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Focusing of phytodetritus deposition beneath a deep-ocean front, Chatham Rise, New Zealand

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Abstract

In October 2001, we observed a deep-ocean phytodetritus deposition event on Chatham Rise beneath the Subtropical Front (STF). The origin of this phytodetritus was probably an extensive phytoplankton bloom that occurred in the STF in the preceding weeks. We assessed the spatial distribution of the deposition event using video images from benthic lander and epibenthic trawl deployments and sediment pigment analyses at six sites on a north–south transect across Chatham Rise. High surficial sediment chlorophyll *a* concentrations were restricted spatially to the southern flank of Chatham Rise (350–1,200-m depth) with the highest values centered at ~750-m water depth (750 S). This southern 750 S site was also the only site where macroscopic phytodetritus was observed, coincident with elevated benthic biomass and sediment community respiration rates. At 750 S, phytodetritus resuspension was observed on video and corroborated by current meter, sediment trap, and optical

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backscatter measurements, suggesting a threshold erosion current speed for phytodetritus of ~10 cm s^{-1}, equivalent to a shear velocity of 0.5 cm s^{-1} and similar to other deep-ocean studies elsewhere. The restriction of macroscopic phytodetritus deposition to 750 S was related to a zone of current convergence within the STF and lower near-bed current speeds observed across ~1-day that promoted deposition. Observations of high benthic biomass and respiration on the southern flank of Chatham Rise suggest that this focusing process is important in fueling the energy demands of benthic communities, in association with the general west–east advection of organic matter within the STF itself. Such physical focusing of labile organic matter deposition may be an important process in other highly productive frontal systems.

The input of organic matter to the deep ocean is a key determinant in sustaining and controlling the composition and functioning of benthic communities (e.g., Tyler 2003). The rapid transfer of labile phytodetritus, comprising intact phytoplankton cells and other plankton, to the benthic environment stimulates the growth and feeding activity of benthic organisms and triggers reproduction cycles in some deep-sea species (e.g., Kaufmann and Smith 1997; Pfannkuche et al. 1999; Gooday 2002). Such deposition is often highly seasonal or episodic (e.g., Billett et al. 1983; Rice et al. 1986; C. Smith et al. 1996). Once on the seafloor, phytodetritus may be rapidly degraded or ingested and assimilated by heterotrophic communities, mixed into sediments by the actions of bioturbating organisms, or resuspended and transported laterally (reviewed by Beaulieu 2002). Resuspended organic aggregates may be transported considerable distances with residence times of days to weeks in the benthic boundary layer on continental margins (e.g., Thomsen 1999). Resuspension also increases the remineralization potential of fresh organic matter deposited at the seafloor and widens the spatial extent to which such influxes of food may influence the structure and functioning of benthic communities.

Here, we report the observations of the deposition and resuspension of phytodetritus on Chatham Rise in the Southwest Pacific Ocean. The rise lies beneath and constrains geographically the Subtropical Front (STF), a major oceanic front, which is also recognized as a zone of high biological productivity. The STF is a circum-global oceanic front that separates warm, saline, macronutrient-limited subtropical waters to the north from cold, fresh, macronutrient-replete, iron-limited subantarctic waters to the south. The STF is intersected by and diverted around the margins of the submerged continental landmass of New Zealand in the southwest sector of the Pacific Ocean (Fig. 1). East of New Zealand, the STF is manifest by strong gradients in temperature and salinity in surface waters along the eastern shelf-break of the South Island, where it is known as the Southland Front, and along the crest and upper flanks of the Chatham Rise (Heath 1985; Uddstrom and Oien 1999; Sutton 2001). The rise is a narrow (100–170-km wide) submarine ridge with its crest at water depths of ~300–400 m that extends 1,500 km east of the South Island. The STF and Chatham Rise support substantial deep-water fisheries for orange roughy (*Hoplostethus atlanticus*), oreo dories, and blue grenadier (hoki, *Macruronus novaezelandiae*) and are recognized as zones of high biological production (Bradford-Grieve et al. 1999; Murphy et al. 2001). The southern upper slope and crest of the Chatham Rise (<1,200 m depth) are characterized by elevated levels of macro- and meiofaunal biomass and benthic respiration rates as compared to the northern slopes, possibly related to the proximity of the STF (Probert and McKnight 1993; Nodder et al. 2003; Grove et al. 2006). Despite these previous observations, the process maintaining the elevated benthic biomass and activity on the southern slope (via enhanced food supply) has not been elucidated, but is thought to be related to organic matter production within the STF (e.g., Nodder et al. 2003).

The main objectives of the present study were to ascertain the influence of the STF on the structure and functioning of deep-ocean benthic communities and the degree of benthic–pelagic coupling during a time of high biological production (i.e., austral spring). In this context, it was fortuitous that immediately before the start of our study a widespread algal bloom developed in the Chatham Rise area, as described below.

Locally validated, 8-day composites of sea-viewing wide field-of-view sensor (SeaWiFS) ocean color data at 4-km resolution (Richardson et al. 2004) indicate that 1 week before the start of research voyage TAN0116 on 01 October 2001, an extensive phytoplankton bloom, with surface chlorophyll *a* (Chl *a*) concentrations estimated to be >2 mg m^{-3}, developed within the STF along the crest of Chatham Rise (Fig. 2). This biomass accumulation was concentrated across the crest and northern flank of the rise and extended from coastal waters off northeastern South Island almost to the Chatham Islands, 1,500 km to the east, in a narrow band approximately 120 km wide (Fig. 2b). During the first part of the voyage, the bloom dissipated on the rise, and elevated surface Chl *a* concentrations were located to the north in subtropical waters within the Wairarapa Eddy (Fig. 2c). At the time of our study, however, active deposition of algal-rich material was only observed on the southern flanks of Chatham Rise, suggesting that this phytodetrital sedimentation was being focused, perhaps by hydrodynamic processes within the STF, as outlined here.

Methods

The latitudinal transect between 41° and 47°S and along 178°30′E has been the focus of previous studies since 1997 investigating processes in the STF (e.g., Sutton 2001; Nodder et al. 2003). The same benthic sites, as described in Nodder et al. (2003), were reoccupied in austral spring from 29 September–14 October 2001 (Fig. 1). During the 2001 voyage, we determined the benthic biomass within different size compartments, ranging from bacteria to megafauna, as

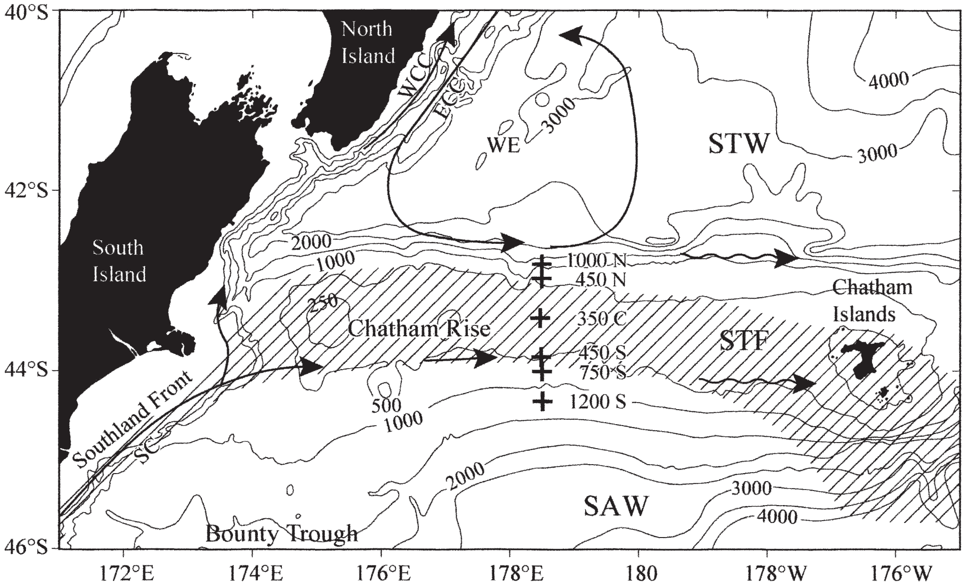

Fig. 1. A map of Chatham Rise region, showing sites sampled on the National Institute of Water and Atmospheric Research research voyage TAN0116 in October 2001 (shown as crosses), physical oceanography (main water masses, fronts and broad circulation patterns), and bathymetric contours (250-m isobath and then every 500 m from 500-m isobath to 4,000 m). Diagonal lines indicate the extent of the STF; STW, subtropical water; SAW, subantarctic water; ECC, East Cape Current; WCC,Wairarapa Coastal Current; SC, Southland Current; WE, Wairarapa Eddy.

well as sediment community respiration rates, sediment physical and chemical properties, and near-bed and upper water column hydrodynamics. Six sites were occupied on the upper flanks and crest of Chatham Rise in water depths ranging from 350 m on the crest to 1,000 m and 1,200 m on the northern and southern flanks, respectively (Fig. 1; Table 1). Sites were sampled sequentially from the northern end of the sampling transect to the southernmost site, with the vessel then returning northward along the same longitude across the Chatham Rise, collecting mainly underway data and resampling selected sites, such as 750 S.

Water column measurements—Conductivity–temperature–depth (CTD) profiles and water samples at each site were obtained using a Seabird *911plus* and 24-bottle Niskin bottle rosette. Water column fluorescence data were collected using a SeaPoint fluorometer (Model SCF), interfaced with the CTD. Water column Chl *a* concentrations were determined from filtered 500-mL samples (GFF filters, frozen in liquid nitrogen) analyzed using standard spectrofluorometric techniques after extraction in 90% acetone.

Surface currents (<200-m depth) were measured using a hull-mounted, 150-kHz RD Instruments broad-band acoustic doppler current profiler (ADCP) as the ship moved between stations. Positional data were supplied by a position and orientation system for marine vessels (POS/MV) GPS system, acquired using VMDAS for Windows (Version 1.3), and processed using the Common Oceanographic Data Access System (CODAS) from the University of Hawaii. Current data were detided using a New Zealand regional barotropic tide model (Walters et al. 2001), following the methods in Sutton and Chereskin (2001). Two ADCP transects across Chatham Rise (one north-to-south, the other south-to-north) were collected ~3–7 days apart, as the ship transited along 178°30′E. Data were averaged across 0.05° latitude bins (~5 km), whereas measurements that were made when the vessel was on station (data not shown) indicate that currents may vary temporally in the order of ~10 cm s^{-1}.

Sediment, bacteria, meio- and macrofaunal sampling—An Ocean Instruments MC-800 multicorer (10 cm diameter cores) was used to sample sediment properties and infauna, following the methods of Nodder et al. (2003). Briefly, particulate organic carbon (POC) and nitrogen contents in dried, acidified (8% v/v sulfurous acid) sediment samples were determined using a carbon-hydrogen-nitrogen (CHN) analyzer (CE Instruments NC2500 with machine precision of ~2%). Phytopigment concentrations were estimated by high-performance liquid-chromatography on freeze-dried, vertically sectioned sediment samples from each site (i.e., surface scrape [<2 mm] plus 0.5-cm thick slices to 1 cm, 1-cm slices to 5 cm, and 2.5-cm slices to 15-cm sediment depth). Additional surface scrapes were collected at phytodetritus-enriched sites and preserved with Lugol's and glutaraldehyde for identifying phytoplankton species using light microscopy.

Sediment bacterial numbers in the top 0–1 cm were estimated by epifluorescence microscopy of slurries prepared from 3.46 cm^2 subcores collected in triplicate at each

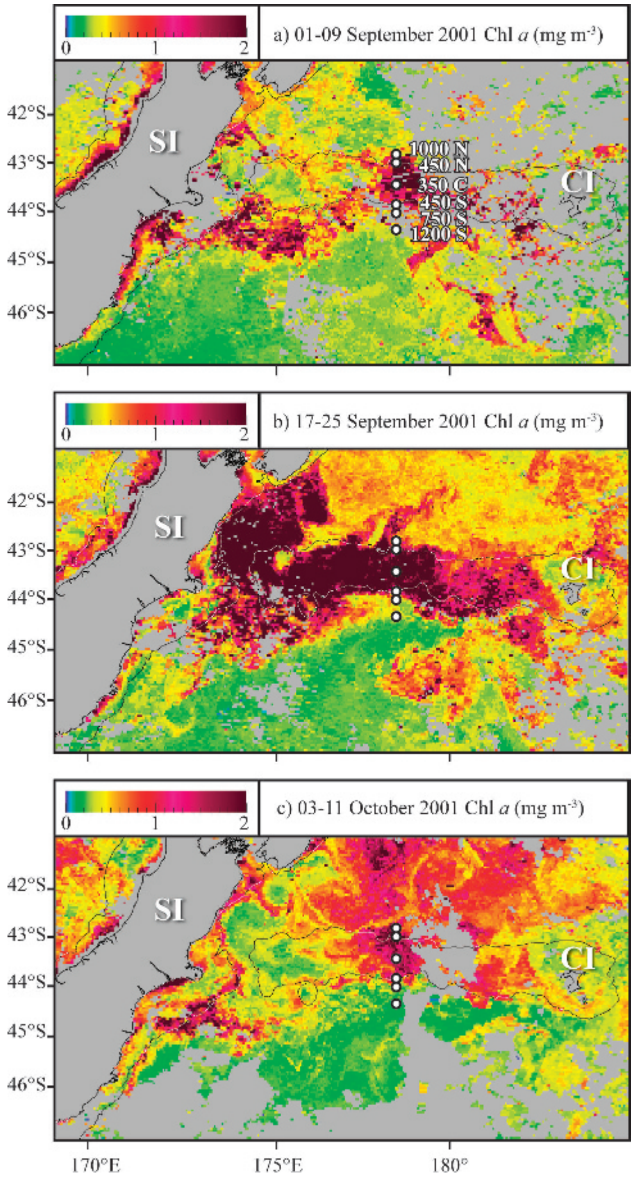

Fig. 2. Eight-day composite SeaWiFS images showing surface Chl *a* concentrations for (a) 01–09 September, (b) 17–25 September, and (c) 03–11 October 2001. The sites occupied in austral spring, 01–22 October 2001, are shown as circles. SI, South Island; CI, Chatham Island with 500-m isobath also depicted. Successive weeks are not able to be shown because of cloud contamination. Images courtesy of SeaWiFS, NASA Goddard Space Center, and Orbimage.

site (*see* Nodder et al. 2003). Meiofauna abundance was determined from 5.3 cm² syringe cores taken to a depth of 5 cm and preserved in 10% buffered formalin with Rose Bengal. Meiofauna were retained on a 45-μm mesh and extracted by Ludox flotation. At each site, the top 10 cm of sediment from four multicore tubes was sieved separately through a 500-μm mesh, and retained macrofauna were preserved with 10% formalin. Total macrobenthic biomass was derived from the blotted wet weight and converted to a carbon equivalent assuming wet weight is 4.3% carbon (Rowe 1983). Megafaunal abundance and biomass at each

Table 1. Site location and environmental data summary. Water column Chl *a* samples were taken from 10-m water depth. Sediment parameters are shown for surface sediment (0–0.5 cm), except for Chl *a* and total pheopigment concentrations (ng g dry wt sediment^{-1}), which were estimated from surface scrapes (<0.2 cm).

					Water column		Sediment properties						
Site	Latitude (S)	Longitude (E)	Date	Water depth (m)	Mixed-layer depth (m)	Surface Chl *a* (mg m^{-3})	Sand (>63 μm) (%)	Mud (>63 μm) (%)	CaCO$_3$ (%)	Organic carbon (%)	C : N (molar)	Chl *a* (ng g dry wt sed^{-1})	Total pheopigments (ng g dry wt sed^{-1})
1000 N	42° 49.192′	178° 30.043′	03 Oct 01	980	50	1.08	46.1	53.9	51.6	0.88	11.41	118	4,033
450 N	42° 58.606′	178° 29.907′	04 Oct 01	441	30	4.48	55.2	44.8	37.0	0.82	10.63	215	6,437
350 C	43° 26.069′	178° 30.132′	05 Oct 01	348	15–20	3.73	56.4	43.6	40.5	0.96	10.18	514	6,231
450 S	43° 49.584′	178° 30.052′	06 Oct 01	460	50	2.55	48.8	51.2	34.0	0.83	12.10	1648	15,010
750 S (1)	44° 00.434′	178° 30.006′	07 Oct 01	753	40	1.61	46.3	53.7	32.1	0.62	10.33	936	6,489
750 S (2)	44° 00.348′	178° 30.022′	13 Oct 01	—	—	—	51.0	49.0	29.7	0.64	9.33	2883	22,599
1,200 S	44° 19.941′	178° 30.068′	08 Oct 01	1,205	25	0.28	23.0	77.0	50.3	0.41	15.94	939	7,204

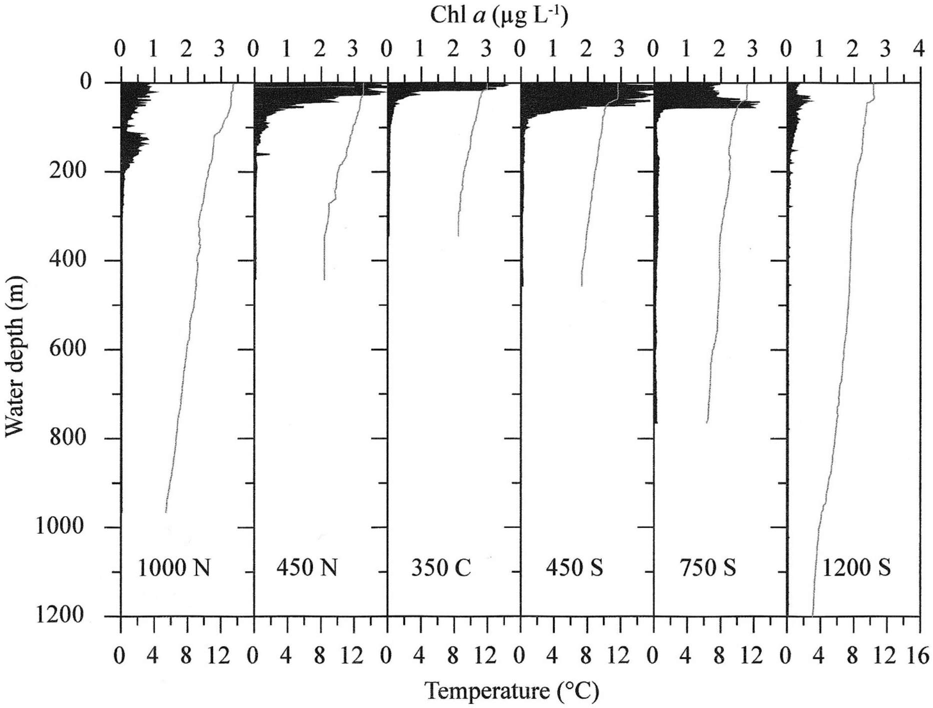

Fig. 3. Temperature (°C, solid line) and Chl *a* concentrations (μg L^{-1}, infilled line) as functions of water depth from CTD profiles at selected sites across Chatham Rise (*see* Fig. 1 and Table 1 for site locations). Chl *a* concentrations were calculated from CTD fluorescence (F) based on an almost 1 : 1 correspondence between these two parameters, where Chl *a* (μg L^{-1}) = 0.98 × (CTD − F) ($r^2 = 0.79$, $n = 33$, all sites).

site were estimated using a large opening-and-closing epibenthic trawl (3.5-m^2 mouth, 1-cm mesh size, ~0.5–1-h trawling times), based on the methods in Lavaleye et al. (2002). The trawl was fitted with a forward-looking video camera (Sony Tr2000E Hi-8 Handycam) and two deep-sea power and light video lamps, which provided continuous video footage during trawl deployments. Trawl catches were compared with the video records to detect any mismatch in species composition and qualitative abundance caused by undersampling by the trawl. No such cases were found.

In situ benthic measurements—Benthic landers from the Royal Netherlands Institute for Sea Research (NIOZ) provided in situ measurements of sediment community oxygen consumption (SCOC), near-bottom particle fluxes and fluorescence, bottom currents, particle concentrations, and video imagery. In situ SCOC rates were measured using three ALBEX chambers with optrodes as used in previous studies in the northeast Atlantic (Duineveld et al. 2004). SCOC rates were also determined from shipboard incubations to complement the in situ data and to enable comparisons with previous shipboard estimates at the same sites (e.g., Nodder et al. 2003).

Particle fluxes and fluorescence within the benthic boundary layer were determined using a SeaPoint fluorometer positioned in the mouth of a conical, 0.05-m^2 Technicap sediment trap, located at the top of the lander frame 2 m above the seafloor (*see* figure in Duineveld et al. 2004). Bottom currents were measured using a FSI-3DACM acoustic current meter at 0.5 m above the seafloor, and near-bed particle concentrations were estimated using optical backscatter SeaPoint sensors placed at 0.5 and/or 2 m above the seafloor on the lander frame. A video camera and lighting system were mounted ~0.75 m above the seafloor to provide continuous footage during lander deployments, which ranged from 26–28.5 h at each site.

Results

Water column processes—CTD data indicate that mixed-layer depths varied from ~15–20 m on the crest of the Chatham Rise to ~50 m at 1,000 N and 450 S (Table 1). Elevated levels of Chl *a* in the surface mixed-layer were observed at sites on the upper flanks and crest of the Chatham Rise (<450-m deep) with moderately high Chl *a* concentrations occurring at 750 S (Fig. 3). CTD sampling at the northern end of the transect was conducted at the start of the voyage (29 September 2001) so that surface fluorescence profiles at these sites do not directly reflect the satellite ocean color composite of 03–11 October (unfortunately, the previous 8-d composite was heavily cloud-contaminated). Nevertheless, the decline in surface fluorescence at the 750 S and 1,000 S sites suggests that the spatial distribution of Chl *a* concentrations shown on the 03–11 October image may be reasonably representative (compare Figs. 3 and 2c).

The ADCP transect data clearly show the presence of two strong, west-to-east zonal jets on the northern and southern flanks of the rise with velocities >40 cm s^{-1} (Fig. 4a,b). A broad zone of generally southward flow across the Chatham Rise and into subantarctic waters was also apparent, although differences between the two transects indicate that there is considerable variability in these patterns with time (Fig. 4c,d). There is an indication from the second ADCP transect of a zone of north–south convergence between 44°S and 44°24′S, which encompasses the 750 S and 1,200 S sites and corresponds to a zone of negative $\delta v/\delta y$. This is separated from 450 S by a narrow zone of current divergence, or positive $\delta v/\delta y$ (Fig. 4f).

Phytodetritus and sediment pigment distributions—Whereas a spatially extensive algal bloom in the water column was evident from remotely sensed satellite (Fig. 2) and CTD data (Fig. 3), evidence from video and chemical analyses of surficial sediments suggested that phytodetritus deposition was restricted primarily to the southern flank and crest of the Chatham Rise. Visual evidence of phytodetritus deposition was most apparent at 750 S. Video footage from the benthic landers and epibenthic trawl showed a patchy mosaic of greenish "fluff" material that had accumulated in shallow depressions on the seafloor and flocs of material that were suspended in the water column immediately above the seafloor (video footage is available at http://www.niwascience.co.nz/rc/coast-oceans/phytodetritus_deposition/). This greenish, flocculent material was also found on the sediment surface recovered in some multicores at 750 S, and subsequent analysis of its biological and chemical composition confirmed that it was phytodetritus (*see* the following discussion). No macroscopic evidence of phytodetritus accumulation was observed at any other site, including 450 S and another site midway between 750 S and 1,200 S where only trawl video footage was collected. Both of these sites were only 17–19 km away from 750 S.

Despite visual evidence of phytodetritus deposition at 750 S, surficial sediment POC values were generally higher on the northern flank and crest of the rise (Table 1). There was no obvious trend in molar carbon : nitrogen (C : N) ratios with water depth, and the physical characteristics of the underlying sediments were consistent across the rise (i.e., glauconite-rich, sandy muds and muddy sands with $CaCO_3$ contents of 30–40% increasing to >50% at sites deeper than 1,000-m depth) (Table 1). In contrast, Chl *a* concentrations in the surface sediments (0–0.5 cm) on the southern flank of the rise were elevated by factors of 2 to 20, compared to sites on the crest and northern flank, with maximum concentrations of 2,900 ng g dry wt sed^{-1} recorded at 750 S. In comparison, Chl *a* concentrations of <520 ng g dry wt sed^{-1} were found on the northern flank and crest and 940–1,650 ng g dry wt sed^{-1} at other southern flank sites. The highest sediment Chl *a* concentrations on the transect were found on the second sampling of site 750 S, 1 week after it was first sampled, perhaps reflecting the high local spatial variability of phytodetritus deposition as observed in video footage. Elevated levels of Chl *a* persisted down to sediment depths of 4–8 cm at the upper slope southern sites (450 S and 750 S), with subsurface maxima also observed between 10 cm and 15 cm (Fig. 5). Chl *a* concentrations declined to negligible amounts below 2–3 cm at the other sites.

Concentrations of Chl *a* degradation products (pheophytins and pheophorbides) in surface sediments were elevated at 750 S and 350 C, and for pheophorbides only (>2,700 ng g dry wt sed^{-1}) at 450 S. Slightly elevated levels of these compounds were observed at depth in the sediments on the uppermost flanks and crest of the rise (Fig. 5). Chl *a* : total pheopigment ratios of 0.1–0.15 in surface sediment (0–2 mm) were observed on the southern flank of the rise, whereas much lower ratios of 0.02–0.03 were found on the northern flank.

In near-bed sediment trap samples from 750 S, other major phytopigments included Chl *c2*; fucoxanthin and diadinoxanthin, which are indicative of diatoms; and minor amounts of 19-hexanoyl fucoxanthin and Chl *c3* (data not shown), suggesting that prymnesiophytes or coccolithophorids were also present (e.g., Wright et al. 1991). As for surficial sediments, the highest Chl *a* : total pheopigments ratios in trap samples were found on the southern flank of Chatham Rise (0.13–0.26) as compared to the northern flank and crest (0.06–0.07) (Fig. 6). Chl *a* : total pheopigment ratios in the trap samples were comparable to ratios in surficial sediments, especially at 450 S and 750 S, suggesting a resuspension source for the trapped phytodetritus.

Microscopic identification of phytoplankton in surficial sediments at 750 S indicated that the phytodetritus flora was dominated by diatoms, especially *Thalassiosira* spp. with abundant *Stephanopyxis turris* and *Rhizosolenia* spp. (Table 2) consistent with the pigment analyses (Fig. 5). Two species of silicoflagellates were also found: *Dictyocha fibula* and *Distephanus speculum.*

A small number of coccolithophorid cells were observed in glutaraldehyde-preserved samples, but could not be identified to genus/species level. In general, the species composition of phytoplankton found in sediments at 750 S compared well with contemporaneous surface water column samples (F. H. Chang unpubl. data) and previous studies in the region (Chang and Gall 1998).

Benthic biomass—Bacterial numbers in the surficial sediments (0–1 cm) across the top of the Chatham Rise were high on the upper northern flank and crest and decreased down the southern flank, ranging from 2.6–2.9 × 10^9 cells mL^{-1} to 1.2–2.0 × 10^9 cells mL^{-1}, respectively (Fig. 7a). This trend was also apparent in the bacterial numbers at 4–5-cm sediment depth. Meiofaunal abundance was highest on the crest and southern flank of the rise, with the highest abundances at 750 S (Fig. 7b). Similarly, macrofaunal biomass was also high on the crest and southern flank of the rise (1.0–2.1 g C m^{-2}), compared to the northern flank (0.6–0.8 g C m^{-2}) (Fig. 7c). Although specific counts were not conducted, it is expected from previous work that macrofaunal biomass would be dominated by deposit feeders, including polychaetes, peracarid crustaceans, and bivalves (e.g., Probert et al. 1996).

Megabenthos abundance and biomass were highest at 1,200 S (19 individuals m^{-2} and 55 g wet wt m^{-2}, in-

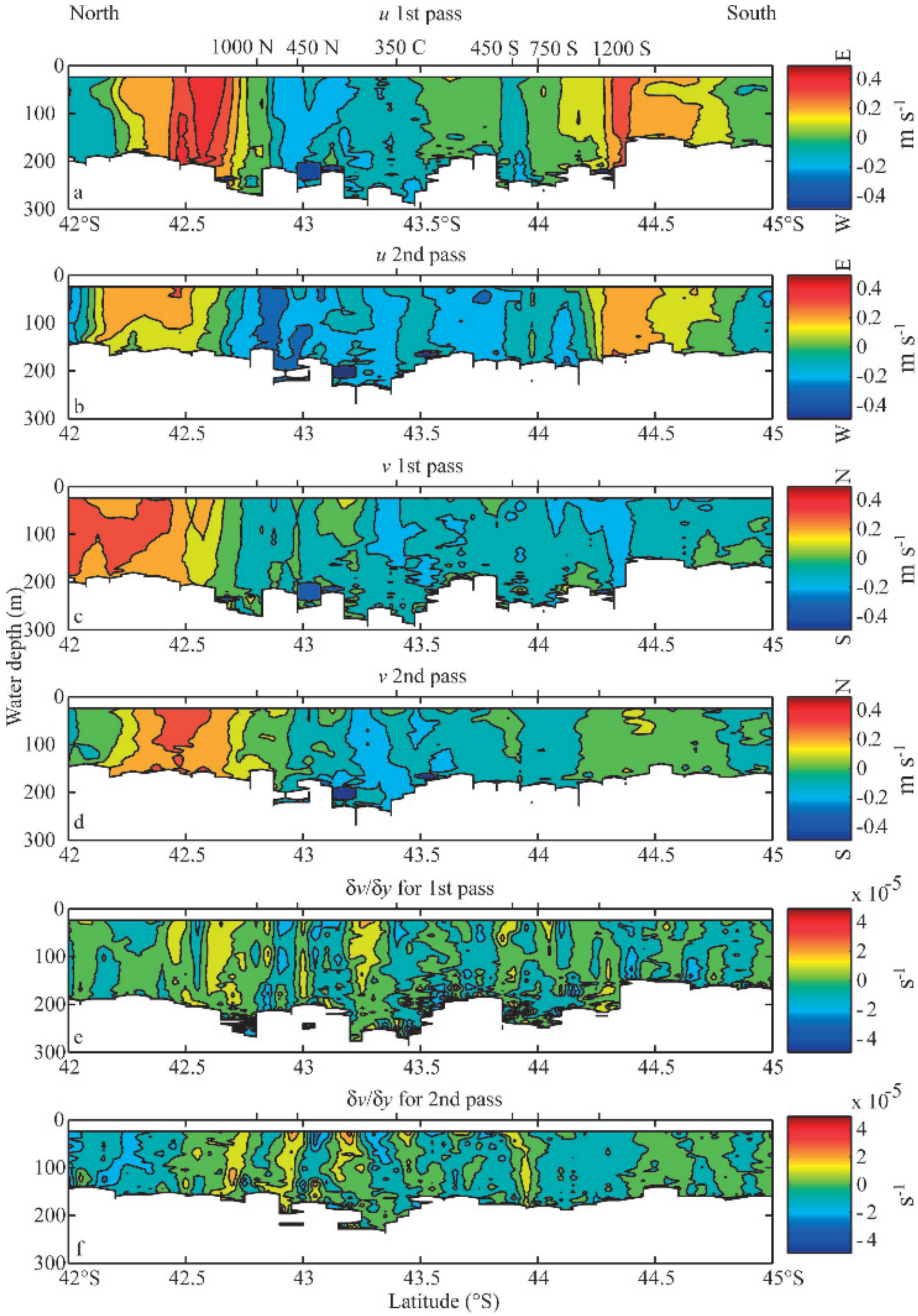

Fig. 4. ADCP data from the upper 200 m on two transects across Chatham Rise in October 2001. The first pass was conducted between 07:36 h, 01 October, and 12:46 h, 10 October (coordinated universal time; UTC), and the second pass from 23:56 h, 10 October, to 04:24 h, 13 October (UTC) (a–d); *u*, E–W zonal flows in m s^{-1} (positive = E, negative = W); *v*, N–S meridional flows (positive = N, negative = S). (e–f) estimates of relative meridional flow convergence ($\delta v/\delta y$), where *v* is meridional flow and *y* is north–south coordinate. Negative values of $\delta v/\delta y$ indicate convergence and positive values divergence.

cluding fish, respectively), dominated overwhelmingly by ophiuroids (Fig. 7d,e). Biomass was also elevated substantially at 750 S (25 g wet wt m^{-2}), but abundance was low compared to other sites, except 1,000 N, with only ~0.3 individuals m^{-2} as compared with ~3 at 350 C and 450 S. The dominant invertebrates in terms of biomass at 750 S were echinoids (predominantly *Gracilechinus multidentatus*), gastropods (*Fusitriton magellanicus*), and holothurians (*Pseudostichopus mollis* and an unnamed species with papillae), which accounted for 94% of the total

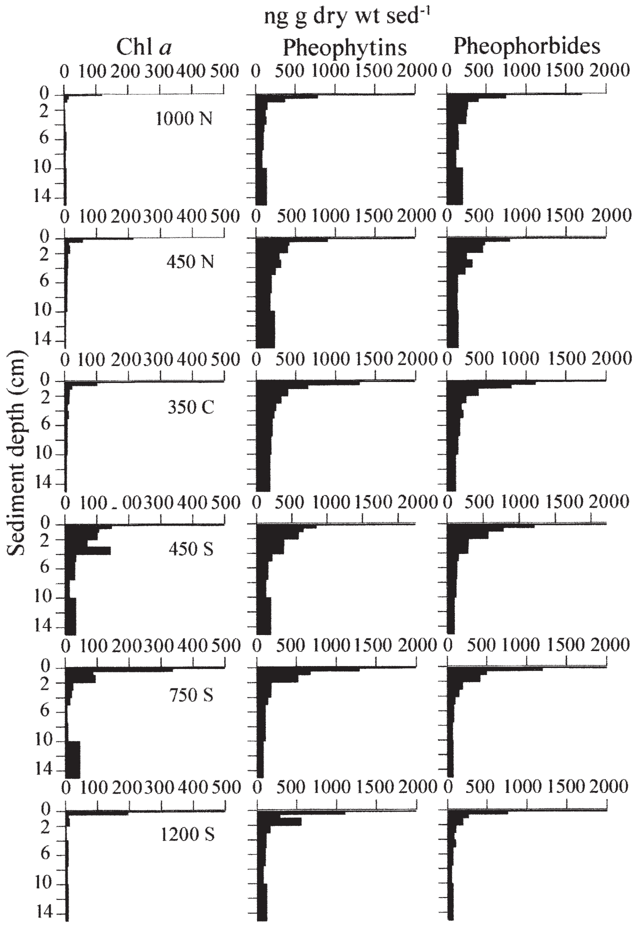

Fig. 5. Concentrations of sediment Chl *a*, pheophytins, and pheophorbides (ng g dry wt sediment^{-1}) in the top 150 mm (*see* Fig. 1 and Table 1 for site locations).

invertebrate biomass. The number of megafaunal species was similar across all the sites (~70–80), with the highest number of species observed at 450 S (~130).

Sediment community oxygen consumption—In situ SCOC measurements were generally higher on the crest and southern flank of the Chatham Rise, with the highest rate measured at 750 S at about 2–3.5-times greater than the rate at adjacent sites (Fig. 8). SCOC rates at 1,200 S were twice that observed at 1,000-m water depth on the northern flank. On average, shipboard measurements of SCOC on the northern flank, crest, and upper slope on the southern flank of the rise were ~2 times higher than in situ estimates, except at 750 S and 1,200 S where they were similar. Despite these differences, the same spatial patterns observed in the in situ measurements were also evident in the shipboard SCOC data, i.e., the highest SCOC rates were measured on the crest and upper southern flank of Chatham Rise and decreased with water depth on the northern flank.

Benthic boundary layer dynamics: near-bottom currents, particle flux, and turbidity—Near-bottom current speeds were generally <20 cm s^{-1} and typically between 5 cm s^{-1} and 15 cm s^{-1} at all of the sites on the southern flank of the rise (Fig. 9). Progressive-vector plots at these sites suggest a mean flow to the northeast (i.e., up- and along-slope), whereas on the Chatham Rise crest flows were generally directed to the south and southwest (Fig. 10).

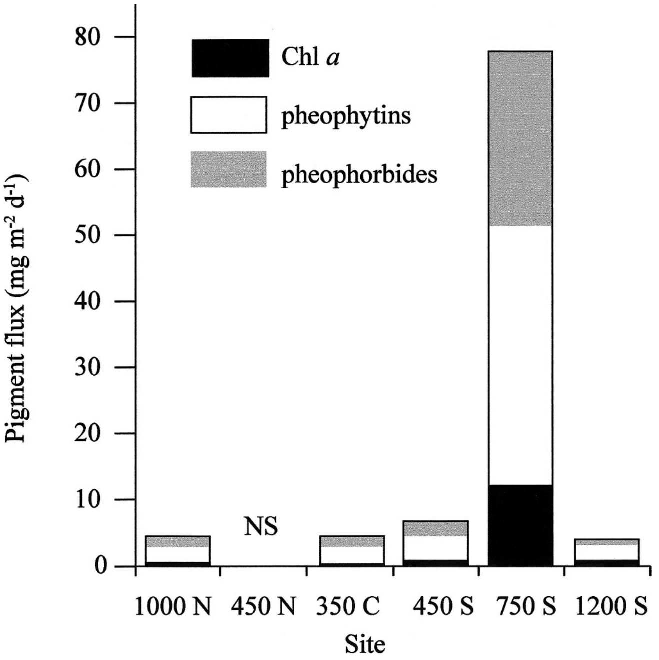

Fig. 6. Daily phytopigment fluxes measured in near-bed sediment traps deployed for more than 24 h at different sites across Chatham Rise in October 2001. No samples (NS) were collected at 450 N.

Although it is acknowledged that flows measured by the current meter on the benthic lander may be affected by local topography, a close temporal relationship between episodic increases in current speed and elevated near-bed turbidity was observed at 750 S, but not the other sites (Fig. 9). At 750 S, when current speeds 0.5 m above the seafloor exceeded 10 cm s^{-1}, there was a rapid increase in turbidity (Fig. 11). As the currents began to wane, turbidity levels declined exponentially: a pattern that is characteristic of local resuspension and deposition cycles. Video observations confirmed that these turbidity events were caused by the resuspension of phytodetritus (see http://www.niwascience.co.nz/rc/coast-oceans/phytodetritus_deposition/). During resuspension events, the OBS signal 2 m above the bed was attenuated, compared to that 0.5 m above the seafloor, suggesting that the bulk of phytodetritus was transported mainly as bed load close to the seafloor. Nevertheless, analysis of the sediment-trapped organic material (Fig. 6) and the time series of trap fluorescence events (Fig. 9) indicate that some phytodetritus was resuspended to at least 2 m above the seafloor.

Previous observations indicate that the threshold erosion current speed of phytodetritus is 7–8 cm s^{-1} (Lampitt 1985; Beaulieu 2003), consistent with the Chatham Rise estimate of approximately 10 cm s^{-1}. Based on this in situ

Table 2. Intact phytoplankton cells identified in surficial sediment scrapes (<0.2 cm) at 750 S. Samples were collected from a benthic lander incubation core (07–08 October) and two multicores (13 October). The number of Xs indicates the relative abundance of phytoplankton species in each sample.

Phytoplankton group	Genus/species	Sample date 07–08 Oct 2001	 13 Oct 2001
Diatoms	*Asterionella glacialis*		X
	Chaetoceros decipiens	X	X
	Chaetoceros concavicornis	X	X
	Chaetoceros spp.	X	X
	Coconeis spp.		X
	Coerthron hystrix	X	X
	Cosinodiscus spp.	X	X
	Ditylum brightwellii	X	X
	Fragilariopsis kergulensis		X
	Guinardia spp.		X
	Leptocylindricus danicus		X
	Navicula spp.		X
	Nitzschia spp.	X	X
	Odontella mobiliensis	X	X
	Pseudonitzschia australis	X	X
	Rhizosolenia setigera	X	X
	Rhizosolenia styliformis	X	X
	Rhizosolenia spp.		XX
	Stephanopyxis turris	XX	XX
	Thalassiosira spp.	XXXX	XXXX
	Trichotoxon reinboldii	X	
Silico-flagellates	*Dictyocha fibula*	X	
	Distephanus speculum	X	

estimate, it would take ~3–4 days for phytodetritus deposited at 750 S to be transported to 450 S, ~18 km away. Furthermore, using this same entrainment velocity, the proportion of time that current flows were below 10 cm s^{-1}, and therefore promoting the retention of deposited phytodetritus, can be calculated for each site. Based on this analysis and assuming a standard sampling period of 24.4 h at each site, corresponding to at least two tidal cycles, flows at 450 S were <10 cm s^{-1} ~27% of the time that near-bed currents were measured, with a median flow speed of 12.4 cm s^{-1}. In contrast, at 750 S, this proportion rose to 60% (median speed = 9.3 cm s^{-1}), and decreased at 1,200 S to 14% with a median speed of 12.4 cm s^{-1}. These calculations highlight the likelihood that phytodetritus deposited at 750 S during periods of low flow was more likely to be retained during the course of the observation period, as compared to sites to the north and south where there was a more frequent occurrence of near-bed currents sufficient to resuspend phytodetritus.

Evidence for fluorescent particles within the benthic boundary layer was found in lander sediment traps at sites only on the upper southern flank and to a lesser extent on the crest of Chatham Rise (Fig. 9). This was apparent especially at 750 S, where the fluorometer signal over-saturated during one 2-h period of the 28-h time series. The highest near-bed Chl *a* and pheopigment fluxes, measured in the lander trap, were observed at 750 S (Fig. 6), consistent with active phytodetritus deposition and resuspension observed at this site.

Discussion

Physical transport, deposition, and resuspension of phytodetritus—One possible explanation for focusing phytodetritus deposition on the southern flank, and specifically at 750 S, may be provided by previous, independent physical descriptions of the current structure within the STF, although it is accepted that the mechanism described below may not necessarily occur all of the time. Sutton (2001) describes the STF as comprising a southern and a northern front, separated by a frontal zone, whereas Uddstrom and Oien (1999) argued against this twin frontal banding and suggested that the strongest gradients in sea-surface temperature and the likely location of the main STF were aligned along the 500-m isobath on the southern flank of the Chatham Rise. An ADCP (150 kHz) study by Chiswell (1994) in austral spring (September) 1991 showed that the current structure across the STF was highly banded with alternating zones of divergence and convergence. One cell of N–S convergent flow was located at ~44°S, the approximate location of the 750 S site. Furthermore, this flow convergence was coherent from the sea surface to at least 500-m water depth and has been observed on the same cross-front transect during previous voyages (e.g., Sutton 2001; NIWA, unpubl. data). ADCP data collected in October 2001 (this study), indicate that, in general, there was southward flow across the rise with northward flow from between ~44°30′S and 45°15′S, but these flows exhibited temporal variability on at least weekly

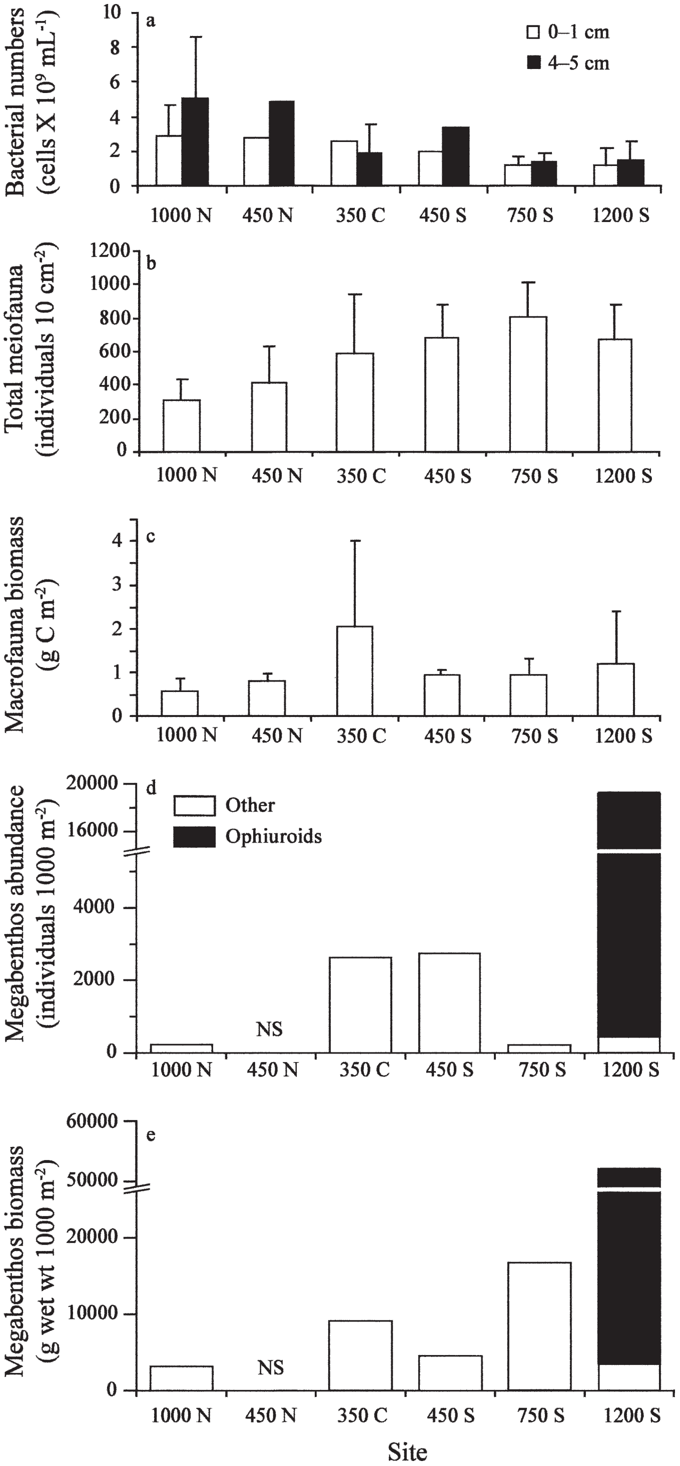

Fig. 7. Benthic community abundance and biomass across Chatham Rise. (a) Bacteria abundance at two sediment depths: 0–1 cm and 4–5 cm (cells × 10^9 mL^{-1}); (b) meiofauna abundance (individuals per 10 cm^2); (c) macrofaunal biomass (g C m^{-2}); (d) megafauna numbers grouped into "ophiuroids" and "others" (numbers per 1,000 m^2); and (e) megafaunal biomass (g wet wt per 1,000 m^2). All data are means plus one standard deviation, except for megafauna, which are totals collected from a single epibenthic trawl. No megafaunal samples (NS) were collected at 450 N.

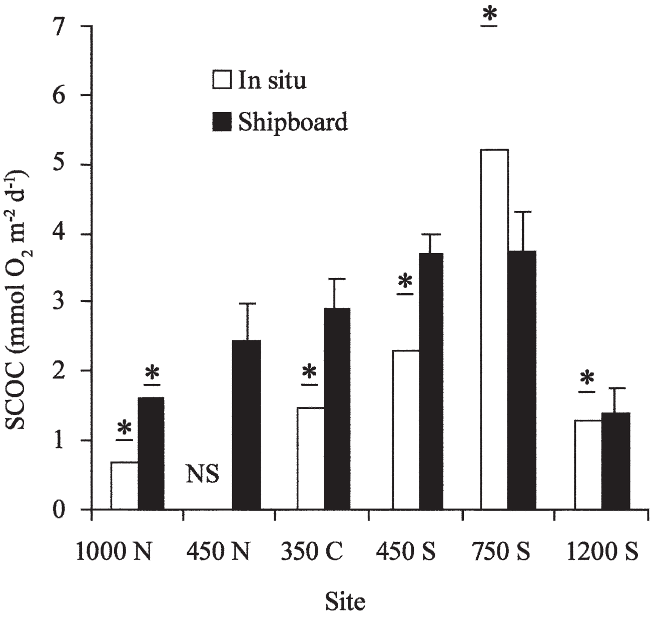

Fig. 8. SCOC rates in mmol O_2 m^{-2} d^{-1} determined in situ and from shipboard incubations (conducted at 1 atm [101.3 kPa] and in situ bottom temperatures). Values for shipboard measurements are means plus one standard deviation (n = 3–4). The upper range of values for sites where n = 2 are asterisked, including all the in situ benthic lander estimates.

time scales (Fig. 4). For flow to be convergent, $\delta u/\delta x + \delta v/\delta y$ must be negative, but since the ADCP transects were undertaken along an N–S line, nothing is known about $\delta u/\delta x$. This may not be critical since eastward flows along the southern flank of Chatham Rise tend to be strong and highly zonal (Nodder and Northcote 2001; Sutton 2001), particularly between 44°15′S and ~45°. Despite the short-term benthic lander deployments (~1 d), the near-bed current meter data are also consistent with these previous observations with northeast- to east-directed residual flows observed at the 450 S and 750 S sites, compared to predominantly south- to southwest-oriented residual flows on the crest of the rise at 350-m depth (Fig. 10).

Thus, the general southward advective component of flow across the rise would tend to transport any organic material produced within the STF zone on the top of Chatham Rise southward. This southward flow would eventually converge with the northward flow, which marks the boundary between the southern STF (Sutton 2001). In addition, physical focusing of suspended and sinking phytoplankton bloom material formed in the STF is also likely to facilitate aggregation and enhance the sedimentation potential of this labile material to the seafloor, especially as large, rapidly sinking diatoms dominated the sedimenting phytodetritus (Table 2). It does not appear that such flow convergence, however, occurs all the time along this longitude because an analysis of repeat ADCP transects across Chatham Rise since 2000 indicates no convergence or divergence on average between 45°S and 43°S (n = 6–7, P. Sutton, unpubl. data.). Nevertheless, since there are occasions when flow convergence does occur at the same time as phytodetritus deposition (Fig. 4a), this

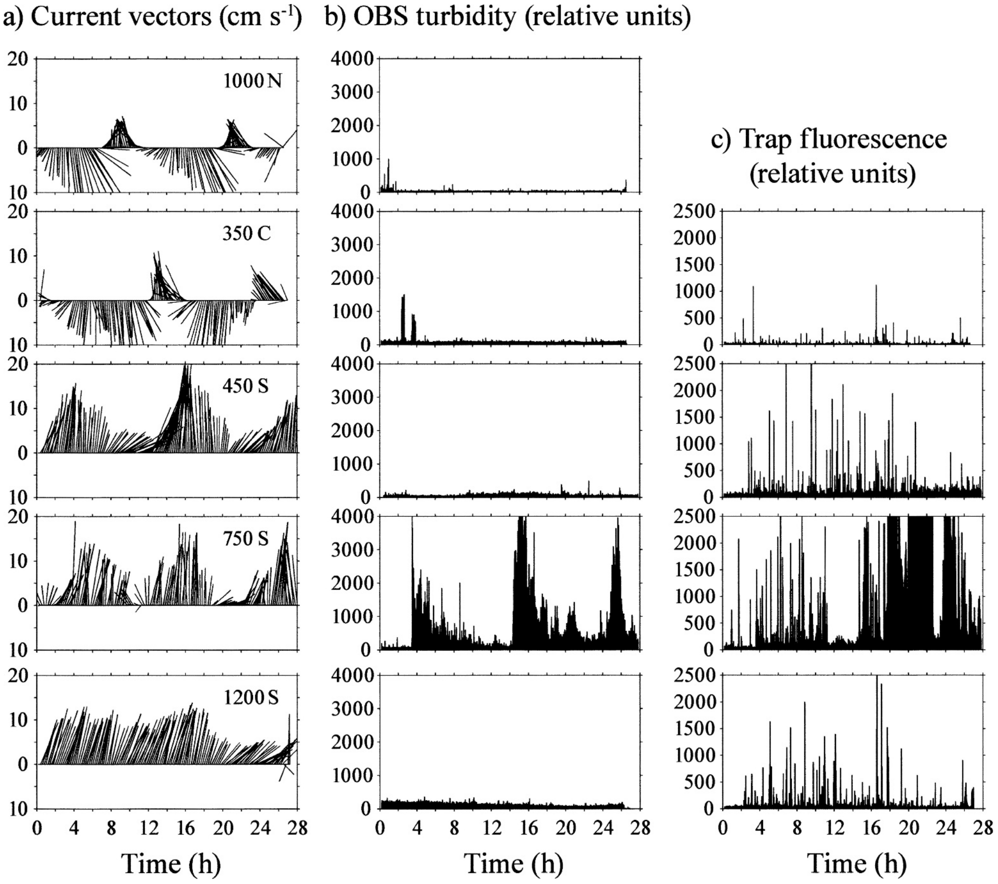

Fig. 9. (a) Current vectors (cm s^{-1}), (b) optical backscatter turbidity (OBS, relative units) and (c) trap fluorometer (relative units) data collected during >24-h benthic lander deployments at sites on Chatham Rise. No lander data were collected from 450 N and only current meter and OBS data were acquired at 1,000 N. For each lander deployment the current meter was mounted 0.5 m above the seafloor, as was the OBS, whereas the fluorometer was located in the mouth of the lander sediment trap, ~2 m above bottom.

physical mechanism has to be sufficiently regular to account for the high benthic activity and biomass observed on southern Chatham Rise.

Once at the seafloor, the recently deposited, labile phytodetritus material may be resuspended and transported by near-bed currents in the STF to other proximal locations on the Chatham Rise. At 750 S, an increase in near-bottom turbidity and resuspended fluorescing particles occurred once instantaneous near-bed velocities, 0.5 m above the seabed, exceeded ~10 cm s^{-1} (Fig. 11). Assuming a standard drag coefficient for deep-sea sediments of 0.0025 (e.g., Beaulieu 2003) and a logarithmic boundary layer profile that goes to zero at the seabed (i.e., "Law of the Wall") this threshold erosion current speed equates to a critical shear velocity (u^{*}_{crit}) for phytodetritus of 0.5 cm s^{-1}. Our in situ estimate of phytodetritus u^{*}_{crit} is similar to other literature values for shallow-water and deep-sea phytodetritus (0.3–0.7 v; Lampitt 1985; Beaulieu

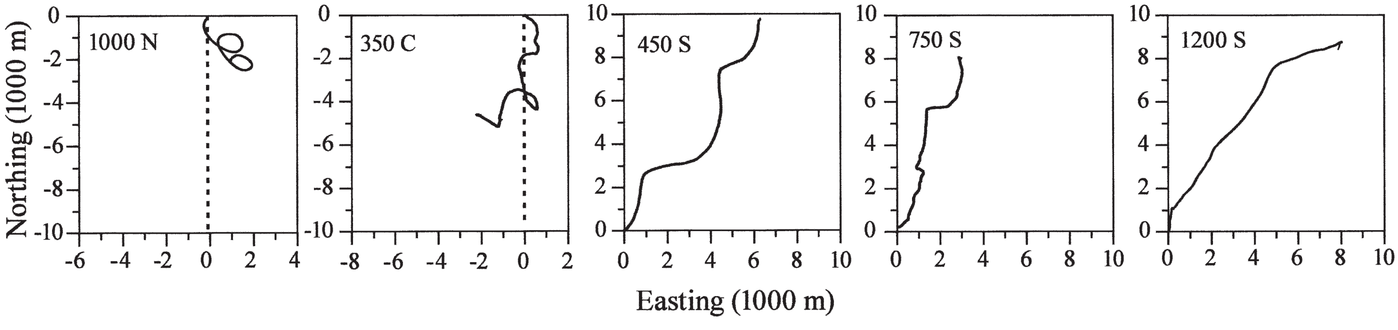

Fig. 10. Progressive vector plots from current meters deployed 0.5 m above the seafloor for >24 h at sites on the crest and southern flank of Chatham Rise. Current direction is relative to true north.

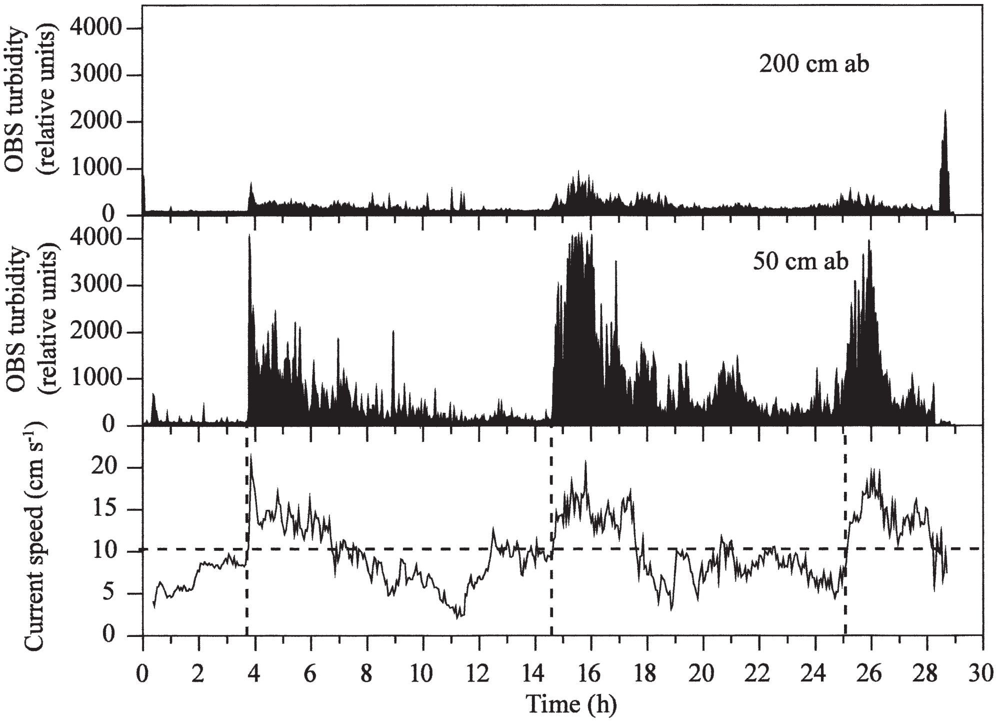

Fig. 11. Current meter data (cm s^{-1}) from 0.5 m above the seafloor and optical backscatter turbidity (OBS, relative units) data from 50 cm and 200 cm above bottom (ab) at 750 S, showing the close temporal relationship between increasing current speed and sediment resuspension. The dashed vertical lines highlight three periods of high currents across the ~28-h deployment and the almost instantaneous increase in turbidity at 0.5 m once the current flows exceeded ~10 cm s^{-1} (horizontal dashed line). Note the attenuation of the resuspension signal at 2 m above the seafloor.

and Baldwin 1998; Williams et al. 1998). If the phytodetritus observed at 750 S originated from a STF bloom (Fig. 2) then it was probably between 7–14 days old (assuming a sinking rate of 100 m d^{-1}; Nodder and Northcote 2001) when it was sampled on 7–8 October, and some microbial decomposition of this material was likely (e.g., Stephens et al. 1997). u^*_{crit} estimates for a natural assemblage of "aged" diatom phytodetritus in flume experiments was between 0.4 cm s^{-1} and 6 cm s^{-1} (Beaulieu 2003) within the range derived in our study.

At 750 S, two bursts of current activity and resuspension during the ~28-h lander deployment indicates that the erosion and transport of phytodetritus and slope sediments could have a tidal periodicity corresponding temporally to the semidiurnal M_2 tide, which is the predominant tidal constituent in the New Zealand region with a period of 12.4 h (e.g., Heath 1985; Stanton et al. 2001). A regional barotropic tidal model (Walters et al. 2001) run across the same time interval as the lander deployment and at the same location as 750 S also indicates two periods of tidal currents when flows would be expected to exceed 10 cm s^{-1}, as we observed. Interestingly, this tidal model indicates that at the 750 S site we were sampling near the end of a spring tide, which was then followed by a period of relatively weak neap tides. This suggests that resuspended particles at 750 S could have a mean residence time in the benthic boundary layer of ~10 h per day, which is less than the ~16–20 h d^{-1} implied by Thomsen and van Weering (1998) on the northeast Atlantic continental margin. Tidal fluctuations in near-bed turbidity have also been observed at abyssal sites in the North Atlantic (Lampitt 1985; Auffret et al. 1994) and Pacific oceans (Beaulieu and Baldwin 1998), whereas Thomsen et al. (2002) showed that tidally modulated flows were responsible for eroding, transporting, and depositing benthic aggregates on the upper northeast Atlantic continental slope.

Thomsen et al. (2002) also measured flow velocities of >10 cm s^{-1} on the northeast Atlantic continental slope, which corresponded to u_{*crit} = 0.5–1 cm s^{-1} for organic-rich aggregates in the benthic boundary layer, similar to our study. Thomsen et al.'s observations suggested net downslope transport distances of ~1 km d^{-1}, whereas our results indicate that resuspended phytodetritus may be transported upslope from 750 S at rates of ~5 km d^{-1}. Our estimate is based on short-term (~1 day) current meter deployments on Chatham Rise by calculating the total time that currents exceed 10 cm s^{-1}, which was ~10 h at 750 S. This transport distance estimate is likely to be a maximum since the resuspension signal is attenuated substantially by 2 m above the seafloor (compare Fig. 11a,b), and the bulk of the phytodetritus will be transported at reduced speeds as bed load lower in the benthic boundary layer. Based on first-order decay rates for Chl *a* of 0.03 d^{-1}, as found in shelf environments (*see* references in Boon and Duineveld 1998), approximately half the Chl *a* biomass would be expected to degrade within 25 days. This indicates that even though phytopigments are very labile and among the first classes of organic matter to decompose, there will still be a substantial amount of fresh phytodetrital material available to fuel the metabolic requirements of benthic communities, even after 25 days. The direction of transport on the southern Chatham Rise flank, however, was predominantly upslope and along the bathymetric contours, such that net downslope transport of particles is inferred to be low, as observed by Thomsen et al. (2002) on the European continental margin. Therefore, phytodetritus deposited at upper slope sites is unlikely to fuel the energy requirements of downslope benthic communities, as advocated in many continental margin studies elsewhere (e.g., Levin and Gooday *in* Tyler 2003), although this statement must be tempered by the fact that the Chatham Rise observations were made over relatively short time frames of only 26–28 h.

Biological and chemical characteristics of surficial sediments—Phytodetritus deposition appeared visually to be restricted to 750 S, whereas sediment analyses and lander fluorometric data indicated that phytoplankton-derived material occurred at all sites sampled on the southern flank, and to a lesser extent on the crest of the rise. This suggests that despite the observation of a spatially extensive phytoplankton bloom in surface waters (Fig. 2), deposition of phytodetritus on the seafloor may have been restricted to a relatively narrow zone, 20 km to 60 km wide, centered on site 750 S, but which nonetheless could be very patchy in its distribution.

Specifically, sediment phytopigment concentrations were enhanced on the southern flank, compared to the northern flank (Fig. 5), but this was not evident in surficial sediment POC content (Table 1). Furthermore on the southern flank of the rise, Chl *a* : total pheopigment ratios were approximately 2–5-times higher in surficial sediments and near-bed resuspended material, compared to the northern flank, indicating more undegraded Chl *a*. In general, sediment organic matter lability was not reflected in C : N ratios (Table 1), which were elevated relative to a C : N Redfield ratio of 6.6. This ratio is an expression of the freshness of organic material, with values higher than 6.6 indicating preferential remineralization of N over C. The lowest ratio of 9.3, however, was found during the second sampling of sediments at 750 S when the highest Chl *a* and pheopigment concentrations were also observed, indicating that the organic matter sampled at this site was relatively fresh. C : N values obtained in austral spring 2001 at all the Chatham Rise sites were lower by 15–40% than those observed at the same locations during the same season in 1997 (Nodder et al. 2003), indicating that the organic matter deposited in surficial sediments in 2001 consisted of more labile, nitrogen-rich organic compounds, compared to spring 1997. In accordance, sediment Chl *a* concentrations in spring 2001 were substantially higher by factors of 20–30 than previous measurements made at the same sites on three previous occasions, including spring 1997 (Nodder et al. 2003).

At sites with high surface concentrations of Chl *a* (i.e., 450 S and 750 S), this labile fraction was transported to depths of 10–15 cm, a consequence perhaps of intense bioturbation related to elevated macrofaunal biomass. Levin et al. (1997) calculated that freshly deposited diatoms could be transported rapidly downward into slope sediments at rates exceeding or equal to 3 cm d^{-1} by burrowing macrofauna, especially maldanid and paraonid polychaetes (particularly *Aricidea quadrilobata*). Probert et al. (1996) identified that paraonids were abundant in Chatham Rise samples and that one species of *Aricidea* was more characteristic of deeper southern stations at water depths between ~800 m and 1,390 m, consistent with the observations of deep vertical transport of fresh organic matter in sediments on southern Chatham Rise (Fig. 5).

Although surficial sediment POC concentrations were not particularly elevated on southern Chatham Rise (Nodder et al. 2003; this study), sediment cores from the southern flank indicate substantially higher organic carbon accumulation rates of 8–16 mg C m^{-2} yr^{-1} at 1,300-m water depth, compared to 4–7 at ~1,000-m water depth on the northern flank (E. Sikes, pers. comm.; Table 3 *in* Nodder et al. 2003). This may reflect a long-term repository for sediment organic carbon on southern Chatham Rise that is in part fueled by preferential deposition of phytodetritus. Burial of relatively undegraded phytocompounds (e.g., Levin et al. 1997; Witte et al. 2003*a,b*) (Fig. 5), may provide an important food resource for benthic communities across much longer time scales than represented by a single flux event (months to seasons; *e.g.*, Josefson et al. 2002). This pool of organic carbon could be used by other components of the benthic food web during extended periods of the year when organic food supplies are insufficient to fuel community respiration and growth, as suggested by Nodder et al. (2003).

Benthic responses to phytodetritus deposition—Phytodetritus deposition is important in the structuring and functioning of many deep ocean benthic communities, although the exact response varies between different groups within the benthic community (e.g., Gooday 2002; Witte et al. 2003*a,b*; Moodley et al. 2005). Previous descriptions of elevated benthic biomass and SCOC on the crest and southern flanks of the Chatham Rise were replicated in the present study and are likely to indicate the effect of higher organic flux at these sites (Probert and McKnight 1993; Nodder et al. 2003; Grove et al. 2006).

High SCOC rates at 750 S, compared to other Chatham Rise sites, reflect the active remineralization of relatively labile phytodetritus (Fig. 8). Similar increases in in situ SCOC rates because of episodic phytodetrital deposition have been reported elsewhere (*e.g.*, Witte et al. 2003*a,b*). The Chl-rich phytodetrital material at 750 S did not support elevated bacterial biomass (Fig. 7a), which suggests that other components of the infaunal community were contributing to the high respiration rates measured at this site. Rapid ingestion and assimilation of enriched organic matter by macrofauna might explain these observations, as reported from deep-sea in situ enrichment experiments (Witte et al. 2003*a,b*). It is possible that the low abundance of bacteria on the southern flank, as compared to the northern flank, may have been the result of increased meiofaunal predation or attributable to time delays in the bacterial biomass response, as observed in other simulated in situ phytodetritus studies (e.g., up to a 23-d lag response at abyssal water depths in the northeast Atlantic Ocean, Witte et al. 2003*a*). Although there were no sediment bacterial production estimates from spring 2001, previous observations suggest that seasonally averaged bacterial production can be slightly higher on the upper southern flanks of the Chatham Rise, as compared to the north (Nodder et al. 2003). Together with the elevated meiofaunal biomass that was observed, this is likely to also contribute to heightened SCOC rates measured on the southern flank during 2001.

Megafaunal deposit feeders have been shown to selectively ingest organic-rich particles (*e.g.*, Lauerman et al. 1997) and increase rates of bioturbation and grazing activity during seasonal pulses of phytodetritus to the deep ocean (Kaufmann and Smith 1997; Witbaard et al. 2000; Bett et al. 2001). In addition, megafauna at abyssal sites in the Atlantic and Pacific Oceans have the capacity to effectively prevent the accumulation of organic matter on the seafloor because of their mobility and foraging activity (Kaufmann and Smith 1997; Bett et al. 2001). At 750 S, where phytodetritus deposition was observed directly, the epibenthos was characterized by a predominance of a few, large surface deposit feeders, such as echinoids and holothurians, as well as carnivorous gastropods (e.g., *Fusitriton magellanicus*). The urchin *Gracilechinus multidentatus* was a conspicuous component of the megafauna at 750 S. Related echinoids (e.g., *Echinus affinis*) feed on fresh phytodetritus in the North Atlantic (Campos-Creasey et al. 1994), which suggests that *G. multidentatus* may take advantage of phytodetritus inputs. Video observations showed the phytodetritus had accumulated mainly in pits and depressions and not substantially on the flat seabed. It is implausible, however, that the low numbers of megafauna observed on the video at 750 S (i.e., mainly echinoids at estimated abundances of <1 per 14 m^2) had any control over the distribution and accumulation of phytodetritus at the seabed between frequent resuspension events, which may occur at least twice every 24 h (cf. Bett et al. 2001).

In contrast, at 1,200 S epifaunal biomass and abundance was dominated almost exclusively by ophiuroids (98% of individuals and 88% of the biomass, mainly *Ophiomusium lymani*) (Fig. 7d,e), which were not observed on video imagery collected at a site on the same transect at 1,000-m depth approximately 15 km away. Food supply is a principal factor causing zonation of slope fauna. On northeast Atlantic slopes, for example, narrow depth bands of mega- and macrofaunal filter feeders were found to be related to local alterations of the food supply caused by interaction between hydrography and the seabed, giving rise to variations in sites of sediment erosion, resuspension, and deposition (*e.g.*, Flach and Thomsen 1998; Witbaard et al. 2005). Dense mats of ophiuroids have also been observed on slopes off Tasmania and Nova Scotia (Metaxas and Giffin 2004 and references therein). In these cases, food supply (i.e., enhanced rates of particle delivery) was thought to explain the aggregations. Many ophiuroids are omnivorous and have also been recognized as active phytodetritus grazers and deposit feeders (e.g., Pearson and Gage 1984). It is possible that the dense ophiuroid band found at 1,200 S reflects regular occurrence of deposition events like the one we observed at 750-m water depth. Although the short-term current measurements from 750 S exclude a significant downslope transport of phytodetritus from this site to 1,200 S (Fig. 10), we cannot discount the possibility of this process occurring. Strong eastward currents have been observed across most of the annual cycle at a site near 1,200 S with mean and maximum current speeds of ~10 cm s^{-1} and 26 cm s^{-1}, respectively, recorded in spring 1996 at 1,000 m depth, 500 m above the seafloor, on southern Chatham Rise (Nodder and Northcote 2001). These data suggest that sediment deposition may be precluded and erosion facilitated at this location over longer time scales (weeks to months) than the ~1-d lander deployments. Alternatively, these persistent eastward currents may be responsible for supplying organic material from sources further to the west (e.g., Nodder et al. 2003).

Despite the likely spatial and temporal variability in water column and near-bed currents (e.g., Auffret et al. 1994; Beaulieu and Baldwin 1998; Thomsen et al. 2000; *see* above), the fact that elevated levels of biomass were observed in all faunal compartments, up to megabenthic organisms, as well as across seasonal time scales (Nodder et al., 2003), suggests that organic particle production and flux to the seabed on the southern flank of Chatham Rise must be temporally sustained or at least episodic in space and time, but common enough to support the high benthic biomass. In a global sense, however, bacteria and meiofauna abundance from Chatham Rise were not particularly high (e.g., Soltwedel 2000). Similarly, macrofauna biomass estimates were similar to values from the temperate northwest Atlantic (Levin and Gooday *in* Tyler 2003), but higher than the Californian margin (C. Smith and Demopoulus *in* Tyler 2003). Excluding the very high abundance and biomass of ophiuroids at 1,200 S, megafauna values were also comparable to, if not lower than, estimates at similar water depths from the temperate and polar Atlantic Ocean (Lavaleye et al. 2002; Levin and Gooday *in* Tyler 2003).

The first in situ observations of active phytodetritus deposition and resuspension on the southern flank of Chatham Rise support the original contention by Nodder et al. (2003) that this organic material plays a critical role in supporting the growth and functioning of benthic communities. Whereas strong west-to-east transport was hypothesized in the previous study, it is apparent that zonal transportation of organic matter across the Chatham Rise and flow convergence along the southern flank are also important processes that serve to concentrate deposition across narrow depth ranges on southern Chatham Rise. This advected material provides a highly labile, easily eroded and transportable food source that is then readily available to suspension- and deposit-feeding organisms that dominate the diverse and biomass-rich communities found on the southern rise flanks. The advection and possible physical focusing of phytodetritus deposition by convergent current cells within the STF suggest that the fate of exported phytoplankton bloom products from the front may be predictable, although current flows across the frontal zone exhibit considerable temporal variability. Such physical focusing of labile organic matter deposition may be an important process in other highly productive frontal systems. However, the west–east lateral extent of the effect of phytodetritus deposition along the southern Chatham Rise flank remains to be determined, because strong zonal jets observed within the STF and other continental margin studies suggest that such transport could be extensive.

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