



The effect of experimentally increased near-bottom flow on metazoan meiofauna at a deep-sea site, with comparison data on macrofauna

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Abstract

It has been argued that strong near-bottom flows affect macrofauna and meiofauna in the deep sea, but the evidence comes largely from studies that compared sites separated geographically by hundreds to thousands of kilometers and in depth by hundreds of meters. In this paper, the results of the first experimental investigation of the effects of strong near-bottom flow on deep-sea metazoan meiofauna are presented. At a site (32° 27.581' N, 127° 47.839' W) at 583 m depth on the Fieberling Guyot summit plain, the submersible *Alvin* emplaced weirs designed to increase the near-bottom flow locally. After 6.5 weeks, sediments in the weirs and unmanipulated locations in the vicinity were sampled. The abundances of nematodes, harpacticoid copepods, ostracods, and kinorhynchs, considered collectively and as individual taxa, were significantly lower in the weir samples than in the background samples. Parallel responses were observed in total macrofaunal and mollusk abundances. Proportional declines in kinorhynchs and mollusks were observed as well. These results suggest that strong near-bottom flow can reduce the abundance of meiofauna and macrofauna in the deep sea and alter assemblage composition. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Meiofauna; Nematoda; Harpacticoida; Ostracoda; Kinorhyncha; Seamount; Deep sea; Disturbance; Macrofauna

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1. Introduction

Near-bottom flows in much of the deep sea are only a few centimeters per second. Although these flows can move the very lightest materials on the sea floor (e.g. phytodetritus, Lampitt, 1985), they are too slow to erode the seabed or the infauna. In contrast, in some parts of the deep sea, near-bottom flows can be much faster (Hollister *et al.*, 1984; Kontar and Sokov, 1994; Paterson and Lamshead, 1995). For example, at the HEBBLE site (Hollister and Nowell, 1991), in the abyssal northwest Atlantic, near-bottom flows strong enough to erode the top millimeters of sediment occur several times annually (Gross and Williams, 1991).

When macrofaunal assemblages at strong-flow deep-sea sites and at other deep-sea sites have been compared, differences have been discovered that have been attributed to the contrast in flow regime. Near-surface-living tanaids were significantly less abundant at strong-flow sites (Reidenauer and Thistle, 1985), as were near-surface-living isopods (Thistle and Wilson, 1987, 1996). Gage *et al.* (1995; see also Paterson and Lamshead, 1995) found that the species richness and the equitability of certain taxa were significantly lower at strong-flow sites. These results are suggestive, but the comparisons have been made between locations hundreds to thousands of kilometers apart or differing by hundreds of meters in depth, and factors other than the hydrodynamic regime could have contributed to the observed differences. Unambiguous demonstration of the effects of near-bottom flow in the deep sea requires experimental manipulation of flow. Levin *et al.* (1994) reported some results for macrofauna from the first such experiment.

Strong near-bottom flows do affect metazoan meiofauna (called meiofauna hereafter) in shallow water (Palmer and Molloy, 1986; Fegley, 1987; Thistle *et al.*, 1995), and a between-site comparison (Thistle, 1983) suggests that flow affects deep-sea meiofauna as well. In this paper, we present the results of the first experimental investigation of the response of deep-sea meiofauna to strong near-bottom flows. Macrofaunal data from the same samples are then compared to our meiofaunal results.

2. Locality

Fieberling Guyot rises from a base at 4300 m depth to a summit plain of 9 km² between 500 and 700 m depth (see Levin *et al.*, 1994, their Fig. 1). Much of the summit plain is rock. The study site (White Sand Swale = WSS) (32° 27.581' N, 127° 47.839' W) was on the summit plain in a swale about 300 m long and 30–40 m wide between 580 and 585 m depth. The swale floor was covered with white, calcareous sand (Fig. 1) composed of foraminiferan tests. Ripples a few centimeters tall with a wavelength between 10 and 20 cm were present; their orientation suggested that flow was along the major axis of the valley.

At Fieberling, the near-bottom velocities over the summit were high by deep-sea standards. In a current-meter record from 18 m above bottom about 2 km from WSS, 50% of the velocities were greater than 11.2 cm s⁻¹, and velocities as great as 47 cm s⁻¹ were recorded (Wichman *et al.*, 1993). Levin *et al.* (1994) used these data and

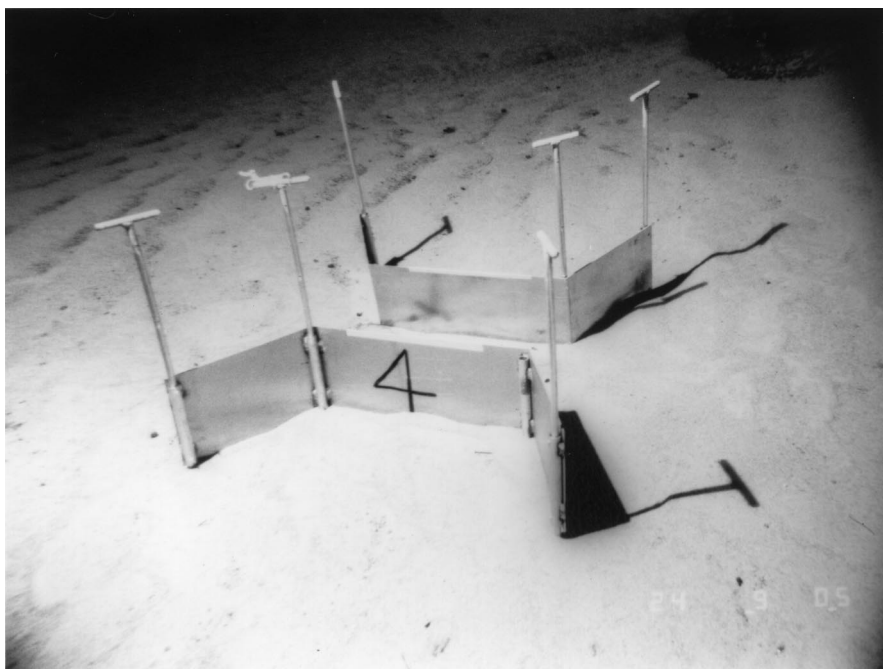


Fig. 1. A weir at White Sand Swale at about 580 m depth on the summit of Fieberling Guyot.

short-term measurements by the Benthic Acoustic Stress Sensor to estimate that near-bottom flow moved the modal size class of sediment daily at WSS. During a four-day measurement period in October 1990, shear velocity exceeded 0.5 cm s^{-1} 45% of the time and 1.0 cm s^{-1} 10% of the time (Levin *et al.*, 1994). Observation of sharp-crested ripples during each dive of three *Alvin* dive series (October 1990, December 1990, June 1991) supported the interpretation of frequent ripple migration (Levin *et al.*, 1994).

3. Materials and methods

In October 1990, we used *Alvin* to place weirs of the sort used in shallow water by Fegley (1987) at WSS to accelerate the near-bottom flow locally. Weirs consisted of paired, 20-cm-tall aluminum plates. Each plate had a 48-cm-long straight section and a 30-cm-long flange at each end, at a 120° angle to the straight section. The plates were placed such that the straight sections were parallel, 30 cm apart, and the flanges formed a funnel-like region at each end (Fig. 1). The flanges compressed the streamlines of the incoming flow, accelerating it through the corridor between the straight sections. The long axis of the corridor was placed perpendicular to the crests of the sediment ripples.

In December 1990 (6.5 weeks after deployment), a $15 \times 15 \text{ cm}^2$ Ekman-style corer was used to sample the corridors of three weirs. Six additional samples were taken from WSS, four with a $15 \times 15 \text{ cm}^2$ Ekman-style corer and two with a $16.2 \times 16.2 \text{ cm}^2$ Ekman-style corer. Cores were divided into quarters on board ship. One quarter was processed for analyses of particle size, organic matter and carbonate content, and microbial abundance as described in Levin *et al.* (1994) (Table 1). The top 10 cm of the three remaining quarters were processed for macrofauna (Table 2) as in Levin *et al.* (1994). Two of the quarters processed for macrofauna were selected at random for the study of meiofauna (resulting in samples of 112.5 cm^2 from the

Table 1

Environmental measures for sediments from cores examined in this study. S.D. = standard deviation; *N* is number of samples. *P* values are for *t*-tests. Bacterial abundances (acridine orange counts) were measured for the 0–1 cm layer and are reported as numbers $\times 10^8 \text{ ml}^{-1}$; methods given by Levin *et al.* (1994)

Parameter	Background			Weir			<i>P</i>
	Mean	S.D.	<i>N</i>	Mean	S.D.	<i>N</i>	
% Sand + gravel	94.5	1.4	5	94.9	2.7	3	NS
% Silt	2.2	1.4	5	1.5	1.5	3	NS
% Clay	3.3	1.7	5	3.5	1.3	3	NS
% Organic carbon	0.119	0.036	6	0.104	0.010	3	NS
% Organic nitrogen	0.014	0.004	6	0.013	0.002	3	NS
% Calcium carbonate	83.4	6.9	6	81.0	6.0	3	NS
Bacterial abundance	2.29	0.18	4	1.85	0.32	3	0.067

Table 2

Number of macrofauna in background and weir samples. Note that samples 22-5 and 22-6 were taken with the larger corer; the table entries have not been adjusted to the area of the smaller corer

	Background						Weir		
	22-5	22-6	23-2	23-4	30-2	30-3	22-2	26-1	26-2
Polychaeta									
Ampharetinae sp. B	0	0	1	0	0	0	0	0	0
<i>Lysippe</i> sp.	2	0	0	0	0	1	0	0	0
Ampharetid juveniles	0	0	1	0	0	0	0	0	0
<i>Leiocapitellides</i> sp.	1	0	0	0	0	2	1	0	0
<i>Notomastus</i> sp.	0	0	0	0	1	0	0	0	0
<i>Caulerella</i> sp. C	2	0	2	1	0	0	0	0	0
<i>Protodorvillea</i> sp. 3	0	0	0	0	4	1	2	2	1
<i>Bonuania</i> sp.	0	0	0	0	0	1	0	0	0
Near <i>Podarkeopsis</i> sp.	0	0	0	0	0	0	0	0	1
Hesionid juveniles	0	1	0	0	2	0	0	1	0
Lumbrineridae sp. 1	0	0	0	0	1	0	0	0	0
<i>Nothria</i> sp.	0	0	0	1	1	0	0	0	0
<i>Paraonis</i> sp.	0	0	2	0	0	0	0	0	0
<i>Synelmis dineti</i>	3	1	1	1	0	6	2	0	3
Sabellidae sp. A	0	0	1	0	0	0	0	0	0
Terebellid juveniles	0	0	0	1	0	0	0	0	0
<i>Flabelligella</i> sp.	0	0	0	0	0	0	0	0	1
Unidentified juveniles	0	1	0	0	0	0	1	0	0
Other vermes									
Oligochaeta sp. A	0	0	1	1	0	0	0	0	0
Oligochaeta sp. B	0	0	0	1	0	0	0	0	0
Nemertea sp. B	0	0	0	0	0	0	0	1	0
Nemertea sp. C	0	1	0	1	1	0	0	0	0
Nemertea sp. D	0	0	1	0	0	0	2	0	0
Sipuncula sp. A	3	0	4	3	1	1	1	1	0
Turbellaria sp. 1	0	0	0	2	0	0	0	0	0
Turbellaria sp. 2	0	0	0	3	2	0	0	1	2
Unidentified vermes sp. H	0	0	0	0	0	0	2	0	0
Unidentified vermes sp. I	0	0	0	0	0	0	0	0	1
Mollusca									
Aplacophora sp. A	5	2	0	2	1	0	0	0	1
Aplacophora sp. B	0	0	2	2	1	3	0	0	0
Aplacophora sp. C	0	0	1	1	0	0	0	0	0
Neomeniomorpha (1)	2	0	0	1	1	0	0	0	0
Neomeniomorpha (3)	1	0	0	0	1	0	1	0	0
Bivalvia sp. A	0	0	1	0	0	0	0	0	0
Bivalvia sp. C	0	1	0	1	2	0	0	0	0
Bivalvia sp. F	0	0	0	3	0	0	0	0	0
Bivalvia sp. G	0	2	0	0	0	0	0	0	0
Cuspidaridae	0	1	0	1	0	0	0	0	0
Gastropoda sp. 3	0	0	0	0	1	0	0	0	0

(continued on next page)

Table 2 (continued)

	Background					Weir			
	22-5	22-6	23-2	23-4	30-2	30-3	22-2	26-1	26-2
Crustacea									
Tanaidacea sp. B	1	0	0	0	0	0	0	0	0
Echinodermata									
Holothuria sp. A	1	0	0	0	0	0	0	0	0
Holothuria sp. B	0	1	0	0	0	0	0	0	0
Echinoidia sp.	1	0	0	0	0	0	0	0	0
Porifera	0	0	0	0	1	0	0	0	0
Total	22	11	18	26	21	15	12	6	10

Table 3

Number of meiofaunal individuals in the 0–2 cm layer of background and weir samples. Note that samples 22-5 and 22-6 were taken with the larger corer; the table entries have been adjusted to make them comparable with the other samples

Sample	Taxon			
	Nematoda	Harpacticoida	Ostracoda	Kinorhyncha
<i>Background</i>				
22-5	874	138	19	62
22-6	230	61	10	8
23-2	1057	176	30	59
23-4	1543	257	35	96
30-2	342	65	30	11
30-3	298	39	2	12
<i>Weir</i>				
22-2	93	11	1	2
26-1	188	28	2	3
26-2	150	45	2	3

smaller and 131.2 cm² from the larger Ekman corer). The 0–1 cm and 1–2 cm layers were sliced from each quarter and preserved in buffered 10% formalin. We divided each sample into three size fractions using 300, 150 and 63 μ m sieves. The meiofauna were concentrated from the fraction caught on the 63 μ m sieve with the aid of a Barnett (1968) trough. After rose-bengal staining, animals were picked from the concentrate and from the two larger fractions, except for nematodes, which were counted but not removed (Table 3). The adult harpacticoids were identified to working species (Table 4).

For comparisons of total abundance, abundance of major taxa, and the proportional composition of the fauna, we normalized the data from the larger sampler (131.2 cm²) to the area of the smaller sampler (112.5 cm²).

Table 4

Number of adult harpacticoid copepods in the 0–2 cm layer of background samples and weir samples. Tentative identifications of the working species are available from the first author. Note that samples 22-5 and 22-6 were taken with the larger corer; the table entries have not been adjusted to the area of the smaller corer

Species	Background samples						Weir samples		
	22-5	22-6	23-2	23-4	30-2	30-3	22-2	26-1	26-2
501	10	2	3	6	1	0	0	0	3
502	7	2	3	0	0	1	0	0	0
503	19	7	19	28	5	1	0	1	9
504	1	7	1	3	4	3	2	1	4
505	1	2	1	9	1	1	0	1	1
506	10	1	3	13	3	0	2	3	0
507	0	0	0	0	1	0	0	0	0
509	0	1	1	6	0	0	0	0	0
510	3	0	2	4	0	0	0	0	0
511	0	0	1	1	0	0	0	0	0
512	2	0	0	0	0	0	0	0	0
513	2	1	1	4	0	1	0	0	0
514	5	0	4	2	1	0	0	0	0
515	1	8	2	6	4	3	1	1	1
517	3	0	0	3	0	0	0	0	0
518	6	1	8	9	1	2	1	1	3
519	4	1	1	4	0	0	0	0	0
520	0	2	1	3	0	0	0	0	1
521	0	0	0	1	1	0	0	0	1
522	5	0	3	5	0	1	0	3	0
523	0	5	0	0	0	0	1	0	0
524	0	2	1	3	0	2	0	1	0
525	0	0	0	4	0	0	0	0	0
526	1	0	0	0	0	0	0	0	0
527	1	0	0	1	0	0	0	0	0
529	8	0	16	9	0	0	0	0	1
530	0	0	1	0	0	0	0	0	0
531	1	0	2	1	0	0	0	0	0
534	1	0	0	0	0	0	0	0	0
535	1	0	0	0	1	0	0	0	0
536	0	0	1	0	0	0	0	0	0
537	0	0	0	1	0	0	0	0	0
538	2	0	2	3	2	0	0	3	1
539	8	1	4	5	4	0	0	3	1
540	0	0	0	0	1	0	0	1	1
541	4	0	1	1	0	0	0	0	0
542	0	0	0	1	0	0	0	0	1
544	0	0	0	0	1	0	0	0	0
545	2	1	4	4	1	1	0	1	1
557	0	0	0	1	0	0	0	0	0
Copepodites	52	27	90	116	33	23	4	8	16
Total	160	71	176	257	65	39	11	28	45

To compare diversity in weir samples to that in background samples at WSS, we used Tipper's (1979) procedure, which involved calculating rarefaction curves to estimate the number of species that would have been found if fewer individuals had been collected in each sample (Sanders, 1968; Hurlbert, 1971). Rarefaction assumes that the distribution of individuals among samples is homogeneous for each species. To test this assumption, we calculated dispersion-chi-square statistics (Jumars, 1975) for each set of data. In this procedure, Fisher's index of dispersion is calculated and summed over species. This total is partitioned into "pooled" and "heterogeneity" components. The latter measures discordance in species' abundances among samples. If it is significantly greater than random expectation, some species are abundant where others are rare, and rarefaction will overestimate diversity (Jumars, 1975). Only individuals that had been assigned to species-level categories were included in the diversity calculations.

We used the Mann–Whitney U-test (Tate and Clelland, 1957) to test for differences between medians and *t*-tests to test for differences between means. In this exploratory paper, we did not correct for multiple testing.

4. Results

Means of sediment grain size, organic C and N content, carbonate content, and bacterial abundance in weir samples did not differ significantly from those in background samples (Table 1), but bacterial abundances in each of the weir samples were lower than any of the abundances in background samples, and the *p* value for the difference between means was 0.067.

4.1. Meiofauna

We found that the median of total abundance of meiofauna (which in this study consisted of nematodes, harpacticoid copepods, ostracods, and kinorhynchs; Table 3) was significantly lower ($p < 0.05$, two-tailed) in the weir samples (median = 200 per 112.5 cm²) than in the background samples (median = 771 per 112.5 cm²). Similarly, we found that the median abundances of nematodes (150 versus 608), harpacticoids (28 versus 102), ostracods (2 versus 25), and kinorhynchs (3 versus 36) were significantly lower in the weir samples than in the background samples ($p < 0.05$ in all cases, two-tailed tests).

We compared the composition of the meiofauna in the two sets of samples by calculating the proportion of the total meiofauna in a sample that each of the four taxa constituted. We tested two-tailed for a difference in the medians of these proportions between weir and background samples. Only for kinorhynchs was the difference significant (1.6% in weir samples versus 3.9% in background samples, $p < 0.05$).

The anticipated lower species richness (Gage *et al.*, 1995) in the weir samples than in the background samples was not found for harpacticoids ($p > 0.10$, Tipper procedure, one-tailed) (Fig. 2A). The heterogeneity-chi-square values (Table 5) were significant,

indicating that the estimates were biased (Jumars, 1975). The ratio of the heterogeneity-chi-square value to its degrees of freedom (Table 5) is greater for the background samples than for the weir samples. Under these circumstances, rarefaction overestimated the species richness of the background samples to a greater degree than it did in the case of the weir samples, making this bias conservative.

We tested for the anticipated lower evenness in the weir samples than in the background samples (Gage *et al.*, 1995) by calculating evenness values (the “*J*” statistic (natural logarithm base), Pielou, 1969) for the harpacticoid data. The medians of *J* for the weir (0.94) and background samples (0.88) did not differ significantly. The lack of a significant difference is unlikely to be the result of insufficient statistical power, because the rank order of the medians is the opposite of expectation.

We could not investigate the expectation from Thistle (1983) that surface-living harpacticoids would be proportionately less abundant in the weir samples, because only two individuals of this functional group were present in the background samples and none were present in the weir samples, too few to permit a meaningful test.

4.2. Macrofauna

The total abundance of macrofauna (Table 2) in weir samples (median = 10) did not differ significantly ($p > 0.10$, two-tailed test) from that in background samples (median = 18.4). For the two abundant macrofaunal taxa, the abundance of polychaetes in the weir samples (median = 6) did not differ from that in the background (median = 7.5) samples, but the abundance of mollusks did (weir median = 1, background median = 6.1) ($p < 0.05$, two-tailed test).

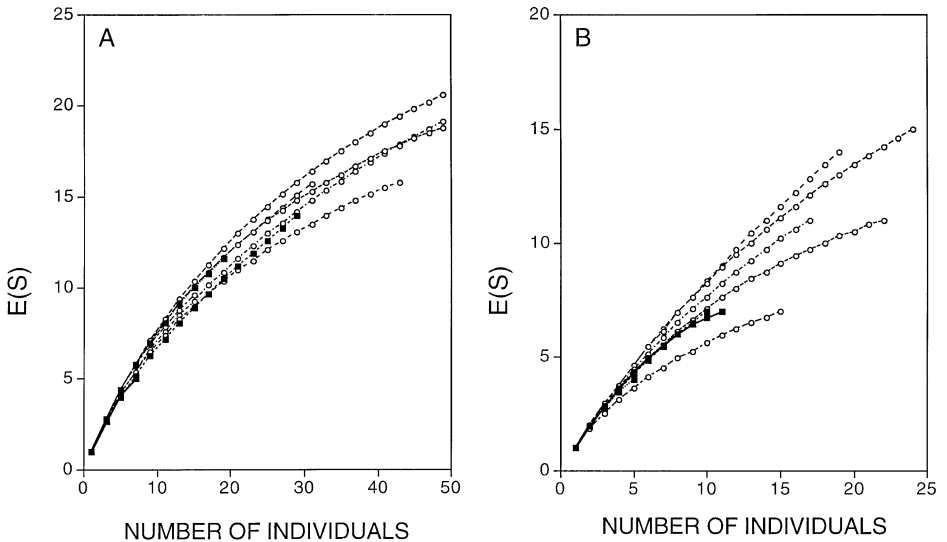


Fig. 2. Hurlburt (1971) rarefaction curves for (A) adult harpacticoid copepods and (B) total macrofauna for weir samples (filled squares) and background samples (open circles). *E(S)* is the estimated number of species at a given number of individuals. Each curve represents a single core.

Table 5

Heterogeneity-chi-square statistics (Jumars, 1975) for adult harpacticoid copepods and total macrofauna

Site	Heterogeneity chi square	Degrees of freedom	Ratio
<i>Harpacticoid copepods</i>			
Background	284.8	195	1.46
Weir	41.9	34	1.23
<i>Total macrofauna</i>			
Background	214.5	165	1.30
Weir	25.8	24	1.08

To compare the composition of the macrofauna in the two sets of samples, we tested for a difference between background and weir samples in the proportion that polychaetes and mollusks constituted of the total macrofauna. The median proportion of polychaetes was 0.40 in the background and 0.50 in the weirs; the difference was not significant. The median proportion of mollusks was 0.36 in the background and 0.08 in the weirs, a significant difference ($p < 0.05$, two-tailed test).

None of the macrofaunal major taxa was individually abundant enough to be usefully analyzed with the Tipper (1979) procedure, so we compared the species richnesses of total macrofauna in background and weir samples. The difference was not significant ($p > 0.10$, Fig. 2B). The heterogeneity-chi-square value for the background samples was significant; that for the weir samples was not. Rarefaction can be expected to overestimate the species richness of the former relative to the latter. Given that greater species richness was anticipated in the background samples but not found, this bias is conservative.

We tested for differences in evenness between background and weir samples. For polychaetes, the median J 's for the weir (0.93) and background samples (0.95) did not differ significantly. For mollusks, the abundances in the weir samples (Table 2) did not permit a meaningful test.

5. Discussion

The question we sought to answer with our experiment was whether strong near-bottom flows had a detectable effect on the meiofauna. We used weirs, which force near-bottom water to flow through a smaller cross section, increasing its speed and therefore the shear stress it exerts on the seabed (Fegley, 1987; Judge *et al.*, 1992), as a means of manipulating near-bottom flow. We did not measure the speed of the flow in the weirs, but the sediment in each of the weir corridors was scoured (Levin *et al.*, 1994), so we infer that the near-bottom flow in the weir corridors was, at least intermittently, faster than that in areas without weirs at WSS.

The abundances of nematodes, harpacticoids, ostracods, and kinorhynchs both taken together and taken as individual taxa were significantly lower in weir samples

than in background samples. The proportion of the meiofauna consisting of kinorhynchs was also significantly lower in the weir samples. Therefore, artificially increased near-bottom flow influences the density and structure of the meiofaunal assemblage at WSS.

Similar effects were found for the macrofauna. The median macrofaunal abundance in the weir samples was only 54% of that in background samples (versus 26% for meiofauna). Mollusks were significantly less abundant in weir than in control samples, as was the proportion of the macrofauna that they constituted. Therefore, artificially increased near-bottom flow does affect the macrofauna of WSS (see also Levin *et al.*, 1994).

Because we could do only a single experiment, we do not know whether the changes we observed persisted. For example, our samples may have been taken near the time of maximum negative effect, and a new, high-flow-tolerant fauna may have recruited subsequently. Samples from such a fauna might not show the lower abundances and different faunal compositions we observed. Despite this limitation, our main point appears valid: strong near-bottom flows can affect deep-sea meiofauna.

Several mechanisms could underlie the effects on meiofauna. In shallow water, meiofauna can be eroded during periods of increased near-bottom flow (Palmer and Gust, 1985; Thistle *et al.*, 1995), so the lower abundances of meiofauna in the weirs could have arisen because the faster flow in the weirs eroded the meiofauna more frequently there than in the background.

If the meiofauna had been affected in the weirs and not the macrofauna, the view that erosion of meiofaunal individuals was the mechanism would have been supported. That is, erodability increases as particles decrease in size, decrease in density, and increase in proximity to the sediment surface. The average meiofaunal individual is smaller and less dense and lives nearer the sediment surface than the average macrofaunal individual and does not have the ability to extend a tube or a foot as an anchor into the sediment below the layer reworked by the flow. This difference in average susceptibility to erosion may be part of the explanation, but the fact that mollusks were rarer in the weir samples than in the background samples suggests that the effect of increased near-bottom flow on the fauna is more complicated than simply the erosion of individuals. In particular, animals may emigrate from sediment where the biomass of microbes per unit mass of sediment is decreased. Although the difference was not significant ($p = 0.067$), weir sediments had fewer bacteria than did background sediments, indicating that this hypothesis is worth further study.

Our results may be conservative. Because White Sand Swale experienced near-bottom flows strong enough to rework the sediment on a daily basis, the fauna from the background samples should already have been adapted to strong flows. This effect would make the differences between the background fauna and that in the weirs smaller than would occur if the control data had been obtained from a less-energetic site. This circumstance may explain why we did not find the anticipated difference in harpacticoid or total macrofaunal diversity or in harpacticoid and polychaete equitability (Gage *et al.*, 1995). It may also explain why surface-living harpacticoids were so rare that we could not test for the expected difference between the weir and background samples (Thistle, 1983).

Our results for meiofaunal abundance differed from those at the high-energy HEBBLE site. At the HEBBLE site, the meiofauna appeared to be susceptible to erosion by the benthic storms that occur there (Thistle, 1983), but the abundances of nematodes and harpacticoids there were not lower than at quiescent localities (Thistle *et al.*, 1985, 1991). In contrast to that in weir sediments at Fieberling, food for the benthos appeared to be unusually abundant at the HEBBLE site (Aller and Aller, 1986; Thistle *et al.*, 1991). Higher population growth rates of meiofauna may compensate for the erosive losses at the HEBBLE site.

Near-bottom flows that occasionally cause erosion around roughness elements (see Gage, 1977) could create patchiness (by decreasing the abundance of meiofauna) on a scale that promotes diversity (Grassle, 1989). Faster or more frequent flows could lower diversity by destroying the small-scale patchiness that maintains it (Thistle, 1998).

These effects, and perhaps others to be discovered, may occur in a variety of deep-sea settings where near-bottom flows are strong, such as seamount summits, the floors of submarine canyons, and regions exposed to benthic storms.

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