

ORIGINAL ARTICLE

Community structure of bathyal decapod crustaceans off South-Eastern Sardinian deep-waters (Central-Western Mediterranean)

Maria Cristina Follesa, Cristina Porcu, Alice Gastoni, Antonello Mulas, Andrea Sabatini & Angelo Cau

Department of Animal Biology and Ecology, University of Cagliari, Cagliari, Italy

Keywords

Deep-sea; decapod crustaceans; faunal zonation; Sardinian deep-waters; Mediterranean.

Correspondence

Maria Cristina Follesa, Department of Animal Biology and Ecology, University of Cagliari, Via T. Fiorelli n.1, 09126 Cagliari, Italy. E-mail: follesac@unica.it

Conflicts of interest

The authors declare no conflicts of interest.

doi:10.1111/j.1439-0485.2009.00323.x

Abstract

Community structure and faunal composition of bathyal decapod crustaceans off South-Eastern Sardinian deep-waters (Central-Western Mediterranean) were investigated. Samples were collected during 32 hauls between 793 and 1598 m in depth over the 2003–2007 period. A total of 1900 decapod specimens belonging to 23 species were collected. Multivariate analysis revealed the occurrence of three faunistic assemblages related to depth: (i) an upper slope community at depths of 793–1002 m; (ii) a middle slope community at depths of 1007–1212 m and (iii) a lower slope community at depths greater 1420 m. In the upper and middle slopes the benthic (*Polycheles typhlops*) and epibenthic–endobenthic feeders (mainly *Aristeus antennatus* and *Geryon longipes*), which eat infaunal prey, were dominant, followed by the macroplankton–epibenthic feeders such as *AcanthePHYRA eximia* and *Plesionika acanthonotus*. In the deepest stratum, the most remarkable feature was the prevalence of macroplankton–epibenthic feeders (*A. eximia* and *P. acanthonotus*). A small percentage of the benthic deep-sea lobster *Polycheles sculptus* was also present. The biomass presented higher values in the middle slope and declined strongly in the lower slope. There was no general pattern of mean individual weight/size *versus* depth among decapods, and the changes seemed to be species-specific with different trends.

Problem

The study of the distribution of species along environmental gradients has traditionally been important for characterising the organisation of animal communities in aquatic systems (Wenner & Boesch 1979). In particular, in deep-sea marine environments, species and communities often change with increasing depth rather than along horizontal gradients (Gage & Tyler 1991; Cartes *et al.* 2004, 2007a), suggesting the idea of depth bands of high faunal homogeneity separated by boundaries of faunal renewal. Moreover, the structure of megafaunal assemblages in the continental slope is largely determined by a combination of both abiotic (the structure and type of the bottom and oceanographic conditions) and biotic (resource availability and food web structure) factors (Moranta *et al.* 1998, 2008), which may also play a funda-

mental role in the local zonation pattern (Maynou & Cartes 2000; Carbonell *et al.* 2003).

In this context, bathyal decapod crustaceans represent, after the ichthyofauna, a dominant faunal component in the benthic communities of the Mediterranean Sea (Abelló & Valladares 1988; Cartes & Sardà 1992; Sardà *et al.* 1994; Maynou & Cartes 2000; Company *et al.* 2004) and are a key taxon linking lower and higher trophic levels (Wenner & Boesch 1979; Cartes 1998). Their high abundance in the Mediterranean in comparison with other oceans, in which the echinoderms predominate among invertebrates (Tyler & Zibrowius 1992; Sardà *et al.* 1994), is probably due to the oligotrophic nature of Mediterranean (Company *et al.* 2004).

Community assemblages, distribution and abundance of decapod crustacean fauna have been described in detail in the Western Mediterranean basin (Abelló *et al.* 1988,

2002; Cartes & Sardà 1993; Mura & Cau 1994; Maynou *et al.* 1996; Maynou & Cartes 2000; Moranta *et al.* 2000; Cartes *et al.* 2001; Morales-Nin *et al.* 2003; Company *et al.* 2004; Fanelli *et al.* 2007; García Muñoz *et al.* 2008) and in the Central and Eastern Mediterranean (Pipitone & Tumbiolo 1993; Ungaro *et al.* 1999, 2005; Kallianotis *et al.* 2000; Colloca *et al.* 2003; Company *et al.* 2004; Galil 2004; Politou *et al.* 2005).

In Sardinian waters (Central-Western Mediterranean), the knowledge available on the deep-sea decapod crustaceans concerns the bio-ecology (mainly reproduction and trophism) of a few deep-sea species (Mura *et al.* 1993; Follesa *et al.* 2007; Cabiddu *et al.* 2008). In fact, the studies in this area are limited to the epibathyal and the mesobathyal levels (mostly at depths of less than 750 m) generally subject to intense trawl fishing. Mura (1987) and Mura & Cau (1992, 1994) described the faunistic composition and bathymetric distribution of the decapod crustaceans present in the lower part (down to 1050 m) of the mesobathyal zone of the Sardinian Channel.

The object of this paper was to update the data on bathyal decapod crustaceans (faunal composition, bathymetric distribution, zonation, abundance, biomass and length frequency distribution) in Sardinian waters (Central-Western Mediterranean). Despite the limitations of bathyal sampling, this study represents the first attempt to identify the deep-sea crustacean assemblages down to 1000 m and to improve knowledge of this area, considered the link between the Western and Eastern Mediterranean (Hopkins 1988).

Methods

The data analysed in the present work came from 32 hauls carried out during experimental trawl survey cruises intended to study the bottom-living community in the continental slope. Sampling was conducted on compact mud bottoms off South-Eastern Sardinian deep-waters (Sardinian Channel, Central-Western Mediterranean) (Fig. 1). All hauls were performed at main depths of 793–1598 m over the 2003–2007 period.

On board, trawl data (date, position and duration) were recorded (Table 1). The duration of each haul (bottom time) varied between 64 and 164 min. The towing speed was about 2.2 knots for all hauls. The otter trawl used was equipped with a 20-mm stretch mesh size cod end. Gear selectivity was assumed to be constant because the same fishing gear for each trawl was used.

Usually, the monitoring of crustacean assemblages is confined to the economically important depths (<750 m). For this reason, due to the lack of long-time series of data on deep-sea assemblages, catches from

different years and seasons have been pooled in our analysis.

For each haul, crustaceans were sorted by species and abundance (N) and biomass (g) data were noted and standardised to 1 h of haul ($N \cdot h^{-1}$). In the laboratory, the carapace length (CL, in mm, from the posterior margin of the eye socket to the posterior end of the carapace), individual weight (g) and sex of each species were also determined. Moreover, the crustaceans were classified as mesopelagic species, nektobenthic species or benthic species on the basis of their relative location in the water column (Maynou & Cartes 2000).

Standardised abundance data of decapod crustaceans were pooled in a matrix of species abundance with the PRIMER (v6) package. Cluster analysis was performed using the Bray–Curtis similarity index and group linkage was used for the dendrogram (Bray & Curtis 1957; Field *et al.* 1982). Prior to analysis, standardisation and fourth-root transformation were applied.

Analysis of similitude (ANOSIM) was used to test the significance of species assemblages between trawl surveys (Clarke 1993) and similarity percentage (SIMPER) was also applied to detect bathymetric differences.

The ecological parameters such as mean abundance ($N \cdot h^{-1}$) and mean biomass ($g \cdot h^{-1}$), and the measures of species diversity, such as species richness (S) (DIVERSE routine), Shannon–Wiener index (H') (Shannon & Weaver 1949) and evenness (J') (Pielou 1977) were calculated for all hauls of the main groups obtained by prior classification.

Between-assemblage differences in species richness, diversity indexes, abundance and biomass spectra were tested using repeated ANOVA measures (Zar 1999). Each haul was considered an observation and the data of abundance and biomass were normalized [$\ln(x + 1)$] to adjust residuals to normality.

A bubble scatterplot was applied to the individual mean weight (g) of the most frequent species to detect the abundance tendencies with depth.

To show the bathymetric distribution of the main species, the overall length frequency distribution (2 mm size class) by sex for each depth interval was determined.

Results

During the trawl surveys, a total of 1900 individuals (total weight 11,919 g), subdivided in 23 species of bathyal decapod crustaceans, were collected and are listed in Table 2. Within the investigated depth range, *Plesionika acanthonotus* was present in all hauls and *Polycheles typhlops*, *Sergia robusta* (97% frequency of occurrence) and *Aristeus antennatus* (91% frequency of occurrence) were present at nearly all stations. A high frequency of occur-

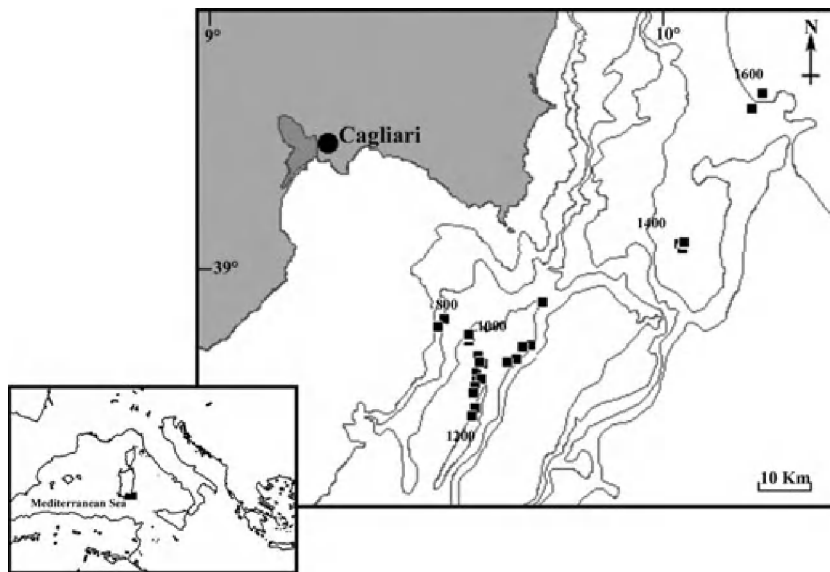


Fig. 1. Map of the study area and positions of trawl stations (black squares) off the South-Eastern Sardinian deep-waters (Central-Western Mediterranean).

haul code	date	mean depth (meters)	starting position		haul duration (minutes)
			latitude (N)	longitude (E)	
1	16/06/2003	1007	38°53'94"	9°27'04"	106
2	16/06/2003	991	38°50'99"	9°31'93"	103
3	10/11/2003	996	38°57'39"	9°37'06"	112
4	10/11/2003	995	38°52'65"	9°34'07"	108
5	11/11/2003	793	38°54'83"	9°22'58"	90
6	11/11/2003	1002	38°45'36"	9°27'22"	97
7	12/11/2003	1035	38°53'95"	9°26'79"	90
8	12/11/2003	842	38°55'58"	9°23'45"	65
9	17/01/2005	961	38°52'75"	9°34'99"	73
10	18/01/2005	1166	38°49'92"	9°27'78"	64
11	23/05/2005	1033	38°53'79"	9°26'75"	74
12	27/05/2005	1145	38°51'02"	9°28'21"	76
13	27/05/2005	1188	38°46'16"	9°27'60"	79
14	19/01/2006	1147	38°51'34"	9°28'25"	111
15	19/01/2006	974	38°51'34"	9°33'16"	109
16	15/05/2006	1020	38°53'35"	9°26'81"	146
17	15/05/2006	1163	38°50'82"	9°28'61"	142
18	15/05/2006	1099	38°49'10"	9°27'74"	126
19	16/05/2006	1037	38°53'79"	9°26'88"	164
20	16/05/2006	1086	38°48'39"	9°27'62"	131
21	18/07/2006	1420	39°03'27"	9°56'04"	135
22	21/11/2006	1212	38°47'84"	9°27'45"	96
23	21/11/2006	1421	39°03'49"	9°56'07"	103
24	21/11/2006	1598	39°19'37"	10°06'93"	89
25	06/03/2007	1133	38°49'74"	9°28'02"	107
26	06/03/2007	1151	38°48'45"	9°27'47"	154
27	07/03/2007	1420	39°03'38"	9°55'52"	138
28	24/04/2007	1044	38°53'74"	9°26'95"	111
29	24/04/2007	1115	38°51'66"	9°27'93"	130
30	24/04/2007	1105	38°49'31"	9°28'48"	88
31	03/09/2007	1573	39°17'82"	10°05'53"	105
32	03/09/2007	1421	39°02'90"	9°55'88"	125

Table 1. Characteristics of hauls (date, mean depth, position, time period of hauls) carried out off South-Eastern Sardinian deep-waters (Central-Western Mediterranean).

rence (%F > 50) of *AcanthePHYra eximia*, *AcanthePHYra pelagica*, *Ponthophilus norvegicus* and *Geryon longipes* was observed (Table 2). In terms of total abundance, the predominant species were found to be *A. antennatus* (23.6%) and *P. typhlops* (18.4%). In terms of biomass, *A. antennatus* (31.6%), and *G. longipes* (21.05%) were the species with the highest percentage of contribution (Table 2).

The similarity dendrograms of the trawls revealed the presence of three main groups (Fig. 2), which can be clearly identified along the bathymetric gradient. The first group consisted of the deepest stations covering a depth range of 1420–1598 m (six hauls, mean depth 1475.5, SD 85.57) (lower slope) (Fig. 2). A second group was made up of stations investigated at 793–1002 m depth (eight

Table 2. Bathyal decapod crustacean species collected off South-Eastern Sardinian deep-waters (Central-Western Mediterranean) between 793 and 1598 m with their bathymetric range, occurrence's frequency (%F), percentage of abundance (%Abundance) and biomass (%Biomass).

species	depth range (m)	%F	%abundance	%biomass
<i>suborder Dendrobranchiata</i>				
superfamily Penaeoidea				
family Aristeidae				
<i>Aristaeomorpha foliacea</i> (Risso, 1827)	793–1037	3	0.1	0.57
<i>Aristeus antennatus</i> (Risso, 1816)	793–1598	91	23.6	31.6
<i>Gennadas elegans</i> (S. I. Smith, 1882)	1163–1421	13	0.3	0.01
family Penaeidae				
<i>Parapenaeus longirostris</i> (H. Lucas, 1846)	793	3	0.2	0.88
superfamily Sergestoidea				
family Sergestidae				
<i>Sergestes arcticus</i> Krøyer, 1855	842–1188	19	0.3	0.01
<i>Sergia robusta</i> (S.I. Smith, 1882)	793–1598	97	11.2	2.8
<i>suborder Pleocyemata</i>				
infraorder Caridea				
family Oplophoridae				
<i>AcanthePHYra eximia</i> S. I. Smith, 1884	793–1598	88	12.3	16.93
<i>AcanthePHYra pelagica</i> (Risso, 1816)	996–1573	59	3.4	3.03
family Pasipheidae				
<i>Pasiphaea multidentata</i> Esmark, 1866	793–1573	44	1.4	1.48
family Pandalidae				
<i>Plesionika acanthonotus</i> (S. I. Smith, 1882)	793–1598	100	13.2	1.6
<i>Plesionika martia</i> (A. Milne-Edwards, 1883)	793	3	0.1	0.03
family Crangonidae				
<i>Pontocaris lacazei</i> (Gourret, 1887)	793	3	0.1	0
<i>Ponthophilus norvegicus</i> (M. Sars, 1861)	1020–1598	63	3.5	0.25
infraorder Thalassinidea				
family Axiidae				
<i>Calocaris macandreae</i> Bell, 1853	1421	3	0.1	0.01
infraorder Palinura				
family Polychelidae				
<i>Polycheles sculptus</i> S. I. Smith, 1880	1037–1598	50	2.6	1.08
<i>Polycheles typhlops</i> Heller, 1862	793–1598	97	18.4	13.2
infraorder Anomura				
family Paguridae				
<i>Pagurus alatus</i> (Fabricius, 1775)	793	3	0.1	0.03
family Galatheididae				
<i>Munida tenuimana</i> G. O. Sars, 1871	793–1598	34	2.4	0.42
infraorder Brachyura				
family Xanthidae				
<i>Monodaeus couchii</i> (Couch, 1851)	793	3	0.1	0.02
family Homolidae				
<i>Paromola cuvieri</i> (Risso, 1816)	974–1212	38	1	4.54
family Geryonidae				
<i>Geryon longipes</i> A. Milne Edwards, 1881	842–1421	69	5.6	21.05
family Portunidae				
<i>Bathynectes maravigna</i> (Prestandrea, 1839)	793–1105	6	0.2	0.32
<i>Macropipus tuberculatus</i> (Roux, 1830)	995	3	0.1	0.1

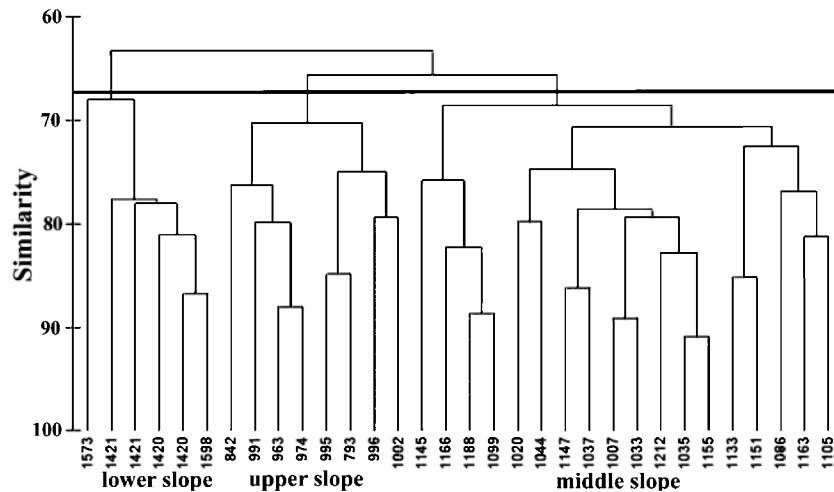


Fig. 2. Dendrograms of hauls using group-average clustering from Bray-Curtis similarity by depth strata in terms of standardised abundance ($N \cdot h^{-1}$) of total catches off South-Eastern Sardinian deep-waters (Central-Western Mediterranean). Mean depth of each sample is given. The upper line indicates groups at the 66% level of similarity.

hauls, mean depth 944.5, SD 80.48) (upper slope). The third aggregation consisted of six hauls (mean depth 1107, SD 64.06) carried out at middle depths of 1007–1212 m (middle slope).

The pair-wise test comparisons (ANOSIM) showed, in terms of abundance, a low level of overlap between the hauls ($R = 0.534$, $P < 0.01$).

The results of the SIMPER routine showed a high percentage of similarity for the assemblages identified by clustering (Table 3). In the upper slope (793 and 1002 m), the species which took part in the assemblage appeared to be *P. typhlops*, *A. antennatus* and *S. robusta* (59.06%). *Aristeus antennatus*, *P. typhlops*, *P. acanthonotus* and *S. robusta* contributed 58.74% of the middle slope assemblage (1007–1212 m). The most typical species of the deepest bottoms (1420–1598 m) were *A. eximia* (19.10%), *P. acanthonotus* (14.83%) and *A. antennatus* (14.13%). Moreover, in the lower slope, *Polycheles sculptus* was a common species (13.65%).

Mean values of the ecological parameters of each assemblage are reported in Table 4. Significant differences in species richness (S) were observed ($F_{11,86}$; $P < 0.05$).

The highest value (an average of 2.47 species) was found on the middle slope, followed by the lower (2.32 species) and the upper slope (1.79 species). The highest diversity (H') was obtained for the lower ($H' = 1.89$, $J' = 0.86$) and the middle slope ($H' = 1.8$, $J' = 0.81$), with significant differences between assemblages ($F_{5,25}$; $P < 0.05$).

The mean values of abundance showed an increase with depth (24, 36, 37 individuals per hour, respectively), with significant differences between assemblages ($F_{3,43}$; $P < 0.05$), whereas no significant difference ($F_{1,95}$; $P > 0.05$) was observed between the mean biomass that showed a maximum value in the middle stratum.

The relative abundance analysis of the species caught in each identified group (Fig. 3A,C,E) generally highlighted a species' dominance similar to that obtained from the SIMPER analysis (Table 3). Moreover, in terms of relative biomass, *A. antennatus*, *P. typhlops* and *G. longipes* were the most abundant species in the upper and middle slopes (Fig. 3B and D). In the deepest strata, *A. eximia* and *A. antennatus* were the predominant species (Fig. 3F).

Regarding their relative depth distribution, in the shallowest stations the crustacean decapods could be charac-

Table 3. Results of the SIMPER routine to analyse the percentage contribution of typifying species (over 7%) to within-group similarity resulting from cluster analysis for crustacean samples during trawl surveys off the South-Eastern Sardinian deep-waters (Central-Western Mediterranean).

793–1002 m		1007–1212 m		1420–1598 m	
average similarity: 73.74		average similarity: 72.41		average similarity: 75.59	
species	contrib%	species	contrib%	species	contrib%
<i>Polycheles typhlops</i>	21.35	<i>Aristeus antennatus</i>	16.42	<i>Acantheephyra eximia</i>	19.10
<i>A. antennatus</i>	18.93	<i>P. typhlops</i>	16.16	<i>Plesionika acanthonotus</i>	14.83
<i>Sergia robusta</i>	18.78	<i>P. acanthonotus</i>	14.41	<i>A. antennatus</i>	14.13
<i>A. eximia</i>	17.44	<i>S. robusta</i>	11.75	<i>Polycheles sculptus</i>	13.80
<i>P. acanthonotus</i>	15.07	<i>Geryon longipes</i>	8.97	<i>S. robusta</i>	13.65
–	–	<i>A. eximia</i>	8.03	<i>Ponthophilus norvegicus</i>	9.11
–	–	<i>Acantheephyra pelagica</i>	7.88	<i>Munida tenuimana</i>	7.93
–	–	<i>P. norvegicus</i>	7.83	–	–

Table 4. Some ecological parameters (mean and deviation standard) in the three groups resulting for the cluster analysis.

ecological parameters	upper slope	middle slope	lower slope
	793–1002 m	1007–1212 m	1420–1598 m
mean abundance (N·h ⁻¹)	24 ± 10.78	36 ± 13.31	37 ± 12.03
mean biomass (g·h ⁻¹)	205.48 ± 141.38	224.25 ± 106.27	121.81 ± 42.80
number of species	11	17	13
mean species richness (S)	1.79 ± 0.28	2.47 ± 0.34	2.32 ± 0.32
diversity (H')	1.56 ± 0.26	1.81 ± 0.20	1.89 ± 0.20
evenness (J')	0.83 ± 0.11	0.81 ± 0.08	0.86 ± 0.03

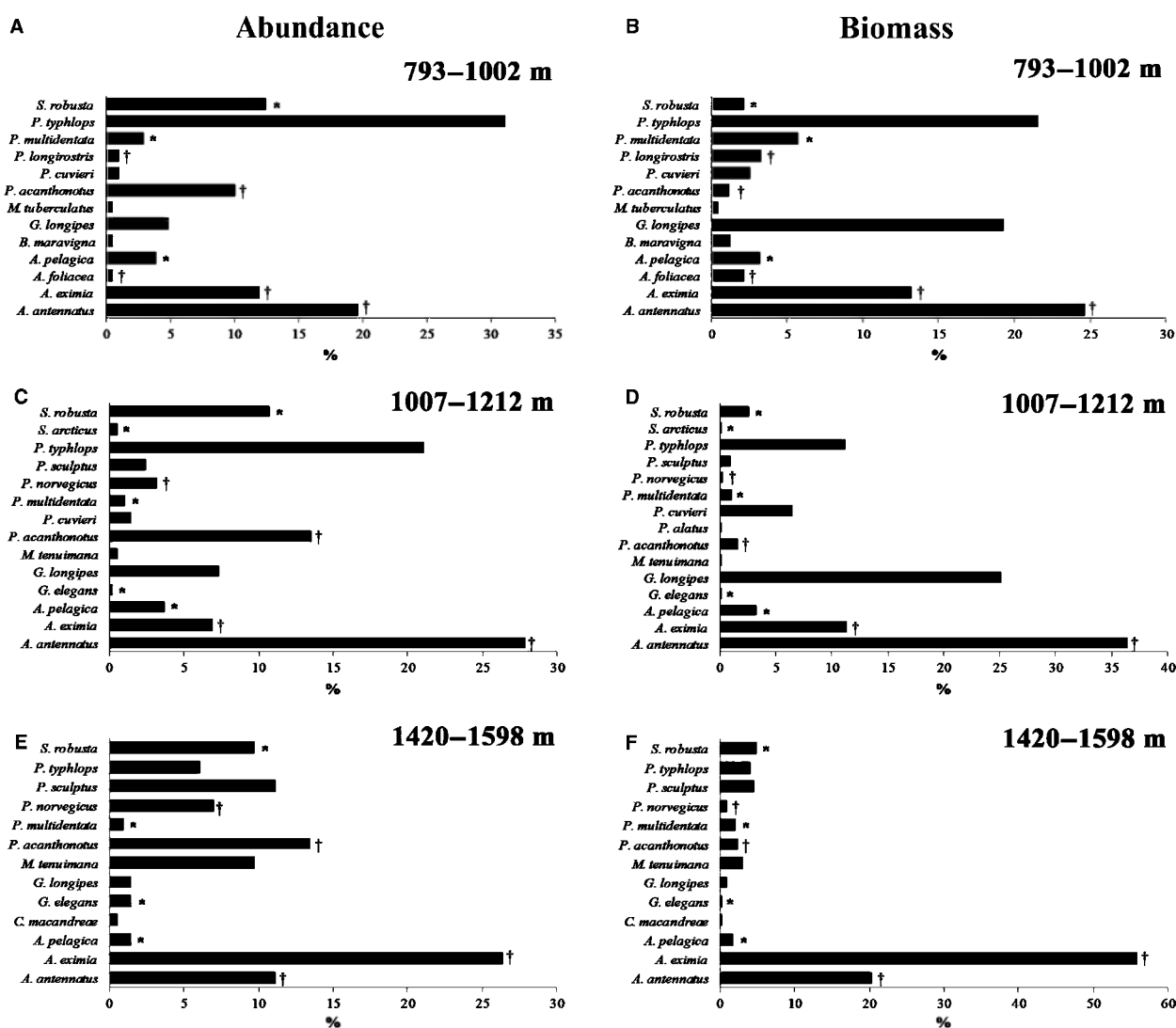


Fig. 3. Relative abundance and biomass of the most abundant deep-sea decapods collected off South-Eastern Sardinian deep-waters (Central-Western Mediterranean). *Mesopelagic species; †nektobenthic species; all other species are benthic.

terised mainly by nektobenthic and benthic species (43% and 38% in number and 44% and 45% in weight, respectively) (Fig. 5). In the middle slope, nektobenthic species again dominated both in weight and number, while the benthic species were also present with a high percentage in biomass (44%), probably due to the occasional presence of large-bodied species such as the brachyuran crab *G. longipes*. The deepest range was inhabited by nektobenthic species (principally *A. eximia* and *A. antennatus*) but also by benthic decapods (29%), which became significant in number probably as consequence of the high abundance of the small deep-sea lobster *P. sculptus*.

The bubble plot for the bathyal decapod crustaceans showed different mean weight tendencies with depth depending on the species (Fig. 4). *Aristeus antennatus*, *A. eximia*, *A. pelagica*, *P. typhlops* and *G. longipes* showed a negative correlation between individual mean weight and depth, probably due to the recruitment of small individuals in the deepest waters. Otherwise, *Munida tenuimana* and *S. robusta* presented a 'bigger-deeper' trend, with mean weight increasing with depth. On the lower slope, the deepest species *P. sculptus* and *P. norvegicus*, which were captured for the first time below 1000 m, were characterized by small to medium sized individuals.

Figure 5 shows the size frequencies and sex distribution by depth interval of the main bathyal decapod species. Juveniles of *A. antennatus* (CL < 20 mm; Sardà *et al.* 2004) were most representative in the deepest part of range (below 1420 m), with a high percentage of females; between 793 and 1212 m (middle slope), the adults appeared well represented, with an elevated proportion of males. On the upper and middle slopes, *A. eximia* showed a range in size of 20–38 mm CL, with males mainly represented only by the smallest size class, whereas on the lower slope, juveniles (CL 14–18 mm) were also present. *Plesionika acanthonotus* showed a range in size of between 4 and 22 mm CL and a sex-ratio in favour of females increasing with depth. An inverse sex-ratio was observed in *S. robusta* (range 8–26 mm CL). It was difficult to find a clear pattern for the population structure of *P. norvegicus* because the individuals were present exclusively below 1000 m and were relatively scarce in all depth intervals.

Discussion

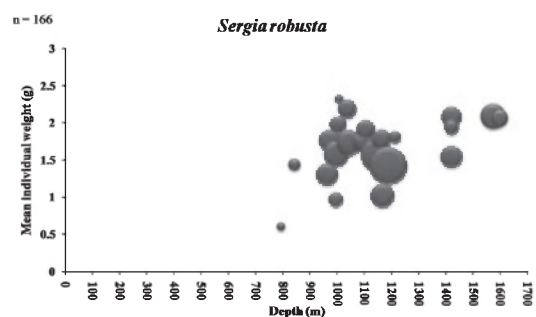
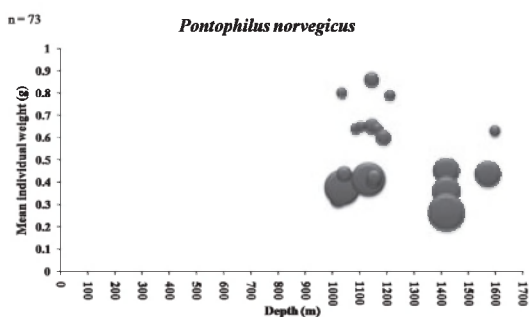
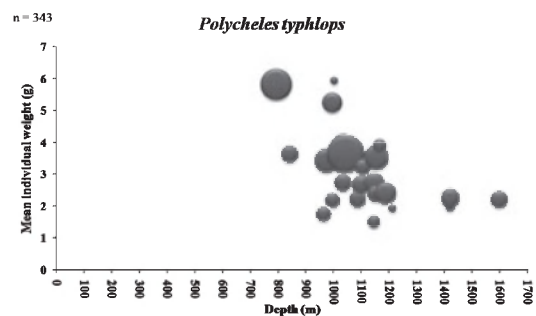
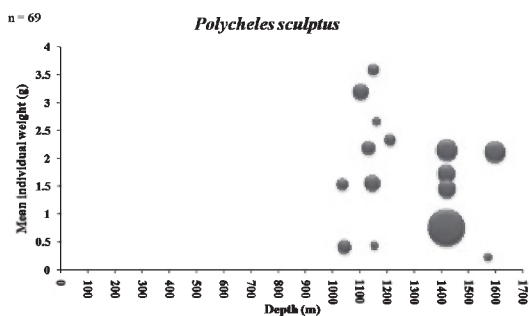
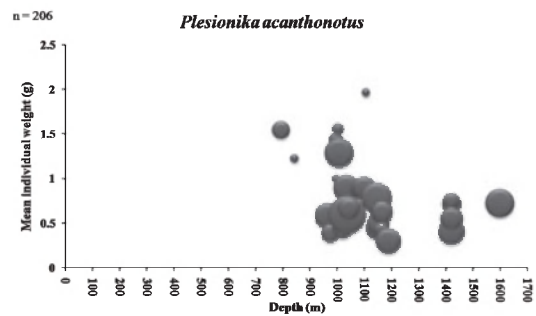
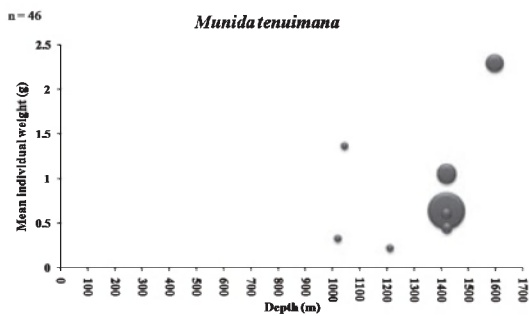
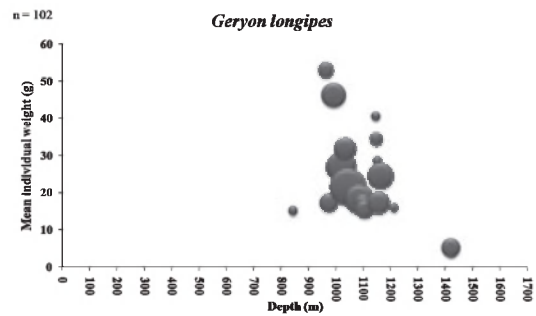
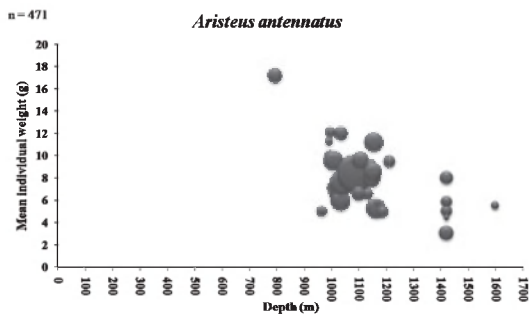
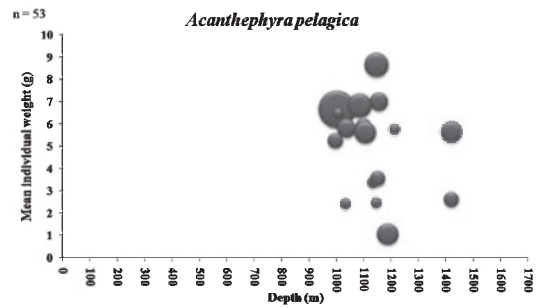
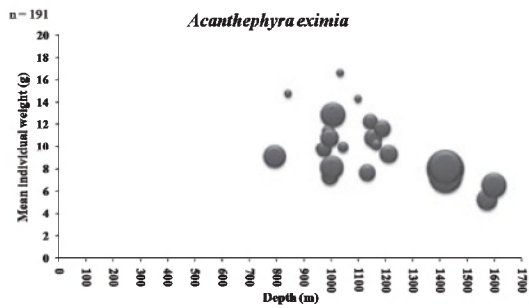
Our results confirm the importance of decapod crustaceans in Mediterranean deep-sea benthic communities because they may be more competitive than other invertebrate groups, in contrast to more productive oceans like the Atlantic (Tyler & Zibrowius 1992).

Depth represents the main structuring factor in many areas of the Mediterranean Sea (Abelló *et al.* 1988, 2002; Cartes & Sardà 1993; Ungaro *et al.* 1999; Kallianotis *et al.*

2000; Morales-Nin *et al.* 2003; Gaertner *et al.* 2005; Masuti & Reñones 2005; Abad *et al.* 2007; Fanelli *et al.* 2007), although it has often been argued that marine organisms may respond to a combination of depth-related factors such as food availability, light, temperature and pressure (Cartes *et al.* 2004). Trophic issues have often been used to explain community organisation at different spatial and temporal scales (Gage & Tyler 1991) and seasonally averaged phytoplankton pigment concentration has also been utilised to describe the organic vertical flux and food supply for demersal megafauna (Rex *et al.* 1993).

The bathyal decapod crustacean community of the South-Eastern Sardinian deep-waters (Central-Western Mediterranean) presented a clear zonation effect, with a series of well-defined bathymetric boundaries that seemed to be connected to depth-related factors. Three faunistic assemblages along the continental slope were identified by means of cluster analysis. The lowest values of species richness (S) were found in the upper and lower slope, which could be explained best by a decrease in food supply enhancing competitive exclusion of the species; the highest mean value of species richness was found in the mid-bathyal interval (1002–1212 m), probably implying low trophic pressure or diminished competition with fish (Maynou & Cartes 2000). This phenomenon, also reported in various taxa among macrofauna (*e.g.* gastropods; Rex 1973), generates a typical bell-shaped response along depth or other environmentally mediated gradients (Gage & Tyler 1991).

Following the feeding classification of Cartes (1998) for the main bathyal decapod species in the Catalan Sea, our study area showed in the upper and middle slope (between 793 and 1212 m), a prevalence of benthic (*P. typhlops*) and epibenthic–endobenthic feeders (mainly *A. antennatus* and *G. longipes*) that eat infaunal prey, with a low percentage of macroplankton–epibenthic feeders such as *A. eximia* and *P. acanthonotus*. In contrast, in the deepest stratum [the main boundary similar to the lower subzone defined by Pérès (1985), Cartes & Sardà (1993) and Stefanescu *et al.* (1993)] the most remarkable feature was the prevalence of macroplankton–epibenthic feeders (*A. eximia* and *P. acanthonotus*), followed by the benthic deep-sea lobster *P. sculptus*. A similar distribution of feeders in the continental slope was found by Maynou & Cartes (2000) off the South-West Balearic Islands (Western Mediterranean), where the distance from the mainland and the absence of submarine canyons justify the low values of superficial primary production and the consequent dominance of the macroplankton–epibenthic feeders. This result differs greatly from what was registered in the Catalan Sea (Cartes *et al.* 1994), where advective inputs of organic carbon via submarine canyons represent an additional contribution to deposit feeders and epibenthic–endobenthic feeders



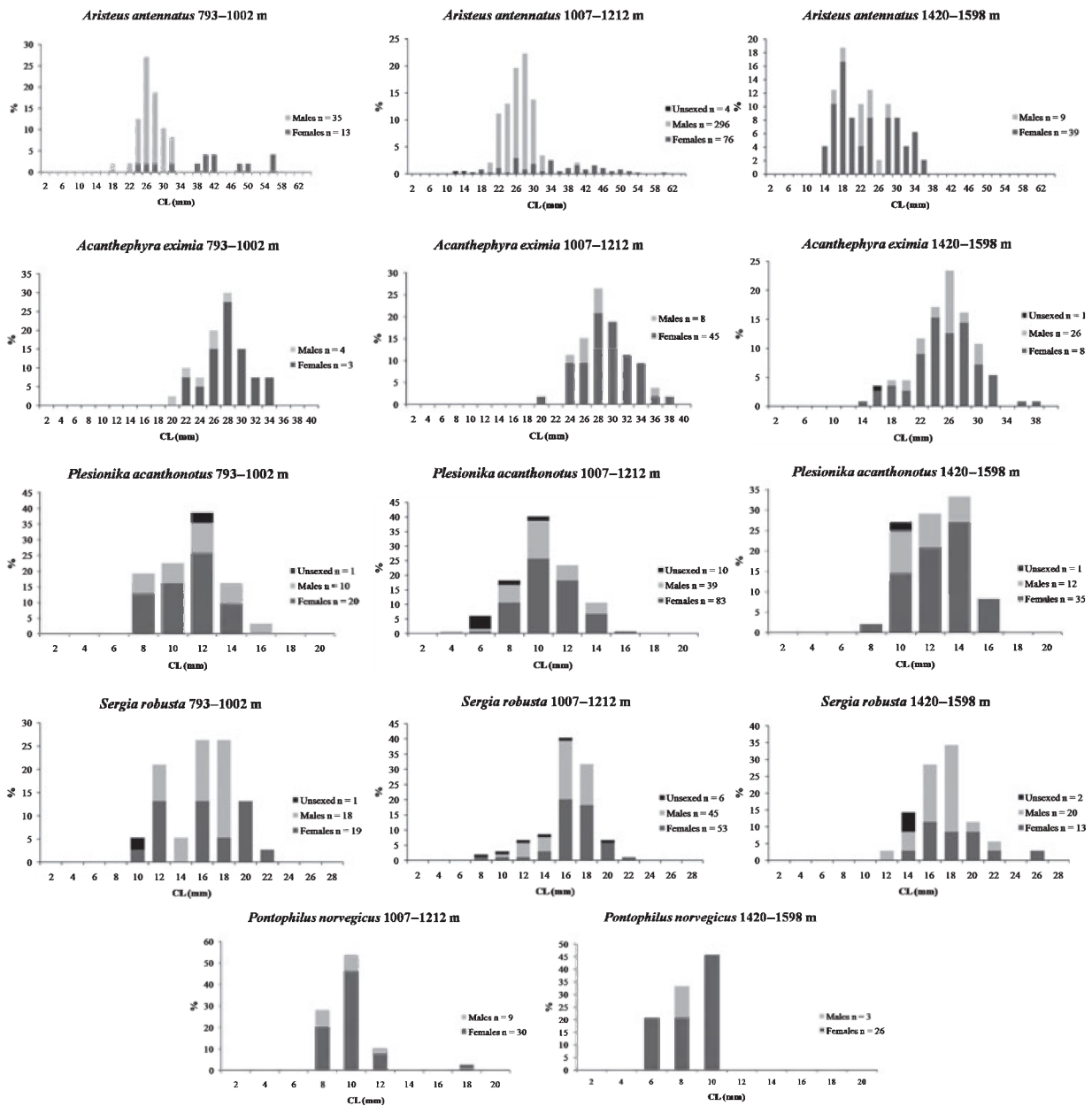


Fig. 5. Size frequencies and sex distribution of any bathyal decapod species collected off South-Eastern Sardinian deep-waters (Central-Western Mediterranean).

(Maynou & Cartes 2000). This phenomenon, supporting the food availability and local geographic conditions as responsible for species distribution, also highlighted the presence of a remarkable west–east productivity gradient in the Mediterranean, probably mainly due to the variability

in the vertical fluxes of organic carbon to the sea floor (Danovaro *et al.* 1999). Many studies have compared the phytoplankton pigment concentrations (PPC) in the Mediterranean Sea, highlighting differences of an order of magnitude between the west and eastern basin, and con-

Fig. 4. Bubble plot showing the relationship between depth strata and mean individual weight (g) of the decapod crustacean species predominant off South-Eastern Sardinian deep-waters. N = number of analysed individuals. The diameter of the bubble is proportional to the number of individuals.

firming the increase of oligotrophy in the west *versus* east (Maynou & Cartes 2000; Cartes *et al.* 2004; Company *et al.* 2004; Tselepidis *et al.* 2004; Politou *et al.* 2005).

The decrease of total decapod biomass with depth has been established in oceans worldwide (Haedrich *et al.* 1980; Lampitt *et al.* 1986). The data available in the Mediterranean are consistent with the general decrease down to 2200 m in the Western Mediterranean (Cartes & Sardà 1992) and down to 1000 m in the Cretan Sea (Kallianotis *et al.* 2000). On the whole, this trend was confirmed for the South-Eastern Sardinian deep-waters, where the biomass showed a strong decrease in the deepest slope (1420–1598 m), probably due to the small size of specimens caught (principally *A. eximia*, *P. acanthonotus* and *P. sculptus*). The highest value of biomass was found between 1007 and 1212 m, due to the presence of big size species (*A. antennatus* and *G. longipes*).

The relationship between mean individual weight/size and depth has been the subject of a considerable number of studies in deep-sea biology, basically focused on fish (Stefanescu *et al.* 1992; Moranta *et al.* 2000, 2004; Morales-Nin *et al.* 2003) rather than on decapods (Polloni *et al.* 1979; Cartes & Sardà 1993; Morales-Nin *et al.* 2003; Company *et al.* 2004). In our study there was no general pattern of mean individual weight/size *versus* depth among decapods, and the changes seemed to be species-specific. *Aristeus antennatus*, *A. eximia* and *P. typhlops*, according to Abelló & Cartes (1992), Company (1995), Company *et al.* (2004), Sardà *et al.* (2004), Follesa *et al.* (2007) and Guijarro *et al.* (2008), showed a significant 'smaller deeper trend' (Stefanescu *et al.* 1992), with juvenile specimens mainly distributed in the deepest part of the continental slope (below 1420 m). Instead, a 'bigger-deeper pattern' was only found for *S. robusta* and *M. tenuimana*, which showed a progressive increase of size or mean individual weight below 1200 m, as reported by Morales-Nin *et al.* (2003) and Cartes *et al.* (2007b). The bigger-deeper pattern, described also for fish such as *Phycis blennoides* (Massutí *et al.* 1996), *Trachyrhynchus scabrurus* (Massutí *et al.* 1995), *Lepidion lepidion* and *Mora moro* (Rotllant *et al.* 2002), has been attributed to the fact that the metabolic demands per unit weight of a large animal are less than for a small one (Haedrich *et al.* 1980). Therefore, in our results the simultaneous existence of 'smaller and bigger deeper trends' in the whole fauna highlighted the co-existence of small and large-size specimens at increasing depth. Fishery activity might also be considered a factor that could affect individual characteristics as mean size and species size structure (Mytilineou *et al.* 2001).

In conclusion, this study provides useful information about the composition, distribution and structure of bathyal decapod crustaceans in the Central-Western Mediterranean, considered the link between the western and

eastern basin. Further investigations should be devoted to increasing the bathymetric range of the research to improve knowledge of the Mediterranean Sea fauna.

References

- Abad E., Preciado I., Serrano A., Baro J. (2007) Demersal and epibenthic assemblages of trawlable grounds in the northern Alboran Sea (western Mediterranean). *Scientia Marina*, **71**(3), 513–524.
- Abelló P., Cartes J.E. (1992) Population characteristics of the deep-sea lobsters *Polycheles typhlops* and *Stereomastis sculpta* (Decapoda: Polychelidae) in a bathyal mud community of the Mediterranean Sea. *Marine Biology*, **114**, 109–117.
- Abelló P., Valladares F.J. (1988) Bathyal decapod crustaceans of the Catalan Sea (Northwestern Mediterranean). *Mésogée*, **48**, 97–102.
- Abelló P., Valladares F.J., Castellón A. (1988) Analysis of the structure of the decapod crustacean assemblages off the Catalan coast (North-West Mediterranean). *Marine Biology*, **98**, 39–49.
- Abelló P., Carbonell A., Torres P. (2002) Biogeography of epibenthic crustaceans on the shelf and upper slope off the Iberian Peninsula Mediterranean coasts: implications for the establishment of natural management areas. *Scientia Marina*, **66** (Suppl. 2), 183–198.
- Bray J.R., Curtis J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 325–349.
- Cabiddu S., Follesa M.C., Gastoni A., Porcu C., Cau A. (2008) Gonad development of the deep-sea lobster *Polycheles typhlops* (Decapoda: Polichelidae) from the Central Western Mediterranean. *Journal of Crustacean Biology*, **28**(3), 495–502.
- Carbonell A., Palmer M., Abelló P., Torres P., Alemany R., Gil de Sola L. (2003) Mesoscale geographical patterns in the distribution of pandalid shrimps *Plesionika* spp. in the Western Mediterranean. *Marine Ecology Progress Series*, **247**, 151–158.
- Cartes J.E. (1998) Feeding strategies and partition of food resources in deep-water decapod crustaceans (400–2300 m). *Journal of the Marine Biological Association of the United Kingdom*, **78**, 509–524.
- Cartes J.E., Sardà F. (1992) Abundance and diversity of decapod crustaceans in the deep-Catalan Sea (Western Mediterranean). *Journal of Natural History*, **26**, 1305–1353.
- Cartes J.E., Sardà F. (1993) Zonation of deep-sea decapods fauna in the Catalan Sea (Western Mediterranean). *Marine Ecology Progress Series*, **94**, 27–34.
- Cartes J.E., Company J.B., Maynou F. (1994) Deep-water crustacean communities in the northwestern Mediterranean: influence of submarine canyons and season. *Marine Biology*, **120**, 221–229.
- Cartes J.E., Maynou F., Morales-Nin B., Massutí E., Moranta J. (2001) Trophic structure of bathyal benthopelagic boundary

- layer community south of the Balearic Islands (southwestern Mediterranean). *Marine Ecology Progress Series*, **215**, 23–35.
- Cartes J.E., Maynou F., Moranta J., Massutí E., Lloris D., Morales-Nin B. (2004) Patterns of bathymetric distribution among deep-sea fauna at local spatial scale: comparison of mainland vs. insular areas. *Progress in Oceanography*, **60**, 29–45.
- Cartes J.E., Madurell T., Fanelli E., López-Jurado J.L. (2007a) Dynamics of suprabenthos-zooplankton communities around the Balearic Islands (western Mediterranean): influence of environmental variables and effects on the biological cycle of *Aristeus antennatus*. *Journal of Marine Systems*, **71**, 316–335.
- Cartes J.E., Serrano A., Velasco F., Parra S., Sánchez F. (2007b) Community structure and dynamics of deep-water decapod assemblages from Le Danois Bank (Cantabrian Sea, NE Atlantic): influence of environmental variables and food availability. *Progress in Oceanography*, **75**, 797–816.
- Clarke K.R. (1993) Non parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Colloca F., Cardinale M., Belluscio A., Ardizzone G. (2003) Pattern of distribution and diversity of demersal assemblages in the central Mediterranean sea. *Estuarine, Coastal and Shelf Science*, **56**, 469–480.
- Company J.B. (1995) *Estudi comparatiu de les strategies biològiques dels crustacis decàpodes del talus de la Mar Catalana*. Ph.D. thesis, Universitat de Barcelona.
- Company J.B., Maiorano P., Tselepides A., Politou C.-Y., Plaity W., Rotllant G., Sardà F. (2004) Deep-sea decapod crustaceans in the western and central Mediterranean Sea: preliminary aspects of species distribution, biomass and population structure. *Scientia Marina*, **68** (Suppl. 3), 73–86.
- Danovaro R., Dinet A., Duineveld G., Tselepides A. (1999) Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions-Catalan Sea (western Mediterranean) and the Cretan Sea (eastern Mediterranean). *Progress in Oceanography*, **44**, 287–312.
- Fanelli E., Colloca F., Ardizzone G. (2007) Decapod crustacean assemblages off the West coast of central Italy (western Mediterranean). *Scientia Marina*, **71**(1), 19–28.
- Field L.G., Clarke K.R., Warwick R.M. (1982) A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**, 37–52.
- Follesa M.C., Cabiddu S., Gastoni A., Cau A. (2007) On the reproductive biology of the deep-sea lobster, *Polychaetes typhlops* (Decapoda, Palinura, Polychelidae), from the central-western Mediterranean. *Crustaceana*, **80**(7), 839–846.
- Gaertner J.C., Bertrand J.A., Gil de Sola Simarro L., Durbec J.P., Ferrandis E., Souplet A. (2005) Large spatial scale variation of demersal fish assemblage structure on the continental shelf of the NW Mediterranean Sea. *Marine Ecology Progress Series*, **297**, 245–257.
- Gage J.D., Tyler P.A. (1991) *Deep-Sea Biology: a Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge: 504 pp.
- Galil B.S. (2004) The limit of the Sea: the bathyal fauna of the Levantine Sea. *Scientia Marina*, **68** (Suppl. 3), 63–72.
- García Muñoz J.E., Manjón-Cabeza M.E., García Raso J.E. (2008) Decapod crustacean assemblages from littoral bottoms of the Alborán Sea (Spain, west Mediterranean Sea): spatial and temporal variability. *Scientia Marina*, **72**(3), 437–449.
- Guijarro B., Massutí E., Moranta J., Díaz P. (2008) Population dynamics of the red shrimp *Aristeus antennatus* in the Balearic Islands (western Mediterranean): short spatio-temporal differences and influence of environmental factors. *Journal of Marine Systems*, **71**, 385–402.
- 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. (1988) Recent observations on the intermediate and deep-water circulation in the Southern Tyrrhenian Sea. *Oceanologica Acta*, **9**, 41–50.
- Kallianotis A., Sophronidis K., Vidoris P., Tselepides A. (2000) Demersal fish and megafaunal assemblages on the Cretan continental shelf and slope (NE Mediterranean): seasonal variation in species density, biomass and diversity. *Progress in Oceanography*, **46**, 429–455.
- Lampitt R.S., Billet D.S.M., Rice A.L. (1986) Biomass of the invertebrate megabenthos from 500 to 4100 m in the north-east Atlantic Ocean. *Marine Biology*, **93**, 69–81.
- Massutí E., Reñones O. (2005) Demersal resources assemblages in the trawl fishing grounds off the Balearic Islands (western Mediterranean). *Scientia Marina*, **69**, 167–181.
- Massutí E., Morales-Nin B., Stefanescu C. (1995) Distribution and biology of five grenadier fish (Pisces: Macrouridae) from the upper and middle slope of the northwestern Mediterranean. *Deep-Sea Research I*, **42**, 307–330.
- Massutí E., Morales-Nin B., Lloris D. (1996) Bathymetric distribution and recruitment patterns of *Phycis blennoides* (Pisces: Gadidae) from the slope of the northwestern Mediterranean. *Scientia Marina*, **60**, 481–488.
- Maynou F., Cartes J.E. (2000) Community structure of bathyal decapod crustaceans off south-west Balearic Islands (western Mediterranean): seasonality and regional patterns in zonation. *Journal of the Marine Biological Association of the United Kingdom*, **80**(5), 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.
- Morales-Nin B., Maynou F., Sardà F., Cartes J., Moranta J., Massutí E., Company J., Rotllant G., Bozzano A., Stefanescu C. (2003) Size influence in zonation patterns in fishes and crustaceans from deep-water communities of the Western Mediterranean. *Journal of Northwest Atlantic Fishery Science*, **31**, 413–430.

- Moranta J., Stefanescu C., Massutí 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., Massutí E., Morales-Nin B. (2000) Fish catch composition of the deep-sea decapod crustacean fisheries in the Balearic islands (western Mediterranean). *Fisheries Research*, **45**, 253–264.
- Moranta J., Palmer M., Massutí E., Stefanescu C., Morales-Nin B. (2004) Body fish size tendencies within and among species in the deep-sea of the western Mediterranean. *Scientia Marina*, **68**(3), 141–152.
- Moranta J., Quetglas A., Massutí E., Guijarro B., Hidalgo M., Diaz P. (2008) Spatio-temporal variations in deep-sea demersal communities off the Balearic Islands (western Mediterranean). *Journal of Marine Systems*, **71**, 346–366.
- Mura M. (1987) Crostacei decapodi batiali della Sardegna meridionale. *Rendiconti seminario Facoltà Scienze Università Cagliari*, **87**, 189–199.
- Mura M., Cau A. (1992) Osservazioni su alcune comunità di vertebrati e macroinvertebrati demersali mesobatiali del Canale di Sardegna. *Oebalia*, **17**, 67–73.
- Mura M., Cau A. (1994) Community structure of the decapod crustaceans in the middle bathyal zone of the Sardinian Channel. *Crustaceana*, **67**(3), 259–266.
- Mura M., Campisi S., Cau A. (1993) Considerazione sull'alimentazione di alcune specie di vertebrati e macroinvertebrati dei fondi mesobatiali del Canale di Sardegna. *Biologia Marina Mediterranea*, **1**, 155–160.
- Mytilineou Ch., Maiorano P., Kavadas S., D'Onghia G., Kapiris K., Capezzuto F. (2001) Size structure comparison in some demersal species between two areas of different fishing impact in the deep-water of the eastern-central Mediterranean (Ionian Sea). *Deep Sea Fisheries Research*, **7**. NAFO SCR Doc 01/1250.
- Péres J.M. (1985) History of the Mediterranean biota and the colonization of the depths. In: Margalef R. (Eds), *Key Environments: Western Mediterranean*. Pergamon Press, New York: 198–232.
- Pielou E.C. (1977) *Mathematical Ecology*. John Wiley and Sons, New York: 385 pp.
- Pipitone C., Tumbiolo M.L. (1993) Decapod and stomatopod crustacean from the trawlable bottoms of the Sicilian Channel (central Mediterranean Sea). *Crustaceana*, **65**, 358–364.
- Politou C.-Y., Maiorano P., D'Onghia G., Mytilineou C. (2005) Deep-water decapod crustacean fauna of the Eastern Ionian Sea. *Belgian Journal of Zoology*, **135** (Suppl. 2), 235–241.
- Polloni P., Haedrich R.L., Rowe G.T., Clifford C.H. (1979) The size-depth relationship in deep ocean animals. *Hydrobiologia*, **64**(1), 39–46.
- Rex M.A. (1973) Deep-sea species diversity: decreased gastropod diversity at abyssal depth. *Science*, **181**, 1051–1053.
- Rex M.A., Stuart C.T., Hessler R.R., Allen J.A., Sanders H.L., Wilson G.D.F. (1993) Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature*, **365**, 636–639.
- Rotllant G., Moranta J., Massutí E., Sardà F., Morales-Nin B. (2002) Reproductive biology of three gadiform fish species through the Mediterranean deep-sea range (147–1850 m). *Scientia Marina*, **66**(2), 157–166.
- Sardà F., Cartes J.E., Company J.B. (1994) Spatio-temporal variations in megabenthos abundance in three different habitats of the Catalan deep-sea (Western Mediterranean). *Marine Biology*, **120**, 211–219.
- Sardà F., D'Onghia G., Politou C.-Y., Company J.B., Maiorano P., Kapiris K. (2004) Deep-sea distribution, biological and ecological aspects of *Aristeus antennatus* (Risso, 1816) in the western and central Mediterranean Sea. *Scientia Marina*, **68** (Suppl.3), 117–127.
- Shannon C.E., Weaver W. (1949) *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Stefanescu C., Recubado J., Lloris D. (1992) Depth-size trends in western Mediterranean demersal deep-sea fishes. *Marine Ecology Progress Series*, **81**, 205–213.
- Stefanescu C., Lloris D., Recubado J. (1993) Deep-sea fish assemblages in the Catalan Sea (Western Mediterranean) below a depth of 1000 m. *Deep-Sea Research*, **40**, 695–707.
- Tselepidis A., Lampadariou N., Hatzianni E. (2004) Distribution of meiobenthos at bathyal depths in the Mediterranean Sea. A comparison between sites of contrasting productivity. *Scientia Marina*, **68**(3), 39–51.
- Tyler P.A., Zibrowius H. (1992) Submersible observations of invertebrate fauna on the continental slope south west of Ireland. *Oceanologica Acta*, **15**, 211–226.
- Ungaro N., Marano C.A., Marsan R., Martino M., Marzano M.C., Strippoli G., Vlorà A. (1999) Analysis of demersal species assemblage from trawl surveys in the South Adriatic Sea. *Aquatic Living Resources*, **13**, 177–185.
- Ungaro N., Marano C.A., Ceriola L., Martino M. (2005) Distribution of demersal crustaceans in the southern Adriatic Sea. *Acta Adriatica*, **46**(1), 27–40.
- Wenner E.L., Boesch D.F. (1979) Distribution patterns of epibenthic decapods Crustacea along the shelf-slope coenocline, Middle Atlantic Bight, USA. *Bulletin of the Biological Society of Washington*, **3**, 106–133.
- Zar J.H. (1999) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Englewood Cliffs, NJ: 662 pp.