

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.

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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 $\sim 190 \text{ mg m}^{-2} \text{ d}^{-1}$ for the western and eastern Arabian Sea, respectively at depths of $\sim 3000 \text{ m}$; Haake et al., 1993; Honjo et al., 2008). The 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 $< 22 \mu\text{M}$ ($< 0.5 \text{ mL L}^{-1}$; 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 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

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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

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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, b) and the Hydrogen Index (HI; Peters, 1986).

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 could not be used to distinguish “live” foraminifera as this could alter 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

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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).

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3.2.1 Depth trends in isotopic signature

Calcareous foraminifera were significantly depleted in ^{13}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}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}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,

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$F_{2,10} = 0.534$, $p = 0.602$, $\delta^{15}\text{N}$: 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}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‰ 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‰ (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

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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 μM); the lower boundary (1103–1414 m; DO = 16.5 to 29.9 μM) and below the OMZ (2030–3185 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, 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}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}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, $F_{1,11} = 1.345$, $p = 0.304$).

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Whitney U test: $p < 0.030$). Similarly, *Globobulimia* spp. (a mixture of *G. turgida* and *G. affinis*) were depleted in ^{15}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‰ 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 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

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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

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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‰ (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 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 $\delta^{15}\text{N}_{\text{NO}_3}$

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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}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,

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(2) consumers of more degraded organic matter, unselective deposit feeders and (3) bacteriovores.

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 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 *Cancriis 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 and 300 m on the Pakistan margin, appears to derive its carbon requirements from fresh

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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}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

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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.

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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	
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 ± 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

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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 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)

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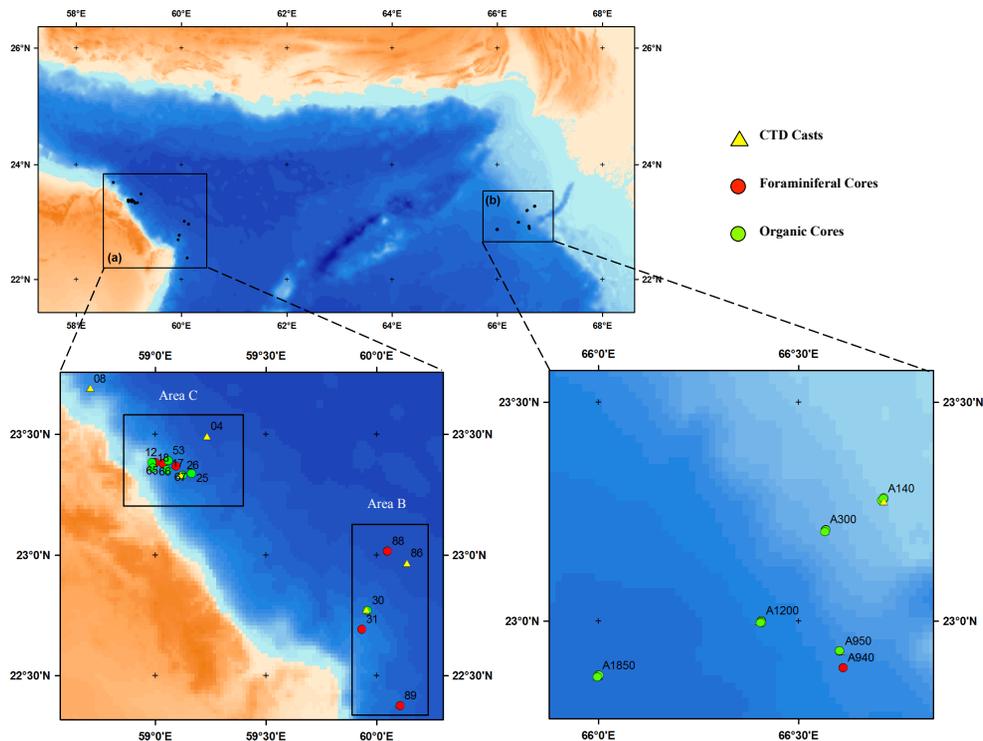


Figure 1. Location of sampling sites in the Arabian Sea. Inset shows the location of the Oman margin (a) and Pakistan margin working areas (b) within the northern Arabian Sea. Map (a) of the Oman margin shows sampling area B and C on the continental rise as defined in Billet et al. (2006). Map (b) shows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

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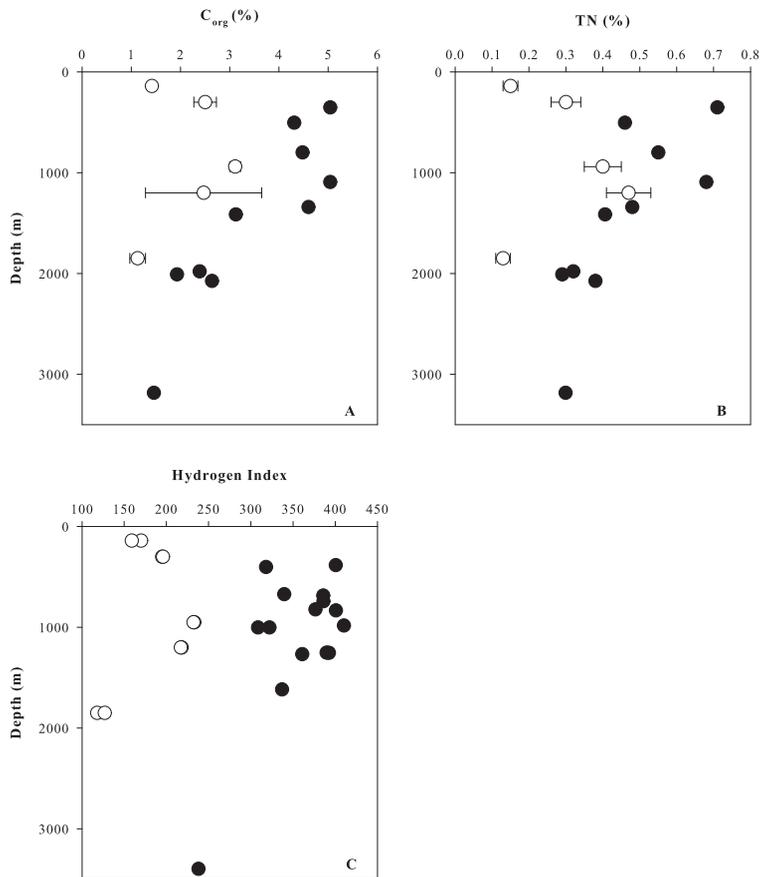


Figure 2. (a) Total organic carbon concentrations, (b) total nitrogen concentrations, and (c) hydrogen index values of surface sediments (0–1 cm) across the Pakistan margin (unfilled circles) and Oman margin (filled circles). For the Pakistan margin each point represents a mean ($n = 3$) \pm 1 SD. For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

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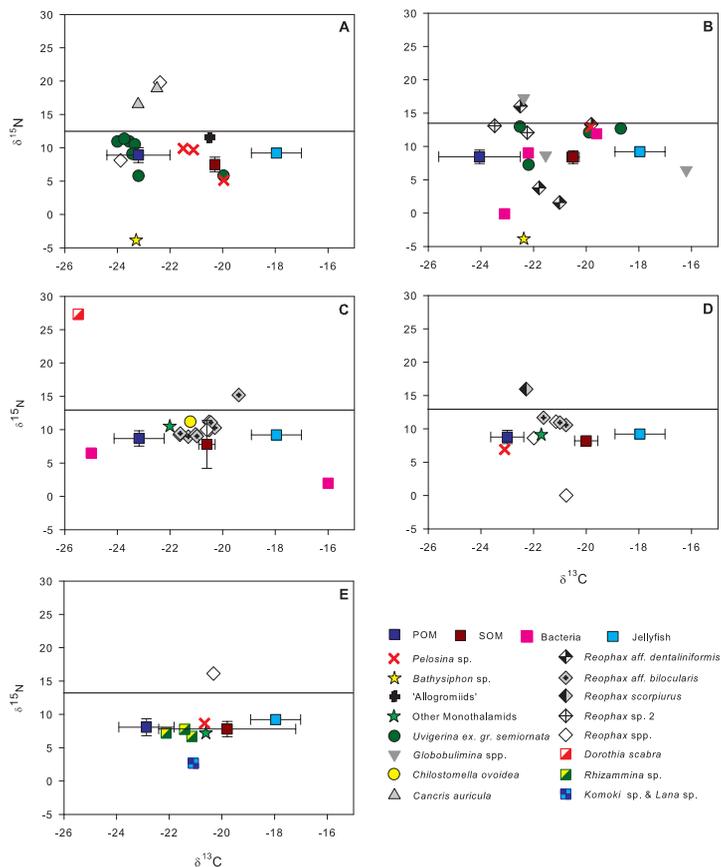


Figure 3. Species level, dual stable carbon nitrogen biplots of foraminifera (> 300 mm) from the Pakistan margin, (a) 140, (b) 300 (c) 940, (d) 1200, (e) 1850 m. Each point denotes a single measurement. The isotopic composition of POM, SOM and jellyfish are also indicated. The solid line represents 1 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.

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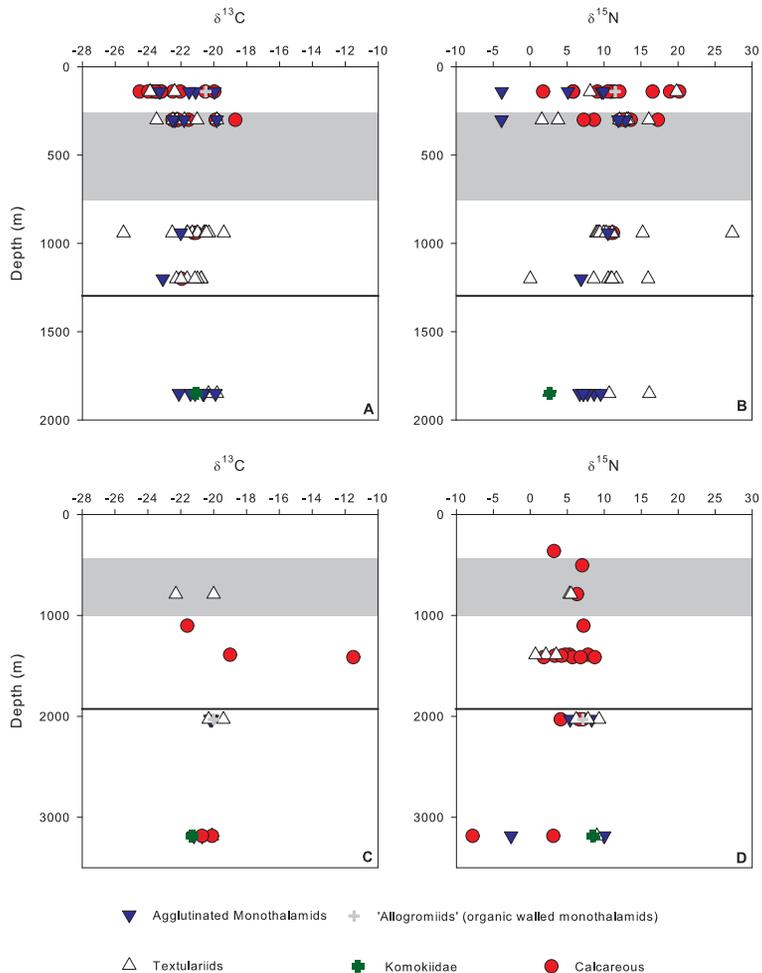


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Figure 4. Stable carbon (**a** and **c**) and stable nitrogen (**b** and **d**) isotope composition of foraminifera plotted by foraminiferal grouping, from Pakistan margin (**a** and **b**) and Oman margin (**c** and **d**). Light grey shaded areas 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.

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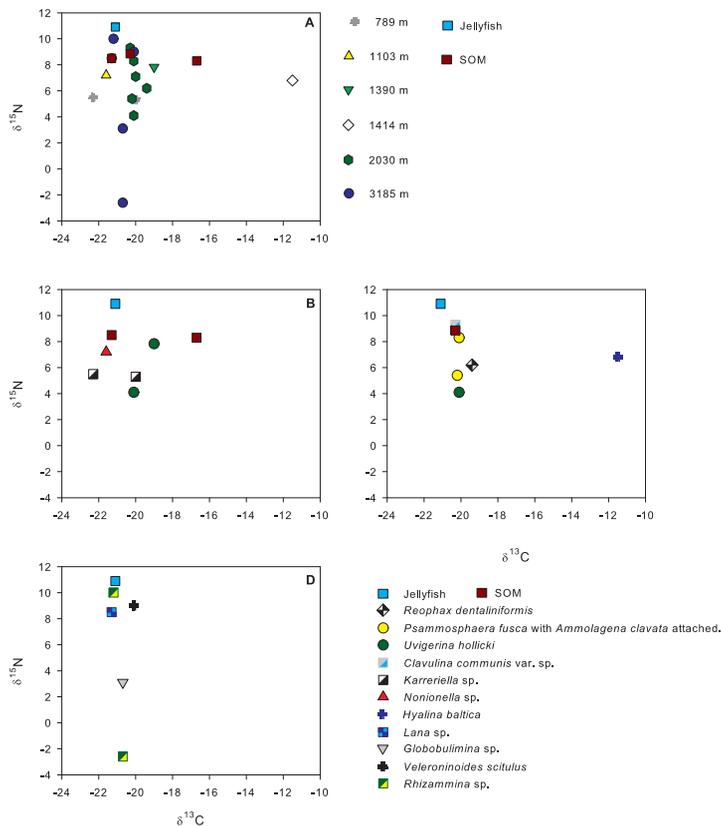


Figure 5. Dual stable carbon nitrogen biplots of foraminifera (> 300 mm) from the Oman margin, **(a)** Foraminifera plotted as a function of depth **(b–d)** Foraminifera plotted as a function of species **(b)** 789 to 1390 m, slope and canyon sites from Area C **(c)** 1414 m and 2030 m, area B **(d)** 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)**.