

Biogeosciences, 12, 1781–1797, 2015
www.biogeosciences.net/12/1781/2015/
doi:10.5194/bg-12-1781-2015

© Author(s) 2015. CC Attribution 3.0 License.



The trophic and metabolic pathways of foraminifera in the Arabian Sea: evidence from cellular stable isotopes

R. M. Jeffreys¹, E. H. Fisher¹, A. J. Gooday², K. E. Larkin³, D. S. M. Billett⁴, and G. A. Wolff¹

¹University of Liverpool, Department of Earth, Ocean and Ecological Sciences, School of Environmental Science, Liverpool, L69 3GP, UK

²National Oceanography Centre, University of Southampton Waterfront Campus, Southampton, SO14 3ZH, UK

³Marine Board, Wandelaarkaai 7, 8400 Oostende, Belgium

⁴Deep Seas Environmental Solutions Ltd. Meadowsweet, 132 Woodlands Road, Ashurst, Hampshire, SO40 7AP, UK

Correspondence to: R. M. Jeffreys (rachel.jeffreys@liv.ac.uk)

Received: 6 October 2014 – Published in Biogeosciences Discuss.: 20 December 2014

Revised: 27 February 2015 – Accepted: 28 February 2015 – Published: 18 March 2015

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 from 100 to 1000 m water depth. We compared the trophic ecology of foraminifera on the Oman and Pakistan margins of the Arabian Sea (140–3185 m water depth). These two margins are contrasting both in terms of the abundance of sedimentary organic matter and the intensity of the OMZ. 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 ($< 250 \text{ mg HC mg TOC}^{-1}$). The $\delta^{13}\text{C}$ 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, particularly at the Oman margin, may reflect feeding on chemosynthetic bacte-

ria. We suggest that differences in productivity regimes may be responsible for the differences observed in foraminiferal isotopic composition. In addition, at the time of sampling, whole jellyfish carcasses (*Crambionella orsini*) 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.

1 Introduction

The Arabian Sea's seasonally reversing monsoons drive one of the most energetic current systems on Earth (Goes et al., 2005; Schott and McCreary, 2001). The SW (summer) monsoon (June–September) is characterised 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 higher in the western compared to the eastern Arabian Sea (Cowie, 2005) and lead to the highest globally recorded fluxes of both particulate matter and partic-

ulate organic carbon (POC) to the deep ocean (~ 600 and $\sim 190 \text{ mg m}^{-2} \text{ d}^{-1}$ for the western and eastern Arabian Sea, respectively at depths of $\sim 3000 \text{ m}$; Haake et al., 1993; Honjo et al., 2008). The heterotrophic utilisation 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 $< 22 \mu\text{M}$ ($< 0.5 \text{ mL L}^{-1}$; 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 particulate organic matter (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 sulfur bacteria in the genera *Thioploca* and *Beggiatoa* (Jørgensen and Gallardo, 1999). In the Arabian Sea, chemosynthetically fixed carbon from such microorganisms may be an 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 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 analysis (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

($< 1 \text{ ‰}$; 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 sulfide 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 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 sub-surface 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 ~ 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 northwest 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 monsoon), a period of presumed low particulate flux for the western Arabian Sea ($\sim 100 \text{ mg m}^{-2} \text{ d}^{-1}$; Haake et al., 1993; Honjo et al., 1999). The majority of samples from the Pakistan margin were collected during two back-to-back cruises. Foraminifera, sediments and filters for POM were collected during CD150 and CD151 (September–October 2003; post-SW monsoon), a period of high partic-

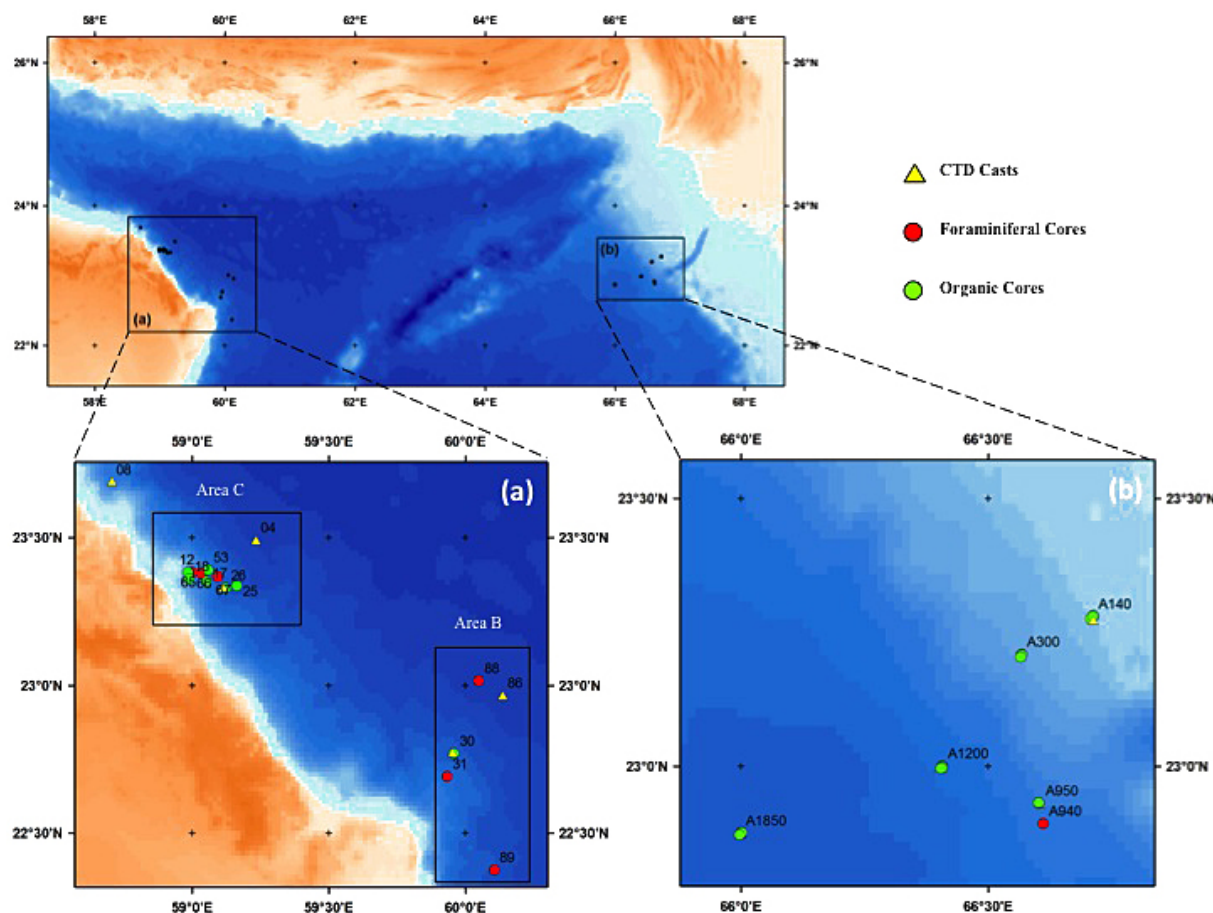


Figure 1. Location of sampling sites in the Arabian Sea. Insets show the location of the Oman margin (a) and Pakistan margin working areas (b) within the northern Arabian Sea. Map (a) of the Oman margin shows sampling area B and C on the continental rise as defined in Billet et al. (2006). Map (b) shows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

ulate flux for the eastern Arabian Sea ($\sim 125 \text{ mg m}^{-2} \text{ d}^{-1}$, Haake et al., 1993) immediately after the SW monsoon. In addition, during CD146 (March–April 2003; pre-SW monsoon), a period of presumed low particulate flux for the eastern Arabian Sea ($\sim 60 \text{ mg m}^{-2} \text{ d}^{-1}$; Haake et al., 1993), nine dead jellyfish were obtained using an Agassiz trawl from depths of $\sim 1850 \text{ m}$.

Bottom-water oxygen data were obtained from 4 and 22 CTD casts off Oman and Pakistan, respectively, between bottom-water depths of 140 and 2900 m. The CTD was deployed as close to the seafloor as possible ($\sim 5 \text{ m}$ above the bottom). The CTD was fitted with an SBE 43 dissolved oxygen polarographic probe (Brand and Griffiths, 2009) and was calibrated using micro-Winkler titration (Hansen, 1999). On the Pakistan margin, the micro-Winkler calibration of the CTD oxygen profile returned a correlation coefficient of 0.997 for 33 water samples measured during the pre-SW monsoon period on cruise CD145. This calibration was used on CD146 and CD151 because oxygen concentrations within the OMZ were very low during these cruises and produced

negative calculated concentrations from the micro-Winkler titration (Brand and Griffiths, 2009). At the Oman margin the micro-Winkler calibration of the CTD oxygen profile returned a correlation coefficient of 0.98 for 32 water samples. Oxygen data from all casts were amalgamated and averaged in 5 m depth intervals to produce summary profiles for each cruise. At the Pakistan margin in situ DO concentrations were determined using a microelectrode profiler as described in Breuer et al. (2009).

Sediments were collected using a hydraulically damped Bowers and Connelly megacorer equipped with eight core tubes (inner diameter of 9.6 cm). During each cruise, sediment cores were collected for geochemical analyses ($n = 1$ per water depth at the Oman margin and $n = 3$ per water depth for each cruise at the Pakistan margin). The surface layer (0–1 cm) was frozen, freeze-dried and analysed for the following parameters: organic carbon content (% C_{org}), total nitrogen (TN%) and stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) ratios, as described in Jeffreys et al. (2009a and b) and the Hydrogen Index (HI; Peters, 1986). The HI is cal-

culated using the following equation: $HI = (S2/TOC) \times 100$, where S2 is the amount of hydrocarbon generated through thermal cracking of nonvolatile organic matter at 550 °C in mg HC g⁻¹ and TOC is total organic carbon [g].

During the cruise CD151 at the Pakistan margin two cores per megacorer deployment at each depth were processed for foraminifera (> 300 µm). Each core was sectioned into horizontal layers at intervals of 0.5 to 2 cm. Sections were wet sieved on a 300 µm screen and “live” foraminifera (assumed to have been living when collected, based on the presence of cytoplasm within the test) and filamentous bacteria were picked from the sieve residues. The residues were kept chilled (< 5 °C) to prevent biochemical decomposition and the foraminifera were sorted as quickly as possible in a Petri dish on ice under a low-power binocular microscope. The organic stain Rose Bengal was not used to distinguish “live” foraminifera as this alters their biochemical composition. Instead, specimens were judged to be “live” (and therefore feeding) at the time of sampling based on the presence of obvious test contents in most or all constituent chambers. Foraminifera were sorted to species level and cleaned in filtered (2 µm screen) seawater to remove any attached organic particles. Approximately 30–100 individuals per species were placed into silver capsules and frozen at –20 °C. Foraminifera from the Oman margin were sorted from frozen cores following the cruise. Briefly, on board at each water depth, the top 2 cm from sediment cores was sectioned and frozen at –20 °C immediately. In the laboratory, samples were thawed and wet sieved and sorted as described above.

2.2 Stable isotope analysis

Vapour phase digestion was used to remove carbonate from sediment samples. Calcareous foraminifera were acidified with 10 % v/v HCl prior to analysis. Foraminifera from the Pakistan margin were analysed using a Europa Hydra 20/20 isotope ratio mass spectrometer (University of California Davis); $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of sediments and POM were analysed using VG Prism III isotope ratio mass spectrometer (University 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 $(\delta X)\text{‰} = [R_{\text{sample}} / R_{\text{standard}} - 1] \times 1000$, where X is either ^{13}C or ^{15}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 N₂, respectively. Analytical accuracy for Pakistan margin samples was determined using a sucrose standard for $\delta^{13}\text{C}$ and was $-23.84\text{‰} \pm 0.04\text{‰}$ and using an ammonium sulfate standard for $\delta^{15}\text{N}$ at $1.28\text{‰} \pm 0.19\text{‰}$. Analytical accuracy for Oman margin samples was determined using acetanilide for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Values were: $\delta^{13}\text{C} -29.50\text{‰} \pm 0.11\text{‰}$ and $\delta^{15}\text{N} -0.42\text{‰} \pm 0.45\text{‰}$ for

samples analysed in 2009 and $\delta^{13}\text{C} -29.27\text{‰} \pm 0.24\text{‰}$ and $\delta^{15}\text{N} -0.46\text{‰} \pm 0.28\text{‰}$ 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 standard deviations were $-15.01\text{‰} \pm 0.16\text{‰}$ for $\delta^{13}\text{C}$ and $12.10\text{‰} \pm 0.17\text{‰}$ $\delta^{15}\text{N}$ ($n = 10$) for Pakistan margin samples analysed in 2005. Mean values and standard deviations for Oman margin samples were -15.71‰ for $\delta^{13}\text{C}$ and 11.99‰ $\delta^{15}\text{N}$ ($n = 1$) for samples analysed in 2009 and $-15.45\text{‰} \pm 0.23\text{‰}$ for $\delta^{13}\text{C}$ and $12.08\text{‰} \pm 0.23\text{‰}$ 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 internal standard with N contents ranging from ~ 1 to 11 µg 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 internal standard 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 %C_{org}, %TN, HI, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between the Oman and Pakistan margins irrespective of depth, i.e. each depth represented one 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 test and Levene’s homogeneity of variance test. If data had a normal distribution and equal variance a one-way ($p < 0.05$) ANOVA was performed to ascertain statistical differences. The post hoc 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 (~ 1100 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 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 $\delta^{13}\text{C}$ composition of POM was significantly depleted relative to the sedimentary organic matter (SOM), whilst the $\delta^{15}\text{N}$ composition of POM and SOM were not significantly different (Jeffreys et al., 2009b). The $\delta^{15}\text{N}$ values of SOM did not exhibit any trends with depth on the Pakistan margin and were significantly lighter on the Pakistan margin compared to the Oman margin (Mann–Whitney U test: $p = 0.030$; Table 2). The $\delta^{13}\text{C}$ values of SOM on the Pakistan margin were significantly heavier at 1850 m compared to shallower depths ($F_{4,24} = 5.664$, $p = 0.002$; Table 2). There was no significant difference in sedimentary $\delta^{13}\text{C}$ values between the two margins (Table 2).

3.2 Isotopic composition of foraminifera at the Pakistan margin

On the Pakistan margin, $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ composition of foraminifera on the Pakistan margin was more variable, ranging from -3.9 to 27.3 ‰ (Fig. 3).

3.2.1 Depth trends in isotopic signature

The $\delta^{13}\text{C}$ composition of the calcareous species *Uvigerina* ex gr. *semiornata* was significantly depleted in ^{13}C at 140 m compared to 300 m (Fig. 3a and b, Mann–Whitney U test: $p = 0.024$), while there was no significant difference in its $\delta^{15}\text{N}$ composition between these sites (Fig. 3a and b). Three

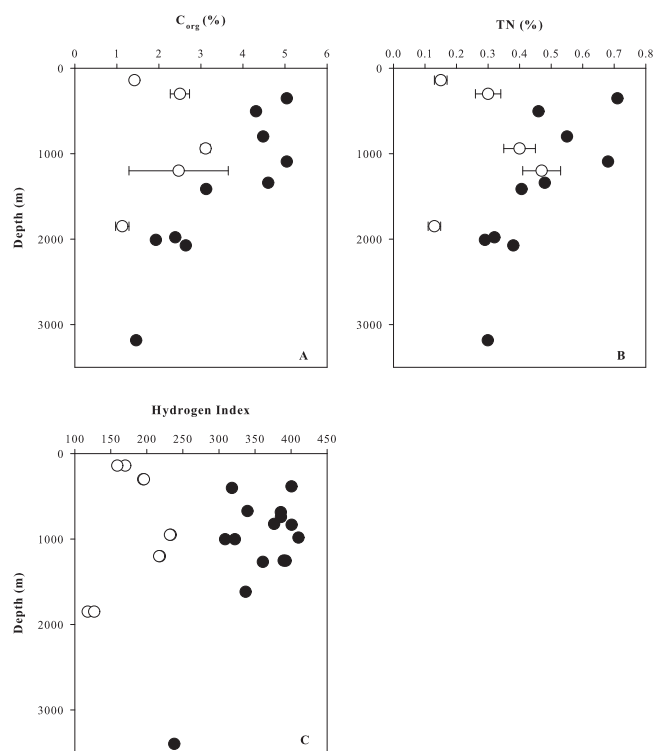


Figure 2. (a) Total organic carbon concentrations, (b) total nitrogen concentrations, and (c) Hydrogen Index values of surface sediments (0–1 cm) across the Pakistan margin (unfilled circles) and Oman margin (filled circles). For the Pakistan margin each point represents a mean ($n = 3$) ± 1 standard deviation. For the Oman margin $n = 1$.

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 m to 1200 m (Fig. 3b–d). 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).

3.2.2 Trends among main foraminiferal groups and species

At 140 m, *Uvigerina* ex gr. *semiornata* was marginally depleted in ^{13}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). 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).

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 ‰ and were broadly similar, with the majority falling

Table 1. Bottom-water oxygen concentrations in μM 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	No data
Oman	790	10.4	5.8	No data
Oman	1105	8.1	9.2	No data
Oman	1390	6.1	27.2	No data
Oman	1414	5.9	29.9	No data
Oman	2030	3.1	83.1	No data
Oman	3165	1.8	105.6	No data
Pakistan	140	18.2	4.9	1.0 ± 0.4
Pakistan	300	14.8	4.9	~ 0.0
Pakistan	940	9.3	7.6	2.8 ± 0.7
Pakistan	1200	7.5	15.6	12.6 ± 0.3
Pakistan	1850	3.7	73.6	80.3 ± 4.5

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 ± 1 standard deviation. 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)

within the range of potential food sources (Figs. 4 and 5). The $\delta^{15}\text{N}$ composition of foraminifera on the Oman margin was more variable, ranging from -7.8 to 10.8 ‰ (Figs. 4 and 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. 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). 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 we observed no significant difference in foraminiferal $\delta^{15}\text{N}$ composition between 1414, 2030 and 3185 m (Figs. 4b and 5a).

Using the oxygen concentrations from the CTD and the definitions of Gooday et al. (2009) as a guide, we categorised the stations into distinct regions of the OMZ. The OMZ core (504 to 789 m; DO = 5.1 to 6.3 μM); the lower boundary (LB: 1103 to 1414 m; DO = 16.5 to 29.9 μM) and below the OMZ (2030 to 3185 m; DO = 90.6 to 166 μM). 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). Foraminiferal $\delta^{15}\text{N}$ composition did not differ significantly with depth (Figs. 4d and 5a). Similarly, foraminiferal $\delta^{15}\text{N}$ composition did not differ significantly between the OMZ core, lower OMZ boundary or below the OMZ (Fig. 4d).

Calcareous foraminiferal $\delta^{15}\text{N}$ compositions did not differ significantly across the Oman margin (Fig. 4d). Textulariids were depleted in ^{15}N at the lower OMZ boundary (2.1 ‰ ± 1.4 ‰) compared to those found below the

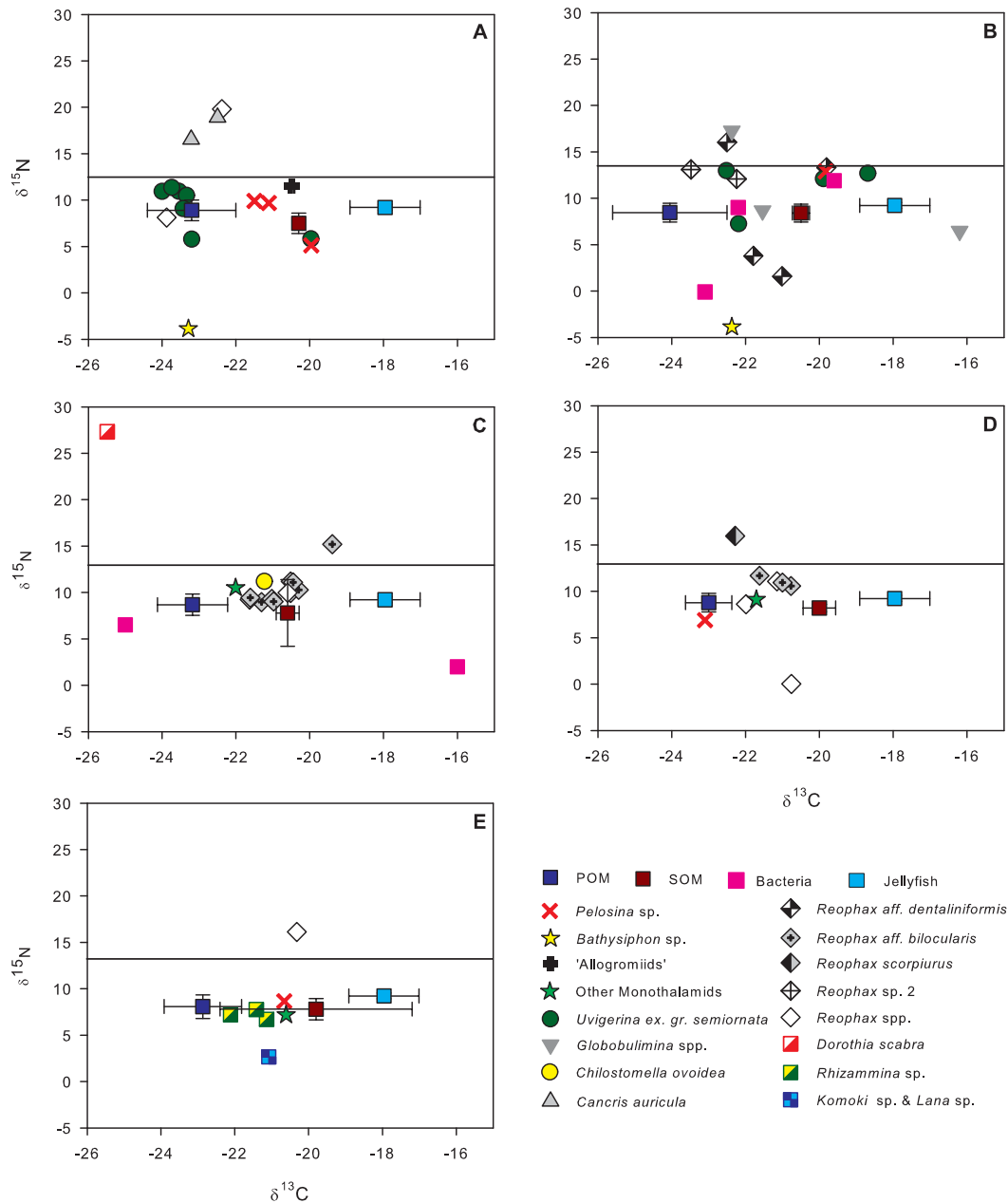


Figure 3. Species level, dual stable carbon nitrogen biplots of foraminifera (>300µm) from the Pakistan margin: (a) 140 m (b) 300 m (c) 940 m (d) 1200 m (e) 1850 m. Each point denotes a single measurement. The isotopic composition of POM, SOM and jellyfish are also indicated. The solid line represents one 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.

OMZ (water depths >2000 m; $8.1\text{‰} \pm 5.1\text{‰}$: 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). Similarly, the $\delta^{15}\text{N}$ composition was not significantly different between foraminiferal groups across the whole margin (Fig. 4d).

Calcareous foraminifera were significantly enriched in ^{15}N ($5.5\text{‰} \pm 2.2\text{‰}$) compared to textulariids at the lower OMZ boundary ($2.1\text{‰} \pm 1.4\text{‰}$: Fig. 4d, water depths 1103 to 1414 m; $F_{1.11} = 6.722$, $p = 0.025$). Below the OMZ (water depths 2030 to 3185 m) no significant differences were observed in $\delta^{15}\text{N}$ composition between agglutinated monothalamid, textulariid or calcareous species (Fig. 4d).

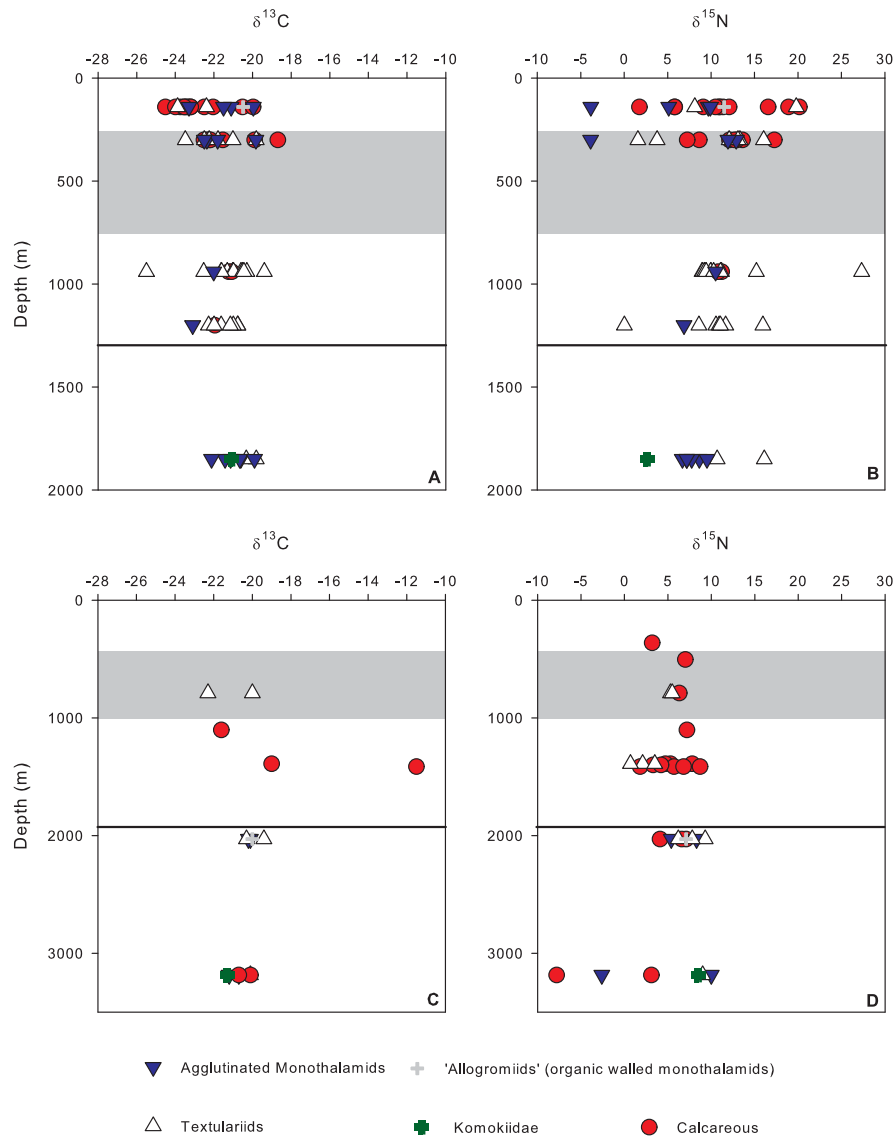


Figure 4. Stable carbon (a, c) and stable nitrogen (b, d) isotope composition of foraminifera plotted by foraminiferal grouping, from Pakistan margin (a, b) and Oman margin (c, d). Light grey shaded areas represent the OMZ core, the solid line separates the lower OMZ boundary from stations below the OMZ (below the line). Note that the 140 m site was hypoxic during the late monsoon. All data shown are from the late/post monsoon period. Legends are below the plots.

3.4 Inter-margin differences in the isotopic composition of foraminifera

There were significant differences in both foraminiferal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition between the two margins (Mann–Whitney U test: $p < 0.0001$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, not accounting for foraminiferal groupings, water depth or oxygen concentration). $\delta^{13}\text{C}$ values were enriched ($\delta^{13}\text{C} = -19.9\text{‰} \pm 2.4\text{‰}$; $-21.7\text{‰} \pm 1.4\text{‰}$), while $\delta^{15}\text{N}$ values were depleted ($\delta^{15}\text{N} = 5.4\text{‰} \pm 3.7\text{‰}$; $10.2\text{‰} \pm 5.1\text{‰}$) at the Oman margin compared to the Pakistan margin, respectively.

There were no significant differences in the $\delta^{15}\text{N}$ composition of foraminifera from the OMZ cores ($\text{O}_2 = 5.1\text{--}5.8\ \mu\text{M}$ at 504 to 789 m water depth on the Oman margin and $4.9\ \mu\text{M}$ at 300 m on the Pakistan margin; Fig. 4b and d), nor from below the OMZ on both margins ($\text{O}_2 = 83.1\ \mu\text{M}$ at 2030 m water depth on the Oman margin and $73.6\ \mu\text{M}$ at 1850 m on the Pakistan margin; Fig. 4b and d). However, foraminifera from below the OMZ on the Oman margin (2030 m) were significantly enriched in ^{13}C compared to those collected below the OMZ on the Pakistan margin at 1850 m (Fig. 4a and c, $F_{1,17_3} = 5.627$, $p = 0.034$).

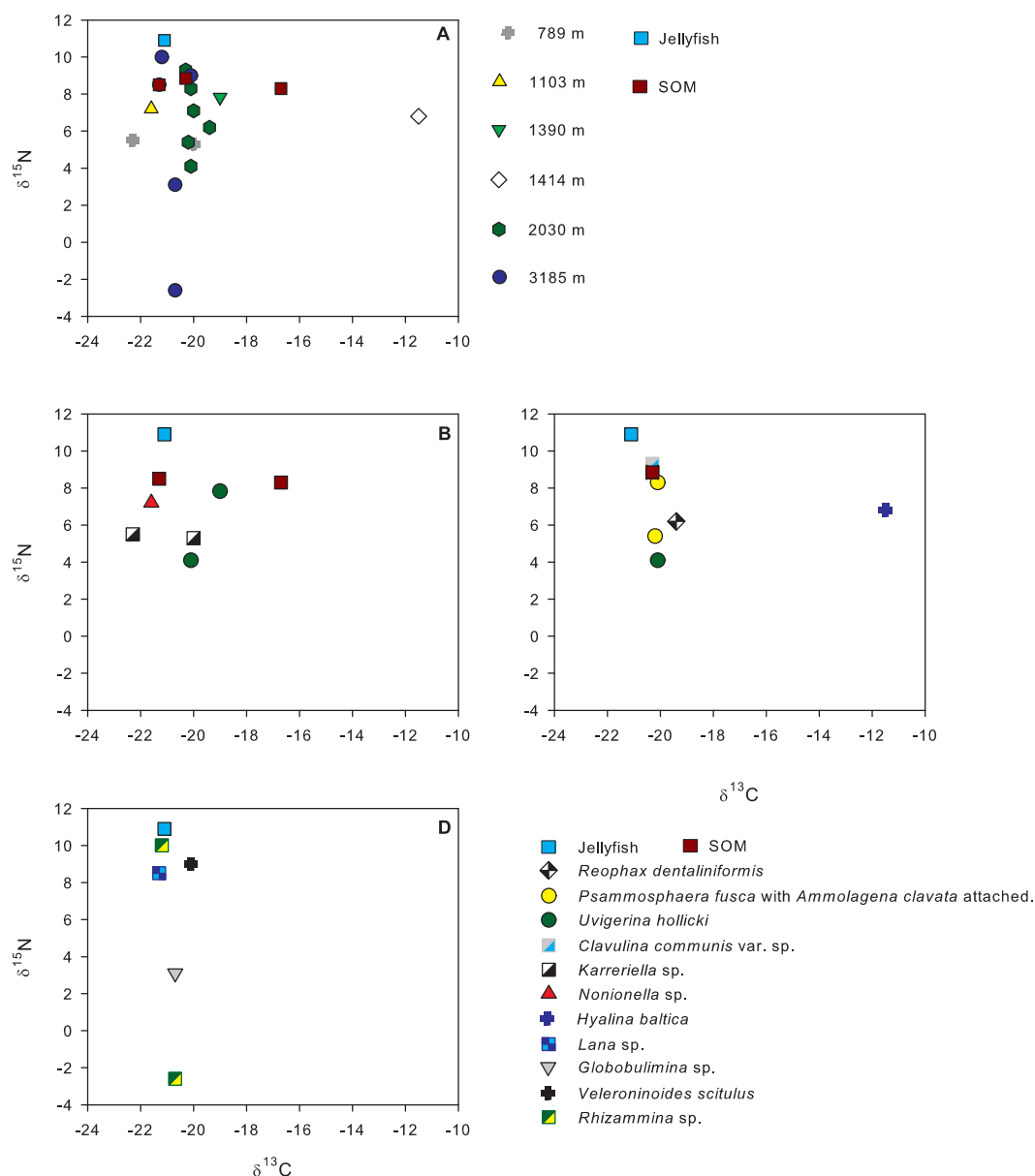


Figure 5. Dual stable carbon nitrogen biplots of foraminifera ($> 300 \mu\text{m}$) from the Oman margin. (a) Foraminifera plotted as a function of depth. (b–d) Foraminifera plotted as a function of species: (b) 789 to 1390 m, slope and canyon sites from area C; (c) 1414 & 2030 m, area B; (d) 3185 m,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

Agglutinated monothalamid foraminifera had similar isotopic compositions on both margins (Fig. 4), while textulariids had significantly depleted $\delta^{15}\text{N}$ values on the Oman margin ($5.5 \text{‰} \pm 3.0 \text{‰}$) compared to those on the Pakistan margin ($10.8 \text{‰} \pm 5.2 \text{‰}$, Fig. 4b, d; Mann–Whitney U test: $p < 0.0001$). The $\delta^{13}\text{C}$ composition of textulariids was similar on both margins (Fig. 4a, c). The isotopic compositions of calcareous foraminifera on the Oman margin were significantly enriched in ^{13}C and depleted in ^{15}N compared to those

on the Pakistan margin (Fig. 4; $\delta^{13}\text{C}$: Mann–Whitney U test: $p = 0.011$; $\delta^{15}\text{N}$: Mann–Whitney U test: $p < 0.0001$).

Differences in $\delta^{15}\text{N}$ composition at species level (not accounting for depth) were also evident. *Uvigerina hollicki* (Oman, $\delta^{15}\text{N} = 3.2 \text{‰} \pm 7.6 \text{‰}$) was depleted in ^{15}N compared to *U. ex. gr. semiornata* (Pakistan margin, $\delta^{15}\text{N} = 10.1 \text{‰} \pm 2.6 \text{‰}$; Supporting information Table S2, Mann–Whitney U test: $p < 0.030$). Similarly, *Globobulimina* spp. (a mixture of *G. turgida* and *G. affinis*) were depleted in ^{15}N off Oman ($\delta^{15}\text{N} = 4.9 \text{‰} \pm 2.0 \text{‰}$) compared

to *G. cf. G. pyrula* off Pakistan ($\delta^{15}\text{N} = 15.4\text{‰} \pm 5.0\text{‰}$; Table S2, $F_{1,5} = 11.024$, $p = 0.021$). The $\delta^{15}\text{N}$ composition of *Reophax dentaliniformis* was similar on both margins (Supporting information Table S2: Pakistan $\delta^{15}\text{N} = 8.7\text{‰} \pm 7.1\text{‰}$; Oman $\delta^{15}\text{N} = 4.9\text{‰} \pm 3.7\text{‰}$).

4 Discussion

4.1 Methodological issues

Different preservation methods were used for foraminifera collected 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‰ for Oman and -3.9 to 27.3‰ for Pakistan) suggests this is unlikely.

4.2 Oxygen dynamics and organic matter supply to the sediments

This study was part of 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 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 and Gooday (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 the Pakistan margin (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 vs. 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 determined by Gaye-Haake et al. (2005), having $\delta^{13}\text{C}$ values typical of mid-latitude algae (Sackett et al., 1965), and were similar on both margins. Nitrogen isotopes of food sources are enriched in ^{15}N , 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 the calcareous foraminifera *Uvigerina* ex. gr. *semiornata* reflected that of POM and SOM at the Pakistan margin. *Uvigerina* ex. gr. *semiornata* rapidly consumes fresh phytodetritus and has also been inferred to ingest sedimentary bacteria (Larkin et al., 2014; Woulds et al., 2007).

$\delta^{15}\text{N}$ 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

Table 3. C/N ratios, total concentration (mg g^{-1} of dry sediment) of HMW ($>C_{24}$) fatty acids and n-alcohols of sedimentary organic matter (0–0.5 cm) from the Pakistan and Oman margins. Pakistan margin data are from Jeffreys et al. (2009a) and Oman margin data are from Smallwood and Wolff (2000). Numbers in parentheses are ± 1 standard deviation, $n = 3$ for all samples.

Oman Margin Depth (m)	C/N	HMW Fatty acids	HMW n-alcohols	Pakistan Margin Depth (m)	C/N	HMW Fatty acids	HMW n-alcohols
409	8.0 (0.5)	8.0 (9.8)	3.6 (1.6)	140	9.1 (1.5)	4.3 (2.2)	4.8 (3.8)
827	8.9 (0.3)	5.1 (4.0)	1.8 (0.7)	300	9.7 (1.1)	13.3 (3.1)	7.3 (5.1)
981	9.5 (0.1)	1.8 (0.3)	0.5 (0.3)	940	8.7 (0.7)	5.5 (1.2)	10.4 (13.7)
1254	8.8 (1.5)	4.1 (2.9)	1.1 (0.9)	1200	8.8 (0.9)	14.5 (17.2)	2.2 (2.8)
				1850	9.6 (0.3)	155 (230)	131 (199)

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 sulfide oxidation, were observed on the continental rise at the time of sampling (Billett et al., 2006). A chemosynthetic bacterial input derived from the anaerobic decomposition of jelly detritus could therefore have led to the enriched $\delta^{13}\text{C}$ values observed at 500 m and 1100 m, as carbon fixation fuelled by energy derived from sulfide oxidation involving Rubisco II leads to enriched $\delta^{13}\text{C}$ values of -9 to -16‰ (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}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}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 at depths of 1850 m 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 at depths of 2030 m foraminifera closely reflected the SOM carbon isotopic signature and there was less variation in isotopic

composition suggesting reduced variation in possible food sources.

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 $\delta^{15}\text{N}_{\text{NO}_3}$ 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 may occur 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}N , several species of *Reophax*, including *R. aff. dentaliformis*, *R. aff. bilocularis*, *R. scorpiurus* and an unidentified species, had enriched $\delta^{15}\text{N}$ values across the margin from the hypoxic core to the more 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 ni-

trate 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 the foraminifera store nitrate and use either pathway (1) or (2), although we cannot discern the exact mechanism. Koho et al. (2010) have demonstrated that *Globobulimina* migrate through the sediment along a concentration gradient to access nitrate; the sediments of the Pakistan margin are a sink for nitrate (Woulds et al., 2009), so this is a plausible strategy.

In contrast, at the Oman margin, foraminifera were generally depleted in ^{15}N . Higher quality SOM at the Oman margin could lead to more efficient benthic remineralisation and higher rates of nutrient effluxes from sediment porewaters (Grandel et al., 2000) than at the Pakistan margin. Incomplete utilisation of N_{org} is known to result in isotopic fractionation producing isotopically depleted NH_4^+ and enriched SOM (Reynolds et al., 2007; Velinsky et al., 1991). Uptake of depleted inorganic nitrogen by foraminifera could lead to their relatively low $\delta^{15}\text{N}$ values at the Oman margin.

At the time of sampling, large numbers of dead jellyfish (*Crambionella orsini*) were observed at the seafloor (Billett et al., 2006); this led to an increase in the standing stock of organic carbon, which was estimated at between 1.5 and 78 g C m^{-2} (Billett et al., 2006). Such a large deposition of organic matter could lead to large increases in rates of remineralisation. In mesocosm experiments, West et al. (2009), observed the rapid breakdown of dead jellyfish leading to a >450 % increase in the NH_4^+ flux from the sediments, which they attributed to bacterial decomposition. Live jellyfish are known to excrete large amounts of dissolved free amino acids ($15 \text{ mg N g dw}^{-1} \text{ d}^{-1}$), alanine and glycine being the most abundant (Webb and Johannes, 1967). Furthermore, Macko and Estep (1984) demonstrated that bacterial cultures utilising alanine as a substrate become depleted in ^{15}N by up to 12.9 % relative to the substrate during deamination and produce a pool of NH_4^+ depleted in ^{15}N . The jellyfish obtained from the Oman margin in this study had a $\delta^{15}\text{N}$ value of 10.9 %, and foraminifera had $\delta^{15}\text{N}$ values ranging from -7.0 to 10.8 %. We suggest that the observed isotopically light nitrogen signatures may result from feeding on bacteria associated with the jelly detritus. On the continental rise (areas B and C), a thin layer of jelly slime on the sediment underlain by a thin layer of black sediment suggested the presence of reduced sulfur species, which could be utilised by sulfur-oxidising bacteria. Oxygen minimum zones often support mats of large sulfur-oxidising bacteria, including *Thioploca*, *Beggiatoa*, *Thiomargarita* (Levin, 2003), and bacterial mats have been observed previously at the Oman margin (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, colonising both single jellyfish and jelly detritus (Billett et al., 2006). Sulfur-oxidising bacteria at cold seeps are characterised 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), (E) monothalamous species that may be bacterivores, and (F) 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 μm 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 six 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, (2) consumers of more degraded organic matter, unselective deposit feeders and (3) bacterivores.

4.4.1 Opportunistic deposit feeders

The carbon isotopic compositions of the majority of foraminifera mirrored POM and SOM, suggesting both selective ingestion of phytodetritus during periods and at sites where it is available and ingestion of SOM at other times. Natural observations and pulse-chase experiments in conjunction with fatty acid analyses have shown that foraminifera are important consumers of phytodetritus (Gooday, 1988; Moodley et al., 2002; Nomaki et al., 2005; Suhr et al., 2003) and, at least at the Pakistan margin, are as important as bacteria in the processing of organic matter (Woulds et al., 2007). The stable carbon and nitrogen isotope values of *Uvigerina* ex. gr. *semiornata* at 140 m on the Pakistan margin reflect those of POM and are consistent with selective deposit feeding on phytodetritus. Stable carbon isotope values of *U.*

ex. gr. *semiornata* and *Globobulimina* cf. *G. pyrula* at 300 m on the Pakistan margin were more enriched than those of *U. ex. gr. semiornata* at 140 m, which suggests a lower supply of phytodetritus at 300 m. Sedimentary fatty acid distributions support this, with relative concentrations of fatty acids indicative of phytodetritus inputs being higher at 140 m compared to 300 m, albeit with seasonal variations (Jeffreys et al., 2009a). Both *U. ex. gr. semiornata* and *G. cf. G. pyrula* can be classed as omnivores taking advantage of phytodetritus when available and feeding on SOM when phytodetritus is absent (Nomaki et al., 2005). At the Oman margin, *Uvigerina hollicki* and *Globobulimina* sp. both appear to feed on fresh phytodetrital material, having $\delta^{13}\text{C}$ compositions nearer to the pelagic jellyfish than to SOM. The carbon isotope values of *Uvigerina* and *Globobulimina* on both margins were consistent with values observed for these genera at Sagami Bay (Nomaki et al., 2008). Similarly, the calcareous foraminifera *Cancris auriculus* (Pakistan) and *Nonionella* sp. (Oman) also had $\delta^{13}\text{C}$ compositions consistent with feeding on phytodetritus.

The agglutinated monothalamid *Bathysiphon* sp. nov., present at 140 m and 300 m on the Pakistan margin, appears to derive its carbon requirements from fresh 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., *Hyperammmina* 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.

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 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 one 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. was 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 centimetre 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, 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 *Psammospaera 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 Bacteriovores

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}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.

Sulfur 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, oxygen concentrations and nitrogen dynamics at the two margins. Using stable isotopes we have demonstrated a tight coupling be-

tween 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 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/bg-12-1781-2015-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. We are grateful to two anonymous reviewers for their helpful comments on the paper. This work was supported by the Natural Environment Research Council, UK (NER/A/S/2000/01381 and NE/F011024/1).

Edited by: H. Kitazato

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.
- 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.
- 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.
- 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.
- 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., John D Lambshhead, P., 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.
- Cowie, G.: The biogeochemistry of Arabian Sea surficial sediments: A review of recent studies, *Prog. Oceanogr.*, 65, 260–289, 2005.
- Cowie, G., Calvert, S., Pedersen, T., Schulz, H., and Rad, von, U.: Organic content and preservational controls in surficial shelf and slope sediments from the Arabian Sea (Pakistan margin), *Mar. Geol.*, 161, 23–38, 1999.
- 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.
- 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.
- Dannheim, J., Struck, U. and Brey, T.: Does sample bulk freezing affect stable isotope ratios of infaunal macrozoobenthos?, *J. Exp. Mar. Bio. Ecol.*, 351, 37–41, 2007.
- 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, *Mar. Ecol.*, 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. 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.
- Feuchtmayr, H. and Grey, J.: Effect of preparation and preservation procedures on carbon and nitrogen stable isotope determinations from zooplankton, *Rapid Commun Mass Spectrom.*, 17, 2605–2610, 2003.
- 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, *Biogeochemistry*, 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.
- 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., Jeffreys, R., Lamont, P. A., Larkin, K. E., Murty, S. J., Schumacher, S., Whitcraft, C., and Woulds, C.: Faunal responses to oxygen gradients on the Pakistan margin A comparison of foraminiferans, macrofauna and megafauna, *Deep-Sea Res. Pt. II*, 56, 488–502, 2009.
- Graf, G.: Benthic Pelagic Coupling in a Deep-Sea 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.
- 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.
- 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.
- Jørgensen, B. B. and Gallardo, V. A.: *Thioploca* spp.: filamentous sulfur bacteria with nitrate vacuoles, *FEMS Microbiol. Ecol.*, 28, 301–313, 1999.
- 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.
- 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.
- 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.
- 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.
- Larkin, K. E., Gooday, A. J., Woulds, C., Jeffreys, R. M., Schwartz, M., Cowie, G., Whitcraft, C., Levin, L., Dick, J. R., and Pond, D. W.: Uptake of algal carbon and the likely synthesis of an “essential” fatty acid by *Uvigerina* ex. gr. *semiornata* (Foraminifera) within the Pakistan margin oxygen minimum zone: evidence from fatty acid biomarker and ^{13}C tracer experiments, *Biogeosciences*, 11, 3729–3738, doi:10.5194/bg-11-3729-2014, 2014.
- Levin, L. and Michener, R.: Isotopic evidence for chemosynthesis-based nutrition of macrobenthos: The lightness of being at Pacific methane seeps, *Limnol. Oceanogr.*, 1336–1345, 2002.
- Levin, L., Gage, J., Lamont, P., Cammidge, L., Martin, C., Patience, A. and Crooks, J.: Infaunal community structure in a low-oxygen, organic-rich habitat on the Oman continental slope, NW Arabian Sea, in: *The responses of marine organisms to their environments: Proceedings of the 30th European Marine Biology Symposium*, University of Southampton, Southampton, UK, 223–230, 1997.
- Levin, L. A.: Oxygen minimum zone benthos: adaptation and community response to hypoxia, *Oceanogr. Mar. Biol.*, 41, 1–45, 2003.
- Lipps, J. H. and Valentine, J. W.: The role of foraminifera in the trophic structure of marine communities, *Lethaia*, 3, 279–286, 1970.
- Macko, S. A. and Estep, M. L.: Microbial alteration of stable nitrogen and carbon isotopic compositions of organic matter, *Org. Geochem.*, 6, 787–790, 1984.
- Macko, S. A., Fogel, M. L., Hare, P. E., and Hoering, T. C.: Isotopic fractionation of nitrogen and carbon in the synthesis of amino acids by microorganisms, *Chem. Geol.*, 65, 79–92, 1987.
- McCutchan, J., Lewis, W., Kendall, C., and McGrath, C.: Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur, *Oikos*, 102, 378–390, 2003.
- McGoldrick, D. J., Barton, D. R., Power, M., Scott, R. W., and Butler, B. J.: Dynamics of bacteria–substrate stable isotope separation: dependence on substrate availability and implications for aquatic food web studies, *Can. J. Fish. Aquat. Sci.*, 65, 1983–1990, 2008.
- Minagawa, M. and Wada, E.: Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age, *Geochim. Cosmochim. Ac.*, 48, 1135–1140, 1984.
- Mojtahid, M., Zubkov, M. V., Hartmann, M., and Gooday, A. J.: Grazing of intertidal benthic foraminifera on bacteria: Assessment using pulse-chase radiotracing, *J. Exp. Mar. Biol. Ecol.*, 399, 25–34, 2011.
- Moodley, L., Middelburg, J. J., and Boschker, H.: Bacteria and Foraminifera: key players in a short-term deep-sea benthic response to phytodetritus, *Mar. Ecol.-Prog. Ser.*, 236, 23–29, 2002.
- Murray, J. W.: *Ecology and Applications of Benthic Foraminifera*, Cambridge Univ Press, Cambridge, UK, 440 pp., 2006.
- Nair, R., Ittekkot, V., Manganini, S., Ramaswamy, V., Haake, B., Degens, E., Desai, B., and Honjo, S.: Increased particle flux to the deep ocean related to monsoons, *Nature*, 338, 749–751, 1989.
- 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. Foram. Res.*, 35, 103–113, 2005.
- Nomaki, H., Heinz, P., and Nakatsuka, T.: Different ingestion patterns of ^{13}C -labeled bacteria and algae by deep-sea benthic foraminifera, *Mar. Ecol.-Prog. Ser.*, 310, 95–108, 2006.
- Nomaki, H., Ogawa, N., 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_2 fixation in the North Atlantic Ocean?, *Global Biogeochem. Cy.*, 21, GB4015, doi:10.1029/2006GB002886, 2007.
- Risgaard-Petersen, N., Langezaal, A. M., Ingvarsdén, 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., and van der Zwaan, J.: Evidence for complete denitrification in a benthic foraminifera, *Nature*, 443, 93–96, 2006.
- 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.*, 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., Rad, von, U., and Imhoff, J.: Oxygen-minimum zone sediments in the north-eastern Arabian Sea off Pakistan: a habitat for the bacterium *Thioploca*, *Mar. Ecol.-Prog. Ser.*, 211, 27–42, 2001.
- Schott, F. A. and McCreary, J. P., Jr: 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. Ann. Rev.*, 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.*, 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.
- 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.
- 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.