



PERGAMON

Deep-Sea Research I 46 (1999) 2041–2052

DEEP-SEA RESEARCH
PART I

Physical reworking by near-bottom flow alters the metazoan meiofauna of Fieberling Guyot (northeast Pacific)

David Thistle^{a,*}, Lisa A. Levin^b, Andrew J. Gooday^c,
Olaf Pfannkuche^d, P. John D. Lambshead^e

^a*Department of Oceanography, Florida State University, Tallahassee, FL 32306-4320, USA*

^b*Marine Life Research Group, Scripps Institution of Oceanography, La Jolla, CA 92093-0218, USA*

^c*Institute of Oceanographic Science, Southampton Oceanography Centre, European Way,
Southampton SO14 3ZH, UK*

^d*GEOMAR, Wischhofstrasse 1-3, 24148 Kiel, Germany*

^e*The Natural History Museum, Cromwell Road, London SW7 5BD, UK*

Received 27 April 1998; received in revised form 9 October 1998; accepted 12 January 1999

Abstract

Although much of the deep sea is physically tranquil, some regions experience near-bottom flows that rework the surficial sediment. During periods of physical reworking, animals in the reworked layer risk being suspended, which can have both positive and negative effects. Reworking can also change the sediment in ecologically important ways, so the fauna of reworked sites should differ from that of quiescent locations. We combined data from two reworked, bathyal sites on the summit of Fieberling Guyot (32°27.631'N, 127°49.489'W; 32°27.581'N, 127°47.839'W) and compared the results with those of more tranquil sites. We tested for differences in the following parameters, which seemed likely to be sensitive to the direct or indirect effects of reworking: (1) the vertical distribution of the meiofauna in the sea bed, (2) the relative abundance of surface-living harpacticoids, (3) the proportion of the fauna consisting of interstitial harpacticoids, (4) the ratio of harpacticoids to nematodes. We found that the vertical distributions of harpacticoid copepods, ostracods, and kinorhynch were deeper on Fieberling. In addition, the relative abundance of surface-living harpacticoids was less, the proportion of interstitial harpacticoids was greater, and the ratio of harpacticoids to nematodes was greater on Fieberling. These differences between Fieberling and the comparison

* Corresponding author. Tel.: 001-850-644-6700; fax: 001-850-644-2581.

E-mail address: thistle@ocean.fsu.edu (D. Thistle)

sites suggest that physical reworking affects deep-sea meiofauna and indicate the nature of some of the effects. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Meiofauna; Nematoda; Harpacticoida; Seamount; Deep sea; Disturbance

1. Introduction

Much of our knowledge of soft-bottom deep-sea communities comes from regions that do not experience near-bottom flows strong enough to rework the sediment. More recent studies have discovered areas of the deep sea where sediments are reworked by near-bottom flow (Gross and Williams, 1991; Kontar and Sokov, 1994), and interest in determining the consequences of this physical reworking (hereafter reworking) for the fauna has been substantial (Thistle et al., 1985, 1991; Aller, 1989, 1997; Levin et al., 1994; Gage et al., 1995; Paterson and Lambshead, 1995).

Reworking of sediments should affect meiofauna. These animals are comparable in size to fine sand and are much less dense than sediment particles, so when the sediment around them begins to move, they risk being suspended. Suspension can be beneficial; for example, it can increase dispersal and relieve benthic crowding (Service and Bell, 1987). Suspension can also be detrimental; for example, animals can be damaged while being removed from the sea bed, they can be expatriated, and they can be exposed to water-column predators (d'Amours, 1988; Shearer, 1998). A suspended animal may be unable to conduct its usual activities efficiently, so, for example, its energy stores can become depleted (Thistle et al., 1995).

In our study, we found that the metazoan meiofauna (hereafter meiofauna) of two reworked sites on the summit of Fieberling Guyot were similar enough to be combined and used for comparison with other sites. We then tested for evidence that reworking altered the combined Fieberling meiofauna by comparing it to that of deep-sea sites that were relatively unaffected by reworking. We assumed that the distribution of a variable of interest at the comparison sites we chose was representative of such sites generally and inferred that significant differences between Fieberling and the comparison sites were due to reworking. Given the limitations of the data set, only four types of comparison could be made. Still, though our study was not an exhaustive investigation of reworking, we found many differences that seemed attributable to its effects.

We focused first on features of the meiofauna that seemed likely to be sensitive to the direct effects of reworking. Reworking occurs most frequently and intensely in the upper sediment layers, and its effects can be both positive (Service and Bell, 1987) and negative (d'Amours, 1988). If reworking confers a net benefit on the members of a group, then the vertical distribution of the group should be shifted toward the sediment surface relative to that at a comparison site. The opposite pattern would indicate a net negative effect. (1) We tested for a difference in vertical distribution between Fieberling and a comparison site for each meiofaunal major taxon.

Some deep-sea meiofauna taxa appear to be obligately associated with the sediment surface (Thistle, 1982) and are therefore particularly exposed to the effects of reworking. If the net effect of reworking on these taxa is negative, their abundance should be less where reworking is greater. A net positive effect should produce the opposite. (2) We tested for a difference in surface-living harpacticoid-copepod abundance between Fieberling and a comparison site.

Reworking could also affect the meiofauna indirectly. Reworking removes fine particles disproportionately, increasing the amount of interstitial space, which will increase the proportion of the deposit with conditions favorable for interstitial harpacticoids. (3) We tested for an increase in the proportion of interstitial to other harpacticoids on Fieberling relative to that at a comparison site. In shallow water, an increase in interstitial space results in an increase in the abundance of harpacticoids relative to that of nematodes (Wieser, 1959). (4) We tested for an increase in the ratio of harpacticoids to nematodes on Fieberling relative to that at a comparison site.

2. Localities

Fieberling Guyot is in the northeast Pacific about 992 km west of San Diego. It rises from 4300 m depth to a summit plain of 9 km² lying mostly between 500 and 700 m depth (see Levin et al., 1994, their Fig. 1). Much of the summit plain is exposed rock, but two sediment-covered sites were located for study. Sea Pen Rim (SPR) (32°27.631'N, 127°49.489'W) was between 630 and 640 m depth. The sediment was a medium sand consisting primarily of basalt particles (Table 1). For a frequency distribution of particle sizes, see Levin et al. (1994, their Fig. 4). Sediment ripples a few centimeters high with wavelengths of 10–30 cm were present. White Sand Swale (WSS) (32°27.581'N, 127°47.839'W) was 2.3 km to the east in a valley about 300 m long and 30–40 m wide between 580 and 585 m depth. The sediment was also a medium sand but included less gravel (Table 1) and consisted primarily of globigerinacean foraminiferan tests (Levin et al., 1994). Organic carbon content and

Table 1

Environmental measures from sediments at Sea Pen Rim and White Sand Swale (Fieberling Guyot). Entries are means; standard deviations are in parentheses. For methodological details see Levin et al. (1994)

	Sea Pen Rim	White Sand Swale
% Gravel	2.66 (3.01)	0.05 (0.05)
% Sand	93.09 (2.11)	96.02 (2.95)
% Silt	3.60 (2.79)	1.56 (1.60)
% Clay	0.93 (0.66)	2.38 (2.18)
% Organic carbon	0.134 (0.028)	0.119 (0.034)
% Organic nitrogen	0.016 (0.002)	0.014 (0.004)
% Calcium carbonate	19.9 (9.6)	82.4 (6.7)
Bacterial counts ($\times 10^8$ ml ⁻¹) (0–1-cm layer)	2.06 (0.98)	1.91 (0.66)

bacterial numbers were comparable to those at SPR (Table 1). Sediment ripples a few centimeters high with wavelengths of 10–20 cm were present.

Near-bottom currents on Fieberling's summit were strong (20 cm s^{-1} at 4 m above bottom) and were dominated by diurnal fluctuations driven by tides (Eriksen, 1991). Modal-size particles moved daily at WSS but less frequently at SPR. The sediment at each site contained only a small proportion of fine particles (Levin et al., 1994), as would be expected for reworked sediments. The dissolved oxygen concentration near Fieberling was $\sim 0.8 \text{ ml/l}$ (Levin and Gage, 1998). The presence of a lush benthic megafauna at each site (Levin et al., 1994) suggests that the oxygen concentration of the near-bottom water was not physiologically limiting.

Because our comparisons depended on accurate sampling of animals at the sediment–water interface, we chose to use only data taken by multiple corer, remotely operated vehicle, or research submarine (Barnett et al., 1984; Bett et al., 1994). For comparisons of vertical distributions by major taxon, we used data from samples collected by multiple corer from a site in the Porcupine Seabight (PSB) (northeast Atlantic, $51^{\circ}36'N$, $13^{\circ}00'W$) between 1320 and 1340 m depth (see Gooday et al., 1996, for details) (Table 2). The sediment at PSB was a well-oxygenated *Globigerina* ooze (57% clay and 35% silt) (Gooday, 1986) with an organic carbon content of 0.5% (Rice et al., 1991). Near-bottom currents in this region were $\leq 13 \text{ cm s}^{-1}$ at 1.3 m above bottom (Billett et al., 1983). They were intermittently strong enough to move phytodetritus (Lampitt, 1985), but there have been no reports of sediment motion, and no sediment ripples have been observed (AJG, personal observation). When reworking is intense enough to cause particles to move in bedload transport, ripples are

Table 2

Abundance data from the Porcupine Seabight (Discovery station 51502) (see Gooday et al., 1996, for site description and sampling methods). The data are means of syringe (3.46 cm^2) subsamples from multiple-corer samples

Deployment	Nematoda		Ostracoda	
	0–1-cm layer	1–2-cm layer	0–1-cm layer	1–2-cm layer
1	136.3	64.0	4.0	0.8
2	227.5	132.0	2.3	0.0
4	175.8	62.5	3.8	0.0
5	158.0	144.3	3.5	0.5
6	195.5	119.0	6.8	1.3
8	193.3	154.3	5.3	0.7
	Harpacticoida		Kinorhyncha	
1	23.0	1.0	0.5	0.5
2	16.0	1.8	2.0	0.0
4	12.8	0.8	2.5	0.0
5	23.8	5.3	1.3	0.0
6	15.8	0.5	0.8	0.0
8	17.5	3.0	2.7	0.3

produced. The absence of ripples at PSB indicates that the reworking regime there is much less intense than that on Fieberling.

Data on the proportion of the harpacticoid fauna that were surface living and the proportion that were interstitial were unavailable from PSB, so we used data from samples collected by remote underwater manipulator from a site at 1220 m depth in the San Diego Trough (SDT) (eastern North Pacific, 32°35.75'N, 117°29.00'W) (Thistle, 1978) for these comparisons. The sediment at SDT was a hemipelagic green mud with an organic carbon content of 1–3% (Emery and Hulsemann, 1963). In San Diego Trough, the modal current speed at 1 m above bottom was 3 cm s⁻¹; the maximum speed was 10 cm s⁻¹ (Thistle and Eckman, 1990). No ripples were present at the SDT site (DT, personal observation). SDT could not be used for the other comparisons because only harpacticoid data were available.

3. Materials and methods

We used the submersible *Alvin* and a 15-cm- \times -15-cm Ekman-style corer to take four cores at SPR and four at WSS. We took two additional cores from WSS with a 16.2-cm- \times -16.2-cm Ekman-style corer. Sediments were sampled to a depth of 10 cm. Cores were divided into quarters on board ship; two quarters from each corer were selected at random for the study of meiofauna (resulting in samples of 112.5 cm² for the smaller and 131.2 cm² for the larger Ekman corer). The 0–1- 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 was concentrated from the fraction caught on the 63- μ m sieve with a modification of the Barnett (1968) troughing procedure. After rose-bengal staining, animals were transferred from the concentrate and from the two larger fractions to slides, except for nematodes, which were counted but not transferred. Adult harpacticoids were identified to working species (most harpacticoid species on Fieberling are undescribed). For comparisons in which species identifications were not necessary, both adult and juvenile (copepodite-stage) harpacticoids were included.

For abundance comparisons of meiofaunal major taxa, we combined the 0–1- and 1–2-cm values from the two quarters of each core (Table 3) and normalized this value to 10 cm². For functional-group comparisons of harpacticoids, we generally followed Thistle (1982), assigning members of the Anchorabolidae, *Eurycletodes*, and a dorsoventrally flattened species (*cf.* Zausodiinae) to the surface-living group and vermiform species with reduced pereopods from families known to contain primarily interstitial species (Cylindropsyllidae and Paramesochridae) to the interstitial group. Many species (72%) did not belong to either group and were not included in these comparisons. To compare the relative abundances of harpacticoids and nematodes, we calculated the ratio of harpacticoids to the sum of harpacticoids and nematodes (= the H/(H + N) ratio) in the 0–2-cm layer. The comparison data from SDT were from the 0–1-cm layer, so the 0–1-cm layer data from Fieberling were used when SDT was the comparison site.

Table 3

Number of individuals per 112.5 cm² of meiofauna by layer in the four samples from Sea Pen Rim and the six samples from White Sand Swale

Sea Pen Rim		White Sand Swale	
0–1-cm layer	1–2-cm layer	0–1-cm layer	1–2-cm layer
Nematoda			
185	200	471	403
510	355	87	142
199	156	539	518
538	239	851	692
		150	192
		212	86
Harpacticoida			
51	36	80	57
74	34	16	45
45	11	76	100
122	84	170	87
		25	40
		29	10
Ostracoda			
2	3	12	7
12	7	2	8
0	2	25	5
24	12	19	16
		9	21
		1	1
Kinorhyncha			
0	0	32	30
14	2	3	5
3	3	28	31
12	7	53	43
		5	6
		8	4

Tests for differences between medians were done by randomization with replacement (4999 trials) (Bruce, 1991). Confidence limits were calculated by bootstrap (5000 replications) (Bruce, 1991). We tested two tailed except where our *a priori* hypotheses were directional. In this exploratory study, we did not correct for multiple testing; the alpha level for each test was 5%.

4. Results

4.1. Sea Pen Rim versus White Sand Swale

SPR and WSS did not differ significantly in either median abundance (per 10 cm²) (Table 4A) or ratio of 0–1- to 0–2-cm abundance (Table 4B) for any meiofaunal major taxon. The 95% confidence limits overlapped extensively.

Table 4

(A) Medians and 95% confidence levels for abundances (number of individuals per 10 cm²) of meiofaunal major taxa in the 0–2-cm layer. (B) Medians and 95% confidence limits for the ratio of number of individuals in the 0–1-cm layer to that in the 0–2-cm layer. (C) Medians and 95% confidence limits for the proportion of the harpacticoid fauna belonging to the interstitial and surface-living groups of the 0–2-cm layer

	Sea Pen Rim			White Sand Swale		
	Median	Lower	Upper	Median	Lower	Upper
A.						
Nematoda	51.7	31.6	76.9	53.8	23.5	115.6
Harpacticoida	8.7	5.0	18.3	9.1	4.5	19.2
Ostracoda	1.1	0.2	3.2	2.2	0.5	2.9
Kinorhyncha	1.0	0.0	1.7	3.2	0.9	7.0
B.						
Nematoda	0.58	0.48	0.69	0.52	0.41	0.63
Harpacticoida	0.64	0.59	0.80	0.51	0.32	0.70
Ostracoda	0.60	0.50	0.67	0.53	0.39	0.64
Kinorhyncha	0.63	0.50	0.88	0.50	0.40	0.61
C.						
Interstitial	0.45	0.26	0.61	0.37	0.26	0.54
Surface-living	0.01	0.00	0.06	0.00	0.00	0.05

SPR and WSS did not differ significantly in the median proportions of the surface-living and interstitial groups of harpacticoids; the 95% confidence limits were nearly coextensive (Table 4C). SPR and WSS did not differ significantly in H/(H + N) ratios (medians = 0.160 and 0.142, respectively); the 95% confidence limits were nearly coextensive (0.111–0.209 and 0.130–0.186).

4.2. Fieberling versus comparison sites

Because the meiofaunas at SPR and WSS were similar (see below), data from the two sites were combined (and are referred to as the Fieberling meiofauna) in comparisons with the more quiescent sites.

The ratios of 0–1- to 0–2-cm abundance for harpacticoids, ostracods, and kinorhynchans were all significantly less (i.e., the population was shifted deeper) at Fieberling than at PSB (Fig. 1). For nematodes, the median ratio was less at Fieberling Guyot than at PSB (Fig. 1), but the difference was not significant ($p = 0.22$). The median proportion of the harpacticoid fauna that was surface living was significantly less at Fieberling than at SDT (0.00 versus 0.04). The median proportion of the Fieberling harpacticoid fauna that was interstitial was significantly greater than that at SDT (0.40 versus 0.08).

The H/(H + N) ratio was significantly greater on Fieberling than at PSB (0.14 versus 0.06). We also compared the H/(H + N) ratio on Fieberling to those at 13 relatively quiescent deep-sea sites that had been sampled by multiple corer (Table 5).

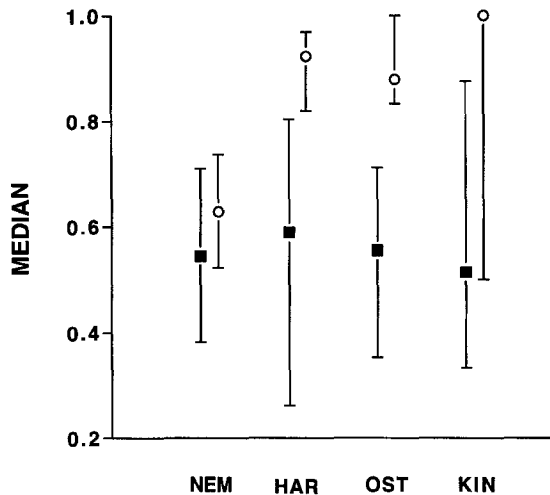


Fig. 1. Ratio of 0–1-cm layer to 0–2-cm layer abundance for Nematoda (NEM), Harpacticoida (HAR), Ostracoda (OST), and Kinorhyncha (KIN) from Fieberling (filled squares) and Porcupine Seabight (open circles). Bars represent ranges.

Table 5

The ratio of harpacticoids to the sum of harpacticoids and nematodes ($H/(H + N)$ ratio) for the 0–2-cm layer

Source	Station	Depth	$H/(H + N)$ ratio
A	511-12	510	0.027
A	511-03	960	0.023
A	511-05	2000	0.067
B	226	582	0.021
B	229	502	0.028
B	235	339	0.014
B	241	458	0.011
B	245	492	0.083
B	248	633	0.092
B	249	708	0.042
B	250	806	0.017
B	252	1185	0.017
B	253	1958	0.045
C	Sea Pen Rim	635	0.160
C	White Sand Swale	583	0.152

A = Pfannkuche's (1985) data from the Porcupine Seabight. B = Herman and Dahms' (1992) data from the Weddell Sea. C = Data from this paper. For Pfannkuche (1985) and Herman and Dahms (1992), the 0–2-cm-layer data were estimated from information on vertical distribution of the fauna.

To make the spatial scale of the sampling more comparable, we used the average $H/(H + N)$ ratios from SPR and from WSS rather than ratios from individual cores. The $H/(H + N)$ ratio on Fieberling ($n = 2$) was significantly greater than the ratios at the relatively quiescent, finer-grained sites ($n = 13$) (0.16 versus 0.03).

5. Discussion

5.1. *Sea Pen Rim versus White Sand Swale*

Although SPR and WSS are within a few kilometers of each other and differed by only tens of meters in depth, there are differences in the physical environments for meiofauna at the two sites. The most marked difference is that the sediment at WSS consists predominantly of the tests of planktonic foraminifera but that at SPR consists predominantly of more dense basaltic particles (Levin et al., 1994). The sediment moves daily at WSS but less frequently at SPR (Levin et al., 1994). SPR had longer ripple wavelengths and more large particles than WSS.

Despite the physical differences, we found the meiofauna of the two sites to be very similar. For meiofaunal major taxa, there were no significant differences in abundance or in vertical distribution. The two sites did not differ significantly in the proportion of surface-living and interstitial harpacticoid species or in H/(H + N) ratio. For only one of the 41 harpacticoid species did abundances at the two sites differ significantly (Thistle, 1998).

The paucity of significant differences was not, of course, sufficient to establish the similarity of the faunas of SPR and WSS. We therefore examined medians and 95% confidence limits for the several comparisons (Table 4). In most cases, the differences between medians were small, and the 95% confidence limits overlapped extensively. If more samples had been available, our tests would have been more powerful, but given the small differences between medians, the differences between sites would have remained small. We concluded that the meiofaunas of SPR and WSS were similar enough to be combined for comparative studies.

This result was unexpected. For macrofauna, SPR and WSS differed in composition, vertical distribution, lifestyles, and recolonization rates, and the differences appeared to be related to the environmental differences between sites (Levin et al., 1994; Levin and DiBacco, 1995). Given previous work on deep-sea meiofauna (Thistle, 1983; Carman et al., 1987), the observed environmental differences between SPR and WSS (e.g. sediment type, sediment-transport regime) seemed sufficient to cause differences in the meiofauna as well, but we found none.

5.2. *Fieberling versus comparison sites*

We looked in four ways for evidence that reworking affects meiofauna. When we compared the Fieberling meiofauna to that of sites that experience much less reworking, we found harpacticoids, ostracods, and kinorhynchs to be deeper in the seabed, and we found the proportion of the harpacticoid fauna that was surface-living on Fieberling to be less, results that suggest negative direct effects of reworking on these groups. We also found a higher proportion of interstitial harpacticoids and a higher H/(H + N) ratio at Fieberling, suggesting positive indirect effects of reworking on these groups. Therefore, we infer that reworking does affect the meiofauna on Fieberling. The environmental conditions on the summit of Fieberling Guyot are not unique. Thousands of seamounts exist (Smith and Jordan, 1988), and many have

patches of physically reworked sediment (Levin and Thomas, 1989). We suspect that the meiofaunas of these locations are similarly modified.

Because Fieberling is an island, the effects of reworking on its fauna may differ from those on faunas from nonisland, reworked sites. The latter will be surrounded by similar habitat (e.g. the HEBBLE site, Thistle et al., 1985; Aller, 1989), whereas the summit sediment community on Fieberling is geographically isolated (the nearest seamount summit is >10 km away). This difference will have consequences for immigration, emigration, and species richness (MacArthur and Wilson, 1967). Thus, the effects of reworking seen on Fieberling are most relevant to other deep-sea island settings. They can suggest potential effects in nonisland reworked settings, but only research on such habitats will reveal the extent of the modifications that reworking imposes on their faunas.

Because the deep sea is undersampled, comparison sites of comparable depth were unavailable. PSB and SDT are roughly twice as deep as the Fieberling sites. Although we focused on likely effects of physical reworking, we acknowledge that some unmeasured, depth-related factor could influence the differences that we found.

For deep-sea macrofauna, comparisons of sites that differ in reworking have revealed patterns consistent with those reported here. For example, isopods (Thistle and Wilson, 1987, 1996) and tanaids (Reidenauer and Thistle, 1985) that live on or close to the sediment surface are proportionately less abundant at reworked than at quiescent sites. Levin et al. (1994) found that the macrofauna lived significantly deeper at the more reworked of two seamount sites (see also Gage et al., 1995 and Aller, 1997).

Additional comparative studies would help to refine our understanding of the observed patterns. For example, Levin and Thomas (1989) reported harpacticoid and nematode data from three seamount sites in the central North Pacific (1480, 1840, and 3150 m depth) with sand:silt:clay proportions of 84:10:6, 70:18:12, and 48:22:30. Their H/(H+N) ratios were 0.35, 0.39, and 0.40. As expected, the H/(H+N) ratios were greater than those of muddy, deep-sea sites (see Table 5), but the trend in the H/(H+N) ratio among the three sites was the opposite of that expected from their assumed differences in amount of interstitial space (see also Levin et al., 1991). Clarification of the mechanisms underlying these patterns may require experimentation.

Acknowledgements

S. Boa, S.C. Ertman, C. Huggett, and A. Wonnacott helped take and process the samples. The comments of L. Bouck, L. Dunning, S.C. Ertman, J.D. Gage, R.R. Hessler, P. Leitman, K. Suderman, A.B. Thistle, and two anonymous reviewers improved the manuscript. We thank these people and the captain, crew, and submersible pilots of the *R/V Atlantis II* and *DSRV Alvin* (legs 125-14 and 125-18). This research was supported by ONR grants N00014-92-J-1025 to D.T. and N00014-89-J-3072 and N00014-92-J-1857 to L.A.L.

References

- Aller, J.Y., 1989. Quantifying sediment disturbance by bottom currents and its effect on benthic communities in a deep-sea western boundary zone. *Deep-Sea Research* 36, 901–934.
- Aller, J.Y., 1997. Benthic community response to temporal and spatial gradients in physical disturbance within a deep-sea western boundary region. *Deep-Sea Research I* 44, 39–69.
- Barnett, P.R.O., 1968. Distribution and ecology of harpacticoid copepods of an intertidal mudflat. *Internationale Revue de gesamten Hydrobiologie* 53, 177–209.
- Barnett, P.R.O., Watson, J., Connelly, D., 1984. A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanologica Acta* 7, 399–408.
- Bett, B.J., Vanreusel, A., Vincx, M., Soltwedel, T., Pfannkucke, O., Lamshead, P.J.D., Gooday, A.J., Ferrero, T., Dinert, A., 1994. Sampler bias in the quantitative study of deep-sea meiobenthos. *Marine Ecology Progress Series* 104, 197–203.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302, 520–522.
- Bruce, P.C., 1991. Resampling stats. Resampling Stats Arlington, VA.
- Carman, K.R., Sherman, K.M., Thistle, D., 1987. Evidence that sediment type influences the horizontal and vertical distribution of nematodes at a deep-sea site. *Deep-Sea Research* 34, 45–53.
- D'Amours, D., 1988. Vertical distribution and abundance of natant harpacticoid copepods on a vegetated tidal flat. *Netherlands Journal of Sea Research* 22, 161–170.
- Emery, K.O., Hulsemann, J., 1963. Submarine canyons of southern California. Part I. Topography, water, and sediments. *Allan Hancock Pacific Expeditions* 27, 1–80.
- Eriksen, C.C., 1991. Observations of amplified flows atop a large seamount. *Journal of Geophysical Research* 96, 15227–15236.
- Gage, J.D., Lamont, P.A., Tyler, P.A., 1995. Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary results: I. Introduction and diversity comparisons. *Internationale Revue de gesamten Hydrobiologie* 80, 235–250.
- Gooday, A.J., 1986. Meiofaunal foraminiferans from the bathyal Porcupine Seabight (northeast Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. *Deep-Sea Research* 33, 1345–1373.
- Gooday, A.J., Pfannkucke, O., Lamshead, P.J.D., 1996. An apparent lack of response by metazoan meiofauna to phytodetritus deposition in the bathyal northeast Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 76, 297–310.
- Gross, T.F., Williams, A.J., III, 1991. Characterization of deep-sea storms. *Marine Geology* 99, 281–301.
- Herman, R.L., Dahms, H.U., 1992. Meiofauna communities along a depth transect off Halley Bay (Weddell Sea, Antarctica). *Polar Biology* 12, 313–320.
- Kontar, E.A., Sokov, A.V., 1994. A benthic storm in the northeastern tropical Pacific over fields of manganese nodules. *Deep-Sea Research* 41, 1069–1089.
- Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Research* 32, 885–898.
- Levin, L.A., DiBacco, C., 1995. The influence of sediment transport on short-term recolonization by seamount infauna. *Marine Ecology Progress Series* 123, 163–175.
- Levin, L.A., Gage, J.D., 1998. Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. *Deep-Sea Research II* 45, 129–163.
- Levin, L.A., Thomas, C.L., 1989. The influence of hydrodynamic regime on infaunal assemblages inhabiting carbonate sediments on central Pacific seamounts. *Deep-Sea Research* 36, 1897–1915.
- Levin, L.A., Huggett, C.L., Wishner, K.F., 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. *Journal of Marine Research* 49, 763–800.
- Levin, L.A., Leithold, E.L., Gross, T.F., Huggett, C.L., DiBacco, C., 1994. Contrasting effects of substrate mobility on infaunal assemblages inhabiting two high-energy settings on Fieberling Guyot. *Journal of Marine Research* 52, 489–522.

- MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, 203 pp.
- Paterson, G.L.J., Lamshead, P.J.D., 1995. Bathymetric patterns of polychaete diversity in the Rockall Trough, northeast Atlantic. *Deep-Sea Research I* 42, 1199–1214.
- Pfannkuche, O., 1985. The deep sea meiofauna of the Porcupine seabight and abyssal plain (NE Atlantic): population structure, distribution, standing stocks. *Oceanologica Acta* 8, 343–353.
- Reidenaer, J.A., Thistle, D., 1985. The tanaid fauna from a region of the deep North Atlantic where near-bottom current velocities are high. *Oceanologica Acta* 8, 355–360.
- Rice, A.L., Billett, D.S.M., Thurston, M.H., Lampitt, R.S., 1991. The Institute of Oceanographic Sciences biology programme in the Porcupine Seabight: background and general introduction. *Journal of the Marine Biological Association of the United Kingdom* 71, 281–310.
- Service, S.K., Bell, S.S., 1987. Density influenced active dispersal of harpacticoid copepods. *Journal of Experimental Marine Biology and Ecology* 114, 49–62.
- Shedden, M., 1998. Grazing predation on a population of *Ampelisca tenuicornis* (Gammaridae: Amphipoda) off the south coast of England. *Marine Ecology Progress Series* 164, 253–262.
- Smith, K.D., Jordan, T.H., 1988. Seamount statistics in the Pacific Ocean. *Journal of Geophysical Research* 93, 2899–2919.
- Thistle, D., 1978. Harpacticoid dispersion patterns: implications for deep-sea diversity maintenance. *Journal of Marine Research* 36, 377–397.
- Thistle, D., 1982. Aspects of the natural history of the harpacticoid copepods of San Diego Trough. *Biological Oceanography* 1, 225–238.
- Thistle, D., 1983. The stability-time hypothesis as a predictor of diversity in deep-sea soft-bottom communities: a test. *Deep-Sea Research* 30A, 267–277.
- Thistle, D., 1998. Harpacticoid copepod diversity at two physically reworked sites in the deep sea. *Deep-Sea Research II* 45, 13–24.
- Thistle, D., Eckman, J.E., 1990. The effect of a biologically produced structure on the benthic copepods of a deep-sea site. *Deep-Sea Research* 37, 541–554.
- Thistle, D., Wilson, G.D.F., 1987. A hydrodynamically modified, abyssal isopod fauna. *Deep-Sea Research* 34, 73–87.
- Thistle, D., Wilson, G.D.F., 1996. Is the HEBBLE isopod fauna hydrodynamically modified? A second test. *Deep-Sea Research I* 43, 545–554.
- Thistle, D., Yingst, J.Y., Fauchald, K., 1985. A deep-sea benthic community exposed to strong near-bottom currents on the Scotian Rise (western Atlantic). *Marine Geology* 66, 91–112.
- Thistle, D., Ertman, S.C., Fauchald, K., 1991. The fauna of the HEBBLE site: patterns in standing stock and sediment-dynamic effects. *Marine Geology* 99, 413–422.
- Thistle, D., Weatherly, G.L., Wonnacott, A., Ertman, S.C., 1995. Suspension by winter storms has an energetic cost for adult male benthic harpacticoid copepods at a shelf site. *Marine Ecology Progress Series* 125, 77–86.
- Wieser, W., 1959. The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnology and Oceanography* 4, 181–194.