



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} ($4.5 \mu\text{mol L}^{-1}$), an in situ isotope labeling experiment (^{13}C , ^{15}N) was performed on the western continental slope of India at 540 m water depth (OMZ core region). The assemblage of living foraminifera ($> 125 \mu\text{m}$) in the uppermost centimeter at this depth is characterized by an unexpectedly high population density of $3982 \text{ individuals } 10 \text{ cm}^{-2}$ 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 foraminiferal 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 labeled phytodetritus during the 4 day experimental phase. In total, these nine species had assimilated $113.8 \text{ mg C m}^{-2}$ (17.5 % of the total added carbon). 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). The 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 the observed

species-specific differences are related to species biomass and specific feeding preferences. In summary, the experiment in the OMZ core region shows rapid processing of fresh phytodetritus by foraminifera under almost anoxic conditions. The uptake of large amounts of organic matter by few species within four days suggests that foraminifera may play an important role in short-term carbon cycling in the OMZ core region on the Indian margin.

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's 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, characterized by dissolved oxygen concentrations $< 0.5 \text{ mL L}^{-1}$ ($22.3 \mu\text{mol L}^{-1}$), are especially well developed at intermediate water depths in the North Pacific, the Arabian Sea, and the Bay of Bengal (Helly and Levin, 2004; Wyrki, 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 regions of OMZs.

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 off 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 in 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 (e.g., Witte et al., 2003; Nomaki et al., 2005; Enge et al., 2011). In OMZ sediments on the Pakistan margin, Woulds et al. (2007) and Andersson et al. (2008) performed a series of labeling experiments along a depth transect (140–1850 m) focusing on the role of the benthic fauna in sedimentary processes. Both studies demonstrated the influence of oxygen on the processing of organic matter by organisms and the importance of foraminifera to

carbon cycling in oxygen-depleted environments. Though Woulds et al. (2007) and Andersson et al. (2008) included foraminifera in their studies, they did not discriminate between species but compared the foraminiferal response to the reaction of macrofauna, meiofauna and bacteria.

In our experiments, we were interested to study the response of individual species of foraminifera to a pulse of fresh phytodetritus under low-oxygen concentration. To ensure almost anoxic conditions, an in situ labeling experiment was carried out in the core region of the OMZ ($< 0.1 \text{ mL O}_2 \text{ L}^{-1}$) on the Indian margin. Recently, Jeffreys et al. (2013) performed a dual labeling experiments on macrofauna-sized foraminifera in the abyssal northeast Pacific, but did not discriminate between species. In the present study, the following hypotheses will be tested: (1) foraminifera from the OMZ core display a positive feeding response to phytodetritus within four days, (2) uptake rates will vary between species, and (3) relative uptake of carbon to nitrogen is species-specific.

2 Material and methods

2.1 Study area

The study was part of an international research project on 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. The area of interest was the sea floor of the Indian margin in the Arabian Sea, exposed to the OMZ water mass. Detailed sampling sites are shown in Hunter et al. (2012). OMZ influenced sediments of the Indian margin are found between 120–1100 m (Helly and Levin, 2004).

The feeding 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 ($16^\circ 58' \text{ N}$ and $71^\circ 55' \text{ E}$). This depth is located in the core region of the Indian margin OMZ and corresponds to station T1 540 in the study of Hunter et al. (2011).

The area of interest shows a moderate to high average yearly productivity of $> 0.5\text{--}0.75 \text{ g C m}^{-2} \text{ d}^{-1}$ (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). This results in distinctly seasonal surface primary production and organic matter flux. In October 2008, the particulate organic carbon concentration was $100\text{--}200 \text{ mg m}^{-3}$ (SeaWiFS, NASA OceanColor; monthly POC data). Environmental data 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). At the time of sampling, in situ oxygen concentrations ranged between 0.02 mL L^{-1} ($0.9 \mu\text{mol L}^{-1}$) and 0.05 mL L^{-1} ($2.4 \mu\text{mol L}^{-1}$) and temperature was 12°C (Table 1). As recordings of environmental parameters were continuous, values given in Table 1 represent averages for 540 m depth. Surface sediment characteristics (% total organic carbon (TOC), % total nitrogen (TN), porosity) are given in Hunter et al. (2011).

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 L1 culture medium, enriched with 99 % ^{13}C -bicarbonate ($\text{NaH}^{13}\text{CO}_3$, Cambridge Isotope Laboratories, Inc., USA) and 50 % ^{15}N -sodium nitrate ($\text{Na}^{15}\text{NO}_3$, Cambridge Isotope Laboratories, Inc., USA). 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 lyophilized (-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 consisted of a transparent polycarbonate tube (25 cm inner diameter, 30 cm length) and a lid that contained the suspension of *T. weissflogii* (650 mg C m^{-2} , 160 mg N m^{-2}). More detailed information about the construction can be found in Hunter et al. (2012). On 9 October 2008, the manipulator arm of the manned submersible *Shinkai 6500* pushed three spreaders straight into the undisturbed sea floor until they stood firmly upright. By pushing the plunger on the lid, the suspension of algae was released from the container and settled to the enclosed sediment surface. To ensure complete deposition of the algae mass onto the sediment surface, the spreader lid was removed several hours after the deployment of the spreader. 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 (plastic tube, 70 mm inner diameter) for foraminiferal analysis was recovered from inside each spreader by the submersible. The Oceanlab spreader system was removed afterwards. On board the research vessel, the push core was immediately sliced horizontally in 1 cm intervals down to 3 cm depth. Each slice was frozen at -80°C and then stored at -25°C until analyzed. For our study, we investigated the assemblage and the isotope composition of foraminifera from the 0–1 cm layer of

one push core. We concentrated on the upper 1 cm because living foraminifera in OMZ sediments of the Arabian Sea are 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 analyze carbon in duplicate batches for four species (Table 2).

2.4 Sample preparation

In the laboratory, the 0–1 cm sediment sample was thawed and washed over a mesh ($125 \mu\text{m}$) 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 the residue in a petri dish, which was placed on a cooling plate for the entire duration of the picking process. The entire 0–1 cm sample was investigated for faunal composition of living foraminifera. We identified foraminifera by species level as far as possible. Counts showed that nine taxa were represented by sufficient specimens and biomass for stable isotopic analyses. To meet the minimum of biomass requirements for isotope analysis, individuals of one species were pooled. The required number of individuals varied among species according to size and biomass, the maximum number per analysis being 1500 individuals (Table 2).

Before processing, material for isotopic analysis, glassware and silver cups were 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 $10 \mu\text{L}$ of filtered seawater, foraminifera were transferred into cups with a brush. Subsequently, we dried the filled cups at 50°C for several hours before adding hydrochloric acid (6.25 %) to ensure complete dissolution of carbonate.

We observed that the decalcification process involved production of carbon dioxide, which could cause overflow of organic matter out of the silver cup. Hence, the transfer of foraminifera into one cup had to be performed stepwise and not at once. The procedure of transferring specimens to silver cups, heating and adding hydrochloric acid was repeated until all calcareous parts of the foraminifera were dissolved. Finally, samples were kept at 50°C for three days to allow complete drying.

Table 1. Environmental parameters at 540 m water depth during the time of the experiment. Data derive from CTD recordings and measurements by an optical oxygen sensor during deployment and recovery of spreaders/push cores.

Date	Water depth (m)	Longitude	Latitude	O ₂ (μmolL ⁻¹)	O ₂ (mLL ⁻¹)	Temperature (°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

Table 2. Number of specimens analyzed for ¹³C/¹²C (nine species) and ¹⁵N/¹⁴N (three species), the calculated content of C and N per individual (average) and the δ¹³C and δ¹⁵N of foraminifera after exposure to labeled food.

Species	Measured individuals	C content (μg individual ⁻¹)	N content (μg individual ⁻¹)	δ ¹³ C (‰)	δ ¹⁵ N (‰)
<i>Bolivina</i> aff. <i>B. dilatata</i>	400	0.124	–	700.4	–
	400	0.128	–	723.4	–
	1500	–	0.010	–	5258.3
<i>Bulimina gibba</i>	250	0.312	–	2630.3	–
	600	–	0.023	–	14 924.7
<i>Cassidulina</i> sp.	300	0.108	–	505.0	–
	300	0.103	–	374.7	–
	1500	–	0.010	–	7191.0
<i>Ehrenbergina pacifica</i>	350	0.251	–	174.6	–
	300	0.226	–	115.5	–
<i>Epistominella rugosa</i>	400	0.140	–	674.6	–
<i>Hoeglundina</i> cf. <i>elegans</i>	200	0.235	–	6182.6	–
<i>Lenticulina</i> spp.	200	0.565	–	230.9	–
<i>Uvigerina schwageri</i>	200	1.363	–	9516.3	–
<i>Uvigerina peregrina</i>	350	0.265	–	4903.4	–
	300	0.232	–	5000.7	–

2.5 Calculation of phytodetritus uptake

Total C and N content of foraminiferal cytoplasm as well as ¹³C/¹²C and ¹⁵N/¹⁴N ratios were measured at SI Science Co., Ltd. (Japan) using an elemental analyzer/isotope-ratio mass spectrometer (EA/IRMS). Hereafter, the ratios ¹³C/¹²C and ¹⁵N/¹⁴N will be expressed as atom%¹³C and atom%¹⁵N. Formulas given in this section apply to the calculation of carbon uptake. Uptake of nitrogen was calculated with the same formulas but with different standards and different natural background values.

Carbon isotope composition was measured against the international Vienna Pee Dee Belemnite standard (VPDB) and nitrogen isotope composition relative to atmospheric nitrogen. Differences between sample and standard are expressed in δ-notation: δ¹³C [‰] = ((atom%¹³C_{sample}) / (atom%¹³C_{VPDB}) - 1) × 1000. Incorporation of ¹³C and ¹⁵N by foraminifera was defined as excess above background (bkgd):

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

while

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

Natural isotope (background) signatures for benthic foraminiferal cytoplasm of δ¹³C = -20.3 and δ¹⁵N = 8.0 derived from Enge et al. (2011), Nomaki et al. (2005, 2006, 2008), and Sweetman et al. (2009). In literature, δ¹³C literature values were available for different sediment depths and foraminiferal species. For our calculation, we used only natural signatures from calcareous species in the 0–1 cm layer. The natural signatures of the diatom *Thalassiosira weissflogii* (and food source in our experiment) with δ¹³C = -21.2 and δ¹⁵N = 4.9 were taken from Aberle and Malzahn (2007).

Uptake (mg C) was calculated as product of excess in the sample and total carbon/nitrogen content in the sample, divided by the excess of 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 analyzed specimens (Table 2) and then multiplying the individual uptake (mg C individuals⁻¹) by the abundance (individuals m⁻²) found in the uppermost centimeter. The fraction (*f*) of carbon and nitrogen originating from added alga material in the TOC/TON (total organic nitrogen) of analyzed foraminifera, was calculated after Nomaki et al. (2006):

$$f_c = \left(\text{atom}\%^{13}\text{C}_{\text{sample}} - \text{atom}\%^{13}\text{C}_{\text{bkgd foram}} \right) / \left(\text{atom}\%^{13}\text{C}_{\text{algae}} - \text{atom}\%^{13}\text{C}_{\text{bkgd algae}} \right). \quad (3)$$

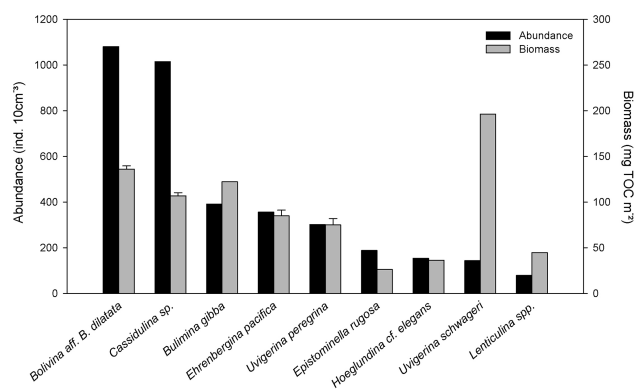


Fig. 1. Abundance (black bars) and biomass (grey bars, \pm SD) of the nine dominant species ($> 125\mu\text{m}$) in the 0–1 cm sediment layer.

In addition, f_C also represents the biomass-normalized uptake of species, calculated as total C uptake per sample (mg C) divided by the TOC content of the sample (mg C). We also used the expression $f \times 100$ (%) because calculated f values were very small.

Species biomass for each species was estimated on the basis of mean individual TOC content and its abundance (in relation to sediment area).

3 Results

3.1 Foraminiferal assemblage at 0–1 cm

The analyzed 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 individuals 10 cm^{-3} in the uppermost cm at 540 m water depth. Abundances of taxa ranged between 0.3 and 1081 individuals 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 absent in the $> 125\mu\text{m}$ fraction. The community of living foraminifera in the analyzed size class was dominated by a low number of species. *Bolivina* aff. *B. dilatata* and *Cassidulina* sp. were the numerically most important taxa with densities of 1015 and 1081 individuals 10 cm^{-3} (Fig. 1), accounting for 27% and 25% of the entire foraminiferal abundance, respectively. The taxa *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 total population density.

The TOC content of species (calculated from the total TOC in the sample and the analyzed number of individuals), as well as species biomass, varied considerably among the nine most abundant species (Table 2, Fig. 1). *Uvige-*

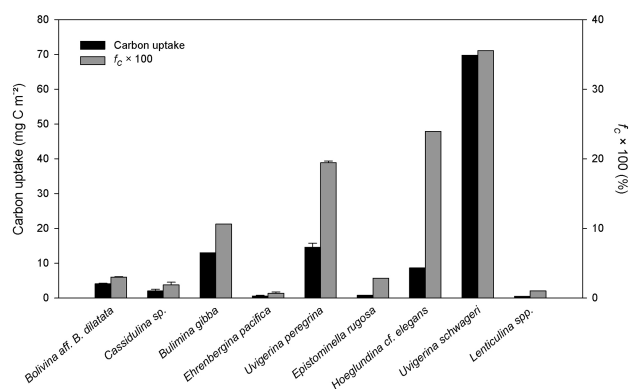


Fig. 2. Total carbon uptake of species and percentage of carbon originating from labeled algae in TOC of foraminiferal cytoplasm ($f_C \times 100$). Standard deviation is given for species with two replicate measurements.

rina schwageri yielded the highest TOC content and species biomass and was also largest in size. Based on the calculated individual TOC content and the total abundances of specimens in the 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). Figure 1 shows the great variation of biomass between the nine foraminiferal taxa.

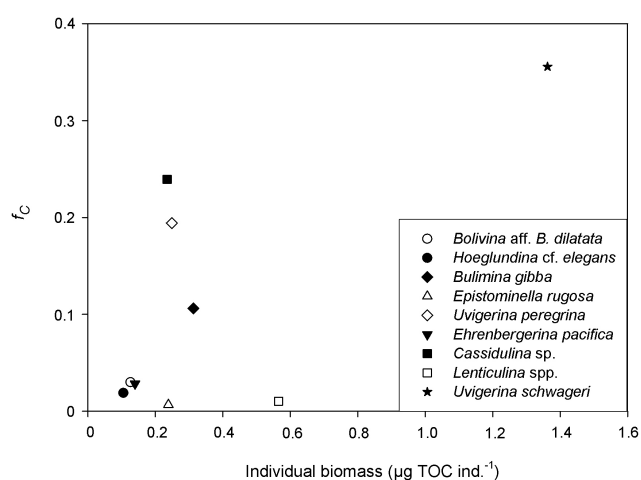
3.2 Response to added carbon

Uptake of phytodetritus was investigated for the nine most abundant species. They represented 93.5% of the total assemblage and were present in sufficient number for isotope analysis. In total, the cytoplasm of 7550 living individuals (Table 2) was analyzed for $^{13}\text{C}/^{12}\text{C}$ (nine taxa) and $^{15}\text{N}/^{14}\text{N}$ (three taxa). Measured $\delta^{13}\text{C}$ values of 115.5–9516.3‰ exceeded natural isotopic values (-20.3‰) substantially for all nine investigated species (Table 2). After four days, the nine taxa had taken up 113.8 mg C m^{-2} , which accounts for 17.5% of the added (labeled) carbon at the beginning of the experiment. The total uptake of carbon (as product of individual uptake and abundance) varied considerably among species (Fig. 2). Total carbon uptake was highest for *U. schwageri* with 69.8 mg C m^{-2} (Table 3). *Bulimina gibba*, *Hoeglundina* cf. *elegans* and *U. peregrina* exhibited similar carbon uptake, ranging between 8.7 and 14.6 mg C m^{-2} . Lowest uptake ($< 1\text{ mg C m}^{-2}$) was observed for *E. pacifica* and *E. rugosa*.

The uptake of labeled carbon per individual (representing an average value for all individuals of the species) also varied considerably between taxa. 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 was a function of foraminiferal biomass, we calculated the biomass-normalized uptake or the fraction of algal carbon

Table 3. (Mean) Carbon and nitrogen uptake (\pm 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 individual ⁻¹)	Total C uptake (mg C m ⁻²)	$f_C \times 100$ (%)	N uptake (ng N individual ⁻¹)	Total N uptake (mg N m ⁻²)	$f_N \times 100$ (%)
<i>Bolivina</i> aff. <i>B. dilatata</i>	3.8 \pm 0.2	4.1 \pm 0.2	3.0	0.6	0.6	5.6
<i>Bulimina gibba</i>	33.2	13.0	10.6	3.6	1.4	15.5
<i>Cassidulina</i> sp.	2.0 \pm 0.5	2.0 \pm 0.5	1.9	0.7	0.7	7.7
<i>Ehrenbergina pacifica</i>	1.6 \pm 0.5	0.6 \pm 0.2	0.7	–	–	–
<i>Epistominella rugosa</i>	4.0	0.7	2.8	–	–	–
<i>Hoeglundina</i> cf. <i>elegans</i>	56.2	8.7	23.9	–	–	–
<i>Lenticulina</i> spp.	5.8	0.5	1.0	–	–	–
<i>Uvigerina schwageri</i>	484.4	69.8	35.6	–	–	–
<i>Uvigerina peregrina</i>	48.2 \pm 3.9	14.6 \pm 1.2	19.4	–	–	–

**Fig. 3.** Estimated individual TOC content of dominant species in relation to their biomass-normalized carbon uptake (f_C).

in foraminiferal cytoplasm (f_C). As illustrated in Fig. 3, *U. schwageri* displayed the highest biomass-normalized carbon content (0.36), followed by *Hoeglundina* cf. *elegans* (0.24), and *U. peregrina* (0.19). Lowest biomass-normalized uptake was calculated for *E. pacifica*.

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 by *B. gibba* (1.4 mg N m⁻²) was twice as high as by *B.* aff. *B. dilatata* and *Cassidulina* sp. (Table 3). The uptake of nitrogen for all three taxa was 2.7 mg N m⁻², which represents 1.7 % of the added nitrogen 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.

The somatic C:N ratio after the experimental phase ranged between 11 and 13.5 for the investigated taxa. Total uptake of carbon was higher than nitrogen for all

species (Fig. 4) yet considerable differences occurred between species (C:N of 6.6 for *B.* aff. *B. dilatata*, 2.7 for *Cassidulina* sp., and 9.6 for *Bulimina aculeata*).

4 Discussion

4.1 Limitations of the study

The vertical distribution of benthic foraminifera within the sediment is greatly influenced by the availability of food and the oxygen concentration with the pore water (Corliss and Emerson, 1990). In our analysis we concentrated on the response of foraminifera to food in the uppermost centimeter of the sediment (0–1 cm) because living foraminifera in the core region of OMZ sediments are mainly restricted to the upper sediment layer (e.g., Jannink et al., 1998, Schumacher et al., 2007) due to the extremely low-oxygen concentrations in these environments (see Table 1). Living foraminifera may be found in deeper sediment layers but with abundances negligible compared to the high numbers found in the 0–1 cm layer. Hence the results should represent an adequate picture of the foraminiferal community response in the size-fraction studied (> 125 μ m). The results reported here derive from the extensive and time-consuming processing of sediment from one push core (0–1 cm), containing about 15 300 counted specimens, of which 7550 were prepared and analyzed for stable isotope measurement. Due to limited manpower, the 63–125 μ m size fraction was not included in this study, which excludes a high number of smaller foraminifera and therefore underestimates the impact of the entire foraminiferal community on the phytodetritus processing. Despite these shortcomings, our data provide important information that is comparable to other studies. Carrying out experiments in the deep sea is not only limited by time and sampling equipment, but also by technical problems or bad weather. After the 4 day feeding experiment performed on the Indian margin at 540 m depth, only one push core from one spreader was available for foraminiferal analysis; the other push cores were used for other taxa.

4.2 Species-specific response to phytodetritus

Individual responses to the added phytodetritus varied considerably among the nine taxa investigated with species uptake ranging 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 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 the numerically dominating taxa *B. aff. B. dilatata* and *Cassidulina* sp. to show the highest uptake. However, uptake was lower 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 is not the only control on species-level uptake of phytodetritus. Unfortunately, a correlation of species biomass and uptake was not observed for all species (e.g., *B. gibba*, *U. peregrina*, and *Hoeglundina cf. elegans*), although largest individual and species biomass was exhibited by *U. schwageri*, which also demonstrated the highest uptake of all species (Fig. 2) and highest content of labeled food after the experiment (Fig. 3).

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 Madhuratap, 1996). In our experiment the cosmopolitan diatom species *Thalassiosira weissflogii* was selected as a food source. The very high uptake by *U. schwageri* could suggest a preference for these diatoms, whereas *T. weissflogii* might be less acceptable to *E. pacifica* or *Lenticulina* spp., which exhibit lower levels of uptake. A preference of diatoms over coccolithophores was discovered for foraminifera in the abyssal Pacific by Jeffreys et al. (2013). 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 phytophagous species that ingested phytodetritus selectively. Different feeding preferences among species could be of advantage in an environment where competition for space and food must be very high among foraminiferal individuals, considering the standing stock of about $4000 \text{ individuals } 10 \text{ cm}^{-3}$.

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

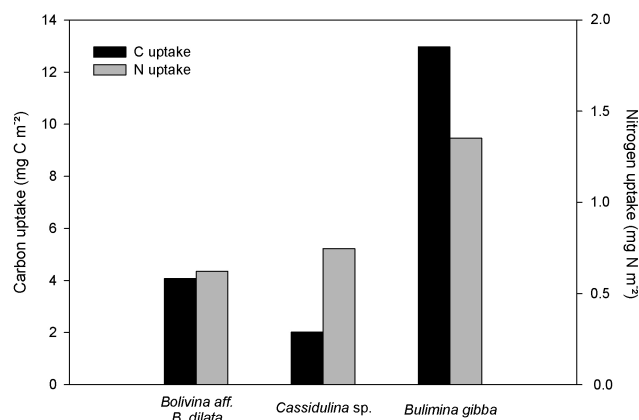


Fig. 4. Uptake of carbon (black) and nitrogen (grey) by the three most abundant species.

suggested by Loubere and Fariduddin (1999). In the eutrophic Sagami Bay, *Uvigerina akitaensis* and *Bulimina aculeata* dominated the foraminiferal response to phytodetritus during an in situ feeding experiment (Nomaki et al., 2005). Hence our observation of highest uptake by *U. schwageri*, *U. peregrina*, and *B. gibba* is consistent with these earlier observations and with the results of Woulds et al. (2007) where *Uvigerina* dominated short-term phytodetritus processing in the OMZ core on the Pakistan margin.

4.3 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 $> 125 \mu\text{m}$. As we have no carbon uptake data for the remaining species at this sediment depth and excluded the size fraction $< 125 \mu\text{m}$, our results represent the minimum response of the entire assemblage. Therefore, carbon uptake by the entire foraminiferal community is expected to be higher and the impact on the benthic community utilization of fresh organic matter even greater.

The only comparable experimental studies to investigate the response of foraminifera to phytodetritus deposition in an OMZ setting were undertaken on the Pakistan margin by Woulds et al. (2007) and Andersson et al. (2008). The foraminiferal uptake in the OMZ core region (300 m depth) of the Pakistan margin ranged between 6 and 20 mg C m^{-2} after 5 days of in situ incubation. The lower uptake compared to our experiment at the Indian margin (114 mg C m^{-2}) is very likely caused by the use of different mesh sizes. In our experiment, we used a $125 \mu\text{m}$ mesh and found abundances

of almost 4000 individuals 10 cm^{-3} , whereas the study at the Pakistan margin yielded 200–336 individuals 10 cm^{-3} using a $300\text{ }\mu\text{m}$ mesh (Woulds et al., 2007). As the calculation of carbon uptake per area is based on the estimated abundance of foraminifera, we assume that the exclusion of the 125–300 μm size fraction at the Pakistan study led to a lower abundance and hence to lower uptake. Foraminiferal uptake is thus comparable between the two OMZ core sites in the Arabian Sea.

Our results indicate that benthic foraminifera are able to utilize organic matter at oxygen concentrations of $< 0.1\text{ mL}^{-1}$ as fast as in non-oxygen-depleted deep-sea environments (Kitazato et al., 2003; Nomaki et al., 2005; Enge et al., 2011; Nomaki et al., 2011). This suggests that foraminifera in the OMZ core on the Indian margin represent species highly adapted to low oxygen in order to be able to ingest large amounts of food. The absence of macrofauna at the investigation site (Hunter et al., 2012) might have also contributed to the observed uptake of phytodetritus by the foraminifera due to reduced competition for food. Where present on continental margins, metazoan 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). Comparison of uptake to other potential consumers of phytodetritus like meiofauna or bacteria is hampered as relevant data are not available so far.

In situ experiments in the core region of the Pakistan margin OMZ (300 m) showed greater uptake of phytodetritus by bacteria than by foraminifera (Andersson et al., 2008). Similar environmental conditions between the two sites leads to the assumption that foraminifera on the Indian margin could also be important in short-term phytodetritus processing, as they are on the Pakistan margin.

4.4 Uptake of nitrogen by foraminifera

The three foraminiferal taxa that were analyzed 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 on species level. More foraminiferal biomass and hence a greater number of specimens is required for the analysis of the nitrogen isotopic composition (Table 2) in comparison to carbon. 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.

The nitrogen uptake was lower in comparison to the uptake of carbon for all three species. The higher absolute uptake of labeled carbon by foraminifera, which has been also observed by Jeffreys et al. (2013), follows the natural higher demand for carbon over nitrogen to meet energetic requirements (Redfield ratio of 106:16). Though the absolute uptake

of carbon was higher than for nitrogen in all three species, great differences were found in the species-specific uptake of C and N (see Sect. 3.3), suggesting that species have different metabolic demands in order to achieve homeostasis (Raubenheimer and Simpson, 2004).

5 Conclusions

The observed rapid response of foraminifera to fresh food input within 4 days is similar to that observed in other deep-sea environments and is advantageous at times of enhanced food flux to the sea floor. The distinct variation in response to the presence of food stresses the importance of working at the species level in order to identify key species such as *Uvigerina schwageri*. The focus on individual species and their responses to food inputs can thus be very helpful for identifying key species for specific habitats and their use, for example, for paleo-reconstruction. The importance of a particular species in the processing of phytodetritus does not solely rely on its abundance but also on its size (biomass) and feeding preferences. Hence other key players might be found among the less abundant or smaller species. The high total uptake by these few species shows that foraminifera are well adapted to extremely low-oxygen concentrations and contribute to the carbon cycling in OMZ sediments. The ratio of C : N uptake is different between species, which suggest that they may have different metabolic energy demands and possibly, therefore, different nutrition preferences.

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