Structure of the deep demersal fish fauna off Newfoundland

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ABSTRACT: Bottom trawls on the Newfoundland continental slope at depths from 204 to 2325 m near Carson Submarine Canyon (45°30′ N, 48°40′ W) took 4222 individuals in 39 species of demersal fishes. The fauna was not strictly zoned, but showed a fairly uniform addition of species with increasing depth over the entire range. Lack of zonation may be related to the high production of the area, and its absence here casts doubt on the idea that faunal regions continuously rim the ocean basins. Dominant species were mainly macrourids (*Macrourus berglax*, *Coryphaenoides rupestris*, *Nezumia bairdii*, *Nematonurus armatus*) and the morid *Antimora rostrata*. Overall abundance, biomass, and diversity were least at the greatest depths. Only *A. rostrata* and *C. rupestris* were bigger-deeper; juveniles of both are abundant in shallow northern waters. The proportion of species belonging to shallow-water groups decreases steadily with depth, a pattern also seen in other data and implying ongoing invasion of the deep sea by fishes from the continental shelves.

INTRODUCTION

The deep demersal fish fauna has been examined both south (Haedrich et al. 1975) and north (Haedrich & Krefft 1978) of Newfoundland's continental slope. The work off New England found a clear pattern of zonation with depth, whereas the one farther north off Iceland found a mosaic where depth and temperature co-described the distribution patterns. The present study, in an area between these 2 regions, seeks to determine whether the Newfoundland fish fauna is intermediate in composition and relative abundance, and what sort of zonation patterns may be present. Vertical zonation in the distribution of benthic organisms is well documented (e.g. Day & Pearcy 1968, Menzies et al. 1973, Haedrich et al. 1980, Pearcy et al. 1982, Carney et al. 1983), but it is not a ubiquitous feature of the ocean bottom. Merrett & Marshall (1980) found no zonation in fishes on the Northwest African slope. They attributed this absence to the high productivity of the area, arguing that increased food availability broke down the zones that might otherwise have been expected. Because the Newfoundland region is one of high primary production, it might be expected that zonation could be weak or absent.

We have approached the question with data from a 3 yr study conducted in the Carson Canyon region on the eastern edge of the Grand Bank of Newfoundland (45°30′ N, 48°40′ W, Fig. 1). Sampling by the M/V
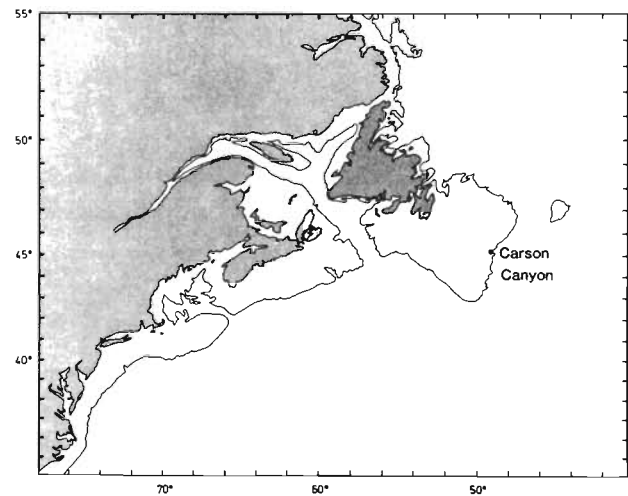

Fig. 1. Location of study area in the region of Carson Submarine Canyon on the eastern edge of the Grand Banks of Newfoundland, northwest Atlantic Ocean. Isobath follows the 200 m depth contour

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'Gadus Atlantica' was undertaken in June 1980 and May 1981 and by the R/V 'Oceanus' in September 1982. There were 32 successful deep benthic tows encompassing a depth range of 204 to 2325 m. The data obtained from these trawls have been used to describe the faunal composition and vertical distribution of the fishes there, and to evaluate the results in the light of other similar studies.

MATERIALS AND METHODS

Station data associated with the samples are given in Table 1. An objective of the 'Oceanus' cruise was to obtain material for physiological studies (e.g. Graham et. al. 1985); trawling times on this cruise tended to be short and depths deep, and thus the number of species and specimens per individual trawl appears smaller than in those from the 'Gadus' cruises. Positions of the stations are plotted on the chart of Fig. 2. Representative material from the study has been deposited in the Newfoundland Museum, St. John's and the National Museum of Natural History, Ottawa.

The gear and sampling protocol are the same as that used in a similar program in the New York Bight (Haedrich et al. 1980). A 12.5 m Gulf-of-Mexico shrimp trawl (Marinovich Company) of 3.7 cm stretch mesh with a 2.5 cm heavy knotted liner in the cod end was used. Steel V-doors measuring 80×120 cm were attached to 20 m bridles. The head rope was buoyed with a 30 cm diameter glass float (Benthos Company), and light chain was lashed at intervals along the footrope. The effective opening of this net is about 8 m (Bullis & Cummins 1963) and an estimated bottom area of $2.2 \times 10^4 \, m^2$ can be swept in an hour by a ship moving at 1.5 kn. Sampling time included only the time after the winch had stopped paying out and

Table 1. Station data associated with bottom trawl collections made on the continental slope off Newfoundland

| Station	Ship	Cruise	Latitude	Longitude	Date	Mean bottom depth (m)	Time	No. of species	No. of speci- mens	Weight (kg)
816	'Gadus'	37	45°23' N	48°29' W	3 Jun 80	900	1231–1250	13	158	25.9
838	'Gadus'	37	45°18' N	48°36' W	4 Jun 80	1425	0812–0832	12	246	28.4
839	'Gadus'	37	45°18' N	48°36' W	5 Jun 80	1200	1140–1220	10	58	13.8
853	'Gadus'	37	45°18' N	48°33' W	5 Jun 80	1280	1410–1430	10	64	18.4
865	'Gadus'	37	45°25' N	48°36' W	8 Jun 80	1050	0110–0130	7	1566	132.8
951	'Gadus'	51	45°28' N	48°30' W	15 May 81	601	1402–1422	12	181	27.4
952	'Gadus'	51	45°27' N	48°28' W	15 May 81	754	1700–1720	10	388	85.3
955	'Gadus'	51	45°31' N	48°29' W	15 May 81	204	2030–2050	5	18	70.0
957	'Gadus'	51	45°30' N	48°29' W	15 May 81	305	2245–2305	5	72	40.2
958	'Gadus'	51	45°29' N	48°29' W	16 May 81	412	0000–0020	2	2	0.9
959	'Gadus'	51	45°31' N	48°22' W	16 May 81	809	0820–0840	11	161	35.1
960	'Gadus'	51	45°31' N	48°25' W	16 May 81	499	1053–1117	8	159	14.7
961	'Gadus'	51	45°33' N	48°23' W	16 May 81	405	1225–1245	10	48	14.3
962	'Gadus'	51	45°33' N	48°10' W	16 May 81	1305	1410–1430	11	146	47.8
964	'Gadus'	51	45°36' N	47°56' W	16 May 81	1475	1920–1940	4	8	3.4
1350	'Oceanus'	126	45°29' N	48°31' W	11 Sep 82	283	1205–1235	7	111	63.5
1352	'Oceanus'	126	45°18' N	48°35' W	11 Sep 82	1350	1730–1800	8	147	46.0
1354	'Oceanus'	126	45°21' N	47°43' W	12 Sep 82	2325	0635–0710	4	31	16.1
1356	'Oceanus'	126	45°18' N	47°51' W	12 Sep 82	2215	1545–1615	7	33	9.4
1357	'Oceanus'	126	45°24' N	47°46' W	13 Sep 82	1985	0600–0635	4	18	9.6
1359	'Oceanus'	126	45°33' N	47°36' W	13 Sep 82	1710	1325–1345	5	16	6.2
1360	'Oceanus'	126	45°33' N	47°30' W	13 Sep 82	1863	1605–1630	3	18	10.8
1361	'Oceanus'	126	45°41' N	47°37' W	13 Sep 82	1360	1955–2015	6	27	7.9
1363	'Oceanus'	126	45°17' N	48°34' W	14 Sep 82	1205	1015–1035	10	92	31.8
1365	'Oceanus'	126	45°08' N	48°45' W	14 Sep 82	1045	1555–1615	5	15	2.9
1366	'Oceanus'	126	45°20' N	48°34' W	14 Sep 82	1175	1953–2013	6	191	25.0
1367	'Oceanus'	126	45°19' N	48°37' W	15 Sep 82	1250	0730–0750	9	87	43.1
1368	'Oceanus'	126	45°10' N	48°33' W	15 Sep 82	1343	1135–1155	4	26	8.3
1370	'Oceanus'	126	45°18' N	48°32' W	15 Sep 82	1438	2030–2045	3	9	4.8
1372	'Oceanus'	126	45°17' N	48°34' W	16 Sep 82	1118	0645–0700	5	85	30.0
1373	'Oceanus'	126	45°17' N	48°26' W	16 Sep 82	1713	0955–1010	3	4	0.3
1376	'Oceanus'	126	45°19' N	48°34' W	16 Sep 82	1090	2105–2130	5	45	17.8
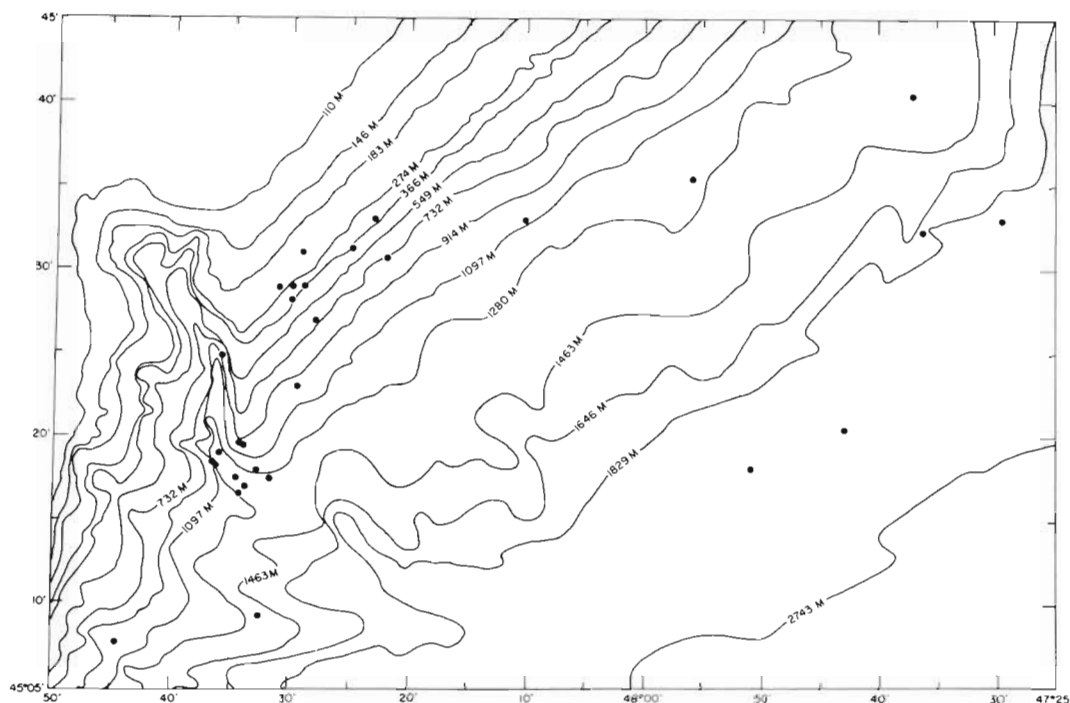
Fig. 2. Chart showing location of successful bottom trawl stations in the Carson Canyon region. Soundings in meters

before retrieval was begun. The speed of the ship during sampling was about 1.5 kn, so the average 20 min trawl swept an area of about 7.4×10^3 m^2.

The material collected was either measured immediately and discarded (but only in the case of the more numerous and easily identified species), or fixed in 10 % buffered formalin. The fixed material was later transferred to alcohol for identification, counting, and weighing in the laboratory. Single specimens of *Hydrolagus affinis* and *Harriotta raleighana* were taken at Station 1363 (depth 1205 m) but were not weighed or preserved because of their great size. They are included in the chi-square analysis and depth range profiles but excluded from all other analyses. *Lycodonus mirabilis* was caught at Station 951 (depth 601 m) but was not kept or weighed. Length-weight regressions based on preserved specimens were used to estimate the biomass of those fishes discarded at sea.

The problems associated with net samples are well known. Cohen & Pawson (1977) observed net avoidance by *Synaphobranchus kaupi* and Haedrich et al. (1975) were able to conclude, through comparison with observations from submersibles, that trawling consistently underestimates absolute abundance. Ohta (1983) has recently considered this problem in considerable detail. Problems in keeping the net fully open may have been an important factor in some samples, and large tears in the net also reduced the number of stations that could be used. Bottom terrain also influenced sampling. Rolling hills between 400 m

and 600 m may have contributed to ineffective sampling. There were no stations completed between 2000 m and 2200 m. This portion of the lower slope was particularly rough, and several nets were lost attempting to trawl.

To establish whether zonation was present, a variation of the chi-square test was employed. This method (Gardiner & Haedrich 1978) tests the distribution across the area of upslope (i.e. deeper to shallower) and downslope (i.e. shallower to deeper) species boundaries using the formula:

$$\chi^2 = (Q/K) \times (V - [K^2/Q]) \qquad (1)$$

where Q = number of regions into which the area is arbitrarily divided; K = total number of species; V = sum of squares of boundaries (upslope or downslope) occurring in each region. The values calculated for the chi-square are compared to values in a chi-square table with degrees of freedom equal to Q − 1. If the calculated value exceeds the value obtained from the table, the boundaries are distributed non-randomly, i.e. they are zoned. For details of the method, the original reference (Gardiner & Haedrich 1978) should be consulted.

The chi-square test is quite applicable to this type of data according to an overview presented by Carney et al. (1983). A potential pitfall lies in the importance of the limits of each species as established by the sampling. Inconsistent sampling effort over the depth range can obscure zonation, particularly if an extremely wide

range is sampled. Our sampling range, however, was not too extreme, and effort was directed as widely as the topography of the slope would permit.

Percentage similarity, PS, a commonly-used measure of faunal overlap, was calculated according to the formula of Whittaker & Fairbanks (1958):

$$PS = 100 \, \Sigma \min(p_{ia}, \, p_{ib}) \quad (2)$$

where p_{ia} = the proportion assumed by species i in sample a; p_{ib} = the proportion assumed by species i in sample b. Diversity, H, was calculated using the information function (Shannon & Weaver 1963):

$$H = -\Sigma p_i \ln p_i \quad (3)$$

where p_i = the fraction of the total comprised by species i in a region. Evenness, J, was calculated according to:

$$J = H/H_{max} \quad (4)$$

where $H_{max} = N \times abs|1/N \ln 1/N|$.

Regressions were performed on individual species and on all taxa combined to establish whether a correlation between size and depth of occurrence existed. The SAS statistical package (Ray 1982) was particularly useful for standard statistical procedures.

RESULTS

A complete list of species taken is given in Table 2. The chi-square test was run on all stations, grouped

Table 2. Alphabetical list of species, catch statistics, and depth range over which each species occurred for fishes taken on the Newfoundland Continental Slope

	No. of stations	No. of specimens	Weight (kg)	Depth range (m)
Alepocephalus sp. Risso 1820	7	15	34.86	1118–2325
Anarhichas lupus Linnaeus 1758	2	2	39.00	307–405
Antimora rostrata Gunther 1878	26	402	147.02	499–2325
Aspidophoroides monopterygius (Bloch) 1786	1	1	0.001	283
Careproctus reinhardti Kroyer 1862	1	2	0.002	900
Centroscyllium fabricii (Reinhardt) 1825	6	16	21.32	900–1350
Chalinura brevibarbis Goode & Bean 1896	1	12	3.37	2215
Coryphaenoides rupestris Gunnerus 1765	20	2429	223.78	405–1712
Cottunculus microps Collett 1875	9	20	2.45	499–1475
Gadus morhua Linnaeus 1758	3	17	6.98	204–307
Gaidropsarus ensis (Reinhardt) 1838	7	10	1.34	405–1425
Glyptocephalus cynoglossus (Linnaeus) 1758	5	11	3.78	405–1200
Halosauropsis macrochir (Gunther) 1878	1	1	0.06	2215
Harriotta raleighana Goode & Bean 1895	2	2	0.03	1205–2215
Hippoglossoides platessoides (Fabricius) 1780	1	3	0.03	204
Hydrolagus affinis (Capello) 1867	2	3	0.63	1205–2215
Lionurus carapinus (Goode & Bean) 1883	5	12	0.69	1710–2325
Lycenchelys sarsi (Collett) 1871	2	4	0.23	499–601
Lycodes atlanticus Jensen 1904	2	5	2.15	1305–1360
Lycodes esmarki Collett 1875	4	21	17.92	283–809
Lycodes perspicillus Kroyer 1845	1	1	0.11	283
Lycodes vahli Reinhardt 1831	3	5	2.25	405–809
Lycodonus mirabilis Goode & Bean 1883	6	29	0.51	601–1425
Macdonaldia rostrata (Collett) 1889	3	4	0.60	1250–1475
Macrourus berglax Lacepede 1801	24	585	181.20	204–1438
Nematonurus armatus (Hector) 1875	4	15	3.20	1710–2325
Nezumia bairdii (Goode & Bean) 1877	15	218	30.18	405–1475
Notacanthus chemnitzii Bloch 1788	2	12	0.78	1200–1425
Phycis chesteri Goode & Bean 1878	2	4	1.66	601–754
Raja jenseni Bigelow & Schroeder 1950	2	4	3.82	1205–1360
Raja radiata Donovan 1808	7	21	90.54	204–1305
Raja senta Garman 1885	2	2	0.91	809–900
Reinhardtius hippoglossoides (Walbaum) 1792	9	25	54.95	754–1425
Scophthalmus aquosus (Mitchill) 1815	2	4	4.35	809–1305
Sebastes sp.	8	169	32.01	283–1050
Synaphobranchus kaupi Johnson 1862	23	141	17.81	405–1863
Trachyrhynchus murrayi Gunther 1887	1	1	0.44	900
Triglops murrayi Gunther 1887	1	2	0.01	204
Zoarcid	3	4	1.96	1200–1425

into regions of 200 m depth increase. Values of chi-square exceeded the lowest acceptable significance level of 0.05 (df = 8) but not a level of 0.01. This indicates that the distribution is zoned, but weakly, between 200 and 2300 m.

The species recruitment curves along the depth gradient are shown in Fig. 3; the upper curve is for first
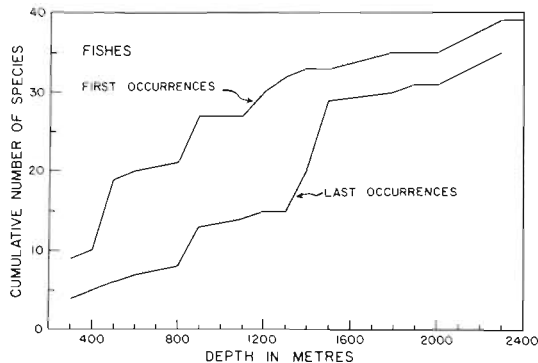

Fig. 3. Cumulative number of fish species taken on the Newfoundland continental slope as depth is increased by 100 m increments

occurrences (i.e. species encountered for the first time as depth of sampling is increased) and the lower curve is for last occurrences (i.e. species encountered for the last time as depth of sampling is increased). The curve of first occurrences approaches an asymptote rather smoothly in comparison to the stepped recruitment curves shown in Haedrich et al. (1980: p. 168, Fig. 3), another indication that zonation is weak. There is a moderate step in the curve at about 900 m which is matched by a similar step in last occurrences. The abrupt increase in the number of last occurrences at about 1500 m is not matched in the curve of first occurrences.

The potential boundaries suggested by the patterns in the recruitment curves were examined by calculating PS between the regions involved. PS measured across the 900 m level was 47 %. Across the 1500 m level PS was 12 %, and it is only here that a case for a faunal boundary can be made. However, this situation results only from species dropping out, not from encountering new ones (Fig. 3). The data thus do not suggest any pronounced pattern of zonation. Nonetheless, faunal composition in the shallow regions is quite different from that of the deeper sections. In order to quantify these differences, we divide the stations into 2 groups: those shallower than 1500 m and those deeper.

Table 3 shows how overall community parameters vary between shallow and deep sections. Abundance and biomass estimates both decline, with markedly lower catch rates on the lower slope. Fewer species occur deeper. As measured by H, diversity is the same

Table 3. Community parameters and catch rates for fish assemblages at shallow (<1500 m) and deep (>1500 m) continental slope depths off Newfoundland

	Shallow (200–1475 m)	Deep (1712–2335 m)
No. of species	33	10
Diversity, H	1.5	1.5
Evenness, J	0.4	0.7
No. of specimens	4109	121
No. of stations	26	6
Duration of trawls (h)	9.0	2.7
Specimens h^{-1}	455.7	45.0
Kg h^{-1}	93.1	19.7

at both depths, but evenness J is somewhat greater in the deep region.

No one species is dominant over the whole sampling range, but *Antimora rostrata* is among the top 6 both shallow and deep (Table 4). By far the most important family in terms of both number and biomass is the macrourids (*Macrourus berglax, Coryphaenoides*

Table 4. The 6 most abundant demersal fish species at shallow (<1500 m) and deep (>1500 m) continental slope depths off Newfoundland. Values are percentages of total number and of total biomass

Species	Number (%)	Biomass (%)
Shallow (200–1475 m)		
Coryphaenoides rupestris	59.1	26.5
Macrourus berglax	14.2	21.4
Antimora rostrata	8.2	12.8
Nezumia bairdii	5.3	3.6
Sebastes sp.	4.1	3.8
Synaphobranchus kaupi	3.4	2.0
Deep (1712–2335 m)		
Antimora rostrata	53.3	74.1
Nematonurus armatus	12.5	6.1
Chalinura brevibarbis	10.0	6.5
Lionurus carapinus	10.0	0.9
Alepocephalus sp.	6.7	9.4
Synaphobranchus kaupi	3.3	1.6

rupestris, Nezumia bairdii, and *Nematonurus armatrus*), which is the most numerous group in all regions less than 1600 m, and comprises the dominant biomass in most regions shallower than 1200 m. In those areas where macrourids do not dominate, they are second only to the morid *A. rostrata*. Below 1200 m, this species comprises the dominant biomass, and is the most abundant species below 1600 m.

Each species has a unique vertical depth range (Fig. 4). Those of *Synaphobranchus kaupi, Antimora rostrata,* and *Alepocephalus sp.* are quite wide, while
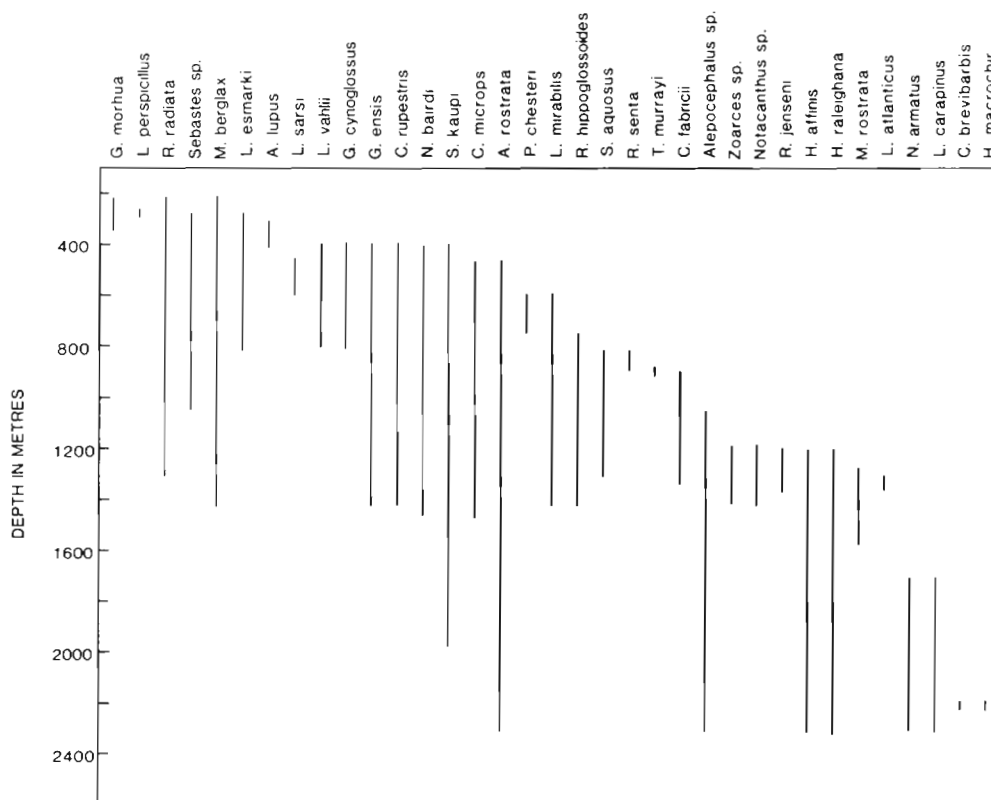
Fig. 4. Vertical depth ranges for fish species taken in bottom trawls on the Newfoundland continental slope

other species such as *Anarhichas lupus, Phycis chesteri, Centroscyllium fabricii,* and *Lycenchelys sarsi* occurred in very narrow zones.

The regression of mean weight per individual for all taxa combined versus depth was not significantly different from zero. Of individual species, only *Antimora rostrata* (Fig. 5) and *Coryphaenoides rupestris* (Fig. 6) showed a significant bigger-deeper relation.
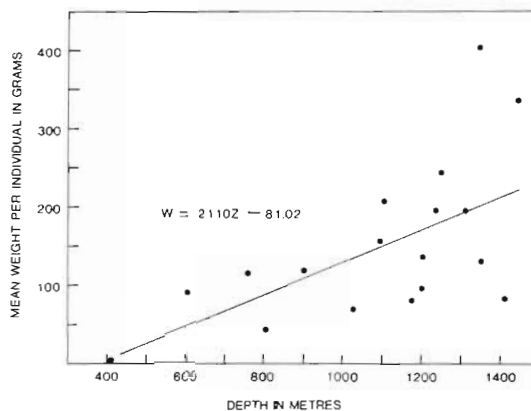

Fig. 6. *Coryphaenoides rupestris.* Size-depth relation. The regression is significant: r = 0.63, p < .008. N = 2424; only the mean value for each station is plotted

DISCUSSION

Deep demersal fish faunas seem to follow the general rule of decline in species number with increasing latitude. Seventy-two species were taken off New England between 200 and 2400 m (Haedrich et al. 1980), 39 off Newfoundland, and 39 between Greenland and Iceland (Haedrich & Krefft 1978). Off northwest Africa,

Fig. 5. *Antimora rostrata.* Size-depth relation. The regression is significant: r = 0.52, p < .007. N = 402; only the mean value for each station is plotted

between 8° and 27°N, about 148 species were taken over a comparable depth range (Merrett & Marshall 1980). In the Pacific at about 45°N, Pearcy et al. (1982) recorded 61 species on the continental slope. Ohta (1983) reports 79 fish species between 200 and 2400 m in Suruga Bay, Japan (ca 35°N). Different gear and varying numbers of stations in these studies mean that results may not be absolutely comparable, but the trend is clear. Sulak (1984), using gear identical to ours but with many more stations, took 74 fish species at slope depths in the Middle Atlantic Bight (ca 37°N) and 85 in the Bahamas (ca 24°N). For these data, the regression of number of fish species on latitude, S = 153 − 2.03 L, is significant (r = .85, p < .01, n = 8)

Haedrich et al. (1980) found that macrourids such as *Nezumia bairdii* and *Coryphaenoides rupestris* are quite important on the New England continental slope from about 653 m to 1290 m, and Haedrich & Krefft (1978) found *Macrourus berglax* and *C. rupestris* dominated the 500 m to 1500 m range in the Denmark Strait. Both of these findings are consistent with ours, as is the dominance of *Antimora rostrata* from about 1500 m to the base of the slope. Pearcy et al. (1982) also found a macrourid (*Coryphaenoides acrolepis*) and a morid (*Antimora microlepis*) dominated the Northeastern Pacific slope.

Coryphaenoides rupestris appears to be most abundant in the canyon environment. All 11 stations made in Carson Canyon took this species, with an average catch rate of 557 individuals and 48.9 kg h⁻¹. Of 21 stations outside the Canyon, only 9 took *C. rupestris*, and the average catch rate at these was 116 individuals and 13.9 kg h⁻¹. We have re-examined the data of Haedrich et al. (1980), and find that there, off New England, canyon stations accounted for 95 % of the *C. rupestris* taken. Nine stations in canyons took this species (25 individuals, 4.8 kg h⁻¹) but only 1 station outside canyons did (7 individuals, 1.5 kg h⁻¹). Hecker (pers. comm.; see 1983) found that *C. rupestris* off New York occurred only in canyons, and was never encountered on the open slope.

Longfin hake *Phycis chesteri* and the eel *Synaphobranchus kaupi* were dominant on the upper slope off New England (Haedrich et al. 1980). Both species were much less abundant off Newfoundland, and the Grand Banks region would seem to be the northern limit of the distribution for these fishes (Methven & McKelvie 1986). Several species found on the Newfoundland continental slope are new records for the area. *Chalinura brevibarbis, Halosauropsis macrochir, Lionurus carapinus*, and *Lycodes perspicillus* have not been described previously from Canadian waters (Steigerwald & McAllister 1982). None of these were particularly abundant, and *H. macrochir* and *L. perspicillus* were represented only by single specimens.

The weak vertical zonation in our study is similar to the findings of Merrett & Marshall (1980) on the Northwest African Slope. They attributed this situation to the high productivity of that area. High production is also characteristic of the Newfoundland slope (Koblentz-Mishke et al. 1970). However, a modest degree of zonation was found on the Oregon slope (Pearcy et al. 1982), which is also highly productive. The similarity of these areas makes it difficult to evaluate the influence of productivity on zonation, and only the examination of a very unproductive area could properly address the question. Sulak (1984) found little evidence for zonation among deep benthic fishes of the relatively oligotrophic waters of the Bahamas.

Based on the ideas of Menzies et al. (1973), several zones should be encompassed within our sampling range. Those authors define a Shelf Faunal Province (about 5 to 250 m), an Archibenthal Zone of Transition (about 445 to 900 m), and an Upper Abyssal Zone (about 940 to 2635 m), as well as others that go well below our sampling range. Haedrich et al. (1980) define a broader archibenthal zone (300 to 1300 m) and divide the slope into upper (300 to 700 m) and lower (700 to 1300 m) zones. Thus, although our sampling range was more restricted than those of Haedrich et al. (1980) and Pearcy et al. (1982), the absence of the expected distinct zones within our range indicates that zonation of fish assemblages is not present off Newfoundland. The failure to find pronounced zones here undermines the belief that regions containing uniform and predictable assemblages of species continuously rim the ocean basins (Menzies et al. 1973). Breaks in supposedly continuous faunal zones have been found in shallower depths (Dauer & Simon 1975) and on the continental slope (Markle & Musick 1974, Cutler 1975).

The 'bigger-deeper' phenomenon (e.g. Polloni et al. 1979, Wenner & Musick 1977) has been reported for several of the species we found in large numbers. *Antimora rostrata, Synaphobranchus kaupi, Nematonurus armatus*, and *Nezumia bairdii* are all species which Polloni et al. (1979) found to be bigger-deeper. Only *A. rostrata* and *Coryphaenoides rupestris* showed a significant bigger-deeper relation in our Newfoundland study.

The bigger-deeper relation observed in *Antimora rostrata* and *Coryphaenoides rupestris* may be related to a number of factors. Podrazhanskaya (1971) found the shallow waters of the North Atlantic slope to be the major area of development for *C. rupestris* young, and Wenner & Musick (1977) suggested *A. rostrata* may also mature in this area. The presence of immature individuals in the shallower samples could create the appearance of a bigger-deeper relation where there was no such phenomenon. Larger individuals would

be sampled at all depths whereas immatures would be seen only in shallow samples, creating the appearance of a bigger-deeper relation where one did not, in fact, exist. Selective net avoidance by larger fishes would further enhance this effect (Pearcy et al. 1982), a factor that could also have contributed to the bigger-deeper relation found by Polloni et al. (1979) and others.

The absence of a general bigger-deeper relation on the Newfoundland slope supports the possibility that the relation is not merely an artifact of selective net avoidance. The equipment used by Polloni et al. (1979) was identical to that used in our sampling, yet their study found fishes (all taxa combined) to be bigger-deeper while ours did not. Were net avoidance the only factor involved, we would also have found a bigger-deeper relation for fishes in general. The bigger-deeper relation may in fact be a geographically limited phenomenon. Sulak (1984) found it to be characteristic of fishes in the Middle Atlantic Bight, a situation he reported to be in sharp contrast to the Bahamas where the relation was absent.

Wenner & Musick (1977) noted an absence of smaller specimens of *Antimora rostrata* in their study near Norfolk Canyon, U.S.A., and suggested that spawning occurred in the north. Two aspects of our data support this hypothesis. First, the standard lengths of their fishes, except in a few instances, were consistently over 20 cm, and they noted a marked absence of small specimens. The Newfoundland samples contain numerous specimens between 10 and 20 cm, particularly at shallow depths; this relates to the second point. Except for 1 specimen caught at 792 m, Wenner & Musick (1977) did not obtain specimens from any samples shallower than 1000 m. *A. rostrata* frequently occurred in many of our samples between 500 and 1000 m. The northwest North Atlantic can be considered a nursery area for *Coryphaenoides rupestris*, but parasitological evidence indicates that this population migrates a considerable distance to the Mid-Atlantic Ridge to spawn (Zubchenko 1985).

Andriashev (1954) defined primary species as those deep water fishes whose evolutionary radiation took place in the deep ocean, as opposed to secondary deep water fishes which evolved in shallow water and have been able to colonize deeper water secondarily Of those groups represented in our sampling, the families Alepocephalidae, Chimaeridae, Macrouridae, Halosauridae, Moridae, Notacanthidae, and Synaphobranchidae are all primary, while all others are secondary.

The percentage of primary species increases steadily with depth (Fig. 7). The general rate of increase in primary species, as expressed by the slope of the relation, is the same (m = 4.2 and 4.3 respectively, z in km) as that reported by Haedrich & Krefft (1978) for the Irminger Sea and steeper than the slope (m = 2.8)

calculated from the original data of Haedrich et al. (1980) off New England. Haedrich & Krefft (1978) suggested this situation might indicate an ongoing invasion of the deep sea from shallow waters at high latitudes. Working with invertebrate faunas that have more complete fossil histories than fishes, Zinsmeister & Feldmann (1984) and Buzas & Culver (1984) have recently supported such a view. In the Isopoda, Wilson
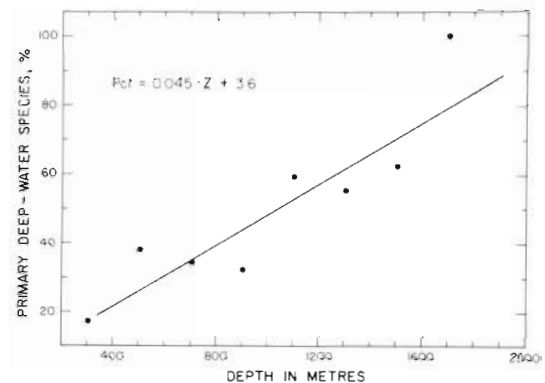
Fig. 7. Percentage of primary deep-water fish species in the fauna as a function of depth, by 200 m increments, on the Newfoundland continental slope. The regression is significant: r = 0.86, p < .01

(1980) points out an interesting contrast between the Munnidae, which appear to be entering the deep sea from both poles, and the Pleurogoniidae, which entered the deep sea from the Antarctic, diversified in deep water, and re-emerged in the Arctic.

A review by Somero et al. (1983) on the biochemical adaptations of deep-sea animals offers some insight concerning colonization of the deep sea by shallow-water forms from polar regions. They point out that deep-sea species possess enzymes and other cellular adaptations to high pressure and low temperature which enable them to function at great depths. It is possible that the shallow-water fishes present in the Denmark Strait area have physiological adaptations to the cold environment that have made invasion of the cold, but high pressure environment possible. Patton (1975) found that the phospholipid composition of the deep-sea *Antimora rostrata* and the cold-adapted, Antarctic shallow-water fish *Pagothenia borchgrevinki* were not significantly different. Adaptations such as a reduction in phospholipid fatty acid saturation not only enable fishes to invade a cold environment, but may also allow penetration into deep waters. This would mean the shallow-water, cold-adapted northern species might be more able to invade deep waters than species living in more temperate waters, and far-northern deep-water assemblages would thus tend to be more a mixture of primary and secondary species.

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