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Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean

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Abstract

The Macrouridae are the most common fish caught in demersal trawls on the continental slope and rise of the Rockall Trough. They represented 41% of all fish caught, with *Coryphaenoides rupestris* amounting to 28% of the catch. No previous study of the trophic interaction of these fish has been made over a wide bathymetric range. Samples were obtained at 250-m intervals of depth between 400 and 2 900 m in the period 1975 to 1981. The stomachs of 5 326 fish belonging to 12 species were examined to define their diets. Eight species are primarily benthopelagic feeders while four are primarily epibenthic feeders. The bathymetric centres of distribution of the populations of the benthopelagic feeding *Trachyrhynchus murrayi, Malacocephalus laevis, Coryphaenoides rupestis, C. guentheri, Nematonurus armatus, Chalinura brevibarbis, C. leptolepis* and *C. mediterranea* are different from each other. Similar differences in bathymetric distribution occurred among the epibenthic feeding *Nezumia aequalis, Coelorhynchus coelorhynchus, C. occa* and *Lionurus carapinus.* These differences decrease competition among species that exploit similar resources.

Introduction

The continental slope and rise of the Rockall Trough extend through a bathymetric transect ranging from approximately 400 to 2 900 m depth. The resources exploited by the fish are not uniform throughout this transect nor do the distributions of the individual species of fish extend throughout it. Earlier studies, such as those of Pearcy and Ambler (1974) and Sedberry and Musick (1978), concentrated on defining the diets of the marourids without taking account of partitionment of the bathymetric range. Macpherson (1979, 1981) collected fish from 200 to 800 m depth in the western Mediterranean from successive 200-m zones; this bathymetric transect, however, is restrictive in terms of the distributions of the macrourids as is the range of 750 to 1 100 m from which Du Buit (1978) obtained samples in the vicinity of the Wyville Thomson Ridge.

The object of the present study was to examine the diets of the macrourids of the continental slope and rise through a total bathymetric range of 400 to 2 900 m partitioned at approximately 250-m intervals. It forms part of a more comprehensive study of the biology and trophic inter-relationships of the pelagic and demersal fish of the Rockall Trough (Mauchline and Gordon, 1983 a, b).

Material and methods

Macrourids occurred in the demersal samples collected from various regions and bathymetric zones of the Rockall Trough as described by Mauchline and Gordon (1983 a, b). About 11 000 fish, comprising 12 species, were caught and 5 326 of them were examined for food. Measurement of the body length of individuals was often inaccurate because of a broken or regenerated tail. Consequently, total body length and head length were both measured on undamaged fish and the biometrical relationship between these measurements determined for each species. Total length was then calculated from head length of individuals with damaged tails.

The German Expedition referred to later is a cruise of the F.F.S. "Walther Herwig" to the Rockall Trough in October, 1981 during which some supplementary observations were made.

A similarity index is employed to compare the diets within and between species. Bloom (1981) and Wallace (1981) have discussed the relative merits of various such indices and, on the basis of their comparisons, Czekanowski's Quantitative Index, also known as the Bray-Curtis Index and Schoener Index, is used

$$S_{jk} = \frac{2 \min (\chi_{ij}, \chi_{ik})}{(\chi_{ij} + \chi_{ik})}$$

where χ_{ij} and χ_{ik} are the Cn values of comparable items in species j and k, the minimum values being summed. The indices are multiplied by 100 so that they range from 0 to 100 instead of from 0 to 1. Crustacean fragments occurring among the stomach contents are usually, but not always, derived from the identified crustaceans recorded in the stomachs. Consequently, they are omitted from the calculation of the similarity index.

Diets of species

Trachyrhynchus murrayi Günther, 1887

This species was caught in the 1 000- to 1 500-bathymetric zones. Only 28 (Fig. 1) of the 636 examined had food present (Table 1), with most fish having everted stomachs. The particle size of the food is small and the diet consists predominantly of copepods and amphipods supplemented by a variety of other organisms. No obvious changes in the diet take place as the fish increase in size. A further 18 fish were caught at depths of 1 200 to 1 500 m on the Hebridean Terrace by the German Expedition and 12 of them had empty stomachs; four fish had only unidentifiable soft tissues in their stomachs while one had a *Sergestes arcticus* and six calanoid copepods; a sixth fish had fragments of polychaetes, amphipods and decapods.

This species feeds on benthopelagic organisms although the occurrence of *Balanus hameri* and polychaetes suggests that it may also forage on the sediment surface. The total quantities of food within the stomachs were small and although all stomachs except one contained unidentifiable soft tissues, the volume of these tissues was not large and they could have originated from the crustaceans.

Geistdoerfer (1978) examined 34 stomachs and found a diet dominated by decapod crustaceans, fish, mysids and supplemented by copepods, polychaetes and gastropod molluscs.

Nezumia aequalis (Günther, 1878)

This species occurred in demersal trawls in the 750- and 1 000-m bathymetric zones; only a single fish was caught in the 1 250-m zone and none in the 500-m zone. A total of 1 013 individuals were examined, 164 of which had everted stomachs and 75 empty stomachs. Two modal size groups of fish were present in the samples (Fig. 1). The diet consists of a wide variety of organisms (Table 1) dominated by amphipods, which occurred in approximately 80% of all stomachs with food and represented 50 to 60% of its volume. The bulk of the crustacean fragments recorded were derived from amphipods. Unidentifiable soft tissue also occurred in 80% of the stomachs but was fragmented and only represented about 10% by volume of the contents. Some of this tissue was recorded as "cephalopod mollusc" but, since only a single cephalopod beak was found, this identification is probably wrong. Calanoid copepods occurred in about 35% of the stomachs; their body size was small and they are thus a minor dietary component. The mysids, mostly 8 to 12 mm in body length, are significant components, being 20 to 25% of the volume of the food. Benthic polychaetes, isopods, decapods and brittle stars are minor but significant contributors to the diet.

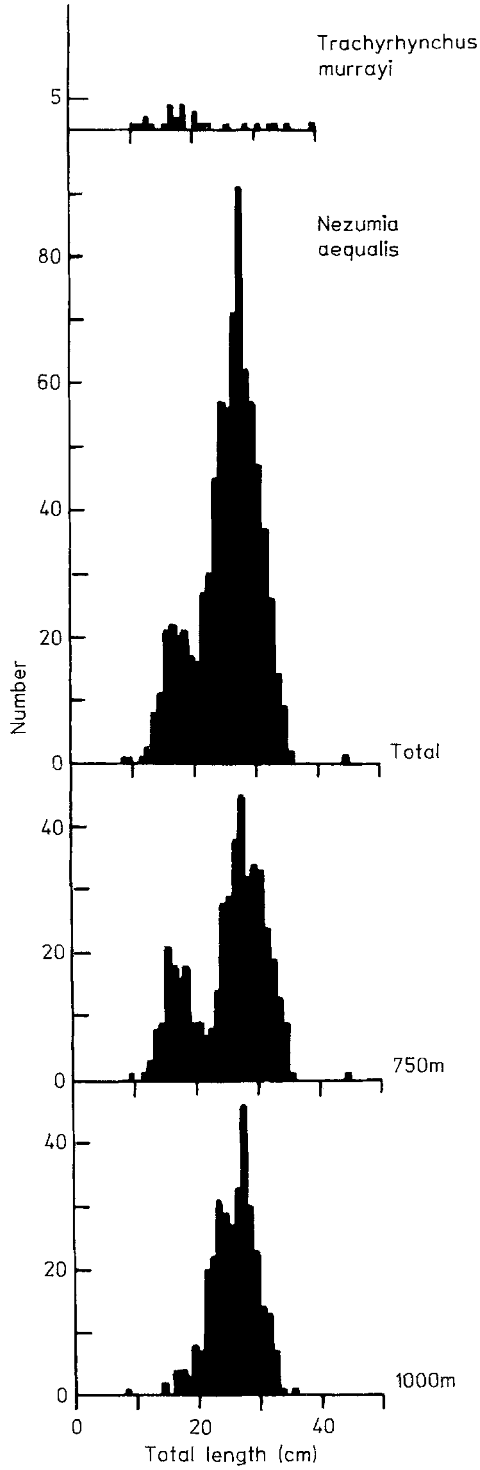

Fig. 1. Macrouridae. Frequency distributions of total body lengths of fish with food present in their stomachs. *Nezumia aequalis* caught at 750 and 1 000 m are shown separately

The samples were taken throughout the year and were analysed to discover any seasonal changes in the diet but none was apparent. The diets of the fish within the two size modes caught at 750 m depth (Fig. 1) are shown in Table 1. The similarity index is 94 (Table 7) and so no ontogenetic changes in the diet are evident. The larger fish probably eat more mysids, decapods and brittle stars than smaller fish, these being the largest organisms occurring in the diet. The fish caught in the 1 000-m zone are comparable in size to the larger fish caught at 750 m depth (Fig. 1), but any differences in their diets in the two zones probably reflect the bathymetric distributions of the prey organisms; the similarity index is 78 (Table 7).

The diet, although consisting of a wide variety of prey, has a very limited size spectrum. The decapods consumed were juvenile and of the same general body size as the amphipods and mysids. The lack of larger organisms in the food is a feature of this species. All organisms eaten are epibenthic or closely associated with the sediment surface. No hyperiid amphipods or pelagic ostracods were present in the stomachs.

Geistdoerfer (1978) examined 21 stomachs and recorded a diet of polychaetes, amphipods and mysids supplemented by ostracods, copepods, isopods, cumaceans and decapods. Marshall and Merrett (1977) found that 44 *Nezumia aequalis* caught off northwest Africa had been feeding on mixed crustaceans, mainly copepods and ostracods, and polychaetes. Merrett and Marshall (1980) presented an analysis of the contents of the stomachs of 52 fish stating that a diet of copepods and polychaetes was supplemented by mysids and amphipods. No details of the species of prey are given, although they remark that *N. aequalis* feeds on a mixed diet of pelagic and benthic organisms. Its diet in the western Mediterranean has been examined in a sample of 135 stomachs with food by Macpherson (1979, 1981). Polychaetes represented 33% and the benthic decapod *Calocaris macandreae* a further 32.4% by weight of the food; amphipods represented 7.4%, the mysid *Pseudomma* sp. 6.6% and brittle stars 10.4% by weight. The remaining 10% of the diet consisted of copepods, cumaceans, ostracods, isopods, euphausiids, tanaids, and other benthic decapods. Macpherson (1983), examining populations off Namibia, found a diet dominated by copepods and supplemented by polychaetes and amphipods. Du Buit (1978) found amphipods and brittle stars, supplemented by decapod crustaceans, in four stomachs of *N. aequalis* caught in the region of the Wyville Thomson Ridge. These data confirm the epibenthic nature of the diet.

Malacocephalus laevis (Lowe, 1843)

This species occurred in demersal trawls in the 500-m bathymetric zone. The 15 fish with food present ranged in total length from 32.5 to 54.0 cm. Their diet is shown in Table 1 and is dominated by small *Munida bamffica* of 4- to 10-mm carapace length and by fragments of fish, eye lenses being very common.

Koefoed (1927) found a crustacean decapod, *Chlorotocus* sp., of 10-cm length, some schizopods (mysids and/or euphausiids), isopods and copepods in the stomach of a fish of 45-cm length. Marshall (1973) records squid beaks in a stomach while Okamura (1970), examining the stomach contents of nine fish from the Pacific coast of Japan, found euphausiids, squid and bottom sediment. These few data indicate a benthopelagic diet.

Coelorhynchus coelorhynchus (Risso, 1810)

This species was caught in demersal trawls in the 500- to 750-m bathymetric zones. The diet is varied (Table 1) but dominated by decapod crustaceans, especially young *Munida bamffica* of 5- to 7-mm carapace length, and by amphipods and polychaetes with isopods and mysids as supplementary items. The particle size of the food is small, the majority of the decapods being young juveniles. Amphipods, although the commonest item, were 5 to 10 mm in total length and, considered on a weight/volume basis, are less important than the decapods as a dietary component. Polychaetes are most common in the diet of the larger fish (Table 1) along with isopods (also epibenthic) while copepods, the mysid *Pseudomma affine* and several juvenile decapods are more common in that of the smaller fish. The larger fish tend to live deeper than the smaller fish (Fig. 2) and so some apparent ontogenetic changes in the diet may reflect the bathymetric distributions of the prey organisms. The similarity index of the diets at 500 and 750 m is 64.

Macpherson (1979, 1981) described the diet from an examination of 160 stomachs of fish caught in the western Mediterranean. Polychaetes represented 50% by weight of the food. Decapod crustaceans were important, especially to the larger fish, but were dominated by the benthic *Calocaris macandreae*. Amphipods contributed only 5% of the weight of the food. Other organisms were also present but were primarily benthic in habit.

Du Buit (1978) only reported on the contents of six stomachs, and these consisted of mixed crustaceans. Geistdoerfer (1973, 1974, 1977, 1978) studied the diet, buccal morphology and digestive system of this species. The food consisted of small organisms closely associated with the water-sediment interphase, being dominated by amphipods, euphausiids, decapods, polychaetes and isopods but supplemented by a variety of other organisms.

Coelorhynchus occa (Goode and Bean, 1886)

This species occurred in demersal trawls over a wide bathymetric range of 1 000 to 2 000 m (Fig. 2). The diet consists of small organisms and is dominated by copepods supplemented by polychaetes, amphipods, mysids and small quantities of unidentifiable soft tissues (Table 1). The small copepod *Aetideopsis multiserrata* is eaten by all sizes of fish, with as many as 40 individuals occurring

Table 1. Diets of macrourids. Dominant prey species are named while the incidence and numbers of rare identified species in various taxonomic orders are given. F: percentage of stomachs containing food that had each item present; Cn: each item is expressed as a percentage of the total numbers of prey items; r: occurs at less than 0.1% of prey items

Species	*Trachyrhynchus murrayi*		*Nezumia aequalis*						*Malacocephalus laevis*		*Coelorhynchus coelorhynchus*				*Coelorhynchus occa*			
Bathymetric zone (m)			750				1 000											
Size class (cm)			8.0–21.4		21.5–45.0						19.0–31.4		31.5–43.0		7.6–27.0		27.1–38.0	
	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn
Polychaeta	14.3	1.9	11.6	1.6	7.2	0.8	3.1	0.5			30.2	3.2	60.9	8.6	42.9	6.5	36.3	5.1
Cirripedia	3.6	0.5																
Ostracoda	7.1	1.4	3.6	0.5	4.8	0.5	4.3	0.6	6.7	1.0							4.5	0.5
Copepoda, unidentified	21.4	8.6	6.3	1.0	4.8	0.5	5.2	1.1			5.7	0.4	3.1	0.4	7.1	0.9	27.3	4.1
Aetideus armatus	14.3	4.8	4.5	0.8	5.1	0.6	13.5	2.7					3.1	0.3	14.3	2.8	4.5	0.5
Aetideopsis multiserrata	53.6	19.6	18.8	3.6	23.6	3.5	35.2	12.7			32.1	3.5	7.8	1.0	42.9	54.6	63.6	59.2
Rare species: Cn (number of species)		0.5(1)		0.1(1)		0.6(7)		0.3(3)								2.8(2)		3.5(5)
Cumacea					0.6	r	0.6	0.1					1.6	0.1				
Amphipoda, unidentified	42.9	19.6	65.1	35.3	74.6	38.1	72.2	37.2	13.3	2.0	83.0	21.3	85.9	35.4	42.9	6.5	18.2	2.6
Ampelisca spp.			21.4	5.3	18.5	3.6	17.4	6.4			9.4	0.7	12.5	4.3	7.1	1.9		
Erichthonius hunteri			11.6	11.8	17.6	6.6	0.9	2.2					1.6	0.6				
Rare species: Cn (number of species)		12.5(3)		2.1(7)		3.3(18)		1.6(13)				1.7(6)		1.5(4)				
Isopoda, unidentified	3.6	0.5	2.7	0.3	2.7	0.3	4.9	0.9			7.5	0.5	25.0	6.7	7.1	0.9	9.1	1.0
Rare species: Cn (number of species)				0.1(1)		0.1(2)		0.2(4)				0.1(1)		0.1(1)		0.9(1)		
Tanaidacea	3.6	0.5	3.4	0.5	1.2	0.1	0.3	0.3										
Mysidacea, fragments											5.7	0.4						
Erythrops microps			8.0	1.6	10.4	1.8	0.3	r			1.9	0.1	3.1	0.4				
Pseudomma affine	3.6	0.5	35.7	13.0	46.9	16.2	5.2	1.1			22.6	3.6	10.9	1.7	7.1	0.9		
Rare species: Cn (number of species)		1.0(1)		0.3(2)		0.4(4)		0.4(4)				0.3(3)		0.7(2)		2.8(2)		
Euphausiacea																		
Meganyctiphanes norvegica							0.3	r	6.7	1.0	5.7	0.7			7.1	0.9	4.5	0.5
Decapoda, fragments	10.7	1.4	3.6	0.5	2.4	0.2	1.5	0.2	13.3	2.0	28.3	2.7	9.4	1.3				
Pandalina brevirostris			0.9	0.1	2.1	0.2	0.3	r			37.7	11.4	3.1	0.3				
Pontophilis norvegicus	3.6	1.0			11.0	1.1	11.6	1.8			11.3	1.0	9.4	1.0				
Pontophilus spinosus					0.3	r					11.3	1.0	1.6	0.1				
Philocheras echinulatus			2.7	0.3	7.8	0.9					17.0	1.9	14.1	2.0				
Crangonid fragments	3.6	0.5	2.7	0.3	7.2	0.9	6.1	0.9			7.5	0.5	10.9	1.1				
Munida bamffica			0.9	0.2	4.2	0.5	1.8	0.3	73.3	27.6	66.0	19.1	31.3	15.5			4.5	0.5
Larvae											22.6	15.1			7.1	0.9		
Rare species: Cn (number of species)				0.1(1)		0.3(5)		0.4(5)				0.5(4)		0.4(4)				
Pycnogonida							0.6	0.1										
Crustacean fragments	75.0	10.0	64.3	8.3	73.1	7.2	68.8	9.3	13.3	2.0	64.2	4.2	51.6	4.6	14.3	1.9	40.9	4.6

Mollusca																		
Bivalvia					1.2	0.1	0.3	r							7.1	0.9		
Cephalopoda, tissues			10.7	1.4	13.1	1.3	4.3	0.6			13.2	0.9	18.8	1.7			4.5	0.5
beak			0.9	0.1					6.7	1.0			3.1	0.3				
Echinodermata																		
Amphipholis squamata							0.3	0.2										
Ophiocten sp.			7.1	1.2	17.0	2.6	20.8	4.5									22.7	2.6
Chaetognatha									6.7	1.0			1.6	0.1				
Egg					0.3	r	0.9	0.1										
Pisces, fragments	3.6	0.5							66.7	12.2			1.6	0.1			4.5	0.5
scale	14.3	1.9			1.8	0.2	0.9	0.1	20.0	3.1	3.8	0.2	15.6	1.4			27.3	3.1
lens									86.7	40.8			1.6	0.1				
otolith									13.3	4.1								
Unidentifiable tissues	96.4	12.9	72.3	9.4	77.3	7.6	89.9	12.1	13.3	2.0	69.8	4.6	85.9	7.9	100	13.0	95.5	10.7
No. of fish examined	636		131		426		456		24		55		102		50		109	
% with everted stomachs	92.1		3.1		18.5		17.8		0		1.8		26.5		46		65.1	
% with empty stomachs	3.5		11.5		2.8		10.5		37.5		1.8		10.8		26		14.7	
% with unrecognizable food	0.2		0.8		1.6		2.2		0		1.8		0		0		0.9	
% with recognizable food	4.2		84.7		77.0		69.5		62.5		94.5		62.7		28		19.3	
No. of prey items	209		864		3 411		2 422		98		807		717		108		196	

within a single stomach. Small amphipods are eaten more commonly by smaller fish while brittle stars and fish fragments only occurred in the stomachs of larger fish. There is a tendency for larger fish to live deeper than smaller fish (Fig. 2). A comparison was made between the diets of fish caught in the 1 000-, 1 250- and 1 500- to 2 000-m bathymetric zones (Table 2). Brittle stars were consumed at the two shallower zones while copepods were eaten more frequently in the deepest zones; this could indicate a more benthic diet at shallower depths than in the deeper regions.

Koefoed (1927) found a portion of an ascidian, *Sergestes* sp., an ostracod and copepod fragments in the stomach of a single fish. Marshall and Merrett (1977) recorded polychaetes and crustaceans (unidentified) as the food of a single fish while Du Buit (1978), examining two fish, found amphipods and natant decapods that were not identified. McLellan (1977) notes that two fish had been feeding on isopods and polychaetes. Marshall and Iwamoto (1973) listed myctophid fish, copepods, decapods and a pagurid crab in the stomachs of three fish. These last are the largest organisms recorded in the diet and such organisms may only be consumed on rare occasions or only in certain regions.

Coryphaenoides rupestris Gunnerus, 1765

This species was caught in demersal trawls over a bathymetric range of 750 to 1 750 m (Fig. 3). The diet consists predominantly of copepods, decapods and fish supplemented by mysids, euphausiids, amphipods and cephalopod molluscs when considered on a weight or volume basis. Other organisms occur in the food but are relatively unimportant because of their low frequency or small body size. The diets of the different size classes show ontogenetic changes (Table 3) and these are reflected in the values of the similarity indices shown in Table 7. The smallest fish feed predominantly on calanoid and cyclopoid copepods supplemented by a variety of other small organisms; a small but significant quantity of soft unidentifiable tissues is also present among the food. The diets of the three size classes of larger fish show progressive changes in composition with increasing size of the fish (Table 3). Calanoid copepods remain a major constituent but cyclopoid copepods are not present in the food of the largest fish. Amphipods, mysids, euphausiids, decapods and especially fish all become increasingly prominent in the diets of the largest *Coryphaenoides rupestris.*

The food of *Coryphaenoides rupestris* in different bathymetric zones was examined (Table 4). The size distributions of the fish in these zones is shown in Fig. 3. The distribution of size classes with depth is irregular, the medium size range 21.5 to 63.4 cm in length, of fish occurring deeper. Polychaetes are significant components of the diet of this size range of fish in the 1 500- to 1 750-m depth zones and there is also an increase in the proportion of unidentifiable soft tissues present among the contents.

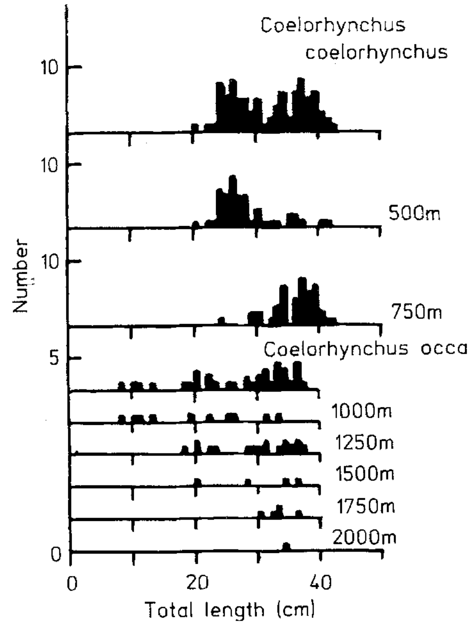

Fig. 2. Macrouridae. Frequency distributions of total body length of the total samples of *Coelorhynchus* species with food present in their stomachs. The partitioning of the size classes between the different bathymetric zones is also shown

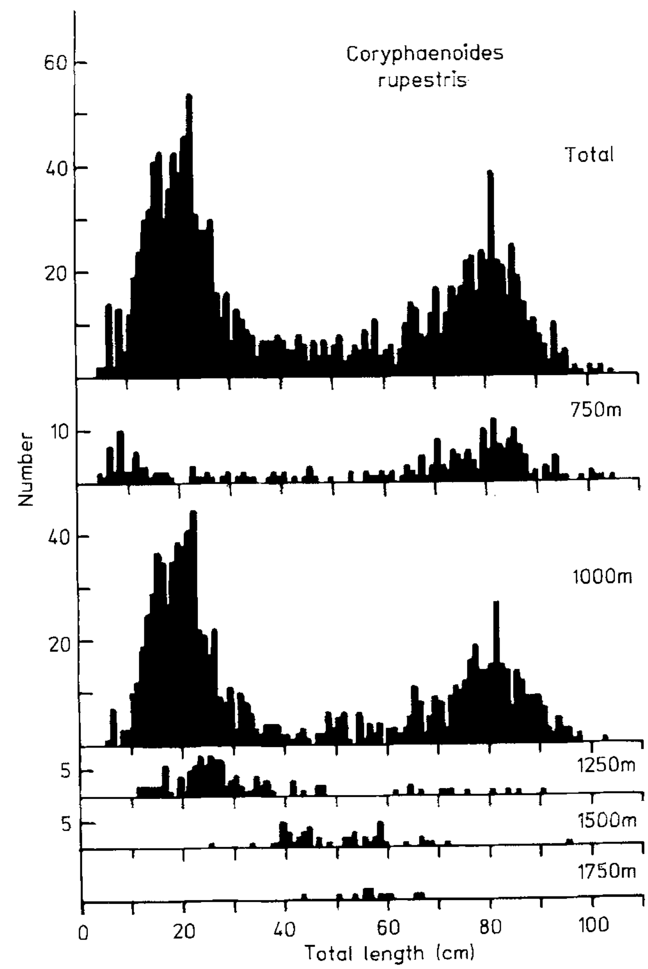

Fig. 3. *Coryphaenoides rupestris.* Frequency distribution of total body lengths of the entire sample with food present in their stomachs and of the corresponding samples taken within each bathymetric zone

Table 2. *Coelorhynchus occa.* Similarity indices for the diets in different bathymetric zones, showing the number (*n*) of full stomachs examined

Zone	*n*	1 250	1 500	1 750
1 000	10	78	52	56
1 250	25		61	65
1 500	18			88
1 750	13			

Other changes in the diet probably reflect the bathymetric distributions of the prey organisms.

Podrazhanskaya (1968) examined the diet of 1 182 fish ranging in length from 46 to 170 cm and caught at depths of 400 to 750 m off southwest Iceland. A further 685 (37%) had stomachs that were empty. The diet was dominated by the decapod *Pasiphaea* sp. as previously indicated by the few stomachs examined by Nordgaard (1917) from Norwegian waters. Euphausiids, copepods, amphipods, cephalopods and fish were supplementary items. Du Buit (1978) examined 135 full stomachs of fish caught near the Wyville Thomson Ridge at depths of 700 to 1 100 m; their length ranged from 45 to 100 cm. The decapod *Pasiphaea tarda* dominated the diet and *Meganyctiphanes norvegica* and *Gnathophausia zoea* were common. Many other organisms were present as supplementary items. Copepods, including *Euchaeta* spp., were only minor components. All these analyses are comparable to those of the diets of the largest size classes examined in the Rockall Trough. The main difference between those diets and that in the Rockall Trough is the insignificance of the copepods in them. The diet of the Rockall Trough fish is apparently more diverse than those described from other areas.

Coryphaenoides guentheri (Vaillant, 1888)

This species also occurs over a wide bathymetric range, 1 000 to 2 500 m (Fig. 4). A further 39 fish, ranging in total length from 20 to 47 cm, were obtained by the 1981 German Expedition at depths of 1 500 to 1 750 m. The individual lengths of the fish were not measured and so they are not included in Fig. 4. The data from their stomach contents, however, are included in the analysis in Table 3.

The diet consists predominantly of copepods and amphipods supplemented by mysids and a wide variety of other organisms. The mysids, because of their larger body size, are significant components. There are differences between the diets of the different size classes (Table 7). The smallest fish, 8.0 to 24.4 cm in length, occur predominantly in the 1 000- to 1 250-m bathymetric zones (Fig. 4) and feed on small amphipods supplemented by calanoid copepods and to a lesser degree by polychaetes and a variety of other small organisms. The other two size classes of larger fish are absent from the 1 000- to 1 250-m bathymetric zones, occurring at depths of 1 500 to 2 500 m

Table 3. Diets of *Coryphaenoides* species. Further details as in legend to Table 1

	Coryphaenoides rupestris Size class (cm)								*Coryphaenoides guentheri* Size class (cm)					
	4.0–12.4		12.5–21.4		21.5–63.4		63.5–105.0		8.0–24.4		24.5–39.4		39.5–48.0	
	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn
Coelenterata					0.2	r	1.2	0.1						
Polychaeta	1.4	0.2	16.4	1.5	27.3	2.6	9.0	0.8	50	5.2	31.3	3.1	54.2	5.1
Cirripedia, larvae	15.9	2.2	24.3	2.3	9.2	0.9	0.2	r	2	0.2				
Ostracoda	8.7	1.8	13.2	2.0	11.3	1.8	11.3	1.5	8	0.8	9.5	0.7	10.4	0.8
Copepoda, unidentified	42.0	17.2	35.6	14.1	38.0	17.4	21.1	5.9	18	9.2	61.1	30.1	37.5	13.7
Aetideopsis multiserrata	23.2	5.7	37.2	9.9	38.2	13.3	28.3	7.1	36	13.4	48.5	38.2	60.4	44.2
Euchaeta norvegica	7.2	1.8	20.5	6.0	21.3	9.7	33.2	17.1			0.8	0.1	4.2	0.3
Euchaeta spp.	2.8	0.4	7.5	1.1	8.7	1.5	8.8	1.2			2.6	0.3	4.2	0.4
Xanthocalanus profundus									2	0.2	5.3	0.4	10.4	1.0
Pleuromamma robusta	4.3	1.0	11.7	17.5	15.4	16.3	18.0	15.5						
Rare species: Cn (number of species)		0.4(2)		5.4(12)		7.6(26)		11.8(42)				0.5(9)		0.2(1)
Cyclopoida	18.8	43.4	20.8	20.5	8.5	1.7			2	0.2	0.8	0.1		
Cumacea									6	0.6	3.1	0.2	4.2	0.3
Amphipoda unidentified	5.8	1.0	3.5	0.7	8.5	4.3	11.1	3.9	88	54.4	68.7	13.0	45.8	13.7
Ampelisca spp.	1.4	0.4	1.6	0.6	1.5	1.0	2.3	2.5	4	0.6				
Rare species: Cn (number of species)				0.1(1)		0.2(3)		0.5(7)		1.0(5)		0.2(6)		
Isopoda, unidentified			0.9	0.1	3.8	0.5			14	2.4	12.2	1.3	10.4	0.8
Rare species: Cn (number of species)						(1)		1.3(1)		0.2(1)				
Tanaidacea									12	1.4	3.8	0.3	4.2	0.3
Mysidacea, fragments			0.9	0.1	0.9	0.1	0.2	r	2	0.2	5.3	0.6	6.3	0.8
Boreomysis spp.	7.2	1.8	1.8	0.3	6.2	1.0	2.4	0.3			1.5	0.1	4.2	0.4
Rare species: Cn (number of species)				0.1(2)		0.6(4)		2.8(4)		1.8(5)		1.8(13)		3.9(8)
Euphausiacea, fragments					0.4	r	1.6	0.2						
Meganyctiphanes norvegica	1.4	0.2	0.9	0.1	1.5	0.3	11.5	3.9			0.4	r		
Rare species: Cn (number of species)						r(1)		0.2(2)						
Decapoda, fragments	1.4	0.6	3.2	0.3	7.9	1.1	5.3	0.7	2	0.2	2.3	0.2	2.1	0.2
Pasiphaea tarda			2.8	0.3	4.1	0.5	23.4	3.9	2	0.4				
Rare species: Cn (number of species)				0.2(3)		0.9(10)		1.9(12)		0.4(2)		0.3(7)		0.4(2)
Crustacean, fragments	49.3	6.7	73.5	6.9	65.7	6.3	45.9	3.8			1.9	0.1		
Mollusca														
Gastropoda											0.4	r	2.1	0.2
Bivalvia											9.9	0.9	16.7	1.5
Cephalopoda, tissues					2.1	2.2	3.5	0.3			0.8	0.1	2.1	0.2
beak					3.2	0.4	18.4	2.2			0.4	0.1		
Echinodermata														
Ophiocten sp.											0.8	r	4.2	0.3
Spatangoidea											0.4	r		
Holothuroidea											0.4	r	2.1	0.2
Chaetognatha	24.6	3.3	11.4	1.1	3.4	0.3	0.8	r						
Ctenophora/Salpidae					1.3	0.1	3.3	0.3						
Larvaceae					0.2	0.1	0.6	0.7						
Pisces, fragments			2.2	0.2	11.3	1.1	46.5	3.8			0.8	r		
scale			0.3	r	3.0	0.3	8.4	0.7			8.4	0.6	12.5	1.0
lens					0.9	r	1.4	0.1	2	0.2				
Xenodermichthys copei					0.2	r	0.8	r						
Notolepis rissoi							0.4	r						
Synaphobranchus kaupi							0.8	r						
Unidentified species					0.2	r	0.8	r						
Egg											0.4	r	2.1	0.2
Unidentified tissues	89.9	12.1	92.4	8.7	81.2	7.7	84.6	7.0	70	7.0	88.5	6.4	87.5	6.9
No. of fish examined	78		375		769		945		59		410		75	
% with everted stomachs	5.1		12.5		33.8		41.3		15.3		32.2		30.7	
% with empty stomachs	6.4		2.9		5.2		7.1		0		3.9		5.3	
% with unrecognizable food	9.0		10.4		4.7		5.6		3.4		3.7		8.0	
% with recognizable food	79.5		74.1		56.3		46.0		81.4		60.2		56.0	
No. of prey items	511		3362		4925		5921		500		3650		613	

Table 4. *Coryphaenoides rupestris.* Similarity indices for the diets in different bathymetric zones, showing the number (*n*) of full stomachs examined

Zone	*n*	1 000	1 250	1 500	1 750
750	230	60	37	26	25
1 000	952		49	32	34
1 250	113			42	48
1 500	84				58
1 750	36				

Table 5. *Coryphaenoides guentheri.* Similarity indices for the diets in different bathymetric zones, showing the number (*n*) of full stomachs examined.

Zone	*n*	1 500	1 750	2 000	2 200	2 500
1 250	30	41	52	34	32	36
1 500	50		78	82	83	65
1 750	65			68	67	56
2 000	75				92	59
2 200	111					60
2 500	48					

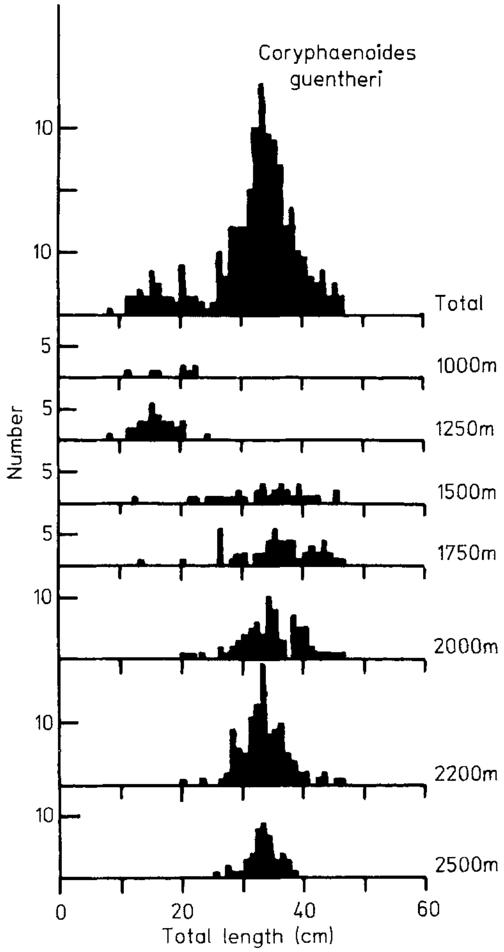

Fig. 4. *Coryphaenoides guentheri.* Frequency distribution of total body lengths of the entire sample with food present in their stomachs and of the corresponding samples taken within each bathymetric zone

(Fig. 4). Copepods are more important relative to amphipods in their diets and mysids and a variety of other organisms contribute significantly.

The rather different diet of the fish in the 1 250-m zone from that of fish in deeper zones (Table 5) is probably a direct result of the smaller size of the fish and their selection of smaller sized prey organisms. Bathymetric differences in the diets of the larger fish reflect the bathymetric distributions of the food organisms as well as an increasing ability to feed on larger organisms.

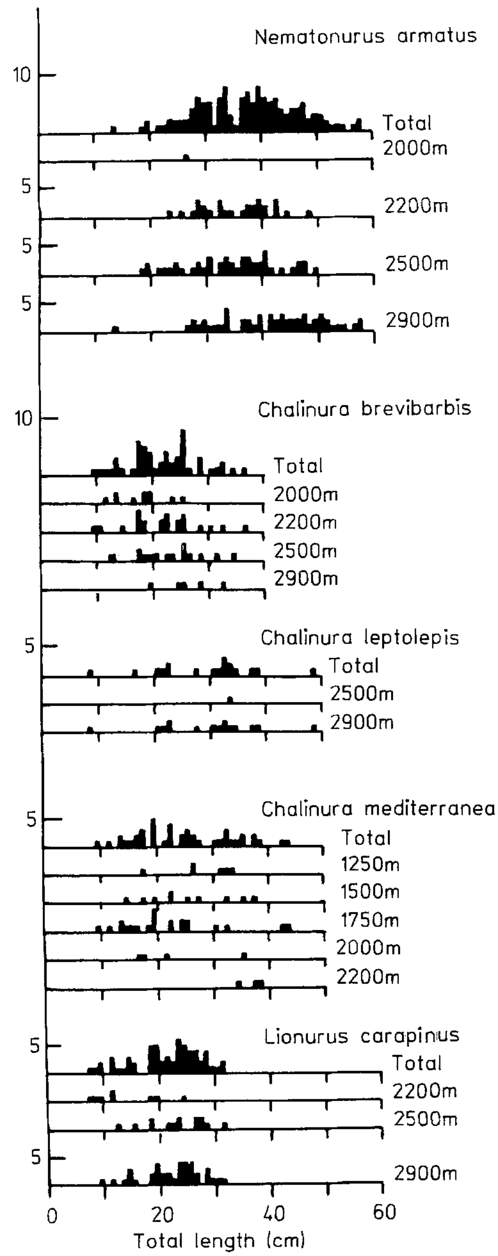

Fig. 5. Macrouridae. Frequency distributions of total body lengths of the entire samples with food present in their stomachs of different species and also of the corresponding samples taken within each bathymetric zone

Nematonurus armatus (Hector, 1875)

This species was caught in demersal trawls over a depth range of 2 000 to 2 900 m (Fig. 5). It was, however, most common at depths of 2 500 to 3 000 m and its distribution probably extends well beyond 3 000 m south of the Rockall Trough. Its diet consists of a large variety of organisms. The smaller fish, however, feed more commonly on copepods and amphipods supplemented by mysids while the larger fish include an increased proportion of decapods, squid and fish (Table 6). Larger fish tend to live deeper than smaller fish (Fig. 5) and so ontogenetic changes in the diet will also reflect the distributions of the prey organisms, although the similarity index of 82 (Table 7) shows that the diet is relatively constant.

The food described here in the Rockall Trough is very similar to that described by Haedrich and Henderson (1974) and Sedberry and Musick (1978) in the western Atlantic and by Pearcy and Ambler (1974) in the eastern Pacific off Oregon. Pearcy and Ambler found that benthic crustaceans were most common in the diets of the smaller fish whereas cephalopods and fish were of increased importance in the diets of the larger fish. Haedrich and Henderson (1974) found a similar situation in which the smaller fish had a predominantly benthic diet. This is not entirely true in the Rockall Trough where few strictly benthic organisms occur in the diet and then only as minor components, a situation found in the ten fish examined by Sedberry and Musick (1978). This species appears to feed on organisms in the water column immediately above the sea bed in the Rockall Trough rather than select organisms from off the surface of the sediment. This is supported by the general lack of sediment among the stomach contents, only 5% of stomachs with food containing any.

Chalinura brevibarbis Goode and Bean, 1896

This species was caught in demersal trawls in the 1 750- to 2 900-m bathymetric zones (Fig. 5), but principally in the 2 000- to 2 500-zones. Its diet is mixed, but dominated by amphipods, mysids and calanoid copepods. The similarity index for the diets of the smaller and larger fish (Table 7) is 73. The smaller fish tend to eat more polychaetes and amphipods than larger fish which have higher proportions of mysids, decapods and probably squid in their diets (Table 6). Calanoid copepods are eaten to the same extent by all sizes of fish. There is a tendency for larger fish to occur in deeper zones than smaller fish (Fig. 5), but the number of fish sampled is small and the overlap of sizes between zones such that the present data cannot be used to examine bathymetric changes in the diet.

Chalinura leptolepis (Günther, 1877)

This species was caught in demersal trawls in the 2 500- to 2 900-m bathymetric zones but principally in the 2 900-m zone (Fig. 5). It feeds on a variety of organisms (Table 6), the amphipods being numerically, and by weight, dominant. Polychaetes had only been eaten by the seven fish less than 29 cm in total length and these seven fish had also consumed 75% of the copepods but only 25% of the amphipods found in all stomachs. Mysids, decapods, *Ophiocten* sp. and fish remains only occurred in the stomachs of fish greater than 29-cm total length. Only 17 fish had food present and so these data are only indicative of ontogenetic changes in the diet.

Pearcy and Ambler (1974) found that this species depended upon crustaceans for its food in the eastern Pacific off Oregon. Benthic crustaceans were most important in the diet of smaller fish while pelagic crustaceans became more dominant in that of larger fish.

Chalinura mediterranea Giglioli, 1893

This species was caught in demersal trawls in the 1 250- to 2 200-m bathymetric zones (Fig. 5), but extends to the 2 500-m zone. A further 20 fish were caught in the 1 500- and 1 750-zones by the 1981 German Expedition. They were not measured individually and so are not included in Fig. 5; their ranges of length were determined relative to the two size classes in Table 6 and so they are included in the analysis given there.

The diet consists of a range of organisms dominated by crustaceans. Copepods are dominant numerically but on a weight basis are probably co-dominant with amphipods and mysids. The larger fish eat fewer copepods and more mysids and decapods than the smaller fish (Table 6); the similarity index for these diets (Table 7) is 82.

Lionurus carapinus (Goode and Bean, 1883)

This species occurred in demersal trawls in the 2 200- to 2 900-m bathymetric zones (Fig. 5); it is most numerous in the 2 900-m zone and its distribution extends deeper in regions to the south of the Rockall Trough. Many of the fish were damaged and measurements of their total body length are only approximate or are derived from measurements of head length.

The diet consists of polychaetes, amphipods and isopods supplemented by a variety of other small organisms (Table 6). A significant proportion of the stomach contents consists of unidentifiable soft tissues. The smaller fish tend to consume more copepods, cumaceans and amphipods than the larger fish, which supplement their diet with other organisms; the similarity index for these diets (Table 7) is 73. No obvious relationship between the size of the fish and its depth of occurrence is present in Fig. 5, and so bathymetric changes in diet reflect distributions of prey organisms rather than ontogenetic changes.

Haedrich and Polloni (1976) examined 108 stomachs, 84 of which contained food, of this species in the western

Table 6. Diets of macrourids. Further details as in legend to Table 1

	Nematonurus armatus Size class (cm)				*Chalinura brevibarbis* Size class (cm)				*Chalinura leptolepis*		*Chalinura mediterranea* Size class (cm)				*Lionurus carapinus* Size class (cm)			
	14.0–35.5		35.5–59.0		9.0–21.4		21.5–38.0				9.0–21.0		21.1–46.0		7.0–20.4		20.5–33.0	
	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn	F	Cn
Polychaeta	19.6	1.9	17.3	2.8	46.2	6.7	20.7	2.1	35.3	5.0	23.1	1.8	11.8	1.4	45.8	9.6	36.1	12.4
Echiurida	2.0	0.2	7.4	1.2														
Sipunculida			1.2	0.2														
Nemertea			1.2	0.2														
Cirripedia, cypris					3.8	0.6												
Ostracoda	5.9	1.4	1.2	0.2			13.8	2.1							4.2	0.9		
Copepoda, unidentified	43.1	8.3	9.9	3.4	50.0	14.0	48.3	15.2	47.1	17.6	80.8	61.2	55.9	45.4	12.5	2.6		
Aetideopsis multiserrata	27.5	6.4	6.2	1.8	30.8	6.7	27.6	7.6	5.9	0.8	11.5	8.8	26.5	13.4	12.5	6.1	2.8	0.9
Euchaeta spp.	5.9	0.5	1.2	0.2	11.5	1.7	20.9	2.4			7.6	0.6	5.8	0.6			2.8	0.9
Xanthocalanus profundus	39.2	17.3	19.8	6.9			13.8	1.4	5.9	0.8	7.6	0.9	8.8	0.8				
Xanthocalanus spp.	27.5	4.9	24.7	6.7	11.5	3.4	10.3	1.4										
Rare species: Cn (number of species)		6.8(7)		1.8(5)		2.3(3)		3.0(4)		1.6(2)		0.6(1)		0.6(2)				
Cyclopoida	5.9	0.5	3.7	0.6														
Harpacticoida			2.5	1.6											8.3	1.7		
Cumacea	5.9	0.5			3.8	0.6	3.4	0.3			7.7	0.6			12.5	4.3		
Amphipoda, unidentified	52.9	21.7	43.2	18.5	69.2	30.2	75.9	23.4	76.5	40.3	61.5	10.6	32.4	9.8	66.7	39.1	47.2	31.0
Rare species: Cn (number of species)		3.4(4)		3.2(4)										0.3(1)		6.1(3)		6.3(4)
Isopoda, unidentified	13.7	3.2							11.8	2.5	3.8	0.3	2.9	0.3	20.8	5.2	25.0	9.7
Tanaidacea			2.5	0.4	3.8	0.6									8.3	1.7	8.3	2.7
Mysidacea, fragments	3.9	0.4	1.2	0.2	3.8	0.6	6.9	1.0	11.8	1.7	3.8	0.3	2.9	0.3				
Boreomysis spp.	2.0	0.2	1.2	0.2	11.4	1.8	27.5	3.8			23.0	2.4	26.4	5.9				
Dactylerythrops gracilura			2.5	0.4	7.7	1.1	13.8	3.4			7.7	0.6	8.8	0.8				
Amblyopsoides ohlinii	11.8	1.6	1.2	0.2	11.5	5.0	17.2	6.9	5.9	0.8			5.9	0.6				
Paramblyops rostrata	3.9	0.5			7.7	1.1	3.4	0.3			7.7	0.6	8.8	0.8				
Rare species: Cn (number of species)		0.7(2)		2.4(3)		1.2(2)						0.3(1)		0.6(2)				
Nebaliacea	2.0	0.2					6.9	0.7										
Euphausiacea													2.9	0.3				
Decapoda	19.6	1.8	28.4	2.6	7.7	1.1	3.4	0.3	23.5	3.4	3.8	0.3	11.7	1.1			2.8	0.9
Acanthephyra pelagica	5.9	0.5	14.8	2.8					5.9	0.8								
Nematocarcinus ensifer							6.9	0.7			3.8	0.6	20.6	5.0				
Rare species: Cn (number of species)		1.0(2)		2.0(5)				0.9(3)						0.3(1)				
Pycnogonida							3.4	0.3										
Crustacean fragments	58.8	5.3	44.4	7.1	26.9	3.9	24.1	2.4	41.2	5.9	19.2	1.5	23.5	2.2	4.2	0.9	2.8	0.9
Mollusca, shells	2.0	0.2															2.8	0.9

Gastropoda															4.2	0.9		
Bivalvia							3.4	0.3							4.2	0.9	11.1	3.5
Cephalopoda, tissues	2.0	0.2	7.4	1.2	3.8	0.6			11.8	1.7	3.8	0.3					2.8	0.9
beak	9.8	1.3	14.8	3.6	7.7	1.1	6.9	5.9	17.6	2.5	3.8	0.3	2.9	0.3	8.3	1.7	2.8	0.9
lens							6.9	0.7					5.9	0.6				
Echinodermata																		
Ophiocten sp.					3.8	0.6			5.9	0.8							2.8	0.9
Holothuroidea	2.0	0.2	1.2	0.2														
Chaetognatha			1.2	0.2	34.6	5.0	31.0	3.1			23.1	1.8	14.7	1.4				
Pisces, fragments	33.3	3.0	58.0	9.3					5.9	0.8			5.9	0.6			2.8	0.9
scale	11.8	1.1	9.9	1.6	7.7	1.1	3.4	0.3	11.8	1.7	7.7	0.6	8.8	0.8	4.2	0.9	2.8	0.9
lens	2.0	0.2					10.3	1.0	5.9	0.8			5.9	0.6				
Micromesistius poutassou			1.2	0.2														
Unidentified species	2.0	0.2																
Egg							3.4	0.3										
Unidentified tissues	96.1	8.7	93.8	15.0	65.4	4.5	82.8	8.3	70.6	10.1	57.7	4.5	55.9	5.3	83.3	17.4	80.6	25.7
No. of fish examined	101		242		26		30		22		30		68		30		38	
% with everted stomachs	48.5		65.7		0		3.3		22.7		13.3		41.2		0		0	
% with empty stomachs	1.0		0.4		0		0		0		0		8.8		20.0		5.3	
% with unrecognizable food	2.0		0.8		0		0		0		3.3		2.9		6.7		15.8	
% with recognizable food	48.5		32.6		100		96.7		77.3		83.3		47.1		73.3		78.9	
No. of prey items	566		507		179		290		119		330		357		115		113	

Atlantic off New England; the diet consisted almost entirely of benthic organisms and is closely similar to that found here. No ontogenetic changes were observed except that ophiuroids were not eaten by the smallest fish. Geistdoerfer (1978), investigating five stomachs, listed three polychaetes, eleven copepods, seven amphipods, one isopod and five mysids. The present data suggest that this species in the Rockall Trough also feeds close to the sediment surface although no sediment occurred among the stomach contents.

Bathymetric distribution and comparison of the diets

Macrourids occur throughout the entire demersal range of depth, 400 to 2 900 m, in the Rockall Trough. They accounted for 41% of the total number of fish caught, 28% of which were the single species *Coryphaenoides rupestris.* The trawls were taken at 250-m intervals of depth down the Hebridean Terrace (Mauchline and Gordon, 1983 a) and the bathymetric range of each species can be approximated (Fig. 6). The species are grouped in Fig. 6 and Table 7 according to whether their diet defines them as predominantly benthopelagic or epibenthic feeders. Their vertical placement in Fig. 6 indicates a gradient from entirely benthopelagic feeders (*Coryphaenoides* spp.) to predominantly epibenthic feeders such as *Nezumia aequalis.*

Seasonal variation exists within the diets of each species but the total number in most species is insufficient to examine this aspect. Table 8 shows comparisons of the diets determined on single samples of *Coryphaenoides*

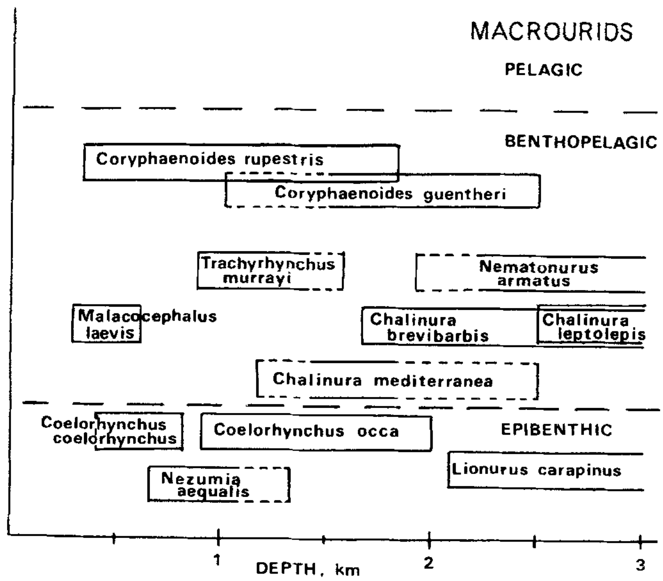

Fig. 6. Macrouridae. Their bathymetric distributions and trophic relationships within the Rockall Trough. The pelagic, benthopelagic and epibenthic environments are indicated. The horizontal extent of the species boxes defines the limits of their bathymetric range; open-ended boxes indicate that insufficient data are available to define these limits. Solid horizontal lines define centres of distribution while hatched extensions indicate continuing presence of the species

Table 7. Macrourids. Similarity indices for the diets of the various species and size classes detailed in Tables 1, 3 and 6

	Body length (cm)	Approximate depth range (m)	Code	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Malacocephalus laevis		500	1	9	7	11	15	5	5	6	12	15	21	8	18	10	12	12	29	26	7	11	7	7	7	8	9
Coryphaenoides	4.0–12.4	1 000	2		72	51	32	26	33	30	26	34	29	34	37	36	41	38	16	17	23	30	26	23	30	24	17
rupestris	12.5–21.4	1 000–1 250	3			81	58	32	36	36	42	36	27	34	38	37	42	35	17	19	26	33	26	24	33	23	14
	21.5–63.4	1 000–1 750	4				71	41	49	45	50	44	35	43	50	43	47	47	25	28	34	41	31	29	39	27	21
	63.5–105	1 000?	5					28	28	28	35	39	33	27	29	31	35	28	22	24	26	30	27	26	29	26	17
Coryphaenoides	8.0–24.4	1 000–1 250	6						49	52	56	52	37	37	41	59	53	68	37	55	36	34	54	55	66	65	49
guentheri	24.5–39.4	1 500–2 500	7							81	55	42	32	59	64	46	49	46	28	27	59	58	29	28	39	36	27
	39.5–48.0	1 500–2 200	8								57	44	34	43	48	50	51	43	28	31	68	69	30	29	40	38	31
Trachyrhynchus murrayi		1 000–1 500	9									61	55	39	47	53	53	55	41	45	52	51	54	47	68	50	42
Nematonurus armatus	14.0–35.4	2 200–2 900	10										65	38	41	58	60	60	42	47	32	36	48	45	51	53	45
	35.5–59.0	2 200–2 900	11											28	30	48	48	55	38	42	30	32	46	42	47	51	47
Chalinura mediterranea	9.0–21.0	1 500–2 000	12												82	47	50	41	25	23	25	26	25	24	30	31	21
	21.1–46.0	12 50–2 200	13													50	54	44	25	25	32	34	26	25	35	29	22
Chalinura brevibarbis	9.0–21.4	2 000–2 500	14														73	68	41	52	29	30	51	49	52	55	49
	21.5–38.0	2 000–2 900	15															62	36	40	30	30	43	41	47	48	39
Chalinura leptolepis		2 900	16																41	65	28	34	60	61	63	65	58
Coelorhynchus	19.0–31.4	500	17																	64	25	22	46	48	43	36	35
coelorhynchus	31.5–43.0	750	18																		30	26	63	64	66	63	61
Coelorhynchus occa	7.6–27.0	1 000–1 250	19																			82	28	25	43	36	30
	27.1–38.0	1 000–1 750	20																				28	27	41	31	25
Nezumia aequalis	8.0–21.4	750	21																					94	77	56	50
	21.5–45.0	750	22																						78	55	46
	8.0–36.0	1 000	23																							63	52
Lionurus carapinus	7.0–20.4	2 200–2 900	24																								73
	20.5–33.0	2 200–2 900	25																								

Table 8. *Coryphaenoides rupestris.* Similarity indices for the diets in different months in 1975 at 750 and 1 000 m depth. The numbers (*n*) of full stomachs are shown

	n	May	May	July	September	November
750 m						
March	39			37	59	41
July	30				53	42
September	91					60
November	37					
1000 m						
March	105	63	67	33	51	25
May	102		78	47	61	30
May	67			39	56	28
July	289				62	30
September	151					39
November	152					

rupestris trawled from the 750- and 1 000-m stations in different months in 1975. The diet in March in the 750-m zone was dominated by amphipods (Cn = 40%), while that in July was dominated by the copepod *Euchaeta norvegica* (Cn = 45%); hence, the index between these two samples is only 37. The diet in November was dominated by the copepod *Pleuromamma robusta* (Cn = 31%) and so lower indices are present for the comparisons between this sample and those of March and July (Table 8). The diet in the 1 000-m zone in November was also dominated by *P. robusta* (Cn = 65%), resulting in less similarity between the diet in this month and those in other months. The diet in March was dominated by the small calanoid *Aetideopsis multiserrata* (Cn = 33%) and amphipods (Cn = 12%), while that in July was dominated by *Euchaeta norvegica* (Cn = 19%) and cyclopoid copepods (Cn = 20%); the resulting index is 33 (Table 8). The two samples collected in May have the highest index, a value of 78.

A similar analysis of the diets of *Nezumia aequalis* in different samples is shown in Table 9. In the 750-m zone, there is a tendency for an inverse relationship between the occurrence in the diets of total amphipods and the mysid *Pseudomma affine* (Fig. 7). The diets in two samples, where mysids had Cn values of 1 and 2% respectively, had a third dominant food compartment that is of only minor importance in the diets of other samples; *Ophiocten gracilis,* calanoid copepods and unidentified tissue had total Cn values of 37 and 31 respectively, whereas in all other samples their Cn values ranged from 10 to 21 except in January, 1979 when a value of 27 occurred. The diets of *Nezumia aequalis* at the 1 000-m depth did not include *P. affine* except in November, 1975 (Cn = 1.4%), April, 1977 (Cn = 0.6%) and January, 1979 (Cn = 11%). The most distinct difference was between the diets in November 1975 and April 1976. The diet in November was mixed, amphipods having a Cn value of 30% and copepods 28% while that of April was dominated by amphipods (Cn = 81%) and copepods (Cn = 7%).

Table 9. *Nezumia aequalis.* Similarity indices for the diets in different months of different years at 750 and 1 000 m depth. The numbers (n) of full stomachs are shown

	n	November	April	June	October	October	April	May	January
750 m									
September 1975	89	68	61	65	50	49	59	67	48
November 1975	49		61	75	59	50	73	53	58
April 1976	52			61	53	57	61	54	54
June 1976	24				74	56	79	58	69
October 1976	62					53	66	42	77
October 1977	79						50	56	62
April 1978	11							55	64
May 1978	18								42
January 1979	55								
1 000 m									
September 1975	23	74	60	67	73		76		70
November 1975	54		48	54	62		69		60
April 1976	15			62	57		64		61
June 1976	69				67		76		69
October 1976	42						74		73
April 1977	26								73
January 1979	21								

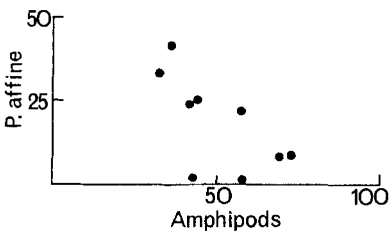

Fig. 7. *Nezumia aequalis.* The Cn values (see legend to Table 1) for the occurrence of total amphipods and the corresponding occurrence of the mysid *Pseudomma affine* among stomach contents of samples from the 750-m bathymetric zone

The diets between samples of *Coryphaenoides rupestris* and *Nezumia aequalis* caught in the 750-m bathymetric zone are slightly less similar (mean indices of 49 and 59 respectively) than the diets of samples of these species caught at 1 000 m (mean indices of 56 and 66 respectively).

Thus, these analyses suggest that quite distinctive changes occur in the diets of these two species of fish in different months of the year but do not indicate whether they are regular seasonal changes or result primarily from opportunistic feeding strategies. The number of stomachs examined in some months is relatively small. Mattson (1981) applied a method for determining the adequateness or otherwise of samples for describing the breadth of the diet. He examined the cumulative number of first records of food species in the diet related to the number of fish with food present at every twentieth fish and produced curves for five coastal species. This has been done for the total dietary samples of macrourids in Fig. 8. A variety of organisms in the stomach contents were identified the first time that they were recorded but, if of rare occurrence, were not necessarily identified to species level on subsequent occasions but only ascribed to a genus, family or order as "unidentified". This applied not only to polychaetes and several amphipods but also to rare cumaceans, some ostracods and other organisms. Some organisms were not identified but only noted as "type A", "type B" etc. These, however, can all be used in the cumulative species curves. The curves will still underestimate, in the majority of fish, the total number of species consumed by any single species of fish. This results, primarily, from the numbers of species of amphipods, isopods and to a certain extent copepods that were not recognized; these were juvenile or semi-digested individuals in a damaged or fragmented state. The degree of underestimation in a species such as *Coryphaenoides rupestris* is thought to be on the order of 20 to 30%.

The diets of *Nezumia aequalis, Coryphaenoides rupestris, C. guentheri* and possibly *Nematonurus armatus* appear to be adequately defined. There are occasionally quite marked inflexions in the curves that reflect a sample from a different depth, size group, sea area or season. It is especially noticeable in the upper part of the curve for *C. rupestris* where 12 prey species were recorded for the first time in stomachs, 980 to 1 020 (Fig. 8). This is a special feature of fish species occurring over a wide bathymetric range; *C. rupestris* was sampled at all depth zones between 750 and 1 750 m. The curve for *C. guentheri* has large irregularities, especially between fish 80 to 160 and 160 to 220 (Fig. 8) and this is the species with the greatest bathymetric range, 1 000 to 2 500 m. Changing the sequential order of samples prior to compilation of a second cumulative species curve for any one fish would produce a curve that would have a different detailed shape but would remain, in essence, the same. With the possible

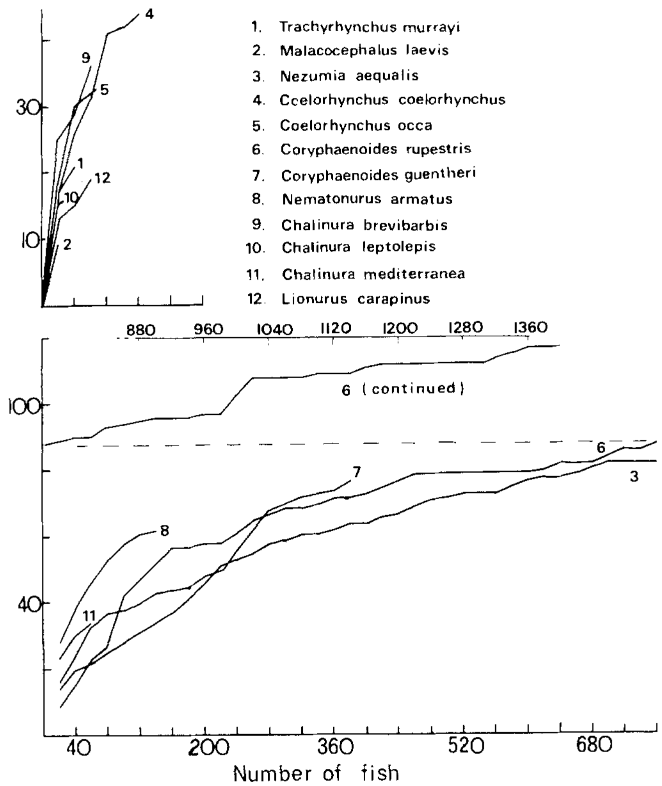

Fig. 8. Macrouridae. Cumulative numbers of first records of prey species at every 20th fish with food present. The curve for *Coryphaenoides rupestris* (6) is broken and continued above on the inserted additional scale

exception of the curves for *Malacocephalus laevis, Chalinura leptolepis* and *Lionurus carapinus,* the other curves indicate prey complements of more than 50 species and in some cases of more than 100 species. *M. laevis,* the shallowest living macrourid, has a diet dominated by the epibenthic *Munida bamffica* and fish (Table 1) and its food may very well be less diverse than that of the majority of macrourids. The same is probably not true of *C. leptolepis* and *L. carapinus.* The stomachs of fish of both these species (Table 6) have a high proportion of unidentified amphipods and *L. carapinus* has in addition a marked proportion of unidentified tissue present. The amphipods were small but may have represented a variety of species as might have the unidentified tissues. These two macrourids may therefore have diverse diets.

The species are grouped in Table 7 according to their tendency to have a benthopelagic or epibenthic diet and, within these categories, are approximately in order of increasing depth of occurrence. The diet of *Malacocephalus laevis,* the shallowest living species (Fig. 6), is not adequately defined (Fig. 8) and this probably contributes to its apparent uniqueness in Table 7. The two *Coryphaenoides* species have over-lapping bathymetric ranges (Fig. 6) although their centres of distribution are separated. The diet of *C. rupestris* is variable (Table 8) and different from that of *C. guentheri,* especially at depths where they overlap. A direct comparison was made between the diets of these two species in the 1 250- and 1 500-m bathymetric zones; the similarity indices were 18 and 22 respectively. The centre of distribution of *Trachyrhynchus murrayi* is between those of the two *Coryphaenoides* species (Fig. 6). Its diet is not well-defined (Fig. 8), overlaps those of the *Coryphaenoides* species but may include a larger epibenthic component. *Nematonurus armatus* is the commonest of the deep living species; it preys less heavily on amphipods and more on other organisms than does the rarer *Chalinura leptolepis.* The other two *Chalinura* species have their centres at shallower and different depths (Fig. 6). They coexist with *C. guentheri* and show some dietary overlap (Table 7).

Among the primarily epibenthic feeders, *Coelorhynchus coelorhynchus* shows considerable dietary overlap with *Nezumia aequalis* in the 750-m zone (Table 7); the latter has a diet, however, dominated by amphipods while the former exploits decapods to a greater extent than amphipods. The centres of distribution of the two *Coelorhynchus* species do not overlap and there are marked differences between their diets (Table 7). *Lionurus carapinus* lives much deeper than the others and its diet is different from that of the benthopelagic feeders associated with it (Fig. 6, Table 7).

Discussion

The method of assessing the information on diets derived from Mattson (1981) and used in Fig. 8 examines potential diversity. It is, however, often more important to examine size class or ecological type of prey organism in a generalist feeder, the identification of the individual species of prey organisms being of less significance than in the diet of a specialist feeder. All these macrourids appear to be generalist feeders, probably with asymptotic numbers of prey species, allowing for underestimation, of 100 to 150 (Fig. 8). Many of these prey species are probably rare components consumed opportunistically or incidentally with the major prey species.

Comparisons of the diets of macrourids in the Rockall Trough with those in other regions are difficult, especially when considering lists of prey species per se. Hynes (1950) discussed the expertise of the investigator relative to the subjective inaccuracies in the resultant data. There is undoubtedly a bias in the present data towards naming crustaceans, especially copepods, mysids, euphausiids, decapods and the larger sized amphipods and a bias against recognizing species of polychaetes, isopods, small amphipods, cephalopods and various benthic organisms such as small holothurians and echinoids. The data of Macpherson (1979) appear to emphasize species of polychaetes at the expense of crustaceans in the diets of *Nezumia aequalis* and *Coelorhynchus coelorhynchus.* The apparent diversity inherent in his data is about half that found here. A comparison, however, of his data with the present, in terms of ecological constitution of the diet, is unaffected by these biases.

The present study shows the macrourids to be partitioned bathymetrically within the Rockall Trough. Macpherson (1979) examined ecological overlap between four microurids within the restricted bathymetric range of 200 to 800 m in the western Mediterranean; differences in the diets and distributions of the species were evident. Pearcy and Ambler (1974) compared the diets of five abyssal Pacific species off Oregon, found them to be generalised feeders with marked dietary overlap in certain size groups between species; bathymetric partitioning of these size groups was not examined. Merrett and Marshall (1980) examined the bathymetric distribution of species in the depth range 261 to 6 059 m off northwest Africa. They concluded, on their relatively cursory examination and classification of the diets, that there was evidence of differences between species. Further, the bathymetric centres of distribution also tended to be different, reinforcing the dietary differences as a means of niche separation.

The macrourids do not live in isolation from the other cohabitant species of fish of the continental slope and rise. Consequently, detailed examination of resource or other partitioning among macrourids is of limited value unless within the context of the fish associations of the region as a whole. This will be attempted for the Rockall Trough in a later paper.

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