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Zonation and faunal composition of epibenthic populations on the continental slope south of New England

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ABSTRACT

The epibenthic macrofauna, including demersal fishes, between 140 and 1900 m on the continental slope south of New England was found to be distributed in three zones: shallow (141–285 m), middle (393–1095 m), and deep (1270–1928 m). Faunal boundaries were associated with the transition zones from shelf to upper continental slope and from upper to lower continental slope. The small Alvin Canyon was not faunally distinct. Fishes and echinoderms were the most abundant taxa, the former predominant in shallow and middle depths and the latter predominating deeper. The macrofauna was less diverse than the macrobenthic infauna of the same region, but the biomass of each fraction of the fauna was of the same order of magnitude.

1. Introduction

The fauna of the continental shelf and slope off southern New England has been an object of study since the early days of the U.S. Fish Commission and the first cruises of the BLAKE and the ALBATROSS. Deep-water collections from the area have provided rich material for systematic investigations, commencing with the classic work on fishes by Goode and Bean (1877 *et seq.*) and molluscs by Verrill (1884) and continuing to the present day (e.g., Sanders and Allen, 1973; Musick, 1973). Such extensive systematic work provides a sound basis for faunal and other ecological studies, but, surprisingly, the number of such works is very few, those concerned with the epibenthic macrofauna comprising only a handful. The first appeared less than 20 years ago, when Schroeder (1955) discussed the distribution of the fish fauna to a depth of about 1300 m. This study drew upon the collections made in an extensive trawling survey, but was essentially a group-by-group account, with emphasis on a relatively few commercial species. Using photographic data, Wigley and Emery (1967) and Grassle *et al.* (in press) have estimated the abundance and distribution of the numerically dominant macrofauna at various depths, with emphasis on the invertebrates. Quite recently, Markle and Musick (1974) report the composition and diversity of fishes taken in three trawls between 823 and 951 m.

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In none of these studies, however, were the data of sufficient density or completeness to assess the extent to which the macrofauna was zoned with depth across the continental slope, and whether distinct faunal groupings could be recognized.

The zonal depth distribution of the deep epibenthic macrofauna has been examined in more detail in other areas, particularly by Day and Pearcy (1968) off Oregon and by Rowe and Menzies (1969) off North Carolina. Day and Pearcy (1968) based their study on the fishes taken in trawls. They recognized four distinct species assemblages between 40 and 1829 m. The assemblages were zoned with depth, with faunal breaks at about 100 m, 400 m, and 1200 m that correlated to some extent with a subtle gradient in the sediment type. Rowe and Menzies (1969) analyzed the data contained in numerous photographs made from the upper continental slope to 5000 m, providing quantitative information on the distribution of large invertebrates. These were zoned with depth, in part correlated with particular physiographic or hydrographic conditions. A faunal break was apparent at about 1000 m on the slope. Menzies *et al.* (1973) have combined this work with other data to define faunal zones on the bottom off the Carolinas. On the shelf and slope, these are (1) the shelf faunal province (5–246 m), (2) the archibenthal zone of transition (445–940 m), and (3) the upper abyssal zone (940–2635 m). These same faunal zones were recognizable in other areas wherever sufficient sampling had been conducted, although the depths of the zones could be quite different from place to place.

Zonation of the animals living in the bottom may be somewhat different from that of the larger epifauna. Examination of the infauna along the Gay Head-Bermuda transect south of New England (Sanders and Hessler, 1969) revealed only a single faunal break, at about 200 m and accompanying the transition from shelf to slope. Below this depth, the fauna was said to change in composition gradually and continuously to almost 5000 m, with no distinct faunal zones being recognized.

The present study began as a modest attempt to gather data on the nature of slope epibenthic communities for later comparison with communities at similar depths in submarine canyons. The success of the trawling, the relatively close spacing of the samples and their location along the Gay Head-Bermuda transect, and the fact that nearly all the material, both fish and invertebrate, could be identified to species resulted in a body of macrofaunal data more extensive and complete than any heretofore reported for slope depths. This material and the completion of an extremely detailed report on the overall geology and sedimentary regime in the sampling area (MacIlvaine, 1973) led us to examine the question of zonation in the various components of the epibenthic macrofauna and in the fauna as a whole. Of particular interest was whether the composition of the fauna changed continuously, as Sanders and Hessler (1969) found for the infauna of the area, or whether there were patterns of zonation such as those described by Menzies *et al.* (1973) off Carolina. Also of interest was to make comparisons between community structure and abundance in the slope epibenthic macrofauna with the same parameters in the infauna.

2. Methods

During August 1972, we made 25 trawl collections from R/V GOSNOLD as she stood picket duty near the DSRV ALVIN dive site at 39°44′N, 70°58′W. Seventeen hauls were made on the continental slope between 200 and 1900 m (the limit of GOSNOLD's trawl wire), six were made between 200 and 1500 m in the small Alvin Canyon (Emery and Ross, 1968), and one was made on the shelf. To these were added four trawls made in July in the area from R/V ALCOA SEAPROBE.

Collections were made with a 16-foot (4.8 m) semiballoon trawl obtained from the Marinovich Trawl Company. This net is constructed of $1^1/_2$ inch (3.7 cm) stretch mesh with a bait seine liner (6 mm) in the cod-end. For deep-water work, the head rope was buoyed with floats of syntactic foam. Light chain was lashed at intervals along the foot rope. The effective opening is assumed to be 3 m wide and 1 m high. Thus, an hour of trawling at $1^1/_2$ kn should cover a minimum of 8.3×10^3 m^2 of bottom. Time on the bottom was estimated as the interval from the time the winch stopped paying out to the time retrieval was begun. Half-hour tows were used in shallower depths, and one-hour tows in deeper ones. An attempt was made to sample at least every 100 m increase in depth, but this was not always possible. Material was preserved in $10^0/_0$ buffered formalin, and was later transferred in the lab to $70^0/_0$ ethanol and individual weights, measurements, and identifications were made. Not all material of particularly abundant species was saved. For these few, mostly echinoderms, counts, weights and identifications were made at sea immediately after the trawl was emptied. Some *Geryon* weights were later calculated from size data. In general, smaller animals, such as polychaetes and isopods, were excluded from consideration on the presumption that these groups are not well sampled by the trawl.

Certainly the data obtained with the 16-foot trawl are not without limitations. The biases inherent in the use of trawls are a recurrent theme in the literature (e.g., Oviatt and Nixon, 1973). Different gear can give different results (Day and Pearcy, 1968), and bigger nets appear to catch disproportionately more and bigger fish (Schroeder, 1955). Nets are known to be selective, and the smaller the gear the greater the avoidance. In our experience off southern New England, however, we find that the rank abundance of species in the 16-foot net is much the same as that obtained with a commercial 40-foot net fished at the same level (cf. Markle and Musick, 1974), and are thus satisfied that the smaller net gives a reasonably good qualitative sample of the dominant species.

Quantification of such samples is considerably more difficult (Bullis and Struhsaker, 1970). The uncertainties with respect to the actual configuration of the net on the bottom, the actual time spent on the bottom, the overall efficiency of the net, and the degree of avoidance must all be taken into account. The extent to which any of these factors contribute individually to the trawl bias is almost impossible to quantify. The practice has been to concede, as we do here, that trawl samples underestimate absolute abundance. In reporting such values, we recognize that they are to be considered minimal. The usefulness of abundance estimates increases in relative comparisons between samples in which the same net was used.

It should be possible to calibrate trawl samples through direct observation of an area with cameras and deep submersibles, although the biases inherent in the use of such relatively new techniques (Barham, Ayer, and Boyce, 1967) are probably less well-understood than those for the more traditional trawls (Taylor, 1953; Clark, 1974). The ideal is a combination of the two methods at one site. We have made photographic observations off southern New England, and will occasionally refer to some of this data. Of particular interest is an examination of the slope fauna made between 500 and 1800 m on dives in DSRV ALVIN in 1967, 1968 and 1972 (Grassle *et al.*, in press). The 1972 dive (No. 436) was during the period in which we were trawling. Data from this study suggest that the 16-foot trawl may underestimate absolute abundance by an order of magnitude or more, but that its estimates of rank abundance are quite good.

A decided advantage in the use of trawls is that specimens are retained for direct identification and examination, and that a very large area can be surveyed in a relatively short time. Even the small trawls used in this study, for example, covered more than 180,000 m^2, fifteen times the area surveyed by ALVIN in the study mentioned above and 90 times the area surveyed by Rowe (1971) using bottom cameras in Hatteras Canyon.

Two methods were used to assess faunal change with depth, transect and cluster analyses. For transect analysis, the trawl collections made on the slope were arranged in order of increasing depth and were examined for faunal change across the depth gradient using the "first-plus-last-captures" method (Backus *et al.*, 1965; Peters, 1971; Hazel, 1972). The method depends on presence or absence only and employs a chi-square test to generate an index of change. The index represents departures from the expected distribution, assuming a homogeneous fauna, of first and last captures in proceeding along the transect. The expected distribution of first captures is described by

$$a_e(x) = k - \frac{k}{N}\sum_{n=0}^{x-1} a_e(n)$$

where $a_e(x)$ is the number of species captured for the first time at station x in the transect series, k is the average number of species captured at each station, N is the total number of species in the population being sampled, and $\sum_{n=0}^{x-1} a_e(n)$ is the sum of first captures from previous stations in the transect. The expected distribution of last captures, $b_e(x)$, is given by the same expression, but in the reverse order. Values of the expected distribution $a_e(x) + b_e(x-1)$ in each station interval are compared with the observed distribution $a_0(x) + b_0(x-1)$ corrected for sample size. For further details, the original reference (Backus *et al.*, 1965) should be consulted. In practice, it has been found useful (Backus *et al.*, 1969) to run a series of such analyses, suc-

Table 1. Station and catch data, GOSNOLD 197 and SEAPROBE.

Station	Latitude	Longitude	Date (1972)	Time	Depth Range	Mean Depth	Number of Specimens	Weight (gm)
SEAPROBE 18	40 04 N	70 29 W	24 July	2300–2330	256–273	264	238	477.1
„ 20	40 06 N	70 25 W	25 July	2038–2150	121–161	141	284	3578.3
„ 24	39 58 N	70 59 W	1 August	2222–2322	393–393	393	41	1777.0
„ 25	39 56 N	71 03 W	2 August	0120–0220	613–626	619	32	451.0
GOSNOLD 102	39 58 N	70 43 W	10 August	0925–1018	460–490	475	119	3367.0
„ 103	39 55 N	70 49 W	10 August	1145–1230	540–560	550	135	7160.0
„ 104	39 54 N	70 53 W	10 August	1350–1425	630–670	650	31	1278.0
„ 105	39 51 N	70 56 W	10 August	1558–1642	875–880	873	1	70.0
„ 106	39 52 N	70 56 W	10 August	1902–1945	910–925	918	4	3.6
„ 107	39 53 N	70 54 W	11 August	0820–0909	780–800	790	43	2677.8
„ 108	39 49 N	70 57 W	11 August	1204–1304	1070–1120	1095	25	2867.1
„ 109	39 49 N	70 55 W	11 August	1742–1840	1250–1290	1270	75	4770.5
„ 110	39 57 N	70 43 W	12 August	0642–0722	430–445	430	38	359.0
„ 111	40 00 N	70 47 W	12 August	0853–0938	275–290	283	78	1939.0
„ 112	40 03 N	70 49 W	12 August	1110–1202	190–190	190	297	1280.4
„ 113	39 53 N	70 44 W	12 August	1548–1630	625–680	653	149	4110.0
„ 114	39 51 N	70 45 W	12 August	1847–1943	925–940	933	23	990.7
„ 115	39 47 N	70 47 W	13 August	0735–0836	1450–1500	1475	241	1151.3
„ 116	39 46 N	70 50 W	13 August	1156–1257	1600–1630	1615	95	404.5
„ 117	39 49 N	70 56 W	13 August	1716–1816	1380–1380	1380	195	5687.2
„ 118	39 44 N	70 53 W	14 August	0812–0932	1925–1930	1928	1449	17796.9
„ 120	39 50 N	70 32 W	16 August	1015–1100	750–775	768	44	4071.0
„ 121	39 50 N	70 31 W	16 August	1325–1407	910–950	930	9	483.1
„ 122	39 54 N	70 32 W	16 August	1729–1830	1510–1575	1543	684	6605.9
„ 123	39 55 N	70 31 W	17 August	0951–1035	550–600	575	188	14362.5
„ 125	40 03 N	70 31 W	17 August	1340–1410	175–180	178	183	418.0

cessively eliminating from consideration those species which occur only at one, two, three, and four stations. Peak values of the index which persist in all runs are considered to show the station intervals of greatest faunal changes.

Cluster analyses were based on all collections, using species composition to group stations. All combinations of the measures percentage similarity (Whittaker, 1952), Canberra metric (Stephenson *et al.*, 1970), and average species shared (Grassle and Smith, in prep.) and the clustering strategies of unweighted pair-group (Williams, 1971) and flexible grouping with $\beta = -0.25$ (Lance and Williams, 1967) were used on data rarified (Sanders, 1968) to 1 and to 50 individuals per station. All gave similar results, with best agreement between runs using percentage similarity and average species shared. The percentage similarity measure, which we prefer, is given by (Whittaker and Fairbanks, 1958)

$$PS = 100(1.0 - 0.5\,\Sigma\,|p_{ia} - p_{ib}|) = 100\,\Sigma \min(p_{ia}, p_{ib})$$

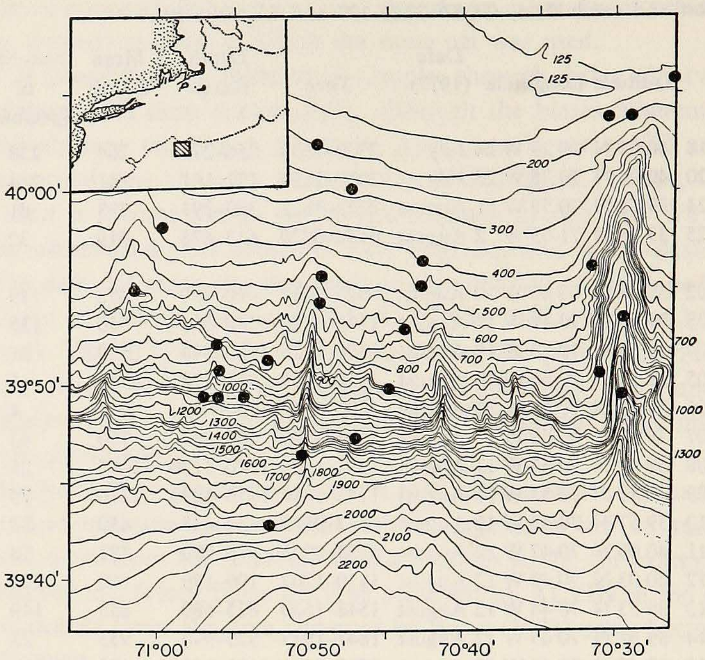

Figure 1. Approximate location of trawl stations, GOSNOLD cruise 197 and ALCOA SEAPROBE. Inset shows relationship of the area to southern New England. Bathymetric chart from MacIlvaine (1973).

where p_{ia} is the fraction composed by species i in collection a, and p_{ib} is the same for collection b.

Cluster analysis tests the results of the transect analysis in a separate and quite independent manner. In the transect analysis, it was assumed that the peak values in the index of change separated areas which included stations containing a relatively homogeneous fauna. Cluster analysis, when applied to the same data, should group such stations into distinct units. Because the between-sample measure takes relative abundance of species into account, cluster analysis should provide better resolution than transect analysis, which examines only presence or absence.

Diversity was calculated using the information function (Shannon and Weaver, 1963)

$$H = -\Sigma p_i \log_e p$$

where p_i is the fraction composed by species i in the sample. Evenness (Lloyd and Ghelardi, 1964; Pielou, 1966) was calculated by

$$E = \frac{e^H}{N}$$

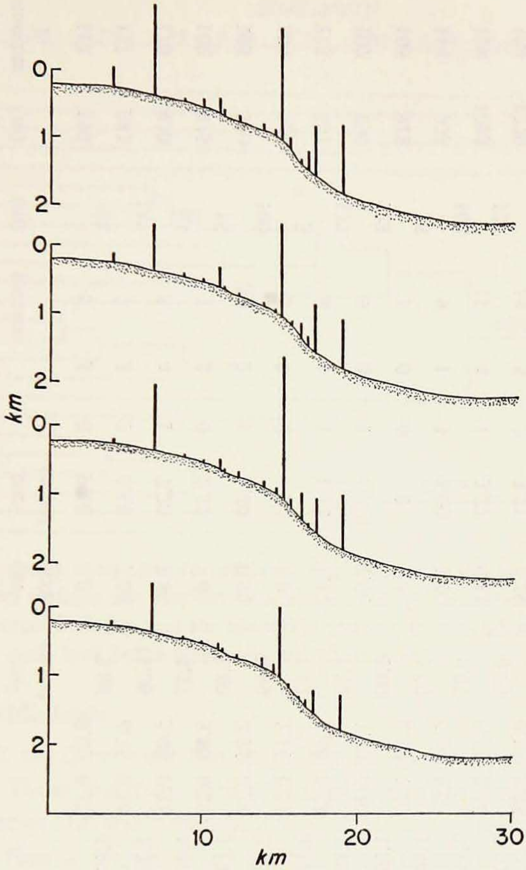

Figure 2. The index of change across the depth gradient for all taxa. Vertical lines are scaled values of the index, from Table 2, plotted at the appropriate depth on the average topographic profile of the area, from MacIlvaine (1973). Vertical exaggeration about 4.2:1. The analyses shown successively omitted, from top to bottom, species ocurring only once, twice or less, three times or less, and four times or less.

where *H* is as defined above and *N* is the total number of species in the sample. Catch rates were standardized with respect to assumed time on the bottom, and are expressed in terms of catch per hour trawled.

Data associated with the collections are presented in Table 1, along with certain catch data. The positions of the stations are plotted on a bathymetric chart of the area (MacIlvaine, 1973) in Figure 1. The station and species data upon which this report is based are on file and are available from the National Oceanographic Data Center, Rockville, Maryland, under acquisition number 74072. The material is housed in the Museum of Comparative Zoology, Harvard University.

Table 2. Values for collections and intervals used in the transect analysis when species occurring only once are omitted. The index of change values for analyses excluding species occurring twice or less, three times or less, and four times or less, and including all species are also listed. Figure 2 was drawn using these values.

Station number	Mean depth (m)	Interval distance (m)	Number of species	a_0	b_0	a_0 corrected	b_0 corrected	a_0+b_0 corrected	a_e	b_e	a_e+b_e	$(a_0+b_0)-(a_e+b_e)$	Index < 2 omitted	Index < 3 omitted	Index < 4 omitted	Index < 5 omitted	Index all species
112	190		5	5	0	9.00	0		9.00	0.12							
		93						3.86			6.87	-3.01	1.32	0.45	0.20	0.12	1.05
111	283		7	3	3	3.86	3.86		6.75	0.16							
		147						11.06			5.22	5.83	6.52	3.30	4.78	3.46	5.32
110	430		5	4	1	7.20	1.80		5.06	0.21							
		45						4.37			4.01	0.36	0.03	0.13	0.00	0.08	0.61
102	475		7	2	0	2.57	0		3.80	0.29							
		75						1.80			3.13	-1.33	0.57	0.05	0.06	0.16	2.81
103	550		10	2	1	1.80	0.90		2.85	0.38							
		100						0.90			2.52	-1.62	1.04	1.41	0.73	0.45	3.77
104	650		5	0	0	0	0		2.14	0.51							
		3						1.12			2.11	-0.98	0.46	0.05	0.10	0.31	3.00
113	653		8	1	1	1.12	1.12		1.60	0.68							
		137						1.12			1.88	-0.75	0.30	0.00	0.30	0.24	1.49
107	790		9	0	1	0	1.00		1.20	0.90							
		128						1.00			1.80	-0.80	0.36	0.01	0.24	0.59	1.71
106	918		1	0	0	0	0		0.90	1.20							
		15						1.00			1.88	-0.88	0.41	0.00	0.30	0.47	3.00
114	933		9	1	3	1.00	3.00		0.68	1.60							
		162						6.27			2.11	4.16	8.22	6.80	10.36	5.15	0.60
108	1095		11	4	1	3.27	0.82		0.51	2.14							
		175						4.03			2.52	1.52	0.91	0.23	0.50	0.01	0.00
109	1270		14	5	2	3.21	1.29		0.38	2.85							
		110						3.79			3.13	0.65	0.14	1.04	1.94	0.02	0.00
117	1380		18	5	7	2.50	3.50		0.29	3.80							
		95						6.27			4.01	2.26	1.27	0.70	0.01	0.43	0.11
115	1475		13	4	1	2.77	0.69		0.21	5.06							
		140						0.69			5.22	-4.53	3.93	3.57	2.53	1.63	5.29
116	1615		9	0	1	0	1.00		0.16	6.75							
		313						1.00			6.87	-5.87	5.02	3.56	3.89	2.55	3.16
118	1928		14	0	14	0	9.00		0.12	9.00							

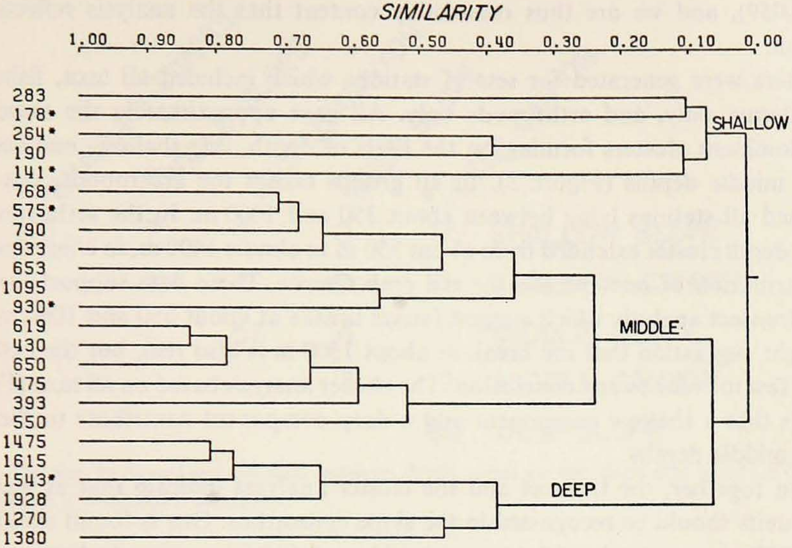

Figure 3. Stations clustered using data for all taxa. The column to the left is the mean depth of each station. Canyon stations are marked with an asterisk (*). The between-samples measure of overlap is percentage similarity and the clustering strategy is unweighted pair-group. Stations 105 and 106, which each took but a single species, are omitted.

3. Faunal change with depth

Separate transect analyses were run including all species taken, fishes only, and echinoderms only. These last two were the most abundant major taxa, each comprising over 25 species. In the remaining major taxa, too few species were taken to give meaningful results. Figure 2 is a graphical presentation of the slope transect analysis for all taxa. The base is the average topographic profile in the area, taken directly from MacIlvaine (1973). The vertical lines are the scaled values of the index of change, each plotted in the middle of the appropriate station interval. Shown are successive runs which excluded from consideration species occurring once, twice, thrice, and four times. The data used in the figure, including all the values to calculate the index when single occurrences are omitted, appear in Table 2. Consistently high values in the index of change occur at about 350 m (in the station interval 111–110) and 1000 m (in the station interval 114–108), with an area of relatively little change between. Deeper, breaks might occur at about 1500 and 1700 m.

It could be argued that the unequal spacing of the stations across the depth gradient might seriously affect the index of change. Where a fauna changes continuously, as suggested for the infauna in this region by Sanders and Hessler (1969), large depth gaps would result in large values of the index, since the larger the gap the more species would drop out and be replaced in the interval. To test whether such a situation might be biasing our results, values of the index based on all species (Table 2) were plotted against the corresponding depth interval. There was no correlation

(r = 0.059), and we are thus reasonably content that the analysis reflects a real situation.

Clusters were generated for sets of stations which included all taxa, fishes only, echinoderms only, and arthropods only. All gave approximately the same result, three dominant clusters forming on the basis of depth, one shallow, one deep, and one at middle depths (Figure 3). In all groups except the arthropods, one cluster contained all stations lying between about 350 and 1000 m. In the arthropods, this middle depth cluster extended from about 350 m to almost 1400 m, in effect describing the distribution of one species, the red crab *Geryon.* These data support the results of the transect analysis which suggest faunal breaks at about 350 and 1000 m. There is a slight suggestion that the break at about 1500 m is also real, but the collections are too few to come to any conclusion. The cluster analysis based on all taxa (Figure 3) suggests that a shallow component and a deep component contribute to the faunal unit at middle depths.

Taken together, the transect and the cluster analyses indicate that at least three faunal units should be recognized in the slope epibenthos. One is found shoaler than about 350 m, a second, with some possible subdivisions, extends between about 350 and 1000 m, and a third is found below about 1000 m. For convenience, we hereafter refer to the three areas as the shallow (141–285 m), middle (393–1095[2] m), and deep (1270–1928 m) portions.

Finally, all stations within a zone were lumped, and the overlap with other zones measured by percentage similarity. *PS* from shallow to middle was 3.4°/₀ for all taxa, 4.7°/₀ for fishes, 2.2°/₀ for arthropods, 62.5°/₀ for coelenterates, and 0°/₀ for echinoderms. *PS* from shallow to deep was 0.04°/₀ for all taxa, 0.0°/₀ for fishes, 0°/₀ for arthropods, 7.1°/₀ for coelenterates and 0°/₀ for echinoderms. *PS* from middle to deep was 3.6°/₀ for all taxa, 26.5°/₀ for fishes, 40.5°/₀ for arthropods, 13.3°/₀ for coelenterates and 16.6°/₀ for echinoderms. These data support the basic division for the fauna as a whole, but indicate that the various major taxa recognize the boundaries to varying degrees and with differing patterns.

4. The distinctiveness of the canyon fauna

Since it were possible that Alvin Canyon might harbor its own particular fauna, the seven successful trawls made there were omitted from the transect analyses. These were included in the cluster analyses, however, and should have clustered separately if the fauna were distinct. This did not prove to be the case, each canyon trawl clustering in the appropriate depth range with the slope trawls (Figure 3). To further test this overlap, the slope collections within each depth zone were lumped and were compared using percentage similarity with similarly lumped canyon collections on the basis of all taxa, fishes only, and echinoderms only. The matrix of

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[2] The transitional station at 1095 m was not consistent in its clustering, sometimes falling in the middle group and sometimes in the deep. We include it in the middle group because it fell there in the cluster based on all taxa (Figure 3).

SHALLOW CANYON	MIDDLE SLOPE	MIDDLE CANYON	DEEP SLOPE	DEEP CANYON	
45	7	4	0	0	SHALLOW SLOPE
	1	1	0	0	SHALLOW CANYON
		57	4	3	MIDDLE SLOPE
			3	2	MIDDLE CANYON
				69	DEEP SLOPE

Figure 4. Overlap in faunal composition between depth zones on the slope and in Alvin Canyon. The measure is percentage similarity.

Figure 4, for all taxa, indicates what all analyses showed, that the overlap within depth zones is high and between depth zones is low. Thus, this small canyon cannot be said to have a distinct fauna. Nonetheless, there is some evidence here that certain species could prove to be "canyon indicators" such as were indicated in a study of photographs from the considerably larger Hatteras Canyon (Rowe, 1971). The echinoderm *Amphilimna olivacea*, for example, occurred only in the shallow canyon collections where it was taken in great abundance. Conspicuously absent from the canyon was the quill worm *Hyalinoecia artifex*, which within its depth zone was the most abundant animal on the slope.

Animals may have been slightly more abundant in the canyon. Catch rates for all slope stations combined were 228 specimens/hr (all taxa) and 3.4 kg/hr. Catch rates for all canyon stations were 368 specimens/hr and 5.7 kg/hr. Comparing only the deeper stations, those from the middle and deep zones and hence below the area of possible direct shelf influence, slope rates were 225 specimens/hr and 4.1 kg/hr while canyon rates were 392 specimens/hr and 7.6 kg/hr.

5. Faunal composition and diversity

In all, the trawls took 4701 specimens weighing more than 88 kg and representing 72 species. Fishes (26 species) and echinoderms (29 species) were important constituents of the fauna. Nine arthropod species (eight crustacea and one pycnogonid), six coelenterates, one polychaete, and one octopod comprised the remainder. Catch statistics for the various higher categories overall and within the three depth zones are found in Table 3. A list of all species, numbers, and weights by depth zone is given in Table 4.

Catch rates, in terms of numbers, were in general at their lowest at the middle

Table 3. Catch rates for major taxa, for all stations ($N = 26$) and arranged by depth zone.

	All Stations		Shallow, 141–285 m		Middle, 393–1095 m		Deep, 1270–1928 m	
Hours	21.41		3.82		11.24		6.35	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight
Fish – total	867	32825.1	381	5202.1	420	17827	66	9796.0
– per hour			99.8	1363.0	37.4	1586	10.4	1542.7
Echinoderms – total	3119	25793.9	499	603.8	13	751	2607	24439.1
– per hour			130.6	158.2	1.2	66	410.5	3848.7
Arthropods – total	423	23457.9*	186	1710.9	182	20063.8*	55	1683.2*
– per hour			48.7	448.3	15.2	1785.0*	8.7	265.1*
Coelenterates – total	49	2879	14	176.0	24	2325	11	378
– per hour			3.7	46.1	2.1	206.9	1.7	59.5
Polychaetes – total	236	1192	–	–	236	1192	–	–
– per hour			–	–	21.0	106.0	–	–
Molluscs – total	7	1871	–	–	7	1871	–	–
– per hour			–	–	0.53	160.2	–	–
All taxa – total	4701	88018.9	1080	7692.8	882	44029.8	2739	36296.3
– per hour			282.7	2015.6	78.5	3911.2	431.3	5716.0

* Contains some calculated *Geryon* weights.

depths, and highest in the deep zone, the increase there caused by the great numbers of echinoderms. The numbers of fish declined with depth, but the weight stayed about the same since bigger specimens were caught deeper. The numbers of coelenterates declined slightly with depth, whereas weights were markedly higher in middle and deep zones. Numbers of arthropods declined as well, but weights, due to dominance by the large red crabs *Geryon*, were at a maximum in the middle zone.

The dominant species in each depth zone are shown in Table 5. For each zone, the species listed comprised 90% or more of the total specimens taken in that zone. Top-ranking species in the shallow zone were the starfish *Astropecten*, the galatheid *Munida*, the ophiuroid *Amphilimna*, and four fish (*Citharichthys*, *Lepophidium*, *Merluccius*, and *Helicolenus*). Top-ranking in the middle zone were the quill worm *Hyalinoecia*, the red crab *Geryon*, and five fish (*Synaphobranchus*, *Nezumia*, *Phycis*, *Lycenchelys*, and *Glyptocephalus*). Top-ranking species in the deep zone were all echinoderms: two brittlestars (*Ophiomusium* and *Homalophiura*), three urchins (*Echinus affinis*, *E. alexandri*, and *Phormosoma*), and the starfish *Porcellanaster*. The fishes are thus important members of the community in both the shallow and middle depths, whereas echinoderms dominate the deep assemblage. No top-ranking species in either the shallow or deep zone occurred in any other zone. In the middle zone, the crab, the eel *Synaphobranchus*, and the rattail *Nezumia* also occurred deeper, although in lesser numbers, and the longfin hake *Phycis* occurred shallower. The witch flounder *Glyptocephalus* was found shallower also, but 96% of the specimens taken came from middle depths. In contrast to other species, the witch flounder is unusual in that it only spends its juvenile life on the slope, moving onto the continental shelves as an adult (Powles and Kohler, 1970).

Table 4. Numbers and weights (in *gm*) of each species taken, by depths zone.

		Shallow		Middle		Deep	
		141–285 m		393–1095 m		1270–1928 m	
		Number	Weight	Number	Weight	Number	Weight
Fish	*Argentina striata*	2	13.0	–	–	–	–
	Coelorinchus carminatus	3	51.0	2	99.0	–	–
	Chlorophthalmus agassozo	7	59.0	–	–	–	–
	Citharichthys arctifrons	144	482.0	–	–	–	–
	Glyptocephalus cynoglossus	1	45.0	45	1510.0	–	–
	Helicolenus dactylopterus	44	394.0	–	–	–	–
	Lepophidium cervinum	68	1027.0	–	–	–	–
	Lophius piscatorius	3	116.0	–	–	–	–
	Merluccius albidus	55	430.1	1	486.0	–	–
	Monolene sessilicauda	1	31.0	–	–	–	–
	Myxine glutinosa	15	652.0	–	–	–	–
	Paralichthys oblongus	2	196.0	–	–	–	–
	Peristedion miniatum	1	42.0	–	–	–	–
	Phycis chesteri	14	93.0	61	8517.0	–	–
	Pisodonophis cruentifer	14	160.0	–	–	–	–
	Urophycis regius	7	1411.0	–	–	–	–
Echinoderms	*Amphilimna olivacea*	146	34.0	–	–	–	–
	Astropecten americanus	352	559.8	–	–	–	–
	Brisaster fragilis	1	10.0	–	–	–	–
Arthropods	*Acanthocarpus alexandri*	6	45.4	–	–	–	–
	Cancer borealis	14	646.0	–	–	–	–
	Collodes robustus	8	1.5	–	–	–	–
	Munida valida	158	1018.0	4	18.2	–	–
Coelenterates	*Bolocera tuediae*	13	170.0	15	222.0	–	–
	Pennatula aculeata	1	6.0	–	–	1	6.0
Fish	*Antimora rostrata*	–	–	3	572.0	27	6245.0
	Coryphaenoides rupestris	–	–	2	3.0	–	–
	Cottunculus thompsoni	–	–	3	377.0	–	–
	Lycenchelys paxillus	–	–	5	65.0	1	15.0
	Lycenchelys verrilli	–	–	50	175.0	–	–
	Nezumia bairdii	–	–	84	1975.0	30	2882.0
	Synaphobranchus kaupi	–	–	164	4048.0	3	161.0
Echinoderms	*Hygrosoma petersii*	–	–	1	599.0	15	2728.0
	Ophiomusium lymani	–	–	2	0.2	1468	1324.7
	Mediaster bairdii	–	–	2	22.0	–	–
	Plutonaster intermedius	–	–	7	109.8	16	139.4
	Pseudarchaster parelii	–	–	1	20.0	–	–
Arthropods	*Collosendeis colossea*	–	–	1	4.0	18	55.0
	Geryon quinquedens	–	–	177	20041.6	22	1599.0
Annelids	*Hyalinoecia artifex*	–	–	236	1192.0	–	–
Coelenterates	*Actinauge verrilli*	–	–	7	1686.0	1	300.0

(continued.)

Table 4 (continued).

		Shallow 141–285 m		Middle 393–1095 m		Deep 1270–1928 m	
		Number	Weight	Number	Weight	Number	Weight
Coelenterates	*Actinostola callosa*	–	–	1	348.0	–	–
	Flabellum goodei	–	–	1	69.0	7	61.0
Molluscs	*Bathypolypus typicus*	–	–	7	1871.0	–	–
Fish	*Aldrovandia affinis*	–	–	–	–	1	23.0
	Alepocephalus agassizi	–	–	–	–	3	355.0
	Centroscyllium fabricii	–	–	–	–	1	115.0
Echinoderms	*Asteronyx loveni*	–	–	–	–	1	0.2
	Asteroschema sp.	–	–	–	–	3	20.0
	Benthopecten spinosus	–	–	–	–	3	2.1
	Brissopsis sp.	–	–	–	–	1	25.0
	Solaster benedicti	–	–	–	–	2	110.2
	Echinus alexandri	–	–	–	–	147	8378.0
	Echinus affinis	–	–	–	–	355	8034.3
	Homalophiura inornata	–	–	–	–	232	251.3
	Molpadia musculus	–	–	–	–	14	22.2
	Ophiochondrus sp.	–	–	–	–	1	0.1
	Ophiothrix sp.	–	–	–	–	5	1.0
	Ophiura sp.	–	–	–	–	2	0.2
	O. ljungmani	–	–	–	–	21	1.7
	O. sarsi	–	–	–	–	5	0.8
	O. signata	–	–	–	–	1	0.1
	Pectinaster forcipatus	–	–	–	–	7	13.4
	Phormosoma placenta	–	–	–	–	182	2606.0
	Bathybiaster vexillifer	–	–	–	–	1	9.8
	Psolus sp.	–	–	–	–	2	1.0
	Zygothuria lactea	–	–	–	–	16	656.8
	Porcellanaster caeruleus	–	–	–	–	107	112.8
Arthropods	*Lithodes agassizii*	–	–	–	–	1	6.0
	Munidopsis curvirostrata	–	–	–	–	4	0.2
	Stereomastis nana	–	–	–	–	10	23.0
Coelenterates	*Umbellula* sp.	–	–	–	–	2	11.0

A summary of the number of species taken and the diversities of the species assemblages, by taxon, is shown in Table 6. Fishes decreased in diversity *H* from shallow to deep, but echinoderms, arthropods and coelenterates increased. Evenness values, which are inversely proportional to the extent to which overall diversity is influenced by a few dominant species, increased slightly with depth in fishes, arthropods, and coelenterates, but decreased markedly in echinoderms. The two dominant groups, the fishes and echinoderms (which together comprise more than 75$^0/_0$ of all species taken), thus display quite different patterns with respect to their diversity, just as they did with respect to relative abundance (Table 3).

Table 5. Dominant species by numbers in each depth zone.

	Shallow 141–285 m		Middle 393–1095 m		Deep 1270–1928 m	
	Number	Percent	Number	Percent	Number	Percent
Astropecten americanus	352	32.6	–	–	–	–
Munida valida	158	14.6	4	0.5	–	–
Amphilimna olivacea	146	13.5	–	–	–	–
Citharichthys arctifrons	144	13.3	–	–	–	–
Lepophidium cervinum	68	6.3	–	–	–	–
Merluccius albidus	55	5.1	1	0.1	–	–
Helicolenus dactylopterus	44	4.1	–	–	–	–
Hyalinoecia artifex	–	–	236	26.8	–	–
Geryon quinquedens	–	–	177	20.1	22	0.8
Synaphobranchus kaupi	–	–	164	18.6	3	0.1
Nezumia bairdii	–	–	84	9.5	30	1.1
Phycis chesteri	14	1.3	61	6.9	–	–
Lycenchelys verrilli	–	–	50	5.7	–	–
Glyptocephalus cynoglossus	1	0.09	45	5.1	–	–
Ophiomusium lymani	–	–	2	0.2	1468	53.6
Echinus affinis	–	–	–	–	355	13.0
Homalophiura inornata	–	–	–	–	232	8.5
Phormosoma placenta	–	–	–	–	182	6.6
Echinus alexandri	–	–	–	–	147	5.4
Porcellanaster caeruleus	–	–	–	–	107	3.9

6. Homogeneity with depth zones

Although the shallow, middle, and deep faunas display a certain internal integrity, the distribution of the various species is not uniform within each area. Figure 5 shows the distribution according to depth on the continental slope for fishes, the most widely abundant taxon in our samples. The kite diagrams for each species reflect, to the left, the number of specimens/hr and, to the right, the overall weight/hr. The two faunal breaks are indicated by dashed lines, the one at about 350 m operative for many species and the one at about 1000 m for fewer, but most notably for *Antimora* and *Phycis chesteri*. *Synaphobranchus*, as noted previously (Table 4), crosses the deep boundary but appeared much less abundant below it than above it. Within the middle zone, only *Glyptocephalus* occurs fairly uniformly. Of particular interest is

Table 6. Number of species, diversity H, and evenness E by taxon and by depth zone.

	All Stations	Shallow, 141–285 m			Middle, 393–1095 m			Deep, 1270–1928 m		
	Species	Species	H	E	Species	H	E	Species	H	E
Fish	26	16	1.9	.42	11	1.7	.47	7	1.2	.47
Echinoderms	29	3	0.6	.62	5	1.3	.74	24	1.5	.19
Arthropods	9	4	0.6	.44	3	0.1	.38	5	1.3	.74
Coelenterates	6	2	0.3	.65	4	0.9	.62	4	1.0	.70
Polychaetes	1	–	–	–	1	–	–	–	–	–
Molluscs	1	–	–	–	1	–	–	–	–	–
All taxa	72	25	2.1	.34	25	2.1	.32	35	1.8	.15

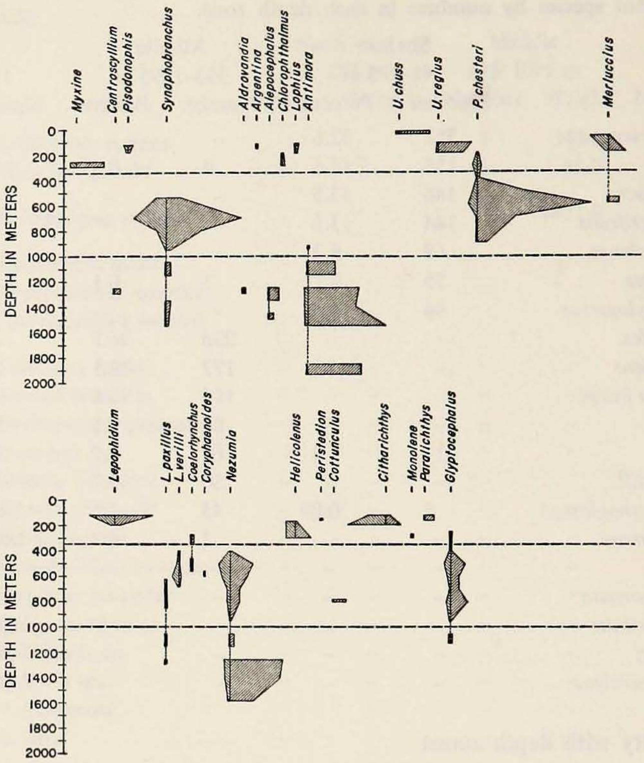

Figure 5. Depth range and relative abundances of fishes on the slope. The left-hand side of each kite diagram reflects relative number per hour, and the right-hand side relative weight per hour. Dashed horizontal lines indicate the approximate depth of the two faunal boundaries.

the distribution of the congeners *Lycenchelys verrilli* and *L. paxillus*, the former occurring in the upper part of the middle zone and the latter in the lower. This dichotomy, suggested in Figure 3, is supported by other taxa as well. The top-ranking species, *Hyalinoecia* (Table 5), was found in abundance only to 650 m, and *Geryon*, while found throughout the zone and to 1400 m, was most abundant at a depth of about 550 m.

Although there is some indication that different species do have different depth preferences within a zone, patchiness alone could also account for the apparent heterogeneity. Our data are inadequate to resolve the question of which factor is most important. Both, of course, could contribute. An effect of either would be to produce the relatively loose clustering, particularly as seen among the shallow stations, of Figure 3.

7. Discussion

The methodology employed here, applied to all taxa of the larger epifauna, suggests that important faunal boundaries exist on the continental slope at about 300–400 m and 1000–1100 m. Both boundaries can be associated with physical changes in the slope environment there, drawing largely on the important descriptive work of MacIlvaine (1973). The topography in our Figures 1 and 2 is taken directly from this work; the significant change in gradient described below can be easily visualized therein.

The shallower boundary corresponds approximately to the transition zone from shelf to slope. The sediments at the shelf/slope break are dominated by quartzose sand, and suspended sediment near the bottom exists in concentrations of up to 250 μg/1. Offshore on the upper continental slope the holocene sediments are silty sand and sandy silt with suspended sediment in concentrations of 50–60 μg/1. The region inshore of the boundary is shoal enough to be influenced by the seasonal thermocline, while offshore it is not. The deeper boundary corresponds approximately to the transition from the upper to the lower continental slope. The upper slope, with a gradient of 1.4°, is characterised by sedimentation rates of 15 cm/1000 yr. The combination results in medium scale slumping (10's of meters), which, when it occurs, results in material being only partially removed. The sediment, mentioned above, is relatively homogeneous, and is soft enough to show current scours. The lower continental slope has a considerably steeper gradient, 7.6°, and the sedimentation rate is only 2 cm/100 yr. Small-scale slumping (1 to a few meters) allows no accumulation of material and leaves a consolidated, erosion-resistant surface exposed. The sediment, a clayey silt, is quite stiff and suspended sediment concentrations are low, of the order of 20 μg/1. The lower continental slope is much more variable than the upper, with four distinct bottom types (smooth sediment, hummocky sediment, talus slopes, and rock outcrops) being recognized instead of only one. From the standpoint of temperature, the deep boundary lies near the bottom of the permanent thermocline.

The two boundaries set off a faunal zone on the upper continental slope, a zone which itself may be divisible into an upper and a lower portion. This zone agrees very nearly with the region (200–300 to 1000 m) occupied by the amphipod "slope fauna" as determined by Mills (1972), studying material from the Gay Head-Bermuda transect, and corresponds approximately to the east coast archibenthal zone of transition (445 to 940 m) defined by Menzies *et al.* (1973) on the basis of the distribution of isopods. Further removed from our area, Day and Pearcy (1968) recognize similar zones for assemblages of fishes off Oregon, with their species association III found at depths between 594 and 1143 m. The upper boundary of such a zone was found by Bullis and Struhsaker (1970) in the fish fauna of the western Caribbean, but their collections did not extend deep enough to define the lower boundary.

Such zones, thus, have considerable horizontal extent and coherence, an idea which is not particularly new (LeDanois, 1948), but the faunas of a zone are not the same everywhere. Faunal replacement along an isobath (within a zone) is probably somewhat of a gradual phenomenon, as was found for the fish fauna at 900 m in the Middle Atlantic Bight by Markle and Musick (1974). Our rather meagre data suggest that zones extend right through submarine canyons, but that animals are somewhat more abundant in the canyon. Canyon enhancement is in keeping with the suggestion

Table 7. Comparison between community parameters for fishes from four investigations on the upper continental slope off southern New England.

Investigation	Depth (m)	Gear	Specimens/ 1000 m^2	Gm/m^2	H(log$_e$)	E
Present study	393–1095	16-ft net	4.5	0.2	1.7	0.47
Markle and Musick (1974)	823–951	40-ft net*	12.4	–	1.5	0.22
Schroeder (1955)	550–732	60-ft net	6.4	2.1	–	–
Grassle *et al.* (in press)	992–1000	Photographs	27.1	–	1.6	0.48

* Assumed to sweep 3.2×10^4 m^2 per hour (Haedrich and Henderson, 1974).

(Rowe, 1972) that submarine canyons may form important conduits for channeling food-rich sediment from the shelf into the deep ocean.

Where comparisons can be made, our observations of the large epifauna on the upper continental slope are in fair agreement with those made by others. The dominant fish species, *Synaphobranchus* (Table 5), was also the top-ranking species observed by Markle and Musick (1974) at 900 m and Grassle *et al.* (in press: Dive 282, 992–1000 m). The rank order for the top fish species is very similar in our list and that of Markle and Musick (1974), with two exceptions. *Lycenchelys verrilli* is our fourth-ranking fish within the zone, but occurs shallower than Markle and Musick fished (Figure 5). *Coryphaenoides rupestris* was ranked third by Markle and Musick (1974), but only two small specimens appeared in our collections (Table 4). 84% of their specimens, however, came from near Hudson Canyon, where we have found this species to be locally abundant (unpub. data). Schroeder (1955) also took relatively few *C. rupestris* in the slope area. Table 7 lists some overall community parameters for fish assemblages in the area derived from the data of four investigations. The greatest differences are in the estimates of absolute abundance. As would be predicted the small net gives the lowest estimate and the photographs give the highest, the difference in numbers being about six-fold. Only two estimates could be gotten for fish biomass, that from the largest net used is ten times that from the small net. Thus, in an absolute sense, abundance and biomass estimates (Table 3) from the small net should probably be considered low by about an order of magnitude. Nonetheless, similar trends in the relative abundance of animals are found in the data from our study and that based on the ALVIN transects (Grassle *et al.*, in press). Both show a 4:1 decrease in fish abundance when comparing depths above and below about 1000 m (i.e. middle *vs.* deep). The values for diversity and evenness are quite close, particularly between our study and the photographic survey.[3] Those measures from Markle and Musick (1974) are slightly lower because their larger net, sweeping about 4.8×10^4 m^2, took larger rare species which most likely avoided the small net and were not seen by the submarine because of the relatively small area (2580 m^2) photographed.

The diversity *H* of the total epibenthic macrofauna investigated by us declined

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[3] Visual observations made on Dive 436 by D. M. Cohen, however, saw more species than either the nets or photographs sampled, and relative abundances were different.

slightly with depth, from 2.1 to 1.8 (Table 6). In contrast, the diversity of the major components of the infauna (polychaetes and bivalves) in the same region increases with depth (Sanders, 1968). The values of the index are somewhat higher for the infauna than for the large epifauna, being 2.8 at 300 m (shallow), 3.1 at 487 m (middle), and 3.3 at 2086 m (deep). The abundance and biomass of the infauna is 6405 specimens/m^2 and 12.0 gm/m^2 at 550 m and 2020 specimens/m^2 and 15.6 gm/m^2 at 1900 m (Rowe *et al.*, 1974). The density of animals in the large epifauna is of course much lower than that in the infauna, our data (Table 3) suggesting a differential of some three to four orders of magnitude. The biomass values, however, are much more comparable. The catch rates in Table 3 imply a biomass of 0.5 gm/m^2 at middle depths and 0.7 gm/m^2 at deep depths, and these are minimal estimates low by perhaps a factor of 10. The biomass contained in the large epifauna on the slope is thus nearly the same order of magnitude as that contained in the infauna. A consequence is that the epifauna must depend on sources other than the infauna for a portion of its food. Presumably these sources must be pelagic, and there is certainly evidence that pelagic food is important to slope-dwelling fishes (Pearcy and Ambler, 1974). Quantification of the degree of dependence must await further investigation. Data on turnover rates in the deep-living infauna are critically needed.

In the slope epifauna, the two dominant major taxa show patterns of diversity quite opposite to one another. The fishes decrease in diversity and the echinoderms increase. The same situation can be found in other deep-sea groups, some showing increased diversity with increasing depth, for example cumaceans (Jones and Sanders, 1972), while others, for example gastropods (Rex, 1973), do not. The increase in diversity by the echinoderms is probably a function of the increased variability (MacIlvaine, 1973) in the bottom on the lower continental slope. For these animals, which adhere quite closely to and even bury in the substrate, the diversity of microhabitats provides more opportunities for speciation than on the much more uniform upper continental slope. Abele (1974) has shown that a good correlation exists between substrate variability and species diversity in shallow marine areas. Fishes, being much more mobile, are probably less influenced by the nature of the bottom directly, but could respond more to food availability. On the continental rise at 2600 m, where fish diversity *H* appears even lower than on the slope, dominant species are quite generalized feeders (Haedrich and Henderson, 1974). On the slope, however, where food is more abundant, including particularly pelagic sources, greater food specialization seems to occur (Pearcy and Ambler, 1974). The mobility of fishes combined with a diversity of feeding types would allow efficient exploitation of this resource.

8. Summary

Transect analysis, which uses presence or absence to identify faunal boundaries in proceeding across some gradient, and cluster analysis, which groups similar samples on the basis of relative abundance of species, were used independently to

examine zonation in the epibenthic macrofauna living on the continental slope south of New England. The data were those from 26 16-ft semiballoon trawl samples made between 140 and 1900 m. Both methods suggested faunal boundaries at about 300–400 m and about 1000–1100 m. The shallow boundary may be associated with the lower part of the transition from shelf to slope and with the changeover from a region with seasonal temperature fluctuations to one of little annual variation. The deeper boundary may be associated with the lower part of the transition from upper to lower continental slope and with the changeover from a region lying within the main thermocline to an essentially isothermal region lying below it. The presence of two boundaries on the slope indicates that the epibenthic macrofauna occurs there in at least three rather distinct zones: shallow (141–285 m), middle (393–1095 m), and deep (1270–1928 m). The fauna of a small submarine canyon in the same area appears similarly zoned, and cannot be considered distinct.

Fishes, with 26 species, and echinoderms, with 29, were the most abundant taxa. Nine arthropod species, 6 coelenterates, 1 polychaete, and 1 octopod were also taken. Separate consideration of the fish, echinoderm, coelenterate, and arthropod fractions of the fauna from zone to zone showed differing responses to the boundaries, and different patterns of diversity and relative abundance. Within zones, animals were not distributed completely uniformly, but whether this apparent heterogeneity was a result of real differing depth preferences by different species or of patchiness only could not be ascertained. The abundance and diversity of fishes declined with depth while that of the echinoderms increased. Increased echinoderm diversity on the lower continental slope may reflect the fact that four distinct bottom types are present there, instead of only one as is found shallower. Increased fish diversity at shallower depths might result from increased food specialisation there, including pelagic sources, but the data are inadequate to resolve the question. Comparison of the results of this study with the relatively few observations made on the macrofauna in the same area by other workers shows fair agreement with respect to dominant species and general patterns. With respect to absolute abundance, however, estimates derived from the small net used by us appear low by an order of magnitude.

The infauna of the continental slope is more diverse than the epibenthic macrofauna, and is 10^3 to 10^4 times more abundant numerically. The biomass of the infauna and that of the macrofauna are, however, of the same order of magnitude. Unless turnover rates in the infauna are very high, the macrofauna must depend at least in part on other sources, presumably pelagic, for food.

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