

Diets of deep-water pandalid shrimps on the Western Mediterranean slope

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ABSTRACT: The feeding habits of 3 deep-water species of pandalid shrimps occurring in the Catalan Sea (Western Mediterranean) were studied. All specimens were collected from 1988 to 1990 using bottom trawls at depths ranging between 380 and 1249 m. A total of 71 specimens of *Plesionika edwardsi*, 176 of *P. martia*, and 213 of *P. acanthonotus* were analyzed. Pandalid shrimps were active predators of macroplankton species. The diets of *P. edwardsi* and *P. martia* were quite similar and consisted primarily of benthopelagic eucarid crustaceans (*Pasiphaea* sp., euphausiids). *P. acanthonotus* is smaller, and its diet was based on smaller prey (siphonophores, hyperiids, euphausiids). Seasonal changes in the diets of bathyal pandalids were important. Planktonic organisms were their main food resource, and pandalid diets corresponded with changes in the abundance of available planktonic resources in the Western Mediterranean. Thus, bathymetric distribution and abundance of pandalid shrimps along the slope were related to the influence of the mesopelagic fauna on bathyal communities, which is commonly accepted to decrease with depth. The bathymetric distribution of pandalids is also discussed in relation to a possible competitive interaction for similar resources among certain pandalid species.

INTRODUCTION

The Pandalidae (Decapoda, Caridea) comprise different genera with a high diversity of species. A large number of species within the bathyal genus *Plesionika* are distributed mainly in tropical and subtropical areas (Zariquiey Alvarez 1968, Crosnier & Forest 1973). *Plesionika edwardsi* (Brandt, 1851), *P. martia* (A. Milne Edwards, 1883), and *P. acanthonotus* (S. I. Smith, 1882) are characteristic and abundant in bathyal mud assemblages in the deep slope of the Catalan Sea (Western Mediterranean), where environmental parameters (temperature and salinity) in the water column are fairly constant below 200 m (Fredj & Laubier 1985).

Plesionika edwardsi is distributed in the upper slope of the Catalan Sea between 256 and 512 m, attaining its maximum abundance between 300 and 400 m (Abelló et al. 1988). Large sizes are linked to the submarine canyons (Cartes 1991, unpubl. data). *P. martia* is distributed deeper than *P. edwardsi* in the upper middle slope between 300 and 900 m (maximum abundance between 400 and 800 m), whereas *P. acanthonotus* is found almost exclusively on the middle slope of

the Catalan Sea between 300 and 1600 m (Abelló et al. 1988, Cartes 1991, 1993a).

The trophic habits of some pandalids have been reported on (Lagardère 1972, 1977, Wienberg 1980). Lagardère (1972) described the diet of *Plesionika martia* in the NW African slope. *P. martia* was found to prey exclusively on euphausiids (*Meganyctiphanes norvegica*) and mesopelagic decapods (*Pasiphaea sivado*). In contrast, in the Bay of Biscay this species has been suggested to scavenge (Lagardère 1977). There are no previous data about the feeding habits of the other 2 deep-Mediterranean species, although a scavenging habits has been suggested for *P. edwardsi* based on commercial catches obtained using pots (Massuti 1967, Lagardère 1976b).

Plesionika acanthonotus is a small species [Cephalothorax length (CL) between 6 and 17 mm]. Its bathymetric distribution overlaps with that of *P. martia* on the upper middle slope. Both species are distinctly separated by their size ranges. *P. martia* and *P. edwardsi* coincide in distribution within the submarine canyons, where a certain degree of size range overlap is also observed.

The objective of the present paper is to describe the diets and feeding habits of the 3 deep-bathyal pandalids occurring in the western Mediterranean Sea, discussing the influence of depth and seasonality in the diet and patterns of dietary overlap among these species.

MATERIAL AND METHODS

Specimens were collected using bottom trawls on the deep slope in the Catalan Sea. CL was recorded for all specimens. A total of 83 specimens of *Plesionika edwardsi*, 282 of *P. martia*, and 463 of *P. acanthonotus* were studied to establish the foregut fullness (f) for each species. The foregut fullness of each individual was recorded; foreguts for which $f \geq 75\%$ were classified as very full, while values of $f < 20\%$ were classified as empty. Only contents from the fullest stomachs were selected for the analysis of diet, to reduce any bias associated with digestion (Sardà & Valladares 1990, Cartes 1991). Consequently, only 71 specimens of *P. edwardsi*, 176 of *P. martia*, and 213 of *P. acanthonotus* were analyzed (Table 1).

Prey identification was carried out to species whenever possible. The results are presented in terms of percentage frequency of occurrence (%F) and percentage abundance (%N) (cf. Hyslop 1980, Cartes & Sardà 1989). Percentage volume was estimated using the subjective points method (Swynnerton & Worthington 1940) for the different prey-species or prey-groups.

General affinities between the samples (diets) were established using a multivariate cluster analysis (cf. Cartes & Abelló 1992) for *Plesionika martia* and *P. acanthonotus*. Each sample combined the individuals taken in one haul. Linear correlation, applied to log-transformed data, was used as a similarity index. This index mainly considers information from the most abundant prey items. Uncommon prey items which occurred only once in the diet were removed from the data matrix. The aggregation algorithm used was UPGMA (Pielou 1984). Analysis results revealed general trends on the influence of spatial and temporal factors (depth and seasonality) in the diet of the studied species. Information obtained from previous studies on deep-water decapod diets, especially *Aristeus antennatus* (cf. Cartes 1991, Cartes & Abelló 1992, Cartes 1993b), showed that dietary changes were dependent on depth and season. Based both on these results and on some general trends derived from the cluster analysis, the diet of each species was studied by seasonal period and by depth stratum. Three depth strata were established: canyons in the upper slope (380 to 530 m); upper middle slope (552 to 730 m); and lower middle slope (861 to 1249 m). Detailed information about seasonal data for each established group (winter, spring–summer, autumn) is given in Table 1.

Trophic diversity was calculated using the Shannon-Wiener index, H' (Shannon & Weaver 1963, Mauchline & Gordon 1985), which is influenced both by dominance and number of species (prey items in this study) (Edgar 1983), for each of the established bathymetric and seasonal sample groups. Intraspecific and interspecific

Table 1. Sampling data for *Plesionika* species in the present study. C: canyon sample

Stn	Date	Location	Depth (m)	Number of individuals		
				<i>P. edwardsi</i>	<i>P. martia</i>	<i>P. acanthonotus</i>
P7	23 Mar 88	41° 03' N, 02° 13' E	570–585	–	11	–
P15	19 Feb 89	41° 08' N, 01° 56' E	380–530 C	10	11	–
P25	13 Jul 89	41° 03' N, 02° 03' E	650–700	–	8	–
P26	14 Jul 89	41° 03' N, 02° 04' E	640–700	–	27	21
P27	14 Jul 89	41° 03' N, 02° 03' E	640–660	–	30	15
P288	14 Jul 89	41° 03' N, 02° 03' E	710–730	–	31	–
P29	14 Jul 89	41° 02' N, 02° 03' E	610–640	–	8	13
P33	20 Oct 89	41° 04' N, 02° 04' E	552–644	–	20	49
P34	20 Oct 89	41° 04' N, 02° 04' E	552–644	–	13	18
DN2	21 Oct 90	41° 07' N, 02° 02' E	380–525 C	61	17	–
B3/15	03 Jul 88	40° 49' N, 01° 36' E	1011–946	–	–	12
B3/16	04 Jul 88	40° 49' N, 01° 51' E	1249–1193	–	–	9
B3/24	07 Jul 88	39° 53' N, 02° 24' E	980–1019	–	–	10
B3/25	07 Jul 88	39° 58' N, 02° 18' E	1224–1184	–	–	12
B5/11	28 Oct 88	40° 53' N, 01° 45' E	1036–994	–	–	12
B5/14	28 Oct 88	40° 56' N, 02° 07' E	1158–1034	–	–	9
B5/17	29 Oct 88	41° 00' N, 02° 27' E	861–1100	–	–	24
SP/2	16 Oct 89	41° 00' N, 01° 34' E	862–989	–	–	5

dietary overlaps were calculated based on %N results using the percentage of similarity index (Schoener 1970). Significance of differences between diets was tested using the chi-square method for contingency tables (Zar 1984) and the Spearman correlation coefficient (Sokal & Rohlf 1979).

RESULTS

Size distribution for each species in the 3 bathymetric slope regions where pandalids were distributed is presented in Fig. 1. Although all size frequencies were significantly different between species ($p < 0.01$; non-parametric Kolmogorov-Smirnov test) the highest degree of size overlap was observed between *Plesionika martia* and *P. edwardsi* inside submarine canyons.

Diet composition

Plesionika edwardsi (canyons)

In winter the most important prey for this species were euphausiids (*Meganyctiphanes norvegica*), the mesopelagic decapod *Pasiphaea sivado*, and polychaetes (Table 2). In contrast, fish remains were a secondary food item. Results in terms of percentage volume (Fig. 2) were similar among the various prey.

Plesionika martia

Cluster analysis of the diet composition for *Plesionika martia* showed segregation of some groups of samples (Fig. 3; see also Table 1). The most homogeneous group included all the samples collected during the spring-summer period in the upper middle slope. Samples collected in autumn on the upper middle slope (Stns P33 & P34) were grouped with a sample from a shallower submarine canyon station sampled in winter (Stn P15). The individuals collected in the canyons during autumn (Stn DN2) were clearly distinct.

Collections of *Plesionika martia* were grouped into 4 bathymetric and seasonal groups, only partially corresponding to groups resulting from the cluster analysis (see 'Material and methods'). The first group included a few specimens collected in a winter canyon sample (380 to 540 m). Predominant prey in the diet (Table 3, Fig. 4) were *Meganyctiphanes norvegica* and *Pasiphaea sivado*. In this case the high incidence of euphausiids was the main factor contributing to the high affinity recorded between the second and third groups of *P. martia*. *P. sivado* was the dominant prey species in the diet of the specimens collected in the canyons during autumn (Stn DN2). Fish remains, polychaetes (*Glycera* sp., *Nephtys* sp., Nereidae), and *Sergestes arcticus* were secondary prey (Table 3, Fig. 4).

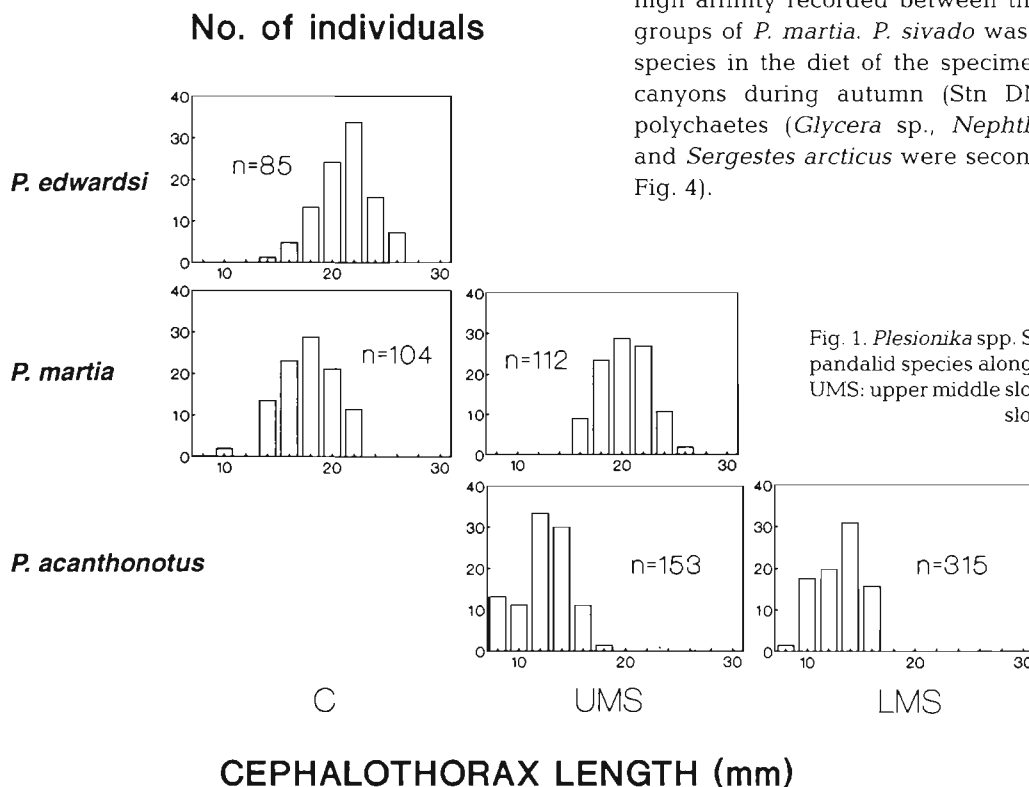


Fig. 1. *Plesionika* spp. Size distribution of the 3 pandalid species along the slope. C: canyons; UMS: upper middle slope; LMS: lower middle slope

Table 2. Composition of the diet of *Plesionika edwardsi* in the 2 seasonal groups established. %F = frequency of occurrence; %N = percentage abundance

Prey	No. of specimens:	Canyons			
		Winter (Feb)		Autumn (Oct)	
		%F	%N	%F	%N
		10		61	
POLYCHAETA		50.0	13.1	37.7	16.9
Aphroditida		10.0	2.6	-	-
<i>Glycera</i> sp.		-	-	11.5	4.7
<i>Hyalinoecia</i> sp.		-	-	1.6	0.7
Eunicida (<i>Marphysa belli</i>)		30.0	7.9	-	-
Nereidae		-	-	18.0	7.4
Unidentified		10.0	2.6	9.8	4.1
CRUSTACEA					
Decapoda					
Natantia					
Mesopelagic species		50.0	13.2	82.0	39.2
<i>Pasiphaea</i> sp.		50.0	13.2	73.8	31.1
Sergestidae		-	-	18.0	7.4
<i>Gennadas elegans</i>		-	-	1.6	0.7
Unidentified Natantia		20.0	5.3	4.9	2.0
Anomura					
<i>Pagurus alatus</i>		10.0	2.6	-	-
Euphausiacea		60.0	23.7	-	-
Mysidacea		10.0	2.6	21.3	20.3
<i>Boreomysis arctica</i>		-	-	21.3	20.3
Unidentified		10.0	2.6	-	-
Amphipoda					
Gammaridea		20.0	5.3	-	-
Isopoda					
<i>Cirolana borealis</i>		10.0	2.6	-	-
Cumacea		10.0	2.6	-	-
Unidentified Crustacea		20.0	5.3	1.6	0.7
MOLLUSCA					
Bivalvia		20.0	5.3	-	-
<i>Abra longicallus</i>		10.0	2.6	-	-
Other Bivalvia		10.0	2.6	-	-
Gastropoda		10.0	2.6	6.6	3.4
Pteropoda		10.0	2.6	1.6	0.7
Other Gastropoda		-	-	6.6	2.7
Cephalopoda		-	-	6.6	2.7
Unidentified		20.0	5.3	-	-
ECHINODERMATA					
Echinoidea		20.0	5.3	1.6	0.7
CHAETOGNATA		-	-	1.6	0.7
OSTEICHTHYES		20.0	5.3	21.3	8.8
<i>Cylothone</i> sp.		-	-	3.3	1.4
Myctophidae		-	-	6.6	2.7
Other Osteichthyes		20.0	5.3	11.5	4.7
CHONDRICHTHYES		-	-	8.2	3.4
UNIDENTIFIED		-	-	3.3	1.4
FORAMINIFERA		30.0		4.9	
<i>Pyrgo</i> sp.		-		1.6	
Other benthic species		30.0		4.9	

A fourth group included specimens collected in the spring-summer period (March to July) on the upper middle slope. *Pasiphaea multidentata* was the dominant prey, accounting for more than 1/3 of the diet (Table 3). Less important were *Calocaris macandreae* or fish remains. Euphausiids were almost absent from the diet. The volumetric results were similar (Fig. 4). Euphausiids and fish remains were the most important prey items in the diet of the specimens collected during autumn on the upper middle slope. Gastropods (mainly pteropods) and mesopelagic decapods (*P. multidentata*, *S. arcticus*) were secondary prey (Table 3, Fig. 4).

Plesionika acanthonotus

Two main groups were detected in the cluster analysis (Fig. 5). Temporal variations (seasonality) seemed to be more important than depth in sample aggregation. Thus, the first group included all the samples collected in summer, between 610 and 1249 m. The second group associated all the specimens collected in autumn, between 552 and 1158 m. Within these major groups samples seemed to be clustered on the basis of depth. Thus, as with the results for *Plesionika martia*, samples were classified into 4 bathymetric and seasonal groups.

Fish remains were dominant in the diet of this species on the upper middle slope in summer. Siphonophores (*Chelophyes appendiculata*), *Pasiphaea multidentata*, and isopods were secondary prey (Table 4, Fig. 6). In contrast, some prey such as *Calocaris macandreae* and *Meganyctiphanes norvegica* were very scarce in the diet. During autumn on the upper middle slope (552 to 644 m) euphausiids were more abundant than fish remains in the diet. Gastropods and hyperiids were also relatively important prey (Table 4, Fig. 6).

The diet was more diversified (Table 4, Fig. 6) on the lower middle slope (980 to 1265 m) in summer. Siphonophores and hyperiids (mainly *Vibilia armata*) were important prey and fish remains were also a dominant resource. Among hyperiid amphipods *V. armata* was the preferred species in the diet of *Plesionika acanthono-*

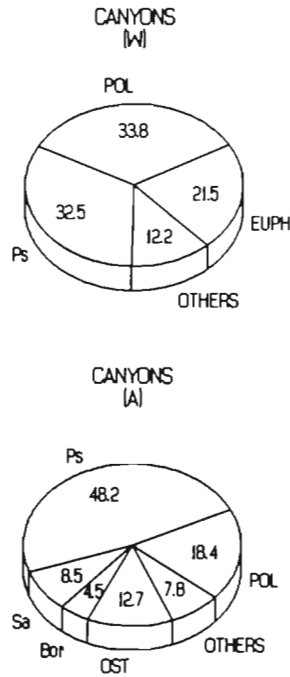


Fig. 2. Proportion (% volume) of prey species in the diet of *Plesionika edwardsi*. POL: polychaetes; Ps: *Pasiphaea sivado*; Sa: *Sergestes arcticus*; EUPH: Euphausiacea; Bor: *Boreomysis arctica*; OST: Osteichthyes. (W) winter; (A) autumn

tus, probably due to its smaller size. On the lower middle slope (862 to 1165 m) in autumn fish remains were predominant in the stomach contents. Euphausiids, pteropod debris, the gastropod *Benthonella tenella*, polychaetes, and foraminiferans were also important resources (Table 4, Fig. 6).

Feeding activity

The global results of the percentage of empty stomachs were 28 % for *Plesionika edwardsi*, 42 % for *P. martia* and 57 % for *P. acanthonotus*. In *P. martia* the highest percentage of very full stomachs was observed in submarine canyons during autumn (Table 5). Outside the canyons the proportion of empty stomachs was always higher. In *P. acanthonotus* stomach fullness was lower when depth increased (Table 5). As a whole, considering only bathymetric results for the 3 combined *Plesionika* species, significant differences ($p < 0.01$; chi-square criterion) were recorded in the percentage of empty foreguts ($f < 20\%$) within the 3 bathymetric groups established (see Fig. 1, Table 5). Thus, stomach fullness for pandalid species decreased significantly with depth.

Trophic diversity

Trophic diversity in *Plesionika edwardsi* was relatively low (Fig. 7). In *P. acanthonotus* diversity was relatively high for the different groups established (Fig. 7) and H' was higher in summer than in autumn for both bathymetric groups. Considering all the species as

a whole within the 3 bathymetric levels studied (see 'Material and methods'), a non-parametric Kruskal-Wallis test was applied to H' values. Only a weak significant trend ($p < 0.1$) of increasing diet diversification with increasing depth (Fig. 7) was recorded, although the obtained test value (5.61) is close to the chi-square 0.05 significance level (5.99, 2 degrees of freedom). Comparing H' values obtained outside and inside the canyons a significant value ($p < 0.05$) was recorded, confirming a higher dietary specialization for the studied species inside the submarine canyons.

Dietary affinity

The diet overlap value was very low between the 2 seasonal groups in *Plesionika edwardsi* (24.573). In *P. martia* the overlap results were generally low (Table 6). The maximum value occurred when the canyon samples in autumn and the upper middle slope samples in spring-summer were compared. In contrast, the lowest overlap value occurred when the diets of these 2 bathymetric zones in autumn were compared. In *P. acanthonotus* dietary overlap values (Table 6) were quite high. The maximum value was recorded between both summer groups (60.144) whereas the lowest values occurred between the spring-summer (lower middle slope) and autumn (upper middle slope) samples.

Interspecific overlap between *Plesionika edwardsi* and *P. martia* samples was high in the canyons. The dietary affinity between *P. acanthonotus* and *P. martia* in the upper middle slope was relatively high only during autumn (Table 6).

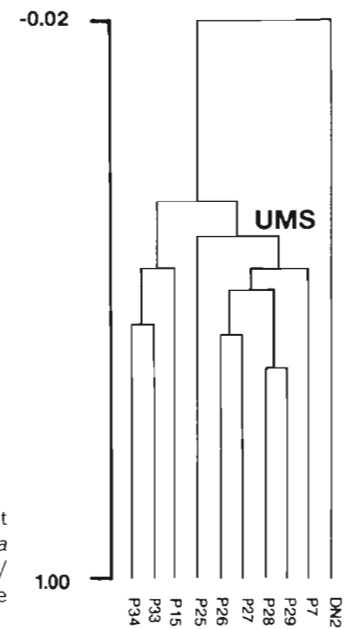


Fig. 3. Aggregation of foregut content samples for *Plesionika martia* (linear correlation/UPGMA). UMS: upper middle slope grouping

Table 3. Composition of the diet of *Plesionika martia* in each bathymetric and seasonal group established. %F = frequency of occurrence; %N = percentage abundance

Prey	No. of specimens:	Canyons (400–500 m)				Upper middle slope (550–750 m)			
		Winter (Feb)		Autumn (Oct)		Spring–summer		Autumn (Oct)	
		%F	%N	%F	%N	%F	%N	%F	%N
HYDROZOA		–	–	–	–	1.7	1.1	3.0	1.2
<i>Chelophyes appendiculata</i>		–	–	–	–	1.7	1.1	3.0	1.2
POLYCHAETA		–	–	41.2	21.9	6.1	3.4	6.1	2.4
Aphroditida		–	–	–	–	3.5	2.3	6.1	2.4
<i>Glycera</i> sp.		–	–	23.5	9.8	–	–	–	–
<i>Nephtys</i> sp.		–	–	5.9	2.4	–	–	–	–
Nereidae		–	–	5.9	2.4	–	–	–	–
Unidentified		–	–	17.6	7.3	1.7	1.1	–	–
CRUSTACEA									
Decapoda									
Natantia									
Bathypelagic species		63.6	38.9	70.6	41.5	60.9	38.1	36.4	14.1
<i>Pasiphaea</i> sp.		63.6	38.9	58.8	31.7	60.0	34.7	27.3	10.6
<i>Sergestes arcticus</i>		–	–	29.4	9.8	7.0	3.4	9.1	3.5
Benthic species		–	–	5.9	4.8	4.3	2.9	6.1	2.4
<i>Aristeus antennatus</i>		–	–	–	–	0.9	0.6	–	–
<i>Plesionika</i> sp.		–	–	–	–	0.9	0.6	6.1	2.4
<i>Processa canaliculata</i>		–	–	5.9	2.4	–	–	–	–
<i>Alpheus glaber</i>		–	–	–	–	2.6	1.7	–	–
Unidentified		–	–	5.9	2.4	10.4	6.3	12.1	4.7
Macrura									
<i>Calocaris macandreae</i>		–	–	–	–	31.3	19.9	18.2	7.1
Anomura		–	–	–	–	3.5	2.2	–	–
<i>Pagurus alatus</i>		–	–	–	–	1.7	1.1	–	–
<i>Munida tenuimana</i>		–	–	–	–	1.7	1.1	–	–
Brachyura		–	–	–	–	0.9	0.6	–	–
Post-larvae		–	–	11.8	4.9	–	–	–	–
Unidentified		–	–	5.9	2.4	2.6	1.7	3.0	1.2
Euphausiacea (<i>Meganyctiphanes norvegica</i>)		63.9	38.9	–	–	0.9	0.6	42.4	17.7
Mysidacea		–	–	5.9	4.9	0.9	0.6	–	–
<i>Boreomysis arctica</i>		–	–	5.9	4.9	–	–	–	–
Unidentified		–	–	–	–	0.9	0.6	–	–
Amphipoda									
Gammaridea		–	–	–	–	0.9	0.6	3.0	1.2
Lysianassidae		–	–	–	–	0.9	0.6	–	–
Synopiidae		–	–	–	–	–	–	3.0	1.2
Hyperidea		9.1	5.6	–	–	5.2	3.3	15.2	6.0
<i>Phrosina</i> sp.		9.1	5.6	–	–	3.5	2.2	6.1	2.4
<i>Vibilia armata</i>		–	–	–	–	–	–	3.0	1.2
Other Hyperidea		–	–	–	–	1.7	1.1	6.1	2.4
Isopoda (<i>Cirolana borealis</i>)		–	–	–	–	4.3	2.8	–	–
Tanaidacea Apseudomorpha		–	–	–	–	2.6	1.1	–	–
Cumacea (<i>Epileucon longirostris</i>)		–	–	–	–	1.7	1.1	–	–
Ostracoda Cypridinidae		–	–	–	–	0.9	0.6	–	–
Copepoda Harpacticoidea		–	–	–	–	–	–	3.0	1.2
Unidentified Crustacea		9.1	5.6	–	–	1.7	1.1	6.1	2.4
MOLLUSCA									
Bivalvia		–	–	–	–	1.7	1.1	–	–
Gastropoda		–	–	17.6	7.3	2.6	1.7	27.3	11.8
Pteropoda		–	–	–	–	2.6	1.7	18.2	7.1
<i>Benthonella tenera</i>		–	–	–	–	–	–	12.1	4.7
Other Gastropoda		–	–	17.6	7.3	–	–	–	–
Unidentified		–	–	–	–	–	–	6.1	2.4
ECHINODERMATA									
Echinoidea		–	–	–	–	0.9	0.6	3.0	1.2
Ophiuroidea		–	–	–	–	0.9	0.6	3.0	1.2
CHAETOGNATA		9.1	5.6	17.6	7.3	13.0	8.5	42.4	38.1
OSTEICHTHYES		9.1	5.6	17.6	7.3	13.0	8.5	42.4	38.1
<i>Cyclothone</i> sp.		–	–	–	–	–	–	3.0	2.4
Myctophidae		–	–	5.9	2.4	2.6	1.7	6.1	3.6
Other Osteichthyes		9.1	5.6	11.8	4.9	13.0	6.8	33.3	32.1

Table 3 (continued)

Prey	No. of specimens:	Canyons (400–500 m)				Upper middle slope (550–750 mm)			
		Winter (Feb)		Autumn (Oct)		Spring–summer		Autumn (Oct)	
		10	%F	%N	61	%F	%N	10	%F
OTHERS		–	–	–	–	0.9	0.6	–	–
UNIDENTIFIED		–	–	5.9	2.4	0.9	0.6	12.1	4.7
FORAMINIFERA		–	–	11.8	–	4.3	–	12.1	–
<i>Uvigerina</i> sp.		–	–	–	–	1.7	–	–	–
<i>Ammodiscus</i> sp.		–	–	–	–	0.9	–	–	–
<i>Gyroidina soldanii</i>		–	–	5.9	–	3.5	–	6.1	–
Globigerinae		–	–	5.9	–	4.3	–	6.1	–
Mud		–	–	–	–	–	–	3.0	–
Micromolluscs remains		–	–	–	–	1.7	–	9.1	–

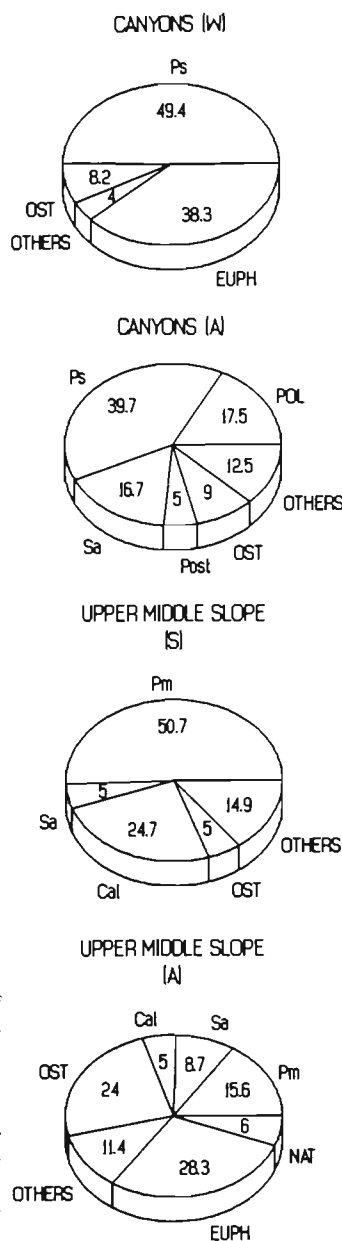


Fig. 4. Proportion (% volume) of prey species in the diet of *Plesionika martia*. POL: polychaetes; Ps: *Pasiphaea sivado*; Pm: *Pasiphaea multidentata*; Sa: *Sergestes arcticus*; NAT: natantian; Cal: *Calocaris macandreae*; Post: decapod post-larvae; EUPH: Euphausiacea; OST: Osteichthyes. W: winter; A: autumn; S: summer

Dietary affinities among all the bathymetric and seasonal groups established were tested using the chi-square criterion for contingency tables (Zar 1984). No comparisons were statistically significant ($p < 0.05$). So, the dietary overlap results in this study must be considered as relative. Results of the semi-quantitative Spearman coefficient (Table 6), where the order of importance by prey is the factor determining dietary affinities, were only significant ($p < 0.05$) between the 2 *Plesionika* species occurring inside submarine canyons during autumn and between both seasonal groups of *Plesionika acanthonotus* established on the lower middle slope.

DISCUSSION

Pandalid shrimps on the deep slope in the Catalan Sea were active predators on macroplankton, although

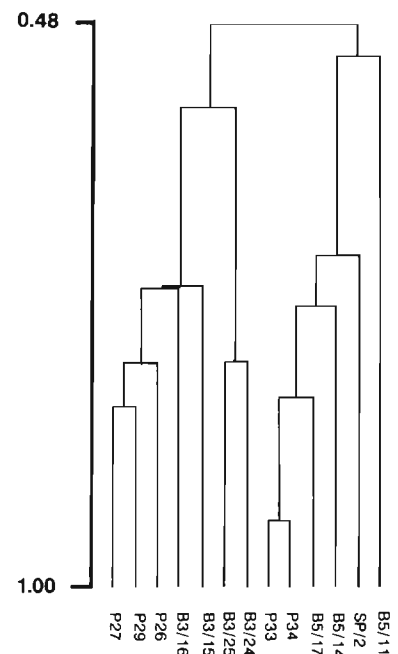


Fig. 5. Aggregation of foregut content samples for *Plesionika acanthonotus* (linear correlation / UPGMA)

Table 4. Composition of the diet of *Plesionika acanthonotus* in each bathymetric and seasonal group established. %F = frequency of occurrence; %N = abundance

Prey	No. of specimens:	Upper middle slope				Lower middle slope			
		Summer (Jul)		Autumn (Oct)		Summer (Jul)		Autumn (Oct)	
		%F ⁴⁹	%N	%F ⁷¹	%N	%F ⁴⁷	%N	%F ⁵⁰	%N
HYDROZOA		18.4	10.9	5.6	1.8	38.3	13.0	10.0	5.2
<i>Chelophyes appendiculata</i>		-	-	-	-	1.7	1.1	3.0	1.2
POLYCHAETA		8.2	4.4	9.7	4.8	21.3	6.6	22.0	7.9
Aphroditida		-	-	4.2	1.8	6.4	2.2	-	-
<i>Glycera</i> sp.		-	-	-	-	-	-	2.0	0.9
<i>Hyalinoecia</i> sp.		-	-	-	-	-	-	2.0	0.9
Nereidae		-	-	-	-	-	-	2.0	0.9
Spionidae		-	-	-	-	8.5	2.2	8.0	3.5
Other (Serpulidae)		-	-	-	-	2.1	0.7	-	-
Unidentified		8.2	4.4	8.3	3.0	4.3	1.5	4.0	1.8
CRUSTACEA									
Decapoda									
Natantia									
Bathypelagic species		10.2	3.3	4.2	1.8	19.1	6.6	24.0	10.3
Sergestidae		-	-	1.4	0.6	-	-	-	-
<i>Acanthephyra</i> sp.		-	-	-	-	6.4	2.2	4.0	1.8
<i>Pasiphaea multidentata</i>		10.2	3.3	2.8	1.2	12.8	4.4	20.0	8.6
Benthic species									
<i>Plesionika</i> sp.		2.0	1.1	-	-	4.3	1.5	2.0	0.9
Unidentified		4.1	2.2	2.8	1.2	10.6	3.6	4.0	1.8
Macrura									
<i>C. macandreae</i>		4.1	2.2	1.4	0.6	2.1	0.7	-	-
Anomura									
<i>Pagurus alatus</i>		6.1	3.3	1.4	0.6	-	-	-	-
Unidentified		6.1	3.3	1.4	0.6	6.4	2.2	6.0	2.6
Euphausiacea		2.0	1.1	68.1	32.0	6.4	2.9	30.0	15.5
Mysidacea									
<i>Boreomysis arctica</i>		-	-	-	-	6.4	2.2	-	-
Unidentified		-	-	-	-	2.1	0.7	-	-
Amphipoda									
Gammaridea		4.1	2.2	2.8	1.2	4.3	1.5	6.0	2.6
Lysianassidae		-	-	-	-	2.1	0.7	-	-
Oedicerotidae		-	-	1.4	0.6	-	-	-	-
<i>Rhachotropis</i> sp.		4.1	2.2	-	-	-	-	-	-
Synopiidae		-	-	1.4	0.6	-	-	-	-
Unidentified		-	-	-	-	2.1	0.7	6.0	2.6
Hyperiidea		4.1	6.6	12.5	5.4	55.3	-	8.0	4.4
<i>Phrosina semilunata</i>		6.1	3.3	4.2	1.8	19.1	6.5	2.0	0.9
<i>Vibilia armata</i>		-	-	5.6	2.4	31.9	12.3	2.0	0.9
<i>Phronima sedentaria</i>		6.1	3.3	2.8	1.2	8.5	3.6	6.0	2.6
Isopoda		16.3	10.1	4.2	1.8	2.1	2.2	-	-
<i>Cirolana borealis</i>		6.1	3.3	-	-	2.1	0.7	-	-
<i>Munnopsurus atlanticus</i>		8.2	4.4	4.2	1.8	-	-	-	-
Other Paraselloidea		2.0	1.1	-	-	-	-	-	-
Unidentified		2.0	1.1	-	-	4.3	1.5	-	-
Tanaidacea Apseudomorpha		-	-	4.2	1.8	-	-	-	-
Cumacea		2.0	1.1	-	-	8.5	2.9	4.0	1.8
<i>Epileucon longirostris</i>		2.0	1.1	-	-	6.4	2.2	-	-
<i>Cyclaspis longirostris</i>		-	-	-	-	2.1	0.7	4.0	1.8
Unidentified		-	-	-	-	-	-	-	-
Ostracoda		2.0	1.1	1.4	0.6	4.3	1.5	-	-
Myodocopa		-	-	-	-	2.1	0.7	-	-
Platycopa		2.0	1.1	1.4	0.6	2.1	0.7	-	-
Copepoda		-	-	1.4	0.6	4.3	1.5	4.0	1.8
Harpacticoida		-	-	1.4	0.6	-	-	-	-
Calanoidea		-	-	-	-	4.3	1.5	4.0	1.8
Unidentified Crustacea		2.0	1.1	5.6	2.4	4.3	1.5	2.0	0.9
PYCNOGONIDA		-	-	-	-	-	-	2.0	0.9
MOLLUSCA									
Bivalvia		-	-	2.8	1.2	-	-	4.0	1.8
<i>Abra longicallus</i>		-	-	2.8	1.2	-	-	4.0	1.8
Other Bivalvia		-	-	-	-	-	-	4.0	1.8

Table 4 (continued)

Prey	No. of specimens:	Upper middle slope				Lower middle slope			
		Summer (Jul)		Autumn (Oct)		Summer (Jul)		Autumn (Oct)	
		49	71	47	50	%F	%N	%F	%N
Gastropoda		8.1	5.4	19.4	7.7	6.4	3.0	22.0	13.8
Pteropoda		8.1	5.4	12.4	4.7	4.3	1.5	16.0	6.9
<i>Alvania</i> sp.		-	-	1.4	0.6	-	-	-	-
<i>Benthonella tenella</i>		-	-	4.2	1.8	4.3	1.5	16.0	6.0
Other Gastropoda		-	-	1.4	0.6	-	-	2.0	0.9
Cephalopoda		-	-	-	-	-	-	2.0	0.9
Unidentified		2.0	1.1	9.7	4.1	2.1	0.7	2.0	0.9
ECHINODERMATA									
Ophiuroidea		-	-	1.4	0.6	-	-	-	-
SIPUNCULOIDEA				6.9	3.0	-	-	-	-
OSTEICHTHYES		71.4	36.9	61.1	26.1	66.0	22.5	58.0	28.5
Myctophidae		6.1	4.4	4.2	1.8	-	-	-	-
Other Osteichthyes		65.3	32.6	56.9	24.3	66.0	22.5	58.0	28.5
Unidentified		-	-	2.8	1.2	2.1	0.7	2.0	0.9
FORAMINIFERA		34.7		15.3		17.0		38.0	
<i>Robulus</i> sp.		4.1		-		2.1		4.0	
<i>Uvigerina</i> sp.		2.0		-		-		6.0	
<i>Pyrgo</i> sp.		-		1.4		4.3		-	
Other benthic species		2.0		-		4.3		-	
Globigerinae		34.7		13.9		6.4		34.0	
Mud		-		1.4		-		2.0	
Micromolluscs remains		8.2		8.3		-		8.0	

they also made substantial use of benthic resources. The cycle of daily activity was also an important factor in their feeding habits (Cartes 1991, unpubl. data). Thus, the diet of *Plesionika martia* underwent an important quantitative change on the upper middle slope between daytime and nighttime. The daytime diet was based almost exclusively on the mesopelagic shrimp *Pasiphaea multidentata*.

The diet of *Plesionika edwardsi* consisted primarily of benthopelagic eucarid crustaceans, especially *Pasiphaea sivado*. *Plesionika martia* has been described as a specialized predator of bathypelagic species (Lagardère 1972). In the present study, although the prey species consumed changed with depth, benthopelagic eucarids were the predominant prey in pandalid diets. *P. edwardsi* also feeds on endobenthic prey, mostly polychaetes. Such feeding behaviour is fairly unusual among the pandalids here studied, although *P. martia* exhibited a similar trend in the submarine canyons. Polychaete consumption among the pandalids was considerable on the upper slope in the Bay of Biscay (Lagardère 1977). The feeding habits of *P. martia* and *P. edwardsi* were thus similar in the submarine canyons, the only slope region where these 2 species co-occur, (also exhibiting a certain degree of size overlap). *P. edwardsi* occurred in the submarine canyons on the upper middle slope but was replaced by *P. martia* at greater depths (Abelló et al. 1988, own unpubl. data). According

to the hypothesis of Rex (1977), both the high trophic level occupied by the 2 pandalids and the relatively high affinity exhibited between their diets may be consistent with a bathymetric displacement between these species.

Plesionika acanthonotus is smaller, and although it exploits a similar type of resource, it directed its activities towards smaller prey items (siphonophores, hyperiids, euphausiids). Benthic prey and Osteichthyes remains were also important. The feeding strategies of *P. acanthonotus* and *P. martia* are similar (directed to pelagic resources). However, selection of different prey sizes by these 2 species attenuates the exploitation of the same resource (cf. Macpherson 1981). Predation on euphausiids in autumn, the only common resource exploited, probably does not imply inter-specific competition, in view of a possible different selection of prey size and because of the very high abundance of euphausiids in the plankton during autumn (Franqueville 1971). A similar resource partitioning by size has been suggested to occur among pasiphaeid species (Lagardère 1976b).

Scavenging is a secondary activity in the feeding habits of pandalids. The proportion of Osteichthyes and Chondrichthyes remains in the diet of *Plesionika edwardsi* and *P. martia* was small (5 to 15%), with occasional otoliths or mandible arches of myctophids and *Cyclothone* sp., suggestive of active hunting of small fishes. These results conflict with the classifica-

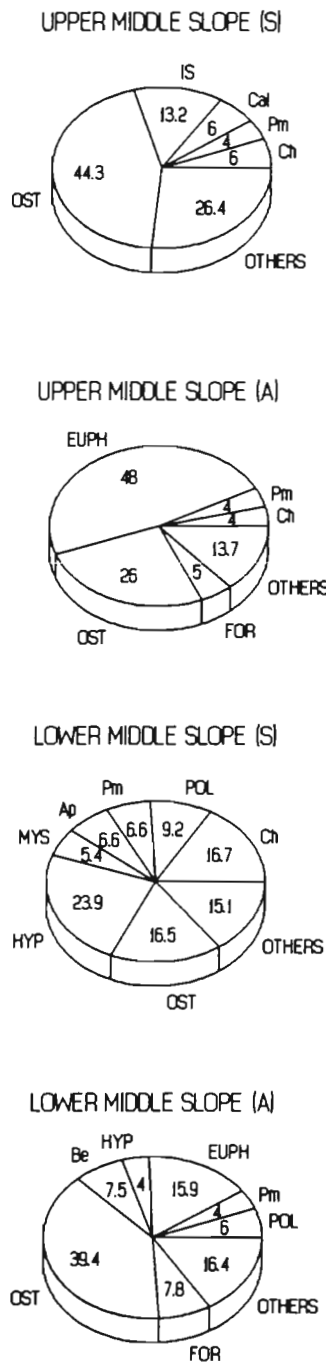


Fig. 6. Proportion (% volume) of prey species in the diet of *Plesionika acanthonotus*. Ch: Siphonophora; POL: polychaetes; Ap: *Acanthephyra* sp.; Pm: *Pasiphaea multidentata*; Cal: *Calocaris macandreae*; EUPH: Euphausiacea; MYS: Mysidacea; HYP: Hyperideia; IS: Isopoda; Be: *Benthonella tenella*; OST: Osteichthyes; FOR: Foraminifera. (A): autumn; (S): summer

tion of *P. edwardsi* as an active scavenger (Lagardère 1976a) based on large catches achieved using pots (Massuti 1967). *P. acanthonotus* seemed to exhibit the most pronounced scavenging activity, though in many cases (60%) Osteichthyes remains consisted of large isolated scales. Its advanced digestion state (Cartes 1991) precluded the possibility of net feeding; rather, scales were probably ingested in the water column (Hopkins & Baird 1975), an activity more in keeping

with passive predation on slow-moving resources above the bottom than with scavenger behaviour.

The proportion of benthic prey items in the diets of pandalids was low. Such prey items tended to be slow-moving (sedimented pteropod shells, molluscs, and fish remains), while mobile epibenthic resources such as peracarids always occurred sporadically in the diet.

Seasonal changes in pandalid diets followed a common pattern with respect to euphausiids, which were basic components of the diets of both *Plesionika martia* and *P. acanthonotus* on the middle slope in autumn. In the submarine canyons the seasonal pattern was different, and euphausiids were only important in winter. This same pattern of feeding on euphausiids was common to all the bathyal decapods in the study area (Cartes 1991) and was in accordance with the abundance of this group in the water column (Franqueville 1971). Siphonophores and hyperiids were also seasonally important in the diet of *P. acanthonotus*, being abundant in summer. The siphonophore species identified (*Chelophyes appendiculata*) and certain hyperiid species (*Phrosina semilunata*, *Phronima sedentaria*) attain peak abundance levels in the Western Mediterranean in summer (Franqueville 1971). Seasonal differences in the diets of bathyal decapods in the Catalan Sea were most important for those species which, like the pandalids, relied on planktonic organisms as their main resource (Cartes 1991).

The influence of the mesopelagic fauna on bathyal benthic communities is commonly accepted to decrease with depth (Lagardère 1977). Pérès (1958) reported that euphausiid shoals tended to aggregate near topographical features in the sea bed, such as the slopes of submarine canyons down to 1000 m. Some

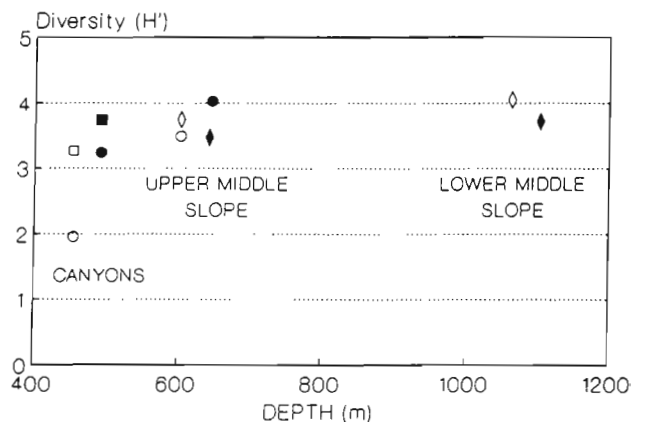


Fig. 7. Trophic diversity (H') in the diet of pandalids determined by depth and seasonal groups. (\diamond , \blacklozenge) *Plesionika acanthonotus*; (\square , \blacksquare) *P. edwardsi*; (\circ , \bullet) *P. martia*. Open symbols: winter-summer values; filled symbols: autumn values

Table 5. Percentage of stomach fullness (*f*) in *Plesionika edwardsi*, *P. acanthonotus* and *P. martia* by depth and season

		Canyons (400–500 m)		Upper middle slope (550–750 m)		Lower middle slope (1000–1200 m)	
		Feb	Oct	Mar–Jul	Oct	Jul	Oct
<i>P. edwardsi</i>	No. of specimens	12	71				
	<i>f</i> < 20 %	41.6	25.4				
	20 % ≤ <i>f</i> < 75 %	50.0	43.6				
	<i>f</i> ≥ 75 %	8.3	31.0				
<i>P. martia</i>	No. of specimens	192	20	175	68		
	<i>f</i> < 20 %	42.1	20.0	40.0	45.6		
	20 % ≤ <i>f</i> < 75 %	47.4	45.0	36.0	35.3		
	<i>f</i> ≥ 75 %	10.5	35.0	24.0	19.1		
<i>P. acanthonotus</i>	No. of specimens			75	72	129	187
	<i>f</i> < 20 %			58.6	23.6	48.1	75.9
	20 % ≤ <i>f</i> < 75 %			37.4	44.5	41.8	19.3
	<i>f</i> ≥ 75 %			4.0	31.9	10.1	4.8

Table 6. Intraspecific and interspecific dietary overlaps between the different bathymetric and seasonal groups in *Plesionika* species. S: similarity; r: Spearman correlation; (*): significant value; UMS: upper middle slope; LMS: lower middle slope

INTRASPECIFIC DIETARY AFFINITY							
<i>P. edwardsi</i>		Canyons (Oct)					
		S	r				
Canyons (Feb)		24.573	-0.293				
<i>P. martia</i>		Canyons (Oct)		UMS (Jul)		UMS (Oct)	
		S	r	S	r	S	r
	Canyons (Feb)	38.462	0.045	43.056	0.548	38.497	0.556
	Canyons (Oct)			47.276	0.057	26.727	0.075
Upper middle (Jul)					45.120	0.288	
<i>P. acanthonotus</i>		UMS (Oct)		LMS (Jul)		LMS (Oct)	
		S	r	S	r	S	r
	Upper middle (Jul)	49.511	0.243	60.144	0.17	57.717	0.058
	Upper middle (Oct)			45.626	0.215	57.519	0.123
Lower middle (Jul)					59.927	0.436 (*)	
INTERSPECIFIC DIETARY AFFINITY							
Canyons		Winter		Autumn			
		S	r	S	r		
<i>P. edwardsii</i> vs <i>P. martia</i>		46.153	0.423	64.691	0.544 (*)		
UMS		Spring–Summer		Autumn			
		S	r	S	r		
<i>P. edwardsii</i> vs <i>P. acanthonotus</i>		34.492	0.155	56.932	-0.133		

samples taken in the benthic boundary layer have pointed to a decrease in euphausiid densities on the lower slope (Hargreaves et al. 1984). In accordance with this finding, euphausiids were more abundant in the shallowest samples (650 to 730 m) than on the lower middle slope (862 to 1265 m) in the diet of pandalid species in the present study. In the Catalan Sea, there is a distinct boundary, at around 1200 to 1300 m, limiting the influence of euphausiids and mesopelagic fishes in the diets of deep-water decapods (Cartes 1991). In contrast, siphonophores and hyperiids were most abundant in the deepest samples in the diet of *Plesionika acanthonotus*. The abundance of gelatinous plankton near the bottom is apparently higher below 1000 m, as indicated by direct results (Hargreaves et al. 1984, Hargreaves 1985) and by indirect results, such as on the bathymetric distribution of benthopelagic fishes of the genus *Alepocephalus* (Gordon & Mauchline 1990, Stefanescu 1991), which are highly specialized exploiters of this type of resource.

Dietary diversity in pandalids seemed to be associated with sample depth. Dietary diversity was low in *Plesionika edwardsi* as compared to the other 2 species outside the canyons. This pattern was also observed for *P. martia* in the canyons. The cause underlying this finding could be a specialization towards a specific type of resource (*Pasiphaea sivado*, euphausiids), which is probably more abundant in a more highly productive zone (Haedrich et al. 1980). Thus, the consistently higher stomach fullness values in the canyons were also attributable to greater food abundance there. In *P. acanthonotus*, the deepest distributed pandalid species, dietary diversity was higher as specific resources became less abundant in the environment. On the lower middle slope the behavioural pattern of *P. acanthonotus* was more like that of a non-selective predator (Dayton & Hessler 1972).

Because of the rather specialized nature of pandalid diets, the distribution and abundance of these species seemed to be strongly conditioned by the abundance of their preferred resources. Thus, *P. martia* based more than one-third of its diet on a single prey item (*Pasiphaea multidentata*) in summer. Preferred prey items also included *Meganyctiphanes norvegica* and *Calocaris macandreae*. The abundance of all these species falls off sharply below 1000 m (Lagardère 1977, Cartes 1991), where the distribution range of *P. martia* (depth distribution 400 to 900 m) ends. The drop in abundance of *P. acanthonotus* towards 1200 to 1300 m may well be related to the nearly total absence of euphausiids below this level.

Despite the dependence of bathyal pandalids on planktonic resources, these species were not present in samples collected from various levels in the water

column (planktonic hauls). Predatory activity by pandalids on planktonic organisms would thus appear to take place in the benthic boundary layer located a few meters above the bottom (Wishner 1980, Hargreaves 1984, Angel 1990). The results of some samples obtained over 24 h sampling periods carried out in the same area suggest that the periodicity of such activity was unclear and may be irregular (Cartes et al. 1993).

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