Int. Revue ges. Hydrobiol.	80	1995	2	217–234

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Observations on the Diet of Some Slope Dwelling Fishes of Southern Portugal

key words: fish, diet, continental slope

Abstract

The diets of 33 fish species from the southern Portuguese slope, at depths between 498 and 740 m were studied through the examination of stomach contents. Species of scyliorhinids, squalids, rajids, chimaerids, anguilliforms, notacanthids, macrourids, gadids and merluccids, with pelagic, benthopelagic and benthic modes of life were examined. *Nezumia sclerorhynchus* feeding habits were studied in detail. Its diet its dominated by amphipods. No differences of prey preferences were recorded corresponding to predator size classes. The studied predators can exploit a wide range of prey, but they feed mainly on benthopelagic and epibenthic material. Consequently it is difficult to establish distinct feeding guilds, so confirming a generalist type of feeding for most of the upper slope dwelling fishes.

1. Introduction

The feeding habits of slope-dwelling fishes have been investigated in the Atlantic and the Mediterranean by several authors (e.g. SORBE, 1972; GEISTDOERFER, 1978; MCLELLAN, 1977; MARSHALL and MERRETT, 1977; DU BUIT, 1978; SEDBERRY and MUSICK, 1978; RELINI and WURTZ, 1979; MACPHERSON, 1979 , 1980a, 1980b, 1981, 1983; MERRETT and MARSHALL, 1981; MAUCHLINE and GORDON, 1984a, b, c; 1985; MERRETT and DOMANSKI, 1985 and SAVVATIMSKY, 1989). While the ichthyofauna of the Portuguese slope is relatively well known (e.g. NOBRE, 1935; ALBUQUERQUE, 1954–56; HUREAU and MONOD, 1973; WHITEHEAD *et al.,* 1984–86), very little information exists about fish feeding for Portuguese waters.

Far less is known about the biological and ecological aspects of most of the slope dwelling fish species, including their feeding habits, than it is for some of economic interest, whose distribution includes the outer shelf and the upper slope. In fact the Portuguese upper slope is a fishing ground for several fish and crustacean species, and the understanding of the dynamics of the benthic and benthopelagic communities would contribute to the evaluation of natural variability as well as to fisheries management. This paper is a contribution to the knowledge of the diets of some fishes of the Portuguese slope.

2. Material and Methods

2.1. Work at Sea

Material was collected during the cruise 02071090 of the N.E. *Noruega,* from 8 to 15 October 1990 off southern Portugal (Fig. 1). A total of six hauls was carried out, using a commercial otter trawl

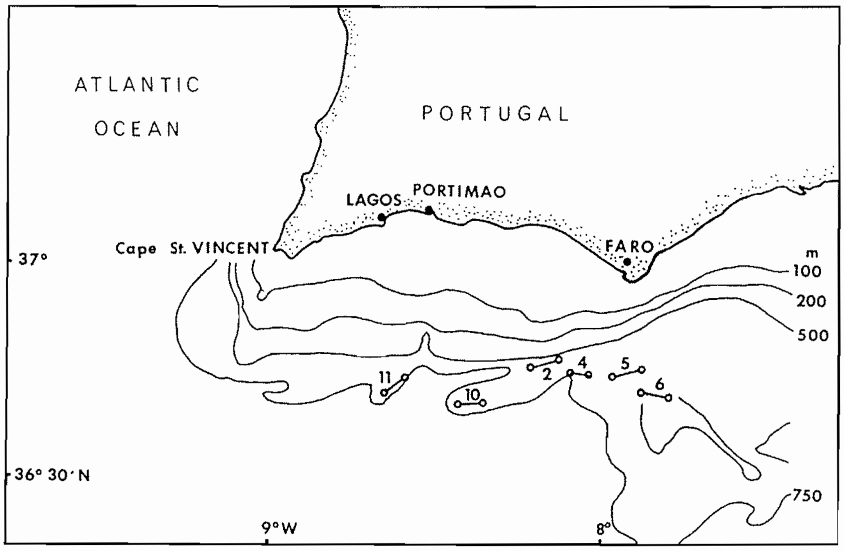

Figure 1. Sampled area off southern Portugal (Stations: 2, 4, 5, 6, 10 and 11).

(mouth opening 2,2 m high and 23 m wide) of 35 mm mesh. Positions, depths and trawling times are given in Table 1. Towing speed was around 2 knots.

Table 1. Station list.

Station	Date	Position Start	Position End	Depth (meters)	Gear	Time of trawling (hours)
2	9/10/90	36°46.6	36°47.0	540	otter trawl	1
		8°11.6	8°07.5	498	35 mm shrimp net	
4	9/10/90	36°44.4	36°45.0	725	otter trawl	1
		8°06.6	8°02.9	740	35 mm shrimp net	
5	10/10/90	36°45.2	36°46.3	630	otter trawl	1
		7°57.5	7°53.5	675	35 mm shrimp net	
6	10/10/90	36°43.5	36°42.2	689	otter trawl	1
		7°47.2	7°44.0	698	35 mm shrimp net	
10	11/10/90	36°40.2	36°40.6	708	otter trawl	1
		8°21.9	8°26.0	722	35 mm shrimp net	
11	12/10/90	36°41.1	36°45.1	710	otter trawl	1.5
		8°38.6	8°36.6	739	35 mm shrimp net	

2.2. *Stomach Content Analyses*

Fishes were dissected aboard and the stomachs preserved in 10% formalin. Material from all the otter-trawl operations was used and 33 species were selected. Species of commercial interest currently studied by the Fisheries Institute of Portugal (IPIMAR) were excluded (e.g. *Micromesistius poutassou),* which represented nearly 39 % of the total number of species collected.

The analyses of stomach contents for all species other than *Nezumia sclerorhynchus* were only taken to the level of higher systematic groups, due both to the difficulty in identifying the digested material and to the evidently high diversity and low frequency of occurrence of prey items. Consequently a total of 19 prey classes was considered, including a "non identified material" class, used for highly digested contents. For general information some conspicuous prey were identified to species level.

For each predator species, the total number of individuals analyzed is presented, together with their average total length and weight and the vacuity and eversion indices. The eversion index is the direct ratio of everted stomachs to the total number of individuals, while the vacuity index is the ratio of empty stomachs to the total of "non-everted" stomachs.

For each predator species and each prey type, an average prey number was computed as the ratio between the total number of occurrences of that prey, and the number of non everted stomachs per species.

2.3. *Nezumia sclerorhynchus*

Nezumia sclerorhynchus stomach contents deserved detailed study due to the high number of stomachs examined (803). This was more than one order of magnitude above the second most abundant species *(Galeus melastomus)* with only 56 stomachs examined. Also, the level of resolution of stomach contents of *N. sclerorhynchus*, was much higher than for the other species. Although prey classes could have been made compatible, the abundance of *N. sclerorhynchus* would have increased prey diversity, to make comparisons incompatible.

Nezumia sclerorhynchus were allocated to size classes of 12.5 mm (class 1: 27,5–40 mm to class 19: 252,5–265 mm) for each station, corresponding to 5 % of the maximum length recorded (see CERRATO, 1980). Stomach contents of *N. sclerorhynchus* were identified to species level whenever possible. Prey size (total length) was measured using only undigested specimens in good condition. For crustaceans (e.g. amphipods, isopods and natant decapods), the most abundant material, total length was measured between the anteriormost part of the head excluding the antennae, to the end of the telson. For each prey category, an average value was calculated.

Prey diversity was calculated for each station, using the SHANNON-WIENER index, and the results expressed in nat (natural logarithm).

2.4. *Abbreviations Used:*

Avg. depth	– average depth
Avg. len.	– average total length
Avg. weight	– average weight
Div.	– diversity
Ever. indx.	– eversion index
nat	– natural logarithm
NC	– non available value
N. id.	– not identified
No. ind.	– number of individuals
No. empty stom.	– number of empty stomachs
St.	– station
Tot.	– total
Vac. indx.	– vacuity index
W	– total weight

3. Results and Discussion

3.1. *Fish Assemblages*

Table II presents values for both number of individuals and total weight – in kg – for each of the 54 fish species collected. Average depth for each trawl is also included. The six stations sampled yielded a restricted number of abundant species, together with a large group of poorly sampled ones. All these species are currently found along the Portuguese southern upper-slope (NOBRE, 1935; ALBUQUERQUE, 1954–56; unpubl. pers. observ.).

Nezumia sclerorhynchus is recorded for the first time in Portuguese waters. The identification criteria of MARSHALL and IWAMOTO (1973) (i.e. less than 20 serrations on the 2nd

Table II. Catch composition at sampling stations.
Avg. – average depth.; W – total weight (in kg); No – number of individuals

Sampling station Avg. Depth (m)			2 519.0	4 732.5	5 652.5	6 693.5	10 715.0	11 724.5
Scyliorhinidae	*Scyliorhinus canicula*	W	2.520					
		No	5					
	Scyliorhinus stellaris	W			0.277		0.410	0.011
		No			13		4	0.667
	Galeus melastomus	W	3.280	15.100	0.340	19.000	0.500	23.333
		No	13	33	13	42	3	44.444
Squalidae	*Centrophorus granulosus*	W		NC		0.013		
		No		1		1		
	Centrophorus uyato	W				9.500		
		No				2		
	Deania calceus	W			0.840	4.058	2.035	7.000
		No			6	30	21	7.333
	Etmopterus spinax	W		0.542	2.900	4.350	0.036	0.248
		No		3	21	25	1	2
	Etmopterus princeps	W		0.558				0.233
		No		6				2
	Etmopterus pusillus	W	0.610	0.203				0.075
		No	3	1				0.667
	Etmopterus sp.	W					0.009	
		No					2	
	Dalatias licha	W			1.300		2.600	3.600
		No			1		4	0.667
Rajidae	*Raja circularis*	W		4.000			2.450	
		No		1			1	
	Raja clavata	W	6.850	0.175			1.470	
		No	1	3			1	
	Raja miraletus	W	0.200					
		No	1					
	Raja montagui	W		0.006				
		No		1				
	Raja naevus	W		NC				
		No		1				
	Raja oxyrinchus	W				25.000		
		No				1		
	Raja sp.	W	0.650	0.230				0.021
		No	12	4				0.667
Chimaeridae	*Chimaera monstrosa*	W	5.450	4.420		2.680	5.323	4.337
		No	8	5		2	10	7
Gonostomatidae	*Polymetme corythaeola*	W		0.014				
		No		1				
Sternoptychidae	*Argyropelecus aculeatus*	W			0.004	0.002	0.008	
		No			2	2	3	
	Argyropelecus hemigymnus	W						0.000
		No						0.667
Myctophidae	*Diaphus metopoclampus*	W	0.036	0.002	0.003	0.021		
		No	1	1	2	2		
Nettastomatidae	*Nettastoma melanurum*	W					0.019	0.178
		No					1	2.667
	Facciolella oxyrhyncha	W					0.012	
		No					1	
Congridae	*Conger conger*	W	0.839	9.023	3.000	16.000	6.000	11.667
		No	3	4	2	5	4	4
Synaphobranchidae	*Synaphobranchus kaupi*	W	0.016	0.023	0.003			0.003
		No	3	3	1			0.667

Table II. Cont.

Sampling station Avg. Depth (m)			2 519.0	4 732.5	5 652.5	6 693.5	10 715.0	11 724.5
Notacanthidae	*Notacanthus bonapartei*	W		0.193		0.028		0.152
		No		4		1		3.333
	Notacanthus chemnitzii	W		0.133				
		No		3				
Macrouridae	*Coelorhynchus*	W	0.210					0.683
	coelorhynchus	No	1					2.667
	Malacocephalus laevis	W				0.170		0.022
		No				1		0.667
	Nezumia sclerorhynchus	W	2.548	2.378	1.895	1.450	2.318	3.213
		No	240	182	154	101	179	180
Merluciidae	*Merluccius merluccius*	W	0.380		3.560	5.680		
		No	1		2	4		
Gadidae	*Micromesistius poutassou*	W		1.440	95.000	14.500	1.880	0.213
		No		8	297	87	8	1.333
	Antonogadus megalo-	W		0.017	0.016	0.010		0.003
	kynodon Gaidropsarus	No		2	2	2		0.667
	cf. mediterraneus	W			0.040			
		No			2			
	Gaidropsarus cf. vulgaris	W				NC		
		No				1		
Moridae	*Gadella maraldi*	W	0.016					
		No	1					
	Gadomus dispar	W					0.033	
		No					1	
	Gadiculus argenteus	W	0.009					
		No	1					
	Mora moro	W		0.200				
		No		1				
	Phycis blennioides	W				3.500	1.100	
		No				5	1	
	Phycis phycis	W						1.433
		No						1.333
Caproidae	*Capros aper*	W	0.030					
		No	1					
Trachichthyidae	*Hoplostethus*	W	0.033	0.320	0.312	3.233	0.119	0.005
	mediterraneus	No	5	9	24	85	4	0.667
Serranidae	*Serranus sp.*	W						0.146
		No						0.667
Apogonidae	*Epigonus denticulatus*	W	0.002		0.022			
		No	1		1			
Trichiuridae	*Benthodesmus elongatus*	W				0.237	0.246	
		No				1	2	
	Lepidopus caudatus	W	0.426					
		No	2					
Centrolophidae	*Centrolophus niger*	W				0.799		
		No				1		
Scorpaenidae	*Helicolenus dactylopterus*	W	0.065			0.100		0.173
		No	2			2		0.667
Soleidae	*Bathysolea profundicola*	W					0.038	
		No					2	
Lophiidae	*Lophius budegassa*	W	3.150					
		No	1					
	Lophius piscatorius	W			5.500			
		No		0	1			

spine, lack of scales under the snout and spinules of scales needle-like) allowed this species to be distinguished from *Nezumia aequalis,* currently confused in southern Portuguese waters with *N. sclerorhynchus.* The horizontal and vertical distribution of the two species along the Portuguese coast remains to be clarified.

3.2. Feeding Habits

Table III summarizes the prey recorded in the stomachs (average prey numbers) of the fish species selected.

3.2.1. Scyliorhinids and Squalids

Scyliorhinus canicula and *S. stellaris* live usually on the continental shelf (cf. WHITEHEAD *et al.,* 1984–86). The present records at bathyal depths are unusual. The specimens of *S. canicula* collected, showed that they were feeding mainly on polychaetes, followed by crustaceans (natant and reptant decapods) and fishes in equal proportions. *Scyliorhinus stellaris* had a diet based on vagile prey, essentially on natant crustaceans (50 % were *Pasiphaea sivado*) and euphausids, fishes and other crustaceans.

Galeus melastomus was found to feed mainly on fishes with myctophids dominating the diet. Natant decapods (60 % of which are *Pasiphaea sivado*) and cephalopods were also present in the stomachs, as well as sponges, ascidians, amphipods, euphausids and mysids. This diet is close to that found for the same species by MATTSON (1981) in a west Norwegian fjord and based on crustaceans (decapods and euphausids), fish and cephalopods. These findings are in agreement with other authors (e.g. MAUCHLINE and GORDON, 1983; MACPHERSON, 1980 b, 1981; MATTSON, 1981).

Sponges and ascidians found in the stomachs of *G. melastomus* (accidentally ingested or not) account for the wide spectrum of prey exploited by this species, ranging from very mobile to sessile prey. This broad prey spectrum is in accordance with the results of other authors. While MAUCHLINE and GORDON (1983) found this species to feed on benthopelagic and epibenthic prey, the results of DU BUIT (1983) show a pelagic or benthopelagic type of feeding.

Specimens of *Centrophorus granulosus* had only unidentified fishes in their stomachs.

Fishes were the bulk of the *Deania calceus* diet and among them myctophids are very important. *Deania calceus* is a benthopelagic shark living along the slope and foraging not very far from the bottom (SALDANHA, 1977, WHITEHEAD *et al.,* 1984–86). Myctophid fishes also occurred near the bottom, for instance they were collected with the benthic pump of the bathyscaphe *Archimède,* over the bottom (cf. SALDANHA, 1977). Natant decapods (62 % of which were *Pasiphaea sivado*), other crustaceans (non identified) and cephalopods were also present in the stomach contents. A similar diet was also found by MAUCHLINE and GORDON (1983). These authors and DU BUIT (1983) also concluded that the species appears to feed at some distance from the sediment surface.

The diet of the specimens of *Etmopterus spinax* from the southern Portuguese slope accorded with that found in other regions: northwest Africa, Mediterranean, Rockall Trough, (CLARKE and MERRETT, 1972; MACPHERSON, 1980 b, 1981; MAUCHLINE and GORDON, 1983). This diet was based on benthopelagic animals such as fish and crustaceans (in equal proportions in our material), supplemented by cephalopods. *Pasiphaea sivado* represented 100 % of the natant decapods present in the stomachs.

Etmopterus princeps had a similar diet to *E. spinax,* with *Pasiphaea sivado* representing 40 % of the natant crustaceans present in the stomachs. MAUCHLINE and GORDON (1983) concluded that *E. princeps* fed on benthopelagic prey, predominantly on decapod crustaceans and fish. Squids were also included in its diet.

Table III. Analysis of stomach contents (average prey numbers)

	Scyliorhinus canicula	*Scyliorhinus stellaris*	*Galeus melastomus*	*Centrophorus granulosus*	*Deania calceus*	*Etmopterus spinax*	*Etmopterus princeps*	*Etmopterus pusillus*	*Dalatias licha*	*Raja circularis*	*Raja clavata*	*Raja montagui*	*Raja naevus*	*Chimaera monstrosa*	*Polymetme corythaeola*	*Argyropleclus aculeatus*
No. ind.	7	31	56	2	43	8	9	4	2	2	6	1	1	32	1	7
Avg. len. (mm)	459.0	267.5	573.3	NC	358.3	267.0	290.0	341.5	NC	422.0	289.0	119.0	313.0	813.9	155.0	48.7
Avg. weight (g)	378.2	125.3	623.0	NC	136.3	126.5	100.8	112.1	NC	1369	340.6	5.9	158.5	747.0	14.3	2.1
Vac. indx.	0.14	0.16	0.07	0.00	0.35	0.38	0.11	0.50	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Evers. indx.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.57
Pisces n. id.	0.14	0.22	0.8	1	0.56	0.25	0.77	0.25	0	1	0.16	0	0	0.03	1	0
Myctophiidae sp.	0	0	0.12	0	0.46	0	0	0	0	0	0	0	0	0	0	0
Ascidiacea	0	0	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0
Cephalopoda	0	0	0.18	0	0.02	0.125	0.11	0	0	0	0	0	0	0	0	0
Bivalvia	0	0	0	0	0	0	0	0	0	0	0	0	0	0.28	0	0
Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0.15	0	3.42
Crustacea n. id.	0.14	0.22	0.07	0	0.02	0	0	0	0	0	0	0	0	0.34	1	0
Copepoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausiacea	0	0.38	0.018	0	0	0	0	0	0	0	0	0	0	0	0	0
Mysidacea	0	0.03	0.018	0	0	0	0	0	0	0	2.5	0	0	0	0	0.14
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0.03	0	0
Amphipoda	0	0	0.036	0	0	0	0	0	0	0	2.67	1	0	0.65	0	0.14
Reptantia	0.14	0.03	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0
Natantia	0.14	0.51	0.18	0	0.19	0.25	0.66	0.25	0.5	0.5	1.5	0	3	0.21	0	0
Polychaeta	0.43	0.03	0	0	0	0	0	0	0	0	0	0	0	0.12	0	0
Calycophora	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthozoa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Porifera	0	0	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0
N. id. material	0.28	0.09	0.03	0	0	0.125	0	0	0	0	0	0	0	0.15	0	0

Table III. Cont.

	Diaphus metopoclampus	*Nettastoma melanurum*	*Facciolella oxyrhyncha*	*Conger conger*	*Synaphobranchus kaupi*	*Notacanthus bonapartei*	*Malacocephalus laevis*	*Merluccius merluccius*	*Antonogadus megalokynodon*	*Gadomus dispar*	*Capros aper*	*Hoplostethus mediterraneus*	*Benthodesmus elongatus*	*Helicolenus dactylopterus*	*Bathysolea profundicola*	*Lophius piscatorius*
No. ind.	6	5	1	15	12	10	2	8	7	1	22	45	18	3	2	1
Avg. len. (mm)	95.0	512.0	285.0	583.0	217.0	277.0	300.0	231.0	113.0	230.0	116.1	103.0	529.0	147.0	145.0	NC
Avg. weight (g)	102.0	57.0	12.3	2269	5.2	44.9	102.0	110.7	6.9	32.6	20.2	19.3	71.2	50.8	19.2	5500
Vac. indx.	0.50	0.60	0.00	0.07	0.08	0.20	0.00	0.13	0.14	0.00	0.36	0.13	0.50	0.33	0.50	0.00
Evers. indx.	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0
Pisces n. id.	0	0	0	0.83	0.33	0	0	0.5	0	0	0.15	0	0.55	0	0	1
Myctophiidae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ascideacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cephalopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalvia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea n. id.	0	0	0	0.17	0.25	0	1	0.13	0.43	1	0.125	0.09	2.94	0	0	0
Copepoda	0	0	0	0	0	0	0	0	0	0	0.21	0	0	0	0	0
Euphausiacea	0	0	0	0	0	0	0	0	0	0	0.03	0	0.39	0	0	0
Mysidacea	0.17	0	0	0	0	0	0	0	0	0	0.06	1.35	0	0	0	0
Isopoda	0	0	0	0	0	0.1	0	0	0	0	0	0.47	0.05	0	0	0
Amphipoda	0	0	0	0	0	0	0	0	0	0	0.03	1.22	0	0	0	0
Reptantia	0.17	0	0	0.33	0.08	0	0	0	0.14	0	0	0	0	0	0	0
Natantia	0.17	0.4	0	0.33	0.25	0	0	0.13	0.28	0	0	0.11	0.11	0	0	0
Polychaeta	0	0	0	0	0	0	0	0	0	0	0.03	0	0	0	0	0
Calycophora	0	0	0	0	0	0	0	0	0	0	0.09	0	0	0	0	0
Anthozoa	0	0	0	0	0	0.8	0	0	0	0	0	0	0	0	0	0
Porifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N. id. material	0	0	1	0	0.08	0.1	0	0.375	0	0	0	0	0	0.66	0.5	0

The two specimens of *Etmopterus pusillus* collected, fed on fish and *Pasiphaea sivado* in equal proportions. The only specimen of *Dalatias licha* had ingested one natant decapod crustacean.

3.2.2. Rajids

Raja circularis fed on natant decapods and unidentified fishes.

Raja clavata prey ranged from amphipods and mysids, the two main items, to natant (50 % of which are *Solenocera membranacea*) and reptant decapods and fishes. CUNHA *et al.* (1987) found that *R. clavata* fed mainly on decapod crustaceans, supplemented by fishes, euphausids, mysids and cephalopods according to the size of the predators. Epibenthic prey like polychaetes were also recorded.

Raja montagui and *R. naevus* contained respectively amphipods and natant decapods in their stomachs. For *R. montagui,* CUNHA *et al.* (1987) found a diet based on natant decapods also. The results obtained by these authors for *R. clavata* and *R. montagui* are very close to those of DU BUIT (1974) and QUINIOU and ANDRIAMIRADO (1979). For *R. naevus,* CUNHA *et al.* (1987) found a diet of natant crustaceans and fishes and pointed out that the bigger specimens fed mainly on fishes. This was also found by DU BUIT, 1974 and HOLDEN and TUCKER, 1974.

Our results and those of the other authors show that the rays studied have a mixed diet of benthopelagic and epibenthic animals.

3.2.3. Chimaerids

Chimaera monstrosa was shown to feed mainly on amphipods and other crustaceans, largely natant decapods. Isopods were also present. Molluscs were represented by bivalves and gastropods. Polychaetes and fishes were also included in the diet.

MAUCHLINE and GORDON (1983) also found amphipods in the stomachs of *C. monstrosa* from Rockall Trough, but the diet was dominated by anemones and their tubes. Echinoderms may also occur. Based on their findings and those of other authors (e.g. MACPHERSON, 1980 a), the species is evidently a benthic feeder in the North Sea, Mediterranean and Rockall Trough and the composition of its diet is very different in each region. Thus *C. monstrosa* feeds essentially on epibenthic (anemones, ophiurans, gastropods, amphipods, polychaetes) and endobenthic prey (bivalves, spatangoids).

3.2.4. Anguilliforms

The anguilliform fishes (see Table III), *Conger conger, Nettastoma melanurum* and *Synaphobranchus kaupi,* confirmed the diet based on fishes and crustaceans (natant and reptant decapods) already known (cf. SALDANHA, 1980).

The diet of *Nettastoma melanurum* was based on natant decapod crustaceans. *Conger conger* fed primarily on fish and on natant and reptant decapod crustaceans.

In our material, *Synaphobranchus kaupi* fed primarily on fish and natant and reptant decapod crustaceans. Nevertheless, a much broader dietary spectrum including cephalopods, amphipods, euphausids and mysids has been reported for this species (SEDBERRY and MUSICK, 1978; SALDANHA, 1980; MERRETT and MARSHALL, 1981; MERRETT and DOMANSKI, 1985).

3.2.5. Notacanthids and Macrourids

Notacanthus bonapartei seemed to feed on slow mobile epibenthic prey such as isopods. *Malacocephalus laevis* fed on crustaceans (non-identified). MAUCHLINE and GORDON (1984 a) also found a diet based on crustaceans for this species, and MCLELLAN (1977) reported a diet containing cephalopods, euphausids and copepods. Cephalopods were also found by MARSHALL and IWAMOTO (1973) and OKAMURA (1970).

3.2.6. Gadids and Merlucids

Antonogadus megalokynodon was shown to feed essentially on natant and reptant crustaceans. *Gadomus dispar* also had a diet based on crustaceans. Fish dominates the diet of *Merluccius merluccius,* supplemented by crustaceans.

3.2.7. Other Fish Taxa

Fishes like *Polymetme corythaeola, Argyropelecus aculeatus, Diaphus metopoclampus, Capros aper, Hoplostethus mediterraneus* and *Benthodesmus elongatus,* which range from pelagic to a benthopelagic distribution (WHITEHEAD *et al.,* 1984–86), showed a variety of food items, both of pelagic and benthic origin. Fishes and crustaceans were the food items found in *P. corythaeola* and *Capros aper* stomachs. In the latter, copepods were also present (the bulk of the diet), together with mysids, euphausids and amphipods, as well as polychaetes and calycophores. Crustaceans were found to be the main prey of *H. mediterraneus* (predominately mysids and amphipods, but also isopods and natant decapods) and of *D. metopoclampus* (mysids and natant and reptant decapods). MARSHALL and MERRETT (1977), DU BUIT (1978) and MERRETT and MARSHALL (1981) found that *H. mediterraneus* had a mixed diet but fed primarily on benthopelagic natant decapods. At the Porcupine Seabight, GORDON and DUNCAN (1987) observed a diet based primarily on decapods, mysids and amphipods that is close to what we found in our material. Fish and cephalopod remains were also present.

Argyropelecus aculeatus fed mainly on gastropods, likely of pelagic origin, but also on mysids and amphipods. MERRETT and ROE (1974) found that *A. aculeatus* fed primarily on ostracods and also on copepods.

Benthodesmus elongatus fed essentially on crustaceans supplemented by fishes.

3.3. Diet of Nezumia sclerorhynchus

3.3.1. Prey Partitioning and Comparison of Feeding Habits

The stomach contents of *N. sclerorhynchus* showed a very wide variety of organisms (see Table IV) ranging from plant fibres (very probably taken by chance) to ophiurans. Amphipods comprised by far the bulk of the diet (Fig. 2). Mysids were the second most abundant prey except at station 10 and 11, where isopods were in second place. Far less abundant were other crustaceans such as tanaids, natant and reptant decapods. Polychaetes, sponges, cumaceans, euphausids, ostracods, pycnogonids, molluscs and ophiurans also occurred but in very low numbers.

GEISTDOERFER (1978) studied the feeding habits of Mediterranean and Atlantic populations of *N. sclerorhynchus.* He concluded that the diet presented the same characteristics in both regions; a large variety of prey belonging to 18 zoological groups and nearly two times more prey was recorded in the Atlantic than in the Mediterranean (GEISTDOERFER, *op. cit.*). The diet was dominated by amphipods and copepods. Mysids also contributed to the diet and gastropods, bivalves and echinoderms were also present. Crustaceans were equally abundant in Mediterranean and Atlantic diets. The same author also stresses that over all 66.3 % of the zoological groups were of pelagic origin, 14.7 % benthic and 18.9 % mixed. The Atlantic specimens depended on only 12.2 % benthic prey (21.6 % in the Mediterranean). GEISTDOERFER also concluded that the diet is more diverse as the fishes increase in size, and he found that bigger individuals tend to feed mainly on benthos. MCLELLAN (1977) also pointed out the primarily benthic origin of stomach contents from *N. sclerorhynchus,* based on the presence of polychaetes and other benthic taxa. Our data does not give any evidence of diet change with increasing individual size, and the results show striking similarities with the diets of other species of *Nezumia,* like *N. bairdii*

(Savvatimsky, 1989) and *N. aequalis* (e.g. Sorbe, 1972; Geistdoerfer, 1978; Du Buit, 1978; Merrett and Marshall, 1981; Macpherson, 1979, 1981, 1983; Mauchline and Gordon, 1984 a; Carrasson and Matallanas, 1989), which are considered generalists.

Table IV. Diet composition of *N. sclerorhynchus* at the six stations. Tot# – total prey number; Avg# – average prey number per stomach; Size (mm) – average prey size.

	Station 2	Station 4	Station 5	Station 6	Station 10	Station 11
No. ind.	202	141	142	35	93	167
Vac. indx.	0.02	0.02	0	0	0	0
Evers. indx.	0.06	0.05	0	0.11	0.06	0.04

	Station 2			Station 4			Station 5			Station 6			Station 10			Station 11		
	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)
Plant fibres				1	1.00	–												
Porifera n. id.				3	1.00	–										1	1.00	–
Polychaeta n. id.	6	1.20	–	4	1.00	–				8	1.00	–	1	1.00	–	6	1.20	–
Onuphis sp.	3	1.50	–				14	1.75	–	19	1.00	–	1	1.00	–			
Diopatra sp.							2	1.00	–									
Amphipoda n. id.	289	4.74	–	89	1.60	8.16	105	2.33	4.48	16	1.60	–	63	3.00	76.22	163	3.00	4.10
Ampeliscidae n. id.	1	1.00	–				2	1.00	–	2	2.00	–	4	2.00	–			
Ampelisca sp.	7	2.33	3.61				16	1.45	3.03	2	1.00	2.65						
Phoxocephalidae n. id.							8	1.60	3.63							6	1.00	2.66
Amphilochidae n. id.	3	1.00	0.75	1	1.00	7.20	2	1.00	2.75							1	1.00	7.50
Amphilocoides cf.																		
odontonyx	5	2.50	1.91				4	1.33	2.44				6	1.20	4.07			
Leucothoidae n. id.	3	1.50	7.35										2	2.00	1.59			
Leucothoe cf. *marina*													4	1.30	3.28			
Leucothoe sp.	6	1.20	4.50															
Stenothoidae													3	1.50	5.33			
Stenothoe cf. *marina*	9	4.50	–										1	1.00	3.69			
Eusiridae n. id.	1	1.00	–				2	1.00	–									
Eusirus longipes	2	1.00	–	1	1.00	11.30	12	1.00	5.38							3	1.00	8.80
Gammaridae n. id.	33	2.36	0.12	1	1.00	8.30	25	1.47	4.03	16	1.80	–	67	3.90	3.89	64	3.40	5.19
Apherusa sp.				1	1.00	–	6	1.20	2.92									
Ceradocus orchestiipes	5	1.25	0.83				12	1.09	7.15	1	1.00	–	2	1.00	5.40			
Maera grossimana	4	1.00	–				9	1.29	7.94				2	2.00	–			
Maera hirondellei?	1	1.00	5.24				7	1.40	9.48				1	1.00	–	1	1.00	9.38
Maera inaequipes	10	2.50	3.59				3	1.50	5.16	2	2.00	4.85						
Maera othonis																3	1.50	8.80
Maerella tenuimana?	4	2.00	–															
Aoridae n. id.	1	1.00	–															
Jassidae n. id.	6	2.00	–															
Lysianassidae n. id.							15	1.50	2.13							8	2.00	3.88
Lilljeborgiidae n. id.							1	1.00	5.63									
Pleustidae n. id.				2	2.00	8.15												
Corophiidae n. id.	9	1.13	1.93													2	1.00	–
Caprellidae n. id.				2	1.00	–												
Caprella aequilibra?	2	1.00	–															
Caprella sp.	3	1.00	–				6	1.00	2.53				5	1.30	2.87	6	1.50	6.26
Cumacea n. id.	2	1.00	3.02	2	1.00	–	11	1.83	–							1	1.00	1.90
Isopoda n. id.	19	1.27	–	10	1.40	–	27	1.35	2.88				3	1.50	–	23	1.80	4.92
Cirolanidae n. id.	8	4.00	–										2	2.00	–			
Cirolana sp.	1	1.00	9.37				5	1.00	7.31	5	5.00	2.90	17	2.40	3.45	1	1.00	–
Sphaeromatidae n. id.				1	1.00	–												
Janiridae n. id.													142	4.40	3.05	33	2.50	3.48
Arcturidae																		
Astacilla sp.				1	1.00	–												
Munidae n. id.				15	1.70	–										6	1.50	3.00
Anthuridae n. id.				1	1.00	–												
Cyathura carinata?													4	1.00	1.91			
Euphausiacea n. id.	3	1.00	3.07				13	2.17	3.13				2	1.00	4.34			
Tanaidacea n. id.							1	1.00	–				1	1.00	–			
Apseudidae n. id.				1	1.00	–	3	1.00	–									
Apseudes grossimanus?	2	1.00	–				16	1.23	5.02	2	1.00	–	4	4.00	3.19			

Table IV. Cont.

	Station 2			Station 4			Station 5			Station 6			Station 10			Station 11		
No. ind.	202			141			142			35			93			167		
Vac. indx.	0.02			0.02			0			0			0			0		
Evers. Indx.	0.06			0.05			0			0.11			0.06			0.04		
	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)	Tot #	Avg #	Size (mm)
Apseudes latreillei?				1	1.00	11.30												
Apseudes sp.				1	1.00	–										1	1.00	–
Mysidacea n. id.	145	2.90	0.17	53	2.40	24.00	147	2.33	7.33	17	1.10	–	6	1.20	–	4	1.00	7.20
Amblyops abbreviata	9	3.00	4.59	12	6.00	–	32	2.46	7.12	4	1.30	4.14	1	1.00	–	8	1.60	8.01
Paramblyops rostrata	8	1.60	2.08				29	1.61	8.05				1	1.00	3.69	8	2.00	10.16
Ostracoda n. id.				1	1.00	–												
Pycnogonida n. id.																1	1.00	–
Decapoda																		
Reptantia n. id.	32	2.13	–	13	1.20	4.47	3	1.50	–							8	1.10	5.49
Paguridae n. id				1	1.00	–												
Diogenes sp.													1	1.00	5.74			
Galatheidae n. id.							1	1.00	–									
Portunidae																		
Macropipus tuberculatus	4	2.00	–				1	1.00	–									
Bathynectes longipes	20	1.33	3.69				6	2.00	4.29							16	1.50	5.03
Geryonidae																		
Geryon sp.				1	1.00	4.80												
Decapoda Natantia n. id.	22	1.22	–	1	1.00	–	6	1.50	–				8	1.30	7.94	4	2.00	4.45
Crangonidae n. id.	2	1.00	–				1	1.00	–									
Philocheras echinulatus	4	1.33	7.04				2	1.00	14.10	1	1.00	9.25						
Processidae	3	1.00	–															
Processa caniculata							1	1.00	–									
Mollusca																		
Gastropoda n. id.				3	1.50	–							9	4.50	1.40			
Ophiuridae n. id.				1	1.00	–										4	2.00	–

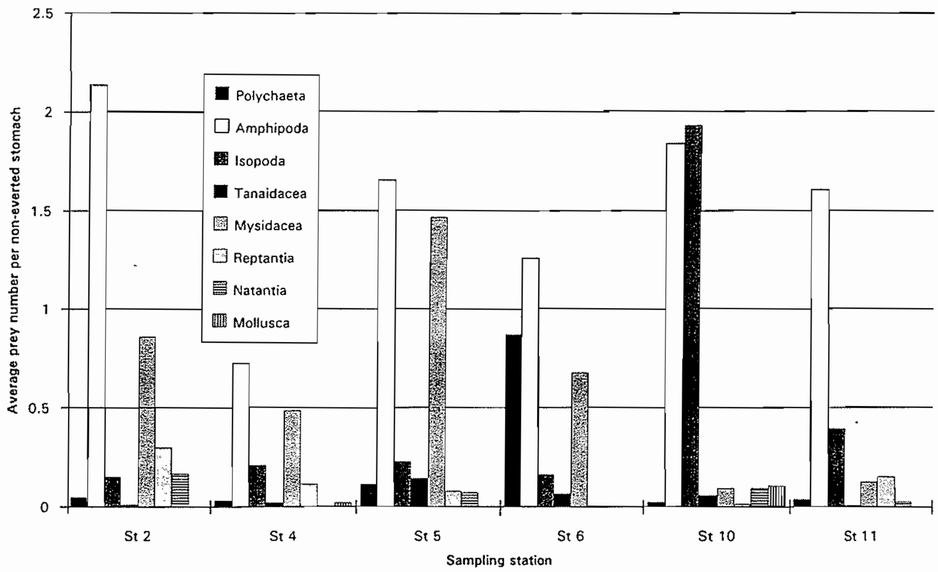

Figure 2. Average prey number in *Nezumia sclerorhynchus* for the six sampling stations.

In conclusion, our results are in general agreement with the findings of other authors (e.g. McLellan, 1977; Merrett and Marshall, 1981). Only the proportions of zoological groups represented were found to be different, with amphipods outnumbering all other prey.

3.3.2. Numerical Studies

Size classes were examined for stations 2, 4, 5, 6, 10 and 11. Absolute size class frequencies (Fig. 3) present the widest distribution in Station 2 (the shallowest one with

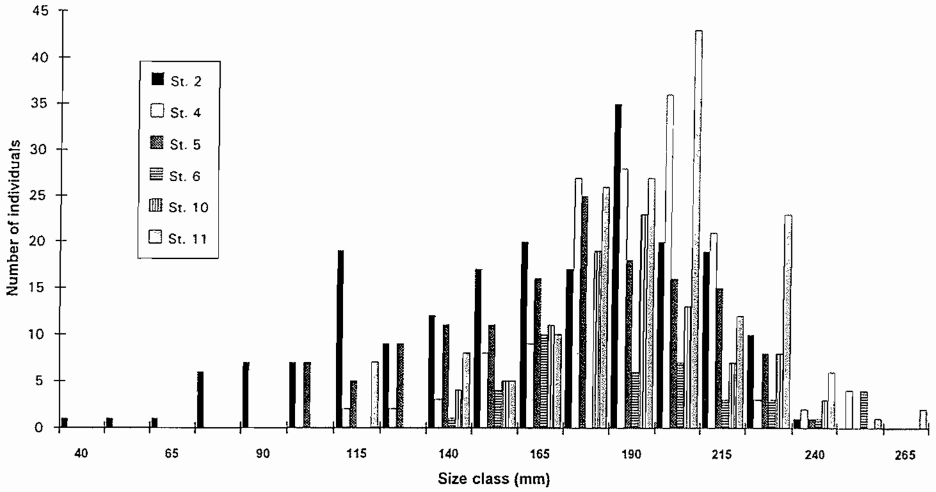

Figure 3. Size distribution of *Nezumia sclerorhinchus* in absolute frequencies.

540–498 m), with the presence of the smaller size classes found. *Nezumia sclerorhynchus* was least abundant at Station 6. Modal values vary between 165 mm (St. 6) and 215 mm (St. 4 and 11), with a concentration between 190 and 215 mm.

In view of the lack of physical characterization of the station localities, no other inferences could be made on the size distribution of the individuals. Data on the distribution and availability of prey is also non-existent for the sampling area.

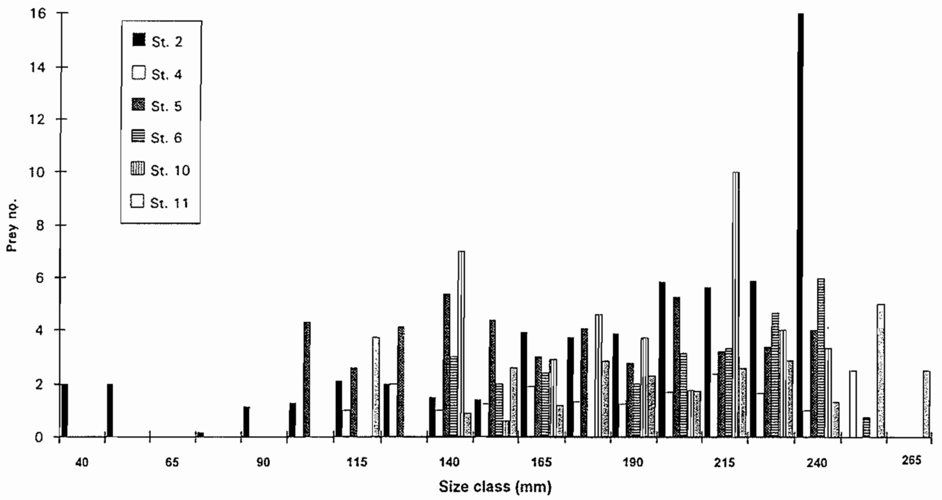

Figure 4. *Nezumia sclerorhynchus* – Average prey number per stomach contents.

The average number of prey per stomach (Fig. 4) was greatest among size classes from 215 to 240 mm. Average prey size (Fig. 5) has an irregular distribution (see Chap. 2.3.). While data from sampling stations 2, 5 and 6 suggests an increase in prey size with predator size, no trend appears in stations 4, 10 and 11. In general mean prey size increases with increasing predator size and with increasing predator-prey pursuit distance (optimal

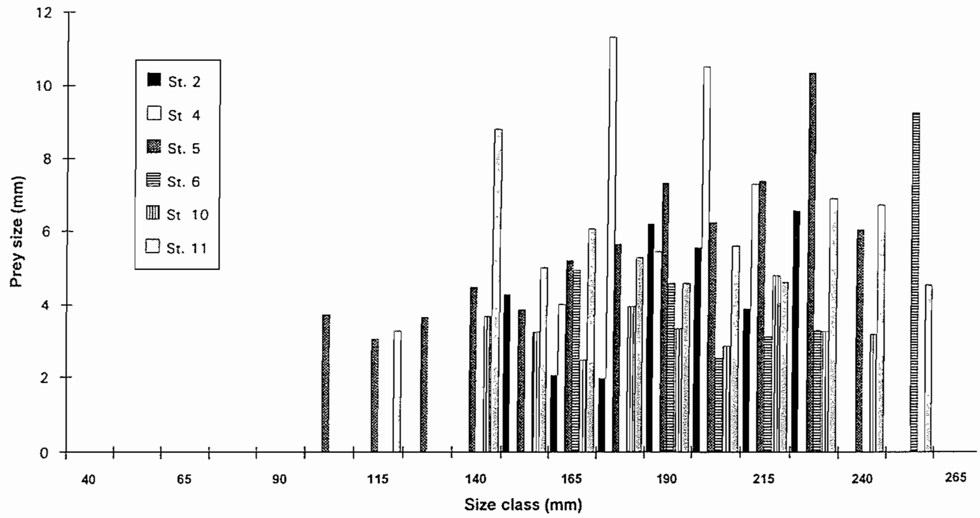

Figure 5. *Nezumia sclerorhynchus* – Average prey size.

foraging, KOCK, 1992). Due to the bias in prey measurements in which only non-digested material was measured (see Material and Methods), it is difficult to determine whether increasing prey size was selected according to increasing predator size (as in stations 2, 5 and 6) or if prey were so easily available that no selection was made at all (as in stations 4, 10 and 11).

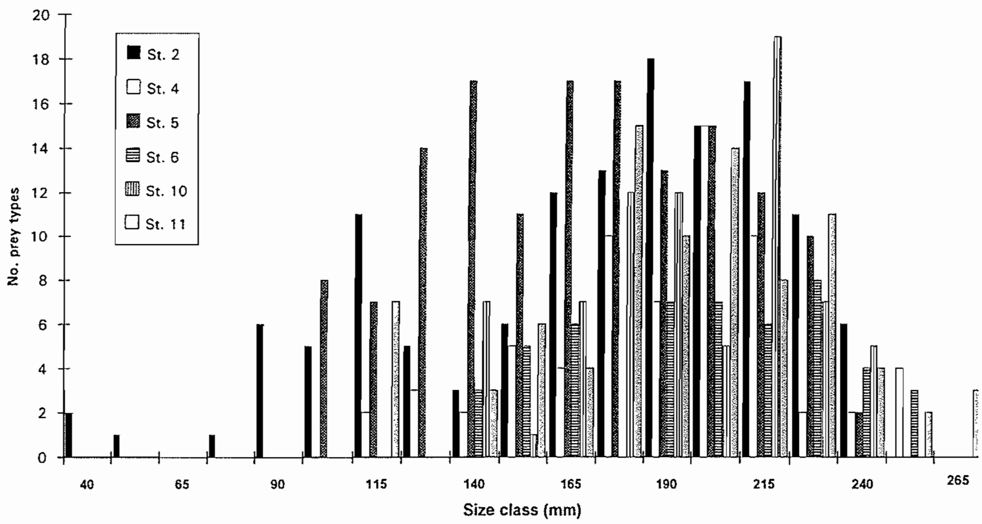

Figure 6. *Nezumia sclerorhynchus* – Prey richness in total number of prey types.

Except for station 5 and 6, both prey richness, measured as total prey types (Fig. 6) and prey diversity (Fig. 7) show a general trend, with a maximum for size classes between 190 and 215, with the number of different prey ingested ranging from 7 to 19, and a diversity always in excess of 2 nat. In station 5, the highest prey richness occurs in size classes 140

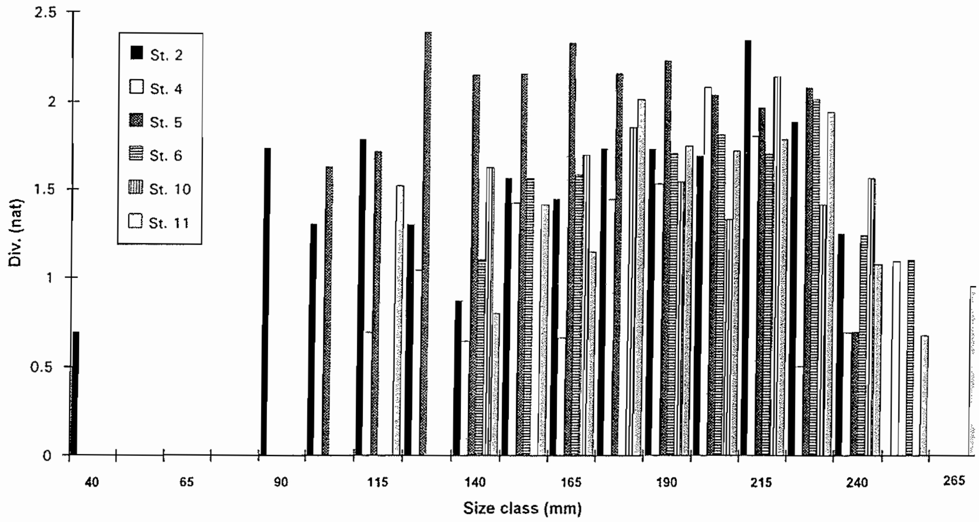

Figure 7. *Nezumia sclerorhynchus* – Prey diversity (in nat).

and 165 mm, with a total of 17 different prey types ingested, and a maximum prey diversity of 2.4 nat for class 127.5 mm. In station 6, both the highest prey richness, corresponding to 7 different prey types ingested and prey diversity of 2 nat, correspond to size class 227.5 mm.

This reflects perhaps the full capacity of fishes of medium size classes to exploit all possible sources of food, but could also result from the reduced sample size in the small and large size classes.

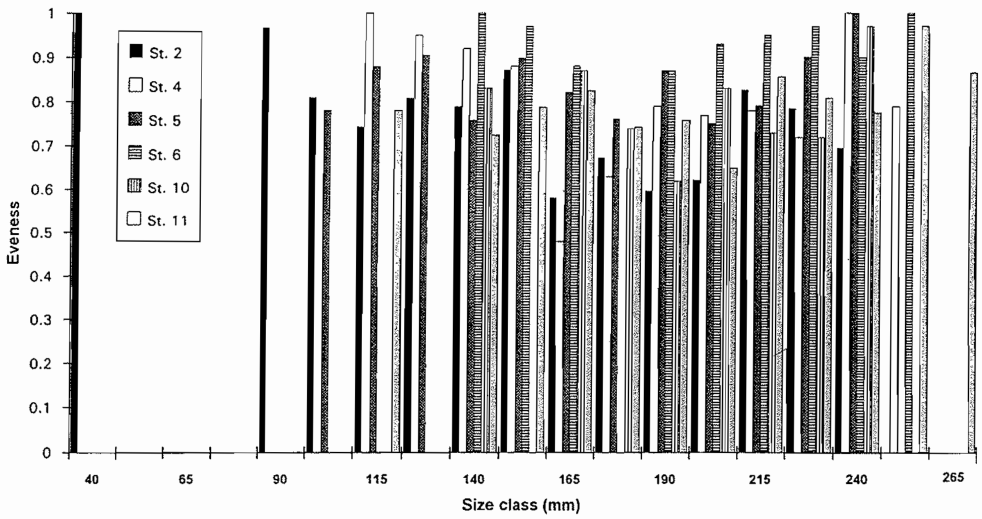

Figure 8. *Nezumia sclerorhynchus* – Prey eveness.

The regular occurrence of individual prey types, which accounts for the high values of diversity, also reflects in the eveness values (Fig. 8), always in excess of 0.6, except for size class 165 mm in station 4. In a large number of cases, this merely reflects the low number of different prey ingested, as in the smaller and larger size classes of most sampling stations. Although lowest eveness values occurred for size class 177.5, eveness remains very close to 1 for the size classes 190 through 240, where the highest prey richness values were found. This suggests that even when a large number of individual prey is ingested, different prey types are taken in equal proportions.

These results suggest that availability of prey, rather than active prey selection is important. In fact, *Nezumia sclerorhynchus* individuals of all but the smaller sizes appear to ingest prey of a size corresponding to its availability. Also, prey richness only seems to relate to the number of individuals sampled, since it behaves in a similar pattern to size distribution. Since prey diversity is also related to this same pattern and prey eveness presents only small variations, it is again arguable that prey ingestion is a measure of prey availability, rather than the result of selection by the predator. Such selection would be reflected in a decrease of prey diversity and eveness with the increase of prey richness, due to the ingestion of less frequent prey.

4. Conclusions

From our results and those of other authors (see above), in which a wide range of prey is exploited by the predators studied, it seems possible to confirm a generalist type of feeding, at least for most of the slope-dwelling species (see e.g. HAEDRICH *et al.*, 1980).

Differences in diet composition of the same predator species from the same or different geographical areas, probably depend on prey patchiness (at different scales) and seasonal or diurnal availability, for which, in the present case, no data exists.

The feeding affinities of the species studied are schematically presented in Fig. 9. In this scheme, prey were grouped in four categories, according to their assumed usual distribu-

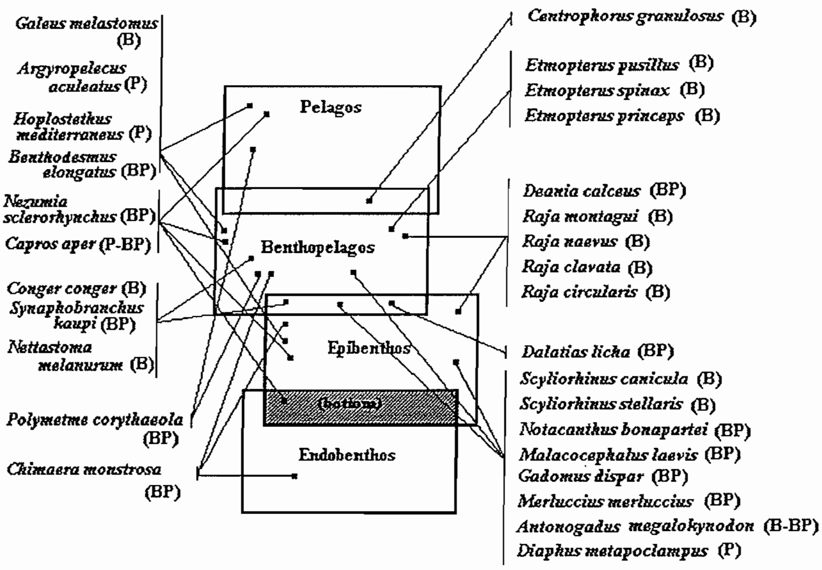

Figure 9. Feeding preferences and habitats of the studied fishes (B – benthic, BP – benthopelagic, P – pelagic).

tion patterns: pelagic, benthopelagic, epibenthic and endobenthic. Predator groups were then defined from the diets found. The life-style (benthic, benthopelagic or pelagic) of each fish species is also given (WHITEHEAD *et al.*, 1984–86).

As it can be seen, most of the studied upper slope species target their feeding on benthopelagic and epibenthic prey. It is also evident that pelagic, benthopelagic and benthic fishes can exploit prey of the same origin, with consequent difficulty in establishing distinct feeding guilds among these fishes.

5. Acknowledgments

This work was funded by the EU-Mast contract Mast-0037-C "Natural variability and the prediction of change in marine benthic ecosystems". Thanks are due to CARLOS REIS (President of IPIMAR) and AURA RIBEIRO for their help in the preparation and during the cruise of the *NE Noruega*. We are indebted to NIGEL MERRETT and JOHN GORDON for the critical reading of the manuscript. An anonymous referee helped to improve the manuscript quality.

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