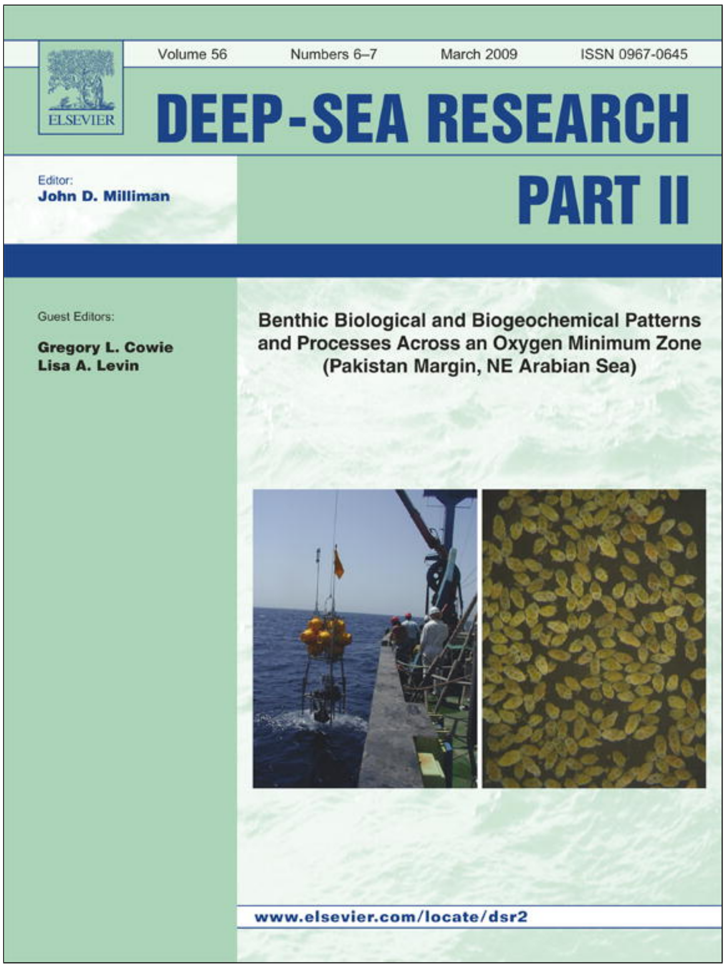

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The short-term fate of organic carbon in marine sediments: Comparing the Pakistan margin to other regions

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ABSTRACT

Pulse-chase experiments with isotopically labelled phytodetritus conducted across the Pakistan margin reveal that the impact of biological activities on benthic C-cycling varies markedly among sites exhibiting different seafloor conditions. In this study, patterns of biological C-processing across the Pakistan margin oxygen minimum zone (OMZ) are compared with those observed in previous tracer studies. Variations in site environmental conditions are proposed to explain the considerable variations in C-processing patterns among this and previous studies. Three categories of C-processing pattern are identified: (1) respiration dominated, where respiration accounts for $>75\%$ of biological C-processing, and uptake by metazoan macrofauna, foraminifera and bacteria are relatively minor processes. These sites tend to show several (although not necessarily all) of the properties of being cold and deep, and having low inputs of organic carbon to the sediment and relatively low-biomass metazoan macrofaunal communities; (2) active faunal uptake, where respiration accounts for $<75\%$, and metazoan macrofaunal, foraminiferal and bacterial uptake each account for 10–25% of biological C-processing. This type is further split into metazoan macrofaunal- and foraminiferal-dominated situations, dictated by oxygen availability; and (3) metazoan macrofaunal uptake dominated, characterised by metazoan macrofaunal uptake accounting for ~50% of biological C-processing, due to unusually large biomasses of the phytodetritus-consuming animals. Total respiration rates (of added C) on the Pakistan margin fell within the range of rates measured elsewhere in the deep sea ($\sim$0.1–2.8 mg C m^{-2} h^{-1}), and seem to be dominantly controlled by seafloor temperature. Rates of metazoan macrofaunal uptake of organic matter (OM) on the Pakistan margin are larger than those in most other studies, and this is attributed to the large and active metazoan macrofaunal communities in the lower OMZ, characteristic of OMZ boundaries. Finally, biological mixing of Pakistan margin sediments was reduced compared to that observed in comparable tracer studies on other margins. This probably reflects faunal feeding and burrowing strategies consistent with low oxygen concentrations and a relatively abundant supply of sedimentary OM.

1. Introduction

The least-well understood aspect of C-cycling and burial in marine sediments is the complex and highly variable role played by benthic communities. Through their burrowing, ventilation, digestion and metabolic activities, benthic organisms influence organic matter (OM) re-mineralisation and burial in a wide variety of ways. The effects of these processes have been investigated in detail using microcosm experiments to study single taxa and processes (e.g., Sun et al., 1999; Thomas and Blair, 2002), but the most holistic pictures are provided by whole-community stable isotope pulse-chase experiments (e.g., Moodley et al., 2002, 2005; Witte et al., 2003a). These powerful experiments utilise the fact that in many areas, the majority of OM input to the seafloor occurs during pulses of fresh phytodetritus following phytoplankton blooms (Lampitt et al., 2001), rather than as a constant slow supply of degraded matter. Experiments that mimic these OM pulses are therefore conducted by adding ^{13}C-enriched OM (algal detritus) to intact sediments, and tracing the isotopic label into pools representative of different biological processes. Thus uptake and/or incorporation of C by micro-organisms, foraminifera and metazoans of various sizes, together

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with total community C re-mineralisation are quantified and compared.

Whole-community ^{13}C-labelling studies have been conducted at a range of sites representing several types of benthic environments, from the deep Porcupine Abyssal Plain (Witte et al., 2003a, b) to an intertidal site in the Scheldt estuary (Moodley et al., 2005). Both similarities and differences exist between the patterns of C-processing observed in pulse-chase experiments that have been conducted to date. For example, while some studies agree that uptake and respiration by foraminifera and bacteria are, in the long term, the dominant processes (Moodley et al., 2002; Witte et al., 2003b), it also has been shown that metazoan macrofaunal ingestion and respiration can equal microbial respiration in magnitude (Woulds et al., 2007). Environmental and biotic features of sites, including oxygen availability, natural OM supply and benthic community composition, have been shown to influence the way OM is processed by organisms on the seafloor (Blair et al., 2001; Woulds et al., 2007), and this should now make it possible to explain some of the previously observed variability. Comparisons between studies, however, are still hampered by the fact that not all C-processing pathways are considered in most studies (Moodley et al., 2005).

Here we compare the C-processing patterns revealed by ^{13}C pulse-chase experiments conducted along oxygen, temperature, and OM gradients found across the Pakistan margin, to those found in previous studies.

The Pakistan margin exhibits a permanent and pronounced oxygen minimum zone (OMZ) ($<9\,\mu$M between ~150 and 1000 m water depth). Low-oxygen conditions are roughly co-incident with maximal values of sediment OM quantity and quality (maximal value = 3.4 wt% OM (%C$_{org}$), Cowie et al., 1999). Oxygen gradients are also accompanied by variations in benthic community structure, with metazoan macrofauna abundant above and below the OMZ (Hughes et al., 2009). Within the OMZ the community is dominated by foraminifera with only a very few polychaetes surviving (Gooday et al., 2009). We show that the steep environmental gradients in conditions across the Pakistan margin produce sites exhibiting biological C-processing patterns similar to those observed in many previous experiments, over a wide range of environment types. This leads us to propose a short-term C-cycling classification system for benthic marine environments, based on fates of ^{13}C-labelled phytodetritus. Specific elements of interest include the relative importance of rapid respiration vs. incorporation into tissues of biota and the organisational level (protozoan vs. metazoan) of major faunal consumers. It is hoped that this approach will facilitate prediction generation for future studies, and aid the extrapolation of the results of ^{13}C pulse-chase experiments up to regional and global scales.

2. Methods

Study site conditions as well as experimental and analytical techniques are described in greater detail elsewhere (Woulds et al., 2007, Cowie et al., 2009).

Briefly, stable isotope pulse-chase experiments were conducted at sites spanning the Pakistan margin OMZ. They ranged in depth from 140 m, where OM abundance was mid-range (1.4 wt%), through 300 m in the OMZ core (dissolved oxygen $<5\,\mu$M) and 850–1000 m near the OMZ lower boundary (6–7 μM) and OM peak (3.3 wt%), to 1200 m (15 μM) and finally 1850 m, which showed minimal OM (1.2 wt%) and maximal O_2 (80 μM) availabilities. Metazoan macrofaunal abundance was maximal at the 140-m site, but biomass showed a marked maximum in the lower OMZ (at the 850 and 940 m sites, Hughes et al., 2009; Levin et al., 2009). Metazoan macrofauna were rare in the core of the OMZ (300 m). Foraminifera were present at all sites, with higher-biomass, calcareous-dominated communities at shallower sites; and lower-biomass, agglutinated-taxa dominated communities at deeper sites (Gooday et al., 2009).

The study was conducted in the inter-monsoon period immediately preceding, and in the period just after the summer monsoon of 2003, in order to assess any seasonal variation in the system in response to monsoon-induced upwelling, productivity and flux of OM to the sediment. These two seasons will be referred to as inter- and post-monsoon, respectively. The only marked change in site conditions (temperature, dissolved oxygen, sediment %C$_{org}$) between these two seasons was a drop in dissolved oxygen concentration at the 140 m site, from ~90 to ~5 μM. The biomass of various faunal classes did not vary greatly between seasons (Gooday et al., 2009, and references therein).

Experiments were conducted on board the ship using recovered cores (10 cm i.d.), and also in-situ (at the sediment-water interface) using a benthic chamber lander (30 × 30 cm). Freeze-dried diatoms (*Thalassiosira*) labelled with ^{13}C (~80%) were added to the sediment-water interface of shipboard cores at a dose of ~700 mg C m^{-2} (360 mg C m^{-2} for lander experiments). Cores were then sealed and incubated in the dark, at seafloor temperature, with gentle stirring for either 2 or 5 days. Core-top seals were designed such that label introduction and sample withdrawal through the cap was possible. In addition, ambient dissolved oxygen levels were maintained by pumping core-top water through ‘oxystat’ gills, which in turn were submerged in a reservoir maintained at the ambient seafloor concentration (Schwartz, unpublished). At five time points during each experiment the overlying water was sampled for dissolved inorganic carbon (DIC) and δ^{13}C of DIC. Lander experiments commenced when the chamber lid closed, and lasted 2.5 days. As with shipboard incubations the chamber water was stirred, and the oxygen concentration was maintained by pumping chamber water through an ‘oxystat’ gill in contact with the ambient bottom water. Samples were withdrawn during lander experiments by a pre-programmed array of syringes. *In situ* experiments were terminated when a shovel was closed beneath the chamber, and the lander returned to the surface. Differences were observed between the results from core incubations and lander experiments. However, these were not systematic, and between-site trends were maintained. For a more complete discussion of this issue see Woulds et al. (2007).

At the end of experiments, cores were sectioned (the lander box core was sub-sampled using short 10-cm i.d. tubes). Each section was divided in half. One half was dedicated to extraction of metazoan macrofauna ($>300\,\mu$m) and macrofaunal foraminifera. This sediment was immediately wet sieved, and residues from 300-, 150- and 63-μm sieves were retained. Metazoan macrofauna were extracted from all of the >300-μm residues, down to 10 cm depth. Foraminifera were extracted from >300-μm residues from the top 1 cm of the sediment. Some 150–300 μm residues from the top 1 cm were sorted for foraminifera, and these samples comprise ~10% of the foraminiferal biomass in each experiment. The other half of each sediment slice was used for extraction of porewaters and to provide samples of the sediment. Metazoan meiofauna were very rare, thus their role in C-processing could not be quantified, and they will not be considered further.

For the purposes of replication, shipboard experiments were conducted simultaneously on duplicate cores. Due to sample limitation, data from the replicate cores were pooled when reported.

For isotopic analyses, soft-bodied fauna, and hard-shelled fauna and sediment (10–30 mg), were de-carbonated by addition of 0.1 and 6 N HCl, respectively. They were analysed for their ^{13}C

Table 1
Sources and site details of previous ^{13}C pulse-chase experiments to which Pakistan margin experiments will be compared, and site detail of Pakistan margin sites.

Study	Site	Length (h)	Depth (m)	Temp (°C)	Organic C in surface 1 cm ($g\,C\,m^{-2}$)	Metazoan macrofaunal biomass ($g\,C\,m^{-2}$)	Foraminiferal biomass ($g\,C\,m^{-2}$)	Bacterial biomass ($g\,C\,m^{-2}$)
Buhring et al. (2006b)	Cretan Sea	36	1540	>13	–	0.06	–	0.4
Moodley et al. (2005)	N Aegean	24	102	14	31	0.07	–	0.52
	E Med.	24	3859	14	17	0.004	–	0.31
	NE Atlantic	24	2170	4	34	0.14	–	0.31
	North Sea	24	37	16	52	0.73	–	2.30
	Scheldt estuary 2	24	Intertidal	18	66	1.36	–	1.26
Witte et al., 2003a	Sognefjord	72	1265	7	–	0.25	–	8.5
Witte et al., 2003b	Porcupine Abyssal Plain	552	4800	<4	2	0.12	0.015	2.5
Heip et al. (2001)	Goban Spur	See caption	208–1034	11–4	4–27	1.07–0.88	0.016–0.71*	3.62–2.88
			2182		39	0.14	0.015	2.22
Moodley et al. (2000)	Scheldt estuary 1	6	Intertidal	10	87	(17111 ind. m^{-2})	1.23 (+1.39 metazoan meiofauna)	4.3–5.8
Buhring et al. (2006a)	German Bight	30	19	9	–	4.9	–	–
This study	140 m	44–118	140	20	7	0.11 ± 0.05	0.13 ± 0.1	1.1 ± 0.4
	300 m	60–155	300	15	13	Unmeasurable	0.10 ± 0.04	1.0 ± 0.3
	940 m	48–113	940	9	18	0.91 ± 0.61	0.07 ± 0.03	0.7 ± 0.3
	1200 m	114	1200	7	17	0.06 ± 0.09	0.04 ± –	–
	1850 m	48–117	1850	4	7	0.11 ± 0.15	0.38 ± 0.14	0.3 ± 0.2

The Heip et al. (2001) study involved theoretical division of responsibility for sediment community oxygen consumption (SCOC) between faunal classes, not a ^{13}C pulse-chase experiment. Temperatures were not published for the Porcupine Abyssal Plain or the Goban Spur at 2182-m, so these values are estimated from data for nearby sites in the same or different studies. Sediment $g\,C\,m^{-2}$ data for the Porcupine Abyssal Plain and the Pakistan margin sites is estimated from weight percentage organic carbon data, assuming a surface porosity of 80% and a dry density of $2.65\,g\,cm^{-3}$. Metazoan macrofaunal biomasses for the Pakistan margin and German Bight sites are estimated from wet weights (averages from five 10-cm diameter cores) given in Hughes et al. (2009) and Buhring et al. (2006a), respectively, assuming that the dry weight is 7.8% of the wet weight, and that dry biomass is 25.6 wt% C (average of measurements on a sub-set of Pakistan margin metazoan macrofauna). Foraminiferal biomass data for the Pakistan margin is derived only from the samples extracted from ^{13}C labelling experiments, and therefore do not represent fully replicated estimates * indicates total meiofauna (not just foraminifera), – indicates data not available.

content on a Europa Scientific (Crew, UK) Tracermass isotope ratio mass spectrometer (IRMS) with a Roboprep Dumas combustion sample converter, and quantified against appropriately sized acetanillide standards. Where possible sample sizes were tailored to yield between 200 and 400 μg of C, however it was also possible to analyse samples as small as 0.1 mg of dry metazoan macrofaunal tissue. Foraminiferal samples tended to contain 20 or more individuals. Replicate analyses produced an average relative standard deviation of 4.6% for $\%C_{org}$ and a standard deviation of 0.7‰ for $\delta^{13}C$ ($n = 27$). Acidified blanks did not contain measurable amounts of C. Porewater and overlying water samples were analysed for δ^{13}DIC as described by Moodley et al. (2000) in order to quantify respiration of added ^{13}C. Sediments were also analysed for the quantity and isotopic makeup of bacterial phospholipid fatty acids as described by Boschker and Middelburg (2002), in order to quantify incorporation of label into the bacterial biomass. The compounds isoC14:0, isoC15:0 and anteisoC15:0 were used as bacterial biomarkers. It was assumed that these represented 12% of all bacterial PLFAs, which in turn comprised 5.6% of total bacterial C.

The results of these experiments are compared to several other previously published similar studies. The studies and sites considered in the comparison are shown in Table 1.

3. Results

3.1. C-processing patterns on the Pakistan margin

On average $15\pm9\%$ of the added label was processed by the benthic community over 2–5 days, and was recovered from the bacterial, foraminiferal or metazoan macrofaunal biomass, or from the CO_2 dissolved in porewater or overlying water. The percentage of added C that was processed tended to be maximal at the 140-m site and minimal at the 1200- and 1850-m sites. The 300-m site showed slightly lower percentages than might be expected, probably as a result of low oxygen concentrations; and the 940- and 1000-m sites showed higher percentages, possibly due to their high-biomass metazoan macrofaunal communities (Table 2). Biologically processed ^{13}C did not account for the total observed loss of ^{13}C from the particulate ^{13}C pool, which is unsurprising as the production of ^{13}C-labelled dissolved organic carbon was not measured. Furthermore, these types of experiment tend not to show 100% label recovery (Woulds et al., 2007).

The pattern of biological C-processing varied among sites (Table 2, Fig. 1). Respiration tended to be the dominant fate of processed C at most sites, generally accounting for 40–95%. The other three processes varied considerably in relative dominance, with bacterial, foraminiferal and metazoan macrofaunal uptake exhibiting typical ranges of 2–32%, 1–17% and 0–46%, respectively.

Total respiration most dominated C-processing at the 1850- and 1200-m sites, where it accounted for 85–95%. At these sites foraminiferal uptake and bacterial uptake accounted for most of the remainder (1–10%), and metazoan macrofaunal uptake was minor (1–4%). In stark contrast, respiration of ^{13}C-labelled algae was least dominant in the lower OMZ (850, 940 and 1000 m), where it accounted for only 16–55%. Most of the remainder was accounted for by metazoan macrofaunal uptake (42–83%), and foraminiferal and bacterial uptake were minor processes (typically 1–3%, although bacterial uptake was 14% in one instance). Respiration accounted for similar proportions of total C-processing at the 140- and 300-m sites (55–75%). The main difference between these sites was that metazoan macrofaunal uptake occurred at the 140-m site (5–17%) but not at the 300-m site. Bacterial uptake was generally greatest at the 300-m site (8–32%, compared to 0–11% at the 140-m site). In the *in situ* experiment at the 140-m site there appeared to be almost no bacterial uptake. This surprising result is likely to be due to imperfect recovery of the sediment-water interface by the benthic lander; and therefore loss of the part of the sediment that typically contains most of the microbial community (Table 2, Fig. 1).

Table 2
Experimental details and the percentages of total biologically processed label recovered from the different processed pools in Pakistan margin experiments.

Season	Site depth (m)	Duration (h)	Dose (mg C m^{-2})	% of total label processed	Percentages of total processed label in processed pools			
					Total respiration (all classes) (%)	Uptake by bacteria (%)	Uptake by foraminifera (%)	Uptake by metazoan macrofauna (%)
Inter	140	68	749	34±1	75±1	5±0.7	3±1	17±2
Post	140	44	632	21±1	69±2	11±5	13±4	7±5
Post	140	118	620	31±1	72±1	7±2	16±1	5±2
Post	140	60 *in situ*	398	14	74	0.3±0.6	15±4	11±3
Inter	300	61	633	5±0.2	75±9.8	8±0.9	17±4	0±0
Inter	300	127	667	7	74±29	13±5	13±1	0±0
Post	300	58	628	9±2	71±	22±23	9±1	0±0
Post	300	155	636	21	55±0.4	32±16	13±0.5	0±0
Post	300	60 *in situ*	398	4	14±	13±7	73±6	0±0
Inter	850	46	973	9	55±3	3±1	No data	42±
Inter	940	112	659	16±2	50±5	2±2	1.3±0.9	46±16
Post	940	113	637	23	38±14	14	0.7±0.0	47±8
Post	940	48 *in situ*	288	16	16	0.5±0.4	1±0	83±1
Inter	1000	57	650	21	41±	2±	No data	57±2
Inter	1200	114	637	5	95±33	2±0	2±1	1±0.5
Inter	1850	48	653	2	28±5	No data	68±5	4±1
Inter	1850	117	974	6±0.3	85±3	2±1	10±2	1.9±0.9
Post	1850	86	1805	13	94±1	0.9	4±0	2±1

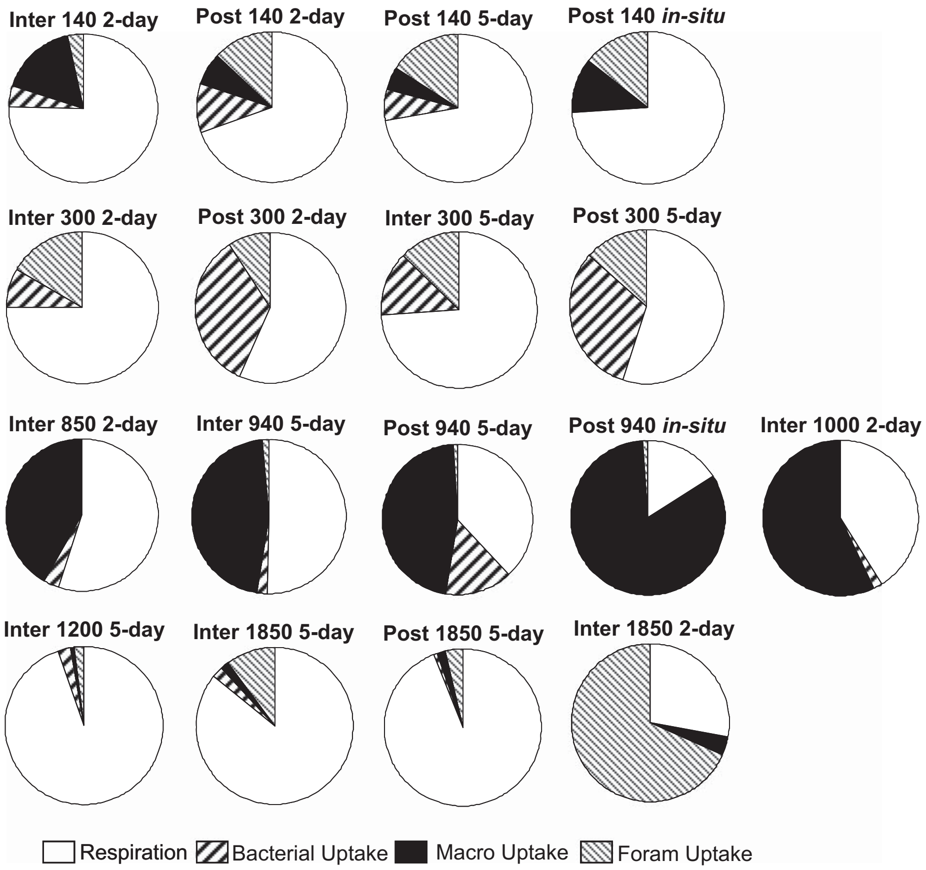

Fig. 1. The partitioning of C among processed pools on the Pakistan margin.

3.2. *Process rates*

The rates of respiration and uptake by metazoan macrofauna were calculated for each experiment by simply dividing the (area-normalised) total amount of C subject to each process by the experiment duration. The calculated rates are therefore averaged over the entire experiment duration, and it should be noted that rates will have altered systematically during experiments.

Respiration rates of added C ranged between ~0.1 and 2.8 mg C m^{-2} d^{-1}; they were maximal at the 140-m site, and

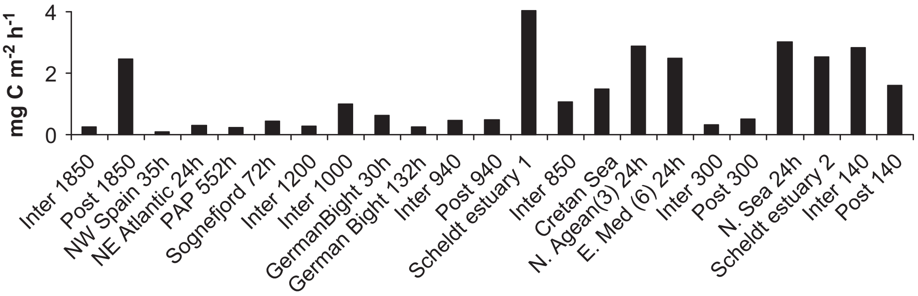

Fig. 2. Respiration rates of added C for Pakistan margin sites and sites of previous studies, arranged in order of increasing temperature from left to right. Note that the value for the Scheldt estuary 1 site was 7.8 mg C m^{-2} h^{-1}, and so is not fully displayed on this scale. For sources of data from previous studies see Table 1.

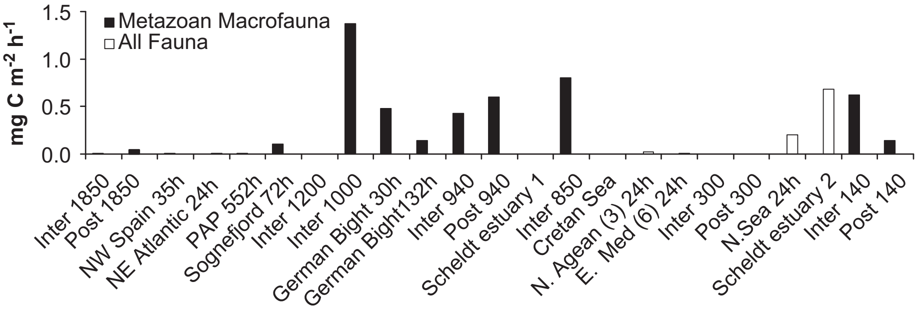

Fig. 3. Metazoan macrofaunal uptake rates for Pakistan margin sites and sites of previous studies, arranged in order of increasing site temperature (left to right). For sources of data from previous studies see Table 1. Where data is for 'all fauna' this includes metazoan macrofauna, meiofauna and foraminifera.

minimal at the 1200- and 1850-m sites (Fig. 2). Metazoan macrofaunal uptake rates were maximal at the 850-, 940- and 1000-m sites, and at the 140-m site in the pre-monsoon season, and were otherwise very low. The full range was 0–1.4 mg C m^{-2} d^{-1} (Fig. 3).

3.3. Sediment mixing

Transport of labelled algae downcore was rarely measurable, once experimental artefacts were accounted for. Time-zero control cores (cores that were sectioned immediately after addition of labelled algae) showed background δ^{13}C values of ∼−20‰ below depths of 1.25 cm (Fig. 4). Downcore δ^{13}C values in excess of this background were only seen in experiments at the 140- and 940-m sites (data not available for the 850- and 1000-m sites). Here, sub-surface δ^{13}C peaks between ∼−10 and −16‰ were present, never deeper than 2.75 cm. In one exceptional case a sub-surface peak (at 2.5 cm depth) in an experiment at the 940-m site reached a value of +107‰ (Fig. 4). At the other sites, δ^{13}C profiles were indistinguishable from time-zero controls, except for a single sub-surface peak value of −11‰ at 2.5 cm depth at the 1850-m site (Fig. 4).

4. Discussion

The pattern of biological C-processing varied considerably across the Pakistan margin, and this can be linked to site conditions (Fig. 1).

The 1200- and 1850-m sites showed foraminiferal and bacterial uptake rates that were comparable to or slightly greater than macrofaunal uptake, with rapid respiration of labelled carbon being ultimately favoured. If it is assumed that the bulk of the respiration at these sites was performed by bacteria (Moodley et al., 2002), this is consistent with the common observation that smaller organisms dominate benthic communities at deeper sites, usually attributed to their relatively limited food supply (e.g. Rowe et al., 1991).

Biological C-processing at the 140-m site was characterised by a greater proportion of 'faunal' (metazoan macrofauna plus foraminifera) uptake relative to respiration, consistent with the greater faunal biomass and food availability there (Table 1).

At the 300-m site, low oxygen levels resulted in a near absence of metazoan macrofauna (Hughes et al., 2009) thus metazoan macrofaunal uptake was an extremely minor process (unmeasurable, Fig. 1), and C uptake was accomplished by the foraminifera and bacteria.

The lower OMZ sites were home to relatively high-biomass metazoan macrofaunal communities, and this led to a dominance of C-processing by metazoan macrofaunal uptake (which in some instances exceeded total respiration in magnitude). The presence of this high macrofaunal biomass is thought to be an OMZ edge effect (Levin, 2003), which occurs where sediments relatively rich in un-degraded (bioavailable) OM occur at oxygen levels just tolerable to metazoan macrofauna.

4.1. C-processing categories

Many of the patterns of biological C-processing observed in this study are similar to those seen in previous studies (Table 1), and this has led us to propose the following categories (Fig. 5).

The first category is termed 'respiration dominated', and most sites that fall into it are from lower slope and abyssal depths (Fig. 5). They include the Pakistan margin 1200 and 1850-m sites, and sites from the E Mediterranean, N Aegean, NE Atlantic and Porcupine Abyssal Plain. In this category respiration, accounts for >75% of the total biological C-processing. Metazoan macrofaunal, foraminiferal and bacterial uptake are all relatively minor processes, accounting for <10% each. Most of these sites show relatively great depths and low bottom-water temperatures; however, the N Aegean site is relatively warm and shallow

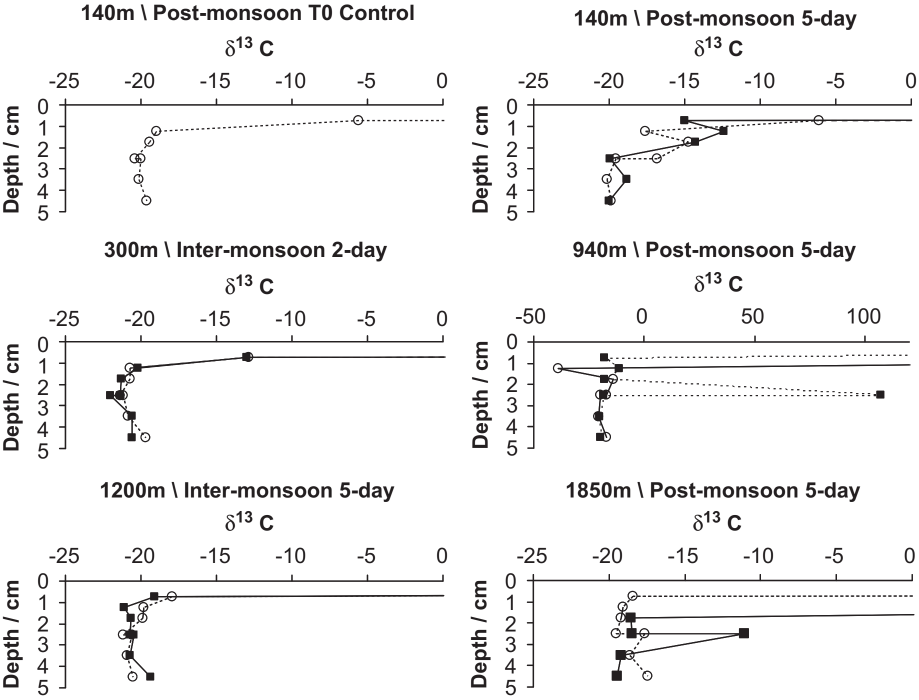

Fig. 4. Typical downcore profiles of sediment δ^{13}C at the end of experiments. Note the different scale in the 940-m/post-monsoon 5-day plot. Where two sets of data points are shown they represent the two replicate cores of the experiment in question. The average standard deviation of δ^{13}C values is 0.7‰, and error bars are smaller than data points.

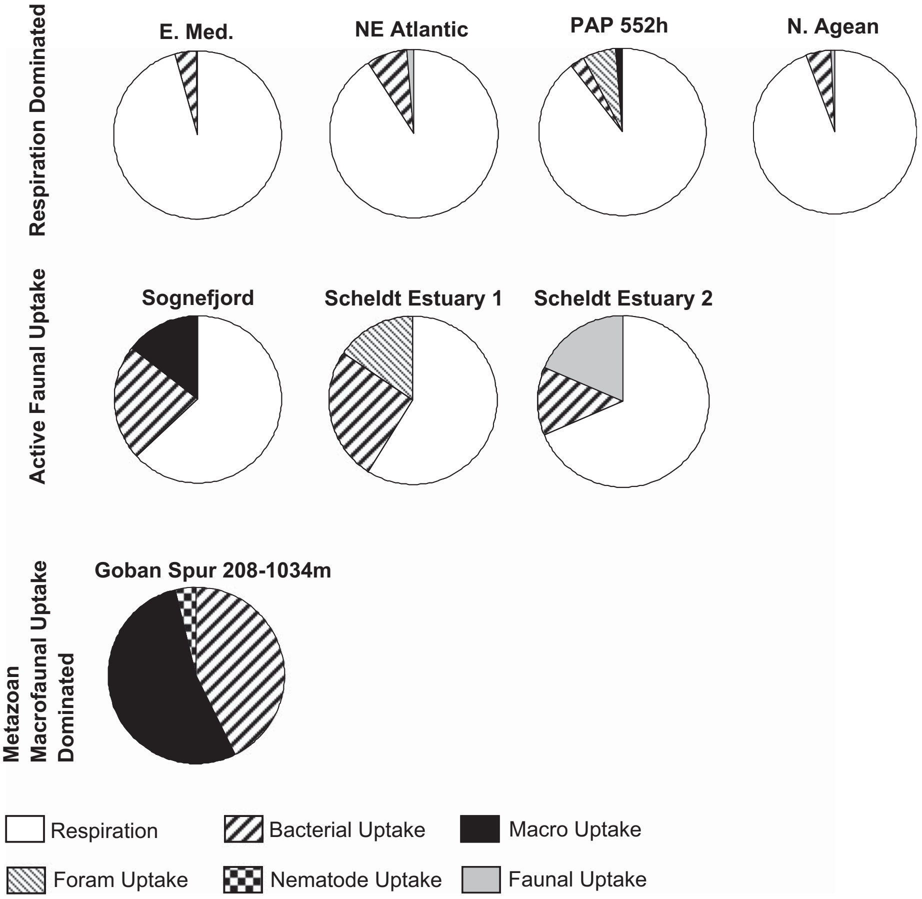

Fig. 5. Carbon processing patterns from previous studies utilising ^{13}C pulse-chase experiments on the seafloor. For the sources of these data see Table 1.

(Table 1) (Moodley et al., 2005). The common property that this site shares with the others is that it has a comparatively low concentration of sedimentary OM (for an indication of organic carbon availability see inventories in Table 1). This suggests that it is principally the comparative lack of food supply (POC input), and the correspondingly low biomasses of metazoan macrofauna (0.06–$1.2\,\mathrm{g\,C\,m^{-2}}$) of these sites that determines their C-processing pattern. Unexpectedly, the inter-monsoon 2-day experiment at the Pakistan margin 1850-m site did not fit into this category, with foraminiferal uptake dominating over respiration (Fig. 1). While patchiness in the foraminiferal community may be the cause, this C-processing pattern could be an artefact of variation in the area-specific added C dose used in the experiment, which was lower than in the other two experiments at the same site (Table 2). Buhring et al. (2006b) showed that after the addition of low doses of C, bacterial assimilation was favoured over respiration; whereas a 10-fold increase in C addition reversed the situation. Our results from the 1850-m site therefore support their conclusion that carbon flow pathways are partly determined by the amount of organic C that is deposited.

In terms of area, the majority of the seafloor is relatively deep and sediments have low $\%C_{org}$ (DeMaison and Moore, 1980). These areas are probably inhabited by relatively low-biomass faunal communities (Rowe et al., 1991) and are therefore likely to show ‘respiration dominated’ type biological C-processing.

The second category is termed ‘active faunal uptake’, and is characterised by respiration accounting for $<75\%$ of processed C, and eukaryotic (metazoan macrofaunal plus foraminiferal) uptake for 10–25%. This category contains a wide range of sites including the 140- and 300-m sites on the Pakistan margin, two intertidal estuarine sites (Moodley et al., 2000, 2005), and the deep (1265 m) Sognefjord. Results from a sandy site in the German Bight (Buhring et al., 2006a) suggest that this setting also falls into the active faunal uptake category, although, for confirmation, further work is required. Sites in the active faunal uptake category tend to be moderately food rich, and/or exhibit slightly higher faunal biomasses than the sites in the previous category (Table 1). This is in line with previous findings that greater faunal biomass (especially metazoan macrofaunal biomass) and naturally available high-quality OM enhance the amount of C processed by the metazoan macrofauna (Woulds et al., 2007). At first glance it may seem surprising that the Pakistan margin 140-m site falls into this category, as it showed similar metazoan macrofaunal biomass and sediment $\%C_{org}$ to the 1850-m site (Cowie et al., 2009; Hughes et al., 2009). However, the metazoan macrofauna and foraminifera were demonstrably more active in C uptake at the 140-m site (Fig. 1). This suggests that the 140-m site has a higher food input than the 1850-m site. This is supported by amino acid degradation index data (Dauwe and Middelburg, 1998; Vandewiele et al., 2009), which shows that sedimentary OM at the 140-m site was fresher and of higher food quality (Dauwe et al., 1999) than that at the 1850-m site.

The ‘active faunal uptake’ category can be split into two sub-categories (where the available data are sufficiently detailed). In the first of these, due to faunal community composition, ‘faunal’ uptake is mostly accomplished by metazoan macrofauna, and this is exemplified by the 140-m site on the Pakistan margin, the Sognefjord and the estuarine intertidal sites.

The Pakistan margin 300-m site can be allocated to the second sub-category, in which the faunal uptake is predominantly carried out by foraminifera. This pattern was the result of extremely low oxygen levels ($<5\,\mu\mathrm{M}$) and the near absence of metazoan macrofauna at the 300-m site, thus oxygen availability can exert a strong influence over the type of fauna responsible for OM uptake. This influence was also evident at the 140-m site, which switched from metazoan macrofaunal to foraminiferal domination of faunal uptake in response to a monsoon-induced reduction in oxygen availability (Fig. 1, Woulds et al., 2007). Uptake of C by metazoan macrofauna as opposed to foraminifera may have implications for its longer-term fate. The two types of organism are likely to vary in their assimilation efficiencies and metabolic rates (Mahaut et al., 1995), and in their positions in benthic food webs. Therefore C uptake by metazoan macrofauna vs. foraminifera is likely to alter the rate at which it is subsequently respired, and the path it takes to higher trophic levels. Further, metazoan macrofaunal processing can result in re-packaging and vertical transport of OM, both of which can influence its ultimate preservation or decay (e.g., Aller, 1982; Josefson et al., 2002).

Sites displaying ‘active faunal uptake’ type biological C-processing are likely to be found in shallower regions, including continental shelves and coastal systems. These tend to exhibit higher surface productivity and greater bulk sedimentation rates, leading to sediments richer in food (Canfield, 1994) and consequently larger faunal biomasses (Rowe et al., 1991; Soetaert and Heip, 1989). On the Pakistan margin low-oxygen conditions influenced the type of fauna responsible for OM uptake. It is expected that other variables that influence the species makeup of benthic communities, including hydrodynamics, turbidity, substrate, salinity, depth, OM supply and predation will similarly affect the faunal type responsible for faunal OM uptake. The breadth of the potential variation in benthic community composition renders the taxa responsible for faunal C uptake extremely difficult to predict.

The third, ‘metazoan-macrofaunal-uptake-dominated’, category contains only the Pakistan margin lower OMZ sites (850, 940 and 1000 m), and is characterised by metazoan macrofaunal uptake accounting for 42–85% of biological C-processing. The particularly notable feature of these sites was their large metazoan macrofaunal biomasses compared to other continental margin sites (Table 1). In addition they exhibited relatively high OM availability (again compared to continental margin sites), and oxygen concentrations (5–$7\,\mu\mathrm{M}$) that were presumably only just sufficient to support metazoan macrofauna (given the near absence of metazoan macrofauna from the 300-m site where the oxygen concentration was 4.5–$4.9\,\mu\mathrm{M}$). There have been no previous pulse-chase experiments conducted either at sites thus impacted by an OMZ, or at sites with similar benthic communities, possibly explaining why none of the other sites considered here showed a similar C-processing pattern.

A study carried out by Heip et al. (2001), however, suggests that sites with similar C-processing patterns may exist on continental margins not impacted by OMZs. They measured total sediment community oxygen consumption (SCOC), and partitioned it between the different faunal classes, based on biological survey data and theoretical respiration rates (related to body size, Mahaut et al., 1995). They found that on the continental shelf and upper slope (depths $<1034\,\mathrm{m}$), the metazoan macrofauna accounted for upto 50% of SCOC. In common with lower OMZ sites, their shelf and upper slope sites tended to exhibit a considerably greater biomass than other, deeper sites (Table 1). By analogy, it seems likely that at lower OMZ sites on the Pakistan margin the metazoan macrofauna may not only dominate short-term C-processing by ingesting large amounts of freshly deposited OM, but may also make a considerable contribution towards total OM re-mineralisation.

The North Carolina slope off Cape Hatteras (850 m) is another region where rapid significant ingestion and deep, rapid mixing of ^{13}C-labelled phytodetritus by metazoan macrofauna has been observed within several days (Blair et al., 1996; Levin et al., 1997, 1999; Fornes et al., 1999). Although complete carbon budgets were not generated, large-bodied macrofauna clearly consumed more ^{13}C-labelled algae at this site with exceptionally high OM flux; and foraminifera played a larger role in processing C at a less OM rich station (off Cape Fear NC) (Levin et al., 1999; Blair et al., 2001).

Metazoan macrofaunal uptake dominated biological C-processing is likely only to be found where unusually large biomasses of metazoan macrofauna exist, and this may prove difficult to predict. Plentiful food supply (such as seen off Cape Hatteras) may be a good indication, however the sites most readily predicted to exhibit this type of biological C-processing are those in the lower reaches of other OMZs, such as on Volcano 7 in the eastern tropical Pacific (Levin et al., 1991) and on the Oman margin (Levin et al., 2000), where large metazoan macrofaunal biomasses have been observed.

It is hoped that we provide a useful summary of the current knowledge of the short-term fate of OM on the seafloor. The proposed categories should allow predictions to be made about the unexplored majority of marine settings, and this in turn could facilitate the scaling up of results to regional and global scales.

4.2. Respiration rates of added carbon

The rate of total C-processing by the benthic community would be a logical parameter to consider when grouping sites into C-processing categories. It is not used in the above classification however, as the sites in each category show the full range of total C-processing rates. The driving force behind total biological C-processing rates at most sites was respiration (hence respiration was the dominant fate of processed C at most sites, Figs. 1 and 5), and respiration rates seem to be determined by factors other than those invoked above to account for the variation in biological C-processing patterns. Therefore a discussion of respiration rates is given here. Note that the respiration rates referred to below are all the rates at which added labelled C was respired, and are not background rates.

Respiration rates (averaged over whole experiments) on the Pakistan margin were within the range published for other sites, including the Porcupine Abyssal Plain and estuaries in the Netherlands (Fig. 2). Generally speaking, rates decreased with increasing water depth, implying control by temperature. This is consistent with observations made by Moodley et al. (2005), who showed that incubating samples from a shallow site (normal temperature 16°) at 4 °C caused the rate of respiration to fall, and become similar to that measured for sediments of deep-sea origin. Accordingly, respiration rates at the 140-m site (22 °C) were similar to those measured for the N Aegean, E Mediterranean, Cretan Sea and North Sea (13–16 °C). Rates measured at the lower OMZ stations (9 °C) were similar to those published for the Sognefjord (7 °C) and German Bight (9 °C), and respiration rates measured at the 1200- and 1850-m sites (3–7 °C) were similar to those previously seen in the NE Atlantic and on the Porcupine Abyssal Plain (~4 °C) (Table 1, Fig. 2). Thus it seems that temperature may exert an overall control on respiration rates, and thus on total biological C-processing rates, at least at sites where respiration is the dominant fate of processed C.

The relationship between respiration rates and temperature is, however, overprinted by the effect of oxygen availability. On the Pakistan margin, low oxygen availability at the 300-m site, and at the 140-m site in the post-monsoon season, appears to have produced unexpectedly low respiration rates (Fig. 2). It is somewhat surprising that micro-organisms, many of which are anaerobic, and which are assumed to be responsible for the majority of respiration at the 300-m site, are affected by low oxygen concentrations, however it is consistent with the fact that OM decay is widely found to be reduced and/or slowed in the absence of oxygen (e.g., Canfield, 1994; Hartnett et al., 1998; Sun et al., 2002).

The addition of fresh phytodetritus to seafloor sediment had been observed to result in an increase in benthic respiration rates (Witte et al., 2003b; Buhring et al., 2006b). Therefore the relationship between respiration rates and temperature is likely to be further interrupted by variation in the amount (both absolute, and relative to natural OM concentration) of C added in each experiment. The surprisingly high respiration rate measured at the 1850-m site in the post-monsoon season on the Pakistan margin may be an artefact of relatively high C addition (Table 2), which has been shown to enhance the rate of overall C-processing, and to favour respiration over other pathways (Buhring et al., 2006b).

4.3. Metazoan macrofaunal uptake rates

Metazoan macrofaunal uptake rates (Fig. 3) must be considered with caution, as these organisms tend initially to rapidly ingest relatively large amounts of labelled algae, after which their net content of ^{13}C may not increase (though their total throughput does) (Witte et al., 2003b, Woulds et al., 2007). Thus, uptake rates for shorter experiments may appear artificially greater than those for longer experiments. However, as most of the experiments considered here were between 24 and 72 h long, a comparison is thought to be justified.

The most notable features of metazoan macrofaunal uptake rates on the Pakistan margin are the unprecedented high values at the lower OMZ stations, and in the inter-monsoon season, at the 140-m site. These are matched in previous studies only by an estuarine site (Moodley et al., 2005), in which case the measured uptake was by ‘fauna’ (metazoan macrofauna, meiofauna and foraminifera), and thus will not have all been accomplished by the metazoan macrofauna. The high uptake rates on the Pakistan margin are attributable to the presence of large and active metazoan macrofaunal communities between 850 and 950 m, thought to be an OMZ edge effect (Gooday et al., 2009; Levin et al., 2009).

Metazoan macrofaunal uptake rates at other Pakistan margin sites (the 1200- and 1850-m sites) are well matched with those at other deep, relatively OM poor sites (the Porcupine Abyssal Plain, NE Atlantic, N Aegean and E Mediterranean), which exhibit similarly low metazoan macrofaunal biomasses (Fig. 3, Table 1).

4.4. Biological mixing

Biological transport of ^{13}C-labelled algae on the Pakistan margin was relatively difficult to detect over the timescale of the experiments (2–5 days). Unsurprisingly, the sites where it was measurable (the 140- and 940-m sites) were those with the highest metazoan macrofaunal abundances and biomasses respectively (Hughes et al., 2009; Gooday et al., 2009).

When compared with other studies, biological transport of label to depth in the sediment on the Pakistan margin was relatively slow. For example, in an open in-situ experiment on the North Carolina margin, at a water depth of 850 m, sub-surface peaks, and generally enriched tracer concentrations were observed at and below 10 cm depth after only 1.5 days (Blair et al., 1996, Levin et al., 1997). In addition, Witte et al. (2003b) observed transport of label to 5–10 cm in just 3 days at a 1265-m site in the Norwegian Sognefjord. They speculated that this was a food capture and storage strategy, induced by highly episodic food delivery.

Such a pulsed food supply also applies to the Pakistan margin (Haake et al., 1993), however, a combination of often low bottom-water dissolved oxygen concentrations, small oxygen penetration depths (Breuer et al., 2009) and generally OM-rich sediments may account for the fact that most fauna on the Pakistan margin are found within the surface 3 cm (Hughes et al., 2009). This is consistent with the observations of Smith et al. (2000) who found reduced mixed-layer depths within the Oman margin OMZ compared to those found on similar oxygenated margins. Notably the dominant fauna at the lower OMZ stations on the Pakistan margin does not penetrate much below 6 cm (Hughes et al., 2009; Levin et al., 2009), and does not appear to cache phytodetritus within burrows. A further, intuitive, explanation for the lack of deep label subduction compared to other regions is that large and deep burrowing organisms were not present during pulse-chase experiments (even if their occurrence was suspected at some sites).

Reduced biological mixing on the Pakistan margin compared to other sites is likely to be accompanied by a difference in biologically influenced C-cycling patterns. On the North Carolina margin, the rapid subduction of OM was accompanied by labelling of sub-surface dwelling meio- and macro-fauna (Levin et al., 1997). Further, rapid sequestration of freshly deposited OM at depth has been observed to slow mineralisation, and extend the period during which food is available to the benthic community (Josefson et al., 2002). Thus the lack of biological mixing on the Pakistan margin is likely to impact food availability and overall C-burial efficiency.

5. Conclusions

The variation in site conditions across the Pakistan margin OMZ is accompanied by a cross-margin variation in the pattern of biological C-processing. This has led us to propose categories of biological C-processing patterns, and to suggest which factors influence the occurrence of those patterns. It is hoped that this will allow predictions to be made about areas of the seafloor that have not been studied directly, and facilitate the extrapolation of existing results to regional and global scales.

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