STRUCTURE OF THE ABYSSAL MACROBENTHIC COMMUNITY IN THE ROCKALL TROUGH

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ABSTRACT

A sampling study of the abyssal and bathyal benthos of the Rockall Trough area was initiated by the S.M.B.A. in 1973. This paper reports on a preliminary analysis of macrobenthic community structure from six large quantitative samples taken from RRS Challenger in 1975 with a 0.25m^2 spade corer from a depth of 2875m in the southern Rockall Trough. The cores were taken within an area measuring 2 x 1 nautical miles between 55°03 - 04'N and 12°02 - 06'W.

Total non-foraminiferal wet-weight biomass averaged 3.67g. m^{-2} from 1853 macrofaunal specimens.m^{-2}, disregarding the weights of the occasional very large specimens. These data exceed the range of published values obtained from comparable depths and positions, relative to the continental land mass, in the northwestern Atlantic. Moreover, the relative proportions of the macrofaunal groups represented in the box core samples more closely resembled samples obtained from depths greater, rather than lesser, than 4000m in the N W Atlantic and the central N Pacific.

The Rockall Trough fauna clearly displays a much smaller average size than benthos from shallow water, with many macrofaunal taxa being of meiofaunal dimensions. Meiofaunal taxa were also well represented, particularly nematodes and foraminiferans. Agglutinating foraminiferans were numerically most numerous, but biomass estimates were frustrated owing to difficulty in identifying living plasma.

The identities of the species collected and the proportional representation showed little variation between cores. Expected species diversities of the polychaete/bivalve fraction showed macrofaunal species diversity to be high, though not as high as at abyssal depths in the central N Pacific or bathyal depths on the Californian continental borderland.

Between-core differences in expected species diversity were computed to fall within the limits of multinomial sampling error. This did not support any hypothesis of large-scale patchiness in faunal dispersion that might enhance diversity estimates from towed samplers such as the epibenthic sledge.

INTRODUCTION

Despite the recent spectacular increase in effort, particularly in America, on the deep-sea ecosystem, sampling of the deep-sea macrobenthos continues predominantly to employ gears such as the epibenthic sled (Hessler & Sanders 1967) that are towed for often quite long distances over the ocean floor. Consequently information on any possible fine scale spatial inhomogeneity is lost and because of the sampling bias to which such gear is subject, quantitative data on the density and community structure of the fauna of this

MATERIAL AND METHODS

In order to obtain reliable sample estimates of community parameters where the degree of spatial homogeneity of the fauna is unknown, it is desirable to take as many replicate samples as possible. The present study is of a series of six successful samples (out of a total of 10 lowerings) using a modified form of the 0.25m^2 United States Naval Electronics Laboratory (USNEL) spade or box corer within an area of 1 x 2 nautical miles in the southern Rockall Trough (Fig. 2), in a depth of 2875m. The cores were obtained on cruise 12B/75 of RRS Challenger in September, 1975.

Sample positions (Table 1) were fixed with satellite navigator.

TABLE 1 Positions of box-core samples (Stations 46 - 51)

Station	Latitude	Longitude
46	55°03.7'N	12°06'W
47	55°03.5'N	12°03.5'W
48	55°03.9'N	12°03.9'W
49	55°03.4'N	12°05.3'W
50	55°04.1'N	12°02.6'W
51	55°03.3'N	12°02.7'W

The box corer used in September, 1975 deviated slightly from the description of Hessler & Jumars as follows: a) a hinged hook rather than a friction release freed the spade arm on bottom contact of the gear and b) spring-loaded hinged steel flaps over large unscreened vents were mechanically restrained open in order to allow free flow of water through the sample box during lowering and hence a much reduced bow-wave effect on approach to the sediment surface; the flaps were allowed to close on release of the spade arm. Winch speeds and other operational details were as detailed by Hessler & Jumars (1974).

The corer was monitored acoustically using an IOS 'H'-type pinger.

The sediment surface of the recovered cores, after draining off the supernatant water, appeared to be only slightly disturbed. This usually only amounted to small surface cracks and fissures probably resulting from manipulating the heavy gear (0.7 tonnes in air empty) back on to the deck. There were usually burrow openings visible together with small ophiuroids and, on one core, a pocket of what appeared to be faecal pellets. The core depth ranged from roughly 17 - 30cm; this variation being caused in part by a slight tilting of the surface of the core. This was likely caused by the spade arm exerting a progressive lifting moment as it described its turning arc through the sediment.

The cores revealed a very marked vertical stratification in the sediment. Below a relatively soft, light brown superficial layer of calcareous pelagic ooze there was a sharp demarcation with an underlying, much harder material consisting of a very stiff greenish clay.

On this occasion it was not possible to remove the full sample box from the sampler. Consequently, the core could not be sectioned or dissected before washing.

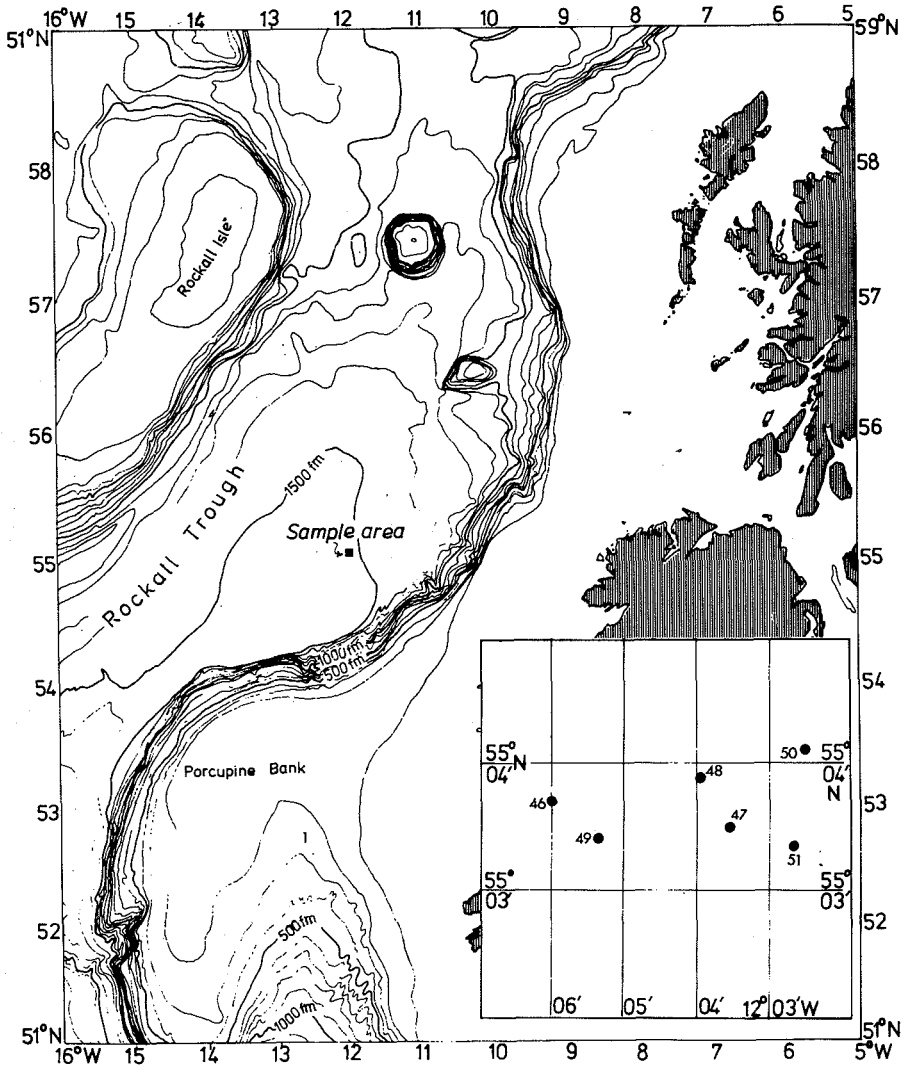

Fig. 1 Location of sample area within southern Rockall Trough. Inset map shows positions of separate core samples. Bathymetry is given in fathoms; contours drawn at 100 fm intervals.

still little-known biotope are still very few.

The present study reports on an analysis of the standing crop and community of the abyssal fauna of one small deep-sea area lying about 90 nautical miles west of the Irish mainland.

The entire core was then carefully washed through a 420μm square mesh sieve, using the elutination technique of Sanders, Hessler & Hampson (1965). Contamination of the sample with pelagic animals (especially copepods) that were present in the ship's fire hose supply used for sample washing was reduced by means of a 250μm sintered woven wire mesh industrial filter interposed in the system. The washed sample was then fixed in buffered formalin and transferred a few days later to a preservative sorting fluid buffered to pH 7.5 consisting of 2.5% formalin, 1% propylene phenoxytol, 10% propylene glycol and 86.5% deionized water. Rose Bengale was used to facilitate separation of living fauna from detrital material and to more easily separate living specimens from dead shells of animals such as molluscs, ostracods and foraminiferans.

Sorting aimed at a total extraction of the living fauna and a subsequent sorting to species level. A considerable effort was made to separate all fauna to the constituent species whether they could be identified or not. In fact, to date only a fraction of the material has been examined by taxonomic specialists. Consequently, the accuracy of sorting species will have varied with the different groups because the criteria separating species are more easily discernible, to a taxonomic generalist, in some groups than others. It is to be hoped that any undersorting will have been balanced by oversorting into species so that sample estimates of community structure based on the species abundance data obtained will not seriously be in error.

Biomass was estimated from the total fauna extracted from the samples before sorting to species. The organisms were gently blotted as a mass and air-dried on filter paper for 2 minutes before weighing. Probably because of the propylene glycol content of the preservative used, the fauna suffered little or no damage through dehydration as a result of this treatment.

BOTTOM ENVIRONMENT

Soundings taken both in the course of cruise 12B/75 and on previous cruises have suggested that the bottom topography in the sample area is flat. Observations of bottom temperature and salinity (P R Barnett personal communication) and dissolved oxygen (Ellett & Martin 1973) indicate stable conditions (2.7 - 2.8°C, 35.0‰ S, and ca. 6 $ml.l^{-1}$ dissolved O_2). Seabed photographs (Fig. 2) taken by Dr Barnett in the area of the present sampling show elongated sediment tails and slight scour marks on opposing sides of small scale features such as projecting worm tubes. The unidirectional deflection of what appears to be protruding polychaete tubes in line with the sediment tails and scour marks suggests bottom currents of several centimetres per second. Recent indications (Fig. 2B) from the deflection of short string 'streamers' attached, with a compass, to a crosswire within the camera's field of view suggest that the bottom current flow may be intermittent. No clear directionality in flow has as yet been detected from such records over the relatively short (ca. 1 min) duration of bottom contact of the camera.

It is of interest to note that Heezen & Hollister (1964) consider that traction velocities necessary for transport of deep sea sediments probably range from 4 - 60 cm/sec. Geological evidence presented by Jones, Ewing, Ewing & Eittreim (1970) and Roberts (1975) suggests that a southgoing current may be an established feature at the floor of the Rockall Trough, although their same evidence suggests that its route is mainly constrained along the western margin of the Trough. We have as yet no information on the possible presence of a tidal component.

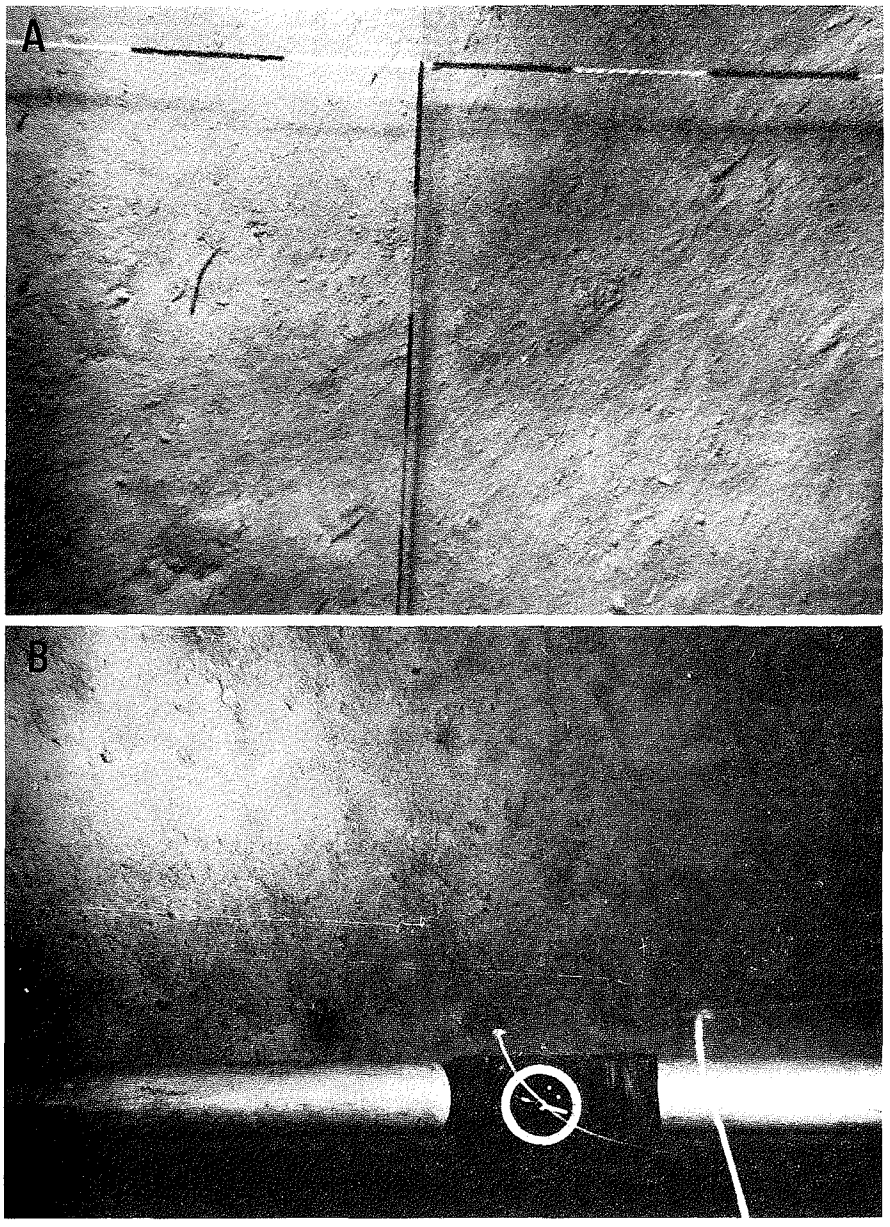

Fig. 2 The bottom at the sample area. A shows a view with the camera looking straight down onto the sediment surface. The crosswires visible are marked at 10cm intervals. B shows another overhead view. The limp state of the string 'streamers' visible do not suggest any appreciable bottom current. The compass indicates that N. is towards the left hand margin of the photograph.

Table 2 Faunal composition and standing crop in six 0.25m^2 box cores (listed as 'Stations 46 - 51') from the southern Rockall Trough

	Station 46		47		48		49		50		51	
Macrofaunal taxa	N	S	N	S	N	S	N	S	N	S	N	S
Porifera	✓	1	✓	2	✓	2	✓	2	✓	1	✓	1
Cnidaria	✓	2	✓	4	✓	3	✓	3	✓	3	✓	3
Polychaeta	261	42	291	62	252	52	294	56	284	46	118	36
Sipuncula	-	-	3	2	4	4	9	4	3	3	4	3
Nemertina	12	2	25	5	14	5	34	3	5	3	-	-
Pogonophora	-	-	1	1	-	-	-	-	-	-	-	-
Tanaidacea	44	15	53	12	45	18	40	15	38	13	19	8
Isopoda	25	10	13	8	20	13	26	13	19	8	8	5
Amphipoda	8	4	13	8	18	6	16	7	17	5	5	4
Cumacea	1	1	2	2	1	1	3	3	1	1	1	1
Other Crustacea	-	-	-	-	-	-	1	1	-	-	-	-
Aplacophora	8	5	3	2	5	2	3	2	3	1	2	1
Bivalvia	37	9	31	10	64	10	53	11	32	9	33	9
Gastropoda	3	2	3	2	3	3	9	3	1	1	2	2
Scaphopoda	13	4	11	3	33	3	23	4	5	3	4	3
Ophiuroidea	6	2	2	1	32	1	12	1	-	-	12	1
Asteroidea	-	-	-	-	2	1	1	1	1	1	-	-
Echinoidea	-	-	-	-	2	2	1	1	1	1	-	-
Holothuroidea	-	-	-	-	1	1	-	-	1	1	-	-
Ectoprocta	-	-	-	-	-	-		1	✓	1	✓	1
Ascidiacea	-	-	-	-	-	-	1	1	-	-	-	-
Total N	431		451		496		526		412		208	
Total N.m^{-2}	1724		1804		1984		2104		1648		832	
Total S		99		124		127		132		101		78
Total S.m^{-2}		396		496		508		528		404		312
Meiofaunal taxa												
Foraminifera	-	-	-	-	-	22	-	-	-	-	-	-
Nematoda	301		200		198		231		221		127	
Copepoda	11	7	4	3	10	3	8	5	6	4	1	1
Ostracoda	-	-	3	2	5	1	3	1	12	2	5	2
Total N	312		207		213		242		339		133	
Total W/W (g) excluding forams	1.18		0.64		0.82		0.92		1.54		0.40	
Total W/W Foraminifera	NM		NM		0.13		0.28		0.27		0.53	

Macrofaunal taxa	Mean N*	Mean S*	%N*	%S*	Total S*
Porifera		1.6		1.4	
Cnidaria		3.6		2.6	
Polychaeta	276.4	51.6	59.6	44.2	105
Sipuncula	3.8	0.4	1.1	2.2	
Nemertina	18	3.6	3.9	3.1	
Pogonophora	0.2	0.2		0.2	
Tanaidacea	44	14.6	9.5	12.5	
Isopoda	20.6	10.4	4.5	8.9	
Amphipoda	14.4	6.0	3.0	5.1	
Cumacea	1.6	1.6	0.4	1.4	
Other Crustacea	0.2	0.2		0.2	
Aplacophora	4.4	2.4	0.9	2.0	
Bivalvia	43.4	9.8	9.3	8.4	18
Gastropoda	2.4	2.2	0.9	1.9	
Scaphopoda	17	3.4	3.7	2.9	
Ophiuroidea	10.4	1.0	2.2	0.8	
Asteroidea		0.6	0.2	0.5	
Echinoidea	0.8	0.8	0.2	0.7	
Holothuroidea	0.4	0.4	0.1	0.3	
Ectoprocta		0.4		0.5	
Ascidiacea	0.2	0.2	0.04	0.2	
Total N	463.2				
Total N.m^{-2}	1852.8				
Total S		116.6			
Total S.m^{-2}		466.4			
Meiofaunal taxa					
Foraminifera					
Nematoda	230				
Copepoda	7.8	4.4			
Ostracoda	4.6	1.2			
Total N	262.6				

Mean W/W(g) excluding forams = 0.92 ($\equiv$ 3.67 g m^{-2})

N = number of individuals, S = number of species, %N and %S = percentage of total N or total S. ✓ designates a positive occurrence of taxa where species could not be enumerated as individuals. NM = not measured. W/W = wet weight. Owing to taxonomic difficulty the total number of species occurring through the sample series was enumerated only for polychaetes and bivalves.

*excluding station 51

RESULTS AND DISCUSSION

Standing Crop

The total numbers of the individuals of the various taxonomic groupings, together with total wet-weight values per core are given in Table 2. Agglutinating forms of the Foraminifera were numerically most numerous in the samples. However, because of difficulty in many cases in identifying living plasma with any great degree of certainty, their biomass was measured separately. The values given should be regarded as approximate until a more certain separation of living from dead tests is achieved.

Although not numerous, there were present also several small clusters of anastomosing tubules tentatively identified as belonging to the new rhizopod subclass Xenophyophoria (Tendal 1972, Hessler 1974).

Published data on deep sea standing crop are summarised in Zenkevitch, Filatova, Balyaev, Lukyanova & Suetova (1971), Menzies, George & Rowe (1973), Rowe, Polloni & Horner (1974) and Thiel (1975). Although much higher values than those of the present investigation have been recorded (e.g. Kusnetzov 1960) from the N Atlantic, these have come from depths less than 1500m. However, it is difficult to make close comparisons with other published data because of (a) differences in sampling gear and screen size and (b) because most of the values given tend to be derived from single samples, the sample variance is unknown.

In general, it seems that standing crop is high compared to data obtained from similar depths elsewhere. For example, the values of 3.67 $g.m^{-2}$ non-foraminiferal wet-weight biomass and 1853 macrofaunal individuals m^{-2} that were obtained in the present study are considerably more than the largest values obtained by Rowe et al. (1974) at comparable depths on the continental rise of N America. However, the samples of Rowe et al. were taken with a deep-sea anchor dredge (Sanders, Hessler & Hampson 1965) or $0.5m^2$ van Veen grab. The sampling efficiency in deep water of the van Veen compared to box corers is unknown; however, Smith & Howard (1972) and Beukema (1974) claim the $0.06m^2$ USNEL and Reineck box corers to be considerably more efficient than grabs on shallow hard sand. The anchor dredge may be less efficient than either grab or box corer. In the sampler comparisons of Dickinson & Carey (1975) and Gage (1975) the anchor-box dredge (which is essentially similar to the Sanders anchor dredge) was found to yield samples defficient in vagile Crustacea (mostly amphipods) and bivalves compared to grab samples. It is also of interest to compare the results (Table 3) obtained by the present anchor-box dredge samples on positions very close to those of the present study. Assuming a 10-cm sampling depth, the fauna extracted give an estimate of non-foraminiferal standing crop at least half that from the present large box cores. Sanders, Hessler & Hampson (1965), however, give values, derived from their anchor-dredge samples of the range of standing crops, in terms of numbers of individuals to be expected along their Gay-Head Bermuda transect, that are considerably in excess of those given by Rowe et al. (1974) from the same area and over a comparable depth range (2500 - 2870m), but which are still less than the values obtained in the present study.

TABLE 3 Wet-weight biomass of total fauna excluding Foraminifera from two anchor-box dredge hauls (Stations 44 and 45) at positions close to box core samples

Station	44	45
Date	6 Sept. 1975	
Position	55°03.5'N 12°01.5'W	55°03.8'N 12°03'W
Depth (m)	2875	2875
Vol. sediment (l)	ca. 50	ca. 50
Biomass (g)	1.03	1.21
Biomass.m^{-2} (approx.)	2.06	2.42

Unfortunately, no other wet-weight biomass data from box core samples are known to the present author, although Hessler & Jumars (1974) and Jumars (1975, 1976) give data on faunal densities in the central N Pacific and Californian continental borderland, respectively. These authors estimate macrofaunal abundance (numbers of individuals) from samples taken with a 0.25m^2 USNEL box corer similar to that used in the present study. Although a 297μm mesh sieve was used by Hessler & Jumars rather than the 420μm of the present study, values exceeding their mean value (from ten samples) by more than 16 times, were obtained in the present study. On the other hand, Jumars (1976) gives values from 5 box cores of macrofaunal density that are quite similar to those of the present study. Hessler & Jumars (1974) relate the low benthic standing crop in the central N Pacific to the unproductive (100 mg $C.m^{-2}$ day^{-1}, Koblents-Mishke 1965) nature of the euphotic zone. Considerably higher standing crops would be expected both in the Californian continental borderland and the Rockall Trough since both are situated in or near areas of regional upwelling with consequently relatively high (250 - 500 mg $C.m^{-2}$ day^{-1}, Koblents-Mishke, Volkovinskii, & Kabanova (1968) surface productivity.

Average size of fauna

As reported by other workers (see Thiel 1975), the average size of individual specimens of taxa normally considered as macrofaunal (see McIntyre 1969) seems minute compared to shallow water specimens. For example, the total macrofaunal standing crop of the soft mud in Loch Creran, Argyllshire, Scotland, was estimated from four 0.1m^2 van Veen grab hauls at 169.8 $g.m^{-2}$ from 4360 individual specimens, giving a biomass/number of individuals ratio of 0.039, an order of magnitude difference when compared to the ratio of 0.002 for the six abyssal box cores.

It was also apparent that many individuals of taxa normally considered meiofaunal did not seem to follow this trend. For example many of the Nematoda which were numerically very conspicuous in the box cores were at least an order of magnitude larger than many of the traditionally macrofaunal specimens such as isopods. However, it remains likely that most of the Nematoda component was lost in washing through the 420 micron sieve used. Many of the Foraminifera were also of a relatively large size. Indeed the putative Xenophyophoria specimens were several millimetres in diameter.

Faunal composition and its proportional representation in the cores

The identities of the species collected and their proportional representation (Table 2) showed little variation between cores. Similarities are apparent when the percentage representation of the major taxonomic groups is compared (Table 4) with comparable data of Hessler & Jumars (1974) from the central N Pacific gyre. Hessler & Jumars compare their values with data obtained previously from the Gay Head-Bermuda transect in the N W Atlantic (Sanders, Hessler & Hampson 1965), but because these faunal data are derived from anchor-dredge samples there must remain some doubt of their accuracy as community estimates where the more vagile elements are concerned. However, it does seem safe to conclude that the present samples more closely resemble the values (summarised in Hessler & Jumars (1974), Table 4) from samples taken deeper rather than shallower than 4000m depth along the Gay Head-Bermuda transect. Because, however, the present taxon percentages, even if not showing a statistically significant difference from those from the abyssal central N Pacific, do in fact show most resemblance to the faunal composition reported by Sanders et al (1965) on the lower continental slope and abyssal rise (depth ranges 823 - 2086m and 2500 - 2870m, respectively).

TABLE 4 Faunal composition of southern Rockall Trough compared to central N Pacific.

Taxon	Pacific	Rockall
Polychaeta	55.1	59.6
Oligochaeta	2.1	-
Sipuncula	0.4	1.1
Nemertina, Pogonophora	-	3.9
Tanaidacea	18.4	9.5
Isopoda	6.0	4.5
Amphipoda	-	3.0
Cumacea	-	0.4
Other crustacea	-	0.1
Aplacophora	0.4	0.9
Bivalvia	7.1	9.3
Gastropoda	0.4	0.9
Scaphopoda	2.5	3.7
Ophiuroidea	0.7	2.2
Echinoidea	-	0.2
Asteroidea, Holothuroidea	0.4	0.2
Bryozoa	2.0	0.1
Brachiopoda	0.7	-
Ascidiacea	1.1	0.1

Values are taxon percentage contributions to the mean total number of macrofaunal individuals in the sample units of each study. Percentages whose differences are not significant at the 95% confidence level are jointly underlined.

As found by other workers using relatively fine screens for sample washing, the polychaetes comprise the single most abundant group of fauna. These have been sorted into at least 31 families and 105 species. The best represented were, in order of relative abundance, the Spionidae (13 species) followed by the Opheliidae (12), the Cirratulidae (9) and the Paraonidae (6). The second most abundant group were the Crustacea which were also represented by numerous species. In general, the relative proportions of the dominant crustacean subgroups, the tanaids, isopods, amphipods and cumaceans, fell within the range given by Sanders et al. (1965) for the abyssal rise of the N W Atlantic.

Unlike the other faunal components, the numerical proportion of protobranchs (80.6%) to eulamellibranchs (19.4%) showed most resemblance to samples from the abyssal plain (Sargasso Sea) area of the Gay Head-Bermuda transect. These results from the Rockall Trough support the contention that while the standing crop of the deep-sea depends mainly on local hydrographic conditions that control trophic input, the faunal composition at higher taxon level may be roughly predicted on the basis of depth.

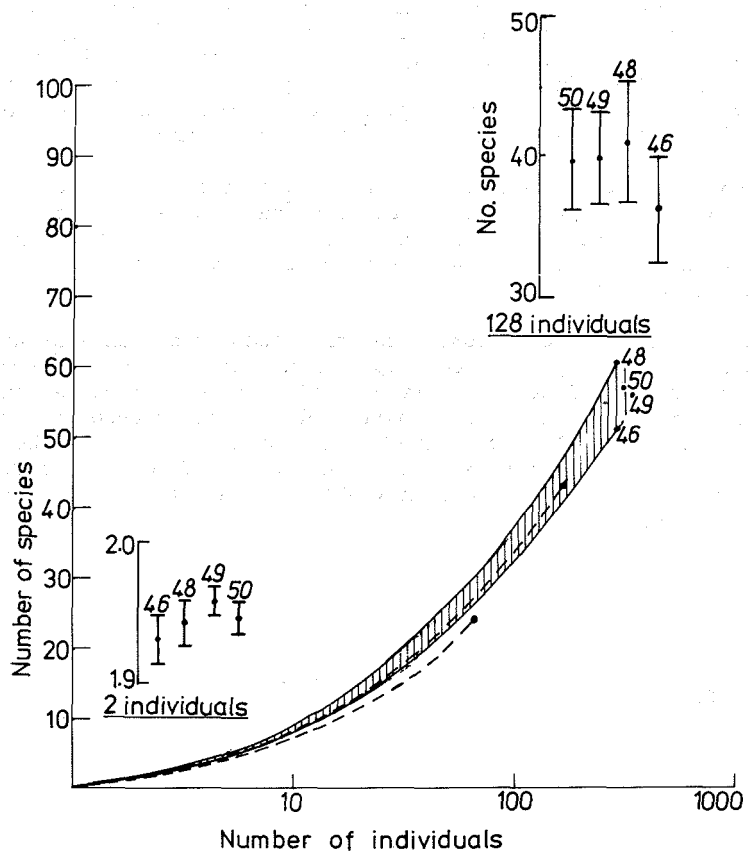

Fig. 3 Expected species diversity for four box-core replicates (Stations 46, 48, 49 and 50). All fall within shaded area of curve. Sampling errors for 2 and 128 individuals are given as vertical bars each two standard deviations above and below the estimated number of species. The two broken lines represent curves of expected species diversity from two anchor-box dredge samples taken from the box-core sampling area.

Faunal diversity

Although data on deep-sea benthic diversity are few, it is of considerable interest to compare values obtained from different areas, particularly in view of (a) the somewhat unexpectedly high deep-sea diversities reported in the last 15 years and (b) the current controversy (Slobodkin & Sanders 1969, Dayton & Hessler 1972, Grassle & Sanders 1973, and Jumars 1975, 1976) on the factors controlling benthos diversity.

Faunal diversity in the present investigation is expressed graphically (Fig. 3) an interpolation of the number of species to be expected amongst smaller numbers of individuals drawn randomly, without replacement, from the total sample. It is being better recognised by benthic workers and others that such

a description of species diversity is to be preferred to the many single point estimator diversity measures, which have unsatisfactory sampling properties especially when the sample size is small (Sanders 1968, Hurlbert 1971, Smith & Grassle in press). The expected species curves indicate a slightly lower benthic diversity in the Rockall Trough compared to the central N Pacific (Hessler & Jumars 1974) and the San Diego Trough (Jumars 1975). Expected species curves in the two studies slightly exceed those for the Rockall Trough despite their being derived from the polychaete data only.

Curves generated (Fig. 3) from two anchor-box dredge samples (420µm sieved) from positions close to or within the box-core sampling area closely resemble those from the box cores. This may indicate that at least for the polychaete/bivalve fraction results from anchor dredging will not seriously underestimate species diversity.

Smith & Grassle, who should be consulted for a theoretical understanding of expected species diversity, have developed an unbiased estimator of sampling variance based on a multinomial sampling model. The estimated variance may itself be partioned into that due to multinomial sampling error and that caused by spatial variability over the total sampling area. For the present samples, Fig. 3 shows that for each core the 95% confidence limits for expected species diversity are generally all less than the total range of values for the cores.

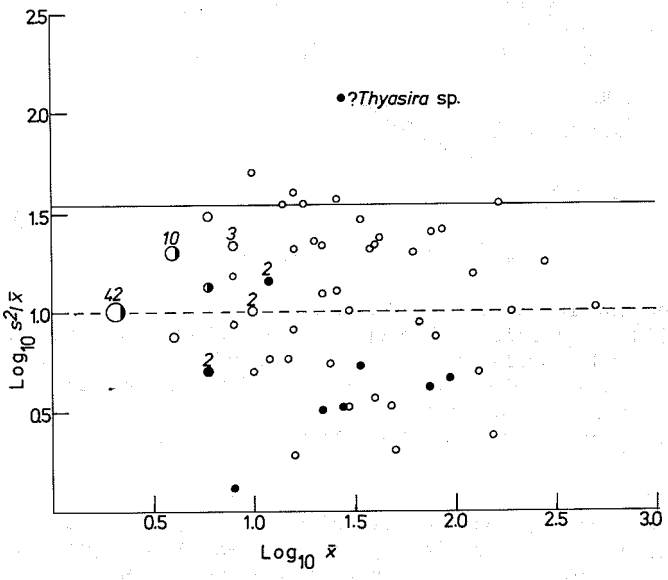

Fig. 4 Logarithm of 'coefficient of dispersion' ($\underline{s}^2/\bar{\underline{x}}$) plotted against logarithm of mean number of individuals ($\bar{\underline{x}}$) per core for all polychaete (open circles) and bivalve (filled circles) species encountered in box-core samples. Numerals denote number of species in excess of one giving identical plots. Upper horizontal line denotes upper 95% confidence limit for Poisson distribution while dotted line denotes the Poisson expectation where $\underline{s}^2 = \bar{\underline{x}}$.

As has been pointed out by Jumars (1976) the resolution of spatial scales of deep-sea benthic diversity will likely clarify the issues involved concerning the possible causative mechanisms for the high diversity observed, and also help to determine whether the diversities recovered by towed samplers such as deep-sea trawls or dredges are artifactually enhanced by traversing a mosaic of patches, each at its individual and less diverse stage of succession following a previous disturbance event. Results from other box-core sampling (Hessler & Jumars 1974, and Jumars 1975, 1976) have likewise shown low sample variance. Jumars' (1975) results indicated that the characteristic scale of these controlling processes would be that approaching the size of single macrofaunal individuals, and hence not detectable between whole large box-core samples taken at the scale of the present sampling. Analysis of individual between-core dispersions (Fig. 4) from the present sample series supports such a conclusion: for only a modest number (11 out of 105 species) did the values of the 'coefficient of dispersion' $s^2/\bar{x}$ exceed the upper 95% confidence level of the Poisson expectation. This result may be compared to a shallow west Scottish sealoch where 41 - 56% of species showed a significant aggregation at a scale of 0.1km (Gage 1973).

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