An introduction
to a sample time-series
of abyssal macrobenthos:
methods and principle
sources of variability

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ABSTRACT

A sequential series of ten large samples of deep-sea macrobenthos, spanning three years, was obtained using the epibenthic sled from a 2 900 m deep permanent station in the southern Rockall Trough (Northeast Atlantic). As an introduction to later studies of dynamic aspects of the populations of the highly diverse community sampled, the physical characteristics of the bottom environment, as far as they are known, and the sampling methods, are described.
In order to assess the comparability of the large samples obtained, the data set, consisting of numbers of different taxa, was simplified using correspondence analysis. Methodological variability in the form of the degree of sample washing during gear recovery and possibly also the speed of towing the bottom sampler over the bottom were the inferred sources of considerable variation in the series. However, the dominant source of variation, unexpectedly, was biological, and derived solely from a massive annual recruitment in the brittlestar *Ophiura ljungmani*.

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RÉSUMÉ

Prélèvements de macrobenthos abyssal,
répartis en séries sequentielles :
Méthodes et origines de la variabilité

Des prélèvements du benthos abyssal ont été effectués à une station permanente située par 2900 m de profondeur au sud du bassin de Rockall, dans le nord-est de l'océan Atlantique. Une drague épibenthique qui retient des volumes importants de sédiment a été utilisée. Ces prélèvements, au nombre de dix, ont été répartis en une série séquentielle, couvrant une période de 3 ans. Les caractéristiques physiques du fond sont décrites avec un maximum de détails, de même que les méthodes d'échantillonnage, comme introduction à des recherches futures à propos de la dynamique de ces peuplements très diversifiés.
Dans un but de comparaison, l'information contenue dans les prélèvements a été résumée au moyen de l'analyse des correspondances; ce qui a permis de mettre en évidence qu'une bonne part de la variabilité des résultats est liée à la vitesse de remorquage de la drague ainsi qu'à l'importance du lavage de l'échantillon au cours de la remontée. Toutefois, la raison première des variations est d'origine biologique; elle est due à l'importance inattendue du recrutement annuel de l'Ophiure, *Ophiura ljungmani*.

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INTRODUCTION

Our understanding of the composition and structure of the deep-sea benthos has been much expanded within the past two decades, yet we still have only meagre knowledge of the nature and rate of biological activity at the benthic boundary in the deep sea. Such information is not easily obtained, and although some recent studies have yielded a few data on short-term rates by means of direct measurements of community meta-

bolism and sediment colonization (Smith, Teal, 1973; Grassle, 1977; Smith, 1978), these approaches do not readily lend themselves to study of longer-term processes such as population growth and reproduction.

Certain deductions on these processes are possible by examining population size-structure in large samples (e. g., Schoener, 1968; Hessler, 1970; Cherbonnier, Sibuet, 1972; Gardiner, 1975; Grassle, Sanders, 1973; Rokop, 1974, 1977 a, 1979; Rex et al., 1979; Thurston, 1979; Aldred et al., 1979). The potential of such an approach in estimating growth and recruitment usually is limited to indirect measurements since only in the case of Rokop's studies was it possible repeatedly to sample deep-sea populations in a time series. This is because in the past most deep-sea sampling has been constrained to spatial rather than temporal sampling designs. Comparisons of such samples in order to assess growth and reproduction, even if collected from different times of the year, may be unrewarding since it is not possible to be certain that the comparison is applied to the same, or to reproductively isolated, populations.

On available data, Rokop (1974, 1977 a, b, 1978) suggests that year-round reproduction is the common pattern in the deep-sea benthos, while Thiel (1975) speculates generation times being one or two orders of magnitude longer than in shallow water.

The present study attempts to study such processes in populations of deep-sea macrobenthos by obtaining a long-term, sequential series of large samples of the populations present at one fixed location.

We sampled a site deeper than the 1 240 m deep location studied by Rokop (1974) in order to eliminate the possible presence of populations extending from the continental shelf and to provide a depth more representative of deep-sea basins. Furthermore, our observations extend over a period of 3 years, rather than the single year of Rokop's study, in order to study processes such as population growth and mortality, as well as reproduction.

In introducing this study of a sample time-series from a deep-sea benthic community, this paper also addresses certain questions that may crucially affect the interpretation of the results of later study of reproduction and growth of the component populations. Of these, the first asks whether the physical and biological environment of the sample station is representative of the deep-sea. The two remaining problems are mutually dependent in seeking, first, to assess the comparability of the samples by identifying likely sources of methodological variation and, second, in detecting possible gross biological changes in the fauna when considered in terms of the representation of major taxa in the samples.

STUDY AREA

The study site was located as a Permanent Station in soundings of around 2 900 m in the southern Rockall Trough and centred on 54°40′N, 12°16′W (Fig. 1).

Rockall Trough (Fig. 1) is shallower (1 200-3 000 m deep) than the 3 932 m mean depth of the Atlantic Ocean excluding coastal seas (Shepard, 1948), but it was chosen for this investigation because physical properties, circulation and geological structure have been intensively studied (Ellett, Martin, 1973; Roberts, 1975; Lonsdale, Hollister, 1979).

Precision echo soundings taken in the course of the sampling indicate a flat bottom with a slight trend to increase in depth from NE to SW. Evidence from large scale photographs taken from a deeply-towed instrument package in the southern Rockall Trough (Lonsdale, Hollister, 1979) shows a streamlined microtopography of the sediment surface and, in places, a high bottom-water turbidity. Direct measurements of bottom currents at the Permanent Station are not presently available. However, tidal flow of 10 cm.sec^{-1}, or more, may be inferred from measurements elsewhere in Rockall Trough (Lonsdale, Hollister, 1979; D. Edelsten, D. J. Ellett, (pers. comm.)

Observations of standard hydrographic parameters for the bottom water were not made at the time of sampling, but published data (Ellett, Martin, 1973; Lonsdale, Hollister, 1979) and unpublished data (D. J. Ellett, personal communication) indicate that temperatures range from 2.95 to 3.16°C, and salinities from 34.94 to 34.97°/$_{oo}$ with dissolved oxygen content of about 6 ml.l^{-1}.

Figure 1

Chart showing sampling area (hatched square) and the position of Station 6 (cross). Inset chartlet shows sampling area and the direction and probable track on the bottom of the sled hauls comprising the time series. Bathymetry in fathoms (fm) where 1 fm = 1.829 m.
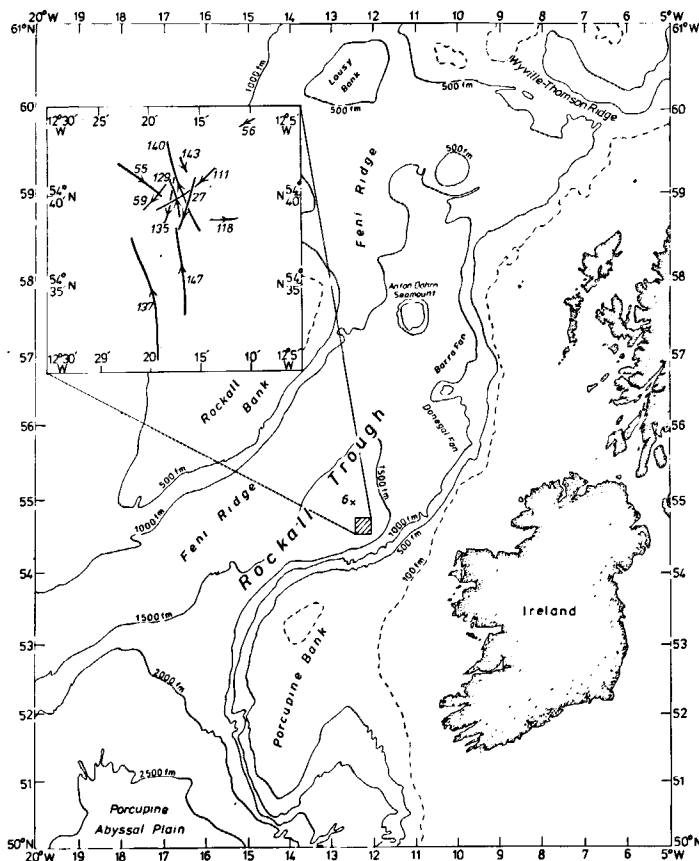
Table 1
Granulometry of superficial sediment at the Permanent Station.

	Sand								Silt						Clay	
Phi unit	0.5	1.1	1.5	2	2.5	3	3.5	4	4.5	5	5.5	6	7	8	9	10
μm	1000-710	710-500	500-351	351-250	250-177	177-125	125-88	88-62	62-44	44-31	31-22	22-16	17-7.8	7.8-3.9	3.9-1.9	1.9-1.0
Percent by weight	0.04	0.25	1.01	3.2	5.3	9.6	3.2	4.8	7.5	5.6	8.3	4.9	7.3	6.7	8.3	9.3
	(wet sieving)								(pipette analysis)							

Gage (1977) provides some observations of the sediment in the vicinity of the Permanent Station. The present authors subsequently have analysed some of the physical and chemical properties of the superficial layer from samples taken by box coring (see Gage, 1977) at 54°37'N, 12°31'W in 2916 m depth. The sediment contained about 67% by weight of calcium carbonate, apparently derived mostly from pelagic Foraminifera, and a very small content of organic carbon [0.47% determined by the wet oxidation method of Gaudette et al., (1974)]. Results (Table 1), from sediment particle-size analysis compare well with those from stations of roughly equivalent depth along the Gay Head-Bermuda transect (Sanders et al., 1965) in the Northwest Atlantic.

The proximity of the Permanent Station to the Irish mainland (about 160 km) and to the shelf edge of the Irish continental margin (about 55 km) might suggest. a possible coastal or terrigenous influence in the shape of transport of mineral and organic particulates to the adjacent deep-sea floor. However, recognisably extraneous organic debris such as macroalgal fragments, grass and leaves have never been found in the present authors' examination of many epibenthic sled or Agassiz trawl hauls from the Rockall Trough.

METHODS

The samples were taken using the Woods Hole Oceanographic Institution pattern epibenthic sled (Hessler, Sanders, 1967) fitted with either a 1.2 or 2 m long extension bag fabricated from 0.5 mm mesh monofilament nylon netting and protected by canvas aprons secured to the after edges of the sled. Loss of faunal elements caused by washing out through the mouth of the sampler during gear recovery was reduced by means of a spring-loaded gate (constructed to drawings kindly made available by Dr. H. L. Sanders of Woods Hole Oceanographic Institution) fitted to the mouth of the sled that was held open during deployment. The gate was closed before gear recovery by use of a precision timer-controlled compact release (Williams, Fairhurst, 1977) that electrically actuated a pressure squib (Holex, Inc., Hollister, California, Model 6100).

In order to ensure we obtained a good sample on the soft ooze encountered it was found important to set the hinged biting edges of the sled so that their leading edges were parallel, or even slightly converging, so as not to cut into the sediment surface (Gage, 1975). The bottom haul was standardised at 1 hour, with the ship steaming at about 1 knot. However, the actual distance of bottom haul varied considerably because of the difficulty in towing slowly enough over the bottom when the tow direction coincided with the probable directions of both surface and bottom drift. This is evident from the tracks of the sled on the bottom, calculated from the ship's position (using Decca and Satellite navigation fixes) and wire payout and tension, that are shown inset in Figure 1. Other details of the hauls made in connection with the present investigation are listed in Table 2.

Subsequent treatment of the muddy material in the hauls followed the elutriation procedure described by Sanders et al., (1965) using a 420 μm mesh aperture sieve. Sea water from the ship's fire hose supply was filtered using an industrial filter cartridge with 40 μm apertures in order to remove plankton. Care was taken to standardise the sieving technique as much as possible. The residue remaining on the sieve was fixed in 4% formalin in sea water and buffered to pH 7.5 with borax.

In order to reduce the labour of sorting the usually large and faunally rich samples, and also to render the smaller hauls more easily compared to the larger ones, the latter were subsampled. This was accomplished using a water-filled plastic measuring cylinder as a sedimentation column, fitted with a divided collector bucket.

The samples were then sorted into 44 taxa. Of these only 24 occurred in numbers justifying numerical comparison between samples, or easily enumerated as individual organisms. These taxa hence excluded colonial forms such as Porifera, Hydroidea and Bryozoa and rarely occurring taxa such as Scyphozoa, Madreporaria, Pennatulacea, Oligochaeta, Priapulida, Phoronida and Crinoidea. The 24 taxa (listed in Table 2) also exclude those (Foraminifera, Nematoda, Ostracoda and Harpacticoidea) which on taxonomic grounds are considered as belonging to the permanent meiofauna (McIntyre, 1969). The remaining fauna would normally be considered as constituting the macrofauna although a few species, such as Ophiomusium lymani Wyville Thomson and Neolithodes grimaldii Milne Edwards and Bouvier, that might be considered as part of the megafauna, also occurred in the samples.

SAMPLE COMPARISON

In order to provide some indication of the numbers of species present amongst the major taxa enumerated in this comparison, data from a complete sorting of Station 6 are summarised in Table 3. Although not taken within the area delimited as the Permanent Station,

Table 2

Details of epibenthic sled hauls from the Permanent Station, and nearby (Station 6), that are considered in the present paper. Only Stations 55-147 constitute the series taken at roughly quarterly intervals; Station 27 while on the Permanent Station was taken 2 years previously. Numbers of individual animals are given only for the most numerically important taxa.

Station No.		6	27	55	56(4)	56(7)	59	111	118	129	135	137	140	143	147
Date		2 July 1973	3 Nov. 1973	17 Nov. 1975	1 March 1976		21 June 1976	22 Oct. 1976	28 Jan. 1977	7 Apr. 1977	7 Aug. 1977	22 Feb. 1978	13 Apr. 1978	14 Apr. 1978	2 June 1978
Mean depth (m)		2900	2880	2878	2886		ca. 2900 c	2886	2910	ca. 2900 c	2900	2900	2912	2892	2921
Sea conditions		Moderate	Moderate	Heavy	Heavy		Moderate	Heavy	Heavy	Moderate	Good	Moderate	Moderate	Moderate	Moderate
Mouth closing gate		Not fitted	Not fitted	Failed	Operated		Operated	Operated	Operated	Failed	Operated	Failed	Operated	Operated	Operated
Proportion b of total catch sorted		All	$\frac{1}{8}$	All	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	All	All	$\frac{1}{8}$
Taxon	Taxon No.	(Nos. of animals)													
Actinaria	1	243	6	49	11	9	3	6	5	1	1	7	7	9	2
Platyhelminthes	2	5	–	–	–	–	–	1	–	–	–	–	–	–	–
Nemertea	3	100	46	2	2	5	2	–	4	14	4	24	9	41	57
Hirudinea	4	10	–	1	–	–	–	–	–	–	–	–	–	–	–
Polychaeta	5	3406	574	97	282	266	439	104	845	1050	962	1067	666	1300	1412
Sipuncula	6	198	27	8	14	6	6	5	–	20	2	10	42	42	34
Leptostraca	7	1	–	–	–	–	–	–	–	5	3	1	1	2	3
Cirripedia	8	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Cumacea	9	547	130	39	84	65	282	25	54	281	407	626	203	38	989
Tanaidacea	10	309	83	29	45	38	221	7	45	179	194	320	72	97	555
Isopoda	11	705	182	79	65	68	253	23	69	330	516	599	249	102	1319
Amphipoda	12	713	182	33	59	64	159	29	29	401	280	536	179	96	741
Eucarida	13	2	–	1	–	–	–	–	–	1	–	–	–	–	–
Pycnogonida	14	–	–	–	3	10	23	1	5	21	58	43	9	1	52
Aplacophora	15	86	12	1	7	13	21	5	9	29	92	36	28	37	67
Gastropoda	16	110	21	116	42	18	32	21	9	39	90	119	367	39	115
Scaphopoda	17	777	172	231	103	101	268	33	59	292	598	335	335	105	328
Bivalvia	18	14908	875	1946	568	528	658	308	154	741	1381	1525	3318	585	1370
Brachiopoda	19	95	18	2	3	5	1	1	1	10	3	3	2	1	2
Asteroidea	20	838	41	33	25	30	21	26	11	38	35	53	514	12	46
Ophiuroidea	21	3048	176	855	281	259	2883	182	81	492	17466	762	1056	118	11134
Echinoidea	22	76	4	–	5	3	10	2	4	8	11	9	7	5	57
Holothuroidea	23	1929	181	218	143	118	79	75	24	120	62	201	148	30	169
Ascidiacea	24	105	25	8	–	2	3	1	–	2	8	13	6	10	16

a Sea conditions were assessed from ship's log entries of estimated wave height. b Part samples were obtained by subsampling as described in text. c Estimates only owing to echo-sounding deficiencies.

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Table 3

Numbers of species and individuals of the numerically most important taxa sorted from Station 6.

Taxon	Estimated No. Species S	No. individuals N	Percent of total N [a]	Percent of total S [a]
Actinaria	6	243	0.86	1.81
Platyhelminthes	1	5	0.02	0.30
Nemertea	3	100	0.35	0.91
Hirudinea	2	10	0.04	0.60
Polychaeta	81	3 406	12.07	24.47
Sipuncula	6	198	0.70	1.81
Leptostraca	1	1	< 0.01	0.30
Cirripedia	1	1	< 0.01	0.30
Cumacea	20	547	1.94	6.04
Tanaidacea	15	309	1.10	4.53
Isopoda	58	705	2.50	17.52
Amphipoda	43	713	2.53	12.99
Eucarida	2	2	0.01	0.60
Aplacophora	19	86	0.30	5.74
Gastropoda	19	110	0.39	5.74
Scaphopoda	6	777	2.75	1.81
Bivalvia	21	14 908	52.84	6.34
Brachiopoda	1	95	0.34	0.30
Asteroidea	1	838	2.97	1.21
Ophiuroidea	6	3 048	10.80	1.81
Echinoidea	3	76	0.27	0.91
Holothuroidea	10	1 929	6.84	3.02
Ascidiacea	3	105	0.37	0.91
TOTAL [a]	331	28 212		

[a] Totals refer only to the taxa listed

but from a position (Fig. 1) nearby (subsequently abandoned as the study site following loss there of the towing warp on a later deployment), it is believed these data are representative of the remaining samples. The remaining samples of this comparison were taken at roughly quarterly intervals from November 1975 until June 1978. A single sample taken on the Permanent Station in November 1973 is also included for comparison over a longer time interval.

Since in most cases one or more subsamples only of the total haul were sorted, it was necessary in comparing the values listed in Table 2 and shown diagrammatically in Figure 2 to estimate the variance contributed by subsampling. Application of a t-test to the two subsamples of Station 56 shows ($t = 2.00$ for 18 df) that subsampling probably did not contribute significantly to the observed variability. Moreover, comparison of two sled hauls (Stations 140 and 143) that were taken on consecutive days of the same research cruise show as much difference in terms of percent taxon representation as that displayed between any other samples.

Although a high species richness was apparent, but is as yet unquantified, in the time-series samples it was also clear from preliminary examination that there was considerable variation between hauls in terms of the abundance of one species of ophiuroid, *Ophiura ljungmani* (Lyman). Closer investigation of this species showed that the numerical variation was entirely caused by a summertime recruitment of juveniles (Tyler, Gage, 1980).

The other component species of the major taxa listed in Table 2 remain incompletely sorted in the sample time-series. However, there is as yet no indication of marked differences between samples in terms either

of the ratio of individuals to species comprising each taxonomic grouping, or from seasonal recruitment of a scale approaching that of *Ophiura ljungmani*, amongst any other taxa sorted. Therefore it seemed likely that the residual variation in numbers and proportions of non-ophiuroid fauna was largely caused by technical aspects of the sampling operation.

Two trends seem to emerge from a comparison of the relative proportions of non-ophiuroid taxa present in the samples (Fig. 2). The first of these is an apparently reciprocal relationship between the numbers of Bivalvia and of the peracarid crustaceans Tanaidacea, Isopoda and Amphipoda: where bivalves are numerous peracarids are proportionally fewer, and vice versa, while the proportionality of other taxa,' such as asteroids and holothurians remains less affected. The second trend appears to be towards a marked enhancement of the polychaetes in proportion to all other taxa.

In order better to define these relationships the technique of multivariate ordination was applied to the data (without *Ophiura ljungmani*). The attributes of the method applied, Correspondence Analysis (Benzecri, 1969; Hill, 1973, 1974) provide a powerful tool for the analysis of benthic taxon/sample data sets (Chardy, Glemarec, Laurec, 1976).

Figure 2

Isometric histograms comparing the percent representation of taxa (see Table 5 for listing of faunal entities identified by each number) in the samples of the time series (Stations 27-147) and Station 6 (heavy stipple). The two subsamples (Nos. 4 and 7) of Station 55 are shown with a light stipple. In order to simplify the comparison, the less abundant taxa listed in Table 2 are omitted.
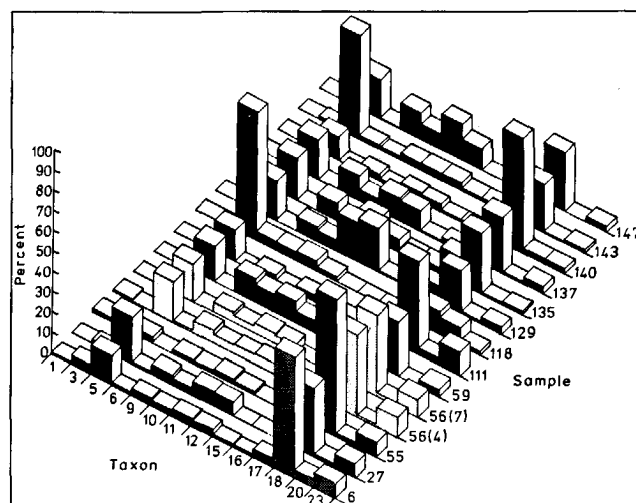

The results for the first two eigenvectors are shown in Figures 3 and 4. The three clusters of samples separated distinguish (*a*) samples rich in the various peracarid crustacean taxa, together with the Leptostraca and Pycnogonida, while relatively poor in bivalves, brachiopods and asteroids; (*b*) those samples showing an opposite relationship; (*c*) a small cluster comprising Stations 118 and 143 that are rich in the same taxa as the first cluster, but also markedly rich in polychaetes.

Although the taxa ordinated in Figure 4 are not noticeably clustered, their arrangement nevertheless reflects the differences apparent between samples: those taxa (peracarids etc.) found enhanced in the first cluster

Figure 3

Plot of scores of sled samples (excluding Ophiura ljungmani*) on the first and second axes of correspondence analysis. Numerals identify Station (sample) number.*
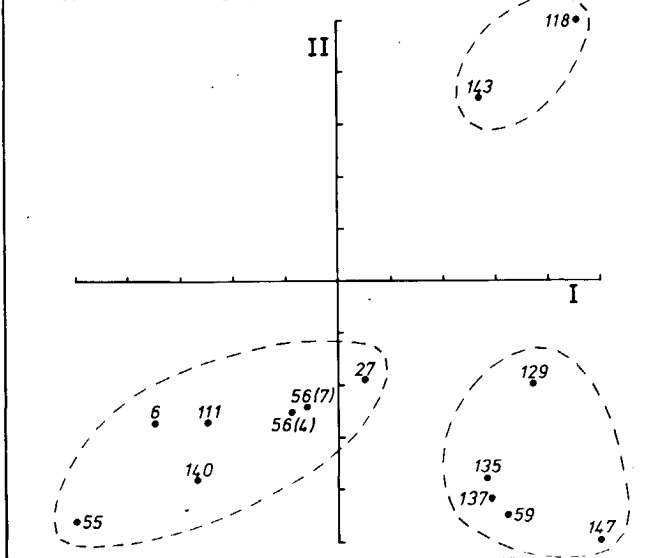
of samples ordinated are ranged towards one end of the first axis of the taxon ordination; while those taxa (bivalves, asteroids, actinians, etc.) found enhanced in the second cluster samples are ranged towards the other. As expected, on the second axis of the taxon ordination the polychaetes are separated from all other taxa. Figures 3 and 4 also suggest that the second axis effect is dependent on the first since (as is indicated in Figure 2) the high-polychaete samples are also rich in peracarids relative to bivalves.

It should be mentioned here that, as might be expected, correspondence analysis of the data including *Ophiura ljungmani* clearly clustered the summertime samples rich in freshly settled postlarvae from the remainder. No further seasonal correlation was evident after removal of *Ophiura ljungmani* from the data. It may also be noted that the sample clustering (Fig. 3) separates the two samples (Stations 140 and 143) taken on consecutive days as far apart as almost any pair of the samples ordinated.

Methodological sources of sample variation

It is known that winnowing of epibenthic sled samples caused by heaving of the vessel transmitted as surge on the wire to the sampler during recovery will lead to a selective loss of fauna, presumably through the mouth of the sled (Hessler, Sanders, 1967). The hydro-dynamically lightest elements, such as peracarid crustacea, are most affected and the relatively heavy bodied fauna, such as heavily calcified large bivalves and echinoderms, least affected.

In order further to define this apparently likely cause of at least some of the variation in the time series, the relative buoyancy of the faunal elements was measured. The sinking rates of specimens of the various taxa sorted from samples where these effects appeared smallest was measured (Table 4) in columns of the fluid in which they were preserved (usually 90% ethanol). Although living animals would yield different values, the results, since they depend largely on ratios of body

surface to volume, remain valid as indicative of relative buoyancy. The values in Table 4 are significantly correlated with the axis I scores shown in Figure 4 (Spearman's $R_v = 0.78$ with a Student's $t = 3.59$ giving $P = 0.01$). This supports the conclusion that sample winnowing, resulting in a selective loss of the lighter and less buoyant taxa, was the source of much of the observed variation between sled samples, and particularly that ordinated along the first axis of correspondence analysis. That the operation of the mouth-closing gate on the sled clearly reduced this winnowing effect, particularly on recovery of the gear in heavy seas, is evident by comparing Station 55, for which the gate failed to release, with other hauls. A similar conclusion would be reached by comparing later hauls with Stations 6 and 27 which were obtained before the gate mechanism was fitted. However, these later hauls are by no means consistently richer in the lighter bodied fauna. But the exceptions (Stations 111 and 140) may be explained by washing that resulted from observed damage to the net.

It is less easy to identify the source of variation associated with the second axis of correspondence analysis (Figs. 3 and 4). These scores may result from a varying efficiency in sampling the burrowing and attached fauna; scores for the taxa appearing to reflect a gradient in mode of life in relation to the sediment. Those organisms whose morphology would suggest an epifaunal mode of life are ranged towards the pycno-gonids at one pole; while those likely to be burrowed or at least anchored to the sediment (brachiopods and ascidians) are ranged towards the polychaetes at the other. This latter group includes the Ophiuroidea (without *Ophiura ljungmani*), many of which were the burrowing species, *Amphilepis norvegica* Ljungman.

It seemed likely that such qualitative differences in catch may result from differences in towing speed: at slow speeds a greater depth of sediment and fauna is disturbed, and hence enters the sled, than at higher towing speeds simply because the gear will sink more

Figure 4

Plot of scores of taxa (excluding Ophiura ljungmani*) in the samples on the first and second axes of correspondence analysis. The taxa are denoted by numbers that may be identified by reference to the listing given in Table 2*
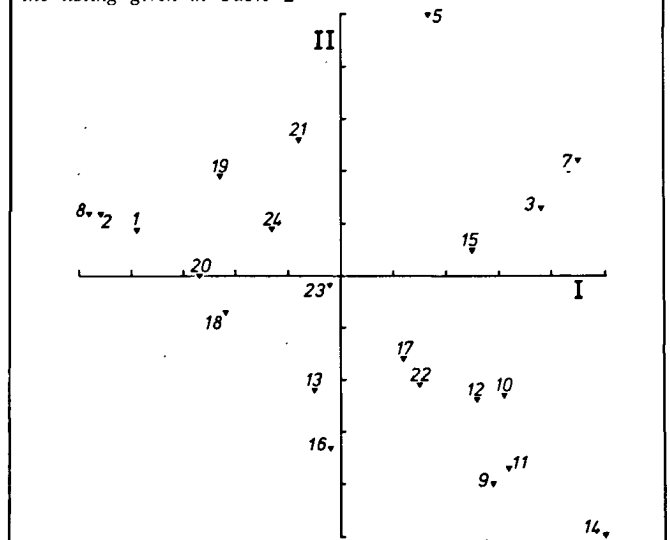
Table 4

Drop speed in ethyl alcohol of randomly chosen individuals of various taxa. The Ophiuroidea tested did not include Ophiura ljungmani; N = total number tested.

Taxon	N	Mean speed (cm.s^{-1})	S.D.
Actinaria	10	6.02	1.51
Nemertea	40	0.83	0.63
Polychaeta	111	1.70	5.80
Sipuncula	36	1.50	1.50
Tanaidacea	82	0.81	0.49
Isopoda	36	1.48	0.92
Amphipoda	20	1.18	0.59
Aplacophora	33	1.97	1.18
Gastropoda	35	5.81	4.35
Scaphopoda	36	3.31	1.74
Bivalvia	99	4.89	3.32
Ophiuroidea	12	4.97	2.61
Echinoidea	16	1.60	1.51
Holothuroidea	26	4.84	2.59
Ascidiacea	10	4.27	1.29

deeply into the soft ooze. It may be significant that the bottom tracks of the two hauls (Stations 118 and 143) that are separated from the rest along axis II (Fig. 3) are both short relative to some of the rest, so that the towing speed over the bottom must have been 1 knot (1.8 km.hr^{-1}) or less. The towing speed of other hauls ranges up to an estimated 4 knots (7.4 km.hr^{-1}) or more for Station 137, when the direction of tow coincided with a presumed northeastward set of the bottom water. Although the bottom tracks of two other hauls (Stations 56 and 59) were also relatively short, they were directed southwest, against the probable set of bottom current. This might have increased the actual speed of the haul through the water although it is not known whether such circumstances would affect the qualitative composition of the fauna caught.

If this interpretation of the effect of towing speed on the effective depth of sediment disturbance is correct, then one would naturally expect a greatly enhanced polychaete content, since they comprise almost 60% of the total macrofauna in box cores taken nearby (Gage, 1977).

Further support for this interpretation comes from a comparison of epibenthic sled hauls taken in Loch Creran at 20 m depth at the site of previous gear comparisons (Gage, 1975). The results (Table 5) show a markedly lower numerical representation of Polychaeta from a "fast" tow compared to a "slow" haul, and when compared to grab samples that are here taken as estimates of actual polychaete abundance in the sediment. On the basis of unpublished data on the predominatingly infaunal life styles of the Polychaeta at this station, it would seem reasonable to conclude that the fast haul caught fewer worms because the gear disturbed a shallower depth of sediment than the slow haul.

DISCUSSION AND CONCLUSIONS

Effect of spatial pattern

Variation amongst the samples from towed samples conceivably may be generated from aggregated pattern

in the dispersion of the fauna. This may result from large-scale patchiness of dimension approaching the length of bottom tow, or of smaller patches possibly of varying demographic composition, such as described for shallow subarctic benthos (Curtis, Petersen, 1977). Although not providing data on such possible small-scale heterogeneity, comparison of fauna in box cores spaced roughly 1 km apart near the Permanent Station indicated considerable homogeneity both in faunal composition and dispersion of individual species (Gage, 1977). Furthermore, study of dispersion in deep-sea macrobenthos elsewhere indicates predominating scales of less than 0.1 m^2 (Jumars, 1975; 1977). Therefore, on the basis of present knowledge, it seems reasonable to assert that such patchiness as is present is small enough in scale as to be cumulatively neutralised by the sampling track of an epibenthic sled haul and thus will not contribute towards significant variance between hauls.

Table 5

Proportion of sample comprised of Polychaeta in 1/8th subsamples of epibenthic sled hauls made at different towing speeds in Loch Creran (Scotland) at Station C12 (see Gage, 1975) on 20 June 1979. Value in parenthesis was obtained earlier from van Veen grabs on this station (derived from data in Gage, 1978).

"Fast" haul (3.6 knots = 6.7 km.hr^{-1} towing speed) (%)	"Slow" haul (0.7 knots = 1.3 km.hr^{-1} towing speed) (%)
31.5	52.6 (55.6)

Generality of results

Do the known physical and biological characteristics of the environment at the Permanent Station accord with physical conditions at this site and its fauna as representative of the deep sea? Information on the species composition in the present samples might permit assessment on whether the fauna is typical of the deep sea. However, it is probable that any such judgement would be premature in view of our presently incomplete knowledge of the taxonomy and zoogeography of the deep-sea macrobenthos. Furthermore, although it is possible to argue that evidence indicates exceptionally strong bottom flow in Rockall Trough, we contend that our present knowledge is too incomplete to permit characterization of "typical" conditions in the deep sea. Moreover, present knowledge suggests that deep oceanic floors adjacent to the continental margin are quite likely to be exposed to currents of considerably greater velocity than those found near the centre of oceans basins. It is not known to what extent regional differences in macrobenthic standing crop and composition may reflect such conditions. At the Permanent Station the bottom current is non-erosional and may reduce the expected flux of organic particulates to the benthic boundary from the eutrophic zone because the bulk of the deep water has a southerly origin under less eutrophic surface conditions (Ellett, Martin, 1973; Lonsdale, Hollister, 1979). However, the relatively high primary production at the surface in the region of the Rockall Trough (Koblents-Mishke et al., 1968) may well explain an apparently high benthic standing crop (Gage, 1977).

In analysis of the time-series samples we have inferred as sources of variation two aspects of the sampling process that were subject to sea conditions (one only in combination with gate malfunction) and hence beyond the control of the investigators. By identifying their effect other possible sources of variability in the composition of the populations present in the samples will be more clearly recognized. That no seasonal or longer term pattern was evident, apart from that ascribed to the seasonal cycle of *Ophiura ljungmani*, although such cycles are conspicuous amongst the benthos of the temperate shelf (Thorson, 1946; Buchanan *et al.*, 1978) is not unexpected in view of the physical stability of the deep sea. However, it must be stated that quantitative samples, rather than the qualitative hauls of the present study, will be required to detect clearly year-to-year changes of macrobenthic community structure in the deep sea.

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