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Live foraminiferal faunas (Rose Bengal stained) from the northern Arabian Sea: links with bottom-water oxygenation

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Abstract

Live (Rose Bengal stained) benthic foraminifera from the Murray Ridge, within and below the northern Arabian Sea Oxygen Minimum Zone (OMZ), were studied in order to determine the relationship between faunal composition, bottom-water oxygenation

- $_{5}$ (BWO), pore-water chemistry and organic matter (organic carbon and phytopigment) distribution. A series of multicores were recovered from a ten-station oxygen (BWO: 2–78 μ M) and bathymetric (885–3010 m depth) transect during the winter monsoon in January 2009. Foraminifera were investigated from three different size fractions (63–125 μ m, 125–150 μ m and > 150 μ m). The larger foraminifera (> 125 μ m) were strongly
- dominated by agglutinated species (e.g. *Reophax* spp.). In contrast, in the 63–125 µm fraction, calcareous taxa were more abundant, especially in the core of the OMZ, suggesting an opportunistic behaviour. On the basis of a Principal Component Analysis, three foraminiferal groups were identified, reflecting the environmental parameters along the study transect. The faunas from the shallowest stations, in the core of th
- OMZ (BWO: 2 μM), were composed of "low oxygen" species, typical of the Arabian Sea OMZ (e.g., *Rotaliatinopsis semiinvoluta, Praeglobobulimina* spp.-, *Bulimina exilis, Uvigerina peregrina* type *parva*). These taxa are adapted to the very low BWO conditions and to high phytodetritus supplies. The transitional group, typical for the lower part of the OMZ (BWO: 5–16 μM), is composed of more cosmopolitan taxa tol-
- 20 erant to low-oxygen concentrations (*Globocassidulina subglobosa*, *Ehrenbergina trigona*). Below the OMZ (BWO: 26–78 μM), where food availability is more limited and becomes increasingly restricted to surficial sediments, more cosmopolitan calcareous taxa were present, such as *Bulimina aculeata*, *Melonis barleeanus*, *Uvigerina peregrina* and *Epistominella exigua*. Miliolids were uniquely observed in this last group,
- reflecting the higher BWO. At these deeper sites, the faunas exhibit a clear depth succession of superficial, intermediate and deep-infaunal microhabitats, because of the deeper oxygen and nitrate penetration into the sediment.

1 Introduction

Oxygen minimum zones (OMZs) are present at intermediate water depths (250– 1500 m) along the continental margin of the eastern Pacific, off southwest and northwest Africa, in the Bay of Bengal and in the northern Indian Ocean (Arabian Sea).

- OMZs are defined as areas where the oxygen concentration in the water column is < 22 μM (Levin, 2003; Helly and Levin, 2004). Mostly, they are also areas of high primary productivity where low-oxygen concentrations develop naturally and have persisted over geological timescales (Reichart et al., 1998), due to enhanced organic matter (OM) degradation. Where the OMZs intersect with the continental margin, the</p>
- ¹⁰ ocean floor is exposed to low-oxygen levels. Despite very low oxygen concentrations, protozoan and metazoan assemblages thrive in these environments (e.g. Jannink et al., 1998; Levin et al., 2000; Levin, 2003; Schumacher et al., 2007). These low-oxygen tolerant benthic assemblages can attain high densities, but have typically a low diversity (e.g. den Dulk et al., 1998; Jannink et al., 1998; Schumacher et al., 2007). The poor
- ventilation also impacts biogeochemical processes in the water column and within the sediment. This results in enhanced sequestration of organic material in the sediment. Consequently, OMZs are considered as important organic carbon sinks (e.g. Cowie, 2005; van der Weijden et al., 1999; Koho et al., 2013).
- The intensity of the Arabian Sea OMZ is closely related to the Indian monsoon system (Wyrtki, 1973). During the summer (SW) monsoon (May to September), an intense coastal upwelling develops off the coast of Somalia, Oman and southwestern part of India. This upwelling triggers high biological productivity in the photic zone (e.g. Ryther and Menzel, 1965; Caron and Dennett, 1999; Rixen et al., 2000), leading to high export of organic carbon to intermediate water depths, where it is intensely recycled
- and remineralized. A second high biological productivity event occurs during the winter (NE) monsoon (e.g. Caron and Dennett, 1999; Rixen et al., 2000), due to convective mixing of the sea-surface water (Banse and McClain, 1986; Madhupratap et al., 1996). The intensity of the Arabian Sea OMZ is particularly strong, with oxygen concentrations

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< 2 µM in its core (Paulmier and Ruiz-Pino, 2009). This is not only due to high biological productivity, but is also related to the semi-enclosed nature of the northern Arabian Sea (Wyrtki, 1973; Shetye et al., 1994), in combination with the renewal of intermediate waters by relatively oxygen-poor intermediate water-masses from the South and West (Swallow, 1984; Olson et al., 1993).

- To date, only few studies have dealt with living (Rose Bengal stained) benthic foraminiferal faunas from the Arabian Sea OMZ. These studies have mostly focused on the Pakistan (Jannink et al., 1998; Maas, 2000; Erbacher and Nelskamp, 2006; Schumacher et al., 2007; Larkin and Gooday, 2009) and Oman margins (Stubbings, 1939;
- Hermelin and Shimmield, 1990; Naidu and Malmgren, 1995; Gooday et al., 2000). In addition, Kurbjeweit et al. (2000) and Heinz and Hemleben (2003, 2006) compared the foraminiferal distribution during different periods of the monsoonal cycle in the central, eastern and western parts of the Arabian Sea. Most of these studies described a general zonation of benthic foraminiferal faunas across the OMZ. However, since geo-
- chemical measurements were generally not included in these studies, no clear, specific correlations could be established with the controlling environmental parameters. Foraminiferal abundances and distributions are suggested to be controlled by organic matter supply and oxygen content. Oxygen and organic matter content are inversely correlated parameters which make their interpretation difficult.
- Here, we explore for the first time the distribution and abundant fliving benthic foraminiferal faunas from the Murray Ridge, Northern Arabian Sea. The Murray Ridge is a seamount with its top culminating in the core of the OMZ, and offers an ideal natural laboratory for investigation of biological process along BWO and organic carbon gradients. Live benthic foraminifera were investigated from three size fractions (63–
- 125 μm, 125–150 μm and > 150 μm) ther, for a miniferal data were correlated with geochemical data obtained at the same stations from the studies of Kraal et al. (2012) and Koho et al. (2013), including BWO content, oxygen and nitrate pore water profiles, phytopigments concentrations and organic carbon, in order to examine the influence of environmental parameters on for a miniferal distribution along the study transect.

2 Material and methods

2.1 Study area

During the interdisciplinary PASOM cruise (Process study on the Arabian Sea Oxygen Minimum Zone) in January 2009, a ten station transect was sampled along the

- ⁵ Murray Ridge, north Arabian Sea (Fig. 1), along a strong oxygen gradient. The cruise was designed to cover a transect through the OMZ (885–3010 m), specifically targeting the transition zone from low oxygen to more oxic conditions below the OMZ. All sediment samples were retrieved with a multicorer, allowing the recovery of undisturbed surface sediment samples. The multicorer was equipped with eight cores measuring
- 6.6 cm in diameter and four cores measuring 10 cm in diameter. All cores collected for foraminiferal (Ø 6.6 cm) and geochemical analysis (Ø 6.6 cm and 10 cm) were retrieved from the same multicore cast. Most cores were sliced at 0.5 cm resolution down to 2 cm sediment depth, at 1 cm intervals between 2 and 6 cm and then every 2 cm intervals down to 10 cm. Only the cores used for pore water extraction and organic carbon (C_{org})
- analyses were sliced differently: 0.5 cm intervals in the top 2 cm, 1 cm intervals down to 6 cm and 2 cm intervals down to 10 cm.

2.2 Foraminiferal analyses

Onboard, samples were stained in Rose Bengal (Walton, 1952) in 95% ethanol solution (1 g L^{-1}). They were gently shaken for several minutes and further stored in the

- ²⁰ Rose Bengal solution. In the laboratory, sediment samples were wet sieved into 150-, 125- and 63-µm fractions. To obtain a good staining, the samples were treated again with Rose Bengal for a minimum of 48 h. All well-stained foraminifera were picked wet (50 % ethanol –50 % water) from > 150 µm and 125–150 µm fractions from all levels until 10 cm depth under a binocular microscope. Foraminifera from the small size fraction
- 25 (63–125 μm) were only investigated from the first centimetre of the sediment (0–0.5 cm and 0.5–1 cm).

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The use of the Rose Bengal technique is an inexpensive and easy method (Walton, 1952; Bernhard, 1988, 2000). However, it has been shown that especially in low-oxygen settings, Rose Bengal may stain protoplasm of recently dead foraminifera (Corliss and Emerson, 1990; Bernhard, 2000). Therefore, to minimize the chance of

- ⁵ bias in our counts of living foraminifera, very strict staining criteria were always applied. Specimens were considered living only when all chambers expect the last one were well stained. Furthermore, doubtful specimens were compared with perfectly stained specimens of the same species and non-transparent agglutinated and miliolid taxa were broken to inspect their contents. Fragments of branching and tubular foraminifera
- (e.g. *Hyperammina, Rhizammina*) were not included in the data analyses because of their easily breakable tests, which makes it very difficult to quantify them correctly. Foraminiferal taxonomy was based on commonly used taxonomic reference works (e.g. Loeblich and Tappan, 1988; Jones, 1994) and on some taxonomic studies with emphasis on Arabian Sea and anoxic zones (e.g. Mass, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009); see taxonomic appendix for more details
- For all stations, diversity indices, including species richness (S; count of number of taxa in a sample), Shannon index (H(S)), and evenness (J) were calculated using the free statistical software "PAST" (PAleontological STatistics; Version 2.14; Hammer et al., 2001).
- To better constrain the relationship between species variability and environmental conditions, Principal Component Analysis (PCA) was conducted using the free statistical software "R" (http://cran.r-project.org/). The PCA was run on geochemical/environmental data and on species that contributed for > 2 % to the total abundance of the entire database. Two PCA analyses were carried; the first one investigating the
- entire core (down to 10 cm, > 125 µm fraction), and the second one the top cm of the sediment (0–1 cm, > 63 µm fraction).

2.3 Dissolved oxygen and nitrate

In short, BWO concentrations water-column and bottom-water dissolved O_2 concentrations were measured with an oxygen sensor (Sea-Bird SBE43, accuracy 2%; Sea-Bird Electronics Inc., 2011) that was built into the framework of a conductivity, temperature

- and depth (CTD) profiler (all data published in Koho et al. (2013); see Fig. 2 for details). The pore-water oxygen concentration was determined immediately following core recovery in a temperature controlled laboratory set up at in situ temperature (some data published in Kraal et al., 2012; see Fig. 2 for details). All measurements were done with Unisense oxygen microelectrodes (OXO100 or OXO50). The microelectrodes were two
- $_{10}$ point calibrated at 100 % O_2 saturated seawater (bubbled with oxygen) and in a solution containing sodium ascorbate (0.1 M) to obtain the 0 % reading.

The details of pore-water extraction for nitrate analyses are outlined in Kraal et al. (2012). In short, sediment slicing was carried out in a N_2 -purged glovebox in a temperature controlled laboratory set at in situ temperature (some data are published

- ¹⁵ in Kraal et al., 2012; see Fig. 2 for details). Sediment samples were transferred to 50 ml plastic centrifuge tubes under N₂ atmosphere and centrifuged for 20 min at 4500 rpm outside the glovebox. The centrifuge tubes were then transferred back into the glovebox where the supernatant pore-water was filtered over 0.45 μ m Teflon filters and frozen (-20 °C) until the analyses. Pore-water nitrate concentrations were measured by an
- ²⁰ autoanalyzer at the Royal Netherlands Institute for Sea Research (NIOZ) in Den Burg, Netherlands

2.4 Organic carbon and phytopigment analyses

The details of organic carbon analyses are outlined in Koho et al. (2013) (all data published in Koho et al., 2013; see Fig. 2 for details). In short, the sediment, from which the pore waters were extracted, was further used for solid phase analyses and frozen

the pore waters were extracted, was further used for solid phase analyses and frozen at -20°C until analyses. In the laboratory, sediment was weighted, freeze-dried and decalcified by reacting twice with 1 mol L⁻¹ HCl (4 h and 12 h). After two subsequent

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rinses with ultrapure water, the decalcified samples were freeze-dried and organic C and N were measured with a CNS analyzer (Fisons Instruments NA 1500).

The phytopigments were extracted from a different core than the one used for C_{org} analyses. However, the core came from the same multicore cast. The details of phy-

- ⁵ topigment analyses are outlined in Koho et al. (2013). In short, the samples were stored at -80 °C until analysed and freeze-dried prior to pigment extraction in 10 mL of acetone : water (90 : 10). The full pigment composition was obtained through application of high-performance liquid chromatography (HPLC) equipped with a C₁₈ reverse phase column at the Royal Netherlands Institute for Sea Research (NIOZ – YERSEKE).
- ¹⁰ The calibration was based on working standards prepared from commercially available compounds (DHI, Denmark). The pigment concentrations are reported per μ g/g of sediment.

3 Results

- On the basis of BWO values, four consecutive zones can be distinguished: (1) the core of the OMZ, where BWO is around 2 μ M (Paulmier and Ruiz-Pino, 2009), (2) the lower part of the OMZ with BWO < 22 μ M (Helly and Levin, 2004; Middelburg and Levin, 2009), (3) the dysoxic zone where BWO is between 22 and 45 μ M (Bernhard and Sen Gupta, 1999; Levin, 2003; Helly and Levin, 2004), and (4) relatively well-ventilated deeper "oxic" sites where BWO is >45 μ M (Bernhard and Sen Gupta, 1999; Levin,
- 2003). According to these definitions, our 885 m (PA1) and 1013 m (PA2) stations are located in the core of the OMZ, stations between 1172 and 1379 m (PA3, PA4 and PA5) depths are in the lower part of the OMZ, the 1495 m (PA6) station is located in the dysoxic zone, and stations from 1791 m to 3010 m (PA7, PA8, PA9 and PA10) are in the oxic zone (Fig. 2).

3.1 Environmental parameters

Details of the environmental parameters related to this study have been published in Kraal et al. (2012) and Koho et al. (2013). Here, some new data together with a summary of the existing data sets are presented in order to link them with the foraminiferal distribution and abundance (Fig. 2).

- Organic carbon (C_{org}) and chlorophyll *a* (Chl *a*) contents, for the top first centimetre, progressively change along the study tranect (Fig. 2; Koho et al., 2013). The highest concentrations ($C_{org} = 5.7$ wt%; Chl *a* = 2.6 µg g⁻¹) are observed in the core of the OMZ (885 m and 1013 m). In the dysoxic (1495 m) and oxic zones (1791 m to 3010 m), C_{org} and Chl *a* values are lower, < 2 wt% and < 0.5 µg g⁻¹, respectively (Fig. 2). Min-
- ¹⁰ C_{org} and Chl *a* values are lower, <2 wt% and <0.5 μ g g⁻¹, respectively (Fig. 2). Minimum concentrations (C_{org} = 0.82 wt%; Chl *a* = 0.1 μ g g⁻¹) are found at the deepest site (3010 m). Generally, C_{org} and Chl *a* concentrations decrease with increasing water depth and BWO.

The oxygen penetration depth into the sediment increases along the transect and is

¹⁵ strongly related to the BWO content ($r^2 = 0.8$, g. 2). At the shallowest site (885 m, BWO~ 2 µM), within the OMZ, oxygen penetration is about 0.1 cm whereas at the deepest site (3010 m, BWO ~ 78.3 µM) oxygen is available until 1.8 cm depth. The nitrate penetration depth shows weaker yet relatively strong regression with the BWO content ($r^2 = 0.4$), increasing from the 1.2 cm at 885 m (OMZ site) to 7.5 cm at 3010 m (oxic site).

3.2 Foraminiferal assemblages of the 0-10 cm interval (> 125 µm fraction)

3.2.1 Total abundance

miniferal abundances for the whole cores (down to 10 cm) were investigated in three different size fractions: $125-150 \,\mu$ m, > $150 \,\mu$ m and > $125 \,\mu$ m (Fig. 3a), the

 $_{\rm 25}$ $\,$ >125 μm fraction being the sum of the first two. All size fractions show a similar dis-

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tribution of foraminiferal absolute abundance, and no clear trend is seen along the transect (Fig. 3a).

In the > 125 μ m fraction, total live foraminiferal abundance varies from ~ 90 to ~ 970 ind/50 cm²-, the two extremes being observed in the two sites from the core of the

- OMZ (at 885 m and 1013 m, respectively). The lower OMZ stations (1172 m, 1306 m and 1379 m) show values from 215 ind/50 cm² to 450 ind/50 cm², the dysoxic site (1495 m) contains ~ 970 ind/50 cm², whereas the oxic sites (1791 m to 3010 m) show densities varying from ~ 400 ind/50 cm² to ~ 870 ind/50 cm² (Fig. 3a).
 Agglutinated foraminifera are dominant at all stations. They always constitute more
- ¹⁰ than half of the total assemblage (Fig. 3a). In the lower part of the OMZ (stations at 1172, 1306 and 1379 m), they attain ~ 70% on average. Abundance of hyaline taxa varies along the transect without a clear pattern. Miliolids are only present at the oxic sites (1791 m to 3010 m depth), constituting less than 14% of total standing stocks.

3.2.2 Diversity and dominance

- ¹⁵ A total of 191 species have been identified, of which 71 are agglutinants are hyaline and 21 are miliolid species. Species richness (*S*) differs considerably between the OMZ stations (core and lower part) and the dysoxic sites (1495 m) (Fig. 3a). The lowest number of species (17) is observed at 1013 m depth, in the core of the OMZ. At the dysoxic site (1495 m) a maximum of 68 species is recorded. At the oxic sites (1791 m
- to 3010 m), species richness is more constant, with about 50 species at all stations (Fig. 3a). The species richness trend follows generally that of the total abundance $(r^2 = 0.5)$, suggesting that the number of foraminifera found is largely determined by the sample size. However, in general higher *S* coincides with a higher Shannon index (*H*(*S*)) and a lower evenness (*J*) (Fig. 3a). Species are also distributed fairly evenly at all sites evenness varying from 0.4 to 0.6 (Fig. 3a).
 - Shannon diversity (H(S)) is minimal in the core of the OMZ (2.3 to 2.5). It is higher at the dysoxic and oxic sites, where values around 3.0 are observed. Maximum H(S)

values are observed in the lower part of the OMZ at 1379 m (H(S) = 3.1) and more oxygenated site at 2470 m (H(S) = 3.2) (Fig. 3a).

3.2.3 Distribution patterns of individual species

Foraminiferal species distribution shows important changes along the transect (Fig. 4), although some agglutinated species, such as Reophax agglutinans, Reophax mi-

caceus and Lagennaminna difflugiformis are found at most of the stations.

In the core of the OMZ, where oxygen and nitrate penetration are very shallow (~0.1 cm and ~1.3 cm respectively) faunal density maximum is concentrated in the upper 1.5 cm (Fig. 4). Nevertheless, at both sites, living foraminifera are found down to 3-

- ¹⁰ 4 cm. The fauna of both stations is dominated by the agglutinated species Reophax agglutinans, Lagenammina difflugiformis, Ammodiscus sp., Cribrostomoides cf. jeffreysii, Verneuilinulla propingua, Reophax dentaliniformis and Hormosina guttifera and the hyaline species Uvigerina peregrina type parva, Rotaliatinopsis semminvoluta, Praeglobobulimina sp., Fursenkoina mexicana, Bulimina exilis, Chilostomella oolina, Gyroidina soldanii and Fursenkoina sp.
- In the lower part of the OMZ (1172 to 1379 m), maximum densities are consistently observed in the first cm of the sediment, but small numbers of stained specimens are present down to 6-8 cm depth (Fig. 4). Here, the oxygen and nitrate penetration depth increase to 0.6 cm and 3.5 cm depth, respectively. The faunas of this zone are domi-
- 20 nated by the agglutinated species Reophax cf. spiculifer, Reophax agglutinans, Lagenammina difflugiformis and Verneuilinulla propingua and the hyaline species Bulimina cf. mexicana, Ehrenbergina trigona, Melonis barleeanus, and Uvigerina peregrina. The infaunal taxa are dominated by agglutinated taxa, among which several Reophax species, whereas only some scarce individuals of the hyaline taxa Chilostomella oolina and Fursenkoina sp. are found deeper in the sediment (3-4 cm).
 - At the dysoxic (1495 m) and oxic (1791 to 3010 m) stations, live foraminifera are found down to 10 cm depth (Fig. 4), although maximum densities are recorded in the oxygenated first two cm of the sediment (Fig. 4).

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At the dysoxic site (1495 m), Lagenammina difflugiformis, Reophax agglutinans, Bulimina aculeata, Uvigerina peregrina dominate the fauna. Both B. aculeata and U. peregrina show two in-sediment maxima here: in the first half cm, which is well oxygenated and at 3–5 cm depth, below the oxygen and nitrate penetration depth.

- At the oxic sites (1791 m to 3010 m), miliolid taxa appear (Fig. 4). Among these, Pyrgo murrhina is most frequent and is found at the 1970 and 2470 m sites (Fig. 4). Other species, with maxima close to the sediment surface, include Uvigerina peregrina, Lagenammina difflugiformis, Bulimina aculeata, and Reophax agglutinans. Also the density of intermediate and deep infaunal species increases at these sites. Melonis
- barleeanus is found down to 3-4 cm (1791 to 2470 m) and Fursenkoina sp. is found in 10 small numbers from 1791 to 2470 m, down to the 6-8 cm level. Furthermore, Reophax species are found down to 10 cm depth regardless of the absence of oxygen and nitrate in the sediment. Different species are found at 3010 m site, Here, faunas are dominated by agglutinated species, such as, Hormosina guttifera, Reophax agglutinans and Lagenammina difflugiformis, and by the hyaline Oridorsalis umbonata.

3.3 Foraminiferal faunas of the 63–125 µm fraction (0–1 cm)

3.3.1 Total foraminiferal abundance and diversity

The 63–125 µm fraction has only been examined in the topmost 1 cm from the same cores-site investigated for the > 125 μ m fraction (Fig. 3b). In the first cm, all investigated size fractions ($63-125 \,\mu$ m, > 125 μ m) show a similar pattern, and no clear trend is seen 20 along the transect (Fig. 3b).

On average, for miniferal abundances in the > 63 μ m fraction of the 0–1 cm level (Fig. 3b) are at least twice as high as the densities in the > $125 \,\mu$ m fraction. The abundance of small (63–125 µm) for minifera is particularly high in the core and lower part of

²⁵ the OMZ and at the dysoxic station (1495 m) where this fraction accounts for 62-84 % of the total foraminiferal abundance (Fig. 5). At the oxic stations (1791 m to 3010 m), for aminifera of the 63–125 μ m fraction and > 125 μ m fraction are more even; the 63– 125 μ m fraction contributing for 44–49 % of the total assemblage. At 3010 m, the 63–125 μ m is dominant again, accounting for ~ 67 % of the total fauna (Fig. 5).

In general, the $63-125 \,\mu\text{m}$ fraction is dominated by calcareous taxa (~ $30-65 \,\%$). Consequently, in the > $63 \,\mu\text{m}$ fraction, the relative abundance of calcareous taxa is higher than in the > $125 \,\mu\text{m}$ fraction (Fig. 3b).

Similarly to > 125 μ m fraction (top 10 cm), Shannon diversity (*H*(*S*)) of the > 63 μ m fraction (top 1 cm) is relatively low (2.8) in the core of the OMZ (885 m and 1013 m), but increases to 3.3 to 3.5 at deeper sites (1172 m, 1306 m and 1379 m) (Fig. 3b). Species richness has a similar trend as *H*(*S*) (Fig. 3b). Evenness values do not show a very

clear trend, although low evenness values are generally found where high values of species richness and H(S) are recorded. In general, all diversity indices are systematically higher when the 63–125 µm size class is included (Fig. 3b).

3.3.2 Faunal composition of the $> 63 \mu m$ fraction (0–1 cm level)

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Figure 5 shows the species distribution along the transect for the > 63 μm fraction
 (0–1 cm only). As expected, the foraminiferal species repartition observes important change between sites.

Small hyaline species, such as *Bolivina seminuda* and *Nuttalides pusillus*, are common in the OMZ core (885–1013 m). In addition, small individuals of *Uvigerina peregrina* type *parva* are abundant. The agglutinated species *Trochammina* sp.1, *Veleroni*-

noides wiesneri and Reophax bilocularis are also only observed abundantly in the 63–125 µm fraction. As in the larger size classes, many OMZ taxa are either restricted to these sites, or occur only in very low abundances at deeper sites.

In the lower part of the OMZ, small hyaline species, *Gyroidina* sp.2, *Bolivina* aff. *dilatata, Bolivina* sp. 1, *Nuttalides pusillus, Gavelinopsis translucens* and *Epistominella*

exigua, are abundant. In addition, as in the > 125 μm fraction, *Reophax* species are common at these sites (Fig. 5).

The foraminiferal assemblages at the dysoxic site (1495 m) and in the oxic zone (1791 m to 3010 m) show high abundances of *E. exigua, G. subglobosa, Nutallides*

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spp., *U. peregrina*, *M. barleeanus*, *Pullenia* spp., *Reophax* spp. and *Cribrostomoides* spp. (Fig. 5). Of these taxa, only *Nuttalides* spp. is largely restricted to the 63–125 μ m fraction and others are also found in abundance in the > 125 μ m fraction. At the deepest and best ventilated sites (1970 and 2470 m depth), *Pyrgo murrhing* goella sphaera and *Pyrgo lucernula* are the best represented miliolid taxa (Fig. 5).

and *Pyrgo lucernula* are the best represented milliolid taxa (Fig. 5)

3.4 Foraminiferal assemblages and relation to environmental parameters: principal component analyses (PCA)

Our PCA analysis is based on the relative abundances of the dominant species (> 2 %) in the > 125 μ m (0–10 cm) size fraction and the geochemical data (Fig. 6). Axis 1 explains about ~ 33 % and axis 2 about 15 % of the total variance. Three faunal groups

- are clearly identified in the PCA analyses (Fig. 6). Group 1 is characterized by species living in the core and lower part of the OMZ (Figs. 4 and 6), and plot together with high C_{org} and pigment values. Group 2 mainly consists of species present in the lower part of the OMZ and in the dysoxic zone (Fig. 6). It seems to represent a transitional as-
- semblage between the faunas of the OMZ and of the oxic sites (Fig. 6) ally, group 3 contains the species dominating the faunas at the deeper, oxic sites. They plot together with high BWO, nitrate and oxygen penetration and water depth.

A second PCA analysis was performed on the basis of the relative abundance data of dominant species in the > 63 μ m fraction (0–1 cm). As in the PCA presented above, three very similar groups were obtained (see Supplement C), with only few changes in species composition (e.g. *Nuttalides pusillus, Bolivina* spp.) are observed. Due to the

- similarity of the two PCA analyses, only the PCA based on the > 125 μ m size will be discussed further. We feel this one is more robust as it is based on the complete core with foraminifera analysed down to 10 cm depth in sedimen preover, most paleo-
- ceanographic studies are based on > 125 μ m fraction.

4 Discussion

4.1 Environmental conditions and their implications to benthic foraminifera

The organic carbon availability in the benthic environment depends to a large degree on primary production (PP) in the surface waters, and the subsequent flux of organic

- remains to the seafloor. In the Arabian Sea, these parameters are strongly linked to the monsoonal cycle. The SW (June-September) and NE (December-March) monsoons lead to intense seasonal changes of surface hydrography and vertical particle flux to the deep-sea (Nair et al., 1989; Haake et al., 1993; Rixen et al., 1996). Nutrient enrichment in surface waters, and thus maximum PP, occur during times of moderate to strong
- winds associated with SW and NE monsoons (Banse and McClain, 1986; Banse, 1987; Rao et al., 1989). Intensity of the NE and SW monsoon, and also the ensuing PP, show important interannual variability (Wyrthing 1973; Burkill et al., 1993). Our samples were taken in January 2009, during the wing NE monsoon, when PP was quite high (surface Chl *a*~0.5–0.7 mg m⁻³, www.nasa.gov). During the intermonsoon (April–May
- and October–November), PP is lower at this site (Chl $a \sim 0.3-0.5$ mg m⁻³, www.nasa. gov) and higher during the summer SW monsoon (Chl $a \sim 0.7-0.1$ mg m⁻³, www.nasa. gov).

Benthic foraminifera generally respond to the quantity and quality of the organic material arriving to the sea-floor (e.g. Jorissen et al., 2007; Mojtahid et al., 2009). In our

- samples, the percentage of C_{org}, an integrative parameter indicative of OM quantity (Fig. 2) shows a clear exponential decline with increasing BWO content (Koho et al., 2013). Chl *a* content, giving somewhat more information about the quality of OM available for benthic organisms, describes a decrease with increasing depth and BWO content (Fig. 2). Other parameters that could potentially influence benthic foraminiferal
- distribution are the oxygen concentration in the bottom waters, and the oxygen and nitrate penetration into the sediment, which have been partly described by Kraal et al. (2012). These three parameters are strongly interdependent and related to amount of C_{org} arriving at the seafloor and its degradation in the sediment during the early di-

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agenesis. This results in a progressive increase in oxygen and nitrate penetration into the sediment with increasing water depths and BWO and decreasing C_{ora} .

4.2 Foraminiferal densities and diversities

- Despite food availability generally considered as the main ecological parameter con trolling the foraminiferal distribution and abundance on continental margin settings (e.g. Jorissen et al., 1995, 2007; Koho, 2008), the standing stocks of foraminifera on the Murray Ridge do not show a clear trend with any
 measured environmental parameter, including C_{org}, Chl a BWO or water depth (Figs. 2 and 3). This observation appears to be in contrast with previous studies of foraminifera from the Arabian Sea OMZ where
- a decreasing of the TSS with water depth was observed (Jannink et al., 1998; Schumacher et al., 2007; Fig. 7). However, since very few environmental parameters were included in these studies, a genuine comparison of foraminiferal abundances remains difficult. The work of Schumacher et al. (2007) was performed off the Pakistan continental margin during the spring intermonsoon (March-April 2003) from 136 m to 1870 m
- ¹⁵ depths. When comparing foraminiferal abundances from similar depths, higher values are observed in our study transect (Fig. 7). We would expect the opposite since seasurface Chl *a* content (~ 1–2.5 mg m⁻³; www.nasa.gov) and BWO were higher during the sampling time of Schumacher et al. (2007) (Fig. 7). The study of Jannink et al. (1998) investigated two transects (from 500 to 2000 m depths) from the Pakistan
- ²⁰ margin (fall intermonsoon, October 1992), which showed large differences (a 4-fold difference) in foraminiferal abundances (Fig. 7). The authors tentatively explained it by the different sampling times: a three week time lag between the two samplings would have led to a very different OM input data are generally similar to foraminiferal abundances from Jannink et al. (1998), especially in transect I (Fig. 7). Kurbjeweit et al. (1998), especially in transect I (Fig. 7).
- al. (2000) compared six sites (from 1916 to 4425 m) across the Arabian Sea during the fall intermonsoon (September/October 1995). Although only two sites are comparable with our transect (~ 1916 m and ~ 3100 m), similar foraminiferal abundances are observed (Fig. 7).

When the finer size fraction (63–125 μ m, first cm only) is also examine miniferal TSSs increase considerably (Fig. 3b). Small-sized foraminifera account for up to 72% of the total assemblage at the OMZ sites whereas at deeper sites they count for 54% (Fig. 5). Similar observations were made in the Pakistan margin of the Arabian

Sea OMZ (Jannink et al., 1998; Larkin and Gooday, 2009). The dominance of small foraminifera could partly be due to pulsed Composition provide the second state of the second state of

Unlike foraminiferal TSSs, diversity parameters show somewhat clearer trends along the studied transect (Fig. 3). Within the OMZ, diversity tends to be lower than at deeper

- sites, which is in agreement with previous studies in the area (Jannink et al., 1998; Schumacher et al., 2007). The lower diversity in the core and lower part of the OMZ could be the result of a disappearance of species sensitive to very low oxygen concentrations. Alternatively, it could be that the very high (and potentially episodic) food input favours opportunistic taxa, thereby decreasing the diversity indices hough most
- ¹⁵ benthic foraminifera are supposed to be insensitive to low BWO down to at least 22 μM (1 mL L⁻¹) (Jorissen et al., 2007), the very low concentrations in the core of the OMZ are probably beyond the tolerance levels of many species.

4.3 Dominance of agglutinated species along the study transect

The high proportion of agglutinated species (up to 72%) along the studied transect seems independent of the BWO or C_{org} content. Indeed, some agglutinated species (*Reophax* spp. and *Lagenammina difflugiformis*) are present all along the transect. Earlier studies from the Arabian Sea have not observed such a high dominance of agglutinated foraminifera. Although, Kurbjeweit et al. (2000) described a strong dominance of agglutinated species at the deepest sites of their transect. However, these sites were located below our depth-transect between 1916 to 4425 m.

The ecological preferences of agglutinated foraminifera are not well understood. It has been suggested that they are less dependent on fresh food input than calcareous taxa (e.g. Koho, 2008; Phipps, 2012a). Therefore, agglutinated taxa could colonise en-

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vironments less suitable for calcareous taxa (Phipps, 2012a). A clear decline is seen both in the quality and quantity of OM along our study transect (Koho et al., 2013). Therefore, the lower OM quality could limit calcareous species and favour the expansion of agglutinated ones.

- ⁵ Alternatively, the abundance of agglutinated foraminifera may be related to the carbonate chemistry of the study setting. Due to the enhanced organic matter recycling and associated CO₂ release into the pore waters, the benthic habitat may become acidified (Berger, 1970). This acidification would make carbonate minerals less stable and thus the habitat would be less suitable for hyaline foraminifera. Visual inspection of
- samples revealed relatively poorly preserved (planktonic) foraminiference is was especially evident in samples from the transitional setting towards more ventilated sites. Furthermore, the bottom water carbonate saturation index (Ω) was also calculated to be < 1, suggesting calcite under saturation, at four sites (885 m, 1306 m, 1791 m, 1970 m) (Reichart, unpublished data
- Previous work on agglutinated foraminifera has also suggested that in general, agglutinated foraminifera are less tolerant to low-oxygen conditions than calcareous foraminifera (Moodley et al., 1997; Gooday et al., 2000, 2001, 2009; Neira et al., 2001). However, the strong dominance of agglutinated species at all stations of our BWO gradient implies the contrary; they appear to be just as tolerant of strongly oxygen depleted conditions as calcareous taxa.

4.4 Species zonation

Three faunal groups were identified by PCA analyses (Fig. 7). These three groups are very distinct in their faunal composition, which present a clear succession along the transect, mainly reflecting the change of BWO and OM. Group 1 is characterised by

the taxa inhabiting the core of the OMZ, Group 2 the lower OMZ and Group 3 the dysoxic and oxic taxa. In the following three paragraphs, we will discuss the ecology of the dominant taxa of each of these three groups.

4.4.1 Taxa dominating the faunas in the core of the OMZ

In the PCA, thes a plot together with positive values of quantitative C_{org} and OM quality indicator (Chl *a*). This suggests that they are favoured by a high content of relatively fresh OM. The OMZ taxa are mainly composed of hyaline species, which are

- s exclusively found in the OMZ (*Bulimina exilis, Uvigerina peregrina* type *parva, Rotali-atinopsis semiinvoluta, Praeglobobulimina* sp. and *Fursenkoina* sp.) (Fig. 6). Also some agglutinated species plot in this group (*Reophax agglutinans, Reophax dentaliniformis, Cribrostomoides* cf. *jeffreysii* and *Ammodiscus* sp.), which is not surprising since agglutinated taxa represent ~ 70 % of the TSS (> 125 µm fraction) in the OMZ (from 885 m to 1306 m) (Fig. 3a).
 - Among the agglutinated taxa, only two species appear strictly restricted to the OMZ: *Ammodiscus* sp. and *Cribrostomoides* cf. *jeffreysii* (Fig. 4). *C*. cf. *jeffreysii* has been described by Maas (2000) and Schumacher et al. (2007) in the core of the OMZ. Also the presence of *Ammodiscus* sp. in the OMZ is consistent with previous observations
- ¹⁵ from the Arabian Sea (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007), which characterised this taxon as highly tolerant to low-oxygen conditions and feeding on relatively fresh O mmodiscus sp. was described as *A. cretaceous* from 233 m to 902 m water depths by Maas (2000).
- Reophax agglutinans, was present along the whole depth transect, however in the PCA analyses showed to OMZ taxa. The omnipresence of this taxon suggests that it is less dependent on the availability of labile OM, than other species characterising the core of the OMZ.

Calcareous taxa in general present a much clearer species succession than agglutinated ones (Fig. 4), and therefore appear to be more sensitive to the ecological param-

eters (BWO and OM quantity and quality). These observations also suggest that these hyaline species are very tolerant to low-oxygen conditions. *Bulimina exilis* is one of the most common species encountered in the core of the OMZ from the North-Eastern Arabian Sea (Jannink et al., 1998; Schumacher et al., 2007; Larkin and Gooday, 2009).

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Previous studies have demonstrated that this taxon thrives under conditions of high input of relatively fresh phytodetritus (Caralp, 1989; Jannink et al., 1998) is able to survive in environments that are very low in oxygen (e.g. Jannink et al., 1998; Mass, 2000). Further, *B. exilis* is a common species of high productivity and/or low-oxygen

- environments in the OMZ of SW Africa (Schmiedl et al., 1997) and off Cape Blanc (Morigi et al., 2001), Another common species in this group is *R. semiinvoluta*, which occurs only at the 885 m and 1172 m stations. Our data confirms previous findings of *R. semiinvoluta* in the Arabian Sea (Jannink et al., 1998), and suggest that this species is specific to the OMZ of the Arabian Sea, and adapted to live under very low-oxygen
- ¹⁰ conditions with a strong and intermittent flux of fresh organic matter. In a paleoceanographic study of the Arabian Sea, den Dulk et al. (1998), suggested that *R. semiinvoluta* may rapidly respond to changes in BWO, occurring at the base of the OMZ where it could thrive seasonally. However our data cannot confirm this hypothesis due to the fact that the samples reflect a single moment in time rather than a time series. *Prae*-
- ¹⁵ globobulimina sp. is also only present at the 885 m and 1013 m sites. This specie is similar to the one described in den Dulk et al. (2000), Maas (2000) and Schumacher et al. (2007). Likewise, in these studies, *Praeglobobulimina* sp. is restricted to the core of the OMZ. Therefore, we suggest it is adapted to the very low oxygen conditions and may feed on relatively fresh OM.
- Uvigerina peregrina inhabits a wide range of continental slope and margin environments, including relatively low-oxygen environments (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007) but also relatively well-ventilated sites (e.g. Fontanier et al., 2005; Koho, 2008; Mojtahid et al., 2010). It abounds in settings with relatively highly OM content (e.g. Lutze and Colbourn, 1984, Hermelin and Shimmield, 1990;
- Schmiedl and Mackensen, 1997) but also in areas with more moderate OM enrichment (e.g. Fontanier et al., 2005; Mojtahid et al., 2010). It has been described previously as a dominant faunal element in the Arabian Sea OMZ (e.g. Hermelin and Shimmield, 1990; Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007). In this study, we observed two different morphotypes of *U. peregrina* (Fig. 8). Specimens found in the

core of the OMZ are somewhat smaller, smoother and have weakly developed lower costae. They correspond to *U. peregrina* forma *parva* of Lutze (1986) (Figs. 3–4 and 8). At deeper sites, specimens have larger and higher costae and become more spinose (Figs. 1–2 and 8). These specimens present morphotypes from typical *U. peregrina*

- ⁵ sensu stricto to *U. auberiana* (d'Orbigny, 1839) (fully spinose specimens). A similar morphological variation in *U. peregrina* has been noted in the Eastern Atlantic (e.g. Lutze, 1986; Schönfeld, 2006; Koho, 2008; Gooday and Jorissen, 2012). *Uvigerina peregrina* forma *parva* and *U. peregrina* do not occur together. *U. peregrina* type *parva* is only present in the core of the OMZ where BWO is very low and where food availabil-
- ity is probably much higher, whereas *U. peregrina* occurs from 1306 to 2407 m (Fig. 4).
 Because most of the deeper sites show a continuous variability from *U. peregrina* s.s.
 to *U. auberiana*, they have been counted together as *U. peregrina*. These two taxa appear to be indicative of slightly higher BWO and lower OM supplies.

4.4.2 Dominant taxa of the lower OMZ

- These are focussed at the 1172 m and 1306 m sites, where the BWO content is between ~ 5 and ~ 17 μM (Fig. 6), and where C_{org} content is still high (3.5–2.80 wt %). The major species of this group are: *Reophax* cf. *spiculifer*, *Ehrenbergina trigona*, *Pullenia bulloides*, *Globocassidulina subglobosa*, *Cribrostomoides brady*, *Bulimina* cf. *mexicana* and *Verneuilinulla propinqua*. In the literature, most of these species have been described as tolerant to relatively low-oxygen conditions (e.g. den Dulk et al., 1998, 2000):
- scribed as tolerant to relatively low-oxygen conditions (e.g. den Dulk et al., 1998, 2000; Jannink et al., 1998; Schumacher et al., 2007).
 Although Q. subschere is a metion in the lower part of the QMZ it is also.

Although *G. subglobosa* is a major species in the lower part of the OMZ, it is also found in small numbers at deeper sites. *G. subglobosa* is known to have a cosmopolitan character; it is found in the Atlantic Ocean (Gofas, 1978; Weston, 1982; Murray et

al., 1986), in the central Pacific (Gofas, 1978) and in the Indian Ocean (Lagoe, 1977; Corliss, 1983b; Peterson, 1984). Its presence in the small fraction at deepest sites can be explained by the opportunistic behaviour: rapid colonization of episodic fresh phytodetritus (Jorissen et al., 2007 and reference therein). The environmental preferences

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of *E. trigona* are poorly known. Along the sampled transect this species is only present at the 1306 and 1379 m sites. The presence of *E. trigona* in the lower part of the OMZ is consistent with the observations of Hermelin and Shimmield (1990), who found this species at mid bathyal depths (770 m, 955 m and 1048 m) within and below the core of

⁵ the OMZ. These authors also suggested that *E. trigona* could be an endemic species to the Arabian Sea OMZ environment. If so, *E. trigona* could be an indicator species for the lower part of the OMZ, which would make it a potential tracer for past variability of the base of the OMZ.

Little is known about ecological preferences of agglutinated species in this group (*R.cf. spiculifer, C. brady, V. propinqua*). However, based on our data, these species

¹⁰ (*R*.ct. spiculiter, *C. brady, V. propinqua*). However, based on our data, these species may be tolerant to relatively low-oxygen condition, with elevated levels of OM still available.

The depth limit of the lower OMZ has been shown to vary over geological history (e.g. Reichart et al., 1997, 1998; den Dulk et al., 2000; Schmiedl and Leuschner, 2005).

- Den Dulk et al. (2000) observed fluctuations in the depth of the OMZ based on the benthic foraminiferal assemblages during the last 225 000 years. Further, Schmiedl and Leuschner (2005) suggested these vertical shifts of the OMZ boundary through time correspond to the combined effects of enhanced OM fluxes and changes in the intensity of deep-water circulation. The foraminifera living in this transitional environment at the
- lower part of the OMZ can be used to track these changes in the past and aid in reconstruction of OMZ dynamics. The presence of both cosmopolitan (e.g. *Pullenia bulloides* and *Cribrostomoides brady*) and potentially endemic species (*Ehrenbergina trigona*), make this assemblage unique to Arabian Sea.

4.4.3 Taxa dominant at more oxygenated deeper sites

²⁵ Rather diverse foraminiferal assemblages, including miliolids, hyaline and agglutinated species (Fig. 6), are found at all deeper sites, with BWO > 26μ M. At these sites, OM availability is lower, as is indicated by the lower ChI *a* and C_{org} contents (Fig. 2).

This third group defined by the PCA analysis is mainly dominated by agglutinated species such as *Lagenammina difflugiformis*, *Reophax micaceus*, *Hormosina guttifera*, *Reophax subfusiformis* and *Trochammina* spp. The increase in proportions of agglutinated species towards deeper waters is usually attributed to increasingly oligotrophic

- ⁵ conditions, resulting in a change in OM quantity and quality (e.g. Ohga and Kitazato, 1997; Schmiedl et al., 1997; Kurbjeweit et al., 2000; Koho, 2008; Phipps et al., 2012). However, this assemblage contains also hyaline taxa, the most common ones being *Bulimina aculeata, Oridorsalis umbonata, Melonis barleeanus, Epistominella exigua* and *Uvigerina peregrina*. The presence of *B. aculeata* below the OMZ is consistent
- with previous studies of the Arabian Sea (e.g., Zobel, 1973; Jannink et al., 1998). *O. umbonata* has been observed in various well-oxygenated environments. Mackensen et al. (1995) relate this species to environments with low food supply. Also, the conspicuous occurrence of the intermediate infaunal taxon *M. barleeanus* suggests a relative dominance of refractory OM (Caralp, 1989; Koho et al., 2013) whereas the presence
- ¹⁵ of *E. exigua* euggests episodic fresh phytodetritus reaching the seafloor (Gooday et al., 1996). *E-gua* is mainly present in the 63–125 μm size fraction (Fig. 5) below the OMZ. However the OM data here, do not suggest the presence of fresh OM. Hence, *E. exigua* may also feed on more refractory OM. In our dataset, miliolids (*Pyrgo murrhina, Pyrgoella sphaera, Pyrgo lucernula*) are absent from the core and lower part of the
- OMZ, and are exclusively found in fair numbers below the OMZ. Similar observations have been made in other Arabian Sea studies (e.g. Jannink et al., 1998; den Dulk et al., 2000; Schumacher et al., 2007). In general, miliolids are rare or absent in oxygen deficient environments (e.g. Mullineaux and Lohmann, 1981; Nolet and Corliss, 1990; Jorissen et al., 1995) thereby implying that they could be more sensitive to oxygen
- stress compared to other species. In a study of two piston cores collected from 920 m and 1470 m, Den Dulk et al. (2000) suggested that a high abundance of miliolids could reflect periods of periodically increased BWO. In fact, Den Dulk et al. (2000) speculate that the percentage of miliolids could be a robust proxy for reconstructing past changes in bottom and pore-water oxygenation. However, miliolid tests, due their high Mg/Ca

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ratio, are more sensitive to alkalinity changes of the bottom-water. Acidic bottom waters, such as those in the core of the OMZ potentially would result in the loss of these shells.

4.5 Vertical distribution

- Generally, highest foraminiferal abundances are found in the first cm of the sediment. Towards deeper sites, with increased BWO and deeper oxygen and nitrate penetration into the sediment, the vertical range of the foraminiferal faunas increases. Only at the 885 m station, the density maximum was not found in the topmost level, but in the 1–1.5 cm interval, roughly corresponding to the depth of maximum nitrate penetration
- (Fig. 4). However, the very similar composition of the upper three half cm samples, with an absence of exclusively infaunal taxa, suggests that this deeper maximum could be an artifact, due to the mixing of the very soupy superficial sediment during sample retrieval. In the lower part of the OMZ (1172 to 1379 m), oxygen penetration is only 1 to 6 mm, whereas living foraminifera are present in fair numbers down to 2 to 5 cm
- ¹⁵ depth. This maximum microhabitat depth roughly corresponds to the maximum depth of nitrate penetration (2.5 to 3.5 cm). At 1495 and 1791 m depths, substantial numbers of living foraminifera are found until 5 to 6 cm depth, much deeper than maximal oxygen and nitrate penetration. At the deepest sites, the living fauna tends to be limited to the upper 3 cm of the sediment. At 3010 m depth, the living faunas become very scarce
- ²⁰ below 3 cm, well above the limit of nitrate penetration. These species distribution may also be influenced by macrofaunal bioturbation, which may have transported some specimens below or above their preferential living-depth. However, both calcareous and agglutinated foraminifera show an exponential decrease in standing stock toward sediment-depth.
- The distribution of calcareous and agglutinated foraminifera in the sediment appears to be systematically different. While the calcareous taxa are mainly concentrated in the first three cm (0–3 cm depth), the agglutinated species are mostly present down to 10 cm. In the core of the OMZ, *Bulimina exilis* and *Fursenkoina mexicana* display

clear infaunal maxima, the latter species occurring deeper than the first one (Fig. 4). At 885 m depth, *B. exilis* is present in maximum numbers in the 1.5–2 cm level, slightly deeper than the maximum nitrate penetration, whereas *F. mexicana* occurs between 1.5 and 3 cm depth, in completely anoxic conditions. Another *Fursenkoina* species is

- ⁵ present at stations between 1791 and 2470 m, where it occurs in low numbers in a deep infaunal microhabitat, in completely anoxic sediments between 4 and 8 cm depth. Consistent with our study, *B. exilis, F. mexicana* and *Fursenkoina* sp. are mainly described as intermediate and deep infaunal taxa living below the oxygen penetration depth (Jorissen et al., 1998). *Melonis barleeanus* appears in fairly high numbers in a specific depth.
- intermediate infaunal microhabitats at all stations from 1495 to 3010 m depth. Its microhabitat depth mimics the oxygen penetration depth, and gradually deepens from 0 to 1 cm at 1495 m, 0.5/1 to 3 cm at 1791 and 1970 m, and 2 to 3 cm at 3010 m depth. The occurrence of *M. barleeanus* below the oxygen penetration depth and above the nitrate penetration depth is consistent with numerous previous studies (e.g. Jorissen).
- et al., 1995, 1998; Koho, 2008; Mojtahid et al., 2010). It appears that this species is able to thrive in absence of oxygen as long as nitrate is present in the pore-water. The presence of intermediate and deep infaunal taxa in anoxic sediments could be explained by a facultative anaerobic metabolism of the concerned species. It is possible that in absence of oxygen, these taxa are able to shift to nitrate reduction. Such
- a facultative anaerobic metabolism is also envisaged for some of the species living in the core of the OMZ, where the BWO is very low. It has been demonstrated recently that many foraminiferal species accumulate intracellular nitrate in low-oxygen settings (Pina-Ochoa et al., 2009). However, until now, nitrate respiration has only been shown for a limited number of taxa (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010;
- ²⁵ Koho et al., 2011). Unfortunately, no measurements of denitrification rates have been performed for the dominant species of the Arabian Sea OMZ so that the possibility of an anaerobic metabolism of some of the dominant OMZ taxa remains speculative.

The agglutinated species here are mainly composed of *Reophax* species (*Reophax* agglutinans, *Reophax dentaliniformis*, *Reophax micaceus*) and *Lagenammina difflugi-*

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formis (Fig. 4). Unlike hyaline taxa, the distribution of these agglutinated taxa does not seem to follow a geochemical boundary. Instead their distrbution appears to be independent of oxygen and nitrate penetration depth. Phipps (2012a) suggested that most agglutinated taxa have lower trophic requirements than calcareous taxa which would

enables them to live in deeper, more food-limited sediment layers. Alternatively, some authors suggested that agglutinated species would prefer living deeper in the sediment to avoid competition with calcareous species (e.g., Buzas et al., 1989; Van der Zwaan et al., 1999; Gooday, 2003; Phipps, 2012a).

5 Conclusions

- ¹⁰ Foraminiferal standing stocks from the Murray Ridge do not show any clear correlation with any of the measured environmental parameters. This observation is inconsistent with previous studies from the Arabian Sea. The standing stocks appear to reflect a complex mix of the environmental parameters, which cannot be directly uncoupled here.
- ¹⁵ The diversity of benthic foraminifera change with bottom water oxygenation. The lowest diversities are generally seen in the core of the OMZ and the highest in the lower part of the OMZ and the deeper more ventilated sites. The prevailing, extremely low oxygen concentrations in the core of the OMZ (BWO $\pm 2 \,\mu$ M) may limit the occurrence of species in this zone, leading to low diversity assemblage
- Agglutinated foraminifera form a dominant part of the foraminiferal assemblage in the Murray Ridge. Up to 72 % of the species assemblage is made of agglutinated taxa. Their distribution seems independent of the BWO and they are present in all sites, including the core of the OMZ. Therefore, agglutinated foraminifera appear to be equally tolerant to oxygen depletion than hyaline taxa. In the Murray Ridge, the dominance of
- agglutinated taxa may be related to relatively corrosive bottom water conditions as a result of enhanced organic matter cycling, limiting the occurrence of hyaline species. In

addition, the agglutinated foraminifera may be favoured by the relatively refractory OM present in the lower OMZ and at the more oxic sites.

Three clear foraminiferal zones were observed across the study transect: (i) species inhabiting the core of the OMZ, (ii) species observed in the transitional zone, including

the lower part of the OMZ and the dysoxic area, (iii) species found in the relatively oxic sites. The distribution of these groups is closely tied to environmental parameters, including redox conditions and food availability. In further application, these three groups can be used to reconstruct the OMZ dynamics in the Arabian Sea.



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Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/10/15257/2013/ bgd-10-15257-2013-supplement.zip.

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Fig. 1. (a) Study area and stations location on the Murray ridge, northern Arabian Sea. The red square correspond to the bathymetric – oxygen transect in **(b)**. **(b)** Water depths of the studied stations and their location within the bottom water oxygenation transect (CTD oxygen values from this study). The seafloor line was extrapolated between stations.

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Fig. 2. Environmental parameters: bottom-water oxygenation, organic carbon (C_{org} ; 0–1 cm), chlorophyll *a* (Chl *a*, 0–1 cm), oxygen and nitrate penetration-depths. In red: the results from this study; In blue: The results published in Koho et al. (2013); in black: The results published in Kraal et al. (2012).



Fig. 3. (a) Live (Rose Bengal stained) foraminiferal abundances (individuals/50 cm²) in the 125–150 µm, > 150 µm and > 125 µm fraction for the entire core (0–10 cm) and foraminiferal biodiversity indices (in the > 125 µm fraction) along the sampling transect. **(b)** Live foraminiferal abundances (individuals/50 cm²) in the 63–125 µm, > 125 µm, > 63 µm fractions for the first cm (0–1 cm) of the sediment and foraminiferal biodiversity indices (in the > 63 µm fraction) along the sampling transect.

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Fig. 4. (Caption on next page.)

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Fig. 4. Vertical densities (individuals/50 cm³) and abundances (individuals/50 cm³) of the dominant live foraminiferal species (> 2 % for each station) in the > 125 µm fraction. The first panel represents the total foraminiferal densities. The black dotted line refers to the oxygen limit penetration (cm) into the sediment, and the red dotted line to the nitrate depth penetration (cm). The second panel represents the vertical distribution of the dominant agglutinated taxa. The third panel represents the vertical distribution of the dominant hyaline and miliod taxa. Species of same gender were grouped under the same color. Note the different horizontal scale between panels.



Fig. 5. (a) Species composition and abundance (individuals/50 cm³) in the > 63 μ m fraction (sum of > 125 μ m and 63–125 μ m) for the upper centimeter of the sediment. Species of same gender were grouped under the same color consistent with Fig. 4; **(b)** Relative abundances comparison between the two size fractions (63–125 μ m and > 125 μ m).

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Fig. 6. (Caption on next page.)

Fig. 6. (a) PCA plot based on the relative abundances of the dominant species (> 2% in at least one sample) for the entire core (0-10 cm) in the > 125 μ m size fraction, together with geochemical data: chlorophyll a (Chl a), organic carbon (Corg), bottom-water oxygenation (BWO), oxygen depth-penetration (O_2), nitrate depth-penetration (NO_3) and water depths. (b) Plot of the percentages of the three defined groups at the different sites. Abbreviation: Group 1: Ammodiscus sp. (A. sp.), Bulimina exilis (B. exi.), Chilostomella oolina (C. ool.), Cribrostomoides cf. jeffreysii (C.cf. jef), Fursenkoina Mexicana (F. mex.), Gyroidina soldani (G. sol.), Praeglobobulimina sp. (P. sp.), Reophax agglutinans (R. agg.), Reophax dentaliniformis (R. den.), Rotaliatinopsis semiinvoluta (R. sem.), Uvigerina peregrina type parva (U. per. type parva). Group 2: Bulimina cf. mexicana (B. cf. mex.), Cribrostomoides brady (C. bra.), Cribrostomoides scitulum (C. sci.), Ehrenbergina trigona (E. tri.), Globocassidulina subglobosa (G. sub.), Pullenia bulloides (P. bul.), Reophax cf. spiculifer (R. cf. spi.), Verneuilinulla propinqua (V. pro). Group 3: Bulimina aculeata (B. acu.), Cibidoides robertsonianus (C. rob.), Cribrostomoides subglobosus (C. sub.), Cyclammina cancellata (C. can.), Epistominella exigua (E. exi.), Hormosina guttifera (H. gut.), Lagenammina difflugiformis (L. dif.), Melonis barleeanus (M. bar.), Oridorsalis umbonata (O. umb.), Pyrgo lucernula (P. luc.), Pyrgo murrhina (P. mur.), Pyrgoella sphaera (P. sph.), Reophax bilocularis (R. bil.), Reophax micaceus (R. mic.), Reophax scorpiurus (R. sco.), Reophax subsufisiformis (R. sub.), Saccammina sphaerica (S. sph.), Trochammina spp. (T. spp.), Uvigerina peregrina (U. per.).

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Fig. 7. Foraminiferal abundance (individuals/50 cm³) and BWO comparisons with previous studies from the Arabian Sea (Jannink et al., 1998; Kurbjeweit et al., 2000; Schumacher et al., 2007). Note the scale difference.



Fig. 8. (Caption on next page.)

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Fig. 8. SEM pictures of the main foraminiferal taxa. Scale bar = $100 \mu m$. 1: *Uvigerina auberiana* (d'Orbigny 1839), PA8 (1–1.5 cm), > 150 μm . Regrouped with *Uvigerina peregrina* s.s. under *U. peregrina*. 2: *Uvigerina peregrina* s.s. (Cushman 1923), PA8 (1–1.5 cm), > 150 μm 3–4: *Uvigerina peregrina* type *parva* (Lutze 1986), PA1 (1–1.5 cm), 3: 63–125 μm , 4: > 150 μm 35: *Praeglobobulimina* sp., PA1 (1–1.5 cm), > 150 μm 6–7: *Ehrenbergina* trigona (Goes 1896), PA4 (0–0.5 cm), > 150 μm 8–10: *Rotaliatinopsis semiinvoluta* (Germeraad 1946), PA1 (1–1.5 cm), 63–125 μm 11: *Bulimina aculeata* (d'Orbigny 1826), PA8 (1–1.5 cm), > 150 μm 12: *Globocassidulina subglobosa* (Brady 1881), PA3 (0–0.5 cm), > 150 μm 13: *Ammodiscus* sp., PA2 (0-0.5 cm), > 150 μm 14: *Lagenammina difflugiformis* (Brady 1879), PA8 (0–0.5 cm), > 150 μm 15–16: *Reophax agglutinans* (Cushman 1913), PA8 (0–0.5 cm), > 150 μm