

F. Sardà · J. E. Cartes · J. B. Company

## Spatio-temporal variations in megabenthos abundance in three different habitats of the Catalan deep-sea (Western Mediterranean)

Received: 26 December 1993 / Accepted: 5 March 1994

**Abstract** The spatio-temporal variations in the megafauna (fishes, crustaceans, and other invertebrates) in three different habitats on the slope in the Western Mediterranean (Catalan coast off Barcelona) have been investigated. Samples were collected at two fixed stations during 1991 and 1992, one inside and one outside a submarine canyon (at depths between 450 and 600 m) and additional samples were collected at another station on the lower slope (at a depth of 1200 m) in each season of the year. Three replicates of each sample were taken at each station. Differences observed between habitats, seasons, and zoological groupings were verified statistically by factorial ANOVA. The habitat appeared to be the main factor responsible for the differences observed in biomass and abundance values for the zoological groupings considered. Decapod crustacean biomass was higher in the submarine canyon than in neighbouring zones, and smaller species and juveniles were more abundant inside the canyon in the case of both fishes and crustaceans. Fish biomass was most abundant in the lower slope. Seasonality was also a factor, although to a lesser extent. Seasonal variations in biomass, especially fish biomass, were recorded in the deepest zone (1200 m). Crustaceans displayed lower sensitivity to seasonal factors, whereas other invertebrates did not, on the whole, exhibit seasonal variations.

### Introduction

The continental margin in the Western Mediterranean is characterized by the presence of depths >1000 m just a few miles offshore, with deep canyons traversing the continental slope. Submarine canyons differ in type, depending upon their geomorphology (Shepard et al. 1974; Alonso et

al. 1991). Monaco et al. (1990) reported that canyons played a major role in the transfer of particulate organic matter from the shelf to the bathyal zone. These same authors also referred to seasonal variations in the biogenic and abiogenic processes associated with discharges of continental run-off, and described the responses of the habitats on different spatio-temporal scales. Thiel (1983), De Bovée et al. (1990) and Monaco et al. (1990), pointed out the relationship between meiofaunal and macrofaunal biomass, production processes in the surface layers of the water column, and seasonality for specific habitats. Evidence for the seasonal deposition of detritus to the deep-sea floor has been recorded by other authors (Billett et al. 1983; Lampitt 1985; Deuser 1986). Studies of the biomass and composition of megabenthic communities on the continental slope are abundant but often fail to give consideration to temporal aspects and/or tend to focus solely on a given taxocenosis (Haedrich et al. 1975, 1980; Rowe et al. 1982; Houston and Haedrich 1984; Lampitt et al. 1986; Hecker 1990; Merrett et al. 1991; Cartes and Sardà 1992; Stefanescu et al. 1992). Moreover, the structure of communities and the biomass of organisms in submarine canyons is poorly known (Reyss 1971; Houston and Haedrich 1984).

In addition, an important deep-water fishery is conducted at about 1000 m in the Western Mediterranean (Bas et al. 1985; Sardà and Martín 1986); this fishery specializes in species distributed on fishing grounds located at the margins of submarine canyons (Tobar and Sardà 1987). The fishery is characterized by temporal fluctuations in catches and local shifts in the location of exploitable shoals, since the behaviour of certain species appears to be related to the depth structure of the bottom; it has been suggested that this is linked to certain water masses (Ghidalia and Bourgois 1961). Thus, *Aristeus antennatus* carries out temporal migrations towards the inside of the canyons (Tobar and Sardà 1987; Sardà et al. 1994). Other authors have also detected spatio-temporal variations in both the internal population structure of certain species, e.g. *A. antennatus* (Relini and Orsi Relini 1987) and *Micromesistius poutassou* (Bas 1963; Bas and Calderón-Aguilera 1989),

Communicated by J. M. Pérès, Marseille

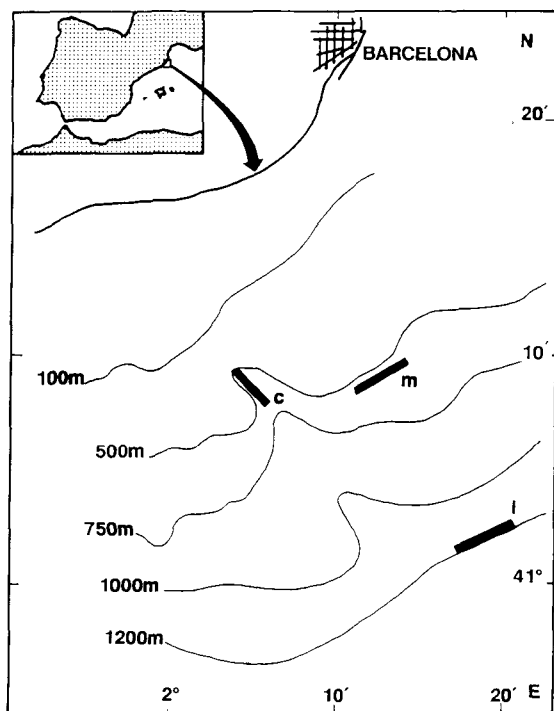
F. Sardà (✉) · J. E. Cartes · J. B. Company  
Instituto de Ciencias del Mar (CSIC),  
Paseo Nacional, s/n,  
E-08039 Barcelona, Spain

as well as in the trophic relationships of the decapod crustacean community on the continental slope (Cartes 1993 a, b).

As a result of all the foregoing, it was decided to examine spatio-temporal variations in megabenthic communities inhabiting the slope. The study areas on the upper (canyon) and middle slopes are exploited, although not intensively, by a trawl fishery. The submarine canyons are occasionally exploited by the fishing fleet. The lower slope is not subjected to any exploitation at all. The object of the present investigation was to study spatio-temporal variations in biomass in the main megabenthic communities on the deep slope in a specific area in the Western Mediterranean (the Catalan Sea off Barcelona).

## Materials and methods

A sampling scheme was designed to survey spatio-temporal features in the different slope habitats (Fig. 1) in which *Aristeus antennatus* is commonly distributed. The submarine canyon (Habitat c) known as "La Merenguera", located on the upper slope at a depth of  $\approx 450$  m ( $41^{\circ}07'75''\text{N}$ ;  $02^{\circ}04'43''\text{E}$ ), and the area known as the "Abisinia" fishing grounds on the middle slope (Habitat m), at a depth of 600 to 650 m ( $41^{\circ}06'34''\text{N}$ ;  $02^{\circ}12'05''\text{E}$ ), are two areas where *A. antennatus* is traditionally fished; trawls within the canyon are carried out along its interior margins. A third station was located on the upper part of the lower slope (Habitat l) at a depth of  $\approx 1200$  m ( $41^{\circ}54'63''\text{N}$ ;  $02^{\circ}06'90''\text{E}$ ); here there is no fishing activity, but the station provided a reference for comparison with deeper waters. Decapod crustacean communities have previously been described from different depths in the Catalan Sea (Abelló et al. 1988; Cartes



**Fig. 1** Map of study area, showing location of three sampling stations on continental slope of Western Mediterranean (c, Habitat c, submarine canyon; m, Habitat m, middle slope; l, Habitat l, lower slope; black bars are haul distances)

and Sardà 1992, 1993). Three replicate samplings were made at each habitat (c, m and l) on each of four surveys, in summer, autumn, winter and spring (Table 1). The three replicate samples at each station were carried out within a period of  $<12$  h.

The trawl gear was a "Maireta system" (MS) [Spanish Patent No. 9200614, Instituto de Ciencias del Mar (CSIC)], which consists of a semi-balloon otter trawl with square panels and wings and a 25 m headline. The gear is towed by a single warp attached to two wires on a crowfoot, which is in turn connected to two 450 kg iron otter boards (Stefanescu et al. 1994). The horizontal gear opening (14 m) was measured using a SCANMAR system; cod-end mesh size was 12 mm. Trawls were carried out by the V. R. "García del Cid" (38 m length, power: 1500 hp). Towing speed was 2.5 knots for all trawls. The position at the start and at the end of each trawl was recorded using a GPS (Global Positioning System).

Sample catches were weighed, counted, and identified to species level. To provide an overview of the general dynamics, the species were classified into the following major zoological groups: fishes (F), decapod crustaceans (C), echinoderms (E), cephalopods (CE) and cnidarians (CN). The less abundant taxa (other non-decapod crustaceans, bivalves, gastropods, scaphopods, etc.) were grouped together as "others" (OT). The relationships between the different zoological groups and each habitat were established by correspondence analysis (Benzecri 1980) using only the biomass (weight) data. Detailed considerations concerning each of the groupings will be addressed separately.

In order to determine which species were mainly responsible for the variations observed, the most prevalent species in each depth stratum were expressed in terms of abundance and percentage of total species, for each season. Only species with a percentage of  $\approx 5\%$  were taken into account when evaluating the data.

Spatio-temporal differences among habitats (c, m, l) and seasons of the year were analyzed by multifactorial ANOVA. The normality of the data was verified using the Kolmogorov-Smirnov test and the homogeneity of variance values using the Cochran's C-test ( $p < 0.05$ ). The possible presence of seasonal variations in each habitat was examined using one-way ANOVA, applying Tukey's test to each habitat separately. The acceptance level of significance was  $p < 0.05$  for all analyses. Data for fishes (F), decapod crustaceans (C), and all other invertebrates combined (OT) were considered in these analyses. The various ANOVA procedures and the different tests were carried out using the STATGRAPHICS statistical package for PCs (Statistical Graphics System Version 5.0, 1991, Statistical Graphics Corporation, USA). Statistical treatment of the data encompassed biomass ( $\text{g h}^{-1}$ ), abundance (number of individuals  $\text{h}^{-1}$ ), and mean weight (g). In view of the heterogeneous nature of the OT category, which included colonial, sessile, endobenthic, and mobile forms, etc., and the fact that the relative abundance of the members of this category was lower than that of the other categories, mean weight was not taken into account for this category nor for the megabenthos as a whole.

## Results

### Distribution of biomass and abundance

#### *Spatio-temporal variations in total megabenthos*

Total megabenthic biomass was significantly different ( $p < 0.05$ ) among the three habitats (c, m, l; Fig. 2); the biomass for Habitats c and l was higher than that for Habitat m. Abundance, however, followed a different trend. Abundance was significantly higher ( $p < 0.05$ ) in the canyon only (Fig. 2; Table 2).

Fig. 3 shows the biomass distributions for the different taxa by habitat and season. The highest biomass for echi-

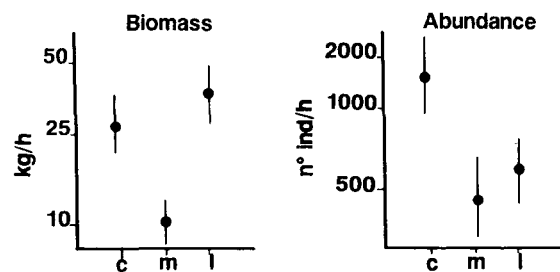
**Table 1** Sampling data and biomass ( $\text{kg h}^{-1}$ ) and abundance (individuals  $\text{h}^{-1}$  in parentheses) of fishes, crustaceans and other invertebrates (OT). (Ref sample reference number; H habitat; S season; c canyon; m middle slope; l lower slope; p spring; s summer; a autumn; w winter

Ref.	H	S	Date	Haul time (h)	Depth (m)	Biomass (abundance)		
						fishes	crustaceans	OT
R1/1	m	p	23.IV.1991	1.00	570	7 623 (143)	2 173 (260)	990 (96)
R1/2	m	p	23.IV.1991	1.50	600	10 726 (191)	4 843 (575)	768 (152)
R1/3	m	p	23.IV.1991	1.67	692	13 250 (265)	4 755 (705)	501 (102)
R1/4	u	p	23.IV.1991	1.00	455	25 561 (413)	3 775 (667)	3 061 (292)
R1/5	u	p	23.IV.1991	1.00	459	13 760 (223)	4 612 (688)	9 245 (307)
R1/6	u	p	23.IV.1991	1.00	390	27 544 (1241)	7 316 (1476)	7 691 (357)
R1/7	l	p	25.IV.1991	1.00	1 160	24 136 (213)	1 304 (171)	1 201 (62)
R1/9	l	p	25.IV.1991	1.00	1 230	30 896 (241)	1 061 (249)	300 (98)
R2/7	m	a	12.IX.1991	1.00	625	11 541 (153)	376 (697)	60 (133)
R2/8	m	a	12.IX.1991	1.00	613	2 627 (130)	650 (512)	524 (118)
R2/9	m	a	12.IX.1991	2.00	562	6 501 (170)	397 (266)	37 (196)
R2/1	u	a	12.VIII.1991	0.42	433	3 493 (344)	5 564 (115)	1 109 (14)
R2/2	u	a	12.VIII.1991	0.50	455	4 359 (474)	8 782 (161)	1 174 (18)
R2/3	u	a	12.VIII.1991	0.50	504	8 427 (239)	3 150 (190)	2525 (44)
R2/4	l	a	12.VIII.1991	1.00	1 265	62 080 (40)	593 (31)	128 (1)
R2/5	l	a	12.IX.1991	1.00	1 274	71 491 (26)	1 160 (48)	342 (37)
R2/6	l	a	12.IX.1991	0.50	1 252	34 369 (69)	2 225 (127)	495 (5)
R3/1	m	w	03.XII.1992	0.83	565	6 081 (116)	6 918 (386)	189 (36)
R3/2	m	w	03.XII.1992	0.75	545	945 (24)	2 226 (263)	1 134 (284)
R3/3	m	w	03.XII.1992	0.75	545	1 633 (43)	3 671 (305)	329 (55)
R3/4	u	w	03.XII.1992	0.50	355	6 807 (66)	909 (71)	521 (34)
R3/5	u	w	03.XII.1992	0.50	447	12 001 (173)	1 403 (251)	4 059 (188)
R3/6	u	w	03.XII.1992	0.50	508	5 590 (54)	809 (56)	3 022 (110)
R3/7	l	w	13.III.1992	1.00	1 235	26 245 (162)	305 (47)	26 (3)
R3/8	l	w	13.III.1992	1.00	1 275	45 969 (280)	549 (107)	110 (6)
R3/9	l	w	13.III.1992	1.00	1 210	47 119 (352)	864 (188)	565 (31)
R4/1	m	s	26.VII.1992	1.00	605	6 472 (45)	1 631 (160)	552 (24)
R4/2	m	s	26.VII.1992	1.00	611	11 444 (255)	2 684 (505)	61 (4)
R4/3	m	s	26.VII.1992	1.00	616	16 447 (332)	4 270 (639)	218 (14)
R4/4	u	s	26.VII.1992	0.50	426	8 459 (136)	12 764 (966)	1 007 (42)
R4/5	u	s	26.VII.1992	0.42	400	6 170 (191)	5 100 (502)	3 750 (167)
R4/6	u	s	26.VII.1992	0.50	440	13 862 (250)	5 782 (470)	2 712 (198)
R4/7	l	s	27.VII.1992	1.00	1 260	25 355 (282)	1 806 (252)	166 (12)
R4/8	l	s	27.VII.1992	1.00	1 286	28 471 (300)	1 263 (249)	769 (53)
R4/9	l	s	27.VII.1992	1.00	1 272	26 131 (277)	4 979 (689)	540 (17)

**Table 2** Comparison of multifactorial ANOVA of biomass and abundance of megabenthos in the three different habitats. (c, m, l canyon, middle and lower slopes, respectively)

Habitat comparison	Statistical significance	
	biomass	abundance
m-c	*	*
m-l	*	NS
c-l	*	*

\* Significant at  $p < 0.05$



**Fig. 2** Total log biomass and log abundance of Sampling Habitats c, m and l

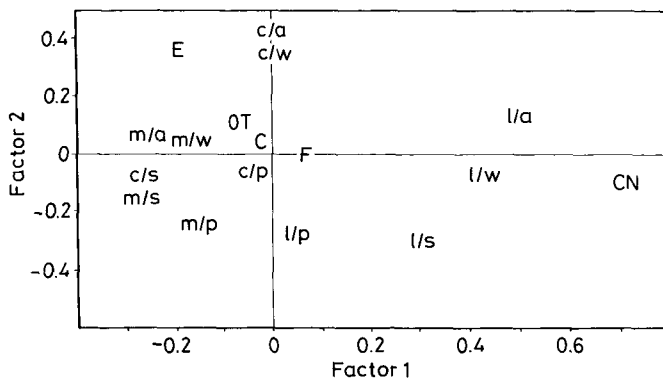
noderns (E) was associated with canyon samples, while the highest biomass for cephalopods (CE) was recorded on the middle slope. Cnidarians (CN) were most abundant on the lower slope, where *Isidella elongata* was prevalent. Fishes, decapod crustaceans, and other invertebrates were

distributed in all three habitats, although fish (F) were most important on the lower slope, and decapod crustaceans (C) and other invertebrates (OT) were more prevalent in the canyon samples. The first axis of the correspondence analysis accounted for 47.17% of the variance. The samples

**Table 3** Results of multifactorial ANOVAS of biomass, abundance and mean weight of zoological groups as a function of habitat (*H*), season (*S*) and interaction (*HS*). Letters indicate habitats and seasons where differences are significant. (*c* canyon; *m* middle slope; *p* spring; *s* summer; *a* autumn; *w* winter)

Zoological group	Biomass					Abundance					Mean weight				
	Comparison			ANOVA		Comparison			ANOVA		Comparison			ANOVA	
	H	S	HS	H	S	H	S	HS	H	S	H	S	HS	H	S
Fishes	***	NS	**	*	NS	***	NS	NS	m-c	NS	**	NS	*	m-c	NS
<i>F</i> -ratio	54.3	1.3	4.1			21.5	2.7	2.2	m-l		8.5	2.1	2.5		
Crustaceans	***	***	***	*	p-a	***	***	***	m-c	a-s	**	NS	NS	m-c	NS
<i>F</i> -ratio	18.9	9.6	9.2		p-w s-a s-w	18.2	6.9	5.6	c-l	w-s	6.1	1.0	0.8		
Other invertebres	***	NS	NS	m-c	NS	***	*	**	m-c	p-a	**	**	**	c-l	p-s
<i>F</i> -ratio	28.5	1.6	1.2	c-l		25.7	3.6	3.7	c-l	p-s	7.2	5.3	5.0		

\* · \*\* · \*\*\* Significant at  $0.05 > p > 0.01$ ,  $0.01 > p > 0.001$ ,  $p < 0.001$ , respectively

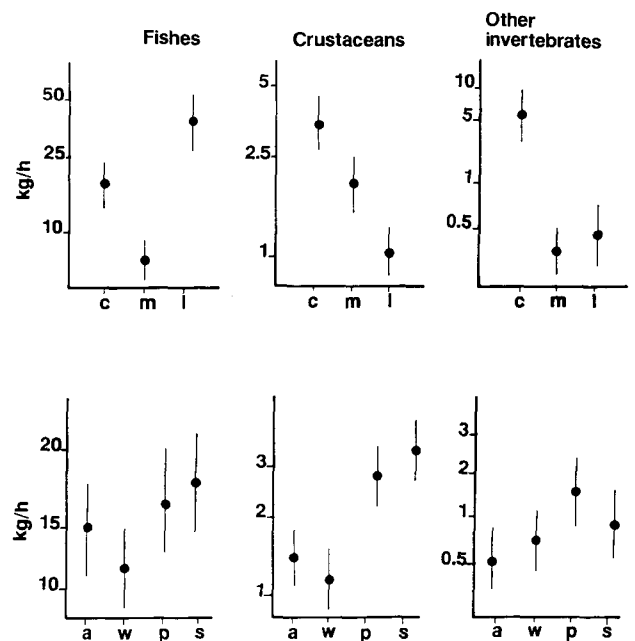


**Fig. 3** Plots of scores of two correspondence axes for entire set of samples (*c* canyon; *m* middle slope; *l* lower slope; *p* spring; *s* summer; *a* autumn; *w* winter. *F* fishes; *C* crustaceans; *E* echinoderms; *CE* cephalopods; *CN* cnidarians; *OT* other invertebrates)

collected on the lower slope (*l*) were clearly separated from those collected in Habitats *c* and *m* along this axis. Thus, the first axis would appear to be related to the variable depth, and the data for the samples collected at the station on the lower slope appear clearly separated in the right-hand section of Fig. 3. The second axis explained 38.05% of the variance and was associated with season, samples taken in spring (*p*) and summer (*s*) appearing in the negative region of the coordinate axis, and the autumn (*a*) and winter (*w*) samples in the positive region.

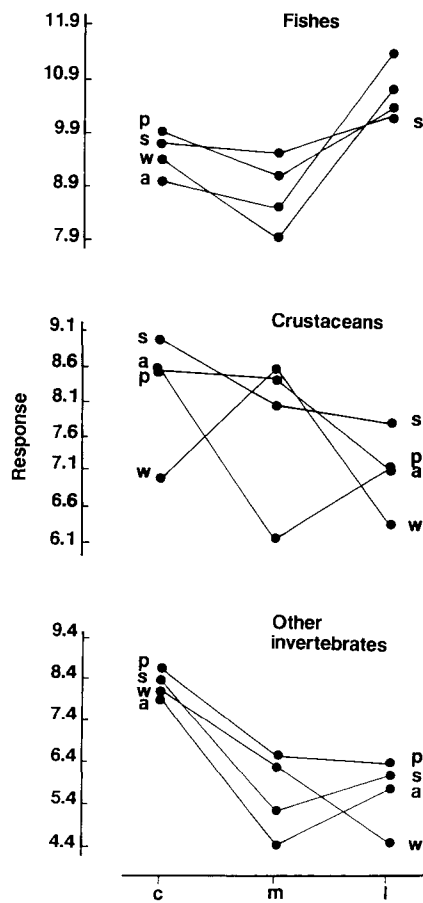
#### Spatio-temporal variations within each grouping

Table 3 presents the results of a multifactorial analysis of variance comparing the different habitats and seasons of the year for each species group based on biomass, abundance and mean weight.



**Fig. 4** Logarithmic biomass as a function of habitat and season for each zoological group (abbreviations as in Fig. 3)

**Biomass.** Differences in the biomass values for the different habitats tended to be highly significant for the zoological groups (Table 3: "Biomass, Comparison H"), except for "other" invertebrates in Habitats *m* and *l* (Fig. 4). The biomass of crustaceans and other invertebrates was relatively highest in the canyon, whereas fish biomass was highest in Habitat *l* because of the presence of highly abundant large species such as *Alepocephalus rostratus*, *Mora moro*, and *Trachyrhynchus trachyrhynchus* (see Table 5). The high contribution of these species to the biomass also accounts for the higher total megabenthic biomass in Habitat 1 (Fig. 2). The decapod *Aristeus antennatus* and the



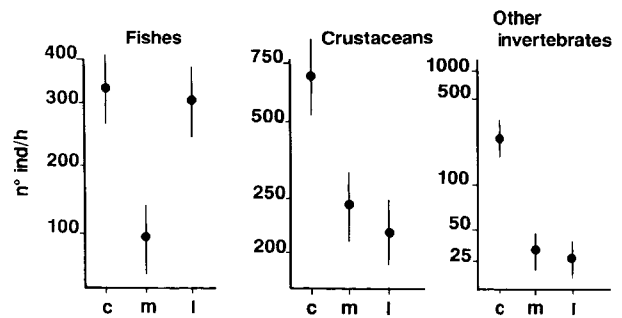
**Fig. 5** Interaction between habitat and season obtained by multifactorial ANOVA, for each zoological group (abbreviations as in Fig. 3)

osteichthians *Phycis blennoides* and *Helicolenus dactylopterus* were the predominant species contributing to the biomass in the canyon (c). Fig. 5 graphically illustrates the interactions and corroborates the results in Table 3.

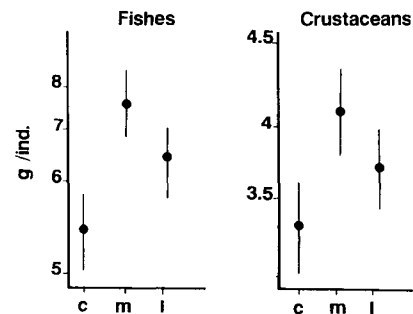
Only fishes and crustaceans exhibited significant differences ( $p < 0.001$ ) in biomass as a function of season (Fig. 4). The trends for both groups reflected an increase in biomass in spring and summer and a drop in autumn and winter. The interaction of these two sources of variation (HS: habitat, season) was significant for fish biomass ( $p < 0.1$ ) and highly significant for crustacean biomass ( $p < 0.01$ ).

Between-habitat comparison revealed significant differences for all taxa except for the other invertebrates (OT group). Biomass for this group was similar in Habitats m and l (Fig. 4; Table 2: "Biomass, Comparison H"). There were seasonal differences for crustaceans in spring-summer (p-s) and autumn-winter (a-w) (Table 3: "Biomass, Comparison S").

**Abundance.** Variations in abundance of each zoological group were highly significant ( $p < 0.001$ ) between habitats (Fig. 6). Fishes were most abundant in Habitats c and l,



**Fig. 6** Logarithmic abundance (no. of individuals  $h^{-1}$ ) as a function of habitat for each zoological group (abbreviations as in Fig. 1)



**Fig. 7** Logarithmic mean weight ( $g\ individual^{-1}$ ) as a function of habitat for fishes and crustaceans (abbreviations as in Fig. 1)

while decapod crustaceans and the OT group were most abundant inside the canyon only. This also explains the higher total megafaunal abundance in Habitat c (Fig. 2). Seasonal differences were significant only for decapod crustaceans and the OT group (Table 3: "Abundance, Comparison S").

The comparisons among the three habitats for each zoological group revealed significant differences ( $p < 0.05$ ) between Habitat c and the other habitats, except in the case of fish, which were appreciably less abundant in Habitat m (Table 3: "Abundance, Comparison S").

**Mean weight.** Increased abundance of all groups in Habitat c (Fig. 6) was accompanied by a decrease in mean weight (Fig. 7), indicative of the greater abundance of smaller individuals inside the canyon in the two groups for which mean weight values were calculated. Differences between the habitats were significant ( $p < 0.01$ ) in all cases. The highest mean weight for fish was recorded in Habitat m, which combined the presence of large individuals of *Phycis blennoides* and *Trachyrhynchus trachyrhynchus* with rather low levels of total abundance. The pattern for

**Table 4** Significant differences (one-way ANOVA) between habitats and seasons for each zoological group. Further details as in Table 3

Zoological groups	Habitats		
	c	m	l
Fishes	s-w	NS	p-a p-w a-w s-a s-w s-w
Crustaceans	p-a a-w s-a	p-w a-w s-w	s-w
Other invertebrates	NS	NS	NS

decapod crustaceans was similar due to the presence of large individuals of *Aristeus antennatus* and other species (*Polychaetes typhlops*, *Plesionika martia*) on the middle slope.

No differences were recorded between the groups (Table 3: "Mean weight, Comparison S") in the various seasons, excluding the OT group, which included highly distinct morphological and ecological forms (see "Materials and methods"). The differences between habitats for each zoological group were corroborated by the significance of the comparisons ( $p < 0.05$ ) in Table 3 ("Mean weight, Comparisons H and S"). No clear trends were distinguishable between seasons, again probably because of the distinct morphological forms of the OT group.

**Table 5** Abundance (*N*) and percentage (% of total species) as a function of habitat and season

Upper slope (canyon)	<i>N</i>	(%)	Middle slope	<i>N</i>	(%)	Lower slope	<i>N</i>	(%)
<b>Spring 1991</b>								
<i>Aristeus antennatus</i>	309.0	(16.4)	<i>Aristeus antennatus</i>	241.4	(39.3)	<i>Munida tenuimana</i>	94.5	(18.3)
<i>Brissopsis lyrifera</i>	140.6	(7.4)	<i>Cymbulia peroni</i>	93.3	(15.2)	<i>Alepocephalus rostratus</i>	86.5	(16.8)
<i>Phycis blennoides</i>	126.3	(6.7)	<i>Plesionika martia</i>	37.5	(6.0)	<i>Lepidion lepidion</i>	55.0	(10.6)
<i>Plesionika gigliolii</i>	112.3	(5.9)	<i>Phycis blennoides</i>	31.7	(5.2)	<i>Aristeus antennatus</i>	47.0	(9.1)
<i>Calocaris macandreae</i>	93.3	(4.9)			<i>T. trachyrhynchus</i>	35.5	(6.9)	
<i>Pasiphaea sivado</i>	89.3	(4.7)			<i>Pontophilus norvegicus</i>	34.5	(6.7)	
<i>Plesionika edwardsi</i>	84.3	(4.5)			<i>Dentalium agile</i>	32.5	(6.3)	
					<i>Cymbulia peroni</i>	30.5	(5.9)	
Totals	1888.1			614.8			517.0	
<b>Autumn 1991</b>								
<i>Aristeus antennatus</i>	278.3	(18.0)	<i>Pandalina profunda</i>	18.3	(14.3)	<i>Alepocephalus rostratus</i>	228.0	(33.7)
<i>Sergestes arcticus</i>	167.9	(10.9)	<i>Aristeus antennatus</i>	15.3	(12.0)	<i>Munida tenuimana</i>	78.3	(11.6)
<i>Plesionika martia</i>	112.7	(7.3)	<i>Phycis blennoides</i>	13.7	(10.7)	<i>Lepidion lepidion</i>	67.7	(10.0)
<i>Calocaris macandreae</i>	106.9	(6.9)	<i>Calocaris macandreae</i>	13.7	(10.7)	<i>Aristeus antennatus</i>	59.3	(8.8)
<i>Symphurus nigrescens</i>	105.1	(6.8)	<i>Nezumia aequalis</i>	8.0	(6.3)	<i>Bathypterois mediterraneus</i>	59.0	(8.7)
<i>Brissopsis lyrifera</i>	98.4	(6.4)	<i>Molpadia musculus</i>	6.7	(5.2)	<i>Mora moro</i>	32.7	(4.8)
					<i>AcanthePHYRA eximia</i>	32.3	(4.7)	
Totals	1542.4			128.0			676.2	
<b>Winter 1992</b>								
<i>Phycis blennoides</i>	83.3	(14.9)	<i>Aristeus antennatus</i>	173.0	(28.4)	<i>Alepocephalus rostratus</i>	119.3	(30.4)
<i>Brissopsis lyrifera</i>	80.6	(14.4)	<i>Calocaris macandreae</i>	103.7	(17.0)	<i>Bathypterois mediterraneus</i>	52.7	(13.4)
<i>Calocaris macandreae</i>	58.0	(10.4)	<i>Molpadia musculus</i>	51.1	(8.4)	<i>Lepidion lepidion</i>	48.7	(12.4)
<i>Aristeus antennatus</i>	41.3	(7.4)	<i>Phycis blennoides</i>	32.4	(5.3)	<i>Munida tenuimana</i>	45.0	(11.5)
<i>Plesionika gigliolii</i>	32.7	(6.8)			<i>Aristeus antennatus</i>	29.7	(7.6)	
<i>Sergestes arcticus</i>	32.7	(6.8)						
<i>Symphurus nigrescens</i>	32.0	(5.7)						
Totals	558.0			608.8			392.5	
<b>Summer 1992</b>								
<i>Aristeus antennatus</i>	396.9	(20.9)	<i>Sergia robusta</i>	171.0	(25.9)	<i>Aristeus antennatus</i>	217.7	(30.6)
<i>Pasiphaea sivado</i>	289.3	(15.2)	<i>Aristeus antennatus</i>	118.7	(18.0)	<i>Alepocephalus rostratus</i>	108.0	(15.2)
<i>Sergestes arcticus</i>	232.9	(12.3)	<i>Sergestes arcticus</i>	48.0	(7.3)	<i>Bathypterois mediterraneus</i>	86.3	(12.1)
<i>Plesionika martia</i>	130.6	(6.9)	<i>Phycis blennoides</i>	47.0	(7.1)	<i>Munida tenuimana</i>	70.1	(9.8)
<i>Calocaris macandreae</i>	121.4	(6.4)	<i>Melanostigma atlanticum</i>	41.3	(6.3)	<i>Lepidion lepidion</i>	58.7	(8.3)
<i>Brissopsis lyrifera</i>	84.9	(4.6)	<i>Hymenocephalus italicus</i>	29.8	(4.5)	<i>AcanthePHYRA eximia</i>	56.3	(7.9)
<i>Phycis blennoides</i>	84.0	(4.5)						
Totals	1900.2			659.3			711.4	

### Seasonality within each habitat: one-way analysis results

Two sources of variation for each zoological group, habitat, and season as well as the interactions between these were considered. However, while the interaction values calculated by multifactorial ANOVA (Fig. 5) revealed whether or not there were differences between seasons, they provided no specific information of which factors were actually responsible for the differences detected for each interaction. A one-way ANOVA was therefore designed for application only to the biomass values within each habitat; the results are given in Table 4.

Fish exhibited variations in Habitat c in contrasting seasons (w-s) and in Habitat l in nearly all seasons (mainly in winter), probably due to variations in the catches of *Alepocephalus rostratus* and *Mora moro*. The greatest differences in decapod crustaceans were in Habitat c in autumn and in Habitat m in winter, whereas the only differences recorded at greater depth (Habitat l) were between the contrasting seasons s and w. The other invertebrates did not exhibit seasonal variations in any of the habitats. The composition of the main species was most stable at the station located below 1000 m depth, where five species were consistently predominant over time, the teleost fishes *Alepocephalus rostratus*, *Lepidion lepidion*, and *Bathypterois mediterraneus* and the decapod crustaceans *Aristeus antennatus* and *Munida tenuimana* (Table 5). Variability in the predominant species was much higher in the canyon (c) and on the middle slope (m).

### Discussion

The system commonly used to sample the deep-water megabenthos, the OTSB-14 otter trawl (Merrett and Marshall 1981), which has a moderate vertical opening (1.5 m), underestimates catches of species that are highly developed swimmers (mesopelagic and nektobenthic species) (Gordon and Duncan 1985; Merrett et al. 1991). The MS gear captures benthopelagic species more efficiently and achieves a species composition that is closer to that of the catches taken using large commercial gears (authors' own unpublished data) and biomass values that are more representative of the actual biomass values associated with the substrate. Unlike the OTSB-14 gear (Pearcy et al. 1982), depth does not appear to decrease the effectiveness of the MS gear.

Various authors (Rowe 1971; Houston and Haedrich 1984; Monaco et al. 1990) have discussed the importance of canyons as geomorphological structures that play a role in concentrating sediment and transporting it to deeper oceanic regions. The canyons display seasonal responses to influxes of organic matter that translate into variations in the meiofauna (De Bovée et al. 1990). The biomass of crustaceans and invertebrates was particularly high in the "La Merenguera" canyon. Thus, the canyon proved to be an area of high productivity with abundant resources. Less general studies (Sardà et al. 1994; Stefanescu et al. 1994)

have reported concentrations of juveniles of certain species which suggest that the canyons may be recruitment areas, this is consistent with the lower mean weights (corresponding to smaller sizes) for fishes and crustaceans recorded in the present study. Submarine canyons generally also appear to be areas of highly dynamic water circulation near the bottom (Shepard et al. 1974; Gardner 1989; Monaco et al. 1990), subject to temporal variations in the extent of resuspension taking place within them in response to changes in the stability of the water masses (Gardner 1989).

Responses by benthic organisms to inputs of organic material to the ocean floor have been observed also by De Bovée et al. (1990) and Gooday and Turley (1990). Some fisheries data from the Catalan Sea (Tobar and Sardà 1987; Sardà et al. 1994; Stefanescu et al. 1994) point to large seasonal fluctuations in catches of fishes and crustaceans linked to migrations into and out of the canyons. To date the relationship between such fluctuations and the dynamics of hydrographics and production in the canyons in the region is poorly understood, and hence for the time being no new working hypotheses can be proposed.

For all the zoological groups, biomass and abundance on the middle slope (m) were lower than those recorded in the canyon. Habitats c and m are subject to fisheries exploitation, although fishing pressure is not intense (Demestre 1990). On the whole, the effect of trawling on the structure of the communities in the study area is relatively slight and only affects certain aspects of the community. The mean weights for fishes and decapods were higher in Habitat m than in Habitat l, indicating that the populations there are composed of larger individuals and that these populations are not subject to intensive overfishing. Seasonality was not pronounced in Habitat c; differences between summer and winter were slight for fishes, while differences for crustaceans were mainly discernible in autumn, probably associated with migrations of *Aristeus antennatus* shoals (Sardà et al. 1994).

The canyon and the middle slope are characterized by high densities of endobenthic species (deposit-feeders), probably because of richer deposits of organic matter in the sediment in these regions. This trend was especially pronounced in the submarine canyon, where echinoderms (mainly *Brissopsis lyrifera*) and decapods (*Calocaris macandreae* and *Alpheus glaber*) make up a large part of the megabenthic community and are a major food resource, supporting the food web (Cartes 1993 a, b).

Biomass was highest on the lower slope (Habitat l) only for fishes. In addition, fishes were influenced by seasonal processes that did not affect crustaceans or other invertebrates. Variations in fish biomass in Habitat l were primarily due to variations in abundance of a single dominant species, *Alepocephalus rostratus*, and (to a lesser extent) of *M. moro*, whereas the (largely non-significant) variations observed in the shallower habitats, c and m, were caused by variations in different fish species. The diets of the predominant fish species in Habitat l (e.g. *Alepocephalus rostratus*, *Bathypterois mediterraneus*) are based on benthopelagic organisms (medusae, siphonophores, copepods)

(Mauchline and Gordon 1985; Carrasson and Matallanas 1990), which also contribute to the diet of decapods in these habitats (Cartes 1993 a, b). In the Northwest Atlantic, peak abundance of this type of food resource has been recorded near the sea floor (Hargreaves et al. 1984), and seasonal fluctuations in medusae and siphonophores in the plankton have been reported in the Northwestern Mediterranean (Franqueville 1971). Changes in fish biomass recorded at ~1200 to 1300 m in depth may be related to possible variations in this type of food resource near the sea bed. The station on the lower slope was located relatively close to a submarine canyon, and might thus have been influenced to some extent by sediment inputs and deep-sea currents associated with structural features of the canyon which, in turn, could affect inputs of organic matter and processes of resuspension (Angel 1990; Monaco et al. 1990). This could result in seasonal changes in the megabenthic biomass in response to the abundance of the exploited resources, particularly in the case of highly developed swimmers such as fishes.

The species composition of the deep-sea communities on the lower slope was more uniform over time, in consonance with what is commonly accepted for deep-sea zones below 1000 m (Tyler 1988; Gage and Tyler 1990). Nevertheless, the results of the present study point to significant seasonal variations in fish biomass and thus highlight the influence of season on deep-sea systems (Tyler 1988).

In conclusion, the biomass of decapod crustaceans and other invertebrates was higher in the submarine canyon (Habitat c) than in neighbouring areas, and smaller-sized fishes and crustaceans predominated in the canyon. Fish biomass was highest in the deepest zone (Habitat l). Habitat was the main factor responsible for the differences observed in biomass and abundance, although season also exerted a smaller influence. Specifically, seasonal differences in fish biomass were recorded in the deepest zone (1200 m). Crustaceans were sensitive to seasonal factors in habitats c and m, whereas other invertebrates failed to exhibit seasonal variations.

**Acknowledgements** The present study was made possible by a research project subsidized by the Ministry of Research and Science (CICYT, MAR90/757). The authors wish to thank Drs. M. Ballesteros, L. Dantart, B. Morales, E. Massuti, and C. Stefanescu for their assistance in collecting and classifying the samples. They likewise wish to express their appreciation to the fishing master, Mr. A. Albiol, for his invaluable practical assistance as well as to the crew of the research vessel "García del Cid". Messrs. G. Fuster and J. M. Anguita are thanked for their technical assistance and their help in preparing the manuscript. Mr. R. Sacks prepared the English version.

## References

- Abelló P, Valladares FJ, Castellón A (1988) Analysis of the structure of decapod crustacean assemblages off the Catalan coast (North-West Mediterranean). *Mar Biol* 98: 39–49
- Alonso B, Canals M, Got H, Maldonado A (1991) Sea valleys and related depositional systems in the Gulf of Lion and Ebro Continental Margins. *Bull Am Ass Petrol Geol* 75: 1195–1214
- Angel M (1990) Life in the benthic boundary layer: connections to the mid-water and sea floor. *Phil Trans R Soc* 331: 15–28
- Bas C (1963) Fluctuations de la pêche de *Merlangus poulassou* et quelques considérations sur son contrôle. *Proc tech Pap gen Fish Coun Mediterr* 7: 417–420
- Bas C, Calderon-Aguilera LE (1989) Effect of anthropogenic and environmental factors on the blue whiting *Micromesistius poulassou* off the Catalan coast, 1950–1982. *Mar Ecol Prog Ser* 54: 221–228
- Bas C, Macpherson E, Sardà F (1985) Fishes and fishermen. The exploitable trophic levels. In: Margalef R (ed) *Key environments: western Mediterranean*. Pergamon Press, New York, pp 198–232
- Benzecri JP (1980) L'analyse des données. 2 l'analyse des correspondances. Dunod ed, Paris
- Billett D, Lampitt RS, Rice AL, Mantoura RFC (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature, Lond* 302: 520–522
- Carrasson M, Matallanas J (1990) Preliminary data about the feeding habits of some deep-sea Mediterranean fishes. *J Fish Biol* 36: 461–463
- Cartes JE (1993 a) Diets of deep-water pandalid shrimps on the Western Mediterranean slope. *Mar Ecol Prog Ser* 96: 49–61
- Cartes JE (1993 b) Feeding habits of pasiphaeid shrimps close to the bottom on the Western Mediterranean slope. *Mar Biol* 117: 459–468
- Cartes JE, Sardà F (1992) Abundance and diversity of decapod crustaceans in the deep-Catalan sea (western Mediterranean). *J nat Hist* 26: 1305–1323
- Cartes JE, Sardà F (1993) Zonation of deep-sea decapod fauna in the Catalan Sea (western Mediterranean). *Mar Ecol Prog Ser* 94: 27–34
- Demestre M (1990) *Biología pesquera de la gamba Aristeus antennatus* (Risso, 1816) en el mar Catalán. Tesis doctoral. Universidad de Barcelona, Barcelona
- De Bovée F, Guidi LD, Soyer J (1990) Quantitative distribution of deep-sea macrobenthos in the northwestern Mediterranean (Gulf of Lion). *Contin Shelf Res* 10: 1123–1146
- Deuser WG (1986) Seasonal and interannual variations in deep-water particle fluxes in the Sargasso Sea and their relation to surface hydrography. *Deep-Sea Res* 33A: 225–246
- Franqueville C (1971) Macroplankton profond (invertébrés) de la Méditerranée nord-occidentale. *Téthys* 3: 11–56
- Gage JD, Tyler PA (1990) *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge University Press, Cambridge, UK
- Gardner WD (1989) Baltimore canyon as a modern conduit of sediment to the deep sea. *Deep-Sea Res* 36A: 323–358
- Ghidalia W, Bourgois F (1961) Influence de la température et de l'éclairement sur la distribution des crevettes des moyennes et grandes profondeurs. *Stud Rev gen Fish Coun Mediterr* 16: 1–53
- Gooday AJ, Turley CM (1990) Responses by benthic organisms to inputs of organic material to the ocean floor: a review. *Phil Trans R Soc (Ser A)* 331: 119–138
- Gordon JDM, Duncan JAR (1985) The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, northeastern Atlantic. *Prog Oceanogr* 15: 37–69
- Haedrich RL, Gilbert T, Polloni PT (1975) Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *J mar Res* 33: 191–212
- Haedrich RL, Rowe GT, Polloni PT (1980) The megabenthic fauna in the deep sea south of New England, USA. *Mar Biol* 57: 165–179
- Hargreaves PM, Ellis CJ, Angel MV (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 radioactive waste. *Inst oceanogr Sciences (Wormley, Godalming) Rep* 185: 1–121
- Hecker B (1990) Variations in megafauna assemblages on the continental margin south of Georges Bank. *Deep-Sea Res* 37: 37–57
- Houston KA, Haedrich RL (1984) Abundance and biomass of macrobenthos in the vicinity of Carson Submarine Canyon, north-west Atlantic Ocean. *Mar Biol* 82: 301–305



- Lampitt RS (1985) Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent repercussion. *Deep-Sea Res* 32A: 885–897
- Lampitt RS, Billett DSM, Rice AL (1986) Biomass of the invertebrate megabenthos from 500 to 4100 m in the northeast Atlantic Ocean. *Mar Biol* 93: 69–81
- Mauchline J, Gordon JDM (1985) Trophic diversity in deep-sea fish. *J Fish Biol* 26: 527–535
- Merrett NR, Haedrich RL, Gordon JDM, Stehmann M (1991) Deep demersal fish assemblages structure in the Porcupine Seabight (eastern North Atlantic): results of single warp trawling at lower slope to abyssal soundings. *J mar biol Ass UK* 71: 359–373
- Merrett NR, Marshall NB (1981) Observations on the ecology of two deep-sea bottom-living fishes collected off northwest Africa (08°N–27°N). *Prog Oceanogr* 9: 185–244
- 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. *Contin Shelf Res* 10: 809–839
- Pearcy WG, Stein DL, Carney RS (1982) The deep-sea benthic fish fauna of the northeastern Pacific Ocean on Cascadia and Tufts abyssal plains and adjoining continental slopes. *Biol Oceanogr* 1: 375–428
- Relini G, Orsi Relini L (1987) The decline of shrimps stock in the Gulf of Genoa. *Investigación pesq* 51: 245–260
- Reyss D (1971) Les canyons sous-marins de la mer Catalane le rech su cap et le rech Lacaze-Duthiers. IV-Étude Synécologique des peuplements de macrofaune benthique. *Vie Milieu* 23B: 101–142
- Rowe GT (1971) Observations on bottom currents and epibenthic populations in Hatteras Submarine Canyon. *Deep-Sea Res* 18: 569–581
- Rowe GT, Polloni PT, Haedrich RL (1982) The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. *Deep-Sea Res* 29: 257–278
- Sardà F, Cartes JE, Norbis W (1994a) Spatio-temporal structure of the deep-water shrimp *Aristeus antennatus* Risso, 1816 (Decapoda: Aristeidae) population in the Western Mediterranean. *Fish Bull US* 92: 599–607
- Sardà F, Martin P (1986) Les pesqueries a Catalunya: evolució en els últims decennis. *Quad Ecol apl (Barcelona)* 9: 91–112
- Shepard FP, Marshall NF, McLoughlin PA (1974) Currents in submarine canyons. *Deep-Sea Res* 21: 691–706
- Stefanescu C, Lloris D, Rucabado J (1992) Deep-living demersal fishes in the Catalan Sea (Western Mediterranean) below a depth of 1000 m. *J nat Hist* 26: 197–213
- Stefanescu C, Morales-Nin B, Massuti E (1994) Fish assemblages on the slope in the Catalan Sea (Western Mediterranean): influence of a submarine canyon. *J nat Hist* (in press)
- Tobar R, Sardà F (1987) Análisis de la evolución del recurso de gamba rosada, *Aristeus antennatus* (Risso, 1816), en los últimos decenios en Cataluña. *Infms téc Inst Invest pesq* 142: 1–20
- Thiel H (1983) Meiobenthos and nanobenthos of the deep-sea. In: Rowe GT (ed) *Deep-sea biology. The Sea. Vol 8.* John Wiley & Sons, New York, pp 167–230
- Tyler PA (1988) Seasonality in the deep sea. *Oceanogr mar Biol A Rev* 26: 227–258