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Spatial distribution of deep-sea decapods and euphausiids near the bottom in the northwestern Mediterranean

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Abstract

This study presents data on the occurrence and relative abundance of deep-sea decapod crustaceans and euphausiids, collected between 389 and 1859 m depth, in the water layer immediately adjacent to the bottom (10–140 cm above the bottom). Species were collected using an automatic opening and closing suprabenthic Macer-Giroq sledge in the Catalan Sea slope (western Mediterranean) during 1991 and 1992. The gear consisted of three rectangular mouths (40 × 80 cm) arranged in three tiers, one above the other, sampling simultaneously three separate levels (subsamples) between 10 and 50, 55 and 95, and 100 and 140 cm above the bottom. Results revealed how mesopelagic species [euphausiids, *Sergestes arcticus* Kroyer, *Pasiphaea sivado* (Risso), and *Gennadas elegans* (S.I. Smith)] and some nektobenthic species were concentrated in the uppermost levels, according to high values in indexes of swimming activity (K2, K1). In contrast, endobenthic species (e.g. *Calocaris macandreae* Bell, *Alpheus glaber* (Oliv), and Crangonidae) were closely associated with the lowermost level. The partitioning of vertical space was analogous to that deduced from stomach contents analysis in deep-sea decapods in the same area. Almost all the specimens of *Sergestes arcticus* and *Gennadas elegans* captured were adults. The presence of large individuals of mesopelagic species near the sea floor is ascribed to ontogenetic migrations, which indicate differences between population structure of mesopelagic species near the bottom and in the midwater.

Key words: Benthopelagic boundary layer; Decapod; Deep-sea; Euphausiid; Mediterranean

1. Introduction

Decapod crustaceans and euphausiids are among the predominant groups in the mesopelagic fauna and also form part of the bathyal communities on the upper and

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middle regions of the continental slope (Lagardère, 1970; Markle et al., 1988; Cartes & Sardà, 1992). These species inhabit the greater portion of the water column and carry out diel vertical migrations (Franqueville, 1971; Casanova, 1974; Fasham & Foxton, 1979; Roe, 1984; Heffernan & Hopkins, 1981; Hargreaves, 1984, 1985). Despite the great importance of mesopelagic species in the flow of energy towards the bathyal zone, there is very little information on the distribution and density of these species near the bottom (Omori & Ohta, 1981). Data collected by bottom trawls (Stefanescu & Cartes, 1992; Cartes et al., 1993) are an important source of information, even though this type of gear is not the most suitable for sampling pelagic fauna near the bottom (Merrett, 1986).

There is likewise very little information on possible migrations by nektobenthic species (Pandalidae, Penaeoidea, etc.) in the bathyal zone (Cartes et al., 1993). Sporadic catches of nektobenthic organisms by plankton nets (Haedrich, 1974; Pearcy, 1976; Domanski, 1986) suggest that such excursions are rare or on a shorter time scale than for mesopelagic species (Mauchline & Gordon, 1991).

In addition, there is still no clear explanation for the frequent occurrence of pelagic organisms in the diets of deep-water benthic species (Pearcy, 1976; Sedberry & Musick, 1978; Tyler, 1988; Angel, 1990). In deep-sea communities megabenthic and macrobenthic biomass values are roughly of the same order (Haedrich & Rowe, 1977), which suggests that the biomass of the macrobenthos is insufficient to sustain megabenthic density. Trophic balance is thus attained due to the input of pelagic organic matter, as indicated in other studies (Houston & Haedrich, 1986; Cartes, 1993a,b). The input of pelagic material may be the result of: (1) the influx of particulate organic matter to the bottom sediment, ranging from the carcasses of large nektonic organisms to the rain of phytoplankton detritus (Billet et al., 1983; Bathmann, 1988; Hecker, 1990); (2) active predation by benthic organisms on pelagic species that migrate to the sea bottom (Lagardère, 1977; Vinogradov & Tseitlin, 1983). The presence of pelagic species close to the deep-water sea bed reported in recent studies (Hargreaves, 1984; Hargreaves et al., 1984; Angel, 1990) would appear to support the second possibility. An increase in plankton biomass has been reported at around 100 to 20 m off the bottom within the Benthopelagic Boundary Layer (BBL). Similar results have been obtained for deep-sea zooplankton nearer the bottom in samples collected using submersibles (Wishner, 1980) or by means of direct observations on the upper slope (Omori & Ohta, 1981) or on the deep slope (Pérès, 1958; Casanova, 1974).

This study therefore presents data on the occurrence and relative abundance of deep-water species, particularly mesopelagic species, in the water layer immediately adjacent to the bottom (10–140 cm above the bottom). The species caught are commonly found in the diets of deep-sea decapods and fishes on the slope in the Western Mediterranean (Macpherson, 1981; Cartes & Abelló, 1992; Stefanescu & Cartes, 1992; Carrasson et al., 1992; Cartes, 1993b,c) and other deep-sea regions in the North Atlantic (Sedberry & Musick, 1978; Mauchline & Gordon, 1991). The significance of the results in explaining deep-sea food webs is also discussed.

2. Materials and methods

All the samples were collected using a Macer-Giroq suprabenthic sledge (Dauvin & Lorgere, 1989), a sampling system that has been employed in studies on the suprabenthos (Brunel et al., 1978; Sorbe, 1983; Sainte-Marie & Brunel, 1985; Elizalde et al., 1994). This sampling method is still little used, particularly in deep waters. The sledge used included certain modifications in the mechanical opening and closing system and differed slightly in size (Fig. 1). The sampling gear consisted of three rectangular mouth openings 40×80 cm on a side arranged in three tiers, one above the other. The distance from the bottom to the lower edge of the first mouth opening was 10 cm. Accordingly, the gear comprised three tiers sampling simultaneously three separate levels at heights of 10–50, 55–95, and 100–140 cm above the bottom. The gear thus sampled the water layer between 0.1 and 1.4 m above the bottom (mab). The mouth openings were opened by a system of levers when the sledge touched the sea floor; a spring pulled the mouth openings shut when the sledge was descending or ascending through the water column (Fig. 2), thereby ensuring that pelagic organisms were not caught while the gear was in transit to and from the sea floor. The mesh size used was 0.5 mm.

Sampling was carried out on the slope in the Catalan Sea (western Mediterranean). A total of 21 bottom samples were taken on four sampling cruises at bottom depths

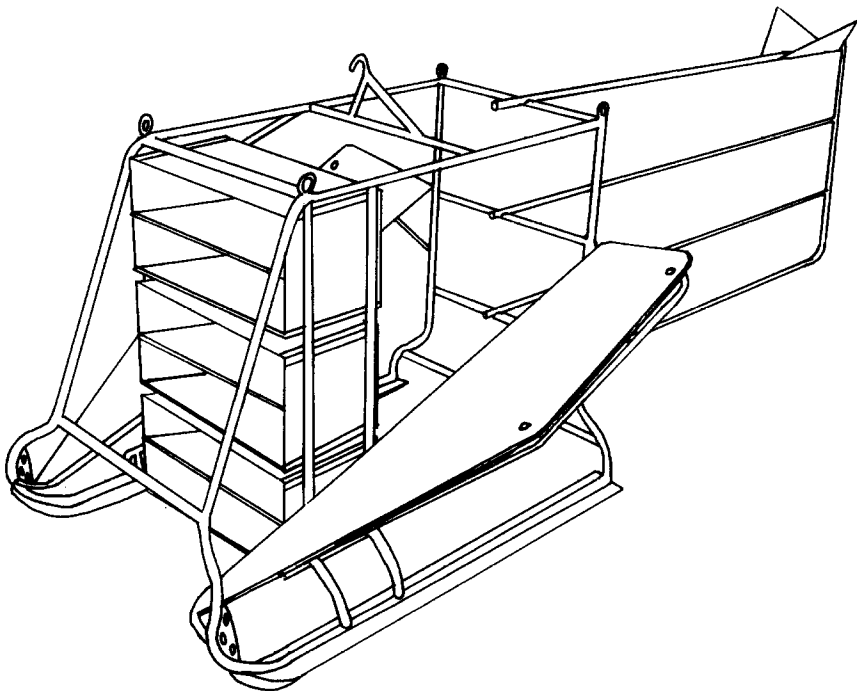


Fig. 1. Schematic general view of the type of Macer-Giroq suprabenthic sledge used in this study.

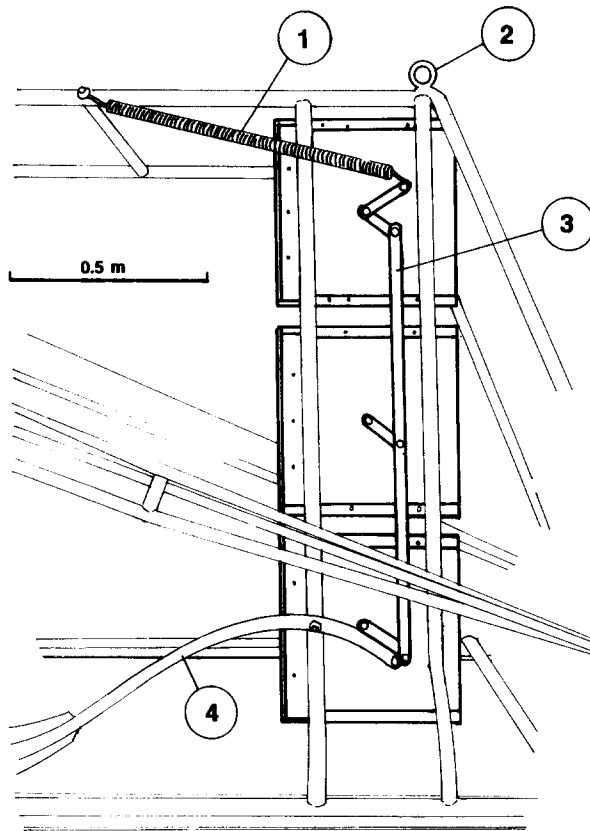


Fig. 2. Lateral view of the opening/closing system in the suprabenthic sledge. 1. Spring to close mouths; 2. float attachment; 3. opening/closing system of levers; 4. basal lever to open mouths.

ranging from 385 to 1 859 m in 1991 and 1992 (Table 1). Towing speed was ≈ 1.8 –2 knots. Four stations were sampled on each of the surveys, one each on the upper slope (Us: 393–400 m), middle slope (Ms: 524–601 m), and lower slope (Ls: 1 253–1 355 m), and one in a submarine canyon (C: 398–504 m). The station in the “La Merenguera” submarine canyon in fact straddled the boundary between the upper and middle slopes. Station Ls was located at the beginning of the lower subzone on the deep slope (Cartes & Sardà, 1992). An additional sampling station at a depth of 1 857–1 859 m was occupied on the R4 survey.

The density of the organisms sampled was estimated with the aid of a flowmeter attached to the middle mouth opening on the sledge. The amount of water filtered through the meshes of the sledge and the towing distance fished by each haul were estimated from the flowmeter data. Density values for each species have been standardized to no. of individuals/100 m².

Decapod crustaceans and euphausiids were identified to species level and counted. The results have been presented for three different depth strata: the upper slope (393–

Table 1
Sampling data corresponding to the present study

Station	Date	Depth (m)	Situation	Sampled area (m ²)
R1/1	25/04/91	549–550	41° 06' 6" N–2° 10' 9" E	200
R1/2	25/04/91	506–501	41° 08' 1" N–2° 04' 3" E	200
R1/3	26/04/91	1355–1354	41° 02' 3" E–2° 27' 9" E	432
R2/1	9/12/91	549–552	41° 06' 2" N–2° 10' 4" E	244
R2/2	9/12/91	552–560	41° 05' 8" N–2° 08' 5" E	204
R2/3	9/12/91	400–402	41° 08' 9" N–2° 08' 7" E	198
R2/4	9/12/91	450–452	41° 08' 0" N–2° 04' 0" E	202
R2/6	9/12/91	1258–1258	40° 54' 2" N–2° 06' 3" E	435
R3/1	14/03/92	1255–1250	40° 54' 3" N–2° 04' 5" E	335
R3/2	14/03/92	1263–1263	40° 54' 4" N–2° 07' 1" E	484
R3/3	14/03/92	525–523	41° 06' 8" N–2° 10' 2" E	203
R3/4	14/03/92	601–601	41° 05' 8" N–2° 10' 5" E	242
R3/5	14/03/92	600–600	41° 06' 4" N–2° 12' 2" E	102
R3/6	14/03/92	400–396	41° 09' 3" N–2° 10' 1" E	197
R3/7	14/03/92	389–400	41° 07' 8" N–2° 04' 5" E	158
R4/1	27/07/92	1284–1273	40° 55' 3" N–2° 10' 7" E	405
R4/2	27/07/92	1280–1271	40° 54' 3" N–2° 07' 4" E	450
R4/3	28/07/92	1859–1857	40° 48' 9" N–2° 35' 4" E	607
R4/4	28/07/92	598–593	41° 05' 6" N–2° 09' 9" E	262
R4/6	28/07/92	392–393	41° 07' 9" N–2° 04' 8" E	122
R4/7	28/07/92	406–405	41° 08' 9" N–2° 08' 8" E	143

450 m), the middle slope (504–601 m), and the lower slope (1 253–1 859 m). The relative abundance values for the most abundant species for all the samples combined have been presented by subsample according to sledge opening level, after standardization of density values. A chi-square test was applied to mean density data (Table 3) to establish the homogeneity in the distribution of species in each subsample (L1 to L3). The index of swimming activity (K1–K2) values, related to the abundance of each species in each subsample (sledge tier), were calculated for the main species caught (cf Brunel, 1972; Sainte-Marie & Brunel, 1985). The formulae $K_1 = N_2/N_t$; $K_2 = N_3/N_t$ have been used in which N_2 and N_3 are, respectively, the abundances recorded from meshes 2 and 3. N_t is the total abundance for all levels ($N_t = \sum N_1, N_2, N_3$). The K1 and K2 indexes are not a direct measure of swimming ability of the species, but the distribution and abundance in each sledge tier can be interpreted as a consequence of the different natatory activity showed by each species. Finally, the carapace length (CL) of certain abundant mesopelagic decapods was also measured.

Some considerations should be made regarding the sampling system employed. The sampling gear was designed to study the suprabenthos, which, based on the size of the organisms, must be classed as part of the macrobenthos. The results obtained indicated that this gear also took larger megabenthic organisms that are normally sampled using bottom trawls (cf Merrett & Marshall, 1981; Haedrich et al., 1980; Cartes & Sardà, 1992). The additional information provided by sledges will contribute to our

understanding of the vertical distribution of certain species in the water layer adjacent to the bottom (10–140 cm). Nevertheless, the efficiency of the Macer-Giroq sledge is low for megabenthic organisms. The vulnerability of organisms to the gear is conditioned by individual size (cf Casanova, 1974). Thus, no large benthopelagic species were caught on the upper and middle slopes, despite the substantial densities of crustaceans and fishes that inhabit this slope region (Cartes & Sardà, 1992; Stefanescu et al., 1992). However, this situation changed at depths below 1 000 m, where large species (*Mora moro* (Risso), *Bathypterois mediterraneus* Bauchot, *Acanthephyra eximia*, *Aristeus antennatus*) were taken by the gear. Therefore, the depth factor also had an effect on the sampling efficiency of the sledge.

Catches of pelagic organisms while the sledge was being towed down to the bottom or up to the surface can be considered negligible, except in the case of very small planktonic organisms (furcilia and calyptopis larvae, *Sardina pilchardus* (Walbaum) larvae, brachyuran zoeae), which may pass through gaps in the closure of the mouth openings on the sledge. Therefore, only juvenile and adult specimens, which, because of their size, were not available to the sledge in the water column, have been taken into account in the present study.

3. Results

Table 2 summarizes the catches of the main species of decapod crustaceans and euphausiids for each depth stratum considered. *Calocaris macandreae*, *Pandalina profunda*, *Processa nouveli*, and *Alpheus glaber* were predominant on the upper slope, where *Sergestes arcticus* and *Pasiphaea sivado* were important among mesopelagic species. *Calocaris macandreae* and *Pandalina profunda* were prevalent on the middle slope. *Pontophilus norvegicus* was the predominant benthic species on the lower slope in where *Gennadas elegans* was the most important pelagic species. The main euphausiid species captured were *Euphausia krohni* and *Nematoscelis megalops*, respectively more abundant on the middle and on the lower slope.

The three subsamples collected concomitantly revealed distinct distributions among the predominant decapod crustacean species. Thus, individuals of the mesopelagic species *Sergestes arcticus*, *Pasiphaea sivado*, and *Gennadas elegans* were homogeneously distributed or concentrated in the upper and middle subsamples (Table 3), commensurate with the indexes of swimming activity. The values of K1 and K2 for these species were particularly high, and in all cases $K2 > K1$ (Table 3). The situation was similar for the nektobenthic species *Acanthephyra eximia* and *Plesionika martia*, though only a very small number (3) of specimens of the latter species were caught. The value of K1 was often high for certain benthic natantian (nektobenthic) species (e.g. *Aristeus antennatus*, *Plesionika giglioli*, *Processa canaliculata*). Nevertheless, in all cases $K2 < K1$, and in many cases $K2 = 0$. The number of specimens of these three species present in the samples was low. Lastly, the endobenthic species *Calocaris macandreae* and *Alpheus glaber*, crangonids, and *Pandalina profunda* were closely associated with the lowermost subsample and had K1 and K2 values that were very low or zero (particularly K2). The situation for euphausiids was similar to that described for the mesopelagic decapods, with $K2 > K1$ and coefficient values greater than 0.30 in all cases.

Table 2

Total number of decapod and euphausiid species collected over the study period on the Catalan Sea slope

	Upper slope			Middle slope			Lower slope		
	L1	L2	L3	L1	L2	L3	L1	L2	L3
Euphausiacea									
<i>Euphausia krohni</i> (Brandt)	1	3	–	6	13	13	3	4	6
<i>Meganyctiphanes norvegica</i> (M. Sars)	–	–	–	1	–	–	–	–	1
<i>Nematoscelis megalops</i> G.O. Sars	5	7	5	6	2	8	5	17	18
<i>Stylocheiron</i> sp. (J)	–	1	–	1	1	1	1	–	5
<i>Stylocheiron longicorne</i> G.O. Sars	–	2	–	–	–	–	1	–	–
<i>Stylocheiron maximum</i> Hansen	–	–	1	–	–	–	–	–	–
Decapoda									
Natantia									
<i>Gennadas elegans</i> (S.I. Smith)	–	–	3	2	4	–	2	4	11
<i>Aristeus antennatus</i> (Risso)	–	1	–	1	–	–	1	2	–
<i>Solenocera membranacea</i> (Risso J)	–	1	1	–	2	1	–	1	–
<i>Sergestes arcticus</i> Krøyer	3	6	14	1	–	2	–	1	–
<i>Sergia robusta</i> (S.I. Smith)	–	–	–	–	–	–	–	1	–
<i>Richardina fredericii</i> Lo Bianco	–	–	–	4	1	–	1	–	–
<i>Acanthephyra eximia</i> S.I. Smith	–	–	–	1	–	–	1	4	9
<i>Nematocarcinus exilis</i> (Bate)	–	–	–	–	–	–	2	1	1
<i>Pasiphaea multidentata</i> Esmark	–	–	–	–	–	–	1	–	–
<i>Pasiphaea sivado</i> (Risso)	2	4	5	–	–	–	–	–	–
<i>Alpheus glaber</i> (Olivi)	16	2	1	3	2	–	–	–	–
<i>Processa canaliculata</i> Leach	4	1	–	2	1	–	–	–	–
<i>Processa nouveli</i> Al-Adhub & Williamson	21	1	1	4	1	–	–	–	–
<i>Periclimenes</i> sp.	1	–	–	–	–	–	–	–	–
<i>Pandalina profunda</i> Holthuis	31	1	–	57	14	–	–	–	–
<i>Plesionika acanthonotus</i> (S.I. Smith)	–	–	–	1	–	–	1	–	–
<i>Plesionika giglioli</i> (Senna)	2	2	–	–	2	–	–	–	–
<i>Plesionika martia</i> (A. Milne Edwards)	–	–	–	1	1	1	–	–	–
<i>Plesionika</i> sp.	1	–	–	–	–	–	–	–	–
<i>Philocheiras echinulatus</i> (M. Sars)	3	–	–	–	–	–	–	–	–
<i>Pontocaris lacazei</i> (Gourret)	4	2	–	2	–	–	–	–	–
<i>Pontophilus norvegicus</i> (M. Sars)	–	–	–	1	–	–	22	1	–
<i>Pontophilus spinosus</i> (Leach)	1	–	–	–	–	–	–	–	–
Reptantia									
<i>Callinassa cf tyrrhena</i> (Petagna)	3	–	–	–	–	–	–	–	–
<i>Calocarides coronatus</i> Trybom	–	–	–	–	–	–	1	–	–
<i>Calocaris macandreae</i> Bell	174	32	6	70	28	1	–	–	–
<i>Polycheles typhlops</i> Heller	–	–	–	–	1	–	2	–	–
<i>Stereomastis sculpta</i> (S.I. Smith)	–	–	–	–	–	–	2	–	–
<i>Munida tenuimana</i> G.O. Sars	–	–	–	–	–	–	4	–	–
<i>Goneplax rhombiodes</i> (Linnaeus)	1	–	–	–	–	–	–	–	–
<i>Monodaeus couchi</i> (Couch)	3	–	–	2	2	–	–	–	–
<i>Dorhynchus thomsoni</i> Thomson	–	–	–	–	–	–	1	–	–

J = juvenile stages.

Table 3

Density (ind. · 100 m⁻²) and indexes of swimming activity (K1, K2) for the most abundant collected species

	Occurrence			Mean abundance			s	K1	K2
	L1	L2	L3	L1	L2	L3			
Euphausiacea									
<i>Euphausia krohni</i>	7	8	9	7.3	10.6	10.8	(-)	0.37	0.42
<i>Nematoscelis megalops</i>	10	11	15	7.6	8.6	7.6	(-)	0.33	0.40
<i>Stylocheiron</i> spp.	3	3	4	4.6	6.4	6.5	(-)	0.32	0.44
Decapoda									
Natantia									
<i>Gennadas elegans</i>	4	6	3	7.3	4.5	13.1	(+)	0.29	0.43
<i>Aristeus antennatus</i>	2	2	-	4.0	4.9	-	(-)	0.55	-
<i>Solenocera membranacea</i> (J)	1	3	2	2.3	7.3	4.6	(-)	0.65	0.28
<i>Sergestes arcticus</i>	5	4	3	5.4	10.4	33.6	(*)	0.25	0.60
<i>Acanthephyra eximia</i>	2	2	4	4.0	3.8	4.4	(-)	0.23	0.53
<i>Nematocarcinus exilis</i>	1	1	1	3.3	1.6	1.6	(-)	0.25	0.25
<i>Pasiphaea sivado</i>	1	2	3	10.1	13.4	11.4	(-)	0.38	0.48
<i>Alpheus glaber</i>	6	4	1	18.3	5.5	8.1	(*)	0.16	0.06
<i>Processa canaliculata</i>	2	2	-	13.9	6.1	-	(*)	0.31	-
<i>Processa noveli</i>	9	2	1	14.5	6.0	5.0	(*)	0.08	0.03
<i>Pandalina profunda</i>	8	5	-	51.8	14.6	-	(*)	0.15	-
<i>Plesionika gigliolii</i>	2	2	-	5.8	5.8	-	(+)	0.50	-
<i>Plsionika martia</i>	1	1	1	3.8	3.8	4.9	(-)	0.30	0.39
<i>Pontocaris lacazei</i>	4	1	-	7.5	5.0	-	(*)	0.14	-
<i>Pontophilus norvegicus</i>	7	-	-	5.3	-	-	(*)	-	-
Reptantia									
<i>Calocaris macandreae</i>	11	9	4	121.6	27.6	7.6	(*)	0.15	0.02
<i>Polycheles typhlops</i>	2	1	-	2.4	3.8	-	(+)	0.44	-
<i>Munida tenuimana</i>	3	-	-	2.5	-	-	(+)	-	-
<i>Monodaeus couchi</i>	3	-	-	8.4	-	-	(*)	-	-

L1 = lower level of the suprabenthic skedje; L2 = intermediate level; L3 = upper level; s = statistical significance level; (-) = not significant; (+) = $p < 0.10$; (*) = $p < 0.05$.

All specimens of *Sergestes arcticus* captured were adults (Fig. 3) approaching the maximum size of 12 mm CL observed in the Catalan Sea. The situation for *Gennadas elegans* was comparable, although some immature individuals (CL < 5 mm) were present in the samples. The size range of *Pasiphaea sivado* in the samples was quite broad, from 2 to 14 mm CL.

4. Discussion

The three subsamples collected using the suprabenthic sledge provided information on the partitioning of vertical space by the species dwelling near the sea floor, be they species inhabiting the water column immediately adjacent to the sea bed, species

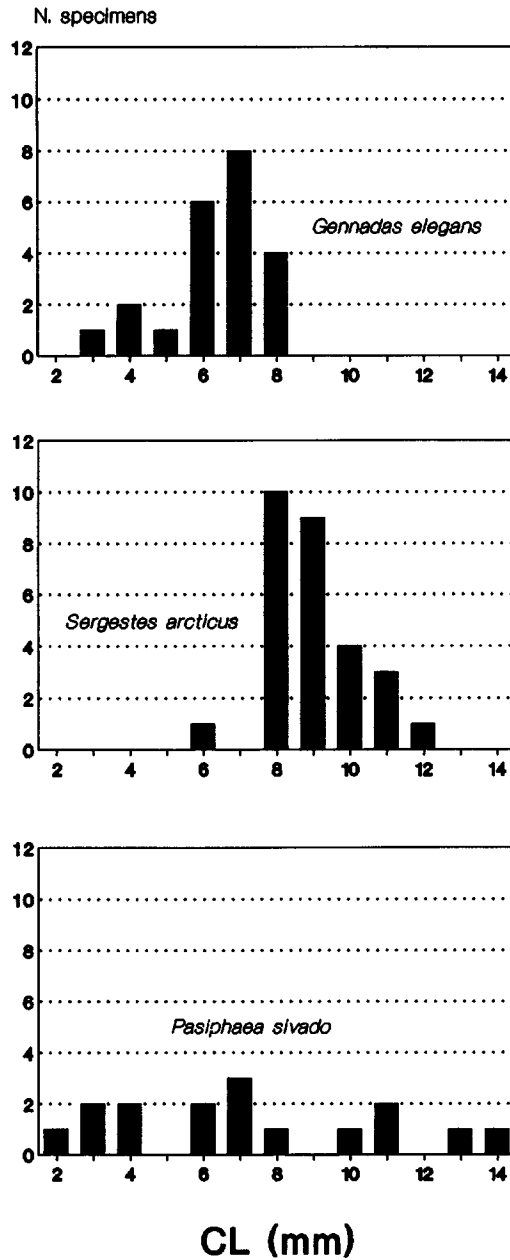


Fig. 3. Frequency size distribution for the three most abundant mesopelagic decapods collected in the Catalan Sea slope. CL = carapace length.

inhabiting the water-sediment interface, or the infauna itself. Comparison of the present results with the results of stomach content analysis for decapod crustaceans indicated

that partitioning of vertical space was analogous to the partitioning of the available trophic resources reported in the study area (Cartes, 1991). Thus, mesopelagic species, whose diet is based on the macro and mesoplankton (Cartes, 1993c), occupied the sampling levels farthest from the bottom (chiefly between 1 and 1.4 mab). Nekto-benthic species (*Aristeus antennatus*, *Plesionika* sp.), which have mixed diets (macroplankton-suprabenthos-endobenthos), occupied the middle and lowermost subsamples (from 0.1 to 0.95 mab), sporadically penetrating into the uppermost layer. In contrast, species whose diets are closely associated with the sediment, such as crangonid shrimps, which feed almost exclusively on polychaetes (Lagardère, 1977; Cartes, 1991), were present only in the lowermost level closest to the bottom (between 0.1 and 0.5 mab). The type of diet would thus appear to be closely related to the swimming activity of each species. Catches of endobenthic species, such as *Calocaris macandreae* and *Alpheus glaber*, in the middle and upper subsamples can probably be attributed to the effect of the sledge's trawl warp digging up the bottom.

The presence of mesopelagic and bathypelagic species close to the bottom was an interesting finding. *Sergestes arcticus*, *Pasiphaea sivado*, and *Gennadas elegans* were the most abundant decapod crustaceans. These three species were most abundant on the summer cruises (Fig. 4), when they were also most abundant in the plankton in the water column in the study area (Franqueville, 1971). The sizes of the individuals of the smaller species, *G. elegans* and, particularly, *Sergestes arcticus*, caught corresponded in all cases to the adult size range, in agreement with the results reported by Hargreaves (1984) in samples taken close to the bottom in the Benthopelagic Boundary Layer in the Northeast Atlantic. The situation for *Pasiphaea sivado* differed, although large individuals (CL > 15 mm) were probably able to avoid capture by the suprabenthic sledge. Specimens of this size are caught in large numbers using bottom trawls on the

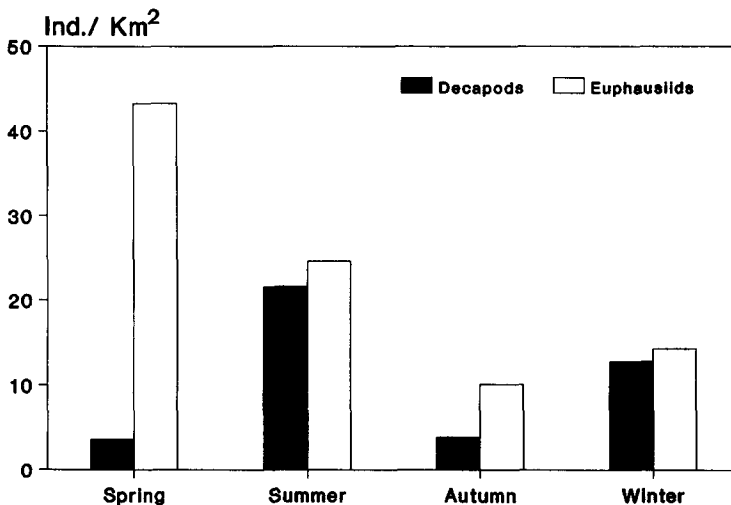


Fig. 4. Seasonal abundance of decapods and euphausiids (ind. · km⁻²) in the present sampling.

upper and middle slopes in the study area (unpublished data). The presence of large individuals of mesopelagic species near the bottom has been ascribed to ontogenetic migrations by both decapods (Hargreaves, 1984; Cartes et al., 1993) and fishes (Stefanescu & Cartes, 1992). This suggests that population density and structure of mesopelagic species near the bottom and in the water column need not be the same. This, in combination with other possible causes such as size selection by predators and seasonal changes in the available pelagic resources, could explain why pelagic prey species occurring in the stomach contents of benthopelagic fish assemblages are not necessarily the most common or prevalent species in the oceanic water column (Mauchline & Gordon, 1991).

The euphausiids caught included species that have eurybathic distributions in the Western Mediterranean, such as *Euphausia krohni* and *Stylocheiron longicorne*, and bathypelagic species, such as *Nematoscelis megalops*, caught at depths down to 2000 m in the Mediterranean (Casanova, 1974). In contrast, epipelagic and mesopelagic species reported by Casanova (1974) were not present in the samples collected in this study. The small number of individuals of *Meganycitiphanes norvegica* caught was not consistent with the abundance of this species in the stomach contents of bathyal benthic species from comparable depth ranges (Cartes & Abelló, 1992; Cartes, 1993b,c). The presence of this species in the stomach contents of crustaceans was recorded in autumn (September–October), when no samples were carried out on the surveys considered here. Large individuals of this same species are often taken by bottom trawls (unpubl. data), which is suggestive of ontogenetic migrations similar to those reported for mesopelagic decapods and fishes.

The suprabenthic sledge also captured various pelagic fish species (i.e. *Cyclothone braueri* Jespersen & Täning, *Argyropelecus hemygymnus* Cocco, *Evermanella balbo* Risso, *Lampanyctus crocodilus* Risso) and other benthopelagic organisms such as siphonophores and chaetognaths (unpubl. data). All the pelagic organisms recorded are also regularly present in the stomach contents of benthic megafaunal species in the study area, as has been reported in other areas (Lagardère, 1977; Mauchline & Gordon, 1991). By way of a general conclusion, the presence of pelagic organisms near the bottom is indicative of the complexity and activity (i.e. in predator/prey relationships) within the deep-sea food webs, at least on the upper and middle slopes that are in contact with the mesopelagic zone. Deep-sea food webs would appear to be based on benthopelagic organisms that may act as facultative detritivores, as in the case of calanoid copepods (Wishner & Meise-Munns, 1984), euphausiids (Mauchline & Fisher, 1969), mysids (Mauchline, 1980) and mesopelagic decapods (Lagardère, 1976). Accordingly, copepods were the predominant organisms in the samples collected using sledges in the present study (unpubl. data) and in the BBL generally (Wishner, 1980; Angel, 1990). Essentially, the diets of these organisms may be based on particulate organic matter and, in spatio-temporal terms, may be intensified in different locations at different times by resuspension phenomena taking place in deep-sea environments (Angel, 1980) in association with seasonal changes in organic matter input (Monaco et al., 1990, and references cited).

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