Resource Partitioning in a Mediterranean Demersal Fish Community

E. Macpherson

Instituto de Investigaciones Pesqueras, Paseo Nacional, s/n, Barcelona, Spain

ABSTRACT: Niche breadths and community matrices were examined for two guilds (benthic and epibenthic) on the western Mediterranean slope. There are a larger number of specialist species in the benthic than in the epibenthic guild. Selachians have broader niches than other species. Most species pairs with significant overlaps present high values in only a few size groups, some of them also showing seasonal or diel patterns of resource partitioning. Analysis of covariance for each niche dimension shows that species are more closely packed with respect to depth distribution than to food. Covariance values of community matrices for each guild indicate that competition is more likely in the benthic than in the epibenthic guild.

INTRODUCTION

Studies on resource partitioning and the structure of fish communities are currently enjoying great popularity (see reviews by Schoener, 1974 and Helfman, 1978). Moreover, recent publications of research in this area have examined the role of resource overlap in the structure and organization of such communities (e. g. Vandermeer, 1972; Cody, 1974; Culver, 1974; Hespenheide, 1975).

The present paper examines the use of different resources and the patterns of interaction between species and their size groups in different dimensions of the Hutchinsonian niche in a western Mediterranean fish community.

Analysis of interaction among coexisting species, using a niche overlap index, is useful in revealing the importance of different niche parameters in community organization and how these niche dimensions are used by fishes to reduce competition and allow species to coexist.

MATERIALS AND METHODS

A total of 17,803 stomachs of 26 benthic and epibenthic species (Table 1) were collected between September 1976 and September 1978. The survey covered the western Mediterranean slope (200–800 m) from Alicante (38 °00' N) to Cape Creus (42 °13' N). Bottom trawls were used in order to restrict sampling effec-

tively to species living directly on or near the bottom.

Diets were determined by stomach-content analysis. The prey organisms found in each stomach were identified to species or genus level wherever possible, and the body weight of each organism was determined. The composition of the diet was obtained as the percentages of the total weight of stomach contents. Frequency of occurrence (in percent) was analyzed for 3 categories of bottom depth (200–400 m, 400–600 m, and 600–800 m).

Parallel to the present study, a series of food-availability surveys were conducted in the same area. The results of these surveys indicated that the availability or frequency of prey items did not vary appreciably with bottom depth in the area under consideration. The analysis of the stomach contents of specimens taken at different bottom depths tended to corroborate these survey results.

Diets and depth distribution were studied for the various size groups (10-cm increments) of the different species. Niche overlap and niche breadth were computed using the following formulas (MacArthur and Levins, 1967; Levins, 1968):

Niche breadth: $B_s = \left[\sum_{i=1}^{s} P_{ih}^2 \right]^{-1}$

Niche overlap: $\alpha_{ji} = \sum_{i=1}^{s} P_{ih} \cdot P_{jh} / \sum_{i=1}^{s} P_{ih}^2;$

$\alpha_{ij} = \sum_{i=1}^{s} P_{ih} \cdot P_{jh} / \sum_{i=1}^{s} P_{jh}^2$

where α_{ji} = overlap of species j on species i; α_{ij} = overlap of species i on species j. P_h is the proportion of a particular food item h (h = 1, . . ., s) in the diet.

An overlap of 0.7 or more is considered high. α_{ji} and α_{ij} may differ if niche breadths are unequal. Because the number of categories was different for each aspect of the niche, niche breadths were normalized by dividing by n (n = number of categories), hence B = B_s/n.

RESULTS

Prey Taxa and Prey Size

220 prey categories and 33 prey sizes were found; however, prey organisms with P_h values of less than about 0.05 have relatively little effect on niche breadth and overlap, especially if the largest value of P_h is greater than 0.5 (Hespenheide, 1975). Therefore, values of less than 0.05 were discarded.

As Root (1967) pointed out, fishes that exploit the same resources in similar fashion may be thought of as forming a guild. Fish species have been divided into

two guilds according to their diets and feeding behaviour. The benthic species guild (marked 'B' in Tables 1 and 2) is composed of species that feed largely on benthic organisms (e. g. polychaetes, ophiuroids, Macrura Reptantia, Brachiura, benthic crustaceans), some of which live buried in the bottom (e. g. *Calocaris macandreae, Alpheus glaber, Lesueurigobius friesii*). However, some species (e. g. *Conger conger* and *Lophius budegasa*) also feed on epibenthic prey items, though, these are probably captured when they are near the bottom (Macpherson, 1977). The regular presence of such prey in the stomach contents examined and some characteristic morphological adaptations (e. g. barbels and long rostra used as sensory probes) imply a close relationship between these species and the bottom (Macpherson, 1977, 1979 and papers cited therein).

On the other hand, species marked 'E' in Table 1 (epibenthic guild) feed heavily on epibenthic and pelagic prey items found near the bottom (e.g. euphausiids, pelagic decapods, myctophids) and seem to live higher up in the water column (all references to 'heights' should be understood in the context of benthic and epibenthic depth zones). A few species

Table 1. (A) Number of stomachs examined. (B) relative abundance of species number of specimens by hour of trawl. (C) percentage of different size groups. Species marked E are considered epibenthic; species marked B, benthic (see text)

Species	(A)	(B)				(C)							
		50	50–100	100–200	200+	5–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79
E *Gadiculus argenteus argenteus*	1434				×	83.2	16.8						
E *Micromesistius poutassou*	1761				×		54.4	44.2	1.4				
E *Merluccius merluccius*	664		×			24.8	51.5	12.4	11.3				
E *Molva dypterigia macrophthalma*	355	×					37.3	56.6	6.1				
E *Hymenocephalus italicus*	323	×					100.0						
E *Etmopterus spinax*	353	×					64.9	27.0	8.1				
E *Galeus melastomus*	1559		×				51.6	35.8	7.5	3.0	2.1		
E *Scyliorhinus canicula*	1009		×				36.5	28.6	14.9	20.0			
E *Scymnorhinus licha*	31	×							48.2	51.8			
E *Lepidopus caudatus*	145	×						5.1	19.8	9.9	52.4	12.8	
E *Epigonus telescopus*	311	×				70.3	29.7						
E *Capros aper*	1067		×			76.9	23.1						
B *Coelorhynchus coelorhynchus*	160	×				16.0	60.0	22.0	2.0				
B *Nezumia aequalis*	168	×					33.3	66.0	0.7				
B *Trachyrhynchus trachyrhynchus*	1670		×				51.7	45.1	3.2				
B *Chimaera monstrosa*	206	×						25.1	39.6	22.2	8.7	4.4	
B *Gnathophis mystax*	218	×					9.8	48.0	42.0				
B *Conger conger*	242	×						7.3	22.6	40.9	17.7	6.0	5.5
B *Phycis blennoides*	2251				×	5.4	72.6	21.3	0.7				
B *Antonogadus megalokynodon*	395	×				52.1	47.9						
B *Lepidorhombus boscii*	669	×				25.5	59.1	15.4					
B *Simphurus nigrescens*	1256			×		71.4	28.6						
B *Lophius budegassa*	337	×					40.5	47.4	10.1	2.0			
B *Trigla lyra*	230	×				15.4	79.5	5.1					
B *Notacanthus bonapartei*	181	×					100.0						
B *Helicolenus dactylopterus dactylopterus*	808	×				18.9	78.0	3.1					

Table 2. Diet of different predators expressed as percentage of total weight in the stomachs

Preys	*Gadiculus*	*Micromesistius*	*Merluccus*	*Molva*	*Hymenocephalus*	*Etmopterus*	*Galeus*	*Scyliorhinus*	*Scymnorhinus*	*Lepidopus*	*Epigonus*	*Capros*	*Coelorhynchus*	*Nezumia*	*Trachyrhynchus*	*Chimaera*	*Gnathophis*	*Conger*	*Phycis*	*Antonogadus*	*Lepidorhombus*	*Simphurus*	*Lophius*	*Trigla*	*Notacanthus*	*Helicolenus*
Mollusca																										
Sepietta oweniana	–	–	–	–	–	11.1	11.1	6.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Annelida																										
Aphroditidae	–	–	–	–	–	–	–	–	–	–	–	–	26.0	11.7	–	–	–	–	–	–	–	13.0	–	–	–	–
Eunicidae	–	–	–	–	–	–	–	–	–	–	–	–	26.2	16.5	–	–	–	–	–	–	–	5.2	–	–	–	–
Ariciidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.4	–	–	–	–
Nephthys sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8.9	–	–	–	–
Polychaeta indeterminated	–	–	–	–	–	–	–	–	–	–	–	–	–	4.7	–	–	–	–	–	–	–	–	–	–	–	–
Arthropoda																										
Copepoda	–	–	–	–	9.0	–	–	–	–	–	22.8	13.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gammaroidea	–	–	–	–	11.2	–	–	–	–	–	–	–	4.8	7.4	–	–	–	–	–	–	–	–	–	–	–	–
Phronima sedentaria	–	–	–	–	–	–	–	–	–	–	–	5.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Boreomysis megalops	–	–	–	–	20.2	–	–	–	–	–	11.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pseudamma sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	6.6	–	–	–	–	–	–	–	–	–	–	–	–
Meganyctiphanes norvegica	32.4	28.5	–	–	–	5.4	6.2	7.7	–	14.0	29.5	12.4	–	–	–	–	–	–	–	5.2	–	–	–	–	–	–
Nyctiphanes couchii	22.9	–	6.1	–	–	–	–	–	–	–	–	41.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Euphausia krhoni	–	–	–	–	–	–	–	–	–	–	–	4.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nematoscellis megalops	4.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Larvae Euphausiacea	–	–	–	–	–	–	–	–	–	–	–	12.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Solenocera membranacea	–	–	–	–	18.5	–	–	–	–	–	–	–	–	–	–	–	–	10.0	–	9.4	–	–	–	–	–	–
Alpheus glaber	4.6	–	–	–	–	–	–	11.2	–	–	–	–	11.7	–	–	33.8	7.5	35.7	21.0	25.8	5.9	14.3	–	–	–	24.9
Pasiphaea sivado	–	10.9	8.0	–	–	9.1	–	6.6	–	47.2	–	–	–	–	–	–	–	–	–	6.4	–	–	4.7	–	–	–
P. multidentata	–	–	–	–	–	4.9	–	–	–	4.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Processa mediterranea	9.4	–	–	–	26.4	–	–	–	–	–	–	–	–	–	–	–	6.5	–	8.8	–	21.2	–	–	–	–	–
Pontocaris lacazei	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.5	–	–
Sergestes arcticus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.3	–	–	–	–	–	–	–	–
Aristeus antennatus	–	–	–	–	–	–	–	–	9.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calocaris macandreae	–	–	–	–	–	–	5.5	–	–	–	–	–	14.6	32.4	88.4	–	15.5	–	13.4	20.8	5.4	20.4	–	–	–	6.3
Goneplax rhomboides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12.9	8.8	–	–	–	–	–	–	–	7.3
Echinodermata																										
Ophiuroidea	–	–	–	–	–	–	–	–	–	–	–	–	–	10.4	–	83.1	–	–	–	–	–	16.8	–	70.1	88.4	–
Crinoidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.3	–
Protochordata																										
Pyrosoma sp.	–	–	–	–	–	–	–	–	–	–	7.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chordata																										
Hymenocephalus italicus	–	–	–	–	–	–	–	–	5.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trachyrhynchus trachyrhynchus	–	–	–	–	–	–	–	–	39.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gnathophis mystax	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.1	–	–	–	–
Etmopterus spinax	–	–	–	–	–	–	–	6.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Galeus melastomus	–	–	–	–	–	–	–	–	10.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Micromesistius poutassou	–	5.7	23.3	–	–	–	–	25.9	–	–	–	–	–	–	–	–	–	16.2	–	–	–	–	–	–	–	–
Phycis blennoides	–	–	–	–	–	–	5.8	–	9.6	–	–	–	–	–	–	–	–	–	–	–	–	–	12.6	–	–	–
Gadiculus argenteus argenteus	–	–	5.5	80.4	–	6.1	11.4	8.6	–	–	–	–	–	–	–	–	–	14.9	–	–	8.0	–	25.7	–	–	21.6
Antonogadus megalokynodon	–	–	–	11.1	–	–	–	–	–	–	–	–	–	–	–	–	–	7.8	–	7.6	–	–	5.0	–	–	13.3
Lesueriogobius friesii	–	–	19.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.9	–	–	11.9	–	–	–	4.6
Notoscopelus elongatus elongatus	–	10.5	4.8	–	–	7.1	6.2	–	5.1	–	–	–	–	–	–	–	–	5.0	–	–	–	–	–	–	–	–
Engraulis encrasicholus	–	–	–	–	–	20.0	13.2	6.6	–	–	–	–	–	–	–	–	–	7.2	–	–	–	–	–	–	–	–
Maurolicus muelleri	–	9.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Simphurus nigrescens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.8	–	–	–
Ciclothone braueri	–	–	–	–	–	–	–	–	–	19.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Notolepis rissoi	–	–	14.7	–	–	15.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mictophum punctatum	–	–	–	–	–	–	5.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pisces indeterminated	7.1	–	–	–	–	–	–	–	5.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

are, however, also found on the bottom, e. g. selachians (Macpherson, 1977 and in press).

In general, values for overlaps of food items in diets are low ($\bar{a} = 0.17$). Nevertheless, some predator species pairs show high overlap values. Table 3 shows that the pairs *Trachyrhynchus trachyrhynchus* on *Antonogadus megalokynodon*, *T. trachyrhynchus* on *Nezumia aequalis*, *Molva dypterigia macrophthalma* on *Conger conger*, *M. d. macrophthalma* on *Galeus melastomus*, *T. trachyrhynchus* on *Simphurus nigrescens*, and *M. d. macrophthalma* on *Lophius budegasa* exhibit by far the highest overlaps. The values be-

tween benthic species are higher ($\bar{a} = 0.34$) than between epibenthic species ($\bar{a} = 0.20$), but this difference is not appreciable.

Mean prey size generally increased with predator body size, as has been observed both in other fishes (e.g. Werner, 1974; Keast, 1977, 1978b) and in other animal groups (e. g. Hespenheide, 1971; Brown and Lieberman, 1973). As Hespenheide (1975) pointed out, this positive correlation between prey size and body size justifies the assumption that differences in predator size confer differences in diet and thereby allow coexistence in competitive environments.

Prey size distributions show higher overlaps than prey type distributions ($\bar{a} = 0.36$, Table 4). When two species are similar in size or their main size groups are nearly identical (Table 1), the overlap values are significant (e.g. *Hymenocephalus italicus* on *Antonogadus megalokynodon*, *Trigla lyra* on *Helicolenus*

Table 3. Interspecific prey type overlap. Overlap of species j on species i (α_{ji}) above diagonal and overlaps of species i on species j (α_{ij}) below

	Gadiculus	Micromesistius	Merluccius	Molva	Hymenocephalus	Etmopterus	Galeus	Scyliorhinus	Scymnorhinus	Lepidopus	Epigonus	Capros	Coelorhynchus	Nezumia	Trachyrhynchus	Chimaera	Gnathophis	Conger	Phycis	Antonogadus	Lepidorhombus	Simphurus	Lophius	Trigla	Notacanthus	Helicolenus
Gadiculus	1	0.75	0.14	0.01	0.15	0.19	0.18	0.28	0.0	0.22	0.51	0.61	0.04	0.02	0.0	0.0	0.16	0.0	0.0	0.29	0.35	0.04	0.03	0.0	0.0	0.14
Micromesistius	0.52	1	0.26	0.03	0.02	0.39	0.60	0.26	0.03	0.40	0.43	0.17	0.0	0.0	0.0	0.0	0.02	0.17	0.02	0.20	0.04	0.0	0.12	0.0	0.0	0.05
Merluccius	0.11	0.28	1	0.08	0.01	0.14	0.42	0.18	0.03	0.24	0.03	0.12	0.0	0.0	0.0	0.0	0.0	0.70	0.04	0.14	0.07	0.0	0.38	0.0	0.0	0.19
Molva	0.0	0.18	0.41	1	0.0	0.48	1.40	0.64	0.03	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.23	1.58	0.02	0.08	0.50	0.0	1.68	0.0	0.0	0.01
Hymenocephalus	0.14	0.02	0.01	0.0	1	0.0	0.03	0.0	0.0	0.0	0.24	0.01	0.04	0.06	0.03	0.0	0.15	0.12	0.10	0.13	0.57	0.09	0.03	0.0	0.0	0.01
Etmopterus	0.11	0.33	0.11	0.08	0.0	1	0.48	0.22	0.03	0.07	0.08	0.03	0.0	0.0	0.6	0.0	0.05	0.17	0.04	0.10	0.04	0.0	0.15	0.0	0.0	0.09
Galeus	0.07	0.32	0.21	0.14	0.01	0.31	1	0.26	0.03	0.12	0.09	0.03	0.0	0.11	0.06	0.0	0.06	0.34	0.10	0.14	0.10	0.10	0.31	0.0	0.0	0.22
Scyliorhinus	0.17	0.22	0.15	0.14	0.0	0.23	0.42	1	0.02	0.22	0.12	0.04	0.07	0.0	0.01	0.0	0.26	0.87	0.17	0.25	0.28	0.06	0.28	0.0	0.0	0.33
Scymnorhinus	0.0	0.05	0.04	0.01	0.0	0.05	0.09	0.03	1	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08	0.0	0.01	0.0	0.0	0.10	0.0	0.0	0.0
Lepidopus	0.32	0.82	0.46	0.0	0.0	0.17	0.47	0.51	0.02	1	0.21	0.13	0.0	0.9	0.0	0.0	0.02	0.15	0.0	0.30	0.02	0.0	0.17	0.0	0.0	0.04
Epigonus	0.56	0.67	0.04	0.0	0.28	0.15	0.27	0.21	0.0	0.16	1	0.29	0.06	0.02	0.0	0.0	0.01	0.0	0.0	0.11	0.0	0.01	0.0	0.0	0.0	0.0
Capros	0.78	0.32	0.20	0.0	0.07	0.07	0.12	0.09	0.0	0.12	0.34	1	0.03	0.0	0.0	0.0	0.0	0.0	0.0	0.08	0.0	0.0	0.0	0.0	0.0	0.10
Coelorhynchus	0.04	0.0	0.0	0.0	0.04	0.0	0.0	0.12	0.0	0.0	0.05	0.02	1	0.74	0.17	0.01	0.41	0.15	0.23	0.42	0.33	0.62	0.05	0.0	0.0	0.29
Nezumia	0.02	0.0	0.0	0.0	0.07	0.0	0.27	0.0	0.0	0.0	0.02	0.0	0.71	1	0.37	0.15	0.32	0.08	0.15	0.52	0.20	0.82	0.0	0.15	0.12	0.21
Trachyrhynchus	0.06	0.0	0.0	0.0	0.15	0.0	0.74	0.04	0.0	0.0	0.0	0.0	0.75	1.68	1	0.05	0.89	0.25	0.50	1.45	0.18	1.56	0.02	0.0	0.0	0.06
Chimaera	0.0	0.0	0.0	0.0	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.60	0.05	1	0.04	0.0	0.02	0.07	0.01	1.28	0.0	1.17	0.94	0.19
Gnathophis	0.15	0.03	0.03	0.06	0.15	0.08	0.15	0.39	0.0	0.01	0.01	0.0	0.38	0.32	0.19	0.01	1	0.61	0.58	0.60	0.82	0.45	0.22	0.02	0.0	1.02
Conger	0.0	0.17	0.43	0.20	0.06	0.13	0.42	0.66	0.04	0.05	0.0	0.0	0.07	0.04	0.03	0.0	0.30	1	0.15	0.21	0.31	0.08	0.43	0.0	0.0	0.48
Phycis	0.0	0.03	0.07	0.0	0.16	0.10	0.38	0.39	0.05	0.0	0.0	0.0	0.34	0.23	0.17	0.01	0.90	0.49	1	0.83	0.97	0.43	0.31	0.0	0.0	0.77
Antonogadus	0.21	0.22	0.13	0.02	0.10	0.13	0.27	0.30	0.0	0.15	0.08	0.04	0.31	0.40	0.24	0.0	0.47	0.34	0.42	1	0.55	0.48	0.16	0.0	0.0	0.56
Lepidorhombus	0.18	0.04	0.07	0.10	0.45	0.06	0.21	0.35	0.0	0.01	0.0	0.0	0.25	0.16	0.03	0.0	0.66	0.51	0.50	0.55	1	0.26	0.29	0.01	0.0	0.63
Simphurus	0.03	0.0	0.0	0.0	0.06	0.0	0.18	0.06	0.0	0.0	0.0	0.0	0.41	0.56	0.23	0.22	0.32	0.11	0.19	0.43	0.23	1	0.02	0.24	0.19	0.25
Lophius	0.02	0.12	0.31	0.33	0.02	0.19	0.60	0.33	0.07	0.09	0.0	0.0	0.03	0.0	0.0	0.0	0.17	0.68	0.15	0.16	0.28	0.03	1	0.0	0.0	0.55
Trigla	0.01	0.0	0.0	0.0	0.0	0.01	0.02	0.02	0.0	0.0	0.0	0.0	0.01	0.43	0.0	0.84	0.07	0.05	0.04	0.04	0.05	1.03	0.01	1	0.79	0.19
Notacanthus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.54	0.0	1.08	0.0	0.0	0.0	0.0	0.0	1.27	0.0	1.24	1	0.18
Helicolenus	0.11	0.06	0.20	0.0	0.01	0.13	0.47	0.44	0.0	0.02	0.0	0.07	0.23	0.18	0.01	0.04	0.88	0.84	0.42	0.61	0.68	0.31	0.61	0.06	0.03	1

Table 4. Interspecific prey size overlap. Overlaps of species j on species i (α_{ji}) above the diagonal and overlaps of species i on species j (α_{ij}) below

	Gadiculus	Micromesistius	Merluccius	Molva	Hymenocephalus	Etmopterus	Galeus	Scyliorhinus	Scymnorhinus	Lepidopus	Epigonus	Capros	Coelorhynchus	Nezumia	Trachyrhynchus	Chimaera	Gnathophis	Conger	Phycis	Antonogadus	Lepidorhombus	Simphurus	Lophius	Trigla	Notacanthus	Helicolenus
Gadiculus	1	0.49	0.69	0.45	0.12	0.41	0.58	0.66	0.02	0.52	0.16	0.39	0.48	0.13	0.38	0.10	0.46	0.13	0.42	0.40	0.54	0.37	0.04	0.83	0.19	1.34
Micromesistius	0.26	1	0.31	0.27	0.07	1.33	1.25	1.38	0.02	0.85	0.03	0.10	0.32	0.11	0.79	0.05	0.86	0.63	0.58	0.57	0.51	0.12	0.24	0.25	0.05	0.77
Merluccius	0.45	0.10	1	0.50	0.07	0.42	0.47	0.55	0.0	0.54	0.09	0.19	0.29	0.08	0.25	0.06	0.33	0.24	0.30	0.29	0.37	0.24	0.40	0.53	0.19	0.93
Molva	0.05	0.05	0.08	1	0.04	0.24	0.27	0.21	0.15	0.15	0.01	0.02	0.09	0.04	0.14	0.01	0.17	0.58	0.16	0.16	0.26	0.04	0.53	0.06	0.02	0.24
Hymenocephalus	0.12	0.12	0.10	0.33	1	0.06	0.11	0.32	0.0	0.02	0.35	0.25	1.40	0.96	1.35	0.29	0.76	0.03	1.52	1.43	1.40	0.71	0.22	0.08	0.37	0.31
Etmopterus	0.10	0.58	0.15	0.53	0.01	1	0.88	0.86	0.10	0.57	0.01	0.03	0.15	0.04	0.47	0.03	0.54	0.79	0.33	0.37	0.27	0.05	0.47	0.03	0.03	0.42
Galeus	0.13	0.51	0.16	0.55	0.02	0.83	1	0.87	0.14	0.44	0.02	0.04	0.19	0.05	0.52	0.06	0.60	0.86	0.39	0.47	0.29	0.09	0.44	0.12	0.06	0.58
Scyliorhinus	0.14	0.54	0.18	0.41	0.07	0.78	0.84	1	0.07	0.53	0.02	0.05	0.26	0.10	0.60	0.21	0.76	0.59	0.48	0.47	0.41	0.26	0.32	0.13	0.22	0.63
Scymnorhinus	0.0	0.01	0.0	0.27	0.0	0.08	0.12	0.07	1	0.0	0.0	0.0	0.02	0.0	0.04	0.0	0.04	0.14	0.04	0.07	0.02	0.0	0.11	0.0	0.0	0.05
Lepidopus	0.22	0.66	0.35	0.57	0.01	1.01	0.84	1.04	0.01	1	0.0	0.08	0.18	0.04	0.45	0.08	0.58	0.58	0.36	0.35	0.33	0.23	0.85	0.22	0.63	0.70
Epigonus	0.17	0.06	0.14	0.09	0.36	0.03	0.09	0.09	0.0	0.01	1	1.07	0.61	0.19	0.55	0.05	0.18	0.0	0.32	0.39	0.32	0.15	0.04	0.08	0.56	0.14
Capros	0.33	0.16	0.24	0.14	0.21	0.12	0.17	0.20	0.0	0.17	0.87	1	0.47	0.07	0.39	0.04	0.17	0.03	0.18	0.26	0.19	0.14	0.0	0.29	0.56	0.45
Coelorhynchus	0.22	0.27	0.20	0.37	0.64	0.29	0.39	0.56	0.04	0.20	0.27	0.26	1	0.62	1.05	0.27	0.76	0.22	1.11	1.06	1.04	0.58	0.17	0.21	0.53	0.58
Nezumia	0.13	0.22	0.13	0.36	1.0	0.19	0.23	0.47	0.01	0.10	0.19	0.09	1.41	1	1.42	0.31	0.88	0.09	1.58	1.49	1.49	0.76	0.24	0.11	0.41	0.40
Trachyrhynchus	0.12	0.45	0.38	0.41	0.41	0.62	0.71	0.87	0.07	0.23	0.17	0.14	0.70	0.42	1	0.27	0.90	0.51	0.93	0.89	0.81	0.44	0.17	0.08	0.29	0.56
Chimaera	0.10	0.08	0.09	0.11	0.26	0.12	0.25	0.92	0.0	0.18	0.04	0.04	0.54	0.28	0.81	1	1.34	0.14	0.76	0.62	0.77	1.13	0.07	0.07	1.03	0.86
Gnathophis	0.13	0.44	0.14	0.43	0.21	0.63	0.75	0.98	0.06	0.38	0.05	0.06	0.46	0.24	0.81	0.40	1	0.51	0.71	0.65	0.62	0.51	0.19	0.11	0.42	0.65
Conger	0.02	0.18	0.06	0.81	0.0	0.51	0.59	0.42	0.11	0.21	0.0	0.01	0.07	0.01	0.25	0.02	0.28	1	0.22	0.28	0.13	0.02	0.58	0.02	0.01	0.31
Phycis	0.13	0.34	0.15	0.47	0.49	0.45	0.57	0.71	0.07	0.28	0.10	0.07	0.77	0.48	0.97	0.26	0.82	0.46	1	0.34	0.89	0.49	0.27	0.12	0.30	0.57
Antonogadus	0.13	0.34	0.14	0.48	0.47	0.51	0.69	0.72	0.12	0.27	0.12	0.10	0.75	0.47	0.94	0.22	0.76	0.58	0.34	1	0.85	0.43	0.32	0.12	0.26	0.56
Lepidorhombus	0.21	0.36	0.22	0.94	0.54	0.43	0.50	0.74	0.05	0.31	0.12	0.09	0.87	0.55	1.01	0.32	0.86	0.34	1.07	1.00	1	0.60	0.25	0.21	0.38	0.68
Simphurus	0.23	0.14	0.22	0.44	0.12	0.24	0.24	0.75	0.0	0.20	0.09	0.10	0.77	0.45	0.88	0.75	1.11	0.67	0.93	0.80	0.95	1	0.14	0.24	0.81	0.89
Lophius	0.0	0.06	0.08	0.64	0.03	0.26	0.26	0.20	0.07	0.27	0.0	0.0	0.05	0.03	0.07	0.01	0.09	0.50	0.11	0.13	0.09	0.03	1	0.0	0.02	0.15
Trigla	0.84	0.47	0.83	0.54	0.09	0.12	0.55	0.61	0.02	0.53	0.07	0.35	0.46	0.10	0.27	0.08	0.39	0.10	0.38	0.36	0.55	0.39	0.04	1	0.18	1.51
Notacanthus	0.16	0.09	0.15	0.13	0.31	0.11	0.23	0.87	0.0	0.20	0.05	0.06	0.62	0.33	0.82	0.95	1.29	0.08	0.81	0.67	0.84	1.13	0.13	0.15	1	0.27
Helicolenus	0.35	0.38	0.38	0.57	0.08	0.47	0.69	0.78	0.07	0.44	0.04	0.14	0.33	0.10	0.48	0.24	0.62	0.53	0.47	0.45	0.46	0.36	0.30	0.40	0.28	1

dactylopterus, and *Nezumia aequalis* on *Trachyrhynchus trachyrhynchus*).

Depth Distribution

All the species sampled have a wide depth distribution, except *Trigla lyra*, *Capros aper*, and *Lophius budegasa*, which exhibited a certain degree of habitat restriction in the study area. It should be recalled that all the species in question are found on or near the bottom, and that it is the bottom depth that varies.

Juveniles of most of the species encountered were concentrated over bottoms located in shallower waters than were adults. This positive size-depth correlation is very common in fishes (see Helfman, 1978 and bibliography cited therein), and – as Keast (1978a) has suggested – it may serve to minimize intraspecific competition.

Table 5 reveals that depth distribution overlaps are very high ($\bar{a} = 0.82$). Only *Nezumia aequalis* shows a low overlap value in several species pair interactions. Those for *Lophius budegasa*, *Capros aper*, *Merluccius merluccius*, and *Gnathophis mystax* on *Conger conger* are distinctly the highest.

Vertical separation in the water column is extremely important in comparing habitats (e. g. Alevizon, 1975; Ebeling and Bray, 1976), since this can affect the real overlap values for either the habitat itself and/or the diet (e. g. Keast, 1978b; Macpherson, 1979). This factor has not been taken into account in the present study, and for this reason the overlap values between the species of different guilds may be overestimated to a certain extent (see above).

Niche Breadth

The accurate determination of niche breadth in natural communities is a very difficult question to settle (Hutchinson, 1978), and a realistic value of B implies that predators make distinctions among available resources similar to those assumed by taxonomists (Hespenheide, 1975).

The niche breadth was evaluated for several resource axes (prey type, prey size, and depth distribution), and the separate values were combined. Two methods of combining these values are commonly applied, i. e. product and summation. The former assumes that niche breadth parameters are independent, while the latter assumes that they exhibit a degree of dependence (e. g. May, 1975; Pianka, 1975; Hanski, 1978). However, as these authors have pointed out, the real situation occurring in nature is probably intermediate; May suggested that the choice of one of these two methods should be made after an intuitive evaluation of the problem.

Table 5. Interspecific habitat overlap. Overlaps of species j on species i (α_{ji}) above the diagonal and overlaps of species i on species j (α_{ij}) below

	Gadiculus	Micromesistius	Merluccius	Molva	Hymenocephalus	Etmopterus	Galeus	Scyliorhinus	Scymnorhinus	Lepidopus	Epigonus	Capros	Coelorhynchus	Nezumia	Trachyrhynchus	Chimaera	Gnathophis	Conger	Phycis	Antonogadus	Lepidorhombus	Simphurus	Lophius	Trigla	Notacanthus	Helicolenus
Gadiculus	1	0.95	0.77	0.83	0.65	1.06	0.89	0.91	1.03	1.13	0.74	0.71	0.45	0.24	1.13	1.12	0.78	1.20	1.12	1.07	0.92	0.96	0.71	0.71	0.87	1.02
Micromesistius	0.89	1	0.66	0.72	0.65	1.06	0.98	0.84	1.10	1.09	0.93	0.58	0.85	0.17	1.07	1.07	0.67	1.07	1.09	0.95	1.01	0.98	0.58	0.58	1.02	0.93
Merluccius	1.23	1.11	1	1.05	0.53	1.09	0.84	1.13	1.10	1.24	0.69	0.93	0.61	0.03	1.23	1.29	1.01	1.42	1.22	1.28	1.06	1.14	0.93	0.93	0.85	1.24
Molva	1.17	1.09	0.95	1	0.54	1.09	0.86	1.09	1.10	1.21	0.73	0.87	0.65	0.05	1.21	1.26	0.95	1.36	1.20	1.23	1.05	1.11	0.87	0.87	0.89	1.19
Hymenocephalus	0.45	0.48	0.23	0.26	1	0.96	0.96	0.34	0.75	0.86	0.74	0.19	0.57	0.71	0.88	0.68	0.23	0.68	0.87	0.56	0.64	0.45	0.19	0.19	0.78	0.48
Etmopterus	0.65	0.70	0.43	0.47	0.85	1	0.96	0.56	0.89	0.96	0.80	0.37	0.66	0.49	0.97	0.85	0.43	0.86	0.97	0.74	0.71	0.67	0.37	0.37	0.87	0.69
Galeus	0.56	0.67	0.34	0.39	0.89	0.99	1	0.49	0.89	0.93	0.86	0.28	0.72	0.53	0.93	0.80	0.34	0.77	0.94	0.66	0.69	0.63	0.28	0.28	0.91	0.60
Scyliorhinus	1.07	1.06	0.85	0.90	0.58	1.08	0.90	1	1.16	1.19	0.77	0.72	0.59	1.16	1.19	0.86	1.26	1.16	1.13	1.03	1.07	0.77	0.77	0.93	1.10
Scymnorhinus	0.73	0.83	0.50	0.55	0.77	1.02	0.99	0.66	1	1.00	0.90	0.43	0.79	0.35	1.00	0.93	0.51	0.91	1.01	0.80	0.85	0.80	0.43	0.43	0.89	0.77
Lepidopus	0.73	0.75	0.51	0.55	0.81	1.01	0.94	0.64	0.92	1	0.78	0.45	0.64	0.43	1.0	0.91	0.51	0.94	1.0	0.82	0.75	0.74	0.45	0.45	0.86	0.76
Epigonus	0.57	0.77	0.34	0.40	0.84	1.01	1.06	0.53	0.99	0.94	1	0.27	0.88	0.42	0.93	0.83	0.35	0.75	0.95	0.64	0.82	0.72	0.27	0.27	1.03	0.62
Capros	1.30	1.14	1.08	1.12	0.49	1.10	0.81	1.20	1.10	1.27	0.63	1	0.56	0.0	1.26	1.34	1.08	1.50	1.25	1.35	1.07	1.18	1.00	1.00	0.83	1.31
Coelorhynchus	0.62	0.87	0.37	0.44	0.80	1.02	1.09	0.59	1.07	0.96	1.09	0.30	1	0.32	0.95	0.88	0.38	0.77	0.98	0.67	0.93	0.86	0.30	0.30	1.12	0.67
Nezumia	0.23	0.21	0.02	0.04	1.18	0.90	0.94	0.57	0.56	0.75	0.62	0.0	0.38	1	0.78	0.48	0.02	0.51	0.76	0.38	0.23	0.19	0.0	0.0	0.64	0.26
Trachyrhynchus	0.72	0.73	0.50	0.55	0.82	1.01	0.94	0.63	0.91	1.01	0.77	0.44	0.63	0.44	1	0.90	0.51	0.94	1.00	0.81	0.74	0.72	0.44	0.44	0.87	0.75
Chimaera	0.84	0.85	0.61	0.66	0.73	1.03	0.94	0.75	0.98	1.05	0.79	0.55	0.68	0.32	1.05	1	0.62	1.04	1.05	0.91	0.85	0.84	0.55	0.55	0.89	0.87
Gnathophis	1.22	1.11	0.99	1.04	0.52	1.09	0.84	1.12	1.10	1.23	0.69	0.92	0.62	0.03	1.23	1.28	1	1.41	1.21	1.27	1.05	1.14	0.92	0.92	0.87	1.23
Conger	0.89	0.84	0.66	0.71	0.73	1.03	0.89	0.79	0.95	1.07	0.71	0.60	0.59	0.33	1.08	1.02	0.67	1	1.07	0.97	0.82	0.84	0.60	0.60	0.83	0.91
Phycis	0.72	0.75	0.50	0.54	0.81	1.01	0.95	0.63	0.92	1.00	0.79	0.44	0.66	0.43	1.00	0.91	0.50	0.93	1	0.81	0.75	0.73	0.44	0.44	0.87	0.75
Antonogadus	0.92	0.87	0.70	0.75	0.70	1.04	0.89	0.83	0.97	1.09	0.71	0.64	0.60	0.29	1.09	0.05	0.71	1.13	1.09	1	0.86	0.88	0.64	0.64	0.84	0.91
Lepidorhombus	0.85	0.99	0.62	0.68	0.86	1.05	1.01	0.80	1.10	1.07	0.96	0.54	0.88	0.19	1.05	1.04	0.63	1.02	1.08	0.90	1	0.96	0.54	0.54	1.05	0.89
Simphurus	0.94	1.02	0.70	0.76	0.64	1.06	0.97	0.88	1.10	1.13	0.90	0.63	0.82	0.16	1.09	1.10	0.72	1.11	1.11	0.99	1.01	1	0.63	0.63	1.01	0.97
Lophius	1.30	1.14	1.08	1.12	0.49	1.10	0.81	1.20	1.10	1.27	0.63	1.00	0.56	0.0	1.26	1.34	1.08	1.50	1.25	1.35	1.07	1.18	1	1.00	0.83	1.31
Trigla	1.30	1.14	1.08	1.12	0.49	1.10	0.81	1.20	1.10	1.27	0.63	1.00	0.56	0.0	1.26	1.34	1.08	1.50	1.25	1.35	1.07	1.18	1.00	1	0.83	1.31
Notacanthus	0.63	0.79	0.39	0.45	0.82	1.01	1.03	0.57	0.91	0.96	0.95	0.33	0.84	0.40	0.95	0.86	0.40	0.81	0.97	0.70	0.82	0.74	0.33	0.33	1	0.67
Helicolenus	0.97	0.94	0.75	0.80	0.66	1.05	0.90	0.89	1.02	1.12	0.76	0.68	0.66	0.22	1.11	1.10	0.75	1.17	1.11	1.00	0.92	0.95	0.68	0.68	0.88	1

Breadths along various dimensions appear to be independent (non-significant correlation coefficients were found between the 3 niche parameters: prey size-depth distribution = 0.13; prey type-prey size = 0.24; prey type-depth distribution = 0.09, $P < 0.01$). For this reason, the product method was considered to be the relevant measure of overall niche breadth in the present instance.

Table 6 gives the niche breadths as calculated for each dimension. In each case, two separate estimates of overall niche breadth were computed, one as the product of the 3 parameters mentioned above and the other as the mean value for prey size times prey type multiplied by the depth distribution value. Both values indicate similar trends: *Chimaera monstrosa, Trigla lyra, Notacanthus bonapartei*, and *Capros aper* present the narrowest overall niches, while selachians (*Galeus melastomus, Etmopterus spinax, Scyliorhinus canicula*, and *Scymnorhinus licha*) and *Conger conger* have the widest, with a larger number of specialist species being observed in the benthic than in the epibenthic guild. These results agree with those obtained by Margalef (1968), who suggested that the number of specialist species is usually larger in more

mature systems (benthos) than in fluctuant systems (epibenthos).

The selachians and, as a rule, other generalist species have certain advantages over specialist species, since they have better control over their environment and are better able to cope with fluctuations in food availability. Moreover, the selachians considered here have a very large and well-developed liver, which allows them to go without food for a rather protracted period of time (e. g. Springer, 1969; Macpherson, in press). In addition, the reproduction rate for these species is very low (e. g. Capape, 1974). As has been pointed out by Margalef (1974), these species may stabilize their populations by decreasing the flow of energy to reproduction.

The greater breadth of the niche of another generalist species, *Conger conger*, may be due to its very distinctive habits, specifically, the fact that only large individuals reproduce, dying thereafter (e. g. Wheeler, 1969). This means that they must be able to react swiftly to changes in the environment in which they live in order to be able to compensate for possible fluctuations, thus ensuring the maximum individual survival rate and thereby at least a minimally acceptable parental population level.

Table 6. Niche breadths for different dimensions and overall niche breadths. (A) Product of three dimensions. (B) Habitat × average prey type and prey size (see text)

Species	Prey type	Prey size	Habitat	Overall niche breadths (A)	(B)
Gadiculus	0.11	0.05	0.61	0.003	0.05
Micromesistius	0.16	0.09	0.65	0.009	0.08
Merluccius	0.15	0.07	0.39	0.004	0.04
Molva	0.03	0.43	0.43	0.006	0.10
Hymenocephalus	0.12	0.05	0.88	0.005	0.07
Etmopterus	0.19	0.20	0.99	0.038	0.19
Galeus	0.30	0.21	0.96	0.060	0.24
Scyliorhinus	0.18	0.22	0.52	0.021	0.10
Scymnorhinus	0.10	0.25	0.86	0.022	0.15
Lepidopus	0.08	0.11	0.94	0.008	0.09
Epigonus	0.10	0.05	0.78	0.004	0.06
Capros	0.09	0.06	0.33	0.002	0.02
Coelorhynchus	0.11	0.10	0.63	0.007	0.07
Nezumia	0.12	0.05	0.54	0.003	0.05
Trachyrhynchus	0.03	0.15	0.95	0.004	0.09
Chimaera	0.03	0.05	0.82	0.001	0.03
Gnathophis	0.12	0.17	0.39	0.008	0.06
Conger	0.24	0.31	0.75	0.056	0.21
Phycis	0.08	0.15	0.95	0.011	0.11
Antonogadus	0.15	0.14	0.71	0.015	0.10
Lepidorhombus	0.15	0.12	0.66	0.012	0.09
Simphurus	0.17	0.08	0.63	0.009	0.08
Lophius	0.15	0.36	0.33	0.017	0.08
Trigla	0.04	0.05	0.33	0.001	0.01
Notacanthus	0.03	0.06	0.85	0.002	0.04
Helicolenus	0.14	0.18	0.65	0.016	0.10

Overall Overlap

As in the case of niche breadth, comparisons between niche parameters can reveal interdependence or independence. Several authors (e. g. Schoener, 1968, 1974; Pianka and Pianka, 1976; Ross, 1977; Hespenheide, 1975) have found either negative or positive correlation among various parameters. In this study, the relationships indicate that the parameters are considerably independent: prey size-depth distribution = 0.04, and prey type-depth distribution = 0.01 (the prey type-prey size relationship, at 0.37, P < 0.01, constituting an exception). Therefore, the product of depth distribution times the mean value of prey type times prey size is probably the best measure for estimating overall overlap.

Table 7 lists the overall overlap values. Some species pairs show high values (e. g. *Molva dypterigia macrophthalma* on *Conger conger, Trigla lyra* on *Simphurus nigrescens, T. lyra* on *Helicolenus dactylopterus*, and *Gnathophis mystax* on *H. dactylopterus*). However, as several authors have pointed out (e. g. Keast, 1978b; Macpherson, 1977, 1979), some of these values may be overestimated, because there are other factors which are likely to exert an influence on the overall overlap (e. g. feeding at different heights in the water column, seasonal fluctuations in diets, etc.).

On the other hand, it is extremely useful to know how these significant values are distributed among the different size groups. As several authors have indicated (see review by Helfman, 1978), ontogenic differences in diet and depth distribution appear to be the rule in fishes.

Table 8 presents the overall overlap values between size groups of species pairs exhibiting high values in Table 7, it being observed, in general, that high values appear in only a few pairs of size groups.

As has just been referred to above, seasonal variations in diet and depth distribution are of considerable importance in the estimation of real overlap. For instance, the overlap values of *Molva* on *Conger conger* are generally low, except between *Molva's* smallest size group and the 40–49 cm size group of *C. conger*. This higher value is chiefly attributable to the fact that both size groups feed basically on *Gadiculus argenteus argenteus*. Nevertheless, this value is overestimated, since these two species make use of this resource in different seasons; *M. d. macrophthalma* feeds on *Gadiculus argenteus argenteus* primarily in spring and summer, whereas *C. conger* preys on this same species mainly in autumn and winter. It was found that high overlap values for depth distribution between these size groups were only significant during summer and autumn.

Similar examples can also be cited, as for instance *Molva d. macrophthalma* on *Lophius budegasa*, with high overlaps for small specimens of *Molva* on the 20–29 cm size group of *L. budegasa*. As in the preced-

Table 7. Overall overlap (habitat × average prey type-prey size). Overlaps of species j on species i (α_{ji}) above the diagonal and overlaps of species i on species j (α_{ij}) below

	Gadiculus	Micromesistius	Merluccius	Molva	Hymenocephalus	Etmopterus	Galeus	Scyliorhinus	Scymnorhinus	Lepidopus	Epigonus	Capros	Coelorhynchus	Nezumia	Trachyrhynchus	Chimaera	Gnathophis	Conger	Phycis	Antonogadus	Lepidorhombus	Simphurus	Lophius	Trigla	Notacanthus	Helicolenus
Gadiculus	1	0.60	0.32	0.19	0.09	0.32	0.34	0.43	0.01	0.42	0.25	0.36	0.17	0.02	0.22	0.06	0.24	0.08	0.24	0.37	0.36	0.20	0.02	0.29	0.08	0.75
Micromesistius	0.35	1	0.19	0.11	0.03	0.91	0.91	0.69	0.03	0.68	0.21	0.08	0.14	0.01	0.42	0.03	0.29	0.47	0.33	0.37	0.28	0.06	0.10	0.07	0.03	0.38
Merluccius	0.34	0.21	1	0.30	0.02	0.31	0.37	0.41	0.02	0.48	0.04	0.14	0.19	0.01	0.15	0.04	0.18	0.67	0.21	0.28	0.23	0.12	0.33	0.25	0.05	0.69
Molva	0.03	0.13	0.23	1	0.01	0.39	0.72	0.46	0.10	0.09	0.01	0.02	0.03	0.01	0.08	0.01	0.13	1.47	0.11	0.15	0.40	0.02	0.96	0.03	0.01	0.15
Hymenocephalus	0.06	0.03	0.01	0.04	1	0.03	0.13	0.05	0.10	0.01	0.22	0.03	0.41	0.36	0.61	0.10	0.10	0.05	0.70	0.44	0.63	0.18	0.02	0.01	0.14	0.08
Etmopterus	0.07	0.32	0.06	0.14	0.01	1	0.65	0.30	0.05	0.31	0.04	0.01	0.05	0.01	0.23	0.01	0.13	0.41	0.18	0.17	0.11	0.02	0.11	0.01	0.01	0.18
Galeus	0.06	0.28	0.06	0.13	0.01	0.56	1	0.28	0.08	0.26	0.05	0.01	0.07	0.04	0.27	0.02	0.11	0.46	0.23	0.20	0.13	0.06	0.11	0.02	0.03	0.24
Scyliorhinus	0.17	0.40	0.09	0.23	0.02	0.55	0.57	1	0.05	0.44	0.06	0.04	0.12	0.02	0.35	0.13	0.44	0.92	0.38	0.41	0.36	0.17	0.23	0.05	0.10	0.53
Scymnorhinus	0.0	0.24	0.01	0.08	0.0	0.07	0.01	0.03	1	0.0	0.0	0.0	0.01	0.0	0.02	0.0	0.01	0.10	0.02	0.03	0.01	0.0	0.05	0.0	0.0	0.02
Lepidopus	0.20	0.56	0.21	0.16	0.01	0.60	0.62	0.50	0.01	1	0.08	0.05	0.06	0.01	0.23	0.04	0.15	0.34	0.18	0.27	0.13	0.05	0.23	0.05	0.04	0.28
Epigonus	0.21	0.28	0.03	0.02	0.27	0.09	0.19	0.08	0.0	0.08	1	0.18	0.29	0.04	0.26	0.02	0.03	0.0	0.15	0.16	0.13	0.08	0.01	0.04	0.08	0.04
Capros	0.72	0.27	0.24	0.08	0.07	0.10	0.12	0.17	0.0	0.18	0.38	1	0.04	0.0	0.25	0.03	0.09	0.03	0.11	0.23	0.10	0.08	0.0	0.15	0.02	0.36
Coelorhynchus	0.08	0.12	0.04	0.08	0.27	0.15	0.21	0.20	0.02	0.10	0.17	0.04	1	0.22	0.58	0.12	0.22	0.14	0.66	0.50	0.64	0.49	0.03	0.03	0.18	0.29
Nezumia	0.02	0.02	0.01	0.01	0.63	0.09	0.24	0.13	0.01	0.04	0.07	0.0	0.40	1	0.70	0.11	0.01	0.04	0.66	0.38	0.19	0.15	0.0	0.0	0.17	0.08
Trachyrhynchus	0.06	0.16	0.03	0.10	0.23	0.03	0.68	0.29	0.03	0.19	0.07	0.03	0.46	0.46	1	0.14	0.46	0.36	0.72	0.95	0.37	0.72	0.04	0.02	0.12	0.23
Chimaera	0.04	0.03	0.03	0.04	0.10	0.06	0.12	0.35	0.0	0.09	0.01	0.02	0.20	0.14	0.45	1	0.43	0.07	0.41	0.31	0.33	1.01	0.02	0.34	0.88	0.46
Gnathophis	0.17	0.26	0.08	0.25	0.19	0.39	0.38	0.77	0.03	0.24	0.02	0.03	0.26	0.01	0.62	0.26	1	0.79	0.78	0.79	0.76	0.55	0.19	0.06	0.18	1.03
Conger	0.01	0.15	0.16	0.36	0.02	0.33	0.45	0.43	0.07	0.14	0.0	0.01	0.04	0.01	0.14	0.01	0.19	1	0.20	0.24	0.18	0.04	0.30	0.01	0.01	0.36
Phycis	0.05	0.14	0.06	0.13	0.26	0.28	0.45	0.35	0.05	0.14	0.04	0.02	0.37	0.15	0.57	0.12	0.43	0.44	1	0.47	0.70	0.34	0.13	0.03	0.13	0.50
Antonogadus	0.16	0.24	0.09	0.19	0.20	0.33	0.43	0.42	0.06	0.23	0.07	0.04	0.33	0.13	0.64	0.12	0.44	0.53	0.41	1	0.60	0.40	0.15	0.04	0.11	0.51
Lepidorhombus	0.17	0.20	0.09	0.35	0.43	0.26	0.36	0.44	0.03	0.17	0.05	0.02	0.49	0.07	0.55	0.17	0.48	0.43	0.85	0.68	1	0.41	0.15	0.07	0.20	0.58
Simphurus	0.12	0.07	0.08	0.08	0.16	0.06	0.20	0.36	0.0	0.11	0.04	0.03	0.48	0.08	0.60	0.54	0.51	0.43	0.62	0.61	0.60	1	0.05	0.15	0.02	0.56
Lophius	0.01	0.10	0.21	0.54	0.01	0.25	0.35	0.32	0.08	0.39	0.0	0.0	0.03	0.0	0.04	0.01	0.14	0.89	0.16	0.20	0.20	0.04	1	0.0	0.01	0.46
Trigla	0.55	0.27	0.45	0.30	0.02	0.07	0.23	0.38	0.01	0.34	0.02	0.18	0.13	0.0	0.17	0.62	0.25	0.11	0.26	0.27	0.32	1.11	0.03	1	0.40	1.11
Notacanthus	0.05	0.04	0.03	0.03	0.13	0.07	0.12	0.25	0.0	0.10	0.02	0.01	0.26	0.17	0.39	0.86	0.26	0.03	0.39	0.23	0.34	0.89	0.02	0.23	1	0.15
Helicolenus	0.22	0.21	0.22	0.23	0.03	0.32	0.52	0.54	0.04	0.26	0.01	0.07	0.28	0.03	0.28	0.13	0.56	0.80	0.49	0.53	0.52	0.33	0.31	0.16	0.14	1

Table 8. Interspecific overall overlap between various size groups of different species pairs. The values represent overlaps of row species on column species. Size groups: 0 = 5–9 cm; I = 10–19; II = 20–29; III = 30–39; IV = 40–49; V = 50–59; VI = 60–69

Left block

		Conger II	III	IV	V	VI
Molva	I	0.05	0.25	0.74	0 26	0.11
	II	0.06	0.41	0.63	0.26	0.16
	III	0.04	0.27	0.33	0.49	0 16

		Conger II	III	IV	V	VI
Scyliorhinus	I	0.24	0.57	0.35	0.11	0 01
	II	0.09	0.43	0.69	0 42	0.20
	III	0.05	0.42	0.63	0.35	0.23
	IV	0.07	0 34	0.78	0.45	0.26

		Conger II	III	IV	V	VI
Lophius	I	0.09	0 50	0.81	0.12	0 11
	II	0.08	0.30	0.38	0.12	0.03
	III	0 08	0.64	0.69	0.09	0.07
	IV	0 03	0.41	0.38	0.13	0.05

		Conger II	III	IV	V	VI
Gnathophis	II	0.48	0.79	0.04	0.07	0.03
	III	0 33	0.76	0.27	0.11	0.04
	IV	0 56	0.53	0.25	0.33	0.06

		Conger II	III	IV	V	VI
Helicolenus	I	0.15	0.40	0 53	0.08	0 08
	II	0.25	0.53	0.42	0.21	0.05
	III	0 40	0.71	0.60	0.59	0.21

		Chimaera II	III	IV	V	VI
Notacanthus	II	0.88	0.84	0.63	1.13	0.29

		Lepidorhombus 0	I	II
Phycis	0	0.99	1.11	0.12
	I	0.36	0.64	0.28
	II	0.38	0.49	0 48
	III	0.04	0.21	0 44

		Lepidorhombus 0	I	II
Gnathophis	II	0 86	1.20	0.16
	III	0.41	0.72	0.16
	IV	0.37	0.56	0.23

		Helicolenus 0	I	II
Gadiculus	0	0.68	0.73	0.03
	I	0.16	0.33	0.02

Middle block

		Galeus I	II	III	IV	V
Micromesistius	I	0.88	0.29	0 07	0.02	0.01
	II	1.25	0.54	0.11	0.02	0.09
	III	0.55	0.45	0.10	0.03	0.03

		Scyliorhinus I	II	III	IV
Gnathophis	II	0.90	0.56	0.25	0.04
	III	0.80	0.85	0.37	0.52
	IV	0.56	0.67	0.52	0.33

		Lophius I	II	III	IV
Molva	I	0.29	0.79	0.22	0.16
	II	0.55	0.44	0.09	0.01
	III	0.09	0.21	0.03	0.03

		Phycis 0	I	II	III
Trachyrhynchus	I	0.35	0 77	0 93	0.05
	II	0.22	0.73	0.77	0.07
	III	0.04	0.53	0.50	0.07

		Phycis 0	I	II	III
Gnathophis	II	1 06	1.49	1.10	0.09
	III	0.54	0 79	0 95	0.06
	IV	0 44	0 71	1 21	0.19

		Phycis 0	I	II	III
Lepidorhombus	0	0 56	0.95	0.81	0.01
	I	0 35	0.89	0.97	0.08
	II	0 06	0.45	1.07	0.26

		Phycis 0	I	II	III
Hymenocephalus	I	0 12	0.69	0.54	0.00

		Etmopterus I	II	III
Micromesistius	I	0.73	0.22	0.01
	II	0.98	0.30	0.01
	III	0 65	0.25	0.02

		Trachyrhynchus I	II	III
Nezumia	I	0 28	0 73	0 07
	II	0 26	0.79	0.11
	III	0.11	0.61	0.39

		Trigla 0	I	II
Helicolenus	0	0.45	0 50	0 44
	I	0.17	0.20	0 19
	II	0.02	0 04	0 29

Right block

		Helicolenus 0	I	II
Gnathophis	II	0.65	1.34	0.43
	III	0.42	1.06	0.33
	IV	0.36	0.97	0.56

		Gadiculus 0	I
Capros	0	0.59	0 11
	I	0.98	0 20

		Simphurus 0	I
Chimaera	II	1.38	0.78
	III	1 41	0.77
	IV	1.56	1.03
	V	1.12	0.84
	VI	0.12	0.40

		Simphurus 0	I
Trachyrhynchus	I	0.65	1 03
	II	0.41	0 62
	III	0.05	0.07

		Simphurus 0	I
Trigla	0	1.06	0.50
	I	0.93	0.46
	II	0.54	0.31

		Simphurus 0	I
Notacanthus	II	1.29	0.71

		Antonogadus 0	I
Trachyrhynchus	I	0.89	0.97
	II	0 62	0.78
	III	0.22	0.52

		Antonogadus 0	I
Gnathophis	II	1.38	1.06
	III	0.81	0.83
	IV	0.62	0 66

ing case, this is mainly due to the presence of *Gadiculus argenteus argenteus* in the diets of both predators, this prey item, however, being captured by *L. budegasa* in the spring and autumn, *M. d. macrophthalma* taking it especially in the autumn and winter. *Scyliorhinus canicula* on *Conger conger* also gives large values, especially for the 40–49 cm size groups. These size groups feed principally on *Gadiculus argenteus argenteus*, *Micromesistius poutassou*, and *Engraulis encrasicholus*, all of which, as in the previous cases, appear in the diets of the different predators in different seasons. There are like cases among

epibenthic species, e. g. *Capros aper* and *Gadiculus argenteus argenteus*, which share two primary resources (*Meganyctiphanes norvegica* and *Nyctiphanes couchii*), using them in different seasons. As some of these cases relate to different guilds that probably inhabit, for the most part, different heights in the water column, the values for depth overlaps, and consequently overall overlaps, may be overestimated.

There are important overlaps between 10–30 cm long specimens of *Micromesistius poutassou* on the smaller size groups of *Galeus melastomus*. These size groups feeed mainly on *Meganyctiphanes norvegica*,

Table 9. Summary of community matrices for each dimension and for each guild. Expected number of species was obtained from Vandermeer's tables (1972)

	$\bar{\alpha}$	Covariance	Number of species observed	Number of species expected
Prey-type overlap	0.17	0.002	26	22
Prey-size overlap	0.36	0.009	26	13
Depth distribution overlap	0.82	−0.01	26	10
Benthic guild (overall overlap)	0.36	0.054	14	5
Epibenthic guild (overall overlap)	0.18	0.005	12	20

with high values being recorded in spring and autumn, at which times this prey species is particularly abundant (Macpherson, 1977). However, their diets are rather different during the rest of the year. *M. potassou* on *Etmopterus spinax* presents a similar situation.

In general, benthic species exhibit diets and depth distribution undergoing little or no seasonal changes, and for this reason significant values remain practically constant all year long (Macpherson, 1977, 1979). For instance, *Chimaera monstrosa, Simphurus nigrescens, Trigla lyra*, and *Notacanthus bonapartei*, which base their diets on ophiuroids, benthic crustaceans, and other benthic organisms, exhibit high overlap values for various size groups throughout the year. Other similar cases can be observed between *Phycis blennoides, Trachyrhynchus trachyrhynchus, Nezumia aequalis, Gnathophis mystax, Lepidorhombus boscii*, and *Antonogadus megalokynodon* on other benthic species feeding mainly on *Alpheus glaber, Calocaris macandreae*, and other benthic crustaceans.

There are other factors affecting estimations of overlap, e. g. the differences in the vertical distribution of the various species already referred to above, differences in diel resource utilization, etc. Such diel feeding patterns have been observed in various fish species (e. g. Bray and Ebeling, 1975; Ebeling and Bray, 1976; Keast and Welsh, 1968; Hobson, 1974).

For the most part, the species considered in the present study did not present important variations between daytime and nighttime activity (Macpherson, 1977), with the exception of *Gnathophis mystax*, which has strictly nocturnal habits (Macpherson, 1977; Rucabado et al., 1978). This tends to indicate that the overall overlaps of this species on the other species are to some extent overestimated.

DISCUSSION

The analysis of overlaps between niche parameters shows that interaction between parameters reduces competition and allows species to coexist (e.g. Schoener, 1974; Brown, 1975; Pianka, 1975; Keast 1978a, b). Segregation of and competition between species may

be the result of combinations of several niche aspects (depth distribution, diet, etc.), one of these possibly being preponderant over the others (e.g. Schoener, 1974). Hespenheide (1975) found in bird communities that it is easier for a species to adjust its foraging zone or method to avoid competition than it is to change its food habits. Schoener (1974) showed that habitat separation is far more effective than food separation in preventing species overlap, though it is less frequently important in aquatic than in terrestrial animals. Other authors (e. g. Gascon and Legget, 1977 and papers cited therein) have found that food is the principal mechanism behind ecological segregation in most freshwater fish communities.

Analysis of the covariance of α_{ij} and α_{ji} and of the mean value of α for each niche dimension separately shows how the species are packed (Vandermeer, 1972; Hespenheide, 1975). Covariance values for the calculated overlap and the mean value of α (Table 9) indicate that the species are more closely packed with respect to depth distribution than to food (one would expect 10 species in the community on the basis of depth distribution, and 13 and 22 on the basis of prey size and prey type, respectively). This result, therefore, implies that the diet dimension is, at least in the community studied, the most important factor contributing to the segregation of fish species and also to the avoidance of possible competition, which agrees with the results of Fryer and Iles (1972), Gascon and Legget (1977), Keast (1978a) and others.

Fishes in general change their diet and habitat with size, hence it can be argued that fish species occupy several niches or subniches simultaneously (Deselle et al., 1978; Keast, 1978a; Margalef, 1978), as has been argued with regard to the males and females of some bird species (see Hutchinson, 1978 and papers cited therein). The overlap analysis between species size-groups shows that most species pairs with significant overlaps present high values in only a few size-group pairs. Furthermore, some of these also exhibit a seasonal or diel pattern of resource partitioning, so the overlap values as calculated may be overestimated. It can be observed from the results obtained that some species utilizing the same resources in actual fact

exploited them at different times or in different situations, thus reducing the real level of overlap between them.

On the other hand, overlap values increase when a resource peaks in abundance and several species are attracted to it; overlaps tend to be smallest when food is relatively scarce (Zaret and Rand, 1971; Lowe-McConnel, 1975; Macpherson, 1977; Keast, 1978a). This was particularly apparent in the present study for those size groups of epibenthic predator species feeding on prey items undergoing substantial seasonal fluctuations in abundance, e. g. *Meganyctiphanes norvegica* and *Sergestes arcticus* (Franqueville, 1971; Macpherson, 1977). This was not the case for benthic predators, which feed on prey items that undergo no significant seasonal variations (Camp, pers. comm.). These high overlap values are not sufficient evidence of competition, for, as Pianka (1976) has pointed out, 'overlap need not necessarily lead to competition unless resources are in short supply'.

However, as Brown (1975) suggested, indirect evidence of interspecific competition comes from inverse correlations of predator abundance. There is a strong inverse relationship between the abundance of comparable predator species or comparable predator species size groups (Table 1) using similar resources, especially in benthic species (e. g. *Lepidorhombus boscii* on *Phycis blennoides*, *Trachyrhynchus trachyrhynchus* on *P. blennoides*, and *Notacanthus bonapartei* on *Simphurus nigrescens*). Roughgarden (1974) found similar results in coral reef fish communities.

Vandermeer (1972) and Culver (1974) have shown that lower covariance values indicate the coexistence of a greater number of species, which in turn implies lower levels of competition. Table 9 shows the covariance values of community matrices for each guild (epibenthic and benthic). The data indicate that the covariance of the epibenthic guild may be lower than that of the benthic guild. Therefore, although both communities possess mechanisms designed to avoid competition, such competition is more likely in the benthic than in the epibenthic guild. As Margalef (1974) pointed out, if the supply of resources is fluctuating rather than constant (e. g. epibenthic and pelagic prey items) several species can coexist and segregation is less than when the supply of available resources is uniform and stable (benthic prey items).

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