



## Abstract

The Arabian Sea is a region of elevated productivity with the highest globally recorded fluxes of particulate organic matter (POM) to the deep ocean, providing an abundant food source for fauna at the seafloor. However, benthic communities are also strongly influenced by an intense oxygen minimum zone (OMZ), which impinges on the continental slope at bathyal depths. We compared the trophic ecology of foraminifera on the Oman and Pakistan margins of the Arabian Sea (140–3185 m water depth). Organic carbon concentrations of surficial sediments were higher on the Oman margin ( $3.32 \pm 1.4\%$ ) compared to the Pakistan margin ( $2.45 \pm 1.1\%$ ) and sedimentary organic matter (SOM) quality estimated from the Hydrogen Index was also higher on the Oman margin ( $300\text{--}400 \text{ mg HC (mg TOC)}^{-1}$ ) compared to the Pakistan margin ( $< 250 \text{ mg HC (mg TOC)}^{-1}$ ).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of sediments were similar on both margins ( $-20$  and  $8\%$ , respectively). Stable isotope analysis (SIA) showed that foraminiferal cells had a wide range of  $\delta^{13}\text{C}$  values ( $-25.5$  to  $-11.5\%$ ), implying that they utilise multiple food sources; indeed  $\delta^{13}\text{C}$  values varied between depths, foraminiferal types and between the two margins. Foraminifera had broad ranges in  $\delta^{15}\text{N}$  values ( $-7.8$  to  $27.3\%$ ). The enriched values suggest that some species may store nitrate to utilise in respiration; this was most notable on the Pakistan margin. Depleted foraminiferal  $\delta^{15}\text{N}$  values were identified on both margins, particularly the Oman margin, and may reflect feeding on chemosynthetic bacteria. We suggest that differences in productivity regimes between the two margins may be responsible for the differences observed in foraminiferal isotopic composition. In addition, at the time of sampling, whole jellyfish carcasses (*Crambionella orsinii*) and a carpet of jelly detritus were observed across the Oman margin transect. Associated chemosynthetic bacteria may have provided an organic-rich food source for foraminifera at these sites. Our data suggest that foraminifera in OMZ settings can utilise a variety of food sources and metabolic pathways to meet their energetic demands.

### The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 1 Introduction

The Arabian Sea's seasonally reversing monsoons drive one of the most energetic current systems in the world (Goes et al., 2005; Schott and McCreary, 2001). The SW (summer) monsoon (June–September) is characterized by southwesterly winds and the Findlater Jet (Findlater, 1969), inducing NE flowing surface currents. These drive strong coastal upwelling of nutrient rich water near Oman resulting in some of the highest recorded values for oceanic primary productivity (Ryther et al., 1966). In contrast, the NE (winter) monsoon (November–February) is characterised by a reversal in the direction of the winds and much less intense primary production (Smith and Codispoti, 1980). Levels of primary production are highest in the western compared to the eastern Arabian Sea (Cowie, 2005) and lead to the highest globally recorded fluxes of both particulate matter and particulate organic carbon (POC) to the deep ocean (~ 600 and ~ 190 mgm<sup>-2</sup> d<sup>-1</sup> for the western and eastern Arabian Sea, respectively at depths of ~ 3000 m; Haake et al., 1993; Honjo et al., 2008). The associated heterotrophic utilization of the phytoplankton blooms, coupled with local hydrography, are responsible for the formation of an oxygen minimum zone (OMZ), defined as a region where oxygen concentrations are < 22 µM (< 0.5 mL L<sup>-1</sup>; Levin, 2003). In the northern Arabian Sea, the OMZ extends from ~ 100 to 1000 m water depth (Gupta and Naqvi, 1984). The coupling of these characteristics results in the enrichment of organic carbon at the seafloor (Cowie et al., 1999; Hedges and Keil, 1995; van der Weijden et al., 1999), creating an abundant food source for benthic organisms.

The majority of deep-sea benthic communities obtain their energy in the form of POM originating from the surface waters (Graf, 1989; Tyler, 1988). This food source often takes the form of highly seasonal pulses of phytodetritus (Billett et al., 1983; Smith et al., 1996; Gooday, 2002). OMZs are known to support large filamentous sulphur bacteria in the genera *Thioploca* and *Beggiatoa* (Jørgensen and Gallardo, 1999). In the Arabian Sea, chemosynthetically fixed carbon from such microorganisms may be an

BGD

11, 18145–18188, 2014

### The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



important additional source of nutrition for benthic organisms, either through symbiosis or heterotrophic consumption of chemosynthetic bacteria (Levin, 2003).

Foraminifera are unicellular eukaryotes (protists) and are an abundant component of marine benthic communities at all depths in the ocean (Murray, 2006). Although some are carnivorous, many benthic foraminifera feed at a low trophic level (Gooday et al., 1992; Lipps and Valentine, 1970), responding rapidly to phytodetritus with reproduction and not an population growth. They are one of the most important heterotrophic consumers in the deep sea (Gooday, 1988; Moodley et al., 2002; Nomaki et al., 2005) and act as an important link between phytodetritus and metazoan consumers in deep-sea food webs (Nomaki et al., 2008). Foraminifera have also been shown to influence the nitrogen cycle through the anaerobic respiration of nitrate (Bernhard et al., 2012; Pina-Ochoa et al., 2010; Risgaard-Petersen et al., 2006), a process that may be mediated by symbiotic bacteria (Bernhard et al., 2011). It has been suggested that the role of foraminifera in the removal of fixed nitrogen through nitrate respiration may equal the importance of bacterial denitrification in oceanic sediments (Glock et al., 2013; Pina-Ochoa et al., 2010).

In order to better understand their role in food webs and elemental cycles, we compared the trophic ecology of foraminifera at the Oman and Pakistan margins of the Arabian Sea, across a depth gradient from 140 to 3150 m, using stable isotope analyses (SIA). SIA is a useful tool for establishing trophic relationships and determining food sources. The stable isotopic signature of an organism's tissues is related to its food source. Stable carbon isotopes are particularly useful in determining food sources as  $\delta^{13}\text{C}$  does not fractionate heavily during transfer between trophic levels (< 1‰; DeNiro and Epstein, 1978; Fry and Sherr, 1984) and different carbon fixation pathways involve distinct isotopic fractionation. Typically, phytoplankton-derived organic matter has  $\delta^{13}\text{C}$  signatures ranging from -15 to -25‰ (Fry and Sherr, 1984). Carbon fixation fuelled by energy derived from sulphide oxidation involving form I Rubisco produces  $\delta^{13}\text{C}$  values of -27 to -37‰, whilst pathways that involve form II Rubisco or the reverse tricarboxylic acid cycle (rTCA) can lead to heavier  $\delta^{13}\text{C}$  values

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



between  $-9$  and  $-16\%$  (Brooks et al., 1987; Campbell et al., 2003; Robinson and Cavanaugh, 1995). Stable nitrogen isotopic compositions can provide information on both nitrogen sources and trophic level. For example, denitrification leads to enriched  $\delta^{15}\text{N}$  values of subsurface nitrate, which is reflected in particulate and sedimentary organic matter (Altabet et al., 1995; Gaye-Haake et al., 2005), whilst light  $\delta^{15}\text{N}$  values in organic matter can be diagnostic of nitrogen fixation (Brandes et al., 1998). Organisms that have chemoautotrophic symbionts often have light  $\delta^{15}\text{N}$  signatures reflecting nitrogen fixation (Levin and Michener, 2002). Generally,  $\delta^{15}\text{N}$  values are enriched by  $\sim 2$  to  $5\%$  per trophic level, the trophic enrichment factor (TEF; DeNiro and Epstein, 1981; Hobson and Welch, 1992; McCutchan et al., 2003; Minagawa and Wada, 1984) and are used to identify predator/prey relationships.

Here we use both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope signatures of the cell body to assess the feeding ecology of deep-sea benthic foraminifera on the Oman and Pakistan margins. Specifically, we addressed the following questions. (1) Is phytodetritus the sole source of nutrition for foraminifera? If not, what alternative dietary items and foraging modes supplement phytodetritus feeding? (2) Do the trophic roles differ among species, bottom water depths or between the two margins? (3) Is there isotopic evidence for nitrate accumulation in any of the studied species?

## 2 Materials and methods

### 2.1 Study areas and field sampling

This study compares two continental slope regions of the northern Arabian Sea: (1) the Oman margin, 40 km offshore from Ra's al Hadd, and (2) the Pakistan margin, immediately north of the Indus Canyon (Fig. 1).

Sampling was carried out during three cruises of the RRS *Charles Darwin* (CD). We define our sampling periods relative to the SW monsoon. Samples from the Oman margin were collected during CD143 (November–December 2002; post-SW





## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



of Edinburgh). Foraminifera, POM, and sediments from the Oman margin were analysed using a Thermo-Finnigan MAT Delta Plus Advantage Dual isotope analyser (University of California, Santa Barbara). Stable isotope ratios are expressed as  $(\delta X)\text{‰} = [R_{\text{sample}}/R_{\text{standard}} - 1] \cdot 1000$ , where  $X$  is either  $^{13}\text{C}$  or  $^{15}\text{N}$ , and  $R$  is either  $(^{13}\text{C} : ^{12}\text{C})$  or  $(^{15}\text{N} : ^{14}\text{N})$ , respectively. The reference standards for carbon and nitrogen are V-Pee Dee Belemnite and atmospheric  $\text{N}_2$ , respectively. Analytical accuracy for Pakistan margin samples was determined using a sucrose standard for  $\delta^{13}\text{C}$  and was  $-23.84 \pm 0.04\text{‰}$  and using an ammonium sulphate standard for  $\delta^{15}\text{N}$  at  $1.28 \pm 0.19\text{‰}$ . Analytical accuracy for Oman margin samples was determined using acetanilide for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Values were:  $\delta^{13}\text{C} -29.50 \pm 0.11\text{‰}$  and  $\delta^{15}\text{N} -0.42 \pm 0.45\text{‰}$  for samples analysed in 2009 and  $\delta^{13}\text{C} -29.27 \pm 0.24\text{‰}$  and  $\delta^{15}\text{N} -0.46 \pm 0.28\text{‰}$  for samples analysed in 2013. All laboratory working standards were calibrated against USGS 40 and USGS 41. Analytical precision was determined using an internal standard (tissue from the holothurian *Oneirophanta mutabilis*; Iken et al., 2001), which was sent to each lab; mean values and SD were  $-15.01 \pm 0.16\text{‰}$  for  $\delta^{13}\text{C}$  and  $12.10 \pm 0.17\text{‰}$   $\delta^{15}\text{N}$  ( $n = 10$ ) for Pakistan margin samples analysed in 2005. Mean values and SD for Oman margin samples were  $-15.71$  for  $\delta^{13}\text{C}$  and  $11.99\text{‰}$   $\delta^{15}\text{N}$  ( $n = 1$ ) for samples analysed in 2009 and  $-15.45 \pm 0.23\text{‰}$  for  $\delta^{13}\text{C}$  and  $12.08 \pm 0.23\text{‰}$  for  $\delta^{15}\text{N}$  ( $n = 4$ ) for those analysed in 2013. The majority of Oman margin samples had low N contents, and so analytical accuracy and precision were determined using a series of variable mass acetanilide and I.S. with N contents ranging from  $\sim 1$  to  $11 \mu\text{g N}$ . Analytical accuracy of  $\delta^{15}\text{N}$  values for samples containing low N using the acetanilide standard (calibrated using USGS 40 and 41) was  $\pm 1.1\text{‰}$ , analytical precision of  $\delta^{15}\text{N}$  values for samples containing low N using the I.S. was  $\pm 0.93\text{‰}$ .

### 2.3 Statistical analyses

As a result of the limited number of sediment samples from the Oman margin ( $n = 1$  per water depth), we tested for differences in  $\% \text{C}_{\text{org}}$ ,  $\% \text{TN}$ , HI,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between

---

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the Oman and Pakistan margins irrespective of depth, i.e. each depth represented 1 replicate. We tested for differences in the stable carbon and nitrogen isotopic composition of the foraminifera at each margin between (a) depth (b) foraminiferal species or higher taxon, where possible and (c) the composition of the foraminiferal wall e.g. calcareous, agglutinated monothalamid and textulariid species (Table S2 in the Supplement). Foraminiferal samples from the Oman margin were collected in two areas on the continental rise as defined in (Billett et al., 2006, Fig. 1); we tested for differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition of foraminifera between these two areas. We tested for inter-margin differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition in foraminiferal higher taxon, genus and species level where possible and between depths with similar oxygen concentrations. The distribution and variance of the data were ascertained using the Shapiro–Wilk’s test and Levene’s homogeneity of variance test. If data had a normal distribution and equal variance ( $p < 0.05$ ) a 1-way ANOVA was performed to ascertain statistical differences. The posthoc Games–Howell test was performed following ANOVA for subsequent pairwise comparisons. If the data did not meet the assumptions of an ANOVA, a Mann–Whitney  $U$  test or Kruskal–Wallis test was carried out.

### 3 Results

#### 3.1 Oxygen and organic matter gradients

On both the Pakistan and Oman margins during the post-SW monsoon period, CTD and in situ measurements revealed the bottom water to be hypoxic (hypoxic bottom water is defined as having  $\text{DO} < 9\ \mu\text{M}$ ; Kamykowski and Zentara, 1990) within the OMZ and across the transition zones (140 to 940 m). DO increased slightly at the lower boundary ( $\sim 1100$  m to 1250 m) gradually becoming oxygenated at water depths of 1850 to 3200 m (Table 1). Organic carbon concentrations ( $\%C_{\text{org}}$ ; used here as a proxy for the concentration of organic matter) on both margins were highest within

the OMZ and the lower transition zones, then decreased with depth (Fig. 2a). Total nitrogen mirrored the organic carbon profiles, although the difference between the core of the OMZ and sites below the core was less pronounced (Fig. 2b). Both  $C_{org}$  and TN concentrations were significantly higher on the Oman margin compared to the Pakistan margin ( $F_{1,9} = 6.894$ ,  $p = 0.028$ ;  $F_{1,9} = 8.485$ ,  $p = 0.017$ , for  $C_{org}$  and TN, respectively). We use the hydrogen index (HI) here as a proxy for food quality (Cook et al., 2000). Values of the HI were significantly higher on the Oman margin than on the Pakistan margin and highest within the OMZ in both cases ( $F_{1,23} = 6.894$ ,  $p < 0.0001$ ; Fig. 2c). On the Pakistan margin the  $\delta^{13}C$  composition of POM was significantly depleted relative to the SOM, whilst the  $\delta^{15}N$  composition of POM and SOM were not significantly different (Jeffreys et al., 2009b).  $\delta^{15}N$  values of SOM did not exhibit any trends with depth on the Pakistan margin (Kruskal–Wallis test  $p = 0.302$ ) and were significantly lighter on the Pakistan margin compared to the Oman margin (Mann–Whitney  $U$  test:  $p = 0.030$ ; Table 2).  $\delta^{13}C$  values of SOM on the Oman margin were significantly lighter at 300 and 940 m compared to 1850 m and marginally lighter at 140 m compared to 1850 m ( $F_{4,24} = 5.664$ ,  $p = 0.002$ ; Games–Howell test  $p = 0.032$ , 0.010 and 0.053 between 1850 m and 300, 940 and 140 m respectively; Table 2). There was no significant difference in sedimentary  $\delta^{13}C$  values between the two margins (Mann–Whitney  $U$  test:  $p = 1.000$ ; Table 2).

### 3.2 Isotopic composition of Foraminifera at the Pakistan margin

On the Pakistan margin,  $\delta^{13}C$  values of foraminifera ranged from  $-25.5$  to  $-20.5\%$  and were broadly similar with the majority falling within the range of possible food sources (Fig. 3). The  $\delta^{15}N$  composition of foraminifera on the Pakistan margin was more variable ranging from  $-3.9$  to  $27.3\%$  (Fig. 3).

**BGD**

11, 18145–18188, 2014

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



### 3.2.1 Depth trends in isotopic signature

Calcareous foraminifera were significantly depleted in  $^{13}\text{C}$  at 140 m compared to those at 300 m, and 940 and 1200 m combined ( $\delta^{13}\text{C} = -22.9, -21.4$  and  $-21.4\%$  at 140, 300 m, and 940 plus 1200 m combined, respectively; Fig. 4a, Kruskal–Wallis test  $p = 0.022$ ). No significant difference in  $\delta^{15}\text{N}$  was noted (Fig. 4b,  $F_{1,17} = 0.691, p = 0.164$ ). A similar trend was observed in the textulariids, i.e.  $\delta^{13}\text{C}$  values significantly depleted in  $^{13}\text{C}$  at shallower depths (Fig. 4a,  $\delta^{13}\text{C} = -22.1, -21.3$  and  $-21.1\%$  at 140 plus 300 m combined, 940 m and 1200 plus 1850 m combined, respectively; Kruskal–Wallis test  $p < 0.0001$ ) and no significant difference in  $\delta^{15}\text{N}$  with depth (Fig. 4b, Kruskal–Wallis test  $p = 0.817$ ). Agglutinated monothalamids (including *Pelosina* spp., *Bathysiphon* sp. and *Rhizammina* sp.) displayed no significant difference in either  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  composition with depth across the Pakistan margin (Figs. 3 and 4,  $\delta^{13}\text{C}$ :  $F_{3,14} = 1.188, p = 0.350, \delta^{15}\text{N}$ :  $F_{3,13} = 0.293, p = 0.830$ ).

The  $\delta^{13}\text{C}$  composition of the calcareous species *Uvigerina* ex gr. *semiornata* was significantly depleted in  $^{13}\text{C}$  at 140 m compared to 300 m (Fig. 3a and b, Mann–Whitney  $U$  test:  $p = 0.024$ ). There was no significant difference in its  $\delta^{15}\text{N}$  composition between 140 and 300 m (Fig. 3a and b,  $F_{1,9} = 0.627, p = 0.449$ ). Three species of the genus *Reophax*, a textulariid, were present across the Pakistan margin; there was no significant difference in their  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  composition, from 300 to 1200 m (Fig. 3b–d,  $\delta^{13}\text{C}$ :  $F_{2,19} = 1.687, p = 0.212, \delta^{15}\text{N}$ : Kruskal–Wallis test  $p = 0.920$ ). Similarly, at 940 m there was no significant difference in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  composition of *Reophax* aff. *bilocularis* with living depth within the sediment (Table S2,  $\delta^{13}\text{C}$ :  $F_{2,8} = 2.310, p = 0.161, \delta^{15}\text{N}$ : Kruskal–Wallis test  $p = 0.135$ ).

### 3.2.2 Trends among main foraminiferal groups and species

At 300 m there was no significant difference in isotopic composition between calcareous, textulariids or agglutinated monothalamid species (Figs. 3b and 4a,

BGD

11, 18145–18188, 2014

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



$F_{2,10} = 0.534$ ,  $p = 0.602$ ,  $\delta^{15}\text{N}$ : Kruskal–Wallis test  $p = 0.841$ ). Similarly, there were no significant differences in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  composition between calcareous and textulariid species at 940 m (Figs. 3c and 4a,  $\delta^{13}\text{C}$ : Mann–Whitney  $U$  test:  $p = 0.180$ ,  $\delta^{15}\text{N}$ : Mann–Whitney  $U$  test:  $p = 0.734$ ).

At 140 m, *Uvigerina* ex gr. *semiornata* was significantly depleted in  $^{13}\text{C}$  compared to *Pelosina* spp. (Fig. 3a, Mann–Whitney  $U$  test:  $p = 0.048$ ); however, there was no significant difference in  $\delta^{15}\text{N}$  composition between these taxa (Fig. 3a, Mann–Whitney  $U$  test:  $p = 0.279$ ). At 300 m there was no significant difference between *U. ex gr. semiornata* or *Reophax* spp. in either the  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  composition (Fig. 3b,  $\delta^{13}\text{C}$ :  $F_{1,8} = 1.015$ ,  $p = 0.343$ ,  $\delta^{15}\text{N}$ : Mann–Whitney  $U$  test:  $p = 0.831$ ).

### 3.3 Isotopic composition of Foraminifera at the Oman margin

Unfortunately, as a result of small sample sizes,  $\delta^{13}\text{C}$  could not be determined in all samples. However,  $\delta^{13}\text{C}$  values of foraminifera on the Oman margin, ranged from  $-21.3$  to  $-11.5\text{‰}$  and were broadly similar, with the majority falling within the range of potential food sources (Fig. 5). The  $\delta^{15}\text{N}$  composition of foraminifera on the Oman margin was more variable, ranging from  $-7.8$  to  $10.8\text{‰}$  (Fig. 5).

#### 3.3.1 Depth trends in isotopic signature

Using the areas (i.e. B and C) and habitats (i.e. continental slopes, canyons and continental rises) defined by Billett et al. (2006, Fig. 1), we observed no significant difference in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  composition of foraminifera between areas B and C ( $\delta^{13}\text{C}$ : Mann–Whitney  $U$  test:  $p = 0.670$ ;  $\delta^{15}\text{N}$ : Mann–Whitney  $U$  test:  $p = 0.169$ ). Similarly, we noted no significant difference in foraminiferal  $\delta^{15}\text{N}$  composition within area C between slope (363–789 m) and canyon sites (1103–1390 m) ( $F_{1,11} = 0.105$ ,  $p = 0.752$ ). Owing to the limited data set, we were unable to test for differences in foraminiferal  $\delta^{13}\text{C}$  composition between these two habitats. Similarly, within area B

BGD

11, 18145–18188, 2014

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



we observed no significant difference in foraminiferal  $\delta^{15}\text{N}$  composition between 1414, 2030 and 3185 m (Figs. 4b and 5a, Mann–Whitney  $U$  test:  $p = 0.389$ ).

Using the oxygen concentrations from the CTD and the definitions of Gooday et al. (2009) as a guide, we categorized the stations into distinct regions of the OMZ. The OMZ core (504–789 m; DO = 5.1 to 6.3  $\mu\text{M}$ ); the lower boundary (1103–1414 m; DO = 16.5 to 29.9  $\mu\text{M}$ ) and below the OMZ (2030–3185 m; DO = 90.6 to 166  $\mu\text{M}$ ). We observed no significant difference in  $\delta^{13}\text{C}$  composition between foraminifera from the lower OMZ boundary and those found below the OMZ (Figs. 4c and 5a, Mann–Whitney  $U$  test:  $p = 0.389$ ). Foraminiferal  $\delta^{15}\text{N}$  composition did not differ significantly with depth (Figs. 4d and 5a, Kruskal–Wallis test  $p = 0.291$ ). Similarly, foraminiferal  $\delta^{15}\text{N}$  composition did not differ significantly between the OMZ core, lower OMZ boundary or below the OMZ (Fig. 4d, Kruskal–Wallis test  $p = 0.287$ ).

Calcareous foraminiferal  $\delta^{15}\text{N}$  compositions did not differ significantly across the Oman margin (Fig. 4d,  $F_{1,13} = 1.979$ ,  $p = 0.183$ ). Textulariids were depleted in  $^{15}\text{N}$  at the lower OMZ boundary ( $2.1 \pm 1.4\text{‰}$ ) compared to those found below the OMZ (water depths > 2000 m;  $8.1 \pm 5.1\text{‰}$ ; Fig. 4d,  $F_{1,5} = 31.011$ ,  $p = 0.003$ ).

### 3.3.2 Trends among main foraminiferal groups

The  $\delta^{13}\text{C}$  composition was not significantly different between foraminiferal groups (Fig. 4c,  $F_{2,11} = 0.889$ ,  $p = 0.439$ ). Similarly, the  $\delta^{15}\text{N}$  composition was not significantly different between foraminiferal groups across the whole margin (Fig. 4d, Kruskal–Wallis test  $p = 0.751$ ). Calcareous foraminifera were significantly enriched in  $^{15}\text{N}$  ( $5.5 \pm 2.2\text{‰}$ ) compared to textulariids at the lower OMZ boundary ( $2.1 \pm 1.4\text{‰}$ ; Fig. 4d, water depths 1103–1414 m;  $F_{1,11} = 6.722$ ,  $p = 0.025$ ). Below the OMZ (water depths 2030–3185 m) no significant differences were observed in  $\delta^{15}\text{N}$  composition between agglutinated monothalamid, textulariid or calcareous species (Fig. 4d,  $F_{1,11} = 1.345$ ,  $p = 0.304$ ).

## BGD

11, 18145–18188, 2014

### The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





Whitney  $U$  test:  $p < 0.030$ ). Similarly, *Globobulimia* spp. (a mixture of *G. turgida* and *G. affinis*) were depleted in  $^{15}\text{N}$  off Oman ( $\delta^{15}\text{N} = 4.9 \pm 2.0\text{‰}$ ) compared to *G. cf. G. pyrula* off Pakistan ( $\delta^{15}\text{N} = 15.4 \pm 5.0\text{‰}$ ; Table S2,  $F_{1,5} = 11.024$ ,  $p = 0.021$ ). The  $\delta^{15}\text{N}$  composition of *Reophax dentaliniformis* was similar on both margins (Table S2: Pakistan  $\delta^{15}\text{N} = 8.7 \pm 7.1\text{‰}$ ; Oman  $\delta^{15}\text{N} = 4.9 \pm 3.7\text{‰}$ ).

## 4 Discussion

### 4.1 Methodological issues

Different preservation methods were used for foraminiferal samples at each margin (see Sect. 2.1). It has been shown that bulk freezing can lead to discrepancies in isotopic signatures as a result of cell lysis (Feuchtmayr and Grey, 2003; Dannheim et al., 2007). However, the discrepancies in  $\delta^{15}\text{N}$  values for bulk frozen material reported by these studies were inconsistent; Feuchtmayr and Grey (2003) reported an increase in  $\delta^{15}\text{N}$  values by 1‰, whereas, Dannheim et al. (2007) reported a decrease in  $\delta^{15}\text{N}$  values by 1‰. The 1‰ discrepancy reported in  $\delta^{15}\text{N}$  values between bulk frozen sediments/water samples and organisms, which have been frozen directly as individuals, is within the analytical error of our study. We therefore do not expect that our methodologies will have significantly affected our results. Furthermore, the large range in  $\delta^{15}\text{N}$  values observed in foraminifera at both of the margins ( $-7.8$  to  $10.8\text{‰}$  for Oman and  $-3.9$  to  $27.3\text{‰}$  for Pakistan) suggests this is unlikely.

### 4.2 Oxygen dynamics and organic matter supply to the sediments

This study arose from a comprehensive investigation of carbon cycling by benthic communities during different seasons (pre- and post- SW monsoon) and at different water depths (140–1850 m) across the Pakistan margin and from a biological survey conducted at the Oman margin during the post SW monsoon season at water depths

BGD

11, 18145–18188, 2014

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



of ~ 360–3185 m. Detailed descriptions of the environmental conditions and benthic community structure at the Pakistan margin can be found in Brand and Griffiths (2009), Breuer et al. (2009), Cowie et al. (2009), Gooday et al. (2009), Jeffreys et al. (2009a, b), and Larkin et al. (2009). Descriptions of environmental conditions and benthic community structure at the Oman margin relevant to this study can be found in: Gooday et al. (2000), Smallwood and Wolff (2000) and Aranada da Silva and Gooday (2009). Below we give a brief overview of environmental conditions at both margins.

Oxygen profiles on both margins exhibited a sharp decline in concentration in the upper 200 m of the water column to an intense minimum, then increased gradually below ~ 1000 m (Aranda da Silva and Gooday, 2009). DO concentrations in the core of the OMZ on the Pakistan margin (~ 300 m) were lower than in the core on the Oman margin (~ 400 m; Gooday et al., 2009). Upwelling intensity is greater off Oman, resulting in higher productivity and higher particulate fluxes compared to off Pakistan (Burkill et al., 1993; Haake et al., 1993; Nair et al., 1989). This is reflected in the abundance and quality of SOM, with higher  $C_{org}$ , TN concentrations and HI values on the Oman margin compared to the Pakistan margin. This suggests a greater input of fresh organic matter to the Oman margin or less heterotrophic reworking of POM in the water column, presumably leading to a more abundant food supply there.

Stable isotopic signatures of potential food sources, i.e. SOM and POM, were similar to those of Gaye-Haake et al. (2005), having  $\delta^{13}C$  values typical of mid-latitude algae (Sackett et al., 1965), and were similar on both margins. Nitrogen isotopes of food sources reflect the  $\delta^{15}N$  of nitrate in surface waters, which reflect denitrification in the region (Altabet et al., 1995; Cline and Kaplan, 1975; Gaye-Haake et al., 2005). Sediments on the Oman margin were enriched in  $^{15}N$  compared to those on the Pakistan margin. This observation is consistent with a greater proportion of terrestrial organic matter at the Pakistan margin, as shown by its higher C/N ratios and concentrations of terrestrially-derived fatty acids and alcohols relative to the Oman margin (Jeffreys et al., 2009a; Smallwood and Wolff, 2000; Table 3).

## 4.3 Spatial patterns in foraminiferal trophic ecology

### 4.3.1 Depth trends

The uniformity in the  $\delta^{15}\text{N}$  composition of food sources on the Pakistan margin is typical of upwelling margins impacted by OMZs (Cowie et al., 2009). This is also reflected in the isotopic composition of the foraminifera, as no bathymetric patterns in their  $\delta^{15}\text{N}$  values were apparent. The  $\delta^{13}\text{C}$  composition of SOM did exhibit spatial variability, being more enriched below the OMZ. This is consistent with Cowie et al. (2009), who suggested that the minimum in  $\delta^{13}\text{C}$  values observed within the OMZ core reflects a chemosynthetic bacterial imprint on the isotopic composition of SOM. We observed large filamentous bacteria with depleted  $\delta^{13}\text{C}$  values within the core and lower transition zone of the OMZ. Additionally, branched fatty acid concentrations, biomarkers for heterotrophic anaerobic bacteria (Gillan and Johns, 1986), were found in highest concentrations at 140 and 300 m during the post-SW monsoon on the Pakistan margin (Jeffreys et al., 2009a), consistent with an important bacterial contribution to SOM. The  $\delta^{13}\text{C}$  composition of foraminifera reflected that of SOM at the Pakistan margin, i.e. both calcareous and textulariid foraminifera have depleted  $\delta^{13}\text{C}$  values at shallower depths within the OMZ, e.g. 140 and 300 m. It seems likely that the foraminifera at 140 m may be taking advantage of a more abundant phytodetrital food source at this site (Jeffreys et al., 2009a), with  $\delta^{13}\text{C}$  values more closely resembling POM and sediments. At 300 m foraminifera appear to utilise both POM and bacteria.

$\delta^{15}\text{N}$  values of SOM were also invariant across the Oman margin, a pattern reflected in the foraminiferal  $\delta^{15}\text{N}$  compositions. On the other hand,  $\delta^{13}\text{C}$  values were spatially variable, being noticeably heavier at 500 and 1100 m. The presence of large falls of dead jellyfish both on the continental slope, rise and in the canyons of the Oman margin at similar depths might provide an explanation for the enrichment of SOM (Billett et al., 2006). The largest aggregations of jellyfish covered by white bacterial mats, evidence of sulphide oxidation, were observed on the continental rise at the time of sampling (Billett et al., 2006). A chemosynthetic bacterial input derived from

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the anaerobic decomposition of jelly detritus could therefore have led to the enriched  $\delta^{13}\text{C}$  values observed at 500 and 1100 m, as carbon fixation fuelled by energy derived from sulphide oxidation involving Rubisco II leads to enriched  $\delta^{13}\text{C}$  values of  $-9$  to  $-16\text{‰}$  (Robinson and Cavanaugh, 1995). The majority of foraminifera on the Oman margin had  $\delta^{13}\text{C}$  compositions typical of mid-latitude phytoplankton (Sackett et al., 1965) with the exception of *Hyalina baltica* at 1414 m, which had a  $\delta^{13}\text{C}$  composition of  $\sim -12\text{‰}$ , possibly through its utilisation of chemosynthetic bacteria as a food source. This station was located on the continental rise within area B, where decaying jellyfish, white bacterial mats and a thin layer ( $< 10$  mm) of jelly slime covered the surface of the sediments (Billett et al., 2006).

### 4.3.2 Inter-margin differences

The inter-margin spatial variability in the organic geochemistry of the sediments provides evidence of variability in the source, abundance and quality of organic matter. Foraminifera on the Oman margin were enriched in  $^{13}\text{C}$  compared to those on the Pakistan margin, this being driven primarily by the calcareous taxa. It is likely that at the Pakistan margin these foraminifera select for fresh phytodetrital material as their isotopic signatures closely match the POM. Similarly, foraminifera below the OMZ on the Pakistan margin were depleted in  $^{13}\text{C}$  compared to those on the Oman margin. Phytodetritus was present on surficial sediments and within burrows at 1850 m, ( $\text{O}_2 = 73.6 \mu\text{M}$ ) below the OMZ at the Pakistan margin. Foraminifera below the OMZ on the Pakistan margin fell between the range of  $\delta^{13}\text{C}$  values for POM and SOM and so it is likely that they were feeding on relatively fresh material. On the Oman margin foraminifera more closely reflected the SOM carbon isotopic signature.

The most noticeable expression of differences in the trophic ecology of the foraminifera between the two margins was the distinct divergence in stable nitrogen isotope signatures. At the Pakistan margin,  $\sim 14\%$  of foraminifera had  $\delta^{15}\text{N}$  values enriched by more than one trophic level relative to SOM. These foraminifera may store nitrate in their vacuoles for respiration; in such cases, intracellular  $\delta^{15}\text{N}_{\text{NO}_3}$

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



values vary from 15 to 42‰ (Bernhard et al., 2012). The storage of intracellular nitrate for respiration is widespread among foraminifera and has been documented in species from anoxic sediments in a variety of habitats including OMZs (Glock et al., 2013; Bernhard et al., 2012; Pina-Ochoa et al., 2010; Prokopenko et al., 2011; Risgaard-Petersen et al., 2006). In this study, nitrate storage/respiration apparently occurs in the calcareous species *Globobulimina* cf. *G. pyrula* and *Cancris auriculus* within the hypoxic core of the OMZ at 140 and 300 m. These species are known to be “nitrate collectors” (Pina-Ochoa et al., 2010). Textulariids were also enriched in  $^{15}\text{N}$ , several species of *Reophax*, including *R. aff. dentaliniformis*, *R. aff. bilocularis*, *R. scorpiurus* and and unidentified species, had enriched  $\delta^{15}\text{N}$  values across the margin from the hypoxic core to the oxygenated deeper site at 1850 m. Species of *Reophax* have not been observed to store nitrate (Pina-Ochoa et al., 2010). However, Pina-Ochoa et al. (2010) noted that only a few specimens were analysed while Bernhard et al. (2012) observed large variations in foraminiferal nitrate storage between individuals of the same species as well as between different species. *Dorothia scabra*, another textulariid, also from the lower OMZ transition zone at 940 m, had the most enriched  $\delta^{15}\text{N}$  value in the present study.

There are three possible mechanisms which would enable nitrate storage in these foraminifera: (1) transport of nitrate into the vacuoles from the surrounding porewaters as demonstrated by Koho et al. (2010), (2) symbiosis with bacterial denitrifiers, as observed in an allogromiid within the Santa Barbara basin (Bernhard et al., 2011) and (3) intracellular production either *de novo* or *via* nitrifying bacteria. It is unlikely that foraminifera or bacteria are able to produce nitrate via nitrification within the OMZ as this requires oxygen (Bernhard et al., 2012). Foraminifera found below the OMZ at fully oxygenated sites may be able to use this pathway. It is more likely that if the foraminifera store nitrate and use either pathway (1) or (2), although from our data set we cannot discern the exact mechanism. Koho et al. (2010) have demonstrated that *Globobulimina* migrate through the sediment along a concentration gradient to access



2003), and bacterial mats have been observed previously at the OM (Levin et al., 1997). At the time of sample collection, bacterial mats were visible in still images across the Oman margin from depths of 1000 to 3300 m, colonizing both single jellyfish and jelly detritus (Billett et al., 2006). Sulphur-oxidising bacteria at cold seeps are characterized by depleted  $\delta^{15}\text{N}$  signatures (Decker and Olu, 2011; Demopoulos et al., 2010; Levin and Michener, 2002). We do not have isotopic data for bacteria from the Oman margin, but bacteria from the Pakistan margin had  $\delta^{15}\text{N}$  values ranging from  $-0.4$  to  $11.9\%$ , including *Thioploca* sp., which had a  $\delta^{15}\text{N}$  value of  $-0.1\%$ . We suggest, therefore, that the depleted  $\delta^{15}\text{N}$  values of foraminifera on the Oman margin are a result of feeding on isotopically light bacteria associated with jelly detritus.

#### 4.4 Foraminiferal feeding types: species level

Gooday et al. (2008) review the trophic biology of deep-sea foraminifera based on feeding experiments, field observations, cellular stable isotope ratios and fatty acid analyses. They recognise the following general types, which should not be regarded as rigid categories: (A) herbivores (i.e. phytodetritus feeders), (B) opportunistic deposit feeders (omnivores), (C) intermediate- and deep-infaunal sediment deposit feeders, (D) stercomata-bearing species (likely deposit feeders), (F) monothalamous species that may be bacteriovores, and (G) suspension feeding epifaunal foraminifera. Using a combination of pulse-chase experiments and fatty acid biomarkers, Larkin (2006) recognised two trophic types among Pakistan margin foraminifera ( $> 300\ \mu\text{m}$  fraction): (i) phytophagous species that consume fresh phytodetritus and (ii) unselective deposit feeders. These are equivalent to Types A and B identified by Gooday et al. (2008). The present study included species representative of all 6 of the trophic groups recognised by Gooday et al. (2008). Our stable isotope analyses spanned a wide range, as previously observed for foraminifera at both bathyal and abyssal depths (Enge et al., 2011; Iken et al., 2001; Nomaki et al., 2008). These results indicate that the Arabian Sea foraminifera include: (1) those that derive carbon and nitrogen principally from fresh organic matter (phytodetritus) when available, i.e. opportunistic deposit feeders,

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



phytodetrital material with its  $\delta^{13}\text{C}$  values closely resembling POM. This is in agreement with Gooday et al. (2002), who concluded from fatty acid analyses that *Bathysiphon capillare* feeds on a diet that includes phytodetritus. Similarly, a mixture of monothalamid foraminifera (including *Bathysiphon* sp. nov., *Hyperammina* sp. and *Nodellum* sp.) from 940 and 1200 m appear to derive carbon from sedimenting POM. Species of the textulariid genus *Reophax* spp. also appear to feed on sedimenting POM at 140 m on the Pakistan margin.

At the Pakistan margin there was a clear distinction between the carbon isotopic composition of calcareous and textulariid foraminifera. This suggests that calcareous taxa are more selective in their choice of food particles, selecting the freshest organic matter when possible. Fatty acid analyses of foraminifera from the West Antarctic Peninsula continental shelf also demonstrates that calcareous foraminifera feed on more labile organic matter than textulariid species (Suhr et al., 2003). In contrast, no differences were observed between calcareous and textulariid foraminifera on the Oman margin, suggesting that these two types are feeding on similar resources. Similarly, at an abyssal site in the NE Pacific there were no apparent differences in carbon isotopic composition of the calcareous and textulariid foraminifera (Enge et al., 2011). The greater abundance of organic matter at the Oman margin compared to the Pakistan margin could lead to a reduction in competition for resources at the Oman margin between these two foraminiferal types.

### 4.4.2 Unselective feeders

Unselective feeders include epifaunal suspension feeders, intermediate- and deep-infaunal sediment deposit feeders, and stercomata-bearing species (Gooday et al., 2008). The only epifaunal suspension feeder in our material was *Pelosina* sp., which was observed across the Pakistan margin from 140 to 1850 m. The  $\delta^{13}\text{C}$  values of *Pelosina* sp. fell between POM and SOM at both 140 and 1850 m but closer to SOM at 300 m and closer to POM at 1200 m. We suggest that *Pelosina* sp. found on the

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Pakistan margin is a passive suspension feeder trapping both fresh and degraded organic matter, which would explain the variation in  $\delta^{13}\text{C}$  values of this foraminifera across the margin. The  $\delta^{15}\text{N}$  values of *Pelosina* sp. were also variable and generally within 1 trophic level (assuming a trophic enrichment factor of 2.2 to 3.4‰; McCutchan et al., 2003; Post, 2002) of POM and SOM; however, some values fell below the POM and SOM suggesting a bacterial component to the diet.

Several groups of foraminifera on both margins are known to accumulate stercomata: “allogromiids” (organic-walled monothalamids), *Rhizammina* sp., the komokiacean *Lana* sp. and other komokiaceans. The isotopic composition of *Rhizammina* sp. were similar at the Pakistan margin and at the Porcupine Abyssal Plain (PAP) in the NE Atlantic (Iken et al., 2001);  $\delta^{13}\text{C}$  data were consistent with feeding on POM/SOM, while isotopically light  $\delta^{15}\text{N}$  values could reflect a bacterial component in the diet. Similarly, at 3185 m depth at the Oman margin, where jelly detritus was observed on the sediment surface, the  $\delta^{13}\text{C}$  composition of *Rhizammina* sp. was consistent with feeding on POM/SOM, while the wide range of  $\delta^{15}\text{N}$  values suggested ingestion of POM/SOM and bacteria associated with jelly detritus. On both margins, various komokiacean species exhibited consistent isotopic patterns similar to those reported at the PAP (Iken et al., 2001), reflecting probable utilisation of POM/SOM and bacteria. An “allogromiid” at 140 m at the Pakistan margin had a  $\delta^{15}\text{N}$  value one trophic level above that of the sediment and a  $\delta^{13}\text{C}$  value close to that of SOM, suggesting that it was feeding on SOM. “Farming” of bacteria associated with the stercomata of foraminifera has been proposed as a feeding strategy by Tendal (1979). Although this has yet to be confirmed, we cannot discount the influence of stercomata or test particles on the isotopic signatures of these agglutinated taxa.

Intermediate and deep-infaunal deposit feeders include *Chilostomella ovoidea* and various textulariids. The majority of the foraminifera in this study were located in the top cm of sediment. However, *C. ovoidea*, *Dorothia scabra* and *Reophax* aff. *bilocularis* were found in deeper layers (2–10 cm) at 940 m. *Reophax* aff. *bilocularis* was located at 0–2, 2–5, and 5–10 cm with no change in isotopic composition with depth. This,

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



coupled with isotopic signatures falling between POM and SOM, suggest this species is an unselective deposit feeder. Similarly, species of *Reophax* from other sites on the Pakistan margin have intermediate  $\delta^{13}\text{C}$  values, suggesting that they are also unselective deposit feeders, except at 140 m where signatures indicate consumption of phytodetritus. *Chilostomella oolina* is known to feed unselectively on both algae and bacteria (Nomaki et al., 2006), consistent with the isotope values for this species reported in the present study. At the Oman margin, the isotopic composition of *Reophax dentaliniformis* and the monothalamid *Psammosphaera fusca* (which had another monothalamid species, *Ammolagena clavata*, attached to its surface) also closely resembled that of SOM, suggesting unselective deposit feeding.

### 4.4.3 Bacterivores

Some shallow-water foraminifera are known to consume bacteria (e.g. Mojtahid et al., 2011). On the other hand, there is little direct evidence for active predation by deep-sea foraminifera on bacteria (Nomaki et al., 2006). However, our stable isotope data suggest that some deep-sea species do include bacteria in their diets. On the Pakistan margin large sheathed filamentous bacteria ( $\geq 300\ \mu\text{m}$ ) occurred within the OMZ at depths of 300 and 940 m (this study) and across the lower OMZ transition zone from depths of 700 to 1000 m (Jeffreys et al., 2012), while bacterial mats were associated with jelly detritus on the Oman margin (Billett et al., 2006). Filamentous bacteria at 300 and 940 m generally had depleted  $\delta^{15}\text{N}$  values (0 to 5‰), whilst two filaments from 300 m were enriched in  $^{15}\text{N}$  with respect to POM and SOM. The variation in bacterial isotopic signatures reflects the large isotopic shifts that have been observed in both autotrophic and heterotrophic bacteria (Macko et al., 1987; McGoldrick et al., 2008). Depleted  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values derived from the monothalamid *Bathysiphon* sp. at 140 and 300 m, suggested that it was feeding on isotopically depleted bacteria. Fatty acid biomarkers ascribed to bacteria were present in *Bathysiphon* sp. nov.1 at 300 m on the Pakistan margin (Larkin, 2006). Bacterial biomarkers have also been noted in *B. capillare* in the NE Atlantic (Gooday et al., 2002). We suggest that the isotopic

signatures of *Bathysiphon* sp. nov. in this study may reflect a bacterial component to the diet. *Reophax* aff. *dentaliniformis* and *Globobulimina* cf. *G. pyrula* also had depleted  $\delta^{15}\text{N}$  values, implying a bacterial food source. Foraminifera with depleted  $\delta^{15}\text{N}$  values were observed both at the lower OMZ boundary and below the OMZ.

Sulphur oxidising/denitrifying filamentous bacteria in the genus *Thioploca* can form conspicuous mats on the surface of OMZ sediments (Cowie and Levin, 2009; Levin et al., 1997; Schmaljohann et al., 2001). Recently, Prokopenko et al. (2013) demonstrated a consortium between *Thioploca* and anammox bacteria in anoxic sediments of the Soledad basin at the Mexican Pacific margin. At the Pakistan margin, bacterial sheaths have been observed entangled in a network of foraminiferal rhizopodia (Schmaljohann et al., 2001). At the Oman margin 74 % of foraminifera had  $\delta^{15}\text{N}$  compositions falling below the  $\delta^{15}\text{N}$  values of the sediments. These observations suggest that bacteria may provide foraminifera with essential nutrients on both margins.

## 5 Conclusions

Arabian Sea foraminifera appear to exploit a variety of food sources and metabolic pathways. Most utilise carbon and nitrogen from photosynthetic food sources. Depleted (“isotopically light”) foraminiferal  $\delta^{15}\text{N}$  values implies some feeding on bacteria. Isotopically light foraminifera were more common at the Oman margin where a large, recently deposited jellyfish fall had led to the development of bacterial mats (Billett et al., 2006). Enriched  $\delta^{15}\text{N}$  compositions of foraminifera from the Pakistan margin provide evidence for intracellular nitrate collection/respiration, which was not apparent at the Oman margin. Differences in the isotopic compositions of foraminifera between the two margins may reflect processes in overlying primary production and nitrogen dynamics at the two margins. Using stable isotopes we have demonstrated a tight coupling between foraminiferal trophic ecology and metabolic processes associated with the presence of organic matter and its subsequent breakdown. Understanding the trophic and metabolic ecology of foraminifera is important for understanding benthic

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



food webs as these protists are an important trophic link to metazoan fauna (Nomaki et al., 2008) and their distinct isotopic signatures can be passed further up the food web.

**The Supplement related to this article is available online at  
doi:10.5194/bgd-11-18145-2014-supplement.**

*Acknowledgements.* We thank the Master, Crew of the RRS *Charles Darwin* and the scientists who participated in CD143, CD146 and CD151 for their help in collection of the material, particularly Christine Whitcraft, Ana Aranda da Silva and Lisa Levin. We would like to thank Brian Bett for producing the maps in Fig. 1. We are grateful to Greg Cowie, David Harris and Georges Paradis, for the stable isotope analyses. Thanks also to Sabena Blackbird for assistance with elemental analyses. Stable isotopic analyses were carried out by the MSI Analytical Lab (Marine Science Institute, University of California) and the laboratory of David Harris (UC Davis) and Greg Cowie (University of Edinburgh). We thank Claire Mahaffey for useful discussions regarding nitrogen cycling. This work was supported by the Natural Environment Research Council, UK (NER/A/S/2000/01381 and NE/F011024/1).

## References

- 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.
- Aranada da Silva, A. and Gooday, A. J.: Large organic-walled Protista (*Gromia*) in the Arabian Sea: density, diversity, distribution and ecology, *Deep-Sea Res. Pt. II*, 56, 422–433, 2009.
- 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, 2011.
- Bernhard, J. M., Casciotti, K. L., McIlvin, 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, 2012.

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[◀](#)

[▶](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



- Billett, D., Lampitt, R., Rice, A., and Mantoura, R.: Seasonal sedimentation of phytoplankton to the deep-sea benthos, *Nature*, 302, 520–522, 1983.
- Billett, D. S. M., Bett, B. J., Jacobs, C. L., Rouse, I. P., and Wigham, B. D.: Mass deposition of jellyfish in the deep Arabian Sea, *Limnol. Oceanogr.*, 51, 2077–2083, 2006.
- 5 Brand, T. D. and Griffiths, C.: Seasonality in the hydrography and biogeochemistry across the Pakistan margin of the NE Arabian Sea, *Deep-Sea Res. Pt. II*, 56, 283–295, 2009.
- Brandes, J., Devol, A., Yoshinari, T., Jayakumar, D., and Naqvi, S.: Isotopic composition of nitrate in the central Arabian Sea and eastern tropical North Pacific: a tracer for mixing and nitrogen cycles, *Limnol. Oceanogr.*, 43, 1680–1689, 1998.
- 10 Breuer, E. R., Law, G. T. W., Woulds, C., Cowie, G. L., Shimmield, G. B., Peppe, O., Schwartz, M., and Mckinlay, S.: Sedimentary oxygen consumption and microdistribution at sites across the Arabian Sea oxygen minimum zone (Pakistan margin), *Deep-Sea Res. Pt. II*, 56, 296–304, 2009.
- Brooks, J. M., Kennicutt, M. C., Fisher, C. R., Macko, S. A., Cole, K., Childress, J. J., Bidigare, R. R., and Vetter, R. D.: Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources, *Science*, 238, 1138–1142, 1987.
- Burkill, P. H., Mantoura, R., and Owens, N.: Biogeochemical cycling in the northwestern Indian Ocean: a brief overview, *Deep-Sea Res. Pt. II*, 40, 643–649, 1993.
- Campbell, B., Stein, J., and Cary, S.: Evidence of chemolithoautotrophy in the bacterial community associated with *Alvinella pompejana*, a hydrothermal vent polychaete, *Appl. Environ. Microb.*, 69, 5070–5078, 2003.
- 15 Cline, J. D. and Kaplan, I. R.: Isotopic fractionation of dissolved nitrate during denitrification in the eastern tropical north pacific ocean, *Mar. Chem.*, 3, 271–299, 1975.
- Cook, A., Lamshead, P. J. D., Hawkins, L., Mitchell, N., and Levin, L.: Nematode abundance at the oxygen minimum zone in the Arabian Sea, *Deep-Sea Res. Pt. II*, 47, 75–85, 2000.
- 25 Cowie, G.: The biogeochemistry of Arabian Sea surficial sediments: a review of recent studies, *Prog. Oceanogr.*, 65, 260–289, 2005.
- Cowie, G. L. and Levin, L. A.: Benthic biological and biogeochemical patterns and processes across an oxygen minimum zone (Pakistan margin, NE Arabian Sea), *Deep-Sea Res. Pt. II*, 56, 261–270, 2009.
- 30 Cowie, G. L., Calvert, S., Pedersen, T., Schulz, H., and von Rad, U.: Organic content and preservational controls in surficial shelf and slope sediments from the Arabian Sea (Pakistan margin), *Mar. Geol.*, 161, 23–38, 1999.

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Cowie, G. L., Mowbray, S., Lewis, M., Matheson, H., and McKenzie, R.: Carbon and nitrogen elemental and stable isotopic compositions of surficial sediments from the Pakistan margin of the Arabian Sea, *Deep-Sea Res. Pt. II*, 56, 271–282, 2009.

Decker, C. and Olu, K.: Habitat heterogeneity influences cold-seep macrofaunal communities within and among seeps along the Norwegian margin – Part 2: contribution of chemosynthesis and nutritional patterns, *Marine Ecology*, 33, 231–245, 2011.

Demopoulos, A. W. J., Gualtieri, D., and Kovacs, K.: Food-web structure of seep sediment macrobenthos from the Gulf of Mexico, *Deep-Sea Res. Pt. II*, 57, 1972–1981, 2010.

DeNiro, M. J. and Epstein, S.: Influence of diet on the distribution of carbon isotopes in animals, *Geochim. Cosmochim. Ac.*, 42, 495–506, 1978.

DeNiro, M. J. and Epstein, S.: Influence of diet on the distribution of nitrogen isotopes in animals, *Geochim. Cosmochim. Ac.*, 45, 341–351, 1981.

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

Findlater, J.: A major low-level air current near the Indian Ocean during the northern summer, *Q. J. Roy. Meteor. Soc.*, 95, 362–380, 1969.

Fry, B. and Sherr, E. B.:  $\delta^{13}\text{C}$  measurements as indicators of carbon flow in marine and freshwater ecosystems, *Contrib. Mar. Sci.*, 27, 13–47, 1984.

Gaye-Haake, B., Lahajnar, N., Emeis, K., Unger, D., Rixen, T., Suthhof, A., Ramaswamy, V., Schulz, H., Paropkari, A., and Guptha, M.: Stable nitrogen isotopic ratios of sinking particles and sediments from the northern Indian Ocean, *Mar. Chem.*, 96, 243–255, 2005.

Gillan, F. T. and Johns, R. B.: Chemical markers for marine bacteria: fatty acids and pigments, *Meth. Geoch.*, 24, 291–309, 1986.

Glock, N., Schönfeld, J., Eisenhauer, A., Hensen, C., Mallon, J., and Sommer, S.: The role of benthic foraminifera in the benthic nitrogen cycle of the Peruvian oxygen minimum zone, *Biogeosciences*, 10, 4767–4783, doi:10.5194/bg-10-4767-2013, 2013.

Goes, J., Thoppil, P., Gomes, H., and Fasullo, J.: Warming of the Eurasian landmass is making the Arabian Sea more productive, *Science*, 308, 545–547, 2005.

Gooday, A.: A response by benthic foraminifera to the deposition of phytodetritus in the deep-sea, *Nature*, 332, 70–73, 1988.

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffrey et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



- Gooday, A.: Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review, *J. Oceanogr.*, 58, 305–332, 2002.
- Gooday, A. J., Levin, L. A., Linke, P., and Heeger, T.: The role of benthic foraminifera in deep-sea food webs and carbon cycling, in: *Deep-Sea Food Chains and the Global Carbon Cycle*, Springer Netherlands, Dordrecht, 63–91, 1992.
- Gooday, A. J., Bernhard, J. M., Levin, L. A., and Suhr, S. B.: Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas, *Deep-Sea Res. Pt. II*, 47, 25–54, 2000.
- Gooday, A. J., Pond, D. W., and Bowser, S. S.: Ecology and nutrition of the large agglutinated foraminiferan *Bathysiphon capillare* in the bathyal NE Atlantic: distribution within the sediment profile and lipid biomarker composition, *Mar. Ecol.-Prog. Ser.*, 245, 69–82, 2002.
- Gooday, A. J., Nomaki, H., and Kitazato, H.: Modern deep-sea benthic foraminifera: a brief review of their morphology-based biodiversity and trophic diversity, *Geol. Soc. Spec. Publ.*, 303, 97–119, 2008.
- Gooday, A. J., Levin, L. A., Silva, A. A. D., Bett, B. J., Cowie, G. L., Dissard, D., Gage, J. D., Hughes, D. J., Jeffrey, R., Lamont, P. A., Larkin, K. E., Murty, S. J., Schumacher, S., Whitcraft, C., and Woulds, C.: Faunal responses to oxygen gradients on the Pakistan margin: a comparison of foraminiferans, macrofauna and megafauna, *Deep-Sea Res. Pt. II*, 56, 488–502, 2009.
- Graf, G.: Benthic pelagic coupling in a deep-sea benthic community, *Nature*, 341, 437–439, 1989.
- Grandel, S., Rickert, D., Schlüter, M., and Wallmann, K.: Pore-water distribution and quantification of diffusive benthic fluxes of silicic acid, nitrate and phosphate in surface sediments of the deep Arabian Sea, *Deep-Sea Res. Pt. II*, 47, 2707–2734, 2000.
- Gupta, R. S. and Naqvi, S.: Chemical oceanography of the Indian Ocean, north of the equator, *Deep-Sea Res. Pt. I*, 31, 671–706, 1984.
- Haake, B., Ittekkot, V., Rixen, T., Ramaswamy, V., Nair, R., and Curry, W.: Seasonality and interannual variability of particle fluxes to the deep Arabian Sea, *Deep-Sea Res. Pt. I*, 40, 1323–1344, 1993.
- Hansen, H. P.: Determination of oxygen, in: *Methods in Seawater Analysis*, Wiley-VCH Verlag, Weinheim, Germany, 75–89, 1999.
- Hedges, J. I. and Keil, R. G.: Sedimentary organic matter preservation: an assessment and speculative synthesis, *Mar. Chem.*, 49, 81–115, 1995.

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Hobson, K. and Welch, H.: Determination of trophic relationships within a high Arctic marine food web using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis, *Mar. Ecol.-Prog. Ser.*, 84, 9–18, 1992.
- Honjo, S., Dymond, J., Prell, W., and Ittekkot, V.: Monsoon-controlled export fluxes to the interior of the Arabian Sea, *Deep-Sea Res. Pt. II*, 46, 1859–1902, 1999.
- 5 Honjo, S., Manganini, S. J., and Krishfield, R. A.: Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: a synthesis of global sediment trap programs since 1983, *Prog. Oceanogr.*, 76, 217–285, 2008.
- Iken, K., Brey, T., Wand, U., Voigt, J., and Junghans, P.: Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis, *Prog. Oceanogr.*, 50, 383–405, 2001.
- 10 Jeffreys, R. M., Wolff, G. A., and Cowie, G. L.: Influence of oxygen on heterotrophic reworking of sedimentary lipids at the Pakistan margin, *Deep-Sea Res. Pt. II*, 56, 358–375, 2009a.
- Jeffreys, R. M., Wolff, G. A., and Murty, S. J.: The trophic ecology of key megafaunal species at the Pakistan Margin: evidence from stable isotopes and lipid biomarkers, *Deep-Sea Res. Pt. I*, 56, 1816–1833, 2009b.
- 15 Jeffreys, R. M., Levin, L. A., Lamont, P. A., Woulds, C., Whitcraft, C. R., Mendoza, G. F., Wolff, G. A., and Cowie, G. L.: Living on the edge: single-species dominance at the Pakistan oxygen minimum zone boundary, *Mar. Ecol.-Prog. Ser.*, 470, 79–99, 2012.
- Jørgensen, B. B. and Gallardo, V. A.: *Thioploca* spp.: filamentous sulfur bacteria with nitrate vacuoles, *FEMS Microbiol. Ecol.*, 28, 301–313, 1999.
- 20 Kamykowski, D. and Zentara, S.-J.: Hypoxia in the world ocean as recorded in the historical data set, *Deep-Sea Res. Pt. I*, 37, 1861–1874, 1990.
- Koho, K. A., Pina-Ochoa, E., Geslin, E., and Risgaard-Petersen, N.: Vertical migration, nitrate uptake and denitrification: survival mechanisms of foraminifers (*Globobulimina turgida*) under low oxygen conditions, *FEMS Microbiol. Ecol.*, 75, 273–283, 2010.
- 25 Larkin, K. E.: Community and trophic responses of benthic foraminifera to oxygen gradients and organic enrichment, PhD thesis, University of Southampton, 323 pp., 2006.
- Larkin, K. E. and Gooday, A. J.: Foraminiferal faunal responses to monsoon-driven changes in organic matter and oxygen availability at 140 and 300 m water depth in the NE Arabian Sea, *Deep-Sea Res. Pt. II*, 56, 403–421, 2009.
- 30 Levin, L. A.: Oxygen minimum zone benthos: adaptation and community response to hypoxia, *Oceanogr. Mar. Biol.*, 41, 1–45, 2003.



## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Nomaki, H., Heinz, P., Hemleben, C., and Kitazato, H.: Behaviour and response of deep-sea benthic foraminifera to freshly supplied organic matter: a laboratory feeding experiment in microcosm environments, *J. Foramin. Res.*, 35, 103–113, 2005.

Nomaki, H., Heinz, P., and Nakatsuka, T.: Different ingestion patterns of <sup>13</sup>C-labeled bacteria and algae by deep-sea benthic foraminifera, *Mar. Ecol.-Prog. Ser.*, 310, 95–108, 2006.

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

Peters, K. E.: Guidelines for evaluating petroleum source rock using programmed pyrolysis, *Am. Assoc. Petr. Geol. B*, 70, 318–329, 1986.

Pina-Ochoa, E., Hogslund, 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, 2010.

Post, D.: Using stable isotopes to estimate trophic position: models, methods, and assumptions, *Ecology*, 83, 703–718, 2002.

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.

Prokopenko, M. G., Hirst, M. B., De Brabandere, L., Lawrence, D. J. P., Berelson, W. M., Granger, J., Chang, B. X., Dawson, S., Crane, E. J., III, Chong, L., Thamdrup, B., Townsend-Small, A., and Sigman, D. M.: Nitrogen losses in anoxic marine sediments driven by *Thioploca*-anammox bacterial consortia, *Nature*, 500, 194–198, 2013.

Reynolds, S. E., Mather, R. L., Wolff, G. A., Williams, R. G., Landolfi, A., Sanders, R., and Woodward, E. M. S.: How widespread and important is N<sub>2</sub> fixation in the North Atlantic Ocean?, *Global Biogeochem. Cy.*, 21, GB4015, doi:10.1029/2006GB002886, 2007.

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

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



- Robinson, J. J. and Cavanaugh, C. M.: Expression of form I and form II Rubisco in chemoautotrophic symbioses: implications for the interpretation of stable carbon isotope values, *Limnol. Oceanogr.*, 40, 1496–1502, 1995.
- Ryther, J. H., Hall, J. R., Pease, A. K., Bakun, A., and Jones, M. M.: Primary organic production in relation to the chemistry and hydrography of the western Indian Ocean, *Limnol. Oceanogr.*, 11, 371–380, 1966.
- Sackett, W., Eckleman, W. R., Bender, M., and Be, A. H.: Temperature dependence of carbon isotope composition in marine plankton and sediments, *Science*, 148, 235–237, 1965.
- Schmaljohann, R., Drews, M., Walter, S., Linke, P., von Rad, U., and Imhoff, J.: Oxygen-minimum zone sediments in the northeastern Arabian Sea off Pakistan: a habitat for the bacterium *Thioploca*, *Mar. Ecol.-Prog. Ser.*, 211, 27–42, 2001.
- Schott, F. A. and McCreary Jr., J. P.: The monsoon circulation of the Indian Ocean, *Prog. Oceanogr.*, 51, 1–123, 2001.
- Smallwood, B. and Wolff, G.: Molecular characterisation of organic matter in sediments underlying the oxygen minimum zone at the Oman Margin, Arabian Sea, *Deep-Sea Res. Pt. II*, 47, 353–375, 2000.
- Smith, C., Hoover, D., Doan, S., Pope, R., DeMaster, D., Dobbs, F., and Altabet, M.: Phytodetritus at the abyssal seafloor across 10 degrees of latitude in the central equatorial Pacific, *Deep-Sea Res. Pt. II*, 43, 1309–1338, 1996.
- Smith, S. L. and Codispoti, L. A.: Southwest monsoon of 1979: Chemical and biological response of Somali coastal waters, *Science*, 209, 597–600, 1980.
- Suhr, S. B., Pond, D. W., Gooday, A. J., and Smith, C. R.: Selective feeding by benthic foraminifera on phytodetritus on the western Antarctic Peninsula shelf: evidence from fatty acid biomarker analysis, *Mar. Ecol.-Prog. Ser.*, 262, 153–162, 2003.
- Tendal, O. S.: Aspects of the biology of Komokiacea and Xenophyophoria, *Sarsia*, 64, 13–17, 1979.
- Tyler, P. A.: Seasonality in the deep sea, *Oceanogr. Mar. Biol.*, 26, 227–258, 1988.
- van der Weijden, C. H., Reichart, G. J., and Visser, H. J.: Enhanced preservation of organic matter in sediments deposited within the oxygen minimum zone in the northeastern Arabian Sea, *Deep-Sea Res. Pt. I*, 46, 807–830, 1999.
- Velinsky, D. J., Fogel, M. L., Todd, J. F., and Tebo, B. M.: Isotopic fractionation of dissolved ammonium at the oxygen-hydrogen sulfide interface in anoxic waters, *Geophys. Res. Lett.*, 18, 649–652, 1991.

Webb, K. L. and Johannes, R. E.: Studies of the release of dissolved free amino acids by marine zooplankton, *Limnol. Oceanogr.*, 12, 376–382, 1967.

West, E., Welsh, D., and Pitt, K.: Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics, *Hydrobiologia*, 616, 151–160, 2009.

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

10 Woulds, C., Schwartz, M. C., Brand, T., Cowie, G. L., Law, G., and Mowbray, S. R.: Porewater nutrient concentrations and benthic nutrient fluxes across the Pakistan margin OMZ, *Deep-Sea Res. Pt. II*, 56, 333–346, 2009.

**BGD**

11, 18145–18188, 2014

---

**The trophic and metabolic pathways of foraminifera in the Arabian Sea**

R. M. Jeffreys et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



**Table 1.** Bottom water oxygen concentrations in  $\mu\text{M}$  from the CTD SBE 43 sensor. In situ DO concentrations from the Pakistan margin during the post-monsoon are from a bottom lander fitted with Profilur microelectrodes; for details see Breuer et al. (2009).

Margin	Depth (m)	Temperature ( $^{\circ}\text{C}$ )	CTD Oxygen	In situ Oxygen
Oman	365	15.3	6.5	No data
Oman	504	12.9	5.1	
Oman	790	10.4	5.8	No data
Oman	1105	8.1	9.2	No data
Oman	1390	6.1	27.2	
Oman	1414	5.9	29.9	
Oman	2030	3.1	83.1	No data
Oman	3165	1.8	105.6	No data
Pakistan	140	18.2	4.9	$1.0 \pm 0.4$
Pakistan	300	14.8	4.9	$\sim 0.0$
Pakistan	940	9.3	7.6	$2.8 \pm 0.7$
Pakistan	1200	7.5	15.6	$12.6 \pm 0.3$
Pakistan	1850	3.7	73.6	$80.3 \pm 4.5$

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

**Table 2.** Stable isotope values of potential food sources in ‰. SOM = sediment organic matter (surface layer 0–1 cm); POM = particulate organic material from bottom water filters. Numbers in parentheses indicate  $\pm 1$  SD. For SOM and POM from the Pakistan margin  $n = 3$ , for SOM from the Oman margin  $n = 1$ .

Margin	Depth (m)	$\delta^{13}\text{C}$ SOM	$\delta^{15}\text{N}$ SOM	$\delta^{13}\text{C}$ POM	$\delta^{15}\text{N}$ POM
Oman	334	−21.3	8.0	No data	No data
Oman	504	−17.2	9.4	No data	No data
Oman	800	−21.3	8.5	No data	No data
Oman	1093	−16.7	8.3	No data	No data
Oman	2010	−20.3	9.0	No data	No data
Oman	2075	−20.3	8.7	No data	No data
Pakistan	140	−20.3 (0.1)	7.7 (1.2)	−23.4 (1.3)	8.5 (0.7)
Pakistan	300	−20.6 (0.3)	8.6 (0.9)	−24.0 (1.6)	8.4 (1.0)
Pakistan	940	−20.7 (0.3)	7.9 (0.3)	−23.4 (0.9)	8.3 (1.0)
Pakistan	1200	−20.1 (0.3)	7.9 (0.3)	−24.0 (0.4)	8.2 (0.7)
Pakistan	1850	−19.9 (0.3)	7.9 (0.3)	−22.9 (1.1)	8.1 (1.3)

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

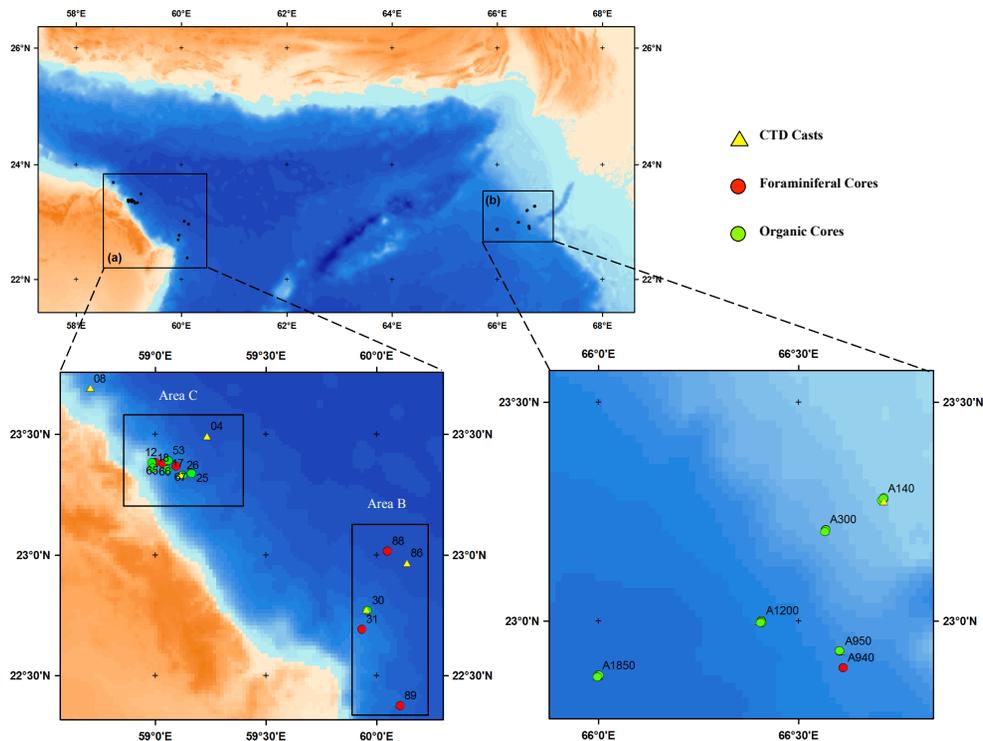
Interactive Discussion





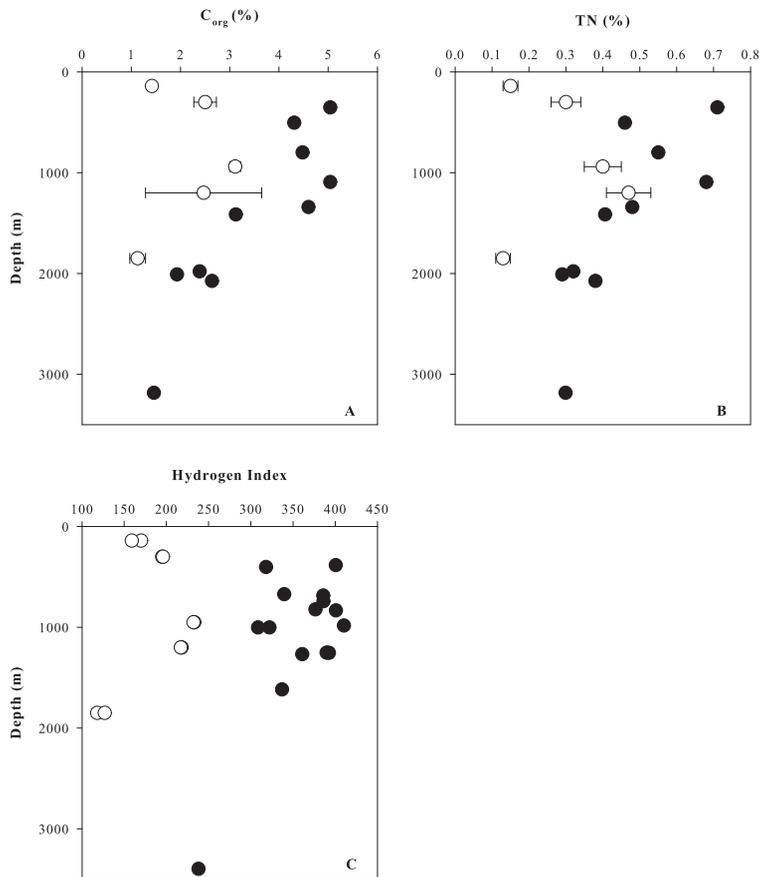
## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.

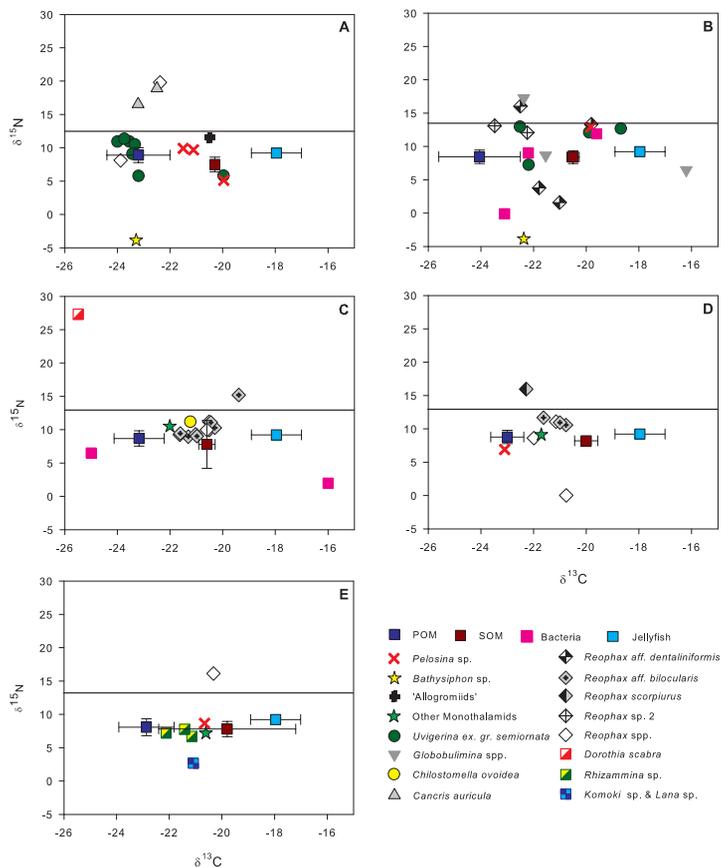


**Figure 1.** Location of sampling sites in the Arabian Sea. Inset shows the location of the Oman margin (a) and Pakistan margin working areas (b) within the northern Arabian Sea. Map (a) of the Oman margin shows sampling area B and C on the continental rise as defined in Billet et al. (2006). Map (b) shows the Pakistan margin sampling sites. Exact locations of sampling sites are given in the Table S1.

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



**Figure 2.** (a) Total organic carbon concentrations, (b) total nitrogen concentrations, and (c) hydrogen index values of surface sediments (0–1 cm) across the Pakistan margin (unfilled circles) and Oman margin (filled circles). For the Pakistan margin each point represents a mean ( $n = 3$ )  $\pm$  1 SD. For the Oman margin  $n = 1$ .



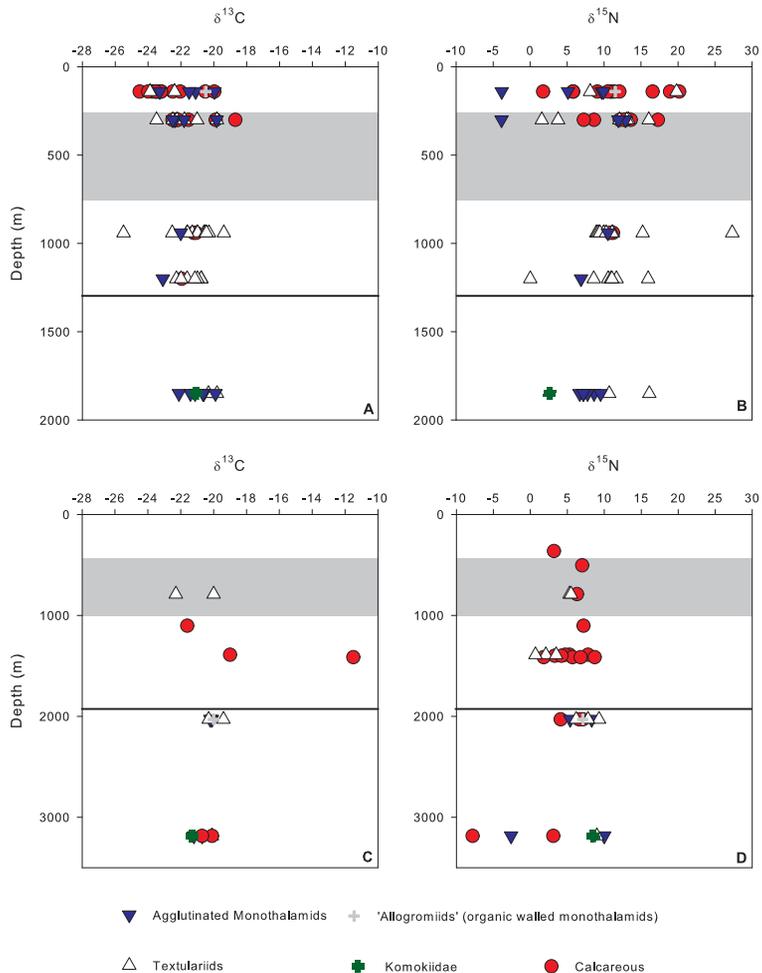
**Figure 3.** Species level, dual stable carbon nitrogen biplots of foraminifera (> 300 mm) from the Pakistan margin, (a) 140, (b) 300 (c) 940, (d) 1200, (e) 1850 m. Each point denotes a single measurement. The isotopic composition of POM, SOM and jellyfish are also indicated. The solid line represents 1 trophic level above the maximum SOM value for each depth, assuming a trophic enrichment factor of 3.4‰ (Post, 2002). Legends are below the plots.

# BGD

11, 18145–18188, 2014

## The trophic and metabolic pathways of foraminifera in the Arabian Sea

R. M. Jeffreys et al.



[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

⏪

⏩

◀

▶

[Back](#)

[Close](#)

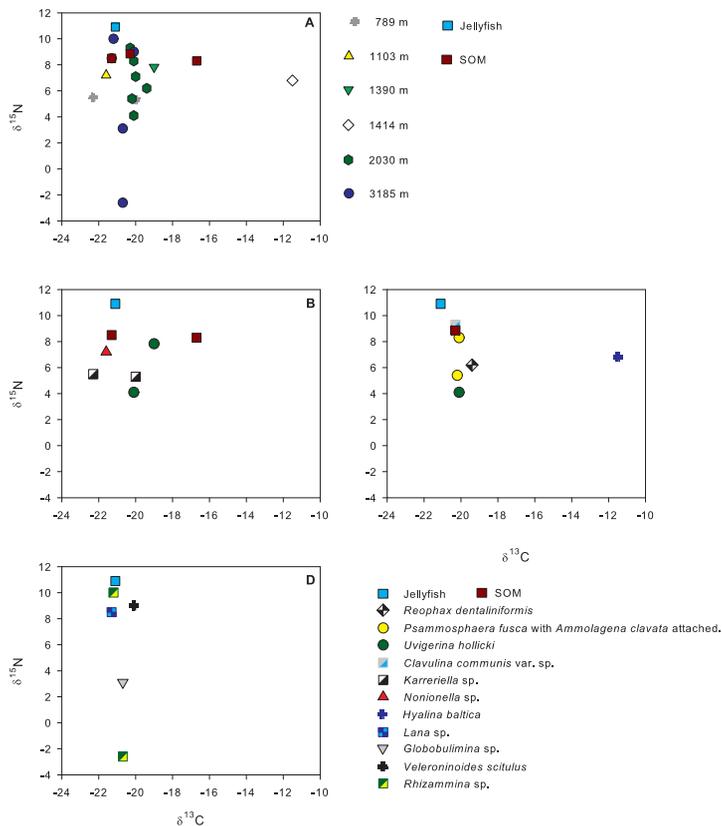
[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)







**Figure 5.** Dual stable carbon nitrogen biplots of foraminifera (> 300 mm) from the Oman margin, **(a)** Foraminifera plotted as a function of depth **(b–d)** Foraminifera plotted as a function of species **(b)** 789 to 1390 m, slope and canyon sites from Area C **(c)** 1414 m and 2030 m, area B **(d)** 3185 m, Area B. Each point denotes a single measurement. The isotopic composition of SOM and jellyfish are indicated. The legends for **(a)** is to the right of the plot and for **(b–d)** are to the right of **(d)**.