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

C. Caulle[1,2]; M. Mojtahid[2]; A. J. Gooday[3]; F. J. Jorissen[2] and H. Kitazato[4]

[1] IFREMER, Laboratoire DYNECO/PELAGOS, Centre de Brest, Technopôle de Brest-Iroise, BP 70, F-29280 Plouzané, France

[2] {UMR CNRS 6112 LPG-BIAF, Recent and Fossil Bio-Indicators, Angers University, 2 Bd Lavoisier, 49045 Angers Cedex 01, France}

[3] {National Oceanographic Centre, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, UK}

[4] {Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushimacho, Yokosuka 237-0061, Japan}

Correspondence to: C. Caulle (clemence.caulle@gmail.com; Clemence.Caulle@ifremer.fr)

Abstract

Rose-Bengal-stained foraminiferal assemblages (> 150µm) 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 µM to 108 µM) bottom waters. Stained benthic foraminifera were investigated from two different size fractions (150-300 µm and >300µ m). Stained foraminiferal densities were very high in the core of the OMZ (at 535 and 649 m) and decreased at deeper sites. The faunas (> 150 µm) were dominated (40-80%) by non-calcareous taxa at all stations. These were mainly species of *Reophax* and *Lagenammina* but

Commentaire [m1]: Comment 2-1

Commentaire [m2]: Comment 1-13

Commentaire [m3]: Comment 2-1

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. These species are presently known only from the Arabian Sea. Because of their association with extremely low-oxygen concentrations, these species may be good markers for very low oxygen concentrations, and could be used to reconstruct past OMZ variability in the Arabian Sea.

Commentaire [m4]: Comment 1-13

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 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 µM; 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; Jannink et al., 1998; Gooday et al., 2000, 2009; Levin et al., 2000; Levin, 2003a; Schumacher et al., 2007; Mallon et al., 2012; Pozzato et al., 2013). In general, meiofaunal organisms (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 and reference therein). 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; Larkin et al., 2014; Enge et al., 2014). 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 on the Indian margin respond to the combination of organic-matter fluxes that are likely to be moderate (as indicated by satellite images of chlorophyll-a) and extremely low oxygen concentration.

Commentaire [m5]: Comment 3-

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 (Helly and Levin, 2004) 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.

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). The sampling sites (five in total) were located in the core of the OMZ at 535 m and 649 m, the lower boundary of the core at 800 m, the lower transition at 1100 and below the OMZ at 2000 m depth. Site characteristics were 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.

Commentaire [m6]: Comment 1-6

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 (wt % 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 µmol/g, respectively) reflect the presence of high quality, labile organic matter (Cowie et al., 2014).

2) At the lower boundary of the OMZ core, at about 800 m depth (BWO ~ 2.2 µM), the sediment is still characterised by high organic matter content and quality (wt % Corg ~ 5.6 % and THAA ~69.8 µmol/g; Cowie et al., 2014).

Commentaire [m7]: Comment 3-9

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 (wt % Corg ~ 4.4 % and THAA ~ 62.9 µmol/g; Cowie et al., 2014).

4) Beneath the OMZ, at 2000 m, well-oxygenated waters (BWO ~136 µM) and poorer trophic conditions occur (wt % Corg ~ 1 % and THAA ~ 17 µmol/g; 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 the *Yokosuka*, each core was sliced and each sediment slice was preserved in 8% borax-buffered formalin. The study of the benthic foraminiferal communities is based on an examination of the first two half-centimeter levels (0-1 cm).

In the laboratory, the fixed sediment from the 0-0.5- and 0.5-1.0-cm layers was washed separately 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 possible future analyses. The 150-300 and > 300 µm fractions of the two sediment layers were sorted wet (in water) under a binocular microscope for all Rose-Bengal-stained foraminifera.

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. All foraminifera 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 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. Since foraminifera are extremely abundant in finer sediment fractions, we confined our study to the >150-µm faction of the 0-1 cm layer.

Commentaire [CC8]: Comment 3-3

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 cm² at 535 m in the OMZ core to ~300 ind./50 cm² 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 species, 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./50cm² (calcareous), respectively, compared to ~150 ind./50 cm² and ~55 ind./50 cm², at the deepest site (2000 m). Monothalamids did not show a clear trends along the transect. The highest densities were found in the core (535 m; ~150 ind. /50cm²) and in the lower part (1100 m; ~115 ind. /50 cm²) of the OMZ. The lowest densities (~25 ind. /50cm²) 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 diversity 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 more elevated 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). For agglutinated taxa Shannon and Fisher indices 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. 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 assemblage composition

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 that includes spirillinids and miliolids (Pawlowski et al., 2013), 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 m and 649 m), where the oxygen concentration was very low, the agglutinated fauna was dominated by *Reophax* sp. 7, *Reophax* sp. 10, *R. 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, with *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 transition zone 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 this site, all calcareous species had relative abundances of 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 Figs. 4A and 4B) 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 would normally 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 core found most of the stained fauna in the first cm of the sediment (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009). In many hypoxic settings, compression of redox profiles leads to the absence of a well-defined vertical sequence of microhabitats and the presence of deep-infaunal taxa close to the sediment surface. Intermediate and deep infaunal taxa were scarce on the Indian margin, and have rarely been reported within the OMZ 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 species were missed at transitional sites and below the OMZ (1100 and 2000 m). However, 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 slightly increased, especially at the deeper sites (1100 and 2000 m). This view 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).

Commentaire [m9]: Comment 2-2

Commentaire [m10]: Comment 1-13

Confining our analyses to the >150 µm size fraction introduces a second source of bias. In low-oxygen settings, small-sized (63-150 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 bathymetric trends in foraminiferal diversity and faunal composition. Although analysing the finer size fractions may add some small-sized species, leading to slight changes in absolute and relative abundances, most of the species found in the small size fraction occurred also in the coarser fraction. Finally, a major advantage of working on the >150 µm size fraction is that it allows direct comparison with paleoceanographic studies, which are mainly based on the >125 or >150 µm fractions.

Commentaire [CC11]: Comment 1-13

Commentaire [m12]: Comment 3-3

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 [illegible]lated to the organic carbon flux to the sea floor, whereas species richness is mainly related to BWO concentrations. In a general sense and at a community scale, our Indian margin density and diversity patterns confirm these conclusions; absolute densities were higher in the core of the OMZ than at deeper sites (Fig. 2) whereas diversity indices described the opposite trend (Fig. 3). Community densities have largely been discussed in previous studies carried in the Arabian Sea OMZ (e.g. Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007; Larkin et al., 2009; Caulle et al., 2014). On the Indian margin, trends in foraminiferal density across the OMZ are very similar to those reported in previous studies in the Arabian Sea and are explained by the large quantities of labile organic matter present in the OMZ sediments (Fig. 2). 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 ~4 µM on the Pakistan margin (Schumacher et al., 2007; Larkin and Gooday, 2009). However, the performance of oxygen sensors is continously improving, and detection limits are decreasing. As a result,

Commentaire [m13]: Comment 1-1- We added community-scale

Commentaire [m14]: Comment 1-1- We added community-scale patterns of diversity

Commentaire [m15]: Comment 1-5:

discrepancies between studies may in part be due to instrumental bias, particularly when there is a substantial time lag between the different sampling periods.

Commentaire [m16]:

Inspite of the very low oxygen concentrations, species richness (i.e. the number of species) in our samples was surprisingly 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 (Taylor amd Gooday, 2014). 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 careful taxonomy was 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 versus ~0.35 µM) (Gooday et al., 2000). Foraminiferal species diversity and richness there were comparable to values reported in the present study (H’(log$_{e}$) ~ 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 their comparison with earlier studies is more straightforward. To facilitate comparisons with the data of Schumacher et al. (2007) and 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 were almost zero (~0.3 µM; at 535 m) at the time of sampling, is particularly striking (Fig. 5). The presence at the 535-m site of a species that we assign to *Hoeglundina* cf. *elegans* is also very surprising (Fig. 4 B). 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; observations of U. Witte reported in Taylor and Gooday, 2014), indicating rapid water movements. A current speed of 15 cm/s was recorded here during the *Yokosuka* cruise (observations of H. Nomaki, reported in Taylor and Gooday, 2014). Intermittent strong currents could lead to short periodic increases of BWO allowing low-oxygen-sensitive species 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 in other oceans 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, 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. Alternatively, the temporal persistence of species that are not known for their tolerance of low-oxygen conditions could be explained by a shift to anaerobic types of metabolism. Many foraminiferal species can accumulate intracellular nitrates in low-oxygen settings (Piña-Ochoa et al., 2010), and some are able to respire these nitrates (Risgaard-Petersen et al., 20xx). Unfortunately, no measurement of nitrate concentrations and denitrification rates are available for the dominant species of the Indian Margin OMZ. Another possibility is that these foraminifera can lower their metabolism (i.e., become dormant) during the most adverse periods. Geslin et al. (2011) showed that most benthic foraminiferal species have low oxygen respiration rates per unit of cytoplasmic volume,

Commentaire [m17]: Comment 3-11

estimated by assuming that the internal test volume corresponds to 75% of the total test volume (Hannah et al., 1994) and is entirely filled with cytoplasm.

Commentaire [CC18]: Comment 1-9

4.3. The tolerance of agglutinated foraminifera to low-oxygen conditions

Agglutinant foraminiferal species 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 the case everywhere. In the Black Sea, soft-shelled monothalamids 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, agglutinated species are the dominant component (up to 76% at 649 m) of foraminiferal assemblages. They include soft-shelled monothalamids, but the majority belong to genera such as *Reophax* and *Hormosinella* together with species of the single-chambered genus *Lagenammina* (Fig. 4B and Table 1). On the Indian margin, where oxygen concentrations during the *Yukosuka* cruise were extremely low in the OMZ core, these multi-chambered uniserial agglutinants are more abundant than calcareous foraminifera.

Commentaire [m19]: Comment 1-1-

Previous studies have observed differences in foraminiferal composition related to sediment characteristics (e.g. Kaminski, 1985). The hydrodynamic context of the Indian margin, and particularly of sites in the OMZ core (535 to 800 m), influences sediment grain size. At the 535 m site, the sand fraction represents 44% of the sediment compared to 9.6% at 800 m (Levin et al., 2013). Therefore, it is possible that the dominance of hormosinacean species at the OMZ sites is partly a consequence of the relatively coarse sediment. However, hormosinaceans, together with *Lagenammina*, are common in many fine-grained, deep-sea settings (e.g. Gooday et al., 2010b). In the Arabian Sea, similar proportions of *Reophax* and *Lagenammina* species have been reported in and below the OMZ on the Murray Ridge (Caulle et al., 2014) and the Oman margin (Gooday et al., 2000), and in the core of OMZ on the Pakistan margin (Larkin and Gooday, 2009) (Fig. 6). The general abundance of hormosinacean species associated with the Arabian Sea OMZ suggests that it cannot be attributed to sediment grain size alone. In fact, these observations reinforce our conclusion that some hormosinaceans can tolerate strong oxygen depletion (Caulle et al., 2014).

Nevertheless, a tolerance to hypoxia does not fully explain why hormosinacean and *Lagenammina* species are so common in our samples. One possible explanation is that it is 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 (Gooday et al., 2010a), 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 in the tests of 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. It is clear, however, that 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) (Fig. 4A and Table 1), and appear to be particularly well adapted to oxygen-poor conditions. It is possible that they dispose a facultative anaerobe metabolism. It has been demonstrated that some foraminiferal species may use nitrate as a second source of electron acceptor for respiration (denitrification) (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010). In fact, Piña-Ochoa et al. (2010) showed that some agglutinated foraminifera collect nitrate, although only four *Reophax* specimens (3 *Reophax micaceus* from the Bay of Biscay and 1 *Reophax* sp. from the Perù OMZ) were measured and no nitrate pool were detected. It can be suggested that hormosinacean species from the Arabian Sea OMZ are able to denitrificate to thrive under this severe environment. However, further investigations are needed before any firm conclusions can be made on this topic.

Commentaire [CC20]: Comment 3-5

Unlike Reophax spp. 7 and 10, *Reophax* aff. *scorpiurus*, *Reophax* spp. 31 and 5 were confined to the deepest site (2000 m) (Fig. 4A and Table 1). Indeed, these species are abundant and diverse in many deep-sea environments, including fully oxic abyssal plains (e.g., Gooday et al., 2010b).

4.4. Distribution of species across the OMZ

There is a succession of both calcareous and agglutinated foraminiferal species along the OMZ transect (Fig. 4 and Table 1). Sites in the core (535 and 649 m) have rather similar assemblages and are dominated (> 2%) 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* as well as *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 elevated 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, 2003) On the Pakistan margin an edge effect of this kind was evident among foraminiferal populations at around 750 m depth (Gooday et al., 2009) and might therefore be expected at our 800 m site (BWO ~2.2 µM). Hence it is rather surprisingly that faunal density are minimal here (~320 ind/50cm²; Fig. 2). If foraminifera do exhibit an edge effect on the Indian margin it must be at some depth between 800 m and the next deepest site at 1100 m.

The assemblage at 800 m comprises a mixture of calcareous species typical of the OMZ 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 here 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 *Cancris auriculus* and *Chilostomella oolina* to colonise the site, resulting in maximum diversity. *Cancris auriculus* is also found in the OMZ (BWO ~ 5 µM) on the Pakistan margin (Larkin and Gooday, 2009) 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

Commentaire [m21]: Comment 3-12

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 µM 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 appears to be more severely depleted in oxygen, in view of possible bias due to instrumental development. 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 (in contrast to the low surface water PP) could be partly explained by the lower oxygen concentrations on the Indian Margin

(Fig. 5) coupled to local hydrodynamics (seasonal development of a belt of intense oxygen depletion linked to northward surface currents) leading to a better preservation of organic matter (Cowie et al., 2014). This would imply that the availability of labile organic carbon on the Indian margin is only partly determined by the sea-surface primary productivity. Instead, severe mid-water hypoxia leading to limited organic matter degradation during transit through the water column may play an important role in the presence of abundant high quality OM on the sea floor. 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 not clear how these indices describe the bio-availability of the organic components. Nevertheless, we think that our data suggest that on the Indian margin [illegible]WO, as well as hydrodynamics, represent a more important control on benthic foraminiferal abundance and species composiion than sea-surface primary production.

The same foraminiferal species are found on the Indian margin and at previously studied sites in the Arabian Sea (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 generally found at oxygen concentrations <10 µM (Fig. 7). This highlights the strong adaptation of these indicator species to hypoxic environments. *Praeglobobulimina* sp. 1 and *B.* aff. *dilatata* have not been reported in other oceanic basins, including the OMZ in the East Pacific or the well-studied upwelling area 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 hypoxia, may induce rapid morphological and genetic changes (Verhallen, 1987) as well as promoting 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 through a combination of molecular genetics and morphological analysis.

Ehrenbergina trigona and *Chilostomella oolina* appear in a BWO interval from ~ 0 to ~ 22 µM (Fig. 7). It appears that many Arabian Sea foraminiferal species are living in a specific range of BWO concentrations, defining ecological niches for the different species. The fact that the same species occur on the Indian margin, the Pakistan margin and the Murray ridge, in the same BWO interval, but probably with very different export production (based on

Commentaire [m22]: Comment 3-1

Commentaire [m23]: Comment 1-10

Commentaire [m24]: Comment 1-12

Commentaire [m25]: Comment 1-11

satellite images of chlorophyll-a), provides strong support for the dominant role of BWO, rather than organic flux to the sea floor, in regulating the benthic foraminiferal assemblages.

Commentaire [m26]: Comment 3-1

4.6. Implications in paleoceanography

Commentaire [m27]: Comment 1-3

Our results suggest that BWO may play the major role in regulating benthic foraminiferal assemblages in the Arabian Sea. This conclusion could have important implications for the reconstruction OMZ variability in the Arabian Sea over geological time scales. Foraminiferal marker 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*, 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. Additionally, absolute foraminiferal diversity indices have to be interpreted very carefully in paleoreconstructions from the Arabian Sea, as our results show that low BWO does not always synonym of low foraminiferal diversity.

Commentaire [m28]: Comment 1-11

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 live 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, which contradicts the commonly accepted paradigm of low oxygen areas being characterized by low diversity faunas, may reflect the adaptation of the predominantly agglutinated species present here to these extreme conditions. However, this high diversity in the OMZ, 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 strong intermittent oxygen fluctuations. Moreover, extremely low oxygen concentrations may enhance the preservation of cellular material after the death of the organism, increasing the apparent diversity of the Rose Bengal stained assemblage.

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, foraminiferal assemblages (both agglutinated and calcareous taxa) change along the oxygen transect. An assemblage comprising species tolerant of severe hypoxia in the core of the OMZ is suceeded by a transitional assemblage in the lower part of the OMZ, and finally a fauna composed of more 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 separates foraminifera typical of the hypoxic core, which probably have a restricted (endemic) 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.

Acknowledgements

We thank the captain and crew of the RV Yokosuka and the pilots and staff of the Shinkai 6500 Human Occupied Vehicle for their assistance with the field operations. We thank the scientists participating in RV Yokosuka cruise YK08-11 for their assistance, especially Kazumasa Oguri and Hisami Suga, who measured dissolved oxygen concentrations, and Will Hunter, Lisa Levin, Hidetaka Nomaki, Ursula Witte and Claire Woulds, who helped with the faunal work at sea. We are grateful for the comments of Dr Anthony Rathburn and two anonymous reviewers, which helped to substantially improve the original submission.

References

Altenbach, A. V.: Die Biomasse der benthische Foraminiferen, in Auswertungen von "Meteor"-Expeditionen im östliche Nordatlantik, University of Kiel, Ph.D. diss., 1985.

Altenbach, A. V.: The measurement of organic carbon in foraminifera, Journal of Foraminiferal Research, 17(2), 106–109, 1987.

Altenbach, A. V., Pflaumann, U., Schiebel, R., Thies, A., Timm, S. and Trauth, M.: Scaling percentages and distributional patterns of benthic foraminifera with flux rates of organic carbon, Journal of Foraminiferal Research, 29(3), 173–185, 1999.

Banse, K. and McClain, C. R.: Winter blooms of phytoplankton in the Arabian Sea as observed by the Coastal Zone Color Scanner, Marine Ecology Progress Series, 34(3), 201–211, 1986.

Bernhard, J. M.: Postmortem Vital Staining in Benthic Foraminifera; Duration and Importance in Population and Distributional Studies, Journal of Foraminiferal Research, 18(2), 143–146, doi:10.2113/gsjfr.18.2.143, 1988.

Bernhard, J. M.: Distinguishing Live from Dead Foraminifera: Methods Review and Proper Applications, Micropaleontology, 46, 38–46, doi:10.2307/1486179, 2000.

Bernhard, J. M. and Gupta, B. K. S.: Foraminifera of oxygen-depleted environments, in Modern Foraminifera, pp. 201–216, Springer Netherlands, 2003.

Bernhard, J. M., Ostermann, D. R., Williams, D. S. and Blanks, J. K.: Comparison of two methods to identify live benthic foraminifera: A test between Rose Bengal and CellTracker Green with implications for stable isotope paleoreconstructions, Paleoceanography, 21(4), doi:10.1029/2006PA001290, 2006.

Cardich, J., Morales, M., Quipúzcoa, L., Sifeddine, A. and Gutiérrez, D.: Benthic Foraminiferal Communities and Microhabitat Selection on the Continental Shelf Off Central Peru, in Anoxia, edited by A. V. Altenbach, J. M. Bernhard, and J. Seckbach, pp. 323–340, 2012.

Caron, D. A. and Dennett, M. R.: Phytoplankton growth and mortality during the 1995 Northeast Monsoon and Spring Intermonsoon in the Arabian Sea, Deep Sea Research Part II: Topical Studies in Oceanography, 46(8), 1665–1690, 1999.

Caulle, C., Koho, K. A., Mojtahid, M., Reichart, G. J. and Jorissen, F. J.: Live (Rose Bengal stained) foraminiferal faunas from the northern Arabian Sea: faunal succession within and below the OMZ, Biogeosciences, 11(4), 1155–1175, doi:10.5194/bg-11-1155-2014, 2014.

Cook, P. L., Revill, A. T., Butler, E. C., Eyre, B. D. and others: Carbon and nitrogen cycling on intertidal mudflats of a temperate Australian estuary. II. Nitrogen cycling, Marine Ecology Progress Series, 280, 39–54, 2004.

Corliss, B. H. and Emerson, S.: Distribution of rose bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine, Deep Sea

Research Part A. Oceanographic Research Papers, 37(3), 381–400, doi:10.1016/0198-0149(90)90015-N, 1990.

Cowie, G., Mowbray, S., Kurian, S., Sarkar, A., White, C., Anderson, A., Vergnaud, B., Johnstone, G., Brear, S., Woulds, C., Naqvi, S. W. A. and Kitazato, H.: Comparative organic geochemistry of Indian margin (Arabian Sea) sediments: estuary to continental slope, Biogeosciences, 11(23), 6683–6696, doi:10.5194/bg-11-6683-2014, 2014.

Diz, P., Francés, G. and Rosón, G.: Effects of contrasting upwelling-downwelling on benthic foraminiferal distribution in the Ría de Vigo (NW Spain), Journal of Marine Systems, 60(1-2), 1–18, 2006.

Den Dulk, M., Reichart, G. J., Memon, G. M., Roelofs, E. M. P., Zachariasse, W. J. and van der Zwaan, G. J.: Benthic foraminiferal response to variations in surface water productivity and oxygenation in the northern Arabian Sea, Marine Micropaleontology, 35(1–2), 43–66, doi:10.1016/S0377-8398(98)00015-2, 1998.

Enge, A. J., Witte, U., Kucera, M. and Heinz, P.: Uptake of phytodetritus by benthic foraminifera under oxygen depletion at the Indian margin (Arabian Sea), Biogeosciences, 11(7), 2017–2026, doi:10.5194/bg-11-2017-2014, 2014.

Erbacher, J. and Nelskamp, S.: Comparison of benthic foraminifera inside and outside a sulphur-oxidizing bacterial mat from the present oxygen-minimum zone off Pakistan (NE Arabian Sea), Deep Sea Research Part I: Oceanographic Research Papers, 53(5), 751–775, doi:10.1016/j.dsr.2006.02.003, 2006.

Fontanier, C., Jorissen, F. ., Licari, L., Alexandre, A., Anschutz, P. and Carbonel, P.: Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats, Deep Sea Research Part I: Oceanographic Research Papers, 49(4), 751–785, doi:10.1016/S0967-0637(01)00078-4, 2002.

Geslin, E., Risgaard-Petersen, N., Lombard, F., Metzger, E., Langlet, D. and Jorissen, F.: Oxygen respiration rates of benthic foraminifera as measured with oxygen microsensors, Journal of Experimental Marine Biology and Ecology, 396(2), 108–114, doi:10.1016/j.jembe.2010.10.011, 2011.

Gooday, A. J.: Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: environmental influences on faunal characteristics, Advances in Marine Biology, 46, 1–90, 2003.

Gooday, A. J., Bernhard, J. M., Levin, L. A. and Suhr, S. B.: Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas, Deep Sea Research Part II: 47(1–2), 25–54, doi:10.1016/S0967-0645(99)00099-5, 2000.

Gooday, A.J., Bett, B.J., Escobar, E., Ingole, B., Levin, L.A., Neira, C., Raman, A.V., Sellanes, J.: Biodiversity and habitat heterogeneity in oxygen minimum zones. Marine Ecology 31, 125-147, 2010a.

Gooday, A. J. and Jorissen, F. J.: Benthic Foraminiferal Biogeography: Controls on Global Distribution Patterns in Deep-Water Settings, Annual Review of Marine Science, 4(1), 237–262, doi:10.1146/annurev-marine-120709-142737, 2012.

Gooday, A. J., Kitazato, H., Hori, S. and Toyofuku, T.: Monothalamous Soft-Shelled Foraminifera at an Abyssal Site in the North Pacific: A Preliminary Report, Journal of Oceanography, 57(3), 377–384, doi:10.1023/A:1012447015771, 2001.

Gooday, A. J., Levin, L. A., Aranda da Silva, A., Bett, B. J., Cowie, G. L., Dissard, D., Gage, J. D., Hughes, D. J., Jeffreys, R., Lamont, P. A., Larkin, K. E., Murty, S. J., Schumacher, S., Whitcraft, C. and Woulds, C.: Faunal responses to oxygen gradients on the Pakistan margin: A comparison of foraminiferans, macrofauna and megafauna, Deep Sea Research Part II: Topical Studies in Oceanography, 56(6–7), 488–502, doi:10.1016/j.dsr2.2008.10.003, 2009.

Gooday, A.J., Malzone, M.G., Bett, B.J., Lamont, P.A.: 2010. Decadal-scale changes in shallow-infaunal foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. Deep-Sea Research II, 57, 1362–1382, 2010b

Gooday, A. J., Nomaki, H. and Kitazato, H.: Modern deep-sea benthic foraminifera: a brief review of their morphology-based biodiversity and trophic diversity, Geological Society, London, Special Publications, 303(1), 97–119, 2008.

Gooday, A. J., Turley, C. M. and Allen, J. A.: Responses by Benthic Organisms to Inputs of Organic Material to the Ocean Floor: A Review and Discussion, Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences, 331(1616), 119–138, 1990.

Haake, B., Ittekkot, V., Rixen, T., Ramaswamy, V., Nair, R. R. and Curry, W. B.: Seasonality and interannual variability of particle fluxes to the deep Arabian Sea, Deep Sea Research Part I: Oceanographic Research Papers, 40(7), 1323–1344, 1993.

Hammer, Ø., Harper, D. A. T. and Ryan, P. D.: PAST-PAlaeontological STatistics, ver. 1.89, University of Oslo, Oslo, 2009.

Hannah, F., Rogerson, A., Laybourn-Parry, J.,: Respiration rates and biovolumes of common benthic foraminifera (protozoa). Journal of the Marine Biological Association of the UK 74, 301–312, 1994.

Heinz, P. and Hemleben, C.: Regional and seasonal variations of recent benthic deep-sea foraminifera in the Arabian Sea, Deep Sea Research Part I: Oceanographic Research Papers, 50(3), 435–447, doi:10.1016/S0967-0637(03)00014-1, 2003.

Heinz, P. and Hemleben, C.: Foraminiferal response to the Northeast Monsoon in the western and southern Arabian Sea, Marine Micropaleontology, 58(2), 103–113, doi:10.1016/j.marmicro.2005.10.001, 2006.

Heinz, P., Hemleben, C. and Kitazato, H.: Time-response of cultured deep-sea benthic foraminifera to different algal diets, Deep Sea Research Part I: Oceanographic Research Papers, 49(3), 517–537, doi:10.1016/S0967-0637(01)00070-X, 2002.

Helly, J. J. and Levin, L. A.: Global distribution of naturally occurring marine hypoxia on continental margins, Deep Sea Research Part I: Oceanographic Research Papers, 51(9), 1159–1168, doi:10.1016/j.dsr.2004.03.009, 2004.

Hermelin, J. O. R. and Shimmield, G. B.: The importance of the oxygen minimum zone and sediment geochemistry in the distribution of Recent benthic foraminifera in the northwest Indian Ocean, Marine Geology, 91(1), 1–29, 1990.

Hunter, W. R., Oguri, K., Kitazato, H., Ansari, Z. A. and Witte, U.: Epi-benthic megafaunal zonation across an oxygen minimum zone at the Indian continental margin, Deep Sea Research Part I: Oceanographic Research Papers, 58(6), 699–710, 2011.

Hunter, W. R., Veuger, B. and Witte, U.: Macrofauna regulate heterotrophic bacterial carbon and nitrogen incorporation in low-oxygen sediments, The ISME journal, 6(11), 2140–2151, 2012.

Jannink, N. T., Zachariasse, W. J. and Van der Zwaan, G. J.: Living (Rose Bengal stained) benthic foraminifera from the Pakistan continental margin (northern Arabian Sea), Deep Sea Research Part I: Oceanographic Research Papers, 45(9), 1483–1513, doi:10.1016/S0967-0637(98)00027-2, 1998.

Jorissen, F. J., de Stigter, H. C. and Widmark, J. G. V.: A conceptual model explaining benthic foraminiferal microhabitats, Marine Micropaleontology, 26(1–4), 3–15, doi:10.1016/0377-8398(95)00047-X, 1995.

Kitazato, H.: Foraminiferal microhabitats in four marine environments around Japan, Marine Micropaleontology, 24(1), 29–41, 1994.

Koho, K. A.: The dynamic balance between food abundance and habitat instability: benthic foraminifera of Portuguese margin canyons., 2008.

Koho, K. A., García, R., De Stigter, H. C., Epping, E., Koning, E., Kouwenhoven, T. J. and Van der Zwaan, G. J.: Sedimentary labile organic carbon and pore water redox control on species distribution of benthic foraminifera: A case study from Lisbon–Setúbal Canyon (southern Portugal), Progress in Oceanography, 79(1), 55–82, 2008.

Koho, K. A., Nierop, K. G. J., Moodley, L., Middelburg, J. J., Pozzato, L., Soetaert, K., van der Plicht, J. and Reichart, G.-J.: Microbial bioavailability regulates organic matter preservation in marine sediments, Biogeosciences, 10(2), 1131–1141, doi:10.5194/bg-10-1131-2013, 2013.

Koho, K. A. and Piña-Ochoa, E.: Benthic Foraminifera: Inhabitants of Low-Oxygen Environments, in Anoxia, edited by A. V. Altenbach, J. M. Bernhard, and J. Seckbach, pp. 249–285, 2012.

Koho, K. A., Piña-Ochoa, E., Geslin, E. and Risgaard-Petersen, N.: Vertical migration, nitrate uptake and denitrification: survival mechanisms of foraminifers (*Globobulimina turgida*) under low oxygen conditions, FEMS microbiology ecology, 2011.

Kurbjeweit, F., Schmiedl, G., Schiebel, R., Hemleben, C., Pfannkuche, O., Wallmann, K. and Schäfer, P.: Distribution, biomass and diversity of benthic foraminifera in relation to sediment geochemistry in the Arabian Sea, Deep Sea Research Part II: Topical Studies in Oceanography, 47(14), 2913–2955, doi:10.1016/S0967-0645(00)00053-9, 2000.

Larkin, K. E. and Gooday, A. J.: Foraminiferal faunal responses to monsoon-driven changes in organic matter and oxygen availability at 140 and 300 m water depth in the NE Arabian Sea, Deep Sea Research Part II: Topical Studies in Oceanography, 56(6–7), 403–421, doi:10.1016/j.dsr2.2008.05.037, 2009.

Larkin, K. E., Gooday, A. J., Woulds, C., Jeffreys, R. M., Schwartz, M., Cowie, G., Whitcraft, C., Levin, L., Dick, J. R. and Pond, D. W.: Uptake of algal carbon and the likely synthesis of an “essential” fatty acid by *Uvigerina* ex. gr. *semiornata* (Foraminifera) within the Pakistan margin oxygen minimum zone: evidence from fatty acid biomarker and ^{13}C tracer experiments, Biogeosciences, 11(14), 3729–3738, doi:10.5194/bg-11-3729-2014, 2014.

Levin, L.: Oxygen minimum zone benthos: adaptation and community response to hypoxia, 2003.

Levin, L. A., Ekau, W., Gooday, A. J., Jorissen, F., Middelburg, J. J., Naqvi, S. W. A., Neira, C., Rabalais, N. N. and Zhang, J.: Effects of natural and human-induced hypoxia on coastal benthos, Biogeosciences, 6(10), 2063–2098, 2009.

Levin, L. A. and Gage, J. D.: Relationships between oxygen, organic matter and the diversity of bathyal macrofauna, Deep Sea Research Part II: Topical Studies in Oceanography, 45, 129–163, 1998.

Levin, L. A., Gage, J. D., Martin, C. and Lamont, P. A.: Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea, Deep Sea Research Part II: Topical Studies in Oceanography, 47(1–2), 189–226, doi:10.1016/S0967-0645(99)00103-4, 2000.

Levin, L. A., Huggett, C. L. and Wishner, K. F.: Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean, Journal of Marine Research, 49(4), 763–800, 1991.

Levin, L. A., McGregor, A. L., Mendoza, G. F., Woulds, C., Cross, P., Witte, U., Gooday, A. J., Cowie, G. and Kitazato, H.: Macrofaunal colonization across the Indian margin oxygen minimum zone, Biogeosciences, 10(11), 7161–7177, doi:10.5194/bg-10-7161-2013, 2013.

Mackensen, A. and Douglas, R. G.: Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell Sea and the California continental borderland, Deep Sea Research Part A. Oceanographic Research Papers, 36(6), 879–900, doi:10.1016/0198-0149(89)90034-4, 1989.

Madhupratap, M., Kumar, S. P., Bhattathiri, P. M. A., Kumar, M. D., Raghukumar, S., Nair, K. K. C. and Ramaiah, N.: Mechanism of the biological response to winter cooling in the northeastern Arabian Sea, 1996.

Mallon, J., Glock, N. and Schönfeld, J.: The Response of Benthic Foraminifera to Low-Oxygen Conditions of the Peruvian Oxygen Minimum Zone, in Anoxia, edited by A. V. Altenbach, J. M. Bernhard, and J. Seckbach, pp. 305–321, 2012.

Milliman, J. D., Troy, P. J., Balch, W. M., Adams, A. K., Li, Y.-H. and Mackenzie, F. T.: Biologically mediated dissolution of calcium carbonate above the chemical lysocline?, Deep Sea Research Part I: Oceanographic Research Papers, 46(10), 1653–1669, 1999.

Moodley, L., Van der Zwaan, G. J., Herman, P. M. J., Kempers, L. and Van Breugel, P.: Differential response of benthic meiofauna to anoxia with special reference to Foraminifera (Protista: Sarcodina), Marine Ecology Progress Series, 1997.

Mullins, H. T., Thompson, J. B., McDougall, K. and Vercoutere, T. L.: Oxygen-minimum zone edge effects: evidence from the central California coastal upwelling system, Geology, 13(7), 491–494, 1985.

Murray, J. W.: Ecology and palaeoecology of benthic foraminifera, Longman, Harlow., 1991.

Naidu, P. D. and Malmgren, B. A.: Do benthic foraminifer records represent a productivity index in oxygen minimum zone areas? An evaluation from the Oman Margin, Arabian Sea, Marine Micropaleontology, 26(1–4), 49–55, doi:10.1016/0377-8398(95)00014-3, 1995.

Neira, C., Sellanes, J., Levin, L. A. and Arntz, W. E.: Meiofaunal distributions on the Peru margin:: relationship to oxygen and organic matter availability, Deep Sea Research Part I: Oceanographic Research Papers, 48(11), 2453–2472, doi:10.1016/S0967-0637(01)00018-8, 2001.

Nomaki, H., Heinz, P., Hemleben, C. and Kitazato, H.: Behavior and Response of Deep-Sea Benthic Foraminifera to Freshly Supplied Organic Matter: A Laboratory Feeding Experiment in Microcosm Environments, Journal of Foraminiferal Research, 35(2), 103–113, doi:10.2113/35.2.103, 2005.

Oliver, P. G. and Levin, L.: A new species of the family Thyasiridae (Mollusca: Bivalvia) from the oxygen minimum zone of the Pakistan Margin, Journal of the Marine Biological Association of the United Kingdom, 86(02), 411–416, 2006.

Paulmier, A. and Ruiz-Pino, D.: Oxygen minimum zones (OMZs) in the modern ocean, Progress in Oceanography, 80(3–4), 113–128, doi:10.1016/j.pocean.2008.08.001, 2009.

Pawlowski, J., Holzmann, M., Tyszka, J.: New supraordinal classification of Foraminifera: Molecules meet morphology. Marine Micropaleontology 100, 1-10, 2013.

Phipps, M., Jorissen, F., Pusceddu, A., Bianchelli, S. and Stigter, H. D.: Live Benthic Foraminiferal Faunas Along a Bathymetrical Transect (282–4987 M) on the Portuguese Margin (NE Atlantic), Journal of Foraminiferal Research, 42(1), 66–81, doi:10.2113/gsjfr.42.1.66, 2012.

Pina-Ochoa, E., Hogslund, S., Geslin, E., Cedhagen, T., Revsbech, N. P., Nielsen, L. P., Schweizer, M., Jorissen, F., Rysgaard, S. and Risgaard-Petersen, N.: Widespread occurrence of nitrate storage and denitrification among Foraminifera and Gromiida, Proceedings of the National Academy of Sciences, 107(3), 1148–1153, doi:10.1073/pnas.0908440107, 2009.

Pozzato, L., van Oevelen, D., Moodley, L., Soetaert, K. and Middelburg, J. J.: Carbon processing at the deep-sea floor of the Arabian Sea oxygen minimum zone: A tracer approach, Journal of Sea Research, 78, 45–58, doi:10.1016/j.seares.2013.01.002, 2013.

Rathburn, A. E., Levin, L. A., Held, Z. and Lohmann, K. C.: Benthic foraminifera associated with cold methane seeps on the northern California margin: ecology and stable isotopic composition, Marine Micropaleontology, 38(3), 247–266, 2000.

Risgaard-Petersen, N., Langezaal, A. M., Ingvardsen, S., Schmid, M. C., Jetten, M. S. M., Op den Camp, H. J. M., Derksen, J. W. M., Piña-Ochoa, E., Eriksson, S. P., Peter Nielsen, L., Peter Revsbech, N., Cedhagen, T. and van der Zwaan, G. J.: Evidence for complete denitrification in a benthic foraminifer, Nature, 443(7107), 93–96, doi:10.1038/nature05070, 2006.

Rixen, T., Haake, B. and Ittekkot, V.: Sedimentation in the western Arabian Sea the role of coastal and open-ocean upwelling, Deep Sea Research Part II: Topical Studies in Oceanography, 47(9–11), 2155–2178, doi:10.1016/S0967-0645(00)00020-5, 2000.

Rixen, T., Haake, B., Ittekkot, V., Guptha, M. V. S., Nair, R. R. and Schlüssel, P.: Coupling between SW monsoon-related surface and deep ocean processes as discerned from continuous particle flux measurements and correlated satellite data, Journal of Geophysical Research: Oceans, 101(C12), 28569–28582, doi:10.1029/96JC02420, 1996.

Ryther, J. H. and Menzel, D. W.: On the production, composition, and distribution of organic matter in the Western Arabian Sea, in Deep Sea Research and Oceanographic Abstracts, 12, 199–209, 1965.

Sanders, H. L. and Hessler, R. R.: Ecology of the deep-sea benthos, Science, 163 (3874), 1419–1424, 1969.

Schumacher, S., Jorissen, F. J., Dissard, D., Larkin, K. E. and Gooday, A. J.: Live (Rose Bengal stained) and dead benthic foraminifera from the oxygen minimum zone of the Pakistan continental margin (Arabian Sea), Marine Micropaleontology, 62(1), 45–73, doi:10.1016/j.marmicro.2006.07.004, 2007.

Sergeeva, N. G., Gooday, A. J., Mazlumyan, S. A., Kolesnikova, E. A., Lichtschlag, A., Kosheleva, T. N. and Anikeeva, O. V.: Meiobenthos of the Oxic/Anoxic Interface in the Southwestern Region of the Black Sea: Abundance and Taxonomic Composition, in Anoxia, edited by A. V. Altenbach, J. M. Bernhard, and J. Seckbach, pp. 369–401, 2012.

Stubbings, H. G.: The Marine Deposits of the Arabian Sea: An Investigation Into Their Distribution and Biology, Order of the Trustees of the British Museum., 1939.

Taylor, A. and Gooday, A. J.: Agglutinated foraminifera (superfamily Hormosinacea) across the Indian margin oxygen minimum zone (Arabian Sea), Marine Biodiversity, 44(1), 5–25, 2014.

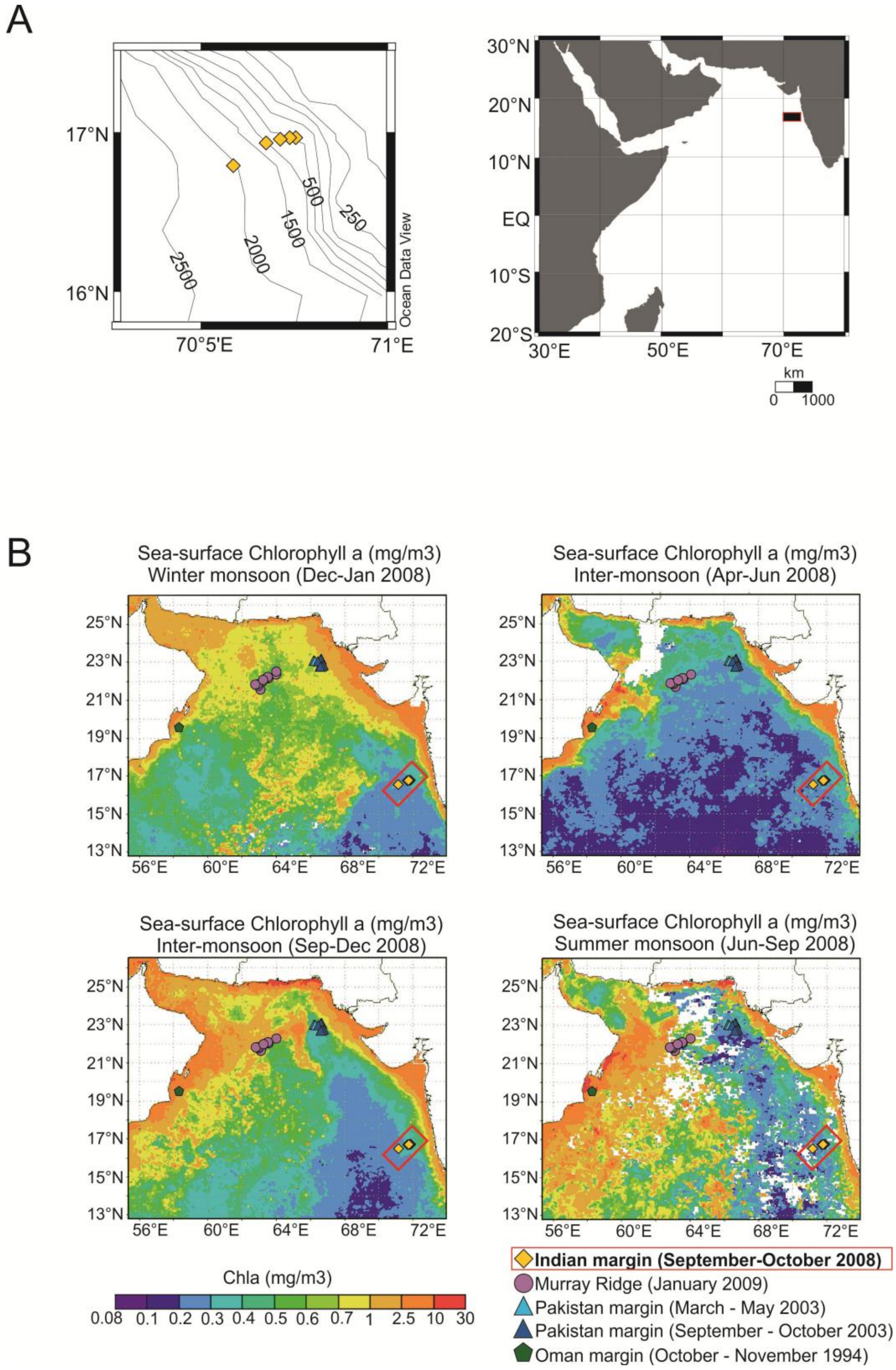
Vandewiele, S., Cowie, G., Soetaert, K. and Middelburg, J. J.: Amino acid biogeochemistry and organic matter degradation state across the Pakistan margin oxygen minimum zone, Deep Sea Research Part II: Topical Studies in Oceanography, 56(6–7), 376–392, doi:10.1016/j.dsr2.2008.05.035, 2009.

Verhallen, P.U.M.: Early development of Bulimina marginata in relation to paleoenvironmental changes in the Mediterranean, Proc. Kon. Ned. Akad. Wetensch. ser. B, 90, 161–180, 1987.

Ward, B. B., Glover, H. E. and Lipschultz, F.: Chemoautotrophic activity and nitrification in the oxygen minimum zone off Peru, Deep Sea Research Part A. Oceanographic Research Papers, 36(7), 1031–1051, 1989.

Wishner, K. F., Ashjian, C. J., Gelfman, C., Gowing, M. M., Kann, L., Levin, L. A., Mullineaux, L. S. and Saltzman, J.: Pelagic and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone, Deep Sea Research Part I: Oceanographic Research Papers, 42(1), 93–115, 1995.

Wishner, K., Levin, L., Gowing, M. and Mullineaux, L.: Involvement of the oxygen minimum in benthic zonation on a deep seamount, Nature, 346(6279), 57–59, 1990.


A
17°N
16°N
70°5'E
71°E
2500
2000
1500
500
250
Ocean Data View
30°N
20°N
10°N
EQ
10°S
20°S
30°E
50°E
70°E
km
0
1000
B
Sea-surface Chlorophyll a (mg/m3)
Winter monsoon (Dec-Jan 2008)
Sea-surface Chlorophyll a (mg/m3)
Inter-monsoon (Apr-Jun 2008)
Sea-surface Chlorophyll a (mg/m3)
Inter-monsoon (Sep-Dec 2008)
Sea-surface Chlorophyll a (mg/m3)
Summer monsoon (Jun-Sep 2008)
25°N
23°N
21°N
19°N
17°N
15°N
13°N
56°E
60°E
64°E
68°E
72°E
Chla (mg/m3)
0.08
0.1
0.2
0.3
0.4
0.5
0.6
0.7
1
2.5
10
30
Indian margin (September-October 2008)
Murray Ridge (January 2009)
Pakistan margin (March - May 2003)
Pakistan margin (September - October 2003)
Oman margin (October - November 1994)

927

Fig. 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 (Gooday et al., 2000; Schumacher et al., 2007; Caulle et al., 2014); http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/

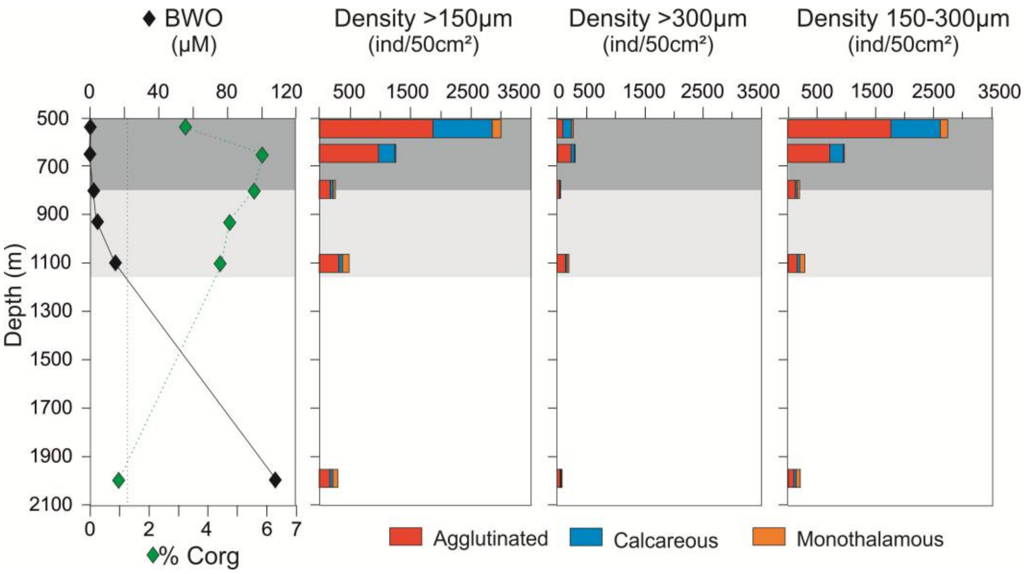


Fig. 2. Total stained foraminiferal abundances (ind/50cm²) in the 150-300 µm, >300 µm and >150 µm (i.e. 150-300 and >300 µm combined) fractions of the first cm (0-1 cm layer) along the sampling transect. The BWO concentration (µM) and Corg content (wt. %) are from Hunter et al. (2012) and Cowie et al. (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 (2-22 µM; Levin, 2003).

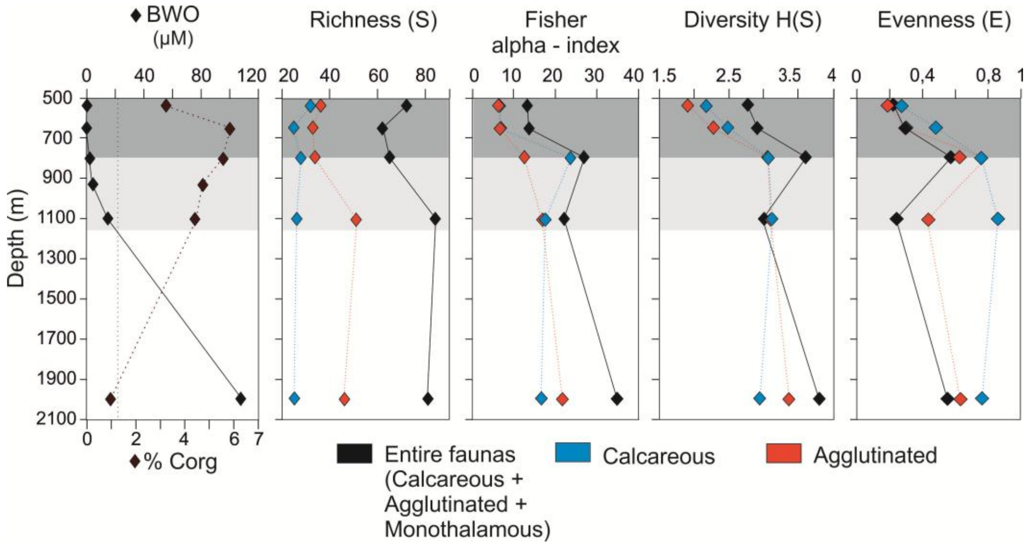
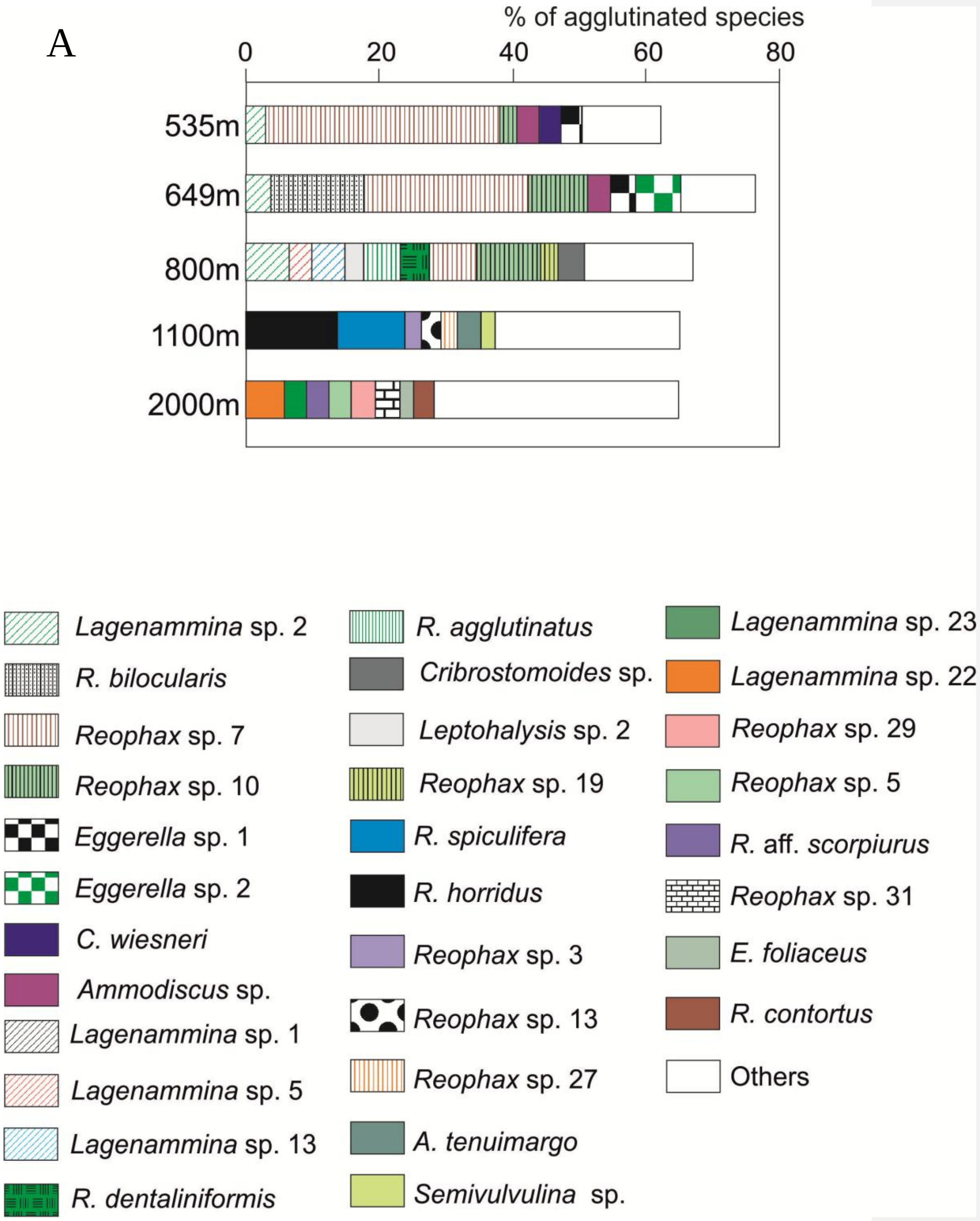


Fig. 3. Stained foraminiferal diversity indices (in the >150µm fraction) along the sampling transect. The Corg content (wt. %) is from Hunter et al. (2012) and Cowie et al. (2014). The dashed line corresponds to the 22 µM limit defining an OMZ according to Levin et al. (2003). The dark grey shadow represent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


A
% of agglutinated species
0
20
40
60
80
535m
649m
800m
1100m
2000m
Lagenammina sp. 2
R. bilocularis
Reophax sp. 7
Reophax sp. 10
Eggerella sp. 1
Eggerella sp. 2
C. wiesneri
Ammodiscus sp.
Lagenammina sp. 1
Lagenammina sp. 5
Lagenammina sp. 13
R. dentaliniformis
R. agglutinatus
Cribrostomoides sp.
Leptohalysis sp. 2
Reophax sp. 19
R. spiculifera
R. horridus
Reophax sp. 3
Reophax sp. 13
Reophax sp. 27
A. tenuimargo
Semivulvulina sp.
Lagenammina sp. 23
Lagenammina sp. 22
Reophax sp. 29
Reophax sp. 5
R. aff. *scorpiurus*
Reophax sp. 31
E. foliaceus
R. contortus
Others

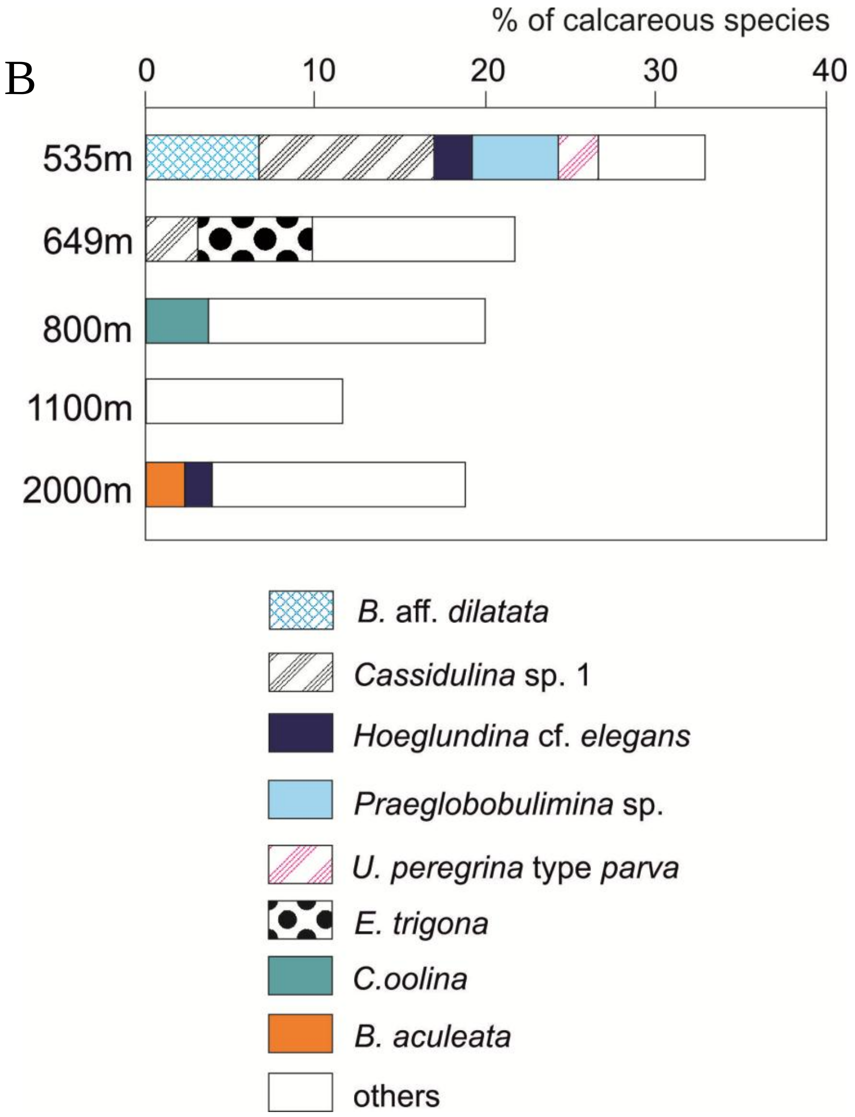


Fig. 4. Relative abundances of 'live' foraminiferal apecies in the >150 µm fraction of the top 1-cm layer at each station. (A) Agglutinated assemblage. (B) Calcareous assemblage. In each case, only the dominant species (>2% at each station) are represented individually.

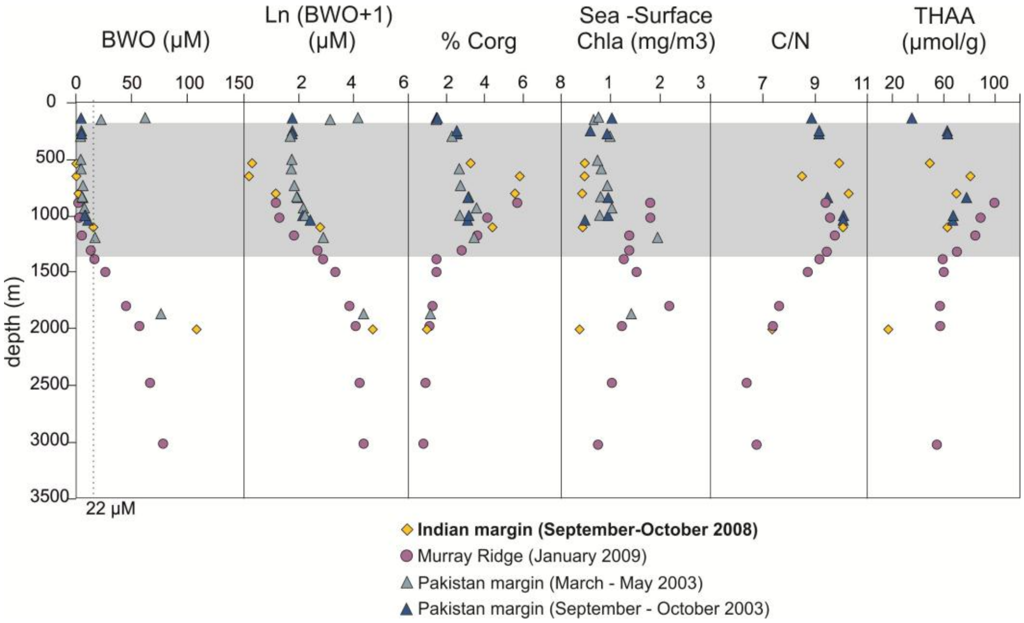


Fig. 5. Regional comparison of the environmental parameters on the Indian and Pakistan margins and the Murray ridge. The Corg content, C/N, THAA concentration and DI data are from Hunter et al. (2012) and Cowie et al. (2014) for the Indian margin; from Vandewiele et al. (2009) for the Pakistan margin;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

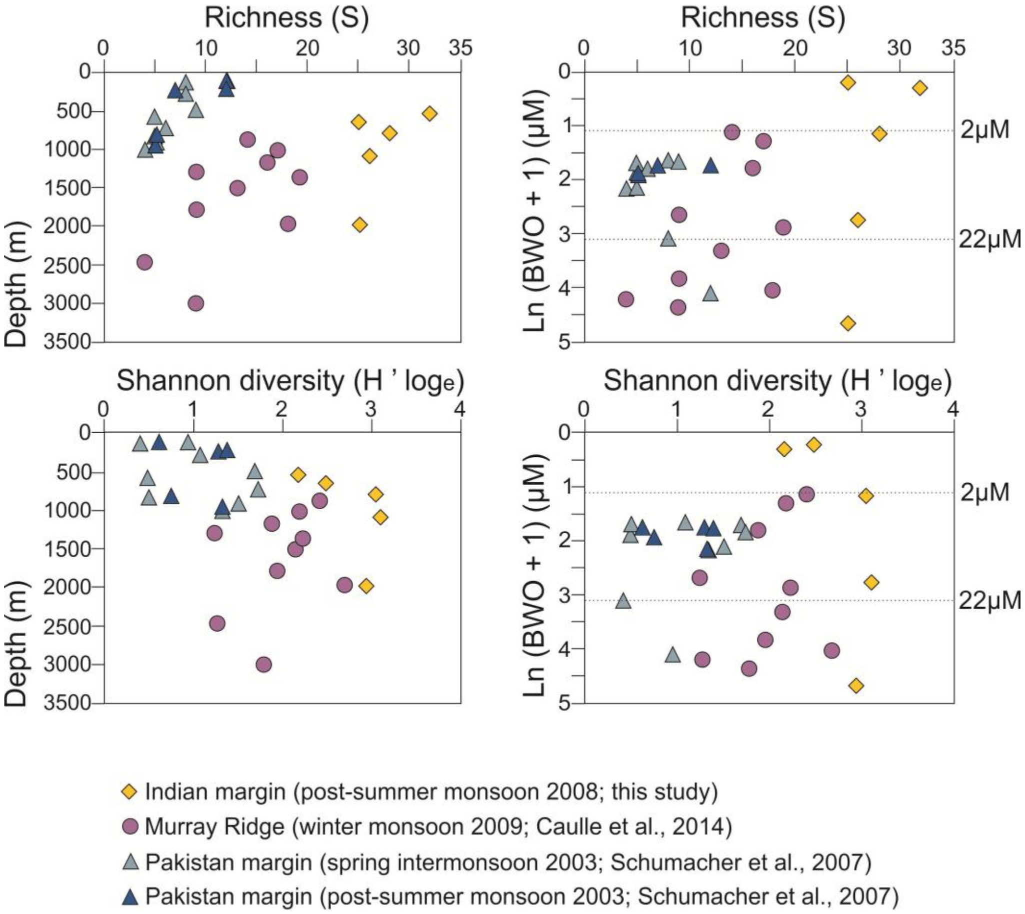
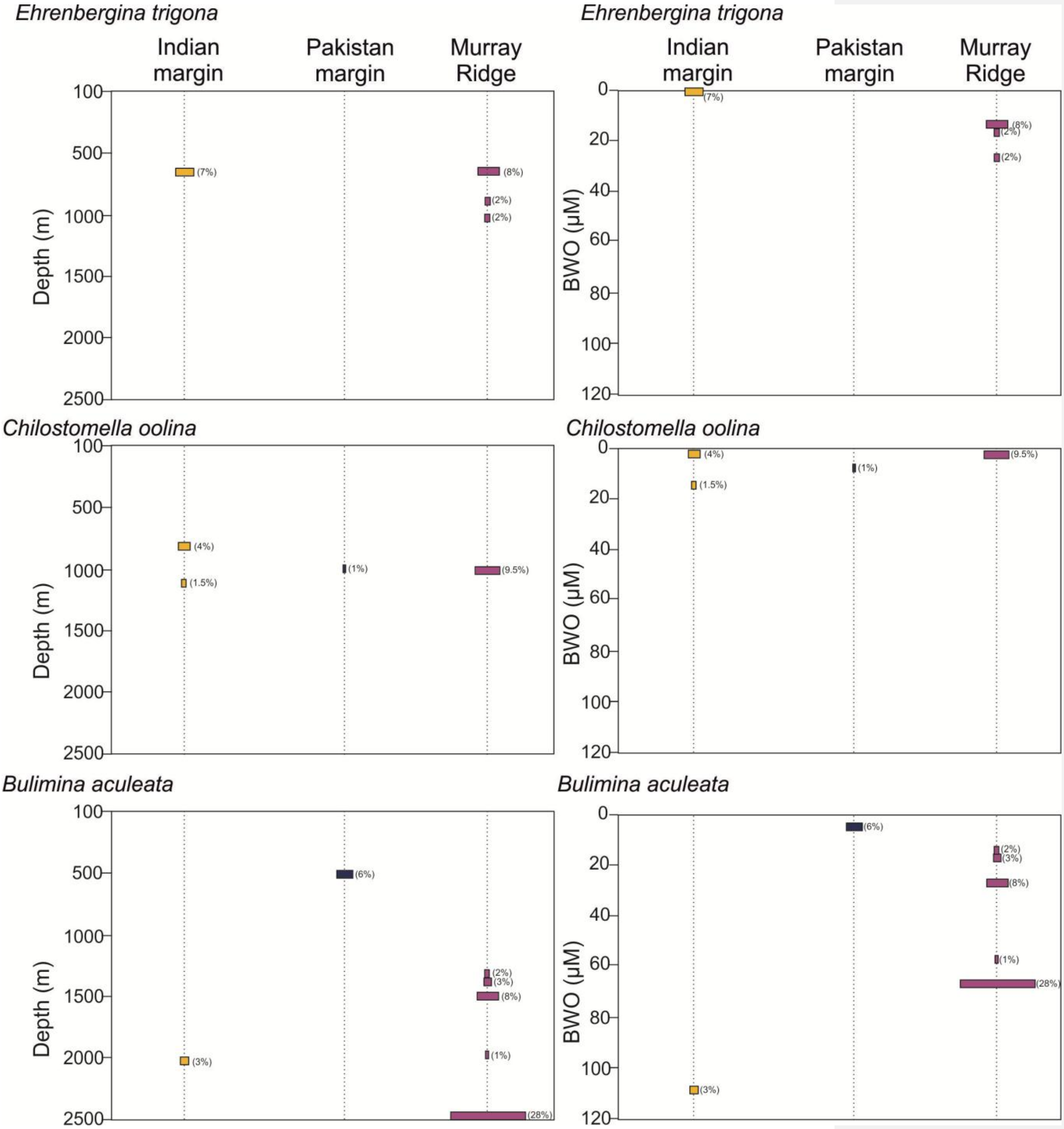


Fig. 6. Species richness and Shannon index (calculated for the calcareous fauna only) vs. depth (m) and Ln (BWO+1) for the Indian margin, the Pakistan margin and the Murray ridge. Because some values were <1, the BWO was expressed using the natural logarithm + 1 (Ln(BWO+1)). The dash lines correspond to the limits of the OMZ core (2μM) and to the lower boundary of the OMZ (22μM).


Ehrenbergina trigona
Indian margin
Pakistan margin
Murray Ridge
Depth (m)
100
500
1000
1500
2000
2500
(7%)
(8%)
(2%)
(2%)
Ehrenbergina trigona
Indian margin
Pakistan margin
Murray Ridge
BWO (μM)
0
20
40
60
80
100
120
(7%)
(8%)
(2%)
(2%)
Chilostomella oolina
Depth (m)
100
500
1000
1500
2000
2500
(4%)
(1.5%)
(1%)
(9.5%)
Chilostomella oolina
BWO (μM)
0
20
40
60
80
100
120
(4%)
(1.5%)
(1%)
(9.5%)
Bulimina aculeata
Depth (m)
100
500
1000
1500
2000
2500
(6%)
(2%)
(3%)
(8%)
(1%)
(3%)
(28%)
Bulimina aculeata
BWO (μM)
0
20
40
60
80
100
120
(6%)
(2%)
(3%)
(8%)
(1%)
(28%)
(3%)

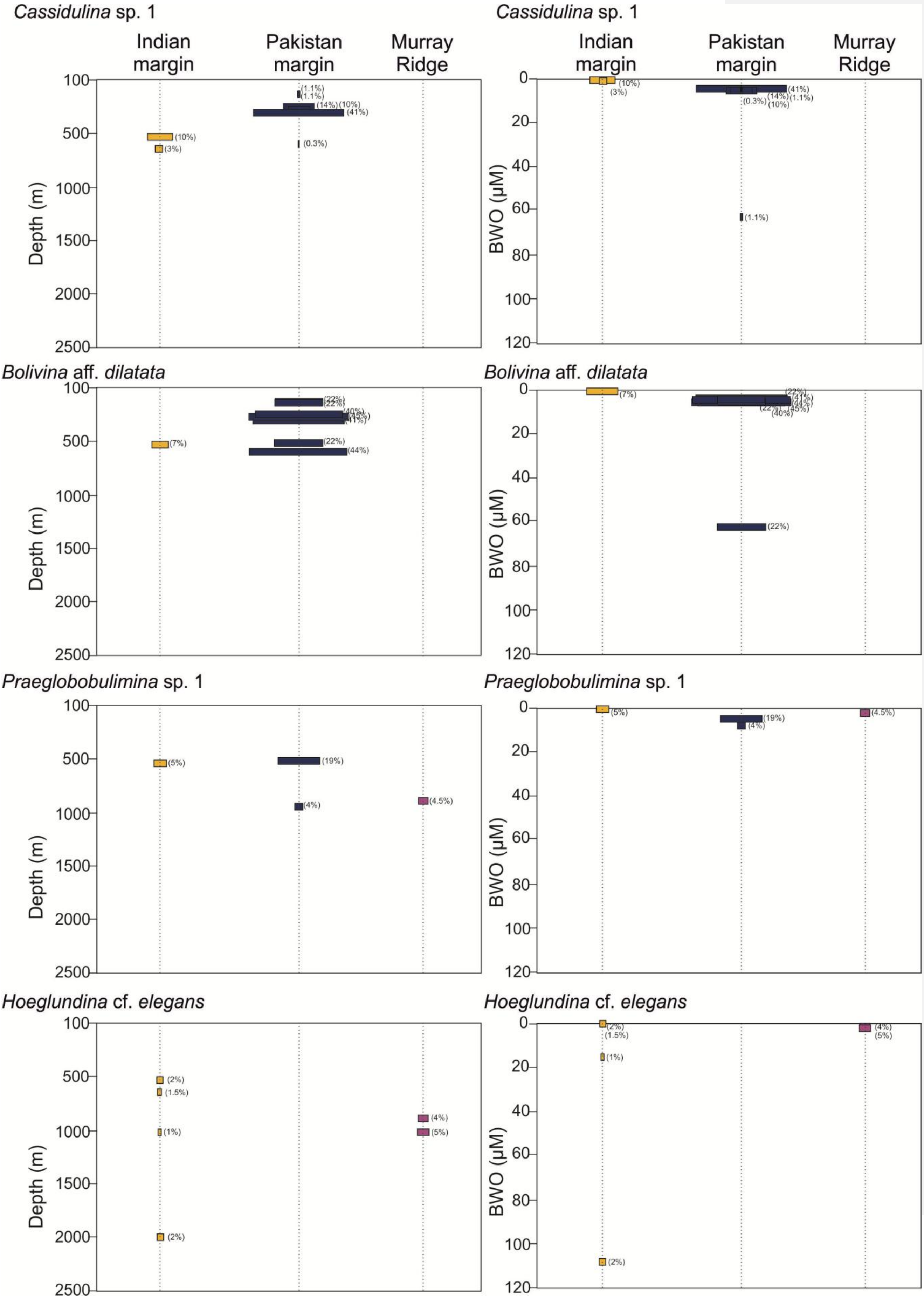

Cassidulina sp. 1
Indian margin
Pakistan margin
Murray Ridge
Depth (m)
100
500
1000
1500
2000
2500
(1.1%)
(1.1%)
(14%) (10%)
(41%)
(10%)
(3%)
(0.3%)
Cassidulina sp. 1
Indian margin
Pakistan margin
Murray Ridge
BWO (µM)
0
20
40
60
80
100
120
(10%)
(3%)
(41%)
(14%) (1.1%)
(0.3%) (10%)
(1.1%)
Bolivina aff. *dilatata*
Depth (m)
(22%)
(22%)
(40%)
(45%)
(41%)
(7%)
(22%)
(44%)
Bolivina aff. *dilatata*
BWO (µM)
(7%)
(22%)
(41%)
(44%)
(22%) (45%)
(40%)
(22%)
Praeglobobulimina sp. 1
Depth (m)
(5%)
(19%)
(4%)
(4.5%)
Praeglobobulimina sp. 1
BWO (µM)
(5%)
(19%)
(4%)
(4.5%)
Hoeglundina cf. *elegans*
Depth (m)
(2%)
(1.5%)
(1%)
(4%)
(5%)
(2%)
Hoeglundina cf. *elegans*
BWO (µM)
(2%)
(1.5%)
(1%)
(4%)
(5%)
(2%)

Fig. 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.. Percentage species occurrences are indicated in brackets.

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)

Table 1. Top 10 ranked species at each site. The number to the right of each name indicate counts of specimens with the relative abundances (%) in brackets.