



## Abstract

The discovery that foraminifera are able to use nitrate instead of oxygen as energy source for their metabolism has challenged our understanding of nitrogen cycling in the ocean. It was evident before that only prokaryotes and fungi are able to denitrify. Rate estimates of foraminiferal denitrification were very sparse on a regional scale. Here, we present estimates of benthic foraminiferal denitrification rates from six stations at intermediate water depths in and below the Peruvian oxygen minimum zone (OMZ). Foraminiferal denitrification rates were calculated from abundance and assemblage composition of the total living fauna in both, surface and subsurface sediments, as well as from individual species specific denitrification rates. A comparison with total benthic denitrification rates as inferred by biogeochemical models revealed that benthic foraminifera account for the total denitrification on the shelf between 80 and 250 m water depth. They are still important denitrifiers in the centre of the OMZ around 320 m (29–56 % of the benthic denitrification) but play only a minor role at the lower OMZ boundary and below the OMZ between 465 and 700 m (3–7 % of total benthic denitrification). Furthermore, foraminiferal denitrification was compared to the total benthic nitrate loss measured during benthic chamber experiments. Foraminiferal denitrification contributes 1 to 50 % to the total nitrate loss across a depth transect from 80 to 700 m, respectively. Flux rate estimates ranged from 0.01 to 1.3 mmol m<sup>-2</sup> d<sup>-1</sup>. Furthermore we show that the amount of nitrate stored in living benthic foraminifera (3 to 705 μmol L<sup>-1</sup>) can be higher by three orders of magnitude as compared to the ambient pore waters in near surface sediments sustaining an important nitrate reservoir in Peruvian OMZ sediments. The substantial contribution of foraminiferal nitrate respiration to total benthic nitrate loss at the Peruvian margin, which is one of the main nitrate sink regions in the world oceans, underpins the importance of previously underestimated role of benthic foraminifera in global biochemical cycles.

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 1 Introduction

Nitrate is a limiting nutrient in surface ocean primary productivity and takes a central role in the marine biogeochemistry (Gruber, 2004; Arrigo, 2005; Lam et al., 2009). In the oceanic nitrogen cycle,  $N_2$  from the atmosphere becomes bioavailable by  $N_2$ -fixation. The loss of nitrogen from the marine ecosystem to the atmosphere as  $N_2$  gas is dominated by two major pathways. One way is nitrate respiration in facultative anaerobic microorganisms which produce  $N_2$  from  $NO_3^-$  (heterotrophic denitrification). The other process is anaerobic oxidation of ammonium (Anammox) by  $NO_2^-$ , which yields  $N_2$  (van de Graaf et al., 1995; Thamdrup and Dalsgaard, 2002; Kuypers et al., 2003).

About 20 to 40 % of the global nitrogen loss in the oceans is estimated to take place in OMZs, although these zones occupy only 0.1 % of the global ocean volume (Gruber and Sarmiento, 1997; Gruber, 2004; Lam et al., 2009). Nitrate is usually depleted in near surface waters due to utilisation by primary producers. Remineralisation of degraded organic matter produces  $NH_4^+$  which is stepwise oxidized to  $NO_3^-$  under aerobic conditions (nitrification). Thus, the  $NO_3^-$  concentration usually increases with water depth. Denitrification also proceeds stepwise with a number of intermediate species involved ( $NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$ ). Nevertheless, only the complete process with the final product  $N_2$  meets the strict definition of denitrification (Zumft, 1997; Lam et al., 2009).

Another concurring nitrate consuming process is dissimilatory nitrate reduction to ammonium (DNRA). It usually takes place under low-oxygen conditions. DNRA by sulfur bacteria (*Thioploca* and *Beggiotoa*) seems to be a major pathway of nitrate-loss at shelf and upper slope at the Peruvian OMZ between 78 and 259 m water depth, while denitrification is the major pathway at depths beyond 319–1005 m (Bohlen et al., 2011; Mosch et al., 2012).

Recent studies showed that several benthic foraminiferal species facultatively may change to nitrate respiration when dissolved oxygen becomes depleted in the water

**BGD**

9, 17775–17817, 2012

### The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



---

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

(Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010a). Four of the analysed foraminiferal species (all from Peruvian OMZ) denitrify to  $N_2O$  rather than to  $N_2$  implying that they might lack nitrous oxide reductase (Piña-Ochoa et al., 2010a). The contribution of foraminiferal denitrification to the total nitrate loss may range from 4 % (Sagami Bay, Japan; Glud et al., 2009) to more than 70 % (Bay of Biscay or Skagerrak; Piña-Ochoa et al., 2010a). Even if the contribution of foraminiferal denitrification is considered low like at the Sagami Bay study site,  $NO_3^-$  stored in foraminiferal cells still comprised  $\sim 80\%$  of the total benthic nitrate pool. Results from Risgaard-Petersen et al. (2006) and Bernhard et al. (2012a) suggested that denitrification in *Globobulimina pseudospinescens* (*Globobulimina turgida* of authors), *Bolivina argentea*, *Fusenkoina cornuta* and *Nonionella stella* is not performed by prokaryotic symbionts. Even after treatment with antibiotics *B. argentea*, was still able to denitrify (Bernhard et al., 2012a). Nevertheless, denitrification in a “Clade L” allogromid from the Santa Barbara Basin was most likely catalyzed by endosymbionts (Bernhard et al., 2012b). *Buliminella tenuata* also hosts abundant endobionts (Bernhard et al., 2012a). Thus, denitrification in some species is performed by symbionts while other species denitrify on their own. Although this foraminiferal denitrification has not been traced to a specific cell organelle yet (Høgslund et al., 2008), there are indications that the pores in some foraminiferal species are involved in the denitrification process (Glock et al., 2011, 2012). The recent proof that benthic diatoms are able to respire nitrate via DNRA shows that foraminifera are not the only important group of marine eukaryotes with the ability of nitrate respiration (Kamp et al., 2011). Other eukaryotes with the ability of denitrification are two fungi, *Fusarium oxysporum* and *Cylindrocarpon tonkinense* (Shoun and Tanimoto, 1991; Usuda et al., 1995), and the eukaryotic protiste *Loxodes* (Finlay et al., 1983). Prokopenko et al. (2011) showed that denitrification in anoxic sediments is strongly supported by biological nitrate transport through cell stored nitrate. They also estimated based on a data constrained model that at least 31 % of the total  $N_2$  production in anoxic sediments is mediated by biological transported nitrate.



## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The sediment from the “glove bag cores” was pushed out of the tube, cut into 10-mm-thick slices and transferred into centrifuge vials. The pore water was separated from sediments with a cooled centrifuge, filtrated with syringe-filters (0.2 nm cellulose-acetate filters) under argon atmosphere and collected in PTFE bottles. Both methods were used to preserve the pore water from oxygen contamination.

At five of these locations, other cores were sampled for pore-water nitrate with an additional method. These cores were cut into 10-mm-thick slices. The pore water was squeezed out of the sediment with a pore water press, filtrated and collected into PTFE bottles. The advantage of this method is that also cell stored nitrate is partly squeezed out of the cells. Comparing nitrate concentrations measured from these samples and centrifugated or rhizon-collected pore waters, a rough estimate of the amount of cell stored nitrate in the sample can be made.

### 2.2 Foraminiferal studies

The foraminiferal samples were washed through stacked sieves with mesh sizes of 2000  $\mu\text{m}$  and 63  $\mu\text{m}$ . The 63–2000- $\mu\text{m}$  size fraction was dried at 50°C and weighed. The residues were subdivided with an Otto (1937) microsplitter until aliquots had a manageable size with a target value of at least 300 well-stained individuals that were considered as living at the time of sampling. Specimens were picked either dry or wet, sorted by species in Plummer cell slides, fixed with glue and counted (Mallon et al., 2012). For the complete faunal references see Mallon (2012).

### 2.3 Calculation of foraminiferal denitrification rates and foraminiferal nitrate storage

The density of living foraminiferal specimens in the sediment under a certain area ( $\text{ind cm}^{-2}$ ; usually defined as standing stock) is referred here as foraminiferal abundance. The foraminiferal abundance was calculated for each species in the individual core slices and referred to the sample surface ( $\text{ind cm}^{-2}$ ). The abundances in each





time interval between the first and the last syringe water sampling. Immediately after retrieval of the observatories, the water samples were transferred to the onboard cool room (4 °C) for further sample processing and sub-sampling. The fluxes of the different nitrogen species were calculated from the linear increase or decrease of their concentrations with time. For the BIGO-T deployments two fluxes were calculated for each nitrogen species, one for the first series of water samples taken prior to the replacement of the chamber water denoted as I1, and another one for the second series of water samples taken thereafter (I2). Negative nitrate flux rates from the lander measurements will be referred as nitrate loss hereafter.

## 2.5 Pore water nitrate concentrations

Nitrate concentrations in pore and bottom waters were measured onboard using a Metrohm 761 compact ion-chromatograph equipped with a Methrom/Metrosep A SUPP5 anion-exchange column (150/4.0 mm) and solution of Na<sub>2</sub>CO<sub>3</sub> (3.2 mM) with NaHCO<sub>3</sub> (1.0 mM) as eluent. The IAPSO seawater standard was used for calibration. The method was described in detail by Grasshoff et al. (1999). Nitrate was measured with a detection limit of 1 μmolL<sup>-1</sup> and a relative error of 5 %.

## 3 Results

### 3.1 Distribution of living benthic foraminifera along 11° S at the Peruvian OMZ

Foraminiferal assemblages in sediments of the centre of the Peruvian OMZ are characterized by low diversities and very high population densities (Mallon et al., 2012). Population densities in the top 5 mm of the sediments can reach values of 1045 indcm<sup>-3</sup> (Table A1). This is comparable to results from other OMZs (Phleger and Soutar, 1973; Baja California, Mexico; Gooday et al., 2000; den Dulk et al., 1998; Jannink et al., 1998; Schumacher et al., 2007; for the Arabian Sea OMZ). Except the station immediately below the OMZ at 697 m, the dominating species are *boliviniidae* (70–95 % of

**BGD**

9, 17775–17817, 2012

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the foraminiferal abundance). At the shallowest station, the total benthic foraminiferal abundance was 344 indcm<sup>-2</sup>. The highest abundances were found at 248 m water depth (616 indcm<sup>-2</sup>). From the centre of the OMZ (317 and 319 m) to the lower OMZ boundary (465 m), the abundances declined down from 496 to 61 indcm<sup>-2</sup>. The lowest values were found below the OMZ (697 m, 13 indcm<sup>-2</sup>). At 78 m water depth the dominant species was *Bolivina costata* (74 %) followed by *Bolivina seminuda* (5 %). *Bolivina seminuda* is dominant at 248 m (90 %) while *B. costata* and *Epistominella obesa* are the second ranked species (3 % each). In the stations in the centre of the OMZ, *B. seminuda* is still the dominant species (67–70 %), followed by *B. costata* (6–15 %) and *B. plicata* (6–13 %). *Cancris carmenensis* was common at one of these stations (6 %). At the lower boundary of the permanent anoxic core of the OMZ (465 m), the most abundant species were *Bolivina interjuncta* (44 %) and *B. seminuda* (20 %). Assemblages were much more diverse at the station below the OMZ core (697 m), where *Uvigerina peregrina* (19 %), *B. spissa* (17 %) and *Cassidulina delicata* (14 %) were frequent. It has to be emphasized that these figures differ from previously published data from surface sediments (Mallon et al., 2012), in that values reported in this paper always refer to the total benthic foraminiferal fauna including both surface and subsurface assemblages.

From this dataset, the benthic foraminiferal denitrification rates were calculated (Table 3). In the three stations from the centre of the OMZ (248–319 m) individual denitrification rates for most of the living foraminifera were known from the literature (76–90 %), and approximations A and B played only a minor role. At the upper and lower boundary of the OMZ (79 m and 465 m) however, approximation A had a strong influence on the calculations (58–74 % of the foraminiferal assemblage). Only at the station immediately below the OMZ (697 m) approximation B had a strong impact on the calculations (54 % of the species). Only for one species comprising 0.1 % of the foraminifera living at this station individual denitrification rates were known from the literature.

## BGD

9, 17775–17817, 2012

### The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

### 3.2 Comparison of foraminiferal denitrification rates to total benthic denitrification rates and nitrate flux rates from lander measurements

At the shallowest station (79 m), the calculated benthic foraminiferal denitrification rate was  $0.45 \text{ mmol m}^{-2} \text{ d}^{-1}$  (Table 4). Foraminiferal denitrification showed a maximum of  $1.31 \text{ mmol m}^{-2} \text{ d}^{-1}$  in the upper part of the OMZ at 248 m water depth. In the center of the OMZ at 300 m, the rates vary between  $0.55$  and  $1.07 \text{ mmol m}^{-2} \text{ d}^{-1}$ . At the lower OMZ boundary (465 m) foraminiferal denitrification was only  $0.10 \text{ mmol m}^{-2} \text{ d}^{-1}$  and reached a minimum of  $0.01 \text{ mmol m}^{-2} \text{ d}^{-1}$  below the OMZ at 697 m where the bottom water oxygen level was  $12.6 \mu\text{mol L}^{-1}$  (Glock et al., 2011). Bohlen et al. (2011) used a dataset including pore water concentration profiles and in situ benthic fluxes of different nitrogen species to calculate rates of denitrification (divided in turnover rates from  $\text{NO}_3^-$  to  $\text{NO}_2^-$  and  $\text{NO}_2^-$  to  $\text{N}_2$ ), nitrification, anammox and DNRA. For our comparison to the benthic foraminiferal denitrification, we used the modelled denitrification rates from  $\text{NO}_3^-$  to  $\text{NO}_2^-$ , hereafter referred to as total benthic denitrification. The benthic foraminiferal denitrification was compared to the total benthic denitrification at different water depths (Fig. 2a, b). The comparison revealed that foraminiferal denitrification almost entirely covered the total benthic denitrification at the shallow stations in the upper OMZ. At the 79 m station, the estimated foraminiferal denitrification exceeded the total benthic denitrification as estimated from the models by  $\sim 28\%$ . This proportion abruptly decreased with water depth. While in the centre of the OMZ foraminifera still contribute about 30–50 % to the total benthic denitrification, their contribution diminished to about 2–5 % at the lower boundary and below the core of the OMZ (465–697 m).

The foraminiferal denitrification rates were compared with the nitrate loss rates as calculated from nitrate concentrations in the benthic chamber experiments (Table 5) in order to assess the demand of foraminiferal denitrification with reference to the total benthic nitrate uptake (Fig. 3a, b). Nitrate uptake rates were particularly low at the shallow station ( $0.9 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) coinciding with low pore water nitrate concentrations in the uppermost sediment. At water depths between 260 and 400 m and well within

**BGD**

9, 17775–17817, 2012

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

the OMZ, nitrate uptake was high ranging from 2.2 to 3.8 mmol m<sup>-2</sup> d<sup>-1</sup>. In the lower part of the OMZ and further below, nitrate uptake declined. The demand of foraminiferal denitrification was constrained to 50 % of the total benthic nitrate uptake at 79 m. The consumption by foraminiferal denitrification was 38 % at 248 m water depth, ranged between 41 % and 18 % in the center of the OMZ, and was in the order of ~1 % at 697 m below the OMZ. It has to be emphasized that despite the high contribution of foraminiferal to total benthic denitrification at the shallower sites, our estimates only consider near surface sediments up to ~5 cm depth. The excess benthic nitrate uptake accounts to DNRA by sulfur bacteria and to anammox processes (Bohlen et al., 2011).

### 3.3 Foraminiferal nitrate storage and pore water nitrate concentrations

The total amount of nitrate stored in foraminiferal cytoplasm in the 0–1 cm sediment was compared with nitrate concentrations in the ambient pore water (Table 4). The pore water nitrate concentrations from glove box or rhizon samples from locations where also foraminiferal data was available ranged from 0.6 to 4.4 μmol L<sup>-1</sup> at the upper and lower OMZ boundaries and in the centre of the OMZ (79–465 m) to 15.8 μmol L<sup>-1</sup> below the OMZ (697 m). The nitrate concentrations obtained from pore water press samples at these locations were with 93.2 μmol L<sup>-1</sup> (79 m) and 102.0 μmol L<sup>-1</sup> (319 m) higher by an order of magnitude (Fig. A1). The calculated foraminiferal nitrate storage ranged from 62.2 μmol L<sup>-1</sup> at the upper OMZ boundary to 705.3 μmol L<sup>-1</sup> in the centre of the OMZ and decreased again to 388.4 μmol L<sup>-1</sup> at the lower boundary of the OMZ. Below the OMZ at 697 m, the calculated foraminiferal nitrate storage was with 2.7 μmol L<sup>-1</sup> relatively low. It has to be mentioned that foraminiferal cells and seawater vacuoles inside the cells are not part of the free pore space. But due to their small size the cell volume is negligible when compared to the sediment or pore water volume.

**BGD**

9, 17775–17817, 2012

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## 4 Discussion

### 4.1 Evaluation of calculated foraminiferal denitrification rates

From 79–465 m water depth, *bolivinidae* are dominating the benthic foraminiferal assemblages. In this depth interval, *Bolivina* species account for 70–95 % of the total foraminiferal fauna comprising surface and subsurface assemblages. Below the OMZ at 697 m, *bolivinidae* account for approximately 25 % of the total standing stock only. Piña-Ochoa et al. (2010a) and Bernhard et al. (2012a) showed that 4 out of 4 analysed *bolivinidae* are able to denitrify including two species from the Peruvian OMZ (*B. seminuda* and *B. plicata*). *Bolivina seminuda* is with 67–90 % the dominant species in the centre of the Peruvian OMZ at 248–319 m where *B. plicata* is also common. At these locations the approximations made for the calculations play only a minor role. At the upper boundary of the OMZ (79 m) the foraminiferal assemblages are dominated by *B. costata* (74 %) while at the lower boundary (465 m) *B. interjuncta* (44 %) and *B. seminuda* (20 %) are the dominating species. Measured denitrification rates were reported for *B. seminuda* and *B. plicata* (Piña-Ochoa et al., 2010a; Bernhard et al., 2012a), while denitrification rates for *B. costata* and *B. interjuncta* are not available. As these species are able to survive under anoxic conditions, it is reasonable to assume that they also can use an electron acceptor different from oxygen for their metabolism. Nitrate appears to be a likely source, because 11 out of 12 benthic foraminiferal species including 4 different *bolivinidae* were proven to denitrify (Piña-Ochoa et al., 2010a). The emerging fact that foraminiferal denitrification is widespread in general further supports our assumptions. Nevertheless, approximation A, which infers average values for non-designated species from the same genus, has a strong influence on the calculation. The denitrification estimate for the location at 697 m below the OMZ contains the highest uncertainty. About 54 % of the species found at this station are from genera for which no denitrification data are available. Therefore, approximation B exerted a strong influence on the calculations. However, the population density and thus the calculated denitrification rate is comparatively low at this location. Even if we assume at this station

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



an error which is several times higher than the calculated value, there would be still an obvious difference to denitrification estimates at stations within the OMZ.

## 4.2 The role of benthic foraminiferal denitrification along the Peruvian OMZ

Despite the novel pathway of nitrogen loss due to foraminiferal denitrification, so far the contribution of foraminiferal denitrification to the total benthic  $N_2$  production has been only determined for a single sampling site in 1450 m water depth at Sagami Bay, Japan (Glud et al., 2009). The data reveal the contribution of foraminiferal denitrification to the overall budget (4%) plays only a minor role at this site. In addition, the benthic foraminiferal abundance is with only  $12 \text{ ind cm}^{-2}$  (size fraction  $> 125 \mu\text{m}$ ) rather low as compared to the OMZ off Peru ( $616 \text{ ind cm}^{-2}$ ). Bottom water oxygen concentration was  $> 55 \mu\text{mol L}^{-1}$  in Sagami Bay and oxygen penetrated  $\sim 3.0\text{--}12.4 \text{ mm}$  into the sediments (Glud et al., 2009). Therefore, foraminifera might not necessarily depend on nitrate respiration in Sagami Bay. Off Peru, bottom-water oxygen may fall below  $0.02 \mu\text{mol L}^{-1}$  revealing essentially anoxic conditions for both bottom waters and subsurface sediments, respectively (Revsbech et al., 2009; Thamdrup et al., 2012). In the Peruvian OMZ, in particular where benthic foraminifera reach abundances of  $616 \text{ ind cm}^{-2}$  and are influenced by anoxic bottom waters, denitrification offers a survival strategy reflected by relatively high denitrification rates.

It has been suggested that benthic foraminifera were responsible for  $\sim 70\%$  of the total denitrification in several regions (Piña-Ochoa et al., 2010a). Our estimates confirm this assumption and reveal that even the entire denitrification might be dominated by benthic foraminifera in the shallow part of the Peruvian OMZ at depths between 79 and 248 m water depth. At 79 m, the estimated foraminiferal denitrification rate tends to be even higher than the total benthic denitrification as inferred by a biogeochemical model (Bohlen et al., 2011). *Bolivina costata* was the dominant species at this station. The individual denitrification rate for this species is yet unknown and has been obtained by using approximation A. Hence, foraminiferal denitrification could be overestimated in our calculations at this site.

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





benthic chambers, since ammonia forming DNRA plays a less important role at these sampling sites. In fact, seafloor observations showed that bacterial mats were scattered and more threadlike in these water depths instead of extensive patchy occurrences at the upper OMZ boundary (Mosch et al., 2012). Since foraminifera were not the quantitative denitrifiers in the centre of the OMZ, prokaryotic denitrification must become more important in these habitats. It is yet unknown which organisms take over the baton from foraminifera as dominant denitrifiers at the deeper stations. Unfortunately, no lander measurements or model-data were available for the 465-m site at the lower OMZ boundary. If the calculated foraminiferal denitrification is compared to the total benthic denitrification as intrapolated from the two closest sites where model data were available (Bohlen et al., 2011), foraminifera only account for 5% to the total benthic denitrification.

Below the OMZ at 697 m, foraminifera play only a minor role in benthic nitrate loss and account for ~ 1% of the total nitrate budget. Contribution to benthic nitrate loss and foraminiferal abundances ( $13 \text{ ind cm}^{-2}$ ) were comparable to those at Sagami Bay (Glud et al., 2009). A direct and more detailed comparison is impeded by largely different environmental settings and a different species composition of foraminiferal assemblages off Japan (Kitazato, 1993; Ohga and Kitazato, 1996).

The fact that foraminiferal denitrification might have an impact on the benthic nitrogen cycle larger than previously thought is challenging. Piña-Ochoa et al. (2010a) already stated that measurements on marine denitrification that rely on  $^{15}\text{N}$  tracer additions (Cabrita and Brotas, 2000; Graco et al., 2001; Rysgaard et al., 2001) or on modeling of nitrate pore-water profiles might underestimate the true total rate of denitrification, because denitrification in intracellular nitrate pools is not considered (Høgslund et al., 2008). Different incubation methods, in particular measuring the decrease of nitrate in the culture vessel fill or the increase of the  $\text{N}_2/\text{Ar}$  ratio in the gas phase that percolates the incubation chambers might be prospective to record foraminiferal denitrification at both, species and assemblage level and with more realistic values (Høgslund et al., 2008; Piña-Ochoa et al., 2010a).

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



### 4.3 The role of benthic foraminifera in the sedimentary nitrate reservoir

The concentration of nitrate in foraminiferal cells can be highly elevated as compared to levels in the ambient pore waters (Risgaard-Petersen et al., 2006; Høgslund et al., 2008; Piña-Ochoa et al., 2010a,b; Bernhard et al., 2012a,b). Even in habitats where the contribution of foraminiferal denitrification to the total benthic nitrate uptake is relatively low, foraminifera may contain the highest proportion of benthic nitrate (Glud et al., 2009). Our calculations revealed that nitrate concentrations in foraminiferal cytoplasm can be three orders of magnitude higher when compared to the levels in the adjacent pore waters. Especially species like *Cancris carmenensis*, having a large biomass and being able to store high amounts of nitrate, make foraminifera in the Peruvian OMZ an important sedimentary nitrate reservoir. Piña-Ochoa et al. (2010a) report very high nitrate concentrations ( $0.26 \mu\text{mol cell}^{-1}$ ) for *Cancris inflatus*, which is probably a synonym of *Cancris carmenensis* from the Peruvian OMZ. Indeed, pore water nitrate concentrations in two samples taken with a pore water press at 79 and 319 m were elevated by two orders of magnitude as compared to corresponding samples taken in a glove box or with rhizons. It is conceivable that released intracellular nitrate may account for this difference. Some amount of nitrate stored in foraminifera could be squeezed out of the cytoplasm in foraminiferal shells. However, another fraction of the excess nitrate might be contributed from squashed *Thioploca* and *Beggiotoa* cells which were common in these habitats (Mosch et al., 2012). The pressure inside the press is not isostatic but directed and thus not comparable with the hydrostatic pressure in the habitat of the foraminifera. An external pressure is exerted on top of the sediment sample. Since the pore water is allowed to leave the system the sediment is intensely compacted and physical properties are severely altered. Even though the exact mechanism of nitrate release from foraminiferal or bacterial cells during pore-water extraction is not yet constrained, so-called “artificial subsurface nitrate peaks” in pore water profiles as found in the Santa Barbara Basin (Bernhard and Reimers, 1991; Reimers et al., 1996; Bernhard et al., 2012a), and also in the Peruvian OMZ (see Table A2; Examples: 78 m,

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



319 m, 465 m, 512 m, 697 m) are considered to originate from the cytoplasm of benthic organisms, most likely with an important contribution of foraminifera.

## 5 Conclusions and implications

Our data highlights the importance of foraminiferal denitrification in one of the major regions for nitrate loss of the world oceans, the Peruvian OMZ, and that there are strong variations in the rate of foraminiferal denitrification even on a regional scale. In the shallow part of the Peruvian OMZ at 79 m and 248 m water depth most likely the entire denitrification is performed by benthic foraminifera. In the centre of the OMZ at 300 m water depth, foraminifera still contribute ~ 30–50 % to the total benthic denitrification while they play only a minor role (~ 1–5 %) at the lower boundary and below the permanent anoxic centre of the OMZ from 465–697 m depth. Foraminiferal denitrification rates at our sampling locations reached up to  $1.31 \text{ mmol m}^{-2} \text{ d}^{-1}$  and thus were among the highest ever estimated. Furthermore, nitrate stored in benthic foraminiferal cells contributes significantly to the benthic nitrate reservoir in this region. However, data on nitrate respiration rates and the knowledge of individual storage capacities of more species are required in order to better constrain the contribution of foraminifera to the nitrate budget of the world oceans.

Several implications emerge from these results and previous studies published on foraminiferal denitrification and nitrate storage. Only few data about nitrogen isotope fractionation processes during foraminiferal denitrification is available at the moment. Recent studies of Bernhard et al. (2012a,b) demonstrated the intracellular nitrate pool of foraminifera fractionated with reference to the  $\delta^{15}\text{N}$  values in pore and bottom waters. The fractionation even increased during foraminiferal denitrification. Furthermore, the fractionation levels varied strongly between different species. These facts and the high amount of nitrate stored in foraminiferal cells imply that foraminiferal stored nitrate might also have a considerable influence on the  $\delta^{15}\text{N}$  values in the sediments. In particular, the nitrogen isotope fractionation of in the water column is relatively low,

### The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



which suggests an influence from denitrification in the sediments (Ryabenko et al., 2012).

*Acknowledgements.* We thank Anna Noffke, Lisa Bohlen, Florian Scholz, Bettina Domeyer, Meike Dibbern, Renate Ebinghaus and Sonja Kriwanek for bottom- and pore-water nitrate and oxygen measurements. Volker Liebetrau supported this study with inspiring discussions. The scientific party on R/V METEOR cruise M77 is acknowledged for their general support and help with multicorer operation and sampling. The Deutsche Forschungsgemeinschaft (DFG), provided funding through SFB 754 “Climate–Biogeochemistry Interactions in the Tropical Ocean”.

The service charges for this open access publication have been covered by a Research Centre of the Helmholtz Association.

## References

- Aanderaa Instruments AS: TD 218 Operating manual oxygen optode 3830 and 3930, 9th Edn., Aanderaa Instruments AS, Bergen, Norway, 44 pp., 2003.
- Altabet, M. A., Francois, R., Murray, D. W., and Prell, W. L.: Climate-related variations in denitrification in the Arabian Sea from sediment  $^{15}\text{N}/^{14}\text{N}$  ratios, *Nature*, 373, 506–509, 1995.
- Arrigo, K. R.: Marine microorganisms and global nutrient cycles, *Nature*, 437, 349–355, 2005.
- Bernhard, J. M. and Reimers, C. E.: Benthic foraminiferal population fluctuations related to anoxia – Santa Barbara Basin, *Biogeochemistry*, 15, 127–149, doi:10.1007/BF00003221, 1991.
- Bernhard, J. M., Visscher, P. T., and Bowser, S. S.: Sub-millimeter life positions of bacteria, protists, and metazoans in laminated sediments of the Santa Barbara Basin, *Limnol. Oceanogr.*, 48, 813–828, 2003.
- Bernhard, J. M., Casciotti, K. L., Mcllvin, M. R., Beaudoin, D. J., Visscher, P. T., and Edgcomb, V. P.: Potential importance of physiologically diverse benthic foraminifera in sedimentary nitrate storage and respiration, *J. Geophys. Res.*, 117, G03002, doi:10.1029/2012JG001949, 2012a.

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

- 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, 2012b.
- Bohlen, L., Dale, A. W., Sommer, S., Mosch, T., Hensen, C., Noffke, A., Scholz, F., and Wallmann, K.: Benthic nitrogen cycling traversing the Peruvian oxygen minimum zone, *Geochim. Cosmochim. Ac.*, 75, 6094–6111, 2011.
- Cabrita M. T. and Brotas V.: Seasonal variation in denitrification and dissolved nitrogen fluxes in intertidal sediments of the Tagus estuary, Portugal, *Mar. Ecol.-Prog. Ser.*, 202, 51–65, 2000.
- Caralp, M., Lamy, A., and Pujos, M.: Contribution a la connaissance de la distribution bathymétrique des Foraminifères dans le golfe de Gascogne, *Rev. Esp. Micropaleontol.*, 2, 55–84, 1970.
- Corliss, B. H.: Microhabitats of benthic foraminifera within deep-sea sediments, *Nature*, 314, 435–438, 1985.
- Den Dulk, M., Reichart, G. J., Memon, G. M., Roelofs, E. M. P., Zachariasse, W. J., and van der Zwaan, G. J.: Benthic foraminiferal response to variations in surface water productivity and oxygenation in the northern Arabian Sea, *Mar. Micropaleontol.*, 35, 43–66, 1998.
- Falkowski, P. G.: Evolution of nitrogen cycle and its influence on the biological pump in the ocean, *Nature*, 342, 637–642, 1997.
- Finlay, B. J., Span, A. S. W., and Harman, J. M. P.: Nitrate respiration in primitive eukaryotes, *Nature*, 303, 333–335, 1983.
- Francis, C. A., Beman, J. M., and Kuypers, M. M. M.: New processes and players in the nitrogen cycle: the microbial ecology of anaerobic and archaeal ammonia oxidation, *ISME J.*, 1, 19–27, 2007.
- Glock, N., Eisenhauer, A., Milker, Y., Liebetrau, V., Schönfeld, J., Mallon, J., Sommer, S., and Hensen, C.: Environmental influences on the pore-density in tests of *Bolivina spissa*, *J. Foramin. Res.*, 41, 22–32, 2011.
- Glock, N., Schönfeld, J., and Mallon, J.: The functionality of pores in benthic foraminifera and bottom water oxygenation, a review, in: *ANOXIA: Evidence for Eukaryote Survival and Paleontological Strategies, Cellular Origin, Life in Extreme Habitats and Astrobiology 21*, edited by: Altenbach, A. V., Bernhard, J. M., and Seckbach, J., Springer Science + Business Media, Dordrecht, Netherlands, 537–552, doi:10.1007/978-94-007-1896-8\_28, 2012.



## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

- Kuypers, M. M. M., Sliemers, A. O., Lavik, G., Schmid, M., Jørgensen, B. B., Kuenen, J. G., Sinninghe Damste J. S., Strous, M., and Jetten, M. S. M.: Anaerobic ammonium oxidation by anammox bacteria in the Black Sea, *Nature*, 422, 608–611, doi:10.1038/nature01472, 2003.
- 5 Lam, P., Lavik, G., Jensen, M. M., van de Vossenberg, J., Schmid, M., Woebken, D., Gutiérrez, D., Amann, R., Jetten, M. S. M., and Kuypers, M. M. M.: Revising the nitrogen cycle in the Peruvian oxygen minimum zone, *PNAS*, 106, 4752–4757, 2009.
- Lutze, G. F.: Relative abundance of live (Rose Bengal stained) benthic foraminifera in the small size fraction of surface sediment off NW Africa (Table 3), in: *Depth Distribution of Benthic Foraminifera on the Continental Margin off NW Africa*, edited by: Lutze, G. F., Meteor Forschungsergebnisse, Deutsche Forschungsgemeinschaft, Reihe C Geologie und Geophysik, Gebrüder Bornträger, Berlin, Stuttgart, C32, 31–80, doi:10.1594/PANGAEA.536260, 1980.
- 10 Lutze, G. F. and Altenbach, A. V.: Technik und Signifikanz der Lebendfärbung benthischer Foraminiferen in Bengalrot, *Geol. Jahrb. A*, 128, 251–265, 1991.
- Mallon, J.: Benthic foraminifera of the Peruvian and Ecuadorian Continental margin, dissertation, Geomar Helmholtz Centre for Ocean Research, Kiel, 2012.
- Mallon, J., Glock, N., and Schönfeld, J.: The response of benthic foraminifera to low-oxygen conditions of the Peruvian oxygen minimum zone, in: *ANOXIA: Evidence for Eukaryote Survival and Paleontological Strategies, Cellular Origin, Life in Extreme Habitats and Astrobiology 21*, edited by: Altenbach, A. V., Bernhard, J. M., and Seckbach, J., Springer Science + Business Media, Dordrecht, Netherlands, 16, 305–321, doi:10.1007/978-94-007-1896-8, 2012.
- 20 Mosch, T., Sommer, S., Dengler, M., Noffke, A., Bohlen, L., Pfannkuche, O., Liebetau, V., and Wallmann, K.: Factors influencing the distribution of epibenthic megafauna across the Peruvian oxygen minimum zone, *Deep-Sea Res. Pt. I*, 68, 123–135, doi:10.1016/j.dsr.2012.04.014, 2012.
- Murray, J. W.: The niche of benthic foraminifera, critical thresholds and proxies, *Mar. Micropaleontol.*, 41, 1–7, 2001.
- 30 Ohga, T. and Kitazato, H.: Seasonal changes in bathyal foraminiferal populations in response to the flux of organic matter (Sagami Bay, Japan), *Terra Nova*, 9, 33–37, 1997.
- Otto, G. H.: Comparative tests of several methods of sampling heavy mineral concentrates, *J. Sediment. Petrol.*, 3, 30–39, 1933.

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Phleger, F. B. and Soutar, A.: Production of benthic foraminifera in three east Pacific oxygen minima, *Micropaleontology*, 19, 110–115, 1973.
- Pierotti, D. and Rasmussen, R. A.: Nitrous oxide measurements in the eastern tropical Pacific Ocean, *Tellus*, 32, 56–72, 1980.
- 5 Piña-Ochoa, E., Høgslund, S., Geslin, E., Cedhagen, T., Revsbech, N. P., Nielsen, L. P., Schweizer, M., Jorissen, F., Rysgaard, S., and Risgaard-Petersen, N.: Widespread occurrence of nitrate storage and denitrification among Foraminifera and *Gromiida*, *P. Natl. Acad. Sci. USA*, 107, 1148–1153, 2010a.
- 10 Piña-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, 2010b.
- Prokopenko, M. G., Sigman, D. M., Berelson, W. M., Hammond, D. E., Barnett, B., Chong, L., and Townsend-Small, A.: Denitrification in anoxic sediments supported by biological nitrate transport, *Geochim. Cosmochim. Ac.*, 75, 7180–7199, 2011.
- 15 Reimers, C. E., Ruttnerberg, K. C., Canfield, D. E., Christiansen, M. B., and Martin, J. B.: Pore-water pH and authigenic phases formed in the uppermost sediments of the Santa Barbara Basin, *Geochim. Cosmochim. Ac.*, 60, 4037–4057, doi:10.1016/S0016-7037(96)00231-1, 1996.
- Risgaard-Petersen, N., Langezaal, A. M., Ingvarsdn, S., Schmid, M. C., Jetten, M. S., Op den Camp, H. J. M., Derksen, J. W. M., Piña-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.
- 20 Ryabenko, E., Kock, A., Bange, H. W., Altabet, M. A., and Wallace, D. W. R.: Contrasting biogeochemistry of nitrogen in the Atlantic and Pacific Oxygen Minimum Zones, *Biogeosciences*, 9, 203–215, doi:10.5194/bg-9-203-2012, 2012.
- 25 Rysgaard S., Fossing H., and Jensen M. M.: Organic matter degradation through oxygen respiration, denitrification, and manganese, iron, and sulfate reduction in marine sediments (the Kattegat and the Skagerrak), *Ophelia*, 55, 77–91, 2001.
- Schmiedl, G., Mackensen, A., and Müller, P. J.: Recent benthic foraminifera from the eastern South Atlantic Ocean: dependance on food supply and water masses, *Mar. Micropaleontol.*, 32, 249–287, 1997.
- 30 Schönfeld, J.: History and development of methods in Recent benthic foraminiferal studies, *J. Micropaleontol.*, 31, 53–72, 2012.

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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.

Shoun, H. and Tanimoto, T.: Denitrification by the fungus *Fusarium oxysporum* and involvement of cytochrome P-450 in the respiratory nitrite reduction, *J. Biol. Chem.*, 266, 11078–11082, 1991.

Sommer, S., Linke, P., Pfannkuche, O., Schleicher, T., Schneider v. Deimling, J., Reitz, A., Haeckel, M., Flögel, S., and Hensen, C.: Seabed methane emissions and the habitat of frenulate tubeworms on the Captain Arutyunov mud volcano (Gulf of Cadiz), *Mar. Ecol.-Prog. Ser.*, 382, 69–86, doi:10.3354/meps07956, 2009.

Sommer, S., McGinnis, D. F., Linke, P., Camilli, R., Mosch, T., and Pfannkuche, O.: Life at the edge – oscillating lower boundary of the Peruvian oxygen minimum zone, *Eos Trans. AGU, Ocean Science Meeting Supplementary*, 91, Abstract BO24C–08, 2010.

Tengberg, A., Hovdenes, J., Andersson, H. J., Brocandel, O., Diaz, R., Hebert, D., Arnerich, T., Huber, C., Körtzinger, A., Khripounoff, A., Rey, F., Rönning, C., Schimanski, J., Sommer, S., and Stangelmayer, A.: Evaluation of a lifetime-based optode to measure oxygen in aquatic systems, *Limnol. Oceanogr.-Meth.*, 4, 7–17, 2006.

Thamdrup, B. and Dalsgaard, T.: Production of  $N_2$  through anaerobic ammonium oxidation coupled to nitrate reduction in marine sediments, *Appl. Environ. Microb.*, 68, 1312–1318, 2002.

Thamdrup, B., Dalsgaard, T., and Revsbech, N. P.: Widespread functional anoxia in the oxygen minimum zone of the Eastern South Pacific, *Deep-Sea Res. Pt. I*, 65, 36–45, doi:10.1016/j.dsr.2012.03.001, 2012.

Timm, S.: *Rezente Tiefsee-Benthosforaminiferen aus Oberflächensedimenten des Golfes von Guinea (Westafrika): Taxonomie, Verbreitung, Oekologie und Korngrößenfraktionen = Recent deep-sea benthic foraminifera from surface sediments of Gulf of Guinea (Westafrika): taxonomy, distributions, ecology and grain size fractions*, dissertation, Geologisch-Paläontologisches Institut und Museum, Christian-Albrechts-Universität, Kiel, Germany, 1992.

Uchio, T.: Ecology of living benthonic foraminifera from the San Diego, California, Area, Cushman Foundation for Foraminiferal Research, Special Publication, 5, 1–72, 1960.

Usuda, K., Toritsuka, N., Matsuo, Y., Kim, D. H., and Shoun, H.: Denitrification by the fungus *Cylindrocarpon tonkinense*: anaerobic cell growth and two isozyme forms of cytochrome P-450nor, *Appl. Environ. Microb.*, 61, 883–889, 1995.

5 Van de Graaf, A. A., Mulder, A., de Bruijn, P., Jetten, M. S. M., and Kuenen, J. G.: Anaerobic oxidation of ammonium is a biologically mediated process, *Appl. Environ. Microb.*, 61, 1246–1251, 1995.

Zumft, W. G.: Cell biology and molecular basis of denitrification, *Microbiol. Molecul. Biol. Rev.*, 61, 533–616, 1997.

**BGD**

9, 17775–17817, 2012

---

**The role of benthic foraminifera in the benthic nitrogen cycle**

N. Glock et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Table 1.** Sampling sites for foraminiferal studies.

| Site             | Longitude (S) | Latitude (W) | Water depth (m) |
|------------------|---------------|--------------|-----------------|
| M77/1-540/MUC-49 | 11°00.01′     | 77°47.40′    | 79              |
| M77/1-583/MUC-65 | 11°06.86′     | 78°03.06′    | 248             |
| M77/1-473/MUC-32 | 11°00.01′     | 78°09.94′    | 317             |
| M77-1-449/MUC-19 | 11°00.01′     | 78°09.97′    | 319             |
| M77/1-456/MUC-22 | 11°00.013′    | 78°19.23′    | 465             |
| M77/1-459/MUC-25 | 11°00.03′     | 78°35.60′    | 697             |

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Table 2.** Individual foraminiferal denitrification rates and nitrate storage for the different species used to calculate total benthic foraminiferal denitrification and nitrate storage at the different sampling sites. Bold numbers represent species where literature data was available for the distinct species. Numbers in italic letters were calculated using approximation A (mean values of other species from the same genus). Data are from Piña-Ochoa et al. (2010) except for the denitrification rate of *Nonionella stella* (Risgaard-Petersen et al., 2006).

| Species                                    | Denitrification<br>( $\text{pmol} \#^{-1} \text{d}^{-1}$ ) | Nitrate storage<br>( $\text{pmol} \#^{-1}$ ) |
|--|--|--|
| <i>Bolivina alata</i> var. A               | 135  | <b>615</b>                                   |
| <i>Bolivina alata</i> var. B               | 135  | <b>615</b>                                   |
| <i>Bolivina costata</i>                    | 135  | 518  |
| <i>Bolivina interjuncta</i>                | 135  | 518  |
| <i>Bolivina (Loxostomum) boltovskoyi</i>   | 135  | 518  |
| <i>Bolivina (Loxostomum) salvadorensis</i> | 135  | 518  |
| <i>Bolivina plicata</i>                    | <b>79</b>  | <b>478</b>                                   |
| <i>Bolivina seminuda</i>                   | <b>216</b>   | <b>564</b>                                   |
| <i>Bolivina spissa</i>                     | 135  | 518  |
| <i>Cancris carmenensis</i>                 |  | 262877                                       |
| <i>Cassidulina auka</i>                    |  | 182  |
| <i>Globobulimina pacifica</i>              |  | 7462   |
| <i>Nonionella stella</i>                   | <b>84</b>  | <b>186</b>                                   |
| <i>Uvigerina auberiana</i>                 |  | 1090   |
| <i>Uvigerina canariensis</i>               |  | 1090   |
| <i>Uvigerina peregrina</i>                 |  | <b>166*</b>                                  |
| <i>Uvigerina striata</i>                   | 46   | 1090   |
| <i>Valvulineria vilardeboana glabra</i>    | 248  | 1067   |

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 3.** Contribution of species with known denitrification rates, approximation A and B in the calculations of benthic foraminiferal denitrification rates at the different sampling sites. The percentage of living individuals of the several species to the total foraminiferal abundances is shown. Without approximation stands for species where literature data for individual was available.

| Site             | Individual denitrification rates (%) | Estimate using approximation A (%) | Estimate using approximation B (%) |
|------------------|--------------------------------------|------------------------------------|------------------------------------|
| M77/1-540/MUC-49 | 21.1                                 | 73.9                               | 5.0                                |
| M77/1-583/MUC-65 | 90.3                                 | 3.4                                | 6.3                                |
| M77/1-473/MUC-32 | 80.0                                 | 15.9                               | 4.1                                |
| M77-1-449/MUC-19 | 76.1                                 | 7.5                                | 16.4                               |
| M77/1-456/MUC-22 | 22.3                                 | 57.7                               | 21.0                               |
| M77/1-459/MUC-25 | 0.1                                  | 45.6                               | 54.4                               |

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

**Table 4.** Calculated approximated total benthic foraminiferal denitrification rates and nitrate storage at the different sampling sites. Also listed are foraminiferal abundances and pore water nitrate concentrations in the top cm of the sediments.

| Site             | Water depth (m) | Foraminiferal abundance (indcm <sup>-2</sup> ) | Total foraminiferal denitrification (mmolm <sup>-2</sup> d <sup>-1</sup> ) | Foraminiferal denitrification approx. a (mmolm <sup>-2</sup> d <sup>-1</sup> ) | Foraminiferal denitrification approx. b (mmolm <sup>-2</sup> d <sup>-1</sup> ) | Foraminiferal nitrate storage (mmolL <sup>-1</sup> ) | Pore water nitrate (rhizons or glovebox) (mmolL <sup>-1</sup> ) | Pore water nitrate (press) (mmolL <sup>-1</sup> ) |
|------------------|-----------------|--|--|--|--|--|---|---|
| M77/1-540/MUC-49 | 79              | 343.7  | 0.57   | 0.43   | 0.02   | 62.1   | 4.4   | 93.2  |
| M77/1-583/MUC-65 | 248             | 616.2  | 13.51  | 1.23   | 0.08   | 439.1  | –   | –   |
| M77/1-473/MUC-32 | 317             | 495.5  | 5.35   | 0.96   | 0.11   | –  | –   | –   |
| M77-1-449/MUC-19 | 319             | 262.4  | 2.30   | 0.44   | 0.11   | 705.3  | 0.6   | 102.0   |
| M77/1-456/MUC-22 | 465             | 61.3   | 0.13   | 0.07   | 0.03   | 388.4  | 2.3   | –   |
| M77/1-459/MUC-25 | 697             | 12.7   | 0.01   | 0.01   | 0  | 2.7  | 15.8  | –   |

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

**Table 5.** Benthic stations where in situ fluxes of nitrate loss (negative nitrate fluxes) were determined. The notation C1 and C2 refers to the chamber 1 and chamber 2, respectively. All stations lie on the latitudinal transect at 11° S.  $T_{inc.}$  denotes the duration of the chamber flux measurements. Negative and positive fluxes indicate uptake and release from the seabed, respectively. During the flux measurements of BIGO T, the chamber water was replaced once with ambient seawater half-way through the incubation period. For these deployments, I1 refers to the time interval after driving the chamber into the sediment, I2 refers to the time interval after the chamber water was replaced. Nitrate fluxes were calculated according to Dale et al. (2012).

| Site              | Chamber/<br>Interval | Water<br>depth<br>(m) | Position<br>(long.) W | $T_{inc.}$<br>(h) | $\text{NO}_3^-$ -loss<br>( $\text{mmol m}^{-2} \text{d}^{-1}$ ) |
|-------------------|----------------------|-----------------------|-----------------------|-------------------|---|
| M77/1-540/BIGO-5  | C1                   | 85                    | 77°47.72'             | 18.0              | 0.9   |
|                   | C2                   |                       |                       |                   | –   |
| M77/1-583/BIGO-T6 | I1                   | 259                   | 78°05.91'             | 19.4              | 3.8   |
|                   | I2                   |                       |                       |                   | 3.0   |
| M77-1-449/BIGO-T4 | I1                   | 309                   | 78°09.13'             | 20.7              | 2.5   |
|                   | I2                   |                       |                       |                   | 2.7   |
| M77/1-473/BIGO-1  | C1                   | 315                   | 78°09.92'             | 17.8              | 3.2   |
|                   | C2                   |                       |                       |                   | 3.1   |
| M77/1- /BIGO-T5   | I1                   | 316                   | 78°09.40'             | 12.7              | 2.2   |
|                   | I2                   |                       |                       |                   | 3.2   |
| M77/1-456/BIGO 2  | C1                   | 695                   | 78°25.55'             | 18.1              | 0.7   |
|                   | C2                   |                       |                       |                   | 0.6   |

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

**Table A1.** Population densities and abundances of living benthic foraminifera as calculated from census data of Mallon (2012). For complete faunal references see also Mallon (2012).

| M77-1 540-MUC-49<br>Living specimens cm <sup>-2</sup> | sediment depth (mm) |        |       |      |       |        |       |       |       |       | Total | %      |       |
|---|---------------------|--------|-------|------|-------|--------|-------|-------|-------|-------|-------|--------|-------|
|   | 0–2                 | 2–4    | 4–7   | 7–10 | 10–15 | 15–20  | 20–25 | 25–30 | 30–35 | 35–40 |       |        | 40–50 |
| <i>Bolivina costata</i>                               | 0.07                | 40.39  | 34.06 | 2.77 | 2.19  | 54.96  | 11.45 | 2.21  | 0.93  | 47.97 | 56.95 | 253.95 | 73.90 |
| <i>Bolivina seminuda</i>                              | 0.02                | 7.92   | 5.33  | 0.15 | 0.12  | 0.44   | 0.05  | 0.06  | 0     | 2.15  | 0     | 16.24  | 4.73  |
| <i>Bulimina pupoides</i>                              | 0.02                | 0      | 0.29  | 0    | 0     | 0.15   | 0.11  | 0.11  | 0.04  | 0.52  | 5.3   | 6.54   | 1.90  |
| <i>Buliminella elegantissima limbosa</i>              |                     | 0.53   | 0.29  | 0.02 | 0.03  | 0      | 0.02  | 0     | 0     | 0     | 0     | 0.89   | 0.26  |
| <i>Buliminella elegantissima tenuis</i>               |                     |        | 0.07  | 0    | 0     | 0      | 0     | 0     | 0     | 0     | 0     | 0.07   | 0.02  |
| <i>Epistominella exigua</i>                           |                     | 0.26   | 0     | 0    | 0     | 0      | 0     | 0     | 0     | 0     | 0     | 0.26   | 0.08  |
| <i>Fursenkoina fusiformis</i>                         | 0.18                | 5.28   | 0     | 0.15 | 0.06  | 0      | 0.07  | 0.02  | 0.06  | 0     | 0     | 5.82   | 1.69  |
| <i>Nonionell stella</i>                               | 0.27                | 44.62  | 8.78  | 0.95 | 0     | 0.73   | 0.14  | 0.08  | 0.08  | 0.07  | 0.55  | 56.27  | 16.37 |
| <i>Pulvinulinella subperuviana</i>                    |                     |        | 0.14  | 0    | 0.03  | 0      | 0.18  | 0.04  | 0.03  | 0     | 0.05  | 0.47   | 0.14  |
| <i>Virgulina texturata</i>                            | 0.4                 | 2.64   | 0.5   | 0    | 0     | 0      | 0     | 0.01  | 0     | 0     | 0     | 3.19   | 0.93  |
| <i>Loxostomum limbatum</i>                            |                     |        |       |      |       |        | 0.02  | 0     | 0.01  | 0     | 0     | 0.03   | 0.01  |
| Total abundance (ind cm <sup>-2</sup> )               | 0.6                 | 101.64 | 49.46 | 4.03 | 2.42  | 56.26  | 12.04 | 2.51  | 1.15  | 50.7  | 62.85 | 343.66 |       |
| Number of counted specimens                           | 27                  | 385    | 687   | 193  | 373   | 388    | 668   | 359   | 148   | 747   | 1259  |        |       |
| Sample volume [cm <sup>3</sup> ]                      | 7.83                | 12.1   | 32.7  | 28.5 | 81.3  | 56.13  | 55.13 | 74.13 | 45.6  | 60.9  | 84.1  |        |       |
| Split   | 1                   | 0.0625 | 0.125 | 0.5  | 1     | 0.0625 | 0.5   | 1     | 1     | 0.125 | 0.25  |        |       |
| Population density [ind cm <sup>-3</sup> ]            | 3.4                 | 509.1  | 168.1 | 13.5 | 4.6   | 110.6  | 24.2  | 4.8   | 3.2   | 98.1  | 59.9  |        |       |

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table A1. Continued.

| M77-1 456-MUC-22<br>Living specimens cm <sup>-2</sup> | sediment depth (mm) |       |       |      |      |       | %     |
|---|---------------------|-------|-------|------|------|-------|-------|
|   | 0–2                 | 2–4   | 4–6   | 6–8  | 8–10 | Total |       |
| <i>Ammodiscus insertus</i>                            |                     |       | 0.04  | 0    | 0    | 0.04  | 0.07  |
| <i>Angulogerina carinata</i>                          | 0.18                | 0.53  | 0.04  | 0.02 | 0    | 0.77  | 1.26  |
| <i>Bathysiphon</i> sp.                                |                     |       | 0.13  | 0    | 0    | 0.13  | 0.21  |
| <i>Bolivina alata</i> var. A                          |                     | 0.46  | 0.13  | 0    | 0    | 0.59  | 0.96  |
| <i>Bolivina alata</i> var. B                          |                     | 0.53  | 0.35  | 0    | 0    | 0.88  | 1.44  |
| <i>Bolivina costata</i>                               | 0.83                | 0.84  | 0.09  | 0.06 | 0    | 1.82  | 2.97  |
| <i>Bolivina interjuncta</i>                           | 10.12               | 10.64 | 4.31  | 1.29 | 0.7  | 27.06 | 44.14 |
| <i>Bolivina plicata</i>                               |                     | 0.23  | 0.18  | 0    | 0    | 0.41  | 0.67  |
| <i>Bolivina (Loxostomum) boltovskoyi</i>              |                     | 0.08  | 0.09  | 0    | 0    | 0.17  | 0.28  |
| <i>Bolivina (Loxostomum) salvadorensis</i>            |                     | 0.08  | 0     | 0    | 0    | 0.08  | 0.13  |
| <i>Bolivina seminuda</i>                              | 1.84                | 7.52  | 2.38  | 0.21 | 0.11 | 12.06 | 19.67 |
| <i>Bulimina pupoides</i>                              | 1.01                | 0.08  | 0.04  | 0.04 | 0.04 | 1.21  | 1.97  |
| <i>Buliminella curta basispinata</i>                  |                     | 0.91  | 0     | 0    | 0    | 0.91  | 1.48  |
| <i>Cancris carmenensis</i>                            | 0.18                | 1.06  | 0     | 0.04 | 0.08 | 1.36  | 2.22  |
| <i>Cassidulina auka</i>                               | 0.74                | 0.08  | 0.18  | 0.02 | 0.02 | 1.04  | 1.70  |
| <i>Cassidulina crassa</i>                             | 0.37                | 0.38  | 0.13  | 0    | 0.02 | 0.9   | 1.47  |
| <i>Chilostomella oolina</i>                           |                     | 0.08  | 0     | 0    | 0    | 0.08  | 0.13  |
| <i>Cibicidoides wuellerstorfi</i>                     |                     |       | 0.4   | 0    | 0    | 0.04  | 0.07  |
| <i>Epistominella obesa</i>                            |                     |       | 0.04  | 0.02 | 0    | 0.06  | 0.10  |
| <i>Ehrenbergina compressa</i>                         |                     | 0.08  | 0.04  | 0    | 0    | 0.12  | 0.20  |
| <i>Fursenkoina fusiformis</i>                         | 0.37                | 1.37  | 1.1   | 0.19 | 0.1  | 3.13  | 5.11  |
| <i>Gyroidina soldanii</i>                             |                     |       | 0.18  | 0    | 0    | 0.18  | 0.29  |
| <i>Gyroidina soldanii multilocula</i>                 | 0.64                | 0.3   | 0.09  | 0.02 | 0.04 | 1.09  | 1.78  |
| <i>Haplophragmoides columbiense evolutum</i>          |                     | 0.23  | 0.04  | 0    | 0    | 0.27  | 0.44  |
| <i>Haplophragmoides sphaeriloculum</i>                |                     | 0.23  | 0     | 0    | 0    | 0.23  | 0.38  |
| <i>Hoeglundina elegans</i>                            |                     |       | 0.09  | 0    | 0    | 0.09  | 0.15  |
| <i>Marsipella granulosa</i>                           |                     | 0.23  | 0     | 0    | 0    | 0.23  | 0.38  |
| <i>Pullenia elegans</i>                               | 0.28                | 0     | 0     | 0    | 0    | 0.28  | 0.46  |
| <i>Pullenia subcarinata</i>                           |                     | 0.3   | 0.04  | 0.02 | 0    | 0.36  | 0.59  |
| <i>Pulvinulinella subperuviana</i>                    | 0.28                | 0     | 0     | 0    | 0    | 0.28  | 0.46  |
| <i>Reophax dentaliniformis</i>                        | 0.28                | 0     | 0     | 0    | 0    | 0.28  | 0.46  |
| <i>Reophax scoriurus</i>                              |                     | 0.15  | 0.04  | 0    | 0    | 0.19  | 0.31  |
| <i>Suggrunda eckisi</i>                               |                     | 0.08  | 0     | 0    | 0    | 0.08  | 0.13  |
| <i>Textularia conica</i>                              |                     | 0.08  | 0     | 0    | 0    | 0.08  | 0.13  |
| <i>Uvigerina striata</i>                              | 1.38                | 0.3   | 0.75  | 0.08 | 0.07 | 2.58  | 4.21  |
| <i>Valvulineria vilardeboana glabra</i>               | 0.46                | 0.99  | 0.75  | 0    | 0.01 | 2.21  | 3.60  |
| <i>Virgulina bradyi</i>                               |                     |       | 0.04  | 0    | 0    | 0.04  | 0.07  |
| Total abundance [ind cm <sup>-2</sup> ]               | 18.95               | 27.82 | 11.35 | 2    | 1.19 | 61.31 |       |
| Number of counted specimens                           | 209                 | 364   | 258   | 104  | 99   |       |       |
| Sample volume [cm <sup>3</sup> ]                      | 8.7                 | 21    | 18.13 | 40.9 | 35.6 |       |       |
| Split   | 0.25                | 0.125 | 0.25  | 0.25 | 0.5  |       |       |
| Population density [ind cm <sup>-3</sup> ]            | 96.1                | 138.7 | 56.9  | 10.2 | 5.6  |       |       |

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table A1. Continued.

| M77-1 449-MUC-19<br>Living specimens cm <sup>-2</sup> | sediment depth (mm) |       |       |        | Total |  |
|---|---------------------|-------|-------|--------|-------|--|
|   | 0–5                 | 5–10  | 10–15 | Total  |       |  |
| <i>Bolivina costata</i>                               | 11.21               | 3.22  | 0.29  | 14.72  | 5.61  |  |
| <i>Bolivina plicata</i>                               | 12.39               | 2.31  | 0.3   | 15     | 5.72  |  |
| <i>Bolivina seminuda</i>                              | 173.46              | 8.89  | 2.51  | 184.86 | 70.44 |  |
| <i>Bulimina pupoides</i>                              | 9.44                | 0.07  | 0     | 9.51   | 3.62  |  |
| <i>Buliminella curta</i>                              | 0.59                | 0     | 0     | 0.59   | 0.22  |  |
| <i>Buliminella elegantissima limbosa</i>              |                     | 0.56  | 0.03  | 0.59   | 0.22  |  |
| <i>Buliminella elegantissima tenuis</i>               | 11.8                | 1.75  | 0.09  | 13.64  | 5.20  |  |
| <i>Cancris carmenensis</i>                            | 12.98               | 1.61  | 0.23  | 14.82  | 5.65  |  |
| <i>Valvulineria vilardeboana glabra</i>               | 4.72                | 0.14  | 0     | 4.86   | 1.85  |  |
| <i>Ammosphaeroidina grandis</i>                       |                     | 0.14  | 0     | 0.14   | 0.05  |  |
| <i>Bolivina alata</i> var. B                          |                     | 0.07  | 0     | 0.07   | 0.03  |  |
| <i>Cassidulina auka</i>                               |                     | 0.07  | 0     | 0.07   | 0.03  |  |
| <i>Epistominella obesa</i>                            |                     | 0.07  | 0     | 0.07   | 0.03  |  |
| <i>Fursenkoina fusiformis</i>                         |                     | 1.05  | 0.09  | 1.14   | 0.43  |  |
| <i>Nonionides grateloupii</i>                         |                     | 1.89  | 0.17  | 2.06   | 0.78  |  |
| <i>Suggrunda kleinpellii</i>                          |                     | 0.14  | 0     | 0.14   | 0.05  |  |
| <i>Verneuilina bradyi</i>                             |                     | 0.14  | 0.02  | 0.16   | 0.06  |  |
| <i>Pulvinulinella subperuviana</i>                    |                     |       | 0.02  | 0.02   | 0.01  |  |
| Total abundance (indcm <sup>-2</sup> )                | 236.59              | 22.12 | 3.72  | 262.43 |       |  |
| Number of counted specimens                           | 401                 | 316   | 248   |        |       |  |
| Sample volume [cm <sup>3</sup> ]                      | 27.1                | 29    | 30.7  |        |       |  |
| Split   | 0.03125             | 0.25  | 1     |        |       |  |
| Population density [indcm <sup>-3</sup> ]             | 473.5               | 43.6  | 8.1   |        |       |  |

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table A1. Continued.

| M77-1 583-MUC-65<br>Living specimens cm <sup>-2</sup> | sediment depth (mm) |       |        |       |
|---|---------------------|-------|--------|-------|
|   | 0–10                | 10–15 | Total  | %     |
| <i>Bolivina alata</i> var. B                          |                     | 0.04  | 0.04   | 0.01  |
| <i>Bolivina costata</i>                               | 19.74               | 0.56  | 20.3   | 3.29  |
| <i>Bolivina plicata</i>                               | 2.82                | 0.24  | 3.06   | 0.50  |
| <i>Bolivina seminuda</i>                              | 538.62              | 15.56 | 554.18 | 89.83 |
| <i>Bolivina spissa</i>                                | 0.47                | 0     | 0.47   | 0.08  |
| <i>Bulimina pupoides</i>                              | 0.47                | 0     | 0.47   | 0.08  |
| <i>Buliminella elegantissima limbosa</i>              | 7.99                | 1.88  | 9.87   | 1.60  |
| <i>Buliminella elegantissima tenuis</i>               | 2.35                | 0.28  | 2.63   | 0.43  |
| <i>Cancris carmenensis</i>                            | 0.47                | 0.56  | 1.03   | 0.17  |
| <i>Cassidulina auka</i>                               | 6.58                | 0.24  | 6.82   | 1.11  |
| <i>Cibicidoides wuellerstorfi</i>                     | 0.47                | 0     | 0.47   | 0.08  |
| <i>Epistominella obesa</i>                            | 16.92               | 0.08  | 17     | 2.76  |
| <i>Fursenkoina fusiformis</i>                         |                     | 0.44  | 0.44   | 0.07  |
| <i>Trochammina nana</i>                               |                     | 0.16  | 0.16   | 0.03  |
| Total abundance (ind cm <sup>-2</sup> )               | 596.9               | 20.04 | 616.94 |       |
| Number of counted specimens                           | 1270                | 501   |        |       |
| Sample volume [cm <sup>3</sup> ]                      | 33.9                | 50.1  |        |       |
| Split   | 0.0625              | 0.25  |        |       |
| Population density [ind cm <sup>-3</sup> ]            | 599.4               | 40.0  |        |       |

Table A1. Continued.

| M77-1 459-MUC-25<br>Living specimens cm <sup>-2</sup> | sediment depth (mm) |      |      |      |      |       | %     |
|---|---------------------|------|------|------|------|-------|-------|
|   | 0–2                 | 2–4  | 4–6  | 6–8  | 8–10 | Total |       |
| <i>Ammobaculites agglutinans</i>                      |                     | 0.04 | 0.01 | 0.01 | 0    | 0.06  | 0.47  |
| <i>Ammodiscus incertus</i>                            | 0.03                | 0    | 0    | 0    | 0    | 0.03  | 0.24  |
| <i>Ammodiscus tenuis</i>                              |                     | 0.06 | 0    | 0    | 0    | 0.06  | 0.47  |
| <i>Ammomarginulina foliaceus</i>                      |                     | 0.71 | 0.01 | 0    | 0    | 0.72  | 5.68  |
| <i>Angulogerina angulosa</i>                          | 0.05                | 0.06 | 0.03 | 0    | 0    | 0.14  | 1.10  |
| <i>Bolivina alata</i> var. A                          |                     | 0.02 | 0    | 0    | 0    | 0.02  | 0.16  |
| <i>Bolivina costata</i>                               |                     | 0.08 | 0    | 0    | 0    | 0.08  | 0.63  |
| <i>Bolivina seminuda</i>                              | 0.01                | 0    | 0    | 0    | 0    | 0.01  | 0.08  |
| <i>Bolivina spissa</i>                                | 0.06                | 0.59 | 0.62 | 0.39 | 0.51 | 2.17  | 17.11 |
| <i>Bolivinita minuta</i>                              | 0.26                | 0.59 | 0.05 | 0    | 0    | 0.9   | 7.10  |
| <i>Cassidulina crassa</i>                             | 0.38                | 0.73 | 0.17 | 0.04 | 0    | 1.32  | 10.41 |
| <i>Cassidulina delicata</i>                           | 0.13                | 1.35 | 0.24 | 0.07 | 0.01 | 1.8   | 14.20 |
| <i>Cyclammina cancellata</i>                          | 0.12                | 0.08 | 0.04 | 0    | 0    | 0.24  | 1.89  |
| <i>Eggerella scabra</i>                               |                     |      | 0.04 | 0    | 0.01 | 0.05  | 0.39  |
| <i>Epistominella obesa</i>                            |                     |      | 0.02 | 0.01 | 0.01 | 0.04  | 0.32  |
| <i>Epistominella pacifica</i>                         |                     | 0.04 | 0.02 | 0    | 0    | 0.06  | 0.47  |
| <i>Fissurina annectens</i>                            |                     | 0.02 | 0    | 0    | 0    | 0.02  | 0.16  |
| <i>Fursenkoina fusiformis</i>                         | 0.34                | 0.18 | 0.09 | 0.05 | 0.05 | 0.66  | 5.21  |
| <i>Globobulimina pacifica</i>                         |                     |      | 0.09 | 0.04 | 0    | 0.13  | 1.03  |
| <i>Gyroidina neosoldanii</i>                          |                     | 0.02 | 0    | 0    | 0    | 0.02  | 0.16  |
| <i>Gyroidina soldanii</i>                             | 0.01                | 0    | 0    | 0    | 0    | 0.01  | 0.08  |
| <i>Lagena gracillima</i>                              |                     |      | 0.1  | 0    | 0    | 0.01  | 0.08  |
| <i>Lagena laevis</i>                                  |                     |      | 0.01 | 0    | 0    | 0.01  | 0.08  |
| <i>Pullenia elegans</i>                               | 0.01                | 0    | 0    | 0    | 0    | 0.01  | 0.08  |
| <i>Pullenia subcarinata</i>                           |                     | 0.04 | 0    | 0    | 0    | 0.04  | 0.32  |
| <i>Quinqueloculina seminula</i>                       |                     | 0.04 | 0    | 0    | 0    | 0.04  | 0.32  |
| <i>Reophax apiculatus</i>                             | 0.26                | 0.83 | 0.03 | 0.01 | 0    | 1.13  | 8.91  |
| <i>Saracenaria stolidota</i>                          |                     |      | 0.01 | 0    | 0    | 0.01  | 0.08  |
| <i>Uvigerina auerberiana</i>                          | 0.03                | 0.02 | 0    | 0    | 0    | 0.05  | 0.39  |
| <i>Uvigerina canariensis</i>                          | 0.01                | 0    | 0    | 0.01 | 0    | 0.02  | 0.16  |
| <i>Uvigerina peregrina</i>                            | 0.72                | 1.31 | 0.18 | 0.17 | 0.01 | 2.39  | 18.85 |
| <i>Valvulina oblonga</i>                              |                     | 0.04 | 0.05 | 0.17 | 0.14 | 0.4   | 3.15  |
| <i>Valvulinera vilardeboana glabra</i>                |                     |      |      |      | 0.04 | 0.04  | 0.32  |
| <i>Virgulina schreibersiana</i>                       |                     |      |      |      | 0.02 | 0.02  | 0.16  |
| Total abundance (ind cm <sup>-2</sup> )               | 2.07                | 7.01 | 1.8  | 0.99 | 0.81 | 12.68 |       |
| Number of counted specimens                           | 157                 | 354  | 189  | 108  | 76   |       |       |
| Sample volume [cm <sup>3</sup> ]                      | 15.8                | 20.5 | 21.2 | 20.2 | 18.1 |       |       |
| Split   | 1                   | 0.5  | 1    | 1    | 1    |       |       |
| Population density [ind cm <sup>-3</sup> ]            | 9.9                 | 34.5 | 8.9  | 5.3  | 4.2  |       |       |

The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table A1. Continued.

| M77-1 473-MUC-32<br>Living specimens cm <sup>-2</sup> | sediment depth (mm) |       |
|---|---------------------|-------|
|   | 0–5                 | %     |
| <i>Bolivina costata</i>                               | 77.72               | 14.88 |
| <i>Bolivina plicata</i>                               | 68.01               | 13.02 |
| <i>Bolivina seminuda</i>                              | 349.76              | 66.94 |
| <i>Buliminella curta</i>                              | 4.32                | 0.83  |
| <i>Buliminella elegantissima limbosa</i>              | 1.08                | 0.21  |
| <i>Buliminella elegantissima tenuis</i>               | 5.4                 | 1.03  |
| <i>Cancris carmenensis</i>                            | 8.64                | 1.65  |
| <i>Cassidulina auka</i>                               | 1.08                | 0.21  |
| <i>Epistominella obesa</i>                            | 1.08                | 0.21  |
| <i>Valvulineria vilardeboana glabra</i>               | 5.4                 | 1.03  |
| Total abundance (ind cm <sup>-2</sup> )               | 522.48              |       |
| Number of counted specimens                           | 484                 |       |
| Sample volume [cm <sup>3</sup> ]                      | 29.6                |       |
| Split   | 0.015625            |       |
| Population density [ind cm <sup>-3</sup> ]            | 1046.5              |       |

## The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

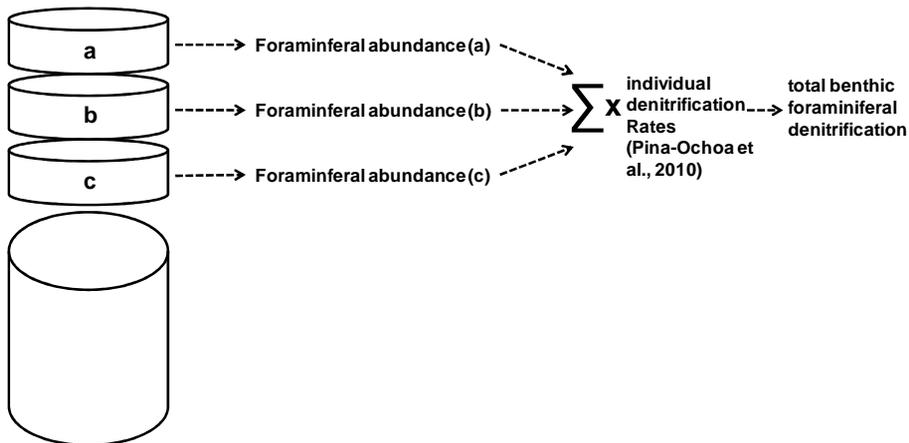
Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table A2.** Sampling sites for pore water nitrate profiles.

| Site             | Longitude (S) | Latitude (W) | Water depth (m) |
|------------------|---------------|--------------|-----------------|
| M77/1-543/MUC-52 | 11°00.01′     | 77°47.40′    | 79              |
| M77/1-470/MUC-29 | 11°00.02′     | 77°56.60′    | 145             |
| M77/1-573/MUC-61 | 11°09.09′     | 78°05.05′    | 309             |
| M77-1-449/MUC-19 | 11°00.01′     | 78°09.97′    | 319             |
| M77/1-481/MUC-33 | 11°00.00′     | 78°14.19′    | 376             |
| M77/1-601/MUC-71 | 11°12.05′     | 78°10.08′    | 394             |
| M77/1-456/MUC-22 | 11°00.013′    | 78°19.23′    | 465             |
| M77/1-516/MUC-40 | 11°00.00′     | 78°20.00′    | 512             |
| M77/1-488/MUC-39 | 11°00.02′     | 78°23.17′    | 579             |
| M77/1-459/MUC-25 | 11°00.03′     | 78°35.60′    | 697             |
| M77/1-445/MUC-15 | 10°59.997′    | 78°30.022′   | 928             |
| M77/1-549/MUC-53 | 10°59.807′    | 78°31.266′   | 1005            |



**Fig. 1.** Scheme for the calculation of total benthic foraminiferal denitrification rates. The cylinder is representing a sediment core. The slices represent the slices of the different sediment depth intervals. Total foraminiferal nitrate storages were calculated in a similar way.

**The role of benthic foraminifera in the benthic nitrogen cycle**

N. Glock et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

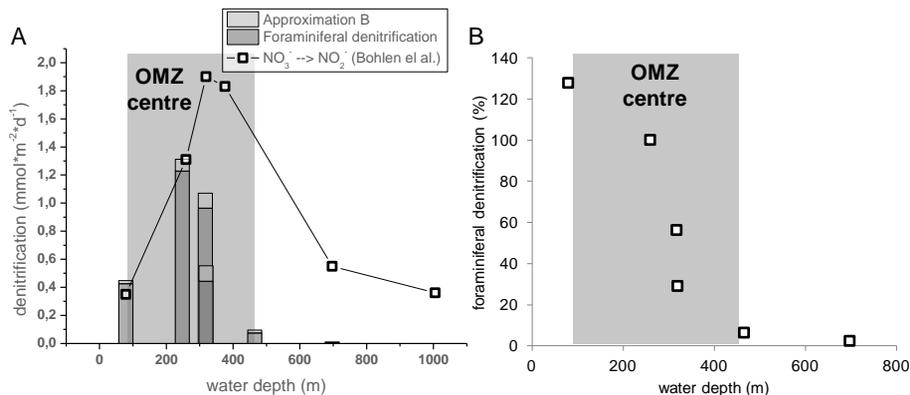
Printer-friendly Version

Interactive Discussion



## The role of benthic foraminifera in the benthic nitrogen cycle

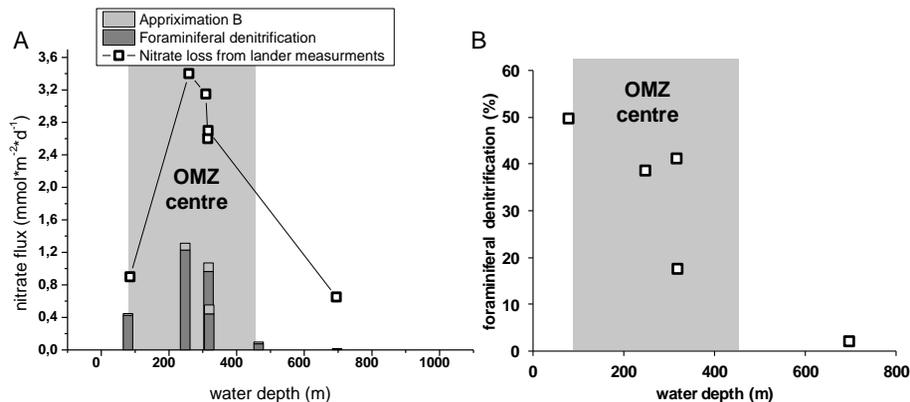
N. Glock et al.



**Fig. 2.** (A) Comparison of benthic foraminiferal denitrification rates and modeled turnover rates from  $\text{NO}_3^-$  to  $\text{NO}_2^-$  (Bohlen et al., 2011) both plotted against water depth. (B) Percentage of the contribution of foraminiferal denitrification to the total benthic  $\text{NO}_3^-$  loss due to denitrification.

## The role of benthic foraminifera in the benthic nitrogen cycle

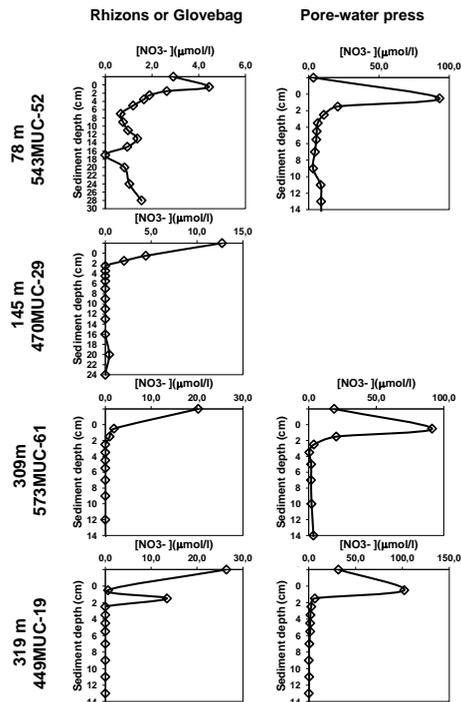
N. Glock et al.



**Fig. 3.** (A) Comparison of benthic foraminiferal denitrification rates to the total benthic  $\text{NO}_3^-$  loss measured in the lander chambers, both plotted against water depth. (B) Percentage of the contribution of foraminiferal denitrification to the total benthic  $\text{NO}_3^-$  loss.

The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.



**Fig. A1.** Pore water nitrate profiles at different water depths along the Peruvian OMZ, including bottom water nitrate concentrations. Profiles on the left represent data from cores sampled with rhizons or in a glovebag. Profiles on the right represent data from cores sampled with a pore-water press. Informations about the sampling sites are shown in Table A2

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

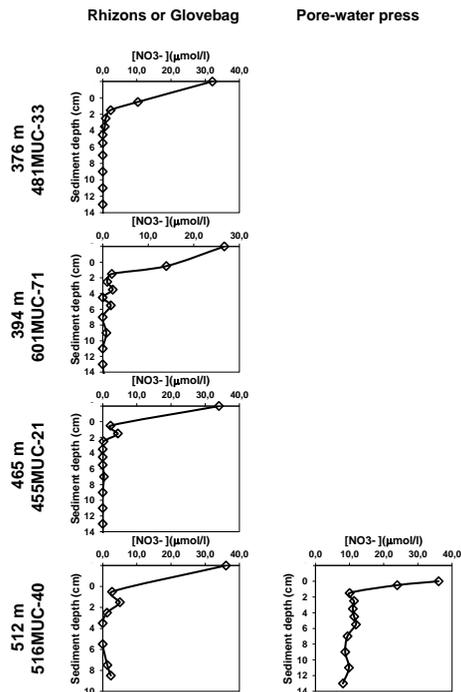


Fig. A1. Continued.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The role of benthic foraminifera in the benthic nitrogen cycle

N. Glock et al.

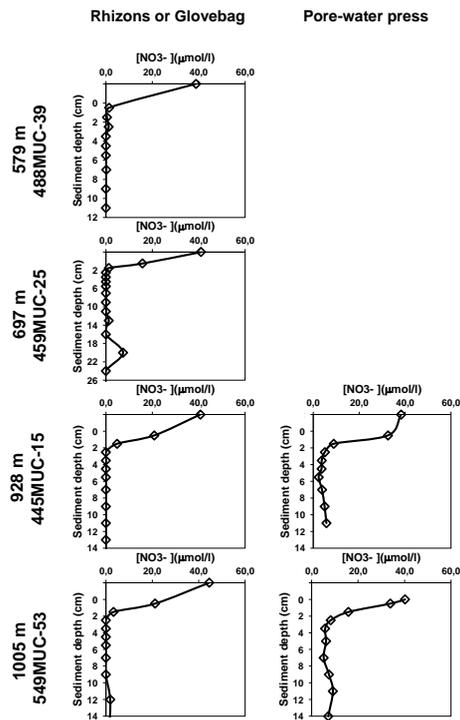


Fig. A1. Continued.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

