^{-2} in Q1 to ~700 g 10,000 m^{-2}.

The decapod crustacean assemblages identified by the multivariate analysis can be characterized as follows (Tables 4 & 5): in Q1, the SST/US assemblage comprised a relatively large number of species (S=25), but 95% of the abundance was accounted for by only six species. This assemblage was clearly dominated by the pandalid shrimps of the genus *Plesionika*, chiefly *P. heterocarpus* and *P. edwardsi* (accounting for 85.7% of abundance in number and 74.4% of abundance in weight; Table 4).

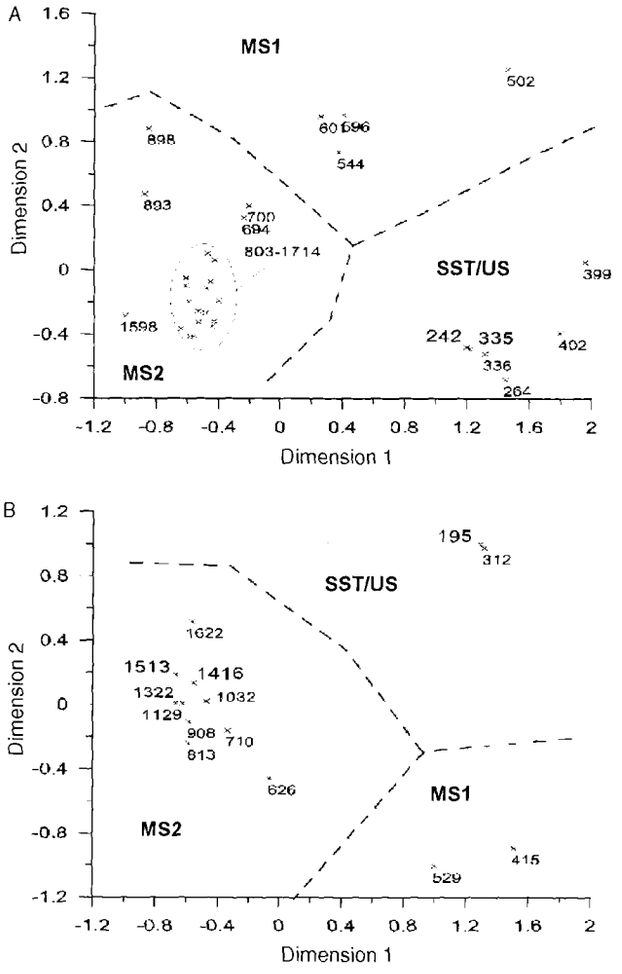

Figure 3. Multidimensional scaling ordination of decapod crustacean samples in (A) cruise Q1 (October 1996, stress of MDS ordination: 0.075); and (B) cruise Q2 (May 1998, stress of MDS ordination: 0.026).

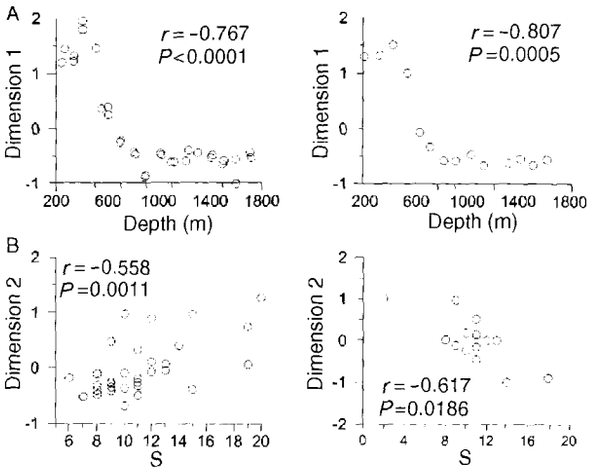

Figure 4. Plot of the first and second dimensions resulting from the MDS ordination vs depth (A) and species richness (B) for cruises Q1 (left) and Q2 (right). Inset in each graph: results of Spearman's rank correlation (r) and associated probability.

Table 3. *Depth distribution, diversity and abundance (mean number and mean weight 10,000 m^{-2} ± SD) of decapod crustacean assemblages classified by MDS.*

Cruise	Assemblage	Depth range (m)	S	Ind	Weight
Q1	SST/US	242–402	25	114.2 ±15.2	340 ±37
	MS1	502–601	28	101.8 ±4.2	550 ±70
	MS2	694–1714	27	32.8 ±5.2	298 ±31
Q2	SST/US	195–312	9	107.8 ±31.2	229 ±49
	MS1	415–529	23	217.3 ±17.3	709 ±59
	MS2	626–1622	23	36.0 ±3.4	249 ±12

In the MS1 assemblage, nektobenthic decapods clearly dominated the species composition (making up 75% of the abundance in number and weight), consisting of pandalids (*P. martia*, *P. acanthonotus* and *P. gigliolii*) and the aristeid *Aristeus antennatus*. In this assemblage, the species richness was higher (S=28) and mesopelagic (*Sergestes arcticus*, *Pasiphaea sivado*) and benthic (*Processa* spp., *Solenocera membranacea*, *Philocheras echinulatus*, *Munida tenuimana*, *Calocaris macandreae*, *Nephrops norvegicus*) species became important. In the MS2 assemblage, species richness was relatively high (S=27) and typical bathyal species became dominant, such as *Acanthephyra* spp. and *Nematocarcinus exilis*, although the species reaching the highest density were the shrimps *A. antennatus* and *Plesionika martia*. It is noteworthy that the deep-sea red crab *Geryon longipes* represented 20.5% of the decapod biomass, although it was not very abundant in number.

In the survey Q2, the dominance of *Plesionika heterocarpus* over the SST/US assemblage was also clear (78% of abundance in number, 47.2% in biomass) and species richness was very low, with only three species accounting for 95% of the abundance. In the MS1 assemblage, the species composition was similar to the composition reported for Q1, but their relative dominance differed. In Q2, the dominant species was *Plesionika gigliolii* (cf. with *P. martia* in Q1) and the mesopelagic *Sergestes arcticus* became very important (21.4% in number although only 1.0% in weight due to its small size). *Aristeus antennatus* diminished in abundance compared with the first survey, while *Nephrops norvegicus* and *P. edwardsii* became more abundant. In the MS2 assemblage, both species composition and relative dominance remained constant between surveys, e.g. *A. antennatus* and *P. martia* were the dominant species in both surveys accounting for most of the abundance, while other typical bathyal species came next in abundance.

Regarding their relative distribution on or above the sea-floor, the crustacean decapods could be characterized as mostly nektobenthic during both cruises in the SST/US assemblage (more than 90% of the abundance in number or weight; Tables 4 & 5). In the MS1 assemblage, nektobenthic species still made up more than 50% of the abundance, but benthic decapods became significant and, to a lesser extent and for cruise Q2 only, mesopelagic decapods also. In the MS2 assemblage, nektobenthic species dominate again, with around 80% of the abundance in each cruise and benthic and mesopelagic species have a small representation. Note, however, that the occasional presence of large-bodied species such as the red crab *Geryon longipes* can contribute significantly to the dominance of benthic species in biomass.

Table 4. *Abundance (number and weight 10,000 m^{-2}, and percentages of total) of decapod crustacean species accounting for more than 95% of abundance in number, for cruise Q1.*

Species/assemblage	Ind	%	Weight	%
A. SST/US				
Plesionika heterocarpus†	76.2	44.9	155	28.3
Plesionika edwardsi†	49.4	29.1	220	40.2
Plesionika gigliolii†	14.7	8.6	26	4.8
Parapenaeus longirostris†	10.8	6.4	105	19.1
Plesionika antigai†	5.3	3.1	6	1.1
Munida iris	2.7	1.6	11	2.1
B. MS1				
Plesionika martia†	43.9	36.3	234	33.9
Plesionika gigliolii†	19.3	15.9	44	6.4
Aristeus antennatus†	15.7	13.0	189	27.4
Plesionika acanthonotus†	10.9	9.0	20	2.9
*Pasiphaea sivado**	4.6	3.8	7.2	1.0
*Sergestes arcticus**	4.5	3.7	1	<1.0
Munida tenuimana	3.5	2.9	24	3.5
Solenocera membranacea	2.6	2.1	6	<1.0
Munida intermedia	2.4	2.0	12	1.7
Calocaris macandreae	2.3	1.9	1	<1.0
Nephrops norvegicus	1.8	1.5	59	8.5
C. MS2				
Aristeus antennatus†	15.2	30.9	113	24.4
Plesionika martia†	11.0	22.4	80	17.4
Acanthephyra eximia†	6.6	13.4	40	8.7
Plesionika acanthonotus†	3.2	6.5	4	<1.0
*Sergia robusta**	2.3	4.6	3	<1.0
Nematocarcinus exilis†	2.1	4.2	2	<1.0
Munida tenuimana	1.6	3.3	4	<1.0
*Gennadas elegans**	1.3	2.6	<1	<1.0
Geryon longipes	0.8	1.9	95	20.5
*Pasiphaea multidentata**	0.9	1.8	3	<1.0
Polycheles typhlops	0.8	1.7	6	1.3
*Acanthephyra pelagica**	0.7	1.5	4	<1.0

*, mesopelagic species; †, nektobenthic species. All other species are benthic.

Table 5. *Abundance (number and weight 10,000 m^{-2}, and percentages of total) of decapod crustacean species accounting for more than 95% of abundance in number, for cruise Q2.*

Species/assemblage	Ind	%	Weight	%
A. SST/US				
Plesionika heterocarpus†	47.8	78.0	74	47.2
Parapenaeus longirostris†	6.8	11.0	53	33.8
Plesionika gigliolii†	2.5	4.1	9	5.4
B. MS1				
Plesionika gigliolii†	66.3	28.4	163	19.8
*Sergestes arcticus**	50.1	21.4	8	1.0
Plesionika martia†	27.8	11.9	57	6.9
Plesionika edwardsii†	23.3	10.0	104	12.7
Plesionika acanthonotus†	16.9	7.2	28	3.5
*Pasiphaea sivado**	12.2	5.2	18	2.2
Nephrops norvegicus	10.2	4.3	232	28.3
Aristeus antennatus†	10.1	4.3	114	13.9
Aristaeomorpha foliacea†	3.2	1.4	14	1.7
Solenocera membranacea	2.8	1.2	6	<1.0
C. MS2				
Plesionika martia†	30.9	44.8	238	45.9
Aristeus antennatus†	15.3	22.2	125	24.2
Acanthephyra eximia†	7.0	10.1	19	3.7
Plesionika acanthonotus†	5.0	7.2	10	1.9
*Sergia robusta**	2.1	3.0	2	<1.0
Nematocarcinus exilis†	2.1	3.0	2	<1.0
Munida tenuimana	0.9	1.3	2	<1.0
Polycheles typhlops	0.9	1.2	7	1.3
*Acanthephyra pelagica**	0.9	1.2	4	<1.0
Geryon longipes	0.5	0.7	37	7.2

*, mesopelagic species; †, nektobenthic species. All other species are benthic.

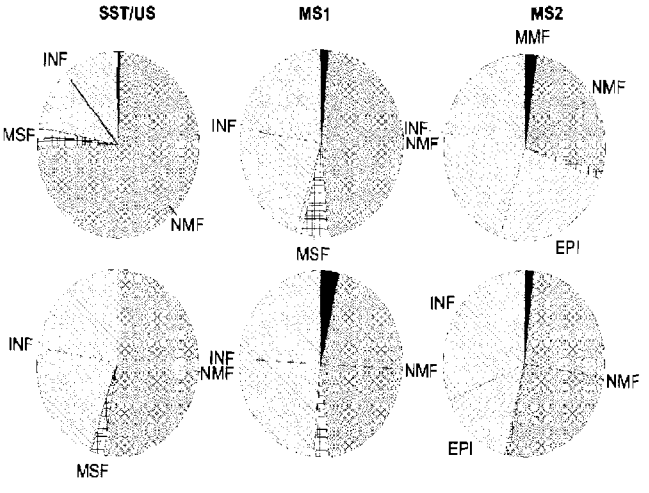

Figure 5. Relative biomass contribution of feeding guilds in each decapod crustacean assemblage for cruises Q1 (top) and Q2 (bottom). SST/US, shelf-slope transition/upper slope assemblage; MS1, middle slope assemblage; MS2, middle slope/lower slope assemblage. INF, infaunal feeders; MSF, macroplankton feeders scavengers; NMF, non-migrator macroplankton feeders; MMF, migrator macroplankton feeders; EPI, epifaunal feeders.

Regarding the food habits of the species studied, non-migrating macroplankton feeders (NMF; Figure 5) made up 50% or more of the decapod crustacean biomass, at all depths sampled, except for the MS2 assemblage in Q1 (October 1996). The contribution of other feeding strategies varied across depths and between cruises: Thus, decapods feeding on infaunal prey (INF; Figure 5) were also important in all assemblages and for the two cruises. On the lowest depth assemblage, MS2, the contribution of epifaunal feeders to the total biomass became very important.

Biogeographical aspects

The expected number of species, ES(n), shows that the MS1 assemblage was the more diverse, followed by the MS2 (Figure 6). The appearance of new, typical deep-sea species contributed to the high diversity of MS2 but it did not suffice to offset the loss of species with depth. Regarding the species composition, the faunistic assemblages reported here represent all species previously reported for the Catalan Sea (excluding *Hymenopenaus debilis*, firstly reported for Mediterranean waters in our samplings; Cartes et al., 2000). Differences do exist, however, as to the contribution in abundance of each species. Fossorial species such as *Nephrops norvegicus*, *Calocaris macandreae*, or *Alpheus glaber* are more abundant in the Catalan Sea by an order of magnitude (cf. Cartes

et al., 1994), probably due to a more suitable substrate for burrowing (terrigenous mud), while pagurid crabs (such as *Pagurus excavatus* or *P. alatus*) were absent in the present samplings. It also is informative to analyse the pattern of first appearances with depth of those species appearing only in the deeper assemblage (MS2), therefore inhabiting the most oligotrophic environment. When the recorded depth of first appearance is drawn across an imaginary west–east axis (Table 6; based on own data and published sources: Mura, 1987; Cartes et al., 1993; Pipitone & Tumbiolo, 1993; Ungaro et al., 1999), most species (*Acanthephyra pelagica*, *A. eximia*, *Nematocarcinus exilis*, *Paromola cuvieri* and *Stereomastis sculpta*) first appear in very deep waters (around or below 1000 m) in the Catalan Sea, while in Sardinia, the Sicilian Channel and the south Adriatic Sea they are first recorded well above 1000 m. The depth of first appearance in the study area, to the south-west Balearic Islands is intermediate between the western and eastern extremes. A visual comparison of surface phytoplankton pigment concentration (PPC) for the Mediterranean Sea (available from NASA's SeaWiFS project image archive) showed that surface PPC for the Catalan Sea was between 0.5 and 1.0 mg m^{-3} at corresponding 200–2000 m depths, while surface PPC was much lower in the south-west Balearic Islands (0.15–0.35 mg m^{-3}) and rarely exceeding 0.30 mg m^{-3} eastwards, towards Sardinia and Sicily. On the other hand, one species did not show this pattern (*Pontophilus norvegicus*), as its first record of appearance was deeper at the easternmost reported locality (Sicilian Channel). It is

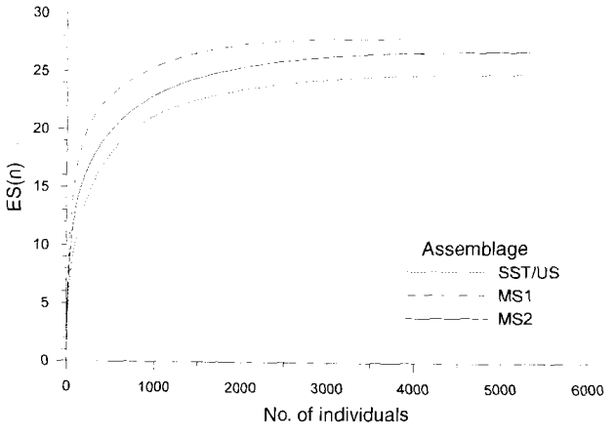

Figure 6. Cumulative species richness in the decapod crustacean assemblages detected in cruise Q1.

Table 6. *Depth of first appearance of deep-water decapod crustaceans at five well-sampled bathyal locations in the Mediterranean Sea, arranged from west to east.*

Species	Catalan Coast[a]	Balearic Islands[b]	Sardinia[c]	Sicilian Channel[d]	South Adriatic[e]
Acanthephyra pelagica	1008	626	480–510	NR	NR
Acanthephyra eximia	969	816	NR	733	NR
Nematocarcinus exilis	1242	1094	NR	NR	NR
Paromola cuvieri	662	626	350–400	267	~400
Pontophilus norvegicus	662	694	480–510	704	NR
Stereomastis sculpta	981	803	NR	NR	NR

NR, not reported; [a], own data and Cartes et al. (1993); [b], this study; [c], Mura (1987); [d], Pipitone & Tumbiolo (1993); [e], Ungaro et al. (1999).

Table 7. *Relative contribution of decapod crustacean feeding guilds at two nearby areas in the western Mediterranean for the shelf-slope transition/upper slope and the middle slope assemblages (abundance index: ind 10,000 m^{-2}). See main text for a definition of feeding guilds. Data for the Catalan Sea recalculated from Cartes et al. (1994).*

	Catalan Sea		South-west Balearic Islands	
	Abundance	%	Abundance	%
1. SST/US				
Deposit feeders	12.6	3.5	1.2	1.0
Infaunal feeders	22.4	6.4	11.0	9.5
Epifaunal feeders	55.6	15.9	0.8	0.7
Macroplankton feeders / scavengers	0.9	0.3	2.0	1.7
Non-migrator macroplankton feeders	61.2	17.5	98.3	85.1
Migrator macroplankton feeders	197.9	56.4	2.2	1.9
2. MS1				
Deposit feeders	27.2	1.7	2.7	1.5
Infaunal feeders	65.3	40.7	23.9	13.5
Epifaunal feeders	15.6	9.7	0.6	0.3
Makroplankton feeders / scavengers	1.3	0.8	4.8	2.7
Non-migrator makroplankton feeders	14.5	9.0	108.3	61.1
Migrator macroplankton feeders	36.7	22.9	37.0	20.9

perhaps remarkable that *Pontophilus norvegicus* is a temperate to subboreal species (for which the Mediterranean Sea is the southernmost limit of its distribution), while the other species are temperate to subtropical.

Comparison with bathyal assemblages from the Catalan Sea

The decapod crustacean biomass for the Catalan Sea (recalculated from Cartes et al., 1994) in autumn (corresponding to Q1) and spring (corresponding to Q2) were 280 g 10,000 m^{-2} and 590 g 10,000 m^{-2} for the SST/US assemblage, and 740 g 10,000 m^{-2} and 690 g 10,000 m^{-2} (MS1), respectively. Comparing these biomass values with our values reported in Table 3, the biomass of crustacean decapods for the two areas is shown to be very similar. However, the relative contribution of each species varies markedly between the two areas: nektobenthic species such as *Plesionika* spp. are more abundant in the south-west Balearic Islands than in the Catalan Sea, while infaunal (burrowing species) such as *Alpheus glaber* and *Calocaris macandreae* are up to ten times more abundant in the Catalan Sea bathyal assemblages (Cartes et al., 1994). These differences are perhaps best illustrated in a comparison of the relative contribution of each feeding guild to the total crustacean decapod abundance (Table 7). Migrator macroplankton-feeders (~mesopelagic decapods) were dominant in the SST/US assemblage in the Catalan Sea (56.4%, Table 7), and very important (22.9%; Table 7) in the MS1 assemblage, while the dominant feeding guild in the south-west Balearic Islands was the non-migrator macroplankton-feeders (mainly pandalid shrimps) at the two depth assemblages (85.1% in SST/US and 61.1% in MS1). Migrator macroplankton played only a secondary role in the south-west Balearic Islands MS1 assemblage (20.9%; Table 7). It is also significant that both the relative and the absolute contributions of those feeding guilds closely related to bottom resources (i.e. epifaunal, infaunal and deposit-feeders) were more abundant in the Catalan Sea in both assemblages (Table 7).

DISCUSSION

It was found that decapod crustaceans are important or even dominant in number at mid-slope depths (400–800 m) when total megafaunal biomass is low. The local importance (in terms of abundance) of decapod crustaceans has been reported for the Catalan Sea (Cartes et al., 1994; Maynou et al., 1996), where they also form a sizeable fraction (40–50%) of the total megafaunal biomass at upper slope and middle slope levels. Our results confirm the importance of decapod crustaceans in Mediterranean deep-sea benthic communities, perhaps because they are more competitive in oligotrophic environments, as opposed to the nearby Atlantic Ocean, where fish always dominate and where echinoderms constitute the major invertebrate group (Haedrich et al., 1980; Lampitt et al., 1986; Markle et al., 1988; Sardà et al., 1994).

The surface productivity regimes differ greatly between the Catalan Sea and the south-west Balearic Islands (yearly-averaged phytoplankton pigment concentrations of 0.5–1.0 and 0.15–0.35 mg m^{-3}, respectively) and this is indirectly reflected in the megafaunal assemblages studied here. On the other hand, advective inputs of organic carbon via submarine canyons are an additional input of food resources in the northern part of the Catalan Sea, (Buscail et al., 1990), and generally, organic C in the sediment surface is lower in interfluves or open sea areas, such as the south-west Balearic Islands. It is proposed that the relative importance of trophic guilds differs between the Catalan Sea and the south-west Balearic Islands, due to the differences in trophic web structure and energy flow. The most remarkable feature in the south-west Balearic Islands is the dominance of the non-migrator macroplankton feeding guild (mainly composed by pandalids of the genus *Plesionika*). The preferential exploitation of food of planktonic origin in an area with lower superficial primary production suggests a diminishing importance of benthos in the trophic webs of our study area, which is also supported by the low densities of deposit-feeders and infaunal-feeders when compared with the Catalan Sea (Table 7), where burrowing species such as *Calocaris macandreae* are an important food resource for crustacean decapods (Cartes & Maynou, 1998).

The decapod crustacean taxocenoses described here were constituted by three clearly differentiated assemblages: a SST/US assemblage, down to 400 m depth, a shallow MS1 assemblage (500–600 m) and a deep MS2 assemblage (below 600 m). These assemblages remained constant between seasons, coinciding with results in the Catalan Sea (Maynou et al., 1996). Depth has been repeatedly reported as the main factor affecting species distribution for benthic species (Abelló et al., 1988; Cartes et al., 1994; Day & Pearcy, 1968; Haedrich et al., 1975, 1980; Wenner & Boesch, 1979) and could be directly related to the first axis in our ordination. Likewise, the species diversity (S) in each assemblage explained the second ordination axis and revealed a species-rich assemblage (MS1) contrasting with a species-poor assemblage (SST/US) and an assemblage with a strong species-richness gradient (MS2), where the disappearance of middle slope species and the appearance of new lower slope species takes place, such as *Acanthephyra pelagica*, *A. eximia*, *Paromola cuvieri*, *Pontophilus norvegicus*, *Dorhynchus thomsoni*, *Stereomastis sculpta*, *Nematocarcinus exilis*, *Bathynectes maravigna* and *Hymenopenaeus debilis*. Among macrofauna, maximum S has also been reported for mid-bathyal depths in a variety of taxa (e.g. gastropods; Rex, 1973). This phenomenon typically generates a bell-shaped response of species richness along depth or other environmentally mediated gradients (Gage & Tyler, 1991). The intermediate disturbance hypothesis is often put forward to explain this pattern, as a mechanism combining varying-frequency disturbances and production/competition dynamics. The high disturbance of the continental shelf could explain the low species richness found in the SST/US assemblage, while the low species richness on the lower slope could be best explained by a decrease in food supply enhancing competitive exclusion and species exclusion (Gage & Tyler, 1991). In our study area, the higher S at mid-bathyal depths coincided with an increase in the dominance by decapods, probably implying low trophic pressure or diminished competition with fish.

Boundaries between assemblages (or communities) for megafauna vary among locations (Day & Pearcy, 1968; Haedrich et al., 1975; Wenner & Boesch, 1979; Haedrich et al., 1980; Markle et al., 1988; Cartes & Sardà, 1993) and perhaps may be meaningfully compared only within regions (Hecker, 1990). In the Catalan Sea, Abelló et al. (1988) and Cartes et al. (1994) reported the boundary between the decapod crustacean assemblages corresponding to our SST/US/MS1 at around 400–500 m, which is close to the boundary reported here (around 400 m), while the boundary between the assemblages corresponding to MS1 and MS2 would be located below 600 m in the Catalan Sea (Cartes & Sardà, 1993). However, this study failed to detect an important faunal discontinuity reported at ~1200 m in the Catalan Sea (Cartes & Sardà, 1992; Cartes, 1993) and in other Atlantic areas (Wenner & Boesch, 1979; Hecker, 1990). This is probably related to the shallower depths occupied by the characteristic deep-water species (*Acanthephyra* spp., *Nematocarcinus exilis* and *Stereomastis sculpta*) in the southwest Balearic Islands than in the Catalan Sea (see also below). Another aspect pointed out by Cartes & Sardà (1993) is the variability of boundary definitions among taxa. Comparing our results with a study on zonation of fish assemblages by Moranta et al. (1998), it can be seen that demersal fish in the northern Algerian Basin are mainly delimited by the 800 m depth contour, with further subassemblages in each group at depths differing from ours for decapod crustaceans. The different response shown by each taxon may be attributed to the distinct trophic levels occupied by different taxa: broadly speaking, fish and the various groups of invertebrates may exploit different fractions of the food resource or food spectrum and should show different response patterns to a depth gradient.

Although distinct assemblages can be discerned when analysing trawl haul data along a depth gradient by multivariate analysis, we agree with Haedrich & Merrett (1990) in that their significance is strictly local and related to the taxocenosis studied. First, one does not uncover consistent or recurring boundaries when analysing invertebrate or vertebrate assemblages (compare Cartes & Sardà (1993) with Stefanescu et al. (1992); Moranta et al. (1998) with the present work), i.e. the faunal discontinuities are not always sharp and they almost never coincide across animal taxa or geographic regions. The uniqueness of assemblage structure can best be explained by the combination of local environmental factors and the biogeographical history in the region considered. Thus although the actual species forming a local taxonomic assemblage is drawn (historically) from a regional pool of available species and linked by more or less well-defined ecological relationships, their observed abundances and relative proportions are best explained by the contemporary environmental conditions prevailing in the study area (Rickleffs, 1987). Clearly, the deep-water Mediterranean decapod crustaceans show the highest affinity with the immediate eastern Atlantic decapod fauna (Cartes, 1993), but it is poorer due to historical factors such as the Messinian salinity crisis (Pérès, 1985; Bouchet & Taviani, 1992), the geographical barrier represented by the Gibraltar Strait and the current oligotrophic environment of the Mediterranean Sea.

Within an environmentally homogeneous area such as the deep Mediterranean, the composition of crustacean decapod assemblages scarcely varies (Abelló et al., 1988; Cartes et al., 1994; Pipitone & Tumbiolo, 1993; Ungaro et al., 1999), but the depth at which typically bathyal species appear does vary. We found a trend of shallower first appearance of bathyal decapods towards the eastern Mediterranean, coinciding with increased oligotrophy (Table 6). The increased oligotrophy reported for the eastern Mediterranean is directly related to low surface primary productivity (phytoplankton pigment concentration differs almost by an order of magnitude between the west and the eastern Mediterranean). Other examples can be found linking primary productivity regimes and the structure of deep-sea macrobenthic and megabenthic communities at mid and large spatial scales (Watts et al., 1992).

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