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Sink or link? The bacterial role in benthic carbon cycling in the Arabian sea oxygen minimum zone

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Abstract

The bacterial loop, the consumption of dissolved organic matter (DOM) by bacteria and subsequent transfer of bacterial carbon to higher trophic levels, plays a prominent role in pelagic aquatic food webs. However, its role in sedimentary ecosystems is not well documented. Here we present the results of isotope tracer experiments performed under in situ oxygen conditions in sediments from inside and outside the Arabian Sea Oxygen Minimum Zone (OMZ) to study the importance of the microbial loop in this setting. Particulate organic matter, added as phytodetritus, was processed by bacteria, protozoa and metazoans, while dissolved organic matter was processed only by bacteria and there was very little, if any, transfer to higher trophic levels within the experimental period. This lack of significant transfer of bacterial-derived carbon to metazoan consumers indicates that the bacterial loop is rather inefficient in these sediments. Moreover, metazoans directly consume labile particulate organic matter resources and thus compete with bacteria for phytodetritus.

1 Introduction

Isotope tracer experiments have been conducted in various settings to assess the processing of particulate labile organic matter (OM) by the benthic community (Moodley et al., 2002, 2005b; Witte et al., 2003a, b; Andersson et al., 2008; Woulds et al., 2009). These studies have revealed that all benthic size classes (bacteria, meiofauna, and macrofauna) were involved and took up some of the labeled OM. These results, although very informative, left one question unanswered: is organic matter assimilated directly by meio- and macrofauna feeding on phytodetritus, or indirectly via ingestion of bacteria that in turn hydrolyzed particulate organic matter (POM) into dissolved organic matter (DOM) and subsequently incorporated it? In other words, are sedimentary bacteria a link or a sink in the benthic food web?

BGD
10, 10399–10428, 2013

Pomeroy (1974) suggested that bacteria and protozoa form an important link between dissolved organic matter produced by primary producers and metazoans higher up in the food web. Following studies confirmed this hypothesis and Azam et al. (1983) named this pathway the "microbial loop" in pelagic ecosystems. Later, Jumars et al. (1989) presented a provocative paper in which this theory was further elaborated: they showed that heterotrophic bacteria were feeding not only on phytoplankton-derived dissolved organic carbon but also on DOM derived from sloppy feeding by zooplankton.

Lee (1980) and Kemp (1988) were among the first to hypothesize that the microbial loop might also be occurring in the sediment, although possibly in a more complex form. According to these authors, sediment bacteria would incorporate DOM via their membranes directly from the pore water or from polymeric materials and particles, after breaking them down to more simple compounds using exoenzymes. Bacteria would then become food for protozoans and metazoans and thereby play a key role in the transfer of carbon and nutrients. Lee (1992) conducted ^{14}C incubation experiments using water samples from an enclosed marine glacial basin, to study carbon preservation under oxic and anoxic condition. She found that biomass and biodiversity of bacterial grazers may explain part of the differences in carbon preservation, supporting the idea of a benthic microbial loop and offering some insights in the relationships between bacteria and their grazers.

Recent observations on the trophic role of bacteria and bacterial-derived carbon in sediments based on isotope tracer experiments revealed however that bacteria are not a major carbon source for intertidal benthos (Van Oevelen et al., 2006b). Consistently, for deep-sea sediments Nomaki et al. (2006) and Guilini et al. (2010) found limited to no bacterivory by meiofauna, previously thought to be major consumers of bacterial production. If faunal grazing does not constitute a main controlling factor of the bacterial community, then the latter must be controlled in a different way. Danovaro et al. (2008) proposed viral infection as heterotrophic bacterial production controlling mechanism in the sediment, asserting that at water depths beneath 1000 m, viral lysis would be

BGD
10, 10399–10428, 2013

responsible for nearly all prokaryotic mortality, transforming bacteria in detritus. The viral shunt hypotheses and the results obtained in bacterivory studies suggest that the microbial loop in sediments is a sink rather than a link in the benthic food web.

The importance of the microbial loop in deep-sea benthic food webs has however been exclusively studied in oxic sediments. Oxygen minimum zones (OMZ) are known for a different biogeochemistry as compared to regular oxic settings. The naturally occurring OMZ in the Arabian Sea is an archetypical example: here OM accumulates in the sediment (Cowie et al., 1999; Middelburg and Levin, 2009). Several explanations have been given for this accumulation: low faunal biomass (Demaison and Moore, 1980; Levin et al., 1991; Jeffreys et al., 2009) and faunal activity (Woulds et al., 2007; Levin et al., 2009), lack of oxidants and interaction of the OM with inorganic material (Hedges and Keil, 1995), incorporation of organic particles in geomacromolecules or humic substances (Mayer, 1994), and the refractory nature of the OM deposited at the bottom (Henrichs, 1992). Focusing on the functioning of this ecosystem, results by Moodley et al. (2011), Pozzato et al. (2013) and Koho et al. (2013) showed that faunal limited activity, oxygen low concentration and low faunal biomass are not exclusively responsible for the OM accumulation. Instead, community functioning and efficiency are more likely to be key factors in determining such phenomenon.

OMZ sediments harboring benthic fauna could offer ample opportunity for an efficient microbial loop because of: high quantity of refractory OM (preferentially degraded by bacteria) and low labile OM concentration (which force fauna to choose other food sources, such as bacteria). Thus, should the microbial loop key role in sediment OM cycling not be confirmed in such a setting, then such loop is unlikely to be important in any soft-sediment.

We investigated the specific role of bacteria in the sediments of the Arabian Sea OMZ to clarify if they are a sink or a link in the benthic food web. We amended sediment from inside and outside the Arabian sea OMZ with two different complex OM tracers, particulate organic matter (POM) and dissolved organic matter (DOM). This approach allowed us to follow the two main routes of OM degradation in the benthic food web:

BGD
10, 10399–10428, 2013

POM degradation by bacteria and metazoans, i.e. the detritivore pathway (Mayer, 1989; Chrost, 1991a, b), and DOM incorporation by bacteria subsequently grazed by fauna, i.e. the microbial loop. This simultaneous tracking of the two pathways allowed us to track the transfer of C up the food web to fauna via bacterivory.

2 Material and methods

2.1 Study area

The study focused on two stations on the Murray Ridge, situated in the northern Arabian Sea between the Indus River delta and the city of Muscat (Fig. 1). Station STOMZ lies in the core of the OMZ and was shallower (22° 32.9′ 64° 02.4′, 885 m) than the deeper station SToutOMZ (22° 18.5′ 63° 24.5′, 1791 m) at the lower boundary of the OMZ. The Murray Ridge is located south west of the Pakistan margin and it starts about 100 km from the coast into the Arabian Sea; it is approximately 20 km wide and 750 km long. The Ridge is composed of three different parts: the southern crest at water depth < 1000 m, the northern zone is subdued with water depths of 2000 m and the > 4400 m deep Dalymple Trough (Gaedicke et al., 2002). The sedimentary cover of the Ridge increases in thickness towards the coast and it progressively widens. The Ridge is a perfect experimental setting to study marine OM processing because it is isolated and far away from shore (Shimmield et al., 1990), preventing confounding terrestrial input to this site. The OMZ starts approximately 150 m below the sea surface and coincides with the seasonal thermocline. At STOMZ a surface mixed layer was recorded by our CTD at depth between 80 and 85 m, whereas SToutOMZ was a fully mixed water column that lacked layers and was thus not stratified.

Three different methods were used to analyze the oxygen concentration in the water column: the oxygen sensor on the CTD, Winkler titration of the water sampled by the rosette sampler and an optode fitted to the multicorer. The CTD was equipped with a sea-Bird SBE43 sensor, detection limit 3 µmol L^{-1}, accuracy 2 %, which was cali-

BGD
10, 10399–10428, 2013

brated using Winkler titration of samples from outside the OMZ. One CTD cast was done per station. Sea surface temperature was 25.2 °C and below the mixed layer the temperature declined to a minimum of 2.1 °C at 2600 m. Salinity profiles showed a distinct maximum of 36.2 at 320 m, probably related to the Persian Gulf outflow. The salinity decreased below 400 m to a minimum of 34.7 at 3000 m.

2.2 Preparation of isotopically labeled substrates

POM and DOM were prepared in the laboratory from axenic cultures of the brown diatom *Thalassiosira pseudonana* that was grown in a 30 % ^{13}C-$NaHCO_3$ enriched F2 medium. Algae were harvested via centrifugation (2000 G), the pellet washed of any residual label with artificial seawater and centrifuged again. The pellets were frozen at −80 °C and freeze-dried. We harvested ∼ 0.8 g dry algae from 9 L of cultured *Thalassiosira pseudonana*. Sterilized Milli-Q water was then added to the freeze-dried pallets to burst the algal cells and release the inner cytoplasm and exudates from the algal frustules. DOM was separated from POM by centrifugation (2000 G). This procedure was repeated three times. The remaining pellet was used as POM substrate. The supernatant was taken as DOM substrate and was filtered through a GF/F pre-combusted filter, filtered through a 0.2 µm syringe filter before being stored in glass vials. Both POM and DOM were portioned, frozen and freeze-dried again before usage in the experiments. The ^{13}C content of the POM was 20 % (equal to a δ^{13}C value of 21 500 ‰) and 18 % of the DOM (equal to a δ^{13}C of 18 500 ‰) as measured by a Thermo Electron Flash EA 1112 analyzer (EA) coupled to a Delta V isotope ratio mass spectrometer (IRMS).

2.3 Sediment core sampling

Intact 10 cm i.d. multicorer cores were retrieved from both stations. Upon arrival on deck, the cores were transferred to a temperature-controlled laboratory and were allowed to acclimatize for 2 days in a water bath at in situ temperature. During this period,

BGD
10, 10399–10428, 2013

the overlying water of the cores was gently bubbled with pre-made air mixtures (certified O_2, CO_2 and N_2 gas mixture by Hoekloos BV, the Netherlands) to give oxygen concentrations of 125 µM O_2 for SToutOMZ and 6 µM O_2 for STOMZ.

2.4 Sediment characteristics

Two additional cores per station were sampled together with the incubation cores and used to determine sediment characteristics. The upper 3 cm of each core was sliced off, homogenized and 10 cm^3 of each slice subsampled and used for analysis. The porosity was calculated on sediment wet/dry measurements using an average sediment density of 2.55 g cm^{-3}. Grounded freeze-dried sediment samples were measured for organic carbon content, molar C : N ratio and background $\delta^{13}C$ values with a Thermo Electron Flash EA 1112 analyzer (EA) coupled to a Delta V isotope ratio mass spectrometer (IRMS). Sediment grain size distribution was assessed with a MALVERN Mastersizer 2000 on freeze-dried sediment samples.

2.5 Experimental incubations

Eight cores were incubated in total: from STOMZ, 2 with the equivalent of 400 mg C m^{-2} POM, 2 with the equivalent of 400 mg C m^{-2} DOM and from SToutOMZ, 2 with the equivalent of 100 mg C m^{-2} POM and 2 with the equivalent 100 mg C m^{-2} DOM. The selected tracer quantities represent 0.31 and 0.19 % of the organic C present in the surface 3 cm of the sediment. The POM was resuspended in 0.2 µm filtered natural seawater and then gently delivered to the sediment surface of each core via a long glass pipette, paying attention not to disturb the sediment. The DOM was dissolved in 0.2 µm filtered natural seawater and subsequently injected down to approximately 4 cm into the sediment with a micro-glass syringe via numerous injections of 10 µL each, equally distributed over the surface of the core. The cores were sealed on the bottom and on the top with O-ring lids and incubated for 7 days under suboxic conditions (6 µM O_2 for STOMZ and 125 µM O_2 for SToutOMZ,), bubbling pre-made mixtures of air (cer-

BGD
10, 10399–10428, 2013

tified O_2, CO_2 and N_2 gas mixture by Hoekloos BV, the Netherlands) in the overlying water of each core. To verify that the oxygen concentration in the core water of the different incubations was matching the desired ones, measurements were carried out with an oxygen-optode probe (Presens, Germany) following standard procedures manual of calibration, according to the optode manual, directly before and after the experiment. The out-flowing air of each core entered into two successively placed CO_2 traps, which were connected to each other and changed every 3.5 days to prevent oversaturation. The CO_2 traps were filled with a solution of Milli-Q water and NaOH (Kristensen et al., 1992) and were prepared in 500 mL sealed-off glass bottles with a screw-on septum cap. At the end of the incubation time, the cores were opened sequentially, oxygen concentration measurements done in the cores and water samples were taken.

2.6 Sample processing

At the end of the incubation, the overlying water of the cores and the content of the CO_2 traps were filtered on GF/F pre-combusted filters. The filters were then analyzed for phospholipid fatty acids (PLFA) to estimate the water column bacterial contribution to OM degradation (see below). The sediment cores where then frozen in their coring tube. While frozen, the upper 10 cm of each core was cut off when still inside the coring tube with a hand saw for later sub-sampling. This procedure was preferred over normal slicing due to the extremely soft nature of the sediment. The intact core sections were stored in a −20 °C freezer and transported to the laboratory at NIOZ-Yerseke.

After arrival in the laboratory, four weeks later, the background and incubation cores were sliced frozen in 2 cm intervals: 0–2 and 2–4 cm with a circular electric saw. While frozen, each slice was portioned as follows: one quarter (approx. 39 mL) was analyzed of bacterial PLFA, two quarters were used for faunal extraction and the remaining quarter was used for total lipids extraction and archaeal biomarkers (Lengger, 2013a). The fatty acid subsample was freeze-dried and stored at −20 °C until further processing. The frozen subsamples for faunal analysis (for background and incubations cores) were immersed in a mixture of 40 % buffered formaldehyde stained with Rose Bengal

BGD
10, 10399–10428, 2013

and allowed to thaw at room temperature. This was preferred over fixing and staining after defrosting to better preserve the fauna. The stained sediment was stored for 2 days at room temperature before sieving, to give the stain sufficient time to color the animals.

2.7 δ^{13}C isotope measurements

2.7.1 Bacteria

The bacterial tracer incorporation was estimated through the isotope enrichment of bacterial-specific PLFAs (Boschker and Middelburg, 2002). Two main biomarkers were chosen for the analysis: iC15:0 and ai15:0 because of their specificity for bacteria and presence in all samples. Fatty acids were extracted using the Bligh and Dyer extraction protocol and analyzed using GC-c-IRMS (Middelburg et al., 2000) and δ^{13}C values were corrected for the C addition during derivatization and also per PLFA-C content differences. Incorporation of ^{13}C into these bacterial PLFAs was converted to incorporation into bacterial biomass by assuming that the specific PFLAs represent 11 % of all bacterial PLFAs, which in turn comprise 5.6 % of total bacterial carbon (following Moodley et al., 2002). The conversion from PLFA gDW to bacterial biomass m^{-2} was done using determined sediment porosity values.

2.7.2 Fauna

Following Rose Bengal staining, the sediment was sieved on stacked 500 and 38 µm sieves to separate macrofauna (retained on 500 µm sieve) and meiofauna (retained on 38 µm sieve). The meiofauna fraction was then further treated with Ludox (colloidal silica) centrifugation (Burgess, 2001) to separate the nematodes from the sediment. The division between macro- and meiofauna was based on size and not on genera. Foraminifera are usually considered to be part of meiofauna, but in our samples of approx. 78 mL sediment, up to 100 specimens were retained on the 500 µm

BGD
10, 10399–10428, 2013

sieve. Residues retained on both mesh sizes, containing the fauna and some sediment particles, were then hand-picked under a binocular microscope and the fauna was divided in: branched and shelled Foraminifera, soft-bodied protists (both Gromiids and Allogromiids), Polychaetes, *Linopherus sp.*, nematodes and "other" (mostly crustaceans. The fauna was transferred into pre-weighed silver cups, oven-dried (50 °C), decarbonated with 10 % HCl (slow addition for Foraminifera and checked under binocular to ensure that bubbling had finished) and again oven-dried. The silver cups were then weighed to establish the dry-weight of the fauna and pinched closed. The samples were then analyzed for carbon and nitrogen concentration and $\delta^{13}C$ value with a Thermo Electron Flash EA 1112 analyzer (EA) coupled to a Delta V. Faunal biomass was determined via dry weight and C content values from the IRMS, combined with measurements of faunal abundance through counting all specimens in the faunal sediment sample (78 mL) under the binocular.

2.8 Uptake calculations

The relative uptake of the isotope tracer is presented in the $\Delta\delta^{13}C$ notation, which represents the enrichment in $\delta^{13}C$ of the sample in excess of its natural background value ($\delta^{13}C_{background}$), and is calculated as

$$\Delta\delta^{13}C_{sample} = \delta^{13}C_{sample} - \delta^{13}C_{background} \quad (1)$$

The ^{13}C enrichment in at % (E) is calculated as

$$E = F_{sample} - F_{control} \quad (2)$$

where

$$F = \frac{^{13}C}{^{13}C + ^{12}C} = \frac{R}{R+1} \quad (3)$$

BGD
10, 10399–10428, 2013

and

$$R = \left(\frac{\delta^{13}\mathrm{C}}{1000} + 1\right) \times R_{\mathrm{ref}} \quad (4)$$

with $R_{\mathrm{ref}} = 0.01118$. The uptake of ^{13}C tracer (I, µg tracer ^{13}C m^{-2}) is then calculated as the product of E and biomass. The total uptake of the DOM and POM substrates (µg tracer C m^{-2}) for both bacteria and fauna was then calculated according to Moodley et al. (2005a), by dividing the total ^{13}C tracer uptake (I) with the fractional abundance of ^{13}C in the tracers (i.e. 0.2 for POM, 0.18 for DOM). Please note that the presented data on relative and total uptake are calculated for each individual experimental core and then averaged. Biomass values are however the average of all cores (i.e. all experimental and background cores per station) since the larger area covered implies a better biomass estimate.

2.9 Respiration measurements

Water samples of ∼ 2 mL for analysis of DIC (dissolved inorganic carbon) from the CO_2-traps (changed every 3 days) and the overlying water of the incubated cores were taken with a sterile plastic syringe, filtered on a GF/F filter attached to the syringe and injected into helium pre-flushed 5 mL glass vials, were sealed with crimp-cap with rubber septum. DIC samples were immediately acidified with 99 % H_3PO_4 (10 µL per mL sample) to stop biological activity and vials were stored upside down at 4 °C until analysis in the laboratory (∼ four weeks after sampling). Shortly before analysis, each vial was further acidified to convert any residual bicarbonate into CO_2, which then accumulates in the vial headspace. The headspace was sampled using a glass syringe and CO_2 concentration and isotope ratio of the gas were measured on a Thermo Electron Flash EA 1112 analyzer (EA) coupled to a Delta V isotope ratio mass spectrometer (IRMS). Total respired ^{13}C-DIC was determined by summing the values obtained from the overlying water and CO_2 trap. The second CO_2-trap in succession showed no to

BGD
10, 10399–10428, 2013

very limited ^{13}C enrichment in the DIC, which indicated that all DIC had been trapped and that the data from the second trap could safely be ignored in the calculations.

3 Results

3.1 Sediment

The sediment was very different between the 2 stations. SToutOMZ was mainly composed of light brown-gray and very compact clay, whereas at STOMZ it was dark brown-black, watery and fluffy, poor in clay but with a high content of foraminiferan shells and diatom frustules. The layering and burrows were still intact, indicating that no alteration of the sediment occurred during sampling and retrieval. The total organic carbon content and C : N ratio were higher inside the OMZ, whereas the $\delta^{13}C$ and $\delta^{15}N$ of the sediment inside and outside the OMZ were comparable (Table 1).

3.2 Benthic biomass

Biomass data per layer and station of both incubated and background cores are shown in Fig. 2 as averages among treatments to account for sediment patchiness. Bacterial biomass was 1000 and 1600 mg C m^{-2} respectively in SToutOMZ and STOMZ, meiofaunal nematode biomass was 19 and 13 mg C m^{-2}, meiofaunal-sized shelled foraminiferan biomass was 42 and 38 mg C m^{-2}. Macrofaunal-sized shelled foraminiferan biomass accounted for 118 and 183 mg C m^{-2} for STOUT OMZ and STOMZ respectively, polychaetes biomass was 87 and 897 mg C m^{-2} with *Linopherus sp.* the most abundant species in STOMZ. Macrofaunal nematodes accounted for 17 mg C m^{-2} in SToutOMZ but were found only in background cores at low biomass in STOMZ, macrofaunal branched foraminifera and soft-bodied protists were found only in SToutOMZ where they accounted for 208 and 497 mg C m^{-2}, respectively. Other eukaryotes accounted for 0.2 mg C m^{-2} and were found only in SToutOMZ.

BGD
10, 10399–10428, 2013

3.3 OM incorporation

Incorporation into biota of the two ^{13}C labeled OM types was evident in both treatments, although the level of enrichment differed per station, benthic group and depth layer (Table 2 and Fig. 3).

At STOMZ, the biota in the upper layer (0–2 cm) accounted for only a small part (3247 µg C m^{-2} or 12 % of the total uptake) of the POM uptake: bacteria incorporated 2181 µg C m^{-2}, meiofaunal nematodes 36.8 and shelled foraminifera 1028 µg C m^{-2}, macrofaunal shelled foraminifera incorporated 0.13 µg C $m^{-2}$and *Linopherus sp.* accounted for 1.18 µg C m^{-2}. Almost all the POM incorporation took place in the deeper 2–4 cm layer (23 000 µg C m^{-2}or 87 % of the total uptake). Meiofaunal nematodes accounted for 2.66 µg C $m^{-2}$and shelled foraminifera for 6.55 µg C m^{-2}, macrofaunal shelled foraminifera accounted for 4.83 µg C m^{-2}, polychaetes for 6133 µg C m^{-2} and *Linopherus sp.* for 16 807 µg C m^{-2}. The bacterial contribution to POM uptake in this deeper layer was negligible. DOM incorporation was strongly dominated by bacteria and thereby clearly different from that of the POM substrate. In the upper layer, most of the total uptake took place 12 314 µg C m^{-2} (87 %): bacteria incorporated 12 312 µg C m^{-2}, followed by meiofaunal nematodes with 2.33 µg C m^{-2}; macrofaunal shelled foraminiferans incorporated 0.02 µg C m^{-2} and *Linopherus sp.* 0.05 µg C m^{-2}. Meiofaunal shelled foraminiferan contribution was negligible. In the deeper layer, 2–4 cm, the uptake was much lower (1818 µg C m^{-2} or 13 %): bacteria again clearly dominated uptake (1803 µg C m^{-2}), while meiofaunal shelled foraminifera accounted only for 8.4 µg C m^{-2}, meiofaunal and macrofaunal nematodes had negligible uptake and macrofauna *Linopherus sp.* accounted for 6.1 µg C m^{-2}.

At SToutOMZ, the largest part of the POM uptake was found in the upper layer: bacteria incorporated 466 µg C m^{-2}, meiofaunal shelled foraminifera 2.06 µg C m^{-2}, macrofaunal nematodes 0.42 µg C m^{-2}, other groups showed negligible uptake. In the deeper layer, only 0.6 % of the total POM was taken up by meiofaunal shelled foraminifera (1.47 µg C m^{-2}) and macrofaunal nematodes (1.80 µg C m^{-2}). DOM uptake in the upper

BGD
10, 10399–10428, 2013

layer was dominated by bacteria (3637 $\mu g\,C\,m^{-2}$), with negligible uptake by the other groups (< 0.01 $\mu g\,C\,m^{-2}$). This pattern was different in the deeper layer: bacteria incorporating 805 $\mu g\,C\,m^{-2}$, meiofaunal shelled foraminifera 63.7 $\mu g\,C\,m^{-2}$, macrofaunal shelled foraminifera 1.94 $\mu g\,C\,m^{-2}$and polychaetes 2.63 $\mu g\,C\,m^{-2}$.

3.4 Respiration

Respiration of POM at STOMZ was twice as high as compared to DOM respiration, 54.5 versus 26.9 $mg\,C\,m^{-2}$, respectively. The same pattern was seen at SToutOMZ, where respiration of POM and DOM were 6.82 and 2.07 $mg\,C\,m^{-2}$, respectively. Most of the POM and DOM tracers was not processed within the 7 days incubation time, but respiration was the dominant fate of processed DOM and POM at both stations (Fig. 4), accounting for up to 13.6 % and 6.73 % of the added tracer on average for STOMZ POM and DOM treatment and 6.80 % and 2.07 % for SToutOMZ (Fig. 4).

4 Discussion

In most environmental settings, the majority of the OM that reaches the ocean floor is used by the benthic community for biomass production and respiration (Burdige, 2006). This processing is thought to occur essentially along two pathways in the benthic food web. The POM pathway involves metazoan ingesting of particulate detritus, while consortia of bacteria hydrolyze POM to DOM first, before taking it up. The DOM pathway involves the microbial incorporation of DOM directly, or after hydrolysis. Microbial carbon, produced through either the POM or DOM pathway, can be transferred to higher trophic levels via predation and grazing in accordance with the microbial loop concept. Woulds et al. (2009) reviewed isotope tracer experiments and showed that all benthic size classes are involved in the POM pathway, in shallow and deep ecosystems, spanning from low to high activity communities and from oxic to suboxic environments. The POM uptake rates in our experiments (Table 2 and Fig. 3), both here and in a similar

BGD
10, 10399–10428, 2013

work (Pozzato et al., 2013), confirm that all size classes take up recently deposited phytodetritus in Arabian Sea sediments. The biomass values of bacteria, protists and fauna in our stations (Fig. 2) were comparable to other deep-sea settings (Moodley et al., 2002, 2005b; Witte et al., 2003b; Woulds et al., 2009; Hunter et al., 2012), which confirms that the benthic community in Arabian Sea sediments underlying oxic and suboxic bottom water is well developed and active.

Although one decade of isotope tracer experiments has established that phytodetritus-derived carbon eventually ends up in all benthic size classes (Woulds et al., 2009), we have little understanding whether this represents direct access of consumers to POM and therefore direct incorporation of the tracer, or whether the POM uptake by fauna is mediated by bacteria. Here we directly address the question by focusing on the carbon flow in parallel incubations using complex ^{13}C enriched DOM and POM substrates and target both microbes and fauna.

In our experiments, the DOM tracer was quickly incorporated by bacteria but no appreciable uptake was seen by benthic fauna (Figs. 3 and 4). This indicates limited bacterivory and the comparison of relative labeling ($\Delta\delta^{13}$C, Table 2) of bacteria versus their potential consumers in other ecosystems (Hall and Meyer, 1998; Van Oevelen et al., 2006b) supports this finding. Few studies (Lee et al., 1966; Delaca et al., 1981; Delaca, 1982) reported foraminifera feeding directly on dissolved organic carbon. Our StoutOMZ samples also showed some enrichment in foraminifera (Fig. 3), thus we cannot exclude direct DOM assimilation or transfer through bacterivory to protists, the latter also suggested by Van Oevelen et al. (2006b) although in relative low amounts. We limited our analysis of the microbial community to bacteria because in a companion study conducted at the same stations, Lengger et al. (2013b) showed that only bacteria and not archaea utilized the ^{13}C enriched POM and DOM, indicating bacteria as dominant active microbial group. Our findings therefore show that, at least in the short term, in the DOM pathway bacteria were not a principal food source for the fauna and that bacterial carbon was not transferred up the food web. Therefore we infer that the fauna uptake in our POM experiments, and most likely in other isotope tracer experiments,

BGD
10, 10399–10428, 2013

must also be due to direct ingestion of the POM substrate rather than ingestion of bacterial biomass. In the POM treatment, the $\Delta\delta^{13}C$ values of fauna are much higher than those of bacteria (Table 2), further supporting that tracer incorporation occurred via direct substrate ingestion.

Kemp (1990) reviewed the fate of benthic bacterial production in shallow/soft sediments and concluded that likely only a small fraction of bacterial production enters the macrofaunal food web (directly and indirectly) and that most bacterial production is remineralized and respired by a microbial food web. Later predation studies (Hondeveld et al., 1992; Starink et al., 1994; Hamels et al., 2001) further debunked the microbial loop theory and Pomeroy's ideas by not finding evidence of bacterial ingestion by their "thought to be" main grazers, protozoa, suggested as link between bacteria and fauna. The limited bacterial-derived carbon transfer was confirmed experimentally by Van Oevelen et al. (2006a, b) who used in situ stable isotope pulse-chase experiments and modeling in a tidal mudflat. They concluded that some bacterial production was lost to the sediment via exchange processes and grazing by meio- and macrobenthos, but that its major fate was mortality (65 %), which inducing recycling of bacterial biomass in the sediment. The same studies reported also that only a small portion (up to 11 %) of the faunal carbon requirements was met by bacterivory, irrespective of dwelling depth and organism size. Hence, they concluded that intertidal meio- and macrofauna depend primarily on carbon sources other than bacteria. Nomaki et al. (2006) conducted feeding experiments with deep-sea foraminifera using ^{13}C-labeled bacteria and algae and found that these protozoa selectively ingested algae or randomly ingested sedimentary organic matter. No selective feeding on bacteria was observed, because bacteria were either not or to a very limited extent assimilated. Guilini et al. (2010) conducted similar experiments in the Arctic targeting nematode feeding habits and reached similar conclusions: bacteria were not a major food source for nematodes and the very limited amount of ^{13}C incorporated could not be attributed to bacterivory. These results by Van Oevelen et al. (2006a, b), Guilini et al. (2010) and Nomaki et al. (2006) support Kemp's conclusion that bacteria are not a major food source for protists and meio- and

BGD
10, 10399–10428, 2013

macrofauna and that faunal carbon requirements are not met by bacterial production. These and our experimental results disagree with other studies (Vanreusel et al., 1995; Iken et al., 2001; Hoste et al., 2007) that suggested transfer of carbon from bacteria to nematodes via direct predation from positive correlations between bacterial density and nematodes abundance in the deep-sea. Along this line, Ingels et al. (2010) found a preferential uptake of bacteria versus phytodetritus-derived carbon by nematodes, but the isotope enrichment of the nematodes was so low that the authors concluded that the contribution of nematodes to benthic mineralisation was limited in deep polar seas. Hence, even though nematodes might be bacterivorous, upwards transfer of bacterial derived carbon via nematodes appears to be minimal.

It has been shown that bacterial standing stocks along a depth gradient of 0–6000 m appears quite stable in sediments (Rex et al., 2006). Hence, if it's not grazing controlling bacterial populations in sediments, then some other mechanism must be responsible. Recently Danovaro et al. (2008) suggested that viral infection controls bacterial production. In their recent review Rowe and Deming (2011) finally proposed a paradigm shift that is in line with most isotope tracer studies. Free-living heterotrophic microbes in marine sediments would play only a minor role in metazoan food webs, providing only a small fraction of metazoans nourishment.

5 Conclusions

Accumulating evidence from the literature and our experimental results suggest strongly that bacteria are a carbon sink in the benthic food web of the Arabian Sea OMZ sediments because no appreciable carbon transfer from bacteria up the food chain to meio- and macrofauna occurs via predation or grazing. This also implies that the POM and DOM processing pathways in this system are separated. The DOM pathway is limited to bacterial exploitation, since no other group showed any uptake of this resource, and no transfer of DOM-derived carbon via bacterial grazing is observed, thus making this processing route a dead end. Within the POM pathway, there is com-

BGD
10, 10399–10428, 2013

petition for food, since bacteria as well as various faunal groups take up this resource, as shown in many short-term experiments. Similarly to what happens with the DOM though, once POM is taken up by bacteria it is lost for faunal secondary production. Protists could have grazed upon bacteria to a minor extent but we could not investigate such predation, due to present lack of technical tools to do so in intact sediment cores. Our results from StoutOMZ indicate that direct DOM uptake by foraminifera may occur, as also found by others, which when predated by bigger fauna, might be an alternative route for carbon transport along the food chain. Evidently, there is great need for future investigation for the role of protozoans and protists in sedimentary food webs to be able to further constrain the apparently weak link between bacteria and protozoan and metazoan consumers in marine sediments.

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10, 10399–10428, 2013

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BGD
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BGD
10, 10399–10428, 2013

Table 1. Station locations, environmental parameters, water and sediment characteristics of the two sampling stations STOMZ and SToutOMZ.

	STOMZ	SToutOMZ
Position	22° 32.9′ 64° 02.4′	22° 18.5′ 63° 24.5′
Depth	885 m	1791 m
Bottom water		
Temperature °C (CTD sensor)	10	4
Salinity (CTD sensor)	34.8	34.9
Dissolved O_2 µmol kg^{-1} (CTD sensor)	2	45
Sediment		
Median grain size µm (0–3 cm)	35.4	16.5
% Total organic carbon (0–3 cm)	6.38	1.03
C : N ratio (0–3 cm)	9.75	7.87
δ^{13}C (‰)	−21.5	−20.0
δ^{15}N (‰)	8.04	8.68

BGD
10, 10399–10428, 2013

Table 2. Relative uptake for POM and DOM treatment. "n.f." means that no specimen of the group was found in the core layer. The terms "Soft bodied protists" represents Gromiids and Allogromiids.

	Relative Uptake $\Delta\delta^{13}$C ‰	Relative Uptake $\Delta\delta^{13}$C ‰
	STOMZ POM	STOMZ DOM
Bacteria		
0–2	80 ± 23	210 ± 46
2–4	0 ± 0.0	65 ± 26
Meiofauna		
Nematodes		
0–2	69 ± 46	5.9 ± 10
2–4	16 ± 5.6	0.4 ± 0.9
Shelled foraminifera		
0–2	685 ± 404	3.6 ± 3.4
2–4	23 ± 6.6	9.3 ± 0.8
Soft-bodied foraminifera		
0–2	n.f.	n.f.
2–4	n.f.	n.f.
Macrofauna		
Shelled foraminifera		
0–2	18 ± 17	5.2 ± 2.7
2–4	1.1 ± 0.3	11 ± 10
Linopherus sp.		
0–2	44 ± 44	1.5 ± 1.5
2–4	136 ± 116	11 ± 9.6
Polycahetes		
0–2	185 ± 167	n.f.

BGD
10, 10399–10428, 2013

Table 2. Continued.

	Relative Uptake $\Delta\delta^{13}C$ ‰	Relative Uptake $\Delta\delta^{13}C$ ‰
	SToutOMZ POM	SToutOMZ DOM
Bacteria		
0–2	13 ± 2.0	40 ± 3.3
2–4	no uptake	26 ± 26
Meiofauna		
Nematodes		
0–2	no uptake	1.8 ± 0.0
2–4	no uptake	no uptake
Shelled foraminifera		
0–2	3.9 ± 1.8	24 ± 20
2–4	0.6 ± 0.6	40 ± 39
Soft-bodied foraminifera		
0–2	n.f.	n.f.
2–4	n.f.	n.f.
Macrofauna		
Nematodes		
0–2	0.8 ± 0.2	2.2 ± 2.0
2–4	n.f.	2.5 ± 1.6
Shelled foraminifera		
0–2	0.2 ± 0.0	0.4 ± 0.2
2–4	n.f.	0.5 ± 0.5
Branched foraminifera		
0–2	no uptake	0.8 ± 0.8
2–4	n.f.	n.f.
Soft bodied foraminifera		
0–2	1.0 ± 1.0	0.3 ± 0.2
2–4	n.f.	6.0 ± 6.0
Polychaetes		
0–2	1.0 ± 1.0	0.3 ± 1.0
2–4	7.3 ± 7.3	0.5 ± 0.4

BGD
10, 10399–10428, 2013

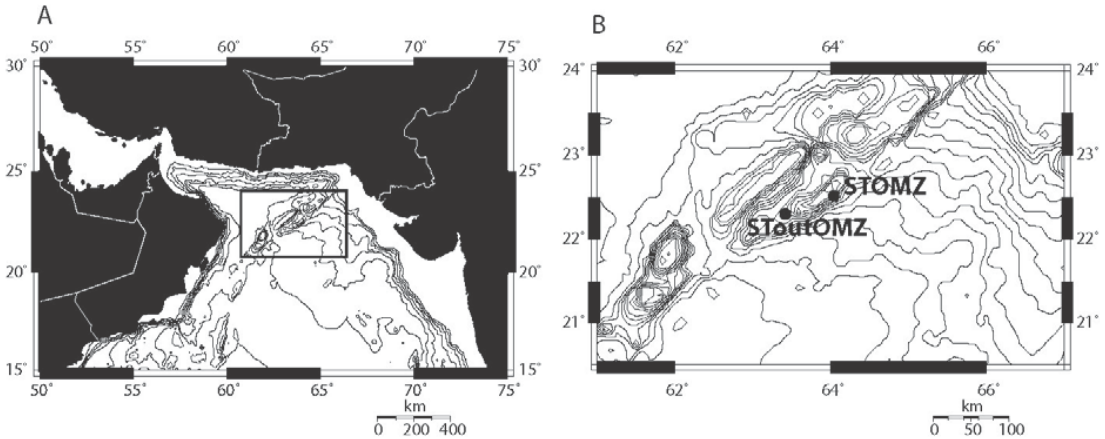

Fig. 1. The Northern Arabian Sea **(A)** and the sampling areas STOMZ and SToutOMZ indicated on the Murray Ridge **(B)**.

BGD
10, 10399–10428, 2013

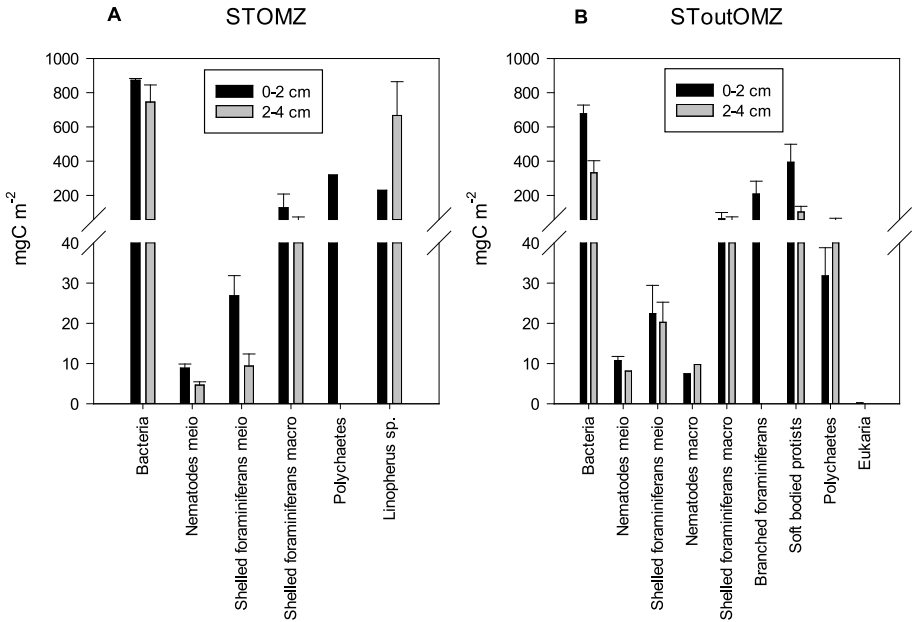

Fig. 2. Group-specific biomass presented per station. Values are averages of all cores, background and incubated ones, both treatments, to better account for heterogeneity.

BGD
10, 10399–10428, 2013

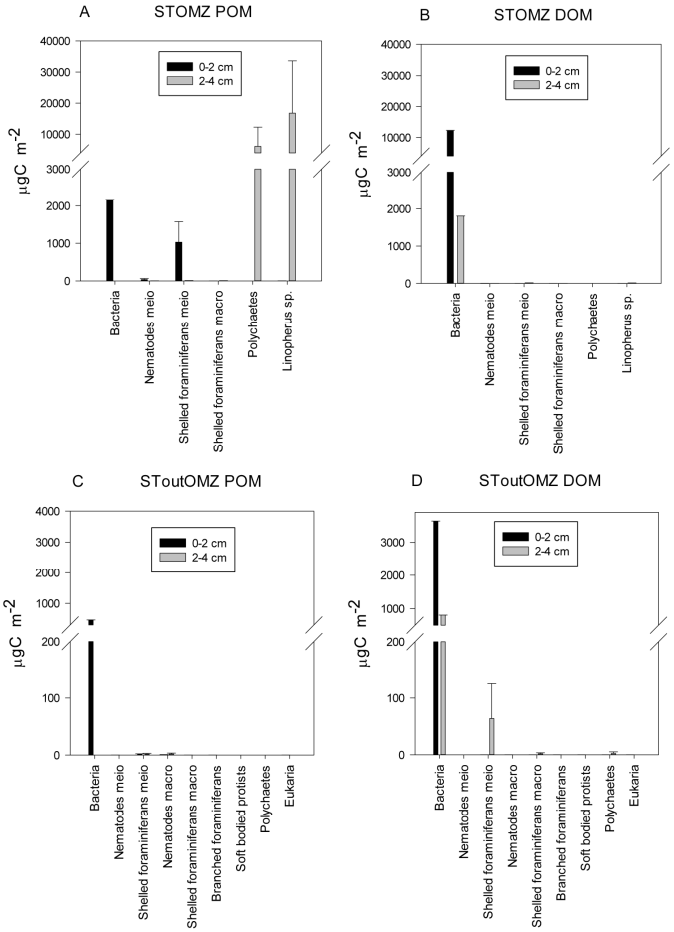

Fig. 3. Total tracer C incorporation in the stations divided per treatment. The term “soft bodied protists” represents Gromiids and Allogromiids.

BGD
10, 10399–10428, 2013

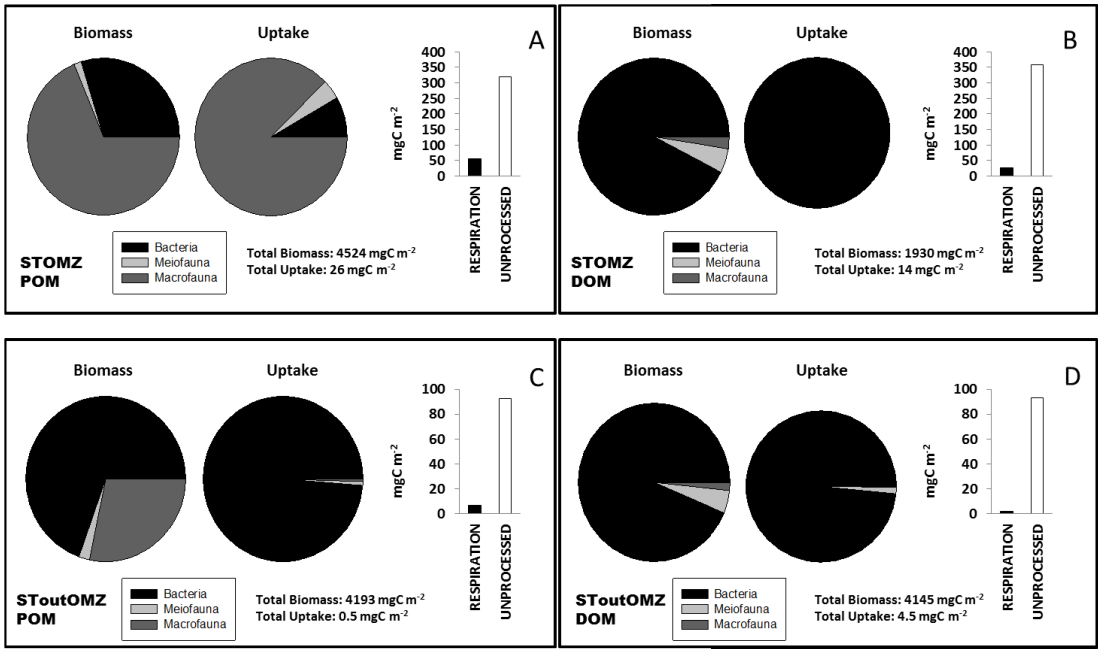

Fig. 4. Comparison between stations and treatments and overview of the benthic community structure and functioning. Biomass values are calculated per treatment and whole core, to allow direct comparison with uptake values.

BGD
10, 10399–10428, 2013