

# The fauna of the HEBBLE site: patterns in standing stock and sediment-dynamic effects

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## ABSTRACT

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At the High Energy Benthic Boundary Layer Experiment (HEBBLE) site at 4820 m depth on the Nova Scotia Rise (40°27'N, 62°20'W), abundances of polychaetes, bivalves, tanaids, and isopods were conspicuously greater than expected for the depth, whereas those of nematodes and harpacticoids, the two dominant meiofaunal taxa, were not. Further, the abundances of polychaetes, bivalves, tanaids, and nematodes were consistent over time and appeared to be unaffected by the periods of strong near-bottom flow that characterized the site. In contrast, isopods and harpacticoid copepods were less abundant in samples taken as a storm abated, apparently because they were eroded during benthic storms. We explore implications of the difference between macrofaunal and meiofaunal abundance for community structure. In addition, because a goal of the HEBBLE project was the parameterization of sediment transport in the deep sea, we summarize ways that the biota affects sediment transport at this high-energy site.

## Introduction

Community organization in the deep-sea benthos is not well understood. The high diversity (Sanders, 1968; Hessler and Jumars, 1974) suggests that it is complex, but the relative inaccessibility of the deep sea makes collection of edifying data unusually difficult. As a consequence, the analysis of pattern remains important. In this paper, we report a striking pattern in standing stock at a site at 4820 m depth on the Nova Scotia Rise. Four macrofaunal taxa are unusually abundant there, yet the two dominant meiofaunal taxa have abundances that are ordinary for the depth. We examine the stability of this pattern in time and attempt to understand its implication for the organization of the community.

The data were collected as part of the High Energy Benthic Boundary Layer Experiment (HEBBLE), a study of sediment transport in the deep sea (Nowell et al., 1982). It was recognized

at the beginning of HEBBLE that biological effects could have an impact on sediment transport, so a biology component was incorporated into the program. We include a summary of what has been learned about the importance of such effects at the HEBBLE site.

## Locality

The HEBBLE site is at 4820 m depth on the Nova Scotia Rise in the western North Atlantic centered at 40°27'N, 62°20'W (Fig. 1). This site experiences intense sediment-transport events ("benthic storms") several times per year (Gross and Williams, this issue). During these events, near-bottom current velocities can exceed 20 cm s<sup>-1</sup>, and as much as a centimeter of sediment can be eroded (Hollister and McCave, 1984). The surface sediment is a bioturbated clayey silt of 100–160% water content by dry weight, which during one visit varied from 0.5 to 11.3 cm in

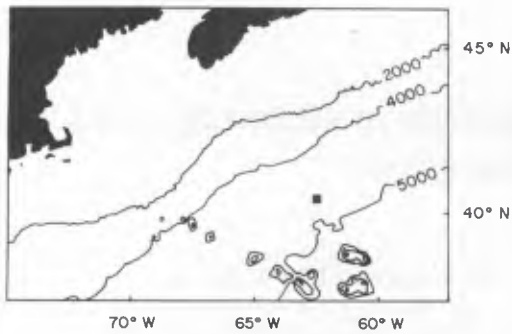


Fig. 1. Chart of the northwest Atlantic showing the location of the HEBBLE site (filled square). Contours are in meters.

thickness over the site (McCave, 1985). Beneath this layer of brown mud lies a sandy layer of  $84 \pm 17\%$  water content, the "sand" being the tests of planktonic Foraminifera (McCave, 1984).

#### Materials and methods

In July 1982 (Hollister and Chandler, 1982), a  $2 \times 4\text{-km}^2$  sampling region, divided into sixteen  $0.5 \times 1.0\text{-km}^2$  areas (see fig. 2 of Reidenauer and Thistle, 1985), was defined relative to in-situ acoustic beacons. A single sample was taken, essentially at random, from each area (see Reidenauer and Thistle, 1985, for details). In June 1983 (Chandler and Hollister, 1983), four samples were taken as above, one from each of four adjacent areas (see fig. 2 of Reidenauer and Thistle, 1985).

The sampling device was a  $0.25\text{-m}^2$  USNEL box corer (Hessler and Jumars, 1974) that had been modified to reduce bow-wave effects (see Thistle, 1983). Nine  $100\text{-cm}^2$  subcores were centered in the core box (see fig. 3 of Reidenauer and Thistle, 1985). Each subcore contained a subsubcore whose lower edges were beveled such that the subcores sampled  $77\text{cm}^2$ . At sea, the water overlying a subcore was filtered through a  $45\text{-}\mu\text{m}$ -aperture sieve, and the residue was added to the 0–1-cm sediment sample. The sediment was then extruded, sliced into layers (0–1, 1–2, 2–3, 3–5, 5–7, 7–10 cm), and preserved in a solution of  $45\text{ }\mu\text{m}$  filtered seawater and formalin (4:1 by volume), buffered to neutrality with sodium borate.

In the laboratory, macrofauna specimens (except polychaetes) were sorted from the  $\geq 0.297\text{-mm}$

fractions from the 0–5-cm layers of each of the nine subcores. Meiofauna (except nematodes) were sorted from the  $\geq 63\text{-}\mu\text{m}$  fractions of two undisturbed subcores selected at random (Carman et al., 1987). Only the 0–1 and 1–2 cm layers were sorted for meiofauna. As an aid to sorting, the meiofauna was concentrated on a  $63\text{-}\mu\text{m}$  sieve with the Barnett (1968) procedure. Polychaetes were sorted from the 0–5 cm layer of the two meiofauna subcores from each box core. Nematodes were sorted by the method of Sherman et al. (1984) from the top 2 cm of sediment from one of the two meiofauna subcores per box core, chosen at random. In 1983, the polychaetes were sorted from nine subcores per box core.

#### Results and discussion

##### *Patterns in standing stock*

Inspection of Figs. 2–5 shows that the HEBBLE values for polychaetes, bivalves, tanaids, and isopods are conspicuously high for their depth and that comparable values are reached elsewhere only in much shallower waters. We tested this qualitative impression by comparing the abundances in the sixteen box cores taken at the HEBBLE site

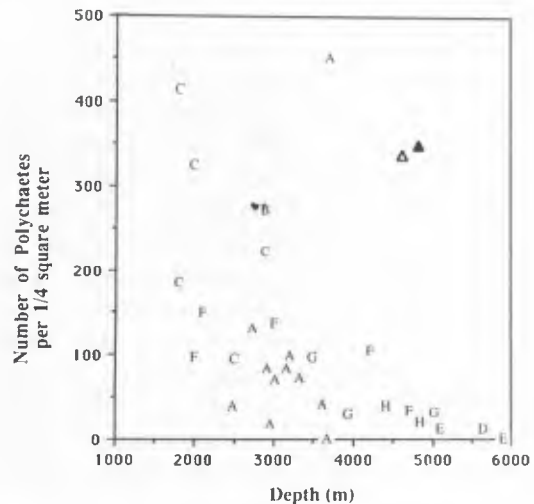


Fig. 2. Median polychaete abundances versus depth. Letters refer to reports in Table 1. The filled triangle is the HEBBLE result (see Table 2). The open triangle is the value reported by Thistle et al. (1985) from a high-energy location near the HEBBLE site.

TABLE 1

Papers reporting deep-sea standing stocks from greater than 1000 m depth that used techniques sufficiently similar to those of HEBBLE to allow comparison. The letters before each entry correspond to those used in Figures 2-7.

Author	Region	Depth (m)	Sieve Aperture (mm)	Sample Depth (cm)
<i>Macrofauna</i>				
A. Dahl et al. (1976)	Norwegian Sea	2479-3718	0.250	0-20
B. Gage (1977)	Rockall Trough	2875	0.420	core depth
C. Gage (1979)	Rockall Trough	1800-2900	0.420	≥25
D. Hessler and Jumars (1974)	Central North Pacific	5634	0.297	0-20
E. Khripounoff et al. (1980)	Vema Fracture Zone	5090-5880	0.250	core depth
F. Laubier and Sibuet (1979)	Bay of Biscay	2000-4700	0.250	—
G. Richardson et al. (1985)	Venezuela Basin	3500, 3950, 5050	0.300	core depth
H. Sibuet et al. (1984)	Demerara Abyssal Plain	4420, 4850	0.250	core depth
I. Thistle et al. (1985)	Nova Scotia Rise	4626	0.297	0-5
<i>Meiofauna</i>				
J. Coull et al. (1977)	Western North Atlantic	4000	0.042	0-10
K. Dinet (1973)	Walvis Ridge	1440-5170	0.040	0-3
L. Dinet (1979)	Norwegian Sea	2479-3709	0.040	0-5
M. Dinet and Vivier (1977)	Bay of Biscay	1939-4645	0.050	0-4
N. Pfannkuche (1985)	Porcupine Seabight	500-4850	0.042	0-5
O. Shirayama (1984)	Western Pacific	2090-5820	0.037	0-30
P. Sibuet et al. (1984)	Demerara Abyssal Plain	4420, 4850	0.040	0-5
R. Thistle et al. (1985)	Nova Scotia Rise	4626	0.062	0-2
S. Woods and Tietjen (1985)	Venezuela Basin	3517, 3858, 5054	0.044	0-6

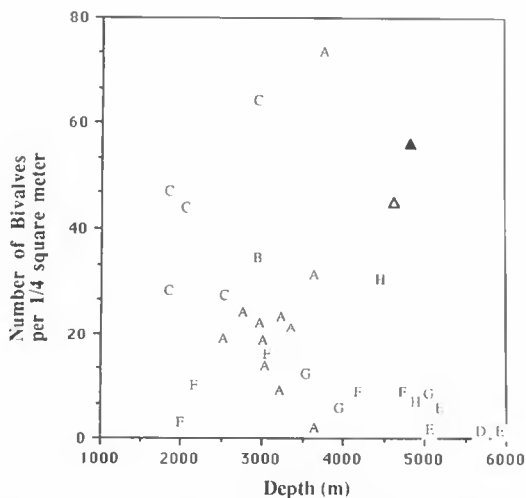


Fig. 3. Median bivalve abundances versus depth. Letters refer to reports in Table 1. The filled triangle is the HEBBLE result (see Table 2). The open triangle is the value reported by Thistle et al. (1985) from a high-energy location near the HEBBLE site.

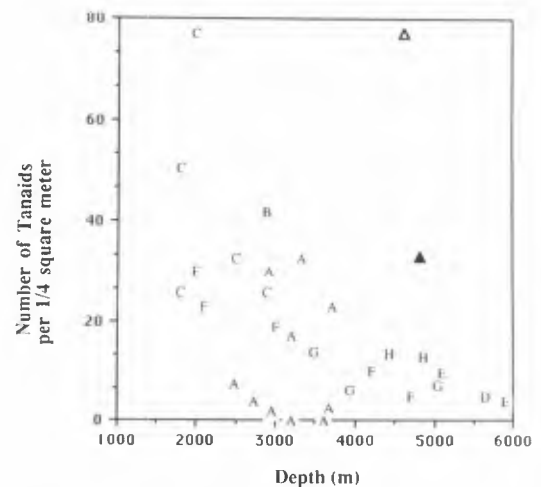


Fig. 4. Median tanaid abundances versus depth. Letters refer to reports in Table 1. The filled triangle is the HEBBLE result (see Table 2). The open triangle is the value reported by Thistle et al. (1985) from a high-energy site near the HEBBLE location.

TABLE 2

Abundances at the HEBBLE site by box core; see Hollister and Chandler (1982) for station data. For macrofauna except Polychaeta, the data given are the total number of individuals in the 0–5 cm layer of sediment summed over nine 77 cm<sup>2</sup> subcores (= 693 cm<sup>2</sup>) per box core. For meiofauna except Nematoda, the data are total number of individuals in the 0–2 cm layer summed over two 77 cm<sup>2</sup> subcores (= 154 cm<sup>2</sup>) per box core. For Polychaeta, the data are from the 0–5 cm layer from the same two subcores as for meiofauna. For Nematoda, the data are from the 0–2 cm layer from one of the two meiofaunal subcores chosen at random.

	Box Core															
	2	4	6	7	9	11	12	14	16	18	21	22	25	27	31	33
<i>Macrofauna</i>																
Polychaeta	22	30	33	16	16	31	21	18	21	21	14	24	17	62	25	29
Bivalvia	7	21	21	15	28	22	19	30	20	9	11	8	10	13	16	8
Gastropoda	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0
Aplacophora	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Tanaidacea	3	15	6	7	8	6	7	12	5	10	16	17	11	15	19	5
Isopoda	9	15	19	15	20	10	5	11	14	13	10	14	20	14	13	12
Amphipoda	2	0	1	0	5	2	2	0	0	1	0	1	2	0	0	0
Cumacea	4	2	4	2	3	2	0	0	0	1	1	3	1	1	3	0
Sipunculida	3	1	1	0	1	0	2	0	3	1	0	0	0	1	1	1
Echiurida	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Ophiuroidea	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Meiofauna</i>																
Nematoda	1129	1130	1098	2400	3094	1359	1489	2523	2228	1126	1448	1468	3584	1328	1540	968
Harpacticoida	147	195	170	281	224	166	196	279	262	166	185	231	269	111	132	96
Ostracoda	20	26	37	35	54	16	25	76	31	28	29	68	47	55	26	22
Kinoryncha	18	9	20	31	29	6	14	35	21	18	17	22	39	16	13	11

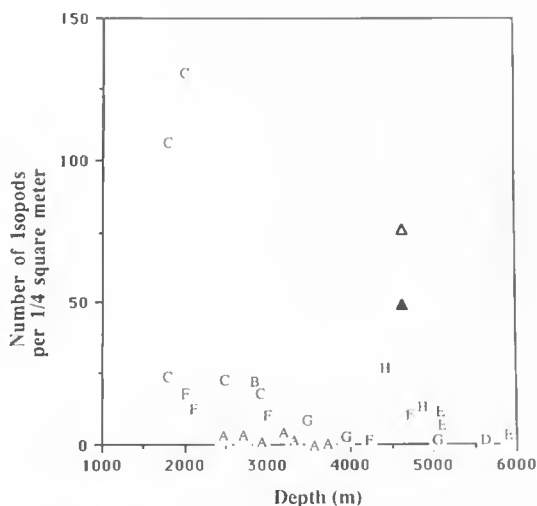


Fig. 5. Median isopod abundances versus depth. Letters refer to reports in Table 1. The filled triangle is the HEBBLE result (see Table 2). The open triangle is the value reported by Thistle et al. (1985) from a high-energy location near the HEBBLE site.

in 1982 to abundances at the site at most nearly the same depth from which values for replicate box cores have been reported (Khripounoff et al., 1980). For each taxon, we found that the abundances at the HEBBLE site were significantly higher (Wilcoxon two-sample test, Sokal and Rohlf, 1969). The results for the meiofauna contrast with those for the macrofauna. Figures 6–7 show that the abundances of the two dominant taxa, nematodes and harpacticoids, are well within the range of observations from similar depths.

To explore the consequences of this disparity for community organization at the HEBBLE site, we examined the feeding habits of the abundant macrofauna. The polychaete fauna (Table 3) is dominated by forms that deposit feed on food concentrated in surface irregularities. Such irregularities may be formed by the animals (e.g., ampharetids, Nowell et al., 1984), or the animals may take advantage of existing features (e.g., spionids, Dauer et al., 1981). In addition to these surface deposit feeders, 38 individuals belong to species that are subsurface deposit feeders, and four speci-

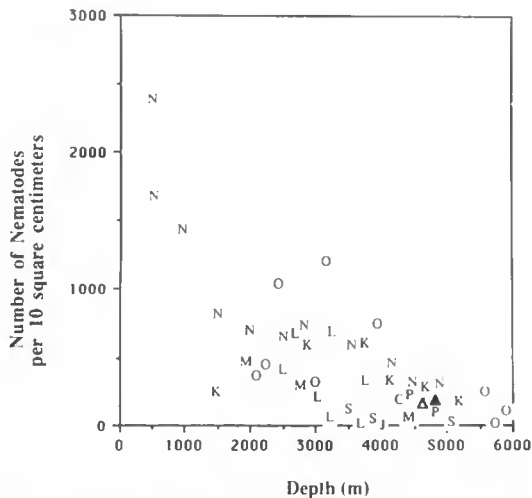


Fig. 6. Median nematode abundances versus depth. Letters refer to reports in Table 1. The filled triangle is the HEBBLE result (see Table 2). The open triangle is the value reported by Thistle et al. (1985) from a high-energy location near the HEBBLE site.

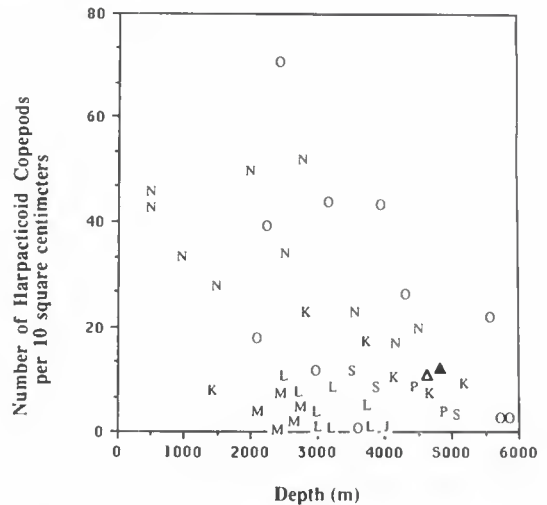


Fig. 7. Median harpacticoid abundances versus depth. Letters refer to reports in Table 1. The filled triangle is the HEBBLE result (see Table 2). The open triangle is the value reported by Thistle et al. (1985) from a high-energy location near the HEBBLE site.

TABLE 3

Polychaetes collected during the 1982 HEBBLE cruise; see Hollister and Chandler (1982) for station data.

Family	Box Core															
	2	4	6	7	9	11	12	14	16	18	21	22	25	27	31	33
Ampharetidae	18	25	25	14	6	22	16	15	16	14	9	19	9	59	19	21
Cirratulidae	1	0	0	0	0	4	1	0	0	1	1	0	1	0	0	0
Cossuridae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Glyceridae	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0
Opheliidae	0	0	0	0	8	0	0	0	0	0	0	0	1	1	0	0
Orbiniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Paraonidae	1	4	2	0	0	0	0	0	3	1	1	0	1	0	0	4
Phyllodocidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pilargiidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Sabellidae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Spionidae	1	1	4	2	2	4	5	3	1	5	2	4	5	0	6	4

mens are known to be carnivores. The bivalves (Thistle et al., 1985), the tanaids (Reidenauer and Thistle, 1985), and the isopods (Menzies, 1962) are also thought to be deposit feeders. Thus, the abundant macrofauna are overwhelmingly deposit feeders and can be expected to ingest all food particles that can fit in their mouths, including meiofauna (Dayton and Hessler, 1972). Therefore, if the macrofauna are feeding at a rate typical for the deep sea, their high standing stock implies an

increased rate of predation on the meiofauna. There is no evidence at the HEBBLE site to indicate that macrofaunal feeding rates are decreased; in fact, the high rates of bioturbation (DeMaster et al., this issue) suggest that macrofaunal activity and particle ingestion are unusually rapid for the depth.

Given this expectation of an increased predation rate on the meiofauna, the fact that their standing stock is not low implies that atypical processes are

at work in structuring this deep-sea community. Either the meiofauna have been released from a source of mortality comparable in magnitude to the increased mortality imposed by the macrofauna, or meiofaunal production has been sufficiently increased over the normal expectation for this depth to compensate for the macrofaunal predation. No data are available with which to assess the possibility of a release from mortality for the meiofauna, but there is evidence that the amount of food available to the meiofauna may be enhanced.

There are several reasons for believing that the flux of food to the seafloor at the HEBBLE site is relatively high. Thistle et al. (1985) document that the site is below a region of moderately high surface productivity, and Aller and Aller (1986) present evidence that high-quality food reaches the sea bed. Further, the HEBBLE site is subject to intermittent, strong horizontal advection. Much of the sediment passing through the HEBBLE region is presumed to originate from the Laurentian Fan on the upper Nova Scotia Rise (Hollister and McCave, 1984). The passage of this hemipelagic, relatively organic-rich sediment could increase the flux of food through the HEBBLE site. Finally, in-situ bacterial production may be enhanced. Several investigators have shown that disruption of the microenvironments of sedimentary microbes, as would be caused by the erosion-deposition cycle of benthic storms at the HEBBLE site, stimulates the growth of sedimentary bacteria (Yingst and Rhoads, 1980; Wainwright, 1987). An increase in sedimentary microbial production should benefit the meiofauna in that 85% of the nematodes at a nearby site appear to be deposit feeders (Thistle and Sherman, 1985), and many harpacticoids are known to feed by scraping microbes from sediment particles (Hicks and Coull, 1983). Therefore, the meiofauna at the HEBBLE site appear to have the opportunity to achieve a high production rate by exploiting a supply of food that is large compared to that at other deep-sea sites and thereby counter the effects of increased macrofaunal predation.

#### *Temporal patterns*

To this point, we have proceeded as if the abundance pattern observed were a constant fea-

ture. In the quiescent deep sea, this assumption might be uncontroversial, but given the strong changes in the physical environment at the HEBBLE site, the temporal consistency of the pattern requires evaluation. We tested for variation in time as follows. In both 1982 and 1983, a box core was taken in each of the four areas in the west corner of the sampling region (see fig. 2 of Reidenauer and Thistle, 1985). For each of the six taxa under consideration, we tested for a difference over time using a randomized-block analysis of variance (area was the blocking factor) (Sokal and Rohlf, 1969), with data transformations as necessary to meet the assumptions of analysis of variance. There was no significant difference over time for polychaetes, bivalves, or tanaids. For polychaetes, the difference in mean abundance is 0.015 individual per 77 cm<sup>2</sup>; for bivalves, the difference is 0.5 individual per 693 cm<sup>2</sup>; for tanaids, the difference is 1.0 individual per 693 cm<sup>2</sup>. The nonsignificant results appear to arise because the differences in abundance are relatively small rather than because the test lacks statistical power (Rotenberry and Wiens, 1985).

Isopods, nematodes, and harpacticoids were significantly less abundant in 1983 (Table 4). Although a variety of alternative hypotheses could be stated, an obvious candidate to explain the difference is an effect associated with benthic storms. That is, because the fauna tends to be concentrated in the surficial sediment (see, e.g., Thistle, 1983; Thistle and Sherman, 1985), it is living in the layer of sediment subject to erosion by benthic storms. If storms do cause the observed decreases in abundance, then the 1983 samples should be found to have been taken during a stormy period, whereas those from 1982 should be found to have been taken during a period between storms. Current-meter data show that the 1982 samples were taken 10 days after the abatement of the most recent storm and that the 1983 samples were taken as a storm was just ending (Weatherly and Kelley, 1985), suggesting that the difference between times could be caused by benthic storms.

Storms could cause the observed decrease in abundance in two ways. First, animals could move into the seabed to escape erosion. The shift of enough of the animals to levels below the depth

TABLE 4

Abundances with depth for isopods and nematodes in the 1982 and 1983 samples from the western portion of the sampling region. Thistle (1988, Table 1) gives the values for harpacticoids.

*Isopods (numbers per 693 cm<sup>2</sup>)*

1982			1983		
Box Core	Layer		Box Core	Layer	
	0-1 cm	1-5 cm		0-1 cm	1-5 cm
2	6	3	2	1	2
9	10	10	5	5	3
16	6	8	6	6	7
24	11	9	8	3	7

*Nematodes (numbers per 77 cm<sup>2</sup>)*

1982			1983		
Box Core	Layer		Box Core	Layer	
	0-1 cm	1-2 cm		0-1 cm	1-2 cm
2	697	432	2	374	204
9	1082	2012	5	874	119
16	812	1416	6	1297	332
24	2372	1212	8	467	309

to which we sampled could account for the observed difference. Alternatively, given the tendency for most taxa to be concentrated near the sediment surface in the deep sea, the storm-caused erosion of the surface sediment could suspend a substantial portion of the fauna.

To distinguish between these hypotheses, we did two analyses. We compared the 0-1-cm layers between 1982 and 1983, testing the null hypothesis of no difference against the one-tailed alternative of a significantly lower abundance in the storm-influenced (1983) samples, using a randomized-block analysis of variance. For isopods and harpacticoids, abundance was significantly lower, as would be expected under either hypothesis. For isopods and harpacticoids, we then compared the abundances in the lower layers between times, testing the one-tailed alternative that abundances would be greater in the lower layers of the storm-influenced samples, as would be expected if animals moved into the seabed to avoid erosion. For both taxa, there was no significant difference between

sampling dates. We were again in the position of failing to reject a null hypothesis. Because the tests of the second null hypothesis were of the same form as those of the first and the abundances were comparable, the test would appear to have adequate statistical power. We conclude that neither isopods nor harpacticoids moved into the lower layers. The results are consistent with the view that isopods and harpacticoids are eroded during storms and kept in suspension long enough that, even as a storm is abating, deposition of individuals advected into the area does not immediately restore abundances to between-storm levels. Thistle and Wilson (1987) and Thistle (1983) argued respectively that surface-living isopods and surface-living harpacticoids are in low abundance in this high-energy environment because they cannot avoid erosion by benthic storms. Our results suggest that even infaunal isopods and harpacticoids do not escape erosion.

The nematodes were neither significantly more abundant in the 1982 0-1-cm layer data nor significantly less abundant in the 1982 1-2-cm layer data despite the significant difference between times when the two layers were combined. Examination of the data reveals considerable variability such that there is no consistent trend in abundance within layer over time. As a consequence, there is no basis for attributing the observed difference in nematode abundance over time to erosion by benthic storms.

To summarize these results, standing stocks of polychaetes, bivalves, and tanaids appear to be relatively constant at the HEBBLE site despite the stormy nature of the physical environment. In contrast, isopod and harpacticoid abundances vary in a manner consistent with the view that they are eroded by benthic storms.

*Sediment-dynamic effects: biologically produced microtopography*

We have documented that the HEBBLE macrofauna is abundant, and the dramatically high bioturbation rates (DeMaster et al., this issue) and the rate of surface-feature production (Wheatcroft et al., 1991) provide evidence of substantial biological activity at the site. Below we summarize how

this abundant and active fauna may be influencing sediment transport.

Biologically produced microtopography appears to be important in sediment transport at the HEBBLE site. Gross and Williams (this issue) report that, on some occasions, strong currents at the HEBBLE site cause extensive erosion. On other occasions, currents of the same magnitude do not cause erosion. Stereophotographs and time-series measurements of bottom stress reveal that the erosive events follow periods in which the organisms have had time to roughen the sediment surface (Gross and Williams, this issue). Wheatcroft et al. (1991) found that the concentration of biologically produced traces reaches 95% of equilibrium concentration in approximately 8.5 days. Given that the average time between storms is about 100 days (Hollister and McCave, 1984; Gross and Williams, this issue), most storms will occur when the bottom is fully roughened. As a consequence, it appears that biologically produced roughness plays an important role in initiating sediment transport at the site.

The physical mechanisms underlying this effect have been studied in shallow water. Eckman and Nowell (1984) have shown that biologically produced microtopography can locally increase boundary shear stress, a measurement of the force exerted between the moving fluid and the bed. As a consequence, microtopography can induce erosion at a velocity lower than that required to do so on a smooth bed (Eckman et al., 1981; Nowell et al., 1981; Eckman and Nowell, 1984). In addition, turbulent perturbations created by these biological "roughness elements" can lead to instability in the near-bottom flow, altering the hydrodynamic nature of the flow and increasing boundary shear stress in general (Nikuradse, 1933; Eckman et al., 1981; Nowell et al., 1981).

#### *Sediment-dynamic effects: biological influence on sediment cohesion and adhesion*

The ease with which fine-grained marine sediments are eroded is largely a function of particle "cohesion" and "adhesion" (sensu Jumars and Nowell, 1984). Infaunal organisms can have two main effects on cohesion, the electrochemical bond-

ing between molecules. In their movement through the sediment, they create voids, and those animals that deposit-feed ingest silt- and clay-sized particles and egest sand-sized fecal pellets (Kraeuter and Haven, 1970), altering sediment packing. Both effects increase the water content of the deposit and increase its erodibility (Rhoads and Young, 1970; see also McCave, 1984).

At the HEBBLE site, the fauna appears to affect sediment cohesion in this way. Many of the bi-valves are subsurface deposit feeders, as are some of the polychaetes. Burrowing sipunculids and large, burrowing echinoids (McCave, 1988; DeMaster et al., this issue) are also important infauna at the site. X-radiographs (e.g., fig. 2 of Yingst and Aller, 1982, and fig. 3 of McCave et al., 1984) show the sediment to be riddled with burrows, even in recently deposited layers. Sediment radio-nuclide profiles confirm the presence of high rates of biological reworking (DeMaster et al., this issue). Although the magnitude of the biological effect cannot be specified, it seems likely that the organisms help maintain and perhaps increase the high water content of the sediment, thus increasing the ease with which it is eroded (Postma, 1967).

Organisms can also alter sediment adhesion, the bonding of particles by an intermediary substance, by secreting sticky organic materials, collectively termed mucus. Sedimentary bacteria produce mucus to attach to sediment grains (Meadows and Anderson, 1968). Nematodes use mucus in burrowing and feeding (Cullen, 1973; Riemann and Schrage, 1978). Some macrofauna use it in locomotion (Nowell et al., 1981), feeding (Jumars et al., 1982), and fecal-pellet formation (Nowell et al., 1981). This material tends to bind sediment particles together, increasing the resistance of the bed to erosion, all else being equal (Rhoads et al., 1978; Grant et al., 1982). Although bacterial abundances (Baird et al., 1985) and macrofaunal abundances are high at the HEBBLE site compared to those at other deep-sea locations, the concentration of mucus in the sediment is less than 1% (D. C. White, unpublished data) of that in shallow-water sediment (Fazio et al., 1982), suggesting that adhesion is unlikely to influence sediment erodibility substantially.



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