Pergamon Progress in Oceanography 41 (1998) 111–139

Progress in Oceanography

Dynamics of the bathyal Benthic Boundary Layer in the northwestern Mediterranean: depth and temporal variations in macrofaunal–megafaunal communities and their possible connections within deep-sea trophic webs

Joan E. Cartes*

CSIC, Institut Mediterrani d'Estudis Avançats, Crta. Valldemossa Km 7.5, 07071 Palma de Mallorca, Spain

Abstract

The distribution patterns of benthopelagic fauna and the macrofauna–megafauna trophic relationships in the Benthic Boundary Layer (BBL) were studied. The study is based on data collected during 6 sampling cruises off the Catalan coast (western Mediterranean) during 1991–1995 at depths ranging from 389–1355 m. Crustaceans were the dominant benthopelagic macrofauna in the BBL level closest to the sea bed (~0–1.5 m above bottom) on the Catalan Sea slope. Copepods and peracarid crustaceans (mysids, amphipods, isopods, and cumaceans) were dominant, whereas euphausiids and natantian decapods, some taxa of gelatinous plankton (siphonophores, medusae, and chaetognaths), and benthopelagic fishes were also well represented groups. Seasonal changes in megafaunal decapod crustaceans abundance seem to be linked to changes in the density and the biological cycle of BBL macrofauna, which constitute an important part of the available food exploited by megafauna. Both the advective and the vertical flow of organic matter in the north-western Mediterranean should simultaneously influence peaks of available food (BBL macrofauna) for bathyal–megafaunal decapods. Recruitment of macrofaunal (suprabenthos and infauna) species at the level of canyons and neighbouring slope zones mainly occurred between late autumn–late winter and would probably be mainly induced by an advective component. However, the macrofaunal sizes consumed by megafaunal decapods are found more abundantly represented in spring and summer populations. In parallel, the vertical fluxes seem to determine maxima in the abundance of planktonic organisms (especially copepods) which also occur in late spring–summer. Size, natatory capability, and energetic value are important factors in the selection of food-resources by

---

* Correspondence address: CSIC, Institut de Ciènces del Mar, Plaça del Mar s/n, 08039 Barcelona, Spain.

PII: S0079-6611(98)00018-4

megafaunal decapods, which would have a greater availability of food in late spring–summer. This would explain both the seasonal maxima of decapod abundance in summer, and maxima in the catches of some commercial species (i.e. the shrimp *Aristeus antennatus*) in spring–summer.

Contents

1. Introduction

The Benthic Boundary Layer (BBL) extends a few tens of metres into the water column immediately overlying the sea bed, and it is an environment of great complexity both from a physical (Gage and Tyler, 1991) and biological (Smith and Hinga, 1983) perspective. One of the most important biological characteristics of the BBL is the progressive increase of planktonic and nektonic biomass near the bottom (from around 100 m above the sea bed) within this layer (Angel, 1990), in contrast to the general exponential decline of pelagic biomass with depth in the water column (Vinogradov and Tseitlin, 1983). Since the first qualitative data obtained on the BBL (Wishner, 1980), the studies carried out on the composition and structure of this environment, both at bathyal and abyssal depths, have been relatively scarce (Hargreaves, 1984, 1985; Wiebe et al., 1988; Angel, 1990; Roe et al., 1990). Benthopelagic organisms, inhabiting the near bottom environment, are a fundamental part of the BBL (Marshall, 1965). These communities of organisms living above the sea bed have been included in distinct concepts, such as suprabenthos (Brunel et al., 1979) and hypoplankton (Mauchline, 1991). The term suprabenthos is linked to the specific sampling methodology of the suprabenthic sledges, and refers to the macrofauna with a natatory capability that inhabit the interface closest to the sea bed (Sainte-Marie and Brunel, 1985; Elizalde et al., 1997). Because of this natatory capability, this fauna is hardly captured using dredges or corers (Elizalde et al., 1997). Recently, Vereshchaka (1995) introduced a complete classification of benthopelagic organisms according to their more or less intense relationship with the sea bed within the BBL.

Excluding hydrothermal vents, the deep-BBL is considered an alocthonous system, dependent on the contribution of particulate organic matter that follows two main paths, one vertical and another advective. The food supply, whose dominant source is the primary production originating in the euphotic zone, penetrates by active or passive mechanisms towards the deep communities. An important component within the general scheme of the deep-trophic webs is the incidence of benthopelagic organisms in the diet of megafauna that inhabit the BBL (Gordon and Mauchline, 1991), which constitute an active transport path from the surface production to the organisms at the end of the trophic chains. The BBL macrofauna, because of its size and high densities, constitutes a very important link between the surface production and the megafauna, and is, specifically, a fundamental part of the diet of deep-water fishes and other megabenthic groups (i.e. decapod crustaceans).

To obtain a sufficient number of replicates or to follow the seasonal biological processes in a study of the deep sea is usually limited by problems of time and cost (Brattegard and Fosså, 1991). Despite this, in recent years certain information on the biological cycle of deep-sea species has been accumulating (Gage and Tyler, 1991). Seasonal environmental signals, among which phytodetritus deposition stands out, appear to operate rapidly and favour aspects of the biological cycle (recruitment, gametogenesis) in some groups of deep-sea macrofaunal species (Bishop and Shalla, 1994; Tyler et al., 1994; Cartes and Sorbe, 1996), and some megafaunal species (Tyler and Gage, 1984; Féral et al., 1990). To date, the study of these coupling processes has been limited to the organisms situated at the lowest levels of the trophic chains—detritivores or those that directly consume organic matter—which can be expected to have a clearer response towards seasonal changes in organic material inputs (Graf et al., 1982). On the other hand, no data on these relationships exist among deep-megafaunal predators (mainly fishes and decapods) and the type of resource that they exploit. In the same way, studies are very scarce on seasonal changes in the composition and abundance of the BBL, and are focused to changes in the overall biomass (Sorbe, 1997).

The Mediterranean Sea is a zone characterized by the annual thermal stability of the water mass (~12.8 °C) below around 200 m (Hopkins, 1985). In the north-western area, different aspects of seasonal changes in primary production (Estrada and Salat, 1989; Estrada, 1991), and in the flux of particles (Buscail et al., 1990; Miquel et al., 1994) have been studied in open waters and on the slope in recent years. In the Catalan Sea, water-column stratification regularly occurs from April to November, while primary production dynamics are characterized by a late winter–spring bloom and by a deep chlororhyll maximum (DCM) in open waters during the stratification period (Estrada, 1991). Muddy sediment dominates along all the slope, with an increase in the biogenous fraction (pteropods, pelagic foraminiferans) with increasing depth (Emelyanov, 1977). In the study area, submarine canyons act as channels of the advective flux over the adjacent slope (Buscail et al., 1990). On the other hand, studies on changes in seasonal zooplankton abundance in the western Mediterranean are very scarce, particularly in open areas and on bathyal bottoms. Franqueville

(1971) and Sardou et al. (1996) carried out some complete seasonal studies of the deep macroplankton, although only on the greater sized fraction (mesh sizes between 3 × 5 to 6 mm). Other studies are restricted to the shelf-slope break (Sabatés et al., 1989), or to epipelagic zones in open areas (Razouls and Kouwnberg, 1993; Fernández de Puelles et al., 1995). At the bathyal level, changes in the abundance of benthopelagic organisms are probably parallel to those of zooplankton, and, without studies on the BBL, data of seasonal changes in zooplankton abundance can be important for comparison. Finally, at the level of studies on megafaunal communities, the deep-western Mediterranean Sea is characterized by the importance of deep-water decapod crustaceans, including the Penaeoidean shrimps *Aristeus antennatus* and *Aristaeomorpha foliacea*, that are of considerable ecological and fishing interest (Pérès, 1985; Cartes and Sardà, 1992; Sardà et al., 1994).

Within this general context, the present work pursues a double objective: (1). The description of the composition and abundance of the BBL at the bathyal level in the north-western Mediterranean, considering both seasonal and bathymetric changes. (2). To establish and discuss the possible implications that these changes could have in the trophic chains at the level of megafauna, in this case crustacean decapods that are a representative and well-studied group in the area. Based on these results and through their possible relation to environmental data available in the literature, a preliminary scheme for the dynamics of the trophic chains and of the possible macrofauna–megafauna coupling in the study area will be established.

2. Material and methods

The present study was carried out on bathyal bottoms of the Catalan Sea area (between the coast of Catalonia and the Balearic Islands; Fig. 1) at depths ranging from 389–1355 m. In this study, benthopelagic macrofauna (using sledges) and megafauna (using bottom trawls) were sampled in a practically simultaneous way at the level of the Benthic Boundary Layer (BBL).

Benthopelagic macrofauna was sampled by means of a Macer-GIROQ suprabenthic sledge (Dauvin and Lorgère, 1989). This sledge consists of three rectangular 40 × 80 cm mouth openings superimposed, with a mechanical open–close system that minimizes the contamination of the samples during the ascent/descent of the gear. Nets of 500 μm were attached to each mouth. The gear samples the water column between 0.1–1.5 m above the bottom (Cartes et al., 1994). A total of 26 samples were obtained, covering the four annual seasons between 1991–1995, within the framework of two different scientific projects (CICYT MAR90/757 and CICYT AMB93/0283). Four sampling cruises were carried out in 1991 and 1992 (R1 - April 1991; R2 - December 1991; R3 - March 1992; and R4 - July 1992), and a total of 18 samples were obtained. More detailed descriptions of R sampling data have already been published (Cartes et al., 1994). Data from 8 samples from cruises BT1 (March 1994) and BT2 (July 1995) were also included in the present work (Table 1). Three bathymetric levels were sampled on the upper slope (between 389–506 m), the middle slope (549–601 m), and the lower slope (1250–1355 m). At the

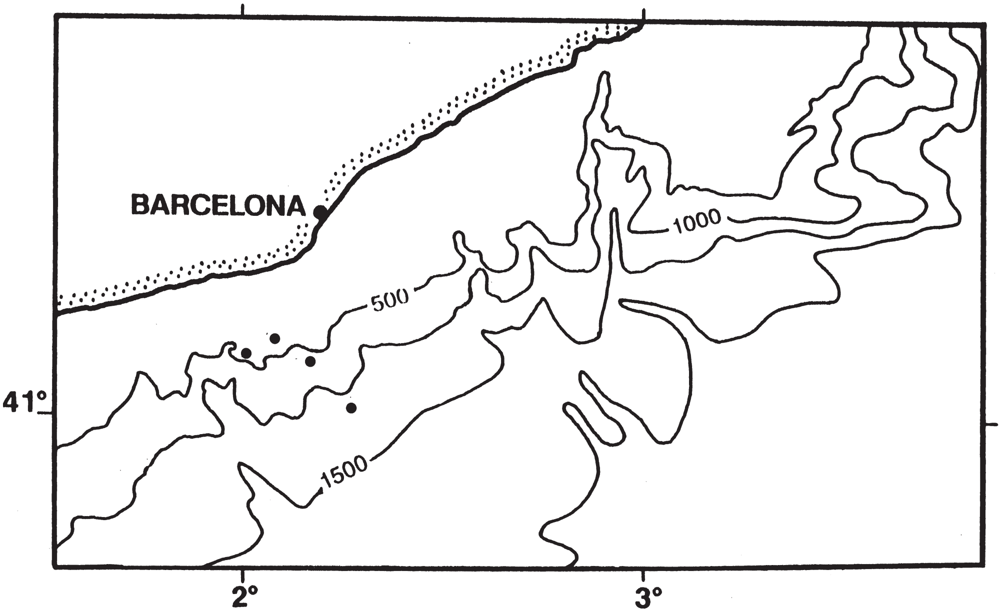

Fig. 1. Map of the study area in the northwestern Mediterranean (off Barcelona), showing the approximate location of stations sampled.

upper slope level two stations respectively situated within and in the vicinity of La Merenguera Canyon were sampled.

During BT1 cruise an opening and closing net was also used to sample the large fraction of mesoplankton near the bottom. Three samples were carried out at bottom depths between 639–663 m (Table 1). This net, with a mouth opening of 1 m^2 had a mesh of 500 μm. It was towed at approximately 1.5–1.7 knots, a speed similar to that of the sledge, and at distances above the sea bed ranging between 13–55 m. The position on the bottom was registered with the aid of a sensor (SCANMAR monitoring system) during BT1 cruise, for both the 1 m net as well as the Macer-GIROQ sledge, but only on the upper and middle slope zones. In spite of the limited number of samples obtained, those from the 1 m plankton net have a high comparative value. In these samples the degree of contamination by epipelagic plankton is nil and the study of their faunistic composition confirms the presence of different mesoplankton groups near the bottom. As in the case of the Macer-GIROQ sledge, the volumes of filtered water were estimated by means of a 2030R standard flowmeter (General Oceanics Inc.) positioned beside the central aperture of the net mouth.

Only the benthopelagic organisms (cf. Marshall, 1965) have been considered in the present study. In practice, in spite of the 10 cm distance between the lower mouth of the sledge and the bottom, the nature of soft muds in the study area resulted in the lower mouth of the sledge being slightly in touch with the sediment, thus allowing groups of infauna and epibenthos to be regularly caught. Amongst these groups, dominant in studies of benthos using grab samples in the same region (Carpine, 1970;

Table 1
Sampling data for BT1 and BT2 cruises

	Date	Situation	Depth (m)	Time (GMT)	Volume (m^3)
BT1					
P1	21/03/94	41°10.5′ N 2°24.4′ E	656–660	10.59–11.13	739
P6	21/03/94	41°01.4′ N 2°17.2′ E	1125–1128	22.54–23.08	840
P11	22/03/94	41°10.6′ N 2°24.3′ E	659–660	19.32–19.44	537
P15	23/03/94	41°00.5′ N 2°17.1′ E	1211–1214	16.51–17.05	742
M3	22/03/94	41°11.2′ N 2°26.3′ E	649–663 (17–43 mab)	15.02–15.22	744
M5	22/03/94	41°11.3′ N 2°25.9′ E	644–660 (14–37 mab)	21.05–21.26	967
M6	22/03/94	41°10.6′ N 2°24.0′ E	639–657 (13–55 mab)	22.54–23.12	781
BT2					
P1	6/07/95	40°53.9′ N 2°07.2′ E	1297–1300	7.36–7.58	1381
P4	6/07/95	41°05.8′ N 2°11.2′ E	649–651	13.47–13.58	763
P5	6/07/95	41°06.1′ N 2°05.0′ E	425–452	15.28–15.36	527
P6	6/07/95	41°08.5′ N 2°08.7′ E	405–406	16.46–17.01	1049

P: sledge samples; M: 1m-plankton net samples. mab: meters above bottom.

Reyss, 1971), the most common were polychaetes, endobenthic decapods (*Calocaris macandreae*, *Alpheus glaber*), mollusca (aplacophorans, bivalves, gastropods), echinoderms (echinoids, ophiuroids, and holothuroids), sipunculans, and tanaids among peracarid crustaceans. The abundances of these organisms in the sledge depends of the degree in which the gear sinks into the mud and, consequently, are not quantitative so they have not been included in the present study. Sampling with box-corers is needed for the quantitative study of this fauna. Large benthopelagic fishes (*Mora moro*, *Bathypterois mediterraneus*, *Lepidion lepidion*), caught sporadically with the Macer-GIROQ sledge, were also excluded from the results.

The density results are presented as the number of individuals/1000 m^3 for the three bathymetric levels and four annual seasons sampled. To compare the similarity between each of the samples within each bathymetric level, the percentage similarity (Whittaker and Fairbanks, 1958) was calculated. A non-parametric Kruskall-Wallis test (Sokal and Rohlf, 1979) was used to compare general abundances between depth strata.

Megabenthic decapod crustaceans were caught using bottom trawls during R cruises. The seasonal abundance and the diet of decapod crustaceans, the most important group of megafauna, together with fishes, in the northwestern Mediterranean (Cartes and Sardà, 1992) were simultaneously determined to cover the second objective of this work. A semi-balloon MTS ("Maireta" Trawl System), equipped with 2 doors and 25 m long briddles, were used in all cases. The size and basic characteristics of the MTS is similar to that of the OTSB-14 bottom trawl (Merrett and Marshall, 1981). All trawling was carried out at 2.6 knots, at which speed the net swept an estimated area of 65005 m^2 in an hour of trawling. The net was covered with a 6 mm mesh codend liner. A total of 47 trawls were performed during the R1 (11 hauls), R2 (12 hauls), R3 (12 hauls), and R4 (12 hauls) cruises at three fixed stations on the upper slope (between 390–508 m), the middle slope (545–692 m) and the lower slope (1160–1286 m) (see detailed aspects of sampling in Sardà et al., 1994). A total of 13078 individuals belonging to 54 different species were caught. Abundance (number of individuals/10000 m^2) for the dominant species was calculated in each slope zone.

Some feeding aspects have been studied for those more abundant megabenthic decapods (Table 2) on the R cruises. A total of 22 species, that represented 84.6% of the total abundance of decapods caught, were studied. A total of 2142 individuals were dissected in order to obtain a stomach fullness index (%f), as a percentage by visual observation under a × 10 stereomicroscope. Diet was recorded as a percentage

Table 2
Dominant megafaunal decapods in the study area selected to feeding analysis–captured with bottom trawls in R cruises

Species	f	N
Aristeus antennatus	490	201
Aristaeomorpha foliacea	12	11
Solenocera membranacea	11	11
Sergestes arcticus	117	64
Sergia robusta	56	35
Acanthephyra eximia	129	84
Pasiphaea multidentata	43	21
Pasiphaea sivado	62	32
Ligur ensiferus	40	14
Processa canaliculata	16	8
Processa nouveli	20	16
Pandalina profunda	44	22
Plesionika acanthonotus	40	25
Plesionika edwardsi	88	47
Plesionika gigliolii	101	59
Plesionika martia	232	132
Pontocaris lacazei	95	30
Pontophilus norvegicus	130	34
Nephrops norvegicus	100	78
Polycheles typhlops	83	33
Munida tenuimana	197	105
Monodaeus couchi	36	20

f: number of individuals analyzed to determine stomach fullness; N: number of individuals analyzed to establish dietary composition.

abundance of the prey (%N) based on 1082 individuals. A more detailed description of methods for obtaining data in decapod diets can be found in previous publications (Cartes and Abelló, 1992; Cartes, 1994 and references cited). Prey were classified to the lowest taxonomic level, although afterwards they were grouped into the same taxa that were established for the BBL composition results, with the objective of establishing a subsequent comparison between prey groups and available trophic resources. Both %f and %N were obtained from subsamples with a sufficient number of individuals from each species (Table 2).

For each of three bathymetric levels sampled a study of food selectivity was carried out, by comparing the overall composition of diet of decapods with the abundance of benthopelagic organisms in the environment. The number of prey per stomach depends of stomach fullness (Cartes, 1991). Thus, the values of the diet for overall decapod assemblages within each bathymetric level was estimated by multiplying the number of prey in each of the 23 prey taxa (derived from BBL results) by the %f index, and by the mean abundance of each species (individuals/10000 m^2) in the environment. The overall diet is deduced from the sum for the total decapod species dominant at each bathymetric level. A linear index of food selection (Strauss, 1979) was used to obtain food selectivity for each prey. This index is simply based on the unweighted difference in proportions

$$L = r_i - p_i$$

where r_i and p_i are the relative proportions of prey item i in the gut and habitat respectively. This index ranges from −1 to +1, with positive values indicating preference and negative values avoidance or inaccessibility, while zero (or close to zero) is the expected value of this index for random feeding. Other properties of this index, above all in comparison with the most commonly used Ivlev index (Ivlev, 1961), are discussed by Strauss (1979). This index does not take into account the different digestion times for each type of prey. The obtained results were also tested by $2 \times 2\ \chi^2$ (Yates correction). Only the benthopelagic organisms have been considered in the diet of decapods. The mean densities for each benthopelagic group in the diet and in the environment were obtained exclusively from the data of the R1, R2, R3 and R4 cruises, in which the study of stomach contents analysis was made.

The natatory capability coefficients (Kt) were estimated for the main taxa. Kt is calculated from the distribution of each taxon in three subsamples of the Macer-GIROQ sledge, according to the formula Kt = (N2 + N3)/Nt, in which N2 is the abundance of organisms in the intermediate net, N3 the abundance in the upper net and Nt the total abundance in the three nets (Sainte-Marie and Brunel, 1985).

For some well represented species or taxa in decapod diets, data of size-frequency distributions for natural populations were obtained and compared to those obtained from stomach contents (Kolmogorov-Smirnov test). Both suprabenthic and infaunal species were included. The sizes were obtained with the aid of an ocular micrometer attached to a stereomicroscope (10 × –40 ×). Among the suprabenthos, isopods, a frequent prey-group in decapod stomachs, were chosen. The asellids *Munnopsurus atlanticus* and *Ilyarachna longicornis*, and the Flabellifera *Cirolana borealis* were the chosen species. Size frequency distributions were obtained from the environment

(LT, in mm), whereas the total lengths of the isopods consumed (LT, in mm) were estimated using linear regressions of highly-calcified structures (telson, uropods or hard cephalic armours in the case of both asellid species) resistant to digestion. In both cases (environment and stomach contents) data were obtained in all four annual seasons. As an example of infaunal species, the burrowing decapod *Calocaris macandreae* was chosen. It is a species that, because of its size and abundance, is a key part of the bathyal food webs in the study area, being widely consumed both by bathyal decapods and fishes (Macpherson, 1979, 1981; Cartes, 1994). Size-frequencies (CL, in mm) for *C. macandreae* populations were measured for each season. Size structure derived from stomach contents was also estimated using regressions between size (CL) and characteristic persistent remains (mandibles and telson). To avoid differences between environment and gut contents in prey size composition by local and seasonal differences, only data exclusively and simultaneously obtained from R samples were tested. Post-larval or early juvenile stages of *C. macandreae*, which were present in late autumn and late winter, were more or less represented in the three subsamples of the sledge. Kt was calculated for these stages in both seasons.

3. Results

3.1. BBL community: faunistic composition, bathymetric and seasonal changes in abundance

Crustaceans were the dominant benthopelagic fauna in the water column closest to the sea bed (between 0.1–1.5 m above the bottom) sampled with the Macer-GIROQ sledge. Among these, copepods were the dominant group in number for all samples (Tables 3–5). Due to their relatively large size (1–20 mm), peracarid crustaceans (mysids, amphipods, isopods and cumaceans) must be considered the dominant group of crustaceans in biomass. Eucarids (euphausiids and natantian decapods) in biomass and ostracods in number were also relatively important.

Another important group was comprised of gelatinous plankton (siphonophores, medusae, chaetognaths, and thaliaceans), whose quantification is subject to a certain error since they are very fragile and are broken and distorted during the manipulation and conservation of samples. Some pelagic molluscs (pteropods, *Cymbulia peroni*), and benthopelagic fishes (Myctophids, *Cyclothone braueri*) completed the list of the principal faunistic groups. Fish and eucarid larvae were also present in these samples. The presence of at least some of these larvae, because of their small size, could be an artefact resulting from certain degree of contamination during the ascent–descent of the suprabenthic sledge in the water column (Cartes and Sorbe, 1993).

The basic composition of the BBL between 13–55 m above the sea bed of the middle slope (Table 6) was similar to that described for the ~0–1.5 m range above the bottom. Only three samples were obtained in March 1994, when crustaceans were also the dominant taxon, with copepods attaining the highest densities. Ostracods (*Conchoecia* sp.) were also important numerically but not in terms of biomass, while meso-bathypelagic decapods and euphausiids must be considered dominant in

Table 3
Density (ind./1000 m^3) of the main benthopelagic taxa on the upper slope level sampled with the Macer-GIROQ sledge

BBL density	R3		R1	BT2		R4		R2	
(ind./1000 m^3)	Mar92		Apr91	Jul95		Jul92		Dec91	
Upper slope (392–506 m)	Us	C	C	Us	C	Us	C	Us	C
	n = 1	*n* = 1	*n* = 1	*n* = 1	*n* = 1	*n* = 1	*n* = 1	*n* = 1	*n* = 1
Medusae	4.2	47.6	-	77.2	132.2	-	-	155.5	49.6
Siphonophora	88.9	84.7	175.0	18.1	42.8	61.6	22.3	205.9	99.2
Polychaeta	-	-	-	-	-	-		-	-
Crustacea Decapoda	71.9	68.9	45.8	8.6	28.5	40.9	67.5	168.0	24.6
larvae + post-larvae	331.8	143.1	58.3	82.6	77.2	299.2	17.5	326.8	86.1
Euphausiacea	12.7	15.8	4.2	102.0	132.8	34.2	29.1	-	24.8
Calyptopis, Furcilia and post-larvae	669.5	280.4	320.4	478.5	717.3	575.3	524.5	75.6	49.6
Mysidacea	56.3	597.9	1602.4	26.7	2466.8	226.0	40.9	589.2	186.0
Amphipoda Gammaridea	1407.5	7349.2	1508.3	25.7	442.2	856.2	862.5	2953.7	735.5
Amphipoda Hyperiidea	25.4	5.3	29.2	22.9	49.3	27.3	17.3	-	12.4
Isopoda	987.3	7634.9	1170.8	13.4	584.4	212.3	262.2	684.9	574.4
Cumacea	411.0	2248.7	372.5	3.8	51.2	335.6	215.6	857.9	314.1
Ostracoda	203.4	412.7	640.8	278.8	941.2	198.6	27.2	105.1	409.1
Copepoda	6915.3	12439.1	15592.4	6282.1	15215.3	5541.1	1131.2	4622.7	2405.0
Nebaliacea	-	142.4	-	-	3.8	-	-	-	4.1
Pycnogonida	-	5.3	-	-	1.9	6.8	-	-	-
Pteropoda	21.1	5.3	-	10.5	54.0	6.8	7.4	8.4	4.1
Chaetognata	55.1	238.1	400.5	64.8	191.8	178.1	91.6	79.8	210.7
Thaliacea	-	-	-	-	-	-	-	-	-
Apendicularia	21.2	21.2	-	-	-	6.8	-	-	-
Pisces	4.2	42.3	16.7	1.9	26.5	6.8	2.5	-	12.4
larvae	12.7	5.3	4.2	43.2	11.4	-	19.8	-	-
OTHER	21.2	3.7	141.7	23.8	35.4	-		50.4	12.4
TOTAL	10,345.4	31,820.8	22,083.7	7564.6	21,206.2	8613.7	3339.1	10,879.2	5218.1

C: canyon samples; Us: out of canyon samples; n: number of samples.

Table 4
Density (ind./1000 m^3) of the main benthopelagic taxa on the middle slope level sampled with the Macer-GIROQ sledge

BBL density	BT1	R3	R1	BT2	R4	R2
(ind./1000 m^3)	Mar94	Mar92	Apr91	Jul95	Jul92	Dec91
Middle slope (549–660 m)	n = 1	n = 2	n = 1	n = 1	n = 1	n = 1
Medusae	2.5	20.5	16.7	279.3	3.2	1191.3
Siphonophora	16.2	104.5	641.7	65.6	41.4	104.0
Polychaeta	-	-	-	-	-	-
Crustacea Decapoda	37.7	28.7	58.3	102.2	143.3	168.1
larvae + post-larvae	32.7	120.9	33.4	56.4	140.1	598.6
Euphausiacea	5.7	22.6	91.7	137.1	9.5	14.4
larvae and post-larvae*	414.3	550.4	200.8	217.7	111.5	65.3
Mysidacea	462.5	474.6	1971.2	4499.6	1885.4	836.2
Amphipoda Gammaridea	620.6	689.3	1183.0	1099.8	4178.3	2902.7
Amphipoda Hyperiidea	11.9	30.6	37.5	5.2	9.5	20.3
Isopoda	415.4	364.2	487.5	1546.4	1828.0	2098.3
Cumacea	65.1	441.6	156.2	370.8	1924.3	695.2
Ostracoda	221.4	592.0	1627.4	765.3	789.8	771.4
Copepoda	7078.0	7805.3	11925.9	17992.4	17019.0	8547.6
Nebaliacea	2.5	-	12.5	-	15.9	8.2
Pycnogonida	-	-	-	-	-	-
Pteropoda	1.5	2.0	-	12.2	-	-
Chaetognata	10.9	81.9	125.4	78.7	38.2	118.1
Thaliacea	1.5	-	116.6	-	-	-
Apendicularia	-	12.3	25.0	-	-	8.1
Pisces	2.6	24.5	87.5	75.9	54.1	28.6
larvae	0.7	8.2	8.3	-	3.2	-
OTHER	3.0	10.2	145.8	-	6.4	
TOTAL	8597.9	11,384.3	20,423.5	27,629.5	28,201.0	18,184.8

n: number of samples. Mean values for stations with n > 1. *Larvae including *Calyptopis, Furcilia*

biomass, because of their large mean size. Peracarid crustaceans were poorly represented, only by hyperid amphipods and some mysids. Gelatinous plankton were also well represented at this level (Table 6), by the same groups that occurred in the interface closest to the sea bed. Mesopelagic fishes (almost uniquely *Cyclothone braueri*) were also important in terms of biomass. Eucarid larvae were abundant in this level too; the shrimp *Gennadas elegans*, for instance, was represented by all the larval stages from *zoea* to *megalopa*, while *Furcilia*, *Calyptopis* and post-larvae forms of euphausiids were also common. A calibration test of this gear was performed, by carrying out the same manoeuvre for the valid samples, but without opening the plankton net. The catches confirmed that there is no contamination of the samples during the ascent–descent of this gear. Suprabenthic, or vagile, epibenthic fauna was poorly represented at this level of the water column (between 13–55 m), and the only suprabenthic peracarid collected was *Boreomysis arctica* (9 specimens in 2 samples over 644–680 m soundings).

Table 5
Density (ind./1000 m^3) of the main benthopelagic taxa on the lower slope level sampled with the Macer-GIROQ sledge

BBL density (ind./1000 m^3) Lower slope (1125–1355 m)	BT1 Mar94 n = 2	R3 Mar92 n = 1	R1 Apr91 n = 1	BT2 Jul95 n = 1	R4 Jul92 n = 1	R2 Dec91 n = 1
Medusae	2.5	9.9	7.7	14.5	1.9	5.7
Siphonophora	66.7	161.7	144.8	45.6	40.7	11.5
Polychaeta	-	-	-	-	-	-
Crustacea Decapoda	22.9	17.3	5.8	13.8	28.5	5.7
larvae + post-larvae	333.6	27.2	12.7	24.6	20.9	5.7
Euphausiacea	9.6	7.5	25.1	34.0	30.8	11.5
larvae and post-larvae*	573.4	144.3	87.8	266.4	255.9	26.8
Mysidacea	313.5	337.2	501.8	231.7	191.1	373.4
Amphipoda Gammaridea	1141.2	1074.4	314.7	309.2	578.6	749.2
Amphipoda Hyperiidea	8.6	21.2	11.6	26.8	27.7	1.9
Isopoda	614.6	184.1	100.4	68.8	64.8	394.6
Cumacea	434.9	327.1	122.4	59.9	166.5	82.8
Ostracoda	128.8	106.9	87.0	234.6	59.3	36.4
Copepoda	5975.6	3927.5	3703.0	6042.8	6859.3	2881.0
Nebaliacea	2.7	-	1.9	2.2	1.9	-
Pycnogonida	-	-	-	-	-	-
Pteropoda	14.4	9.9	1.9	1.4	13.0	7.6
Chaetognata	33.6	77.1	29.0	62.9	38.9	11.5
Thaliacea	4.9	9.9	21.2	-	-	-
Apendicularia	5.4	37.3	11.6	-	-	-
Pisces	11.9	14.9	17.4	23.9	16.7	15.3
larvae	5.6	-	-	20.3	-	-
OTHER	1.3	32.3	13.5	22.0	5.6	3.8
TOTAL	9419.5	6528.1	5221.0	7304.6	8402.1	4624.4

n: number of samples. Mean values for stations with n > 1. *larvae including *Calyptopis, Furcilia*

Comparisons of the data for the three sampled bathymetric levels showed that the abundances of benthopelagic fauna were significantly higher on the middle slope (Kruskall-Wallis test – n = 21; p = 0.036), and significantly decreased on the lower slope—Kruskall-Wallis test (n = 21; p = 0.019). This latter trend is common for all groups (Table 7), although some, such as siphonophora, euphausiid larvae, hyperid amphipods, or fishes, maintained density values on the lower slope closer to those of the upper and middle levels. As a consequence, the megabenthos must have different type of food-resources available on the upper and middle slopes than on the lower slope.

Seasonal trends in densities of benthopelagic organisms differed at the three slope levels sampled. On the middle slope (Table 4), a peak of benthopelagic fauna was clearly detected in summer (Jul92–Jul95), whereas the minimal density was observed in late winter (Mar92–Mar94). Several groups showed a peak in summer, matching

Table 6
Density (ind./1000 m^3; mean value) of zooplankton taxa near the bottom (between 13–55 m above bottom) on the middle slope. Samples collected with an opening-closing plankton net

BBL density (ind./1000 m^3) Middle slope (639–663 m) 13–55 mab	BT1 Mar94 n = 3
Medusae	2.5
Siphonophora	120.5
Polychaeta	3.3
Crustacea Decapoda	34.4
larvae	41.9
Euphausiacea	15.6
Calyptopis, Furcilia and post-larvae	302.5
Mysidacea	7.5
Amphipoda Gammaridea	-
Amphipoda Hyperiidea	41.6
Isopoda	-
Tanaidacea	-
Cumacea	-
Ostracoda	609.1
Copepoda	9530.5
Nebaliacea	-
Pycnogonida	-
Pteropoda	17.8
Chaetognata	7.5
Thaliacea	30.3
Apendicularia	3.3
Pisces	26.5
larvae	-
OTHER	44.2
TOTAL	10,846.1

n: number of samples.

the general peak already mentioned. This applied particularly to copepods, and also partially to decapod crustaceans, euphausiids, and fishes. Peracarid crustaceans, mysids, gammarid amphipods, and cumaceans were also more abundant or showed high density values in summer (Jul92 or Jul95). Siphonophora, Ostracoda and hyperids showed a maximum in spring (Apr91), while for Medusae and isopods the maximum occurred in autumn (Dec91). On the middle slope the highest similarity (91.2) was between the Mar92–Mar94 samples, which suggests a degree of seasonal regularity in the taxonomic composition of the BBL communities.

On the upper slope maximum densities of benthopelagic organisms were observed in late winter (Mar92) at the canyon station (C), and high values also occurred outside the canyon (Us) during this same period (Table 3). Among the dominant taxa in terms of abundance, peracarids (gammarid amphipods, isopods, and cumaceans)

Table 7
Comparison between abundances in decapods diet (per 1000 individuals) and density (ind./1000 m^3) in the environment for benthopelagic taxa

	Upper slope (392–506 m)				Middle slope (549–660 m)				Lower slope (1125–1355 m)			
	Diet	BBL	L	χ^2	Diet	BBL	L	χ^2	Diet	BBL	L	χ^2
Medusae	-	64.2	– 0.005	*	7.0	307.9	– 0.012	**	-	6.3	– 0.001	ns
Siphonophora	42.5	105.4	0.012	**	31.1	222.8	0.004	ns	140.6	89.7	0.062	**
Polychaeta	-	-	-	-	-	-	-	-	-	-	-	-
Decapoda	176.4	69.7	0.078	**	87.6	99.6	0.039	**	126.4	14.3	0.066	**
larvae	-	180.4	– 0.014	**	0.7	223.3	– 0.011	**	-	16.6	– 0.003	ns
Euphausiacea	365.5	20.1	0.170	**	166.2	34.6	0.082	**	13.5	18.7	0.004	ns
larvae	-	356.5	– 0.027	**	-	32.0	– 0.012	ns	-	128.7	– 0.021	**
Mysidacea	70.2	471.2	– 0.003	ns	121.3	1291.9	– 0.005	ns	26.3	350.9	– 0.042	**
Gammaridea	426.7	2248.0	0.032	**	298.3	2238.3	0.035	**	199.4	679.2	– 0.002	ns
Hyperiidea	85.6	17.8	0.039	**	70.2	24.5	0.034	**	134.1	15.6	0.070	**
Isopoda	336.7	1653.8	0.033	**	390.0	1194.5	0.135	**	333.8	186.0	0.150	**
Cumacea	138.8	662.2	0.015	*	232.7	804.3	0.076	**	228.7	174.7	0.095	**
Ostracoda	17.8	260.8	– 0.011	**	218.2	945.2	0.061	**	28.9	72.4	0.004	ns
Copepoda	174.1	6319.6	– 0.397	*	110.7	11324.5	– 0.524	**	15.6	4342.7	– 0.693	**
Nebaliacea	-	73.3	+	*	-	12.2	– 0.002	ns	-	1.9	+	ns
Pycnogonida	7.0	6.1	0.003	**	5.8	-	0.003	**	-	-	-	-
Pteropoda	124.2	8.9	0.003	**	12.6	20.2	0.002	**	-	8.1	– 0.001	ns
Chaetognata	40.5	179.1	0.005	ns	29.5	90.9	0.010	**	24.1	39.1	0.007	ns
Thaliacea	-	16.4	+	ns	-	116.6	-0.006	*	-	15.6	– 0.003	ns
Apendicularia	-	7.0	– 0.001	ns	-	15.1	0.001	ns	-	24.5	– 0.004	ns
Osteichthyes	18.7	14.2	0.008	**	16.4	48.7	0.006	**	19.7	16.1	0.008	**
larvae	-	10.5	– 0.001	ns	-	6.6	0.006	ns	-	8.2	+	ns
OTHER†	40.0	45.9	0.015	**	85.0	54.1	– 0.040	**	255.9	13.8	0.136	**
TOTAL	2126	13186			1990	19548			1850	6194		

L: linear index of food selection (Strauss, 1979); + = less than ± 0.001. χ^2 significant levels: ns = non-significant; * = $p < 0.01$; ** = $p < 0.001$. †soft tissues.

were at their maximum in the canyons during late winter. On the other hand, groups such as mysids, ostracods or copepods were more abundant in summer (Jul95) and/or spring (Apr91), also in the canyon station (although this trend did not appear in Jul92). The seasonal variations between inside and outside the canyon were very important, as is deduced from the very disparate similarity values (Table 8). The majority of the taxa attained their highest densities within the canyon although in different seasons. The interannual variations at the same season (the case of Jul92–Jul95 comparison) were also important. On the upper slope, the similarity between canyon (C) samples was higher than between the outside canyon (Us) samples, and also higher than between Us–C comparisons.

Finally, on the lower slope station, below 1200 m, general peaks of abundance were less striking than at shallower depths (Table 5), and there was only a slight

Table 8
Percentage of similarity between BBL taxa composition sampled with the Macer-GIROQ sledge. Comparisons within each bathymetric level

Upper slope-Canyons (389–506 m)	Mar92 C	Apr91 C	Jul95 C	Jul95 Us	Jul92 Us	Jul92 C	Dec91 Us	Dec91 C
Mar92 Us	28.8	16.7	11.0	10.0	28.2	35.9	32.2	29.4
Mar92 C		58.7	50.0	43.9	61.4	75.1	81.0	76.7
Apr91 C			89.4	77.9	85.2	53.6	66.1	71.3
Jul95 C				83.1	79.9	46.1	57.3	63.7
Jul95 Us					77.1	45.0	48.8	57.3
Jul92 Us						63.1	68.1	73.9
Jul92 C							77.7	69.3
Dec91 Us								80.2

Middle slope (549–601 m)	Mar94	Apr91	Jul95	Jul92	Dec91
Mar92	91.2	86.4	83.6	81.9	71.7
Mar94		82.4	83.3	80.6	67.6
Apr91			87.1	80.7	68.4
Jul95				81.9	69.2
Jul92					82.1

Lower slope (1250–1355 m)	Mar94	Apr91	Jul95	Jul92	Dec91
Mar92	89.0	84.0	73.5	77.5	62.8
Mar94		82.1	76.8	80.9	62.7
Apr91			83.6	86.6	62.5
Jul95				94.0	60.1
Jul92					61.3

maximum in Mar94. Some groups showed peaks of abundance in winter (gammarid amphipods, isopods, and cumaceans), whereas copepods and ostracods, together with euphausiids, and less clearly chaetognaths, were more abundant in summer, mysids were most abundant in Apr91. Similarities between samples (seasons) at this level were always high ($S > 60.1$). In general, similarities were greater between the samples from the middle and lower slope than from the shallowest level (Table 8).

Briefly, among the observed trends the more important were: (1). the seasonal peak of copepods in summer at the three bathymetric levels studied (spring–summer at the upper slope), and (2). the highest densities for the majority of pericarid groups (gammarids, isopods and cumaceans) occurred in the canyon at upper slope depths (Table 3) in late winter (Mar92).

3.2. *Influence in trophic food webs of megabenthic organisms (decapod crustaceans)*

Species of the dominant decapod crustaceans collected with bottom trawls (megafauna) changed at each level down the slope. Maximum total densities were recorded in summer (Jul92) at all three bathymetric levels. The most important fluctuations were among mesopelagic species (*Sergestes arcticus* and *Pasiphaea sivado* on the upper slope; *S. arcticus*, *Sergia robusta* and *Pasiphaea multidentata* on the middle slope), which disappeared from catches at certain seasons (Table 9). *Aristeus antennatus*, one of the most abundant species on the slope, showed maxima in spring (Apr91) and summer (Jul92). Decapod abundances progressively decreased with increasing depth; the most evident result being the almost total disappearance of mesopelagic species (Sergestidae, Pasiphaeidae) at the lower slope station (Table 9).

Although infaunal and epibenthic groups can be dominant in decapods diet as a function of the species' depth and of season, benthopelagic prey-groups are also very important as food resource (Cartes and Abelló, 1992; Cartes, 1994). Numerically about half of the total decapod prey are of benthopelagic origin (Cartes, 1991). Considering the high mean size of different groups (mesopelagic fishes and decapods, euphausiids), the importance of benthopelagic prey in the diet of megabenthic decapods is even greater in terms of weight and from an energetic point of view.

From the results of food-selectivity analysis it was deduced that decapods showed preference for certain prey-groups, particularly crustaceans. Thus, both natantian decapods and some peracarids (hyperid amphipods, isopods, and cumaceans) were consistently more abundant in stomach contents than in the environment (sledge samples) throughout the bathymetric range studied (L between 0.015–0.150; significant χ^2, $p < 0.01$). Furthermore, hyperids, isopods, and cumaceans were more positively selected as the depth increased (Table 7). Euphausiids and gammarid amphipods were positively selected only on the upper and middle slope, while mysids were taken randomly at these same levels and were negatively selected below 1200 m. Little or no preference was shown for the consumption of gelatinous plankton. Only Siphonophora and soft tissues (perhaps attributable to gelatinous taxa) were positively selected, mainly at lower slope depths. Copepods were not consumed by megabenthic decapods throughout the whole bathymetric range sampled, despite their

Table 9
Abundance ind/10000 m^2 by depth and season of the dominant decapod species on the Catalan Sea slope captured with bottom trawls in R cruises

Upper slope (390–508 m)	R3 Mar92 n = 3	R1 Apr91 n = 3	R4 Jul92 n = 3	R2 Dec91 n = 3
Alpheus glaber	1.3	2.4	1.8	3.2
Aristeus antennatus	6.4	47.5	**61.1**	42.8
Calocaris macandreae	8.9	14.4	**18.7**	16.5
Ligur ensiferus	0.1	0.6	0.1	8.6
Monodaeus couchi	0.5	2.0	1.2	1.9
Munida intermedia	0.5	0.5	0.1	2.5
Nephrops norvegicus	1.7	3.8	3.1	1.0
Pandalina profunda	-	*	3.7	5.4
Pasiphaea sivado	-	13.7	**44.5**	0.9
Plesionika edwardsi	1.7	**12.8**	1.6	5.9
Plesionika gigliolii	5.0	**17.3**	9.2	9.0
Plesionika martia	3.2	6.0	**20.1**	17.3
Pontocaris lacazei	1.7	3.2	2.4	4.6
Processa nouveli	0.2	0.6	2.4	6.3
Sergestes arcticus	8.5	0.6	**21.1**	4.1
Solenocera membranacea	0.7	1.2	2.4	1.6
Total	42.2	133.7	**193.8**	143.3
Middle slope (545–692 m)	n = 3	n = 3	n = 3	n = 3
Aristeus antennatus	26.6	**37.1**	18.3	2.4
Calocaris macandreae	**15.9**	3.1	4.2	2.1
Geryon longipes	0.7	0.2	0.2	0.4
Munida tenuimana	3.8	0.3	0.9	0.7
Pandalina profunda	2.2	*	–	2.8
Pasiphaea multidentata	*	0.8	**3.5**	1.6
Plesionika acanthonotus	2.0	1.4	1.3	0.4
Plesionika martia	2.7	**5.8**	2.9	*
Polycheles typhlops	2.0	2.3	1.2	0.7
Sergestes arcticus	0.8	2.0	**7.4**	0.1
Sergia robusta	0.9	2.4	**26.3**	-
Total	62.7	57.0	**66.9**	10.6
Lower slope (1160–1286 m)	n = 3	n = 2	n = 3	n = 3
Acanthephyra eximia	1.8	1.4	**8.7**	5.0
Aristeus antennatus	4.6	7.2	**33.5**	9.1
Gennadas elegans	0.1	0.2	1.4	0.2
Geryon longipes	0.3	0.9	0.4	0.5
Munida tenuimana	6.9	**14.5**	10.8	12.0
Plesionika acanthonotus	0.6	1.2	0.2	0.5
Pontophilus norvegicus	2.3	**5.3**	4.7	4.2
Total	15.8	30.9	**52.3**	28.7

n: number of samples. *: less than 0.1 ind/10000 m^2. Maximum seasonal values highlighted for the most abundant species and the total abundance maxima.

being numerically the dominant group in the bathyal-BBL. For the rest of the groups a selection (positive or negative) could not be deduced in any bathymetric level.

Comparison of sizes of prey found in stomach contents with those in the environment is also interesting. Among suprabenthos (isopods), the most frequent size peaks in the environment were between 2–3 mm LT (Fig. 2) for Asellota and between 5.5-6.5 mm LT for *Cirolana borealis*. In stomach contents, on the other hand, the frequency peaks were between 4–5 mm LT, and 9–11 mm LT respectively (Fig. 2). For Asellota, the 3 mm size-class was relatively abundant in stomach contents. Comparisons between the size-frequency distributions in the natural environment and in stomach contents (Kolmogorov-Smirnov test) showed significant differences for Asellota ($p < 0.01$) and for *Cirolana borealis* ($p < 0.01$). In the case of *Calocaris macandreae* the sizes most abundantly consumed by megabenthic decapods were > 3.5 mm CL (Fig. 3). The sizes corresponding to recruits, between 1–3 mm CL (Fig. 3), were hardly represented in the stomach contents. These size-classes still showed relatively high swimming coefficients (Kt = 0.697 in late autumn; Kt = 0.233 in late winter). The comparison between mean sizes in the environment and stomach contents was also significantly different ($p < 0.01$).

4. Discussion

Bathyal–benthopelagic macrofauna from depths of between 389–1355 m in the Catalan Sea had a similar taxonomic composition to that reported in other studies in the north Atlantic (Hargreaves et al., 1984; Angel, 1990 and references cited), at both bathyal and abyssal depths; copepods were clearly the dominant taxon, with ostracods, chaetognaths and gelatinous plankton also well represented. In our case, the level of the BBL sampled with the suprabenthic sledge (~0–1.5 m above the bottom), is very close to, or includes, the water–sediment interface. Consequently, epibenthic macrofauna with high natatory capability (suprabenthos according to Brunel et al., 1979), basically peracarid and decapod crustaceans, are also collected. Among peracarids the natatory capability varies between species (Cartes and Sorbe, 1995) or even, as in the case of cumaceans, on the sexual state (Cartes and Sorbe, 1996). Therefore, to include a taxon within the concept of epibenthos or suprabenthos implies an unavoidable margin of error if detailed studies on the biology and autoecology of species is not carried out. In the present study, suprabenthic peracarids were almost totally restricted to the narrow interface sampled with the Macer-GIROQ sledge. The one species which was uniquely caught far above the bottom (between 13–55 m), was the mysid *Boreomysis arctica*; this species was also the only benthopelagic mysid sporadically present in midwater samples from previous studies in the western Mediterranean (Macquart-Moulin, 1993). The study of the BBL close to the bottom only using pelagic gears, underestimates the diversity and density of suprabenthic macrofauna, since it can only be sampled effectively with sledges.

Obviously, the lack of replicates in the present study is a drawback when discussing results and trends obtained. Despite this though, Brattegard and Fosså (1991) indicated that there is an acceptable level of similarity between repeated samples

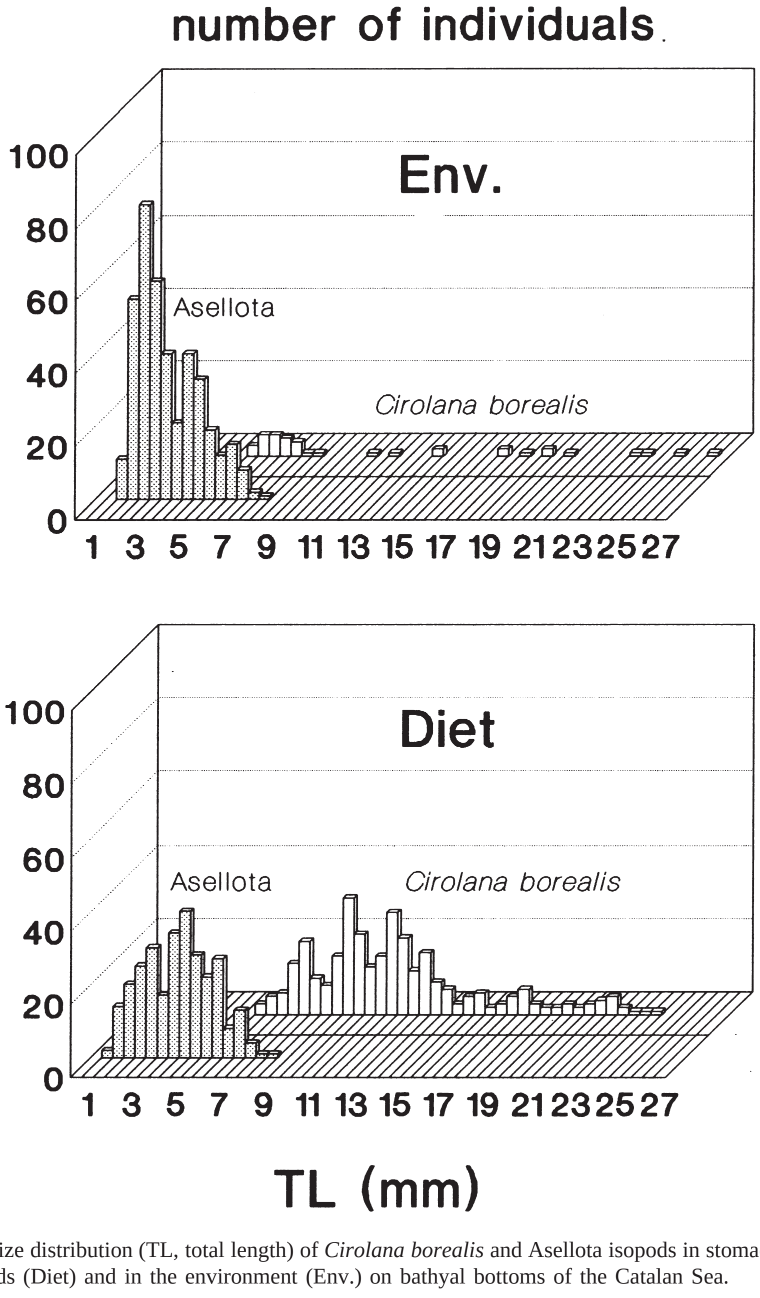

Fig. 2. Size distribution (TL, total length) of *Cirolana borealis* and Asellota isopods in stomach contents of decapods (Diet) and in the environment (Env.) on bathyal bottoms of the Catalan Sea.

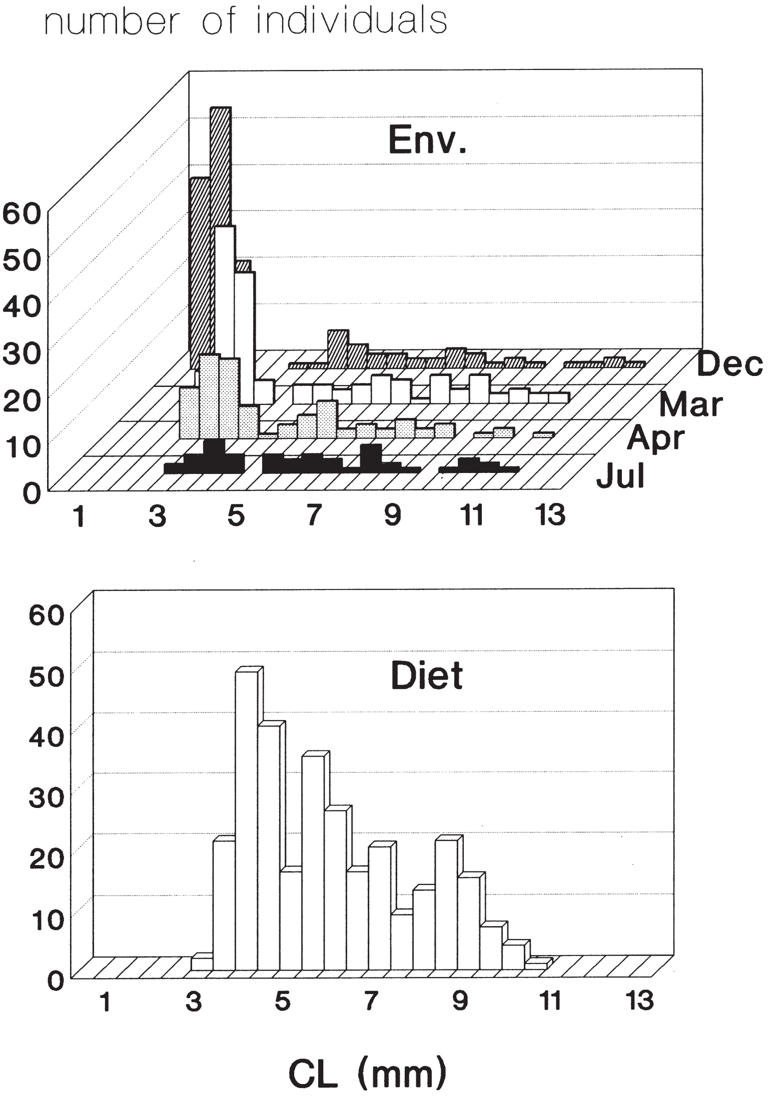

Fig. 3. Size distribution of *Calocaris macandreae* (CL, cephalotorax length) in stomach contents of decapods (Diet) and in the environment (Env.-ordered by moth) in the studied area of the Catalan Sea slope. Dec: December 1991; Mar: March 1992; Apr: April 1991; Jul: July 1992;

obtained with suprabenthic sledges, both in the number of individuals and the species present. Thus, a single haul can be considered to provide a representative sample.

In the bathyal-BBL in the Catalan Sea, the maximum densities of benthopelagic macrofauna were observed during summer (Jul92–Jul94) on the middle slope, whereas on the upper slope the maximum occurred in late winter (Mar92), although the peaks were less marked and subjected to fluctuations between the canyon and the open slope adjacent to canyons. The summer maximum was especially marked for the copepods, the dominant taxon. No similar data on BBL macrofauna abundance exist for the Mediterranean, so comparisons can only refer to zooplankton studies. Our BBL data showed fluctuations which coincided with seasonal changes of zooplankton in the western Mediterranean. Maximum zooplankton biomasses (collected with 200–250 μm meshes) were recorded from different open Mediterranean areas either in May–June (Razouls and Kouwnberg, 1993) or in the early spring (Fernández de Puelles et al., 1995), a maximum was also detected in April-May on the shelf-slope break in the Catalan Sea (Sabatés et al., 1989) associated with a swarm of gelatinous plankton. However, abundance values associated with the copepods tended to reach a maximum in June–July (Sabatés et al., 1989; Fernández de Puelles et al., 1995), which coincides with our BBL density results. The reduction of temporal variations in zooplankton abundance collected in sediment traps with depth (Miquel et al., 1994), is also confirmed by our results, and is an aspect also detected in seasonal changes in taxonomic composition. Abundance of peaks of adult euphausiids, represented in our samples mainly by *Nematoscelis megalops* and *Euphausia krohni* (Cartes et al., 1994), coincided with those cited by Casanova (1974) for these same species, although the maximum abundance of euphausiids on the slope was found in autumn if we consider the larger sized fraction (mesh size used = 6 mm) of zooplankton (Franqueville, 1971). In this fraction *Meganyctiphanes norvegica* is predominant; this species occurred infrequently in our samples.

Copepods are generally considered to be filter-feeders (Vinogradov and Tseitlin, 1983), and consume a large variety of particles or detritus, depending on their availability in the environment (Klepper, 1993). The maximum densities we detected for deep-water copepods (below 549 m) in July could probably be explained as a response coupled to peaks in the vertical flux of organic matter which have been observed in the northwestern Mediterranean slope in summer (Buscail et al., 1990), or more specifically in late June over the upper slope of the neighbouring Ligurian Sea region (Miquel et al., 1994). In contrast, the seasonal regime of particle flux at 1000 m does not show a clear temporal trend (Miquel et al., 1994), which agrees with the apparent lack of temporal variations of the densities of benthopelagic organisms on the lower slope observed in the present study. Other groups with summer peaks on the middle slope, composed of both facultative detritivores (euphausiids, mysids), and small predators (mesopelagic decapods, chaetognaths, and fishes), would also experience their maximum availability of food resources (mainly copepods) in this same season. However, seasonal variations in faunal density differ according to the size of the fauna sampled. Thus, for the same region, the peak of abundance for the larger fraction of macroplankton (caught with a 6 mm mesh-size), is recorded in autumn–winter with a minimum in summer (Franqueville, 1971).

On the upper slope, many of the dominant groups (copepods, euphausiids, mysids, and chaetognaths) showed strong fluctuations in their densities that appeared to be related more to the influence of the submarine canyons than to the seasonal pattern of organic material derived from surface production. The dynamics of downward particle flux in canyon areas can be very different between the axis of the canyon and in open areas over the neighbouring slope, because of substantial differences in advective fluxes and terrigenous inputs (Miquel et al., 1994). Thus, in the Lacaze-Duthier canyon, orgC contents are more important in canyons than on the open slopes between canyons (Buscail et al., 1990), with an important seasonal variation within the canyon. Therefore, submarine canyons at upper slope levels can have a more complex dynamic in the BBL than that of the middle slope zone in this study.

Various groups of peracarids (amphipods, isopods, and cumaceans) showed their maximum densities in late winter in the canyon. Buscail et al. (1990) indicated that there is an increase in the flux of organic matter between early winter–early spring in the Lacaze-Duthier canyon in the Catalan Sea area, as a result of a maximum of fresh matter inputs in late winter. This agrees with the maximum densities found for the groups cited above, which are taxa with a large number of species associated with the sediment. More specific studies carried out in this same area showed that an important recruitment of cumaceans occurs in late winter (Cartes and Sorbe, 1996), and in late autumn–late winter for mysids and amphipods (unpublished data), coinciding with the periods of vertical mixing of the water column. This pattern has been observed in other very different taxa such as bivalves or polychaetes (personal observation), which would affect, in general, the recruitment and biological cycle of macrofauna in the BBL (both infauna and suprabenthic organisms). Among the infaunal species, the decapod *Calocaris macandreae* is one of the most abundant in the communities studied, and is a basic component of the diets of the majority of the megafaunal groups, such as the shrimp *Aristeus antennatus* (Cartes, 1994), crabs (Cartes, 1994), macrourids (Macpherson, 1981), and other fishes (Macpherson, 1979). As a macrofaunal species its relatively large mean size and high biomass (Cartes and Sardà, 1992) makes *C. macandreae* a keystone prey-species from an energetic point of view. It has a recruitment peak in late autumn–late winter. However, the smallest sizes appear in late autumn as recently hatched forms still with vitelline reserves in the cephalothorax (personal observation). In late winter, the peak of recruits, depending on inputs of an external food source also appears to coincide with the maximum input of orgC that, as already mentioned, occurs in the neighbouring area of the Lacaze-Duthier canyon (Buscail et al., 1990).

4.1. Implications in the trophic bathyal webs (megafauna)

In the study area, a considerable amount of information has been published on bathyal trophic webs for both for fish and decapod crustaceans, which are the two clearly dominant groups in megafaunal communities. Decapod diets have been particularly well studied, both over wide bathymetric ranges (between 400–2200 m) and seasonally (Cartes, 1994, 1998). Benthopelagic resources contribute approximately half of the diet of megabenthic decapods collected in bottom trawls, and the bathyal fishes show an even greater dependency on benthopelagic resources than decapods (Macpherson, 1979, 1981; Carrasson et al., 1992; Carrasson, 1994).

To date, studies on the diets of bathyal megabenthic organisms have seldom considered simultaneously sampling of the available resource (Mauchline, 1991) or examining food selectivity. Over the Catalan Sea slope, one of the dominant group in the bathyal-BBL, the megabenthic decapod crustaceans, showed a strong preference for natantian decapods and euphausiids, as well as for peracarid crustaceans, although the low capture rate of decapods and euphausiids by the Macer-GIROQ sledge probably tended to overestimate the selectivity results. On the other hand, very abundant groups in the environment (i.e. copepods) are hardly consumed. Thus, decapod crustaceans caught with bottom trawls select prey of relatively large size (more than ~3 mm LT), and low natatory capability. This would explain their very low consumption of copepods, which combine a small-size with a relatively high Kt (Table 10). Mysids are unique among peracarids, since they are not positively selected for, and this can be explained by the relatively high Kt of the dominant species *Boreomysis arctica* (Cartes and Sorbe, 1995). Obviously, the abundance of a prey species must influence its selection by consumers. In our study, the total density of benthopelagic fauna peaked on the middle slope and decreased below 1000 m; the composition and relative abundance of each group in bathyal benthopelagic communities varied with depth, in agreement with other studies (Hargreaves et al., 1984). Consequently, the available trophic resource for the megafauna differs qualitatively and quantitatively on the upper part of the slope compared to that below 1000 m. In accordance with these bathymetric changes, some gelatinous plankton taxa are only selected by megabenthic decapods on the lower slope, where there is a decrease in the availability of small mesopelagic decapods and euphausiids in the BBL. The low energetic content of gelatinous taxa could be an explanation for why they are only consumed when more energy-rich prey are scarce in the environment.

Table 10
Natatory capability (Kt) of benthopelagic taxa captured with the Macer-GIROQ sledge

BBL (Kt)	
Medusae	0.229
Siphonophora	0.803
Crustacea Decapoda	0.861–0.724 (mesopelagics); 0.150–0.762 (nektobenthics)[1]
larvae + post-larvae	0.664
Euphausiacea	0.732–0.791
larvae + post-larvae	0.681
Mysidacea	0.824 (*Eucopia hanseni*); 0.453–0.102 (suprabenthic)[2]
Amphipoda Gammaridea	0 (*Urothoe corsica*) – 0.336 (*Tmetonyx similis*)
Amphipoda Hyperiidea	0.587 (*Vibilia armata*) – 0.774 (*Phrosina semilunata*)
Isopoda	0.036
Cumacea	0.024–0.676 (*Leucon longirostris*, adult males)
Ostracoda	0.409
Copepoda	0.616
Nebaliacea	0
Pycnogonida	0
Pteropoda	0.764
Chaetognata	0.201
Thaliacea	0.785
Pisces	0.644 (*Cyclothone braueri*) – 0.279 (*Bathypterois mediterraneus*)
larvae	0.859

[1]Cartes et al. (1994); [2]Cartes and Sorbe (1995).

The incidence of prey size as a factor in the diet of bathyal megafaunal decapods is clearly shown by the smallest prey sizes (= recruits) of peracarid crustaceans and *Calocaris macandreae*, hardly being consumed by decapods. Megafaunal decapods would find the maximum availability of suprabenthic peracarids as a food resource in spring and summer, both because of high densities and, above all, for their larger mean size. During this period populations of peracarids, such as mysids or cumaceans are predominantly subadult and adults (Cartes and Sorbe, 1996). In parallel, taking *Calocaris macandreae* as an example, infaunal prey seems to have similar dynamics. Recruitment (specimens between 1–3 mm CL) occurs between late autumn-late winter, probably at greater intensity in or near submarine canyons. On the other hand, the sizes preferably consumed by megafaunal decapods are most abundant in spring and summer. The relatively high natatory capability of *C. macandreae* recruits (between 0.233–0.697) would also contribute to their scarcity in the diets of the decapod crustacean.

Among the large size fraction of deep macroplankton, maximum densities in the north-western Mediterranean occur in winter-spring, and minimum abundances occur in summer (Franqueville, 1971). However, the dominant groups in summer-autumn (Sergestidae, Pasiphaeidae, euphausiids) have a much higher energetic content than the dominant groups in winter-spring (basically gelatinous plankton). Our results confirm that the maximum abundance of mesopelagic decapods occurs in summer.

In summary, different basic trophic resources in decapod diets (suprabenthic peracarids, *Calocaris macandreae,* or mesopelagic decapods) are more abundant in the environment during spring and summer, which are furthermore represented by the sizes consumed by megafaunal decapods. Therefore, a greater availability of trophic resources exist for megafaunal decapods around summer (between late spring-early autumn considering the discontinuity of the present sampling) in the study area, and this coincides with the season during which the maximum density of megafaunal decapods was obtained in our sampling.

At the species level, decapods with biological and trophic strategies as different as *Sergestes arcticus* and *Aristeus antennatus*, had maximum abundances in summer, which coincide with maxima in availability of their preferential food resources. Thus, *Sergestes arcticus,* a mesopelagic decapod of small size, has an specialized diet mainly based on copepods and small euphausiids (Lagardère, 1976; own unpublished data), which showed peak abundances also in summer. For the shrimp *Aristeus antennatus*, the most important fishing resource on the deep-slope in the western Mediterranean (Demestre, 1990), fishing data indicate maximum catches of adults between spring–summer (Tobar and Sardà, 1987; Demestre, 1990; Sardà et al., 1997), which are attributable to a greater aggregation of shoals for reproduction on the middle slope (Sardà et al., 1994). *A. antennatus* bases its diet on a wide variety of infaunal and suprabenthic macrofauna (Cartes, 1994), which also showed abundance peaks of the sizes most consumed by the shrimp, around summer. Other species, however, do not adjust their maximum densities to this proposed scheme. Probably each species is coupled to the cycles of its preferred resource, so that seasonal partitioning of food resources is to be expected among megabenthic species. Although for different deep-sea macrofaunal taxa peaks of food (i.e. phytodetritus deposition) can favour biological processes such as larval release, recruitment or vitellogenesis (Gage and Tyler, 1991; Bishop and Shalla, 1994), the influence that such a maximum of food availability may have on the biological cycle of megafauna are remains unknown. In *Sergestes arcticus*, the largest (= breeders) individuals dominate in summer (Fig. 4). Considering its small size, and its short life (Franqueville, 1971), vitellogenesis of adult individuals in summer would be coupled with the primary production peak of late winter-early spring (Estrada et al., 1985). In the large shrimp *A. antennatus* gonad maturity in females starts around May (Demestre, 1990), also indicating a possible influence of the primary production peak on maturation. Individuals in the process of gonadal maturity, with a period of maturity and reproduction from May to September (Demestre, 1990), would therefore encounter optimal feeding conditions at the stage of their life-cycles when their energetic requirements are high. Understanding the coupling of specific aspects of megafaunal life-histories with the availability of different trophic-resources for other

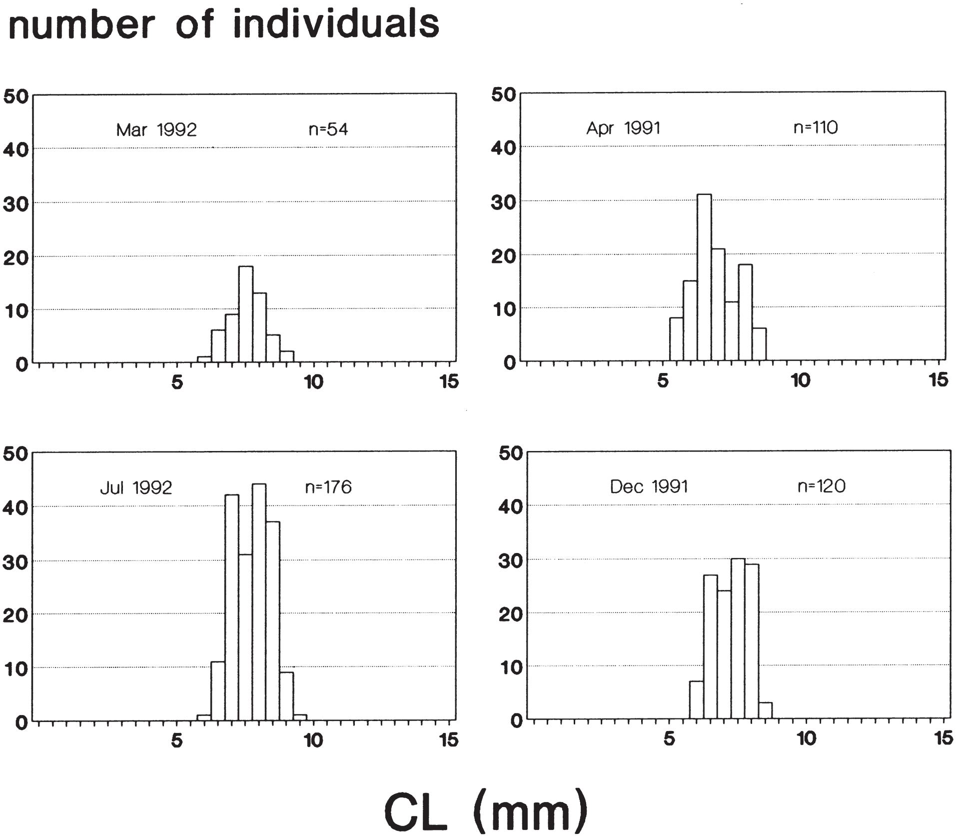

Fig. 4. Seasonal size distribution (CL, cephalotorax length) for the mesopelagic shrimp *Sergestes arcticus* on the Catalan Sea slope between 1991–1992.

species and taxa requires more detailed studies, involving the joint dynamics of the deep macrofauna and zooplankton.

5. Conclusions

In the area studied, seasonal changes in decapod megafaunal abundance seem to be coupled to changes in the food availability exploited. Surface production (flux of organic matter) seems to influence different aspects of the biological cycle (recruitment, abundance) of small suprabenthic and infaunal organisms. The flow of organic matter over the north-western Mediterranean slope shows two important paths, an advective and a vertical component (Monaco et al., 1990). Both paths will simultaneously determine when conditions of maximum food availability occur for bathyal decapods and megafaunal communities in general. The advective flow seems to be more important in the recruitment of suprabenthic and infaunal species at the level of canyons and influence zones between late autumn-late winter (Buscail et al., 1990). The sizes of the organisms consumed by decapods are found more abundant in spring and summer. In parallel, the vertical fluxes seem to determine that the maxima in the abundance of mesoplanktonic organisms (especially copepods) occurs in summer, as may be the case in some macroplankton groups. Size, natatory ability, and energetic value are important factors in the selection of food-resources by decapods. The combination of these factors points towards there being a greater availability of food for decapods between late spring-early autumn, and this would seem to explain both the seasonal values of their abundance (present data), and maxima in the catches of commercial species, such as the case of *Aristeus antennatus*. In future, more detailed studies will be needed to evaluate the applicability of this proposed scheme more generally to other species, of other groups of megafauna (fishes), and to other geographic areas.

6. Acknowledgements

I thank all members of the R and BT cruises (ref. projects MAR90-0575 and PB90-0166 funded by CICYT) for their sampling assistance at the sea, especially to Dr. F. Sardà and to the crew of the “B/O García del Cid”, and also especially to Dr. J.C. Sorbe for his help in the identification of taxa. Thanks also go to Dr. C. Rodgers, who prepared the English translation of this paper.

7. References

Angel, M.V. (1990). Life in the Benthic Boundary Layer: connections to the mid-water and sea floor. *Philosophical Transactions of the Royal Society. London*, *331*, 15–28.

Bishop, J.D.D., & Shalla, S.H. (1994). Discrete seasonal reproduction in an abyssal peracarid crustacean. *Deep-Sea Research*, *41*, 1798–1800.

Brattegard, T. & Fosså, J. H. (1991). Replicability of an epibenthic sampler. *Journal of the Marine Biological Association of the United Kingdom*, *71*, 153-166.

Brunel, P., Besner, M., Messier, D., Poirier, L., Granger, D., & Weinstein, M. (1979). Le traîneau Macer-GIROQ: appareil amélioré pour l'échantillonnage quantitatif étagé de la petite faune nageuse au voisinage du fond. *Internationale Revue der gesamten Hydrobiologique und Hydrographie*, *63*, 815–829.

Buscail, R., Pocklington, R., Daumas, R., & Guidi, L. (1990). Fluxes and budget of organic matter in the benthic boundary layer over the northwestern Mediterranean margin. *Continental Shelf Research*, *10*, 1089–1112.

Carpine, C. (1970). Ecologie de l'étage bathyal dans la Méditerranée occidentale. *Memoires de l'Institut Océanographique de Monaco*, *2*, 1–46.

Carrasson, M. (1994). Relaciones tróficas en las comunidades ícticas bentónicas (de 1000 a 2200 m) en el mar Catalán. Tesis, Universidad Autónoma de Barcelona, 356 pp.

Carrasson, M., Stefanescu, C., & Cartes, J.E. (1992). Diets and bathymetric distributions of two bathyal sharks of the Catalonian deep sea (Western Mediterranean). *Marine Ecology Progress Series*, *82*, 21–30.

Cartes, J. E. (1991). Análisis de las comunidades y estructura trófica de los crustaceos decápodos batiales del Mar Catalán. Tesis, Universitat Politècnica de Catalunya, 627 pp.

Cartes, J.E. (1994). Influence of depth and seasonality in the diet of the deep-water aristeid shrimp *Aristeus antennatus* in the Western Mediterranean. *Marine Biology*, *120*(4), 639–648.

Cartes, J.E. (1998). Feeding strategies and partition of food resources in deep-water decapod crustaceans in relation to depth (between 400-2300 m). *Journal of the Marine Biological Association of the United Kingdom*, *XX*, 000–000.

Cartes, J.E., & Abelló, P. (1992). Comparative feeding habits of Polychelid lobsters in the Western Mediterranean Deep-Sea Communities. *Marine Ecology Progress Series*, *84*, 139–150.

Cartes, J.E., & Sardà, F. (1992). Abundance and diversity of decapod crustaceans in the deep-Catalan Sea (Western Mediterranean). *Journal of Natural History*, *26*, 1305–1323.

Cartes, J.E., & Sorbe, J.C. (1993). Les communautés suprabenthoniques bathyales de la Mer Catalane (Méditerranée occidentale): Données préliminaires sur la répartition bathymétrique et l'abondance des crustacés péracarides. *Crustaceana*, *64*(2), 155–171.

Cartes, J.E., & Sorbe, J.C. (1995). Deep-water mysids of the Catalan Sea: species composition, bathymetric and near bottom distribution. *Journal of the Marine Biological Association of the United Kingdom*, *75*, 187–197.

Cartes, J.E., & Sorbe, J.C. (1996). Temporal population structure of deep-water cumaceans from the western Mediterranean slope. *Deep-Sea Research*, *43*(9), 1423–1438.

Cartes, J.E., Sorbe, J.C., & Sardà, F. (1994). Spatial distribution and swimming activity of deep-sea decapods and euphausiids near the bottom in the northwestern Mediterranean. *Journal of Experimental Marine Biology and Ecology*, *179*, 131–144.

Casanova, B. (1974). Les Euphausiaces de Mediterranée (Systematique et developpement larvaire. Biogéographie et Biologie). These, Université de Provence (Aix-Marseille I), 380 pp.

Dauvin, J.C., & Lorgère, J.C. (1989). Modifications du traîneau Macer-Giroq pour l'amélioration de l'échantillonnage quantitatif étagé de la faune suprabenthique. *Journal de Recherche Océanographique*, *14*, 65–67.

Demestre, M. (1990). Biología perquera de la gamba (*Aristeus antennatus*, Risso, 1816) en el Mar Catalán. Tesis, Universitat de Barcelona, 443 pp.

Elizalde, M., Weber, O., Pascual, A., Sorbe, J. C. & Etcheber, H. (1997). Benthic response of *Munnopsurus atlanticus* (Crustacea, Isopoda) to the carbon content of the near-bottom sedimentary environment on the southern margin of the Cap Ferret Canyon (Bay of Biscay, Northeastern Atlantic Ocean). Deep-Sea Research, in press.

Emelyanov, E. M. (1977). Principal types of recent bottom sediments in the Mediterranean Sea: their mineralogy and geochemistry. In D. J. Stanley (Ed.), *The Mediterranean Sea: A Natural Sedimentation Laboratory*. Dowden, Hutchinson and Ross, Stroudsburg, pp. 355–386.

Estrada, M. (1991). Phytoplankton assemblages across a NW Mediterranean front: changes from winter mixing to spring stratification. *Oecologia Aquatica*, *10*, 157–185.

Estrada, M., & Salat, J. (1989). Phytoplancton assemblages of deep and surface water layers in a Mediterranean frontal zone. *Scientia Marina*, *53*(2,3), 203–214.

Estrada, M., Vives, F., & Alcaraz, M. (1985). Life and the productivity of the Open Ocean. In R. Margalef (Ed.), Western Mediterranean (Key Environments). Pergamon Press, Oxford, pp. 198–232.

Féral, J.P., Ferrand, J.G., & Guille, A. (1990). Macrobenthic physiological response to environmental fluctuations: the reproductive cycle and enzymatic polymorphism of a eurybathic sea-urchin on the northwestern Mediterranean shelf and slope. *Continental Shelf Research*, *10*, 1147–1155.

Fernández De Puelles, M.L., Amengual, B., Gomis, C., Grás, D., Jansá, J., Morillas, A., & Vicente, L. (1995). Zooplankton seasonal variations during a year study in the Majorcan shelf, Baleares, Spain (39°28′59 N; 21°25′63 E). *Rapports du XXXIVe Congrés de la CIESM*, *34*, 206.

Franqueville, C. (1971). Macroplancton profond (Invertébrés) de la Méditerraée nord-occidentale. *Tethys*, *3*(1), 11–56.

Gage, J. D., & Tyler, P. A. (1991). Deep Sea Biology: A Natural History Of Organisms at the Deep-sea Floor. Cambridge University Press, Cambridge, 504 pp.

Gordon, J. D. M., & Mauchline, J. (1991). Depth-related trends in diet of a deep-sea bottom-living fish assemblages of the Rockall Trough. In: Trophic Relationships in the Marine Environments. *Proceedings of the 24th European Marine Biology Symposium*. Aberdeen University Press, pp. 439–452.

Graf, G., Bengtsson, W., Diesner, U., Schulz, R., & Theede, H. (1982). Benthic response to sedimentation events during autumn to spring at a shallow-water station in the Western Kiel Bight. I. Analysis of processes on a community level. *Marine Bilogy*, *67*, 201–208.

Hargreaves, P.M. (1984). The distribution of Decapoda (Crustacea) in the open ocean and near-bottom over an adjacent slope in the northern North-east Atlantic ocean during Autumn 1979. *Journal of the Marine Biological Association of the United Kingdom*, *64*, 829–857.

Hargreaves, P.M. (1985). The distribution of mysidacea in the open ocean and near-bottom over slope regions in the northern North-east Atlantic Ocean during 1979. *Journal of Plankton Research*, *7*, 241–261.

Hargreaves, P. M., Ellis, C. J., & Angel, M. V. (1984). An assessment of biological processes close to the sea bed in a slope region and its significance to the assessment of sea bed disposal of radiactive waste. Institut of Oceanographic Sciences Report, *185*, 121 pp.

Hopkins, T. S. (1985). Physics of the sea. In R. Margalef (Ed.), Western Mediterranean (Key Environments). Pergamon Press, Oxford, pp. 100–125.

Ivlev, V. S. (1961). Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven, CT, 302 pp.

Klepper, G.S. (1993). On the diet of Calanoid Copepods. *Marine Ecology Progress Series*, *99*, 183–195.

Lagardère, J.P. (1976). Recherches sur l = alimentation des crevettes bathypelagiques du talus continentale du Golfe de Gascone. *Revue des Travaux de l'Institut de Pêches maritimes*, *39*(2), 213–229.

Macpherson, E. (1979). Ecological overlap between macrourids in the Western Mediterranean Sea. *Marine Biology*, *53*, 149–159.

Macpherson, E. (1981). Resource partitioning in a Mediterranean demersal fish community. *Marine Ecology Progress Series*, *4*, 183–193.

Macquart-Moulin, C. (1993). Répartition verticale, migrations et stratifications superficielles des Mysidacés et Amphipodes pélagiques sur les marges méditerranéenne et atlantique françaises. *Journal of Plankton Research*, *15*, 1149–1170.

Marshall, N.B. (1965). Systematical and biological studies of the Macrourid fishes (Anacanthini-Teleostii). *Deep-Sea Research*, *12*, 299–322.

Mauchline, J. (1991). Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series*, *74*, 109–115.

Merrett, N.R., & Marshall, N.B. (1981). Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08°-27°N). *Progress in Oceanography*, *9*, 185–244.

Miquel, J.C., Fowler, S.W., La Rosa, J., & Buat-Menard, P. (1994). Dynamics of the downward flux of particles and carbon in the open northwestern Mediterranean Sea. *Deep-Sea Research*, *41*(2), 243–261.

Monaco, A., Biscaye, P., Soyer, J., Pocklington, R., & Heussner, S. (1990). Particle fluxes and ecosystem response on a continental margin: the 1985-1988 Mediterranean ECOMARGE experiment. *Continental Shelf Research*, *10*, 809–839.

Pérès, J. M. (1985). History of the Mediterranean Biota and the colonization of the depths. In R. Margalef (Ed.), Western Mediterranean (Key Environments). Pergamon Press, Oxford, pp. 198–232.

Razouls, C., & Kouwnberg, H.M. (1993). Spatial distribution and seasonal variations of mesozooplankton biomass in the Gulf of Lions. *Oceanologica Acta*, *16*, 393–401.

Reyss, D. (1971). Les canyons sous-marines de la mer Catalane. le rech du Cap et le rech Lacaze-Duthiers. IV. Etude synécologique des peuplements de macrofaune benthique. *Vie e Mileu*, *22*, 529–613.

Roe, H.S.J., Billett, D.S.M., & Lampitt, R.S. (1990). Benthic/midwater interactions on the Madeira Abyssal Plain; evidence for biological transport pathways. *Progress in Oceanography*, *24*, 127–140.

Sabatés, A., Gili, J.M., & Pagès, F. (1989). Relationship between zooplankton distribution, geographic characteristics and hydrodinamic patterns off the Catalan coast (Western Mediterranean). *Marine Biology*, *103*, 153–159.

Sainte-Marie, B., & Brunel, P. (1985). Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of Saint Lawrence. *Marine Ecology Progress Series*, *23*, 57–69.

Sardà, F., Cartes, J.E., & Norbis, W. (1994). Spatio-temporal structure of the deep-water shrimp *Aristeus antennatus* (Decapoda: Aristeidae) population in the western Mediterranean. *Fisheries Bulletin N.O.A.A.*, *92*, 599–607.

Sardà, F., Maynou, F., & Talló, L. (1997). Seasonal and spatial mobility patterns of rose shrimp *Aristeus antennatus* in the Western Mediterranean: results of a long-term study. *Marine Ecology progress series*, *159*, 133–141.

Sardou, J., Etienne, M., & Andersen, V. (1996). Seasonal abundance and vertical distributions of macroplancton and micronecton in the northwestern Mediterranean. *Oceanologica Acta*, *19*, 645–656.

Smith, C. R., & Hinga, K. R. (1983). Sediment community respiration in the Deep Sea. In G. T. Rowe (Ed.), Deep-Sea Biology: The Sea, vol. 8. John Wiley and Sons, New York, pp. 331–370.

Sokal, R. R., & Rohlf, F.J. (1979). Biometria. Principio y métodos estadísticos en la investigación biológica. H. Blume, 832 pp.

Sorbe, J. C. (1997). Deep-Sea macrofaunal assemblages within the benthic boundary layer of the Cap Ferret canyon (Bay of Biscay, EN Atlantic Ocean). Deep-Sea Research, in press.

Strauss, R.E. (1979). Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society*, *108*, 344–352.

Tobar, R., & Sardà, F. (1987). Análisis de las capturas de gamba rosada *Aristeus antennatus* (Risso, 1816) en los últimos decenios en Cataluña. *Infomes Técnicos de Scientia Marina*, *142*, 1–20.

Tyler, P.A., & Gage, J.D. (1984). Seasonal reproduction of *Echinus affinis* (Echinodermata: Echinoidea) in the Rockall Trough, northeast atlantic ocean. *Deep-Sea Research*, *31*, 387–402.

Tyler, P. A., Campos-Creasy, L. A., & Giles, L. A. (1994). Environmental control of quasi-continuous and seasonal reproduction in deep-sea benthic invertebrates. In C. M. Young, & K. J. Eckelbarger (Eds.), Reproduction, Larval Biology and Recruitment of the Deep-sea Benthos. Columbia University Press, New York, pp. 158–178.

Vereshchaka, A.L. (1995). Macroplankton in the near-bottom layer of continental slopes and seamounts. *Deep-Sea Research*, *42*, 1639–1688.

Vinogradov, M. E., & Tseitlin, V. B. (1983). Deep-sea pelagic domain (aspects of bioenergetics). In G. T. Rowe (Ed.), Deep-Sea Biology: The Sea, vol. 8. John Wiley and Sons, New York, pp. 123–165.

Whittaker, R.H., & Fairbanks, C.W. (1958). A study of plankton copepod communities in the Columbia Basin, southeastern Washington. *Ecology*, *39*, 46–65.

Wiebe, P.H., Copley, N., Van Dover, C., Tamse, A., & Manrique, F. (1988). Deep-water zooplankton of the Guaymas Basin hydrotermal vent field. *Deep-Sea Research*, *35*, 985–1013.

Wishner, K.F. (1980). The biomass of the deep-sea benthopelagic plankton. *Deep-Sea Research*, *27*, 203–216.