Abundance and diversity of decapod crustaceans in the deep-Catalan Sea (Western Mediterranean)

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The deep-slope decapod fauna of the Catalan Sea was extensively sampled with an OTSB-14 bottom trawl. A total of 67 bottom tows were taken from 1985 to 1989 at bottom depths ranging from 552 to 2261 m. Species in which abundance decreased with depth were *Plesionika acanthonotus, Polycheles typhlops, Calocaris macandreae* and *Geryon longipes*. Highest densities of *Acanthephyra eximia, Stereomastis sculpta,* and *Nematocarcinus exilis* were attained at the greatest depths studied. Total abundance, biomass and species richness for decapod crustaceans as a whole decreased with depth. Maximum decapod biomass and diversity occurred on the upper-middle slope on soft bottoms in the Catalan Sea and in all regions for which data were available. In the Catalan Sea, an oligotrophic area, the abundance of decapods as a group seemed to be higher than in north-Atlantic eutrophic regions. In these latter areas, other deep-sea benthic invertebrate groups, particularly ophiuroids, predominate.

KEYWORDS: Decapod crustaceans, Mediterranean, abundance, biomass, diversity.

Introduction

The deep-sea decapod crustacean fauna in the Mediterranean has been only qualitatively studied (Carpine, 1970a; Reyss, 1971; Fredj and Laubier, 1985; Pérès, 1985; Abelló and Valladares, 1988; Cartes, 1992 and references cited). Data on abundance, biomass and on the dominant species along the deep slope are particularly scarce.

The structure of bathyal decapod crustacean populations on the upper slope in the northwestern Mediterranean is relatively well known (Zariquiey Alvarez, 1968; Sardà and Palomera, 1981; Abellò *et al.,* 1988) down to a depth of 800 m, with data on species abundance and biomass also available. Below 1000 m such information is very scarce (Carpine, 1970b; Pérès, 1985; Abelló and Valladares, 1988). The lower subzone is characterized by extremely low species diversity, particularly compared with similar zones in the Atlantic (Pérès, 1985). Qualitative data collected using an Agassiz trawl are available for the region between 1020 and 2011 m (Abelló and Valladares, 1988). However, the catching power of this gear is low and hence estimation of species abundance using such data is not reliable.

The present paper provides data on the abundance, biomass, and diversity of bathyal decapod species in the Catalan Sea. This has been made possible by extensive sampling of the deep slope with an OTSB-14 bottom trawl at depths ranging from 552 to 2261 m. The results obtained are discussed in the light of the characteristics of
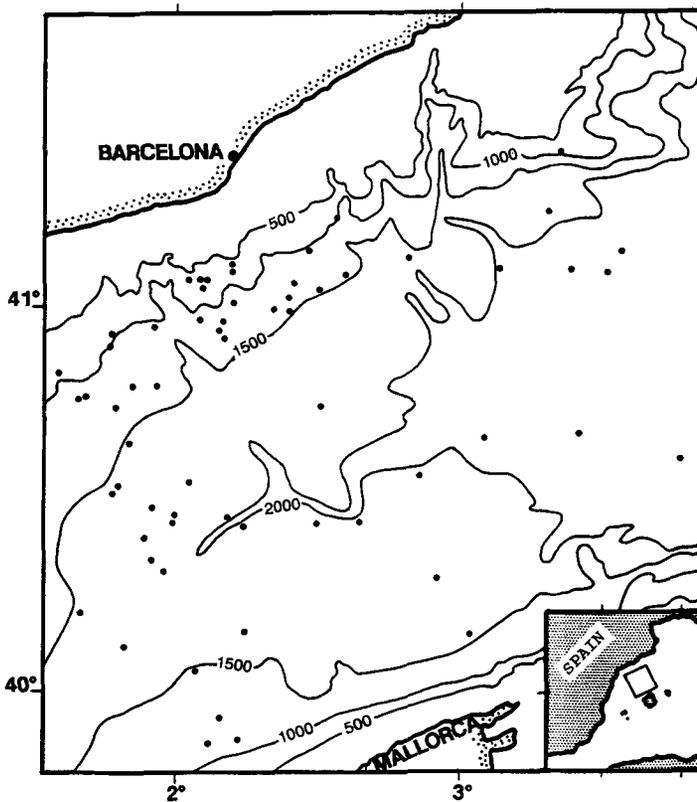
FIG. 1. Location of deep-sea samples (m) collected over the period 1985–1989 using OTSB-14 trawl gear in the Catalan Sea.

the bottom trawl employed and are compared with available data on the deep slope for other oceanic regions.

Materials and methods

A total of 67 bottom trawls were carried out from 1985 to 1989 at bottom depths ranging from 552 to 2261 m in the Catalan Sea (38°45′N to 42°N) (Fig. 1). A detailed description of station data is available in Cartes (1992). Maximum depth in this region is around 2300 m. Physical conditions of the Mediterranean deep-water mass are fairly constant below 200 m: temperature 12·7°C and salinity 38·4‰ (Fredj and Laubier, 1985; Hopkins, 1985). Muddy bottoms were dominant along all the slope (Emelyanov, 1972).

All the material included in the present paper was collected with the same sampling gear, an OTSB-14 bottom trawl (headline length 13·7 m) equipped with two doors and a single trawl warp (Merrett and Marshall, 1981; Sulak, 1982; Rucabado *et al.*, 1991). The size of the OTSB-14 trawl at a towing speed of 2·6 knots was estimated as a vertical opening of 1·5 m and a horizontal opening between the wings of 7 m. These measurements were verified with the aid of a remote acoustic sensing system attached to the gear (unpublished data) and were approximately equal to those reported by Sulak (1982). An hour of trawling with the 13·7 m net at 2·6 knots covers an estimated

area of 33 725 m² of the sea bottom. The end of the net was covered with a 6 mm mesh cod-end liner. All the samples were collected on board the R/V *García del Cid* (engine power: 1500 h.p.; length: 38 m). Sampling covered an extensive slope zone (between 862 and 2261 m) in which 61 bottom trawls were carried out along the depth transect. An additional six bottom tows were made on the upper middle slope at depths between 552 and 710 m for purposes of comparison with deeper samples. Although submarine canyons are important in the area all sampling was carried out outside the canyons. A more detailed explanation of sampling design is available in previous works (cf. Rucabado *et al.*, 1991; Stefanescu *et al.*, 1992).

Table 1.   List of species collected in the present study.

Species	Habits
Gennadas elegans (S. I. Smith, 1884)	M
Aristeus antennatus (Risso, 1816)	N
Solenocera membranacea (Risso, 1816)	B–E
Sergestes articus Kröyer, 1855	M
Sergestes henseni (Ortmann, 1893)	M
Sergestes sargassi (Ortmann, 1893)	M
Sergia robusta (S. I. Smith, 1882)	M
Richardina fredericii Lo Bianco, 1903	B
Acanthephyra eximia S. I. Smith, 1886	N
Acanthephyra pelagica (Risso, 1816)	M
Nematocarcinus exilis (Bate, 1888)	N
Pasiphaea sivado (Risso, 1816)	M
Pasiphaea multidentata Esmark, 1866	M
Alpheus glaber (Olivi, 1792)	E
Ligur ensiferus (Risso, 1816)	N
Processa canaliculata Leach, 1815	B–E
Pandalina profunda Holthuis, 1946	N
Plesionika acanthonotus (S. I. Smith, 1882)	N
Plesionika gigliolii (Senna, 1903)	N
Plesionika martia (A. Milne Edwards, 1883)	N
Philocheras echinulatus (M. Sars, 1861)	B
Pontocaris lacazei (Gourret, 1887)	B
Pontophilus norvegicus (M. Sars, 1861)	B
Nephrops norvegicus (Linnaeus, 1758)	B–E
Calocaris macandreae Bell, 1864	E
Axiidae unidentified	B–E?
Polycheles typhlops Heller, 1862	B
Stereomastis sculpta (S. I. Smith, 1880)	B
Pagurus alatus Fabricius, 1775	B
Pagurus excavatus (Herbst, 1791)	B
Munida tenuimana G. O. Sars, 1872	B
Munidopsis tridentata (Esmark, 1857)	B
Paromola cuvieri (Risso, 1816)	B
Dorhynchus thomsoni Thomson, 1873	B
Macropodia longipes (A. Milne Edwards and Bouvier, 1899)	B
Geryon longipes A. Milne Edwards, 1881	B
Chaceon mediterraneus Manning and Holthuis, 1989	B
Macropipus tuberculatus (Roux, 1830)	B
Goneplax rhomboides (Linnaeus, 1758)	E
Monodaeus couchi (Couch, 1851)	B–E

M: mesopelagic species; N: nektobenthic species; B: benthic species; E: endobenthic species.

Table 2.　Mean abundance (individuals h⁻¹) and standard error for the different species collected by depth stratum on the slope in the Catalan Sea.

	Depth range						
	552–710 m (n = 6)	862–1149 m (n = 14)	1150–1349 m (n = 9)	1350–1549 m (n = 7)	1550–1749 m (n = 13)	1750–1949 m (n = 11)	1950–2261 m (n = 7)
Gennadas elegans	2·2 ± 1·5	0·5 ± 0·7	1·7 ± 1·8	2·9 ± 3·6	1·9 ± 1·1	0·6 ± 1·0	0·3 ± 0·3
Aristeus antennatus	5·5 ± 2·3	8·3 ± 6·7	14·7 ± 4·6	10·3 ± 6·2	5·8 ± 4·1	5·0 ± 6·4	3·7 ± 2·2
Solenocera membranacea	0·7 ± 10	—	—	—	—	—	—
Sergestes arcticus	3·5 ± 4·6	1·2 ± 2·2	1·1 ± 1·8	0·1 ± 0·2	0·2 ± 0·3	—	0·1 ± 0·1
Sergestes henseni	—	*	*	—	—	—	—
Sergestes sargassi	0·2 ± 0·4	—	—	—	—	—	—
Sergia robusta	0·3 ± 0·5	1·2 ± 2·8	2·3 ± 3·5	1·3 ± 1·6	1·0 ± 0·8	0·6 ± 0·6	1·2 ± 0·4
Richardina fredericii	—	*	—	—	—	—	—
Acanthephyra eximia	—	3·5 ± 3·7	15·1 ± 11·0	27·4 ± 17·7	27·6 ± 24·4	33·6 ± 21·7	68·5 ± 59·4
Acanthephyra pelagica	—	0·4 ± 0·6	1·6 ± 2·4	1·6 ± 1·2	0·8 ± 0·6	0·6 ± 0·6	1·7 ± 1·5
Nematocarcinus exilis	—	—	1·9 ± 3·6	0·9 ± 1·7	3·6 ± 2·6	5·6 ± 3·7	22·9 ± 13·3
Pasiphaea sivado	0·2 ± 0·4	—	—	—	—	—	—
Pasiphaea multidentata	1·4 ± 1·4	0·6 ± 0·8	0·8 ± 0·7	0·8 ± 0·6	0·4 ± 0·5	0·2 ± 0·2	0·5 ± 0·3
Alpheus glaber	4·7 ± 3·1	—	—	—	—	—	—
Ligur ensiferus	0·1 ± 0·3	—	—	—	—	—	—
Processa canaliculata	3·6 ± 4·5	—	—	—	—	—	—
Pandalina profunda	5·8 ± 7·6	—	—	—	—	—	—
Plesionika acanthonotus	12·0 ± 7·9	9·9 ± 8·0	7·5 ± 8·4	1·5 ± 2·1	*	—	—

Plesionika gigliolii	0·3 ± 0·4	—	—	—	—	—	—
Plesionika martia	12·1 ± 8·7	—	—	—	—	—	—
Philocheras echinulatus	0·8 ± 1·2	0·1 ± 0·3	—	—	—	—	—
Pontocaris lacazei	12·7 ± 9·9	12·3 ± 9·8	17·4 ± 11·6	11·8 ± 6·1	11·2 ± 5·3	3·8 ± 3·5	0·3 ± 0·4
Pontophilus norvegicus	4·8 ± 8·1	—	—	—	—	—	—
Nephrops norvegicus	1·2 ± 1·5	—	0·6 ± 1·2	0·6 ± 0·8	*	—	—
Calocaris macandreae	437·7 ± 421·0	4·8 ± 9·2	—	0·1 ± 0·1	*	*	—
Unidentified Axiidae	—	—	—	—	—	—	—
Polycheles typhlops	16·8 ± 4·8	5·5 ± 5·0	1·7 ± 1·1	1·1 ± 1·1	0·8 ± 1·2	0·3 ± 0·9	—
Stereomastis sculpta	—	0·1 ± 0·2	8·7 ± 1·5	4·3 ± 3·8	14·8 ± 15·0	30·1 ± 17·8	45·9 ± 39·1
Pagurus alatus	7·8 ± 8·8	0·5 ± 1·0	—	—	—	—	—
Pagurus excavatus	0·1 ± 0·2	—	—	27·4 ± 9·3	—	—	—
Munida tenuimana	47·1 ± 26·5	20·1 ± 13·1	36·2 ± 13·4	—	18·0 ± 10·6	20·5 ± 13·4	—
Munidopsis tridentata	—	*	—	—	0·1 ± 0·3	—	—
Paromola cuvieri	0·6 ± 0·5	0·2 ± 0·3	*	0·1 ± 0·2	—	—	—
Macropodia longipes	—	*	—	—	—	—	—
Dorhynchus thomsoni	1·0 ± 0·7	0·2 ± 0·3	0·2 ± 0·3	—	—	—	*
Macropipus tuberculatus	—	*	—	0·2 ± 0·3	—	—	—
Geryon longipes	6·4 ± 1·4	4·8 ± 7·2	1·7 ± 1·5	0·2 ± 0·3	0·1 ± 0·2	0·1 ± 0·1	—
Chaceon mediterraneus	—	—	—	—	—	—	0·2 ± 0·2
Goneplax rhomboides	0·7 ± 1·4	—	—	—	—	—	—
Monodaeus couchi (Table 1)	21·3 ± 14·5	*	—	—	—	—	—

*Mean abundance less than 0·1 individual h^{-1}; n = no. of samples.

Table 3. Mean biomass (g h⁻¹) and standard error for the different species collected by each depth stratum on the slope in the Catalan Sea.

	Depth range						
	552–710 m (n = 6)	862–1149 m (n = 13)	1150–1349 m (n = 7)	1350–1549 m (n = 7)	1550–1749 m (n = 12)	1750–1949 m (n = 11)	1950–2261 m (n = 7)
Gennadas elegans	0·4 ± 0·4	0·1 ± 0·2	0·2 ± 0·5	0·6 ± 0·8	0·4 ± 0·3	0·1 ± 0·3	*
Aristeus antennatus	74·0 ± 40·7	104·1 ± 94·7	139·0 ± 64·2	82·1 ± 40·1	48·3 ± 33·2	20·8 ± 21·1	35·1 ± 22·8
Solenocera membranacea	1·9 ± 2·4	—	—	—	—	—	—
Sergestes arcticus	1·1 ± 1·5	0·1 ± 0·2	0·1 ± 0·4	*	0·1 ± 0·2	—	*
Sergestes henseni	—	—	*	—	—	—	—
Sergestes sargassi	*	*	—	—	—	—	—
Sergia robusta	0·4 ± 0·8	1·2 ± 1·7	1·3 ± 3·1	2·7 ± 3·2	1·9 ± 1·6	1·4 ± 1·3	2·0 ± 1·1
Richardina fredericii	—	*	—	—	—	—	—
Acanthephyra eximia	—	22·7 ± 24·5	96·3 ± 66·9	182·3 ± 99·0	159·3 ± 110·0	152·9 ± 118·0	218·7 ± 204·2
Acanthephyra pelagica	—	2·5 ± 4·2	1·5 ± 2·0	8·2 ± 6·8	4·8 ± 4·1	3·0 ± 3·6	9·1 ± 7·9
Nematocarcinus exilis	—	—	0·5 ± 1·2	0·2 ± 0·4	4·9 ± 3·7	7·8 ± 5·2	27·8 ± 14·8
Pasiphaea sivado	0·2 ± 0·5	—	—	—	—	—	—
Pasiphaea multidentata	4·3 ± 4·7	2·4 ± 2·7	4·9 ± 6·5	4·2 ± 3·1	3·3 ± 4·2	1·6 ± 1·7	2·8 ± 3·0
Alpheus glaber	2·3 ± 1·2	—	—	—	—	—	—
Ligur ensiferus	0·3 ± 0·6	—	—	—	—	—	—
Processa canaliculaya	1·0 ± 1·7	—	—	—	—	—	—
Pandalina profunda	0·8 ± 1·0	—	—	—	0·1 ± 0·2	—	—
Plesionika acanthonotus	22·6 ± 14·5	21·5 ± 16·0	20·5 ± 19·2	2·8 ± 3·4			

Species							
Plesionika gigliolii (Table 2)	0.5 ± 0.7	—	—	—	—	—	—
Plesionika martia	73.4 ± 49.4	—	—	—	—	—	—
Philocheras echinulatus	0.5 ± 0.6	—	—	—	—	—	—
Pontocaris lacazei	8.6 ± 6.1	*	—	—	—	—	—
Pontophilus norvegicus	2.3 ± 5.0	7.4 ± 5.6	8.5 ± 5.2	8.0 ± 5.0	7.2 ± 2.9	2.5 ± 2.6	0.2 ± 0.3
Nephrops norvegicus	10.8 ± 14.0	—	*	*	*	—	—
Calocaris macandreae	213.8 ± 206.5	1.7 ± 3.7	0.3 ± 0.6	*	0.1 ± 0.3	*	—
Unidentified Axiidae	—	—	—	—	—	—	—
Polycheles typhlops	223.5 ± 161.0	22.5 ± 15.4	5.7 ± 4.7	2.5 ± 2.3	1.7 ± 2.6	*	—
Stereomastis sculpta	—	0.5 ± 1.2	1.3 ± 1.2	9.3 ± 8.3	33.4 ± 37.0	72.1 ± 37.5	89.7 ± 63.1
Pagurus alatus	16.5 ± 18.1	1.5 ± 2.6	—	—	—	—	—
Pagurus excavatus	0.4 ± 0.8	—	—	—	—	—	—
Munida tenuimana	108.7 ± 57.0	37.1 ± 22.7	197.0 ± 154.2	92.5 ± 33.9	56.2 ± 34.1	58.8 ± 41.4	—
Munidopsis tridentata	—	*	—	*	*	—	—
Paromola cuvieri	73.0 ± 91.6	6.7 ± 11.1	—	0.2 ± 0.5	—	—	—
Macropodia longipes	0.1 ± 0.2	0.1 ± 0.5	0.1 ± 0.3	—	—	—	—
Dorhynchus thomsoni	—	*	0.1 ± 0.2	—	—	—	*
Macropipus tuberculatus	435.6 ± 332.4	0.3 ± 0.5	114.9 ± 88.7	5.3 ± 8.3	5.6 ± 11.3	1.1 ± 1.8	—
Geryon longipes	—	365.0 ± 574.1	—	—	—	—	12.1 ± 15.7
Chaceon mediterraneus	2.3 ± 4.2	—	—	—	—	—	—
Goneplax rhomboides	74.7 ± 69.3	—	—	—	—	—	—
Monodaeus couchi (Table 1)	—	0.1 ± 0.3	—	—	—	—	—

* Mean biomass less than $0.1\,g\,h^{-1}$; n = no. of samples.

Samples were preserved in 70% alcohol. Specimens were identified, counted, and weighted at the laboratory. All trawl results were first standardized to 1 h tows. Abundance (individuals/h) and biomass (grams/h) were calculated by species and for all decapod crustaceans combined for seven arbitrary 200 m depth strata (between 552 and 2261 m), established after sampling. Slope areas were categorized according to the bathymetric zonation previously established in the Catalan Sea decapod communities (Cartes, 1991; Cartes and Sardà, unpublished) as: upper-middle slope (between 552 and 710 m); lower-middle slope (862–1300 m); lower slope (below 1300 m).

Mean and absolute species richness, diversity (Shannon and Weaver, 1963), and dominance (Simpson, 1949; Magurran, 1988) were calculated for each depth stratum. Abundance and biomass data were transformed (ln (x)) and homogeneity of variances were tested, using a F_{max} test (Sokal and Rohlf, 1969). Analysis of variance (ANOVA) was used to compare the influence of depth in species richness, abundance and biomass. After this, the significance between the mean species richness, abundance, and biomass values for the different strata was established by a method of multiple comparison of means (Scheffe, 1959).

Results

The systematic relationships of the species identified in the present study have been published elsewhere (Abelló and Valladares, 1988; Abelló et al., 1988; Cartes, 1993). A list of the species collected is presented in Table 1.

Table 2 sets out the species abundance values by depth stratum, with the number of trawls collected. Species in which abundance declined with depth included Plesionika acanthonotus, Calocaris macandreae, Polycheles typhlops and Geryon longipes. These species were more characteristic of the upper-middle slope communities. Plesionika acanthonotus and P. typhlops were abundant in catches made between 600 and 1200 m. From that point, catches fell off to a few isolated individuals at greater depths, with some juvenile P. typhlops present at depths down to 1900 (Abelló and Cartes, 1992). Calocaris macandreae was relatively abundant only down to about 1000 m, with isolated individuals appearing down to 1300–1500 m. It was the dominant species at 600 m, where it accounted for 70% of total abundance (Fig. 2). Geryon longipes was abundant between 600 and 1300 m, and only isolated individuals were caught down to 1700–1800 m.

Aristeus antennatus was present over the entire depth range sampled. Below 1000 m this species showed a peak abundance at 1150–1350 m and became progressively less abundant particularly below 1500–1600 m. The caridean Pontophilus norvegicus was abundant over a broad depth range from 1000 to 1700 m. The abundance of this species dropped after 1800 m, and it was extremely uncommon at depths of 2000–2200 m. The anomuran Munida tenuimana followed a similar pattern, and abundance values fell off sharply at 1900 m.

The species with the highest densities at great depth included Acanthephyra eximia, Stereomastis sculpta, and Nematocarcinus exilis (Fig. 3). For all these species, maximum abundance levels were recorded in the deepest sampling stratum (below 2000 m), and must be considered the dominant species on the lower slope.

Abundance for benthopelagic species was low in all cases. Although demersal trawls are not the best method to sample this species, Merrett (1986) remarks on the contribution made by bottom trawl samplings to our knowledge of pseudoceanic species. In our case, Sergestes articus and Pasiphaea multidentata were more
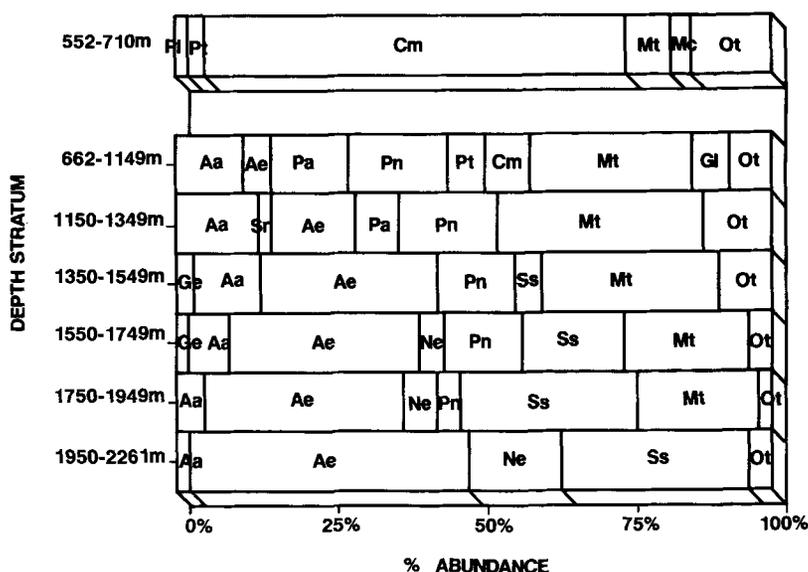
FIG. 2. Relative abundance of dominant species by depth stratum. Aa: *A. antennatus;*
Ae: *A. eximia;* Cm: *C. macandreae;* Ge: *G. elegans;* Gl: *G. longipes;* Mc: *M. couchi;*
Mt: *M. tenuimana;* Ne: *N. exilis;* Ot: Others; Pa: *P. acanthonotus;* Pl: *P. lacazei;*
Pn: *P. norvegicus;* Pt: *P. typhlops;* Sr: *S. robusta;* Ss: *S. sculpta.*

Table 4.   Mean total abundance (individuals h^{-1}) and biomass (g h^{-1}) for decapod crustaceans
by depth stratum.

Depth range (m)	Mean abundance (individuals h^{-1})	Mean biomass (g h^{-1})
552–710	607·8 ± 451·9	1352·7 ± 435·7
862–1149	82·5 ± 36·9	667·2 ± 627·6
1150–1349	116·5 ± 21·9	473·8 ± 269·9
1350–1549	92·1 ± 37·4	402·1 ± 144·9
1550–1749	91·4 ± 43·6	326·8 ± 146·7
1750–1949	95·5 ± 46·7	301·6 ± 169·5
1950–2261	145·4 ± 105·3	400·3 ± 262·5

abundant at shallower depths, while *Acanthephyra pelagica* was more abundant on
the lower slope.

In terms of biomass the brachyuran *G. longipes* predominated on the middle slope
(between 550 and 1349 m), due to its high mean weight (Fig. 4, Table 3). Despite its
low mean weight, *C. macandreae* was important in terms of biomass on the upper-
middle slope, because of its high abundance. The caridean *A. eximia* was the dominant
species in terms of biomass on the lower slope below 1300–1400 m. *M. tenuimana* was
important between 1200 and 1900 m, as was *S. sculpta* at depths greater than 1800 m
(Fig. 4, Table 3).

Mean abundance, biomass and species richness for decapod crustaceans as a whole
declined with depth (Tables 4 and 5). Variances were homogeneous in the abundance,
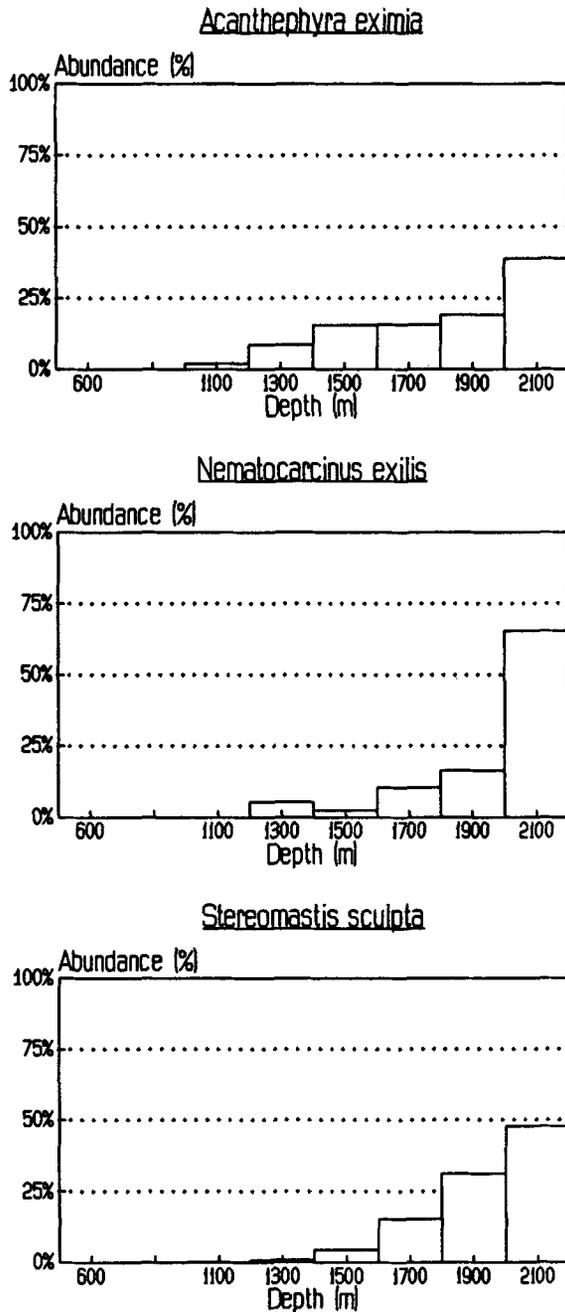
FIG. 3. Distribution of abundance for the three most predominant species on the lower slope.

biomass and species richness data (Table 6), and ANOVA results showed a significant ($P < 0.01$) effect of depth in each case (Table 6). Decline was significant ($P < 0.05$) when abundances values for the interval between 552 and 710 m were compared with the values below 1000 m (Table 6). Conversely, abundance increased slightly from
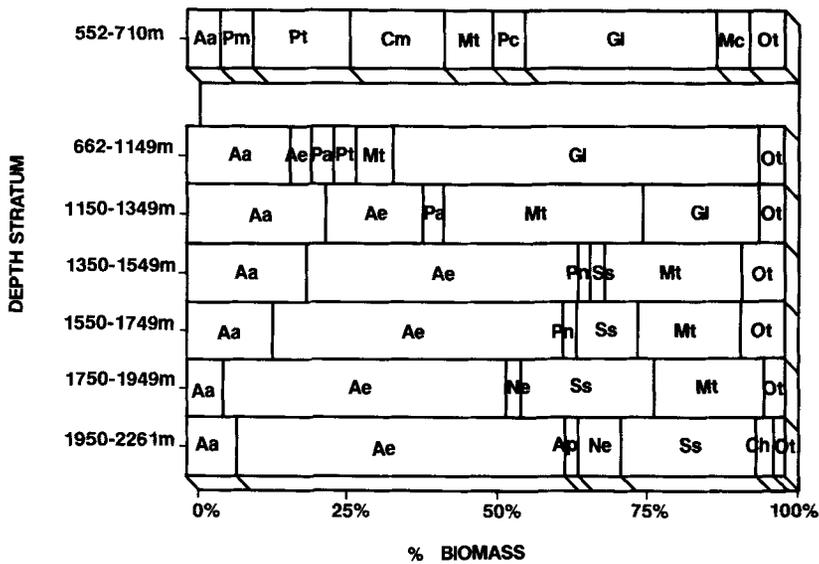
FIG. 4. Relative biomass of dominant species by depth stratum. Aa: *A. antennatus;* Ae: *A. eximia;* Ap: *A. pelagica;* Ch: *Ch. mediterraneus;* Cm: *C. macandreae;* Gl: *G. longipes;* Mc: *M. couchi;* Mt: *M. tenuimana;* Ne: *N. exilis;* Ot: others; Pa: *P. acanthonotus;* Pc: *P. cuvieri;* Pm: *P. martia;* Pn: *P. norvegicus;* Pt: *P. typhlops;* Sr: *S. robusta;* Ss: *S. sculpta.*

Table 5. Mean number of species, species richness, diversity (Shannon–Wiener index) and dominance (Simpson index) by depth stratum on the slope in the Catalan Sea.

Depth range (m)	No. of samples	Mean number of species	Species richness	Diversity (H')	Dominance (Simpson)
552–710	6	19.00 ± 2.76	29	1·90	0·53
862–1149	14	12.43 ± 1.72	24	3·17	0·15
1150–1349	9	12.00 ± 2.66	21	3·18	0·21
1350–1549	7	11.14 ± 1.64	19	2·72	0·21
1550–1749	13	10.54 ± 1.08	18	2·72	0·21
1750–1949	11	8.73 ± 1.54	13	2·43	0·25
1950–2261	7	8.57 ± 1.18	14	1·82	0·33

2000 m, though the increase was not significant. In terms of biomass significant differences ($P < 0.05$) were found between the values for the upper-middle slope and those for the depth strata below 1350 m (Table 6). Mean species richness values for the upper-middle slope were significantly different ($P < 0.05$) from the values for depths greater than 1000 m (Table 6). Differences between the values for the strata from 862 to 1349 m and the values for the strata at depths greater than 1750 m were significant in all cases except between the values for the 1150–1349 m and the 1950–2261 m strata.

Diversity (H') decreased with depth beyond 1000 m (Table 5). The values obtained for the upper-middle slope can be attributed in part to methodological causes (under-estimation of mobile species), which also account for the dominance values in this same zone (Table 5).

Table 6. F_{max}, ANOVA and Scheffe test results for the abundance, biomass and mean number of species by each depth strata.

F_{max} results

	F	Degree of freedom (a, n − 1)	Significance
Abundance (individuals h⁻¹)	3·29	(7,6)	**
Biomass (g h⁻¹)	4·32	(7,6)	**
Species richness	6·54	(7,5)	**

ANOVA results

	F	Degree of freedom (a − 1, (Σn − a))	Significance
Abundance (individuals h⁻¹)	9·74	(6,60)	**
Biomass (g h⁻¹)	4·88	(6,60)	**
Species richness	22·99	(6,60)	**

Scheffe results

	862–1149 m	1150–1349 m	1350–1549 m	1550–1749 m	1750–1949 m	1950–2261 m
Abundance						
552–710 m	*	−	*	*	*	*
862–1149 m		−	−	−	−	−
1150–1349 m			−	−	−	−
1350–1549 m				−	−	−
1550–1749 m					−	−
1750–1949 m						−
Biomass						
552–710 m	*	−	*	*	*	*
862–1149 m		−	−	−	−	−
1150–1349 m			−	−	−	−
1350–1549 m				−	−	−
1550–1749 m					−	−
1750–1949 m						−
Species richness						
552–710 m	*	−	*	*	*	*
862–1149 m		−	−	−	*	*
1150–1349 m			−	−	*	−
1350–1549 m				−	−	−
1550–1749 m					−	−
1750–1949 m						−

a = Number of depth strata; n: number of samples; ** significant value (P < 0·01); * significant value (P < 0·05); −, non-significant value.

Discussion

There have been few studies dealing with species abundance in deep-sea mega-faunal communities, particularly relating to decapod crustaceans. The reasons for this have been chiefly methodological, i.e. the different types of bottom trawls used and an element of bias towards results on species population density (Gordon and Duncan, 1985; Merrett *et al.,* 1991). The catchability of the OTSB-14 gear is sufficient to justify inclusion of the results on decapod species abundance in the present study.

Changes in species composition along the slope in the Catalan Sea were reflected more by changes in species abundance than species occurrence, in view of the broad depth ranges inhabited by the dominant decapod species in this area (Cartes, 1991, 1993). The most important quantitative boundary was located at around 1200–1300 m, which separated the decapod communities on the middle and lower slopes (Cartes, 1991). The species that displayed the highest abundance values on the middle slope communities (between 550 and 1300 m) in the Catalan Sea were *Plesionika acanthonotus, Calocaris macandreae, Polycheles typhlops,* and *Geryon longipes. Plesionika martia, Pontocaris lacazei,* and *Monodaeus couchii* were also abundant on the upper-middle slope. *Munida tenuimana* and *Pontophilus norvegicus,* for which the highest abundance was recorded on the middle slope, also attained high densities on the upper part of the lower slope (from 1400 to 1900 m). The middle slope is comparable with the middle subzone of Pérès (1985). *Aristeus antennatus* is especially abundant between 500 and 800 m in the Western Mediterranean (Maurin, 1962; Pérès, 1985) where it is an important commercial species in fisheries (Tobar and Sardà, 1987). The abundance of this species in the present study on the upper-middle slope was underestimated, due to the small size of the OTSB-14 trawl employed. The most abundant species on the lower slope were *Acanthephyra eximia,* with *Nematocarcinus exilis,* and *Stereomastis sculpta,* which were also cited by Pérès (1985) as the dominant species in the lower subzone.

In the Catalan Sea the characteristics of the gear used may have biased the results for the upper-middle slope. Thus, the abundance of benthopelagic and nektobenthic species in this zone is underestimated by small gear such as the OTSB-14 trawl, down to 1000 m (Pearcy *et al.,* 1982; Gordon and Duncan, 1985; unpublished data). OTSB-14 trawls are not well-suited to catching bathypelagic species that dwell near the bottom, probably because of their small vertical opening. Thus, when commercial gears, with a larger vertical opening (up to 5 m) than the OTSB-14 have been employed, Pasiphaeidae and Sergestidae have been caught in abundance on the upper and middle slope in the Catalan Sea (Abelló *et al.,* 1988; Cartes, 1991). These benthopelagic species play an essential role in the food web of bathyal communities (Lagardère, 1977; Relini-Orsi and Relini, 1990; Cartes, 1991; Cartes and Abelló, 1992). These methodological considerations affected the values for *H'* on the upper-middle slope and also may explain the high dominance values in this zone, ascribable to the high relative abundance of the burrowing decapod *Calocaris macandreae.*

Considering the OTSB-14 as a standard gear, results obtained with this trawl in different areas should be comparable (cf. Haedrich and Merrett, 1988). However, comparison of decapod results, especially abundance data, in the different studies poses considerable difficulty in view of the varied methodology employed in sampling (Table 7) and in the presentation of results. Cod-end mesh size is probably the most important aspect affecting results, and in decapod studies the smallest size used (6 mm) would be the most suitable mesh size. Despite all these considerations, the abundance of the benthic genus *Stereomastis* spp. would seem to be lower in all other areas than

in the Mediterranean. On the lower slope, *Acanthephyra eximia,* the dominant species in the Mediterranean, were more abundant than the dominant species in the other zones for which data were available. Off Nova Scotia, total decapod abundance was of the order of half, or even less, that recorded in the Mediterranean, even though samples were collected with a larger bottom trawl (Markle *et al.,* 1988). Off New England (Haedrich *et al.,* 1975, 1980), decapod population densities were always lower than in the Catalan Sea. Decapod density was also negligible on the lower slope in the vicinity of the Rockall Trough (Stefanescu, personal communication 1991).

The absolute biomass values obtained using the OTSB gear were higher (4320–3572 g h^{-1}) on the upper and middle slopes down to 1300 m in the Northwest Atlantic (Haedrich *et al.,* 1980) than in the Catalan Sea, whereas on the lower slope the values recorded from the Catalan Sea below 2000 m were of the same order or even higher. On the basis of available comparable data, the abundance and biomass values recorded for deep-sea decapod crustaceans appeared to be higher in the Catalan Sea than the values reported for eutrophic regions in the North Atlantic, particularly on the lower slope (Haedrich *et al.,* 1975, 1980; Wenner and Boesch, 1979; Markle *et al.,* 1988). Arthropod biomass, mainly *Geryon (= Chaceon) quinquedens,* was higher on the middle slope than on the lower slope off New England (Haedrich *et al.,* 1975), as was the case for *Geryon longipes* in the Catalan Sea. Decapod biomass in that same region peaked on the upper slope (283–650 m) and on the middle slope (653–1290 m), which was attributable to *G. quinquedens,* whereas the maximum for the megabenthos was between 1380 and 2481 m, linked to fishes and echinoderms, the clearly dominant groups in density and biomass. Decapod crustaceans were also more abundant in the deeper, more oligotrophic zones of the abyssal plain (Sokolova, 1972) between 3879 and 4986 m in the Atlantic Ocean.

Maximum abundances of decapods were also located on the upper-middle slope in the Middle Atlantic Bight (Wenner and Boesch, 1979) and off Nova Scotia (Markle *et al.,* 1988). In general, all available data point towards higher abundance of decapod crustaceans on soft bottoms on the upper-middle slope, where maximum species richness values were recorded as well.

Decapod abundance seemed to be higher in the Mediterranean than in other regions studied, especially on the lower slope. These results highlight the important role of decapod crustaceans in the deep Mediterranean. Concomitantly, the echinoderm population on the lower slope is low in the Catalan Sea (Fredj and Laubier, 1985; Alvà, 1987). Echinoderms, particularly ophiuroids, are the dominant group in eutrophic zones in the North Atlantic and the Pacific (Rowe and Menzies, 1969; Haedrich *et al.,* 1975, 1980; Smith and Hamilton, 1983; Lampitt *et al.,* 1986). In contrast, ophiuroids are not present on the lower slope in the Mediterranean (Alvà, 1987).

Generally speaking, decapod biomass on the deep slope could be sustained by a high density of benthopelagic organisms (Wishner, 1980; Hargreaves, 1984; Angel, 1990), which would furnish sufficient food, either directly or indirectly, for the communities dwelling in that zone. In neighbouring Atlantic regions (Hargreaves *et al.,* 1984), micronekton densities near the bottom were appreciable down to depths below 2000 m. The level occupied by these organisms should be sufficiently close to the bottom to enable the detritus generated to reach the benthos relatively undegenerated with minimal qualitative change in the organic matter reaching the bottom sediment (Wishner, 1980; Lampitt *et al.,* 1982).

Finally, the patterns observed for diversity with depth were in agreement with the abundance and biomass values. Species richness was highest on the upper-middle

Table 7. Abundances (individuals h^{-1}) of a benthic species (*Stereomastis* spp.), the dominant species and decapods from deep-sea areas where this information was available, with the main technical aspects of the bottom trawl used.

| Gear | Nova Scotia Western IIA | New England | | | MAB OTSB–14 | Catalan Sea OTSB–14 |
		1 OTSB	2 OTSB–13			
Headline length (m)	23	4,8	12,5		13,7	13,7
Cod-end mesh (mm)	19	6	25		12,7	6
Stereomastis spp abundance	1–3,6	0,6	—		(<15)	4–46
Dominant species abundance	*Acanthephyra pelagica* (16,8)	*Geryon (= Chaceon) quinquedens* (15,7)	(—)		*Glyphocrangon sculpta* (<29)	*Acanthephyra eximia* (65,8)
Total decapod abundance	27–58	6–16	10–53		(<85)	82–608

Results between parentheses were deduced from other papers (see references).
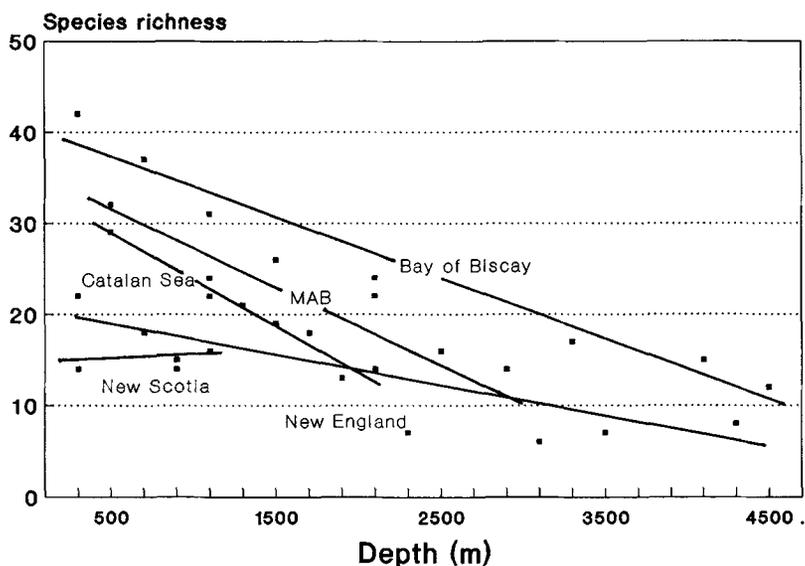
FIG. 5.   Species richness by depth in different areas in where deep-sea decapod studies have been carried out.

slope in the Catalan Sea. In decapod crustaceans, species richness is affected by latitude, being highest in tropical regions (Abele, 1982). Thus, species richness in high-latitude regions like the deep-sea zone in the Northwest Atlantic (Haedrich *et al.*, 1980; Markle *et al.*, 1988) is similar to that on the lower slope in the Mediterranean (Fig. 5). When species richness in different regions at similar latitudes is compared (Crosnier and Forest, 1973; Lagardère, 1977; Wenner and Boesch, 1979; Saint Laurent, 1985), the Mediterranean decapod fauna on the lower slope is poorer in both benthic and pelagic species (Foxton, 1970; Crosnier and Forest, 1973; Fasham and Foxton, 1979; Heffernan and Hopkins, 1981; Hargreaves, 1984; Domanski, 1986; Macpherson, 1991). In particular, bathypelagic species are poorly represented in the Mediterranean.

According to the trend in species richness values with depth, maximum decapod crustacean diversity occurs on the upper-middle slope on soft bottoms in all regions for which data are available (Fig. 5). Consideration of the *H'* values is more problematic, since these values are based on the abundance of each species, which is linked to the sampling methods employed. Maximum decapod diversity occurred at intermediate depths, which is in agreement to the findings for other macrofaunal groups (Rex, 1973, 1983; Valentine, 1976; Haedrich *et al.*, 1980), although for decapods the maximum value occurred in shallower zones on the slope.

Bathyal decapod crustaceans may possibly be better adapted to zones that are poor in resources. The large number of empty stomachs found when examining the stomach contents of deep-water species supports this conclusion (Cartes, 1991) as occurred, for instance, in polychelid lobsters, a characteristic deep-sea decapod family (Cartes and Abelló, 1992). A consequence of this would be the predominance of decapods in oligotrophic regions, for instance, the Mediterranean, the Bay of Biscay (Sulak, 1982), or in abyssal zones (Haedrich *et al.*, 1980). In contrast, other deep-sea benthic invertebrate groups, particularly ophiuroids, predominate in more eutrophic zones.

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