

Comparative feeding habits of polychelid lobsters in the Western Mediterranean deep-sea communities

J. E. Cartes, P. Abelló

Institut de Ciències del Mar, Passeig Nacional s/n, E-08039 Barcelona, Spain

ABSTRACT: Feeding habits of the 2 deep-water species of polychelid lobsters occurring in the Balearic Basin (Western Mediterranean) were examined. Samples were taken with an OTSB-14 bottom trawl from depths between 550 and 2300 m in 1988-89. *Polycheles typhlops* and *Stereomastis sculpta* occupy a well-defined trophic niche, between the uppermost level of the bottom sediment and the water layer immediately adjacent to the sea bed. Scavenging plays an important role in feeding. However, ontogenetic changes in the diet were clear in both species. Small individuals based their diet on epibenthic peracarid crustaceans, whereas scavenging and ingestion of inert remains became more important in the adult diet. The trophic habits of the 2 species were rather similar; differences recorded are more consistent with depth-related changes in available prey resources than with changes in the position of the 2 species in the food web. The progressive decrease of abundance of *P. typhlops* with increasing depth coincided with greatly reduced densities of some of its preferential prey (i.e. *Calocaris macandreae*, *Cirolana borealis* or euphausiids) and with a different feeding strategy. *S. sculpta* shows a more microphagic and passive feeding habit. Feeding activity, quite low in both species, was lower in *S. sculpta*. All these results suggest that *S. sculpta* is better adapted to the more oligotrophic conditions found on the lower slope. Competitive trophic interaction may also account for the separate depth distributions of the 2 species. These interactions may be especially important on the deep-sea bottoms in the Mediterranean Sea, where environmental parameters like temperature and salinity are constant.

INTRODUCTION

The Polychelidae (Decapoda, Palinuroidea) are one of the most characteristic families in deep-sea communities, with different species distributed in bathyal and abyssal oceanic regions (Kensley 1968, Wenner & Boesch 1979, Gore 1984, Saint Laurent 1985, Abelló & Valladares 1988). *Polycheles typhlops* Heller, 1862 and *Stereomastis sculpta* (S.I. Smith, 1880) are two of the most characteristic and abundant species in bathyal mud assemblages in the Western Mediterranean (Cartes 1991, Cartes et al. in press). *P. typhlops* is one of the dominant species in the middle subzone (500 to 1200 m) of the continental slope (Abelló & Valladares 1988, Abelló et al. 1988, Cartes 1991). *S. sculpta* is one of the more abundant species in the lower subzone (below 1200 m) (Péres 1985, Cartes 1991, Cartes et al. in press). The separation in the depth ranges of these 2 species is quite clear. Their distribution ranges do overlap below 1000 m, but densities of *P. typhlops* are

very low there (Abelló & Cartes in press). The size ranges of these species are similar. Environmental conditions of the Mediterranean deep-water mass in the bathyal zone are fairly constant: temperature 12.7 °C and salinity 38.4 (Fredj & Laubier 1985, Hopkins 1985).

Some isolated data have been published on the trophic habits of various polychelidae of the genus *Stereomastis* by Wenner (1979) and of the abyssal genus *Willemoesia* by Gore (1984) in the Atlantic. The feeding pattern of *Polycheles typhlops* has occasionally been studied. Santucci (1932) reported that feeding in this species was chiefly based on scavenging. In contrast, Lagardère (1977) described this species as a predator of bathypelagic crustaceans, with scavenging activity merely a complement to the diet. Based on the analysis of a few specimens, this same author suggested that the feeding pattern of *S. sculpta* was similar to that of *P. typhlops*. Some preliminary data on the feeding habits of *P. typhlops* and *S. sculpta* were presented by Cartes & Abelló (1990).

The object of the present study was to describe the diets of these 2 species over their entire distribution ranges and to analyze the effect of depth on diet. Given the similar morphology and size of the 2 species, types of prey could be similar although the precise species preyed upon may vary as a function of the differential distribution ranges of the species. Consideration has also been given to the level of dietary similarity as a possible contributing factor to the distinctly separate depth distributions of these species and to the ecological role of this crustacean group, which is characteristic in, and well adapted to, the deep-sea environment.

MATERIALS AND METHODS

Specimens were collected from the Balearic Basin using an otter trawl semi-balloon (OTSB-14) (Merret & Marshall 1981) in July and October 1988 (1000 to 2300 m; 15 samples) and July and October 1989 (550 to 750 m; 9 samples). A total of 459 specimens of *Polycheles typhlops* and 1271 specimens of *Stereomastis sculpta* were dissected. The stomach fullness (f) of each specimen was recorded; foreguts for which $f < 20\%$ were classified as empty, while those for which $f \geq 50\%$ were classified as full. Food-containing stomachs were preserved in 70% alcohol. Individual size (cephalothorax length, CL) was also recorded.

In all, the contents of 193 *Polycheles typhlops* stomachs and 163 *Stereomastis sculpta* stomachs were studied. The diet composition was analyzed by depth intervals and in the case of *P. typhlops* from the upper middle slope also by season (see Table 1). The diet was also analyzed by comparing size classes of the same species. Three size classes were considered: < 20 mm, 20–30 mm, > 30 mm CL in *P. typhlops*; < 16 mm, 16–25 mm, > 25 mm CL in *S. sculpta*. Specimens in the smallest size class were immature; those in the 2 largest size classes were mature (Abelló & Cartes in press).

Diets are presented in terms of percentage frequency of occurrence (%F) and percentage abundance (%N) by prey item (Hyslop 1980, Cartes & Sardà 1989). Quantification was relatively simple (Cartes 1991). The mandibles of Polychelidae contain a well-developed cutting incisor process but no molar process. Thus, prey items are usually found whole or in a few, readily identifiable fragments. Foraminiferans were not quantified in this study and only the percentage occurrence of these organisms was recorded. Percentage volume values for the different prey groups have been expressed by the subjective points method (Swynnerton & Worthington 1940). Prey identification was carried out to species level whenever possible.

To detect possible changes in the daily feeding pattern of *Polycheles typhlops* a continuous 24 h sampling was performed on the upper middle slope. Samples of both species collected from below 1000 m at different times of the day were analyzed. The occurrence of significant differences in foregut fullness was tested using a homogeneity chi-squared test. A subjective estimate of the state of digestion of prey was also established (Amezaga 1988, Sardà & Valladares 1990, Cartes 1991).

Cumulative trophic diversity curves (Mauchline & Gordon 1985) for both species were constructed using the Shannon-Wiener index (Shannon & Weaver 1963). Asymptotic stabilization of the curves yielded the minimum number of stomachs that need to be analyzed to produce sufficiently reliable results.

Multivariate cluster analysis was used to analyze general affinities between the samples (diets) of the 2 species. Each sample combined the individuals taken in one haul. Uncommon prey items that occurred only once in the samples were removed from the data matrix. Linear correlation (with previous logarithmic transformation of the data) was used as the similarity index. The aggregation algorithm used was the Unweighted Paired Method using Arithmetic Averages (UPGMA).

For purposes of comparison samples were aggregated according to species, depth strata and season. Overlap between the diets was calculated using the Schoener (1974) index and trophic diversity was established using the Shannon-Wiener index. These 2 indexes were calculated for each of the resulting sample groups established.

RESULTS

The basic prey type for the 2 species studied consisted of fish remains and benthic peracarid crustaceans. Cumulative trophic diversity values stabilized for both species after analysis of the contents of 15 to 20 stomachs. There is a low degree of prey manipulation; the ability to ingest prey items whole has been confirmed on different occasions.

Sample aggregations

Linear correlation analysis pointed to a clear separation between the samples of the 2 polychelid species (Fig. 1). Only one *Polycheles typhlops* sample (from the lower middle slope) was associated with *Stereomastis sculpta*. No evident groups were detected within either of the 2 main clusters discriminated by the analysis (Fig. 1).

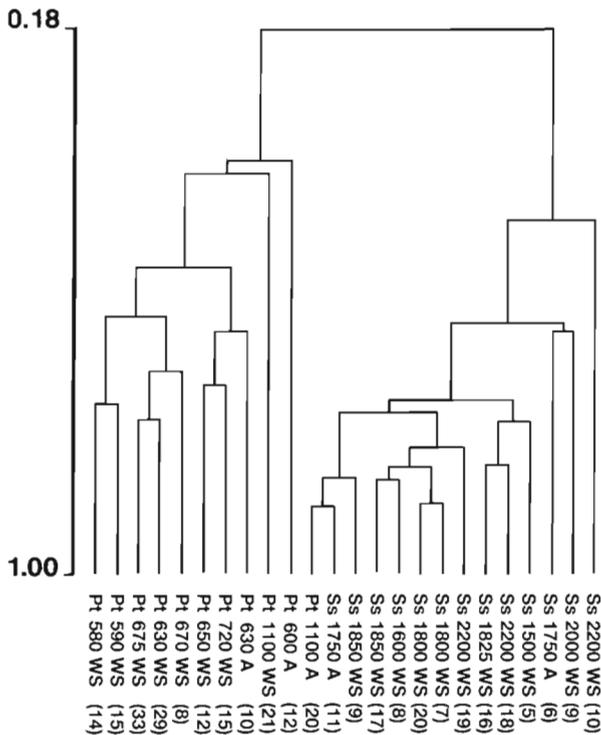


Fig. 1. *Polycheles typhlops* (Pt) and *Stereomastis sculpta* (Ss). Aggregation of foregut content samples for 2 polychelid species (linear correlation-UPGMA). The number of foregut contents studied in each sample is given in brackets, with the mean depth and time of year. WS: samples taken between winter and summer; A: samples taken in autumn

Diet composition

***Polycheles typhlops*: upper middle slope (550 to 750 m).** In spring and summer samples the diet was based on fish remains, the burrowing macruran *Calocaris macandreae*, and remains of the shrimp *Aristeus antennatus*. Other important prey were the mysid *Boreomysis arctica* and the isopod *Cirolana borealis*. These prey together accounted for nearly 60 % of the diet (Table 1).

In autumn the most important prey were fish remains and *Calocaris macandreae*. Together with echinoids, euphausiids (*Meganyctiphanes norvegica*) and gammarid amphipods (Lysianassidae), these prey items accounted for around 60 % of the diet. The share of euphausiids in the diet was quite high (Table 1, Fig. 2).

***Polycheles typhlops*: lower middle slope (1000 to 1200 m).** In terms of abundance (%N) fish remains, asellid isopods (*Munnopsurus atlanticus*), pteropod remains, and polychaetes (Aphroditidae) contributed about 60 % of the diet (Table 1). Results in terms of frequency of occurrence were similar, and foraminiferans were also common.

In terms of percentage volume, the diet appeared considerably more diverse than in the samples from the upper middle slope (Fig. 2).

***Polycheles typhlops*: lower slope (1400 to 1900 m).** Twenty-five individuals, all immature (CL: 9 to 19 mm), of *P. typhlops* were analysed. Only 7 of the stomachs contained food remains. The prey were asellid isopods [*Ilyarachna* sp. (2), *Munnopsurus atlanticus* (2)], an unidentified isopod (1), gammarid amphipods [*Rhachotropis* sp. (1), Pandaliscidae (1)], pteropod debris with the encrusting foraminiferan *Ammolagena* sp. (2), aphroditid polychaetes (2), and fish scales (1). These results suggest a diet based on suprabenthic crustaceans.

***Stereomastis sculpta*: lower slope (1400 to 2300 m).** Diet analysis was performed separately for the samples taken above and below 2000 m (Table 1), since this depth constitutes an ecological discontinuity in deca-

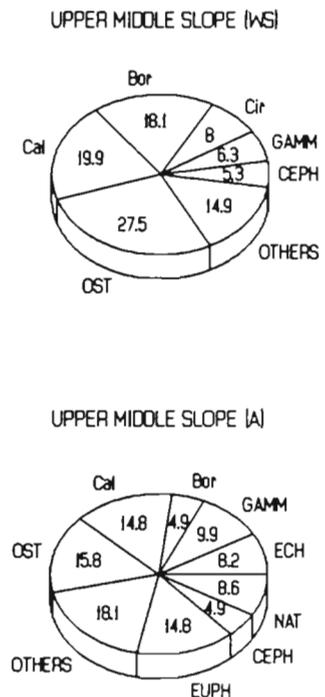


Fig. 2. *Polycheles typhlops*. Proportion (by volume) of prey species by group in the diet by depth interval and season. POL: polychaetes; NAT: natantian decapods; Pont: *Pontophilus norvegicus*; Cal: *Calocaris macandreae*; EUPH: euphausiids; Bor: *Boreomysis arctica*; GAMM: gammarid amphipods; Cir: *Cirolana borealis*; ASELL: asellid isopods; ECH: echinoids; CEPH: cephalopods; OST: fishes

Table 1 *Polycheles typhlops* and *Stereomastis sculpta*. Diet composition of the 2 polychelid species. %F: percentage frequency of occurrence; %N: percentage abundance of prey item

Prey	No. of specimens:	<i>Polycheles typhlops</i>						<i>Stereomastis sculpta</i>			
		550–750 m		1000–1200 m		1400–1900 m		2000–2300 m			
		Mar–Jul 104	Oct 22	Jul–Oct 41	Jul–Oct 41	Jul–Oct 99	Jul 56	%F	%N		
HYDROZOA											
<i>Stephanoscyphus</i> spp.		–	–	–	–	2.4	1.8	–	–	–	–
POLYCHAETA		3.9	1.8	4.5	2.7	12.2	10.9	12.1	6.7	14.3	8.4
Aphroditida		1.0	0.4	–	–	12.2	9.1	10.1	5.2	7.1	3.4
<i>Glycera</i> sp.		–	–	–	–	–	–	1.0	0.5	–	–
<i>Nephtys</i> sp.		1.0	0.4	4.5	2.7	–	–	–	–	1.8	0.8
Unidentified		1.9	0.9	–	–	2.4	1.8	2.0	1.0	5.4	2.5
NEMATODA		–	–	–	–	–	–	1.0	0.5	3.6	1.7
CRUSTACEA											
Decapoda natantia											
Bathypelagic		3.8	1.8	–	–	–	–	1.0	0.5	3.6	3.6
<i>Genadas elegans</i>		–	–	–	–	–	–	1.0	0.5	3.6	1.7
Sergestidae		1.9	0.9	–	–	–	–	–	–	–	–
<i>Pasiphaea multidentata</i>		1.9	0.9	–	–	–	–	–	–	–	–
Benthonic		27.9	15.9	13.6	13.5	9.8	7.2	7.1	3.6	12.5	7.6
<i>Aristeus antennatus</i>		18.3	8.2	–	–	–	–	–	–	–	–
<i>Plesionika</i> sp.		4.8	2.6	4.5	2.7	–	–	–	–	–	–
<i>Acanthephyra</i> sp.		1.0	0.4	–	–	–	–	4.0	2.1	7.1	3.4
<i>Pontophilus norvegicus</i>		1.9	1.7	4.5	2.7	9.8	7.2	3.0	1.5	5.4	2.5
<i>Alpheus glaber</i>		1.0	0.4	4.5	2.7	–	–	–	–	–	–
Unidentified		6.7	2.6	9.1	5.4	–	–	1.0	0.5	3.6	1.7
Macrura		29.8	15.1	18.2	8.1	2.4	1.8	1.0	–	1.8	0.8
<i>Calocaris macandreae</i>		28.8	14.7	13.6	8.1	2.4	1.8	–	–	–	–
Polychelidae		1.0	0.4	–	–	–	–	1.0	0.5	1.85	0.8
Anomura		–	–	–	–	4.9	3.6	2.0	1.0	–	–
<i>Pagurus alatus</i>		–	–	–	–	2.4	1.8	–	–	–	–
<i>Munida tenuimana</i>		–	–	–	–	2.4	1.8	2.0	1.0	–	–
Brachyura		1.0	0.4	–	–	–	–	–	–	–	–
Unidentified		6.7	3.0	–	–	2.4	1.8	–	–	–	–
Euphausiacea		1.0	0.4	13.6	8.1	–	–	–	–	–	–
Mysidacea		17.3	15.6	4.5	2.7	14.6	10.8	13.1	6.7	16.1	7.6
<i>Boreomysis arctica</i>		12.5	12.6	4.5	2.7	12.2	7.2	13.1	6.7	16.1	7.6
<i>Parapseudomma</i> sp.		2.9	1.7	–	–	2.4	3.6	–	–	–	–
Unidentified		1.9	1.3	–	–	–	–	–	–	–	–
Amphipoda											
Gammaridea		2.9	6.5	9.1	8.1	9.8	7.2	9.1	4.6	5.4	2.4
Lysianassidae		–	–	4.5	5.4	2.4	1.8	–	–	–	–
<i>Harpinia</i> sp.		–	–	–	–	–	–	1.0	0.5	1.8	0.8
<i>Leucothoe</i> sp.		–	–	–	–	–	–	1.0	0.5	–	–
Oedicerotidae		–	0.4	4.5	2.7	–	–	–	–	1.8	0.8
<i>Eusirus longipes</i>		1.0	0.9	–	–	–	–	–	–	–	–
<i>Rhachotropis</i> sp.		1.0	2.6	–	–	4.9	3.6	4.0	2.1	1.8	0.8
Other Gammaridea		1.0	1.3	–	–	2.4	1.8	–	–	–	–
Unidentified		1.0	1.3	–	–	–	–	3.0	1.5	–	–
Isopoda		7.7	7.8	4.5	2.7	19.5	14.5	10.1	5.1	5.4	6.1
<i>Cirolana borealis</i>		7.7	5.2	4.5	2.7	–	–	–	–	–	–
<i>Munnopsurus atlanticus</i>		–	2.2	–	–	17.1	12.7	6.1	3.1	1.8	0.8
<i>Ilyarachna</i> sp.		1.0	0.4	–	–	–	–	2.0	1.0	3.6	2.5
Other Paraselloidea		–	–	–	–	2.4	1.8	2.0	1.0	1.8	0.8
Tanaideacea		–	–	–	–	–	–	4.0	2.6	1.8	1.7
Apseudomorpha		–	–	–	–	–	–	1.0	0.5	–	–
Tanaidomorpha		–	–	–	–	–	–	4.0	2.1	1.8	1.7
Cumacea		1.9	0.9	–	–	–	–	2.0	1.0	5.4	5.8
<i>Epileucon longirostris</i>		1.9	0.9	–	–	–	–	–	–	–	–
<i>Cyclaspis longicaudata</i>		–	–	–	–	–	–	1.0	0.5	1.8	0.8
Unidentified		–	–	–	–	–	–	1.0	0.5	3.6	1.7
Ostracoda Platycopa		–	–	–	–	–	–	–	–	5.4	3.3
Copepoda Harpacticoidea		–	–	–	–	–	–	2.0	1.0	1.8	0.8
Unidentified		1.9	0.9	–	–	–	–	4.9	1.0	2.0	2.5

Table 1 (continued)

Prey	No. of specimens:	<i>Polycheles typhlops</i>						<i>Stereomastis sculpta</i>			
		550–750 m		1000–1200 m		1400–1900 m		2000–2300 m			
		Mar–Jul 104	Oct 22	Jul–Oct 41	Jul–Oct 99	Jul 56					
	%F	%N	%F	%N	%F	%N	%F	%N			
MOLLUSCA											
Bivalvia		–	–	–	–	–	2.0	1.0	–	–	
Gastropoda		3.8	1.8	–	–	19.5	12.7	60.6	35.0	39.3	20.2
Pteropoda		1.9	0.9	–	–	19.5	12.7	60.6	34.5	39.3	20.2
<i>Alvania</i> sp.		1.0	0.4	–	–	–	–	–	–	–	–
<i>Benthonella tenella</i>		1.0	0.4	–	–	–	–	1.0	0.5	–	–
Cephalopoda		4.8	2.2	4.5	2.7	7.3	5.4	–	–	–	–
Unidentified		–	–	–	–	–	–	3.0	1.0	–	–
ECHINODERMATA		3.8	1.7	27.3	16.2	–	–	6.1	3.1	10.7	5.0
Echinoidea		1.0	0.4	27.3	16.2	–	–	1.0	0.5	1.8	0.8
Ophiuroidea		2.9	1.3	–	–	–	–	–	–	–	–
<i>Brisingella coronata</i>		–	–	–	–	–	–	5.1	2.6	8.9	4.2
OSTEICHTHYES		46.2	22.6	54.5	32.4	26.8	18.2	33.3	17.9	37.5	19.3
<i>Cyclothone</i> sp.		–	–	–	–	–	–	1.0	0.5	–	–
Myctophidae		6.7	3.5	9.1	5.4	–	–	3.0	1.5	5.4	2.5
Macrouridae		5.8	2.6	9.1	5.4	–	–	2.0	1.0	7.1	3.4
Other osteichthyes		33.7	16.5	36.4	21.6	26.8	18.2	29.3	14.9	28.6	13.4
Turridae eggs		–	–	–	–	2.4	1.8	–	–	–	–
OTHER		1.9	0.9	4.5	0.9	4.8	3.6	7.1	3.6	1.8	0.8
UNIDENTIFIED		1.9	0.9	–	0.9	–	–	5.1	2.6	1.8	0.8
FORAMINIFERA		10.6		4.5		36.6		61.6		46.4	
Benthic foraminifera		6.8		4.5		4.8		14.1		7.2	
Globergerinae		6.7		–		36.6		61.65		46.4	
Mud		–		4.5		12.2		22.2		8.9	
Micromollusc remains		1.0		4.5		4.9		56.6		46.4	

pod communities (Cartes 1991). Both groups exhibited very similar diets (see below, 'Diversity and dietary overlap').

Numerical values were highest for pteropod shells, foraminiferans, and fish remains. In terms of abundance small calcified benthic ostracods were also important (Table 1).

Pteropod remains were the most important prey item in volume (Fig. 3). These shells bore attached bottom mud, small encrusting foraminiferans (*Ammolagena* sp.), minute sponges, and polyps (*Stephanoscyphus* spp.).

Size differences in diet composition

***Polycheles typhlops*.** The following results are based on individuals from the upper middle slope, where the highest abundances of *P. typhlops* occur. The diet was quite similar in the 2 size classes larger than 20 mm CL (Table 2; see also Table 4).

Immature *Polycheles typhlops* (smaller than 20 mm CL) prey mainly on suprabenthic organisms, in par-

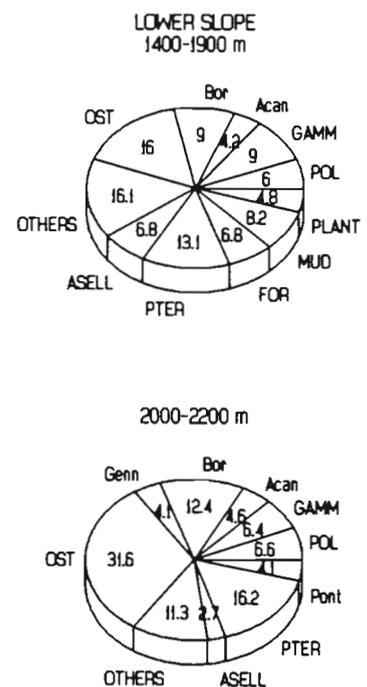


Fig. 3. *Stereomastis sculpta*. Proportion (by volume) of prey species by group in the diet by depth interval. Acan: *Acanthephyra* sp.; FOR: foraminiferans; PTER: pteropod remains; PLANT: plant matter. For explanation of all other abbreviations see Fig. 2

Table 2. *Polycheles typhlops*. Diet composition by size class in the depth range 550 to 750 m

Prey	No. of specimens:	CL > 30 mm 66		30 > CL > 20 37		CL < 20 mm 24	
		%F	%N	%F	%N	%F	%N
POLYCHAETA		1.5	0.9	5.4	2.9	4.2	2.1
Aphroditida		-	-	-	-	4.2	2.1
<i>Nephtys</i> sp.		-	-	2.7	1.4	-	-
Unidentified		1.5	0.9	2.7	1.4	-	-
CRUSTACEA							
Decapoda natantia							
Bathypelagic		3.0	1.8	5.4	2.8	-	-
<i>Pasiphaea multidentata</i>		1.5	0.9	2.7	1.4	-	-
<i>Sergestes arcticus</i>		1.5	0.9	2.7	1.4	-	-
Benthic		27.3	16.1	29.7	15.7	8.4	4.2
<i>Aristeus antennatus</i>		16.7	9.8	21.6	11.4	-	-
<i>Plesionika (acanthonotus)</i>		6.1	3.6	2.7	1.4	4.2	2.1
<i>Acanthephyra eximia</i>		1.5	0.9	-	-	-	-
<i>Pontophilus norvegicus</i>		1.5	0.9	5.4	2.9	4.2	2.1
<i>Alpheus glaber</i>		1.5	0.9	-	-	-	-
Unidentified		4.5	2.7	5.4	2.9	-	-
<i>Calocaris macandreae</i>		28.8	17.0	35.1	18.6	8.4	4.3
<i>Polycheles typhlops</i>		-	-	2.7	1.4	-	-
Brachyura		1.5	0.9	-	-	-	-
Unidentified		6.1	3.6	8.1	4.3	-	-
Euphausiacea (<i>Meganyctiphanes norvegica</i>)		1.5	0.9	-	-	-	-
Mysidacea		15.2	8.9	21.6	11.5	45.8	36.1
<i>Boreomysis arctica</i>		10.6	6.2	16.2	8.6	54.2	31.9
<i>Paraseudomma</i> sp.		1.5	0.9	5.4	2.9	4.2	2.1
Unidentified		3.0	1.8	-	-	4.2	2.1
Amphipoda Gammaridea		4.5	2.7	2.7	1.4	33.3	23.2
Oedicerotidae		-	-	-	-	4.2	2.1
<i>Eusirus logipes</i>		-	-	2.7	1.4	4.2	2.1
<i>Rhachotropis</i> sp.		1.5	0.9	-	-	20.8	10.6
Other Gammaridea		1.5	0.9	-	-	8.4	4.2
Unidentified		1.5	0.9	-	-	8.4	4.2
Isopoda		6.1	3.6	13.5	7.1	37.5	19.1
<i>Cirolana borealis</i>		6.1	3.6	10.8	5.7	16.7	8.5
<i>Munnopsurus atlanticus</i>		-	-	-	-	20.8	10.6
<i>Ilyarachna</i> sp.		-	-	2.7	1.4	-	-
Cumacea (<i>Epileucon longirostris</i>)		1.5	0.9	2.7	1.4	-	-
Unidentified		1.5	0.9	2.7	1.4	4.2	2.1
MOLLUSCA							
Gastropoda		4.5	2.7	8.1	1.4	-	-
Pteropoda		1.5	0.9	2.7	1.4	-	-
<i>Alvania</i> sp.		1.5	0.9	-	-	-	-
<i>Benthonella tenella</i>		1.5	0.9	-	-	-	-
Cephalopoda		4.5	2.7	5.4	2.9	-	-
ECHINODERMATA		4.5	2.7	2.7	1.4	-	-
Echinoidea		1.5	0.9	-	-	-	-
Ophiuroidea		3.0	1.8	2.7	1.4	-	-
OSTEICHTHYES		48.5	28.6	40.5	21.5	16.7	8.5
Myctophidae		6.1	3.6	5.4	2.9	4.2	2.1
Macrouridae		6.1	3.6	5.4	2.9	-	-
Unidentified		36.4	21.4	29.7	15.7	12.5	6.4
OTHERS		3.0	1.8	-	-	-	-
UNIDENTIFIED		1.5	0.9	2.7	1.4	-	-
FORAMINIFERA		15.1		5.4		29.2	
Benthic foraminifera		9.1		5.4		8.3	
Globigerinae		9.1		2.7		20.7	
Mud		1.5		-		-	
Micromollusc remains		3.0		-		-	

Table 3. *Stereomysis sculpta*. Diet composition by size class in the depth range 1400 to 2300 m

Prey	No. of specimens:	CL > 25 mm		25 > CL > 16		CL < 16 mm	
		%F	%N	%F	%N	%F	%N
POLYCHAETA		–	–	12.2	6.4	26.3	13.1
Aphroditida		–	–	6.8	3.3	21.0	10.5
<i>Glycera</i> sp.		–	–	1.4	0.7	–	–
Unidentified		–	–	5.6	2.7	5.3	2.6
NEMATODA		2.5	1.1	1.4	0.7	5.3	2.6
CRUSTACEA							
Decapoda							
<i>Gennadas elegans</i>		2.5	1.1	2.8	1.3	–	–
<i>Acantheephyra</i> sp.		7.5	3.4	4.2	2.0	–	–
<i>Pontophilus norvegicus</i>		2.5	1.1	5.6	2.7	5.3	2.6
Unidentified natantia		–	–	2.8	1.3	–	–
<i>Stereomastis sculpta</i>		2.5	1.1	–	–	–	–
<i>Munida tenuimana</i>		2.5	1.1	1.4	0.7	–	–
Mysidacea		7.5	3.4	16.2	7.9	31.6	13.2
<i>Boreomysis arctica</i>		7.5	3.4	16.2	7.9	31.6	13.2
Amphipoda Gammaridea		7.5	3.4	6.9	3.4	21.0	10.5
<i>Harpinia</i> sp.		–	–	1.4	0.7	–	–
<i>Leucothoe incisa</i>		–	–	–	–	5.3	2.6
Oedicerotidae		2.5	1.1	–	–	–	–
<i>Rhachotropis</i> sp.		2.5	1.1	4.2	2.0	–	–
Unidentified		2.5	1.1	1.4	0.7	15.8	7.9
Isopoda		12.5	5.6	8.3	4.7	26.3	13.2
<i>Munnopsurus atlanticus</i>		2.5	1.1	5.6	2.7	10.5	5.3
<i>Ilyarachna</i> sp.		7.5	3.4	1.4	0.7	10.5	5.3
Other Paraselloidea		2.5	1.1	2.8	1.3	5.3	2.6
Tanaidacea		10.0	4.5	4.2	2.0	–	–
Apseudomorpha		–	–	1.4	0.7	–	–
Tanaiidomorpha		10.0	4.5	2.8	1.3	–	–
Cumacea		7.5	4.5	–	–	5.3	2.6
<i>Cyclaspis longicaudata</i>		5.0	2.3	–	–	–	–
Unidentified		2.5	1.1	–	–	5.3	2.6
Ostracoda		10.0	16.9	–	–	–	–
Myodocopa		–	–	–	–	5.3	2.6
Ostracoda Platycopa		10.0	16.9	–	–	–	–
Copepoda Harpacticoida		2.5	1.1	2.8	1.3	–	–
Unidentified		–	–	4.2	2.0	–	–
MOLLUSCA							
Bivalvia		–	–	2.8	1.3	–	–
Gastropoda		57.5	31.5	51.4	30.6	42.1	18.4
Pteropoda		57.5	31.5	51.4	29.1	42.1	18.4
<i>Benthonella tenella</i>		–	–	1.4	0.7	–	–
Unidentified		2.5	1.1	1.4	0.7	–	–
ECHINODERMATA		2.5	1.1	11.1	5.3	5.3	2.6
Echinoidea		–	–	2.8	1.3	–	–
<i>Brisingella coronata</i>		2.5	1.1	8.3	4.0	5.3	2.6
OSTEICHTHYES		35.0	15.7	38.9	19.3	21.0	10.5
Myctophidae		2.5	1.1	5.6	2.7	–	–
Macrouridae		–	–	5.6	2.7	–	–
Unidentified		32.5	14.6	29.2	13.9	21.0	10.5
OTHERS (Plant debris)		7.5	3.4	6.9	3.3	5.3	2.6
UNIDENTIFIED		–	–	8.3	4.0	5.3	2.6
FORAMINIFERA		82.5		65.3		38.9	
Benthic foraminifera		15.0		8.4		15.9	
Globigerinae		82.5		61.1		31.6	
Mud		30.0		18.1		10.6	
Mollusc remains		60.0		52.8		36.8	

ticular mysids (*Boreomysis arctica*, *Parapseudomma calloplura*), gammarid amphipods (*Rhachotropis grimaldii*, *Eusirus longipes*, *Niccipe tumida*), and isopods (*Munnopsurus atlanticus*, *Cirolana borealis*). In all, suprabenthic crustaceans made up 82.7 % of the total diet. Remains attributable to scavenging activity were of rather minor importance (7 %).

Dietary overlap between the 2 largest size classes and the smallest size class was very low (see Table 6).

***Stereomastis sculpta*.** The diets of the 2 largest size classes were dominated by pteropod and fish remains (Table 3), which accounted for nearly 50 % of the diet. In immature individuals the proportion of these 2 prey items in the diet dropped to 29 %. The share of suprabenthic crustaceans (45 %) grew in importance in the diet of the smallest size class, whereas the contribution of this group of prey was much lower in the medium and large size classes.

The mysid *Boreomysis arctica* and the asellid isopods *Munnopsurus atlanticus*, *Ilyarachna* sp., and *Janirella* sp. were particularly important in the diet of the smallest individuals.

Feeding activity

The proportion of empty stomachs was very high in both species (Table 4). In *Polycheles typhlops* 67.8 % of all individual stomachs either were empty or contained few food remains. The proportion was even higher (74.3 %) in *Stereomastis sculpta*.

No significant differences were found in the degree of foregut fullness at different times of the day in either species ($p \leq 0.05$), though perhaps they may be

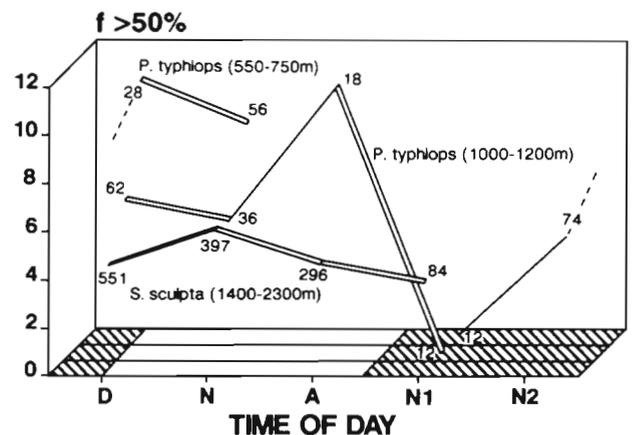


Fig. 4. *Polycheles typhlops* and *Stereomastis sculpta*. Percentage of full stomachs by depth according to time of day. Number of specimens appears next to each data point. D: daybreak; N: noon; A: afternoon; N1, N2: nighttime

important in view of the low feeding intensity recorded in these 2 species (Fig. 4). Very few differences in the type of prey ingested were also recorded at the periods considered.

Diversity and dietary overlap

Trophic diversity in *Stereomastis sculpta* increased with depth (Table 4). This trend is not evident for *Polycheles typhlops*. There seem to be seasonal differences in the latter species.

Diversity in *Polycheles typhlops* was higher in the larger size classes (Table 5) than in individuals smaller

Table 4. *Polycheles typhlops* and *Stereomastis sculpta*. Trophic diversity and feeding activity by depth interval

	<i>Polycheles typhlops</i>			<i>Stereomastis sculpta</i>	
	550-750 m Mar-Jul	550-750 m Oct	1000-1200 m Jul-Oct	1400-1900 m Jul-Oct	2000-2300 m Jul
No. of specimens	191	58	139	727	412
$f < 20$ %	56.3 %	52.6 %	76.9 %	78.2 %	79.9 %
$f \geq 50$ %	8.9 %	8.6 %	2.9 %	2.2 %	3.4 %
Diversity (H')	4.307	3.668	3.561	3.754	4.117

Table 5. *Polycheles typhlops* and *Stereomastis sculpta*. Trophic diversity and feeding activity by size class

	<i>Polycheles typhlops</i>			<i>Stereomastis sculpta</i>		
	CL > 30 mm	30 > CL > 20	CL < 19 mm	CL > 25 mm	25 > CL > 18	CL < 17 mm
No. of specimens	148	115	74	227	841	71
$f < 20$ %	69.7 %	72.6 %	62.4 %	75.3 %	79.9 %	80.6 %
$f \geq 50$ %	5.1 %	0.9 %	13.1 %	4.0 %	2.0 %	5.6 %
Diversity (H')	4.093	3.980	3.668	3.438	3.966	3.671

Table 6. *Polycheles typhlops* (Pt) and *Stereomastis sculpta* (Ss). Dietary overlap between the different groups established and between the different size classes in samples. UMS: upper middle slope; LMS: lower middle slope; LS: lower slope

<i>Polycheles typhlops</i> , <i>Stereomastis sculpta</i>	Pt (UMS) 550–750 m Oct	Pt (LMS) 1000–1200 m Jul–Oct	Ss (LS) 1400–1900 m Jul–Oct	Ss (LS) 2000–2300 m Jul
UMS (550–750 m, Jul)	48.146	41.273	40.039	38.987
UMS (550–750 m, Oct)	–	32.108	25.508	29.593
LMS (1000–1200 m)	–	–	54.144	48.252
LS (1400–1900 m)	–	–	–	65.538
<i>Polycheles typhlops</i>	30 < CL < 20	CL > 20 mm	<i>Stereomastis sculpta</i>	25 > CL > 17 CL < 17 mm
CL > 30 mm	77.857	31.858	CL > 25 mm	65.340
30 mm > CL 20 mm	–	35.593	25 mm > CL > 17 mm	–

than 20 mm CL. In contrast, the largest *Stereomastis sculpta* size class did not show the highest diversity values. The maximum value of H' was shown by individuals in the medium size class (Table 5).

The overlap index values for the sample groups were generally low (Table 6). The maximum value occurred between samples of *Stereomastis sculpta* and samples of *Polycheles typhlops* from the lower middle slope (1000 to 1200 m). The minimum value (27.623) between species was between the diets in the most distant bathymetric zones.

The maximum overlap value between size classes within each species was between the medium and large size classes (Table 6). The minimum overlap value was between the extreme size classes (the smallest and the largest size classes) in both cases.

DISCUSSION

Polycheles typhlops and *Stereomastis sculpta* have similar morphologies and sizes. In addition, the depth areas in which each species is most abundant are distinctly separate (Abelló & Cartes in press). These 2 species appear to occupy a similar niche, encompassing the uppermost level of the bottom sediment and the water layer immediately adjacent to the sea bed, judging from the predominance of prey items from these layers in their diets. Planktonic prey (hyperiid, siphonophores, chaetognaths, calanids, etc.) were almost completely absent. Such organisms are present in the diet of nektobenthic species like *Aristeus antennatus* (Cartes & Sardà 1989), which are abundant in the same areas as polychelid lobsters. These prey groups are also present in samples collected with suprabenthic sleds equipped with automatic opening/closing systems, particularly in the upper subsample (50 to 100 cm from the bottom)

(Sorbe 1983, authors' unpubl. data).

The proportion of polychaetes and other endobenthic prey (other than *Calocaris macandreae*) was small, especially in *Polycheles typhlops*. Aphroditids and *Nephtys* sp. were the predominant polychaetes. These 2 groups are regarded as slow-moving predators on the surface of the sea bed (Fauchald & Jumars 1979). In contrast, glycerids were absent from the diets. Glycerids include species that dwell permanently in burrows, like *Glycera rousii*, a predominant species in the bathyal macrobenthic mud assemblages in the Catalan Sea (Reyss 1971). Glycerids are prevalent in the diet of *Aristeus antennatus*, a species well equipped to root in the substrate in search of prey (Cartes & Sardà 1989, Cartes 1991).

The gammarid amphipods identified were epibenthic and highly mobile, like the eusirids (*Eusirus longipes*, *Rhachotropis* sp.), regarded as active predators of calanids and other crustaceans, and the Lysianassids, generally regarded as scavengers (Lagardère 1976, Slattery & Oliver 1986). In contrast, endobenthic species like *Harpinia pectinata* and *Urotioe corsica* (Enequist 1949), common prey of *A. antennatus*, were almost absent from the diet.

Based on a few specimens of *Stereomastis sculpta*, Lagardère (1977) suggested that its diet was similar to that of *Polycheles typhlops*. In our results the maximum interspecific overlap value was obtained for the samples from the closest depth strata. This value, 54.144, was relatively high (Schoener 1974), indicating that the trophic habits of the 2 species in their areas of distribution overlap are similar. Habitat separation is important in preventing species competitive interactions (Schoener 1974, Rex 1977). This could be the case for *P. typhlops* and *S. sculpta*. Thus, only the deepest *P. typhlops* sample was associated with *S. sculpta*. In fact both species based their diets in similar prey groups with variation in prey species due to changes in ben-

thic communities with depth (Pérès 1985, Cartes 1991, Stefanescu 1991).

Scavenging activity plays an important role in the feeding of both species, and both can be classified as active scavengers according to the classification of Lagardère (1976). The presence of large decapod crustaceans, fishes, and cephalopods remains can be ascribed to such scavenging activity. In all cases parts of these prey items were present, providing a means of gauging the size of the whole animal. Based on the estimated sizes, active hunting seems unlikely, particularly in view of the relatively unaggressive nature of *Polycheles typhlops* (Santucci 1932). The fish remains were chiefly scales, some vertebrae and/or spines, and in a very few instances only, small otoliths of Myctophidae or the nearly whole axial skeletons of small fish, probably the result of active predation.

The contribution of scavenging activity to the diet of adult *Polycheles typhlops* on the upper middle slope was nearly 40%; the impact of this trophic strategy was much smaller in the diet of small individuals. This type of activity may have been stimulated by commercial trawler operations carried out in the region at depths down to between 700 and 800 m, either directly or through discarding of non-commercial species. The importance of scavenging activity in the diet of *P. typhlops* on the lower middle slope decreased. In contrast, it was replaced by a new strategy, namely, the ingestion of pelagic matter from the sediment (pteropod remains and foraminiferans). Pteropod remains were abundant in the biogenic sediments of the lower slope in the Catalan Sea, while in less deeper zones the terrigenous sediments were dominant (Emelyanov 1977, Fredj & Laubier 1985, Cartes 1991).

Scavenging behaviour made only a small contribution to the diet of *Stereomastis sculpta*, similar to *Polycheles typhlops* in the lower middle slope. It was complemented by the ingestion of pteropod remains, mud, plant debris, and/or foraminiferans.

Epibenthic prey were important in both species, above all in immature individuals. The presence of euphausiids (mainly *Meganyctiphanes norvegica*) in the samples taken in the upper middle slope in autumn was notable. This group is also present in the diets of all the other decapods inhabiting the middle slope at this same season (Cartes 1991). On the lower middle slope, the share of epibenthic prey and peracarid crustaceans became more important, accounting for over 40% of the diet.

The lower density of *Polycheles typhlops* on the lower middle slope as compared to the upper middle slope coincided with greatly reduced densities of some of this species' preferred prey items (*Calocaris macandreae*, *Cirolana borealis* and *Meganyctiphanes norvegica*), which were abundant in the upper middle

slope (Pérès 1958, Carpine 1970, Reyss 1971, Cartes 1991) and with a different feeding strategy. These are likely factors contributing to the progressive decrease in the population of this species with depth.

On the middle slope both adult and immature individuals of *Polycheles typhlops* are abundant (Abelló & Cartes in press). However, only small *P. typhlops* were collected on the lower slope (between 1400 and 1900 m). The diet of these small individuals was dominated largely by peracarid crustaceans, still abundant at those depths (Pérès 1985). Adults may not be able to dwell at those depths since their main prey items are unavailable. This appears to occur concomitantly with a decrease in the size of the macrobenthic fauna comprising the basic diet of polychelids at greater depths (Jumars & Gallagher 1982, Pérès 1985, Sokolova 1990). The diet of small individuals on the lower slope was similar to that described for immature *P. typhlops* on the upper middle slope.

The presence of *Stereomastis sculpta* marks the lower limit of the distribution range of *Polycheles typhlops*. *S. sculpta* exhibits quite similar trophic preferences, and seems to be better adapted to environments with lower prey densities (Jumars & Gallagher 1982, Rowe 1983, Thiel 1983, Pérès 1985) or with less nutritional food resources (pteropod remains or foraminiferans). The tendency of species that inhabit relatively unproductive (oligotrophic) zones like deep-sea bottoms to be more omnivorous and microphagous has been reported for a variety of invertebrate groups (Carey 1972, Sokolova 1972) and appears to be part of a general pattern of trophic adaptation to conditions in which resources are scarce. Thus, *S. sculpta* appears to match the definition of cropper species put forward by Dayton & Hessler (1972) for deep-water predators. These results are in agreement with those reported for other deep-sea polychelids (Wenner 1979, Gore 1984).

Ontogenetic changes in diet were clearly seen in both species. On the whole, small individuals based their diet on epibenthic peracarid crustaceans, whereas scavenging activity and ingestion of inert remains from the bottom sediment became more important in the diets of medium and large individuals. Santucci (1932), basing his study on large specimens, concluded that *Polycheles typhlops* was almost exclusively a scavenger. Lagardère (1977) in turn reported that the diet of *P. typhlops* was based on euphausiids and mysids. These findings partially agree with the results reported herein for sizes smaller than 30 mm CL. However, in the present samples euphausiids were important only seasonally.

The results for the diet of *Stereomastis sculpta* were to a certain extent parallel to those for *Polycheles typhlops* on the basis of size class. Thus, while the diet of adults was based on slow-moving or even sedentary

prey items (mud, dead matter, etc.) juveniles were much more specialized, active predators of small prey like peracarids. Medium-sized individuals exploited both types of food resource, hence their diet was more diversified. However, for all the size classes combined as well as for each size class separately, *S. sculpta* tended to exploit less mobile prey items (polychaetes, benthic ostracods, etc.) more than *P. typhlops* did. The behaviour of this latter species, and especially that of immature individuals, was more consistent with the behaviour of a more active predator. Comparing the diets of the smallest size classes of the 2 species indicates that small *S. sculpta* are better adapted to exploit inert remains (pteropods), while small *P. typhlops* specialized nearly exclusively in the capture of live prey.

Feeding intensity was quite low in both species, particularly since the digestion rate must be relatively slow, given the low constant bottom temperature of 12.7 °C in the bathyal Mediterranean regions. This was more pronounced in *Stereomastis sculpta*, despite the possible longer digestion times for calcareous remains (pteropods, foraminiferans) (Joll 1982) in the foregut of this species. The high proportion of empty stomachs has been reported previously by Wenner (1979) and Gore (1984) and would seem to be a general pattern in the Polychelidae as an adaptation to oligotrophic deep-sea areas.

Lagardère (1977) reported predacious activity only during the daytime in *Polycheles typhlops*, justified by the presence of mesopelagic species that carry out vertical migrations and dwell close to the bottom during daytime hours. Our results do not show significant differences in daily feeding rhythm, probably due to the small influence of mesopelagic species in the diet.

In summary, the trophic habits of the 2 polychelid species in the Western Mediterranean were rather similar. The differences recorded seem to be more consistent with depth-related changes in the composition of available prey resources and faunal communities than to changes in the position of the two species in the food web. Moreover, various indicators suggest that the deeper-dwelling species, *Stereomastis sculpta*, is better adapted to an environment poorer in resources. A possible competitive trophic interaction may also account for the separate depth distributions of the 2 species, as postulated by Rex (1977). Such trophic interactions may be especially important on the deep-sea bottoms of the Mediterranean Sea, where environmental parameters like temperature and salinity are constant.

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