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Uptake of phytodetritus by benthic foraminifera under oxygen depletion at the Indian Margin (Arabian Sea)

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Abstract

Benthic foraminifera in sediments on the Indian margin of the Arabian Sea where the oxygen minimum zone (OMZ) impinges on the continental slope are exposed to particularly severe levels of oxygen depletion. Food supply for the benthic community is high but delivered in distinct pulses during upwelling and water mixing events associated with summer and winter monsoon periods. In order to investigate the response by benthic foraminifera to such pulsed food delivery under oxygen concentrations of less than 0.1 mL L^{-1} (4.5 µmol L^{-1}), an in situ isotope labeling experiment (^{13}C, ^{15}N) was performed at the western continental slope of India at 540 m water depth (OMZ core region). The assemblage of living foraminifera (> 125 µm) in the uppermost centimeter at this depth is characterized by an unexpectedly high population density of 3982 ind. 10 cm^{-2} and a strong dominance by few calcareous species. For the experiment, we concentrated on the nine most abundant taxa, which constitute 93 % of the entire foraminifera population at 0–1 cm sediment depth. Increased concentrations of ^{13}C and ^{15}N in the cytoplasm indicate that all investigated taxa took up the labeled phytodetritus during the 4 day experimental phase. In total, these nine species had assimilated 113.8 mg C m^{-2} (17.5 % of the total added carbon). The uptake of nitrogen by the three most abundant taxa (*Bolivina* aff. *B. dilatata*, *Cassidulina* sp., *Bulimina gibba*) was 2.7 mg N m^{-2} (2 % of the total added nitrogen) and showed the successful application of ^{15}N as tracer in foraminiferal studies. The short-term response to the offered phytodetritus varied largely among foraminiferal species with *Uvigerina schwageri* being by far the most important species in short-term processing whereas the most abundant taxa *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. showed comparably low uptake of the offered food. We suggest that the observed species-specific differences are related to individual biomass of species and to specific feeding preferences. The high numbers of living foraminifera and their rapid response to deposited fresh phytodetritus demonstrate the importance of foraminifera in short-term carbon cycling under oxygen-depleted conditions. We propose that foraminifera at the studied site benefit

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from unique adaptations in their metabolisms to nearly anoxic conditions as well as from the exclusion of macrofauna and the resulting relaxation of competition for food and low predation pressure.

1 Introduction

Most benthic deep-sea organisms feed on the organic matter that settles onto the sea floor and therefore depend on this material as their food source. Phytoplankton detritus (phytodetritus), which is a main food source for benthic foraminifera (Gooday and Hughes, 2002; Lambshead and Gooday, 1990), typically arrives at the sea floor in pulses delivered from seasonal surface production (Beaulieu and Smith, 1998; Gage and Tyler, 1991; Gooday, 2002; Gooday and Turley, 1990). Benthic foraminifera can respond very quickly to the pulses of phytodetritus to the sediment surface (Altenbach, 1992; Drazen et al., 1998; Enge et al., 2011; Gooday and Turley, 1990; Graf, 1989; Linke et al., 1995). Additionally, they are common inhabitants of marine sediments. Therefore, they play a quantitatively important role in short-term processing of phytodetritus on the floor of the world oceans (Moodley et al., 2002).

Oxygen-depleted water masses (oxygen minimum zones, OMZs) develop in areas with high surface production and limited water replenishment (Kamykowski and Zentara, 1990). These natural hydrographic features, characterised by dissolved oxygen concentrations $< 0.5\,mL\,L^{-1}$ ($22.3\,\mu mol\,L^{-1}$), are especially well developed at intermediate water depths in the North Pacific, the Arabian Sea, and the Bay of Bengal (Helly and Levin, 2004; Wyrtki, 1971). Where they impinge on continental margins at shelf to upper bathyal depths, strong bottom-water oxygen gradients are developed. Sediments rich in organic matter are typically associated with OMZs. Benthic organisms found within these sediments can benefit from this enhanced food supply, but they must be able to tolerate the very low oxygen concentrations that are permanently present in the core region of OMZs.

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An unusually high tolerance to hypoxia among eukaryotic benthos has been observed for benthic foraminifera in strongly oxygen-depleted areas such as the Southern California borderland basins, Scandinavian fjords, and OMZ sediments (Bernhard and Sen Gupta, 1999). Being able to perform respiration by denitrification in the absence of oxygen was first observed for two benthic species by Risgaard-Petersen et al. (2006). This surprising ability to accumulate nitrate and its respiration to dinitrogen gas was later confirmed in benthic foraminifera in OMZ sediments at the Chilean coast (Hogslund et al., 2008) and demonstrated in laboratory experiments (Pina-Ochoa et al., 2010). However, in at least one species, symbiotic bacteria appear to be responsible for respiring the nitrate, not the foraminifera (Bernhard et al., 2012). Since most other eukaryotic organisms, especially macrofauna, are not as tolerant to hypoxia as foraminifera (Josefson and Widbom, 1988), they often are absent from sediments at the core of the OMZ (Gooday et al., 2009). Due to their unique metabolism, combined with the absence of macrofaunal competition, foraminifera are thus able to proliferate under extreme low-oxygen conditions. In the OMZ sediments in the Arabian Sea, recent foraminifera are abundant components of the benthic community as observed in studies performed on the Pakistan margin (Gooday et al., 2009; Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007) and Oman margin (Gooday et al., 2000; Hermelin and Shimmield, 1990).

Their abundant occurrence in OMZ sediments, combined with the ability to utilize fresh labile organic matter and tolerate low oxygen concentrations, suggest that benthic foraminifera might play an important role in carbon cycling in OMZ sediments in the Arabian Sea. In-situ feeding experiments using ^{13}C-labeled food have been shown to be an effective approach to study the metabolic response of foraminifera to phytodetritus deposition under natural conditions. In OMZ sediments on the Pakistan margin, Woulds et al. (2007) and Andersson et al. (2008) performed a series of experiments along a depth transect (140–1850 m), demonstrating variable responses of the foraminiferal community to artifical phytodetritus at different water depths. All of the existing in situ feeding experiments on foraminifera, including those in the OMZ influenced sediments

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off Pakistan, were carried out at oxygen concentrations $> 0.17\,mL\,L^{-1}$ ($7.6\,\mu mol\,L^{-1}$). Under these conditions, the advantages of nitrate metabolism in foraminifera and the exclusion of competition by macrofauna are not yet obvious. Therefore, the aim of our study was to investigate benthic foraminifera and their response to phytodetritus under almost anoxic conditions ($< 0.1\,mL\,L^{-1}$) by performing an in situ feeding experiment in an OMZ core region.

We conducted a stable isotope labelling experiment on the Indian margin in order to follow the fate of organic matter in form of the labeled diatom *T. weissflogii* in single species of foraminifera. In addition to the ^{13}C tracer, we simultaneously tracked ^{15}N. This is the first foraminiferal study to utilise two stable isotope tracers. Hunter et al. (2012) had previously applied this approach successfully to macrofauna on the Indian margin.

2 Material and methods

2.1 Study area

This experiment was carried out as a part of an international study of benthic ecology, geochemistry and biogeochemical processes across the oxygen minimum zone on the Indian margin in the Arabian Sea. The collaborative research cruise "YK08-11" aboard the R/V *Yokosuka* of the Japan Agency for Marine–Earth Science and Technology (JAMSTEC) took place between September and November 2008.

Our experiment was carried out from 9 to 13 October 2008 (post-monsoonal period) during the first leg of the cruise at 540 m water depth on the Indian margin (16°58′ N and 71°55′ E). At this site, the sea floor is influenced by an OMZ water body that impinges on the continental margin of India at water depths of about 120–1100 m (Helly and Levin, 2004). Therefore, the investigated depth of 540 m is located in the core region of the Indian margin OMZ and corresponds to station T1 540 in Hunter et al. (2011). The area of interest shows a moderate to high average yearly productivity of > 0.5–

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0.75 g C m^{-2} d^{-1} (Babu et al., 1999). The intense productivity in the Arabian Sea is driven by monsoon-induced upwelling in summer (SW monsoon) and deep mixing of water masses in winter (NE monsoon), resulting in distinctly seasonal surface primary production and organic matter flux. Environmental data at this site were obtained during dives by the submersible *Shinkai* 6500 (JAMSTEC, 2007) and derive from CTD recordings and measurements with an optical oxygen sensor (Hunter et al., 2011). The sampling site was characterised by in situ oxygen concentrations of 0.02 mL L^{-1} (0.9 µmol L^{-1}) and 0.05 mL L^{-1} (2.4 µmol L^{-1}) and an average temperature of 12 °C (Table 1).

2.2 Preparation of ^{13}C and ^{15}N-labeled algae

Before the cruise, an axenic clone of the diatom *Thalassiosira weissflogii* (CCMP, Bigelow Laboratories for Ocean Science, USA) was cultured in artificial seawater and *L*1 culture medium, enriched with 99 %-^{13}C-bicarbonate ($NaH^{13}CO_3$, Cambridge Isotope Laboratories, Inc., USA) and 50 %-^{15}N-sodium nitrate ($Na^{15}NO_3$, Cambridge Isotope Laboratories, Inc.). Algae were cultured at 16 °C for 28 d (light: dark = 16 : 8; 35 PSU), harvested by centrifugation (500 G; 30 min), sonicated (2000 Hz; 5 min) and rinsed three times in ultrapure water to remove inorganic salts and dissolved organic carbon. Harvested algae were lyophilised (−60 °C; −0.0001 mbar; 24 h) to produce phytodetritus containing 27.75 atom%^{13}C and 33.70 atom%^{15}N (Hunter et al., 2012).

2.3 Experimental setup

For the feeding experiment we used Oceanlab spreader systems. This in situ mesocosm consists of a transparent polycarbonate tube (25 cm inner diameter, 30 cm length) and a lid. More detailed information about the construction can be found in Hunter et al. (2012). On 9 October 2008, three spreaders were pushed straight into the undisturbed sea floor by the manipulator arm of the manned submersible *Shinkai* 6500, until standing firmly upright. The spreader lid held a container with the suspension of *T.*

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weissflogii (650 mg C m^{-2}, 160 mg N m^{-2}), which was applied to the enclosed sediment surface by pushing a plunger that released the algae. The spreader lid was removed several hours after the deployment of the spreader to ensure that the algae slurry had completely deposited onto the sediment surface. Incubation of the enclosed sediment surface with the labeled diatoms lasted four days. The amount of food applied and the open system with continuous water exchange guaranteed optimal simulation of natural conditions.

After four days, one push core for foraminiferal analysis (plastic tubes, 70 mm inner diameter) from the inside of each spreader was recovered by the submersible and the Oceanlab spreader system was removed. On board of the research vessel, the push cores were immediately horizontally sliced in 1 cm intervals down to 3 cm depth. Each slice was frozen at −80 °C and then stored at −25 °C until analysed. For our study, the assemblage and the isotope composition of foraminifera from the 0–1 cm layer from one push core were investigated. We concentrated on the upper 1 cm of the push core as the living foraminifera assemblage in OMZ sediments of the Arabian Sea is largely restricted to the upper sediment layer (e.g. Jannink et al., 1998; Larkin and Gooday, 2009; Maas, 2000; Schumacher et al., 2007). The need for between 200 and 1500 individuals for a single isotope measurement made replication difficult given the available time and manpower. However, we were able to analyse carbon in duplicate batches for four species (Table 2).

2.4 Sample preparation

In the laboratory at the University of Tübingen, the 0–1 cm sediment sample was thawed and washed over a mesh (125 µm) with artificial seawater (composition see Enge et al., 2011). After sieving, the residue was frozen at −25 °C until further processing. Separation of living and dead specimens was based on visual assessment of cytoplasm presence and the degree to which it filled the test (Moodley et al., 2002; Nomaki et al., 2005, 2006; Sweetman et al., 2009). Foraminifera were wet-picked from

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the residue in a petrie dish, which was placed on a cooling plate for the entire duration og the picking process. Foraminifera were identified to species level as far as possible. The entire 0–1 cm sample was investigated for the faunal composition of living foraminifera. The nine most abundant taxa were each represented by enough specimens and biomass for stable isotopic analyses. To meet the minimum of biomass requirements, individuals of one species were pooled. The required number of individuals varied among species according to size and biomass, the maximum number per silver cup being 1500 (Table 1).

Before processing, material for isotopic analysis, glassware and silver cups was combusted (450 °C, 5 h) and picking tools were cleaned with a mixture of Dichloromethane and Methane (1 : 1, *v* : *v*) to be free of organic contaminants. All foraminifera were carefully brushed and washed twice in filtered artificial seawater to ensure they were free from organic matter adhering on the outside of the test. After filling silver cups with 10 µL of filtered seawater, foraminifera were transferred into these cups with a brush. Subsequently, the filled cups were dried at 50 °C for several hours before adding hydrochloric acid (6.25 %) to ensure complete dissolution of carbonate. Because the decalcification process involves the production of carbon dioxide and can cause overflow of organic matter out of the silver cup, the transfer of foraminifera into cups had to be performed stepwise and not at once. Thus, transferring specimens to silver cups, heating and adding Hydrochloric acid had to be repeated until all calcareous parts of the foraminifera were dissolved. Finally, samples were kept at 50 °C for three days to allow complete drying.

2.5 Calculation of phytodetritus uptake

The total C and N content of foraminiferal cytoplasm as well as $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were measured using an elemental analyzer/isotope-ratio mass spectrometer (EA/IRMS) at SI Science Co., Ltd. (Japan). Hereafter, the ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$ will be expressed as atom% ^{13}C and atom% ^{15}N. Formulas given in this section apply to the calculation of carbon uptake. The assimilation of nitrogen was calculated in the

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same way, although with different standards and natural background values from carbon calculations.

Carbon isotope composition was measured against the international Vienna Pee Dee Belemnite standard (VPDB) and the nitrogen isotope composition relative to the atmospheric nitrogen. Differences between sample and standard are expressed in the δ-notation: $\delta^{13}\mathrm{C}\ [‰] = ((\mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{sample}}) / (\mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{VPDB}}) - 1) \times 1000$. Incorporation of ^{13}C and ^{15}N by foraminifera was defined as excess above background:

$$\mathrm{excess}_{\mathrm{foram}} = \left(\mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{sample}} - \mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{backgr.\ foram}}\right) / 100, \quad (1)$$

while

$$\mathrm{excess}_{\mathrm{algae}} = \left(\mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{alga}} - \mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{backgr.\ alga}}\right) / 100. \quad (2)$$

Natural isotope (background) signatures for benthic foraminiferal cytoplasm of $\delta^{13}\mathrm{C} = -20.3$ and $\delta^{15}\mathrm{N} = 8.0$ derived from Enge et al. (2011), Nomaki et al. (2005, 2006, 2008), and Sweetman et al. (2009). Where δ^{13}C values are available for different sediment depths and foraminiferal species, we used only data for calcareous species in the 0–1 cm layer. The diatom *Thalassiosira weissflogii*, which was used as the algal food source, shows natural signatures of $\delta^{13}\mathrm{C} = -21.2$ and $\delta^{15}\mathrm{N} = 4.9$ (Aberle and Malzahn, 2007).

Uptake (mg C) was calculated as the product of the excess in the sample and the total carbon/nitrogen content in the sample, divided by the excess of the labeled algae. Species uptake per sea-floor area (mg C m^{-2}) was obtained by dividing the uptake per sample (mg C) by the number of analysed specimens (Table 2) and then multiplying the individual uptake (mg C ind.$^{-1}$) by the abundance (ind. m^{-2}) found in the uppermost centimeter. The fraction (f) of carbon and nitrogen originating from added alga material in the TOC/TON of the analysed foraminifera was calculated after Nomaki et al. (2006):

$$f_{\mathrm{C}} = \left(\mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{sample}} - \mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{backgr.\ foram}}\right) / \left(\mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{alga}} - \mathrm{atom\%}^{13}\mathrm{C}_{\mathrm{backgr.\ alga}}\right).$$

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(3)

The calculated f_C also represents the biomass-normalized uptake of species, which is the same as the total C uptake per sample (mg C) divided by the TOC content of the sample (mg C). Because f values were very small, we used $f \times 100$ (%).

3 Results

3.1 Foraminiferal assemblage at 0–1 cm

The analysed sediment (volume 38.5 cm^3) yielded 15 322 foraminifera assumed to have been living at the time of sampling. This amounts to a population density of 3982 ind. 10 cm^{-3} in the uppermost cm at 540 m water depth. Abundances of taxa ranged between 0.3 and 1081 ind. 10 cm^{-3}. The assemblage consisted almost entirely of calcareous taxa (99.5 %). Agglutinated foraminifera represented the rest of the assemblage (0.5 %) while miliolids, allogromids, xenophyophores and soft-walled (agglutinated) foraminifera were not present in the > 125 µm fraction. The community of living foraminifera in the analysed size class was dominated by a small number of species. *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. were the numerically most important taxa with densities of 1015 and 1081 ind. 10 cm^{-3} (Fig. 1), accounting for 27 % and 25 % of the entire foraminiferal abundance, respectively. *Bulimina gibba* (10 %), *Ehrenbergina pacifica* (9 %), *Uvigerina peregrina* (8 %), *Epistominella rugosa* (5 %), *Hoeglundina* cf. *elegans* (4 %), *Uvigerina schwageri* (4 %), and *Lenticulina* spp. (2 %) were also abundant. In total, these nine taxa accounted for 93.5 % of the population density.

The TOC content of species (calculated from the total TOC in the sample and the analysed number of individuals) varied considerably among species, ranging from 0.1 to 1.4 µg TOC per individual on average, (Table 2). The lowest cytoplasmic TOC values were found in *Cassidulina* sp. and *B.* aff. *B. dilatata* whereas *U. schwageri* yielded the overall highest TOC content of all investigated taxa and was also largest in size. Based on the calculated individual TOC content and the total abundances of specimens in the

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uppermost cm, we estimated the mean individual TOC content of each taxon in relation to the area of sediment (hereafter referred to as species biomass). As shown in Fig. 1, species biomass exhibited a great variation between the nine foraminiferal taxa.

3.2 Response to added carbon

Because of the high dominance of a few taxa at the studied site within the OMZ, only the response of the most abundant species to the labeled algal material has been studied. In total, the cytoplasm of 7550 living individuals (Table 2) was analysed for $^{13}C/^{12}C$ (9 taxa) and $^{15}N/^{14}N$ (3 taxa). Measured $\delta^{13}C$ values of 115.5 ‰ to 9516.3 ‰ exceeded natural isotopic values (−20.3 ‰) substantially for all nine investigated species (Table 2). The total uptake (as product of individual uptake and abundance) after four days of incubation for all taxa is shown in Fig. 2 and varied considerably among the analysed species.

Total carbon uptake was highest for *U. schwageri* with 69.8 mg C m^{-2} (Table 3). *Bulimina gibba*, *Hoegludina* cf. *elegans* and *U. peregrina* exhibited similar uptake, ranging between 8.7 and 14.6 mg C m^{-2}. Lowest uptake (< 1 mg C m^{-2}) was observed for the two species *E. pacifica* and *E. rugosa*. After four days, the nine dominating taxa had taken up 113.8 mg C m^{-2}, which accounts for 17.5 % of the total added labeled carbon at the beginning of the experiment.

The uptake of labeled carbon per individual (representing an average value for all individuals of the species) varied considerably between the investigated taxa. On average, one single foraminifera ingested 71 ng C within the four days of incubation with a high variation between species. Lowest individual uptake was exhibited by *E. pacifica* with 1.6 ng C, while the C uptake by *U. schwageri* yielded 484 ng C per individual (Table 3). In order to test whether food uptake is a function of foraminiferal biomass, we calculated the biomass-normalized uptake, which represents the fraction (f_C) of the carbon originating from the labeled food in the cytoplasm of the analysed foraminifera. *U. schwageri* was the species with the highest labeled carbon content (36 %), followed

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by *Hoeglundina* cf. *elegans* (24 %), and *U. peregrina* (19 %). Lowest added carbon signal was calculated for *E. pacifica* with 0.7 % (Table 3).

3.3 Response to added nitrogen

Nitrogen isotope measurements were obtained for the three most abundant taxa (*B.* aff. *B. dilatata*, *Cassidulina* sp., and *B. gibba*). Uptake of labeled nitrogen was twice as high for *B. gibba* (1.4 mg N m^{-2}) as for *B.* aff. *B. dilatata* as well as for *Cassidulina* sp. (Table 3). The total uptake of nitrogen by the three taxa of 2.7 mg N m^{-2} represents 1.7 % of the applied 160 mg N m^{-2} at the start of the experiment. The same three taxa took up 19.1 mg C m^{-2}, which accounts for 2.9 % of the 650 mg C m^{-2}.

4 Discussion

4.1 Species-specific response to phytodetritus

Individual responses to the added phytodetritus varied considerably among the nine taxa investigated. These differences, combined with the differing abundances of species, yielded in a total per-species uptake that varied strongly between species (Table 3), from 0.5 mg C m^{-2} for *Lenticulina* spp. to 69.8 mg C m^{-2} for *U. schwageri*. Similar pronounced differences in short-term processing of phytodetritus between foraminiferal species under in situ experimental conditions have been also observed in the bathyal Sagami Bay (Kitazato et al., 2003; Nomaki et al., 2005), the abyssal North Pacific (Enge et al., 2011) as well as on the Carolina margin (Levin et al., 1999). We suspect that several factors contribute to the occurrence of species-specific uptake of fresh phytodetritus in an environment of sufficient food supply but hostile environmental conditions.

As the calculation of total per-species uptake (per area) in our study is based on individual abundances, we expected that the numerically dominating taxa *B.* aff. *B. dilatata* and *Cassidulina* sp. would show the highest uptake. However, uptake was lower

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than average for both taxa, contributing less to short-term carbon cycling than species that were far less common at this site. This observation shows that the abundance of a species does not control its total uptake of phytodetritus and other factors are responsible for species-specific differences in the utilization of fresh phytodetritus.

The rate of uptake of a species might to some extent be related to its biomass. In our study, *U. schwageri* not only demonstrated the highest uptake of all species (Fig. 2) as well as the largest individual and species biomass, it also showed the highest content of labeled food after the experiment (Fig. 3). Also, species with lower individual biomass (*Cassidulina* sp., *B*. aff. *B. dilatata*, *E. rugosa*) exhibited the lowest carbon uptake. On the other hand, *B. gibba*, *U. peregrina*, and *Hoeglundina* cf. *elegans* which were feeding well, showed no correlation between biomass and uptake, although they fed on the labeled algae. Hence, a direct relationship between biomass and uptake is not apparent for all species, and uptake also reflects additional parameters.

As suggested by Nomaki et al. (2005) for foraminiferal populations from Sagami Bay, feeding preferences might play a very important role in the rate of uptake. In the Eastern Arabian Sea diatoms are the dominating element of the phytoplankton community throughout the year (Sawant and Madhupratap, 1996). In our experiment we used the cosmopolitan diatom species *Thalassiosira weissflogii* as a food source. The very high uptake by *U. schwageri* could suggest a preference for these diatoms whereas *T. weissflogii* might not be the favorite food source for the species that demonstrated lowest uptake in our experiment, such as *E. pacifica* or *Lenticulina* spp. In the laboratory, Heinz et al. (2002) found higher numbers of individuals of foraminiferal species after feeding on *Amphiprora* sp. (diatom) and *Pyramimonas* sp. (green alga) than after feeding on *Dunaliella tertiolecta* (green alga), all three being common algae species. In another in situ experiment, Nomaki et al. (2006) were able to identify selective feeders and random feeders on phytodetritus and sedimentary organic matter. *Uvigerina akitaensis* was one of the phytophageous species that ingested phytodetritus selectively. Different feeding preferences among species could be of advantage in an environment

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where competition for space and food must be very high among foraminiferal individuals, considering the standing stock of about 4000 ind. 10 cm^{-3}.

In our study, *U. schwageri* showed highest uptake of all species by far; a third of this species' carbon content originated from labeled food. The association of the genera *Uvigerina* and *Bulimina* with areas of high productivity was suggested by Loubere and Fariduddin (1999), while *U. akitaensis* and *B. aculeata* dominated the foraminiferal response to phytodetritus in an in situ feeding experiment performed in the eutrophic Sagami Bay (Nomaki et al., 2005). The fact that uptake by *U. schwageri*, *U. peregrina*, and *B. gibba* was higher than that of other taxa in our experiment is consistent with these earlier observations. Woulds et al. (2007) reported that a *Uvigerina* species dominated short-term phytodetritus processing in the OMZ core on the Pakistan margin. These taxa seem to be highly adapted to high food concentrations and are able to react to and ingest large amounts of organic material very fast.

4.2 Impact of foraminifera on carbon cycling in OMZ sediments

Despite high interspecific differences in the uptake of food, all the investigated species demonstrated a positive reaction towards the presence of fresh phytodetritus within a very short amount of time. Within four days, foraminifera had taken up 114 mg C m^{-2} with *U. schwageri* as the most important contributor. Our results reflect the uptake of food by the nine most abundant species in the size fraction > 125 µm. As we have no uptake data for other species present at this sediment depth and excluded the size fraction < 125 µm, our results are minimum values of carbon uptake. Carbon uptake by the entire foraminiferal community must be higher and the impact on the benthic community utilization of fresh organic matter even greater.

The observed response to fresh phytodetritus during the experiment on the Indian margin shows that even under dysoxic conditions foraminifera are able to utilize food rapidly. In particular, *U. schwageri* ingested large amounts of labeled material and might be best adapted to the environmental conditions simulated by the experiment: the presence of fresh phytodetritus arriving in a pulsed event. That deep-sea foraminifera are

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able to react very quickly to offered organic matter has been observed during in situ feeding experiments by Kitazato et al. (2003), Nomaki et al. (2005), Enge et al. (2011), and Nomaki et al. (2011). Foraminifera at 2170 m depth in the North Atlantic ingested ~ 2 mg C m^{-2} within 35 h (Moodley et al., 2002). In Sagami Bay, *Uvigerina akitaensis* and *Bulimina aculeata* were the most important rapidly responding species, responsible for utilizing 31 mg C m^{-2} within 11 days (Nomaki et al., 2005). Comparison of uptake between foraminifera at our investigated site and in these previous studies is difficult because of major between-site differences in oxygen concentrations, food supply, or foraminiferal assemblage composition and abundances.

The only comparable experimental approach to investigating the response of foraminifera to phytodetritus deposition in an OMZ setting was undertaken on the Pakistan margin by Woulds et al. (2007) and Andersson et al. (2008). During the same cruise, ^{13}C-labeled phytodetritus was offered in situ and ex situ to the benthic community, including foraminifera, along a depth transect including OMZ influenced sediments (140–1850 m). At 300 m depth in the OMZ core, the uptake of the entire foraminiferal community after 5 days of incubation ranged between 6 and 20 mg C m^{-2}. These values are at least five times lower than observed in our experiment on the Indian margin at 540 m. Moreover, *Uvigerina* ex gr. *U. semiornata* dominated uptake on the Pakistan margin, rather than *U. schwageri*, as in our experiment. Since both experiments were carried out in a similar hypoxic habitat in the Arabian Sea, we expected foraminiferal uptake to be more similar. The different foraminiferal responses may result from differences in foraminiferal densities and water depth. The calculation of carbon uptake per area is based on the number of living foraminifera found at the study site. Abundances at 540 m on the Indian margin (3982 ind. 10 cm^{-3}) are much higher than at 300 m on the Pakistan margin (200–336 ind. 10 cm^{-3}). If densities on the Indian margin were only 336 specimens/10 cm^3, the estimated uptake of about 9 mg C m^{-2} would be very similar to the measured uptake on the Pakistan margin with 6–20 mg C m^{-2}. The observed high uptake on the Indian margin is hence probably a product of the large population densities of living foraminifera at this site. At the same time, our study site at 540 m

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depth is located in the center of the OMZ (Hunter et al., 2011) where oxygen concentrations are $< 0.1\,mL\,L^{-1}$ ($4.5\,\mu mol\,L^{-1}$) and macrofauna are absent (Hunter et al., 2012), whereas the site at 300 m investigated by Woulds et al. (2007) and Andersson et al. (2008) is in the upper part of the core region where oxygen conditions are not as stable and adaptation of foraminifera to environmental conditions might not be as strong as for foraminifera under constant hypoxic conditions (such as at 540 m on the Indian margin).

Our results indicate that benthic foraminifera are able to utilize organic matter under oxygen concentrations of $< 0.1\,L\,m\,L^{-1}$ as fast as in non-oxygen-depleted environments. This suggests that foraminifera in the OMZ core on the Indian margin must be highly adapted to low oxygen in order to be able to ingest large amounts of food. In eutrophic environments, foraminifera are adjusted to the presence of organic matter and do not need to activate their metabolism, as has been suggested by Nomaki et al. (2005) or Witte et al. (2003) to explain the delayed response to phytodetritus pulses of "starved" deep-sea foraminifera in oligotrophic environments. The higher uptake by foraminifera at our site in comparison to the Pakistan margin assemblage could also result from the absence of the macrofauna (Hunter et al., 2012). Where present on continental margins, macrofaunal organisms (polychaetes, nematodes,) are important consumers of phytodetritus, reacting very quickly to its deposition (Andersson et al., 2008; Blair et al., 1996; Hunter et al., 2012; Levin et al., 1999; Woulds et al., 2007). Due to the absence of macrofaunal animals, foraminifera at 540 m on the Indian margin are less exposed to competitors for food and space. Competition with meiofaunal metazoans at this depth is possible, but this cannot be assessed because relevant data are not available. Macrofauna assemblages at 800 and 1100 m depth on the Indian margin include polychaetes, nematodes, crustaceans, and molluscs (Hunter et al., 2012) of which some representatives are known to feed selectively on foraminifera (Lipps, 1983; Nomaki et al., 2008). There is no information about selective predation on foraminifera by other benthic organisms in this part of the Arabian Sea, although unselective predation by detritivores is believed to regulate foraminiferal densities (Goo-

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day, 1986; Lipps, 1983). Reduced predation pressure on foraminifera resulting from the absence of macrofauna at 540 m depth cannot be excluded and may have contributed to the high densities of foraminifera and their clear reaction to phytodetritus.

Their high abundance and ability to rapidly ingest large amounts of organic material suggests that benthic foraminifera must play a very important role in the early decomposition of sinking organic carbon in the core region of OMZ sediments. Other possible consumers of phytodetritus at our study site are bacteria, which we assume will exhibit higher uptake rates than foraminifera. In oxygen-depleted environments where high amounts of organic matter are present, bacteria are also very likely to occur in high numbers. In sediments from 300 m depth within the Pakistan margin OMZ, there was no uptake of ^{13}C tracer by macrofauna, which was represented by less than 0.5 g wet weight m^{-2} (Woulds et al., 2007). The largest pool of labeled carbon was respired (41 mg C m^{-2}) and uptake by bacteria was higher than by foraminifera (Andersson et al., 2008). While Moodley et al. (2002) found bacteria and foraminifera to account for 50 % of the short-term response to phytodetritus in the bathyal North Atlantic, Witte et al. (2003) reported low tracer uptake by foraminifera during the first week of an in situ experiment in the abyssal North Atlantic, but the highest uptake of carbon among all investigated benthic groups after 3 weeks. Apparently, the role of foraminifera in cycling of organic matter on the sea floor can show much variation between environments characterised by differing physico-chemical conditions (e.g. oxygen content, nutrient supply, water depth) and biological interactions (competition, predation), all of which can influence phytodetritus assimilation.

4.3 Uptake of nitrogen by foraminifera

The three foraminiferal taxa that were analysed for stable N isotopes all displayed high ^{15}N values after the experiment, indicating that they had ingested nitrogen and that ^{15}N can be used as a marker for food consumption. However, because analytical sensitivity is lower for nitrogen than for carbon, more foraminiferal biomass is required for the analysis of the nitrogen isotopic composition. Hence, the analysis of nitrogen uptake

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at species level requires high abundances of species or high individual biomass. For example, in our experiment we pooled 1500 living individuals of *Cassidulina* sp. for one measurement. Therefore, ^{15}N is highly suitable as a marker for species with high population densities whereas at abyssal or hadal depths its application could be hampered by the generally lower number of living foraminifera (e.g. Gooday, 1996; Ohkushi and Natori, 2001) compared to assemblages on continental margins.

Nitrogen uptake was positive for the three taxa investigated (*B.* aff. *B. dilatata*, *Cassidulina* sp., *B. gibba*) but was lower than observed for carbon and exhibited greater interspecific variations (Fig. 4). This might be due to the applied dose of both components at the beginning of the experiment. The phytodetritus (*T. weissflogii*) deployed at the sea floor contained 160 mg N m^{-2} and 650 mg C m^{-2}, and nitrogen and carbon uptake by the three foraminifera hence responds to 1.7 % and 2.9 % of the phytodetrital dose mass. Although the difference in the relative uptake of carbon and nitrogen was less than the absolute uptake, foraminifera still ingested almost twice the amount of carbon than nitrogen. Because this is the first dual labelling experiment that has been successfully conducted with foraminifera, comparisons are limited. The higher uptake of carbon than nitrogen by foraminifera contrasts with data for intertidal meio- and macrofauna in the North Sea (Rossi, 2007; Evrard et al., 2010). Rossi (2007) found that nitrogen was ingested faster and in greater quantities than carbon by the macrofauna, while Evrard et al. (2010) observed preferential ingestion of nitrogen by meiofauna. However, in contrast to the results of Rossi (2007), Evrard et al. (2010) observed that the macrofauna either assimilated more carbon than nitrogen, or ingested material with a higher carbon content. The only other study using ^{13}C and ^{15}N in deep-sea experiments was performed by Hunter et al. (2012) on the macrofauna during the same cruise to the Indian margin as ours. At 800 and 1100 m depth (no macrofauna present at 540 m), macrofauna also ingested more carbon than nitrogen. Their carbon assimilation accounted for ~ 1 % of the phytodetritus dose, while only ~ 0.4 % of the offered nitrogen was ingested. The results of these studies show strong discrepancies

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in the relationship between carbon and nitrogen assimilation between faunal groups and sites.

Carbon and nitrogen are important components of all organic compounds, although carbon is present at much larger amounts. The higher requirement for organic carbon might hence explain the higher uptake of carbon during the experiment. However, foraminifera not only ingest organic material to meet their nutritional demands, they also eliminate particles or compounds from their body. Hence we cannot be certain that all food ingested during the experiment was also incorporated into the cytoplasm analysed for isotopic composition. The applied method does not discriminate between ingested carbon/nitrogen atoms and atoms assimilated into the foraminiferal biomass. Excretion of nitrogenous waste products could have also occurred during the experimental period and the measured nitrogen amounts present in the foraminiferal cytoplasm would not reflect the total amount ingested during the entire time.

5 Conclusions

The in situ experiment revealed that foraminifera are strongly involved in the cycling of organic carbon in almost anoxic sediments of the Indian margin. Relaxed predation pressure and food competition through the absence of the macrofauna, as well as metabolic adaptations to anoxia, allow foraminiferal species to take up fresh phytodetritus in amounts larger than at the Pakistan margin OMZ sites. The observed rapid response (4 days) is advantageous at times of enhanced food flux to the sea floor and highlights their role in short-term carbon cycling in deep-sea sediments. The high variation between the nine most abundant taxa to the presence of food stresses the importance to work at species level rather than with groups (e.g. calcareous foraminifera) in order to identify key players such as Uvigerina schwageri. Because the uptake of a species does not solely rely on its abundance (but also on their size and feeding preferences), other key players might be found among the less abundant species.

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References

Aberle, N. and Malzahn, A. M.: Interspecific and nutrient-dependent variations in stable isotope fractionation: experimental studies simulating pelagic multitrophic systems, Oecologia, 154, 291–303, 2007.

Altenbach, A. V.: Short-term processes and patterns in the foraminiferal response to organic flux rates, Mar. Micropaleontol., 19, 119–129, 1992.

Andersson, J. H., Woulds, C., Schwartz, M., Cowie, G. L., Levin, L. A., Soetaert, K., and Middelburg, J. J.: Short-term fate of phytodetritus in sediments across the Arabian Sea Oxygen Minimum Zone, Biogeosciences, 5, 43–53, doi:10.5194/bg-5-43-2008, 2008.

Babu, C. P., Burmsack, H.-J., and Schnetger, B.: Distribution of organic carbon in surface sediments along the eastern Arabian Sea: a revisit, Mar. Geol., 162, 91–103, 1999.

Beaulieu, S. E. and Smith, K. L. J.: Phytodetritus entering the benthic boundary layer and aggregated on the sea floor in the abyssal NE Pacific: macro- and microscopic composition, Deep-Sea Res. Pt. II., 45, 781–815, 1998.

Bernhard, J. M. and Sen Gupta, B. K.: Foraminifera of oxygen-depleted environments, in: Modern Foraminifera, edited by: Sen Gupta, B. K., Kluwer Publishers, 201–216, 1999.

Bernhard, J. M., Edgcomb, V. P., Casciotti, K. L., McIlvin, M. R., and Beaudoin, D. J.: Denitrification likely catalyzed by endobionts in an allogromiid foraminifer, ISME J., 6, 951–960, 2012.

Blair, N. E., Levin, L. A., DeMaster, D. J., and Plaia, G.: The short-term fate of fresh algal carbon in continental slope sediments, Limnol. Oceanogr., 41, 1208–1219, 1996.

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Drazen, J. C., Baldwin, R. J., and Smith, K. L. J.: Sediment community response to a temporally varying food supply at an abyssal station in the NE Pacific. Deep-Sea Res. Pt. II, 45, 893–913, 1998.

Enge, A. J., Nomaki, H., Ogawa, N. O., Witte, U., Moeseneder, M. M., Lavik, G., Ohkouchi, N., Kitazato, H., Kucera, M., and Heinz, P.: Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific, Mar. Ecol.-Prog. Ser., 438, 129–142, 2011.

Gage, J. D. and Tyler, P. A.: Deep-sea biology: a natural history of organisms at the deep-sea floor, Cambridge University Press, Cambridge, 504 pp., 1991.

Gooday, A. J.: Meiofaunal foraminiferans from the bathyal Porcupine Seabight (north-east Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment, Deep-Sea Res. Pt. I, 33, 1345–1375, 1986.

Gooday, A. J.: Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes, Deep-Sea Res. Pt. I, 43, 1395–1421, 1996.

Gooday, A. J.: Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review, J. Oceanogr., 58, 305–332, 2002.

Gooday, A. J. and Hughes, J. A.: Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages, Mar. Micropaleontol., 46, 83–110, 2002.

Gooday, A. J. and Turley, C. M.: Response by benthic organisms to inputs of organic material to the ocean-floor – a review, Philos. Tr. R. Soc. Lond., 331, 119–138, 1990.

Gooday, A. J., Bernhard, J. M., Levin, L. A., and Suhr, S. B.: Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas, Deep-Sea Res. Pt. II, 47, 25–54, 2000.

Gooday, A. J., Levin, L. A., da Silva, A. A., Bett, B. J., Cowie, G. L., Dissard, D., Gage, J. D., Hughes, D. J., Jeffreys, R., Lamont, P. A., Larkin, K. E., Murty, S. J., Schumacher, S., Whitcraft, C., and Woulds, C.: Faunal responses to oxygen gradients on the Pakistan margin: a comparison of foraminiferans, macrofauna and megafauna, Deep-Sea Res. Pt. II, 56, 488–502, 2009.

Graf, G.: Benthic pelagic coupling in a deep-sea community, Nature, 341, 437–439, 1989.

Heinz, P., Hemleben, C., and Kitazato, H.: Time-response of cultured deep-sea benthic foraminifera to different algal diets, Deep-Sea Res. Pt. I, 49, 517–537, 2002.

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10, 15305–15335, 2013

Helly, J. J. and Levin, L. A.: Global distribution of naturally occurring marine hypoxia on continental margins, Deep-Sea Res. Pt. I, 51, 1159–1168, 2004.
Hermelin, J. O. R. and Shimmield, G. B.: The importance of the oxygen minimum zone and sediment geochemistry in the distribution of recent benthic foraminifera in the northwest Indian Ocean, Mar. Geol., 91, 1–29, 1990.
Hogslund, S., Revsbech, N. P., Cedhagen, T., Nielsen, L. P., and Gallardo, V. A.: Denitrification, nitrate turnover, and aerobic respiration by benthic foraminiferans in the oxygen minimum zone off Chile, J. Exp. Mar. Biol. Ecol., 359, 85–91, 2008.
Hunter, W. R., Oguri, K., Kitazato, H., Ansari, Z. A., and Witte, U.: Epi-benthic megafaunal zonation across an oxygen minimum zone at the Indian continental margin, Deep-Sea Res. Pt. I, 58, 699–710, 2011.
Hunter, W. R., Levin, L. A., Kitazato, H., and Witte, U.: Macrobenthic assemblage structure and organismal stoichiometry control faunal processing of particulate organic carbon and nitrogen in oxygen minimum zone sediments, Biogeosciences, 9, 993–1006, doi:10.5194/bg-9-993-2012, 2012.
Jannink, N. T., Zachariasse, W. J., and Van der Zwaan, G. J.: Living (Rose Bengal stained) benthic foraminifera from the Pakistan continental margin (northern Arabian Sea), Deep-Sea Res. Pt. I, 45, 1483–1513, 1998.
Josefson, A. B. and Widbom, B.: Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin, Mar. Biol., 100, 31–40, 1988.
Kamykowski, D. and Zentara, S. J.: Hypoxia in the world ocean as recorded in the historical data set, Deep-Sea Res., 37, 1861–1874, 1990.
Kitazato, H., Nomaki, H., Heinz, P., and Nakatsuka, T.: The role of benthic foraminifera in deep-sea food webs at the sediment–water interface: results from in situ feeding experiments in Sagami Bay, Frontier Research on Earth Evolution, 1, 227–232, 2003.
Lambshead, P. J. D. and Gooday, A. J.: The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic – the assemblage response, Deep-Sea Res., 37, 1263–1283, 1990.
Larkin, K. E. and Gooday, A. J.: Foraminiferal faunal responses to monsoon-driven changes in organic matter and oxygen availability at 140 and 300 m water depth in the NE Arabian Sea, Deep-Sea Res. Pt. II, 56, 403–421, 2009.

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Levin, L. A., Blair, N. E., Martin, C. M., DeMaster, D. J., Plaia, G., and Thomas, C. J.: Macrofaunal processing of phytodetritus at two sites on the Carolina margin: in situ experiments using ^{13}C-labeled diatoms, Mar. Ecol.-Prog. Ser., 182, 37–54, 1999.

Linke, P., Altenbach, A. V., Graf, G., and Heeger, T.: Response of deep-sea benthic foraminifera to a simulated sedimentation event, J. Foramin. Res., 25, 75–82, 1995.

Lipps, J. H.: Biotic interactions in benthic foraminifera, in: Biotic Interactions in Recent and Fossil Benthic Communities, edited by: Tevesz, M. and McCall, P., Plenum Publishing Corporation, 331–376, 1983.

Loubere, P. and Fariduddin, M.: Benthic foraminifera and the flux of organic carbon to the seabed, in: Modern Foraminifera, edited by: Sen Gupta, B., Kluwer Academic Publishers, Great Britain, 181–199, 1999.

Maas, M.: Verteilung lebendgefärbter benthischer Foraminiferen in einer intensivierten Sauerstoffminimumzone, Indo-Pakistanischer Kontinentalrand, nördliches Arabisches Meer, Meyniana, 52, 101–129, 2000.

Moodley, L., Middelburg, J. J., Boschker, H. T. S., Duineveld, G. C. A., Pel, R., Herman, P. M. J., and Heip, C. H. R.: Bacteria and foraminifera: key players in a short-term deep-sea benthic response to phytodetritus, Mar. Ecol.-Prog. Ser., 236, 23–29, 2002.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., and Kitazato, H.: Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: in situ tracer experiments, Limnol. Oceanogr., 50, 134–146, 2005.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Ohkouchi, N., Ogawa, N. O., Kogure, K., Ikemoto, E., and Kitazato, H.: Different ingestion patterns of ^{13}C-labeled bacteria and algae by deep-sea benthic foraminifera, Mar. Ecol.-Prog. Ser., 310, 95–108, 2006.

Nomaki, H., Ogawa, N. O., Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M., Nakatsuka, T., and Kitazato, H.: Benthic foraminifera as trophic links between phytodetritus and benthic metazoans: carbon and nitrogen isotopic evidence, Mar. Ecol.-Prog. Ser., 357, 153–164, 2008.

Nomaki, H., Ogawa, N. O., Takano, Y., Suga, H., Ohkouchi, N., and Kitazato, H.: Differing utilization of glucose and algal particulate organic matter by deep-sea benthic organisms of Sagami Bay, Japan, Mar. Ecol.-Prog. Ser., 431, 11–24, 2011.

Ohkushi, K. and Natori, H.: Living benthic foraminifera of the Hess Rise and Suiko Seamount, central north Pacific, Deep-Sea Res. Pt. I, 48, 1309–1324, 2001.

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10, 15305–15335, 2013

Pina-Ochoa, E., Koho, K. A., Geslin, E., and Risgaard-Petersen, N.: Survival and life strategy of the foraminiferan *Globobulimina turgida* through nitrate storage and denitrification, Mar. Ecol.-Prog. Ser., 417, 39–49, 2010.

Risgaard-Petersen, N., Langezaal, A. M., Ingvardsen, S., Schmid, M. C., Jetten, M. S. M., Op den Camp, H. J. M., Derksen, J. W. M., Pina-Ochoa, E., Eriksson, S. P., Nielsen, L. P., Revsbech, N. P., Cedhagen, T., and van der Zwaan, G. J.: Evidence for complete denitrification in a benthic foraminifer, Nature, 443, 93–96, 2006.

Sawant, S. and Madhupratap, M.: Seasonality and composition of phytoplankton in the Arabian Sea, Current Science, 71, 869–873, 1996.

Schumacher, S., Jorissen, F. J., Dissard, D., Larkin, K. E., and Gooday, A. J.: Live (Rose Bengal stained) and dead benthic foraminifera from the oxygen minimum zone of the Pakistan continental margin (Arabian Sea), Mar. Micropaleontol., 62, 45–73, 2007.

Sweetman, A. K., Sommer, S., Pfannkuche, O., and Witte, U.: Retarded response by macrofauna-size foraminifera to phytodetritus in a deep Norwegian fjord, J. Foramin. Res., 39, 15–22, 2009.

Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W. R., Jorgensen, B. B., and Pfannkuche, O.: In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor, Nature, 424, 763–766, 2003.

Woulds, C., Cowie, G. L., Levin, L. A., Andersson, J. H., Middelburg, J. J., Vandewiele, S., Lamont, P. A., Larkin, K. E., Gooday, A. J., Schumacher, S., Whitcraft, C., Jeffreys, R. M., and Schwartz, M.: Oxygen as a control on seafloor biological communities and their roles in sedimentary carbon cycling, Limnol. Oceanogr., 52, 1698–1709, 2007.

Wyrtki, K.: Oceanographic Atlas of the International Indian Ocean Expedition, National Science Foundation, Washington, DC, 542 pp., 1971.

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Table 1. Environmental parameters at the sampling site, obtained during deployment and recovery of spreaders and push cores. Surface sediment characteristics (% TOC, % TN, porosity) are given in Hunter et al. (2011). Data presented show means for the 540 m depth because recordings were continuous during dives.

Date	Water depth (m)	Longitude	Latitude	O_2 ($\mu mol\,L^{-1}$)	O_2 ($mL\,L^{-1}$)	Temp. (°C)	Salinity (PSU)
9 Oct 2008	540	16°58.8′ N	71°55.3′ E	0.9	0.02	11.7	35.2
13 Oct 2008	540	16°58.8′ N	71°55.3′ E	2.4	0.05	12.1	35.2

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Table 2. Number of specimens analysed for ^{13}C (9 species) and ^{15}N (3 species), the calculated content of C and N per individual and the $\delta^{13}C$ and $\delta^{15}N$ of foraminifera.

Species	Measured individuals	C content ($\mu g\,ind.^{-1}$)	N content ($\mu g\,ind.^{-1}$)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Bolivina aff. *B. dilatata*	400	0.124	–	700.4	–
	400	0.128	–	723.4	–
	1500	–	0.010	–	5258.3
Bulimina gibba	250	0.312	–	2630.3	–
	600	–	0.023	–	14 924.7
Cassidulina sp.	300	0.108	–	505.0	–
	300	0.103	–	374.7	–
	1500	–	0.010	–	7191.0
Ehrenbergina pacifica	350	0.251	–	174.6	–
	300	0.226	–	115.5	–
Epistominella rugosa	400	0.140	–	674.6	–
Hoeglundina cf. *elegans*	200	0.235	–	6182.6	–
Lenticulina spp.	200	0.565	–	230.9	–
Uvigerina schwageri	200	1.363	–	9516.3	–
Uvigerina peregrina	350	0.265	–	4903.4	–
	300	0.232	–	5000.7	–

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Table 3. (Mean) Carbon and nitrogen uptake (± SD) during 4 day experiment and the fractions of carbon (f_C) and nitrogen (f_N) originating from added algal material in foraminiferal cytoplasm.

Species	C uptake (ng C ind.$^{-1}$)	Total C uptake (mg C m^{-2})	$f_C \times 100$ (%)	N uptake (ng N ind.$^{-1}$)	Total N uptake (mg N m^{-2})	$f_N \times 100$ (%)
Bolivina aff. *B. dilatata*	3.8 ± 0.2	4.1 ± 0.2	3.0	0.6	0.6	5.6
Bulimina gibba	33.2	13.0	10.6	3.6	1.4	15.5
Cassidulina sp.	2.0 ± 0.5	2.0 ± 0.5	1.9	0.7	0.7	7.7
Ehrenbergina pacifica	1.6 ± 0.5	0.6 ± 0.2	0.7	–	–	–
Epistominella rugosa	4.0	0.7	2.8	–	–	–
Hoeglundina cf. *elegans*	56.2	8.7	23.9	–	–	–
Lenticulina spp.	5.8	0.5	1.0	–	–	–
Uvigerina schwageri	484.4	69.8	35.6	–	–	–
Uvigerina peregrina	48.2 ± 3.9	14.6 ± 1.2	19.4	–	–	–

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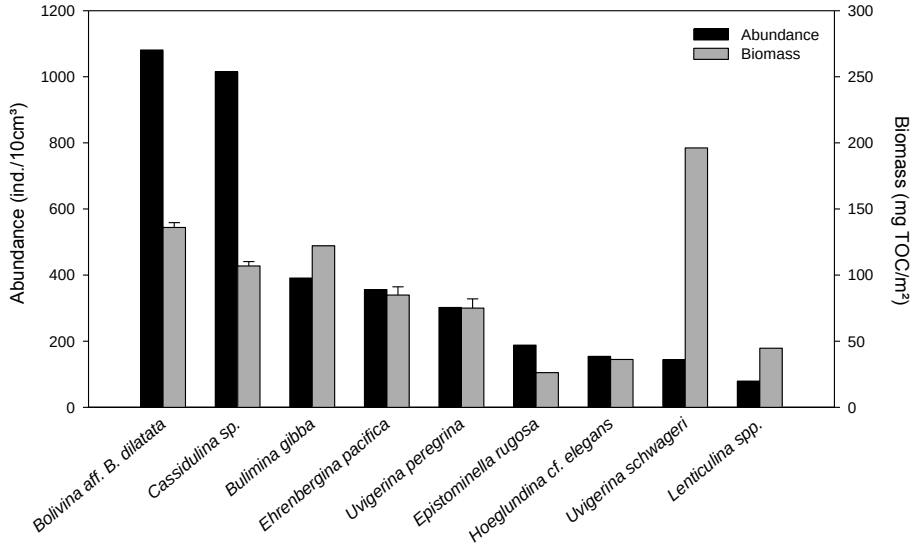

Fig. 1. Abundance (black bars) and biomass (grey bars, ±SD) of the nine dominant species (> 125 µm) in the 0–1 cm layer of the sediment.

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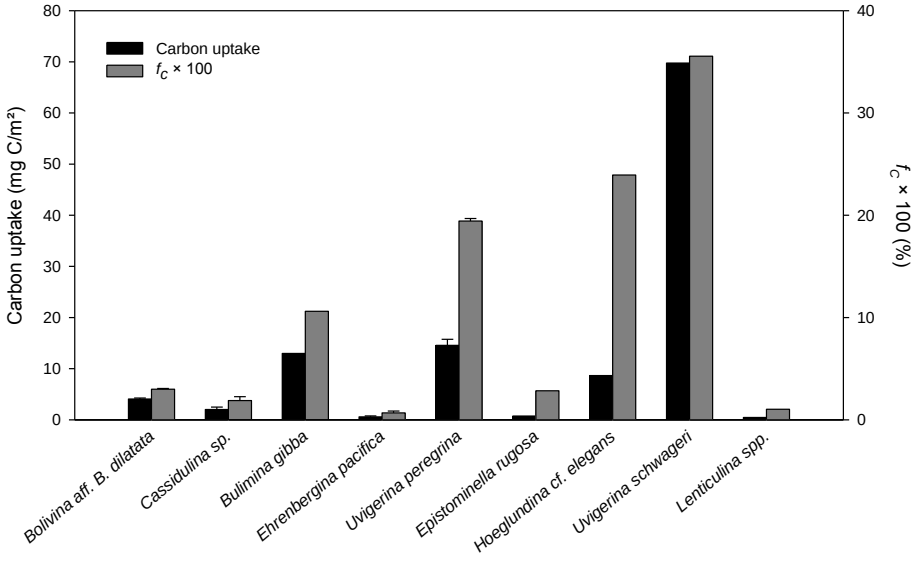

Fig. 2. Total carbon uptake of species and the percentage fraction of carbon originating (f_C × 100) from labeled algae in the analyzed TOC of the cytoplasm of the nine investigated species. Standard deviation is given for the four species with two replicate measurements.

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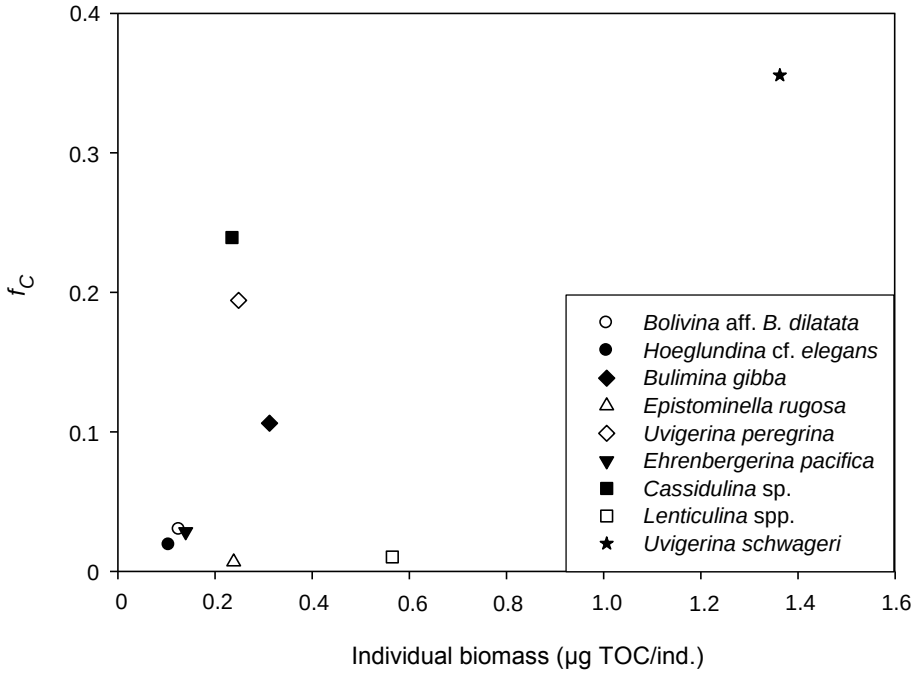

Fig. 3. Estimated individual TOC content of the investigated nine species in relation to the biomass-normalized carbon uptake of species (f_C).

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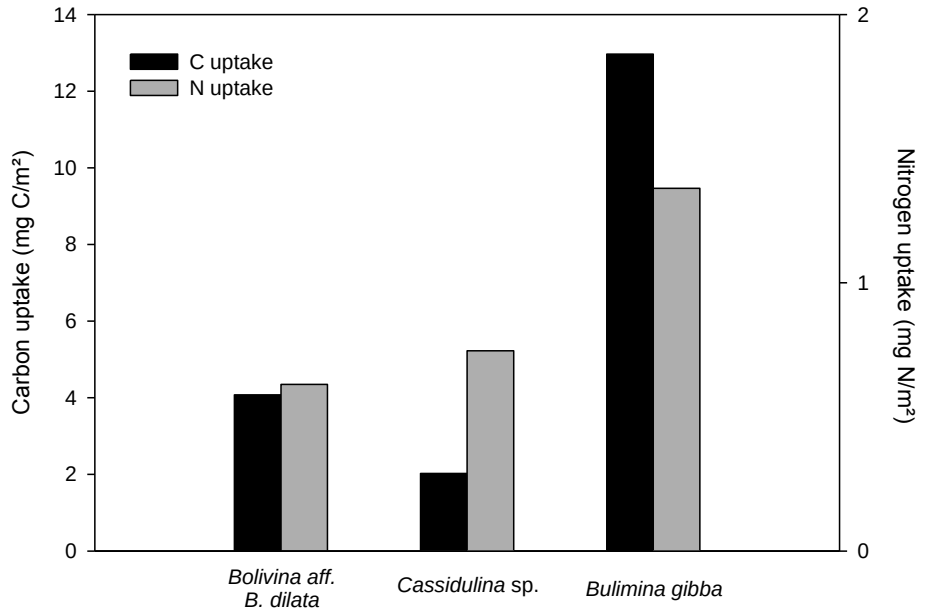

Fig. 4. Uptake of carbon (black) and nitrogen (grey) by the three most abundant species.

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