

Distribution of bathyal meiofauna in the region of the Subtropical Front, Chatham Rise, south-west Pacific

S.L. Grove ^{a,1}, P.K. Probert ^{a,*}, K. Berkenbusch ^a, S.D. Nodder ^b

^a Department of Marine Science, University of Otago, P.O. Box 56, Dunedin, New Zealand

^b National Institute of Water and Atmospheric Research Limited, Private Bag 14-901, Kilbirnie, Wellington, New Zealand

Received 1 July 2005; received in revised form 14 December 2005; accepted 15 December 2005

Abstract

Metazoan meiofauna was sampled along a temperate latitude transect (41–47°S 178°30'E) across the Chatham Rise, south-west Pacific, from water depths of 350–2600 m on three occasions (austral autumn 1997, spring 1997, summer 2000). Samples were collected using a multicorer and extracted on a 63- μ m mesh. Meiofaunal density and biomass were negatively correlated with water depth, median grain-size and sediment calcium carbonate content, and positively correlated with sediment chlorophyll *a*. There were no significant relationships between meiofaunal abundance and biomass and measures of sediment organic matter and bacterial productivity and biomass, except in summer when bacterial and meiofaunal biomass were positively correlated. Vertical penetration of meiofauna into the sediment was related to sediment organic matter and sediment chloroplastic pigments. Variation in meiofaunal abundance at different spatial scales was examined at two sites: at 450 and 2300 m on the northern slope of the rise. At both sites, variation between subcores of a multicore (<10-cm scale) was lower than that of multicores within a deployment (<1-m scale). However, whilst the highest variance component at the shallow site was for multicores within a deployment, it was between multicore deployments (<1-km scale) for the deep site. Meiofaunal density and biomass were generally higher on the southern slope of the rise than on the northern slope, a trend probably attributable to high productivity of the overlying Subtropical Front and the flux of more nutritious organic material to the sea floor.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Bathyal zone; Meiofauna; South west Pacific Ocean; Subtropical Front

1. Introduction

Meiofauna comprises a major functional component of the deep-sea benthos and there has in recent decades been increasing interest in its distribution and relationship

to environmental parameters, particularly food availability (e.g., Thiel, 1975, 1983; Tietjen, 1992; Brown et al., 2001; Galéron et al., 2001). On a global scale, results indicate considerable regional differences in meiofaunal abundance and biomass, although sampling is very uneven (Soltwedel, 2000), and the number of deep-water sites where both meiofaunal abundance and biomass have been calculated is small (Tietjen, 1992). In the Pacific Ocean, studies of meiofaunal distribution along continental margins have been largely confined to north-western temperate regions (Shirayama, 1984;

* Corresponding author. Tel.: +64 3 479 7465; fax: +64 3 479 8336.
E-mail address: keith.probert@stonebow.otago.ac.nz
(P.K. Probert).

¹ Present address: Department of Botany, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.

Shirayama and Kojima, 1994), tropical southern Pacific (Alongi and Pichon, 1988; Neira et al., 2001; Danovaro et al., 2002), and central oceanic areas (Snider et al., 1984; Renaud-Mormant and Gourbault, 1990).

In the temperate south-western Pacific, metazoan meiofauna at bathyal depths has been sampled as part of an interdisciplinary research programme by the National Institute of Water and Atmospheric Research (NIWA) to quantify biological productivity in waters associated with the Subtropical Front (STF), a region where surface subtropical water (STW) to the north meets surface subantarctic water (SAW) to the south. STW is relatively warm, saline, macronutrient-poor and with marked seasonal phytoplankton blooms, whereas SAW is cooler, less-saline, with high macronutrient concentrations and iron-limitation, and low annual cycles of surface chlorophyll abundance (Boyd et al., 1999; Bradford-Grieve et al., 1999; Murphy et al., 2001; Sutton, 2001). In particular, NIWA studies have focused on a region east of New Zealand where the STF overlies the Chatham Rise, a broad submarine ridge that extends eastwards from South Island for some 800 km and has an average width of 100 km (as outlined by the 500 m isobath). The rise is generally flat-topped, the crest being at 200–400 m water depth, but with the northern and southern flanks of the rise descending to more than 2000 m. The STF appears to be bathymetrically locked to the southern flank of the rise near 44°S (Uddstrom and Oien, 1999). Heightened

primary productivity has been observed over the rise with community biomass dominated by diatoms (Chang and Gall, 1998) and elevated chlorophyll concentrations often occurring in a STF zone on the south side of the rise (Murphy et al., 2001). There is evidence for high episodic organic fluxes on the northern flank of the rise (nominally STW), compared with lower, more sustained fluxes on the southern flank (in SAW) (Nodder and Northcote, 2001).

This paper presents meiofaunal density and biomass data from bathyal depths in the temperate south-west Pacific, a region where there is a paucity of such information (Soltwedel, 2000). A particular objective was to examine meiofaunal distribution in relation to physical and biogeochemical properties in the region of the STF, as earlier studies had indicated a marked macrobenthic response to enhanced productivity at the STF (Probert and McKnight, 1993; Probert et al., 1996).

2. Materials and methods

2.1. Sampling and laboratory methods

Samples were collected on three occasions: April–May 1997 (austral autumn), October–November 1997 (spring) and January–February 2000 (summer). Sampling stations were located along a transect at 178°30'E across the Chatham Rise (Fig. 1), between water depths

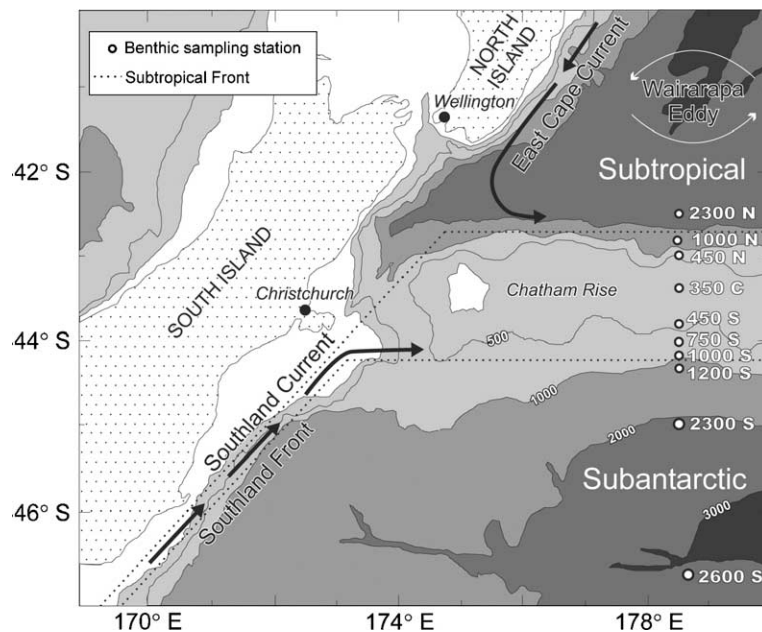


Fig. 1. Location of sampling sites.

Table 1
Multicore sample positions and sediment parameters

Sample site*	NIWA station	Date	Latitude (S)	Longitude (E)	Water depth (m)	Surface (0–1 cm) sediment											Bacteria 0–1 cm ($\times 10^9$ cells cm^{-3})	Bacteria 0–1 cm (mg C m^{-2})	Bacterial productivity 0–1 cm ($\text{mg C m}^{-2} \text{d}^{-1}$)		
						Sand (%)	Silt (%)	Clay (%)	Median (phi)	Sorting (phi)	CaCO ₃ (%)	TOM (%)	Chl <i>a</i> (ng/mg)	Phaeo (ng/mg)	TOC (%)	TON (%)				C:N (mol)	Water (%)
<i>Cruise 3036</i>																					
2300N	S1052	30-Apr-97	42°29.73'	178°30.80'	2330	4.2	41.7	54.1	4.5	1.4	21.88	–	0.027	5.266	1.01	0.08	14.62	72.70	0.333	66.50	0.374
2300N	S1073g	8-May-97	42°29.21'	178°30.39'	2327	4.0	42.1	53.7	–	–	21.95	6.78	0.077	6.350	1.00	0.09	13.46	70.66	–	–	–
1000N	S1053	1-May-97	42°48.54'	178°30.49'	1004	45.6	40.1	14.0	3.5	1.5	40.70	5.33	0.080	5.298	0.60	0.04	16.12	50.08	–	–	–
450N	S1054a	1-May-97	42°58.54'	178°29.64'	442	62.8	29.5	6.8	2.8	1.3	23.55	4.16	0.055	5.154	0.66	0.05	16.31	48.16	0.258	51.60	0.194
450N	S1072c	7-May-97	42°58.61'	178°29.95'	446	–	–	–	–	–	–	–	0.040	2.616	0.37	0.03	12.53	36.23	1.527	305.33	0.158
450N	S1072g	8-May-97	42°58.54'	178°29.59'	439	–	–	–	–	–	–	–	0.044	3.753	0.46	0.04	12.45	40.06	2.020	404.00	–
350C	S1066b	3-May-97	43°26.00'	178°29.90'	350	67.8	26.1	5.9	2.5	1.0	26.90	4.34	0.078	5.099	0.64	0.05	16.92	43.08	0.509	101.87	0.290
450S	S1060b	3-May-97	43°49.35'	178°29.66'	453	64.3	28.1	7.3	2.3	1.5	16.33	3.18	0.065	4.441	0.54	0.04	16.45	41.11	–	–	0.336
1000S	S1065e	5-May-97	44°08.41'	178°30.49'	981	75.0	17.8	7.0	2.0	1.3	18.93	3.83	0.040	2.880	0.44	0.03	15.13	40.48	0.312	62.33	0.216
2300S	S1064f	4-May-97	44°57.18'	178°30.62'	2283	38.7	28.2	33.1	3.8	2.2	68.68	3.49	0.006	1.230	0.26	0.01	22.21	51.77	0.376	75.13	0.089
<i>Cruise 3040</i>																					
2300 N	U1214b	29-Oct-97	42°20.88'	178°32.03'	2294	2.2	–	–	–	–	20.10	8.43	0.025	5.798	1.19	0.08	18.26	69.48	0.999	199.87	–
1000N	U1226b	30-Oct-97	42°47.87'	178°30.24'	1046	40.8	41.6	19.4	–	–	42.83	4.87	0.036	3.979	0.65	0.04	19.29	50.97	1.079	215.70	–
450 N	U1239b	2-Nov-97	42°58.85'	178°30.00'	464	61.4	–	–	–	–	26.40	3.50	0.047	4.563	0.53	0.04	16.26	43.38	3.420	684.00	–
350 C	U1248d	3-Nov-97	43°26.37'	178°30.15'	347	55.9	–	–	–	–	33.30	4.00	0.102	5.553	0.68	0.05	14.68	44.66	–	–	–
450 S	U1204c	26-Oct-97	43°49.18'	178°29.82'	453	62.1	26.7	9.0	–	–	11.20	5.44	0.063	5.047	1.22	0.00	0.00	36.67	1.543	308.67	–
750 S	U1202b	25-Oct-97	44° 00.07'	178° 29.94'	752	51.8	34.2	13.4	3.5	1.3	26.20	4.50	0.047	4.322	0.53	0.03	19.02	41.69	0.690	138.07	–
1000 S	U1249b	4-Nov-97	44° 08.24'	178° 30.39'	974	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1200 S	U1250	4-Nov-97	44° 08.39'	178° 30.64'	1206	21.5	50.0	27.4	–	–	38.80	2.37	0.040	3.590	0.49	0.03	22.86	47.41	–	–	–
2600 S	U1165j	20-Oct-97	46° 44.91'	178° 29.89'	2678	57.6	–	–	–	–	86.43	2.18	0.003	0.557	0.31	0.01	23.06	49.78	2.365	473.00	–
<i>Cruise 3065</i>																					
2300 N	U1628i	5-Feb-00	42° 21.005'	178° 29.868'	2297	–	–	–	–	–	19.90	9.31	0.088	6.528	0.96	0.08	13.70	64.77	1.205	241.00	0.284
1000 N	U1626b	4-Feb-00	42° 47.488'	178° 29.028'	1000	–	–	–	–	–	40.41	5.63	0.064	4.687	0.51	0.05	11.84	52.28	–	–	0.682
450 N	U1631f	6-Feb-00	42° 57.253'	178° 29.944'	494	–	–	–	–	–	32.26	5.04	0.062	3.087	0.47	0.04	15.62	44.57	1.120	224.00	0.424
350 C	U1602a	25-Jan-00	43° 25.729'	178° 29.864'	350	–	–	–	–	–	31.48	5.43	0.097	5.772	0.69	0.06	13.53	44.95	–	–	0.422
450 S	U1617c	2-Feb-00	43° 48.602'	178° 30.419'	450	–	–	–	–	–	12.38	5.42	0.113	6.050	0.61	0.06	11.47	40.72	3.515	703.00	0.670
750 S	U1603b	25-Jan-00	44° 00.072'	178° 29.812'	750	–	–	–	–	–	25.72	4.93	0.050	2.556	0.41	0.03	15.77	39.17	–	–	0.408
1200 S	U1616b	1-Feb-00	44° 19.90'	178° 29.66'	1204	–	–	–	–	–	39.80	3.71	0.058	3.655	0.17	0.01	19.44	48.95	1.953	390.67	0.435
2600 S	U1612k	28-Jan-00	46° 40.69'	178° 30.49'	2600	–	–	–	–	–	–	2.00	0.003	0.199	0.17	0.01	19.82	47.26	0.598	119.61	0.061

*N = north slope, S = south slope, C = crest.

of 350 and 2600 m (Table 1). Samples were obtained using an Ocean Instruments MC-800A multicorer which has eight 10-cm diameter cores. For each multicore deployment, up to three cores (depending on availability) were processed for meiofauna. From each of these cores, three subcores of internal diameter 26 mm (5.3 cm²) were taken to a depth of 5 cm using 60-ml cut-off plastic syringes. Each subcore was divided into three vertical fractions: 0–1, 1–3 and 3–5 cm depth and preserved in 10% buffered formalin (0.4 µm filtered seawater) and stained with rose bengal. The preserved faunal samples were gently washed on a 425-µm mesh to exclude macrofauna (which was processed separately, see Nodder et al., 2003) and extracted on a 63-µm mesh.

Subcores were taken to a depth of 5 cm as earlier sampling had indicated only a small proportion of meiofauna occurring below this depth. For meiofaunal cores taken to 10 cm depth in the central Chatham Rise region in September 1989 at 244–1394 m water depth, a mean of 5.35% (S.D. 5.20) of total meiofaunal individuals were recovered from the 5–10 cm portion ($n=12$) (unpublished data). This is comparable to sediment depth distribution of meiofauna reported in other deep-sea studies (e.g., Shirayama, 1984b; Alongi and Pichon, 1988; Vanreusel et al., 1995a). A 63-µm mesh is coarser than is usually used for extracting deep-sea meiofauna (Thiel, 1983; Tietjen, 1992; Soltwedel, 2000), but was adopted because of logistic constraints on sample processing and because samples were taken primarily to derive estimates of biomass rather than of numerical abundance (see Nodder et al., 2003); using a finer mesh is likely to affect biomass estimates considerably less than estimates of abundance (e.g., McIntyre, 1964; Thiel, 1983). Vanreusel et al. (1995b) found that even at abyssal sites of contrasting food supply where 32- and 64-µm meshes were used, the latter would be expected to retain about 74–77% of nematode biomass.

Meiofauna was extracted from the sediment by Ludox flotation and mounted on microscope slides (Sommerfield and Warwick, 1996). Foraminiferans were not reliably extracted as complete specimens and were excluded from the study. The preservation method also destroyed ‘soft’ meiofauna (e.g., Turbellaria) which must be sorted live (Coull et al., 1977; Thiel, 1983), so these organisms were also discounted.

Meiofauna dimensions were measured by video image analysis (NIH Image 1.60). Volumes were calculated by applying the formula $V=L \times W^2 \times C$, where V is the body volume in nanolitres, L is the length, W is maximum width (both in mm), and C is the appropriate conversion factor for the taxon in question (Feller and Warwick, 1988).

Body volumes were converted to dry weight by assuming a relative density of 1.13 and a dry:wet weight ratio of 0.25 (Feller and Warwick, 1988).

Abundance of major metazoan taxa was recorded for all samples. For volume estimates, up to three subcores from each multicorer deployment were used, with each subcore being from a different multicore. A complete set of subcores was not obtained on each cruise, though this mainly affects results for the spring cruise (see Table 2 for number of subcores processed). Except for nematodes, all meiofauna on each slide were measured. Where nematodes were very numerous, at least 50 randomly selected individuals were measured, and total volume estimated by multiplying by the ratio of number counted to number measured.

Associated physical and biogeochemical properties of the sediment were measured from samples taken from other multicores from that deployment. These parameters, for the 0–1 cm sediment layer, were: sediment grain-size, water content, and organic matter (TOM, POC, TN, and molar C:N ratio), % CaCO₃, chloroplastic pigments (chlorophyll *a* plus phaeopigments) as tracers for phytodetritus, bacterial counts and bacterial productivity. These variables, apart from grain-size and water content, may reflect meiofauna food availability, and are here referred to as ‘potential food variables.’ Total organic matter (TOM) content was determined by loss-on-ignition (500 °C for 4 h), while sediment particulate organic carbon (POC) and total nitrogen (TN) concentrations were measured using a CHN analyser after acidifying samples with sulphurous acid to remove the carbonate component. Chloroplastic pigment contents were estimated using standard spectrophotometric techniques after freeze-drying (to determine water content). Calcium carbonate percentages were determined using a gasometric technique. Bacterial counts were made on microscope slides using epifluorescence microscopy, and bacterial productivity was determined using thymidine-incorporation methods. Details of these methods are given by Nodder et al. (2003).

2.2. Statistical analysis

Statistical procedures were carried out using SPSS 10.0 (SPSS, 1999). Pearson correlation coefficients were made between the factors listed in Table 1, and the following meiofaunal indices for each sample: (a) total meiofaunal density, (b) total meiofaunal biomass, (c) nematode biomass, (d) nematode + harpacticoid biomass, (e) proportions of density and biomass of nematodes and harpacticoids to the

Table 2
Meiofaunal density (individuals 10 cm^{-2}) and biomass (μg dry weight 10 cm^{-2}) for 0–5 and 0–1 cm sediment depths

Sample site	0–5 cm												0–1 cm											
	Meiofauna density			Meiofauna biomass			Nematode biomass			Harpacticoid biomass			Meiofauna density			Meiofauna biomass			Nematode biomass			Harpacticoid biomass		
	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n
<i>Cruise 3036</i>																								
2300 N	333.8	156.0	9	109.3	26.0	3	61.9	10.4	3	7.6	8.3	3	130.6	37.9	9	43.7	22.3	3	15.8	9.4	3	4.1	5.3	3
2300 N	601.5	158.5	9	265.3	274.0	3	58.9	10.5	3	6.8	5.6	3	294.0	141.0	9	182.8	264.1	3	14.1	3.4	3	3.8	5.2	3
1000 N	583.5	127.3	9	168.1	88.7	3	58.0	6.2	3	18.6	7.8	3	303.7	104.9	9	124.1	91.1	3	20.9	10.1	3	11.0	2.1	3
450 N	1037.6	213.3	8	285.0	171.1	3	77.4	26.2	3	24.6	7.9	3	411.9	165.4	9	157.8	55.9	3	17.0	3.6	3	15.7	5.7	3
450 N	631.4	69.0	9	164.0	67.7	3	75.5	31.5	3	19.0	9.5	3	226.4	85.2	9	100.8	89.2	3	31.1	44.3	3	13.5	9.3	3
450 N	638.9	289.9	9	245.8	214.1	3	58.2	48.5	2	23.6	15.3	3	271.9	102.3	9	153.6	103.4	3	9.6	0.9	3	16.4	15.7	3
350 C	1227.8	265.9	9	391.3	105.1	3	174.1	34.3	3	30.9	15.5	3	440.1	196.2	9	186.8	54.0	3	38.4	13.7	3	19.8	12.9	3
450 S	1454.1	207.7	9	435.3	136.8	3	182.4	45.0	3	56.0	37.2	3	558.1	128.0	9	179.0	33.4	3	29.0	2.8	3	34.8	34.4	3
1000 S	866.6	338.6	8	230.0	47.8	3	102.8	43.2	3	19.4	11.7	3	513.7	249.9	8	129.2	49.0	3	45.4	28.0	3	14.3	11.4	3
2300 S	533.4	189.8	9	97.6	14.8	3	43.0	9.3	3	20.8	8.4	3	286.9	95.4	9	68.1	4.4	3	30.7	4.7	3	13.9	8.7	3
<i>Cruise 3040</i>																								
2300 N	223.5	138.5	3	50.3	32.5	3	28.8	17.0	3	6.4	8.4	3	69.7	45.2	3	13.1	9.0	3	8.4	5.2	3	3.4	4.0	3
1000 N	404.0	147.8	2	163.4		1	42.6		1	51.3		1	190.2	23.1	3	75.1		1	5.4		1	48.5		1
450 N	542.4		1	101.8		1	55.2		1	7.7		1	203.4	133.2	2	37.3		1	15.5		1	7.2		1
350 C	1099.3	277.2	3	220.3	53.6	3	111.0	11.0	3	17.1	13.4	3	372.9	209.3	4	87.3	12.6	3	36.9	6.1	3	14.1	9.0	3
450 S	902.2	205.1	5	162.4	23.1	3	105.3	17.7	3	10.2	2.0	3	383.3	175.1	6	70.4	29.9	3	31.9	16.9	3	9.9	2.3	3
750 S	665.3	87.5	4	163.7	14.8	3	74.8	13.9	3	13.0	6.0	3	267.5	104.4	5	69.6	24.7	3	15.8	7.0	3	12.6	6.2	3
1000 S	494.4	185.1	2	104.1		1	60.8		1	10.8		1	229.8	71.9	2	64.5		1	42.4		1	10.8		1
1200 S	364.7	123.1	8	75.1	41.3	3	32.2	15.0	3	4.1	2.2	3	154.2	87.5	9	37.3	20.1	3	14.6	9.2	3	4.0	2.2	3
2600 S	93.3	50.9	9	10.4	7.3	3	4.1	0.8	3	5.2	7.5	3	45.0	27.4	9	6.9	8.3	3	1.5	1.0	3	4.3	7.4	3
<i>Cruise 3065</i>																								
2300 N	356.0	58.0	9	51.3	16.1	3	30.7	13.1	3	14.1	5.4	3	127.2	51.5	9	18.0	17.7	3	10.2	11.0	3	4.5	5.4	3
1000 N	578.9	105.3	9	82.6	17.1	3	40.2	7.5	3	10.4	5.3	3	270.4	80.0	9	41.5	7.8	3	14.1	6.2	3	9.6	4.6	3
450 N	1006.0	578.3	9	130.3	72.2	3	83.8	68.3	3	14.1	15.2	3	468.6	417.9	9	41.5	28.8	3	19.4	20.7	3	4.7	4.8	3
350 C	1022.3	389.3	9	197.4	93.1	3	69.2	23.3	3	24.1	21.8	3	501.0	228.0	9	136.2	54.5	3	27.2	11.7	3	23.7	21.7	3
450 S	1299.2	153.7	9	351.4	44.5	3	145.1	39.8	3	46.7	20.7	3	504.4	116.3	9	169.7	11.0	3	43.5	17.4	3	42.9	17.4	3
750 S	1150.5	276.0	6	216.6	19.5	2	105.5	2.7	2	36.5	6.8	2	640.7	206.9	6	155.5	41.6	2	52.1	20.5	2	36.3	6.6	2
1200 S	1010.2	186.4	6	123.1	25.2	2	71.0	4.1	2	13.2	2.7	2	561.3	123.4	6	64.4	21.5	2	19.7	5.5	2	12.3	4.0	2
2600 S	161.8	201.2	9	13.6	21.7	3	10.7	17.1	3	1.6	2.4	3	61.3	69.7	9	4.0	6.7	3	1.8	3.0	3	1.5	2.5	3

total metazoan meiofauna, and (f) proportions of total meiofauna, nematode and harpacticoid densities and biomass in the top 1 cm of sediment (relative to the top 5 cm).

Correlations were made for each cruise separately and by combining data from all cruises, which had the advantage of increasing the number of data points, but the disadvantage of masking possible seasonal differences.

Lack of true replication prevented a rigorous statistical comparison of different stations and seasons. However, during the autumn cruise, three multicore deployments were made at the 450 N site, and two at the 2300 N site. Variation of meiofaunal abundance at different spatial scales (subcores within a multicore (a few centimetres apart), cores within a multicore deployment (30–70 cm apart), multicore deployments within a site (64 m–1.1 km apart), and among sites (54 km apart)), were assessed at these locations by variance components analysis in a nested ANOVA design. For the purposes of the analysis, the subsampling levels below site were assumed to be independent and random.

3. Results

3.1. Meiofaunal densities and biomass

Mean meiofaunal density per sample ranged from 93 to 1454 individuals 10 cm^{-2} , and mean meiofaunal biomass from 10.4 to 435.3 μg dry weight 10 cm^{-2} (Table 2). The lowest densities and volumes occurred at the deepest sites (2600 m) in spring 1997 and summer 2000, and the highest at the 450 S site in autumn 1997.

Nematodes were numerically dominant at all sites (77–95% of individuals), with harpacticoid copepods (3–12%) and nauplii (<10%) being the next most abundant groups. Annelids and ostracods comprised <1–3% of individuals, and other taxa each comprised <1% of individuals in samples.

Meiofaunal densities along the transect and at different seasons are shown in Fig. 2. Meiofaunal densities tended to be highest towards the crest and southern flank of the rise and decreased with increasing water depth on either side. For the summer and autumn cruises, the highest densities were at 450

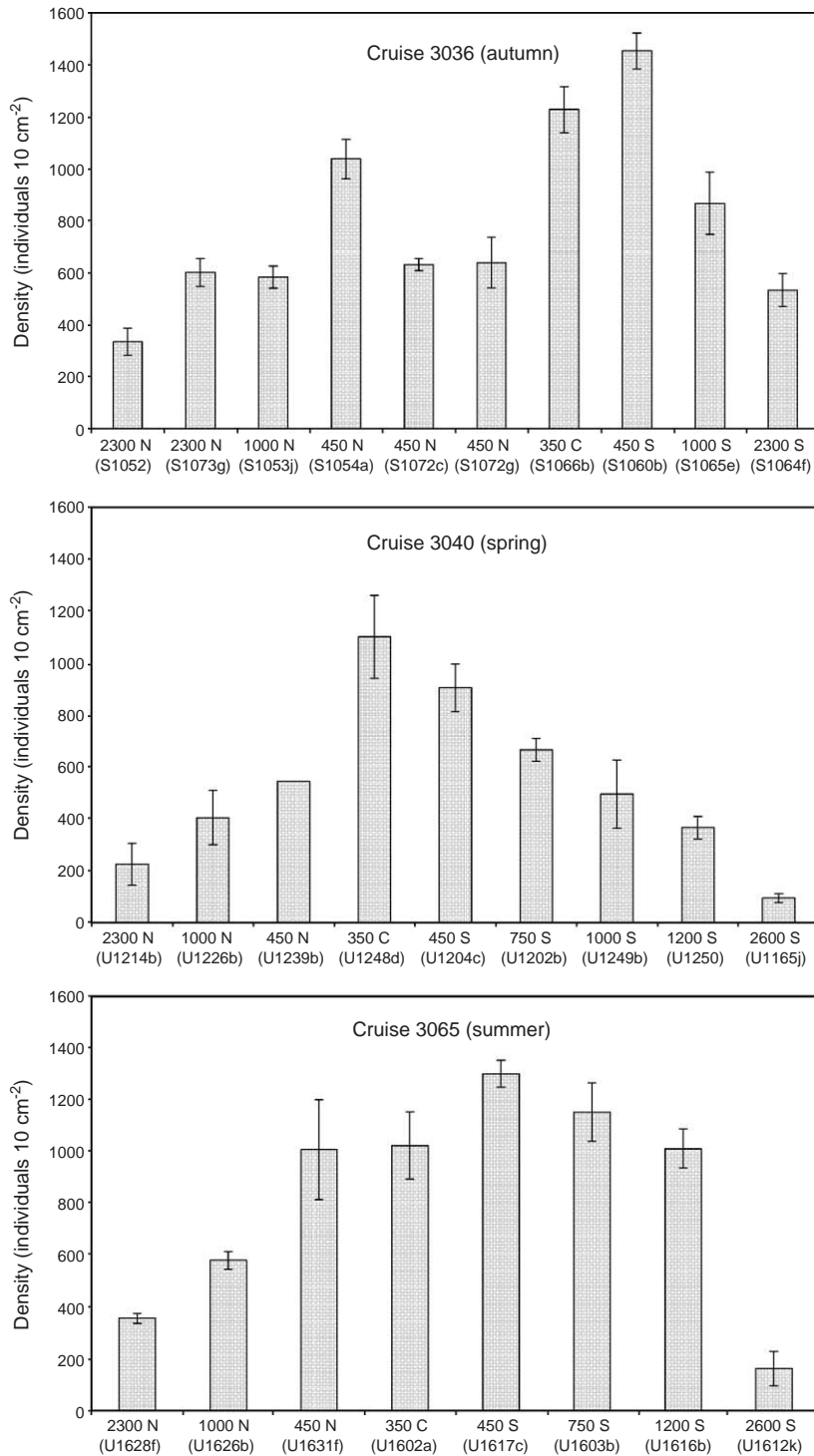


Fig. 2. Mean (\pm S.E.) density of total meiofauna at stations across the Chatham Rise for the three sampling occasions.

S rather than at the crest (350 m). Also, densities at 450 S and 1000 S were generally higher than equivalent depths on the north side of the rise (lack of true replication precludes significance testing).

Similar trends were observed with the biomass estimates (Fig. 3). Total meiofaunal biomass exhibited high variability between subcores, often due to the occurrence of large, rare individuals.

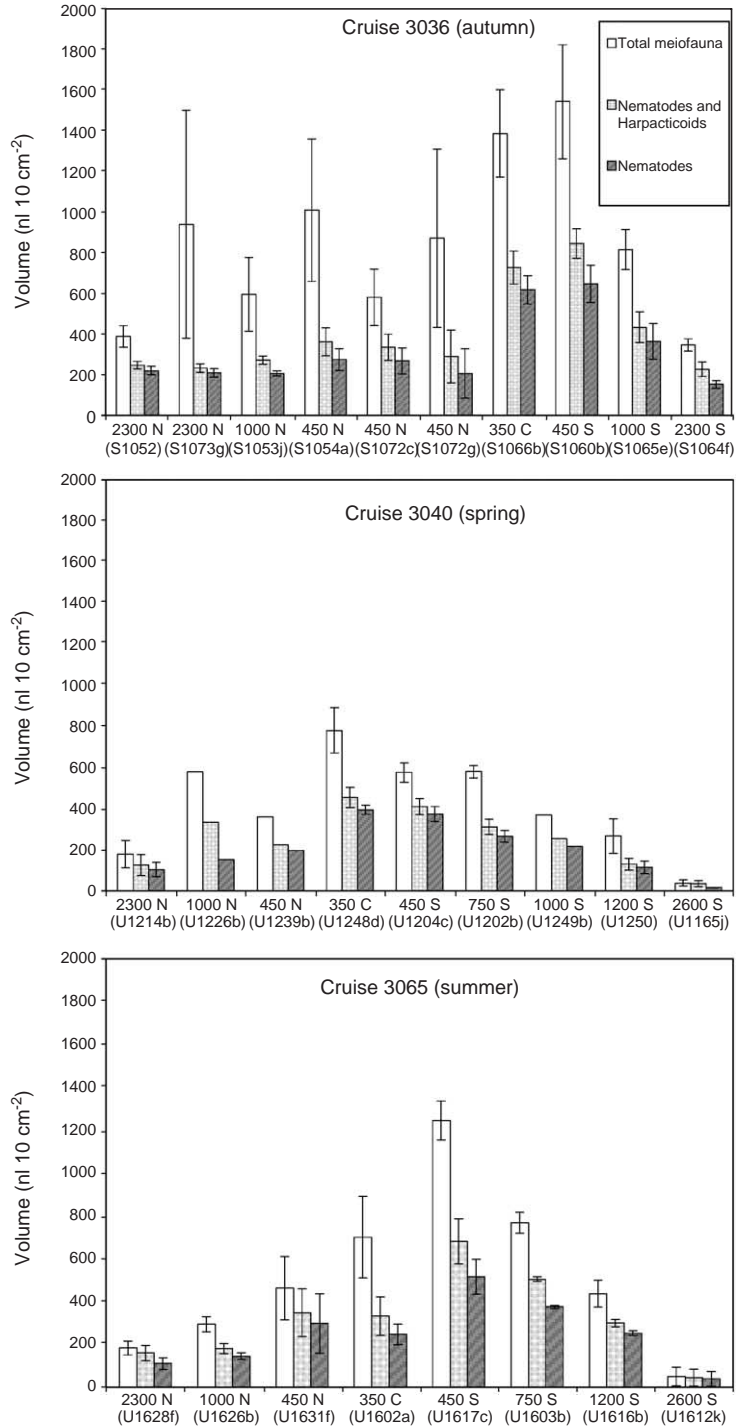


Fig. 3. Mean (±S.E.) biomass of meiofauna across the Chatham Rise for the three sampling occasions.

3.2. Correlations

Results of bivariate correlations showed that when data from all cruises were combined, significant correlations ($p < 0.05$) were found between all the meiofaunal measures and water depth, median grain-size and carbonate (all negative), and chlorophyll *a* (positive). Water content, % sand and % silt were also significantly correlated with all the meiofaunal measures (decreasing with finer sediments), except total meiofauna biomass. These patterns were not entirely consistent when cruises were analysed independently. For the autumn samples, meiofaunal density was significantly related to water depth (negative), but this was not the case for the three measures of biomass. Only total meiofaunal biomass showed a significant relationship with chlorophyll *a* (positive), and only total meiofaunal density and biomass correlated significantly with grain-size parameters. For the spring samples, there were strong depth and chlorophyll *a* relationships, but relationships were weaker with grain-size distributions. The summer samples showed significant correlations between depth and meiofaunal measures, and also between bacterial biomass and meiofaunal biomass. Since a number of the environmental and potential food factors (see Materials and methods), notably sediment organic content, pigment, carbonate, and grain size, were highly correlated with depth, partial correlations were calculated to examine the possible relationships of these sediment and potential food variables with the effect of depth held constant. In this case, however, only chlorophyll *a* retained a significant positive correlation with meiofaunal abundance.

3.3. Relative densities of nematodes and harpacticoids

Trends in the relative density and biomass of the nematodes and harpacticoids varied between cruises. Significant correlations are summarised in Table 3. Relative harpacticoid biomass increased with depth overall, but for the autumn samples correlated negatively with potential food variables (phaeopigments and sediment organic content). The summer samples showed a different pattern, with relative harpacticoid density (but not biomass) positively correlated with sediment organic matter. Summer samples also showed a negative relationship between potential food variables and the relative importance of nematodes, indicating a food-related increase of other metazoan meiofauna at that time.

Table 3

Significant correlations ($p < 0.05$) between environmental variables and the relative density and biomass of nematodes and harpacticoid copepods for the three cruises

Meiofaunal component as fraction of total meiofauna	Variable and correlation (+/–)	Cruise
Harpacticoid biomass	Depth (+)	All combined
	C:N ratio (+)	3036
	Carbonate (+)	3036, 3040, all combined
	Phaeopigments (–)	3036, 3040, all combined
	Sorting (+)	3036
Harpacticoid density	POC, TN, TOM (–)	3036
	C:N ratio (–)	3065
	POC, TN, TOM (+)	3065
Nematode biomass	Bacteria, bacterial prod. (–)	3065
	C:N (+)	3065
	Depth (+)	3065
	Phaeopigments, chl. <i>a</i> (–)	3065
	Nematode density	Phaeopigments, chl. <i>a</i> (–)
POC, TN (–)		3065
TOM (–)		3065, all combined

3.4. Vertical distribution of meiofauna

All samples showed a decrease in meiofaunal density with increasing depth in the sediment. Non-nematode meiofauna was concentrated in the top 1 cm of the sediment, with the 3–5 cm depth fraction being almost entirely nematodes. A mean of 80% (S.D. 17.5%) of non-nematode individuals was found in the top 1 cm of each 5 cm core, whilst in the 3–5 cm section of each core nematodes averaged 97% (S.D. 7%) of individuals.

The relationship between environmental and potential food variables and the proportion of major meiofaunal components in the top 1 cm of sediment was not consistent between cruises (Table 4). However, for all the meiofaunal components examined, phaeopigments and/or sediment organic content showed negative correlations, indicating that as potential food variables increased, meiofauna became less concentrated in the uppermost sediment layer.

3.5. Variability at different spatial scales

Two patterns of spatial variability were evident from the two sites on the autumn cruise where more than one multicore deployment was made (Table 5). At the deeper site at 2300 N, the highest proportion of variance was between the multicorer deployments,

Table 4

Significant correlations ($p < 0.05$) between environmental variables and the proportion of meiofaunal components in the 0–1 cm sediment layer for the three cruises

Proportion of meiofaunal component in the top 1 cm	Variable and correlation (+/-)	Cruise
Meiofauna density	Phaeopigments (-)	3040
	POC (-)	All combined
	TN (-)	3040
Meiofauna biomass	Bacterial prod. (-)	3036
	Carbonate % (+)	3040, all combined
Nematode density	Phaeopigments (-)	3040
	TN (-)	3040
	Carbonate % (+)	All combined
Nematode biomass	Phaeopigments (-)	All combined
	TN (-)	3065
	Carbonate % (+)	3036, all combined
Harpacticoid density	Phaeopigments (-)	3036
	Bacterial prod. (-)	3036
	Water content % (-)	3036, 3065, all combined
Harpacticoid biomass	POC (-)	3036
	TN (-)	All combined
	Water content % (-)	3036, 3040, all combined
	Phaeopigments (-)	3036
	Sand % (+)	3036
	Silt % (-)	3036
	POC (-)	3036
TN (-)	3036, all combined	

whereas at the 450 N site, the highest variance component was “within” the deployments, i.e. on the scale of 30–70 cm, the distance between multicore cylinders. However, for both stations, the centimetre-

scale variation (subcores) was lower than that for the cores within each deployment.

4. Discussion

4.1. Meiofaunal densities and biomass

Meiofaunal density and biomass estimates in this study fall within the ranges reported for similar water depths around the world (Thiel, 1983; Tietjen, 1992; Soltwedel, 2000). Soltwedel's review demonstrates, however, considerable regional differences, probably largely reflecting the degree of benthic-pelagic coupling. For temperate latitudes, extensive data have been available only for the Northern Hemisphere, with meiofaunal densities in the western Atlantic being significantly lower than those for the eastern Atlantic and western Pacific (Soltwedel, 2000). Densities for the Chatham Rise are somewhat lower than those for the eastern Atlantic and western Pacific and with a greater rate of decline with increasing water depth. Soltwedel (2000) points out, however, that differences reported between the Northern Hemisphere temperate regions may also be partly explained by differences in sampling and sample processing techniques.

The negative correlation of meiofaunal abundance and biomass with depth agrees with findings elsewhere (e.g., Shirayama, 1983; de Boveé et al., 1990; Danovaro et al., 1995), although this relationship is not always consistent for different areas (Tietjen, 1992; Vincx et al., 1994), or for all taxa (e.g., nematodes: Alongi and Pichon, 1988; Vanhove et al., 1995). The relationship of meiofaunal standing stocks with depth is generally attributed to food supply, in the form of particulate

Table 5

Variability of total meiofaunal abundance at different spatial scales for sites 2300 N and 450 N of Cruise 3036

ANOVA						
Source of variation	Degrees of freedom		Sum of squares	Mean squares	F ratio	p value
Site	1		257,603.710	257,603.710	2.461	0.215
Deployment (within site)	3		310,446.072	103,482.024	3.613	0.053
Core (within deployment)	10		288,566.375	28,856.637	7.410	0.000
Sub-core (error)	29		112,931.167	3894.178		
Variance components						
Component	Both stations		Site 2300 N		Site 450 N	
	Variance estimate	% of sum	Variance estimate	% of sum	Variance estimate	% of sum
Site	7237.297	26	–	–	–	–
Deployment (within site)	8602.154	30	8219.333	51	8566.574	36
Core (within deployment)	8534.174	30	4416.259	27	11,395.579	47
Subcore (error)	3894.178	14	3657.278	22	4061.402	17

organic carbon (POC) flux. Sediment-bound algal pigments have been correlated with deep-sea meiofaunal densities and biomass in a number of studies (Pfannkuche, 1985; Vanreusel et al., 1995a; Danovaro et al., 1999; Brown et al., 2001). Although we found a positive correlation between sediment chlorophyll *a* and metazoan meiofaunal densities and biomass, the nature of the relationship was not consistent. When the cruises were considered separately, the strongest correlation was found for the spring samples, but chlorophyll *a* levels were not any higher at this time compared to other sampling times (Table 1). Attempts to determine meiofaunal responses to pulsed inputs of organic matter related to primary productivity at the surface have often been inconclusive with regard to metazoan meiofauna (Pfannkuche, 1993; Gooday et al., 1996; Pfannkuche et al., 2000). Whilst bacteria and protists may show an obvious positive response, suggesting that such organisms can exploit pulses of organic matter rapidly, sedimentation events may result in little or no apparent biomass production by metazoan meiofauna, probably for reasons of behaviour, physiology and growth rate (Gooday et al., 1996; Soltwedel et al., 1996; Pfannkuche et al., 1999; Shimanga and Shirayama, 2000). More recently, however, Witte et al. (2003) reported meiofauna (Nematoda) at 2–5 cm depth responding within weeks to a phytodetrital pulse at a North Atlantic abyssal site, whilst at a site at 1920 m in the NE Atlantic, Hughes and Gage (2004) reported a significant increase in meiofaunal numbers from May to July associated with a phytodetrital accumulation.

Measurements of POC, TN and TOM attempt to take into account the organic content of the sediment, which may not be of immediate phytodetrital origin. This may include carcasses of nekton, marine macrophyte debris, resuspended material, and terrigenous material transported from shallower shelf environments (Pfannkuche, 1985). Soetaert et al. (1997) argue that organic matter content is not a good indicator of food input to the sediment because of large differences in the reactivity of organic material arriving at the sediment–water interface. Although POC and TN do not always yield meaningful information (see de Boveé et al., 1990), positive correlations with meiofaunal densities have been reported (de Boveé et al., 1990). Danovaro et al. (1995) found a significant relationship between the ratio of labile organic material to total organic matter and meiofaunal density (no correlation between meiofauna and chlorophyll pigment-equivalents was found), and suggested that the quality of the sediment was more important than quantity in extreme oligotrophic environments.

Sibuet et al. (1989) placed the *flux* of organic matter as the first-order parameter controlling biomass distribution in the deep Atlantic Ocean, whereas the organic matter *deposited* correlated poorly with meiofaunal abundance. Tietjen et al. (1989) found a highly significant positive relationship between particle flux rates (measured in near-bottom traps) and meiofaunal biomass. Nodder and Northcote (2001) observed that particle fluxes on the southern flank of the Chatham Rise were 2–3 times lower than those on the northern flank in spring and less episodic. However, the more prolonged fluxes to the south had a higher proportion of organic carbon, were more labile and inferred to be more protein-rich than those on the northern slope, suggesting the importance of sediment food quality rather than quantity on the south side. This appears to be supported by the distribution of macrobenthic biomass and abundance, which were found to be higher on the southern than on the northern flank of the Chatham Rise (Probert and McKnight, 1993; Probert et al., 1996), and by elevated rates of sediment community oxygen consumption on the crest and southern flank (Nodder et al., 2003), i.e., in a similar pattern to the meiofauna. Nevertheless, although using biochemical descriptors of sedimentary organics, Grémare et al. (2002) found that organic matter availability was not controlling the meiofauna standing stock on the upper slope of the Gulf of Lions.

Attempts to relate meiofaunal densities with microbial standing stocks have also yielded conflicting results. Some have found a positive correlation (Alongi and Pichon, 1988 (for some taxa); Aller and Aller, 1986; de Boveé et al., 1990; Vanreusel et al., 1995a; Brown et al., 2001), but others have found no relationship (Tietjen et al., 1989; Pfannkuche, 1993; Danovaro et al., 1995; Pfannkuche et al., 2000). Sommer and Pfannkuche (2000) found a relationship between bacterial biomass and meiofaunal biomass, but not meiofaunal density. Such a relationship was evident in the present study, but only for the summer samples.

Sediment granulometric parameters were highly correlated with water depth in this study, and did not correlate significantly with the meiofaunal measures when the effect of depth was held constant; nor did water depth correlate significantly with the meiofaunal measures when the effect of median grain-size was held constant. Alongi and Pichon (1988) reported a correlation between total meiofauna (including Foraminifera) and sediment silt content that was independent of depth, but others have failed to find any relationship between granulometric parameters and meiofaunal density (de Boveé et al., 1990; Coull et al., 1982). This could be

attributable to the relative homogeneity of deep-sea sediments. Differing sediment types at similar depths can be so spatially separated that differences in surface productivity confound any relationship observed (Tietjen, 1984). Across the Chatham Rise, however, sediment physical and chemical properties varied along the transect with differences in sediment parameters most obvious at the deepest sites to the north and south: organic-rich, low carbonate, muddy sediments sampled at 2300 N; and organic-poor, carbonate-dominated sandy sediments at 2300 S and 2600 S (Table 1). This reflects the high and low production in STW and SAW, respectively (e.g., Bradford-Grieve et al., 1999). Sediments on the upper flanks and crest of the rise are predominantly glauconitic silty sands with higher organic contents than these southernmost sites, and underlie the highly productive STF (Bradford-Grieve et al., 1997; Uddstrom and Oien, 1999; Murphy et al., 2001; Nodder et al., 2003).

Shirayama (1984a) found sediment calcium carbonate to be one of the main factors explaining variance of meiofaunal abundance in the deep western Pacific (2090–8260 m). This was attributed to the relationship between calcium carbonate and sedimentation rate (increased food availability) and larger inter-particle pore space (as calcareous sediments contain many tests of planktonic foraminifera which increase interstitial space). In the present study, however, carbonate content was highly negatively correlated with potential food variables such as plant pigments and organic material, though positively correlated with sediment sorting (where higher values denote poorer sorting). Flach et al. (2002) found meiofaunal densities to be inversely correlated with CaCO_3 content and positively correlated with both POC and TN at Iberian margin stations. Similarly, Alongi and Pichon (1988) found no relationship between meiofaunal densities and CaCO_3 content at bathyal depths in the western Coral Sea, which they attributed to the more poorly sorted sediments decreasing interstitial space. On the Chatham Rise, carbonate content was not correlated with percentage sand or water content (a possible index of pore size). Water content was positively correlated with clay and silt content and median grain-size (ϕ scale), so if this were an index of pore size, the opposite might be expected.

The inconsistent results for the relationship between Chatham Rise meiofaunal distributions and various potential food variables perhaps reflect the complexity of relationships between meiofauna and environmental factors and the difficulty of estimating actual food availability, at least from the factors

available in this study (e.g., Soetaert et al., 1997). More appropriate descriptors of potential food are likely to be biochemical parameters that reflect organic fractions that are actually bioavailable and digestible (Danovaro et al., 1995; Cartes et al., 2002; Grémare et al., 2002). Also, the transect encompasses a complex area with changes in bathymetry and hydrological regime, and food–meiofauna interactions can be confounded by other environmental factors, such as sediment granulometry, interactions with other faunal groups, and episodic events such as benthic storms (e.g., Tietjen, 1992). Flach et al. (2002), for example, observed low meiofaunal densities at a bathyal site characterised by a high current regime (and low POC and TN).

4.2. Vertical distribution of meiofauna

Penetration of meiofauna into the sediment has been correlated with the input of organic matter to the sediment (Thiel, 1983; Vincx et al., 1994; Lamshead et al., 1995; Sommer and Pfannkuche, 2000), and with increasing water depth (Alongi and Pichon, 1988; Vanaverbeke et al., 1997). This has been related to species interactions, such as the increased activity of larger organisms in more eutrophic areas leading to higher bioturbation and hence penetration into the sediment of both organic matter and meiofauna (Vincx et al., 1994; Lamshead et al., 1995). Penetration of sediment by meiofauna correlated well with increasing organic matter (Table 4).

Increasing carbonate content was correlated to poorer penetration by nematodes, whereas the opposite relation was found by Shirayama (1984b) who attributed a high carbonate content to increased sedimentation rates. In the present study, calcium carbonate content was either negatively or poorly correlated with sediment chloroplastic pigments and organic matter, consistent with recent observations that the Campbell Plateau to the south of the sampling transect is characterised by low POC fluxes (H. Neil, NIWA, personal communication), despite a high CaCO_3 content of the total mass flux.

4.3. Variability at different spatial scales

Variance components analysis of nematode abundance in deep-sea studies, where replicate cores/grabs have been taken, have shown higher within-sample variance than between-sample variance (85.7% and 14.3%, respectively, Coull et al., 1977; 66% and 34%, respectively, Thiel, 1983). A similar pattern was found

at 450 N in this study (allowing for the gear differences), though 2300 N showed the opposite. Snider et al. (1984) found no relationship between abundance or biovolume and distance between samples (from 2.5 to 45.0 cm and 17–110 km) in a deep-water study (5800 m). In a shallow-water study, Li et al. (1997) found subcore variation (centimetre-scale) to be higher than between cores (metre-scale). When components of the meiofauna were considered, the non-nematode meiofauna displayed much higher variation at the smaller scale. These diminished in importance with increased depth. Meiofaunal variation has been related to very small-scale biogenic structures (Aller and Aller, 1986), which are postulated to act as sediment traps for highly reactive, fresh organic matter. Phytodetritus can deposit as a gelatinous layer with aggregates accumulating in relation to surface topography under the action of currents (Thiel et al., 1988/89; de Wilde et al., 1998), and patches of detrital aggregates may exert a noticeable impact on the chemical microenvironment (Smith et al., 1998). Given these small-scale environmental variations, spatial heterogeneity has been attributed to the selective recruitment of meiofauna (Lee et al., 1977).

To conclude, our results provide the first detailed estimates of meiofaunal abundance and biomass for bathyal depths of the temperate south-west Pacific. Across the Chatham Rise, there is a considerable range in physico-chemical and biological characteristics of differing water masses and in the underlying sediment geochemistry of the benthic environment. Despite limitations of the descriptors of food availability, the meiofaunal parameters appeared to provide a good indicator of the likely degree of benthic–pelagic coupling, in particular that associated with the productive STF region.

Acknowledgements

We thank officers and crew of Cruises 3036, 3040 and 3065 of RV *Tangaroa*; Bill Main, Don McKnight and Conrad Pilditch for assistance with sampling; Lisa Northcote for analysis of sediment physical properties; Lindsay Hawke for sediment pigment analysis; Julie Hall and Lisa Reed for sediment bacterial measurements; and anonymous reviewers for constructive comments on the manuscript. The work was funded by the Foundation for Research, Science and Technology (New Zealand) via the *Ocean Fronts* (1996–2000) and *Ocean Ecosystems* (2000–2002) programmes (C01623, C01822, C01X0027). [SS]

References

- Aller, J.Y., Aller, R.C., 1986. Evidence for localised enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. *Deep-Sea Res., A, Oceanogr. Res. Pap.* 33, 755–790.
- Alongi, D.M., Pichon, M., 1988. Bathyal meiobenthos of the western Coral Sea: distribution and abundance in relation to microbial standing stocks and environmental factors. *Deep-Sea Res.* 35, 491–503.
- Boyd, P., LaRoche, J., Gall, M., Frew, R., McKay, R.M.L., 1999. Role of iron, light, and silicate in controlling algal biomass in subantarctic waters SE of New Zealand. *J. Geophys. Res.* 104, 13395–13408.
- Bradford-Grieve, J.M., Chang, F.H., Gall, M., Pickmere, S., Richards, F., 1997. Size-fractionated phytoplankton standing stocks and primary production during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *N. Z. J. Mar. Freshw. Res.* 31, 201–224.
- Bradford-Grieve, J.M., Boyd, P.W., Chang, F.H., Chiswell, S., Hadfield, M., Hall, J.A., James, M.R., Nodder, S.D., Shushkina, E.A., 1999. Pelagic ecosystem structure and functioning in the Subtropical Front region east of New Zealand in austral winter and spring 1993. *J. Plankton Res.* 21, 405–428.
- Brown, C.J., Lamshead, P.J.D., Smith, C.R., Hawkins, L.E., Farely, R., 2001. Phytodetritus and the abundance and biomass of abyssal nematodes in the central, equatorial Pacific. *Deep-Sea Res.* 1 48, 555–565.
- Cartes, J.E., Grémare, A., Maynou, F., Villora-Moreno, S., Dinet, A., 2002. Bathymetric changes in the distributions of particulate organic matter and associated fauna along a deep-sea transect down the Catalan sea slope (Northwestern Mediterranean). *Prog. Oceanogr.* 53, 29–56.
- Chang, F.H., Gall, M., 1998. Phytoplankton assemblages and photosynthetic pigments during winter and spring in the Subtropical Convergence region near New Zealand. *N. Z. J. Mar. Freshw. Res.* 32, 515–530.
- Coull, B.C., Ellison, R.L., Fleeger, J.W., Higgins, R.P., Hope, W.D., Hummon, W.D., Reiger, R.M., Sterrer, W.E., Theil, H., Tietjen, J.H., 1977. Quantitative estimates of the meiofauna from the deep sea off North Carolina, USA. *Mar. Biol.* 39, 233–240.
- Coull, B.C., Zo, Z., Tietjen, J.H., Williams, B.S., 1982. Meiofauna of the southeastern United States continental shelf. *Bull. Mar. Sci.* 32, 139–150.
- Danovaro, R., Della Croce, N., Eleftheriou, A., Fabiano, M., Papadopoulou, N., Smith, C., Tselepidis, A., 1995. Meiofauna of the deep Eastern Mediterranean Sea: distribution and abundance in relation to bacterial biomass, organic matter composition and other environmental factors. *Prog. Oceanogr.* 36, 329–341.
- Danovaro, R., Dinet, A., Duineveld, G., Tselepidis, A., 1999. Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions–Catalan Sea (western-Mediterranean) and the Cretan Sea (eastern-Mediterranean). *Prog. Oceanogr.* 44, 287–312.
- Danovaro, R., Gambi, C., Della Croce, N., 2002. Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. *Deep-Sea Res.* 1 49, 843–857.
- de Boveé, F., Guidi, L.D., Soyer, J., 1990. Quantitative distribution of deep-sea meiobenthos in the northwestern Mediterranean (Gulf of Lions). *Cont. Shelf Res.* 10, 1123–1145.
- de Wilde, P.A.W.J., Duineveld, G.C.A., Berghuis, E.M., Lavaleye, M.S.S., Kok, A., 1998. Late-summer mass deposition of

- gelatinous phytodetritus along the slope of the N.W. European Continental Margin. *Prog. Oceanogr.* 42, 165–187.
- Feller, R.J., Warwick, R.M., 1988. Energetics. In: Higgins, R.P., Thiel, H. (Eds.), *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, Washington, D.C., pp. 181–196.
- Flach, E., Muthumbi, A., Heip, C., 2002. Meiofauna and macrofauna community structure in relation to sediment composition at the Iberian margin compared to the Goban Spur (NE Atlantic). *Prog. Oceanogr.* 52, 433–457.
- Galéron, J., Sibuet, M., Vanreusel, A., Mackenzie, K., Gooday, A.J., Dinert, A., Wolff, G.A., 2001. Temporal patterns among meiofauna and macrofauna taxa related to changes in sediment geochemistry at an abyssal NE Atlantic site. *Prog. Oceanogr.* 50, 303–324.
- Gooday, A.J., Pfannkuche, O., Lamshead, P.J.D., 1996. An apparent lack of response by metazoan meiofauna to phytodetritus deposition in the bathyal north-eastern Atlantic. *J. Mar. Biol. Assoc. U.K.* 76, 297–310.
- Grémare, A., Medemach, L., de Boveé, F., Amouroux, J.M., Vétion, G., Albert, P., 2002. Relationships between sedimentary organics and benthic meiofauna on the continental shelf and the upper slope of the Gulf of Lions (NW Mediterranean). *Mar. Ecol. Prog. Ser.* 234, 85–94.
- Hughes, D.J., Gage, J.D., 2004. Benthic metazoan biomass, community structure and bioturbation at three contrasting deep-water sites on the northwest European continental margin. *Prog. Oceanogr.* 63, 29–55.
- Lamshead, P.J.D., Ferrero, T.J., Wolff, G.A., 1995. Comparison of the vertical distribution of nematodes from two contrasting abyssal sites in the northeast Atlantic subject to different seasonal inputs of phytodetritus. *Int. Rev. Gesamten Hydrobiol.* 80, 327–331.
- Lee, J.J., Tietjen, J.H., Mastropaolo, C., Rubin, H., 1977. Food quality and the heterogeneous spatial distribution of meiofauna. *Helgol. Wiss. Meeresunters.* 30, 272–282.
- Li, J., Vincx, M., Herman, P.M.J., Heip, C., 1997. Monitoring meiobenthos using cm-, m-, and km-scales in the Southern Bight of the North Sea. *Mar. Environ. Res.* 43, 265–278.
- McIntyre, A.D., 1964. Meiobenthos of sub-littoral muds. *J. Mar. Biol. Assoc. U.K.* 44, 665–674.
- Murphy, R.J., Pinkerton, M.H., Richardson, K.M., Bradford-Grieve, J.M., Boyd, P.W., 2001. Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. *N. Z. J. Mar. Freshw. Res.* 35, 343–362.
- Neira, C., Sellanes, J., Levin, L.A., Arntz, W.E., 2001. Meiofaunal distributions on the Peru margin: relationship to oxygen and organic matter availability. *Deep-Sea Res.* 48, 2453–2472.
- Nodder, S.D., Northcote, L.C., 2001. Episodic particulate fluxes at southern temperate mid-latitudes (42–45°S) in the Subtropical Front region, east of New Zealand. *Deep-Sea Res.* I 48, 833–864.
- Nodder, S.D., Pilditch, C.A., Probert, P.K., Hall, J.A., 2003. Variability in benthic biomass and activity beneath the Subtropical Front, Chatham Rise, SW Pacific Ocean. *Deep-Sea Res.* I 50, 959–985.
- Pfannkuche, O., 1985. The deep-sea meiofauna of the Porcupine Seabight and abyssal plain (NE Atlantic): population structure, distribution, standing stocks. *Oceanol. Acta* 8, 343–353.
- Pfannkuche, O., 1993. Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47°N, 22°W. *Deep-Sea Res.* II 40, 135–149.
- Pfannkuche, O., Boetius, A., Lochte, K., Lundgreen, U., Thiel, H., 1999. Responses of deep-sea benthos to sedimentation patterns in the North-East Atlantic in 1992. *Deep-Sea Res.* I 46, 573–596.
- Pfannkuche, O., Sommer, S., Kähler, A., 2000. Coupling between phytodetritus deposition and the small-sized benthic biota in the deep Arabian Sea: analyses of biogenic sediment compounds. *Deep Sea Res.* II 47, 2805–2833.
- Probert, P.K., McKnight, D.G., 1993. Biomass of bathyal macrobenthos in the region of the Subtropical Convergence, Chatham Rise, New Zealand. *Deep-Sea Res.* 40, 1003–1007.
- Probert, P.K., Grove, S.L., McKnight, D.G., Read, G.B., 1996. Polychaete distribution on the Chatham Rise, southwest Pacific. *Int. Rev. Gesamten Hydrobiol.* 81, 577–588.
- Renaud-Mornant, J., Gournault, N., 1990. Evaluation of abyssal meiobenthos in the eastern central Pacific (Clarion–Clipperton fracture zone). *Prog. Oceanogr.* 24, 317–329.
- Shimanga, M., Shirayama, Y., 2000. Response of benthic organisms to seasonal change of organic matter deposition in the bathyal Sagami Bay, central Japan. *Oceanol. Acta* 23, 91–107.
- Shirayama, Y., 1983. Size structure of deep-sea meio- and macrobenthos in the Western Pacific. *Int. Rev. Gesamten Hydrobiol.* 68, 799–810.
- Shirayama, Y., 1984a. The abundance of deep sea meiobenthos in the western Pacific in relation to environmental factors. *Oceanol. Acta* 7, 113–121.
- Shirayama, Y., 1984b. Vertical distribution of meiobenthos in the sediment profile in bathyal, abyssal and hadal deep sea systems of the western Pacific. *Oceanol. Acta* 7, 123–129.
- Shirayama, Y., Kojima, S., 1994. Abundance of deep-sea meiobenthos off Sanriku, Northeastern Japan. *Jpn. J. Oceanogr.* 50, 109–117.
- Sibuet, M., Lambert, C.E., Chesselet, R., Laubier, L., 1989. Density of the major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean. *J. Mar. Res.* 47, 851–867.
- Smith Jr., K.L., Baldwin, R.J., Glatts, G.C., Kaufmann, R.S., Fisher, E.C., 1998. Detrital aggregates on the sea floor: chemical composition and aerobic decomposition rates at a time-series station in the abyssal NE Pacific. *Deep-Sea Res.* II 45, 843–880.
- Snider, L.J., Burnett, B.R., Hessler, R.R., 1984. The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. *Deep-Sea Res.* 31, 1225–1249.
- Soetaert, K., Vanaverbeke, J., Heip, C., Herman, P.M.J., Middelburg, J.J., Sandee, A., Duineveld, G., 1997. Nematode distribution in ocean margin sediments of the Goban Spur (northeast Atlantic) in relation to sediment geochemistry. *Deep-Sea Res.* I 44, 1671–1683.
- Soltwedel, T., 2000. Metazoan meiobenthos along continental margins: a review. *Prog. Oceanogr.* 46, 59–84.
- Soltwedel, T., Pfannkuche, O., Theil, H., 1996. The size structure of deep-sea meiobenthos in the north-eastern Atlantic: nematode size spectra in relation to environmental variables. *J. Mar. Biol. Assoc. U.K.* 76, 327–344.
- Somerfield, P.J., Warwick, R.M., 1996. *Meiofauna in Marine Pollution Monitoring Programmes: A Laboratory Manual*. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, U.K. 71 pp.
- Sommer, S., Pfannkuche, O., 2000. Metazoan meiofauna of the deep Arabian Sea: standing stocks, size spectra and regional variability in relation to monsoon induced enhanced sedimentation regimes of particulate organic matter. *Deep-Sea Res.* II 47, 2957–2977.
- SPSS, 1999. *Statistical Package for Social Science (SPSS) 10.0*. SPSS Inc., Chicago, USA.
- Sutton, P., 2001. Detailed structure of the Subtropical Front over Chatham Rise, east of New Zealand. *J. Geophys. Res.* 106, 31045–31056.
- Thiel, H., 1975. The size structure of the deep-sea benthos. *Int. Rev. Gesamten Hydrobiol.* 60, 575–606.

- Thiel, H., 1983. Meiobenthos and nanobenthos of the deep sea. In: Rowe, G.T. (Ed.), *The Sea. Deep-Sea Biology*, vol. 8. Wiley, New York, pp. 167–230.
- Thiel, H., Pfannkuche, O., Schriever, G., Lochte, K., Gooday, A.J., Hemleben, C., Mantoura, R.F.G., Turley, C.M., Patching, J.W., Riemann, F., 1988/89. Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. *Biol. Oceanogr.* 6, 203–239.
- Tietjen, J.H., 1984. Distribution and species diversity of deep-sea nematodes in the Venezuela Basin. *Deep-Sea Res.* 31, 119–132.
- Tietjen, J.H., 1992. Abundance and biomass of metazoan meiobenthos in the deep sea. In: Rowe, G.T., Pariente, V. (Eds.), *Deep-Sea Food Chains and the Global Carbon Cycle*. Kluwer, Dordrecht, pp. 45–62.
- Tietjen, J.H., Deming, J.W., Rowe, G.T., Macko, S., Wilke, R.J., 1989. Meiobenthos of the Hatteras Abyssal Plain and Puerto Rico Trench: abundance, biomass and associations with bacteria and particulate fluxes. *Deep-Sea Res., A, Oceanogr. Res. Pap.* 36, 1567–1577.
- Uddstrom, M.J., Oien, N.A., 1999. On the use of high-resolution satellite data to describe the spatial and temporal variability of sea surface temperatures in the New Zealand region. *J. Geophys. Res.* 104, 20729–20751.
- Vanaverbeke, J., Soetaert, K., Heip, C., Vanreusel, A., 1997. The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). *J. Sea Res.* 38, 93–107.
- Vanhove, S., Wittoeck, J., Desmet, G., Van den Berghe, B., Herman, R.L., Bak, R.P.M., Nieuwland, G., Vosjan, J.H., Boldrin, A., Rabitti, S., Vincx, M., 1995. Deep-sea meiofauna communities in Antarctica: structural analysis and relation with the environment. *Mar. Ecol. Prog. Ser.* 127, 65–76.
- Vanreusel, A., Vincx, M., Schram, D., Van Gansbeke, D., 1995a. On the vertical distribution of metazoan meiofauna in shelf break and upper slope habitats of the NE Atlantic. *Int. Rev. Gesamten Hydrobiol.* 80, 313–326.
- Vanreusel, A., Vincx, M., Bett, B.J., Rice, A.L., 1995b. Nematode biomass spectra at two abyssal sites in the NE Atlantic with a contrasting food supply. *Int. Rev. Gesamten Hydrobiol.* 80, 287–296.
- Vincx, M., Bett, B.J., Dinert, A., Ferrero, T., Gooday, A.J., Lamshead, P.J.D., Pfannkuche, O., Soltwedel, T., Vanreusel, A., 1994. Meiobenthos of the deep northeast Atlantic. *Adv. Mar. Biol.* 30, 1–88.
- Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.R., Jorgensen, B.B., Pfannkuche, O., 2003. In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. *Nature* 424, 763–766.