

Comparative biomass of sediment benthos across a depth transect, Chatham Rise, Southwest Pacific Ocean

K. Berkenbusch^{1,*}, P. K. Probert¹, S. D. Nodder²

¹Portobello Marine Laboratory, Department of Marine Science, University of Otago, Portobello 9014, New Zealand

²National Institute of Water and Atmospheric Research (NIWA) Limited, Kilbirnie, Wellington 6021, New Zealand

ABSTRACT: The present study examined the partitioning of carbon between benthic meio- and macrofauna at sites between 350 and 3100 m water depth across Chatham Rise, Southwest Pacific Ocean. Biomass declined with increasing depth on both sides of the crest, but showed different patterns for each faunal size grouping at the deepest sites. Meiofaunal biomass was highest on the crest and lowest at 2800 m, south of the rise (76 and 8 mg C m⁻², respectively), whereas macrofaunal biomass peaked on the southern slope (1169 mg C m⁻²), with lowest values at the deep northern sites (88 and 116 mg C m⁻²). Macrofauna dominated total faunal biomass (>80%), although the relative importance of meiofauna increased with increasing depth on the northern side. The meiofauna: macrofauna carbon ratio was correspondingly low across all sites (0.04 to 0.10), except at the deep 3100 and 2300 m northern sites (0.16). These biomass patterns were significantly related to sediment chlorophyll *a* concentration, indicating greater availability of high-quality (labile) organic carbon. The lack of a shift towards the smaller benthic size class with decreasing food supply at the deep southern site (2800 m depth) appeared to be related to relatively high sediment particulate organic carbon and high calcium carbonate contents, which also influenced meio- and macrofaunal biomass. These findings reveal the close link between faunal biomass and food availability in deep-sea habitats and highlight the importance of phytodetritus in structuring benthic assemblages in the Chatham Rise/Subtropical Front region.

KEY WORDS: Metazoan · Sediment characteristics · Phytopigment · Deep sea · Regression models

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INTRODUCTION

Deep-sea sediments have long been recognised as food-limited habitats, with benthic communities greatly dependent on food supplied from overlying waters (Thiel 1979, Gage & Tyler 1991, Giere 2009). Pelagic productivity and processes largely determine the quantity and quality of organic matter reaching the seafloor, which can originate from a variety of sources, including phyto- and zooplankton remains, crustacean moults, macro-aggregates ('marine snow'), and faecal pellets (Rowe & Staresinic 1979, Gooday & Turley 1990). Sedimentation of photosynthetically produced organic matter can lead to the deposition of relatively undegraded material on the seafloor that is rapidly

consumed and/or incorporated into benthic biomass and represents a significant food source for deep-sea benthos (e.g. Richardson & Young 1987, Pfannkuche 1993, Danovaro et al. 1999, Levin et al. 1999, Blair et al. 1996, Witte et al. 2003a,b, Moodley et al. 2005). In this context, seasonal phytoplankton blooms are considered particularly important as they can result in substantial phytodetritus deposition on the seafloor, representing an important (often episodic) food supply (Billett et al. 1983, Witte et al. 2003b, see reviews by Gooday & Turley 1990, Beaulieu 2002, Gooday 2002).

As the flux of organic carbon is directly linked to surface-water productivity, the supply of organic matter generally decreases with increasing water depth (Pace et al. 1987, Carney 1989). The diminishing food supply

*Email: katrin.berkenbusch@otago.ac.nz

is reflected in the decline in abundance and biomass of benthic organisms, which has been documented for deep-sea fauna (i.e. mega-, macro- and meiofauna) and bacteria (Rowe et al. 1982, Shirayama 1983, Pequegnat et al. 1990, Sibuet et al. 1993, Soltwedel 2000, Baguley et al. 2006, 2008, Johnson et al. 2007, Deming & Carpenter 2008). While biomass decreases with decreasing food supply (and increasing depth), the rate of decline differs amongst benthic size components: larger sized fauna, such as mega- and macrofauna, exhibit a greater rate of biomass decline than meiofauna (and bacteria), so that the latter organisms become increasingly important with depth (Snider et al. 1984, Richardson & Young 1987, Pequegnat et al. 1990, Rowe et al. 1991, 2008, Danovaro et al. 1999).

Although organic matter input has been identified as one of the main factors controlling benthic biomass in deep-sea environments (Tyler 2003), few studies have directly examined the partitioning of carbon across faunal groupings over a wide depth range based on samples taken at the same time and locations (but see Flach et al. 1999, Galéron et al. 2000). The quantification of biomass of different faunal size classes is necessary to understand how differences in primary productivity affect different components of the benthic community. This information is vital to establish the flow of energy through deep-sea food webs and to develop carbon models (e.g. Rowe et al. 2008), which, in turn, help to improve understanding of the functioning of deep-sea ecosystems.

The aim of the present study was to assess the partitioning of carbon between benthic meio- and macrofauna at different depths across Chatham Rise, New Zealand, Southwest Pacific Ocean, and to determine if these benthic assemblages exhibit a shift towards smaller fauna with increasing water depth as observed elsewhere (Flach et al. 1999, Galéron et al. 2000).

MATERIALS AND METHODS

Study site. Chatham Rise is a broad, submarine ridge that extends east of South Island, New Zealand. The crest is relatively shallow at 300 to 400 m water depth, with the northern and southern sides of the rise descending to ca. 3000 m depth (Mackay et al. 2005). The region is characterised by the Subtropical Front, where warm, nutrient-depleted subtropical waters from the north mix with cold, nutrient-rich subantarctic waters from the south, thereby supporting high biological productivity (Bradford-Grieve et al. 1999, Sutton 2001).

As benthic communities north and south of the crest experience contrasting productivity regimes and organic fluxes (Nodder & Northcote 2001), sampling sites across the rise provide the opportunity to examine

benthic biomass at comparable water depths in potentially different trophic environments.

Sample collection and processing. Samples were collected at 9 sites across Chatham Rise in austral spring 2001 (29 September to 14 October; Table 1, Fig. 1; see also Nodder et al. 2007). Sampling sites were situated along a latitudinal transect at 178° 30' E, at water depths ranging from 350 (crest) to 3100 m north and 2800 m south of the rise (Table 1). Sediment and infaunal samples were obtained using a multicorer (Ocean Instruments MC-800, 10 cm diameter cores), with several deployments at each site.

Meiofaunal subsamples (5.3 cm² syringe cores, 5 cm sediment depth) were obtained from a single core from each of 3 separate multicorer deployments per site. Samples were preserved in 10% buffered formalin containing Rose Bengal and subsequently sieved on a 45 µm mesh. Meiofauna was extracted by Ludox flotation before being mounted on microscope slides (Sommerfield & Warwick 1996). Using a compound microscope connected to a video image system (Olympus BX51, Soft Imaging System 2007), meiofauna was sorted into main metazoan taxonomic groups and enumerated. Specimen dimensions (maximum length and width) were measured via video image analysis (see Grove et al. 2006) and converted to body volume using standard conversion factors for each taxon (Feller & Warwick 1988). When nematodes were highly abundant, a random subsample of 50 individuals was measured, and total volume was estimated by multiplying the volume of the subsample by the ratio of numbers counted to the numbers measured (see Grove et al. 2006). Body volumes were converted to biomass by assuming a specific gravity of 1.13 and a carbon:wet weight ratio of 0.1 (Feller & Warwick 1988).

Macrofaunal samples were obtained from several cores (generally 6 to 8) per multicorer deployment, based on 3 deployments site⁻¹. Cores were sieved on a 500 µm mesh, either as a whole or by sediment depth sections of 0–1, 1–5, 5–10, 10–15 cm), and preserved in 10% buffered formalin containing Rose Bengal. Macrofauna was sorted into the main taxonomic groups, excluding meiobenthic taxa, i.e. nematodes, harpacticoid copepods, or ostracods. Blotted wet weight was recorded for each taxon (accuracy 0.01 mg) and converted to carbon biomass using conversion factors for each group following Rowe (1983). Data from cores were combined for each multicorer deployment for subsequent analysis.

Sediment cores (different to those sampled for benthic fauna, 1 core site⁻¹) were divided vertically into 11 sections (0.5 cm sections from 0–5 cm sediment depth, and one 1.0 cm section at either 8–9 or 9–10 cm sediment depth). Each section was analysed for sediment grain size, total organic matter (TOM), carbonate

Table 1. Characteristics of sampling sites along transect 178° 30' E across Chatham Rise, New Zealand. Sediment variables included total organic matter (TOM), calcium carbonate (CaCO₃), particulate organic nitrogen (PON), particulate organic carbon (POC), and phytopigments (chlorophyll *a* [chl *a*] and total phaeopigments). Values are averaged (\pm SD) across 11 depth sections to 10 cm sediment depth (but averaged across top 9 cm for sediment fines, CaCO₃, and TOM at Site 450N; PON, POC, and C:N at Site 350CR). Site identifiers are water depth (m) and relative position on Chatham Rise — N: northern flank; CR: crest; S: southern flank

Site	Latitude (S)	Water depth (m)	Sediment fines (%)	TOM (%)	CaCO ₃ (%)	PON (%)	POC (%)	C:N (mol)	Chl <i>a</i> (ng g ⁻¹ dry sediment)	Total phaeopigments (ng g ⁻¹ dry sediment)	Chl <i>a</i> : total phaeopigment ratio
3100N	41° 00'	3118–3125	96.84 \pm 2.31	5.75 \pm 1.56	12.73 \pm 1.77	0.09 \pm 0.01	0.82 \pm 0.09	10.24 \pm 1.03	12.78 \pm 11.19	1333.70 \pm 810.29	0.99 \pm 0.82
2300N	42° 30'	2326–2330	95.47 \pm 1.41	5.21 \pm 1.26	30.10 \pm 1.46	0.15 \pm 0.01	1.28 \pm 0.08	9.78 \pm 0.29	13.41 \pm 12.76	914.06 \pm 592.29	1.43 \pm 0.97
1000N	42° 49'	978–1001	52.22 \pm 2.72	3.48 \pm 0.56	54.19 \pm 1.57	0.06 \pm 0.02	0.64 \pm 0.11	13.31 \pm 1.69	17.90 \pm 37.63	910.38 \pm 1242.25	1.45 \pm 0.86
450N	42° 58'	441–449	28.76 \pm 7.30	3.11 \pm 1.27	27.11 \pm 5.63	0.05 \pm 0.02	0.50 \pm 0.14	12.52 \pm 1.74	38.68 \pm 67.92	1352.67 \pm 1952.05	2.27 \pm 0.67
350CR	43° 26'	347–349	33.35 \pm 6.07	3.58 \pm 0.56	34.48 \pm 4.51	0.08 \pm 0.02	0.78 \pm 0.15	11.45 \pm 0.99	77.89 \pm 166.49	1442.99 \pm 1922.16	3.01 \pm 2.12
450S	43° 49'	453–477	45.09 \pm 5.21	3.67 \pm 1.01	35.24 \pm 1.86	0.06 \pm 0.01	0.67 \pm 0.49	12.54 \pm 1.77	254.57 \pm 524.75	2438.77 \pm 4751.81	10.02 \pm 4.54
750S	44° 00'	744–754	41.63 \pm 5.32	3.40 \pm 0.40	30.21 \pm 1.76	0.06 \pm 0.01	0.46 \pm 0.09	8.90 \pm 0.78	169.23 \pm 305.87	1369.91 \pm 2058.82	7.92 \pm 4.00
1200S	44° 20'	1205–1209	79.73 \pm 1.98	2.00 \pm 0.36	48.50 \pm 1.64	0.03 \pm 0.01	1.02 \pm 0.49	49.63 \pm 27.54	130.96 \pm 309.29	1255.43 \pm 2296.85	4.51 \pm 4.34
2800S	46° 40'	2631–2780	56.88 \pm 4.24	2.16 \pm 0.28	95.65 \pm 7.43	0.04 \pm 0.02	2.89 \pm 1.32	108.12 \pm 47.21	5.31 \pm 12.64	269.76 \pm 502.51	0.67 \pm 1.06

(CaCO₃), particulate organic carbon (POC), and particulate organic nitrogen (PON) contents as well as molar C:N ratio. Sediment grain size was determined by drying subsamples to constant weight and then using a combination of dry-sieving (63 to 500 μ m — percentage sand) and Sedigraph techniques (<63 μ m fraction — percentage silt and clay) (Singer et al. 1988, Bale & Kenny 2005). Percentage TOM was established by loss-on-ignition (500°C for 4 h) (Bale & Kenny, 2005), and the calcium carbonate contents, by CO₂ vacuum-gasometric method (\pm 1% accuracy) (Jones & Kaiteris 1983). POC and PON contents were analysed in dried, acidified (8% v/v sulphurous acid) sediment samples via a carbon-hydrogen-nitrogen (CHN) analyser (CE Instruments NC2500; precision ca. 2%) (Bale & Kenny 2005). Phytopigment concentrations, i.e. chlorophyll *a* (chl *a*) and total phaeopigments, including the degradation products phaeophytin and phaeophorbide, were determined in sediment cores sliced vertically into 10 depth sections: surface scrape (0 to 0.1 cm), 0.5, and 1 cm sections to 5 cm sediment depth, and 2.5 cm sections to 15 cm, with freeze-dried sediment from each section analysed via high-performance liquid chromatography (Jeffrey et al. 1997).

Data analysis. Differences in meio- and macrofaunal biomass (wet weight and organic carbon) across sites were tested using 1-way ANOVA, after assessing normality and homogeneity of variance (Shapiro-Wilks and Levene's tests, respectively; Zar 1984). When necessary, data were log₁₀-transformed to meet requirements of parametric tests, although transformation did not achieve normality of macrofaunal wet weight and carbon data. Nevertheless, macrofaunal data were tested using this analysis, as ANOVA is relatively robust to non-normality (Underwood 1997).

The influence of sediment parameters on meiofaunal and macrofaunal biomass (organic carbon) and on the ratio between meiofaunal and macrofaunal carbon were analysed using multiple regressions with the following predictors (independent variables): sediment grain size, %TOM, %CaCO₃, %POC, %PON, chl *a*, total phaeopigment concentrations, and chl *a*:total phaeopigment ratio. Water depth was not included as a predictor variable to avoid collinearity. A maximum of 3 predictors was included in each regression model to ensure that the number of observations sufficiently exceeded that of predictors (i.e. 6- to 10-fold; Quinn & Keough 2002). As a consequence, all possible combinations of predictors were tested to obtain a regression model that had the highest significant coefficient of determination (*r*²). For significant relationships, partial regression plots (graphing the residuals) were used to illustrate the nature of the relationship between each biomass variable and individual predictors. These residual plots were also used as diagnostic tools to assess

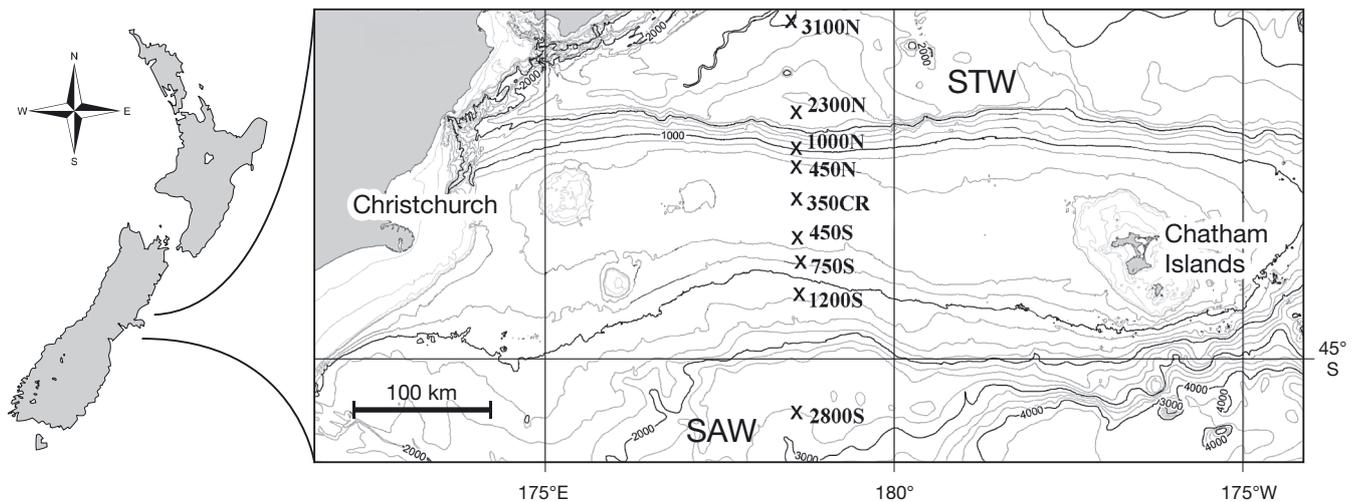


Fig. 1. Deep-sea benthos study sites across Chatham Rise, New Zealand, Southwest Pacific Ocean. Site identifiers: water depth (m) and relative position on Chatham Rise (N: northern flank; CR: crest; S: southern flank). Associated surface water masses that mix in the Chatham Rise region include subtropical water (STW) and subantarctic water (SAW)

that assumptions of linear regression were met. Normality, presence of outliers, and homogeneity of variance were assessed visually using the residual graphs, and collinearity was assessed by examining tolerance and condition index values; Cook's distance and leverage values were used to determine potential outliers (Quinn & Keough 2002). All data were \log_{10} -transformed.

RESULTS

Sediment variables

Sediment parameters showed some variability in relation to water depth and/or position relative to the Chatham Rise crest, with differences particularly evident at the deep sites (>1000 m water depth) on either side of the rise (Table 1). These deep sites were characterised by a high percentage of sediment fines, which was particularly pronounced on the northern side, where sediment consisted of >95% fines, while also containing a relatively high proportion of TOM (ca. 5 to 6%). In contrast, TOM content was low at the deep southern sites (ca. 2%), whereas %CaCO₃ was high, especially at 2800S (>95%). Sediment %PON and %POC were relatively high at deep sites (ca. 1 to 2%), with %PON elevated on the northern side, but %POC was considerably higher at 2800S (ca. 3% cf. <1% at 3100N). At this site (and 1200S), the C:N molar ratio was also particularly high (≥ 50), indicating highly refractory organic matter, while it was markedly lower at deep northern sites (10 to 13). Sediment chl *a* concentration was highest at 450S, with high values also at the

other shallow southern sites (130 to 255 ng chl *a* g⁻¹ dry sediment), but substantially lower concentrations at 350CR and all northern sites (12 to 78 ng chl *a* g⁻¹ dry sediment), and a drastic decline at 2800S (5 ng chl *a* g⁻¹ dry sediment). Total phaeopigment concentrations showed a similar pattern on the southern side, but with high values also at all northern sites, although without a substantial decrease with increasing water depth from 350CR to 3100N. The chl *a*:total phaeopigment ratios corresponded closely with chl *a* concentrations across sites, indicating the availability of relatively undegraded pigmented organic material at shallow sites. There was considerable variability within cores across sediment depth (0 to 10 cm) owing to extremely high values in surface sediments (see Nodder et al. 2007) and markedly lower values with increasing sediment depth, resulting in large variability in the depth-integrated data (Table 1).

Meio- and macrofaunal biomass

Meiofaunal biomass (wet weight) showed a clear pattern across Chatham Rise, ranging from 0.6288 mg 10 cm⁻² at the shallowest site (350CR) to a minimum of 0.0682 mg 10 cm⁻² at 2800S. There was a considerable decrease in biomass with increasing water depth on either side of the rise (Fig. 2A), but this trend was more pronounced on the northern side, with higher biomass values on the southern side. Values at 750S and 1200S were similar to those at 450N (0.4 to 0.5 mg 10 cm⁻²), with lowest values at 2800S (<0.1 mg 10 cm⁻²). There was considerable within-site variability on the crest at 350CR, owing to large differences in polychaete

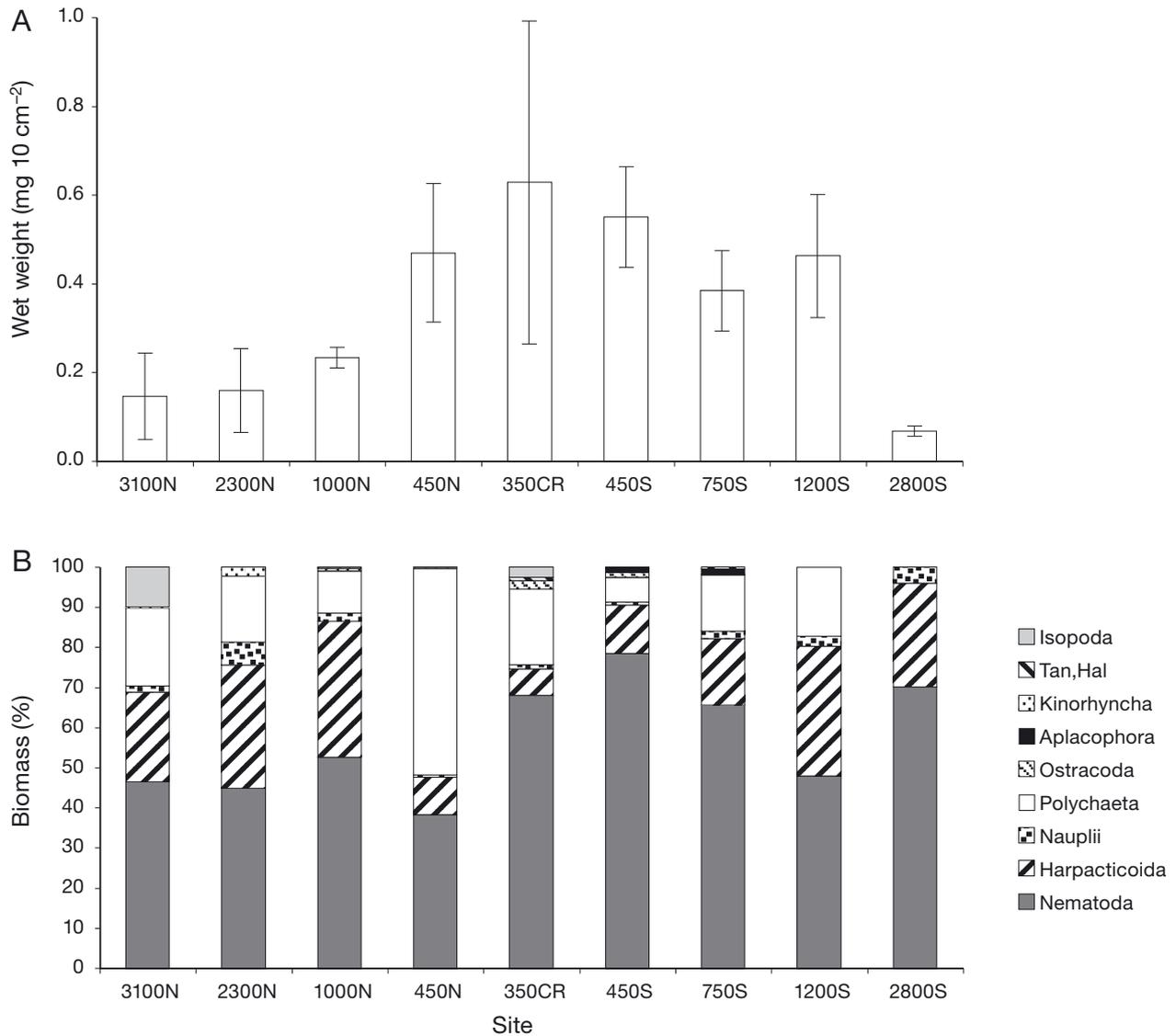


Fig. 2. Meiofaunal biomass (wet weight, mg 10 cm⁻²; average \pm 1 SD, n = 3) and contribution of different taxa to total biomass across Chatham Rise, New Zealand. Site identifiers: water depth (m) and relative position on Chatham Rise (N: northern flank; CR: crest; S: southern flank). Tan, Hal: Tanaidacea and Halacaridae combined

biomass among replicate samples at this site (data not shown). Meiofaunal biomass differed significantly across sites (1-way ANOVA, $F_{8,18} = 5.173$, $p < 0.005$); it was significantly lower at 3100N than at 450S, and at 2800S compared with each of the shallow sites (450N to 450S) (post hoc Tukey test, $p < 0.05$).

Nematodes consistently dominated total meiofaunal biomass (ca. 45 to 78%), and combined with harpacticoid copepods and nauplii, constituted ca. 48 to 97% of the meiofaunal biomass across all sites (Fig. 2B). The contribution of these meiofaunal groups was lowest at 450N, where polychaetes accounted for a substantial proportion of overall biomass (ca. 51%). Polychaete biomass varied at the other sites (between 6.05 and 19.44%), and polychaetes were absent at 2800S. Other

faunal groups made only relatively minor contributions to total biomass and included ostracods (absent at sites >1000 m water depth, 0.09 to 2.10% at shallower sites), kinorhynchans (0.01 to 2.18%, absent at 2800S), aplacophorans (only at 450S and 750S, 1.00 and 1.53%, respectively), tanaidaceans and halacarids (combined 0.20 to 0.66%, only at 350CR to 750S), and isopods (only at 3100N and 350CR, 2.65 and 9.99%, respectively) (Fig. 2B).

Macrofaunal biomass (wet weight) also showed a depth-related pattern across the rise, with similar, high values at shallow sites, 1000N to 1200S (13 427 to 26 791 mg m⁻²) and highest biomass at 750S (Fig. 3A). Lowest biomass values were at 3100N and 2300N (<2500 mg m⁻²), where biomass was considerably

lower than at the deepest southern site, 2800S (ca. 7400 mg m⁻²). Differences in macrofaunal biomass were statistically significant (1-way ANOVA, log₁₀-transformed data, $F_{8,18} = 30.70$, $p < 0.001$), with values significantly lower at 3100N and 2300N than that at any other site. Biomass at 2800S was significantly lower compared with 350CR and the 2 shallow southern sites, 450S and 750S (post hoc Tukey test, $p < 0.05$).

Polychaetes generally dominated macrofaunal biomass, constituting 36.99 to 76.45% of the total. Other taxa made relatively large contributions (>10%) at some sites, but were absent or contributed little to biomass at others (Fig. 3B). For example, ophiuroids contributed 31.27% of the total biomass at 1200S, but accounted for only 0.95 to 9.24% of total biomass at all other sites; similarly, echinoids accounted for 20.08 and

11.00% of biomass at 1000N and 750S, respectively, but were absent at the deepest northern and southern sites (≥ 1200 m depth) and at low proportions (0.19 to 5.80%) at the shallow sites. Different crustacean groups, including amphipods, isopods, tanaidaceans, and cumaceans, were present at most sites, but generally at low biomass, except at 3100N, where amphipods accounted for 11.50%. Other minor contributors to biomass were holothurians (0.10 to 1.38% at 1000N, 350CR, 1200S), bivalves (all sites, except 2800S, 3.27 to 6.89%), gastropods (absent at several sites, 0.11 to 2.90% at others), and aplacophorans, sipunculans, and mysidaceans (absent at 2800S, combined 0.05 to 1.30% at other sites); anthozoans were present only at 450S (4.40%). Biomass that could not be assigned to a specific taxonomic group was included under 'miscel-

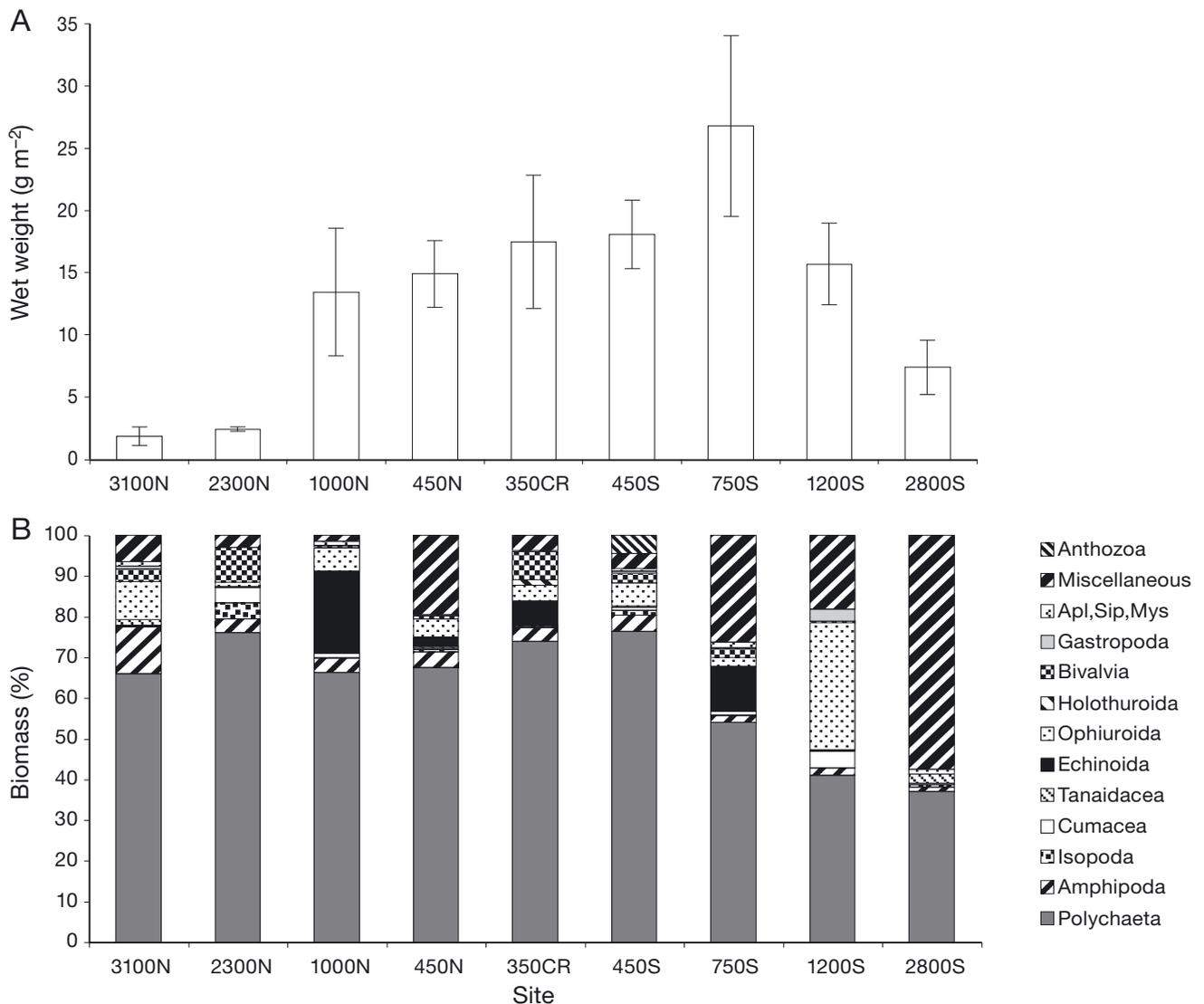


Fig. 3. Macrofaunal biomass (wet weight, g m⁻²; average \pm 1 SD, $n = 3$) and contribution of different taxa to total biomass across Chatham Rise, New Zealand (site identifiers: water depth [m] and relative position on Chatham Rise—N: northern flank; CR: crest; S: southern flank). Apl,Sip,Mys: Aplacophora, Sipuncula and Mysidacea combined

laneous' (e.g. body parts such as crustacean antennae that could not be assigned to amphi- or isopods). At most sites, this category was <10%, but, at 2800S, it constituted 57.49% of total biomass.

Carbon values

Meio- and macrofaunal organic carbon values (mg C m^{-2}) reflected the wet weight patterns across the rise (Table 2). The highest meiofaunal carbon value was at 350CR, the lowest at 2800S, and the greatest drop in value was on the southern side between 1200S and 2800S. Macrofaunal carbon was highest at 750S, lowest at 3100N, and showed the greatest decline on the northern side, between 1000N and 2300N. Total carbon, for both faunal groups combined, followed the macrofaunal carbon trend, as macrofauna contributed on average from 83.78 to 97.47% to total faunal carbon. The meiofaunal contribution was highest at the 2 deepest northern sites, where it constituted around 15% (Table 2).

Accordingly, the ratio of meio- to macrofaunal carbon biomass was highest at the 2 northern deep sites (0.16), where meiofauna made the largest contribution to overall biomass (Fig. 4). At all other sites, the relative importance of meiofauna was similarly low, and ratio values were at a minimum at 750S and 2800S (0.04 and 0.03, respectively).

Biomass in relation to sediment variables

Multiple regressions revealed significant relationships between faunal carbon values and sediment parameters (i.e. sediment chl *a*) across the Chatham Rise (Table 3, Fig. 5). Meiofaunal carbon was significantly related to sediment chl *a* and %POC ($r^2 = 0.702$, $p < 0.001$) and increased with increasing chl *a* concentration, but decreased with increasing %POC. Macro-

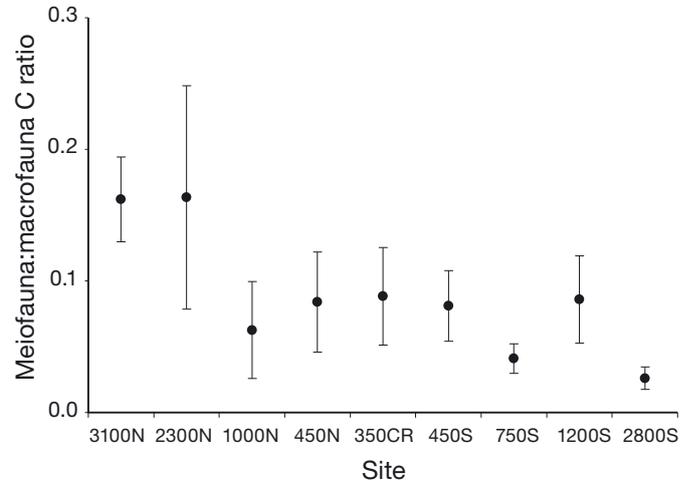


Fig. 4. Ratio of meio- to macrofaunal carbon biomass (mean \pm 1 SD, $n = 3$) across Chatham Rise, New Zealand. Site identifiers: water depth (m) and relative position on Chatham Rise (N: northern flank; CR: crest; S: southern flank)

faunal carbon significantly increased with increasing sediment chl *a* concentration and increasing % CaCO_3 ($r^2 = 0.702$, $p < 0.001$). The meio- to macrofauna carbon ratio was significantly related to sediment chl *a* and % CaCO_3 ($r^2 = 0.400$, $p < 0.005$), with a significant decrease with increasing % CaCO_3 (Table 3, Fig. 5).

DISCUSSION

Both meio- and macrofauna exhibited assemblage compositions that are consistent with those previously reported from this region and elsewhere. Meiofauna samples are generally dominated by nematodes, followed by harpacticoid copepods, and nauplii (Vanaverbeke et al. 1997, Soltwedel 2000, Vanhove et al. 2004, Gambi & Danovaro 2006, Grove et al. 2006, Baguley et al. 2008), whereas polychaetes are frequently the most prevalent macrofaunal taxon (Brown

Table 2. Meio-, macrofaunal, and total biomass (C , mg m^{-2}) and contribution of each faunal grouping to total C in benthic samples at different sites across Chatham Rise, New Zealand. Site identifiers: water depth (m) and relative position on Chatham Rise (N: northern flank; CR: crest; S: southern flank)

Site	Meiofauna	Macrofauna	Total C	Meiofauna (%)	Macrofauna (%)
3100N	17.59 \pm 11.57	87.57 \pm 34.24	105.16 \pm 42.78	16.22 \pm 5.65	83.78 \pm 5.65
2300N	19.40 \pm 11.62	115.65 \pm 9.50	135.05 \pm 7.74	14.21 \pm 7.90	85.79 \pm 7.90
1000N	28.15 \pm 2.97	557.73 \pm 296.14	585.89 \pm 293.90	5.81 \pm 3.24	94.19 \pm 3.24
450N	55.95 \pm 17.78	702.53 \pm 123.12	758.47 \pm 105.63	7.67 \pm 3.25	92.33 \pm 3.25
350CR	75.98 \pm 44.01	802.64 \pm 208.82	878.62 \pm 194.98	9.22 \pm 6.14	90.78 \pm 6.14
450S	66.87 \pm 13.70	854.98 \pm 129.64	921.85 \pm 115.96	7.45 \pm 2.31	92.55 \pm 2.31
750S	46.29 \pm 10.74	1168.58 \pm 309.72	1214.87 \pm 312.33	3.92 \pm 1.04	96.08 \pm 1.04
1200S	55.73 \pm 16.58	663.46 \pm 78.06	719.19 \pm 71.79	7.85 \pm 2.79	92.15 \pm 2.79
2800S	8.32 \pm 1.37	336.05 \pm 76.84	344.37 \pm 76.19	2.53 \pm 0.82	97.47 \pm 0.82

Table 3. Multiple linear regressions between infaunal biomass (carbon) measures, including meiofaunal:macrofaunal C ratio, and sediment parameters at sites across Chatham Rise, New Zealand (all values \log_{10} -transformed). POC: percentage particulate organic matter; CaCO_3 : percentage calcium carbonate; chl a: chlorophyll a, ng g^{-1} dry sediment

Variable	<i>t</i>	<i>p</i>
Meiofaunal biomass		
Total regression: $r^2 = 0.702$, $F_{2,26} = 28.29$, $p < 0.001$		
POC	-2.07	0.49
Chl a	4.31	<0.001
Macrofaunal biomass		
Total regression: $r^2 = 0.702$, $F_{2,26} = 28.23$, $p < 0.001$		
CaCO_3	4.01	<0.002
Chl a	6.87	<0.001
C ratio		
Total regression: $r^2 = 0.400$, $F_{2,26} = 8.01$, $p < 0.005$		
CaCO_3	-4.00	<0.002
Chl a	-0.59	0.56

1991, Paterson & Lamshead 1995, Probert et al. 1996, Smith & Demopoulos 2003).

Total (meio- and macrofaunal) biomass decreased with increasing water depths on both sides of Chatham Rise, but this decline was more pronounced on the northern slope, reflecting different levels of productivity on either side of the crest and the Subtropical Front. Previous Chatham Rise studies across this transect revealed similar biomass patterns, albeit with some differences at deep sites (Nodder et al. 2003, Grove et al. 2006). Encompassing 3 different seasons (austral autumn and spring 1997, summer 2000), meiofaunal biomass was consistently high at the shallow sites and markedly higher on the

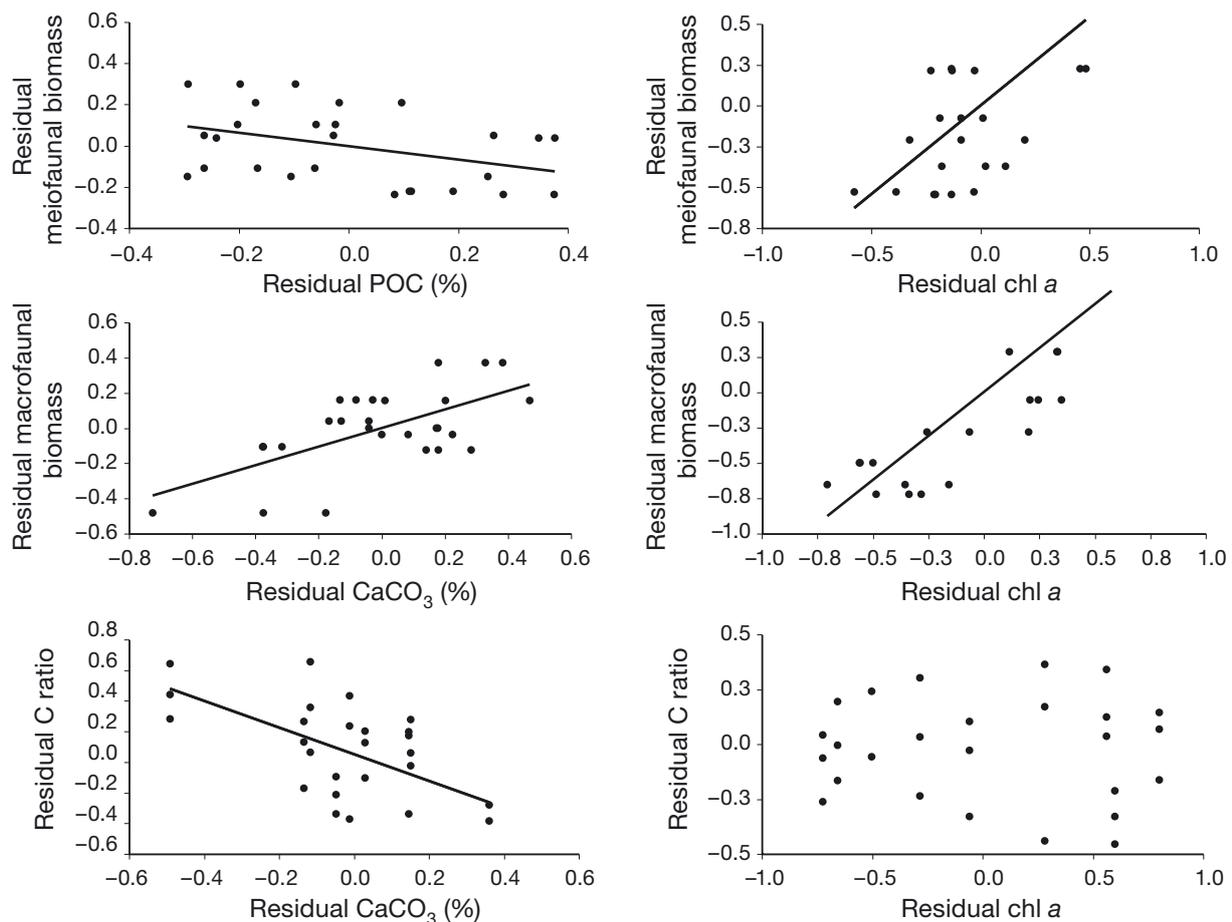


Fig. 5. Partial regression plots of multiple linear regressions between infaunal biomass (carbon) measures, including the meiofaunal:macrofaunal C ratio and sediment parameters at sites across Chatham Rise, New Zealand (all values \log_{10} -transformed). Graphs show the relationship between residuals of each biomass variable versus those of individual predictors. Line of best fit only shown for significant relationships ($p < 0.05$). POC: particulate organic carbon; CaCO_3 : percent calcium carbonate; chl a: chlorophyll a, ng g^{-1} dry sediment

upper southern slope, with maximum values at 450S (Grove et al. 2006). Spring biomass values were comparable to those in the present study, ranging from a minimum of 5 mg C m^{-2} at 2600S (cf. 8 mg C m^{-2} at 2800S, present study) to a maximum of 90 mg C m^{-2} at 350CR (cf. 76 mg C m^{-2} at 350CR); however, biomass values in summer and autumn were noticeably higher, ranging from 20 to 140 mg C m^{-2} and from 40 to 170 mg C m^{-2} , respectively (Nodder et al. 2003). Macrofaunal biomass (recorded in autumn 1997) was also elevated on the upper slopes, particularly the southern flank, with a maximum at 450S (Nodder et al. 2003). It decreased with increasing water depth on either side, but in contrast to the present study, macrofaunal biomass declined more drastically on the southern side: sites below 1000 m water depth supported considerably lower macrofaunal biomass than sites at equivalent depths on the northern slope, and biomass was at a minimum at the deepest southern site, 2300S. Furthermore, biomass values were generally lower than those reported here, with a maximum of 390 mg C m^{-2} at 450S (cf. 1168 mg C m^{-2} at 750S, present study), and a minimum of ca. 90 mg C m^{-2} at 2300S (Nodder et al. 2003) (cf. 336 mg C m^{-2} at 2800S). The differences in faunal biomass values across seasons and studies are likely related to seasonal (and annual) variation in food supply via surface water productivity and phytodetritus deposition.

The observed biomass patterns suggest enhanced phytodetritus deposition on the southern slope, following phytoplankton blooms in surface waters, similar to the event immediately preceding sample collection in the present study (see Nodder et al. 2007). The extensive spring phytoplankton bloom resulted in elevated surface chl *a* concentrations (estimated $>2 \text{ mg m}^{-3}$) in northern subtropical surface waters, but the deposition of phytodetritus was generally limited to the southern slope, focused at 750S (Nodder et al. 2007). These sites were also characterised by high chl *a*:total phaeopigment ratios, denoting relatively undegraded phytodetritus within the sediment. Sediment chl *a* concentration was consistently implicated as influencing benthic biomass across sites, reflecting the availability of labile organic matter that is readily consumed near the sediment–water interface (Richardson & Young 1987, Witte et al. 2003a).

In addition, comparatively high chl *a* concentrations within the sediment profile (at 10 to 15 cm depth) suggest that relatively undegraded phyto-compounds can be buried quickly (e.g. through macrofaunal bioturbation; Witte et al. 2003b), resulting in a pool of labile organic carbon that is available at greater depths and over longer time scales than those immediately associated with episodic flux events (Nodder et al. 2007). The high proportion of high-quality food available at shallow sites and on the southern slope supports consis-

tently greater benthic productivity, as evident in higher faunal biomass and sediment community oxygen consumption rates (Probert & McKnight 1993, Probert et al. 1996, Nodder et al. 2003, 2007, Grove et al. 2006, present study).

A decrease in benthic biomass with decreasing food supply (usually coupled with increasing water depth) is well documented, particularly at deep bathyal and abyssal sites (Snider et al. 1984, Lampitt et al. 1986, Richardson & Young 1987). As deep-sea benthic communities are greatly dependent on organic matter input from the euphotic zone (Gage & Tyler 1991, Tyler 2003), the quantity and quality of organic carbon reaching the seafloor influence the abundance and biomass of benthic organisms (Danovaro et al. 1999, Tyler 2003, Ruhl & Smith 2004, Smith et al. 2009). The findings from the present study support this notion and highlight the close link between (high-quality) organic matter input from surface waters and deep-sea benthic fauna.

In addition to total benthic biomass, there were some differences in relative biomass across Chatham Rise, with a decrease in the relative importance of macrofauna with increasing water depth and decreasing food supply on the northern side. The dominance of macrofauna at shallow sites and the observed shift towards meiofauna with increasing water depth agree with deep-sea studies in other regions that also directly compare different benthic size groups in relation to the partitioning of carbon across a wide depth range (Shirayama 1983, Rowe et al. 1991, 2008, Flach et al. 1999, Galéron et al. 2000). In the western North Atlantic Ocean, meiofaunal biomass (without 'typical' macrofaunal taxa, e.g. polychaetes, amphipods, isopods, tanaisids) declined considerably more slowly and became proportionally more important than macrofauna below 1200 m depth (Rowe et al. 1991). Accordingly, the contribution of meiofauna to total faunal biomass increased from $<3\%$ on the continental shelf (70 to 150 m) to 10% at 450 m and 20% at 4400 m depth. At the abyssal site at 5300 m, meiofauna became prevalent, with its biomass ~ 6 times greater than that of macrofauna, reflecting 86% of faunal biomass (Rowe et al. 1991).

Similarly, at 3 tropical Northeast Atlantic sites characterised by different levels of surface water primary productivity (and depths), total benthic biomass was highest at the eutrophic site (1600 to 2100 m water depth), where meiofauna (i.e. nematodes and copepods only) constituted 12% of this biomass compared with 56 and 32% by mega- and macrofauna, respectively (Galéron et al. 2000). At the meso- and oligotrophic sites (3110 and 4640 m depth), the meiofaunal contribution increased to 27 and 72% of the total, respectively (without accounting for megafauna). Differences in water depth likely enhanced the effects of different degrees of productivity across sites. Another Northeast

Atlantic Ocean study of carbon partitioning between macro- and meiofauna revealed similar findings (Flach et al. 1999). On the continental slope of the Goban Spur, meiofaunal biomass (nematodes only) became increasingly important in comparison with macrofauna at water depths between 208 and 4460 m. Following an initial decrease in meiofaunal biomass on the continental shelf to 1000 m depth, values remained stable, whereas macrofaunal biomass declined drastically between upper slope sites and sites below ca. 1400 m water depth. The different rates of decline were evident in the ratio of meio- to macrofaunal biomass, which increased with increasing water depth; after an initial decline from ca. 0.12 at the shallowest site to a minimum of ca. 0.02 at 1034 m, it increased to ca. 0.10 at 2182 m and to ca. 0.37 at 4460 m water depth (Flach et al. 1999).

These studies highlight the relative shift in importance of meiofaunal biomass with increasing water depth in deep-sea habitats, as observed in the present study. Similarly, this pattern appeared to be determined by a concomitant decrease in food supply, measured as differences in primary productivity (Galéron et al. 2000), carbon input and quality (Flach et al. 1999), or POC flux (Rowe et al. 1991). Food supply, in the form of phytodetritus, was also identified as determining benthic community structure in relation to bathymetry in a global review of biomass patterns in deep-sea benthos (Rex et al. 2006). This analysis of existing data across different regions (but with the Southern Hemisphere under-represented) confirms a general decline in faunal biomass with increasing depth and decreasing organic carbon input across faunal groups. Although macrofaunal biomass was generally higher than that of meiofauna above ca. 2500 m, it was lower below ca. 4000 m, with similar biomasses in-between these depths (Rex et al. 2006).

Chatham Rise deep-sea fauna seems unusual in that the contribution of macrofauna to total biomass did not decline below ca. 80%, and there was no discernible shift towards meiofaunal biomass at the deep southern sites. The more pronounced increase in the relative importance of meiofaunal biomass in the aforementioned studies compared with Chatham Rise benthos may, in part, be related to the greater depth ranges sampled, including abyssal sites. Abyssal sediments are extremely food-deprived, and quantitative estimates of benthic biomass at abyssal sites have revealed the dominance of small-sized organisms (Snider et al. 1984, Richardson & Young 1987). In the North Pacific Ocean, meiofaunal biomass estimates at 5800 m water depth were 33 mg wet weight m^{-2} (excluding foraminiferans), compared with 5.1 mg wet weight m^{-2} of macrofaunal biomass (Snider et al. 1984). Meiofaunal biomass was also prevalent in the deep Venezuela Basin, Caribbean Sea, where the ratio

between meio- and macrofaunal biomass was on average 3.3 (range: 1.2 to 7.1) between 3450 and 5050 m water depth (Richardson & Young 1987). These biomass comparisons demonstrate clearly that the partitioning of energy is most noticeably skewed towards smaller sized benthos, as food resources diminish greatly with increasing depth into the abyssal realm.

The notable lack of a shift towards meiofaunal biomass at 2800S reflects the influence of other sediment variables affecting biomass patterns in addition to sediment chl *a* concentration across Chatham Rise. Meiofaunal biomass was negatively related to %POC, which was highest at 2800S, and the high value possibly indicates a high proportion of refractory carbon, which may not be directly accessible to benthic fauna. The extremely high C:N molar ratio (108) at this site supports this contention, as it reflects preferential remineralisation of nitrogen over carbon, which, in turn, implies that organic compounds are in forms that are difficult for benthic fauna to assimilate. In contrast, at the deep northern sites, relatively high sediment %POC was accompanied by C:N values of ca. 9 to 10. It is, therefore, possible that the low supply of high-quality food in the form of sediment chl *a* at 2800S was exacerbated by high %POC, further limiting the food supply for meiofauna.

In addition, macrofaunal biomass was positively related to %CaCO₃, which was extremely high at 2800S (95.65%) (and low at the deep northern site, 12.73%). The underlying reason for the positive relationship between %CaCO₃ and macrofauna is unclear. Other deep-sea studies have reported positive or negative effects of this variable on meiofauna (Shirayama 1984, Flach et al. 2002, Grove et al. 2006). Positive effects of high CaCO₃ content on meiofaunal densities have been linked to this variable being indicative of high food availability (via increased sedimentation) and the provision of large interstitial spaces (Shirayama 1984). In addition, a recent experimental study suggested that the crystallographic structure of sediment particles may influence the distribution and abundance of marine benthic fauna (Cerrano et al. 1999). Manipulation of the proportion of carbonate versus quartz sand within sediment showed significantly lower meio- and macrofaunal colonisation in relation to increasing quartz content, possibly owing to the adverse impact of released silicon-based radicals caused by water movement across quartz crystal surfaces (Cerrano et al. 1999). In view of these studies, sediment conditions other than food supply (i.e. at 2800S) possibly favour some macrofaunal groups and, thereby, profoundly influence Chatham Rise deep-sea assemblages.

While sediment chl *a* concentration was the single most important sediment variable influencing biomass patterns across Chatham Rise, the exact roles of %POC

and %CaCO₃ in relation to benthic assemblages warrant further investigation. The latter includes examination of the possible influence of lateral particle advection on sediment properties at deep-sea sites in the Chatham Rise region. Ongoing data collection in this region focuses on sediment flux dynamics and experimental manipulation of benthic assemblages to elucidate the processes that determine faunal patterns across Chatham Rise.

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