

Response of an abyssal macrofaunal community to a phytodetrital pulse

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ABSTRACT: The majority of deep-sea benthic communities rely on particulate organic matter (POM) sinking from the euphotic zone for energy, much of which is delivered in pulsed events. But we know little about abyssal plain macrofaunal communities, their response to such events or their role in deep-sea carbon-cycling. In this study, we examined the composition of the macrofaunal community at Station M in the deep NE Pacific and assessed its short-term response to a simulated OM pulse in two 36 h *in situ* enrichment experiments. In each experiment, 1.2 g C m⁻² of ¹³C-labelled *Skeletonema costatum* was deposited onto the seafloor using a benthic chamber lander. Macrofaunal abundance and biomass were significantly higher at 0 to 5 cm depth compared to 5 to 10 cm, and were dominated by the Nematoda and Crustacea, respectively. Twenty-five percent of the macrofauna specimens showed ¹³C signatures indicative of label ingestion, but specific uptake ($\Delta\delta^{13}\text{C}$) and C-turnover rates varied strongly between and within taxa. Two organisms, a single cumacean from 1 chamber and a paraonid polychaete from the second chamber, were responsible for the majority of C-uptake and had ingested up to 2.3% of their body weight in C. Macrofaunal C-turnover was much lower than recorded in the abyssal NE Atlantic, which is most likely due to differences in the timing of the experiments relative to the spring/summer bloom, different experimental durations and disparities in macrofaunal community structure. These results emphasize the degree of plasticity inherent in the macrofaunal response to a food pulse and stress the need for comprehensive *in situ* investigations to further our understanding of deep-sea benthic ecosystem functioning.

KEY WORDS: Abyssal plain · Northeast Pacific · Deep sea · Pulse-chase experiments · $\delta^{13}\text{C}$ · $\delta^{15}\text{N}$ · Natural isotopic signatures · Benthic carbon remineralisation · Macrofauna

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INTRODUCTION

Prior to the early 1980s, it was thought that the majority of deep-sea communities derived their energy from a constant 'drizzle' of relatively refractory organic matter. However, within the last 25 yr it has become apparent that this 'rain' of particulate organic matter (POM) can be punctuated by large, episodic, pulses of labile POM to the seafloor (Deuser & Ross 1980, Billett et al. 1983). It is from these downpours of organic matter that the majority of deep-sea communities obtain most of their energy (Goody 1988, Graf 1989, Pfannkuche 1993), with the

exception of reducing systems. Recent studies have additionally shown from both time-lapse camera systems and sediment trap moorings that large inter-annual variations in the supply of POM to the deep-seafloor do exist, and are regular features of this environment (Smith et al. 1994, 2001, 2006, Baldwin et al. 1998). Furthermore, rapid responses to POM input by a number of deep-sea benthic taxonomic groups from microbes (Pfannkuche 1993, Lochte & Turley 1988) and protozoa (Goody 1988, Drazen et al. 1998), to megafauna (Smith et al. 1994, Lauerman et al. 1997, Bett et al. 2001) have been identified.

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Macrofaunal communities can provide helpful information about the quality and quantity of POM arriving at the seafloor, and can assist in predicting its overall fate within the sediment. For example, the vast majority of macrofauna found at abyssal depths are considered deposit feeders (Hessler & Jumars 1974) that, through bioturbation and feeding, considerably re-work sediment, thus affecting the early diagenesis of recently deposited POM (Levin et al. 1997). However, owing to the inherent costs and difficulties associated with sampling deep-sea environments, especially abyssal habitats, detailed knowledge of deep-sea macrofaunal trophic interactions, including their access to and ingestion rates of POM, have yet to be established.

Conventional analysis using gut contents to infer food-web structure in the deep sea has proved successful for megafauna (Lauerman et al. 1997), but is almost impossible to carry out on small-sized biota, such as macrofauna. Recently, the establishment of stable isotope techniques has created numerous opportunities for studying macrofaunal trophic interactions (Iken et al. 2001), and the development of the pulse-chase approach has allowed direct quantification of C flow through benthic food webs (Middelburg et al. 2000, Witte et al. 2003a). In *in situ* pulse-chase experiments at abyssal depths, Witte et al. (2003a) found during a 60 h experiment that among bacteria, Foraminifera, Nematoda and macrofauna, macrofauna responded to and processed C faster when incubated with fresh phytodetritus. Witte et al. (2003b) reported a similar reaction by infaunal macrofauna from the deep Norwegian Sognefjord (1265 m) during a 3D experiment. Furthermore, a detailed study by Aberle & Witte (2003) revealed that, of the dominant taxa, crustaceans were of minor importance in C cycling in the abyssal NE Atlantic, but cirratulid and spionid polychaetes played a leading role in re-working freshly deposited material, in a similar manner to the maldanid and paraonid polychaetes on the Carolina continental slope (Levin et al. 1997, 1999).

The coupling of pelagic and benthic processes has been studied repeatedly since 1989 in the abyssal NE Pacific at Station M (Smith & Druffel 1998); however, detailed information on macrofaunal community structure and trophic interactions is lacking for this site and for the abyssal Pacific in general. This study therefore examines macrofaunal community composition at Station M and explores food web structure using natural C and N isotopic signatures. We also describe for the first time the short-term response of an abyssal Pacific macrofaunal community to a simulated phytodetritus pulse. We present *in situ* data from 2 replicate enrichment experiments carried out at Station M using a benthic chamber lander in October 2004. Diatoms, labeled

with ^{13}C , were incubated for a period of 36 h over a known area of seafloor and uptake of labelled C into the metazoan macrofauna was subsequently measured. We specifically focused our attention on the polychaetes, since this group comprises a number of dominant functional groups whose diversity is known to affect biogeochemical fluxes (e.g. PO_4^{3-} and O_2), profiles (e.g. O_2 and pH), and transport rates in addition to rates of organic matter remineralisation (Levin et al. 1997, 1999, Aberle & Witte 2003, Waldbusser et al. 2004, Waldbusser & Marinelli 2006).

MATERIALS AND METHODS

In late October 2004, during cruise PULSE 45 of the RV 'New Horizon,' *in situ* pulse-chase experiments were carried out at Station M ($34^\circ 50' \text{N}$, $123^\circ 00' \text{W}$, ca. 4100 m water depth, Fig. 1), located approximately 220 nautical miles west of Point Conception, California, at the base of the Monterey Deep-Sea Fan. The seafloor at Station M is characterised by silty-clay sediments with an organic C content of approximately 17 mg C g^{-1} and possesses little topographical relief ($<100 \text{ m}$ over 1600 km^2) (Smith et al. 1994, 2001, Smith & Druffel 1998).

A non-axenic clone of the diatom *Skeletonema costatum* (Bacillariophyta) was used as a labelled food source in our experiments. This diatom species was chosen as a suitable food source since it occurs within the vicinity of, and has been sampled in sediment traps moored above, the seafloor at Station M (Venrick 1998, Beaulieu & Smith 1998). Algae were cultured in an artificial seawater medium modified with F/2 (Grasshoff et al. 1999). The culture medium was amended by replacing 25% of ^{12}C bicarbonate with $\text{NaH}^{13}\text{CO}_3$. Diatoms were cultured for 3 wk at 15°C under a 16:8 h light:dark cycle and harvested. To harvest, inoculums were concentrated by centrifugation ($404 \times g$, 5 min), washed 4 times in an isotonic solution to remove excess labelled bicarbonate, and freeze dried. Algae possessed a ^{13}C content of $7.9 \pm 0.4 \text{ atom\%}$ ($n = 6$) and a C:N ratio of 9 ± 1 ($n = 6$). Comparatively similar C:N ratios of added algae to seafloor phytodetrital aggregates (C:N = 11) sampled in September 1994 at Station M (Smith et al. 1998) suggest that the POM used was representative of natural phytodetritus entering the benthic boundary layer (BBL) in autumn.

Macrofaunal community structure was assessed from 3 multiple corer (MUC) and 3 benthic chamber sediment samples. Macrofauna from the MUC cores were additionally used for natural or 'background' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements. MUC cores were sampled at a depth of 4062 m, and processed in a cold-room once



Fig. 1. Station M in the NE Pacific

back onboard. All 3 cores (10 cm \varnothing) were sectioned at 0 to 2 cm and 2 to 5 cm, but one core was additionally sampled at 5 to 10 cm. Sectioned sediment horizons were immediately sieved for metazoan macrofauna (>250 μ m) and all sieved organisms were transferred to 4% buffered formaldehyde solution for long-term storage and refrigerated. Macrofauna from the 3 benthic chambers were sampled at 0 to 2 cm, 2 to 5 cm, and 5 to 10 cm sediment depth and processed in the same way as the 3 MUC cores. The macrofaunal abundance and biomass determined from MUC cores and benthic chambers did not differ significantly with sampling technique (macrofaunal abundance *t*-test, $t_4 = 0.693$, $p = 0.526$; biomass *t*-test, $t_4 = 0.953$, $p = 0.394$).

In situ pulse-chase experiments were carried out during a single deployment of a deep-sea benthic chamber lander. The lander carried 3 independent, autonomous benthic chambers (400 cm²), with each chamber separated from the others by approximately 0.5 m. For a description of the lander see Witte & Pfannkuche (2000). Two hours after arriving on the seafloor, approximately 250 mg of labile algal C, equivalent to 1.2 g C m⁻² (or ~40% of the annual C supply to the BBL), was injected into each chamber and stirrers mounted in the chamber lids were activated to homogeneously distribute it over the enclosed sediment surface. Approximately 1 min after algal injection, stirrers were switched off for 1 h to allow the labelled algae to sink. Stirrers were then

turned on and the chamber waters gently mixed (without creating sediment resuspension) for the duration of the 36 h *in situ* incubation. After 36 h, the lander was recalled to the surface, where it was discovered that the algal injector in the third chamber (Chamber 1) failed to work in concert with the other two (Chambers 2 & 3) and only fired during the recovery of the lander, thus contaminating this 'control' chamber. As such, Chamber 1 was only used for macrofaunal abundance and biomass data. Once onboard, half of the enclosed sediment (200 cm²) in each of the 3 chambers was sectioned and processed as above. In an effort to gather greater numbers of animals for C-uptake measurements, an additional core (6 cm \varnothing), initially sectioned and preserved unsieved for Foraminifera (0 to 2 and 2 to 5 cm), was taken from the second half of each chamber and later sieved in the laboratory for metazoan macrofauna (>250 μ m). Sieved animals from both the 28.3 cm² core and 200 cm² sediment samples from 0 to 2 and 2 to 5 cm were then pooled.

In the laboratory, sieved samples were picked for macrofauna (>250 μ m) in cooled artificial seawater (salinity 35) under a binocular microscope and transferred to 4% buffered formaldehyde solution. To derive information from macrofaunal natural isotopic signatures about potential food sources at Station M, $\delta^{13}\text{C}$ signatures from 'background' macrofauna were corrected for formaldehyde preservation effects by adding 1‰ to each $\delta^{13}\text{C}$ value (Kaehler & Pakhomov 2001, Sarakinos et al. 2002). Only 13 of the 25 macrofaunal samples measured for background C and N signatures possessed enough biomass for natural $\delta^{15}\text{N}$ measurements. Preservation effects on stable isotope signatures were considered to be negligible (~0.5 to 1‰, L. Levin & C. R. Smith pers. comm.) compared to tracer uptake; thus, no corrections were applied to 'background' or 'enriched' signatures when calculating specific uptake of ^{13}C and C-uptake. Separate picking utensils were used for background and labelled samples to avoid contamination of stable isotopes. Organisms were identified to major taxon, with polychaetes being identified to family or lowest taxonomic level possible. Crustacea were identified to class or order. Single organisms were cleaned of attached organic debris in cooled, clean artificial seawater (salinity 35), placed in silver caps and dried at 35 to 40°C for a period of 2 wk. Calcareous shelled organisms were decalcified with 2 M HCl in double boated silver caps and dried as above. In order to obtain

sufficient biomass for isotope measurements, some individual organisms (see Table 1) were combined as in Aberle & Witte (2003) and Kamp & Witte (2005). Prior to isotopic analysis, all organisms were weighed on an electronic microbalance (Sartorius) for biomass determinations (mg dry weight).

From the second half of each benthic chamber, a 6 cm (\varnothing) core was taken for determination of total organic (TO) ^{13}C signatures of the sediment ($\Delta\delta\text{TO}^{13}\text{C}$). Each core was extruded at 1 cm intervals from 0 to 5 cm, at a 2 cm interval from 5 to 7 cm, and at a 3 cm interval from 7 to 10 cm. Sectioned sediment cakes were placed in brown glass bottles and immediately frozen at -20°C . Background sediment samples were collected from a fourth MUC core (10 cm \varnothing ; 4062 m depth) and processed in the same way. Upon return to the laboratory, each cutlet was freeze-dried for 4 d and homogenized using a pestle and mortar. From each homogenized horizon, approximately 50 to 100 mg of freeze-dried sediment was transferred to a pre-combusted glass tube (550°C for 5 h) and decalcified overnight with 10% HCl. Decalcified sediment was vigorously washed 4 times with Milli-Q water, concentrated by centrifugation and dried at 50°C for 3 d. Approximately 30 mg of pre-acidified sediment was then transferred to tin caps for isotope ratio mass spectrometry (IRMS) analysis.

The isotopic ratios of the macrofaunal organisms were measured using a Finnigan Delta plus XP (Thermo) Isotope Ratio Mass Spectrometer at MPI Bremen (reproducibility: $\delta^{13}\text{C} = 0.2\text{‰}$, $\delta^{15}\text{N} = 0.8\text{‰}$) and those of the sediment samples analysed using a Europa Integra (enriched isotopes) and Hydra 20/20 (natural isotopes) IRMS at UC Davis (reproducibility: $\delta^{13}\text{C} = 0.02\text{‰}$, $\delta^{15}\text{N} = 0.06\text{‰}$). Macrofaunal C-isotopic ratios ($^{13}\text{C}/^{12}\text{C}$) were measured against a PDB standard and are expressed as delta notation ($\delta^{13}\text{C}$) as relative difference between sample and standard: $\delta^{13}\text{C} (\text{‰}) = [(^{13}\text{C}/^{12}\text{C}_{\text{sample}})/(^{13}\text{C}/^{12}\text{C}_{\text{standard}}) - 1] \times 10^3$. Specific uptake of ^{13}C by macrofaunal organisms was calculated as excess (above background) and is expressed in $\Delta\delta^{13}\text{C}$ notation: $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{background}}$. Incorporation of ^{13}C was calculated as the product of the excess atom% ^{13}C (difference in atom% ^{13}C between sample and background) and C content (expressed as unit weight): ^{13}C incorporation (unit wt ^{13}C) = (atom% $^{13}\text{C}_{\text{sample}} - \text{atom}\% ^{13}\text{C}_{\text{background}}) \times (\text{unit wt C of organism})$. ^{13}C incorporation was then adjusted to account for the ^{13}C algal labelling, yielding total C uptake: C uptake (unit wt C) = ^{13}C incorporation/7.9 atom %. C-uptake was then normalized to 24 h to give total C-turnover. Specific labelling ($\Delta\delta\text{TO}^{13}\text{C}$) of sediment was measured relative to a PDB standard and expressed as excess above background as $\Delta\delta\text{TO}^{13}\text{C} = \delta\text{TO}^{13}\text{C}_{\text{sample}} - \delta\text{TO}^{13}\text{C}_{\text{background sediment}}$.

RESULTS

Macrofaunal abundance and biomass

Total macrofaunal density was 6165 ± 3751 individuals (ind.) m^{-2} / 2462 ± 396 ind. m^{-2} (SD, $n = 4$, including/excluding nematodes). Total biomass was 509 ± 226 mg dry wt m^{-2} / 485 ± 227 mg dry wt m^{-2} (SD, $n = 4$, including/excluding nematodes). The top 2 cm of sediment at Station M comprised the greatest concentration (53%) of macrofauna with 4350 ± 2270 ind. m^{-2} (SD, $n = 6$, including nematodes, Fig. 2a). Macrofaunal abundance decreased below 2 cm sediment depth with 42% (3419 ± 1986 ind. m^{-2} , SD, $n = 6$, including nematodes) and 5% (432 ± 390 ind. m^{-2} , SD, $n = 4$, including nematodes) found within the 2 to 5 cm and 5 to 10 cm horizons, respectively (Fig. 2a). Significantly higher abundances were found in the 0 to 5 cm horizon compared to the 5 to 10 cm layer (t -test, $t_6 = 3.132$, $p = 0.020$) when adjusted for multiple testing (Holm 1979). Maximum biomass values were observed at 0 to 2 cm (Fig. 2b). After correcting for multiple testing (Holm 1979), biomass values were significantly different

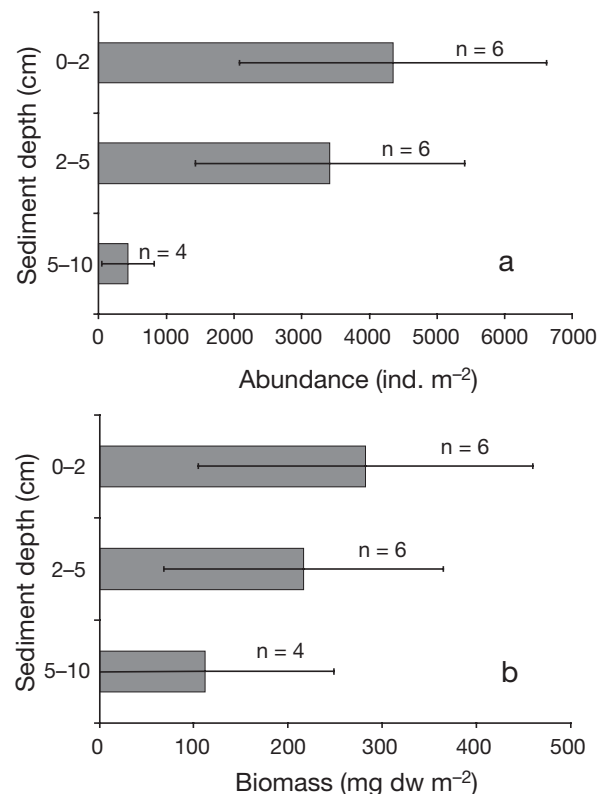


Fig. 2. Vertical distribution of (a) total macrofaunal abundance and (b) biomass within the sediment column (0 to 10 cm) at Station M (± 1 SD). $n = 6$ denotes samples from 3 benthic chambers and 3 MUC cores; $n = 4$ denotes samples from 3 benthic chambers and 1 MUC core

between the 0 to 5 and 5 to 10 cm depths (t -test, $t_6 = 2.998$, $p = 0.024$). The majority of organisms (95%) and biomass (82%) were found within the top 5 cm (Fig. 2). Because the presence of a single large opheliid polychaete (1172 mg dry wt m^{-2}) in Chamber 1 drastically altered biomass estimates, this animal was removed from further analysis. Macrofaunal community composition is given in Fig. 3. Altogether, 10 major macrofaunal taxa were found at Station M. The Nematoda contributed 60% to macrofaunal abundance, but only 6% to overall biomass. The Crustacea were the second most abundant taxon (23%) and made up 43% of the biomass, followed by the Polychaeta, which contributed 8% to overall abundance and 29% to biomass. Although the Harpacticoida were the most abundant (56%) crustacean group, the Ostracoda made up for most of the crustacean biomass (40%). Members of the family Paraonidae (20%) and Pilargidae (15%) were the most common polychaete families found, but the Capitellidae contributed by far the most biomass (65%), followed by the Paraonidae (10%).

Natural isotopic signatures and ^{13}C labelling experiments

Natural $\delta^{13}C$ and $\delta^{15}N$ signatures are summarized in Fig. 4. Delta ^{13}C signatures showed negative values and ranged from -15.8 to -27.8 ‰. The highest and lowest $\delta^{13}C$ signatures were measured for an ostracod (-15.8 ‰) and a syllid polychaete (-27.8 ‰), respectively. Natural $\delta^{13}C$ signatures of polychaetes ($n = 14$) and crustaceans ($n = 7$) were -20.2 ± 2.7 ‰ (SD) and -19.1 ± 2.1 ‰ (SD), respectively. Delta ^{13}C and ^{15}N signatures of surface ($\delta^{13}C = -19.5$ ‰, $n = 2$, $\delta^{15}N = 16.5$ ‰, $n = 2$) and sub-surface deposit feeding polychaetes ($\delta^{13}C = -19.6 \pm 1.1$ ‰, SD, $n = 7$, $\delta^{15}N = 17.8 \pm 1.2$ ‰, SD, $n = 4$) showed little variation amongst functional groups. Carnivorous polychaete families were on average slightly lighter, but comparable (-20.8 ‰, $n = 4$), although they displayed far more variability (range: -17.2 to -27.8 ‰) in ^{13}C over deposit feeding polychaetes. Mean $\delta^{15}N$ signatures of carnivorous (18.1‰, $n = 2$) vs. sub-surface deposit feeding polychaetes were approximately identical. Amongst the polychaetes, a pilargid of the species *Ancistrosyllis homata* showed the highest $\delta^{13}C$ signature (-17.2 ‰), and a syllid polychaete of the genus *Brania* sp. possessed the lowest (-27.8 ‰), whilst $\delta^{15}N$ signatures ranged from 15.6‰ for the Ampharetidae to 19.4‰ for the Opheliidae. Natural $\delta^{13}C$ measurements for the crustaceans ranged from -15.8 ‰ (Ostracoda) to -21.4 ‰ (Tanaidacea), and $\delta^{15}N$ signatures for the harpacticoida and isopoda were 14.3‰ and 15.7‰, respectively. We did not observe background $\delta^{13}C$ signatures

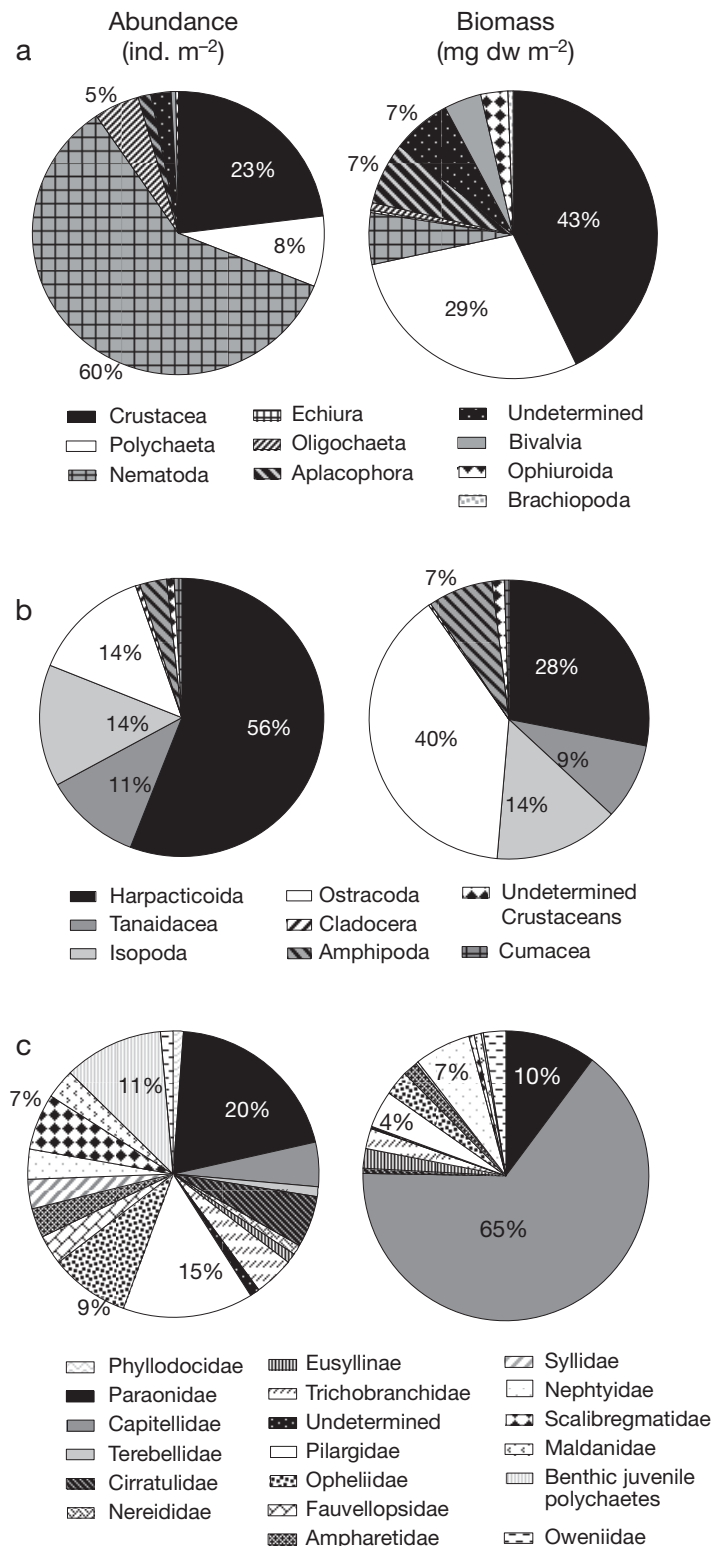


Fig. 3. Relative abundance (individuals m^{-2}) and biomass (mg dry wt m^{-2}) of (a) major macrofaunal taxa (including nematodes), (b) major crustacean taxa, and (c) major polychaete families, at Station M (all data from 3 benthic chambers, 3 MUC cores)

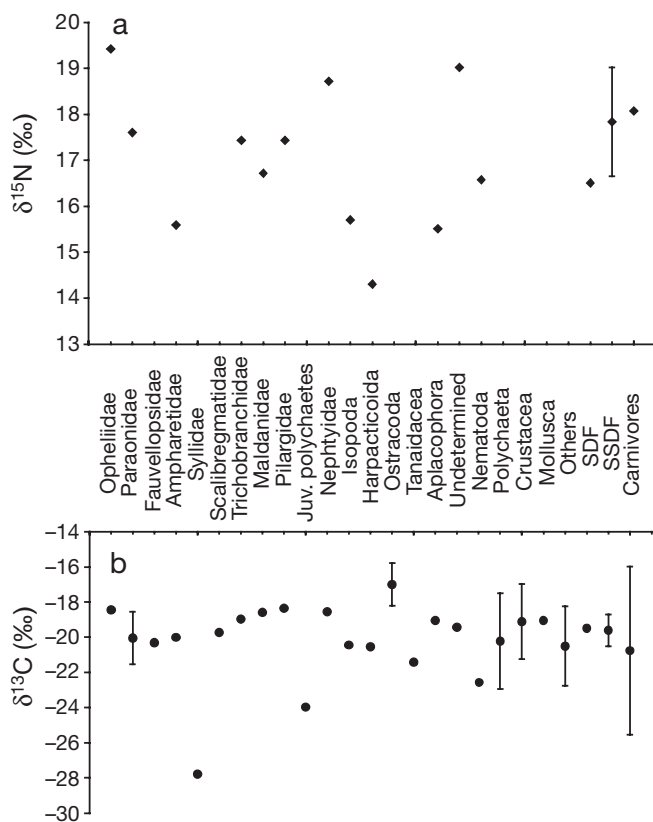


Fig. 4. Natural (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$ signatures of MUC-collected macrofauna taxa at Station M. Groups 'Polychaeta,' 'Crustacea,' 'Mollusca,' 'SDF,' 'SSDF' (surface- and sub-surface deposit feeders, respectively) and 'Carnivores' denote mean of natural isotopic signatures of all polychaetes, crustaceans, molluscs, surface deposit-feeding, sub-surface deposit-feeding and carnivorous polychaetes, respectively. 'Others' refers to mean of $\delta^{13}\text{C}$ signatures of undetermined taxa and nematodes. Feeding guilds of polychaetes were determined from Fauchald & Jumars (1979). Bars denote ± 1 SD

higher than -15.8% . Thus, in our enrichment experiments we considered signatures $> -14\%$ as evidence of incorporation of ^{13}C from our labelled algae (Aberle & Witte 2003). Delta ^{13}C and $\delta^{15}\text{N}$ signatures of decalcified sediment at Station M were $-22 \pm 0.1\%$ (SD, $n = 7$) and $9 \pm 0.1\%$ (SD, $n = 7$), respectively.

The isotopic signatures of macrofaunal organisms retrieved from experimental Chambers 2 & 3 are shown in Table 1. A number of macrofaunal organisms rapidly incorporated the ^{13}C -labelled phytodetritus with 37% (Chamber 2) and 13% (Chamber 3) of the macrofauna showing $\delta^{13}\text{C}$ signatures indicative of phytodetritus ingestion after 36 h (Table 1). Enrichment was modest in most organisms with only 3 individuals, a cumacean ($\Delta\delta^{13}\text{C} = 127\%$) from Chamber 2, and an isopod ($\Delta\delta^{13}\text{C} = 295\%$) and paraonid polychaete ($\Delta\delta^{13}\text{C} = 165\%$) from Chamber 3, showing $\Delta\delta^{13}\text{C}$ signatures greater than

100%. At the same time, a large degree of variation was observed in enrichment between related taxa within and between each chamber. For example, a single paraonid polychaete from Chamber 3 showed a $\Delta\delta^{13}\text{C}$ signature of 165%, whilst additional paraonids in Chamber 3 possessed $\delta^{13}\text{C}$ signatures of $< -14\%$. Similar patterns were also seen amongst the paraonids in Chamber 2 and the isopods in Chamber 3. Highest enrichment occurred in the top 5 cm of sediment (Fig. 5).

C-turnover rates are shown in Table 1. Mean metazoan macrofaunal C-uptake was $3.4 \times 10^{-3}\%$ of the C added. Highest turnover rates were found at 0 to 2 cm where 96% (Chamber 2) and 70% (Chamber 3) of the C was processed. However, there was an order of magnitude difference in C-turnover between Chambers 2 and 3. Counting the 2 amphipods in Chamber 2, 1.7% (Chamber 2) and 3.1% (Chamber 3) of the combined biomass (C) measured by IRMS analysis were directly involved in C-uptake. Profiles of sedimentary $\Delta\delta\text{TO}^{13}\text{C}$ are shown in Fig. 6.

DISCUSSION

Metazoan macrofaunal abundance decreases exponentially with increasing water depth (Flach & Heip 1996, Cosson et al. 1997). Macrofaunal abundance was similar to macrofaunal densities observed in previous investigations at Station M (Drazen et al. 1998, mesh size 300 μm), and higher than those observed at the Porcupine Abyssal Plain (PAP) (Aberle & Witte 2003), the Goban Spur (Flach & Heip 1996), and the southern Arabian Sea (Witte 2000). Previous investigations have noted a linear relationship between organic carbon flux and macrofaunal density (e.g. Cosson et al. 1997). Higher particulate organic carbon (POC) fluxes to the seafloor at Station M ($\sim 2.4 \text{ g C m}^{-2} \text{ yr}^{-1}$, Baldwin et al. 1998) than those found at the PAP ($\sim 1.3 \text{ g C m}^{-2} \text{ yr}^{-1}$, Lampitt et al. 2001) and in the southern Arabian Sea ($\sim 1.3 \text{ g C m}^{-2} \text{ yr}^{-1}$, Honjo et al. 1999), probably account for the higher densities we observed at Station M. Assuming an annual POC flux of $2.4 \text{ g C m}^{-2} \text{ yr}^{-1}$ at Station M (Baldwin et al. 1998), our mean macrofaunal abundance estimates fit well into the regression published by Cosson et al. (1997).

The majority of metazoan macrofauna density and biomass was found in the top-most 5 cm, thus adhering to profiles observed in previously studied continental slope (Blake 1994, Blair et al. 1996) and abyssal habitats, including Station M (Drazen et al. 1998) and the PAP (Aberle & Witte 2003). Metazoan macrofaunal biomass profiles with depth were similar to profiles of macrofaunal abundance and were comparable to previous abyssal studies undertaken by Drazen et al. (1998) and Aberle & Witte (2003). The standard

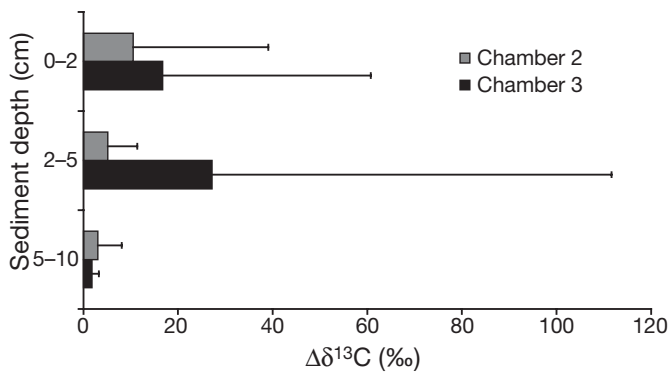


Fig. 5. Vertical distribution of mean $\Delta\delta^{13}\text{C}$ signatures of macrofaunal taxa with sediment depth (0–10 cm) at Station M. Bars denote +1 SD

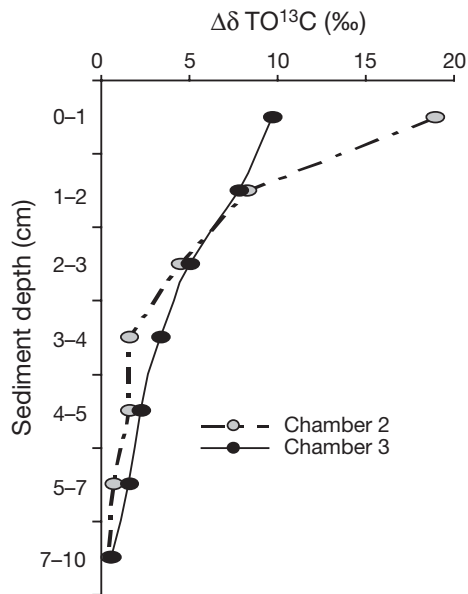


Fig. 6. Specific labelling of total organic (TO) ^{13}C in the sediment ($\Delta\delta\text{TO}^{13}\text{C}$) in each replicate experimental chamber

deviations of macrofaunal density and biomass estimates were extremely large suggesting high spatial heterogeneity amongst the macrofaunal community—a pattern also noted by Drazen et al. (1998). Like Drazen and his co-workers, we found no significant difference in macrofaunal abundance or biomass in relation to sampling technique (multicorer [78.5 cm²] and benthic chamber lander [400 cm²]). Processes that drive macrofaunal community spatial structure—such as the presence or absence of biogenic structures (Levin et al. 1986, Schaff & Levin 1994)—must therefore function at scales different from the area difference enclosed by both sampling devices.

Previous publications point to the dominance of either polychaetes (Schaff & Levin 1994, Flach & Heip

1996, Cosson et al. 1997) or crustaceans at deep-sea environments (Drazen et al. 1998, Witte 2000, Aberle & Witte 2003). In the present study, the crustaceans were the most abundant group (excluding nematodes) and contributed most to overall biomass. However in an earlier investigation at Station M, Drazen et al. (1998) found the polychaetes to contribute more to community biomass, a discrepancy most likely due to the high spatial heterogeneity of macrofauna previously discussed.

As already stated, crustaceans were numerically dominated by the Harpacticoida, but by the Ostracoda in terms of biomass. Drazen et al. (1998) also reported that the Harpacticoida were the most dominant crustacean group in their study, but found the Isopoda to contribute more to overall crustacean biomass. Of the polychaetes sampled, the Paraonidae were most abundant. In a study carried out on the central equatorial Pacific abyssal plain, Glover et al. (2002) reported that the polychaete assemblage was highly dominated by members of the Paraonidae (~17%). Paterson et al. (1998) found relatively high densities of paraonid polychaetes (range: 8.5 to 15.2%) at 3 sites in the equatorial Pacific and Schaff & Levin (1994) reported elevated densities of the paraonid *Levinsenia gracilis* in the vicinity of biogenic structures such as tubes, pits and mounds. Furthermore, in a feeding study conducted on the continental slope off the east coast of the USA, Levin et al. (1999) noted that paraonids were very active sediment and diatom ingesters, leading the authors to postulate that paraonids were opportunistic/flexible feeders. It is this opportunistic lifestyle that probably allows the paraonids to reach high densities in relation to other polychaetes at the food-limited seafloor of Station M.

Lack of accessibility to, and the high costs and risks associated with conducting research in the deep sea means that relatively little is still known about macrofaunal feeding ecology. Very often, inferences on deep-water feeding guilds are drawn based on animal mouth morphologies and/or feeding modes of shallow-water analogues. In recent years the use of natural stable C and N isotope measurements and, more recently, the pulse-chase approach, have provided insightful information about macrofaunal feeding ecology and C flow through deep-sea food webs (Fry & Sherr 1984, Levin et al. 1999, Iken et al. 2001, Aberle & Witte 2003, Witte et al. 2003a). Natural $\delta^{13}\text{C}$ signatures of the macrofauna at Station M ($-19.9 \pm 2.4\%$ SD) suggested a dependency on a phytoplankton-based food web (Fry & Sherr 1984). Natural ^{13}C -isotopic signatures measured in the present study were comparable to those measured from 2 bathyal sites located off the Carolina margin by Levin et al. (1999). In comparison to the PAP, where polychaetes and crustaceans

Table 1. Isotopic signatures and C-turnover of macrofaunal organisms within 2 replicate chambers (Chambers 2 & 3) and their vertical position within the sediment column (0 to 10 cm) at Station M. n: number of organisms combined for 1 measurement. Undet.: undetermined. Note: in Chamber 2, a single amphipod from 0 to 2 cm depth was accidentally combined with an amphipod from 5 to 10 cm depth prior to isotope ratio mass spectrometry (IRMS) analysis. Since different areas of sediment were sampled from these 2 horizons (see 'Materials and methods'), we were unable to calculate a value for C-turnover per unit area for these 2 pooled animals despite the sample showing a $\delta^{13}\text{C}$ signature of $> -14\%$

Taxon	Sediment depth (cm)	Biomass ($\mu\text{g C}$)	n	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	C-turnover ($\times 10^{-3} \text{ mg C m}^{-2} \text{ d}^{-1}$)	C ingestion (% of body wt C)
Chamber 2							
Crustacea							
Amphipoda	2–10	10.69	2	36.71	56.83	...	0.78
Harpacticoida	0–2	33.63	15	-20.93
Tanaidacea	0–2	30.36	5	-20.99
Cumacea	0–2	11.63	1	107.07	127.20	5.94	1.75
Cladocera	5–10	23.56	1	-21.56
Ostracoda	0–2	4.39	1	-20.57
Ostracoda	0–2	2.94	1	-12.36	5.64	0.06	0.07
Ostracoda	0–2	1.83	1	-11.56	6.44	0.05	0.08
Ostracoda	0–2	2.38	1	-12.03	5.97	0.05	0.08
Ostracoda	0–2	1.67	1	-5.73	12.27	0.08	0.17
Ostracoda	2–5	3.03	1	-13.95	4.05	0.05	0.05
Ostracoda	5–10	2.41	1	-9.55	8.45	0.09	0.11
Polychaeta							
Paraonidae	0–2	8.47	1	-8.08	12.97	0.44	0.18
Paraonidae	0–2	35.90	1	-19.29
Phyllodocidae	0–2	10.18	1	-18.96
Capitellidae	2–5	2510.37	1	-18.61
Other metazoa							
Bivalvia	0–2	7.06	1	-15.49
Bivalvia	0–2	3.12	1	-11.27	8.79	0.11	0.12
Bivalvia	2–5	8.93	1	-17.98
Bivalvia	5–10	26.88	1	-17.81
Nematoda	0–2	14.69	1	-19.28
Nematoda	0–2	18.07	10	-21.25
Nematoda	0–2	13.50	19	-20.85
Nematoda	2–5	23.19	8	-20.03
Nematoda	2–5	14.23	2	-19.74
Nematoda	2–5	19.31	24	-22.27
Brachiopoda	2–5	1.89	1	-2.45	19.06	0.15	0.26
Oligochaeta	0–2	13.09	6	-21.22
Undet.	0–2	8.07	1	-20.45
Undet.	0–2	7.66	1	-20.12
Chamber 3							
Crustacea							
Amphipoda	0–2	811.42	1	-21.83
Harpacticoida	0–2	30.84	6	-21.33
Harpacticoida	0–2	26.30	13	-22.05
Tanaidacea	0–2	421.25	1	-16.22
Tanaidacea	0–2	20.15	1	-16.66
Tanaidacea	0–2	19.57	3	-20.21
Cumacea	2–5	25.21	1	-11.18	8.95	0.92	0.12
Isopoda	0–2	22.46	1	-17.02
Isopoda	0–2	14.16	1	-19.62
Isopoda	2–5	5.69	1	-22.38
Isopoda	2–5	11.66	1	273.75	295.19	13.84	4.06
Polychaeta							
Paraonidae	0–2	41.85	1	143.97	165.02	27.82	2.28
Paraonidae	2–5	79.12	1	-21.07
Paraonidae	2–5	21.15	1	-19.06
Paraonidae	5–10	50.43	1	-19.93
Trichobranchidae	0–2	26.56	1	-19.95
Cirratulidae	2–5	25.45	1	-20.31

Table 1. (continued)

Capitellidae	5–10	47.27	1	–20.05
Capitellidae	5–10	1522.89	1	–18.72
Undet.	2–5	14.81	1	–20.38
Other metazoa							
Ophiuroida	0–2	34.26	1	20.57	42.07	5.83	0.58
Nematoda	0–2	52.06	8	–19.40
Nematoda	0–2	43.58	45	–20.18
Nematoda	0–2	25.03	34	–22.83
Nematoda	2–5	63.62	1	–18.50
Nematoda	2–5	46.36	15	–21.37
Nematoda	2–5	33.72	29	–17.39
Nematoda	2–5	24.43	39	–20.68
Nematoda	2–5	18.04	12	–19.95
Nematoda	5–10	36.84	16	–19.86

showed average $\delta^{13}\text{C}$ signatures of -25 and -24% , respectively (Aberle & Witte 2003), polychaetes and crustaceans from Station M exhibited heavier signatures, suggesting more recent ingestion of a fresh C source. Aberle & Witte (2003) conducted their experiments in May/June 2000, before the pulse of exported phytodetritus had settled to the abyssal plain, in contrast to the present investigation, which was carried out in late October 2004, a mere 3 to 4 mo after the peak POM pulse, around the same time as the autumn POM pulse event (Baldwin et al. 1998, Drazen et al. 1998, Smith et al. 2001). Druffel et al. (1998) showed that POC settling at a depth of 3450 m in the water column at Station M in September 1994 possessed a $\delta^{13}\text{C}$ signature of $\sim 21\%$. Thus, if we assume a $\delta^{13}\text{C}$ enrichment of 1% per trophic step (Fry & Sherr 1984), it seems plausible that the heavier signatures measured in our study were the result of fauna assimilating a fresher, more labile food source than those sampled by Aberle & Witte (2003). This assertion is further supported by the results of Iken et al. (2001), who measured natural $\delta^{13}\text{C}$ signatures in polychaetes and crustaceans at the PAP in September 1996 and July 1997 (immediately after the peak POM pulse) and found lower $\delta^{13}\text{C}$ signatures ($-17.4 \pm 1.4\%$ and $-17.9 \pm 1.2\%$, respectively). Mean natural $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of deposit feeding and carnivorous polychaetes were surprisingly similar (Fig. 4), despite carnivores generally living at higher trophic levels and thus exhibiting heavier isotopic signatures compared to deposit-feeding animals. Nevertheless, a large degree of variability was evident in $\delta^{13}\text{C}$ signatures of carnivorous polychaetes owing to a very lightly labelled syllid of the genus *Brania* sp. The majority of the Syllidae have been classified as carnivores by Fauchald & Jumars (1979) and Gaston (1987), but based on the $\delta^{13}\text{C}$ signature found for *Brania* sp., we postulate that this particular genus ingests highly refractory detritus, though it may alter its diet, living as a carrion feeder and/or carnivore when the opportunity arises

(Fauchald & Jumars 1979). Due to the small size of this animal we were unable to measure its $\delta^{15}\text{N}$ signature and, as such, this statement must remain a postulation until further studies are conducted. Surprisingly, of all the taxa measured for $\delta^{15}\text{N}$, none appeared to feed directly on sediment and associated phytodetritus, assuming a ^{15}N enrichment of 3.5% per trophic level (Fry & Sherr 1984, Fry 1988) and a sediment-plus-POM $\delta^{15}\text{N}$ signature of $9 \pm 0.1\%$, which is in good agreement with previous $\delta^{15}\text{N}$ signatures for POM (Iken et al. 2001). Rather, the Harpacticoida, Isopoda, Aplousophora, and Ampharetidae appeared to be feeding at the second trophic level ($\delta^{15}\text{N} > 12.5\%$, Fig. 4a) with the remaining polychaetes, nematodes and those unclassified animals feeding at the third trophic level ($\delta^{15}\text{N} > 16\%$, Fig. 4a). Since trichobranchid and paraonid polychaetes have been previously classified as surface and sub-surface deposit feeders, respectively (Fauchald & Jumars 1979, Gaston 1987, Levin et al. 1997, 1999), it is possible that the large $\delta^{15}\text{N}$ signatures measured for these 2 taxa ($\delta^{15}\text{N} > 17\%$) resulted from IRMS sample reproducibility error. Additionally surprising was the extremely large $\delta^{15}\text{N}$ signature found among opheliid polychaetes analyzed in this study; this suggests a carnivorous, rather than a detritivorous lifestyle, as has been previously proposed in the literature (Fauchald & Jumars 1979). The opheliid polychaetes sampled may have instead been preying on protozoans (Fauchald & Jumars 1979).

Remarkably, only a small fraction of the macrofauna sampled from both experimental chambers showed $\delta^{13}\text{C}$ signatures indicative of ^{13}C ingestion. This differs sharply with *in situ* pulse-chase experiments carried out at the PAP by Aberle & Witte (2003), who found after only 2.5 d, approximately 77% of the polychaetes and crustaceans (ca. 95% of the macrofauna) were already labelled. Vertical $\Delta\delta^{13}\text{C}$ profiles highlighted the relative importance of the top sediment layers (0 to 5 cm) in abyssal C cycling, and indicated that deeper-dwelling macrofauna had far less access to the labelled

food source than those living within the top 5 cm. These findings concur with earlier investigations carried out in the abyssal NE Atlantic (Aberle & Witte 2003, Witte et al. 2003a), deep Sognefjord (Witte et al. 2003b) and a shallow shelf habitat (Kamp & Witte 2005). Jumars et al. (1990) hypothesized that in environments characterized by highly sporadic food-supply and scarce food resources (e.g. abyssal regions), fauna burrow with food to deeper sediment layers in an effort to store food out of reach of competitors. Despite only a single ostracod from a single chamber showing $\Delta\delta^{13}\text{C}$ values greater than -14‰ at 5 to 10 cm depth (Table 1), $\Delta\delta\text{TO}^{13}\text{C}$ profiles did reveal the presence of small amounts of labelled material at 7 to 10 cm depth in both chambers. Although we cannot specifically assign a subduction mechanism for the $\Delta\delta\text{TO}^{13}\text{C}$ profiles observed, it is possible that the presence of capitellid and paraonid polychaetes (Table 1), families known for their burrowing lifestyles (Fauchald & Jumars 1979), contributed to these distributions. If this is true, faunal-mediated burial of organic matter to deeper sediment layers would provide highly reactive, labile resources to fauna and microbes living beneath the surficial sediments (Levin et al. 1997, Witte et al. 2003b).

As stated before, both specific uptake ($\Delta\delta^{13}\text{C}$) and C-turnover rates varied among and within taxa and were almost negligible with the exception of 4 individual organisms. Of the 6 paraonids analysed, 4 showed background isotope signatures indicating no ingestion of our tracer, one had ingested a minor amount, whilst another individual was heavily labelled. In Chamber 2, while ^{13}C uptake was detectable in one third of organisms, only 1 cumacean was heavily labelled and responsible for 85% of C-uptake. In Chamber 3, a total of 3 individuals were significantly labelled, with the above-mentioned paraonid being responsible for 57% of C-uptake. This is especially noteworthy when one considers that these animals accounted for only 0.4 and 1.2% of the total biomass (C), respectively, and had ingested up to 2.3% of their body weight in C.

Total C-turnover rates for the whole macrofaunal community at Station M were approximately 2 orders of magnitude lower than at the PAP (Witte et al. 2003a) in the NE Atlantic. When normalized to both the amount of C added and incubation time, the average C-turnover rate at Station M was 1.3% of that in the NE Atlantic, with $2.3 \times 10^{-3}\%$ of algal C added being processed at Station M (in 24 h) compared to 0.18% at the PAP. While it is important to bear in mind the highly variable response in this study (total C-turnover by the macrofaunal community varied by an order of magnitude between replicates despite similar overall biomass in both chambers), this is likely due to the different fractions of the macrofauna community that

had ingested significant amounts of ^{13}C -labelled POM (6.7 vs. 55% of specimens, representing 1.4 vs. 97% of the biomass at Station M and PAP, respectively) and indicates that macrofaunal response patterns to fresh POM may vary seasonally. Witte et al. (2003a) carried out their investigation immediately prior to the maximum POM pulse settlement, whilst our experiments were carried out at approximately the same time as the autumn POM pulse event (Baldwin et al. 1998, Drazen et al. 1998). Also, sedimentary organic C content during the experiment was 4 times higher at Station M than at PAP (1.7 vs. 0.4 wt%). Therefore, an immediate response by the entire macrofaunal community, coupled with elevated C-turnover rates at the PAP, would be a reasonable trait of a severely food-limited community, as opposed to a macrofaunal population that had very recently ingested fresh-bloom C. Had our experiments been carried out at a similar time of year (i.e. immediately prior to the main POM pulse event when the fauna should naturally be more food-starved), and/or for a similar duration (i.e. 60 instead of 36 h), we may have observed a reaction by the Station M macrofaunal community, both in terms of percentage labelled and macrofaunal C-turnover, that was similar to that measured at the PAP (Aberle & Witte 2003, Witte et al. 2003a).

Dissimilarities in macrofaunal community structure may also help to explain the different response patterns between Station M and the PAP. Aberle & Witte (2003) documented that surface deposit-feeding cirratulid polychaetes (1) were the most abundant polychaete family, (2) contributed most to polychaete biomass, and (3) showed some of the highest ^{13}C signals measured. These results allowed the investigators to speculate that this particular family plays a leading role in reworking freshly deposited POM in the NE Atlantic. At Station M however, the sub-surface deposit-feeding Paraonidae and carnivorous Pilargidae were the most abundant polychaete families found, with the Cirratulidae making up less than 10% of the population. Members of the Paraonidae and sub-surface deposit-feeding Capitellidae also made up the largest fraction of polychaetes in our 2 replicate experiments, making it reasonable to assume that they had far less access to our fresh food source than would surface-deposit feeding polychaetes. Thus, the larger assemblage of sub-surface deposit-feeding polychaetes and the smaller, sometimes absent (Chamber 2), surface deposit-feeding polychaete community in our 2 replicate experiments may additionally explain the comparatively small amount of C processed at Station M.

All of these findings emphasize the amount of heterogeneity and plasticity in the response to a food pulse on the family, taxon and community levels.

Reasons for this variability may stem from variations in POM supply and demand (Aspetsberger 2005, Bühring et al. 2006), particle size (Wheatcroft 1992), age (Smith et al. 1993) and density (Mayer et al. 1993), as well as from variations in metabolic state, infaunal life history, the degree of selective ingestion, and assimilation and feeding modes of the taxa (Aberle & Witte 2003, Fauchald & Jumars 1979). Finally, our results stress the need for long-term, time-series pulse-chase experiments with multiple replications in order to reliably quantify and identify reasons for temporal and spatial variations in macrofaunal C cycling at abyssal depths.

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