A DEEP-SEA BENTHIC COMMUNITY EXPOSED TO STRONG NEAR-BOTTOM CURRENTS ON THE SCOTIAN RISE (WESTERN ATLANTIC)

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ABSTRACT

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This paper gives an overview of the structure of a benthic community at 4626 m depth on the Nova Scotian continental rise. Here, abundances of polychaetes, bivalves, isopods and tanaids are conspicuously high compared to those reported from comparable depths. Bacterial numbers and ATP concentrations are also high. We suspect that these anomalous abundances result from enhanced food availability caused by the strong near-bottom currents that flow through the area. The polychaete and bivalve faunas have few adults and high species dominance suggesting that currents create large-scale, sediment-transporting disturbances. The composition of the crustacean fauna supports this inference in that it is dominated by forms that can enter the seabed and thereby escape adverse conditions on the sediment surface.

INTRODUCTION

Investigation of the deep-sea benthos began in the 1800's (Mills, 1983). Yet, because of the vastness of the realm and the difficulty of obtaining information about the organisms living there, deep-sea communities are far from fully described. Much of our knowledge comes from regions with quiescent hydrodynamic conditions, and, as a result, the deep sea has been characterized as a physically stable environment (Sanders, 1968). It is now being recognized that the deep sea is not always or everywhere quiescent (Heezen and Hollister, 1964; Rowe and Menzies, 1968; Dinet and Vivier, 1977; Gage, 1979; Rowe, 1981). Vast areas have bedforms that appear to have been created by strong near-bottom flows (Hollister and Heezen, 1972). The community described in this paper occurs in a hydrodynamically active area on the Nova Scotian Rise, where strong near-bottom currents (Richardson et al., 1981) episodically erode the surface of the sea bed (Yingst and Aller,

1982; McCave et al., 1984). The description of this community is of interest because it experiences conditions that differ from those of the more familiar, physically stable deep-sea areas, and because it may be representative of communities beneath strong deep-sea currents worldwide. In this paper, we contrast a benthic community on the Scotian Rise with other deep-sea communities and attempt to understand the differences in terms of the impact of the near-bottom flow regime.

The samples upon which our description is based were taken as part of the High Energy Benthic Boundary Layer Experiment (HEBBLE) (Nowell et al., 1982). This project is an interdisciplinary study of sediment transport in the deep ocean where near-bottom current velocities are intermittently high. Because sediment-transport parameters in many environments are significantly altered by the organisms living in the sediment (Rhoads, 1974; Young and Southard, 1978; Nowell et al., 1981; Rhoads and Boyer, 1982), biological studies are an important component of the project.

LOCALITY

The study site is on the Nova Scotian Rise at 4626 m depth (Fig.1). In this region, currents alter seabed topography (Hollister and Heezen, 1972). A nine-month current-meter record taken nearby (33 km away at 4500 m depth) documents frequent, several-day-long periods when daily averaged, current velocities at 10 m above bottom were 20—25 cm s^{-1} (Weatherly and Kelley, 1983). These velocities are conspicuously higher than the 3 cm s^{-1} typical of abyssal conditions (Munk et al., 1970) and are among the highest ever measured in the deep sea (Richardson et al., 1981). These "benthic storms" (Kerr, 1980) erode surficial sediment (Weatherly and Kelley, 1983), producing near-bottom suspended particulate matter concentrations that are, at times, much greater than those of strong nepheloid layers known elsewhere
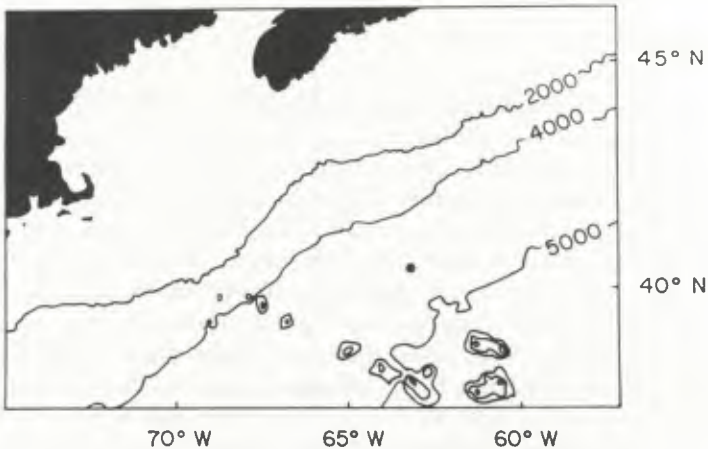

Fig.1. Chart of the northwestern Atlantic showing the sample location (solid circle).

in the world ocean, for example, 0.78 ppm volume concentration of suspended matter versus 0.03 ppm in clear sea water (Weatherly and Kelly, 1983). These periods of rapid erosion appear to alternate with periods of massive deposition (Yingst and Aller, 1982).

Two locations 3 km apart but at the same depth were sampled: Knorr 78 Station 7 (40°24.0'N, 63°07.4'W) and Knorr 78 Station 14 (40°24.3'N, 63°09.6'W). In this region, near-bottom temperature varies between 2.23° and 2.27 °C and the salinity varies between 34.85 and 34.9°/$_{\circ\circ}$ (G.L. Weatherly, pers. commun., 1982). Disaggregated-grain-size analyses show the sediments to be composed of 6.0% sand, 50.6% silt, and 39.3% clay on the average (Tucholke, unpublished data). The clay- and silt-sized particles are incorporated in and mixed with particle aggregates >500 μm including fecal pellets, arenaceous and calcareous foraminiferan tests, and glacially rafted pebbles (Yingst and Aller, 1982; Thistle, 1983a). The sediment is consolidated compared to shallow-water deposits of similar composition (Yingst and Aller, 1982) and is oxidized to at least 10 cm depth. X-radiographs of vertical sediment slabs reveal physically produced sediment layers, abundant tubes and burrows, and localized areas homogenized by biological reworking (Yingst and Aller, 1982; and Fig.2). Organic-carbon and organic-nitrogen concentrations are higher throughout the top 10 cm than in many deep-sea regions and the C/N ratio suggests that the surficial organic matter can be further metabolized (Yingst and Aller, 1982; Yingst and Aller, submitted).

Thistle (1983b) refers to this location as the HEBBLE site. It is not. The HEBBLE site is at 4820 m depth (40°27'N, 62°20'W) about 68.6 km away from the location of these preliminary samples.

MATERIALS AND METHODS

The samples were taken from R/V "Knorr" (cruise 78) using a 1/4 m² box corer (Hessler and Jumars, 1974) equipped with the modifications originated by R.R. Hessler, P.A. Jumars and J. Finger to reduce bow wave (see Thistle, 1983b, for more description). The box-corer box contained removable subsamplers (Fig.3). The central nine 10 × 10 cm subcores contained 5 × 5 cm subsubcores whose bottom edges were beveled such that they sampled 23 cm². Sediment slabs for X-radiography were taken from the 10 × 30 cm region (Fig.3).

Faunal samples (77 cm²) were processed as follows. At sea, the water overlying a subcore was drawn off and passed through a 0.045 mm sieve, and the residue added to the 0—1 cm layer sample. The sediment was then extruded and sliced into the following layers: 0—1, 1—2, 2—3, 3—5, 5—7, and 7—10 cm. Samples were preserved in buffered 20% formaldehyde-filtered seawater. In the laboratory, each layer was washed on sieves with the following apertures: 1.00, 0.500, 0.420, 0.297 and 0.063 mm. The ⩾0.297 mm fractions were rose bengal stained and sorted under a dissecting microscope. The animals in the 0.063 mm fraction were concentrated using the Barnett (1968) procedure [efficiency was 100% for harpacticoids and 99.7% for nematodes (median of
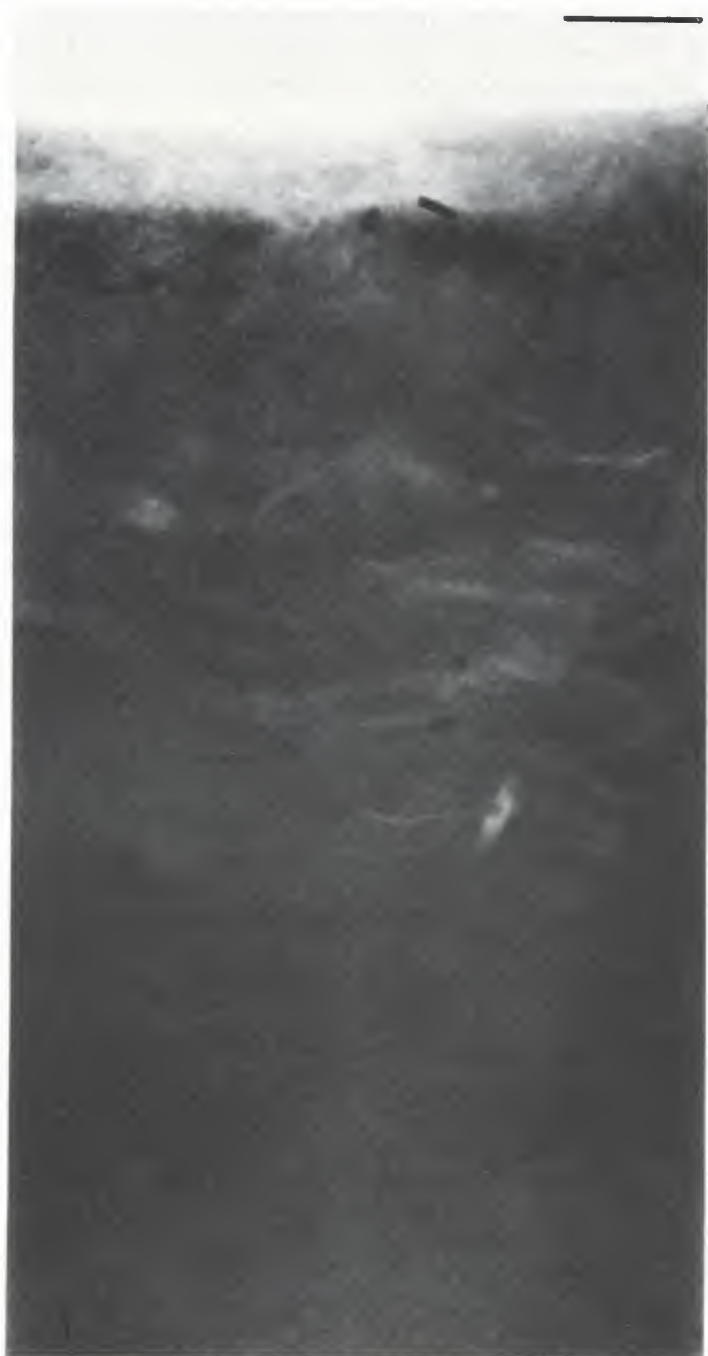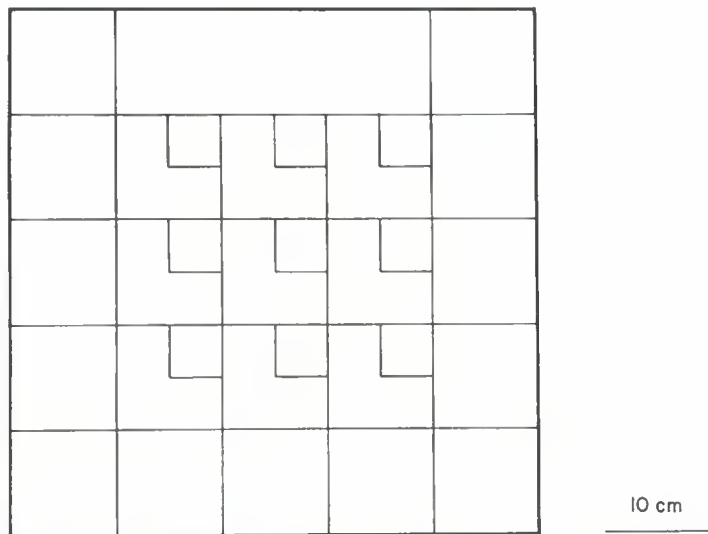
Fig.3. A schematic representation of a core box showing the subsamples.

3 trials)], rose bengal stained, and sorted under a dissecting microscope. Nematodes were counted; other taxa were picked. Values reported for nematodes and harpacticoids include individuals found in all fractions; values reported for macrofauna include only individuals from the $\geqslant 0.297$ mm fractions. The 0—5 cm layers were enumerated for macrofauna. For nematodes and harpacticoids, the 0—2 cm layer data reported account for the bulk of the fauna. For example, the 2—3 cm layer adds a median of 14.8% more nematodes ($N = 18$; Thistle and Sherman, in press).

Bacteria were counted directly from gluteraldehyde-preserved subsamples (0.3% gluteraldehyde in 3% NaCl) using the epifluorescence method of Hobbie et al. (1977) as modified by Watson et al. (1977) (see Aller and Yingst, 1980, for details). Sediment adenosine triphosphate (ATP) concentrations were determined aboard ship as soon after sample collection as possible, usually <4 h, using either the boiling sodium bicarbonate method of Christian et al. (1975) or the boiling phosphate buffer method (Bulleid,

Fig.2. X-radiograph of vertical slab of sediment from a box core taken on the lower continental rise off Nova Scotia. Scale = 2 cm. The upper 1—2 cm of sediment is well burrowed. Differences in the degree of reworking in this zone are reflected in the density of the radiograph; the more intensely reworked areas have higher water contents (>55%) and appear lighter. Intense biogenic reworking, possibly by protobranch bivalves, is apparent as homogenized areas near the sediment—water interface on the right side of the radiograph. Small-diameter, vertically oriented tube-burrow networks are seen near the interface and larger-diameter, horizontally oriented burrows at depth. Burrows coming out of the plane of the radiograph appear as light holes. Pebbles concentrated at 1.5 cm and scattered throughout the top 10 cm illustrate the poorly sorted nature of the deposit. The pebble lag deposits reflect the presence of periodic erosional activity in this deep-sea area (Knorr 78, Sta. 17, 4673 m, 40° 21.52'N, 63° 06.24'W). .

1978). All samples were extracted in duplicate and ATP concentrations calculated using standard curves determined with sediment from this area prepared to be azoic and essentially ATP-free. These curves are designed to correct for interference in the luciferin-luciferase assay caused by chemical characteristics of the sediment that are proportional to the weight of sediment extracted (Yingst, unpublished data).

In our among-site comparison, we have considered each major taxon separately for the taxa that were abundant in our samples. Literature reports and our own data are expressed as the number per $1/4$ m^2 for macrofauna, number per 10 cm^2 for nematodes and harpacticoids, and number per g of sediment for bacteria for each box core. Benthic copepod and harpacticoid copepod abundances are considered to be equivalent because harpacticoids overwhelmingly dominate the benthic copepod assemblage. We tested the abundance of each macrofaunal taxon against Khripounoff et al.'s (1980) results because, of the studies where replicate box cores were taken at a site, their site at 5100 m in the Vema Fracture Zone (station B) most nearly approximates the depth at our site.

RESULTS AND DISCUSSION

Abundance and composition of major taxa

Although deep-sea communities have been sampled since the 1800's, quantitative estimates of infaunal standing stocks have been made only since the advent of box-coring techniques in the 1970's. Quantitative samples using sampling methods comparable to those we used have been taken in only a small number of sites (Table 1). We use these data to compare with our results.

Table 2 gives the composition of the fauna at our site. The taxa listed are among those commonly found in the deep sea. Our list is shorter than most because some rare taxa that have been collected by other investigators were not found. As is typical in the deep sea (Kripounoff et al., 1980, table 5), polychaetes are the most abundant macrofaunal group and nematodes are the most abundant metazoan meiofaunal group.

Polychaetes are conspicuously more abundant at our site than at all but one other site from greater than 3000 m (Fig.4). In particular, their abundance is six times greater than the abundance found at a 4700 m site in the Bay of Biscay (Laubier and Sibuet, 1979) and is significantly greater than that found by Khripounoff et al. (1980).

The polychaete fauna resembles that of the other areas in the deep, northwest Atlantic in that the Paraonidae and Spionidae are important families (Hartman, 1965; and Table 3). However, the fauna differs from that found in other deep-sea locales in several ways. Cirratulidae is not among the dominant families (see stations II2, LL1, JJ1 in Hartman, 1965; Hessler and Jumars, 1974), but Ampharetidae is. The polychaete fauna of other deep-sea sites typically lacks strong dominance at the species level (e.g., Hessler and

TABLE 1

Reports giving deep-sea faunal standing stocks that are comparable to our data. All studies used box corers but differed in details of sample handling including the sieve size used and the lowest depth to which the sediment was sampled. The abundances reported by Dinet et al. (1973) may be artifactually low according to Thiel (1983)

Author(s)	Region	Depth (m)	Sieve aperture (mm)	Sample depth (cm)
Macrofauna				
Hessler and Jumars (1974)	Central North Pacific	5634	0.297	0—20
Dahl et al. (1976)	Norwegian Sea	2479—3718	0.250	0—20
Jumars and Hessler (1976)	Aleutian Trench	7298	0.297	0—8
Gage (1977)	Rockall Trough	2875	0.420	core depth
Gage (1979)	Rockall Trough	1800—2900	0.420	≥25 cm
Laubier and Sibuet (1979)	Bay of Biscay	2000—4700	0.250	—
Khripounoff et al. (1980)	Vema Fracture Zone	5090—5880	0.250	core depth
Meiofauna				
Dinet (1973)	Walvis Ridge	1440—5170	0.040	0—3
Dinet et al. (1973)	Mediterranean	2116—2855	0.050	0—4
Coull et al. (1977)	Western North Atlantic	400—4000	0.042	0—10
Dinet and Vivier (1977)	Bay of Biscay	1939—4645	0.050	0—4
Dinet (1979)	Norwegian Sea	2479—3709	0.040	0—5
George and Higgins (1979)	Puerto Rico Trench	8560—8580	0.062	0—7

Jumars, 1974), whereas, at our site, the summed abundances of two un-described species of Ampharetidae make up 58 and 64% of the polychaetes at Stations 7 and 14, respectively. These ampharetids are small (1.5—3.0 mm body length), as are many of the paraonids and spionids. Further, all of the polychaetes collected were sexually immature.

Although little direct evidence is available to assess the natural history of deep-sea polychaetes, analogies with shallow-water relatives suggest that our fauna is dominated by surface deposit feeders (Ampharetidae, Spionidae, Flabelligeridae, Cirratulidae and perhaps the single Sabellidae individual; Jumars and Fauchald, 1977; Fauchald and Jumars, 1979; and Table 3). This dominance by surface deposit feeders agrees with data from other deep-sea areas (Hessler and Jumars, 1974; Jumars and Hessler, 1976; Gage, 1977).

TABLE 2

For macrofauna, total number of individuals in the 0—5 cm layers of nine 77 cm² sub-cores (693 cm²). For meiofauna, total number of individuals in the 0—2 cm layers of three 77 cm² subcores (231 cm²)

	Station	
	7	14
Macrofauna		
Polychaeta	111	75
Bivalvia	18	7
Aplacophora	1	0
Tanaidacea	9	34
Isopoda	18	24
Amphipoda	2	0
Cumacea	1	1
Sipunculida	5	0
Tardigrada	1	0
Total	166	141
Meiofauna		
Nematoda	4526	3297
Harpacticoida	313	192
Ostracoda	25	15
Kinorhyncha	22	11
Total	4886	3515

The Paraonidae and Cossuridae are subsurface deposit feeders. The members of the Hesionidae and Dorvilleidae and the species of Pilargiidae found in our samples appear to be carnivores. Most of the polychaete species we found belong to families known to be motile or discretely motile; the ampharetids are probably discretely motile despite their tubicolous habit (e.g., *Amphicteis scaphobranchiata*; cf. Nowell et al., 1984).

The abundance of bivalves at our site is greater than that at all but one other site from deeper than 3000 m (Fig.5). Laubier and Sibuet's (1979) sample from the Bay of Biscay is most nearly from the same depth (4700 m); our value is more than four times greater and is significantly greater than that found by Khripounoff et al. (1980).

The bivalves are small in comparison to individuals of the same families and genera collected from similar depths elsewhere (G.R. Hampson and H.L. Sanders, pers. commun., 1982). In addition, no sexually mature individuals were found. These circumstances contrast strongly with those reported by Grassle and Sanders (1973). The majority of the bivalves are protobranchs, e.g., *Malletia abyssorum*; 25% belong to the eulamellibranch family Thyasiridae, e.g., *Thyasira subovata*. Both groups are mobile surface and subsurface deposit feeders and are probably responsible for most of the localized areas of homogenized sediment seen in the X-radiographs where physically
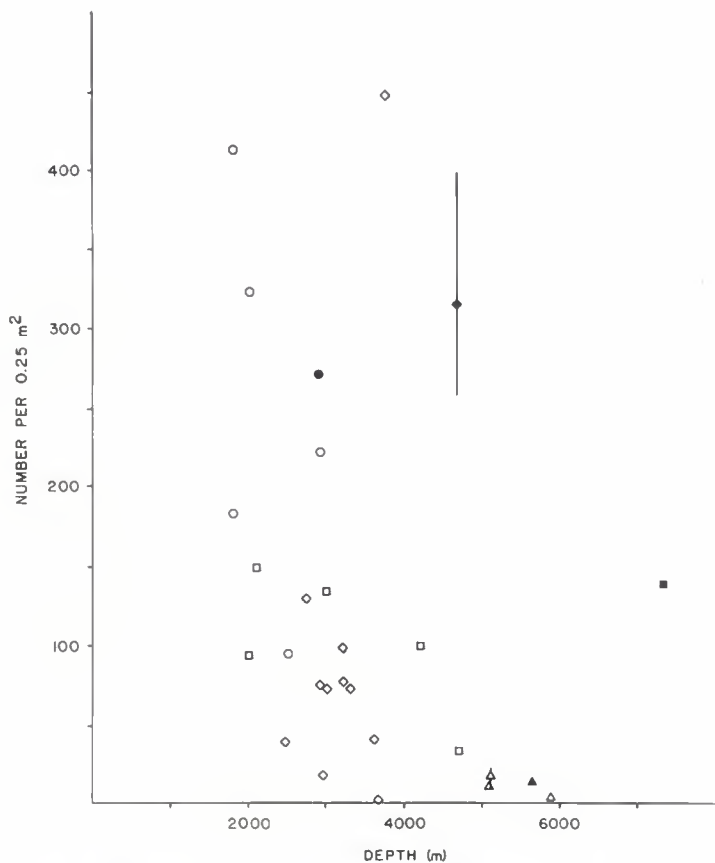
Fig.4. Median polychaete abundances versus depth for the reports in Table 1. Symbols are as follows: Hessler and Jumars (1974), solid triangles; Dahl et al. (1976), open diamonds; Jumars and Hessler (1976), solid square; Gage (1977), solid circles; Gage (1979), open circles; Laubier and Sibuet (1979), open squares; Khripounoff et al. (1980), open triangles; this study, solid diamond. Ranges are shown for Khripounoff et al. (1980) and this study.

produced laminations and biologically produced burrows and tubes have been obliterated (Fig.2).

The abundance of isopods at our site is conspicuously greater than that at sites from similar depths (Fig.6). The median abundance is seven times greater than that found by Laubier and Sibuet (1979) at 4700 m, and the density of isopods is significantly greater than that at Kripounoff et al.'s (1980) 5100 m site. In fact, only Gage's (1979) sites in ≤2000 m depth in Rockall Trough have comparable densities. The isopods we found (Table 4) belong to typical deep-sea families (Hessler and Thistle, 1975), but only six of the 18 deep-sea janiroidean isopod families (Hessler and Wilson, 1983) are represented.

Nannoniscidae is the most abundant isopod family at our site. The species found have a long, thin body that seems more suitable for burrowing than

TABLE 3

The abundance by family of polychaetes found in the 0—5 cm layers of 693 cm²

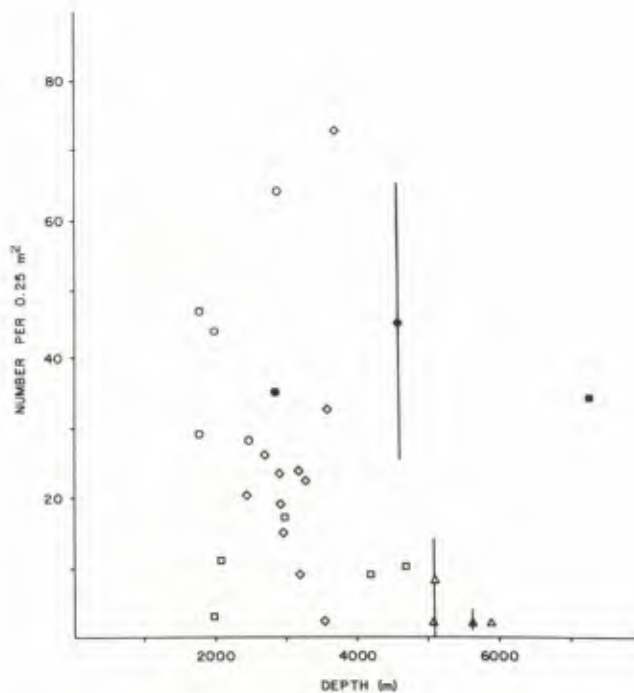| Family	Station	
	7	14
Ampharetidae	64	48
Paraonidae	15	11
Spionidae	16	10
Cirratulidae	4	3
Hesionidae	4	0
Goniadidae	3	1
Cossuridae	1	0
Pilargiidae	1	0
Dorvilleidae	1	0
Sabellidae	1	0
Flabelligeridae	1	1
Phyllodocidae	0	1
Unknown Family A	0	1
Total	111	75

Fig.5. Median bivalve abundances versus depth for the reports in Table 1. Symbols as in Fig.3.
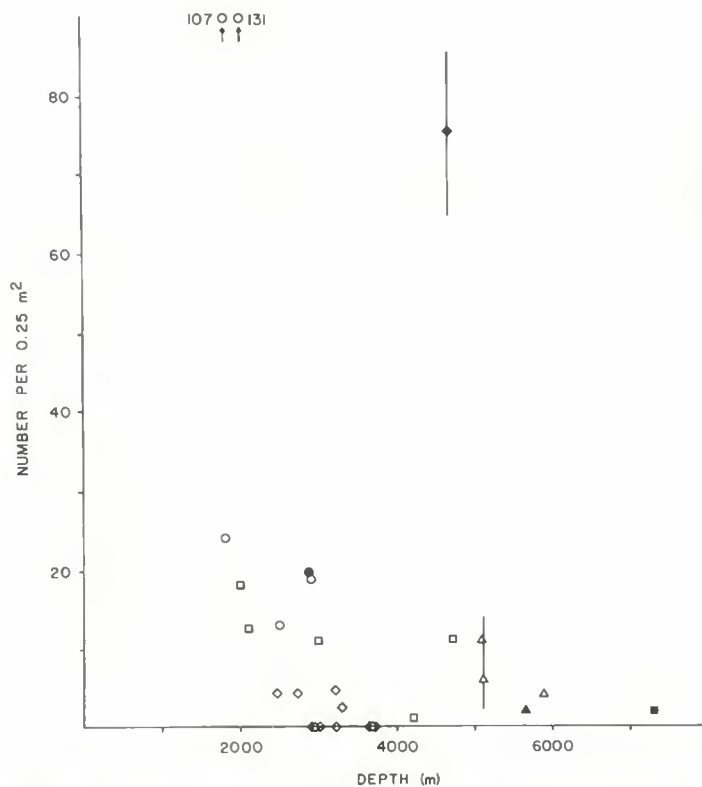
Fig.6. Median isopod abundances versus depth for the reports in Table 1. Symbols as in Fig.3.

TABLE 4

The abundance by family of isopods found in the 0—5 cm layers of 693 cm²

Family	Station	
	7	14
Nannoniscidae	4	13
Ischnomesidae	3	6
Macrostylidae	5	0
Haploniscidae	1	2
Desmosomatidae	0	1
Pseudomesidae	0	2
(unidentifiable mancas)	5	0
Total	18	24

does the broader body characteristic of other species of the family (J.F. Siebenaller, pers. commun., 1982). Ischnomesidae is second in abundance. These isopods have elongate bodies and long walking legs and are reminiscent of the walking-stick insects. Their habits are not well known. Wolff (1976)

found specimens in seagrass rhizomes (see also George and Higgins, 1979); Gooday (1984) found individuals in tube-like foraminiferan tests. We have found individuals in the 1—2, 2—3 and 3—5 cm layers at the HEBBLE site. These observations suggest that ischnomesids are capable of burrowing or tube dwelling. Species of the other abundant isopod family, the Macrostylidae, have morphologies that suggest a tube- or burrow-dwelling life style. In sum, at our site the surface-living isopods seem to be rare, while those that can enter the sediment are unusually abundant in both relative and absolute terms.

The median abundance of tanaids at our site is higher than any value reported from the studies in Table 1 regardless of depth (Fig.7). It is more than an order of magnitude greater than Laubier and Sibuet's (1979) 4700 m value and significantly greater than that of Khripounoff et al. (1980) from 5100 m. All of the tanaids we found belong to the suborder Tanaidomorpha, and the majority belong to typically deep-sea families, the Pseudotanaidae and Leptognathiidae (Table 5; Sars, 1896; Hansen, 1913; Nierstrasz, 1913; Lang, 1968). Many Leptognathiidae species construct tubes (Nierstrasz and Schuurmans Stekhoven Jr., 1930; Grieve, 1967). Although none of our specimens were found inside tubes, the morphology of the Leptognathiidae
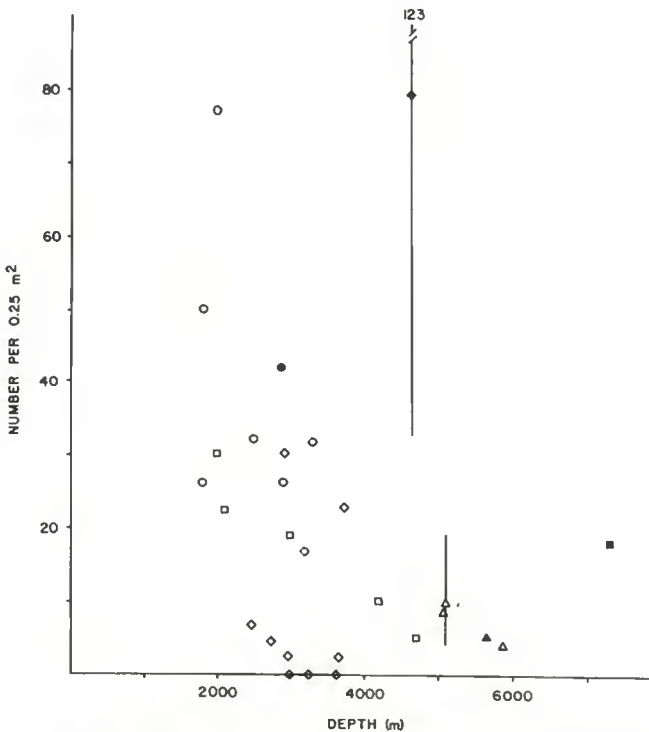

Fig.7. Median tanaid abundances versus depth for the reports in Table 1. Symbols as in Fig.3.

with its short, stout legs, suggests a tube-dwelling habit (Johnson and Attramadal, 1982). Also, individuals of the surface dwelling family Neo-tanaidae are absent from our samples although they are common in other areas of the deep, northwest Atlantic (Gardiner, 1975). The tanaids, too, appear to be dominated by species that can enter the sediment.

Our values for nematode (Fig.8) and copepod densities (Fig.9) fall among reports from similar depths. However, this result should not be taken to imply that the composition of the meiofauna is typical for its depth. In particular, Thistle (1983b) has shown that the harpacticoid fauna is depleted of surface-living individuals and is enriched in burrowing individuals.

There are few estimates based on direct-counting procedures of bacterial standing stocks in sediments with which to compare our results, but in general, bacterial standing stocks appear to decrease with increasing water depth (Yingst and Aller, submitted). In contrast, our densities appear to be unusually high (Table 6). For example, they are comparable to those found at DOS II in 3480 m in the western Atlantic (Yingst, unpublished data), at stations in 100—230 m of water in the vicinity of the Texas Flower Garden Banks in the Gulf of Mexico (Yingst and Rhoads, 1985), and at the Deep station in 40 m of water in Long Island Sound (Aller and Yingst, 1980). Sediment ATP concentrations similarly indicate high bacterial standing stocks in that they are approximately 8 times greater than those found at 6011 m on the Nares Abyssal Plain (Karl et al., 1976) and twice as great as Romano and Dinet (1978) found at 4010 and 4727 m in the northwestern Indian Ocean.

Interpretation of the composition data

In the deep sea, polychaetes and bivalves generally have been found to be relatively abundant and highly diverse (Sanders et al., 1965; Sanders, 1968; Hessler and Jumars, 1974). By shallow-water standards, the distribution of individuals among species tends to be even (i.e., low dominance; e.g., Hessler and Jumars, 1974), and large individuals ($\simeq$ adults) occur in and often domi-nate size-frequency tabulations (e.g., Grassle and Sanders, 1973). The poly-chaetes and bivalves from our site do not fit this pattern. Two polychaete species make up more than 50% of the individuals; the polychaete and bivalve individuals are small pre-adults.

TABLE 5

The abundance by family of tanaids found in the 0—5 cm layers of 693 cm^2

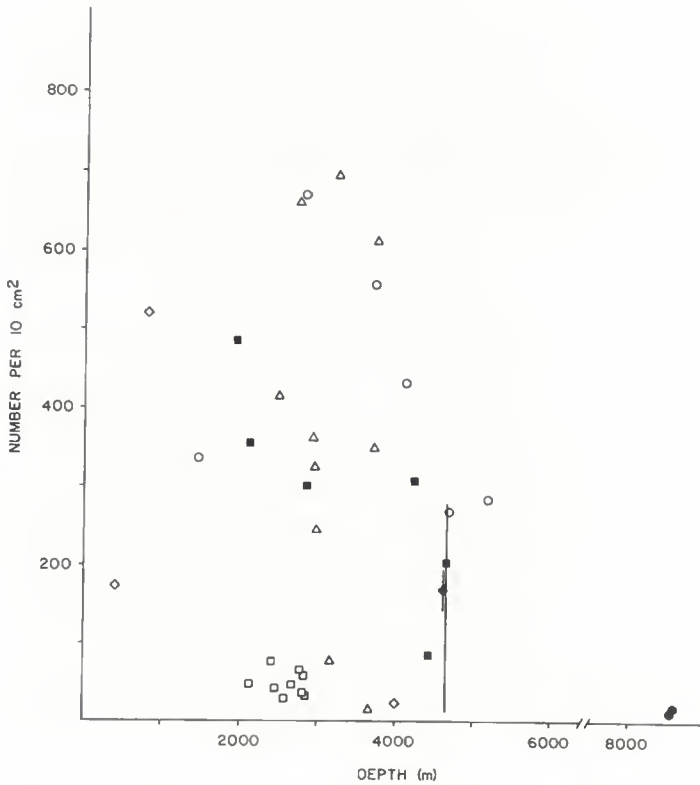| Family	Station	
	7	14
Leptognathiidae	6	31
Pseudotanaidae	1	3
(unidentifiable damaged)	2	0
Total	9	34

Fig.8. Median nematode abundance versus depth for the reports in Table 1. Symbols are as follows: Dinet (1973), open circle; Dinet et al. (1973), open square; Coull et al. (1977), open diamond; Dinet and Vivier (1977), solid square; Dinet (1979), open triangle; George and Higgins (1979), solid circle; this study, solid diamond. Ranges are shown for Dinet and Vivier's (1977) Station 4 and for this study.

The only deep-sea studies that report faunas with these characteristics are those of Grassle (1977) and Desbruyères et al. (1980). Both papers report on recolonization studies at approximately 2000 m. Desbruyères et al. found when they recovered their experiment after six months that one species of polychaete made up 82% of the fauna. Also, they found only sub-adult bivalves and commented on the unusually high ratio of nauplii to adult harpacticoid copepods. Grassle found that *Priapulus atlantisi* dominated the fauna (30%) after two months and that most individuals of all taxa were sub-adults. These studies suggest that dominance by a small number of species and a preponderance of non-adults occurs in the deep sea when a defaunated patch is colonized primarily by larvae.

The similarity between our data and those of the recolonization experiments suggests that some factor at this locality is creating patches that are defaunated to some extent and are colonized by larvae from the water column. We know that locations in this region are subject to periods of intense erosion alternating with times of massive deposition, and such
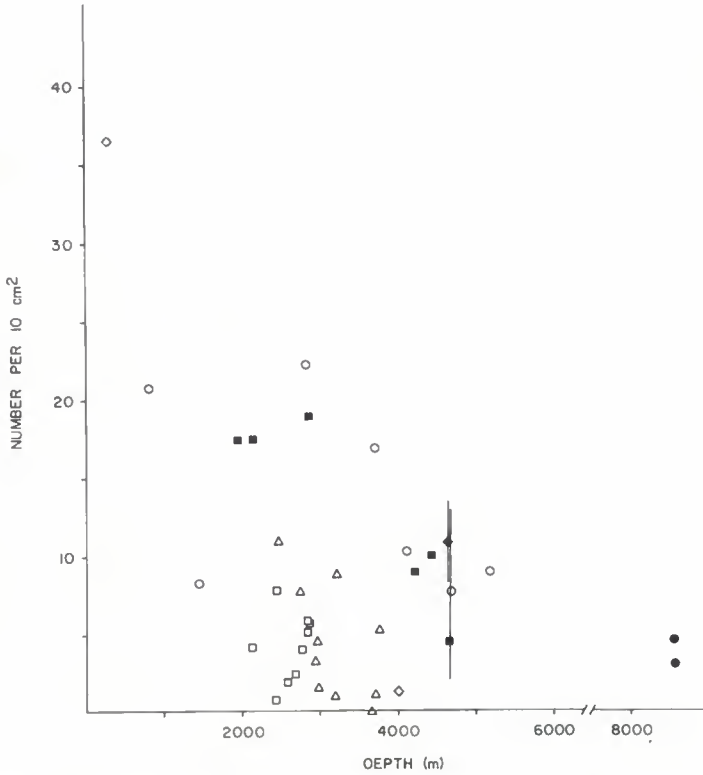
Fig.9. Median harpacticoid copepod abundance versus depth for the reports in Table 1. Symbols as in Fig.8.

physical conditions can create defaunated patches (Eagle, 1975). Given that mesoscale oceanographic phenomena drive the system (Hollister et al., 1984), it is likely that the patches produced will be large relative to the mobility of adult polychaetes and bivalves and that recolonization will be primarily by larvae (see Gerdes, 1977). So, as a working hypothesis, we suggest that our site is part of a region that has a patch structure imposed on it in which defaunation is followed by larval recolonization. The above scenario does not seem to fit the crustacean data. In particular, isopods and tanaids are unusually abundant in our samples. These peracarid crustaceans brood their young until they emerge as miniature adults. Lacking a planktonic stage, tanaids and isopods are thought to be poor dispersers. Why their numbers are high given the physical regime is unclear, but they do show the impact of the hydrodynamic conditions. That is, the only isopod groups abundant in our samples are those that can enter the sediment. The tanaids show the same pattern in that surface-living neotanaids are absent while burrow-dwelling families are extraordinarily abundant. Likewise, the harpacticoid copepod fauna has very few surface-living individuals (Thistle, 1983b). The ability of most of the crustacean species to enter the seabed suggests that these species may be able to mitigate the effects of erosion and deposition at this site.

TABLE 6

Organic carbon, nitrogen, ATP concentrations and bacterial standing stocks ($\pm$S.D., $N = 9$) in discrete depth intervals at Stations 7 and 14

Depth (cm)	ATP (ng g^{-1})	(ng cm^{-2})	Bacteria (10^9 g^{-1})	(10^9 cm^{-2})	Organic carbon (mg g^{-1})	Nitrogen (total) (mg g^{-1})
Station 7						
0—1	12.93 ± 3.2	8.39 ± 2.08	18.26 ± 6.85	11.85 ± 4.45	5.70	0.52
1—2	10.5 ± 1.95	6.98 ± 1.3	12.23 ± 4.24	8.13 ± 2.82	5.20	0.55
2—3	8.05 ± 0.66	5.60 ± 0.44	10.86 ± 2.53	7.56 ± 1.76	4.80	0.47
3—5	7.23 ± 0.79	5.23 ± 0.57	9.74 ± 2.39	7.05 ± 1.73	4.30	0.47
5—7	6.8 ± 1.2	5.48 b 0.97	7.52 ± 1.26	6.06 ± 1.02	3.90	0.62
7—10	5.02 ± 1.73	3.29 ± 1.13	6.61 ± 1.18	4.34 ± 0.77	4.00	0.65
Station 14						
0—1	10.57 ± 1.17	7.28 ± 0.81	21.6 ± 7.05	14.88 ± 4.86	6.07	0.68
1—2	9.28 ± 1.6	8.57 ± 1.48	15.12 ± 4.42	13.97 ± 4.08	5.52	0.77
2—3	7.83 ± 0.33	6.55 ± 0.28	17.37 ± 4.26	14.54 ± 3.57	4.96	0.69
3—5	8.38 ± 0.97	7.74 ± 0.87	15.41 ± 2.52	14.48 ± 2.33	4.08	0.65
5—7	7.71 ± 0.61	8.29 ± 0.66	12.20 ± 2.27	13.12 ± 2.44	3.80	0.65
7—10	6.87 ± 0.51	4.70 ± 0.35	9.89 ± 1.20	6.76 ± 0.82	3.17	0.52

Interpretation of the standing-stock data

Although some typically deep-sea taxa are absent or rare at our site, polychaetes, bivalves, isopods, and tanaids are much more abundant than in other deep-sea regions of comparable depth. The reason for the enhanced abundance is not clear, but it does not seem to be directly related to the productivity of the overlying water (see also Smith et al., 1983). In Table 7, we array the available data against productivity for each of the four taxa. The standing-stocks in our area remain anomalously high.

Although the high standing stocks could come about in a variety of ways, the hydrodynamic regime suggests two possibilities. Given that the mean current velocity at our site is greater than that of quiescent localities, even if the concentration of food in the overlying water is no greater, the flux of food available to animals that can extract suspended particulate food should be larger. For example, on our site a species of Oweniidae appears to be exploiting this food source. These tube-dwelling worms excavate pits around their tubes that passively extract particles from the near-bottom flow by decreasing the water velocity locally, causing material to fall from suspension (see Nowell et al., 1984). Despite the apparently high flux of suspended food particles, ordinary suspension feeders (i.e., animals that use a mechanical filter) are not abundant. Work in shallow water has shown these organisms to be adversely affected by high suspended-sediment concentrations, which clog their filters (Rhoads and Young, 1970). The intermittently high suspended-matter concentrations on our site may exclude animals with this life style.

TABLE 7

The abundance of the four macrofaunal taxa tabulated against water depth and levels of primary productivity in the overlying water. Relative productivity levels were taken from the version of Koblentz-Mishke et al.'s map in Gross (1982); Low = less than or equal to 100 mg C/m²/day, Moderate = 100—250 mg C/m²/day, High = greater than 250 mg C/m²/day. The sources from which the abundances (per 1/4 m²) are taken are as follows: A = Hessler and Jumars, 1974; B = Gage, 1977; C = Gage, 1979; D = Laubier and Sibuet, 1979; E = Khripounoff, Desbruyères and Chardy, 1980; F = our data. Dahl et al.'s (1976) data were omitted because of the difficulty of assessing overlying-water productivities in the Norwegian Sea

	Depth (m)				
	1000—1999	2000—2999	3000—3999	4000—4999	5000—5999
A. Polychaetes					
Low					15 A
					17 E
					11 E
					3 E
Moderate		150 D	136 D	102 D	
		97 D		34 D	
		273 D		336 F	
		96 C			
		325 C			
High	414 C	224 C			
	185 C				
B. Bivalves					
Low					2 A
					8 E
					2 E
					2 E
Moderate		11 D	17 D	9 D	
		3 D		10 D	
		35 B		45 F	
		28 C			
		44 C			
High	47 C	64 C			
	29 C				
C. Isopods					
Low					2 A
					6 E
					11 E
					4 E
Moderate		13 D	11 D	1 D	
		18 D		11 D	
		20 B		76 F	
		23 C			
		131 C			
High	107 C	19 C			
	24 C				

TABLE 7 (*continued*)

	Depth (m)				
	1000—1999	2000—2999	3000—3999	4000—4999	5000—5999
D. Tanaids					
Low					5 A
					10 E
					9 E
					4 E
Moderate		23 D	19 D	10 D	
		30 D		5 D	
		42 B		78 F	
		32 C			
		77 C			
High	50 C	26 C			
	26 C				

Second, recent work has shown that disruption of the microenvironment of sedimentary microbes stimulates their growth (Yingst and Rhoads, 1980; Aller, 1982). The erosion-deposition regime at our site appears to be capable of such disruption, so enhanced microbial production may explain a portion of the enhanced macrofaunal abundances. Further, the elevated bacterial numbers observed suggest that higher macrofaunal standing stocks can be maintained without reducing bacterial abundances to ordinary deep-sea levels, implying a decrease in the efficiency of the coupling between these trophic levels that may be caused by the disturbance regime.

Given the large amount of suspended material observed, the currents at our site could bear enhanced concentrations of food that, in turn, could be supporting the high macrofauna numbers. For example, Gage (1979) speculates that the anomalously high biomass at 2000 m on the Feni Ridge (eastern North Atlantic) is related to a turbid bottom current having its origin in overflow water from the Norwegian Sea.

The circumstances related above suggest ways that the high standing stocks could occur, but before we conclude, we wish to point out a potential artifact of uncertain importance. The standing-stock comparison was based on numbers of individuals (as is typically done; see Thiel, 1983) rather than biomass because the latter data were not available. Given the preponderance of sub-adults among the HEBBLE polychaetes and bivalves (see above), the abundances of these two taxa could be inflated compared to sites where adults dominated the assemblage (assuming adult biomasses are comparable).

In conclusion, this site appears to contrast strongly with more familiar deep-sea soft-bottom habitats. In particular, macrofaunal standing stocks are unusually high and many species are adapted to shelter in the sediment. Both effects seem to be attributable to a hydrodynamic regime that is much more energetic than those in better studied areas of the deep ocean. Given that such energetic current regimes are not rare (Hollister et al., 1984), present generalizations about the ecology of the deep sea may have to be modified.

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