Northwest Atlantic Fisheries Organization

Serial No. N755

NAFO SCR Doc. 83/IX/89

FIFTH ANNUAL MEETING - SEPTEMBER 1983

Food Sources for Deep-sea Fishes of the Newfoundland Continental Slope

by

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ABSTRACT

Stomach contents and parasite faunas of 464 specimens of demersal fishes in 14 species were examined from the upper continental slope of the Grand Banks off Newfoundland, Canada. Individual species tended to feed either primarily on benthic invertebrates or on pelagic food items. Most pelagic predators also fed on benthopelagic organisms. Infestation rate by parasites was 46 percent, with an average of 5.5 worms per fish. Infestation rate was higher in benthic feeders (53.1%) than in pelagic feeders (28.9%). Percent occurrence of metazoan parasites among all fishes was: Trematoda 6.9%, Nematoda 36.7% and Acanthocephala 20.7%. Percent occurrence by group among benthic feeders was: Trematoda 5.8%, Nematoda 53.1% and Acanthocephala 40.9%. Percent occurrence by group among pelagic feeders was: Trematoda 27.8%, Nematoda 72.2% and Acanthocephala 0%. There are more species of benthic feeders (5) than pelagic feeders (3), but pelagic feeders are more abundant (pelagic 70.93%, benthic 20.48%,). Benthic feeders are on average larger ($\bar{x}$ = 270.6 g) than pelagic ($\bar{x}$ = 130.6), but pelagic feeders represent a larger proportion of the biomass (pelagic 43.3%, benthic 25.94%).

INTRODUCTION

Conditions for life near the deep sea floor are most favourable over the upper continental slope at depths of 150 to 1000 meters (Marshall 1980). Such conditions are 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 (Wolff 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 off the middle Atlantic coast of the United States, thereby providing a major source of food for the demersal fishes (Sedberry and Musick 1978).

Fishes, especially rattails (family Macrouridae), 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 a largely unanswered question. Marshall and Bourne (1964) suggested, on the basis of fin pattern and head shape, that Macrouridae and Halosauridae (spiny eels) were both adapted for hovering over the bottom and "rooting the ooze" with the rostrum to feed on small benthic organisms. However, the report 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 far off the bottom (Pearcy 1976, Haedrich 1974), 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 predator 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.

These and other studies have revealed the complexity of feeding relations among marine organisms. By establishing trophic linkages one can determine energy flow pathways through the ecosystem (Hacunda 1981). Whether the sources of food for fishes on the upper continental slope are benthic or pelagic, both pathways depend ultimately on surface primary production. How primary production influences the benthic ecosystem 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). By moving off the bottom to feed, fishes eliminate at least one trophic level. As a result, food reaches these pelagic feeders via a shorter and hence more efficient pathway than that of benthic feeders. By determining the path of energy flow, a hypothetical food web can be constructed based on primary production, fish catches and the biomasses of zooplankton and macrobenthos. This allows comparison of regions such as the Scotian shelf and the Grand Banks, provides us with insights into the general structure of marine ecosystems and allows us to pinpoint deficiencies in our understanding of them. Therefore, information on the types of food consumed is necessary in order to estimate fish production in this region (Mills and Fournier 1979).

The purpose of the present study is to determine if the dominant demersal fishes from the upper continental slope of the Grand Banks consume primarily benthic or pelagic organisms. As an approach to this question, stomach contents have been analysed and prey taxa have been classified as benthic or pelagic 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 ms), indicating that pelagic organisms are may be more important than benthic organisms as a food resource for the dominant demersal fishes.

Stomach content data reveal only what the 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 may be 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 the host within a community food web. Therefore, parasites from the digestive system were collected to provide information on the diet of the individual integrated over time since the parasites are accumulated throughout the life of the fish.

METHODS

Collection of Specimens

Table 1 is a list of the fish species collected and examined. The material was collected on cruises 37 and 51 of the F/V GADUS ATLANTICA in June 1980 and May 1981, respectively, as a part of general oceanographic studies of the Carson Canyon region (bounded by latitudes 45°17'N and 45°33'N and by longitudes 48°06'W and 48°36'W) on the eastern Grand Banks off Newfoundland (Figure 1). Fishes were collected using a 41-foot 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 <u>et al</u>. 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. An hour of trawling with the 41-ft net at this speed covers 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, total length (to nearest cm), total weight (to nearest g), gut, gonad, and liver weight (all to nearest 0.01 g) and sex determinations were made in the laboratory for each specimen prior to removal of the stomach. Standard lengths were also recorded for all species other than rattails. The problem of 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-analfin length (tip of snout to first anal finray) was found to be highly correlated with the total length in rattails (Atkinson 1981), therefore, anal length was measured for all species of rattails in addition to total length.

Stomachs and intestines were removed and placed singly in numbered jars of 70 % ethanol. Prey species were removed from the stomachs, sorted by taxon, 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 or antennal scales (crustaceans), discs (ophiuroids) and other parts.

The food items were for the most part whole animals and could be divided into three categories on the basis of habits and habitats. Fishes and euphausiids (Mauchline and Fisher 1969) are active swimmers usually found in the water column, but may occasionally come in contact with the bottom. 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 included the pelagic families Panaeidae and Sergestidae (Foxton 1970), and the benthic family Pandalidae. These groups, considered separately in the analysis of the data, were rare in the stomach contents examined. Hence, in the results they are reported as one group. Based on previous studies (Marshall and Iwamota 1973, Haedrich and Henderson 1974, Pearcy and Ambler 1974, Geistdoerfer 1975, 1979, and McLellan 1977), fishes, euphausiids, copepods (primarily calanoid) and decapod crustaceans in the Panaeidae and Sergestidae were considered as pelagic prey items. Ostracods, mysids and isopods were considered as benthopelagic prey items, and Pandalidae, polychaetes, tanaids, gastropods, bivalves, echinoderms and amphipods (primarily Gammaridae) were considered as benthic.

Parasitological Analysis

The parasitological examination of fishes was done using 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. Parasites were identified to phylum and class, and the number and taxa were determined for each host individual.

Data Analysis

For each specimen, percentage benthopelagic plus pelagic prey versus percentage benthic prey was calculated. A cluster analysis was done on the entire data set using the CLUSTAN package (Wishart 1975) available at the Memorial University computer facilities. Clustering was done by computing a dissimilarity value on the basis of number of pelagic versus number 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 due to ontogeny. 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 cases comprising a pair or cluster (p), X_{ij} equals the value of variable j for individual i, and N_p denotes the number of cases 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 density of the points constituting a cluster is not a factor in evaluating the resemblance between the two entities (Sneath and Sokal 1973).

The average number of parasitic worms per host fish was determined. Infection rate for each species was calculated as the number of individuals of a species infected versus the number of individuals of the species examined. Infection rate by major taxon of helminths was determined for each host species. Infection rates and number 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.

RESULTS

A total of 464 fishes, representing 14 species from 9 families of fishes were collected from depths of 403 to 1505 meters (means). Coryphaenoides rupestris was by far the dominant species representing 57.80% of the total number of fishes and 24.93% of the biomass of the assemblage. Macrourus berglax was also dominant, representing 13.68% of the total number and 20.19% of the biomass, followed by Antimora rostrata (9.60% of numbers, 16.39% of weight), Nezumia bairdii (5.23% of numbers, 3.36% of weight), Sebastes sp. (3.96% of numbers, 3.56% of weight) and Synaphobranchus kaupi (3.53% of numbers, 1.98% of weight). The remaining species examined, including Lycodonus mirabilis, Reinhardtius hippoglossoides (6.20% of weight), Cottunculus microps, Gaidropsarus ensis, Lycenchelys sarsi, Macdonaldia rostrata, Lycodes esmarki and Lycodes perspecilius, each represent less than 1% of the assemblage of fishes by number and by weight (Snelgrove ms).

Feeding Habits

The stomach contents of the dominant fishes from the study region are summarized in Table 2. Most of the species contained prey from two or three of the pelagic, benthopelagic and benthic categories. Of those species which were found with items from all three categories, the same individual rarely had items from all three groups. Some specimens, primarily the Macrouridae, had the stomach or 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 but are reported here along with those stomachs which were recorded as empty.

The clustering method used classified the predators into two groups: (1) primarily benthic prey in the diet; or (2) primarily pelagic/benthopelagic prey in the diet. Pelagic and benthopelagic prey were numerically dominant in the diets of Coryphaenoides rupestris, Synaphobranchus kaupi and Antimora rostrata.

Food items of Synaphobranchus kaupi include 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%), fishes (6.7%, primarily myctophids), mysids (4%), bivalves (4%) and echinoderms (1.3%).

Of the 34 stomachs of Coryphaenoides rupestris examined, only 1 (2.9%) 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%).

The dominant food item in the stomachs of *Antimora rostrata* was euphausiids (50.0%). 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 126.1 to 155.0 mm TL.

Stomach contents of primarily benthic origin occurred in *Macrourus berglax* (91.6%), *Nezumia bairdii* (86.0%), *Lycodonus mirabilis* (76.2%), *Lycodes esmarki* (97.4%) and *Cottunculus microps* (84.3%). Several of the individuals of these species had consumed large amounts of sediment.

Food items of *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 frequent 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 77.7 to 324.0 mm TL, with an average weight of 316.1 g.

Of the 96 stomachs of *Nezumia bairdii* examined, only 3 (3.1%) 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 of *Lycodonus mirabilis* were amphipods (56.9%) followed by cumaceans (22.9%). Other prey items include polychaete (8.3%), bivalves (7.3%), echinoderms (2.8%), isopods, fish 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 esmarki* 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 taxon of *Cottunculus microps* was amphipods (64.9%), followed by euphausiids (15.8%), bivalves, polychaetes, and cumacaeans (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.

The small numbers of intact stomachs of *Lycenchelys sarsi*, *Lycodes perspicillus*, *Reinhardtius hippoglossoides*, *Sebastes sp.*, *Gaidropsarus ensis* and *Macdonaldia rostrata* that have been 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.

Parasites

A total of 14 species of hosts, representing nine families of fishes, were examined from depths of 403 to 1505 meters (means). Forty-six percent of the 464 fishes examined were infested with 1 to 3 ($\bar{x}$ = 1.9) major taxa of helminths. Intensity of infestation 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 Trematoda 6.9%.

Table 3 summarizes the total helminth infections for all host species examined. Table 4 summarizes the infection rate of the major taxa of parasites found in all host species. The overall infection rate of Trematoda in benthic feeders was only 1.9%, while they comprised 55.9% of the parasites of benthopelagic/pelagic feeders. Nematoda comprised 54.4% of the parasite fauna of benthic feeders and 43.1% of the benthopelagic feeders. Acanthocephala were prominent (43.5%) in the parasite fauna of benthic feeders but were negligable (1%) in that of the benthopelagic/pelagic feeders.

DISCUSSION

In the deep sea, organic matter may be of continental or oceanic origin. On the upper continental slope, food chains involving vertically migrating species appear to be important in the transfer of energy. The direct transfer of energy by overlapping vertical migrations of pelagic organisms and demersal fishes on the upper continental slope appears 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. In addition to feeding relationships, turbidity currents and related phenomena appear to be important vehicles for energy transport, especially near continental margins (Heezen _et al_. 1955, Menzies 1962).

Coryphaenoides rupestris, and _Antimora rostrata_ are numerically dominant species on the slope of the Grand Banks, while _Synaphobranchus kaupi_ is relatively rare (Snelgrove ms). All three species primarily consumed pelagic species, many of which are known vertical migrators (Sedberry and Musick 1978). Other investigators have also found that vertically migrating pelagic organisms are important prey items for these demersal fishes.

Pechenick and Troyanovski (1970) found that _C. rupestris_ in slope waters of the northwest Atlantic feed intensively on zooplankton (shrimps, euphausiids, _Calanus_ and amphipods). They also found the seasonal bathymetric vertical migrations of _C. rupestris_ to be related to changes in the vertical distributions of these pelagic animals. 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 off the mid-Atlantic coast of the USA (Haedrich 1974).

The upper depth range of the vertical migration of _S. kaupi_ overlaps with 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 found in the stomachs of _S. kaupi_ examined.

Pelagic food is also important to _A. rostrata_, a fish usually found on the lower slope. Sedberry and Musick (1978) found 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. In fact, little information on the life habits of this species is available.

Available data on the behaviour of benthopelagic fishes are the result of direct or photographic observations from bathyscaphes or with automatic cameras (Marshall and Bourne 1964, Sedberry and Musick 1978). A. rostrata were observed hovering within one meter of the bottom. Macrourinae, a subfamily of Macrouridae including C. rupestris, Macrourus berglax and Nezumia bairdii, swim above the bottom with a "nose-down" attitude 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 have a terminal mouth and are therefore probably unable to burrow in the sediment like M. berglax and N. bairdii which have a more inferior mouth and a well developed rostrum (Geistdoerfer 1975). The latter two species are among the benthic feeding species in this study.

In his study of Macrouridae, Geistdoerfer (1975) found that none fed exclusively on pelagic or benthic animals, the diet was never composed of only one prey group and 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 2).

N. bairdii, M. berglax, Lycodes esmarki, 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 species are relatively rare (Snelgrove ms).

Other studies have also found M. berglax and N. bairdii to 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).

The food of the two species of zoarcids, Lycodes esmarki and Lycodonus mirabilis, is similar to that for Lycenchelys verrilli from the coast of New England, which Farlow (1980) described 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 (Sedberry and Musick 1978).

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

As a result of differences in diet, individual species of fishes may show marked differences in the composition of their parasite faunas and in infection rates. Infection rate for hosts which were found to feed primarily on pelagic or benthopelagic prey was 28.9%. Infection rate for benthic feeding hosts was 53.1%. Benthic feeders were infested with an average of 2.4 major taxa of parasites and 4.3 worms per fish. Pelagic feeders were infested with an average of 1 taxon and 1.9 worms per fish. This higher rate of infection 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), instead of vertically through the water column as proposed by Collard (1970). Thus, fishes which feed primarily on the benthos are likely to have a higher infestation rate than those which feed more on pelagic or benthopelagic organisms (Noble and Collard 1970).

Collard (1970) also proposed that midwater organisms play an important role as vertical transporters 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 to be abundant in both benthic (53.1%) and pelagic (72.2%) feeders, indicating that both pathways are possible.

Crustaceans, particularly amphipods, are known intermediate hosts for acanthocephalans (Ginetsinskaya 1970). Acanthocephala were relatively abundant in benthic feeders (40.9%)and 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.

Trematoda comprised 27.8% of the helminth fauna of pelagic feeders and only 5.8% of the helminth fauna of benthic feeders. Epifaunal invertebrates have been reported as primary second intermediate hosts for these helminths (Munroe 1976). Since C. rupestris was the only pelagic feeding species infected with Trematoda, benthic organisms may be an important component of their diet at some time in their life.

Zubchenko (1981) reported on the parasite faunas of the three species of Macrouridae studied here. In his study, 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 as a significant part of the diet. M. berglax was infested with 21 species of parasites, many of which have 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, they also had parasites which cycle through benthic organisms. These results suggest that, at some point in their life, pelagic organisms are important prey items for N. bairdii.

Comparison of infection data among deep-sea hosts reveals that all phyletic groups of fishes are not infected by helminths to the same degree. Incidences of infections by Nematoda and Acanthocephala were twofold or greater in the macrourids than for other fishes. Infection by Trematoda was several fold greater in all other species than for 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.

Incidence of infection for all helminths, except Acanthocephala, were greater in Gulf of Mexico fishes (Armstrong 1974) and Hudson Canyon fishes (Munroe 1976) than for fishes examined here (Table 5). These higher levels of infections could be a result of sampling. Only parasites from the gut and body cavity were collected here, while Armstrong (1974) and Munroe(1976) included parasites from the gills, skin and viscera. A comparison between Carson Canyon and Hudson Canyon fishes (Munroe 1976), excluding macrourids, revealed that infections of non-macrourid fishes were similar in trend.

Of the 8 species examined, 5 feed primarily (by number) on benthic organisms and 3 feed primarily on pelagic and benthopelagic organisms. There are more species of benthic feeders than pelagic feeders, but the pelagic feeders are more abundant in actual numbers (70.3% versus 20.5%). These results are similar to those of DuBuit (1978). She found that 62% of food of deep sea fishes off the northeast coast of Scotland and on Bill Bailey Bank is of nectonic origin. 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%).

This and other studies have found that the benthopelagic fishes from the upper continental slope feed on a variety of both benthic and pelagic animals. The analysis of trophic relationships among prey groups and between the demersal fishes and prey groups from this study shows that the fishes are at the top levels of the food web of the continental slope. These demersal fishes, particularly the pelagic feeding species, may represent a connecting link between the pelagial and the benthos. Since they are not confined to the bottom, they may be an important factor in the transfer of energy from pelagic to benthic ecosystems through their remains and feces (Dayton and Hessler 1972), but there is no direct evidence to support this contention. In fact, the large proportion of biomass represented by pelagic feeders, and the low biomass of macrobenthic fauna (Houston and Haedrich ms) indicate that a large proportion of the biomass is being recycled in the water column. These results indicate the importance of pelagic organisms to the assemblage of demersal fishes on the upper continental slope. To understand the dynamics of demersal fish populations, it will be necessary to study the populations and physical environment of the water column.

Reports of Macrouridae falling prey to large Gadidae that make temporary forays onto the upper continental slope (Geistdoerfer 1975) suggest that demersal fishes may provide a link between the deep sea food chain and the continental shelf food chain. These predators of Macrouridae are mainly large fishes that are fished commercially. As well, C. rupestris is already fished commercially and is therefore of economic interest. Hence, the demersal fishes from the upper continental slope are involved in the fishing industry both indirectly as prey to commercial species, and directly as human food.

ACKNOWLEDGEMENTS

I thank R. L. Haedrich, P. Snelgrove, T. J. Benfey, S. McKelvie, and D. Goulet for their comments on the manuscript. The work was supported by Natural Sciences and Engineering Research Council Grant A-7230. Travel grants to attend the NAFO conference were supplied by Dr. R. L. Haedrich, the Biology Department and the Grauate School of Memorial University of Newfoundland.

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Table 1: List of all species collected from sample area (Snelgrove, ms)

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
Centroscyllum fabrica	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 perspecillus	1	1	0.02	1	100
Lycodes vahlii	3	5	0.12	N/E	-
Lycodonus mirabilis	6	29	0.69	28	96.55
Lycenchelys sarsi	2	2	0.05	2	100
Macdonaldia rostrata	3	4	0.10	2	50.0
Macrourus berglax	25	573	13.68	191	33.33
Nematanurus armatus	4	15	0.36	N/E	-
Nezumia bairdii	16	219	5.23	96	43.84
Notocanthus sp.	2	2	0.05	N/E	-
Physis 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
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: Summary of stomach contents of the fishes studied (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
Gaidropsaridae														
Gaidropsarus 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 esmarki	6		X					X	X		X		X	
Lycodes perspecillus	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 3: Comparison of helminth infections for all hosts

Host species	# examined / # infected	% infected	Total helminth taxon recovered	Helminth taxon per host	Intensity per host
Cottidae					
Cottunculus micraps	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 esmarki	6/1	16.7	2	2.0	2.0
Lycodes perspecillus	1/0	0	0	0	0
Lycodonus mirabilis	28/13	46.4	3	1.4	3.7

Table 4: Comparison of infection rate of major taxons 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 esmarki	50.0 (1)	50.0 (1)	0	2
Lycodes perspecillus	0	0	0	0
Lycodonus mirabilis	87.5 (42)	10.4 (5)	2.1 (1)	48

Table 5. Comparison of helmunth 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	46	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

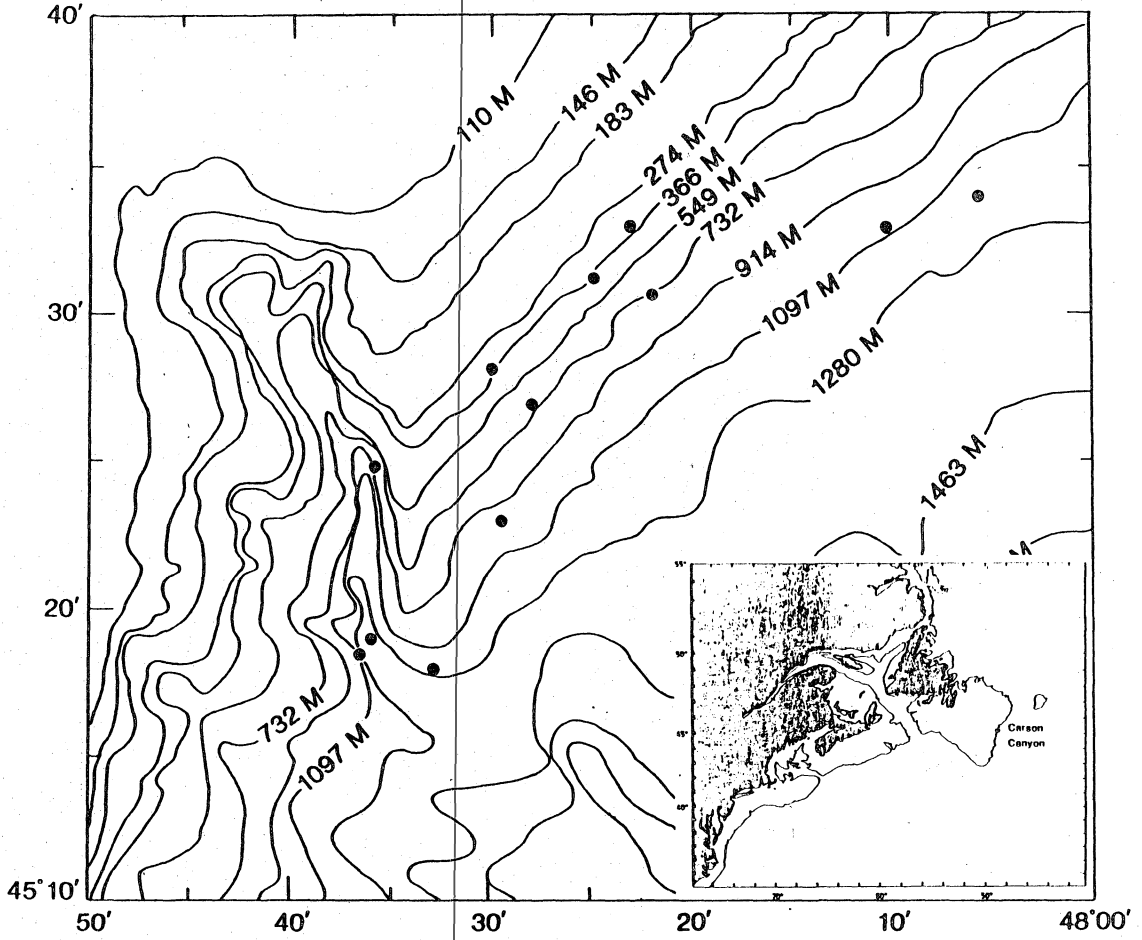

Figure 1: Chart of positions of trawl stations off the coast of Newfoundland.