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Foraging strategies of deep-sea fish

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ABSTRACT: The structure of the stomach contents of 33 species of fish caught at depths between 400 and 2900 m in the Rockall Trough is analysed for information on foraging strategies of individual species. One representative (a single) or several representatives (a multiple incidence) of a prey species can occur in stomachs. The contents of stomachs range from 1 to about 200 individual prey items. These items can comprise singles, singles and a multiple incidence, or singles and co-occurring multiple incidences. Relations between the numbers of items occurring as singles or multiple incidences and the total number of items in the stomachs of the different species of fish were examined. An attempt is made to analyse the progressive accumulation of items in stomachs as they become fuller. Results suggest that fish such as the benthopelagic feeding macrourids are exploiting multi-species patches of prey. Four types of general feeding strategies appear to be present among the species. Ten species are primarily opportunistic feeders that occasionally feed repetitively on single prey species. Five species are also opportunistic feeders but lock-on to a single prey species that they exploit repetitively fairly regularly. Four species feed opportunistically on single items but in addition feed repetitively on 1 or more preferred prey species. Six species combine opportunistic and repetitive feeding much more closely to exploit a wide variety of resources. Data on the remaining 8 of the 33 species were not adequate to define their feeding strategies.

INTRODUCTION

Dietary analyses of a wide variety of species of demersal fish have been made in the Rockall Trough by Mauchline & Gordon (1980, 1983a, b, 1984a, b, c). The analyses are primarily descriptive, seasonal and ontogenetic aspects being taken into account. The relevant literature is reviewed in these papers. A more analytical approach to the data was used to assess sources of diversity within the diets (Mauchline & Gordon 1985). The diets are dominated by relatively few components and diversity within a diet is derived directly from the number of minor components occurring.

The type and size of prey consumed is governed to a considerable extent by the functional morphology of the predatory species of fish concerned. The most detailed comparative studies have been made on the macrourid species (Marshall 1965, Okamura 1970, Geistdoerfer 1973, 1978, McLellan 1977). Similar studies on species in other families are less detailed but the results are comparable. The form of the mouth and its position, the structure of the gill rakers, the functional aspects of the swimbladder, and the disposition and form of the fins relative to an active or lethargic life style in conjunction with the sensory apparatus for location of prey are all involved. These combined with behavioural and distributional differences between populations of the different species allow exploitation of varying compartments of the resources of prey which themselves exhibit heterogeneous behavioural and distributional patterns.

Behavioural and distributional patterns of potential pelagic prey, especially the ecological importance of patchiness, have received recent attention (Steele 1978). This is the fine-scale (metres to hundreds of metres) and micro-scale (1 cm to 1 m) of Haury et al. (1978). Such patches may be of single species (Alldredge et al. 1984), but according to Haury & Wiebe (1982) are more likely to be multi-species in composition. Both these investigations hypothesize the potential ecological importance of such patches in the trophodynamics of oceanic ecosystems.

Horwood & Cushing (1978), in discussing patchiness in the distributions of prey of pelagic fish, point out that it is metabolically cheaper to feed on patches than on evenly distributed prey. Assuming this to be true then patches within the distributions of prey organisms should be detectable in an examination of the stomach contents of fish.

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GENERAL APPROACH

The benthopelagic environment of the slope of the Rockall Trough is exploited for food by the demersal fish (Mauchline & Gordon *loc. cit.*). It is inhabited by a large variety of organisms normally considered members of the pelagic plankton and micronekton. These organisms are a dominant prey of the assemblages of demersal fish (Marshall & Merrett 1977, Mauchline & Gordon *loc. cit.*).

The stomach contents of a fish are a sample of the potential prey species in the environment around the fish. The efficiency of a pelagic net or benthic sampler in procuring a representative sample of the assemblages at which it is targeted depends on its size, design and structural elements (Angel 1977, Holme & McIntyre 1984). A fish as a sampler also has selective biases derived from its functional morphology as outlined above. A grab or corer samples a small area or volume (spot sample) while dredges, trawls and the majority of pelagic nets traverse assemblages in more or less straight lines horizontally, obliquely or vertically. A fish can combine all of these but also digress from any one of them on the fine micro-scales of Haury et al. (1978).

In addition, a feeding fish may be caught when it has filled its stomach or at any stage between commencement of feeding and repletion. Some species have up to 200 prey items in a full stomach, others have 3 to 5, while some stomachs of *Synaphobranchus kaupi* contain only a single large prey. Identified prey items in a stomach that is nearly empty contribute to a dietary list but provide little information on how a meal, represented by the contents of a full stomach, is constructed. A method is required to examine the progressive acquirement of items between commencement of feeding and repletion. This would define any changing structure within the meal and generate ideas on feeding strategy.

What evidence of exploitation of patches of prey might be found within stomach contents of individual fish? To take the simplest case, a fish exploiting a single species patch of either a benthic or pelagic organism could be expected to have several examples (a *multiple incidence* or *multiple*) of that species in its stomach. A fish exploiting a multi-species patch (Haury & Wiebe 1982) would then be expected to have several examples of several species (*co-occurring multiple incidences* or *co-occurring multiples*) in its stomach along with single individuals *(singles)* of species that occur in small numbers (densities) within the patch.

This is illustrated in Fig. 1 which represents a portion of a multi-species patch of prey containing 1 dominant, 3 sub-dominant and 5 rarer species. The species are distributed more or less randomly throughout this portion of the patch. The successively larger concentric circles, each twice the area of the previous, represent increasing foraging areas of a fish between commencement of feeding and repletion. Conceptual circular foraging areas are for diagrammatic simplicity. A true foraging area may be an extended tube, its diameter related to that of the fish's mouth, or it can be a zig-zag path. Such regular or irregular areas can be reduced to the form in Fig. 1 for comparative purposes. The resultant stomach contents, as the prey species in each successive area are consumed, are shown in Table 1.

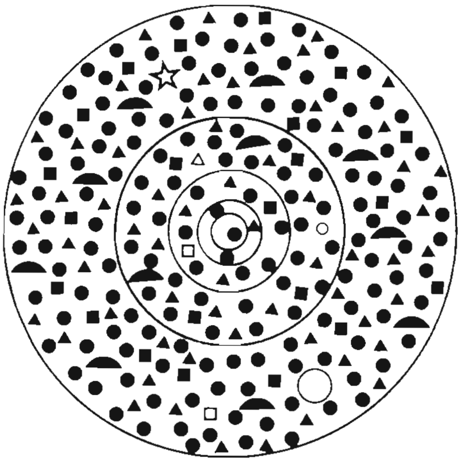

Fig. 1. Diagrammatic illustration of a multispecies patch of zooplankton prey species. The distribution of each species, denoted by different symbols, is random throughout the patch. The concentric circles, each twice the area of the previous, represent successively larger foraging areas of a fish between commencement of feeding and repletion

Table 1. The resultant stomach contents as a fish progressively consumes all organisms in each successively larger concentric circle superimposed on the multispecies patch in Fig. 1

Concentric circles	Cumulative numbers of each species consumed ●	▲	■		□	△	○	◯	✫
Smallest	1								
2	3	1							
3	10	4	1		1				
4	39	15	5	2	1	1	1		
Largest	156	61	22	11	2	1	1	1	1

The stomach contents, therefore, should hypothetically consist first of one or more single representatives of prey species and evolve into a situation where co-occurring multiples are found along with a single representative of additional species (Table 1). This should apply not only to exploitation of pelagic multi-species patches but also to those in the epibenthic regime. This paper examines this hypothesis and also the possibility of other modes of feeding being evidenced by structure within stomach contents.

MATERIALS AND METHODS

The fish were sampled at approximately 250 m bathymetric intervals between 400 and 2900 m depth in the Rockall Trough during the period 1975 to 1981.

Table 2. The numbers of multiple incidences consisting of different numbers of organisms occurring in stomachs of a variety of demersal species of fish. The numbers of stomachs with and without multiple incidences are also given. Nomenclature of the fish is that of Hureau & Monod (1979)

	Number of multiple incidences consisting of different numbers of organisms						No. of stomachs	
	2–5	6–15	16–35	35–37	76–155	>156	With multiple incidences	Without multiple incidences
Scyliorhinidae								
Apristurus sp.	9	7					16	8
Squalidae								
Centroscymnus crepidater (Bocage & Capello 1864)		1					1	11
Deania calcea (Lowe 1839)	1						1	38
Etmopterus spinax (Linnaeus 1758)	8						8	69
Chimaeridae								
Chimaera monstrosa Linnaeus 1758	34	6					40	69
Hydrolagus mirabilis (Collett 1904)	1						1	55
Alepocephalidae								
Alepocephalus bairdii Goode & Bean 1879	15	2	1				15	372
Xenodermichthys copei (Gill 1884)	4						4	94
Argentinidae								
Argentina silus (Ascanius 1775)	1						1	41
Synaphobranchidae								
Synaphobranchus kaupi Johnson 1862	11						9	452
Notacanthidae								
Notacanthus bonapartei Risso 1840	17	9					26	68
Polyacanthonotus rissoanus (Filippi & Verany 1859)	2						2	67
Macrouridae								
Trachyrhynchus murrayi (Günther 1887)	20	4					14	14
Nezumia aequalis (Günther 1887)	519	66	16	1			410	364
Malacocephalus laevis (Lowe 1843)	3	1					4	11
Coelorhynchus coelorhynchus (Risso 1810)	105	22	2				70	47
Coelorhynchus occa (Goode & Bean 1885)	17	4	1	2			19	17
Coryphaenoides rupestris Gunnerus 1765	1016	271	50	25	7	2	618	725
Coryphaenoides guentheri (Vaillant 1888)	180	87	26	5		1	234	78
Nematonurus armatus (Hector 1875)	81	9	1				50	82
Chalinura brevibarbis (Goode & Bean 1896)	27	7	1				19	36
Chalinura leptolepis (Günther 1877)	3						3	14
Chalinura mediterranea (Giglioli 1893)	34	12	1				31	29
Lionurus carapinus (Goode & Bean 1883)	7						6	54
Gadidae								
Gadiculus argenteus thori J. Schmidt 1914	1	1					1	67
Phycis blennoides (Brünnich 1768)	29	11	1				15	2
Moridae								
Halargyreus johnsonii Günther 1862	6	10	2	2			19	14
Lepidion eques (Günther 1887)	58	7					61	242
Trachichthyidae								
Hoplostethus atlanticus Collett 1889	17	2	1				16	22
Apogonidae								
Epigonus telescopus (Risso 1810)	122	8					119	242
Scorpaenidae								
Helicolenus dactylopterus dactylopterus (Delaroche 1809)	18	2					20	135
Scophthalmidae								
Lepidorhombus boscii (Risso 1810)	33	1					21	7
Pleuronectidae								
Glyptocephalus cynoglossus (Linnaeus 1758)	11	4					14	51

The types of gear used, sampling strategy and an assessment of the accuracy of the samples in representing the fish assemblages investigated are given by Gordon & Duncan (1985). The dietary samples are representative of the seasons of the year in addition to the majority of species being collected throughout their total bathymetric range.

The stomach contents were either preserved on board ship or removed from preserved fish for later examination in the laboratory. All taxa were identified to species level where possible but such identifications are biased in favour of species of calanoid copepods, mysids, euphausiids, decapods and against polychaetes, smaller amphipods, isopods and gelatinous organisms. Small numbers, in a few diets larger numbers, of immature or damaged calanoid copepods were not identified to species. All items were counted in each stomach.

Stomachs of fish within any one sample of fish may be everted, empty or contain food. The number of everted and empty stomachs varies between species and between samples taken at different and the same times of the year. Few correlations exist between the occurrence of everted and empty stomachs and body size or depth of capture of the fish. Consequently, their presence is ignored and only stomachs with food present are discussed in this paper. Stomachs with food present exhibit all degrees of fullness. Partial regurgitation of contents during the process of capturing the fish is frequently suspected to have taken place but cannot be proved. Consequently, partially full stomachs with only a few items of food present may include an unknown number in which contents have been partially regurgitated.

RESULTS

The stomach contents of 75 species of demersal fish were examined. Contents were present in only 1 to 12 stomachs of each of 40 species, however, and so data on these species may be unreliable and are excluded from this analysis. Approximately 70 % of the items in the diet of the synaphobranchid *Histiobranchus bathybius* were unidentified fish (Mauchline unpubl.). Similarly, the diet of *Antimora rostrata* consisted of 70 % unidentified tissues (Mauchline & Gordon 1984b). Consequently, these 2 species are not included with the remaining 33 species in the following analysis.

Structure within stomach contents

The occurrence of multiple incidences and single items within the diets of 33 species is shown in Tables 2 and 3. Multiples can range in size from 3 to 100 organisms in any 1 stomach. The proportion of stomachs with and without multiples varies between species (Table 1). The mean number of items in stomachs with multiple incidences is greater than that in stomachs without them (Table 3). This is illustrated for *Coelorhynchus coelorhynchus* in Fig. 2 which shows (inset) that stomachs without multiples have less than 10 items (mean 4.3 ± 2.0) while those with multiples have 5 to 43 items (mean 13.7 ± 7.5). The frequency distributions of stomachs with different numbers of prey are skewed towards stomachs with smaller rather than larger numbers so that the calculation of means and standard deviations are not appropriate; only means are shown in Table 3. The first 2 correlations in Table 4 show that the numbers of co-occurring multiple incidences and the number of items comprising them are directly proportional to the total number of items in the stomachs in most species. The number of single items per stomach, however, is not necessarily related to the total number of items (Table 4) and this will be discussed later.

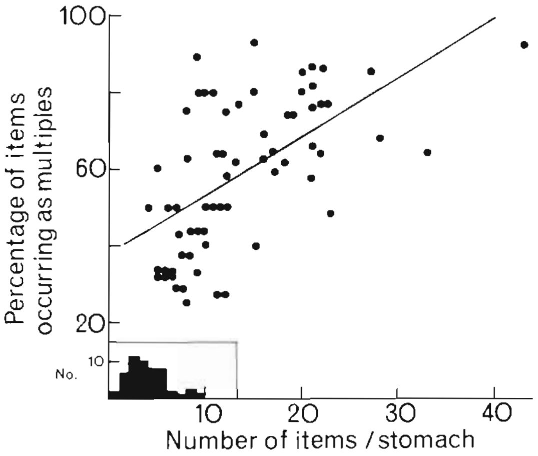

Fig. 2. *Coelorhynchus coelorhynchus*. The proportion of items occurring as multiples increases as the number of items in the stomach. The equation of the line is: $y = 1.53x + 37.82$. The inset histogram shows the numbers of stomachs without multiples present that had different numbers of prey items; none of these stomachs had more than 10 items, whereas stomachs with multiples had 5 to 43 items

An assessment of the importance of multiple incidences in the diets can be made by calculating the percentage of the total prey items in the diet that occur exclusively as multiples and the comparable percentage of total items contained in the stomachs with multiple incidences present (Table 3). Comparison of these 2 percentage values shows, first, whether prey occurring as multiple incidences are an important component of the diet; the percentages occurring as multiples range from 2 to 72 %. Second, the compari-

Table 3. Comparison of the quantities of prey items in stomachs with and without multiple incidences

	Mean no. of prey items per stomach		% of total prey items occurring	
	With multiple incidences	Without multiple incidences	As multiple incidences	In stomachs with multiple incidences
Apristurus sp.	9.1	2.9	60	86
Centroscymus crepidater	6.0	1.2	32	32
Deania calcea	3.0	1.3	6	6
Etmopterus spinax	2.8	1.4	16	19
Chimaera monstrosa	6.4	1.8	48	67
Hydrolagus mirabilis	3.0	2.0	2	3
Alepocephalus bairdii	12.0	1.4	8	27
Xenodermichthys copei	4.0	1.6	7	10
Argentina silus	5.0	2.0	4	6
Synaphobranchus kaupi	2.9	1.3	5	5
Notacanthus bonapartei	4.9	1.3	55	60
Polyacanthonotus rissoanus	5.0	1.2	9	11
Trachyrhynchus murrayi	11.2	3.8	43	75
Nezumia aequalis	11.6	5.3	35	71
Malacocephalus laevis	6.0	6.7	23	24
Coelorhynchus coelorhynchus	13.7	4.3	31	79
Coelorhynchus occa	14.0	2.4	61	87
Coryphaenoides rupestris	20.6	2.7	57	86
Coryphaenoides guentheri	16.1	5.0	46	91
Nematonurus armatus	15.5	3.6	28	72
Chalinura brevibarbis	13.7	5.8	23	56
Chalinura leptolepis	12.3	5.9	5	31
Chalinura mediterranea	16.0	6.5	23	72
Lionurus carapinus	7.7	3.4	7	20
Gadiculus argenteus thori	15.0	1.7	9	12
Phycis blennoides	17.1	4.6	52	97
Halargyreus johnsonii	14.9	2.3	72	87
Lepidion eques	5.7	1.7	25	46
Hoplostethus atlanticus	8.6	2.6	32	70
Epigonus telescopus	5.9	2.4	30	54
Helicolenus dactylopterus dactylopterus	4.7	2.4	14	22
Lepidorhombus boscii	6.0	3.6	45	65
Glyptocephalus cynoglossus	6.2	2.5	26	40

son also shows what proportion of the prey occur in the stomachs with multiples; it is 86 % in *Apristurus* sp. which means that only 14 % of all items were found in stomachs that only contained single items. These stomachs are usually nearly empty.

Most of the total prey items (> 50 %) occur in stomachs with multiple incidences in 17 of the 33 species examined; the proportion of these that occur as multiple incidences in these stomachs, however, ranges from 23 % in *Chalinura brevibarbis* and *C. mediterranea* to 72 % in *Halargyreus johnsonii*. In other words, the proportions of single items co-occurring with the multiples varies as inferred from the number of species, in Table 4, in which the number of items occurring as singles is not correlated with the total number of items in the stomach.

Another list of 12 species in Table 3 has less than 31 % of total prey items occurring as multiples or in stomachs with multiples; multiple incidences in 10 of these species represent less than 10 % of all items recorded in the diet, implying that they are not important.

Samples of most species of fish included all stages between juveniles and adults. Consequently, the number of prey items per stomach in the 33 species was regressed on body length (Table 4) to discover if multiple incidences are more common in stomachs of larger than smaller fish. Positive correlations occur in *Chimaera monstrosa* and *Notacanthus bonapartei* and stomachs of larger fish will, therefore, have more items as multiples than those of smaller fish. Negative correlations occur in the other 3 species (Table 4) and also in *Lionurus carapinus* ($r = -0.402$, $p < 0.05$) where larger fish tend to consume fewer but larger prey and will, therefore, have fewer items occurring as multiple incidences. There was no positive correlation in

Table 4. Species in which prey items occurring in stomachs with multiple incidences represent more than 40 % of the total prey items in the diet (Table 3). The following correlations were attempted for all species but values and significance of *r* are only given where significant.

Correlation 1 Number of multiple incidences/stomach : Total number of items/stomach
2 Number of items occurring as multiple incidences/stomach : Total number of items/stomach
3 Number of items occurring as singles/stomach : Total number of items/stomach
4 Total number of items/stomach : Body length of fish

	Correlation no. 1	2	3	4
Apristurus sp.	+	0.905***		0.515***
Chimaera monstrosa	+	0.845***	0.378*	0.461***
Notacanthus bonapartei	+	0.966***		
Trachyrhynchus murrayi	0.632*	0.801*	0.769***	
Coelorhynchus coelorhynchus	0.492***	0.954***	0.407***	−0.221*
Coelorhynchus occa	0.674**	0.984***		
Coryphaenoides rupestris	0.669*	0.967***	0.539***	
Nematonurus armatus	0.715***	0.848***	0.754***	
Phycis blennoides	0.631*	0.972***		−0.639**
Halargyreus johnsonii		0.993***		
Lepidion eques	0.505***	0.820***	0.552***	
Hoplostethus atlanticus		0.976***	0.578*	
Epigonus telescopus	0.390***	0.856***	0.576***	−0.105*
Lepidorhombus boscii	0.680**	0.929***		
Glyptocephalus cynoglossus	0.537*	0.899***		

\+ These species have only a single multiple incidence in any 1 stomach
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Coryphaenoides rupestris but the mean body lengths of fish with increasing numbers of co-occurring multiples show a trend of increasing size (Table 5).

Prey species that occur as multiple incidences

Some 230 species of prey were identified in the stomach contents. The apportionment of 186 of these is as follows: calanoid copepods 69; amphipods 39; mysids 26; euphausiids 5; decapod crustaceans 28; fish 19. Many of these species are relatively rare among the stomach contents and are not found as multiple incidences. Those that are common as multiples are restricted in number, about 30, and occur in diets of several species of fish (Table 6). A further 10 to 20 species are occasionally recorded as multiples of 2 to 5 individuals. No fish are listed in Table 6 but a few mesopelagic species occur as multiples in stomachs of several predatory species.

Table 5. *Coryphaenoides rupestris.* Mean body lengths of fish with different numbers of multiple incidences per stomach

No. of multiples	No. of fish	Mean total body length ± SD
0	586	44.6 ± 29.9
1	228	42.3 ± 28.9
2	134	46.7 ± 25.6
3	64	51.4 ± 27.8
4	42	45.6 ± 29.7
5	29	51.2 ± 28.3
6	14	60.7 ± 26.5
7	3	69.4 ± 19.9
8	4	80.2 ± 2.8

The dominance of a relatively few prey species in the stomach contents of the fish fauna of the Rockall Trough is further exemplified in the following analysis. The detailed composition of co-occurring multiples in stomachs of *Coryphaenoides rupestris* is examined in Tables 7 and 8. This is the only species examined here that has sufficient numbers of stomachs with 5 or more co-occurring multiple incidences to allow their composition to be examined. The number of times each prey species occurs as the largest, the second largest multiple and so on was determined. The species were then ranked in decreasing order of occurrence within each column (Table 7). The largest multiple was always 1 of 4 species of copepod or, in 1 stomach, the euphausiid *Meganyctiphanes norvegica*. The largest multiple comprises 3 to 5 times the numbers of individuals that represent the second largest multiple and there is less difference in size of successively smaller multiples (see Table 10). The diversity within succes-

Table 6. Recurrent prey species in the diets of the 35 more commonly caught species of demersal fish in the Rockall Trough. The numbers of predatory fish species and the numbers of bathymetric zones in which each prey is consumed are shown. There are 10 bathymetric zones at approximately 250 m intervals between 500 and 2900 m depth

Prey species	No. of predatory fish species	No. of bathymetric zones
Coelenterata		
Anemones	6	9
Copepoda		
Calanus helgolandicus	4	3
Aetideopsis multiserrata	21	10
Euchaeta norvegica	10	8
Xanthocalanus profundus	6	6
Xanthocalanus spp.	7	8
Pleuromamma spp.	4	3
Heterorhabdus norvegicus	5	4
Amphipoda		
Ampellisca spp.	8	5
Erichthonius spp.	3	2
Lanceola spp.	5	7
Mysidacea		
Gnathophausia zoea	9	10
Boreomysis arctica	10	7
Boreomysis tridens	11	6
Dactylerythrops gracilura	4	6
Pseudomma affine	10	5
Michthyops parva	4	5
Amblyopsoides ohlinii	5	5
Parambylops bidigitata	2	4
Parambylops rostrata	5	5
Euphausiacea		
Meganyctiphanes norvegica	18	6
Decapoda		
Acanthephyra pelagica	6	7
Pandalina brevirostris	7	3
Pandalus propinquus	4	3
Sergestes arcticus	15	10
Pasiphaea tarda	13	9
Crangonidae	13	5
Munida bamffica	13	6
Ophiuroidea	10	7

Table 7 *Coryphaenoides rupestris*. Prey species present as multiple incidences in the 43 stomachs with 5 or more co-occurring multiples (See Table 10). Only the 5 largest multiples are considered in stomachs with 6 or more. The prey species are ranked from the commonest to the rarest within each successively smaller multiple. The largest multiples in the 43 stomachs represented only 5 prey species while the second largest (Multiple 2) represented only 9 species

	Successively smaller multiples				
	1	2	3	4	5
Euchaeta norvegica	1	1	3	4	9
Pleuromamma robusta	2	6	3	3	2
Aetideopsis multiserrata	3	4	2	2	4
Calanus helgolandicus	4	2	8	7	4
Meganyctiphanes norvegica	5	7	10	10	
Pasiphaea tarda		3	5	6	6
Heterorhabdus norvegicus		5	1	1	1
Gnathophausia zoea		7	6	10	
Boreomysis tridens		7	8		
Ostracods			6	8	3
Munida bamffica				5	9
Sergestes arcticus				9	8
Scaphocalanus sp.					6
Euchirella curticauda					8
Undeuchaeta plumosa					9
Gaetanus kruppi					9

sively smaller multiples increases (Table 7), as would be expected.

The largest and second-largest multiples in fish with 4 and 3 co-occurring multiples are analysed in Table 8. The commonest 4 species comprising the largest multiples in both groups of fish are the same, and in the same order of dominance, as in fish with 5 or more multiples. The seasonal occurrence of these organisms among the stomach contents is shown in Table 9. *Aetideopsis multiserrata* and *Heterorhabdus norvegicus* are consumed throughout the year. The other 4 species are eaten more commonly at certain seasons but overlap each other. No seasonal pattern in the occurrence of multiple incidences among the stomach contents was detected.

Evidence of exploitation of patches

Possible evidence of exploitation of patches should occur in the 17 species where more than 50 % of the total prey occur in stomachs with multiple incidences and where relatively large numbers of stomachs (> 100) have been examined. There are 7 species in this category (Tables 2 & 3). Multiple incidences occur singly in stomachs of *Apristurus* sp., as can be deduced from Table 2 by summing the number of different sized multiples and comparing with the number of stomachs that contain multiples (16 and 16); this species will be discussed later. *Nezumia aequalis* and *Coryphaenoides guentheri* are excluded because their diets contain more than 38 % of items as unidentified copepods and amphipods (Mauchline & Gordon 1984a); many of these organisms occur as multiples but, since they were not consistently identified to species in all stomachs, the data on these species are incomplete. The remaining 4 species are analysed in Table 10 along with *Lepidion eques* in which 46 % of the total prey occur in stomachs with multiples but in which 303 with food were examined.

The stomachs of the different species of fish have been grouped according to the number of co-occurring

Table 8. *Coryphaenoides rupestris*. Prey species present as multiple incidences in the 42 stomachs with 4 multiples and the 64 stomachs with 3 multiples (Table 10). The prey species are ranked from the commonest to the rarest within the largest (1) and second largest (2) multiple within both groups of fish

	Fish with 4 multiples		Fish with 3 multiples	
	1	2	1	2
Euchaeta norvegica	1	1	1	2
Pleuromamma robusta	2	3	2	3
Aetideopsis multiserrata	3	2	3	1
Calanus helgolandicus	4	3	4	3
Heterorhabdus norvegicus	5	6	5	6
Meganyctiphanes norvegicus	6		6	6
Isopods	6		8	
Oikopleura sp.	6		10	
Pasiphaea tarda		3	7	3
Scolecithrix sp.		6		10
Undeuchaeta plumosa		6		
Gnathophausia zoea		6		
Ampellisca sp.			9	
Ostracods				6
Euchirella curticauda				6

Table 9. *Coryphaenoides rupestris*. Seasonal occurrence of the commonest prey organisms in multiple incidences expressed as the numbers per 100 stomachs with food in the 750 and 1000 m bathymetric zones

	Euchaeta norvegica		*Pleuromamma robusta*		*Aetideopsis multiserrata*		*Calanus helgolandicus*		*Heterorhabdus norvegicus*		*Meganyctiphanes norvegica*	
	750	1000	750	1000	750	1000	750	1000	750	1000	750	1000
Mar	41	28	8	1	269	178	0	1	36	32	36	0
May	101	35	24	3	147	93	0	1	67	28	2	0
Jul	1671	286	84	26	106	129	88	147	101	37	3	0
Sep	83	42	107	40	123	84	32	32	26	11	178	16
Nov	78	15	259	1175	70	154	0	5	24	28	64	4

multiple incidences of prey that each contains (Table 10). The numbers of items per multiple are not distributed normally about a mean because smaller numbers of organisms are more likely to comprise a multiple than large numbers. Stomachs of *Coelorhynchus coelorhynchus* with 1 multiple present have a mean number of items per multiple of 5.3 but the commonest multiple consists of 2 representatives of a species (Table 10). Stomachs with 2 multiples have one commonly of 3 and a second of 2 individuals. Stomachs with 3 multiples have the largest commonly with 5 organisms, the second largest with 3 or 4 and the smallest with 2 organisms. Similar analyses are given for stomachs of *Coryphaenoides rupestris* and *Nematonurus armatus*. Relatively few stomachs of *Lepidion eques* and *Epigonus telescopus* have more than 1 multiple and so they have been grouped into those with 1 and more than 1 multiple, and only the largest multiple is considered.

The stomach contents are like an expanding envelope and there are close similarities between the results in Table 10 and the hypothetical situation described in Fig. 1 and Table 1.

Aspects of this concept of the stomach contents as an expanding envelope can be quantified by examining values of m (Table 11), the slope of the regression line, for some of the correlations in Table 4. The regression equation of Correlation 1 (Table 4) indicates than an additional multiple is obtained by the fish with every 6 to 20 items consumed. In Correlation 2, 5.3 to 10 of every 10 items consumed contribute to multiple incidences, the balance (m values of regressions for Correlation 3) contributing to the single items in the stomachs. Two additional correlations are significant but only within the stomach contents of *Coryphaenoides rupestris* and *Nematonurus armatus*. The number of items occurring as singles per stomach is correlated with the number of multiple incidences per stomach: values of r are 0.457 ($p < 0.001$) ($m = 2.00$) and 0.524 ($p < 0.001$) ($m = 2.23$) respectively. Thus 2 single items occur along with every multiple incidence. This regularity is reflected in a significant correlation between the number of items occurring as singles in the stomach and the number of items occurring as multiples: values of r are 0.302 ($p < 0.001$) ($m = 0.09$) and 0.293 ($p < 0.05$) ($m = 0.24$) respectively. Thus 0.9 to 2.4 items occur as singles along with every 10 items occurring as multiples.

FORAGING STRATEGIES

There is, therefore, a considerable amount of structure within the stomach contents of species that must reflect foraging strategies, and even ontogenetic changes in strategies within species.

The quality and extent of the data on the following species do not allow conclusions on strategy to be drawn:

List 1. *Centroscymnus crepidater*
Nezumia aequalis
Malacocephalus laevis

Table 10. Size of successively smaller multiple incidences of prey species in stomachs which have 2 to 6 co-occurring multiples. The modal number (with mean number in parenthesis) of organisms are given in each class of multiple. The numbers of stomachs with different numbers of co-occurring multiples are also given. Only the mean size of the largest multiple is given in stomachs of *Lepidion eques* and *Epigonus telescopus* where 2 or more multiples occur

No. of co-occurring multiples per stomach	No. of stomachs	Successively smaller multiples					
		1	2	3	4	5	6
Coelorhynchus coelorhynchus							
1	39	2 (5.3)					
2	21	3 (7.1)	2 (3.3)				
3	5	5 (5.0)	3–4 (3.2)	2 (2.2)			
4	4	8 (8.0)	5 (5.3)	4 (4.0)	2 (3.3)		
Coryphaenoides rupestris							
1	228	2 (5.2)					
2	134	3 (11.9)	2 (3.1)				
3	64	4 (12.4)	2 (3.4)	2 (2.4)			
4	42	7–8 (21.2)	4 (5.4)	2 (3.2)	2 (2.3)		
5	29	13 (17.9)	5 (6.6)	4 (4.1)	2 (3.0)	2 (2.1)	
6–10	14	46 (46.4)	5 (8.3)	3–4 (4.8)	2 (3.3)	2 (2.3)	2 (2.0)
Nematonurus armatus							
1	25	2 (4.4)					
2	12	3 (3.7)	2 (2.5)				
3	6	3–6 (6.8)	3 (3.3)	2 (2.5)			
Lepidion eques							
1	40	2 (2.9)					
>1	7	3 (4.9)					
Epigonus telescopus							
1	100	2 (3.0)					
>1	12	3 (3.8)					

Table 11. Values for the slope, *m*, of the regression lines of various correlations detailed in Table 4

	Correlation no.		
	1	2	3
Trachyrhynchus murrayi	0.09	0.53	0.47
Coelorhynchus coelorhynchus	0.08	0.88	0.12
Coelorhynchus occa	0.03	1.00	
Coryphaenoides rupestris	0.04	0.86	0.14
Nematonurus armatus	0.09	0.58	0.42
Phycis blennoides	0.09	0.95	
Lepidion eques	0.08	0.68	0.32
Epigonus telescopus	0.05	0.70	0.30
Lepidorhombus boscii	0.18	0.81	
Glyptocephalus cynoglossus	0.06	0.91	

Coryphaenoides guentheri
Chalinura brevibarbis
Chalinura leptolepis
Chalinura mediterranea
Lionurus carapinus

Stomachs of *Centroscymnus crepidator*, additional to the 12 listed in Table 2, were examined in bulk (Mauchline & Gordon 1983a); 62 of the 75 stomachs contained 1 to 11 myctophid fish, not identified to species but probably representing multiple incidences in several instances. Some 60 % of the stomach contents of *Malacocephalus laevis* are unidentified parts of fish while more than 35 % of the contents of stomachs of the remaining macrourid fish in List 1 are unidentified copepods and amphipods (Mauchline & Gordon 1984a) containing many, but undefined, instances of multiple incidences.

The rest of the 33 species in Table 2 can be ascribed to several categories on the basis of structure within their stomach contents.

The following list of species are those in which only 2 to 13 % of stomachs contain multiple incidences, representing less than 16 % of the total dietary items (Tables 2 & 3).

List 2. *Deania calcea*
Etmopterus spinax
Hydrolagus mirabilis
Alepocephalus bairdii
Xenodermichthys copei
Argentina silus
Synaphobranchus kaupi
Polyacanthonotus rissoanus
Gadiculus argenteus thori
Helicolenus dactylopterus

Individual dietary items in these fishes tend to be large in size relative to the stomach capacity. The mean numbers of items per stomach range from 1.3 to 2.7 (Mauchline & Gordon 1985). The percentage of total dietary items that occur in stomachs with multiples is 3 to 27 % (Table 2). Consequently, the vast majority of stomach contents in these fish consist of a few single items of individual prey species. Foraging strategy is probably opportunistic to obtain prey of suitable size and handling characteristics.

The remaining species in Table 2 all have a greater occurrence of multiple incidences of prey in their stomachs. The following list comprises species where only 1 multiple incidence occurs in the stomach and if 2 or more do occur their occurrence is not related to the total number of items in the stomach (Correlation 1 in Table 4 is not significant):

List 3. *Apristurus* sp.
Chimaera monstrosa
Notacanthus bonapartei
Halargyreus johnsonii
Hoplostethus atlanticus

The mean numbers of items per stomach in these fishes range from 2.3 to 9.9 (Mauchline & Gordon 1985). The first 3 species rarely have more than 1 multiple incidence per stomach. They are selective feeders in that *Apristurus* sp. feeds repetitively on *Sergestes arcticus*, *Chimaera monstrosa* on anemones, and *Notacanthus bonapartei* on brittle stars. The size of the multiple incidence is related to the total number of items in the stomach but the number of co-occurring single items shows a corresponding increase only in *C. monstrosa* (Table 4). This suggests that *Apristurus* sp. and *N. bonapartei* lock on to their preferred prey species while *C. monstrosa* does not. Larger *C. monstrosa* and *N. bonapartei* eat more prey (Table 4), and so more of their preferred species, than smaller individuals. This is not true of *Apristurus* sp. Stomachs of these 3 species with multiples contain more than 60 % of total dietary items (Table 3) implying that the preferred prey and associated organisms are their primary diet. Opportunistic foraging, as described for species in List 2, also takes place but to a lesser degree.

The other 2 species *Halargyreus johnsonii* and *Hoplostethus atlanticus* have 87 and 70 % respectively of the total dietary items contained in stomachs with multiples (Table 3). Multiple incidences in stomachs of *H. johnsonii* are usually of the copepod *Euchaeta norvegica*, as many as 39 occurring in a single stomach (Mauchline & Gordon 1984b). This implies a high degree of repetitive feeding and to the possible exclusion of other species since single items do not show similar increases in number (Table 4). Single items do increase in number as the total number of items in the stomach of *H. atlanticus* and so are consumed along with the preferred prey species.

Consequently, foraging in species in List 3 consists of exploitation of a preferred prey species, even to the partial exclusion of feeding on other dietary items.

A further 4 species in Tables 2 and 3 have a dietary structure similar to species in List 3 except that repetitive feeding takes place on a number of preferred prey species. The fish are:

List 4. *Coelorhynchus occa*
Phycis blennoides
Lepidorhombus boscii
Glyptocephalus cynoglossus

The number of single items does not increase as the total number of items in the stomach and so repetitive feeding on preferred prey seems to be to the exclusion of random foraging. The vast bulk of prey recorded in the stomachs of *Coelorhynchus occa* and *Phycis blennoides* occurred in stomachs with multiples whereas lesser proportions were found in comparable stomachs of the other 2 species (Table 3). These latter 2 species are flatfish whose ranges extend from the shelf to upper slope of the Rockall Trough. Larger *P. blennoides* have fewer items per stomach than smaller individuals (Table 4) because they tend to feed on larger individuals of the same prey species as preferred by the smaller fish. No such relation exists in the diets of the other 3 species.

The remaining species in Table 2 exploit a wide variety of preferred prey repetitively. They are:

List 5. *Trachyrhyncus murrayi*
Coelorhynchus coelorhynchus
Coryphaenoides rupestris
Nematonurus armatus
Lepidion eques
Epigonus telescopus

This list should also probably include the macrourids *Nezumia aequalis*, *Coryphaenoides guentheri*, *Chalinura brevibarbis* and *C. mediterranea* from List 1 but further data on them is required for confirmation.

Lepidion eques and *Epigonus telescopus* had only about half the total dietary items in stomachs with multiple incidences compared with more than 70 % in the other 4 species (Table 3). The principal prey are decapod crustaceans in *L. eques* and decapods, mysids and fish in *E. telescopus* (see Mauchline & Gordon 1980, 1984c). These are, on average, larger prey than consumed by the other species (macrourids) on this list and account for the higher incidences of single items among the stomach contents. Larger *E. telescopus* eat fewer but larger items (Table 4) but no such relation existed in the diet of *L. eques*. A considerable amount of opportunistic foraging for single suitable prey of larger size must take place in these 2 species.

Prey size in the macrourids is restricted within a much narrower size spectrum. Most prey are small relative to the size of the fish (Mauchline & Gordon 1984a). Only 14 to 28 % of dietary items occurred in stomachs of fish that had been feeding exclusively on single prey (Table 3), a large proportion of these stomachs being less than half full. Multiples and the singles associated with them are very important in the diets of these species and opportunistic foraging for single items is probably at a minimum in these species.

CONCLUSIONS

The comparative composition of the contents of individual stomachs of demersal fish from the slope of the Rockall Trough between depths of 400 and 2900 m appear to contain information not exploited during conventional dietary analyses. A large proportion of the species feed primarily on benthopelagic fauna. Those that exploit the epibenthic environment feed primarily on amphipods, brittle stars and anemones. Infaunal elements of the benthos are almost entirely absent from the stomach contents. Diets of some species are diverse while those of others are relatively specialised (Mauchline & Gordon 1985). The particle size of prey items of macrourid fish in particular is small and the contents of individual stomachs can consist of 150 to 200 items. Feeding on patches of prey seems logical, especially as many of the species dominant in stomach contents (Table 6) are known or suspected to aggregate.

Small particle size of prey is very true of *Coryphaenoides rupestris* in considering the 4 species of copepods representing the 4 commonest multiples in the diet (Tables 7 & 8). It is not true, however, of multiples of the euphausiid *Meganyctiphanes norvegica* which is a significantly larger type of prey. In general, however, the largest multiples are of smaller prey simply because stomachs are restricted in capacity. There are exceptions and so availability of prey has some influence inferred, for example, from the occurrence of 82 *M. norvegica* along with a further 6 co-occurring multiples ranging from 2 to 7 individuals of 5 species of copepods and an ostracod in a single stomach of *C. rupestris;* or of 11 myctophid fish, probably of the same species, in a stomach of *Centroscymnus crepidater.* These 2 examples suggest that exploitation of aggregations or shoals of prey organisms takes place. It is generally accepted that the majority of pelagic prey species occur in patches (Angel 1977, Horwood & Cushing 1978), and Rex (1981) reviews evidence of patchiness in the distribution of benthic organisms.

Assuming that fish exploit aggregations and that multiple incidences of prey species in stomachs are a direct reflection of this, then several questions arise. For instance, why does a fish not simply fill its stomach with 1 preferred species at a time? This was not recorded once among 5500 stomachs with food examined in the 33 species discussed here. Thus exclusive feeding on a single prey species is avoided. This is even true of species in List 3 which only repetitively feed on 1 preferred prey species but always have single items present along with multiples.

There is certainly evidence in species in Lists 3 and 4 of locking-on to preferred prey species but this does not totally exclude but rather decreases the proportion of single items in the stomachs. A different interpretation of locking-on would be exploitation of single-species as opposed to multi-species patches. This might account for the occasional single items included. The particular species that might be exploiting single-species patches are *Apristurus* sp., *Chimaera monstrosa, Notacanthus bonapartei, Coelorhynchus occa, Phycis blennoides* and *Halargyreus johnsonii.*

The progressive situation in Table 11 describing the structure of diets of species in List 5 is closely similar to the hypothetical situation in Fig. 1 and Table 2, derived from the data of Haury & Wiebe (1982). It would appear to explain the observed structure within these stomach contents by suggesting that the fish are exploiting multispecies patches. Data on the microstructure within patches are lacking but individual species are more likely to occur in aggregations within the patches rather than be randomly distributed throughout. In addition, a patch may also contain organisms that the species of fish, for one reason or another, may not select; such species are not included in Fig. 1. The converse is also true, namely that one or more species within a multispecies patch may be especially selected by the fish. Neither of these aspects can be resolved in the absence of representative samples of the multispecies patches on which the fish are hypothetically feeding.

Foraging strategies of species in Lists 2 to 5 can be interpreted as showing a progressive development. Species in List 2 are primarily opportunistic feeders that occasionally obtain multiples of a prey species on a haphazard basis. Species in List 3 are also opportunistic feeders but lock on to a preferred single prey species that they exploit fairly regularly on a repetitive basis. Species in List 4 are similar to those in List 3 but exploit several preferred prey species and may or may not lock on to them. Species in List 5 have the most diverse diets and combine opportunistic and repetitive feeding much more closely, suggesting that they may be exploiting multi-species patches on a regular basis.

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