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Living (Rose Bengal stained) benthic foraminiferal faunas along a strong bottom-water oxygen gradient on the Indian margin (Arabian Sea)

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Abstract

Rose Bengal stained foraminiferal assemblages were analysed along a five-station bathymetric transect across the core and the lower part of the oxygen minimum zone (OMZ) on the Indian margin of the Arabian Sea. Sediment cores were collected using the manned submersible *Shinkai* 6500 during RV *Yokosuka* cruise YK08-11 in the post-monsoon season (October 2008) at water depths ranging from 535 to 2000 m, along a gradient from almost anoxic to well-oxygenated (0.3 to 108 µM) bottom waters. Stained foraminiferal densities were very high in the OMZ core (535 m) and decreased with depth. The faunas were dominated (40–80 %) by non-calcareous taxa at all stations. These were mainly species of *Reophax* and *Lagenammina* but also included delicate monothalamous taxa (organic-walled "allogromiids", agglutinated saccamminids, psammosphaerids and tubular forms). These new data from the Indian margin are compared to previous studies from the Murray Ridge, the Pakistan margin and the Oman margin. The fact that similar species were found at sites with comparable bottom-water oxygen concentrations but with very different surface water productivity suggests that, within the strongly developed Arabian Sea OMZ, bottom-water oxygen concentration, and not the organic flux to the sea floor, is the main factor controlling the species composition of the foraminiferal communities. Several foraminiferal species (e.g. *Praeglobobulimina* sp. 1, *Ammodiscus* sp. 1, *Bolivina* aff. *dilatata*) were confined to the core of the OMZ and are presently known only from the Arabian Sea. Because of their association with extremely low-oxygen concentration, these species may prove to be good indicators of past OMZ variability in the Arabian Sea.

1 Introduction

The ocean floor hosts rich and diverse micro-, meio- and macrofaunal communities. The distribution and abundances of these faunas are controlled by many environmental and physical parameters that change from the continental shelf to the deep ocean. In

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particular, organic matter fluxes and bottom-water oxygenation exhibit drastic changes between oceanic basins. Strong gradients in both parameters are found in oxygen minimum zones (OMZ; defined by permanent hypoxia, with dissolved oxygen concentrations $< 22\,\mu M$; Levin, 2003). These mid-water features impinge on the continental slope at upper bathyal depths in the eastern Pacific, the northern Indian Ocean (Arabian Sea and Bay of Bengal), and to a lesser extent off southwest Africa (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009). Many studies have described dense biotic communities within OMZs, despite the low oxygen concentrations (e.g., Wishner et al., 1990; Levin et al., 1991, 2000; Jannink et al., 1998; Gooday et al., 2000, 2009; Levin, 2003a; Schumacher et al., 2007; Mallon et al., 2012; Pozzato et al., 2013). In general, meiofaunal organisms (both protozoan and metazoan, mainly foraminifera and nematodes) attain high densities, although diversity tends to be low (e.g. Jannink et al., 1998; Cook et al., 2004; Schumacher et al., 2007; Larkin and Gooday, 2009; Caulle et al., 2014). Megafaunal and most macrofaunal taxa are more affected by strong hypoxia than smaller organisms and usually exhibit lower abundances, except for polychaetes which are often more resistant and may be abundant, even in the core regions of some OMZs (e.g. Levin et al., 1991; Levin, 2003b; Gooday et al., 2009). However, in all size classes, distinct taxonomic changes are observed across OMZs (e.g. Gooday et al., 2009), making them perfect natural laboratories to examine the influence of oxygen concentration on the density, diversity and species composition of benthic fauna.

In open-ocean settings, the organic flux to the sea floor is often considered as the most important parameter controlling benthic foraminiferal abundance and distribution (e.g. Altenbach, 1985, 1987; Corliss and Emerson, 1990; Gooday et al., 1990; Jorissen et al., 1995; Heinz et al., 2002; Diz et al., 2006; Gooday and Jorissen, 2012). For many foraminiferal species, there is an optimum range of organic input within which they reproduce, are competitive, and attain their maximum abundance (Altenbach et al., 1999). Some species show a strong tolerance to hypoxia and flourish in oxygen-depleted environments (e.g. Mackensen and Douglas, 1989; Gooday et al., 2000; Bernhard and Gupta, 2003; Cardich et al., 2012; Mallon et al., 2012; Sergeeva et al., 2012). Various mechanisms could explain how foraminifera survive in these adverse conditions, which many macro- and mega-faunal animals are unable to tolerate. These include anaerobic metabolic pathways, bacterial symbionts, sequestration of chloroplasts, or proliferation of peroxisomes and mitochondria (Koho and Piña-Ochoa, 2012). In recent studies, Risgaard-Petersen et al. (2006) and Pina-Ochoa et al. (2009) demonstrated the ability of some foraminiferal species to accumulate intracellular nitrate for use as an electron acceptor for respiration instead of oxygen.

In the Arabian Sea, "live" (Rose Bengal stained) benthic foraminifera have been mainly studied on the Oman margin (e.g., Stubbings, 1939; Hermelin and Shimmield, 1990; Naidu and Malmgren, 1995; Gooday et al., 2000) and the Pakistan margin (Jannink et al., 1998; Maas, 2000; Erbacher and Nelskamp, 2006; Schumacher et al., 2007; Larkin and Gooday, 2009). In addition, a few studies have focused on other areas, such as the Murray Ridge (Pozzato et al., 2013; Caulle et al., 2014) and the central, eastern and western parts of the Arabian Sea (Kurbjeweit et al., 2000; Heinz and Hemleben, 2003, 2006). Most of these studies agree that oxygen concentration and organic matter quality and quantity have a strong influence on the abundance and composition of foraminiferal faunas. However, due to the inverse relationship between these two parameters, their relative importance remains difficult to resolve.

Here, we provide the first account of the distribution and abundance of foraminifera across the poorly studied Indian margin in the eastern Arabian Sea (Fig. 1a). The Indian margin displays low sea-surface primary production through the entire monsoonal cycle compared to other Arabian Sea regions (Fig. 1b), suggesting that lower organic resources are available for the benthic foraminiferal faunas. In this context, the present paper focuses on how foraminiferal faunas of the Indian margin respond to the combination of moderate organic matter fluxes and extremely low oxygen concentration of the Indian margin. We are especially interested in the balance between bottom-water hypoxia and the organic flux to the ocean floor as main controls on benthic foraminiferal faunas.

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2 Materials and methods

2.1 Study area

2.1.1 The oxygen minimum zone

The Arabian Sea hosts one of the world's most intense OMZs with almost anoxic conditions in its core (< 2 µM; Paulmier and Ruiz-Pino, 2009). This is the result of the semi-enclosed nature of the northern Arabian Sea, the relatively oxygen-poor intermediate water masses originating from the Persian Gulf, and the effects of the twice-yearly strong intensification of the monsoon system. During the SW or summer monsoon (June–September), intense upwelling develops off Somalia and Oman, and off the southwestern coast of India, due to the anticyclonic surface water circulation. Upwelling leads to an increase of biological production in the photic zone (Fig. 1b; e.g. Ryther and Menzel, 1965; Haake et al., 1993; Rixen et al., 1996), which triggers a strong export of organic carbon to intermediate water-depths, where it is intensely recycled and remineralized. A second maximum in primary production occurs during the NE or winter monsoon (December–March) caused by the convective mixing of the upper water column (Fig. 1b; e.g. Banse and McClain, 1986; Madhupratap et al., 1996; Caron and Dennett, 1999; Rixen et al., 2000). The highly eutrophic surface waters during monsoon periods contrast with the much less fertile conditions during the intermonsoon periods, especially in spring (Fig. 1b). Due to monsoons and their associated change in sea-surface circulation (cyclonic during the NE monsoon and anticyclonic during the SW monsoon), concentration of sea-surface primary production is different between regions and seasons (Fig. 1b). Sea-surface biological production is generally believed to control the organic flux to the sea floor, and thereby the trophic resources for the benthic faunas.

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2.1.2 Oxygen and organic matter characteristics

Samples were collected on the western Indian margin during RV *Yokosuka* cruise YK08-11 (September to November 2008, post-monsoon period) using the manned submersible *Shinkai* 6500 (Fig. 1). Site characteristics are presented by Hunter et al. (2011, 2012), Levin et al. (2013) and Cowie et al. (2014). The YK08-11 cruise was designed to study depositional processes, biogeochemical cycles and biological communities within the intense OMZ, which extends from 150 to 1300 m water depth on the Indian margin. Below is a brief summary of the main environmental characteristics of the OMZ relevant to our study.

(1) In the core of the OMZ, at 535 and 649 m water depths, bottom-water dissolved oxygen concentrations (BWO) are very low, 0.35 and 0.23 µM, respectively. These two sites are enriched in organic matter (Corg ~ 3.2 and ~ 5.8 %, respectively) (Cowie et al., 2014). The high concentrations of Total Hydrolysable Amino Acid (THAA) (~ 48.8 and 79.9 $\mu mol\,g^{-1}$, respectively) reflect the presence of high quality, labile organic matter (Cowie et al., 2014).

(2) At the lower boundary of the OMZ, at about 800 m depth (BWO ~ 2.2 µM), the sediment is still characterised by high organic matter content and quality (Corg ~ 5.6 % and THAA ~ 69.8 $\mu mol\,g^{-1}$; Cowie et al., 2014).

(3) In the lower transitional zone, around 1100 m depth, BWO is still low (~ 15 µM) but the organic matter quantity and quality start to decrease (Corg ~ 4.4 % and THAA ~ 62.9 $\mu mol\,g^{-1}$; Cowie et al., 2014).

(4) Beneath the OMZ, at 2000 m, well-oxygenated waters (BWO ~ 136 µM) and poorer trophic conditions occur (Corg ~ 1 % and THAA ~ 17 $\mu mol\,g^{-1}$; Cowie et al., 2014)

2.2 Foraminiferal analysis

Sediment samples were taken using push-cores (8.3 cm internal diameter, surface area 54.1 cm^2) deployed from the *Shinkai* 6500 submersible. On board of the *Yokosuka*, each core was sliced into 0.5 cm thick layers down to 2 cm sediment depth, 1 cm intervals between 2 and 6, and 2 cm intervals down to 10 cm. Each sediment slice was preserved in 8 % borax-buffered formalin. In the laboratory, the fixed sediment was washed through 300 and 150 µm screens and stained overnight on the sieve in Rose Bengal solution. The < 150 µm size fractions were kept and stored in borax-buffered formalin for future analyses. The 150–300 and > 300 µm fractions of the first centimetre sediment layer (0–0.5 and 0.5–1 cm) were kept wet (in water) under a binocular microscope and all Rose Bengal stained foraminifera were removed.

The Rose Bengal technique is considered to be an inexpensive and easy method to recognize foraminifera that were alive (or recently alive) when collected (Walton, 1952; Murray and Bowser, 2000). However, especially in low-oxygen settings, the cell material may persist long after death, resulting in false positives (Corliss and Emerson, 1990; Bernhard, 2000). In order to minimize over-estimation in the live foraminiferal counts, strict staining criteria were always applied. Specimens were considered "alive" only when all chambers, except for the last one or two, 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. Soft-shelled monothalamous taxa, which are largely undescribed, were included in the data analyses. They were identified to the lowest possible taxonomic level and assigned to informal species categories for diversity analyses. Species identifications followed previous studies from the Arabian Sea (e.g. Maas, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009; Caulle et al., 2014; Taylor and Gooday, 2014). A special effort was made to discriminate hormosinacean species (the superfamily *Hormosinacea* includes genera with uniserial chambers such as *Reophax*, *Hormosina*, *Hormosinella,* and *Nodosinella*), extending the recent taxonomic study of Taylor and Gooday (2013), which was based on different material from the same sites as the present study. Deep-sea hormosinacean species are often difficult to identify; many are undescribed and some widely-reported "species" represent complexes of morphologically similar species (i.e. morphotypes). Hence it was necessary to assign

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many species within the genera *Hormosina*, *Reophax* and the monothalamous genus *Lagenammina* to informal categories. In some cases, these are the same as those illustrated by Taylor and Gooday (2013) but others have not been recognised previously. Further details on species identifications are given in the supplementary taxonomic appendix.

For all stations, diversity indices, including species richness (S; count of number of taxa in a sample), Shannon index ($H' \log_e$), and evenness (J) were calculated using the statistical software "PAST" (PAleontological STatistics; Version 2.14; Hammer et al., 2009). We use the term "entire live" to refer to all stained foraminifera, i.e. agglutinated and calcareous taxa combined.

3 Results

3.1 Foraminiferal densities

The total densities of live (Rose Bengal stained) foraminifera in the upper 1 cm layer (> 150 µm fraction) decreased from ~ 3000 ind/50 cm^2 at 535 m in the OMZ core to ~ 300 ind/50 cm^2 at 2000 m below the OMZ (Fig. 2). Foraminifera were concentrated in the 150–300 µm fraction, which at most stations accounted for about three-quarters of the total density. Faunas were dominated by multichambered agglutinated taxa, which represented between 48 % (2000 m) and 75 % (649 m) of the assemblages, whereas calcareous species did not exceed 32 % (535 m) of the total fauna (Fig. 2 and Table 1). The relative abundance of monothalamids was lowest (2 %) at 649 m and highest (30 %) at 2000 m. The absolute densities of multichambered agglutinated and calcareous species decreased with increasing water-depth (Fig. 2). At 535 m, in the core of the OMZ, their densities were ~ 1870 (agglutinated) and ~ 990 ind/50 cm^2 (calcareous), respectively, compared to ~ 150 ind/50 cm^2 and ~ 55 ind/50 cm^2, at the deepest site (2000 m). Monothalamids did not show any clear trends along the transect. The highest densities were found in the core (535 m; ~ 150 ind/50 cm^2) and in the lower

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part (1100 m; ~ 115 ind/50 cm^2) of the OMZ. The lowest densities (~ 25 ind/50 cm^2) were found at the 649 m site.

3.2 Species richness, diversity and dominance of living foraminiferal faunas

A total of 214 morphospecies was identified (0–1 cm layer, 150 µm size fraction), of which 131 were agglutinated (77 referred to the superfamily *Hormosinacea*), 79 were hyaline and only 4 were miliolids. Monothalamous species, the majority of which were undescribed, were included in the biodiversity analysis.

Species richness (*S*) of the entire live faunas varied along the transect (Fig. 3). In the core of the OMZ, a total of 72 species was recognised at 535 m compared to 62 species at 649 m. Species richness increased at sites below the OMZ core to a maximum of 84 species at 1100 m (Fig. 3). In contrast to the number of multichambered agglutinated species, which more or less mirrored the total number of "live" species, calcareous species richness was more constant between sites, ranging from a maximum of 32 species at 535 m to a minimum of 25 at 649 and 2000 m (Fig. 3). The Shannon (H') and Fisher Alpha indices showed a similar trend toward higher values at greater depth and higher oxygen concentration, but in contrast to species richness, these indices were higher for the entire live fauna at 800 m than at 1100 m. The 1100 m site exhibited a lower H' value (~ 3) than the 800 and 2000 m sites (Fig. 3). In the case of the calcareous component, the trend in the Fisher index was broadly similar to that of the entire live assemblage with a distinct decrease from maximal values at 800 m to lower values at 1100 and 2000 m. This pattern was not seen in the Shannon index, however (Fig. 3). These indices also showed divergent trends for the agglutinated taxa where values for H' and the Fisher index were very similar between 800 and 1100 m (Fig. 3).

Evenness fluctuated along the transect (Fig. 3). There was an increase from low values at 535 m to a peak at 800 m in the total and multichambered agglutinated components, followed by a sharp decline to 1100 m with higher values again at 2000 m.

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For calcareous species, evenness followed a similar trend down to 800 m but then increased further at 1100 m followed by somewhat lower values at 2000 m. The evenness of the calcareous and agglutinated species was consistently higher than that of the entire live fauna. When considering calcareous and agglutinated species separately, diversity measures may be substantially different from those of the entire live fauna.

3.3 Foraminiferal assemblages

In general, the live faunas were mainly represented by perforate calcareous and agglutinated foraminifera. Soft-shelled monothalamous taxa were not considered in this analysis in order to allow a better comparison with previous studies.

Most of the abundant species were agglutinated, in many cases assigned to the genera *Reophax* and *Lagenammina* (Fig. 4a, Table 1). The agglutinated genus *Ammodiscus*, which belongs to a lineage related to spirillinids and miliolids, was common at the 535 and 649 m sites in the OMZ core. Relatively few of the species representing > 2 % of the assemblages were calcareous (Fig. 4b, Table 1). Miliolids were very rare.

The faunal composition displayed important changes along the transect (Fig. 4). In general, different assemblages were observed at different sites, particularly in the case of the calcareous taxa. In the core of the OMZ (535 and 649 m), where the oxygen concentration was very low, the agglutinated fauna was dominated by *Reophax* sp. 7, *Reophax* sp. 10, *Reophax bilocularis*, *Lagenammina* sp. 2, *Eggerella* sp. 1, *Eggerella* sp.2, *Cribrostomoides wiesneri* and *Ammodiscus* sp. The most common calcareous species in the OMZ core were *Bolivina* aff. *dilatata*, *Cassidulina* sp. 1, *Praeglobobulimina* sp. 1, *Hoeglundina* cf. *elegans,* Uvigerina *peregrina* type *parva* at 535 m, and *Cassidulina* sp. 1 and *Ehrenbergina trigona* at 649 m (Fig. 4b). The 800 m site had a very different fauna, mostly composed of *Lagenammina* spp. 1, 5 and 13, *Reophax dentaliniformis, R. agglutinatus, Cribrostomoides* sp. and *Chilostomella oolina*, (Fig. 4). At 1100 m, in the lower part of the OMZ, two *Reophax* species, *R. spiculifera* and *R. horridus*, were predominant; other agglutinated species included *Reophax* spp. 3, 13 and 27, *Ammoscalaria tenuimargo* and *Semivulvulina* sp. 1. At the 1100 m site,

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all calcareous species had relative abundances less than 2 %. Finally, at the deepest site (2000 m), foraminiferal assemblages consisted mainly of *Reophax* aff. *scorpiurus, Reophax* spp. 5, 29 and 31, *Lagenammina* spp. 22 and 23, *Recurvoides contortus, Bulimina aculeata* and *Hoeglundina* cf. *elegans* (Fig. 4).

The cumulative percentage of all species representing < 2 % of the "live" assemblages ("others" in Fig. 4a and b) was large, especially for the calcareous component, at sites below the core of the OMZ (800 to 2000 m). Considering all sites across the transect together, only 8 calcareous species, out of a total of 83, were sufficiently abundant to represent > 2 % of the assemblage at least at one station (Fig. 4b).

4 Discussion

4.1 Limitations of the study

Our analyses were confined to the uppermost (0–1 cm) sediment layer, which could result in an under-representation of deeper-dwelling species. Foraminiferal microhabitats are largely controlled by organic matter input and oxygen penetration into the sediment (Corliss and Emerson, 1990; Jorissen et al., 1995). As a result, although foraminifera often occur in sediment layers down to a depth of 5 cm or more where oxygen is plentiful, they are generally concentrated near the sediment surface in hypoxic, organically-enriched settings. Previous studies of the Arabian Sea OMZ found most of the stained fauna in the first cm of the sediment (e.g. Jannink et al., 1998; Kurbjeweit et al., 2000; Maas, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009; Caulle et al., 2014). In many hypoxic settings, compression of redox profiles leads to an absence of classical microhabitat successions and a concentration of deep-infaunal taxa near the sediment surface. Intermediate and deep infaunal taxa were scarce on the Indian margin, and have rarely been reported in previous Arabian Sea studies (Jannink et al., 1998; Kurbjeweit et al., 2000; Mass, 2000; Schumacher et al., 2007; Larkin et al., 2009; Caulle et al., 2014). In our material, *Chilostomella oolina* was the only species of this type that represented > 2 % of the "live" fauna, being found mainly at 800 m (Fig. 4b). Similar observations were made by Schumacher et al. (2007) on the Pakistan margin, where C*. oolina* was found exclusively in the 0–0.5 cm layer across the OMZ (306–738 m depth). Species of the deep infaunal genus *Globobulimina* are also abundant in the first sediment cm on the Pakistan margin (at 576 m; Erbacher and Nelskamp, 2006). These species occur at several cm depth in the sediment in better oxygenated environments (Corliss and Emerson, 1990; Kitazato, 1994; Rathburn et al., 2000). Since our study was limited to the topmost cm of the sediment, it is possible that intermediate- and deep-infaunal taxa were missed at sites below the OMZ (1100 and 2000 m). However, for the reasons outlined above, we think that it is unlikely that analysis of deeper sediment layers would have led to substantial changes of foraminiferal diversity, although density values may have increased slightly, especially at the deeper sites (1100 and 2000 m). This conclusion is supported by data in Caulle et al. (2014) from sites located along an oxygen gradient on the Murray Ridge (885 to 3010 m depth), where foraminiferal diversity was very similar in the 0–1 and 0–10 cm sediment layers (> 150 µm fraction).

A second source of bias could result from the consideration of only the > 150 µm size fraction. In low-oxygen settings, small-sized (> 63 µm) foraminifera are particularly abundant (e.g. Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007), possibly because small species have a higher tolerance to low-oxygen conditions (Caulle et al., 2014). However, the very considerable time and effort involved in sorting the dense populations present in size fractions < 150 µm precluded their analysis in the present study. Even so, the > 150 µm size fraction alone yielded abundant and diverse faunas with stained assemblages containing between 279 and 3177 individuals, belonging to 214 species. Moreover, Schumacher et al. (2007) and Caulle et al. (2014) demonstrated that adding the small-sized fraction (> 63–150 µm) did not lead to a major change in bathymetrical trends in foraminiferal diversity and faunal composition. In these two studies, the small size fraction comprised mainly juveniles of taxa also occurring in the coarser fraction. Finally, a major advantage of working on the > 150 µm size fraction is that it allows direct comparison with paleo-oceanographic studies, which are mainly based on the > 125 or > 150 µm fractions.

4.2 Dense high diversity assemblages in extreme hypoxic conditions

On the basis of macrofaunal data from the Arabian Sea, Levin and Gage, (1998) concluded that abundance is related to the organic carbon flux to the sea floor, whereas species richness is mainly related to BWO concentrations. In a general sense, our Indian margin data confirm these conclusions; diversity indices were lower in the core of the OMZ (535 and 649 m) than at deeper sites (1100 and 2000 m; Fig. 3). At the time of sampling (September–October 2008), the Indian margin OMZ was extremely hypoxic compared to previous observations in the Arabian Sea (e.g. Maas, 2000; Gooday et al., 2000; Schumacher et al., 2007; Larkin and Gooday, 2009; Vandewiele et al., 2009; Koho et al., 2013; Caulle et al., 2014). Oxygen concentrations in the core of the OMZ were ~ 0.3 µM compared to ~ 2 µM on the Murray Ridge (Pozzato et al., 2013; Koho et al., 2013; Caulle et al., 2014), and to ~ 4 µM on the Pakistan margin (Schumacher et al., 2007; Larkin and Gooday, 2009) (Fig. 5). Nevertheless, in spite of the very low oxygen concentrations, species richness (i.e. the number of species) was high, particularly at the most severely hypoxic site (535 m; Fig. 3) compared to previous data from the Arabian Sea (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009; Caulle et al., 2014). This difference may be the result of our unusually careful taxonomical analysis of the samples, which took into account monothalamids and the diverse hormosinaceans. These species are often difficult to identify and many are undescribed. A total of 77 hormosinacean species was recognized, based on the number of chambers, chamber shape and size, wall construction, and the shape of the apertural neck. Similar methods were applied to a sample from the core of the Oman margin OMZ (412 m depth), where BWO levels were more than one order of magnitude higher than off India, although still very low (~ 5.5 µM vs. ~ 0.35 µM) (Gooday et al., 2000). Foraminiferal species diversity and

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richness there were comparable to values reported in the present study ($H'(\log_e) \sim 2.8$, $S = 64$), although the hormosinaceans were less diverse (Gooday et al., 2000).

Compared to the monothalamids and hormosinaceans, the taxonomy of calcareous foraminifera in the Arabian Sea is better known and more straightforward. To facilitate comparisons with previous studies (Schumacher et al., 2007; Caulle et al., 2014) diversity metrics were recalculated for calcareous species only (Fig. 6). These reveal that faunal diversity within (535 to 1100 m depth) and below (2000 m) the Indian margin OMZ is still higher than in other parts of the Arabian Sea. The high diversity in the core of the OMZ (Fig. 6), where oxygen concentrations are almost zero (~ 0.3 µM; at 535 m), is particularly striking (Fig. 5). The presence at the 535 m site of *Hoeglundina* cf. *elegans* is also very surprising (Fig. 4b). Based on a fossil record from the Murray Ridge (Northern Arabian Sea) spanning the last 120 000 years, den Dulk et al. (1998) concluded that *H. elegans* can tolerate mild hypoxia but not the severely hypoxic conditions found in the core of the OMZ. The occurrence of a morphologically similar species in the OMZ core on the Indian margin could be explained by the hydrodynamic setting of this region. At 535 m, sharp-crested ripples (crests up to 10–12 cm high) were observed (Hunter et al., 2011; Taylor and Gooday, 2014), indicating rapid water movements. A current speed of 15 $\mathrm{cm\,s^{-1}}$ was recorded here during the *Yokosuka* cruise (Taylor and Gooday, 2014). Intermittent strong currents could lead to short periodic increases of BWO allowing low-oxygen-sensitive taxa such as *H.* cf. *elegans* to colonise the area, where they can apparently persist during the severely hypoxic periods. This hypothesis is supported by the occurrence at 535 m of numerous dead thyasirid bivalves and gastropods (between 150–300 µm in size), which usually do not inhabit such severely oxygen depleted environments (Levin, 2003b). Thyasirids have been reported in the lower part of the OMZ on the Pakistan margin, where BWO varies between ~ 4.5 and 9 µM (Oliver and Levin, 2006; Levin et al., 2009). *Hoeglundina elegans* is a commonly reported deep-sea species that is distributed across a wide bathymetric and geographical range in all oceans (Murray, 1991). Most records are from bathyal (< 3000 m) or even sublittoral (e.g., 140 m; Fontanier et al., 2002) depths, but morphologically identical specimens also occur at > 4000 m in the eastern equatorial Pacific (Gooday, unpublished data). The species found in the OMZ core on the Indian margin appears identical to typical examples of *H. elegans* in terms of test morphology. Nevertheless, we refer to it as *H* cf. *elegans* because its occurrrence in a severely hypoxic setting is unexpected, and for consistency with Enge et al. (2014). Whether it is genetically coherent with *H. elegans* from oxic environments remains to be determined.

Another factor that could explain the high diversity of stained foraminifera in the OMZ core off India is the post-mortem preservation of the cell material. In this severely hypoxic environment the cytoplasm could persist for months or longer (Corliss and Emerson, 1990; Bernhard, 2000). Although, as explained above, very strict staining criteria were applied, it might still be difficult to confidently discriminate between individuals that had been dead for some time and those that were alive when collected. More reliable assays, such as the Cell Tracker Green (CTG) technique (e.g. Bernhard, 2000; Bernhard et al., 2006) could give a better estimate of the "living" fauna. Finally, the temporal persistence of taxa that are not known for their tolerance of low-oxygen conditions could be explained by a lowered metabolism during the most adverse periods (i.e., dormancy). Geslin et al. (2011) showed that many benthic foraminiferal taxa have low oxygen respiration rates per unit of bio-volume.

4.3 The tolerance of agglutinated foraminifera to low-oxygen conditions

Agglutinant taxa are often considered to be less tolerant of low-oxygen conditions than calcareous foraminifera (Moodley et al., 1997; Gooday et al., 2000, 2001, 2009; Neira et al., 2001). However, this is not always the case. In the Black Sea, soft-shelled monothalamous taxa were more abundant than calcareous foraminifera in samples taken across the transition from hypoxic to sulphidic conditions (depth range 120–240 m) (Sergeeva et al., 2012). On the Indian margin, stained foraminiferal assemblages are systematically dominated by agglutinated species (up to 76 % at 649 m). These include soft-shelled monothalamids, but the majority belong to genera such as *Reophax* and *Hormosinella* together with species of the single-chambered genus *La-*

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genammina (Fig. 4b and Table 1). Similar proportions of *Reophax* and *Lagenammina* species have been reported in and below the OMZ on the Murray Ridge (Northern Arabian Sea) and in the core of OMZ of the Pakistan margin (Fig. 6; Larkin and Gooday, 2009; Caulle et al., 2014). These observations reinforce our hypothesis that some hormosinaceans can tolerate strong oxygen depletion (Caulle et al., 2014). On the Indian margin, where oxygen concentrations during the *Yukosuka* cruise were lower than at other sites in the Arabian Sea (Fig. 5), these multi-chambered uniserial agglutinants are even more abundant in the OMZ core than calcareous foraminifera.

Why hormosinacean and *Lagenammina* species should be so common in the OMZ core is not clear. It could be related to the quality of the available organic matter. Many agglutinated foraminifera seem to be less dependent on fresh food inputs than calcareous taxa, feeding instead on more refractory material (e.g. Gooday, 2003; Gooday et al., 2008; Koho, 2008; Koho et al., 2008; Phipps et al., 2012; Caulle et al., 2014). Another possible factor is that enhanced organic matter recycling and associated CO_2 release into the pore waters depresses pH within OMZs, making the secretion of a carbonate test more energetically demanding. Seawater pH is reduced to below 7.1 on the Oman margin between 391 and 1265 m (Milliman et al., 1999). Taylor and Gooday (2014) observed that some globigerinacean shells incorporated into stained *Reophax* and *Lagenammina* specimens at our 535 and 800 m sites were partly corroded, and traces of dissolution were evident in our material as well. However, different hormosinacean and *Lagenammina* species display different degrees of tolerance to hypoxia on the Indian margin. For instance, *Reophax* spp. 7 and 10 were mainly found in the core (535–800 m depth) whereas *Reophax* aff. *scorpiurus, Reophax* spp. 31 and 5 were confined to the deepest site (2000 m) (Fig. 4a and Table 1). Indeed, these taxa are abundant and diverse in many deep-sea environments, including fully oxic abyssal plains (e.g., Gooday et al., 2010b). Further investigations are necessary in order to better understand their ecology.

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4.4 Distribution of species across the OMZ

There is a succession of both calcareous and agglutinated foraminiferal species along the transect (Fig. 4 and Table 1). Sites in the core of the OMZ (535 and 649 m) have rather similar assemblages and are dominated by *Reophax* spp. 7 and 10 and *Ammodiscus* sp. 1 (agglutinated), and *Cassidulina* sp. 1, *Bolivina* aff. *dilatata, Praeglobobulimina* sp. 1, *Hoeglundina* cf. *elegans* and *Ehrenbergina trigona* (calcareous) (Fig. 4 and Table 1). Most of these species are restricted to these two sites where oxygen concentrations were extremely low at the time of sampling (BWO ~ 0.2 and 0.3 µM). The calcareous species, except for *H.* cf. *elegans* (see above), are typical of organically-enriched environments with low oxygen concentrations (Bernhard and Gupta, 2003). Many of them (*Hoeglundina* cf. *elegans, Uvigerina peregrina, Cassidulina* sp. 1 and *Praeglobobulimina* sp. 1) demonstrated a large and rapid (~ 4 days) carbon uptake in tracer experiments on the Indian margin using labelled phytodetritus (Enge et al., 2014). *Uvigerina* ex gr. *semiornata* exhibited a similar response in experiments conducted on the Pakistan margin in 2003 (Larkin et al., 2014). The ability of these species to feed rapidly on organic matter under extremely low oxygen concentrations may lead to the development of large population densities.

The lower boundaries of OMZs are often characterised by enhanced biogeochemical activity (Paulmier and Ruiz-Pino, 2009) and enhanced faunal abundance in both the benthic and pelagic communities (e.g. Sanders and Hessler, 1969; Mullins et al., 1985; Ward et al., 1989; Levin et al., 1991; Wishner et al., 1995; Levin, 2003b; Gooday et al., 2009). An "edge effect" of this kind may be evident at our 800 m site below the OMZ core (BWO ~ 2.2 µM). Here, the assemblage comprises a mixture of calcareous species typical of the core (e.g. *Bolivina* aff. *dilatata, Cassidulina* sp. 1) and those that are more widely distributed (e.g. *Cancris auriculus, Chilostomella oolina*), together with *Reophax* spp. 7 and 10 and *Lagenammina* sp. 1 (Fig. 4 and Table 1). Apparently, the oxygen concentration at 800 m is still low enough to allow species adapted to the core of the OMZ to remain competitive, but also high enough to allow taxa such as

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Cancris auriculus and *Chilostomella oolina* to colonise the site. *Cancris auriculus* is also found in the OMZ (BWO ~ 5 µM) on the Pakistan margin (Larkin and Gooday, 2009) whereas *Chilostomella oolina* has more striking ecological preferences (e.g. Nomaki et al., 2005). A different foraminiferal assemblage is observed in the lower part of the OMZ (1100 m; BWO ~ 15 µM), where *Reophax horridus, Reophax spiculifera, Reophax* sp. 10, *Chilostomella oolina, Hoeglundina* cf. *elegans, Globocassidulina subglobosa* and *Bulimina aculeata* (Fig. 4 and Table 1) are all abundant. Most of these species are widely distributed in the bathyal deep sea and, except for *H.* cf. *elegans,* they are not found in the OMZ core. An inability to tolerate very low oxygen concentrations, perhaps combined with strong competition from better adapted species, probably precludes their penetration into this harsh environment. It thus appears that there is a critical oxygen threshold between ~ 2 and ~ 15 µM (i.e. 800 and 1100 m depth) for benthic foraminifera on our Indian margin transect. Due to the sample site spacing, it is difficult to specify a more precise value.

Changes in the composition of foraminiferal assemblages are also observed in other areas of the Arabian Sea. On the Pakistan margin, Schumacher et al. (2007) found transitional assemblages, mainly composed of *Bolivina* aff. *dilatata, Praeglobobulimina* sp. 1, *Uvigerina peregrina* and *Chilostomella oolina,* between ~ 600 and ~ 800 m (BWO 4.7–5.8 µM), a depth range spanning the lower part of the OMZ core and the upper part of the "lower transition zone" (Gooday et al., 2009). On the Murray Ridge, this change occurs at 1172–1306 m (BWO ~ 5.0–13.8 µM) where the widely distributed species (e.g., *Globocassidulina subglobosa, Ehrenbergina trigona, Fursenkoina* spp.) occur together with species typical of the OMZ core that may have more restricted distributions (e.g. *Ammodiscus* sp. 1) (Caulle et al., 2014). These studies are consistent with the existence of a transitional assemblage where the BWO starts to increase, either at the base of the OMZ core, or around the lower boundary of the OMZ.

4.5 BWO, deposit and flux of organic matter, benthic foraminiferal faunas: comparison of study sites

Compared to previous studies in the Arabian Sea (e.g. Maas, 2000; Gooday et al., 2000; Schumacher et al., 2007; Vandewiele et al., 2009; Larkin and Gooday, 2009; Koho et al., 2013; Caulle et al., 2014), the OMZ of the Indian margin was more severely depleted in oxygen. In fact, conditions here were virtually anoxic, at least during the sampling period. On the other hand, the similar values for surface sediment organic matter quantity and quality (THAA content) between study areas suggests an absence of major regional differences in these parameters (Fig. 5; Vandewiele et al., 2009; Koho et al., 2013; Cowie et al., 2014). This is surprising in view of the concentrations of sea-surface chlorophyll *a*, mirroring primary production, which are much lower on the Indian margin compared to the rest of the Arabian Sea (Fig. 1b). The comparably high Corg values of the superficial sediments here (compared to low surface water primary production) could be explained partly by the lower oxygen concentrations on the Indian Margin (Fig. 5) leading to a better preservation of organic matter. If true, this would mean that on the Indian margin, the availability of labile organic carbon is not so much determined by the sea-surface primary productivity, but rather by BWO concentration, which in turn reflects the complex hydrodynamic context (seasonal development of a belt of intense oxygen depletion linked to northward surface currents) (Cowie et al., 2014). However, it has to be kept in mind that there are many indicators of OM quality (e.g. THAA, concentration of single amino-acid, enzymatically hydrolysable amino acids) and their interpretations are often problematic. It is far from clear to what degree each of these indices describes the bio-availability of the organic components. Nevertheless, it appears that on the Indian margin, BWO, as well as hydrodynamics, represent a more important control on benthic foraminiferal abundances than sea-surface primary production.

Stained foraminiferal species from the Indian margin OMZ and below are also found in other regions of the Arabian Sea OMZ (Fig. 7). *Praeglobobulimina* sp. 1 is restricted to extremely low oxygen concentrations (< 10 µM), mainly corresponding to the core of the OMZ on the Indian margin, the Murray ridge and the Pakistan margin, while *Cassidulina* sp. 1 and *Bolivina* aff. *dilatata* are mainly found at oxygen concentration < 10 µM (Fig. 7). This highlights the strong adaptation of these species to hypoxic environments. *Praeglobobulimina* sp. 1 and *B.* aff. *dilatata* have not been reported in other oceanic basins, neither in the OMZ of East Pacific nor off North-West Africa. This raises the issue of whether some species inhabiting OMZs are endemic to particular regions. It has been suggested that severely stressed environments, notably by extreme low oxygen concentration, may induce rapid morphological and genetic changes (Verhallen, 1987) and may promote allopatric speciation though the creation of barriers to gene flow (Rogers, 2000). The visually conspicuous spider crab *Encephaloides armstrongii* is an example of a species that appears to be restricted to the OMZ in the northern Arabian Sea and Bay of Bengal (Creasey et al., 1997). However, the question of endemism within OMZ settings needs to be explored at the molecular genetics level, as well as through morphological analysis.

Ehrenbergina trigona and *Chilostomella oolina* appear in a BWO interval from ∼ 0 to ∼ 22 µM (Fig. 7), but are still present in the OMZ and especially in the lower part of the OMZ. It appears that many Arabian Sea foraminiferal species are living in a specific range of BWO, creating ecological niches for the different species. The fact that the same species occur on the Indian margin, the Pakistan margin and the Murray ridge, at sites with the same BWO interval, but probably with very different export production, provides strong support for the dominant role of BWO, rather than organic flux to the sea floor, in regulating the benthic foraminiferal assemblages. This observation could have important implications in paleoceanography, because it may allow us to reconstruct past-OMZ variability in the Arabian Sea. Foraminiferal species typical of the OMZ (*Praeglobobulimina* sp. 1, *Cassidulina* sp. 1, *Bolivina* aff. *dilatata, Ehrenbergina trigona*) should provide critical and reliable information about past BWO, making it possible to quantitatively reconstruct past changes in intensity and extension of the OMZ. On the other hand, some species, such as *Bulimina aculeata* and *Hoeglundina* cf. *elegans,*

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are both found in the OMZ and below (Fig. 7). It seems that the ecological preferences of these two species differ from site to site. This could suggest a high adaptability of these two species to several environmental conditions (BWO and organic carbon). It could also be the result of the presence of cryptic species, with a very similar morphology. However, due to their wide ecological range, *Bulimina aculeata* and *Hoeglundina* cf. *elegans* cannot be used as tracers of past-oxygen concentrations.

5 Conclusions

This study focused on the response of living (Rose Bengal stained) benthic foraminifera to the combination of low organic-matter fluxes and extremely low oxygen concentrations on the poorly studied Indian margin. A transect through the OMZ yielded a dense and relatively diverse assemblage in the extreme hypoxic conditions prevailing at 535 m in the OMZ core and a much sparser but more diverse assemblage in well-oxygenated waters at 2000 m depth, below the OMZ. The unexpectedly high diversity in the OMZ core may reflect the adaptation of the predominantly agglutinated species present here to these extreme conditions. However, it may also result from periods of higher oxygenation mediated by the activity of bottom currents in this region. The presence of *Hoeglundina* cf. *elegans* and dead thyasariid bivalves support the hypothesis of intermittent oxygen fluctuations. Moreover, extremely low oxygen concentrations may enhance the preservation of cellular material after the death of the organism, increasing the apparent faunal diversity.

The high abundances of *Reophax* and *Lagenammina* species suggest that these agglutinated foraminifera species are more tolerant to low-oxygen settings than previously thought. Although their ecology is not well understood, their presence may be related to the quality and quantity of the organic matter within the OMZ. However, the foraminiferal assemblages (both agglutinated and calcareous taxa) exhibit a shift from an assemblage comprising species tolerant of severe hypoxia in the core of the OMZ, to a transitional assemblage in the lower part of the OMZ, and an assemblage of more

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widely distributed species below the OMZ. We suggest that this faunal succession is mainly controlled by the bottom-water oxygen concentrations. There appears to be an oxygen threshold between 2 and 15 µM that separate foraminifera typical of the hypoxic core, which probably have a restricted distribution, from more cosmopolitan species that are less tolerant of hypoxia and characterise the deeper sites.

A comparison of benthic foraminiferal assemblages from the Indian margin with those reported in previous studies from other parts of the Arabian Sea suggests that similar species are common at sites with the same bottom-water oxygenation but subject to different organic-matter flux regimes. Thus bottom-water oxygen levels may exert the main control on species distributions in this region. This would enhance the utility of foraminiferal species as reliable tools to reconstruct past OMZ variability in the Arabian Sea.

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Table 1. Top 10 rank species at each site, with relative abundances (%) on the right.

535 m BWO: 0.35 µM		649 m BWO: 0.23 µM		800 m BWO: 2.2 µM		1100 m BWO: 15 µM		2000 m BWO: 108 µM	
Reophax sp. 7	1118 (35.1)	*Reophax* sp. 7	329 (24.5)	*Reophax* sp. 7	19 (6.8)	*R. horridus*	76 (7.6)	*Reophax* sp. 29	12 (3.7)
Ammodiscus sp. 1	113 (3.5)	*R. bilocularis*	190 (14.2)	*Lagenammina* sp. 1	18 (6.4)	*R. spiculifera*	53 (5.3)	*Lagenammina* sp. 23	11 (3.4)
C. wiesneri	104 (3.3)	*Reophax* sp. 10	118 (8.9)	*Reophax* sp. 10	18 (6.4)	*A. tenuimargo*	18 (1.8)	*R.* aff. *scorpiurus*	11 (3.4)
Eggerella sp. 2	97 (3.1)	*Eggerella* sp. 2	90 (6.7)	*R. agglutinatus*	15 (5.4)	*Reophax* sp. 13	15 (1.5)	*Reophax* sp. 31	11 (3.4)
Lagenammina sp. 2	92 (3)	*Eggerella* sp. 1	52 (3.9)	*Lagenammina* sp. 13	14 (5)	*Reophax* sp. 27	13 (1.3)	*Reophax* sp. 5	10 (3.1)
Reophax sp. 10	77 (2.4)	*Lagenammina* sp. 2	49 (3.6)	*R. dentaliniformis*	12 (4.3)	*Reophax* sp. 3	12 (1.2)	*R. contortus*	9 (2.8)
Trochammina sp. 1	62 (2)	*Ammodiscus* sp. 1	46 (3.4)	*Cribrostomoides* sp.	11 (4)	*Semivulvulina* sp.	11 (1.1)	*E. foliaceus*	7 (2.2)
R. aff scorpiurus	46 (1.4)	*C. wiesneri*	24 (1.8)	*Lagenammina* sp. 5	9 (3.2)	*Lagenammina* sp. 13	10 (1)	*Lagenammina* sp. 25	6 (1.8)
Eggerella sp. 1	42 (1.3)	*Spiroplectammina* sp. 2	17 (1.3)	*Reophax* sp. 19	8 (3)	*Reophax* sp. 10	9 (0.9)	*P. challengerii*	5 (1.5)
R. bilocularis	35 (1.1)	*R. bilocularis* form 2	14 (1)	*Leptohalysis* sp. 2	7 (2.5)	*Reophax* sp. 1	7 (0.7)	*R. dentaliniformis*	4 (1.2)
				Reophax sp. 13	5 (2.5)				
		E. trigona	89 (6.6)						
Cassidulina sp. 1	324 (10.1)	*Cassidulina* sp. 1	42 (3.1)	*C. oolina*	10 (3.6)	*C. oolina*	6 (0.6)	*B. aculeata*	7 (2.1)
B. aff. *dilatata*	216 (6.8)	*N.* cf. *umboniferus*	22 (1.6)	*C. auriculus*	4 (1.4)	*H. elegans*	4 (0.4)	*Gyroidina* sp. 1	6 (1.8)
Praeglobobulimina sp. 1	161 (5.1)	*H. elegans*	19 (1.4)	*Bolivina* sp.	3 (1.1)	*G. subglobosa*	4 (0.4)	*B. alazensis*	5 (1.5)
H. elegans	72 (2.2)	*L.* cf. *calcar*	18 (1.3)	*Globobulimina* spp.	3 (1.1)	*M. barleeanus*	4 (0.4)	*E. exigua*	5 (1.5)
U. peregrina	72 (2.2)	*Globobulimina* spp.	17 (1.3)	*N.* cf. *umboniferus*	3 (1.1)	*P. bulloides*	4 (0.4)	*H. elegans*	5 (1.5)
U. ex. gr. *U. semiornata*	39 (1.2)	*F. rotundata*	10 (0,7)	*P. quinqueloba*	3 (1.1)	*P. pupoides*	3 (0.3)	*P. bulloides*	4 (1.2)
N. cf. *umboniferus*	36 (1.1)	*C. oolina*	9 (0,7)	*Pullenia* sp	3 (1.1)	*Amphycorina* spp.	2 (0.2)	*C. brady*	3 (0.9)
P. quinqueloba	25 (0.8)	*Praeglobobulimina* sp. 1	9 (0.7)	*B.* aff. *dilatata*	2 (0.7)	*B. aculeata*	2 (0.2)	*G. subglobosa*	3 (0.9)
C. auriculus	15 (0.4)	*Pullenia* sp.	9 (0.7)	*Cassidulina* sp. 1	2 (0.7)	*C. auriculus*	2 (0.2)	*O. umbonata*	3 (0.9)
E. trigona	11 (0.3)	*R. semiinvoluta*	9 (0.7)	*G. orbicularis*	2 (0.7)	*Cibicidoides* sp.	2 (0.2)	*P. murrhina*	2 (0.6)

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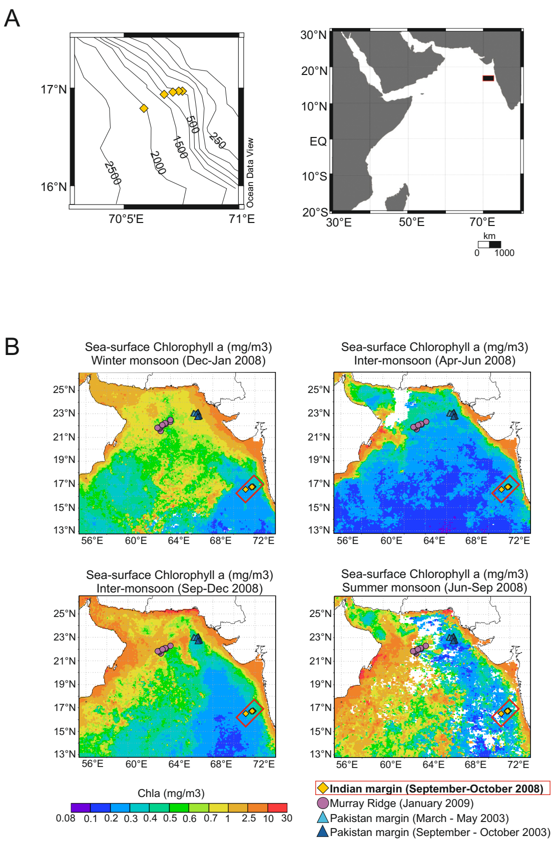

Figure 1. (a) Study area and station location **(b)** Sea-surface chlorophyll *a* concentration (mg m^{-3}) during the monsoonal cycle in 2008 at our study sites and previous studies of live benthic foraminfera from the Arabian Sea (Schumacher et al., 2007; Caulle et al., 2014); http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/.

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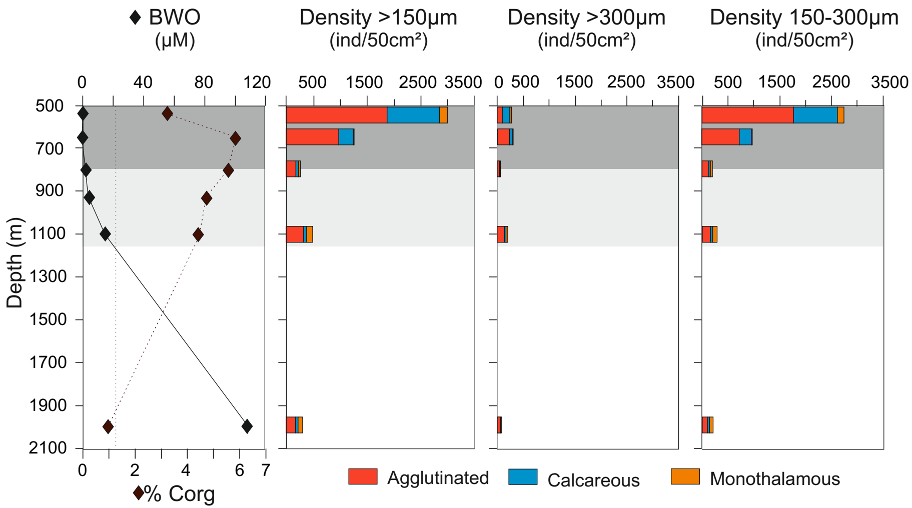

Figure 2. Total stained foraminiferal abundances (ind/50 cm^2) in the 150–300 µm, > 300 µm and > 150 µm for the first cm (0–1 cm) along the sampling transect. The Corg content is from Hunter et al. (2012) and Cowie et al. (2014). The vertical dashed line corresponds to the 22 µM limits defining an OMZ according to Levin et al. (2003). The dark grey shadow represents the core of the OMZ (< 2 µM; Paulmier and Ruiz-Pino, 2009) and the light grey shadow the lower part of the OMZ (< 22 µM; Levin, 2003).

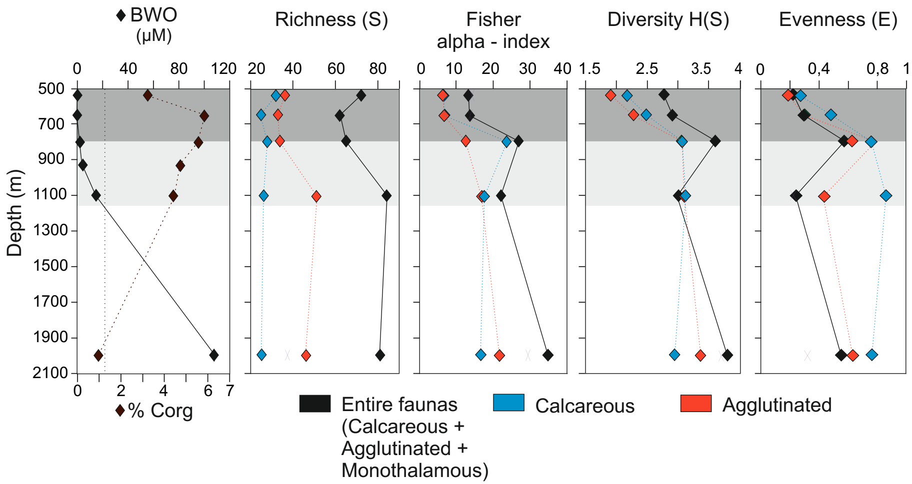

Figure 3. Stained foraminiferal biodiversity indices (in the > 150 µm fraction) along the sampling transect. The Corg content is from Hunter et al. (2012) and Cowie et al. (2014). The dashed line corresponds to the 22 µM limits defining an OMZ according to Levin et al. (2003). The dark grey shadow represent the core of the OMZ (< 2 µM; Paulmier and Ruiz-Pino, 2009) and the light grey shadow the lower part of the OMZ (< 22 µM; Levin, 2003).

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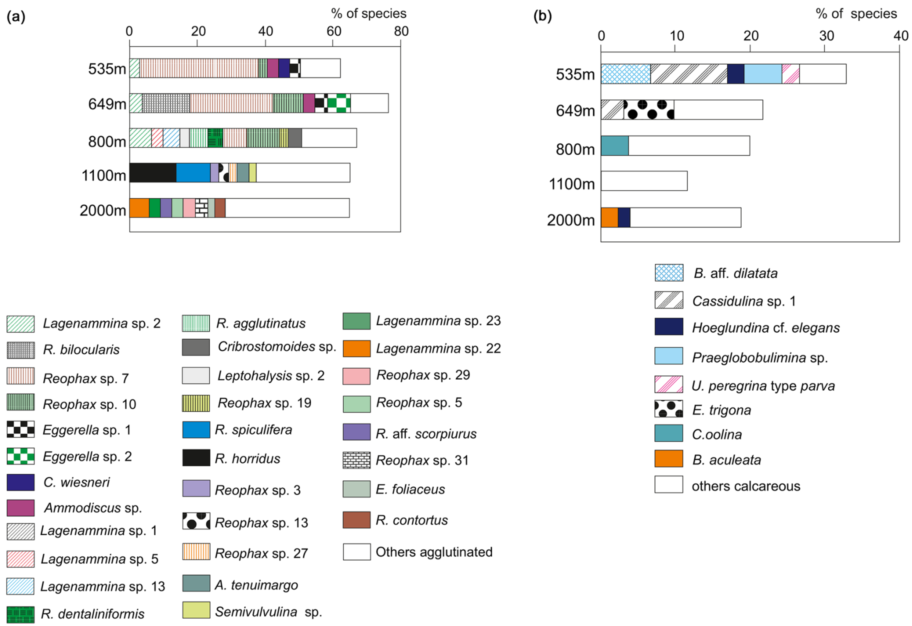

Figure 4. (a) Relative abundances of total fauna, only dominant live agglutinated foraminiferal species (> 2 % for each station) are represented, for the first top cm (0–1 cm) in the > 150 µm fraction. **(b)** Relative abundances of total fauna, only dominant live calcareous foraminiferal species (> 2 % for each station) are represented, for the first top cm (0–1 cm) in the > 150 µm fraction.

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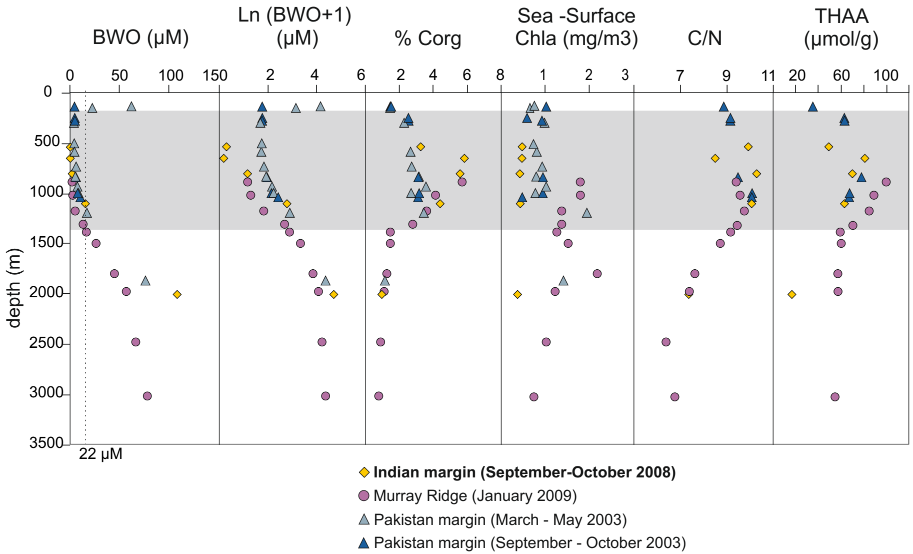

Figure 5. Regional comparison of the environmental parameters between the Indian margin, the Pakistan margin and the Murray ridge. The Corg content, C/N, THAA concentration and DI data are from Hunter et al. (2012) and Cowie et al. (2014) for the Indian margin; from Vandewiele et al. (2009) for the Pakistan margin; from Koho et al. (2013) for the Murray ridge. BWO was also expressed using the natural logarithm + 1 (Ln(BWO+1)) due to the values < 1 µM. The dark grey shadow corresponds to OMZ position.

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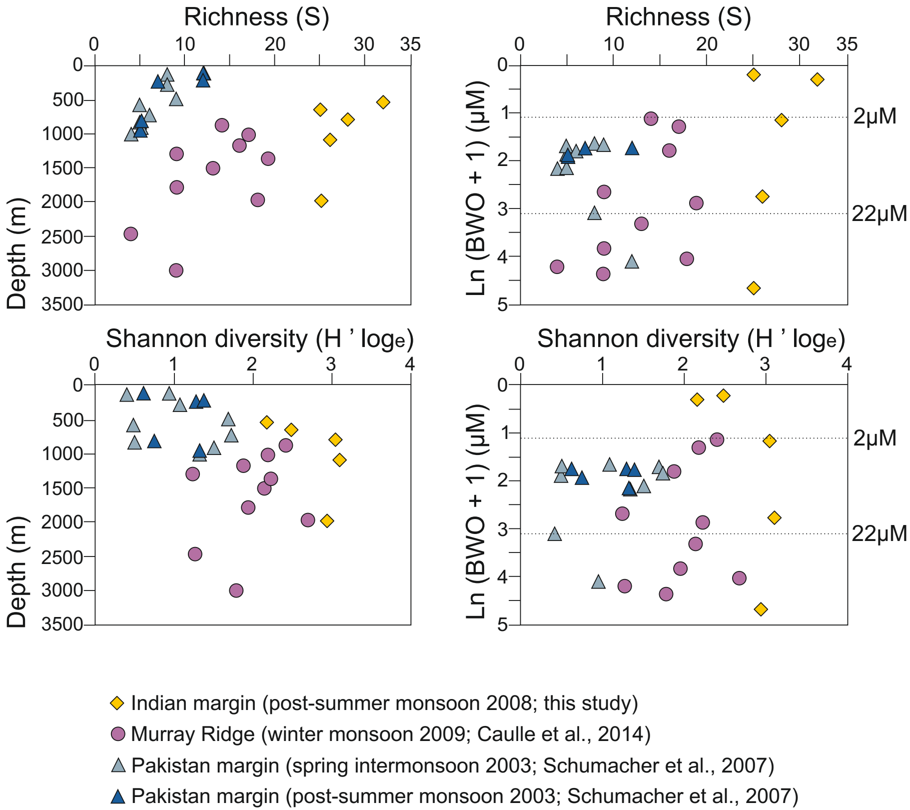

Figure 6. Richness and Shannon index, calculated only on calcareous fauna, vs. depth (m) and Ln (BWO+1) for the Indian margin, the Pakistan margin and the Murray ridge. The BWO was expressed using the natural logarithm +1 due to values < 1. The dash lines correspond to the limit of the core of the OMZ (2 µM) and to the OMZ (22 µM).

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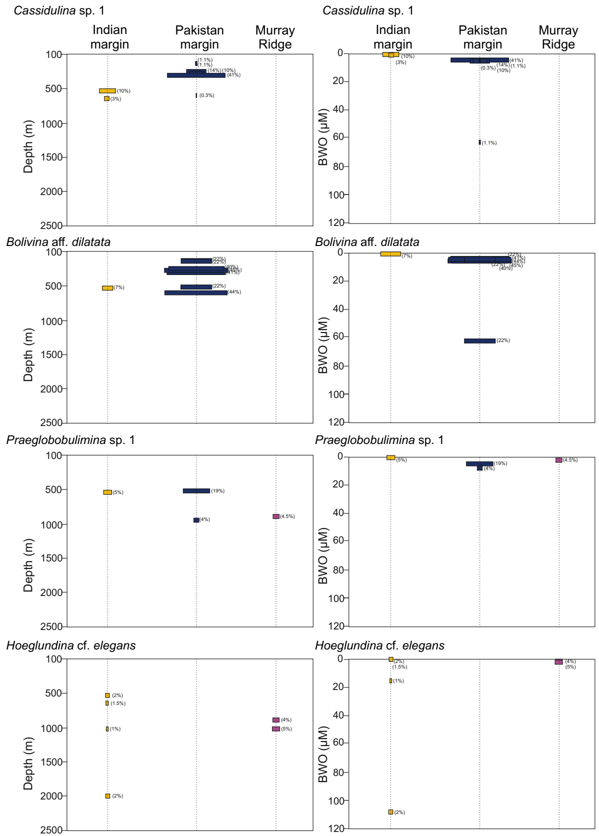

Figure 7. Comparison of species occurrences vs. depth (left panel) and BWO (µM; right panel) for three regions in the Arabian Sea. *Cassidulina* sp. 1 (from the Indian margin) and *Cassidulina laevigata* (Schumacher et al., 2007) was grouped into *Cassidulina* sp. Percentages of species occurrence is indicated in bracket.

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