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Biogeosciences

Short-term fate of phytodetritus in sediments across the Arabian Sea Oxygen Minimum Zone

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Abstract. The short-term fate of phytodetritus was investigated across the Pakistan margin of the Arabian Sea at water depths ranging from 140 to 1850 m, encompassing the oxygen minimum zone (∼100–1100 m). Phytodetritus sedimentation events were simulated by adding ∼44 mmol ^{13}C-labelled algal material per m^2 to surface sediments in retrieved cores. Cores were incubated in the dark, at in situ temperature and oxygen concentrations. Overlying waters were sampled periodically, and cores were recovered and sampled (for organisms and sediments) after durations of two and five days. The labelled carbon was subsequently traced into bacterial lipids, foraminiferan and macrofaunal biomass, and dissolved organic and inorganic pools. The majority of the label (20 to 100%) was in most cases left unprocessed in the sediment at the surface. The largest pool of processed carbon was found to be respiration (0 to 25% of added carbon), recovered as dissolved inorganic carbon. Both temperature and oxygen were found to influence the rate of respiration. Macrofaunal influence was most pronounced at the lower part of the oxygen minimum zone where it contributed 11% to the processing of phytodetritus.

1 Introduction

Phytodetritus arriving in pulses is a major food source for the benthic communities living at ocean margins and deep-sea basins (Gooday, 2002). The occurrence of such intense phytodetritus pulses requires episodic production events and a short transit time through the water column where it would otherwise be degraded, i.e. the settling speed needs to be high. Aggregation of phytoplankton into larger particles (Kriest and Evans, 1999) and ballasting (Francois et al., 2002) contribute to high settling speeds. As diatoms easily form aggregates, they are the most important part of phytodetritus settling to the sea floor (Beaulieu, 2002).

Following the fate of naturally occurring phytoplankton blooms and the resulting detritus deposition on the sea floor is logistically difficult due in part to the unpredictable nature of these sedimentation events. Time-series observations of sediment processes (e.g. as total sediment oxygen consumption) have yielded inconclusive results when compared to measured deposition fluxes (Smith, 1992; Sayles et al., 1994; Soetaert et al., 1996). An experimental approach, where algae enriched in ^{13}C are added directly to the sediment surface facilitates the establishment of carbon budgets, whilst it also enables studying several parts of the benthic food web, such as uptake into bacteria, fauna and respiration, simultaneously (Moodley et al., 2002; Witte et al., 2003b; Moodley et al., 2005).

The biogeochemistry of the Arabian Sea is strongly influenced by the two monsoon periods. Periods vary, but the southwest monsoon occurs from late May to early September and the northeast monsoon from December to March (Wiggert et al., 2005). Primary productivity increases dramatically in these two periods due to higher nutrient levels, caused during the southwest-monsoon by coastal upwelling of nutrient-rich waters and during the north-east monsoon by convective mixing together with subsequent advection by large-scale circulation (Naqvi et al., 2002; Kawamiya and Oschlies, 2003). At the end of the algal blooms, detritus sinks through the water column and on to the sea floor (Haake et al., 1993). The sediments of the Arabian Sea therefore receive fluxes of organic material that display strong seasonal variability.

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Table 1. Station characteristics. Temperature and oxygen concentrations taken from CTD casts.

Depth (m)	T (°C)	O_2 (µM)	Latitude	Longitude
Pre-monsoon				
140	22	92	23°17′ N	66°43′ E
300	15	4.5	23°12′ N	66°34′ E
850	10	5.8		
940	9.0	5.8	22°54′ N	66°37′ E
1000	8.7	6.7		
1200	7.2	15	23°0′ N	66°25′ E
1850	3.5	79	22°52′ N	66°0′ E
Post-monsoon				
140	18	4.9	23°17′ N	66°43′ E
300	15	4.9	23°12′ N	66°34′ E
940	9.3	7.6	22°54′ N	66°37′ E
1850	3.7	76	22°52′ N	66°0′ E

Another prominent feature of the Arabian Sea is the midwater Oxygen Minimum Zone (OMZ), from a water depth of around 100 m down to 1100 m, due to respiration of organic matter in combination with input of intermediate waters, with a low oxygen content, from the Southern Hemisphere (Naqvi, 1987; Warren, 1994). The OMZ coincides roughly with maxima in sedimentary organic carbon, suggesting a link between organic carbon preservation and oxygen availability (Cowie et al., 1999).

The short term fate of phytodetritus has been studied at several places in the ocean (Blair et al., 1996; Moodley et al., 2000, 2002; Witte et al., 2003b), but no study has yet directly compared sites in suboxic and oxic environments. At present low-oxygen environments are only a minor part of the world ocean (Helly and Levin, 2004), but are biogeochemically important for a number of processes such as organic carbon preservation (Hartnett et al., 1998; Burdige, 2007) , metal cycling (Aller, 1994), removal of biologically available nitrogen through denitrification and natural production of N_2O, contributing to global warming (Naqvi et al., 2000). It is also important to note, that the area of oxygen-poor waters is likely to expand due to global warming, both as a direct effect of decreased solubility and indirectly because of enhanced stratification (Keeling and Garcia, 2002).

In this paper we present results from an experimental study on the short-term fate of phytodetritus on the sea floor, at sites spanning the OMZ on the Pakistan margin of the Arabian Sea, before and after the SW monsoon. Phytodetritus sedimentation events were simulated by adding a known amount of ^{13}C labelled diatoms and subsequently tracing the ^{13}C into bacteria, via incorporation into phospholipid-derived fatty acids (PLFAs) specific to bacteria, into foraminifera and macrofauna, and into dissolved organic and inorganic carbon pools. Site depths ranged from 140 to 1850 m, which encompass the OMZ and provided us with a natural laboratory where the effect of oxygen and temperature could be tested under natural conditions.

2 Material and methods

2.1 Study site

Experiments were conducted on cruises CD146 and CD151, before and immediately after the summer monsoon of 2003 on-board RRS Charles Darwin. Thus it was possible to assess changes in benthic community response associated with the biannual monsoon-driven delivery of OM to the sediment. Experiments were conducted at sites along an offshore transect off the Indus River, across the Pakistan margin of the Arabian Sea (Table 1).

2.2 Experimental conditions

Cores (i.d. 10 cm) were taken using a multiple-barrel "megacorer", providing virtually undisturbed samples (Barnett et al., 1984), and immediately transferred to a temperature controlled laboratory set to in situ temperature, where the experiments were conducted.

For the purpose of incubation experiments, cores were fitted with core top seals, and all air bubbles were excluded. The undersides of the seals featured magnetic stir bars, ports for oxygen and temperature microsensors, and a further five ports; one for slurry introduction, two to allow water sampling, and two for the "oxystat" system. The "oxystat" system was designed to maintain core-top oxygen levels at seafloor conditions despite sediment oxygen consumption. On each core the two oxystat ports were connected to each other via 8 m gas-permeable tubing (the oxystat gill), submerged in a reservoir of filtered seawater (the oxystat reservoir). This reservoir was sparged with an air and nitrogen mix tuned to maintain oxygen levels slightly above those at the seafloor. A peristaltic pump circulated core top water out of each core barrel, through its dedicated oxystat gill, and back. Diffusion across the tubing in the reservoir replenished core top water with dissolved oxygen which had been consumed. Sub-aerial parts of the oxystat system were made of gas impermeable tubing.

Diatoms grown in a ^{13}C enriched medium were freeze dried onto silica or kaolin ballast and injected into the barrels, as a slurry dissolved in purified water, through a port in the core lid. The labelled diatoms consisted of 75% ^{13}C, except at the 1850 m station in the post-monsoon season, where a different batch of algae was used consisting of 31% ^{13}C. This resulted in a loading of between 3.6 and 5.8 mg of ^{13}C added to each core (43.9±6.8 mmol $^{13}C\,m^{-2}$).

Each experiment was conducted simultaneously on two replicate cores, and incubated in the dark for 2 or 5 days, exact durations varied slightly due to logistical constraints. All cores were incubated with a gentle stirring of the overlying water. Samples of the overlying water were taken at

the beginning and end of, and at pre-determined intervals, during each experiment. The samples were immediately poisoned with 50 µL of a saturated solution of $HgCl_2$ to vials with volumes of 5 mL, in order to prevent further microbial activity. After termination of each experiment, cores were sectioned at 0.5 cm intervals to 2 cm depth, then at 1 cm intervals to 10 cm depth, and then at 2 cm intervals to 20 cm depth. One half of each slice was placed in a centrifuge tube for porewater extraction, and the other half was placed in a petri dish for faunal sampling. After centrifugation, the supernatant was transferred to vials for subsequent δ^{13}C−DOC and δ^{13}C−DIC analysis (see below). The remaining sediment, used for the analysis of δ^{13}C−POC and bacterial lipids, were transferred to plastic bags and freeze dried. Fauna samples were sieved using filtered sea water, and residues from 300 µm, 150 µm and 63 µm sieves were retained. From the 300 µm and some 150 µm residues all fauna were extracted by sorting at 12–20 X magnification to the lowest possible taxonomic level, and frozen in pre-weighed tin capsules or combusted glass vials.

In addition to the shipboard incubations, labelling experiments were also conducted in situ using a benthic chamber lander (Elinor). The lander system has been described in detail by Glud et al. (1995). On arrival at the sea floor the lander inserted a 30×30 cm chamber into the underlying sediment. Pre-programmed syringes, a stirring motor, an oxygen electrode and an external oxystat gill allowed maintenance of ambient oxygen levels, slurry introduction, sample withdrawal and stirring comparable to the shipboard experiments. In these experiments, 19–27 mg ^{13}C was added, giving a dose of 18–25 mmol ^{13}C m^{-2}. After a 2-day incubation a shovel closed the bottom of the chamber, weights were dropped and the lander ascended to the surface. Sediment from the lander chamber was sub-sampled using two short megacore tubes. These cores were sectioned and the samples were processed as described above.

2.3 Analytical methods

2.3.1 Sediments and fauna

Aliquots of 200–400 µgC of gently disaggregated freeze-dried sediment were weighed into silver capsules. Decarbonation was achieved by carefully adding 2–5 drops of double distilled 6 M HCl. Samples were dried overnight at 60°C and stored in a vacuum desiccator prior to analysis.

Faunal samples were air dried at 45°C and stored in a vacuum desiccator. Soft bodied fauna were de-carbonated in two layers of tin capsule using 2–5 drops of 1 M HCl, followed by drying at 40°C. Macrofauna and Foraminifera were de-carbonated with 6 M HCl, the original tin capsule having been placed inside silver capsules. All samples were analysed on a dedicated Europa Scientific (Crew, UK) Tracermass isotope ratio mass spectrometer with a Roboprep Dumas combustion sample converter.

2.3.2 Bacteria

Bacterial biomass and uptake were quantified by measuring the concentration and isotopic composition of three PLFAs, iC14:0, iC15:0 and aiC15:0 specific to bacteria, following Middelburg et al. (2000).

PLFAs were extracted from 4 g freeze-dried sediment using a modified Bligh and Dyer extraction (Boschker et al., 1999). The lipid extract was fractionated on silicic acid into different polarity classes by sequential elution with chloroform, acetone and methanol. The methanol fraction containing the PLFAs was derivatised to yield fatty acid methyl esters (FAMEs).

The isotopic composition and concentrations were determined using a Varian 3400 gas chromatograph equipped with a HP5 column, coupled via a combustion interface to a Finnigan Delta+ isotope ratio mass spectrometer (IRMS).

2.3.3 Dissolved inorganic/organic carbon

Samples for the determination of dissolved inorganic and organic carbon were stored refrigerated in darkness and upside-down in head-space vials. The vials were sealed with butyl rubber membranes covered with Teflon to prevent gas diffusion through the membrane. Concentrations of dissolved inorganic carbon were measured by coulometric titration. Isotopic compositions were measured independently by injecting head-space gas directly in a continuous stream of helium into a Finnigan Delta+ IRMS via a ConFloII interface following Moodley et al. (2000).

Concentrations and isotopic composition of dissolved organic carbon (DOC) were measured on the same samples used for the determination of δ^{13}C−DIC. Dissolved inorganic carbon was removed by adding sulphuric acid in excess and subsequent stripping with helium. The samples were analysed with a Skalar Formacs^{LT} TOC analyser coupled through a ConFloII interface to a Finnigan Delta S IRMS. The calibration standards were prepared with potassium phtalate dissolved in purified water (MilliQ).

2.4 Data treatment

Incorporation of ^{13}C is reflected as excess (above background) ^{13}C and is expressed in terms of total uptake in millimoles of ^{13}C per square meter as well as specific uptake (i.e. $\Delta\,\delta^{13}\mathrm{C}=\delta^{13}\mathrm{C}_{\mathrm{sample}}-\delta^{13}\mathrm{C}_{\mathrm{control}}$, where δ^{13}C is expressed relative to Vienna Pee Dee Belemnite (VPDB)). Total uptake was calculated as the product of excess ^{13}C (E) and carbon concentrations. Excess ^{13}C is the difference between the fraction ^{13}C of the control (F_{control}) and the sample (F_{sample}) : $E=F_{\mathrm{sample}}-F_{\mathrm{control}}$, where the fraction of ^{13}C (F) was calculated from the ratio (R) of $^{13}C/^{12}C$,

$$F = {}^{13}C/({}^{13}C + {}^{12}C) = R/(R+1). \quad (1)$$

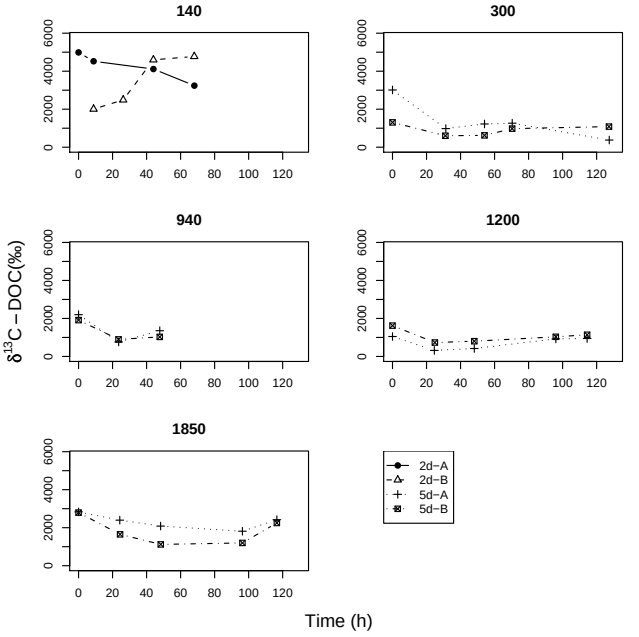

Fig. 1. Isotopic composition of dissolved organic carbon in the overlying water from the pre-monsoon cruise. A, B indicate replicate cores.

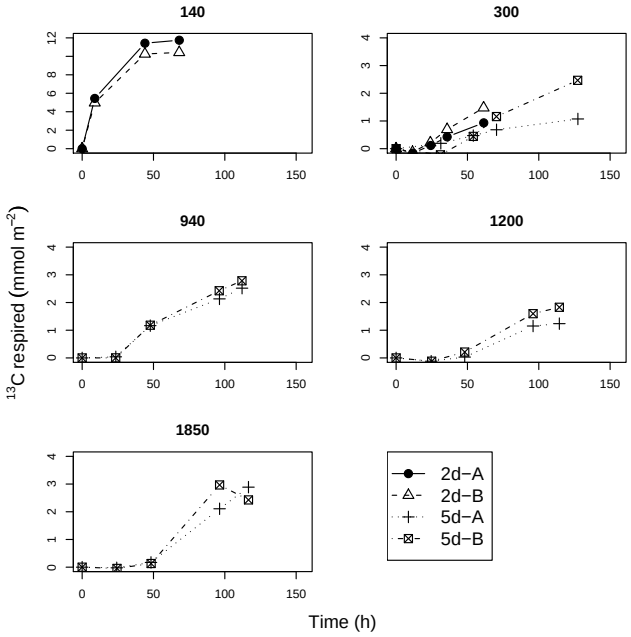

Fig. 2. Respiration of the added tracer during the pre-monsoon cruise. Note the different scale for station 140. See Table 1 for details about the stations. A, B indicate replicate cores.

The carbon isotope ratio (R) was derived from the measured δ^{13}C values as:

$$R = (\delta^{13}C/1000 + 1) \cdot R_{\mathrm{VPDB}}, \tag{2}$$

where R_{VPDB}=0.0112372.

Incorporation into bacterial biomass was calculated in the following way,

$$I_{\mathrm{bact}} = \frac{\sum_{i=1}^{3} I_{\mathrm{PLFA},i}}{F_{\mathrm{PLFA}} \cdot C_{\mathrm{PLFA}}} \tag{3}$$

where F_{PLFA}=0.12 is the fraction of the three PLFA's to total bacterial PLFA's (Moodley et al., 2005) and C_{PLFA}=0.038 is the fraction of PLFA carbon to total bacterial carbon (Boschker and Middelburg, 2002).

3 Results

The oxystat system designed to maintain the oxygen concentration on the shipboard incubations, regulated the oxygen concentrations to within 10% of in-situ values.

The δ^{13}C−DOC values in overlying waters were elevated well above background values (−20±1‰, assuming that natural sedimentary DOC has a similar isotopic composition to that of POC in underlying sediments) at the start of all incubations (Fig. 1), indicating that the added phytodetritus was a source of some DOC as well as POC. The δ^{13}C−DOC values decreased over time as a result of dilution with unlabeled DOC present in the porewater. In several cases the δ^{13}C−DOC increased again after the initial decrease as a result of degradation of labelled POC.

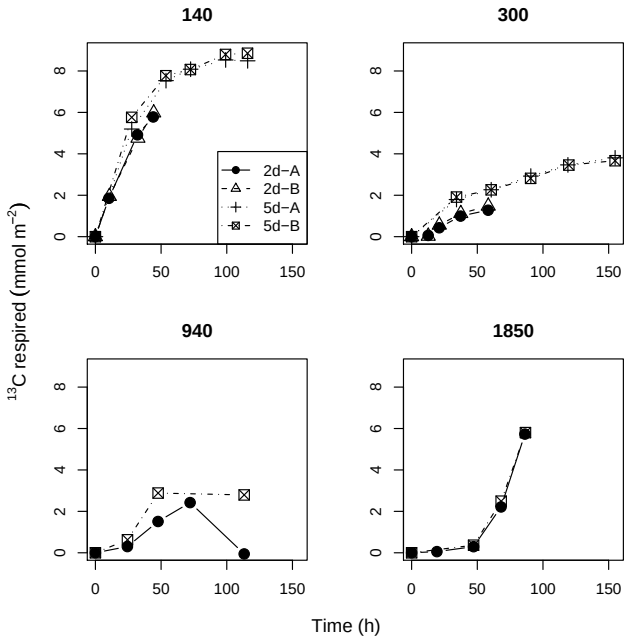

Fig. 3. Respiration of the added tracer during the post-monsoon cruise. See Table 1 for details about the stations. A, B indicate replicate cores.

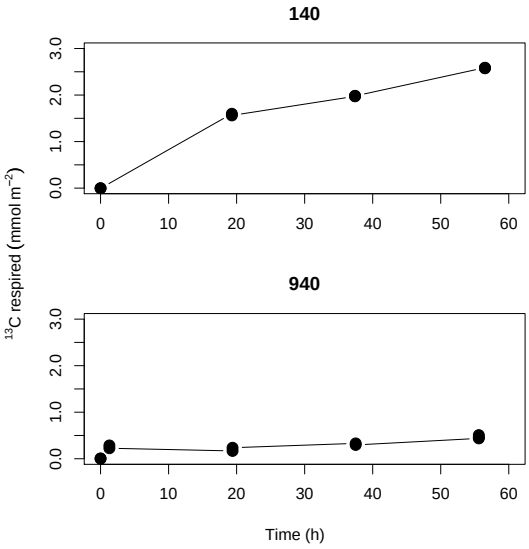

Fig. 4. Respiration of the added tracer during the post-monsoon cruise in in situ incubations. See Table 1 for details about the stations.

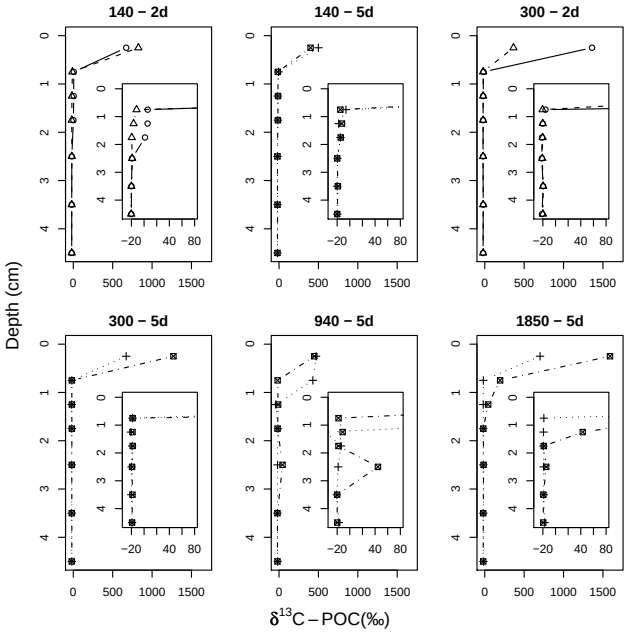

Fig. 5. Excess δ^{13}C−POC from the post-monsoon cruise. Insets zoom in on a limited range in delta values to allow distinguishing small differences between stations with limited and no vertical displacement of added algal ^{13}C.

As the overlying water was sampled for δ^{13}C−DIC and DIC at several times during the incubations, it was possible to investigate the extent and timing of respiration more closely than components such as faunal and bacterial uptake, which were sampled only at the end of the 2- and 5-day incubations. The evolution of excess ^{13}C in DIC over time was in general very comparable between replicate cores although these were collected purposely from different casts. The most intense respiration was found at the shallowest station, at 140 m. This is also the station where respiration of the added phytodetritus was evident already from the start of the incubation (Fig. 2 and 3). Later, however the respiration rate slowed down. The fast initial response followed by gradual slowing down and an apparent eventual halt is found in both the pre- and post-monsoon data at the 140 m station. Respiration of added phytodetritus at 300 m in the OMZ also started immediately, but with a much lower rate. In contrast, respiration at the deeper stations all showed an initial lag phase with very low rates of respiration but a marked increase after this phase. Overall, the length of the lag phase increased with increasing water depth; about one day at station 940 increasing to about two days at the 1200 m and 1850 m stations (Fig. 2).

Due to technical difficulties with the lander, the number of successful in situ deployments was limited. However, respiration of added algal material was evident at both the 140m and 940m stations with relative differences in rates similar to those observed in the shipboard incubations (Fig. 4).

Downcore profiles of sediment δ^{13}C−POC, obtained at the end of the experiments show limited downward mixing of the added algae (Fig. 5) in both 2- and 5-day incubations. Moreover, there was no apparent change over time. Despite the limited vertical displacement, small amounts of labelled material were brought down from the surface to deeper layers at all stations except in the core of the OMZ (300 m station) where all the added phytodetritus remained in the topmost sediment layer (0–0.5 cm).

The δ^{13}C−DIC of pore-waters was highly enriched relative to background values. Enrichment was highest in the top centimeters, exponentially decreasing with depth in the sediment (Fig. 6). Except for one profile from 140 m in the pre-monsoon cruise exhibiting sub-surface peaks, all porewater profiles appear to be the combined result of respiration at the sediment-surface and downward diffusion into the sediment.

Transfer of ^{13}C from phytodetritus to bacteria was highest in the upper two centimeters (Fig. 7). Label assimilation in bacteria was also detectable in the 2–5 cm depth layer, but contributed <1% to the depth-integrated bacterial uptake. The labelling pattern of the three bacteria-specific fatty acids, iC14:0, iC15:0 and aiC15:0 was consistent across stations and depth layers in the sediment. The fatty acid with the highest specific uptake ($\Delta\,\delta^{13}$C) in general is iC15:0. Bacterial uptake was quite similar across the stations above 1000 m depth. Uptake was much lower at greater station depths, even after five days (Table 2). Bacterial uptake of the added algal carbon was on average comparable to macrofaunal and foraminiferal uptake (Woulds et al., 2007). At the 300 m station, where exceptionally low oxygen levels resulted in a near-total absence of macrofauna, bacterial and foraminiferal

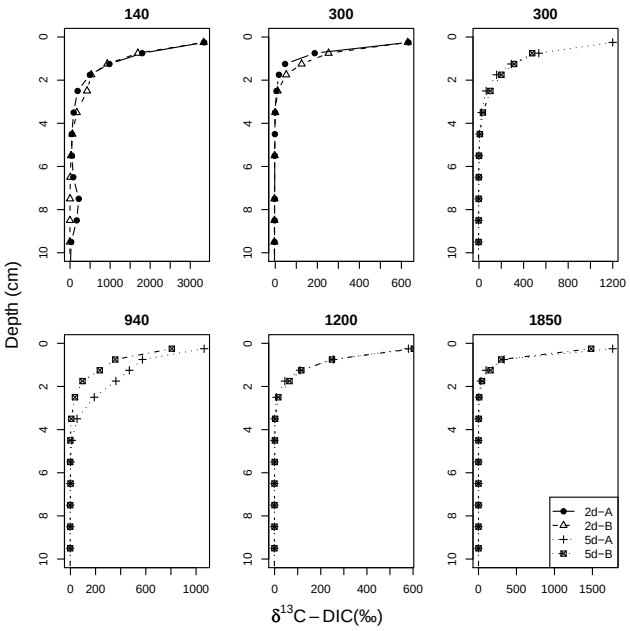

Fig. 6. Isotopic composition of the porewater DIC at the end of the experiments at five different water depths from the pre-monsoon cruise. Results are shown for a maximum depth of 10 cm, although samples were analysed to a depth of 20 cm. A, B indicate replicate cores.

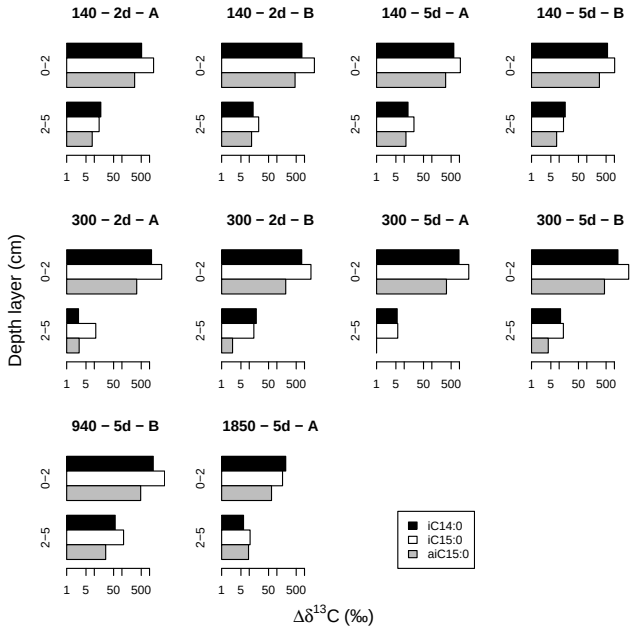

Fig. 7. Specific uptake of ^{13}C into bacterial fatty acids in two depth layers at all stations during the post-monsoon cruise. A, B indicate replicate cores. Note the use of a logarithmic x-axis.

uptake was similar. At the 940 m station, the macrofauna was much more prominent and dominated the carbon processing.

Respiration was measured in incubations lasting both 2 and 5 days. To allow the comparison of all incubations, all respiration values were linearly interpolated from the two closest sampling times to a common time of 44 h (Fig. 8). As some incubations nominally lasting 5 days had to be terminated earlier due to limited processing manpower, these were interpolated to 86 h (Fig. 9). Respiration after 44 h was most intense at the shallowest station and decreased with station depth. However, after 86 h the decrease with station depth is only evident at the 140 to 300 m stations. Note that a different batch of algae was used for the 1850 m station in the post-monsoon cruise, which apparently was more easily mineralised.

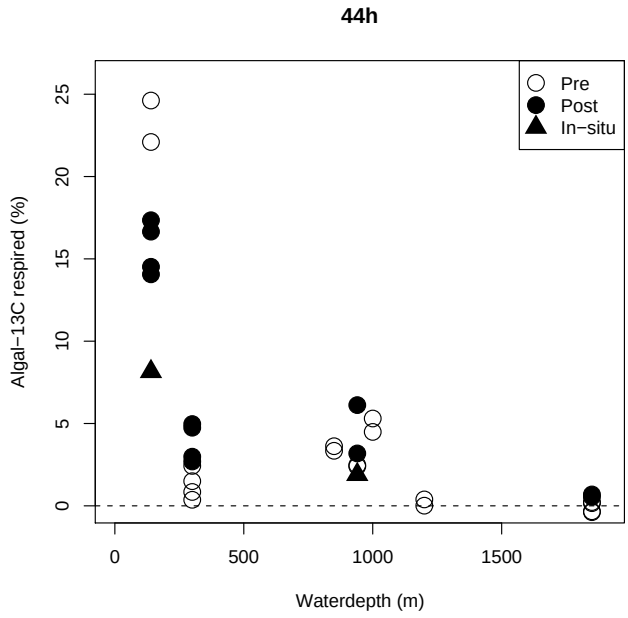

Fig. 8. Interpolated percentage of total label respired after 44 h across the ocean margin. A different batch of algae was used for station 1850 during the post-monsoon cruise. All shipboard experiments were performed in duplicate.

4 Discussion

4.1 Experimental approach

Potential artifacts in shipboard incubations of oceanic sediments have been reported repeatedly (e.g. Glud et al., 1994) and include possible changes due to decompression or warming of the sediment during retrieval and incubation of the cores. At most stations, we also performed in situ incubations to be able to verify the shipboard results. However, the distribution of added phytodetritus in the in situ incubation chamber was very patchy, as highlighted by large differences

Table 2. Mean (and standard deviations) of phytodetrital processing rates in mmol $^{13}C\,m^{-2}$ and recovery in % of the added carbon. Recovery is calculated as the sum of macrofaunal uptake, respired carbon and bulk excess POC, as POC already includes the contribution from both bacteria and foraminifera. Contribution from macrofauna and foraminifera were taken from Woulds et al. (2007). The absolute amount of algae added to in situ incubations were higher than in the shipboard incubations, but lower on a per area basis.

Station	Days	POC	Bacteria	Foraminifera	Macrofauna	Respired	Recovery
Pre-monsoon							
140	2	24.1(10.1)	1.26(0.2)	0.38	2.61	11.1(0.936)	81.6(23.9)
300	2	16(0.854)	0.27(0.03)	0.31	0	1.2(0.383)	44(3.47)
300	5	24.4	0.41(0.15)	0.38	0	1.77(0.986)	61.6
850	2		0.18(0.05)				
940	5	8.34	0.26(0.21)	0.08	3.00	2.65(0.188)	35.0
1000	2		0.17(0.03)				
1200	5	10.2(2.18)	0.05(0)	0.41	0.17	1.53(0.418)	29.7(6.76)
1850	5	48.2(15.5)	0.14(0.08)	0.37	0.068	2.66(0.326)	84.6(27.7)
Post-monsoon							
140	2	32.9(3.22)	1.71(0.815)	1.17	0.587	5.88(0.139)	96(8.52)
140	5	18.6(2.64)	1.6(0.509)	2.19	0.605	8.67(0.258)	69.3(6.53)
140	2 (in situ)	0.5(0.42)	0.29(0.24)	0.628	0.489	2.58	72.0
300	2	33(25.3)	1.93(1.33)	0.321	0	1.38(0.141)	84.8(63)
300	5	36.2(15.8)	2.79(1.36)	1.30	0	3.74(0.0973)	96.8(38.6)
940	5	31.9(4.48)	0.95(1.34)	0.0677	4.38	2.61(0.261)	94.1(11.9)
940	2 (in situ)	0.11(0.01)	0.07(0.01)	0.039	2.96	0.46	36.0
1850	5	32.7(21.6)	0.08	0.228	0.0984	5.77(0.0493)	78.4(44)

in excess ^{13}C-POC and bacterial uptake between subcores (Table 2) at the 140 m site. As a consequence of patchy availability of phytodetritus, a large fraction of bacteria residing at the sediment surface was unable to participate in the processing of this material. Upscaling measurements made on small subcores, such as excess ^{13}C-POC and bacterial uptake rates, introduces large uncertainty in total chamber estimates.

Incubation of sediments from low-oxygen environments poses a major challenge because measures should be taken to maintain oxygen levels close to ambient. Therefore, water from each core was pumped through gas-permeable silicon tubing placed in a reservoir where oxygen concentrations were kept at in situ concentrations. This ensured ambient oxygen levels and thus a close-to-natural functioning of the benthic community. However, since the partial pressure of carbon dioxide was higher in the cores compared to the controlled reservoir, it is possible that carbon dioxide effluxed from the experimental cores and consequently that absolute values of respiration are underestimated.

While core incubations are able to replicate both the temperature and oxygen conditions of the in situ environment, the stirring rate is constant and is set to prevent resuspension. Should resuspension occur in the natural environment, it could alter the fate of phytodetritus by keeping it exposed longer to decomposition in the benthic boundary layer (Beaulieu, 2003).

The natural status of phytodetritus arriving at the seafloor has been found to be highly variable in terms of degradation state and composition, and it is thus not easy to select the appropriate pre-treatment of experimental phytodetritus such

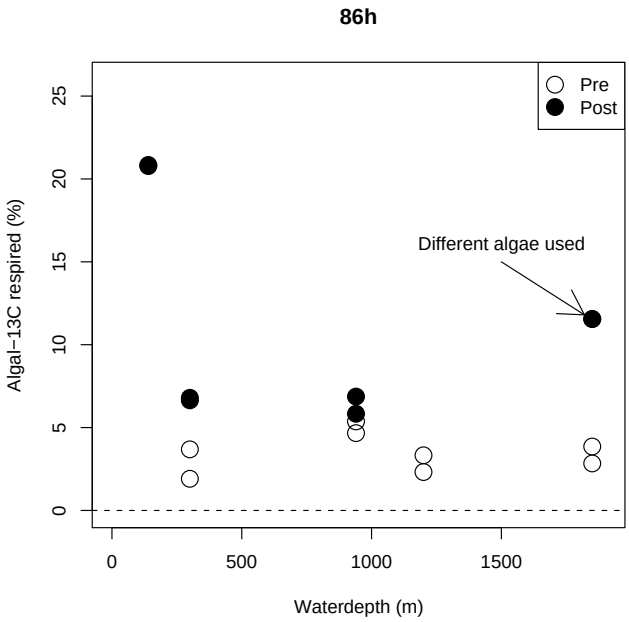

Fig. 9. Interpolated percentage of total label respired after 86 h across the ocean margin. A different batch of algae was used for station 1850 at the post-monsoon cruise, which apparently was more easily mineralised. All experiments were performed in duplicate.

that it resembles natural conditions best (Beaulieu, 2002). Similarly, it was not possible to select proportionally representative amounts of labeled C to add to the different sites. Instead, we chose to add the same material and the same quantity to all sediments, allowing a direct comparison among sites. Adding the same amount of phytodetritus at all depths does not simulate natural inputs, as these would generally be lower at greater depths due to respiration within the water column (Andersson et al., 2004). Our experiments were therefore designed to directly compare the relative potential for phytodetritus processing at different study sites. However, it has been shown that degradation of particulate organic material is slowed down in suboxic water columns such as the one found in the Arabian Sea (Devol and Hartnett, 2001). Thus, in OMZ areas, the flux of organic material arriving at the seafloor is of a more similar magnitude at different depths, than it would be for an entirely oxic water column.

That the nature of reactive organic matter added may be important to experimental results was possibly demonstrated in the response recorded during the post-monsoon period at the 1850 m station. Due to problems with algal cultures, a different batch of labeled diatoms was used, which apparently was much more readily respired. Moreover, the immediate ^{13}C enrichment of DOC in incubations at all stations (Fig. 1) indicates that DOC was added with the freeze-dried algal material despite thorough rinsing procedures. Although this unintended addition of 13C-DOC amounted to less than 5% of total added ^{13}C in all cases, the combined results highlight that benthic carbon processing studies using artificially introduced phytodetritus are not necessarily comparable, because the results may depend on the type of algae used, their preconditioning and the specific carbon loading (Buhring et al., 2006).

Summing up the contribution from all the compartments, i.e. uptake into bacteria, foraminifera, macrofauna, respiration and unprocessed algal carbon remaining in the sediment a recovery can be calculated. POC measurement includes the contribution from both unprocessed algal carbon and carbon taken up by bacteria and foraminifera (macrofauna was picked out). Thus, the recovery was calculated by the sum of the POC pool, the uptake into macrofauna and the DIC pool. The recovery was high in most of the experiments from the post-monsoon cruises and some of the pre-monsoon stations (Table 2). Apparent label losses are primarily due to uncertainty in the measurement of excess ^{13}C-POC. Another potential loss of ^{13}C-DIC was losses of gaseous $^{13}C-CO_2$ through the silicon tubing (see above).

4.2 Fate of phytodetritus

Our results clearly show that, within 2-to-5 day timescales, a minor fraction of total added carbon was processed at all sites, and the fate of the majority of the processed carbon was respiration, in both pre- and post-monsoon seasons. The notable exception was at the 940 m station where in both pre- and post-monsoon seasons, uptake by the abundant macrofauna dominated the phytodetritus processing. The occurrence of the amphinomid polychaete *Linopherus* sp. at this station accounted for most of the macrofaunal uptake and influenced the entire carbon processing (Woulds et al., 2007). When present, animals such as these amphinomid polychaete have a large impact on the mineralisation pathway, by subducting organic matter below the oxic zone (Levin et al., 1997). This demonstrates that short-term carbon cycling pathways can differ dramatically, with possible consequences for the fate of carbon (e.g. burial vs respiration).

At the 140 m site there was a marked shift in the uptake patterns from pre- to post-monsoon due to an upward shift in the upper boundary of the OMZ, which caused bottom waters to become considerably less oxygenated (Table 1). Concurrent with this decrease in oxygen, the uptake shifted from macrofauna-dominated to more equally divided between bacteria, foraminifera and macrofauna. The shift in uptake pattern indicates that changes in oxygen, from fully oxygenated to hypoxic conditions, has a major impact on the pathway of benthic phytodetritus processing (Woulds et al., 2007). Respiration also responded to the shift in oxygen concentration, but in a less dramatic sense.

Specific uptake into bacterial lipids expressed as $\Delta\,\delta^{13}$C in the 0–2 cm layer was always less than 3500‰. Using Eqs. (1) and (2) this corresponds to a fraction of ^{13}C of 4.8%. Thus, even the most active of the bacterial lipids did not experience more than 5% turnover during five days of incubation. The turnover calculation assumes an equal contribution of all bacteria in the 0–2 cm layer.

Transfer of labeled carbon below the surface layer was limited, even at stations where macrofauna was present. Even though the impact of fauna might be less than that found elsewhere (Witte et al., 2003a; Kamp and Witte, 2005), the fauna left a clear imprint at station 940 in the profiles of δ^{13}C−POC, bacterial lipids and in the porewater profiles of δ^{13}C−DIC (Figs. 5, 7, 6), where the penetration of label was deeper and values were more variable.

4.3 Factors governing respiration

The importance of benthic respiration as a fate for phytodetritus on the timescale of days to months is still largely unknown and results reported from the literature are ambiguous. Moodley et al. (2002) examined the fate of phytodetritus in a deep-sea environment (NE Atlantic, 2170 m) on a relatively short timescale, by incubating sediment amended with labelled algae for 35 h. They found that 1.5% of the added algae were respired during these 35 h. However, 40% of the algal carbon was left unaccounted for after the experiment, implying that it might have been lost prior to injection. Assuming that this was the case the respiration would increase to 2.4%. Moodley et al. (2005) later repeated this experiment at several locations, with a large range in water depths

and temperatures, and found that ∼15% of the added algal carbon was respired at all locations after 24 h. Similarly, in our study , respiration accounted for up to 25% of the added algae within 5 days at the 140 m station. It was the dominant fate of the processed phytodetritus. This result is similar to the study of Moodley et al. (2005) where respiration dominated the budget of processed phytodetritus as well, in sites ranging from estuarine to deep-sea environments.

Chemical reaction rates increase with increasing temperatures, including microbially mediated reactions in marine sediments such as organic matter mineralisation (Westrich and Berner, 1988). Effects of temperature on short-term processing of phytodetritus have been studied by Moodley et al. (2005), where they found that a decrease in temperature slowed down respiration considerably. By decreasing the temperature from 16°C in situ to a temperature of 6°C, the contribution of respiration decreased from 17 to 3% of the added algal carbon respectively. In our experiments the length of the lag time in the appearance of excess ^{13}C into the DIC pool showed a smooth transition from warm, shallow sediments where no delay was observed to a lag time of almost two days at the deepest and coldest station. The increase in lag time with increasing station depth, and concurrently decreasing temperatures (Table 1), might be explained by a decoupling in the temperature response between the different functional groups of bacteria taking part in the mineralisation process. One group is responsible for performing the initial hydrolysis of organic matter to DOC and another group the respiration of these compounds to CO_2. Such a decoupling might result in an accumulation of low-molecular weight DOC at low temperatures (Weston and Joye, 2005).

Bottom water oxygen concentrations may have an effect on sediment organic matter (OM) processing, but literature evidence is scattered and sometimes conflicting. Hartnett et al. (1998) and Hedges et al. (1999) have reported correlative evidence that oxygen exposure time determines the extent of OM processing. Experimental studies examining the effect of oxygen on OM degradation have shown it to be small when the material is fresh and larger when it is more refractory (Hulthe et al., 1998; Kristensen et al., 1995), but these experiments were not done with undisturbed sediment originating from naturally suboxic environments. In this study, the effect of oxygen on respiration was not as pronounced as the effects of temperature, but was apparent at the 300 m station where oxygen levels were so low that virtually no macrofauna could exist. An unexpected decrease in oxygen levels at the 140 m station (Table 1), from 92 µM in the pre-monsoon cruise to 5 µM in the post-monsoon cruise, might have caused the respiration to decrease. However, not to the same level as at the 300 m station, which would be expected if the only factor determining respiration factor was oxygen. Concurrent with the decrease in oxygen at the 140 m station was also a decrease in temperature, which probably had a similar effect as the change in oxygen on the respiration.

5 Conclusions

Between 20 and 100% of the added algal carbon was left unprocessed in the sediment, mainly at the surface. Respiration accounted for the largest fraction of processed carbon, between 0 and 25%, and was governed by both temperature and bottom-water oxygen levels The decrease in temperature from shallow to deeper situated sediments caused a progressively longer lag period in the respiration of the algal carbon. Macrofaunal influence was most pronounced at the lower part of the oxygen minimum zone (940 m), where high amounts of food overlaps with a sufficient concentration of oxygen. At this station macrofaunal uptake accounted for 11% of total phytodetritus processing.

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