Analysis of the structure of decapod crustacean assemblages off the Catalan coast (North-West Mediterranean)

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Abstract

We sampled the communities of decapod crustaceans inhabiting the depth zone between 3 and 871 m off the Catalan coast (North-West Mediterranean) from June 1981 to June 1983. The 185 samples comprised 90 species differing widely in their depth distributions. Multivariate analysis revealed four distinct faunistic assemblages, (1) littoral communities over sandy bottoms, (2) shelf communities over terrigenous muds, (3) upper-slope communities, and (4) lower-slope or bathyal communities. The brachyuran crab *Liocarcinus depurator* is the most abundant species of the shelf assemblage, although *L. vernalis* dominates over the shallow sandy bottoms of the shelf. The dominant species of the upper-slope assemblage are nektobenthic species (*Solenocera membranacea, Plesionika heterocarpus, Processa canaliculata*), pelagic species (*Pasiphaea sivado, Sergestes arcticus*), and benthic species (*Macropipus tuberculatus, Munida intermedia, Nephrops norvegicus*). *Aristeus antennatus* comprise most of the biomass of the lower-slope community, which supports a greater diversity than the other assemblages. The main assemblages appear to be related to different hydrological characteristics, the extent of seasonal fluctuations, and to the changes in sediment structure associated with changes in the steepness of the bottom.

Introduction

The study of the benthic animal communities inhabiting the continental shelf and slope is an important aspect of marine ecology, particularly in areas such as the Spanish Mediterranean coast, where these communities have a significant commercial value. Unfortunately, the ecology and biology of the decapod crustacean communities of this area have received little attention. Most studies examine different aspects of the taxonomy of these animals (e.g.

Zariquiey Álvarez 1968, García Raso 1981, 1982, 1984), as well as different biological aspects of the economically important species (Sardá 1980, Sardá et al. 1981, etc.). More recently, some studies of the species distribution of the decapod crustacean communities of the North-West Mediterranean have been published (Sardá and Palomera 1981, Castellón and Abelló 1983, Carbonell 1984, Abelló 1986). However, the quantitative composition of the decapod crustacean communities of this area remain largely unknown, and comparable efforts to those of Arena and Li Greci (1973), Relini (1981), or Tunesi (1986) are lacking.

The present study contributes to the knowledge of the ecology of soft-bottom decapod-crustacean communities off the Catalonian coast by (1) describing their faunistic composition, (2) quantifying the depth distribution and relative abundance of the individual decapod species, and (3) defining the main faunistic assemblages of the area. The composition of the assemblages has been established using cluster analysis and correspondence analysis (Chardy et al. 1976, Lleonart 1981, González Gurriarán 1982, Penas and González Gurriarán 1982, Romero et al. 1982, Wenner and Read 1982, Lleonart and Roel 1984, González Gurriarán 1986, inter alia).

Materials and methods

This study is part of a broader research program of the Instituto de Ciencias del Mar (Barcelona) directed to the study of the demersal fisheries off the Catalan coast. The decapod crustacean communities were sampled from commercial trawlers using bottom nets of 9 mm-mesh size. Trawls of 1 to 2 h were made, depending on the characteristics of the sampling area along the shelf and slope (3 to 871 m depth range, Fig. 1). A total of 185 trawls were completed between June 1981 and May 1983.

The animals captured in each trawl were sorted to species, weighed and counted, and the data for each
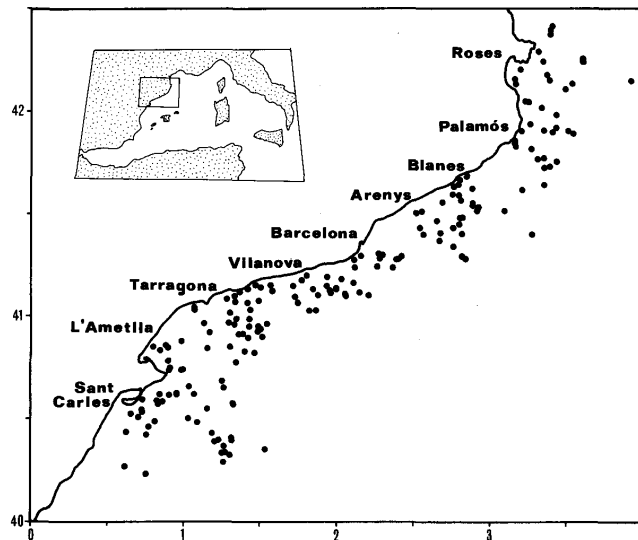
Fig. 1. Position of trawls made in 1981–1983 off the Catalan coast, North-West Mediterranean

species was expressed as number and weight of individuals per hour of trawling. Because the trawls were made using different vessels, the quantitative data gathered can be regarded only as approximative. Any such imprecision must, however, be small, since the differences in the depth distribution and relative abundance of the different species were remarkably clear.

The depth distributions of the various species was obtained by calculating their average abundance over depth intervals of 100 m for the slope (> 200 m deep), and for narrower strata on the shelf (0 to 25 m, 25 to 50 m, 50 to 100 m, 100 to 150 m and 150 to 200 m deep). The narrower depth strata of the shelf zone were selected to account for the greater steepness of the environmental gradients associated with depth variations within this zone. The average depth of each trawl path was used to assign it to a depth stratum.

The composition of the species collected on each trawl was used to define faunistic assemblages. This was achieved through cluster analysis and correspondence analysis applied to the presence-absence data for the most important species (42) obtained in 95 trawls. Only 42 species were used in these analyses because the remaining were too rare (i.e., large number of absences), and therefore must play a minor role in structuring the communities. Those trawls where the difference between maximum and minimum depth was greater than 50 m on the slope and 20 m on the shelf were excluded from the analyses, because they could have sampled different communities. For the analyses, the presence-absence of the species was preferred to their abundances, since a large number of absences weakens the robustness of abundance data (Lleonart 1979, Lleonart and Roel 1984).

The cluster analyses were performed using the point-correlation similarity-index and the UPGMA (unweighted pair group method of analysis) aggregation algorithm (Lleonart and Roel 1984). Correspondence analysis was used because it allows the simultaneous comparison of the distribution of species and their association with particular trawls in the same space. The diversity index was calculated using the equation of Shannon-Wiener (Margalef 1974).

Results

Faunistic composition

The samples were comprised of 90 species of decapod crustaceans (Table 1). The Brachyura was the infraorder with most species (35 species), followed by the Caridea (22 species), Anomura (17), and the suborder Dendrobranchiata (9). Only four species of Palinura were found; the infraorder Thalassinidea was represented by only two species, and the Astacidea by a single species.

Species bathymetric distribution and abundance

The dominant species differed among depth strata (Table 2), confirming the importance of depth in structuring crustacean decapod communities. The depth range, total number of presences, and average abundance within the different strata for each species (Table 3) also demonstrate quantifiable differences in the distribution of crustaceans. The depth differences in the structure of decapod crustacean communities is further evidenced by examination of the relative abundances (Fig. 2) and biomass (Fig. 3) of the dominant species within each depth stratum.

Table 1. Decapod crustacean species (order Decapoda) collected by trawling off Catalan coast (North-West Mediterranean) during sampling program (1981–1983)

Suborder Dendrobranchiata
    Superfamily Penaeoidea
        Family Aristeidae
            Aristaeomorpha foliacea (Risso, 1827)
            Aristeus antennatus (Risso, 1816)
            Gennadas elegans (S. I. Smith, 1884)
        Family Penaeidae
            Parapenaeus longirostris (H. Lucas, 1846)
            Penaeus kerathurus (Forskal, 1775)
        Family Solenoceridae
            Solenocera membranacea (Risso, 1816)
        Family Sicyoniidae
            Sicyonia carinata (Brünnich, 1768)
    Superfamily Sergestoidea
        Family Sergestidae
            Sergestes arcticus Kröyer, 1855
            Sergia robusta (S. I. Smith, 1882)

Suborder Pleocyemata
    Infraorder Caridea
        Family Oplophoridae
            Acanthephyra eximia S. I. Smith, 1886
            Acanthephyra pelagica (Risso, 1816)
        Family Pasiphaeidae
            Pasiphaea multidentata Esmark, 1866
            Pasiphaea sivado (Risso, 1816)
        Family Palaemonidae
            Periclimenes granulatus Holthuis, 1950
        Family Alpheidae
            Alpheus glaber (Olivi, 1792)
        Family Hippolitidae
            Ligur ensiferus (Risso, 1816)
        Family Processidae
            Processa canaliculata Leach, 1815
            Processa nouveli Al-Adhub & Williamson, 1975
        Family Pandalidae
            Chlorotocus crassicornis (Costa, 1871)
            Pandalina profunda Holthuis, 1946
            Plesionika acanthonotus (S. I. Smith, 1882)
            Plesionika edwardsii (Brandt, 1851)
            Plesionika gigliolii (Senna, 1903)
            Plesionika heterocarpus (Costa, 1871)
            Plesionika martia (A. Milne Edwards, 1883)
        Family Crangonidae
            Crangon crangon (Linnaeus, 1758)
            Philocheras echinulatus (M. Sars, 1861)
            Pontocaris cataphracta (Olivi, 1792)
            Pontocaris lacazei (Gourret, 1887)
            Pontophilus norvegicus (M. Sars, 1861)
            Pontophilus spinosus (Leach, 1815)
    Infraorder Astacidea
        Family Nephropidae
            Nephrops norvegicus (Linnaeus, 1758)
    Infraorder Thalassinidea
        Family Axiidae
            Calocaris macandreae Bell, 1846
        Family Upogebiidae
            Upogebia tipica (Nardo, 1869)
    Infraorder Palinura
        Family Polychelidae
            Polycheles typhlops Heller, 1862
        Family Palinuridae
            Palinurus mauritanicus Gruvel, 1911
        Family Scyllaridae
            Scyllarus arctus (Linnaeus, 1758)
            Scyllarus pygmaeus (Bate, 1888)
    Infraorder Anomura
        Family Diogenidae
            Dardanus arrosor (Herbst, 1796)
            Diogenes pugilator (Roux, 1829)
            Paguristes eremita (Linnaeus, 1767)
        Family Paguridae
            Anapagurus bicorniger A. Milne Edwards & Bouvier, 1892

            Anapagurus laevis (Bell, 1846)
            Pagurus alatus Fabricius, 1775
            Pagurus cuanensis Bell, 1845
            Pagurus excavatus (Herbst, 1791)
            Pagurus forbesii Bell, 1845
            Pagurus prideaux Leach, 1815
        Family Galatheidae
            Galathea cenarroi Zariquiey Álvarez, 1968
            Galathea dispersa Bate, 1859
            Galathea intermedia Lilljeborg, 1851
            Munida intermedia A. Milne Edwards & Bouvier, 1899
            Munida iris Zariquiey Álvarez, 1952
            Munida tenuimana G. O. Sars, 1872
        Family Porcellanidae
            Pisidia longicornis (Linnaeus, 1767)
    Infraorder Brachyura
        Section Archaeobrachyura
            Family Homolidae
                Homola barbata (Fabricius, 1793)
                Paromola cuvieri (Risso, 1816)
        Section Oxystomata
            Family Dorippidae
                Ethusa mascarone (Herbst, 1785)
                Medorippe lanata (Linnaeus, 1767)
            Family Calappidae
                Calappa granulata (Linnaeus, 1767)
            Family Leucosiidae
                Ebalia deshayesi Lucas, 1846
                Ilia nucleus (Linnaeus, 1758)
        Section Oxyrhyncha
            Family Majidae
                Dorhynchus thomsoni Thomson, 1873
                Eurynome aspera (Pennant, 1777)
                Inachus communissimus Rizza, 1839
                Inachus dorsettensis (Pennant, 1777)
                Inachus thoracicus (Roux, 1830)
                Macropodia linaresi Forest & Zariquiey Álvarez, 1964
                Macropodia longipes (A. Milne Edwards & Bouvier, 1899)
                Macropodia rostrata (Linnaeus, 1761)
                Maja crispata Risso, 1827
                Maja squinado (Herbst, 1788)
                Pisa armata (Latreille, 1803)
            Family Parthenopidae
                Parthenope macrochelos (Herbst, 1790)
                Parthenope massena (Roux, 1830)
        Section Cancridea
            Family Atelecyclidae
                Atelecyclus rotundatus (Olivi, 1792)
            Family Corystidae
                Corystes cassivelaunus (Pennant, 1777)
            Family Thiidae
                Thia scutellata (Fabricius, 1793)
        Section Brachyrhyncha
            Family Geryonidae
                Geryon longipes A. Milne Edwards, 1881
            Family Portunidae
                Carcinus mediterraneus Czerniavsky, 1884
                Liocarcinus depurator (Linnaeus, 1758)
                Liocarcinus maculatus (Risso, 1827)
                Liocarcinus puber (Linnaeus, 1767)
                Liocarcinus vernalis (Risso, 1816)
                Macropipus tuberculatus (Roux, 1830)
            Family Goneplacidae
                Goneplax rhomboides (Linnaeus, 1758)
            Family Xanthidae
                Monodaeus couchii (Couch, 1851)
                Pilumnus spinifer H. Milne Edwards, 1834
            Family Grapsidae
                Brachynotus sexdentatus (Risso, 1827)
            Family Pinnotheridae
                Pinnotheres pinnotheres (Linnaeus, 1758)

Table 2. Species collected from different depth strata, listed in order of decreasing relative frequency. Only those species appearing in more than half of the trawls made within each stratum have been included

0–25 m	25–50 m	50–100 m	100–150 m	150–200 m
Liocarcinus depurator	*Liocarcinus depurator*	*Liocarcinus depurator*	*Liocarcinus depurator*	*Liocarcinus depurator*
Goneplax rhomboides	*Medorippe lanata*			*Macropipus tuberculatus*
Medorippe lanata				*Solenocera membranacea*
Liocarcinus vernalis				*Macropodia longipes*
				Plesionika heterocarpus

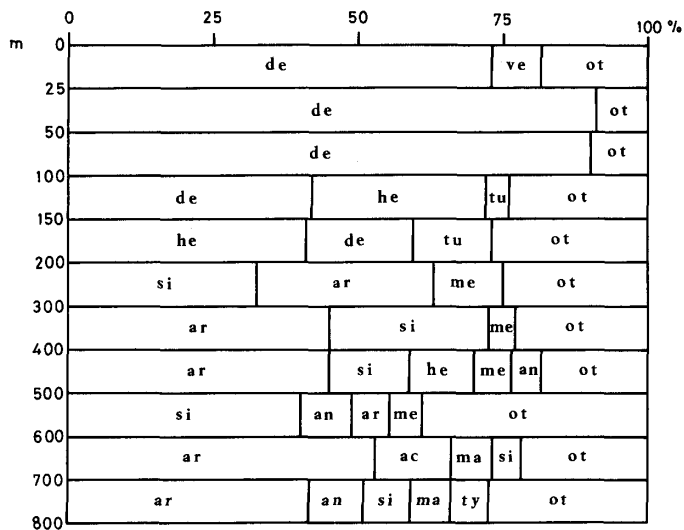| 200–300 m	300–400 m	400–500 m	500–800 m
Munida intermedia	*Pasiphaea sivado*	*Solenocera membranacea*	*Polycheles typhlops*
Nephrops norvegicus	*Nephrops norvegicus*	*Plesionika martia*	*Pasiphaea multidentata*
Liocarcinus depurator	*Munida intermedia*	*Processa canaliculata*	*Plesionika martia*
Macropipus tuberculatus	*Macropipus tuberculatus*	*Nephrops norvegicus*	*Solenocera membranacea*
Solenocera membranacea	*Solenocera membranacea*	*Pasiphaea sivado*	*Munida intermedia*
Plesionika heterocarpus	*Pontophilus spinosus*	*Pontocaris lacazei*	*Pasiphaea sivado*
Processa canaliculata	*Pontocaris lacazei*	*Munida intermedia*	*Pontocaris lacazei*
Pasiphaea sivado	*Processa canaliculata*	*Sergestes arcticus*	*Processa canaliculata*
Pontophilus spinosus	*Liocarcinus depurator*	*Pasiphaea multidentata*	*Sergestes arcticus*
	Sergestes arcticus	*Calocaris macandreae*	*Nephrops norvegicus*
	Pasiphaea multidentata	*Polycheles typhlops*	*Calocaris macandreae*
	Philocheras echinulatus	*Macropipus tuberculatus*	*Pontophilus spinosus*
	Plesionika martia	*Sergia robusta*	*Aristeus antennatus*
		Pontophilus spinosus	*Sergia robusta*
			Munida tenuimana
			Plesionika acanthonotus
			Philocheras echinulatus
			Liocarcinus depurator
			Pagurus alatus

Fig. 2. Relative abundance of dominant species within each depth stratum. ac: *Plesionika acanthonotus;* an: *Aristeus antennatus;* ar: *Sergestes arcticus;* de: *Liocarcinus depurator;* he: *Plesionika heterocarpus;* ma: *Plesionika martia;* me: *Solenocera membranacea;* si: *Pasiphaea sivado;* tu: *Macropipus tuberculatus;* ty: *Polycheles typhlops;* ve: *Liocarcinus vernalis;* ot: other species

Cluster analysis

Classification of trawls

The dendrogram of similarities among trawls shows that the individual trawls displayed somewhat different species distributions (Fig. 4), although four main groups can be clearly defined, probably corresponding to four distinct faunistic assemblages. The first branching of the similarity tree clearly discriminates between shelf (P) and slope (T) trawls (Figs. 4 and 5). The shelf trawls can be further divided into shallow trawls over sandy bottoms (P1), and trawls over terrigenous mud (P2). The assemblage P1 included nine trawls with a mean depth of 22.9 m (stan-
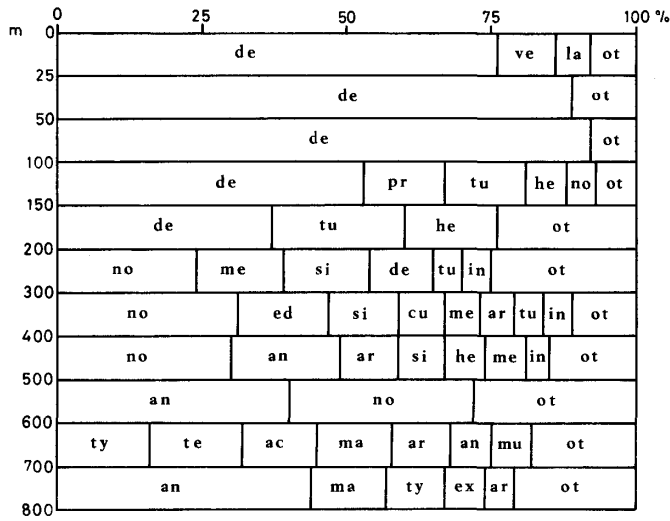
Fig. 3. Relative biomass of dominant species within each depth stratum. ac: *Plesionika acanthonotus;* an: *Aristeus antennatus;* ar: *Sergestes arcticus;* cu: *Paromola cuvieri;* de: *Liocarcinus depurator;* ed: *Plesionika edwardsii;* ex: *Acanthephyra eximia;* he: *Plesionika heterocarpus;* in: *Munida intermedia;* la: *Medorippe lanata;* ma: *Plesionika martia;* me: *Solenocera membranacea;* mu: *Pasiphaea multidentata;* no: *Nephrops norvegicus;* pr: *Pagurus prideaux;* si: *Pasiphaea sivado;* te: *Munida tenuimana;* tu: *Macropipus tuberculatus;* ty: *Polycheles typhlops;* ve: *Liocarcinus vernalis;* ot: other species
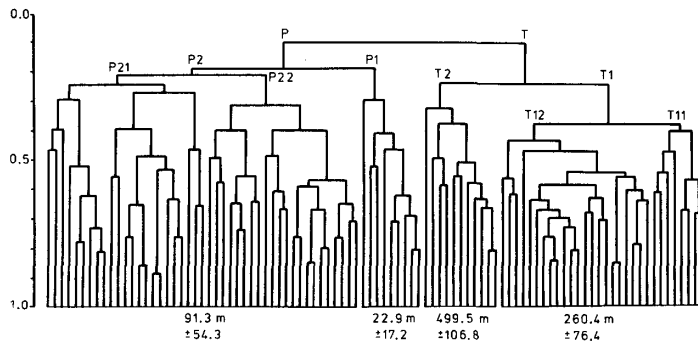

Fig. 4. Similarities between trawls. Cluster analysis. Mean depth (± standard deviation of each major cluster is given. Ordinate shows similarity (correlation). P: shelf assemblage; T: slope assemblage; P1: sand group; P2: muddy-shelf group; P21 and P22: shelf subgroups; T2: deep-slope group; T1: upper-slope group; T11 and T12: upper-slope subgroups
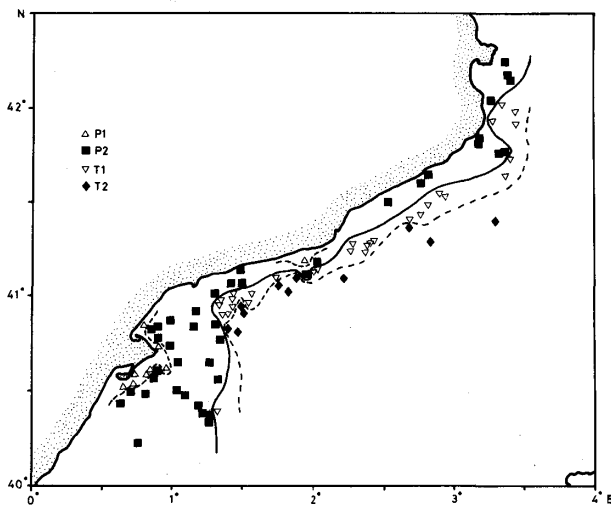

Fig. 5. Location of four groups of trawls discriminated by cluster analysis in sampling zone. P1: sand group; P2: muddy-shelf group; T1: upper-slope group; T2: deep-slope group. Continuous line separates Group P (shelf) trawls from Group T (slope) trauls, and approximately corresponds to 200 m isobath; dashed lines separate P1 from P2 assemblage and T1 from T2 assemblage

Table 3. Average abundance (number of individuals captured per hour of trawling) of decapod species collected during sampling program, depth strata, depth range, and number of presences (i.e., number of trawls in which species were collected). Species arranged in alphabetical order. +: less than one individual per hour of trawling; –: absent

Species	Depth strata (m)											Depth range (m)	(No. of presences)
	0–25	25–50	50–100	100–150	150–200	200–300	300–400	400–500	500–600	600–700	700–800		
Acanthephyra eximia	–	–	–	–	–	–	–	–	–	1	10	549–871	(4)
Acanthephyra pelagica	–	–	–	–	+	–	–	–	+	–	1	176–803	(3)
Alpheus glaber	36	12	58	10	5	5	9	1	1	+	+	3–871	(65)
Anapagurus bicorniger	–	+	–	–	–	–	–	–	–	–	–	26– 26	(1)
Anapagurus laevis	–	–	–	–	–	–	+	–	+	–	–	348–544	(2)
Aristaeomorpha foliacea	–	–	–	–	–	–	+	1	+	1	–	273–748	(9)
Aristeus antennatus	–	–	–	–	+	10	4	55	60	12	27	176–871	(15)
Atelecyclus rotundatus	28	1	+	–	–	–	–	–	–	–	–	9– 37	(9)
Brachynotus sexdentatus	5	–	–	–	–	–	–	–	–	–	–	9– 11	(1)
Calappa granulata	–	–	+	+	–	–	–	–	–	–	–	70–128	(3)
Calocaris macandreae	–	–	–	–	–	+	3	5	2	2	2	201–871	(25)
Carcinus mediterraneus	+	+	–	–	–	–	–	–	–	–	–	15– 26	(2)
Chlorotocus crassicornis	–	–	1	8	1	2	2	–	–	1	–	55–641	(22)
Corystes cassivelaunus	20	–	+	–	–	–	–	–	–	–	–	9– 62	(6)
Crangon crangon	1	–	–	–	–	–	–	–	–	–	–	3– 6	(1)
Dardanus arrosor	+	2	+	+	3	+	1	+	+	–	–	3–723	(28)
Diogenes pugilator	3	–	–	–	–	–	–	–	–	–	–	3– 26	(3)
Dorhynchus thomsoni	–	–	–	–	–	+	–	+	–	–	–	280–454	(2)
Ebalia deshayesi	–	–	–	–	–	–	+	–	–	–	–	348–348	(1)
Ethusa mascarone	1	–	–	–	–	–	–	–	–	–	–	15– 22	(1)
Eurynome aspera	–	+	–	–	–	–	–	–	–	–	–	33– 42	(1)
Galathea cenarroi	–	–	+	–	–	–	–	–	–	–	–	48– 60	(1)
Galathea dispersa	–	+	+	–	–	–	–	–	–	–	–	24– 91	(2)
Galathea intermedia	–	–	+	–	–	–	–	–	–	–	–	51– 91	(2)
Gennadas elegans	–	–	–	–	–	–	+	–	13	+	2	366–803	(5)
Geryon longipes	–	–	–	–	–	–	–	–	1	+	–	439–723	(2)
Goneplax rhomboides	17	7	22	1	2	1	1	4	1	–	–	3–748	(50)
Homola barbata	–	–	–	+	+	–	+	–	+	–	–	128–637	(4)
Ilia nucleus	+	–	–	–	–	–	–	–	–	–	–	15– 22	(1)
Inachus communissimus	1	1	+	+	+	–	–	–	–	–	–	13–174	(10)
Inachus dorsettensis	–	+	+	–	–	–	–	–	–	–	–	26– 91	(4)
Inachus thoracicus	–	+	+	–	–	–	–	–	–	–	–	33– 91	(2)
Ligur ensiferus	–	–	–	–	–	–	–	–	+	–	–	439–871	(1)
Liocarcinus depurator	876	684	1131	113	40	26	8	1	4	4	1	3–871	(135)
Liocarcinus maculatus	+	+	–	–	–	–	–	–	–	–	–	15– 48	(3)
Liocarcinus puber	+	–	–	–	–	–	–	–	–	–	–	3– 22	(3)
Liocarcinus vernalis	102	2	+	–	–	–	–	–	–	–	–	3– 62	(12)
Macropipus tuberculatus	–	–	2	12	29	15	20	15	1	+	–	48–748	(72)
Macropodia linaresi	–	+	–	–	–	–	–	–	–	–	–	26– 59	(1)
Macropodia longipes	5	+	2	4	6	+	1	+	1	–	–	18–748	(48)
Macropodia rostrata	15	1	1	1	+	–	–	–	–	–	–	3–183	(16)
Maja crispata	–	–	+	–	–	–	–	–	–	–	–	66– 95	(1)
Maja squinado	–	–	+	+	–	–	–	–	–	–	–	48–128	(3)
Medorippe lanata	49	13	20	+	2	–	+	+	1	+	+	9–769	(51)
Monodaeus couchii	–	–	–	+	–	–	+	+	+	–	–	137–748	(8)
Munida intermedia	–	+	1	1	2	14	34	42	6	2	2	35–871	(77)
Munida iris	–	–	–	–	–	+	–	–	–	–	–	220–282	(1)
Munida tenuimana	–	–	–	–	–	–	3	1	5	2	1	348–803	(15)
Nephrops norvegicus	–	–	+	3	2	22	71	67	68	8	1	66–871	(76)
Paguristes eremita	1	+	–	–	–	–	–	–	–	–	–	15– 40	(4)
Pagurus alatus	–	–	–	–	+	2	2	1	2	1	–	136–748	(26)
Pagurus cuanensis	1	+	+	+	–	–	–	–	–	–	–	15–146	(7)
Pagurus excavatus	7	1	11	1	1	–	–	–	–	–	–	9–220	(38)
Pagurus forbesii	–	+	–	–	–	–	–	–	–	–	–	37– 58	(1)
Pagurus prideaux	+	2	4	20	2	+	–	–	–	–	–	15–260	(28)
Palinurus mauritanicus	–	–	+	–	–	1	+	+	+	–	–	66–748	(12)
Pandalina profunda	–	–	–	–	–	–	–	+	–	–	–	421–439	(1)
Parapenaeus longirostris	–	–	+	+	1	1	+	1	+	–	–	70–586	(17)
Paromola cuvieri	–	–	–	–	+	+	+	+	+	–	–	136–748	(15)
Parthenope macrochelos	+	–	–	+	+	–	+	–	–	–	–	20–370	(4)
Parthenope massena	+	–	–	–	–	–	–	–	–	–	–	15– 22	(1)

Table 3 (continued)

Species	Depth strata (m)											Depth range (m)	(No. of presences)
	0–25	25–50	50–100	100–150	150–200	200–300	300–400	400–500	500–600	600–700	700–800		
Pasiphaea multidentata	–	–	–	–	+	34	8	20	28	8	3	128–871	(36)
Pasiphaea sivado	–	1	–	+	7	299	524	179	261	19	22	33–871	(56)
Penaeus kerathurus	5	2	+	+	–	–	–	–	–	–	–	3–126	(11)
Periclimenes granulatus	–	–	–	–	–	–	–	–	–	–	–	623–803	(1)
Philocheras echinulatus	–	–	+	+	1	2	13	4	3	2	5	55–871	(34)
Pilumnus spinifer	+	4	+	–	–	–	–	–	–	–	–	16– 88	(5)
Pinnotheres pinnotheres	–	–	+	+	1	–	–	–	–	–	–	48–220	(6)
Pisa armata	–	+	+	–	–	–	–	–	–	–	–	22– 88	(3)
Pisidia longicornis	–	6	+	–	–	–	–	–	–	–	–	22– 91	(6)
Plesionika acanthonotus	–	–	–	–	+	–	4	1	13	48	14	165–803	(17)
Plesionika edwardsii	–	–	–	–	–	1	97	–	–	–	–	256–512	(5)
Plesionika gigliolii	–	–	–	+	–	3	1	–	+	–	–	101–748	(5)
Plesionika heterocarpus	–	–	+	81	89	15	6	140	–	3	–	82–699	(45)
Plesionika martia	–	–	–	–	1	1	8	19	23	26	20	165–871	(41)
Polycheles typhlops	–	–	–	–	–	+	1	3	13	16	18	267–871	(28)
Pontocaris cataphracta	+	7	1	–	–	–	–	–	–	–	–	3– 95	(9)
Pontocaris lacazei	13	5	4	1	1	4	9	8	11	2	2	13–871	(72)
Pontophilus norvegicus	–	–	–	–	–	–	4	+	+	4	1	366–803	(6)
Pontophilus spinosus	–	–	+	10	4	8	9	11	8	–	6	70–871	(61)
Processa canaliculata	–	–	+	1	6	62	116	32	30	9	7	70–871	(73)
Processa nouveli	–	–	–	–	–	2	–	–	–	–	–	212–220	(1)
Scyllarus arctus	–	–	+	–	–	–	–	–	–	–	–	62– 91	(1)
Scyllarus pygmaeus	–	+	–	–	–	–	–	–	–	–	–	37– 58	(1)
Sergestes arcticus	–	–	–	–	–	278	858	586	42	200	117	180–803	(36)
Sergia robusta	–	–	–	–	–	–	2	12	21	6	9	220–871	(24)
Sicyonia carinata	6	+	–	–	–	–	–	–	–	–	–	13– 27	(4)
Solenocera membranacea	1	2	2	3	9	112	92	88	37	4	11	3–871	(91)
Thia scutellata	–	+	–	–	–	–	–	–	–	–	–	26– 59	(1)
Upogebia tipica	+	–	–	–	–	–	–	–	–	–	–	16– 18	(1)

Table 4. Average diversity, standard deviation (*S*) and number of samples (*N*) for each of four assemblages distinguished by cluster analysis

Assemblage	Diversity	*S*	*N*
Shelf-sand	2.05	0.92	9
Shelf-mud	1.46	0.81	45
Upper slope	1.90	0.86	30
Deep slope	2.70	0.58	11

dard deviation = 17.2 m). Cluster P2 comprised 45 samples with a mean depth of 91.3 m (sd = 54.3). The two groups of trawls differ significantly (Student's *t*-test, *P* < 0.05) in their mean depths. Further subdivisions of Cluster P2 (P21, mean depth = 102 ± 63.0 m; P22, mean depth = 80 ± 42 m) do not differ significantly in their mean depths (Student's *t*-test, *P* > 0.05). Examination of the subdivisions of the slope cluster (T) indicates that it can also be separated into an upper (T1), and lower or bathyal subgroup (T2). The mean depth of Group T1 (260.4 ± 76.4 m) is significantly different (Student's *t*-test, *P* < 0.05) from that of Group T2 (499.5 ± 106.8 m). Differences between the mean depths of subdivisions of Cluster T1

(T11 and T12) are close to our *P* = 0.05 significance threshold (Student's *t* = 2.28).

The cluster analysis (Fig. 4) does not allow a clear distinction between a littoral or shallow-water and a shelf assemblage, since both overlap at ca. 40 m. In contrast, the bathymetrical division between the shelf and slope groups is clear, and located at about 150 to 180 m. Finally, the limits between the upper and the lower slope can be located at about 350 to 400 m depth.

Diversity

The average diversity of the four assemblages defined tends to increase with depth (Table 4). This tendency is particularly evident in the comparison of the muddy shelf and the slope assemblages. The diversity reaches a maximum over the deep slope.

Classification of species

Cluster analysis of the species presences revealed the existence of two well-defined species assemblages (Fig. 6). A group comprising the shallow-littoral and shelf species
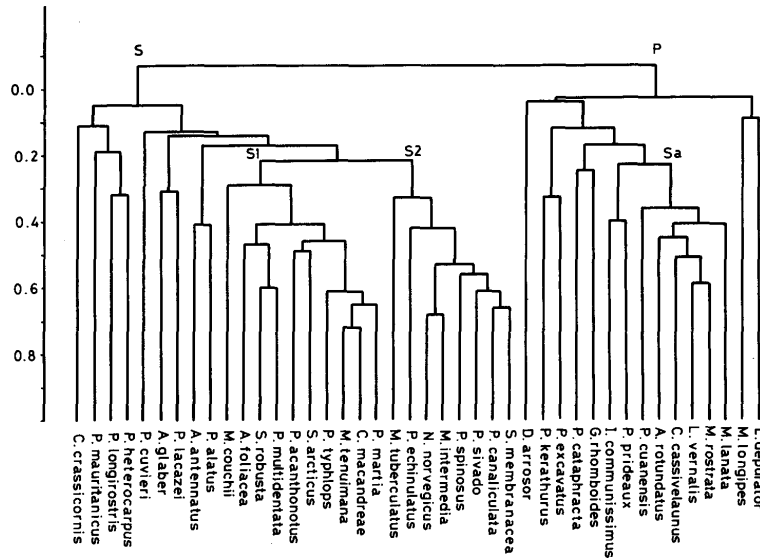
Fig. 6. Similarities among species. (Cluster analysis). Ordinate shows similarity (correlation) P: shelf assemblage; Sa: sand assemblage; S: slope assemblage; S1: deep-slope assemblage; S2: upper-slope assemblage. Full specific names are given in Table 5

Table 5. Species included in correspondence analysis, listed in decreasing order of number of presences. Code numbers (CN) are those used in correspondence analysis shown in Fig. 7

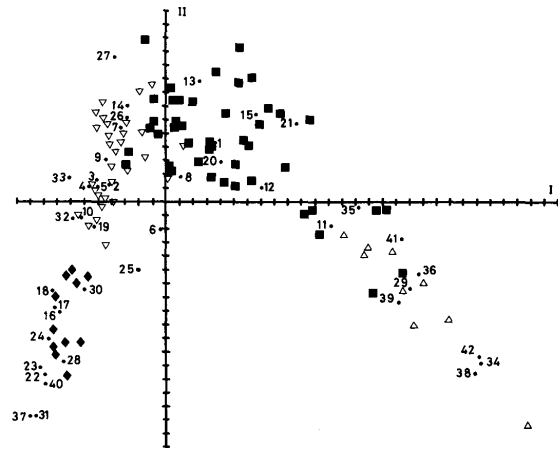| CN	Species	CN	Species
1	*Liocarcinus depurator*	22	*Polycheles typhlops*
2	*Solenocera membranacea*	23	*Calocaris macandreae*
3	*Munida intermedia*	24	*Sergia robusta*
4	*Nephrops norvegicus*	25	*Pagurus alatus*
5	*Processa canaliculata*	26	*Chlorotocus crassicornis*
6	*Pontocaris lacazei*	27	*Parapenaeus longirostris*
7	*Macropipus tuberculatus*	28	*Plesionika acanthonotus*
8	*Alpheus glaber*	29	*Macropodia rostrata*
9	*Pontophilus spinosus*	30	*Aristeus antennatus*
10	*Pasiphaea sivado*	31	*Munida tenuimana*
11	*Medorippe lanata*	32	*Paromola cuvieri*
12	*Goneplax rhomboides*	33	*Palinurus mauritanicus*
13	*Macropodia longipes*	34	*Liocarcinus vernalis*
14	*Plesionika heterocarpus*	35	*Penaeus kerathurus*
15	*Pagurus excavatus*	36	*Inachus communissimus*
16	*Plesionika martia*	37	*Aristaeomorpha foliacea*
17	*Pasiphaea multidentata*	38	*Atelecyclus rotundatus*
18	*Sergestes arcticus*	39	*Pontocaris cataphracta*
19	*Philocheras echinulatus*	40	*Monodaeus couchii*
20	*Dardanus arrosor*	41	*Pagurus cuanensis*
21	*Pagurus prideaux*	42	*Corystes cassivelaunus*

Fig. 7. Correspondence analysis. Distribution of species and trawls as function of first two axes. Symbols representing trawls are same as in Fig. 5 (trawl assemblages obtained with cluster analysis); code numbers of species are as in Table 5

(P), and a group of slope species (S). Further subdivisions allowed the definition of a group of sandy-bottom species (Sa), with high similarity indexes among them. The remaining species of the slope cluster occurred over muddy shelf substrates, and are more loosely related, perhaps reflecting their wide depth ranges. The slope assemblage can be subdivided into a deep slope (S1) group, a group of species that inhabit the upper slope (S2), and a less coherent group of species with wide bathymetric distributions.

Correspondence analysis

The structure underlying the distribution of trawls and species was defined using this analysis. The ordination of the 42 species (Table 5) and 95 trawls is reflected in their position relative to the first two axes (Fig. 7), where the four different assemblages obtained in the cluster analysis of the trawls are represented by different symbols. The first axis explains 16.43% of the variance, the second explains 9.00%.

The position of the trawls and species along the first two axes (Fig. 7) reveals the existence of a gradient associated with depth variations, indicating the presence of the Guttman effect. This phenomenon is characteristic of samples where the species respond in a non-linear fashion to an environmental gradient (Lleonart 1979).

The greater scores for the first axis correspond to sandy-bottom species: *Corystes cassivelaunus* (Code No. 42), *Atelecyclus rotundatus* (38), and *Liocarcinus vernalis* (34); followed by a group of shallow-water shelf species: *Pontocaris cataphracta* (39), *Macropodia rostrata* (29), *Inachus communissimus* (36), *Pagurus cuanensis* (41), *Medorippe lanata* (11) and *Penaeus kerathurus* (35). These two groups have negative scores on the second axis.

A group of typical shelf species has smaller scores for the first axis, but positive scores on the second axis: *Goneplax rhomboides* (12), *Pagurus prideaux* (21), *P. excavatus* (15), *Dardanus arrosor* (20), *Liocarcinus depurator* (1), *Alpheus glaber* (8), and *Macropodia longipes* (13).

The upper-slope species have negative scores for the first axis, and have both positive [*Parapenaeus longirostris* (27), *Plesionika heterocarpus* (14), *Chlorotocus crassicornis* (26), *Macropipus tuberculatus* (7), *Pontophilus spinosus* (9), *Palinurus mauritanicus* (33), *Munida intermedia* (3), *Nephrops norvegicus* (4), *Processa canaliculata* (5) and *Solenocera membranacea* (2)] and negative [*Pasiphaea sivado* (10), *Paromola cuvieri* (32), *Philocheras echinulatus* (19) and *Pontocaris lacazei* (6)] scores for the first axis, the species with positive scores being the most closely associated with the upper slope.

These are followed by species characteristic of the deepest slope: *Pagurus alatus* (25), *Aristeus antennatus* (30), *Sergestes arcticus* (18), *Pasiphaea multidentata* (17), *Plesionika martia* (16), *Sergia robusta* (24), *Plesionika acanthonotus* (28), *Calocaris macandreae* (23), *Polycheles typhlops* (22), *Monodaeus couchii* (40), *Aristaeomorpha foliacea* (37) and *Munida tenuimana* (31), all with negative scores.

The bathyal group of trawls is clearly differentiated from the upper slope. The trawls of the shelf group have a great heterogeneity in their position along the axes, overlapping slightly with the upper-slope group. The shallowest trawls are located at opposite extremes of the gradient, and are associated with the sandy-bottom species.

Discussion

The results provide considerable information about the composition and structure of the communities of demersal decapod crustaceans, and reveal important features of the ecological characteristics and distribution of the species studied. They allow the differentiation of the decapod crustaceans of the Catalan coast into shallow-water shelf species inhabiting sandy bottoms, muddy-shelf species, upper-slope species, and bathyal species.

The delimitation between the shelf assemblage and the littoral or shallow-water assemblage is dependent not only on the bathymetric position of the samples, but also on the substrate granulometry (sand or silt-clay). Although species with a high frequency of presences are rare in the shelf area, there is considerable heterogeneity evidenced in the dispersion of these samples about the correspondence axes. This heterogeneity can result from the hydrological variations experienced in this zone as the result of (1) seasonal changes in water temperature, (2) mixing of surface water of Atlantic origin, intermediate water of eastern Mediterranean origin, and continental water (Salat and Cruzado 1981), and (3) the habitat complexity introduced by differences in sediment composition, rock outcrops, and seagrass meadows. The importance of substrate type is supported by the findings of Desbruyères et al. (1972/1973), who distinguished three different types of benthic communities on the Catalan coast associated with different sediment granulometry (i.e., fine sand, sand-mud transition areas, and muddy substrates).

Brachyuran crabs were the most frequent and abundant species over the continental shelf (< 200 m). Among them, *Liocarcinus depurator* was the dominant species both by biomass and number, particularly in sites <100 m deep. The dominant species of the shallowest zone (<25 m) were, in order of decreasing abundance, *Liocarcinus vernalis, Corystes cassivelaunus* and *Atelecyclus rotundatus.* Other species abundant in this zone were *Goneplax rhomboides* and *Medorippe lanata;* all were characterized by wide bathymetrical distributions over muddy bottoms, but with peak abundance on the shelf.

The communities between 100 and 200 m were dominated by *Macropipus tuberculatus,* together with *Liocarcinus depurator* and *Plesionika heterocarpus,* this being the only nektobenthic caridean abundant on the shelf. This depth range also corresponded to the peak abundance of the shrimp *Alpheus glaber,* and most of the Paguridae and Diogenidae species. However, *Pagurus prideaux* was the only anomuran species which attained sizeable densities in this area.

The area below the geomorphological shelf-slope boundary (ca. 200 m) harbours the centres of distribution of many species (Tables 2 and 3). The upper-slope communities were dominated by *Macropipus tuberculatus, Munida intermedia* and *Nephrops norvegicus.* The latter species is one of the most important local fishery targets. Also very abundant were the nektobenthic species *Solenocera membranacea, Plesionika heterocarpus* and *Processa canaliculata,* which have their maximum abundances in the upper slope (200 to 400 m). Some Crangonidae species of benthic habits (*Pontophilus spinosus, Pontocaris lacazei* and *Philocheras echinulatus*) were also frequent and abundant in this depth range. *Liocarcinus depurator* was also found in this area, although it was not as abundant as in the shelf zone.

The most characteristic benthic species of the deepest portion of the slope were *Polycheles typhlops, Calocaris macandreae, Munida tenuimana* and *Geryon longipes.* The most abundant nektobenthic species of this zone were *Plesionika martia, Aristeus antennatus and P. acanthonotus.*

The differentiation between the two faunistic assemblages corresponding to the slope zone is very sharp, both assemblages containing different species. These observations indicate that the two assemblages described correspond to highly differentiated faunistic communities. The exceptions to this differentiation are the species with pelagic habits (*Pasiphaea multidentata, P. sivado, Sergestes arcticus, Sergia robusta* and *Gennadas elegans*). The differences between the upper- and lower-slope communities can be attributed to hydrological differences between the two habitats. The lower slope is associated with the deep-water mass [temperature = 12.7° to 12.9 °C, salinity = 38.40 to 38.50‰ (Salat and Font 1985)], characterized by a fairly constant temperature over the year. The upper community, in turn, is associated with the warmer intermediate waters located between the upper-water mass of Atlantic origin and the deep-water layer. The depth threshold between the two faunistic assemblages approximately corresponds to the upper limit of the deep-water mass, although this limit can partially disappear in some places and seasons (Salat and Cruzado 1981).

The low diversity of the muddy-shelf bottom-communities can be attributed to the hydrographic heterogeneity characteristic of these uniform and commercially exploited bottoms, where the temperature oscillates widely over the year. The amplitude of seasonal temperature fluctuations decrease with depth. The greater environmental stability of the slope zone allows a more mature, and thus more diverse, community to develop. In addition, the presence of steep bottoms favours the coexistence of pelagic and nektobenthic species (which are relatively independent of benthic resources) with the strictly benthic species, resulting in an increased diversity. The high diversity characteristic of littoral communities inhabiting sandy substrates may be attributed to the influence of neighbouring heterogeneous communities (i.e., coastline, hard bottoms, seagrass meadows).

A similar increase in diversity with increasing depth was reported by Sanders (1968) and Sanders and Hessler (1969), who attributed this observation to increased environmental stability associated with increasing depth. Haedrich et al. (1980) arrived at the same conclusion in explaining the patterns observed in the study of samples collected by trawls from the shelf to the abyssal plain.

Pérès (1985) subdivided the Mediterranean bathyal mud assemblage into three zones of different depths. The upper zone closely corresponds to the upper-slope assemblage defined in this study, the middle zone corresponds to our lower-slope assemblage, and finally his lower subzone corresponds to the deepest bathyal plain. Carpine (1970) placed the limit of the bathyal zone at about 250 to 300 m. Reyss (1972/1973) reported the existence of an ample zone of submarine canyons sharing characteristics of both shelf and bathyal zones (bathylittoral). We located the upper limit of the upper slope zone at about 150 to 180 m and its lower limit at about 350 to 400 m.

In agreement with Wenner and Read (1982), our results demonstrate that the main faunistic discontinuity is that separating the shelf and slope zones. This discontinuity separates a fauna of terrigenous muddy bottoms, experiencing considerable seasonal fluctuations in environmental conditions, from the fauna inhabiting the more stable upper slope. The transition between an upper-slope fauna, and a strictly bathyal fauna is located at about 400 m. The location of the transition zones appears to be defined by hydrological characteristics, the extent of seasonal fluctuations in water temperature, and the changes in sediment structure associated with changes in the steepness of the bottom.

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