

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

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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 ± 1.4 %) compared to the Pakistan margin (2.45 ± 1.1 %) and sedimentary organic matter (SOM) quality estimated from the Hydrogen Index was also higher on the Oman margin (300 – 400 mg HC/mg TOC) compared to the Pakistan margin (< 250 mg HC/mg TOC). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of sediments were similar on both margins (-20 ‰ and 8

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33 ‰, respectively). Stable isotope analysis (SIA) showed that foraminiferal cells had a wide
 34 range of $\delta^{13}\text{C}$ values (-25.5 ‰ to -11.5 ‰), implying that they utilise multiple food sources;
 35 indeed $\delta^{13}\text{C}$ values varied between depths, foraminiferal types and between the two margins.
 36 Foraminifera had broad ranges in $\delta^{15}\text{N}$ values (-7.8 ‰ to 27.3 ‰). The enriched values
 37 suggest that some species may store nitrate to utilise in respiration; this was most notable on
 38 the Pakistan margin. Depleted foraminiferal $\delta^{15}\text{N}$ values, particularly at the Oman margin,
 39 may reflect feeding on chemosynthetic bacteria. We suggest that differences in productivity
 40 regimes may be responsible for the differences observed in foraminiferal isotopic
 41 composition. In addition, at the time of sampling, whole jellyfish carcasses (*Crambionella*
 42 *orsini*) and a carpet of jelly detritus were observed across the Oman margin transect.
 43 Associated chemosynthetic bacteria may have provided an organic-rich food source for
 44 foraminifera at these sites. Our data suggest that foraminifera in OMZ settings can utilise a
 45 variety of food sources and metabolic pathways to meet their energetic demands.

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47 1 Introduction

48 The Arabian Sea's seasonally reversing monsoons drive one of the most energetic current
 49 systems on Earth (Goes et al., 2005; Schott and McCreary, 2001). The SW (summer)
 50 monsoon (June-September) is characterized by southwesterly winds and the Findlater Jet
 51 (Findlater, 1969), inducing NE flowing surface currents. These drive strong coastal upwelling
 52 of nutrient rich water near Oman resulting in some of the highest recorded values for oceanic
 53 primary productivity (Ryther et al., 1966). In contrast, the NE (winter) monsoon (November-
 54 February) is characterised by a reversal in the direction of the winds and much less intense
 55 primary production (Smith and Codispoti, 1980). Levels of primary production are higher in
 56 the western compared to the eastern Arabian Sea (Cowie, 2005) and lead to the highest
 57 globally recorded fluxes of both particulate matter and particulate organic carbon (POC) to
 58 the deep ocean ($\sim 600 \text{ mg m}^{-2} \text{ d}^{-1}$ and $\sim 190 \text{ mg m}^{-2} \text{ d}^{-1}$ for the western and eastern Arabian
 59 Sea, respectively at depths of $\sim 3000 \text{ m}$; Haake et al., 1993; Honjo et al., 2008). The
 60 heterotrophic utilization of the phytoplankton blooms, coupled with local hydrography, are
 61 responsible for the formation of an oxygen minimum zone (OMZ), defined as a region where
 62 oxygen concentrations are $< 22 \mu\text{M}$ ($< 0.5 \text{ ml L}^{-1}$; Levin, 2003). In the northern Arabian Sea,
 63 the OMZ extends from ~ 100 to 1000 m water depth (Gupta and Naqvi, 1984). The coupling
 64 of these characteristics results in the enrichment of organic carbon at the seafloor (Cowie et

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71 al., 1999; Hedges and Keil, 1995; van der Weijden et al., 1999), creating an abundant food
72 source for benthic organisms.

73 The majority of deep-sea benthic communities obtain their energy in the form of POM
74 originating from the surface waters (Graf, 1989; Tyler, 1988). This food source often takes
75 the form of highly seasonal pulses of phytodetritus (Billett et al., 1983; Smith et al., 1996;
76 Gooday, 2002). OMZs are known to support large filamentous sulphur bacteria in the genera
77 *Thioploca* and *Beggiatoa* (Jørgensen and Gallardo, 1999). In the Arabian Sea,
78 chemosynthetically fixed carbon from such microorganisms may be an important additional
79 source of nutrition for benthic organisms, either through symbiosis or heterotrophic
80 consumption of chemosynthetic bacteria (Levin, 2003).

81 Foraminifera are unicellular eukaryotes (protists) and are an abundant component of
82 marine benthic communities at all depths in the ocean (Murray, 2006). Although some are
83 carnivorous, many benthic foraminifera feed at a low trophic level (Gooday et al., 1992;
84 Lipps and Valentine, 1970), responding rapidly to phytodetritus with reproduction and
85 population growth. They are one of the most important heterotrophic consumers in the deep
86 sea (Gooday, 1988; Moodley et al., 2002; Nomaki et al., 2005) and act as an important link
87 between phytodetritus and metazoan consumers in deep-sea food webs (Nomaki et al., 2008).
88 Foraminifera have also been shown to influence the nitrogen cycle through the anaerobic
89 respiration of nitrate (Bernhard et al., 2012; Pina-Ochoa et al., 2010; Risgaard-Petersen et al.,
90 2006), a process that may be mediated by symbiotic bacteria (Bernhard et al., 2011). It has
91 been suggested that the role of foraminifera in the removal of fixed nitrogen through nitrate
92 respiration may equal the importance of bacterial denitrification in oceanic sediments (Glock
93 et al., 2013; Pina-Ochoa et al., 2010).

94 In order to better understand their role in food webs and elemental cycles, we compared
95 the trophic ecology of foraminifera at the Oman and Pakistan margins of the Arabian Sea,
96 across a depth gradient from 140 m to 3150 m, using stable isotope analyses (SIA). SIA is a
97 useful tool for establishing trophic relationships and determining food sources. The stable
98 isotopic signature of an organism's tissues is related to its food source. Stable carbon isotopes
99 are particularly useful in determining food sources as $\delta^{13}\text{C}$ does not fractionate heavily during
100 transfer between trophic levels ($<1\%$; DeNiro and Epstein, 1978; Fry and Sherr, 1984) and
101 different carbon fixation pathways involve distinct isotopic fractionation. Typically,
102 phytoplankton-derived organic matter has $\delta^{13}\text{C}$ signatures ranging from -15% to -25% (Fry

103 and Sherr, 1984). Carbon fixation fuelled by energy derived from sulphide oxidation
 104 involving form I Rubisco produces $\delta^{13}\text{C}$ values of -27 ‰ to -37 ‰, whilst pathways that
 105 involve form II Rubisco or the reverse tricarboxylic acid cycle (rTCA) can lead to heavier
 106 $\delta^{13}\text{C}$ values between -9 and -16 ‰ (Brooks et al., 1987; Campbell et al., 2003; Robinson and
 107 Cavanaugh, 1995). Stable nitrogen isotopic compositions can provide information on both
 108 nitrogen sources and trophic level. For example, denitrification leads to enriched $\delta^{15}\text{N}$ values
 109 of subsurface nitrate, which is reflected in particulate and sedimentary organic matter (Altabet
 110 et al., 1995; Gaye-Haake et al., 2005), whilst light $\delta^{15}\text{N}$ values in organic matter can be
 111 diagnostic of nitrogen fixation (Brandes et al., 1998). Organisms that have chemoautotrophic
 112 symbionts often have light $\delta^{15}\text{N}$ signatures reflecting nitrogen fixation (Levin and Michener,
 113 2002). Generally, $\delta^{15}\text{N}$ values are enriched by ~ 2 to 5 ‰ per trophic level, the trophic
 114 enrichment factor (TEF; DeNiro and Epstein, 1981; Hobson and Welch, 1992; McCutchan et
 115 al., 2003; Minagawa and Wada, 1984) and are used to identify predator/prey relationships.

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

123

124 **2 Materials and Methods**

125 **2.1. Study areas and field sampling**

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

129 Sampling was carried out during three cruises of the RRS '*Charles Darwin*' (CD). We
 130 define our sampling periods relative to the SW monsoon. Samples from the Oman margin
 131 were collected during CD143 (Nov-Dec 2002; post-SW monsoon), a period of presumed low
 132 particulate flux for the western Arabian Sea (~100 mg m⁻² d⁻¹; Haake et al., 1993; Honjo et al.,
 133 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 (Sept-Oct 2003; post-SW monsoon), a period of high particulate 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) 9 dead jellyfish were obtained using an Agassiz trawl from depths of $\sim 1850 \text{ m}$.

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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).

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Sediments were collected using a hydraulically-damped Bowers and Connelly megacorer equipped with 8 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 ($\% \text{ C}_{\text{org}}$), total nitrogen (TN %) and stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) ratios, as described in Jeffreys et al. (2009a & 2009b) and the Hydrogen Index (HI; Peters, 1986). The HI is calculated using the following equation: $\text{HI} = (\text{S2}/\text{TOC}) \times 100$, 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).

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During the cruise CD151 at the Pakistan margin two cores per megacorer deployment at each depth were processed for foraminifera ($>300 \mu\text{m}$). Each core was sectioned into horizontal layers at intervals of 0.5 cm to 2 cm. Sections were wet sieved on a $300 \mu\text{m}$ screen

170 and 'live' foraminifera (assumed to have been living when collected, based on the presence of
 171 cytoplasm within the test) and filamentous bacteria were picked from the sieve residues. The
 172 residues were kept chilled (<5 °C) to prevent biochemical decomposition and the foraminifera
 173 were sorted as quickly as possible in a Petri dish on ice under a low power binocular
 174 microscope. The organic stain Rose Bengal ~~was~~ not used to distinguish 'live' foraminifera as
 175 this ~~alters~~ their biochemical composition. Instead, specimens were judged to be 'live' (and
 176 therefore feeding) at the time of sampling based on the presence of obvious test contents in
 177 most or all constituent chambers. Foraminifera were sorted to species level and cleaned in
 178 filtered (2 µm screen) seawater to remove any attached organic particles. Approximately 30-
 179 100 individuals per species were placed into silver capsules and frozen at -20°C. Foraminifera
 180 from the Oman margin were sorted from frozen cores following the cruise. Briefly, on board
 181 at each water depth, the top 2 cm from sediment cores was sectioned and frozen at -20°C
 182 immediately. In the laboratory, samples were thawed and wet sieved and sorted as described
 183 above.

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184 2.2. Stable isotope analysis

185 Vapour phase digestion was used to remove carbonate from sediment samples. Calcareous
 186 foraminifera were acidified with 10% v/v HCl prior to analysis. Foraminifera from the
 187 Pakistan margin were analysed using a Europa Hydra 20/20 isotope ratio mass spectrometer
 188 (University of California Davis); $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of sediments and POM were analysed using
 189 VG Prism III isotope ratio mass spectrometer (University of Edinburgh). Foraminifera, POM,
 190 and sediments from the Oman margin were analysed using a Thermo-Finnigan MAT Delta
 191 Plus Advantage Dual isotope analyser (University of California, Santa Barbara). Stable
 192 isotope ratios are expressed as $(\delta X) \text{‰} = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$, where X is either ^{13}C or
 193 ^{15}N , and R is either (^{13}C : ^{12}C) or (^{15}N : ^{14}N), respectively. The reference standards for carbon
 194 and nitrogen are V-Pee Dee Belemnite and atmospheric N_2 , respectively. Analytical accuracy
 195 for Pakistan margin samples was determined using a sucrose standard for $\delta^{13}\text{C}$ and was -
 196 $23.84\text{‰} \pm 0.04\text{‰}$ and using an ammonium sulphate standard for $\delta^{15}\text{N}$ at $1.28\text{‰} \pm 0.19\text{‰}$.
 197 Analytical accuracy for Oman margin samples was determined using acetanilide for both $\delta^{13}\text{C}$
 198 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
 199 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
 200 in 2013. All laboratory working standards were calibrated against USGS 40 and USGS 41.
 201 Analytical precision was determined using an internal standard (tissue from the holothurian

205 *Oneirophanta mutabilis*; Iken et al., 2001), which was sent to each lab; mean values and
 206 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
 207 Pakistan margin samples analysed in 2005. Mean values and standard deviations for Oman
 208 margin samples were -15.71‰ for $\delta^{13}\text{C}$ and 11.99‰ $\delta^{15}\text{N}$ (n = 1) for samples analysed in
 209 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
 210 analysed in 2013. The majority of Oman margin samples had low N contents, and so
 211 analytical accuracy and precision were determined using a series of variable mass acetanilide
 212 and I.S. with N contents ranging from ~ 1 to 11 $\mu\text{g N}$. Analytical accuracy of $\delta^{15}\text{N}$ values for
 213 samples containing low N using the acetanilide standard (calibrated using USGS 40 and 41)
 214 was $\pm 1.1\text{‰}$, analytical precision of $\delta^{15}\text{N}$ values for samples containing low N using the I.S.
 215 was $\pm 0.93\text{‰}$.

216 **2.3. Statistical analyses**

217 As a result of the limited number of sediment samples from the Oman margin (n = 1 per
 218 water depth), we tested for differences in % C_{org} , %TN, HI, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between the Oman
 219 and Pakistan margins irrespective of depth, i.e. each depth represented 1 replicate. We tested
 220 for differences in the stable carbon and nitrogen isotopic composition of the foraminifera at
 221 each margin between (a) depth (b) foraminiferal species or higher taxon, where possible and
 222 (c) the composition of the foraminiferal wall e.g. calcareous, agglutinated monothalamid and
 223 textulariid species (Supporting information Table S2). Foraminiferal samples from the Oman
 224 margin were collected in two areas on the continental rise as defined in (Billett et al., 2006,
 225 Fig. 1); we tested for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of foraminifera between these
 226 two areas. We tested for inter-margin differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition in
 227 foraminiferal higher taxon, genus and species level where possible and between depths with
 228 similar oxygen concentrations. The distribution and variance of the data were ascertained
 229 using the Shapiro-Wilk's test and Levene's homogeneity of variance test. If data had a normal
 230 distribution and equal variance a 1-way (p < 0.05) ANOVA was performed to ascertain
 231 statistical differences. The posthoc Games-Howell test was performed following ANOVA for
 232 subsequent pairwise comparisons. If the data did not meet the assumptions of an ANOVA, a
 233 Mann-Whitney U-test or Kruskal-Wallis test was carried out.

234

236 3.1 Oxygen and organic matter gradients

237 On both the Pakistan and Oman margins during the post-SW monsoon period, CTD and *in*
238 *situ* measurements revealed the bottom water to be hypoxic [hypoxic bottom water is defined
239 as having $DO < 9 \mu M$; (Kamykowski and Zentara, 1990)] within the OMZ and across the
240 transition zones (140 m to 940 m). DO increased slightly at the lower boundary (~1100 m to
241 1250 m) gradually becoming oxygenated at water depths of 1850 m to 3200 m (Table 1).
242 Organic carbon concentrations (%C_{org}; used here as a proxy for the concentration of organic
243 matter) on both margins were highest within the OMZ and the lower transition zones, then
244 decreased with depth (Fig. 2a). Total nitrogen mirrored the organic carbon profiles, although
245 the difference between the core of the OMZ and sites below the core was less pronounced
246 (Fig. 2b). Both C_{org} and TN concentrations were significantly higher on the Oman margin
247 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
248 TN, respectively). We use the HI here as a proxy for food quality (Cook et al., 2000). Values
249 of the HI were significantly higher on the Oman margin than on the Pakistan margin and
250 highest within the OMZ in both cases ($F_{1,23} = 6.894$, $p < 0.0001$; Fig. 2c). On the Pakistan
251 margin the $\delta^{13}C$ composition of POM was significantly depleted relative to the SOM, whilst
252 the $\delta^{15}N$ composition of POM and SOM were not significantly different (Jeffreys et al.,
253 2009b). $\delta^{15}N$ values of SOM did not exhibit any trends with depth on the Pakistan margin and
254 were significantly lighter on the Pakistan margin compared to the Oman margin (Mann-
255 Whitney *U*-test: $p = 0.030$; Table 2). $\delta^{13}C$ values of SOM on the Pakistan margin were
256 significantly heavier at 1850 m compared to shallower depths ($F_{4,24} = 5.664$, $p = 0.002$; Table
257 2). There was no significant difference in sedimentary $\delta^{13}C$ values between the two margins
258 (Table 2).

259 3.2 Isotopic composition of Foraminifera at the Pakistan margin.

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

264 3.2.1. Depth trends in isotopic signature

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compared to 1850 m
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0.053 between 1850 m and 300 m, 940 m and 140 m
respectively;
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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 & 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 & b). 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 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 (Supporting information 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 within the range of potential food sources (Figs. 4 & 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 & 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 m - 789 m) and canyon sites (1103 m - 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

Deleted: Calcareous foraminifera were significantly depleted in ^{13}C at 140 m compared to those at 300 m, and 940 m and 1200 m combined ($\delta^{13}\text{C} = -22.9\text{‰}$, -21.4‰ and -21.4‰ at 140 m, 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, $\delta^{13}\text{C} = -22.1\text{‰}$, -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 (Fig. 3 & 4, $\delta^{13}\text{C}$: $F_{3,14} = 1.188$, $p = 0.350$, $\delta^{15}\text{N}$: $F_{3,13} = 0.293$, $p = 0.830$).

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Deleted: At 300 m there was no significant difference in isotopic composition between calcareous, textulariids or agglutinated monothalamid species (Fig. 3b & 4a, $F_{2,10} = 0.534$, $p = 0.602$, $\delta^{15}\text{N}$: 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 (Fig. 3c & 4a, $\delta^{13}\text{C}$: Mann-Whitney *U*-test: $p = 0.180$, $\delta^{15}\text{N}$: Mann-Whitney *U*-test: $p = 0.734$).

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353 | m, 2030 m and 3185 m (Fig. 4b & 5a).

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354 | Using the oxygen concentrations from the CTD and the definitions of Gooday et al.
355 | (2009) as a guide, we categorized the stations into distinct regions of the OMZ. The OMZ
356 | core (504 m to 789 m; DO = 5.1 to 6.3 μM); the lower boundary (LB: 1103 m to 1414 m; DO
357 | = 16.5 to 29.9 μM) and below the OMZ (2030 m to 3185 m; DO = 90.6 to 166 μM). We
358 | observed no significant difference in $\delta^{13}\text{C}$ composition between foraminifera from the lower
359 | OMZ boundary and those found below the OMZ (Fig. 4c & 5a). Foraminiferal $\delta^{15}\text{N}$
360 | composition did not differ significantly with depth (Fig. 4d & 5a). Similarly, foraminiferal
361 | $\delta^{15}\text{N}$ composition did not differ significantly between the OMZ core, lower OMZ boundary or
362 | below the OMZ (Fig. 4d).

Deleted: , Mann-Whitney *U*-test: $p = 0.389$

Deleted: , Kruskal-Wallis test $p = 0.291$

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363 | Calcareous foraminiferal $\delta^{15}\text{N}$ compositions did not differ significantly across the Oman
364 | margin (Fig. 4d). Textulariids were depleted in ^{15}N at the lower OMZ boundary ($2.1\text{‰} \pm$
365 | 1.4‰) compared to those found below the OMZ (water depths > 2000 m; $8.1\text{‰} \pm 5.1\text{‰}$; Fig.
366 | 4d, $F_{1,5} = 31.011$, $p = 0.003$).

Deleted: , $F_{1,12} = 1.979$, $p = 0.183$

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368 | 3.3.2. Trends among main foraminiferal groups.

369 | The $\delta^{13}\text{C}$ composition was not significantly different between foraminiferal groups (Fig
370 | 4c). Similarly, the $\delta^{15}\text{N}$ composition was not significantly different between foraminiferal
371 | groups across the whole margin (Fig 4d). Calcareous foraminifera were significantly enriched
372 | in ^{15}N ($5.5\text{‰} \pm 2.2\text{‰}$) compared to textulariids at the lower OMZ boundary ($2.1\text{‰} \pm 1.4\text{‰}$;
373 | Fig. 4d, water depths 1103 m to 1414 m; $F_{1,11} = 6.722$, $p = 0.025$). Below the OMZ (water
374 | depths 2030 m to 3185 m) no significant differences were observed in $\delta^{15}\text{N}$ composition
375 | between agglutinated monothalamid, textulariid or calcareous species (Fig. 4d).

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Deleted: , $F_{2,11} = 0.889$, $p = 0.439$

Deleted: , Kruskal-Wallis test $p = 0.751$

Deleted: , $F_{1,11} = 1.345$, $p = 0.304$

376 | 3.4 Inter-margin differences in the isotopic composition of foraminifera.

377 | There were significant differences in both foraminiferal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition
378 | between the two margins (Mann-Whitney *U*-test: $p < 0.0001$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, not
379 | accounting for foraminiferal groupings, water depth or oxygen concentration). $\delta^{13}\text{C}$ values
380 | 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

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391 ($\delta^{15}\text{N} = 5.4\text{‰} \pm 3.7\text{‰}$; $10.2\text{‰} \pm 5.1\text{‰}$) at the Oman margin compared to the Pakistan margin,
392 respectively.

393 There were no significant differences in the $\delta^{15}\text{N}$ composition of foraminifera from the
394 OMZ cores ($\text{O}_2 = 5.1\text{--}5.8\text{ }\mu\text{M}$ at 504 to 789 m water depth on the Oman margin and $4.9\text{ }\mu\text{M}$ at
395 300 m on the Pakistan margin; Fig. 4b & 4d), nor from below the OMZ on both margins (O_2
396 = $83.1\text{ }\mu\text{M}$ at 2030 m water depth on the Oman margin and $73.6\text{ }\mu\text{M}$ at 1850 m on the
397 Pakistan margin; Fig. 4b & 4d). However, foraminifera from below the OMZ on the Oman
398 margin (2030 m) were significantly enriched in ^{13}C compared to those collected below the
399 OMZ on the Pakistan margin at 1850 m (Fig. 4a & 4c, $F_{1,173} = 5.627$, $p = 0.034$).

400 Agglutinated monothalamid foraminifera had similar isotopic compositions on both
401 margins (Fig. 4), while textulariids had significantly depleted $\delta^{15}\text{N}$ values on the Oman
402 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;
403 Mann-Whitney U -test: $p < 0.0001$). The $\delta^{13}\text{C}$ composition of textulariids was similar on both
404 margins (Fig. 4a, c). The isotopic composition of calcareous foraminifera on the Oman
405 margin were significantly enriched in ^{13}C and depleted in ^{15}N compared to those on the
406 Pakistan margin (Fig. 4; $\delta^{13}\text{C}$: Mann-Whitney U -test: $p = 0.011$; $\delta^{15}\text{N}$: Mann-Whitney U -test:
407 $p < 0.0001$).

408 Differences in $\delta^{15}\text{N}$ composition at species level (not accounting for depth) were also
409 evident. *Uvigerina hollicki* (Oman, $\delta^{15}\text{N} = 3.2\text{‰} \pm 7.6\text{‰}$) was depleted in ^{15}N compared to *U.*
410 ex. gr. *semiornata* (Pakistan margin, $\delta^{15}\text{N} = 10.1\text{‰} \pm 2.6\text{‰}$; Supporting information Table
411 S2, Mann-Whitney U -test: $p < 0.030$). Similarly, *Globobulimia* spp. (a mixture of *G. turgida*
412 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.*
413 *pyrula* off Pakistan ($\delta^{15}\text{N} = 15.4\text{‰} \pm 5.0\text{‰}$; Supporting information Table S2, $F_{1,5} = 11.024$, p
414 = 0.021). The $\delta^{15}\text{N}$ composition of *Reophax dentaliniformis* was similar on both margins
415 (Supporting information Table S2: Pakistan $\delta^{15}\text{N} = 8.7\text{‰} \pm 7.1\text{‰}$; Oman $\delta^{15}\text{N} = 4.9\text{‰} \pm$
416 3.7‰).

417

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Deleted: , Mann-Whitney U -test: $p < 0.0001$

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Deleted: , $F_{1,17} = 0.880$, $p = 0.361$

Deleted: , $\delta^{13}\text{C}$: $F_{1,19} = 2.590$, $p = 0.124$; $\delta^{15}\text{N}$:
Mann-Whitney U -test: $p = 0.705$

Deleted: , Mann-Whitney U -test: $p = 0.54$

426 4 Discussion

427 4.1 Methodological issues

428 | Different preservation methods were used for foraminifera, **collected** at each margin (See
429 2.1). It has been shown that bulk freezing can lead to discrepancies in isotopic signatures as a
430 result of cell lysis (Feuchtmayr and Grey, 2003; Dannheim et al., 2007). However, the
431 discrepancies in $\delta^{15}\text{N}$ values for bulk frozen material reported by these studies were
432 inconsistent; Feuchtmayr and Grey (2003) reported an increase in $\delta^{15}\text{N}$ values by 1‰,
433 whereas, Dannheim et al., (2007) reported a decrease in $\delta^{15}\text{N}$ values by 1‰. The 1‰
434 discrepancy reported in $\delta^{15}\text{N}$ values between bulk frozen sediments/water samples and
435 organisms, which have been frozen directly as individuals, is within the analytical error of our
436 study. We therefore do not expect that our methodologies will have significantly affected our
437 results. Furthermore, the large range in $\delta^{15}\text{N}$ values observed in foraminifera at both of the
438 margins (-7.8 to 10.8‰ for Oman and -3.9‰ to 27.3‰ for Pakistan) suggests this is unlikely.

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439 4.2 Oxygen dynamics and organic matter supply to the sediments

440 | This study **was part of** a comprehensive investigation of carbon cycling by benthic
441 communities during different seasons (pre- and post- SW monsoon) and at different water
442 depths (140-1850 m) across the Pakistan margin and from a biological survey conducted at
443 the Oman margin during the post SW monsoon season at water depths of ~ 360 -3185 m.
444 Detailed descriptions of the environmental conditions and benthic community structure at the
445 Pakistan margin can be found in Brand & Griffiths (2009), Breuer et al. (2009), Cowie et al.
446 (2009), Gooday et al. (2009), Jeffreys et al. (2009a,b), and Larkin et al. (2009). Descriptions
447 of environmental conditions and benthic community structure at the Oman margin relevant to
448 this study can be found in: Gooday et al. (2000), Smallwood and Wolff (2000) and Aranada
449 da Silva and Gooday (2009). Below we give a brief overview of environmental conditions at
450 both margins.

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451 Oxygen profiles on both margins exhibited a sharp decline in concentration in the upper
452 200 m of the water column to an intense minimum, then increased gradually below ~1000 m
453 (Aranda da Silva and Gooday, 2009). DO concentrations in the core of the OMZ on the
454 Pakistan margin (~300 m) were lower than in the core on the Oman margin (~400 m;
455 (Gooday et al., 2009). Upwelling intensity is greater off Oman, resulting in higher

459 | productivity and higher particulate fluxes compared to ~~the~~ Pakistan margin (Burkill et al.,
460 | 1993; Haake et al., 1993; Nair et al., 1989). This is reflected in the abundance and quality of
461 | SOM, with higher C_{org}, TN concentrations and HI values on the Oman margin ~~vs.~~ the Pakistan
462 | margin. This suggests a greater input of fresh organic matter to the Oman margin or less
463 | heterotrophic reworking of POM in the water column, presumably leading to a more abundant
464 | food supply there.

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

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474 | 4.3 Spatial patterns in foraminiferal trophic ecology

475 | 4.3.1 Depth trends

476 | The uniformity in the $\delta^{15}\text{N}$ composition of food sources on the Pakistan margin is typical
477 | of upwelling margins impacted by OMZs (Cowie et al., 2009). This is also reflected in the
478 | isotopic composition of the foraminifera, as no bathymetric patterns in their $\delta^{15}\text{N}$ values were
479 | apparent. The $\delta^{13}\text{C}$ composition of SOM did exhibit spatial variability, being more enriched
480 | below the OMZ. This is consistent with Cowie et al. (2009), who suggested that the minimum
481 | in $\delta^{13}\text{C}$ values observed within the OMZ core reflects a chemosynthetic bacterial imprint on
482 | the isotopic composition of SOM. We observed large filamentous bacteria with depleted $\delta^{13}\text{C}$
483 | values within the core and lower transition zone of the OMZ. Additionally, branched fatty
484 | acid concentrations, biomarkers for heterotrophic anaerobic bacteria (Gillan and Johns, 1986),
485 | were found in highest concentrations at 140 m and 300 m during the post-SW monsoon on the
486 | Pakistan margin (Jeffreys et al., 2009a), consistent with an important bacterial contribution to
487 | SOM. The $\delta^{13}\text{C}$ composition of ~~the calcareous~~ foraminifera *Uvigerina ex. gr. semiornata*
488 | reflected that of ~~POM and~~ SOM at the Pakistan margin. *Uvigerina ex. gr. semiornata* rapidly

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494 consumes fresh phytodetritus and has also been inferred to ingest sedimentary bacteria
495 (Larkin et al., 2014; Woulds et al., 2007).

496 $\delta^{15}\text{N}$ values of SOM were also invariant across the Oman margin, a pattern reflected in the
497 foraminiferal $\delta^{15}\text{N}$ compositions. On the other hand, $\delta^{13}\text{C}$ values were spatially variable,
498 being noticeably heavier at 500 m and 1100 m. The presence of large falls of dead jellyfish
499 both on the continental slope, rise and in the canyons of the Oman margin at similar depths
500 might provide an explanation for the enrichment of SOM (Billett et al., 2006). The largest
501 aggregations of jellyfish covered by white bacterial mats, evidence of sulphide oxidation,
502 were observed on the continental rise at the time of sampling (Billett et al., 2006). A
503 chemosynthetic bacterial input derived from the anaerobic decomposition of jelly detritus
504 could therefore have led to the enriched $\delta^{13}\text{C}$ values observed at 500 m and 1100 m, as carbon
505 fixation fuelled by energy derived from sulphide oxidation involving Rubisco II leads to
506 enriched $\delta^{13}\text{C}$ values of -9‰ to -16‰ (Robinson and Cavanaugh, 1995). The majority of
507 foraminifera on the Oman margin had $\delta^{13}\text{C}$ compositions typical of mid-latitude
508 phytoplankton (Sackett et al., 1965) with the exception of *Hyalina baltica* at 1414 m, which
509 had a $\delta^{13}\text{C}$ composition of ~ -12 ‰, possibly through its utilisation of chemosynthetic bacteria
510 as a food source. This station was located on the continental rise within area B, where
511 decaying jellyfish, white bacterial mats and a thin layer (<10 mm) of jelly slime covered the
512 surface of the sediments (Billett et al., 2006).

513 4.3.2 Inter-margin differences

514 The inter-margin spatial variability in the organic geochemistry of the sediments provides
515 evidence of variability in the source, abundance and quality of organic matter. Foraminifera
516 on the Oman margin were enriched in ^{13}C compared to those on the Pakistan margin, this
517 being driven primarily by the calcareous taxa. It is likely that at the Pakistan margin these
518 foraminifera select for fresh phytodetrital material as their isotopic signatures closely match
519 the POM. Similarly, foraminifera below the OMZ on the Pakistan margin were depleted in
520 ^{13}C compared to those on the Oman margin. Phytodetritus was present on surficial sediments
521 and within burrows at 1850 m, ($\text{O}_2 = 73.6 \mu\text{M}$) below the OMZ at the Pakistan margin.
522 Foraminifera below the OMZ at depths of 1850 m on the Pakistan margin fell between the
523 range of $\delta^{13}\text{C}$ values for POM and SOM and so it is likely that they were feeding on relatively
524 fresh material. On the Oman margin at depths of 2030 m foraminifera closely reflected the

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536 | SOM carbon isotopic signature and there was less variation in isotopic composition
537 | suggesting reduced variation in possible food sources.

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538 | The most noticeable expression of differences in the trophic ecology of the foraminifera
539 | between the two margins was the distinct divergence in stable nitrogen isotope signatures. At
540 | the Pakistan margin, ~14% of foraminifera had $\delta^{15}\text{N}$ values enriched by more than one trophic
541 | level relative to SOM. These foraminifera may store nitrate in their vacuoles for respiration;
542 | in such cases, intracellular $\delta^{15}\text{N}_{\text{NO}_3}$ values vary from 15 to 42‰ (Bernhard et al., 2012). The
543 | storage of intracellular nitrate for respiration is widespread among foraminifera and has been
544 | documented in species from anoxic sediments in a variety of habitats including OMZs (Glock
545 | et al., 2013; Bernhard et al., 2012; Pina-Ochoa et al., 2010; Prokopenko et al., 2011;
546 | Risgaard-Petersen, et al., 2006). In this study, nitrate storage/respiration may occur in the
547 | calcareous species *Globobulimina* cf. *G. pyrula* and *Cancris auriculus* within the hypoxic
548 | core of the OMZ at 140 m and 300 m. These species are known to be ‘nitrate collectors’
549 | (Pina-Ochoa et al., 2010). Textulariids were also enriched in ^{15}N , several species of *Reophax*,
550 | including *R. aff. dentaliniformis*, *R. aff. bilocularis*, *R. scorpiurus* and and unidentified
551 | species, had enriched $\delta^{15}\text{N}$ values across the margin from the hypoxic core to the more
552 | oxygenated deeper site at 1850 m. Species of *Reophax* have not been observed to store nitrate
553 | (Pina-Ochoa et al., 2010). However, Pina-Ochoa et al. (2010) noted that only a few specimens
554 | were analysed while Bernhard et al. (2012) observed large variations in foraminiferal nitrate
555 | storage between individuals of the same species as well as between different species.
556 | *Dorothia scabra*, another textulariid, also from the lower OMZ transition zone at 940 m, had
557 | the most enriched $\delta^{15}\text{N}$ value in the present study.

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

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572 gradient to access nitrate; the sediments of the Pakistan margin are a sink for nitrate (Woulds
573 et al., 2009), so this is a plausible strategy.

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

581 At the time of sampling, large numbers of dead jellyfish (*Crambionella orsini*) were
582 observed at the seafloor (Billett et al., 2006); this led to an increase in the standing stock of
583 organic carbon, which was estimated at between 1.5 g C m^{-2} and 78 g C m^{-2} (Billett et al.,
584 2006). Such a large deposition of organic matter could lead to large increases in rates of
585 remineralisation. In mesocosm experiments, West et al. (2009), observed the rapid breakdown
586 of dead jellyfish leading to a $> 450\%$ increase in the NH_4^+ flux from the sediments, which they
587 attributed to bacterial decomposition. Live jellyfish are known to excrete large amounts of
588 dissolved free amino acids ($15 \text{ mg N g dw}^{-1} \text{ d}^{-1}$), alanine and glycine being the most abundant
589 (Webb and Johannes, 1967). Furthermore, Macko and Estep (1984) demonstrated that
590 bacterial cultures utilizing alanine as a substrate become depleted in ^{15}N by up to 12.9%
591 relative to the substrate during deamination and produce a pool of NH_4^+ depleted in ^{15}N . The
592 jellyfish obtained from the Oman margin in this study had a $\delta^{15}\text{N}$ value of 10.9% , and
593 foraminifera had $\delta^{15}\text{N}$ values ranging from -7.0% to 10.8% . We suggest that the observed
594 isotopically light nitrogen signatures may result from feeding on bacteria associated with the
595 jelly detritus. On the continental rise (areas B and C), a thin layer of jelly slime ~~on~~ the
596 sediment underlain by a thin layer of black sediment suggested the presence of reduced
597 sulphur species, which could be utilized by sulphur-oxidizing bacteria. Oxygen minimum
598 zones often support mats of large sulphur-oxidising bacteria, including *Thioploca*, *Beggiatoa*,
599 *Thiomargarita* (Levin, 2003), and bacterial mats have been observed previously at the Oman
600 margin (Levin et al., 1997). At the time of sample collection, bacterial mats were visible in
601 still images across the Oman margin from depths of 1000 m to 3300 m, colonizing both single
602 jellyfish and jelly detritus (Billett et al., 2006). Sulphur-oxidising bacteria at cold seeps are
603 characterized by depleted $\delta^{15}\text{N}$ signatures (Decker and Olu, 2011; Demopoulos et al., 2010;

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607 Levin and Michener, 2002). We do not have isotopic data for bacteria from the Oman margin,
608 but bacteria from the Pakistan margin had $\delta^{15}\text{N}$ values ranging from -0.4‰ to 11.9‰,
609 including *Thioploca* sp., which had a $\delta^{15}\text{N}$ value of -0.1‰. We suggest, therefore, that the
610 depleted $\delta^{15}\text{N}$ values of foraminifera on the Oman margin are a result of feeding on
611 isotopically light bacteria associated with jelly detritus.

612 4.4 Foraminiferal feeding types: species level

613 Gooday et al. (2008) review the trophic biology of deep-sea foraminifera based on feeding
614 experiments, field observations, cellular stable isotope ratios and fatty acid analyses. They
615 recognise the following general types, which should not be regarded as rigid categories: A)
616 herbivores (i.e. phytodetritus feeders), B) opportunistic deposit feeders (omnivores), C)
617 intermediate- and deep-infaunal sediment deposit feeders, D) stercomata-bearing species
618 (likely deposit feeders), **E**) monothalamous species that may be bacteriovores, and **F**)
619 suspension feeding epifaunal foraminifera. Using a combination of pulse-chase experiments
620 and fatty acid biomarkers, Larkin (2006) recognised two trophic types among Pakistan margin
621 foraminifera (>300 μm fraction): (i) phytophagous species that consume fresh phytodetritus
622 and (ii) unselective deposit feeders. These are equivalent to Types A and B identified by
623 Gooday et al. (2008). The present study included species representative of all 6 of the trophic
624 groups recognised by Gooday et al. (2008). Our stable isotope analyses spanned a wide range,
625 as previously observed for foraminifera at both bathyal and abyssal depths (Enge et al., 2011;
626 Iken et al., 2001; Nomaki et al., 2008). These results indicate that the Arabian Sea
627 foraminifera include: (1) those that derive carbon and nitrogen principally from fresh organic
628 matter (phytodetritus) when available, i.e. opportunistic deposit feeders, (2) consumers of
629 more degraded organic matter, unselective deposit feeders and (3) bacteriovores.

630 4.4.1. Opportunistic deposit feeders

631 The carbon isotopic compositions of the majority of foraminifera mirrored POM and
632 SOM, suggesting both selective ingestion of phytodetritus during periods and at sites where it
633 is available and ingestion of SOM at other times. Natural observations and pulse-chase
634 experiments in conjunction with fatty acid analyses have shown that foraminifera are
635 important consumers of phytodetritus (Gooday, 1988; Moodley et al., 2002; Nomaki et al.,
636 2005; Suhr et al., 2003) and, at least at the Pakistan margin, are as important as bacteria in the
637 processing of organic matter (Woulds et al., 2007). The stable carbon and nitrogen isotope

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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., *Hyperammina* sp. and *Nodellum* sp.) from 940 m 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 m to 1850 m. The $\delta^{13}\text{C}$ values of *Pelosina* sp. fell between POM and SOM at both 140 m 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

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

694 variable and generally within 1 trophic level (assuming a trophic enrichment factor or 2.2 to
695 3.4‰; McCutchan et al., 2003; Post, 2002) of POM and SOM; however, some values fell
696 below the POM and SOM suggesting a bacterial component to the diet.

697 Several groups of foraminifera on both margins are known to accumulate stercomata:
698 ‘allogromiids’ (organic-walled monothalamids), *Rhizammina* sp., the komokiacean *Lana* sp.
699 and other komokiaceans. The isotopic composition of *Rhizammina* sp. was similar at the
700 Pakistan margin and at the Porcupine Abyssal Plain (PAP) in the NE Atlantic (Iken et al.,
701 2001); $\delta^{13}\text{C}$ data were consistent with feeding on POM/SOM, while isotopically light $\delta^{15}\text{N}$
702 values could reflect a bacterial component in the diet. Similarly, at 3185 m depth at the Oman
703 margin, where jelly detritus was observed on the sediment surface, the $\delta^{13}\text{C}$ composition of
704 *Rhizammina* sp. was consistent with feeding on POM/SOM, while the wide range of $\delta^{15}\text{N}$
705 values suggested ingestion of POM/SOM and bacteria associated with jelly detritus. On both
706 margins, various komokiacean species exhibited consistent isotopic patterns similar to those
707 reported at the PAP (Iken et al., 2001), reflecting probable utilisation of POM/SOM and
708 bacteria. An ‘allogromiid’ at 140 m at the Pakistan margin had a $\delta^{15}\text{N}$ value one trophic level
709 above that of the sediment and a $\delta^{13}\text{C}$ value close to that of SOM, suggesting that it was
710 feeding on SOM. ‘Farming’ of bacteria associated with the stercomata of foraminifera has
711 been proposed as a feeding strategy by Tendal (1979). Although this has yet to be confirmed,
712 we cannot discount the influence of stercomata or test particles on the isotopic signatures of
713 these agglutinated taxa.

714 Intermediate and deep-infaunal deposit feeders include *Chilostomella ovoidea* and various
715 textulariids. The majority of the foraminifera in this study were located in the top cm of
716 sediment. However, *C. ovoidea*, *Dorothia scabra* and *Reophax* aff. *bilocularis* were found in
717 deeper layers (2-10 cm) at 940 m. *Reophax* aff. *bilocularis* was located at 0-2, 2-5, and 5-10
718 cm with no change in isotopic composition with depth. This, coupled with isotopic signatures
719 falling between POM and SOM, suggest this species is an unselective deposit feeder.
720 Similarly, species of *Reophax* from other sites on the Pakistan margin have intermediate $\delta^{13}\text{C}$
721 values, suggesting that they are also unselective deposit feeders, except at 140 m where
722 signatures indicate consumption of phytodetritus. *Chilostomella oolina* is known to feed
723 unselectively on both algae and bacteria (Nomaki et al., 2006), consistent with the isotope
724 values for this species reported in the present study. At the Oman margin, the isotopic
725 composition of *Reophax dentaliniformis* and the monothalamid *Psammosphaera fusca* (which

Deleted: ere

727 had another monothalamid species, *Ammolagena clavata*, attached to its surface) also closely
728 resembled that of SOM, suggesting unselective deposit feeding.

729 **4.4.3. Bacteriovores**

730 Some shallow-water foraminifera are known to consume bacteria (e.g. Mojtahid et al.,
731 2011). On the other hand, there is little direct evidence for active predation by deep-sea
732 foraminifera on bacteria (Nomaki et al., 2006). However, our stable isotope data suggest that
733 some deep-sea species do include bacteria in their diets. On the Pakistan margin large
734 sheathed filamentous bacteria ($\geq 300 \mu\text{m}$) occurred within the OMZ at depths of 300 m and
735 940 m (this study) and across the lower OMZ transition zone from depths of 700 m to 1000 m
736 (Jeffreys et al., 2012), while bacterial mats were associated with jelly detritus on the Oman
737 margin (Billett et al., 2006). Filamentous bacteria at 300 m and 940 m generally had depleted
738 $\delta^{15}\text{N}$ values (0 to 5‰), whilst two filaments from 300 m were enriched in ^{15}N with respect to
739 POM and SOM. The variation in bacterial isotopic signatures reflects the large isotopic shifts
740 that have been observed in both autotrophic and heterotrophic bacteria (Macko et al., 1987;
741 McGoldrick et al., 2008). Depleted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values derived from the monothalamid
742 *Bathysiphon* sp. at 140 m and 300 m, suggested that it was feeding on isotopically depleted
743 bacteria. Fatty acid biomarkers ascribed to bacteria were present in *Bathysiphon* sp. nov.1 at
744 300 m on the Pakistan margin (Larkin, 2006). Bacterial biomarkers have also been noted in *B.*
745 *capillare* in the NE Atlantic (Gooday et al., 2002). We suggest that the isotopic signatures of
746 *Bathysiphon* sp. nov. in this study may reflect a bacterial component to the diet. *Reophax* aff.
747 *dentaliniformis* and *Globobulimina* cf. *G. pyrula* also had depleted $\delta^{15}\text{N}$ values, implying a
748 bacterial food source. Foraminifera with depleted $\delta^{15}\text{N}$ values were observed both at the lower
749 OMZ boundary and below the OMZ.

750 Sulphur oxidising/denitrifying filamentous bacteria in the genus *Thioploca* can form
751 conspicuous mats on the surface of OMZ sediments (Cowie and Levin, 2009; Levin et al.,
752 1997; Schmaljohann et al., 2001). Recently, Prokopenko et al. (2013) demonstrated a
753 consortium between *Thioploca* and anammox bacteria in anoxic sediments of the Soledad
754 basin at the Mexican Pacific margin. At the Pakistan margin, bacterial sheaths have been
755 observed entangled in a network of foraminiferal rhizopodia (Schmaljohann et al., 2001). At
756 the Oman margin 74% of foraminifera had $\delta^{15}\text{N}$ compositions falling below the $\delta^{15}\text{N}$ values
757 of the sediments. These observations suggest that bacteria may provide foraminifera with
758 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 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 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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1048 **Table 1.** Bottom water oxygen concentrations in μM from the CTD SBE 43 sensor. *In situ* DO concentrations from the Pakistan margin
1049 during the post-monsoon are from a bottom lander fitted with Profilur microelectrodes; for details see Breuer et al. (2009).
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Margin	Depth (m)	Temperature (°C)	CTD Oxygen	<i>In situ</i> 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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1061 **Table 2.** Stable isotope values of potential food sources in ‰. SOM = sediment organic matter (surface layer 0-1 cm); POM = particulate
1062 organic material from bottom water filters. Numbers in parentheses indicate ± 1 standard deviation. For SOM and POM from the Pakistan
1063 margin n=3, for SOM from the Oman margin n=1.
1064

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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1068 **Table 3:** C/N ratios, total concentration (mg g⁻¹ of dry sediment) of HMW (>C₂₄) fatty acids and n-alcohols of sedimentary organic matter (0-
1069 0.5 cm) from the Pakistan and Oman margins. Pakistan margin data are from Jeffreys et al. (2009a) and Oman margin data are from
1070 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)

1071 **Figure Legends**

1072 Figure 1: Location of sampling sites in the Arabian Sea. Inset shows the location of the Oman
1073 margin (a) and Pakistan margin working areas (b) within the northern Arabian Sea. Map (a) of
1074 the Oman margin shows sampling area B and C on the continental rise as defined in Billet et
1075 al. (2006). Map (b) shows the Pakistan margin sampling sites. Exact locations of sampling
1076 sites are given in the supporting information Table S1.

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1078 Figure 2. (A) Total organic carbon concentrations, (B) total nitrogen concentrations, and (C)
1079 Hydrogen Index values of surface sediments (0-1 cm) across the Pakistan margin (unfilled
1080 circles) and Oman margin (filled circles). For the Pakistan margin each point represents a
1081 mean ($n=3$) \pm 1 standard deviation. For the Oman margin $n=1$.

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1083 | Figure 3: Species level, dual stable carbon nitrogen biplots of foraminifera ($>300 \mu\text{m}$) from
1084 the Pakistan margin, (A) 140 m (B) 300 m (C) 940 m (D) 1200 m (E) 1850 m. Each point
1085 denotes a single measurement. The isotopic composition of POM, SOM and jellyfish are also
1086 indicated. The solid line represents 1 trophic level above the maximum SOM value for each
1087 depth, assuming a trophic enrichment factor of 3.4‰ (Post, 2002). Legends are below the
1088 plots.

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1090 Figure 4: Stable carbon (A & C) and stable nitrogen (B & D) isotope composition of
1091 foraminifera plotted by foraminiferal grouping, from Pakistan margin (A & B) and Oman
1092 margin (C & D). Light grey shaded areas represent the OMZ core, the solid line separates the
1093 lower OMZ boundary from stations below the OMZ (below the line). Note that the 140-m
1094 site was hypoxic during the late-monsoon. All data shown are from the late/post monsoon
1095 period. Legends are below the plots.

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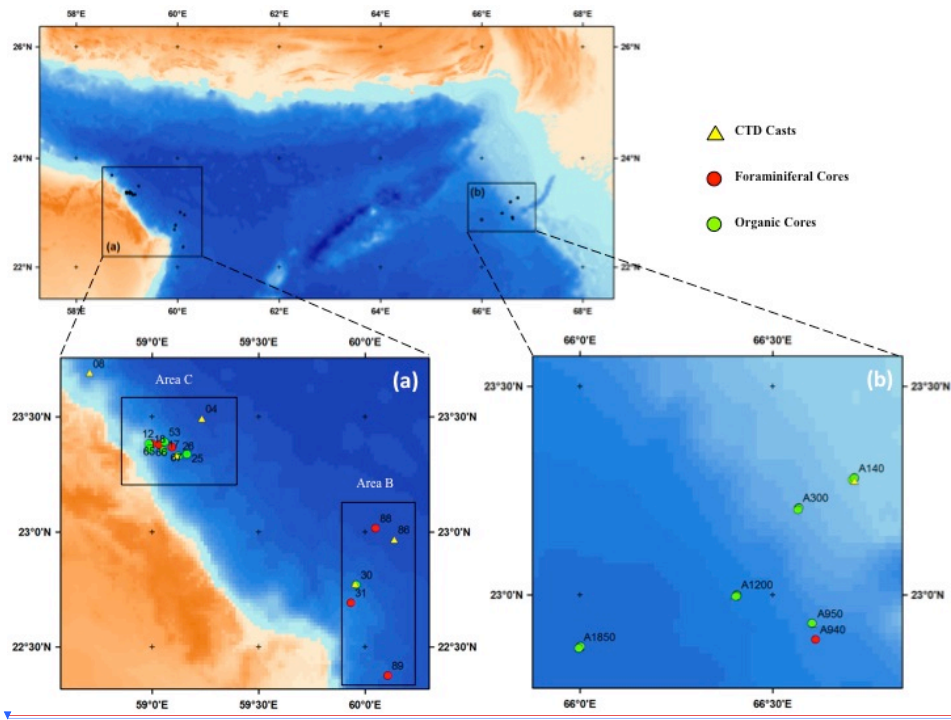
1097 | Figure 5: Dual stable carbon nitrogen biplots of foraminifera ($>300 \mu\text{m}$) from the Oman
1098 margin, (A) Foraminifera plotted as a function of depth (B-D) Foraminifera plotted as a
1099 function of species (B) 789 m to 1390 m, slope and canyon sites from Area C (C) 1414 m &

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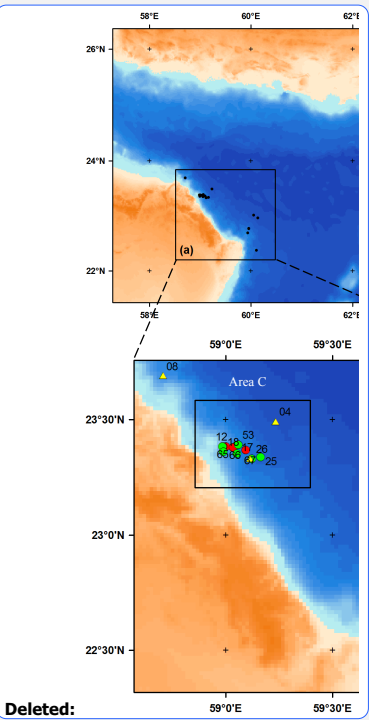
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1102 2030 m, area B (D) 3185 m, Area B. Each point denotes a single measurement. The isotopic
1103 composition of SOM and jellyfish are indicated. The legends for plot A is to the right of the
1104 plot and for plots B to D are to the right of plot D.

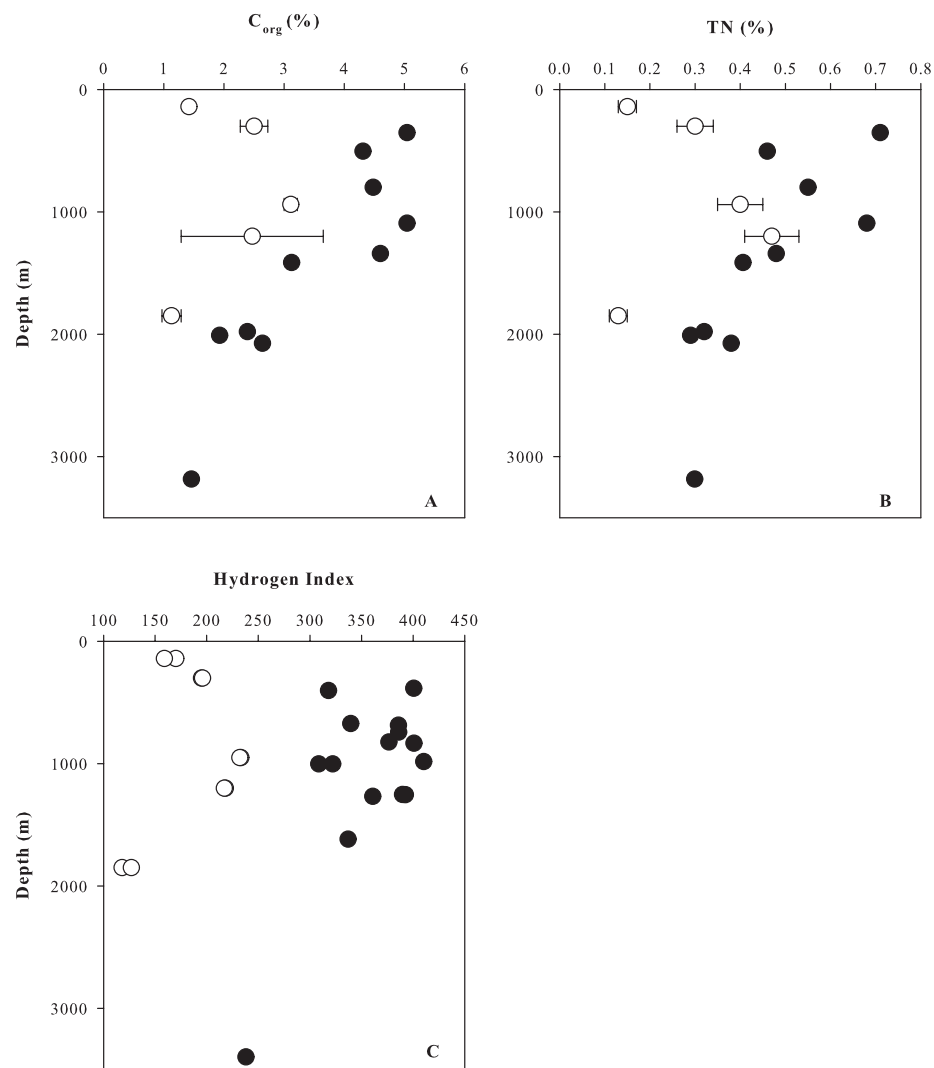
1105 Figure 1



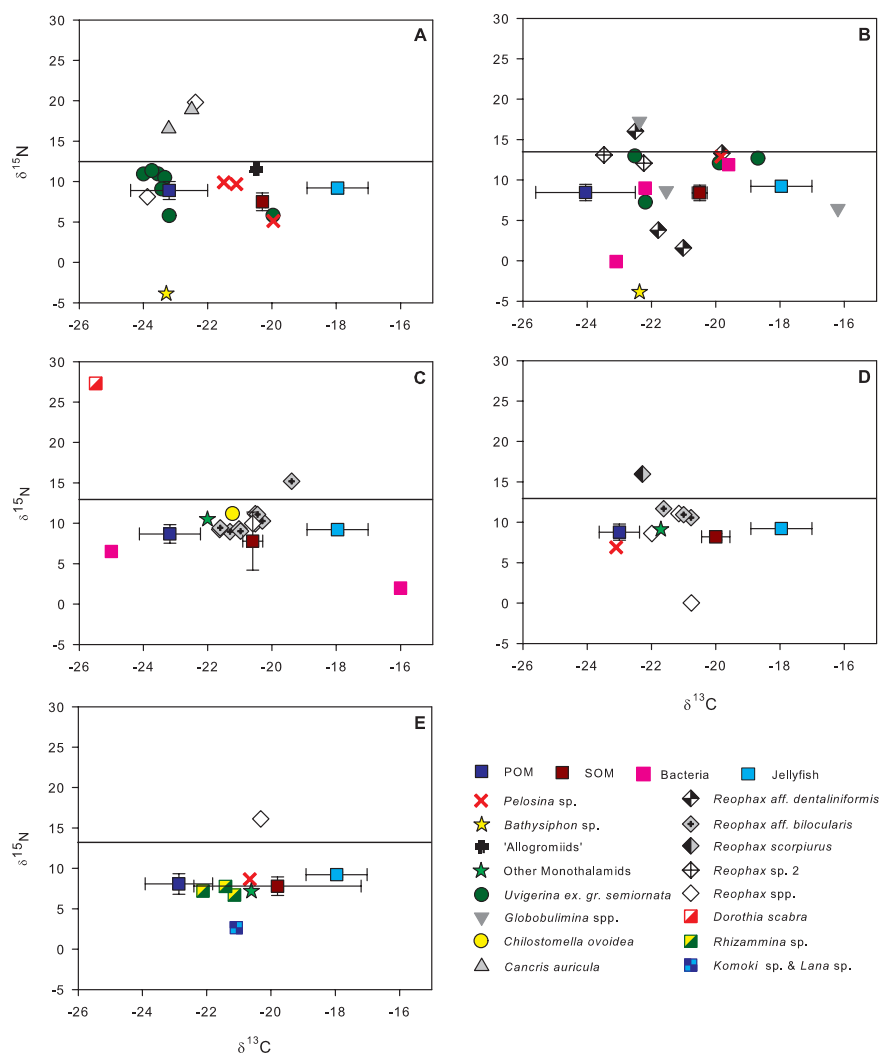
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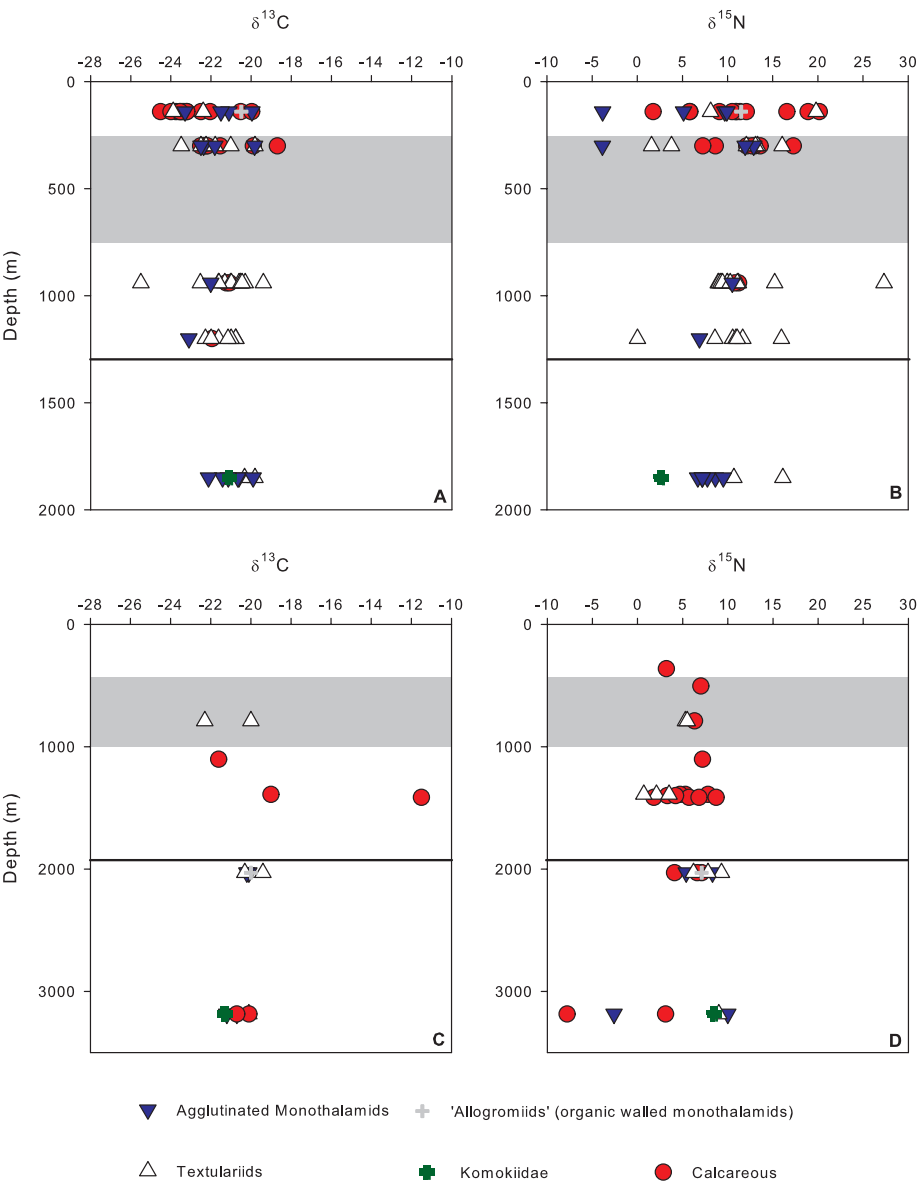


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