FOOD SOURCES FOR DEEP-SEA FISHES FROM THE UPPER CONTINENTAL SLOPE OF THE GRAND BANKS OFF NEWFOUNDLAND

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Food sources for deep-sea fishes from the upper continental slope of the Grand Banks off Newfoundland

by

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ABSTRACT

Stomach contents and parasite faunas of 464 specimens of demersal fishes in 14 species were examined from the Carson Canyon region of the upper continental slope of the Grand Banks off Newfoundland. Individual species tended to feed either primarily on benthic invertebrates or on pelagic food items. Most pelagic predators also fed on benthopelagic organisms. Prevalence of parasites was 46 percent, with an average of 5.5 worms per fish. Prevalence of parasites was higher in benthic feeders (53.1%) than in pelagic feeders (28.9%). Relative abundance by group among benthic feeders was: Digenetic Trematoda 5.8%, Nematoda 53.1% and Acanthocephala 40.9%. Percent occurrence by group among pelagic feeders was: Digenetic Trematoda 27.8%, Nematoda 72.2% and Acanthocephala 0%. There were more species of benthic feeders (5) than pelagic feeders (3), but pelagic feeders were more abundant (pelagic 70.9%, benthic 20.5%). Benthic feeders were on average larger ($\bar{x}$ = 270.6 g) than pelagic ($\bar{x}$ = 130.6), but pelagic feeders represented a larger proportion of the biomass (pelagic 43.3%, benthic 25.94%).

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SYMBOLS:
1 = *C. microps*
3 = *C. rupestris*
4 = *M. berglax*
5 = *N. bairdii*
6 = *A. rostrata*
7 = *M. rostrata*
10 = *S. kaupi*
11 = *L. esmarki*
12 = *L. sarsi*
13 = *L. perspicillus*
14 = *L. mirabilis*
= *R. hippoglossoides* *Sebastes* sp. and *G. ensis*

SHADING:
▨ = Benthic Feeders
■ = Pelagic Feeders

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SIZE CLASSES:
M. beglax: A = 50 - 100 mm TL
B = 101 - 150

C = 151 - 200
D = 201 - 250
E = 251 - 300
F = 301 - 350

N. bairdii: A = 50 - 150 mm TL
B = 151 - 200
C = 201 - 250
D = 251 - 300
E = 301 - 350
F = 351 - 400
G = 401 - 450

S. kaupi: A = 200 - 300 mm TL
B = 301 - 400
C = 401 - 500
D = 501 - 600
E = 601 - 700

C. rupestris: A = 0 - 100 mm TL
B = 101 - 200
C = 201 - 300
D = 301 - 400
E = 401 - 500

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D = 301 - 400
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INTRODUCTION

There are an estimated 160,000 species of marine animals, 98 percent of which are benthic organisms that live in or on the bottom sediment. The remaining two percent are pelagic and benthopelagic organisms adapted for life at all levels between the sea surface and the sea floor (Thorson 1971). Recently, attention has focused on the benthopelagic fauna in the deep sea which includes fishes and other organisms that swim near the ocean floor (Marshall 1965, 1980).

A controversial question in deep-sea biology concerns how energy requirements are met in the benthos (Sokolova 1959; Sanders and Hessler 1969; Grassle and Sanders 1973; Menzel 1974; and others). Various mechanisms have been proposed for the transport of organic matter to the deep sea (see Menzies 1962; Fournier 1972; Wiebe et al. 1976 for reviews). One such mechanism is the sinking of large particles (McCave 1975). Fecal pellets and fecal matter from copepods, euphausiids and some pelagic tunicates appear to constitute a large portion of the transported particulate material (Wiebe et al., 1976; Honjo and Roman 1978; Knauer et al. 1979; Robison and Bailey 1981; Madin 1982). Remains of small organisms (Honjo 1980) or carcasses of large animals may also be important (Isaacs and Schwartzlose 1975; Stockton and DeLaca 1982). Overlapping vertical migrations of predators and prey provide a method of rapid transfer from the surface to the benthos (Wiebe et al. 1976; Hinga et al. 1979). Another theory includes the transport of organic matter from continental shelves via turbidity currents. Flows from these currents likely increase in importance with proximity to the shelf (Heezen et al. 1965).

The upper continental slope (1[illegible]0 meters to 1000 meters) supports more abundant populations than most of the deeper parts of the ocean (Marshall 1980). This is due largely to the relative nearness of the sea floor to both the euphotic zone and the flux of nutrient materials from the land. Surface upwelling at the edge of the shelf provides another potential source of nutrients (Mills and Fournier 1979; Wulff and Field 1983). The deep scattering layer, comprised of vertically migrating organisms, may also be important in the flux of energy over this region (Rowe and Haedrich 1979). Mesopelagic organisms regularly approach the bottom on the continental slope thereby providing a major source of food for benthopelagic fishes (Sedberry and Musick 1978).

In a simplified example of a marine ecosystem (Figure

1), surface primary production either settles to the benthos as part of the particulate flux or is consumed by pelagic organisms. The particulate flux involves the settling of fecal material and dead organisms, or can be accomplished through vertically migrating organisms in the food chains. Once the material reaches the benthos, particles are utilized by infaunal or near-bottom organisms or are buried in the sediment (Hinga et al. 1979). The degree to which primary production influences the benthic ecosystem on the upper slope depends on the amount of food energy produced and the rate at which this energy is transported from the euphotic zone to the bottom (Sedberry and Musick 1978). Demersal organisms which migrate up into the water column or feed on components of the particle flux near the bottom sediments eliminate at least one trophic level. As a result, food reaches these "pelagic" feeders via a shorter and hence more efficient pathway than that available to demersal organisms which feed solely on benthic organisms.

Fishes are prominent members of the deep demersal fauna in the north Atlantic both in numbers of individuals and species (Marshall and Merrett 1977). In spite of their recognized importance in deep benthic communities, little is known of the food habits of many benthopelagic fish species. Whether these demersal fishes feed mostly on pelagic or benthic food is still largely unanswered. There are three possible trophic types among deep-sea benthopelagic fishes: (1) those which feed only on pelagic organisms; (2) those which feed only on benthic organisms; and (3) those which feed on a mixed diet of pelagic and benthic organisms. Marshall and Bourne (1964) suggested, on the basis of fin pattern and head shape, that Macrouridae (rattails) and Halosauridae (spiny eels) were adapted for hovering over the bottom and "rooting the ooze" with their rostrum to feed on small benthic organisms. However, the presence of pelagic animals in the stomachs of some species (Podrazhanskaya 1967; Haedrich and Henderson 1974; Pearcy and Ambler 1974; Geistdoerfer 1975; Sedberry and Musick 1978; DuBuit 1978; Macpherson 1979), as well as the capture of a few species in midwaters (Haedrich 1974; Pearcy 1976), suggests that some benthopelagic species may ascend into the water column to feed. McLellan's (1977) analysis of the functional anatomy of feeding in the Macrouridae indicates a variety of feeding strategies within the group, with highly specialized forms feeding on the benthos, primitive forms feeding on swimming prey near the bottom and intermediate forms feeding on both benthic and pelagic food sources.

Recently the benefits of studying parasites of fishes as indicators of within-community interactions have been recognized. Host specificity of parasites and geographical distribution of parasites are indicators of host feeding habits, distribution and behaviour (Campbell 1983). Various aspects of the ecology of the host may be deduced from the nature of the parasite fauna (Dogiel 1962). This is because the behaviour of the fish, community diversity and population density are of primary importance in determining the parasite load. Therefore, parasites may be useful as biological tags as well as biological indicators to characterize the life histories of deep-sea fishes (Armstrong 1974; Munroe 1976; Campbell _et al._ 1980).

Life histories of digenetic trematodes, nematodes, acanthocephalans and cestodes are complex in that they employ one or more intermediate hosts in addition to the definitive host. Complex helminth life cycles are of value in ecological studies because the parasites utilize food chains to reach the final host wherein the sexually reproducing adults develop. The abundance and incidence of parasites with complex life histories are directly related to the abundance of the benthic fauna as a whole, therefore parasite success in the deep ocean is directly related to abundance and diversity of hosts (Campbell 1983). In many cases, host specificity of adult worms appears to be related more to host ecology through prey selection than to host physiology (Rohde 1982). It also appears that decreased host specificity will be the rule for the most common helminth parasites with complex life cycles, and that their widespread success in the deep sea is directly related to the generalized feeding habits of their hosts (Campbell 1983).

Parasite recruitment throughout the life history of host fish species is a possible indicator of consistencies or changes in feeding habits. Parasite recruitment may follow one of three general patterns: (1) parasites are recruited while the host is young and recruitment declines as the host ages; (2) parasites are absent in young fish and appear with greater frequency as the host ages; or (3) recruitment begins with juvenile hosts and persists throughout its life (Campbell 1983). The first two patterns indicate a change in diet while the third is indicative of a consistent diet.

There are few studies of parasites from deep sea animals (see Noble 1973; Campbell 1983). Records of parasites from deep benthic fishes indicate that these fishes are as heavily parasitized as most shallow water fishes (Campbell _et al._ 1980). Helminths parasitizing deep benthic fishes are not diluted through the water column as envisioned by von Linstow (1888), but are evidently concentrated, and thus more effective in their transmission, within the benthic boundary layer (Campbell 1983). Campbell et al. (1980) believe that deep sea fishes are commonly infected with parasites as a result of this high concentration of larval parasites coupled with host diversity, population density of the benthos, and relative longevity of the parasites. In contrast, bathypelagic (Noble and Orias 1975; Orias 1978) and mesopelagic fishes (Collard 1970; Noble and Collard 1970) are parasite poor. There is some indication that parasite diversity, incidence and prevalence among benthic fishes decreases with increasing depth and distance from the continental shelf (Campbell 1983).

The objective of the present study is to determine if the dominant demersal fishes from the upper continental slope, in the vicinity of Carson Canyon, of the Grand Banks consume primarily benthic or pelagic organisms. The focus is on what types of food organisms are most often consumed by these fishes, not on determining where the fish forage. Stomach contents have been analyzed and prey taxa have been classified as benthic, pelagic, or benthopelagic in order to determine the relative importance of each prey type in the diet of the fishes studied. Preliminary work on benthic infaunal samples collected in the study region revealed a relatively low abundance and biomass of macrofaunal organisms (Houston and Haedrich 1984), indicating that pelagic organisms may be more important than benthic organisms as a food resource for the dominant demersal fishes there.

Stomach content data reveal what an organism was feeding on just prior to capture. Fishes may simply feed on whatever is available to them. Since the amount of specialization in feeding habits of the fishes studied is often difficult to deduce solely from stomach contents, indirect evidence from parasites is used as an indicator of the ecological relationships between hosts in terms of trophic structure (Campbell _et_ _al_. 1980). Noble (1973) pointed out that parasites are part of the fish's environment and that access to the host is determined by diet and living conditions, as well as by evolutionary and zoogeographical factors. As a result, the composition of the helminth fauna of a particular host is an indication of the involvement of that host within a community food web. Since the parasites are accumulated throughout the life of the fish, parasites from the digestive system were collected to provide information on the diet of the individual host integrated over time.

It should be noted that this was an ecological study with the main objective to determine the feeding habits of the fishes from the upper slope. The primary data were obtained from examining stomach contents; this is the traditional method used in feeding habit studies. Indirect evidence of feeding habits based on stomach contents was obtained from the parasite information, and this was used in a supportive mode only.

METHODS

Collection of Specimens

Collections were made on cruises 37 and 51 of the F/V GADUS ATLANTICA in June 1980 and May 1981, respectively, as part of general oceanographic studies of the Carson Canyon region on the eastern Grand Banks off Newfoundland (Figure 2). A total of 34 fish species from these cruises was examined in this study (Table 1). Fishes were collected using a 41-ft Gulf of Mexico Shrimp Trawl (Marinovich Trawl Company) with 80 x 120 cm steel V-doors providing an effective mouth opening of 8 m in width and 2 m in height (Haedrich _et_ _al._ 1980). The net was constructed with 1.5-inch (3.7-cm) stretch mesh with a 1-inch (2.5-cm) heavy knotted liner in the cod-end. The head-rope of the net was buoyed with a 30-cm diameter glass float (Benthos Company) and light chain was lashed at intervals along the foot-rope. The net was paid out and hauled back at 50 m/minute with the ship steaming at 1.5 knots. One hour of trawling with the 41-ft net at this speed covers an area of approximately 3.2×10^4 m^2. Time on the bottom was estimated as the interval from the time the winch stopped paying out to the time retrieval was begun. Twenty to thirty minute tows were used. Samples were fixed in 10% formal saline buffered with borax, and later transferred to 70% ethanol for storage prior to examination.

Stomach Content Analysis

Species determinations (using Goode and Bean 1896, the Fishes of the Western North Atlantic series, Part VI, 1973, and Leim and Scott 1966), total length (± 1.0 mm), total weight (± 1.0 g) and gut weight (± 0.01 g) were made in the laboratory for each specimen. Standard lengths were recorded for all species other than rattails. Tail breakage and regeneration in rattails made it necessary to find a suitable partial length measurement as a replacement for the traditional total length and standard length measurements. The snout-to-anal fin length (tip of snout to first anal finray) is highly correlated with the total length in rattails (r=0.97; Atkinson 1981); anal length was measured for all species of rattails in addition to total length. A regression was done using this anal length in order to estimate a more accurate total length measurement for the rattail species. This total length estimate is the reported value in the present study.

Stomachs and intestines were removed and placed singly in numbered jars of 70% ethanol. Prey species were removed from the stomachs, sorted, and counted using a dissecting microscope. Fragments of animals were keyed to the lowest possible taxonomic level, and numerical abundance of each prey species was estimated by counting pairs of eyes (crustaceans), discs (ophiuroids) and other parts. Prey and parasites were identified to the lowest taxonomic category appropriate to address the objective posed on page 7; i.e. "bivalve" is sufficient to establish that a prey item is benthic; "acanthocephalan" implies amphipods as intermediate hosts.

Several types of measurements have been used to identify dominant or important prey species. They include numerical abundance, volumes or weights, percent frequency of occurrence and caloric value (see Hyslop 1980 for review). Different measurements are usually assumed to contain independent information, therefore several methods have been developed to combine two or more measures in order to avoid loss of information (Macdonald and Green 1982). The necessity to combine all measures into one index has been countered with the argument that it is often desirable to reduce numbers of variables (Green 1979). In many cases the additional information gained decreases rapidly as more variables are included (Kaesler <u>et</u> <u>al.</u>

1974). Macdonald and Green (1982) found numerical abundance, weight and percent occurrence to be highly correlated with each other in a study of spatial and temporal variation in fish diet in the lower Bay of Fundy region in New Brunswick. They concluded that any one of the three variables studied would have adequately described prey species importance regardless of the definition of importance, thus avoiding the difficulties involved in interpretation and statistical analysis of compound indices (Green 1979). With these studies in mind, numerical abundance was chosen as the measure of prey importance in this study.

Food items were divided into three categories: pelagic, benthic and benthopelagic (Table 2). Fishes and euphausiids are active swimmers usually found in the water column, but which may occasionally come in contact with the bottom (Mauchline and Fisher 1969). Animals that dwell within the sediment or rarely leave the surface of bottom muds include polychaetes, echinoderms, gastropods, bivalves, gammarid amphipods (Dickson and Carey 1978), tanaids and cumaceans (Wolff 1977). Copepods (Weikert 1982), decapod crustaceans, ostracods, isopods and mysids include both pelagic and benthic species (Barnes 1980). In this study, decapod crustaceans were represented by the benthic family

Pandalidae and the pelagic families Penaeidae and Sergestidae (Foxton 1970). These groups, considered separately in the analysis of the data, were rare in the stomach contents examined. Hence, they are reported as one group. Based on previous studies (Marshall and Iwamoto 1973; Haedrich and Henderson 1974; Pearcy and Ambler 1974; Geistdoerfer 1975; 1979; McLellan 1977), myctophid fishes, euphausiids, copepods (primarily calanoid) and decapod crustaceans of the families Penaeidae and Sergestidae were considered pelagic prey items. Ostracods, mysids and isopods were considered benthopelagic prey items, and Pandalidae, polychaetes, tanaids, gastropods, cumaceans, bivalves, echinoderms and amphipods (primarily Gammaridae) were considered benthic.

Parasitological Analysis

The parasitological examination of fishes was done according to the methods outlined in Campbell et al. (1980). No live parasites were collected. Parasites were removed from the body cavity and alimentary tract of preserved fish and stored in 70% ethanol. In examining fish for parasites, attempts were made to obtain large samples of the full size range of host species, and stations were selected at regular depth intervals whenever possible.

Whole nematodes were mounted in glycerin. Wholemounts of trematodes and acanthocephalans were stained with Mayer's paracarmine, dehydrated in a graduated ethanol series, cleared in xylene and mounted in Canada Balsam. Parasites were identified to the lowest possible taxonomic level (using Yamaguti 1961a, 1961b, 1975; Munroe 1976), and the number of worms and number of parasite taxa were determined for each individual host.

The parasites were classified as either benthic or pelagic on the basis of the habits and habitats of known intermediate hosts (Table 3). Digenetic trematodes were represented by two families, Hemiuridae and Fellodistomidae. In general, epifaunal invertebrates are the primary second intermediate hosts for Digenea, particularly hemiurids such as *Gonocerca* sp. (Munroe 1976; Zubchenko 1981). Fellodistomid life cycles may involve either benthic (e.g. seastars) or pelagic (e.g. jellyfish) invertebrates (Yamaguti 1975), however, the fellodistome *Steringophorus pritchardae* is believed to cycle through pelagic invertebrates (Campbell *et al*. 1980). Nematoda may also cycle through benthic or pelagic organisms. This group of parasites was represented by the two families

Heterocheilidae and Rhabdochonidae. Amphipods are known intermediate hosts for the heterocheilid Thynnascaris sp. (Uspenskaya 1960; Ginetsinskaya 1970), and midwater fishes are known intermediate hosts for the heterocheilid Contracaecum sp. (Zubchenko 1980). Crustaceans, particularly amphipods, are known intermediate hosts of Acanthocephala (Ginetsinskaya 1970). Based on previous studies (Uspenskaya 1960; Ginetsinskaya 1970; Yamaguti 1975; Munroe 1976; Campbell et al. 1980; Zubchenko 1980, 1981; Campbell 1983), the fellodistome Steringophorus and the heterocheilid Contracaecum were considered indicative of feeding on pelagic organisms while the hemiurid Gonocerca, spirurids, acanthocephalans and the heterocheilid Thynnascaris were considered indicative of feeding on benthic organisms.

Data Analysis

A relative index of stomach fullness was assigned to each specimen. Values ranged from 0 for an empty stomach to 5 for a stomach that was completely full. The fullness value was plotted against the time of sampling and Kendall's rank correlation coefficient (tau) was calculated using the Statistical Package for the Social Sciences

(SPSS) (Nie et al. 1975). Kendall's tau was chosen because it is recommended for data sets containing a large number of common values. The number of prey items per stomach and the number of prey taxa per species were both plotted against the number of specimens of each species examined. The level of significance accepted was $P<0.05$.

The ratio of percentage of pelagic prey (including benthopelagic) versus percentage benthic prey was calculated for each specimen. Individuals were clustered on the basis of this ratio using the CLUSTAN package (Wishart 1975). Clustering was done by computing a dissimilarity value on the basis of percentage of pelagic and benthopelagic versus percentage of benthic prey organisms in the diet of the predator species. Clustering was done on individual fish in order to account for within-species differences. Dissimilarity was computed using the Non-metric (Bray-Curtis) Coefficient according to the formula:

$$\Sigma (U_{jp} - U_{jq}) / \Sigma (U_{jp} + U_{jq})$$

$$\text{with } U_{jp} = \Sigma X_{ij} / N_p$$

where U_{jp} denotes the mean benthic/pelagic ratio (j) for the fishes comprising a pair or cluster (p), U_{jq} denotes the mean benthic/pelagic ratio (j), for the fishes comprising a pair or cluster (q), X_{ij} equals the value of the mean benthic/pelagic ratio (j) for individual i, and N_p denotes the number of individual fishes in the pair or cluster (p). This coefficient was chosen because it is recommended for data sets with a high number of zero entries, and is independent of sample size. Individuals with similar benthic/pelagic ratios had high similarity values (low dissimilarity values) while individuals with very different benthic/pelagic ratios had low similarity values (high dissimilarity values). Clustering was done using the average linkage method. This technique avoids comparison by extreme values in a pair or cluster. The arithmetic average of similarity (or dissimilarity) coefficients between members of two pairs or clusters about to be fused is calculated prior to any further clustering. Thus, the number of individuals comprising a cluster is not a factor in evaluating the similarity between the two groups (Sneath and Sokal 1973). Once clustering was done using the ratio of percent benthic versus percent pelagic and benthopelagic prey, further cluster analyses were done using presence/absence and the percent occurrence of all prey taxa.

The average number of parasitic worms per host fish was determined for each species. The prevalence of each species was calculated as the number of individuals of a species infected versus the number of individuals of the species examined. The prevalence of each major taxon of helminths was determined for each host species. Prevalence and intensity of worms per fish were determined separately for the group of fishes with primarily benthic prey items in the stomach and for the group of fishes with primarily pelagic/benthopelagic prey items in the stomach.

A Fulton condition factor for each specimen was calculated using the formula $(W/L^3) \times 100$ (Carlander 1969). For each species, fullness and prevalence were plotted against the condition factor and data were compared using Kendall's rank correlation coefficient.

RESULTS

A total of 464 fishes, representing 14 species from 9 families was collected at depths from 403 to 1505 meters (Table 1). *Coryphaenoides rupestris* Gunnerus 1765 was the dominant species representing 57.8% of the total number of fishes and 24.9% of the biomass taken over this depth range. *Macrourus berglax* Lacepede 1802 was the second most abundant species, representing 13.7% of the total number and 20.2% of the biomass, followed by *Antimora rostrata* Gunther 1878 (9.6% of total, 16.4% of weight), *Nezumia bairdii* (Goode and Bean) 1877 (5.2% of total, 3.4% of weight), *Sebastes sp.* (4.0% of total, 3.6% of weight) and *Synaphobranchus kaupi* Johnston 1862 (3.5% of total, 2.0% of weight). The remaining species examined, including *Lycodonus mirabilis* Goode and Bean 1883, *Reinhardtius hippoglossoides* (Walbaum) 1792 (6.2% of weight), *Cottunculus microps* Collett 1875, *Gaidropsarus ensis* (Reinhardt) 1838, *Lycenchelys sarsi* (Collett) 1871, *Macdonaldia rostrata* (Collett) 1889, *Lycodes esmarkii* Collett 1875 and *Lycodes perspicillus* Kroyer 1845, each represented less than 1% of the assemblage of fishes by number and by weight (Snelgrove 1983).

Stomach Contents

Table 4 lists the stomach contents found in the dominant fishes from the study region. Most of the species contained prey from two or three ecological zones (pelagic, benthopelagic and benthic). Of those species found with items from all three groups, the same individual rarely had items from all three groups. Some specimens, primarily Macrouridae, had the stomach and gut partially or entirely everted. Prey items remaining in the partially everted guts were identified and included in the analysis. Specimens with guts entirely everted were recorded separately and are reported here with those stomachs recorded as empty. In all cases, except for C. rupestris, there was no significant correlation between gut fullness and the time of sampling, the number of prey taxa and the number of specimens examined or the number of prey items and the number of specimens examined (Table 5).

The cluster analysis using the benthic/pelagic ratio classified the predators into two groups: (1) primarily benthic prey in the diet; or (2) primarily pelagic/benthopelagic prey in the diet. The cluster analysis done on the entire data set as well as that done using the presence/absence data also classified the predators into these two groups. Pelagic and benthopelagic prey were numerically dominant in the diets of Coryphaenoides rupestris (71.7%), Synaphobranchus kaupi (73.3%) and Antimora rostrata (66.7%) (Figures 3 and 4). Stomach contents of primarily benthic origin occurred in Macrourus berglax (91.6%), Nezumia bairdii (86.0%), Lycodonus mirabilis (76.2%), Lycodes esmarkii (97.4%) and Cottunculus microps (84.3%) (Figures 3 and 5). Several individuals of these species had ingested large amounts of sediment.

Food items in Synaphobranchus kaupi included two orders of crustaceans and two families of fishes. Of the 73 stomachs examined, 16 (21.9%) were empty. Specimens ranged in size from 206 to 655 mm TL, with an average weight of 120.4 g. Pelagic organisms comprised 73.3% of the total number of food items of S. kaupi, with euphausiids (66.7%) dominating. Other prey taxa included amphipods (17.3%), myctophid fishes (6.7%), mysids (4%), bivalves (4%) and echinoderms (1.3%).

Only one (2.9%) of the 34 stomachs of Coryphaenoides rupestris examined was empty. Size range of specimens was 173 to 445 mm TL, with an average weight of 92.9 g. Pelagic and benthopelagic organisms comprised 71.7% of the total number of food items in the diet of C. rupestris, with calanoid copepods (68.9%) numerically dominant. Other prey taxa included amphipods (22.2%), cumaceans (4.4%), euphausiids, polychaetes, isopods and ostracods (each 1.1%).

Euphausiids (50%) were the dominant food item in the stomachs of *Antimora rostrata*. Other prey types included amphipods (33.3%) and copepods (16.7%). Pelagic prey types comprised 66.7% of the diet of *A. rostrata*. Of the 7 stomachs examined, 2 (28.6%) were empty. Average weight of specimens was 365.7 g with a size range of 126 to 155 mm TL. This abundant fish almost always has everted stomachs and it is thus difficult to obtain stomach content data.

Food items in *Macrourus berglax* included several orders of crustaceans, polychaetes, echinoderms and mollusks. Of the 191 stomachs examined, 50 (26.2%) were empty. Cumaceans (58.7%) and amphipods (18.0%) were the most frequently occurring food items, followed by polychaetes (7.9%), euphausiids (5.7%), echinoderms (2.8%), tanaids (2.1%), copepods and isopods (each 1.5%), mollusks, mysids, decapod crustaceans and ostracods (all less than 1%). *M. berglax* examined ranged in size from 78 to 324 mm TL, with an average weight of 316.1 g.

Three (3.1%) of the 96 stomachs of *Nezumia bairdii* examined were empty. Numerically dominant prey taxa included cumaceans (35.6%), amphipods (23.9%) and polychaetes (17.0%). Other prey taxa consumed were euphausiids (10.5%), bivalves (7.5%), mysids (2.4%), echinoderms, isopods, copepods, tanaids, ostracods and decapod crustaceans (each less than 1%). Size of specimens ranged from 175 to 407 mm TL, with an average weight of 137.8 g.

The most frequent food items in Lycodonus mirabilis were amphipods (56.9%) followed by cumaceans (22.9%). Other prey items included polychaetes (8.3%), bivalves (7.3%), echinoderms (2.8%), isopods, myctophid fishes and ostracods (each less than 1%). Ten (35.7%) of the 28 stomachs examined were empty. L. mirabilis examined ranged in size from 171 to 330 mm TL, with an average weight of 17.7 g.

Prey taxa found in Lycodes esmarkii stomachs were almost entirely (97.4%) benthic. Cumaceans (39.5%), echinoderms (31.6%) and amphipods (25%) predominated, with fish (2.6%) and isopods (1.3%) being incidental. Of the 6 stomachs examined, 1 (16.7%) was empty. Average weight of specimens was 946 g with a size range of 398 to 569 mm TL.

The numerically dominant prey of Cottunculus microps was amphipods (64.9%), followed by euphausiids (15.8%), bivalves, polychaetes, and cumaceans (each 5.3%). Two stomachs (14.3%) of a total of 14 examined were empty. *C. microps* had an average weight of 135.7 g with a size range of 48 to 232 mm TL.

Kendall's tau was calculated for fullness and prevalence against condition factor for these 8 abundant species. There was a significant correlation between gut fullness and condition factor for *C. rupestris* and *S. kaupi*. Correlations between these two variables were not significant in the other species (Table 4). In all cases there was no correlation between condition factor and prevalence (Table 4).

The small numbers of intact stomachs of *Lycenchelys sarsi*, *Lycodes perspicillus*, *Reinhardtius hippoglossoides*, *Sebastes sp.*, *Gaidropsarus ensis* and *Macdonaldia rostrata* examined do not give an adequate basis for determining the relative importance of the food sources or the degree of specialization in feeding habits of these species.

Two (50%) of the four stomachs of *L. sarsi* examined were empty. Numerically dominant prey taxa included amphipods (38.3%), cumaceans (26.7%) and ophiuroids (26.1%). Other prey taxa consumed included bivalves (5.6%), tanaids (2.2%), polychaetes and isopods (both less than 1%). *L. sarsi* examined ranged in size from 129 to 323 mm

TL, with an average weight of 14.5 g.

The most frequent food items in *L. perspicillus* were cumaceans (39.5%), echinoderms (31.5%) and amphipods (25.0%). The other prey item consumed was bivalves (2.6%). Three (50%) of the 6 stomachs examined were empty or damaged. Size of specimens examined ranged from 43 to 569 mm TL, with an average weight of 399.6 g.

Numerically dominant food items in *G. ensis* included amphipods, euphausiids (both 28.6%) and cumaceans (19.0%). Other food items consumed included pycnogonids (9.5%), polychaetes and tanaids (both 4.8%). Of the 8 stomachs examined, 3 (37.5%) were empty. *G. ensis* examined ranged in size from 60 to 405 mm. TL, with an average weight of 227.8 g.

The numerically dominant prey of *Macdonaldia rostrata* was amphipods (66.7%), followed by euphausiids (13.7%), cumaceans, echinoderms (both 7.8%), polychaetes and tanaids (both 2.0%). The 2 specimens examined were 425 and 501 mm TL and weighed 110.6 g and 134.1 g respectively.

Only 1 stomach of *R. hippoglossoides* was examined. It contained euphausiids (85.7%) and cumaceans (14.3%). The specimen was 318 mm TL, with a weight of 162.3 g.

The 1 stomach of Sebastes sp. examined contained amphipods (87.5%) and polychaetes (12.5%). The specimen was 189.9 mm TL, with a weight of 162.3 g.

The samples of Macrourus berglax were subdivided into 6 size classes. The most apparent trends in the food habits of M. berglax are the decrease in the proportion of cumaceans and the increase in proportion of polychaetes with increasing size of fish (Figure 6). There does not appear to be any shift in the diet from benthic to pelagic prey, but there does appear to be an increase in diversity of prey consumed with increasing size of fish.

Nezumia bairdii samples were subdivided into 7 size classes. There are no obvious trends in the food habits of this species (Figure 6). There is a slight decrease in the fraction of cumaceans with increasing size of fish. There does appear to be an increase in diversity of prey with increasing size although there is no shift from benthic to pelagic prey.

Five size classes were examined for Synaphobranchus kaupi. This species apparently consumes an increasing proportion of euphausiids with increasing size (Figure 6). Benthic organisms do appear to be important in the diet of smaller S. kaupi, but are less prominent in the diet of larger fish. This may be evidence for a shift from benthic to pelagic prey with increasing size. There were no fish found in the stomachs of larger predators. This may be a result of the small numbers of larger fish examined.

Five size classes of Coryphaenoides rupestris were examined. The most apparent trends in the food habits of C. rupestris are an increase in the fraction of copepods along with a decrease in the fraction of amphipods and cumaceans with increasing size of fish (Figure 6). This is indicative of a shift from benthic to pelagic prey with increasing size.

Parasite Faunas

Forty-six percent of the 464 fishes examined were infected with 1 to 3 ($\bar{x}$ = 1.9) major taxa of helminths. The major taxa were represented by the following families: Hemiuridae, Fellodistomidae (Digenea); Heterocheilidae, Rhabdochonidae (Nematoda), and Echinorhynchidae (Acanthocephala). Intensity of infection averaged 5.5 worms per fish. A total of 1176 helminths were obtained. Percent occurrence of metazoan parasites among all fishes was: Nematoda 36.7%, Acanthocephala 20.7% and Digenea 6.9%.

Table 6 summarizes the total helminth infections for all host species examined. Table 7 summarizes the prevalence of the major taxa of parasites found in all host species. The parasite fauna of the 8 major species are summarized in Table 8. The prevalence of digenetic Trematoda in benthic feeders was only 5.8%,, but was 27.8% in benthopelagic/pelagic feeders. Nematoda comprised 53.1% of the parasite fauna in benthic feeders and 72.2% in the benthopelagic feeders. Acanthocephala were abundant (40.9%) in the parasite fauna of benthic feeders but were absent (0%) in that of the benthopelagic/pelagic feeders.

Twenty-nine (39.7%) of the 73 *Synaphobranchus kaupi* examined were infected with an average of 1.3 worms per host. This species was infected solely by Nematoda, in particular *Thynnascaris* sp. and *Contracaecum s.l.*.

Coryphaenoides rupestris was infected by Digenea, in particular *Steringophorus* sp. and an unidentified hemiurid. The Nematoda *Contracaecum s.l.* was also found in this host species. Of the 34 specimens examined, only 4 (11.8%) were infected, with an average of 4.3 worms per host.

None of the 7 *Antimora rostrata* examined were infected by any helminth parasites.

Of the 191 Macrourus berglax examined, 95 (49.7%) were infected with an average of 7.3 worms per host. The majority (62.1%) of the parasites collected were Acanthocephala, probably of the genus Echinorhynchus. Thirty-five percent of the parasites were Nematoda, particularly Spenetectus sp. and Thynnascaris sp., while the remaining 2.9% of the parasites were the digenean Gonocerca sp..

Sixty-three (65.6%) of the 96 Nezumia bairdii examined were infected with an average of 5.4 worms per host. The most abundant parasite was the nematode Thynnascaris sp. (93.9%). The remaining parasites were Acanthocephala of the genus Echinorhynchus.

Lycodonus mirabilis was infected by all three major groups of parasites. The most abundant parasites were Digenea (87.5%), in particular Gonocerca sp. and an unidentified hemiurid. The remaining parasites included the nematode Thynnascaris sp. and an acanthocephalan (likely Echinorhynchus). Of the 28 host specimens examined, 13 (46.4%) were infected, with an average intensity of 3.7 worms per host.

One (16.7%) Lycodes esmarkii was infected with a total of 2 parasites: the digenean Gonocerca sp. and the nematode Thynnascaris sp..

The most abundant parasite found in Cottunculus microps was the nematode Thynnascaris sp. (90%). The remaining parasites collected were the digenean Gonocerca sp. (10%). A total of 6 (42.9%) of the 14 host specimens examined were infected with an average of 3.3 worms per host.

In all of the four species examined according to size, there is a definite accumulation of parasites with increasing size of fish. There is also an increase in the number of fishes infested (Figure 7).

There was a decrease in the number of Digenea (Gonocerca sp.) and a slight increase in the number of Nematoda (Spenetectus sp. and Thynnascaris sp.) in M. berglax with increasing size. The number of acanthocephalans was relatively consistent throughout the size range of this host species (Figure 7).

Nezumia bairdii was infected with a high number of Nematoda (Thynnascaris sp.). Acanthocephala were not present in smaller specimens of this host species, but did appear in specimens greater than 250 mm TL (Figure 7).

Synaphobranchus kaupi was infected solely by Nematoda (Thynnascaris sp. and Contracaecum s.l.). All size classes were infected, however there was a greater percentage of larger fishes infected, with an increase in the number of parasites per host (Figure 7).

A relatively small percentage (11.8%) of the C. rupestris examined were infected, with all small fishes (less than 200 mm TL) being parasite free. Host fishes between 200 and 300 mm TL were infected by Nematoda (Contracaecum s.l.), while fishes larger than 300 mm TL were infected by Digenea (Steringophorus sp.) (Figure 7).

DISCUSSION

Food webs involving vertically migrating species appear to be important in the transfer of energy to the benthos along the upper continental slope (Sedberry and Musick 1978). The direct transfer of energy by overlapping vertical migrations of pelagic organisms and demersal fishes on the upper continental slope is presumed to be energetically more efficient than the indirect pathway via benthic organisms. However, the energy expenditure for capture of prey may be greater for those fishes which move off the bottom to feed.

Available data on the behaviour of benthopelagic fishes are the result of direct or photographic observations from bathyscaphes or automatic cameras (Marshall and Bourne 1964, Sedberry and Musick 1978). Antimora rostrata were observed hovering within one meter of the bottom. Macrourinae, a subfamily of Macrouridae including Coryphaenoides rupestris, Macrourus berglax and Nezumia bairdii, swim above the bottom with a "nose-down" posture as a result of their body shape and fin pattern (Marshall and Bourne 1964). Presumably this position makes it easier to seize prey on the bottom and to burrow. However, C. rupestris has a terminal mouth and is therefore probably unable to burrow in the sediment like M. berglax and N. bairdii which have more inferior mouths and well-developed rostra (Geistdoerfer 1975). The latter two species are among the benthic feeding species in this study.

Geistdoerfer (1975) found that macrourids did not feed exclusively on pelagic or benthic animals. The diet of the fish he examined was never composed of only one prey group; there was always a variety of prey types and sizes in the stomach. He also found a greater number of prey groups in benthic feeders as opposed to pelagic feeders. These observations are consistent with the results of this study (Table 4).

Podrazhanskaya (1967, 1971) reported a diurnal rhythm of feeding for C. rupestris collected in the Iceland, West Greenland, Baffin Island, Labrador and the Northern Newfoundland Bank areas. This was also the case in the present study. In all other species examined, there was no apparent diurnal feeding behaviour as demonstrated by the lack of correlation between gut fullness and time of sampling (Table 5). The lack of any diurnal feeding pattern in the other species could be an artifact of the sampling, since a large proportion of the trawls were done between late morning and late afternoon, with few samples taken in the late evening or early morning.

Pelagic Feeders

Coryphaenoides rupestris and Antimora rostrata are numerically dominant species on the slope of the Grand Banks, while Synaphobranchus kaupi is relatively rare (Snelgrove and Haedrich 1984). All three species primarily consumed pelagic species, many of which are known vertical migrators (Sedberry and Musick 1978). Other investigators have also observed that vertically migrating pelagic organisms are important prey items for these demersal fishes. In this study, C. rupestris and S. kaupi were found to feed more on benthic organisms when small, gradually shifting to pelagic prey items with increasing size (Figure 6).

Pechenik and Troyanovski (1970) reported that C. rupestris in slope waters of the northwest Atlantic fed intensively on zooplankton (shrimps, euphausiids, copepods and amphipods). They also found the seasonal bathymetric vertical migrations of C. rupestris to be related to changes in the vertical distributions of their pelagic prey. Pelagic shrimp, euphausiids and amphipods were common prey items in the diet of C. rupestris from Icelandic waters (Podrazhanskaya 1967), from waters near

Baffin Island (Konstantinov and Podrazhanskaya 1973), and in the Denmark Strait (Haedrich 1974).

The upper depth range of the vertical migration of *S. kaupi* overlaps the lower limit of the daily vertical migrations undertaken by many pelagic animals (Ekman 1953; Gibbs *et al.* 1971; Roper and Young 1975), enabling *S. kaupi* to take advantage of this food supply (Sedberry and Musick 1978). Two major components of the vertically migrating mesopelagic fauna are myctophid fishes and euphausiids (Farquhar 1977), both of which were present in the stomachs of *S. kaupi* examined here.

Pelagic food is also important to *A. rostrata*, a fish usually found on the lower slope. Sedberry and Musick (1978) reported that few of the pelagic animals consumed by *A. rostrata* were known vertical migrators. This is not surprising if Marshall's (1971) lower bathymetric limit of 1000 m for vertically migrating mesopelagic organisms is correct. *C. rupestris* may make extensive vertical migrations in the water column to feed (Haedrich 1974), however, there is no evidence that *A. rostrata* does the same (Wenner and Musick 1977). In fact, little information on the life history of this species is available.

Benthic Feeders

Nezumia bairdii, Macrourus berglax, Lycodes esmarkii, Lycodonus mirabilis and Cottunculus microps primarily consumed benthic organisms. The first two species are numerically dominant on the slope of the Grand Banks while the latter three are relatively rare (Snelgrove and Haedrich 1984).

Other studies have also found that M. berglax and N. bairdii feed intensively on infauna. Benthic organisms such as polychaetes, ophiuroids and gammarid amphipods were dominant in M. berglax caught near Baffin Island (Konstantinov and Podrazhanskaya 1973), in the Barents and Labrador Seas (Geistdoerfer 1979) and in the northeast Atlantic, Mediterranean Sea and Indian Ocean (Geistdoerfer 1975). These organisms were important prey items for N. bairdii from the mid-Atlantic coast of the USA (Farlow 1980). In the present study, there is no dramatic change in diet with the size of either species of fish, although there is an increase in the diversity of prey types taken with increasing size of predator (Figure 6).

The food of the two species of zoarcids, Lycodes esmarkii and Lycodonus mirabilis, is similar to that for Lycenchelys verrilli from the coast of New England. Farlow

(1980) characterized this species as a benthic feeder primarily consuming infaunal organisms. Cumaceans and amphipods, dominant food items for Lycodes atlanticus, were apparently gulped down with large amounts of sediment, as also observed by Sedberry and Musick (1978).

Cottunculus microps ingested a large amount of sediment along with the prey. McDowell (1973) believed that the sediment he found in halosaurid stomachs may have been incidentally consumed along with the infauna and was "non-nutritional", but gave no evidence for this conclusion. As a result of work by Coull (1972) and Thiel (1975), it has been suggested that the importance of meiofaunal prey contained within the sediment for benthic-feeding fish may increase with depth. Because of their small size, meiofaunal prey items may only be ingested with sediment. The nutritional value obtained by ingesting sediment and digesting the associated meiofauna has yet to be determined.

It is difficult to draw any conclusions about the feeding habits of species for which there are few specimens. The two species of eelpouts, L. sarsi and L. perspicillus, appear to feed on a diet similar to that of L. esmarkii and

L. mirabilis. The latter two species were defined as benthic feeders, and this may also be the case for the first two. The remaining four species, G. ensis, M. rostrata, R. hippoglossoides and Sebastes sp. appear to feed on a mixed diet of benthic and pelagic organisms. Without further data it is difficult to classify these species. Based on the available data, they would be included with the benthic group.

Parasite Faunas - Pelagic vs Benthic Feeding Hosts

As a result of differences in diet, individual species of fishes should show marked differences in the composition of their parasite faunas and infection rates. The prevalence for hosts found to feed primarily on pelagic or benthopelagic prey was 28.9%. Prevalence for benthic feeding hosts was 53.1%. Benthic feeders were infected with an average of 2.4 major taxa of parasites and 4.3 worms per fish. Pelagic feeders were infected with an average of 1 taxon and 1.9 worms per fish. This higher rate of infection found in benthic feeders is consistent with the argument that the majority of cycling of helminths of demersal fishes is horizontal through animals in and associated with the benthic community (Campbell et al.

1980), and not vertically through the water column as proposed by Collard (1970).

There was no correlation between condition factor for a fish and gut fullness (except for C. rupestris and S. kaupi) or intensity of parasite prevalence (Table 5). It is often assumed that a host which is heavily parasitized will not be as "healthy" as one which is free of parasites. However, recent studies have drawn attention to the fact that parasites may be of benefit to the individual host (Lincicome 1971). Among marine parasites, nothing is known of potential beneficial effects, however Berland (1980) suggested that ascaridoid nematodes in the stomachs of fishes may mechanically break up large food particles. This action may be important in digestion, since many hosts ingest their food whole or in large chunks (Rohde 1982). The results of this study do not indicate any detrimental or beneficial effects of the parasites on their hosts. The intensity of parasite infection for all species was relatively low compared to that found in other studies (Armstrong 1974, Munroe 1976, Campbell *et al.* 1980).

Zubchenko (1981) reported parasite faunas for the three species of Macrouridae studied here. He found that *C. rupestris* was infected with 14 species of parasites. The majority of these parasites were reported to have pelagic animals as intermediate hosts, indicating pelagic prey were a significant part of the diet. M. berglax was infected with 21 species of parasites, many having benthic organisms as intermediate hosts. Interestingly, the parasite fauna of N. bairdii collected from the Flemish Cap area included a number of species with cycles of development related to planktonic organisms. However, the fish also contained parasites which cycle through benthic organisms. These results suggest that pelagic organisms are important prey items for N. bairdii at some point in its life.

Parasites vs Food Habits

Collard (1970) proposed that midwater organisms play an important role as vectors of nematode parasites from surface waters to the deeper regions of the ocean. Campbell et al. (1980) found nematode parasites to be more common in fishes such as N. bairdii, which they describe as rarely ascending into the water column to feed. Nematoda were found in both benthic (53.1%) and pelagic (72.2%) feeders in this study, indicating that both pathways are possible.

The parasite fauna of N. bairdii was almost completely dominated by nematodes, particularly Thynnascaris sp. S.

kaupi was infected solely by nematodes, in particular Thynnascaris sp. and Contracaecum s.l.. Amphipods are the known intermediate host for nematodes of the genus Thynnascaris (Uspenskaya 1960, Ginetsinskaya 1970), and fishes are known intermediate hosts of Contracaecum aduncum (Zubchenko 1980). Amphipods are important components of the diet of N. bairdii and S. kaupi ((S. kaupi 17.3 %, N. bairdii 23.9 %), while fishes were consumed by S. kaupi only. In both host species, the proportion of infected fishes increases with increasing size of the host (Figure 7). The average number of worms per host is rather consistent in S. kaupi. This lack of apparent parasite recruitment in S. kaupi reflects the decrease in fish consumption with age. In contrast, the number of worms per host increases with increasing size of N. bairdii. The recruitment of parasites throughout the life of N. bairdii is indicative of either a consistent intake or increasing consumption of the intermediate host. This observation agrees with the stomach contents data which reveals that amphipods were consumed by all size classes of fishes (Figure 6).

Crustaceans, particularly amphipods, are known intermediate hosts for acanthocephalans (Ginetsinskaya 1970). Acanthocephala, probably of the genus

Echinorhynchus, were relatively abundant in benthic feeders (40.9%) but absent in pelagic feeders. The abundance of acanthocephalans in benthic feeders suggests that they consume a great number of crustaceans. This contention is supported by gut contents in which amphipods and cumaceans predominated (Figure 5).

Trematoda comprised 27.8% of the helminth fauna of pelagic feeders and only 5.8% of the helminth fauna of benthic feeders. Coryphaenoides rupestris was the only pelagic-feeding species infected with digenetic trematodes, in particular, the fellodistome Steringophorus sp. Fellodistome life cycles are known to involve either benthic invertebrates (e.g. seastars) or pelagic invertebrates (e.g. jellyfish) (Yamaguti 1975), however, Campbell et al. (1980) reported that the presence of the fellodistomes Steringophorus pritchardae or S. blackeri suggests the capture of pelagic prey. The remainder of the host species were infected with the hemiurid Gonocerca sp. and an unknown hemiurid. Epifaunal invertebrates have been reported as primary second intermediate hosts, for digenetic trematodes such as Gonocerca sp. (Munroe 1976; Zubchenko 1981), a finding which supports the stomach content data from host fishes in the present study.

Parasite Infection Rates

All phyletic groups of fishes are not infected by helminths to the same degree (Tables 7 and 8). Prevalence of Nematoda and Acanthocephala were greater by twofold or more in the macrourids than in other fishes. Infection by Trematoda was severalfold greater in all other species than in the macrourids. Overall infection rate was much greater for macrourids (50.5%) than for non-macrourids (36.4%). In general, the higher incidence of helminth infections in macrourids (Armstrong 1974; Munroe 1976; and Campbell et al. 1980) indicates that this group of teleosts is not only more frequently infected but also carries a greater parasite burden than non-macrourid hosts occurring in the same areas.

Prevalence of all helminths, except Acanthocephala, was greater in Gulf of Mexico (Armstrong 1974) and Hudson Canyon fishes (Munroe 1976) than in fishes examined here (Table 9). The higher levels of infections could be a result of sampling. In the present study, only parasites from the gut and body cavity were collected, while Armstrong (1974) and Munroe (1976) included parasites from the gills, skin and viscera. A comparison between Carson Canyon and Hudson Canyon fishes, with macrourids excluded, revealed that infections of non-macrourid fishes exhibited similar trends (Table 9).

Overall Summary and Conclusions

Eight fish species were examined from the Newfoundland continental slope; 5 fed primarily (by number) on benthic organisms and 3 fed primarily on pelagic and benthopelagic organisms. Although there are more species of benthic feeders than pelagic feeders, the pelagic feeders are more abundant in actual numbers (70.3% versus 20.5%). Thus, pelagic feeding is the primary source of nutrition for this assemblage of fishes. These results are similar to those of DuBuit (1978). She found that 62% of the food of deep sea fishes off the northeast coast of Scotland and on Bill Bailey Bank is of nectonic origin. In the present study, the average individual weight for the benthic feeders was 270.6 g while that of the pelagic feeders was 130.6 g. Despite this smaller average size, pelagic feeders still comprised a significant proportion of the biomass (43.3%), with the benthic feeding species studied comprising a smaller proportion (25.9%).

The present work and other studies have found that the demersal fishes of the upper continental slope feed on a variety of benthic and pelagic animals. Demersal fishes, particularly the pelagic feeding species, may represent a connecting link for the transfer of material between the pelagial and the benthos. Since these fishes are not confined to the bottom, they may be an important factor in the transfer of energy from pelagic to benthic ecosystems via their remains and feces (Dayton and Hessler 1972), but there is no direct evidence to support this contention. In fact, the large proportion of the biomass represented by pelagic feeders, and the low biomass of macrobenthic fauna on the slope of the Grand Banks (Houston and Haedrich 1984) indicate that a large proportion of the biomass is being recycled in the water column of this region.

Other studies have similarly found that pelagic organisms are important prey items for demersal fishes on the upper slope (Pearcy and Ambler 1974; Sedberry and Musick 1978; DuBuit 1978). The results from the present study combined with the results of others indicate that feeding from the pelagial at upper continental slope depths is probably the general rule. Therefore, in order to understand the dynamics of fish populations on the bottom, it is necessary to study the biological and physical environment of the water column.

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Table 1. List of all species collected from sample area (Snelgrove, 1983).
N/E means not examined.

Species	# stations	Total number	% Total number	Number Examined	% Examined
Alepocephalus sp.	7	15	0.36	N/E	-
Anarhichas lupus	2	2	0.05	N/E	-
Antimora rostrata	26	402	9.60	7	1.74
Centroscyllium fabricius	5	15	0.36	N/E	-
Chalinura brevibarbis	1	12	0.29	N/E	-
Coryphaenoides rupestris	18	2424	57.80	34	1.40
Cottunculus microps	9	18	0.43	14	77.78
Gadus morhua	3	16	0.38	N/E	-
Gaidropsarus ensis	7	10	0.24	8	80.0
Glyptocephalus cynoglossus	4	10	0.24	N/E	-
Harriotta raleighana	2	2	0.05	N/E	-
Hydrolagus affinis	2	2	0.05	N/E	-
Lionurus carapinus	4	10	0.24	N/E	-
Lycodes atlanticus	2	5	0.12	N/E	-
Lycodes esmarkii	4	19	0.45	6	31.57
Lycodes perspicillus	1	1	0.02	1	100
Lycodes vahlii	3	5	0.12	N/E	-
Lycodonus mirabilis	6	29	0.69	28	96.5
Lycenchelys sarsi	2	2	0.05	2	100.0
Macdonaldia rostrata	3	4	0.10	2	50.0
Macrourus berglax	25	573	13.68	191	33.33
Nematonurus armatus	4	15	0.36	N/E	-
Nezumia bairdii	16	219	5.23	96	43.84
Notocanthus sp.	2	2	0.05	N/E	-
Phycis chesteri	2	4	0.10	N/E	-
Raja jenseni	2	4	0.10	N/E	-
Raja radiata	7	21	0.50	N/E	-
Raja sentra	2	2	0.05	N/E	-
Reinhardtius hippoglossoides	8	23	0.55	1	12.50
Scophthalmus aquosus	2	4	0.10	N/E	-
Sebastes sp.	8	166	3.96	1	0.60

Table I cont'd.

Species	# stations	Total number	% Total number	Number Examined	% Examined
Synaphobranchus kaupi	23	148	3.53	73	49.32
Trachyrhynchus murrayi	1	1	0.02	N/E	-
Zoarces sp.	3	4	0.10	N/E	-
Total		4189		464	11.08

Table 2. Table of prey taxa that occurred in large numbers. Where available, normal habitat (B-benthic, P-pelagic, BP-benthopelagic) is indicated.

Prey Taxa	Habitat Classification
Crustaceans	
Copepoda	
Calanoid	P
Malacostraca	
Euphausiacea	P
Decapoda	
Penaeidae	P
Sergestidae	P
Pandalidae	B
Mysidae	BP
Cumacea	B
Tanaidacea	B
Isopoda	BP
Amphipoda	
Gammaridae	B
Ostracoda	BP
Echinoderms	
Stelleroidea	
Echinoidea	B
Ophiuroidea	B
Annelids	
Polychaeta	B
Mollusks	
Gastropoda	B
Bivalvia	B
Fish	
Myctophidae	P

Table 3. Table of parasite taxa that occurred in large numbers. Where available, the common intermediate host and the host's normal habitat (B-benthic, P-pelagic) is indicated.

Parasite Taxa	Intermediate Host	Habitat Classification	Reference
Acanthocephala	Crustaceans		
Echinorhynchidae			
Echinorhynchus	Amphipods	B	Ginetsinskaya 1970
Digenea			
Hemiuridae			
Gonocerca	Epifaunal invertebrates	B	Munroe 1976; Zubchenko 1981
Fellodistomidae			
Steringophorus	Pelagic invertebrates	P	Yamaguti 1975; Campbell *et al.* 1980
Nematoda			
Heterocheilidae			
Contracaecum	Midwater Fishes	P	Zubchenko 1980
Thynnascaris	Amphipods	B	Uspenskaya 1960; Ginetsinskaya 1970
Rhabdochonidae			
Spinetectus	Unknown		

Table 4. Summary of stomach contents by major taxonomic groups of the fishes studies (presence/absence data).

Predator Species	NO.	FIS	EUP	COP	OST	DEC	MYS	AMP	CUM	TAN	ISO	POL	ECH	MOL
Cottidae														
Cottunculus microps	14		X					X	X			X		X
Galdropsaridae														
Galdropsarus ensis	8							X	X	X				
Macrouridae														
Coryphaenoides rupestris	34		X	X	X			X	X		X	X		
Macrourus berglax	191		X	X	X	X	X	X	X	X	X	X	X	X
Nezumia bairdii	96		X	X	X	X	X	X	X	X	X	X	X	X
Moridae														
Antimora rostrata	7		X	X				X						
Notocanthidae														
Macdonaldia rostrata	2		X					X	X	X	X	X		
Pleuronectidae														
Reinhardtius hippoglossoides	1		X						X					
Scorpaenidae														
Sebastes sp.	1													
Synaphobranchidae														
Synaphobranchus kaupi	73	X	X				X	X					X	X
Zoarcidae														
Lycenchelys sarsi	2		X					X	X	X	X	X	X	
Lycodes esmarkii	6		X					X	X		X		X	
Lycodes perspicillus	1													
Lycodonus mirabilis	28	X			X			X	X		X	X	X	X

NO: Number of specimens examined
FIS: fish
EUP: euphausiid
TAN: tanaid
ISO: isopod
COP: copepod
OST: ostracod
POL: polychaetes
ECH: echinoderms (primarily ophiuroids)
DEC: decapod crustaceans
MYS: mysids
MOL: gastropods & bivalves
AMP: amphipod
CUM cumacean

Table 5. Kendall's rank correlation coefficients (T) for listed variables. TIME = time of sampling; FULLNESS = gut fullness; CONDITION = condition factor; INTENSITY = intensity of parasite infection; * = significant at $p < 0.05$.

Variables	Species	N	T	Significance
TIME with FULLNESS	*M. berglax*	191	0.05	0.45
	N. bairdii	96	-0.10	0.26
	C. rupestris	34	-0.33	0.03*
	S. kaupi	73	-0.13	0.14
	L. mirabilis	28	0.12	0.61
	L. esmarkii	6	0.77	0.16
	C. microps	14	-0.04	0.91
	A. rostrata	7	0.77	0.16
CONDITION with FULLNESS	*M. berglax*	191	0.01	0.84
	N. bairdii	96	0.14	0.07
	C. rupestris	34	0.40	0.01*
	S. kaupi	73	0.23	0.01*
	L. mirabilis	28	-0.19	0.35
	L. esmarkii	6	-0.91	0.07
	C. microps	14	-0.13	0.66
	A. rostrata	7	-0.91	0.07
CONDITION with INTENSITY	*M. berglax*	191	0.07	0.30
	N. bairdii	96	0.05	0.50
	C. rupestris	34	-0.02	0.89
	S. kaupi	73	0.18	0.06
	L. mirabilis	28	-0.13	0.49
	L. esmarkii	6	0.24	0.66
	C. microps	14	-0.29	0.31
	A. rostrata	7	0.24	0.66

Table 6. Comparison of helminth infections for all hosts.

Host species	# examined / # infected	% infected	Total helminth taxa recovered	Helminth taxa per host	Intensity per host
Cottidae					
Cottunculus microps	14/6	42.9	2	1.0	3.3
Gaidropsaridae					
Gaidropsarus ensis	8/1	12.5	2	2.0	7.0
Macrouridae					
Coryphaenoides rupestris	34/4	11.8	2	1.0	4.3
Macrourus berglax	191/95	49.7	3	1.7	7.3
Nezumia bairdii	96/63	65.6	2	1.1	5.4
Moridae					
Antimora rostrata	7/0	0	0	0	0
Notocanthidae					
Macdonaldia rostrata	2/1	50.0	1	1.0	2.0
Pleuronectidae					
Reinhardtius hippoglossoides	1/0	0	0	0	0
Scorpaenidae					
Sebastes sp.	1/0	0	0	0	0
Synaphobranchidae					
Synaphobranchus kaupi	73/29	39.7	1	1.0	1.3
Zoarcidae					
Lycenchelys sarsi	2/1	50.0	1	1.0	9.0
Lycodes esmarkii	6/1	16.7	2	2.0	2.0
Lycodes perspicillus	1/0	0	0	0	0
Lycodonus mirabilis	28/13	46.4	3	1.4	3.7

Table 7. Comparison of infection rate of major taxa of helminths for all hosts (numbers in brackets)

Host species	Trematoda	Nematoda	Acanthocephala	Total Number
Cottidae				
Cottunculus microps	10.0% (2)	90.0% (18)	0%	20
Gaidropsaridae				
Gaidropsarus ensis	71.4 (5)	0	28.6 (2)	7
Macrouridae				
Coryphaenoides rupestris	88.2 (15)	11.8 (2)	0	17
Macrourus berglax	2.9 (20)	35.0 (242)	62.1 (430)	692
Nezumia bairdii	0	93.9 (321)	6.1 (21)	342
Moridae				
Antimora rostrata	0	0	0	0
Notocanthidae				
Macdonaldia rostrata	0	100 (2)	0	2
Pleuronectidae				
Reinhardtius hippoglossoides	0	0	0	0
Scorpaenidae				
Sebastes sp.	0	0	0	0
Synaphobranchidae				
Synaphobranchus kaupi	0	100 (37)	0	37
Zoarcidae				
Lycenchelys sarsi	0	100 (9)	0	9
Lycodes esmarkii	50.0 (1)	50.0 (1)	0	2
Lycodes perspicillus	0	0	0	0
Lycodonus mirabilis	87.5 (42)	10.4 (5)	2.1 (1)	48

Table 8. Summary of parasite taxa of the 8 most abundant species of host fishes examined (presence/absence data).

Predator Species	Number Examined	ECH	GON	STE	CON	THY	SPI
Cottidae							
Cottunculus microps	14		X			X	
Macrouridae							
Coryphaenoides rupestris	34			X	X		
Macrourus berglax	191	X	X			X	X
Nezumia bairdii	96	X				X	
Moridae							
Antimora rostrata	7						
Synaphobranchidae							
Synaphobranchus kaupi	73				X	X	
Zoarcidae							
Lycodes esmarkii	6		X			X	
Lycodonus mirabilis	28	X	X			X	

ECH - *Echinorhynchus* sp.

GON - *Gonocerca* sp.

STE - *Steringophorus* sp.

CON - *Contracaecum* sp.

THY - *Thynnascaris* sp.

SPI - *Spinectus* sp.

Table 9. Comparison of helminth infections for various groups of deep-sea fishes. Numbers are percent occurrences.

	Armstrong (1974)	Munroe (1976)	Munroe* (1976)	Munroe** (1976)	Carson Canyon	Carson* Canyon	Carson** Canyon
Number examined	275	531	253	271	464	143	321
% Infected	90	87	87	100	48	36	51
Trematoda	65	77	76	81	7	26	3
Cestoda	80	34	17	49	-	-	-
Nematoda	75	52	52	53	37	36	54
Acanthocephala	2	6	12	1	21	2	43

* Indicates data excluding that for macrourids

** Indicates data only for macrourids

\- not recorded

FIGURE 1: Simplified schematic potential pathways for the supply of food to benthopelagic fishes in the deep sea.

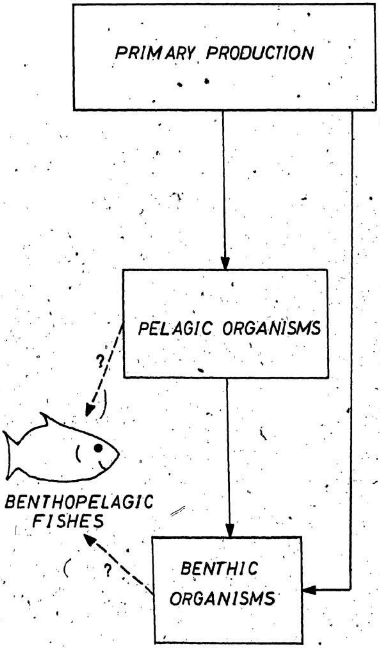

PRIMARY PRODUCTION
PELAGIC ORGANISMS
?
BENTHOPELAGIC FISHES
?
BENTHIC ORGANISMS

FIGURE 2: Chart of positions of bottom trawl stations on the Newfoundland continental slope.

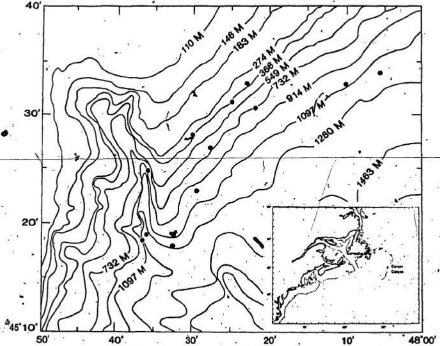

40'
30'
20'
45°10'
50'
40'
30'
20'
10'
48°00'
110 M
146 M
183 M
274 M
366 M
549 M
732 M
914 M
1097 M
1280 M
1463 M
732 M
1097 M
Carson
Canyon

FIGURE 3: Percent by number of pelagic, benthic and benthopelagic prey consumed by each fish species.

SYMBOLS:
1 = *C. microps*
3 = *C. rupestris*
4 = *M. berglax*
5 = *N. bairdii*
6 = *A. rostrata*
7 = *M. rostrata*
10 = *S. kaupi*
11 = *L. sarsi*
12 = *L. sarsi*
13 = *L. perspicillus*
14 = *L. mirabilis*
= *R. hippoglossoides*, *Sebastes* sp. and *G. ensis*

SHADING:
░ = Benthic Feeders
▦ = Pelagic/Benthopelagic Feeders

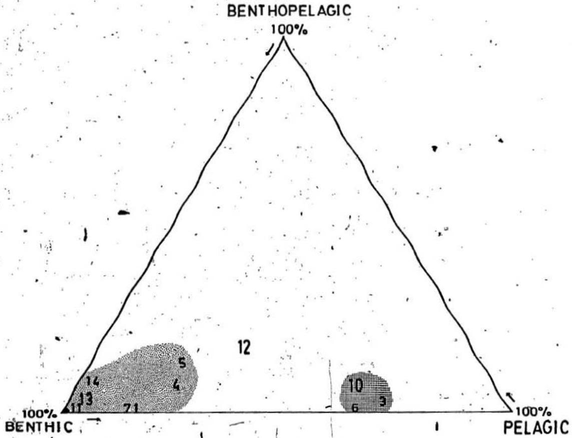
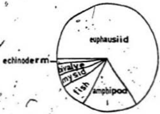

BENTHOPELAGIC
100%
12
5
14
4
13
11
71
10
3
6
100%
BENTHIC
100%
PELAGIC

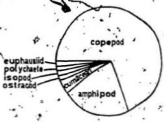
FIGURE 4: Breakdown of diet by major taxa for fish species with primarily pelagic and benthopelagic prey in the diet.

S. KAUPI



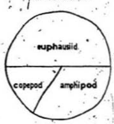
n = 78
empty = 16
pelagic/benthopelagic = 73.3%
benthic = 26.7%

C. RUPESTRIS



n = 34
empty = 2
pelagic/benthopelagic = 71.7%
benthic = 28.3%

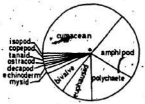
A. ROSTRATA



n = 7
empty = 1
pelagic/benthopelagic = 66.7%
benthic = 33.3%

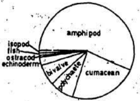
FIGURE 5: Breakdown of diet by major taxa for fish species with primarily benthic prey in the diet.

N. BAIRDII



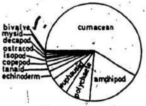
n = 96
empty = 3
pelagic/benthopelagic = 14.0%
benthic = 86.0%

L. MIRABILIS



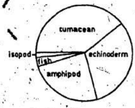
n = 28[illegible]
empty = 10
pelagic/benthopelagic = 23.8%
benthic = 76.2%

M. BERGLAX



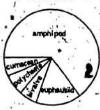
n = 191
empty = 50
pelagic/benthopelagic = 8.4%
benthic = 91.6%

L. ESMARKII



n = 6
empty = 1
pelagic/benthopelagic = 2.6%
benthic = 97.4%

C. MICROPS



n = 14
empty = 2
pelagic/benthopelagic = 15.7%
benthic = 84.3%

FIGURE 6: Breakdown of diet of (a) *Macrourus berglax*, (b) *Nezumia bairdii*, (c) *Synaphobranchus kaupi*, and (d) *Coryphaenoides rupestris* by size class.

SIZE CLASSES:

M. berglax:
A = 50 - 100 mm TL
B = 101 - 150
C = 151 - 200
D = 201 - 250
E = 251 - 300
F = 301 - 350

N. bairdii:
A = 50 - 150 mm TL
B = 151 - 200
C = 201 - 250
D = 251 - 300
E = 301 - 350
F = 351 - 400
G = 401 - 450

S. kaupi:
A = 200 - 300 mm TL
B = 301 - 400
C = 401 - 500
D = 501 - 600
E = 601 - 700

C. rupestris:
A = 0 - 100 mm TL
B = 101 - 200
C = 201 - 300
D = 301 - 400
E = 401 - 500

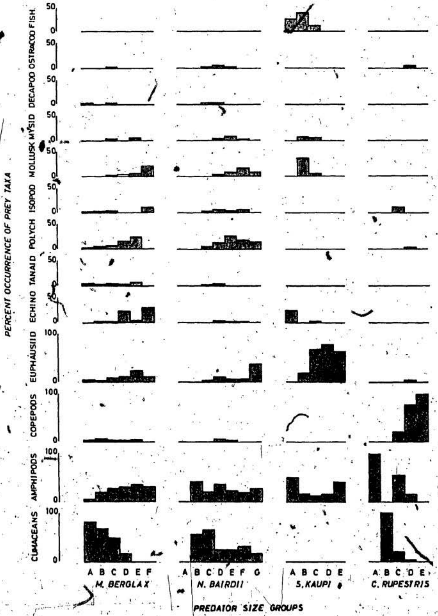

PERCENT OCCURRENCE OF PREY TAXA
FISH.
OSTRACOD
DECAPOD
MYSID
MOLLUSK
ISOPOD
POLYCH
TANAID
ECHINO
EUPHAUSIID
COPEPODS
AMPHIPODS
CUMACEANS
50
0
100
A B C D E F
M. BERGLAX
A B C D E F G
N. BAIRDII
A B C D E
S. KAUPI
A B C D E
C. RUPESTRIS
PREDATOR SIZE GROUPS

FIGURE 7: Breakdown of parasite infection of (a) *Macrourus berglax*, (b) *Nezumia bairdii*, (c) *Synaphobranchus kaupi* and (d) *Coryphaenoides rupestris* by size class.

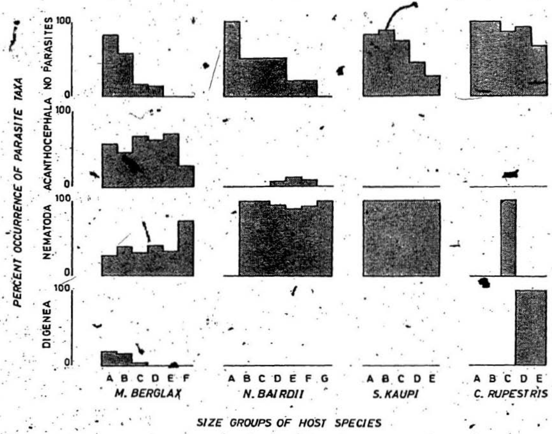
SIZE CLASSES:

M. berglax:
A = 50 - 100 mm TL
B = 101 - 150
C = 151 - 200
D = 201 - 250
E = 251 - 300
F = 301 - 350

N. bairdii:
A = 50 - 150 mm TL
B = 151 - 200
C = 201 - 250
D = 251 - 300
E = 301 - 350
F = 351 - 400
G = 401 - 450

S. kaupi:
A = 200 - 300 mm TL
B = 301 - 400
C = 401 - 500
D = 501 - 600
E = 601 - 700

C. rupestris:
A = 0 - 100 mm TL
B = 10[illegible] 200
C = 201 [illegible] 300
D = 301 - 400
E = 401 - 500


PERCENT OCCURRENCE OF PARASITE TAXA
NO PARASITES
ACANTHOCEPHALA
NEMATODA
DIGENEA
100
0
100
0
100
0
100
0
A B C D E F
M. BERGLAX
A B C D E F G
N. BAIRDII
A B C D E
S. KAUPI
A B C D E
C. RUPESTRIS
SIZE GROUPS OF HOST SPECIES