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Oxygen as a control on seafloor biological communities and their roles in sedimentary carbon cycling

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Abstract

^{13}C tracer experiments were conducted at sites spanning the steep oxygen, organic matter, and biological community gradients across the Arabian Sea oxygen minimum zone, in order to quantify the role that benthic fauna play in the short-term processing of organic matter (OM) and to determine how this varies among different environments. Metazoan macrofauna and macrofauna-sized foraminiferans took up as much as 56 ± 13 mg of added C m^{-2} (685 mg C m^{-2} added) over 2–5 d, and at some sites this uptake was similar in magnitude to bacterial uptake and/or total respiration. Bottom-water dissolved oxygen concentrations exerted a strong control over metazoan macrofaunal OM processing. At oxygen concentrations >7 μmol L^{-1} (0.16 ml L^{-1}), metazoan macrofauna were able to take advantage of abundant OM and to dominate OM uptake, while OM processing at O_2 concentrations of 5.0 μmol L^{-1} (0.11 ml L^{-1}) was dominated instead by (macrofaunal) foraminiferans. This led us to propose the hypothesis that oxygen controls the relative dominance of metazoan macrofauna and foraminifera in a threshold manner, with the threshold lying between 5 and 7 μmol L^{-1} (0.11 to 0.16 ml L^{-1}). Large metazoan macrofaunal biomass and high natural concentrations of OM were also associated with rapid processing of fresh OM by the benthic community. Where they were present, the polychaete *Linopherus* sp. and the calcareous foraminiferan *Uvigerina* ex gr. *semiornata,* dominated the uptake of OM above and below, respectively, the proposed threshold concentrations of bottom-water oxygen.

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Continental margin sediments are important sites for the accumulation and burial of organic matter (OM) (DeMaison and Moore 1980; Berner 1982). While oxygen exposure time generally exerts a dominant long-term control on OM burial efficiency (the proportion of OM delivered to the sediment that is eventually buried) in the marine environment (e.g., Hartnett et al. 1998; Hartnett and Devol 2003), OM burial efficiency in shallower margin environments varies greatly. The activities of macrofaunal and meiofaunal communities have significant effects on benthic OM cycling, and variation in benthic communities may contribute to the observed variation in burial efficiency. Benthic fauna have been shown to affect OM decay rates, and the cycling and burial of OM, through vertical transport during burrowing (Levin et al. 1997; Sun et al. 1999; Thomas and Blair 2002), by altering sediment redox conditions during burrow ventilation (Aller and Aller 1998; Sun et al. 1999, 2002), by stimulating microbial activity (Levin et al. 1997; Sun et al. 1999), and through their own digestive and metabolic processes (e.g., Lauerman et al. 1997).

While these processes have been the subject of considerable previous study, they have generally been studied in isolation; therefore, the total effect of faunal activity is the least well characterized or quantified aspect of OM cycling and burial in marine sediments. Consequently, the inclusion of faunal processes in the modeling of seafloor C cycling is currently restricted to diffusive bioturbation and pore-water irrigation terms, and an exponential decay constant for bulk OM, which is most applicable to microbial processes (Heip et al. 2001). Furthermore, these terms are applied without much consideration of variation in benthic community and environmental conditions between sites. This general lack of information reflects the inaccessibility of the deep seafloor, the localized and patchy nature of faunal communities and processes, and the considerable potential for variation introduced by species-specific effects. Previous studies of the effects of fauna on OM cycling and burial have often concentrated on a single process, and often are undertaken in microcosms, using subsets of the benthic community (e.g., Sun et al. 1999, 2002; Thomas and Blair 2002). A view of the net, combined results of all faunal processes on the fate of organic detritus in a natural setting is therefore lacking.

One powerful approach is to add isotopically labeled phytodetritus and trace the fate of the added carbon through the entire food web. Most previous studies of this kind have been limited to a single coastal or deep-sea site, or an offshore transect with covarying oxygen, OM, and temperature availability (e.g., Witte et al. 2003*a,b*). These limitations have prevented an assessment of how key variables affect faunal OM uptake and cycling. Nevertheless, these studies demonstrate that foraminifera and bacteria take up significant proportions of added label and are probably largely responsible for OM remineralization in sediments (Moodley et al. 2000, 2002). Other studies, however, suggest that the macrofauna carry out the majority of faunal OM uptake over short timescales (Witte et al. 2003*a,b*), as well as transporting fresh OM into the sediment (e.g., Levin et al. 1997) and occasionally accounting for large proportions of total respiration (Heip et al. 2001). It is clear from these contradictory results that much remains to be learned regarding the role of fauna in sedimentary OM cycling.

Globally, OM-rich sediments are found predominantly on continental margins (De Maison and Moore 1980; Berner 1982). Particularly OM-rich sediments are found in regions such as Walvis Bay, the Arabian Sea, and the Pacific margins of North America, where intense productivity and limited water replenishment result in the occurrence of low-oxygen water bodies (oxygen minimum zones, or OMZs) (De Maison and Moore 1980). Moreover, the presence of an OMZ is thought to increase the amount of OM transferred from the surface ocean to the deep sea (Devol and Hartnett 2001). The OMZ of the Arabian Sea is generated and sustained by a combination of monsoon-driven upwelling and productivity, and limited middepth circulation (Sarma 2002), and the result is one of the largest areas of oxygen-depleted continental margin in the world (Helly and Levin 2004). Where such low-oxygen water masses impinge on sloping continental margins, steep oxygen gradients are superposed on the benthic environment, and these further result in steep gradients in sediment geochemistry (Cowie 2005) and benthic community structure (Levin 2003). Thus, an OMZ provides a natural laboratory in which to study the way that environmental factors such as oxygen and OM availability affect the pattern of OM processing by benthic communities.

In this study, we address the role of undisturbed benthic communities in the short-term processing of OM using ^{13}C-labeled algal detritus as a tracer. Our sites spanned the steep gradients in bottom-water oxygen concentration, OM availability, and corresponding faunal changes found across the OMZ on the Pakistan margin of the Arabian Sea. This work was conducted as part of a larger study of benthic biology and biogeochemistry of the Pakistan margin and is thus supported by simultaneously collected biological and geochemical survey data. We hypothesized that variation in bottom-water oxygen concentration in space (cross slope) and time (before vs. after monsoon), as well as variation in natural OM availability, modifies benthic communities in ways that alter processing of organic C. Specifically, we examined C partitioning between total respiration and uptake by bacteria and by benthic metazoan macrofauna and foraminifera under different oxygen regimes. These experiments have led us to hypothesize the existence of oxygen thresholds across which state changes occur in the nature and mechanisms of biological OM processing.

Methods

Study area—The Arabian Sea exhibits a permanent and pronounced midwater oxygen minimum zone (OMZ), where oxygen levels fall below 9 μmol L^{-1} (0.2 ml L^{-1}), between depths of ~150 m and ~1,000 m (Table 1). Where the OMZ impinges on the continental margin, it creates a strong seafloor oxygen gradient. The weight percentage organic carbon contents (%C_{org}) of Pakistan margin sediments varies broadly according to oxygen availability,

Table 1. Site conditions. Temperature and oxygen data are from CTD sensors. Errors are 1 standard deviation from replicate CTD deployments. Sediment $\%C_{org}$ (weight % organic carbon) values are for the surface 0–0.5 cm. Organic matter quality data are DI (an amino acid based degradation index, Dauwe and Middelburg 1998) values averaged over the surface 3 cm (Vandewiele unpubl. data). Metazoan macrofauna diversity data are numbers of species per megacore (surface area 82 cm^2, 10 cm deep) averaged over five cores (P. Lamont unpubl. data). Foraminifera density data are numbers of calcareous individuals, and diversity data are numbers of species, both from the >150-μm sieve fraction in 25 cm^2 of the surface 1 cm of sediment (S. Schumacher unpubl. data). 1 μmol L^{-1} of O_2 = 0.0224 ml L^{-1}.

Station depth (m)	Temperature (°C)	Dissolved oxygen (μmol L^{-1})	Sediment $\%C_{org}$	OM quality (DI)	Metazoan macrofauna biomass (g wet m^{-2}) : diversity	Foraminifera density : diversity
Premonsoon						
140	22.5	92±4	1.46±0.08		9 : 51(±5)	593 : 19
300	15.5	4.2±0.1	2.36±0.09		0.020 (±0.02) : 2(±0.5)	549 : 18
850	9.7	5.8	3.22±0.06			
940	9.0	6.7	3.31±0.12		62(±45) : 12(±1)	80 : 13
1,000	8.7	6.7	3.04±0.01			
1,200	7.2	15.4±0.1	3.27±0.26	−0.49±0.18	0.4(±45) : 13(±2.6)	77 : 16
1,850	3.5	79.5±0.1	1.40±0.10		9(±15) : 53(±6)	24 : 8
Postmonsoon						
140	18.2	5.0±0.4	1.43±0.07	−0.99±0.06	5(±2) : 45(±3)	1,163 : 20
300	14.8	5.0±0.1	2.56±0.29	−0.40±0.12	0.013(±0.019) : 1	839 : 14
940	9.3	7.4±0.3	3.40±0.13	−0.48±0.03	45.7(±0.02) : 13(±1)	
1,850	3.7	74	1.20±0.25	−1.17±0.14	2(±0.9) : 44(±4)	

with maximal values found within and slightly below the OMZ (Cowie et al. 1999). The availability of oxygen across the margin also influences benthic community structure such that above and below the OMZ the sediments are fully bioturbated, while within the core of the OMZ (roughly 250 to 700 m) annual laminations are preserved (Schulz et al. 1996).

Monsoon-driven upwelling in the Arabian Sea (in June–September and November–March) results in twice-yearly blooms and pulsed inputs of OM to the sediment–water interface (maximum particle flux of 180–190 mg m^{-2} d^{-1}, compared with 0.1–60 mg m^{-2} d^{-1} between monsoons; particles are 3.8–10% organic C; Haake et al. 1993), where they form the base of the benthic food chain.

The study was conducted at sites along an offshore transect of the Pakistan margin in an area roughly defined by latitude 23°17′N and 22°52′N, and longitude 65°59′E and 66°43′E (Fig. 1). Sites were visited before (April–May; all sites) and after (September–October; 140-, 300-, 940-, and 1,850-m sites only) the summer monsoon of 2003 during RRS *Charles Darwin* cruises CD146 and CD151, respectively. Study sites were selected above, within, and below the OMZ and, thus, span a range of redox conditions and contrasting benthic communities (Table 1). Partially oxygenated OMZ boundary sites were located at 140-, 850-, 940-, 1,000-, and 1,200-m water depth. The 300-m site was in the hypoxic core of the OMZ, and the 1,850-m site represented a fully oxygenated end member. In addition to the methods and results presented below, a wide range of geochemical and biological parameters were also measured, and these data will be published by others elsewhere.

Oxygen measurements—Bottom-water dissolved oxygen concentrations were measured during conductivity–temperature–depth (CTD) deployments. The CTD was equipped with a Sea-Bird Electronics 43 sensor. Testing shows the instrument to have a precision of ±0.09 μmol L^{-1} (0.002 ml L^{-1}, C. Janzen pers comm.). Errors given for oxygen measurements in the text and in Table 1 are standard deviations from replicate CTD deployments.

Experimental methods—Pulse-chase tracer experiments with a ^{13}C-labeled OM substrate were carried out on intact sediments containing entire benthic communities, both on board ship using recovered sediment cores and in situ using a benthic chamber lander. Experiments of 2-d and 5-

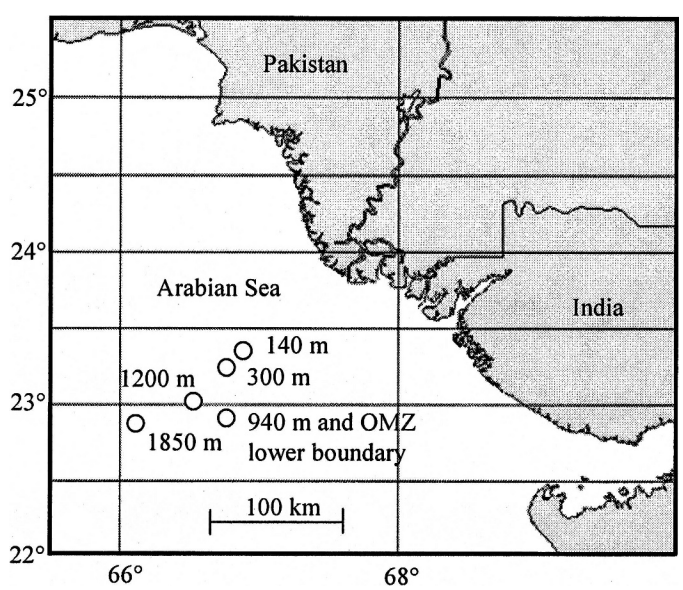

Fig. 1. Map showing the locations of study sites 140, 300, 940, 1,200, and 1,850 m. The 850- and 1,000-m sites were along the same transect as the 940-m site (slightly to the SE of the main transect). The OMZ occurs between depths of ~150 and 1,000 m (O_2 <9 μmol L^{-1}) and follows depth contours along the margin.

Table 2. The quantities of added C recovered from the metazoan macrofauna, the foraminifera, and the total fauna (metazoan macrofauna + foraminifera) in each experiment. Relative appearance of ^{13}C in bacteria, dissolved inorganic carbon, macrofaunal and foraminiferal pools. Errors are 1 standard deviation. Bacterial uptake and respiration data are from Andersson et al. (unpubl. data) and based on the $\delta^{13}C$ of bacterial phospholipid derived fatty acids (Middelburg et al. 2000) and dissolved inorganic carbon (Moodley et al. 2002).

		Absolute uptake by fauna			Percentages of label in pools			
Site	Duration (d)	^{13}C recovered from metazoan macrofauna (μg)	^{13}C recovered from foraminifera (μg)	Total ^{13}C recovered from total fauna (μg)	Bacterial uptake	Total respiration (all classes)	Uptake by macrofauna	Uptake by foraminifers
Premonsoon								
140	2	493±24	102±17	595±6	5±0.7	75±1	17±2	3±1
300	2	0.0	58±7	58±7	8±0.9	75±9.8	0±0	17±4
300	5	0.0	72±3	72±3	13±5	74±29	0±0	13±1
850	2	432±7	N/A	432±7	3±1	55±3	42±	No data
1,000	2	914±207	N/A	914±207	2±	41±	57±2	No data
940	5	563±103	0±0	563±103	2±2	50±5	46±16	1.3±0.9
1,200	5	3±1	8±3	11±4	2±0	95±33	1±0.5	2±1
1,850	2	5±1	90±3	95±3	No data	28±5	4±1	68±5
1,850	5	13±3	70±9	83±12	2±1	85±3	1.9±0.9	10±2
Postmonsoon								
140	2	111±37	210±34	320±3	11±5	69±2	7±5	13±4
140	5	114±24	372±9	486±15	7±2	72±1	5±2	16±1
140	2 (in situ)	92±9	118±13	210±22	0.3±0.6	74	11±3	15±4
300	2	0	61±4	61±4	22±23	71	0±0	9±1
300	5	0.0	218±4	218±4	32±16	55±0.4	0±0	13±0.5
300	2 (in situ)	0.0	156±5	156±5	13±7	14	0±0	73±6
940	5	825±67	13±0	838±68	14	38±14	47±8	0.7±0.0
940	2 (in situ)	557±2	7±0	564±1	0.5±0.4	16	83±1	1±0
1,850	5	19±4	43±1	62±	0.9	94±1	2±1	4±0

d duration were carried out, allowing an assessment of the transfer of label through the sediment system over time (Table 2).

Shipboard experiments—Whole sediment cores (10.2 cm internal diameter) with overlying waters were incubated in the dark, in a controlled-temperature laboratory maintained at seafloor temperature. The cores were sealed during incubation, and ambient dissolved oxygen concentrations were maintained by circulating core-top water through "oxystat" gills (Schwartz et al. unpubl. data).

Tracer experiments were initiated by the introduction of a slurry of ~80% ^{13}C-labeled diatom detritus (*Thalassiosira,* grown by D. Pond at British Antarctic Survey) freeze-dried onto either silica (premonsoon studies) or kaolinite (postmonsoon studies). Each core received 100–150 mg of algal detritus, equivalent to 685 ± 118 mg C m^{-2} (361 ± 63 mg C m^{-2} for lander experiments). After a settling period of 30–60 min, gentle water column stirring was initiated. Overlying waters were sampled for dissolved inorganic carbon (DIC) and $\delta^{13}C$ of DIC at intervals of 0, 12, 24, 36, and 48 h after the start of the experiments for the 2-d incubations, and 0, 24, 48, 96, and 120 h for 5-d incubations. Each experiment was conducted in duplicate simultaneously on megacores from the same corer deployment and thus the same exact coordinates. Oxygen concentration was monitored in one of each pair of cores using a Clark-type oxygen microelectrode and found to remain close to the ambient level (±10%).

Experiments were terminated by sectioning cores at intervals of 0.5-cm thickness to 2-cm depth, then 1-cm thickness to 10 cm, followed by 2 cm thickness to 20 cm. Each section was divided in half; one half was reserved for faunal extraction and the other half for porewater extraction. The sediment residues were transferred to bags and freeze-dried.

Sediment for faunal extraction was immediately wet sieved using filtered seawater, and 300-, 150-, and 63-μm sieve residues were retained and refrigerated. Residues from the 300-μm sieve were examined under ×12 or ×20 magnification, and all live metazoan macrofauna (from all depth horizons to 10 cm) and foraminifera (from the surface 1 cm only) were removed. Foraminifera were also extracted from some 150-μm sieve residues in the premonsoon season at the 300- and 1,850-m sites, and these samples accounted for ~10% of those analyzed from each experiment. Owing to time constraints, foraminifera were not collected from premonsoon experiments at the 850- and 1,000-m sites. Samples were sorted into the lowest taxonomic groups possible, rinsed in ultrapure water, and preserved frozen in glass vials and preweighed tin boats. Nematodes were found only very rarely in the sieve fraction examined and will not be further discussed.

In situ experiments—Benthic lander experiments followed the same principles as shipboard incubations. After the Elinor type lander (Glud et al. 1995; Black et al. 2001) arrived at the seafloor, potentially disturbed sediment was

allowed to settle before the chamber lid was closed. The amount of tracer introduced was scaled up according to the greater surface area of the chamber (30 × 30 cm), and pumping of chamber water through an oxystat "gill" in contact with bottom water prevented significant decline in dissolved oxygen concentration within the chamber. Dissolved oxygen concentration in the chamber was monitored with a Clark-type microelectrode. After incubation for ~48 h, the lander was recovered and the box-core was subsampled with two megacore tubes. These subcores were processed as described above for shipboard incubated megacores.

Bulk isotopic analysis—Sediments were decarbonated by addition of 2–3 drops of double distilled 6 mol L^{-1} HCl and analyzed for C and N content and $\delta^{13}C$ using a Europa Scientific tracermass isotope ratio mass spectrometer (IRMS) with a Roboprep Dumas combustion sample converter. Carbon contents were determined from IRMS peak areas and calibrated against standards of acetanilide. Replicate analyses produced an average relative standard deviation of 4.6% for $\%C_{org}$, and an average standard deviation of 0.7 per mil for $\delta^{13}C$ (n = 27). Acidified blanks did not contain measurable amounts of C.

Soft-bodied fauna were decarbonated using 1–2 drops of 1 mol L^{-1} HCl. Mollusks and foraminifera were treated with 2–3 drops of double distilled 6 mol L^{-1} HCl (H. Nomaki pers. comm.) to ensure complete decarbonation. Fauna samples were analyzed by combustion IRMS as detailed above, with standards tailored to suit very low C samples.

Data treatment—Each experiment was run using two replicate megacores. However, the half-megacore sections available for faunal studies did not yield sufficient material to be representative of the community. Faunal ^{13}C uptake data from the two replicate cores of each experiment were therefore pooled and are reported as one experiment. However, data from each core were also processed individually to generate standard deviations of uptake values (this is the only purpose for which cores were treated separately).

Results

Environmental conditions and benthic communities—Sediment $\%C_{org}$ and OM quality (as indicated by the amino acid degradation index [DI]; Dauwe and Middelburg 1998) reached maxima at the lower OMZ boundary (~940–1,200 m; Table 1). There was no measurable change in sediment $\%C_{org}$ between seasons, but carbohydrates and some lipid classes showed a slight increase in concentration in surface sediments, attributable to a seasonal OM input to the seafloor (C. Woulds and R.M. Jeffreys unpubl. data). Significantly, there was a seasonal decrease in bottom-water dissolved oxygen concentrations at the 140-m site, from 92 ± 4 μmol L^{-1} before the monsoon to 5.0 ± 0.4 μmol L^{-1} (2.1 ± 0.1 ml L^{-1} to 0.11 ± 0.01 ml L^{-1}) after the monsoon, as a result of a ~100 m shoaling of the upper OMZ boundary (Table 1).

Metazoan macrofauna were present above and below the OMZ but almost entirely absent at the 300-m site where organisms in the macrofaunal size range were mainly foraminifera. The 140-m site had the highest metazoan macrofaunal abundance, followed by the 940-, 1,200-, and 1,850-m sites. The OMZ lower boundary sites (the 850-, 940-, and 1,000-m sites; *see* representative 940-m site data in Table 1) displayed the highest metazoan macrofaunal biomass, as a result of large individual animal sizes, followed by the 140-m site, then 1,200- and 1,850-m sites (Table 1). Live foraminifera were present at all sites. Calcareous foraminifera, particularly *Uvigerina* ex gr. *semiornata,* dominated at the shallower 140- and 300-m sites. Agglutinated taxa, notably *Reophax* spp., became more important as depth increased. Macrofaunal foraminiferal populations were reduced at the OMZ lower boundary, where metazoan macrofauna were particularly abundant. Thus, foraminifera dominated the macrobenthic community where oxygen concentrations were lowest, whereas metazoan macrofauna were dominant where high-quality OM was most abundant ($\%C_{org}$ 3.4%, DI −0.48 at the 940-m site, Table 1) and oxygen levels were somewhat higher (6.7–7.4 μmol L^{-1} [0.15–0.17 ml L^{-1}], compared with 4.1–5.0 μmol L^{-1} [0.09–0.11 ml L^{-1}] at the 300-m site).

Overall fate of ^{13}C—On average 15 (±9)% of the total carbon added was "processed" by the benthic community in the 2–5-d incubation periods and was therefore recovered from the respired, bacterial uptake, foraminiferal uptake, and metazoan macrofaunal uptake pools. Most of the unprocessed label remained in the form of algal detritus at the sediment surface. The percentages of added label processed were highest at the metazoan-populated 140- and 940-m sites, and lowest at the foraminifera-dominated 300- and 1,850-m sites. Respiration was typically the dominant fate of processed ^{13}C, accounting for up to 94%, and that dominance was especially pronounced at the 1,850-m site. Metazoan macrofaunal and foraminiferal uptake typically accounted for 0–16% of total OM processing. However, at the 940-m site, metazoan macrofaunal uptake accounted for as much as 82%. Across all sites bacterial uptake was of similar magnitude to metazoan macrofaunal and foraminiferal uptake and accounted for 0.5–22% of total processed label (Table 2).

Faunal uptake of ^{13}C—Total faunal label uptake (=uptake by metazoan macrofauna plus foraminifera) ranged between 11 and 914 μg of C per experiment (two megacores, or 163 cm^2). The highest uptake values by a considerable margin were found at the 940-m site, followed by the nearby 850- and 1,000-m sites. The 140-m site exhibited intermediate levels of faunal uptake, followed by the 300-m site, then 1,200- and 1,850-m sites, at which uptake was extremely low (Fig. 2; Table 2).

The 5-d experiments at the 300-m site in both seasons, and the postmonsoon 5-d experiment at the 140-m site, showed increases in foraminiferal uptake compared with the equivalent 2-d experiments. However, this increase in ^{13}C content with time did not occur in the premonsoon

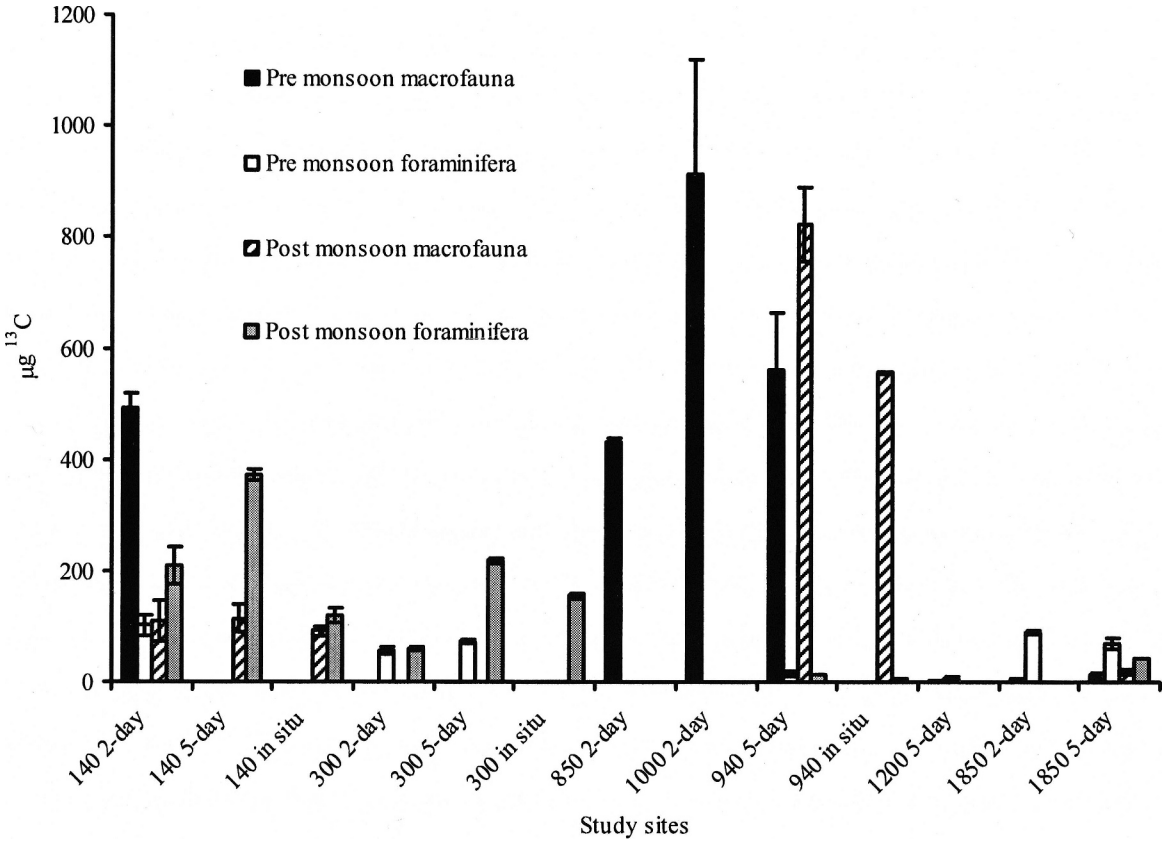

Fig. 2. The quantity of added C recovered from the metazoan macrofauna and foraminifera in each experiment. Error bars are 1 standard deviation.

season at the 1,850-m site and was never observed for metazoan macrofauna (Fig. 2; Table 2).

At the 940- and 300-m sites, during 5-d experiments, the amount of label recovered from the fauna was greater (in excess of error, Fig. 2; Table 2) after the monsoon (September–October) than during the premonsoon season (March–May). Total uptake, however, did not increase after the monsoon in 2-d experiments at the 140- and 300-m sites, or in 5-d experiments at the 1,850-m site.

Bacterial uptake of ^{13}C—Bacterial uptake showed a range of ~3–690 μg C per experiment, with maximal values at the shallower 140- and 300-m sites, and minimal values at the 1,850-m site. As a proportion of total processed label, bacterial uptake showed its greatest contribution (8–32%) at the 300-m site (Table 2).

Dominance of faunal groups—Before the monsoon, the metazoan macrofauna dominated OM uptake at the 140-m site and the 940-m site, being responsible for 87% and 98%, respectively, of total faunal uptake. In contrast, at the deeper 1,200- and 1,850-m sites and at the hypoxic 300-m site, the foraminifera were responsible for 70–100% of faunal OM uptake (Fig. 2).

The 140-m site showed a temporal switch in dominance of faunal OM uptake by different faunal groups under premonsoon and postmonsoon conditions. The decrease in oxygen concentration between April and October 2003 (from 92 ± 4 μmol L^{-1} to 5 ± 0.4 μmol L^{-1}; 2.1 to 0.1 ml L^{-1}) was accompanied by a decrease (from 83% to 43%) in the percentage of total faunal uptake accounted for by the metazoan macrofauna and a corresponding increase in that accounted for by the foraminifera. This was associated with a slight relative change in metazoan macrofaunal and foraminiferal biomass, although the metazoan macrofauna continued to dominate the biomass in both seasons (Fig. 2; Table 2). In addition, the percentage of total processed C accounted for by bacterial uptake increased from 5 ± 0.7 to 11 ± 5 between premonsoon and postmonsoon seasons.

In general there was a positive correlation between total C content (equivalent to animal size) and label content (ρ = 0.65 for all metazoan macrofauna, where the correlation coefficient ρ is equal to the covariance of two data sets divided by the product of their standard deviations), suggesting that taxa take up OM in proportion to their biomass (Fig. 3). However, there were slight deviations from this trend; in particular, the foraminifera at the 140-m site were responsible for a greater proportion of the total OM uptake than they contributed to total biomass (Fig. 3A).

As faunal samples were sorted by taxon, it was possible to observe which taxa consistently consumed a percentage of total OM uptake that was greater than their contribution to the total biomass. This is presented in Table 3 using a "feeding efficiency" parameter, equal to the percentage of total uptake accounted for by a taxon, minus its percentage

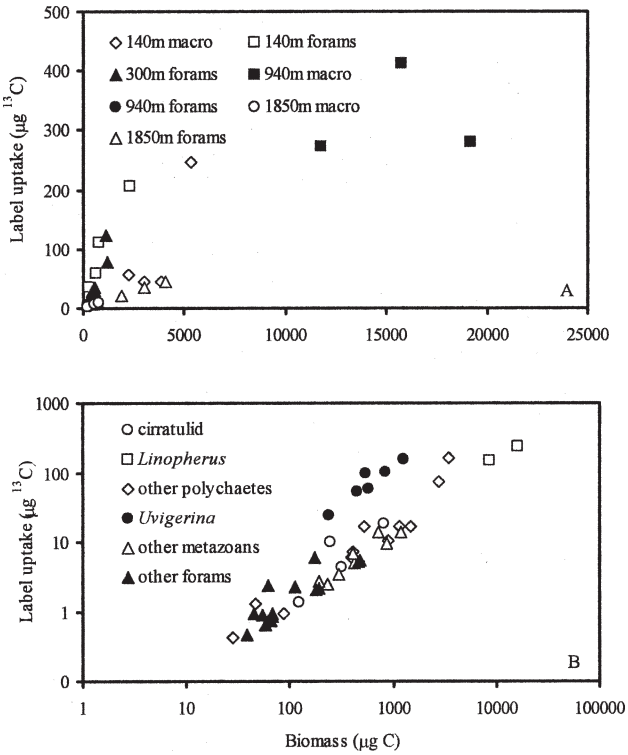

Fig. 3. Plots of label uptake versus sample biomass, illustrating their positive relationship. (A) Shows the total metazoan macrofaunal (macro) and foraminiferal values for all experiments (both seasons), with the site of each experiment indicated. (B) Shows data from all postmonsoon experiments for selected taxa; each data point represents the total biomass and uptake of a particular taxon in a single experiment. Note that *Uvigerina* ex gr. *semiornata* points consistently plot above the main trend.

contribution to the biomass (in a particular experiment, and within either the metazoan macrofauna or foraminifera as appropriate). Relatively efficient feeders (positive feeding efficiency) included a polychaete from the family Ampharetidae, the polychaete genus *Prionospio,* and the calcareous foraminiferan *U.* ex gr. *semiornata*. The amphinomid polychaete *Linopherus* sp., found at the 940- and 850-m sites, consumed less OM than predicted from its biomass (negative feeding efficiency). However, it was so dominant in terms of metazoan macrofaunal biomass at the 940-m site that it also dominated OM processing, despite its relatively inefficient feeding (Fig. 3B).

Discussion

This study took the approach of deliberately adding the same dose of C (685 ± 118 mg C m^{-2}) to each experiment in order to directly compare sites with different oxygen and OM availabilities and benthic communities. This raises the concern that trends in faunal response to OM addition among sites may have been forced by differences in C dosing relative to the natural availability of OM (Moodley et al. 2005). In principle, the stimulus would be more pronounced at OM-depleted sites; in fact the effect does not appear to have been significant. At all sites the added C was

Table 3. The feeding efficiencies (percentage of ^{13}C uptake accounted for by a taxon minus the percentage of biomass it contributed) of several taxa that showed clear tendencies to consume either more or less OM than would be expected considering their biomass. Figures are averages over all experiments (n = number of experiments) in which each taxon was found.

Taxon	Average feeding efficiency index	n
Linopherus sp.	−24±26	4
Ampharetid A	15±13	3
Prionospio sp.	55	1
Uvigerina ex gr. *semiornata*	23±8	9
Reophax sp.	−5±5	9

equivalent to 0.8 ± 0.3% of the organic C naturally present in the surface 1 cm of sediment. There was no systematic (or $\%C_{org}$-related) trend in C dosing between sites. The only experiment for which this was not the case was the postmonsoon experiment at the 1,850-m site, which received C equivalent to 4.7% of that naturally present in the top 1 cm of sediment. This experiment, instead of showing evidence of an increased stimulus, in fact showed the lowest faunal response (Table 2).

The practical challenges of working in a hypoxic environment (the need to monitor and control very low oxygen levels), together with the inaccessibility of the deep seafloor and the time required to extract fauna, led to limited replication of experiments. However, the use of two replicate megacores in shipboard incubations has allowed an assessment of variability introduced by benthic community patchiness. Relative standard deviations for total faunal uptake values (i.e., meiofauna plus metazoan macrofauna) averaged 42% and ranged up to 153%. These are considered reasonable, given the limited degree of replication and small sample sizes. Moreover, trends between sites were outside error limits and were maintained between seasons (Fig. 2; Table 2).

Numerous studies exist that have compared in situ with shipboard methods for quantifying benthic biogeochemical parameters. The majority have indicated that the former technique produces more reliable data (e.g., Glud et al. 1994; Hall et al. 2007). In addition, microorganisms have been shown to exhibit altered activity levels, cell lysis, and death as a result of decompression (e.g., Park and Clark 2002), and this raises the concern that biological OM processing in shipboard incubations might have been substantially different from that which occurs in situ. While this is an unfortunate trade-off for the increased replication and experimental control afforded by the use of a shipboard incubation system, the general lack of systematic differences between shipboard and lander-derived data in this study (Fig. 2; Table 2) suggests that any artifact associated with incubation at atmospheric pressure was small for the depths considered in this study (maximal depth of comparison was 940 m). This is supported by the fact that most studies that have reported differences between in situ and ex situ data were concerned with abyssal depths (2,000–4,000 m), considerably deeper than

any of the sites in this study. Therefore, while the employment of shipboard incubations may have produced some artifacts in the data, these do not appear to be large enough to exceed the other sources of error (e.g., patchiness), to adversely affect interpretation, or to outweigh the benefit of increased duration and replication of experiments.

It was necessary to freeze-dry the labeled algae in order to attach it to the ballast material. Such treatment has been used in the past to show that OM from physically disrupted cells is more easily available to the benthic community than that from whole cells (e.g., Thomas and Blair 2002). Thus freeze-drying the algae will have rendered the added C more available to the benthic community than the OM they usually receive. This is, unfortunately, a necessary evil of the approach used and is common to most experiments of this type (e.g., Moodley et al. 2002; Witte et al. 2003*a*). The effect was minimized by rinsing cells after freeze-drying.

Benthic communities and environmental factors—Variations in benthic community size and composition across the margin provide clues as to how factors such as oxygen and OM availability affect the benthos and its activities. The 140-, 1,200-, and 1,850-m sites between them display the commonly observed decrease in total and individual animal biomass with increasing depth that is usually ascribed to decreasing food availability and temperature (e.g., Rowe et al. 1991; Levin et al. 2000). The presence of the OMZ, however, produces profound deviations from this trend at the 300- and 940-m sites, resulting in the near absence of metazoan macrofauna from the former and a high-biomass metazoan macrofaunal community at the latter (Table 1), similar to those found at OMZ lower boundaries elsewhere (Levin 2003). Thus, it seems that where oxygen availability is just sufficient (~7 μmol L^{-1} [0.16 ml L^{-1}] at the 940-m site, compared with ~5 μmol L^{-1} [0.11 ml L^{-1}] at the 300-m site), metazoan macrofauna are able to take advantage of natural abundances of OM (Rosenberg 2001). Below this apparent threshold (between 5 and 7 μmol L^{-1}), they cannot survive, and foraminifera take over. These environmental controls on the benthic community are further supported by ^{13}C uptake data, as discussed later.

Faunal uptake in total C-processing budgets—Uptake of OM by the biota was observed at all sites (Fig. 2), suggesting that uptake and processing by metazoans and foraminifera are significant influences on the short-term fate of freshly deposited OM in continental margin sediments.

An average of 15% of added ^{13}C was processed by the benthic community over 2–5 d, in line with previous experiments of this duration in deep-water settings and with similar area-specific label addition (e.g., Moodley et al. 2002; Witte et al. 2003*b*). The partitioning of this processed label between the different pools (metazoan macrofaunal uptake, foraminiferal uptake, bacterial uptake, and total respiration) varied among sites (Table 2).

Where respiration dominated total processing (75–95%), such as at the 140- and 1,850-m sites, the pattern of biological processing of OM was comparable with the results of previous experiments from a wide range of environments, including an estuary, a deep Norwegian fjord (Witte et al. 2003*a*), the Porcupine Abyssal Plain (Witte et al. 2003*b*), the North Sea, and shallow and deep Mediterranean and Northeast Atlantic sites (Moodley et al. 2005). The 300-m site, where respiration accounted for ~50% of processed label and bacterial and foraminiferal uptake for the rest, was similar to a 2,170-m–deep site off Northwest Spain (Moodley et al. 2002). The large proportion of processed label in the metazoan macrofaunal uptake pool at the 940-m site was reminiscent of a Goban Spur continental shelf site (Heip et al. 2001). Between them, the previous studies cited here showed considerable variation in the relative importance of metazoan macrofaunal uptake, foraminiferal uptake, bacterial uptake, and total respiration in short-term C cycling. The experiments conducted in this study allow an assessment of factors that may drive some of that variation.

Factors affecting biological processing of organic matter—Oxygen: The switch in dominance of OM uptake from metazoan macrofauna to foraminifera, brought about by a dramatic seasonal drop in dissolved oxygen concentration (from 92 to 5.0 μmol L^{-1}; 2.1 to 0.11 ml L^{-1}) at the 140-m site (Fig. 2), indicates that the availability of oxygen exerts a strong control over the way OM is processed by benthic communities. The shift occurred in spite of the fact that metazoan macrofauna continued to dominate the biomass and seems to indicate that oxygen availability controls the faunal response to an OM pulse in a threshold manner. Notably, an oxygen effect is further indicated by the sharp contrast between the 940-m site (6.7–7.4 μmol L^{-1}), where metazoan macrofauna dominated the biomass and OM uptake, and the 300-m site (5.0 μmol L^{-1}), where foraminifera were dominant in both senses, but which only showed a difference in oxygen concentration of ~2 μmol L^{-1}. We therefore suggest the hypothesis that a threshold oxygen concentration exists below which OM processing tends to be dominated by protozoans. Although this hypothesis was initially prompted by the results of just three experiments at the 140-m site (one premonsoon and two postmonsoon), it is further defined and supported by results from three further experiments at the 940-m site, which allow us to narrow the range of oxygen concentrations in which the proposed threshold value must lie. The hypothesis is consistent with observations that such oxygen thresholds control species distributions across the upper and lower boundaries of OMZs (Levin et al. 2000; Levin 2003). Therefore, our finding extends the influence of the control by oxygen availability to the functioning as well as the occurrence of organisms.

The proposed threshold probably lies between dissolved oxygen concentrations 5.0 μmol L^{-1} (0.11 ml L^{-1}; the postmonsoon value at the 140-m site where foraminifera dominated) and 6.7–7.4 μmol L^{-1} (0.15–0.17 ml L^{-1}, the premonsoon and postmonsoon values, respectively, at the 940-m site, and the lowest bottom-water oxygen concentrations at which metazoan macrofauna dominated). However, the threshold is probably taxon specific (Levin et al. 2000), and could vary in other areas. Below the threshold, the metazoan macrofauna are unable to function effectively

and are out-competed by the foraminifera and bacteria, which then dominate OM uptake. This is reflected by the extreme scarcity of metazoan macrofauna and the dominance of foraminifera at the 300-m site.

The oxygen threshold hypothesis is based on somewhat limited evidence and requires further testing. ^{13}C tracer experiments in which an oxystat system is used to artificially lower and/or raise oxygen concentrations in samples from sites showing steep oxygen gradients (e.g., OMZ boundaries) might be particularly instructive.

There is also evidence that low-oxygen conditions inhibit the functioning of foraminifera. In the postmonsoon season, foraminiferal OM uptake was lower at the intensely hypoxic 300-m site than at the 140-m site, despite similar foraminiferal communities and sufficient OM availability (*see below*) and temperature conditions at the 300-m site. Thus, lack of oxygen suppresses OM processing in all fauna but has a stronger, threshold effect on the efficiency of metazoan macrofaunal activity. However, the threshold may not be identical on all hypoxic margins, since it is probably specific to particular metazoan taxa, and macrofaunal composition may vary between OMZs (Levin 2003).

The general suppression of faunal activity by low oxygen availability is further illustrated by the fact that bacterial uptake showed its greatest contribution to total OM processing at the 300-m site and was the only form of biological C processing that did not show considerable inhibition under low-oxygen conditions. This is relatively unsurprising, since bacteria are the group most able to tolerate hypoxia and anoxia.

Availability of high-quality OM—Faunal communities from sites where higher quality OM (as indicated by higher values of DI, Table 1) was naturally more abundant (the 140-, 850-, 940-, and 1,000-m sites) were better able to respond to an artificial pulse of fresh algal detritus than where it was scarce (the 1,850-m site, Table 1; Fig. 2). In addition, the increase in total uptake in 5-d experiments at the 300- and 940-m sites after the monsoon (and the resultant pulse of OM, Fig. 2) suggests that a seasonal OM pulse could have had a priming effect on these benthic communities, which responded by shifting into a more active and efficient feeding mode. Furthermore, the 940-m site exhibited higher quality and more abundant OM than the 140-m site and had a lower bottom-water dissolved oxygen concentration (premonsoon only, Table 1), but total OM uptake was, on average, a factor of two greater than at the 140-m site (Fig. 2).

Size and abundance of faunal classes—The positive correlation observed between organism biomass and label uptake could partially result from the presence of large quantities of labeled algal matter in metazoan macrofaunal guts or foraminiferal vacuoles. Nonetheless, it still implies that larger individuals and more abundant species played greater roles in OM processing. Thus, the makeup of the benthic community exerts some control over the scale and pattern of its processing of OM. Middelburg et al. (2000) have previously observed this control of community structure on OM processing, when consumption of ^{13}C-labeled benthic algae in an estuarine environment occurred in proportion to consumer biomass.

Those sites where metazoan macrofauna dominated the biomass (the 140-, 850-, 940-, and 1,000-m sites) showed significantly greater (t-test, $t = 5.7$, df = 18, $p = 2 \times 10^{-5}$) total label uptake than at the 300-, 1,200-, and 1,850-m sites, where foraminifera dominated (Fig. 2). The 850-, 940-, and 1,000-m sites in particular exhibited especially high metazoan macrofaunal biomass, above-threshold oxygen levels, and more abundant high-quality OM, and hence showed the highest label uptake values by a considerable margin (Fig. 2).

Temperature—The overall rate of biological C processing (dominated by respiration) and absolute bacterial uptake showed a considerable decrease from the 140-m site to the 1,200- and 1,850-m sites (data not shown). This is linked to the reduction in bottom-water temperatures (~23°C to 4°C) across the margin and is a result of the previously observed temperature dependence of (mostly bacterial) respiration (Moodley et al. 2005).

Relative importance of metazoan macrofauna and foraminifera in OM uptake—Metazoan macrofauna frequently dominated OM uptake in this study (Fig. 2)—particularly at lower OMZ boundary sites. Previous isotope labeling studies in shallow coastal and deep-sea environments (Moodley et al. 2005) have concluded that the bacteria and foraminifera are responsible for a considerably greater percentage of OM uptake than the metazoan macrofauna (Moodley et al. 2000, 2002). The dominance of OM uptake by metazoan macrofauna at our lower OMZ boundary sites is likely to have been due to the unusual high-density and high-dominance metazoan macrofaunal communities that were present. Notably, dominance of metazoan macrofauna over foraminiferans and bacteria in short-term OM uptake has also been observed in selected non-OMZ continental shelf and deep-sea settings (Witte et al. 2003*a*,*b*). At the 140- and 940-m sites, if relatively conservative estimates of polychaete gut turnover times and feeding rates are assumed (18 h, Ahrens et al. 2001, and feeding for 50% of the time, Masson et al. 1995), the metazoan macrofauna can be expected to have processed 20–30% of the added C over 2–5 d. This study therefore supports the suggestion that the metazoan macrofauna, despite their relatively small contribution toward total biomass, can be a major conduit for freshly deposited OM (Blair et al. 1996; Lauerman et al. 1997; Miller et al. 2000).

Dominance of OM uptake by metazoan macrofauna as opposed to foraminifera has profound implications for its short-term fate. Metazoan macrofauna have the potential for active location and selective uptake of food (Fauchald and Jumars 1979) and for significant vertical transport of OM (over 10 cm depth or more, e.g., Levin et al. 1997), making it available to subsurface fauna and bacteria and either burying it or reexposing it to oxygen. In contrast, in eutrophic, hypoxic settings, most foraminifera are forced to the upper 1 cm of sediment (Jorissen et al. 1995) and may only mix the top 0.5 cm of sediment (Nomaki et al. 2005*a*). It has also been suggested that the foraminifera consume

more degraded OM than the metazoan macrofauna (Witte et al. 2003*b*), though significant foraminiferal label uptake was observed after 2–5 d in this study, and this supports observations that some deep-sea foraminifera taxa are capable of selective feeding and of rapidly colonizing and utilizing freshly deposited OM (Gooday 1988; Kitazato et al. 2000; Nomaki et al. 2005*b*).

Feeding efficiency and feeding guilds—Observations of the relative feeding efficiencies of abundant taxa (Table 3) must be interpreted with care, since they could result from species-specific variation in gut volume relative to body size. However, they are nonetheless consistent with previous findings on the feeding preferences of the taxa concerned.

Although there have been a limited number of previous studies, covering a few mainly shallow-water species of each family (e.g., Carrasco and Carbajal 1998), it is highly likely that ampharetids and spionids (to which *Prionospio* belongs) are surface-deposit feeders, which actively select fresh algal detritus. This is consistent with their observed relatively high efficiency at ingesting ^{13}C-labeled algae (Blair et al. 1996; Levin et al. 1999; Aberle and Witte 2003). Conversely, amphinomids (such as *Linopherus* sp.) living on hard substrates are often carnivorous or in the deep sea more likely are scavengers (Fauchald and Jumars 1979 and references therein). Visual observations of some *Linopherus* sp. guts full of algae suggest that it feeds in an opportunistic way, and this, together with its natural stable isotopic composition (R.M. Jeffreys unpubl. data), suggests it is better described as an omnivore, perhaps consistent with its reduced efficiency at ingesting ^{13}C-labeled algae (Table 3).

Lipid biomarkers suggest that the calcareous foraminiferan *U.* ex gr. *semiornata* rapidly consumed freshly deposited OM (Larkin 2006). An herbivorous diet was also observed by Nomaki et al. (2005*a,b*) in the congeneric species *Uvigerina akitaensis*. Other studies have found that, in general terms, calcareous foraminifera have a stronger preference for algal food sources than agglutinated foraminifera such as *Reophax,* which was observed here (Table 3) to feed relatively inefficiently (Gooday 2003; Larkin 2006).

OM remineralization—The dominant C sink in most benthic isotopic labeling studies is respired CO_2 (e.g., Moodley et al. 2002, 2005), and the traditional view is that, since the bacteria generally constitute around 95% of the total sediment biomass, they must also dominate remineralization (Witte et al. 2003*a*; Moodley et al. 2005). This was probably true at several sites in this study, particularly the hypoxic 300-m site where bacterial uptake showed its greatest contribution to total C processing (Table 2). Heip et al. (2001), working along a transect of the Goban Spur, however, divided responsibility for sediment community oxygen consumption (SCOC) between faunal groups using biological survey data and calculated respiration rates for megafauna, macrofauna, and meiofauna (Mahaut et al. 1995). While it should be noted that the application of theoretical individual animal respiration rates is problematic, their study revealed that on the continental shelf and upper slope, although the bacteria vastly dominated the biomass, the metazoan macrofauna were responsible for up to 50% of SCOC. At lower slope and abyssal depths this dropped to 16%. At the 940-m site in the present study the amount of labeled C taken up by the metazoan macrofauna was usually similar to the total amount respired. It seems likely that metazoan macrofauna may also account for a relatively large proportion (20–50%) of total C remineralization at this site.

We show that uptake by macrofaunal metazoans and uptake by foraminifera were important processes determining the short-term fate of freshly deposited OM across the Pakistan margin OMZ. The roles of metazoan macrofauna, macrofauna-sized foraminifera, and bacteria in C cycling varied among sites and were influenced by O_2 availability and broad community composition. In particular, we propose the hypothesis that the availability of oxygen controls the relative dominance of metazoan macrofauna and foraminifera in a threshold manner. Also, faunal uptake of OM is maximized at sites with abundant and higher quality OM and a relatively large metazoan macrofaunal biomass. It can therefore be expected that the variation in previously observed C-processing patterns could be related to the O_2 and OM availability at study sites and the corresponding variation in benthic community composition.

We predict that in very low-O_2 environments and in relatively OM-poor, oxygenated environments, foraminifera will tend to dominate OM uptake and preliminary processing, whereas at selected OM-rich sites with slightly higher O_2 concentrations (such as at lower boundaries of OMZs), metazoan macrofauna will play a primary role in OM uptake and cycling. Global warming and eutrophication may drive the future expansion of natural, low-O_2 environments in fjords, estuaries, coastal waters, and on the continental slope (Helly and Levin 2004). Our results suggest that as hypoxia spreads, foraminifera may take precedence over metazoan macrofauna and come to dominate OM processing, with possible effects for overall OM cycling and burial, and also for the transfer of C up the food chain.

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