# 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 (> 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 >300 μm). 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

28    also included delicate monothalamous taxa (organic-walled 'allogromiids', agglutinated
29    saccamminids, psammosphaerids and tubular forms). These new data from the Indian margin
30    are compared to previous studies from the Murray Ridge, the Pakistan margin and the Oman
31    margin. The fact that similar species were found at sites with comparable bottom-water
32    oxygen concentrations but with very different surface water productivity suggests that, within
33    the strongly developed Arabian Sea OMZ, bottom-water oxygen concentration, and not the
34    organic flux to the sea floor, is the main factor controlling the species composition of the
35    foraminiferal communities. Several foraminiferal species (e.g. *Praeglobobulimina* sp. 1,
36    *Ammodiscus* sp. 1, *Bolivina* aff. *dilatata*) were confined to the core of the OMZ. These
37    species are presently known only from the Arabian Sea. Because of their association with
38    extremely low-oxygen concentrations, these species may be good markers for very low
39    oxygen concentrations, and could be used to reconstruct past OMZ variability in the Arabian
40    Sea.

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42    **1.  Introduction**

43    The ocean floor hosts rich and diverse micro-, meio- and macrofaunal communities. The
44    distribution and abundances of these faunas are controlled by many environmental and
45    physical parameters that change from the continental shelf to the deep ocean. In particular,
46    organic-matter fluxes and bottom-water oxygenation exhibit drastic changes between oceanic
47    basins. Strong gradients in both parameters are found in oxygen minimum zones (OMZ;
48    defined by permanent hypoxia, with dissolved oxygen concentrations <22 μM; Levin, 2003).
49    These mid-water features impinge on the continental slope at upper bathyal depths in the
50    eastern Pacific, the northern Indian Ocean (Arabian Sea and Bay of Bengal), and to a lesser
51    extent off southwest Africa (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009). Many
52    studies have described dense biotic communities within OMZs, despite the low oxygen
53    concentrations (e.g., Wishner et al., 1990; Levin et al., 1991; Jannink et al., 1998; Gooday et
54    al., 2000, 2009; Levin et al., 2000; Levin, 2003a; Schumacher et al., 2007; Mallon et al.,
55    2012; Pozzato et al., 2013). In general, meiofaunal organisms (mainly foraminifera and
56    nematodes) attain high densities, although diversity tends to be low (e.g. Jannink et al., 1998;
57    Cook et al., 2004; Schumacher et al., 2007; Larkin and Gooday, 2009; Caulle et al., 2014).
58    Megafaunal and most macrofaunal taxa are more affected by strong hypoxia than smaller
59    organisms and usually exhibit lower abundances, except for polychaetes which are often more

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60    resistant and may be abundant, even in the core regions of some OMZs (e.g. Levin et al.,
61    1991; Levin, 2003b; Gooday et al., 2009). However, in all size classes, distinct taxonomic
62    changes are observed across OMZs (e.g. Gooday et al., 2009), making them perfect natural
63    laboratories to examine the influence of oxygen concentration on the density, diversity and
64    species composition of benthic fauna.

65    In open-ocean settings, the organic flux to the sea floor is often considered as the most
66    important parameter controlling benthic foraminiferal abundance and distribution (e.g.
67    Altenbach, 1985, 1987; Corliss and Emerson, 1990; Gooday et al., 1990; Jorissen et al., 1995;
68    Heinz et al., 2002; Diz et al., 2006; Gooday and Jorissen, 2012). For many foraminiferal
69    species, there is an optimum range of organic input within which they reproduce, are
70    competitive, and attain their maximum abundance (Altenbach et al., 1999). Some species
71    show a strong tolerance to hypoxia and flourish in oxygen-depleted environments (e.g.
72    Mackensen and Douglas, 1989; Gooday et al., 2000; Bernhard and Gupta, 2003; Cardich et
73    al., 2012; Mallon et al., 2012; Sergeeva et al., 2012). Various mechanisms could explain how
74    foraminifera survive in these adverse conditions, which many macro- and mega-faunal
75    animals are unable to tolerate. These include anaerobic metabolic pathways, bacterial
76    symbionts, sequestration of chloroplasts, or proliferation of peroxisomes and mitochondria
77    (Koho and Piña-Ochoa, 2012 and reference therein). In recent studies, Risgaard-Petersen et al.
78    (2006) and Pina-Ochoa et al. (2009) demonstrated the ability of some foraminiferal species to
79    accumulate intracellular nitrate for use as an electron acceptor for respiration instead of
80    oxygen.

81    In the Arabian Sea, 'live' (Rose-Bengal stained) benthic foraminifera have been mainly
82    studied on the Oman margin (e.g., Stubbings, 1939; Hermelin and Shimmield, 1990; Naidu
83    and Malmgren, 1995; Gooday et al., 2000) and the Pakistan margin (Jannink et al., 1998;
84    Maas, 2000; Erbacher and Nelskamp, 2006; Schumacher et al., 2007; Larkin and Gooday,
85    2009; Larkin et al., 2014; Enge et al., 2014). In addition, a few studies have focused on other
86    areas, such as the Murray Ridge (Pozzato et al., 2013; Caulle et al., 2014) and the central,
87    eastern and western parts of the Arabian Sea (Kurbjeweit et al., 2000; Heinz and Hemleben,
88    2003, 2006). Most of these studies agree that oxygen concentration and organic matter quality
89    and quantity have a strong influence on the abundance and composition of foraminiferal
90    faunas. However, due to the inverse relationship between these two parameters, their relative
91    importance remains difficult to resolve.

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92   Here, we provide the first account of the distribution and abundance of foraminifera across the
93   poorly studied Indian margin in the eastern Arabian Sea (Fig. 1A). The Indian margin
94   displays low sea-surface primary production through the entire monsoonal cycle compared to
95   other Arabian Sea regions (Fig. 1B), suggesting that lower organic resources are available for
96   the benthic foraminiferal faunas. In this context, the present paper focuses on how
97   foraminiferal faunas on the Indian margin respond to the combination of organic-matter
98   fluxes that are likely to be moderate (as indicated by satellite images of chlorophyll-a) and
99   extremely low oxygen concentration.

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101  **2.   Materials and Methods**

102  **2.1. Study area**

103       2.1.1.  The Oxygen Minimum Zone

104  The Arabian Sea hosts one of the world's most intense OMZs (Helly and Levin, 2004) with
105  almost anoxic conditions in its core (< 2 μM; Paulmier and Ruiz-Pino, 2009). This is the
106  result of the semi-enclosed nature of the northern Arabian Sea, the relatively oxygen-poor
107  intermediate water masses originating from the Persian Gulf, and the effects of the twice-
108  yearly strong intensification of the monsoon system. During the SW or summer monsoon
109  (June – September), intense upwelling develops off Somalia and Oman, and off the
110  southwestern coast of India, due to the anticyclonic surface water circulation. Upwelling leads
111  to an increase of biological production in the photic zone (Fig. 1B; e.g. Ryther and Menzel,
112  1965; Haake et al., 1993; Rixen et al., 1996), which triggers a strong export of organic carbon
113  to intermediate water-depths, where it is intensely recycled and remineralized. A second
114  maximum in primary production occurs during the NE or winter monsoon (December –
115  March) caused by the convective mixing of the upper water column (Fig. 1B; e.g. Banse and
116  McClain, 1986; Madhupratap et al., 1996; Caron and Dennett, 1999; Rixen et al., 2000). The
117  highly eutrophic surface waters during monsoon periods contrast with the much less fertile
118  conditions during the intermonsoon periods, especially in spring (Fig.  1B). Due to monsoons
119  and their associated change in sea-surface circulation (cyclonic during the NE monsoon and
120  anticyclonic during the SW monsoon), concentration of sea-surface primary production is
121  different between regions and seasons (Fig.  1B). Sea-surface biological production is

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122    generally believed to control the organic flux to the sea floor, and thereby the trophic
123    resources for the benthic faunas.

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125            2.1.2.  Oxygen and organic matter characteristics

126    Samples were collected on the western Indian margin during RV *Yokosuka* cruise YK08-11
127    (September to November 2008, post-monsoon period) using the manned submersible *Shinkai*
128    6500 (Fig. 1). The sampling sites (five in total) were located in the core of the OMZ at 535 m
129    and  649 m,  the lower boundary of the core at 800 m, the lower transition at 1100 and below
130    the OMZ at 2000 m depth. Site characteristics were presented by Hunter et al. (2011, 2012),
131    Levin et al. (2013) and Cowie et al. (2014). The YK08-11 cruise was designed to study
132    depositional processes, biogeochemical cycles and biological communities within the intense
133    OMZ, which extends from 150 to 1300 m water depth on the Indian margin. Below is a brief
134    summary of the main environmental characteristics of the OMZ relevant to our study.

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

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

143    3) In the lower transitional zone, around 1100 m depth, BWO is still low (~15 μM) but the
144    organic matter quantity and quality start to decrease (wt % Corg ~ 4.4 % and THAA ~ 62.9
145    μmol/g; Cowie et al., 2014).

146    4) Beneath the OMZ, at 2000 m, well-oxygenated waters (BWO ~136 μM) and poorer trophic
147    conditions occur (wt % Corg ~ 1 % and THAA ~ 17 μmol/g; Cowie et al., 2014)

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149    **2.2. Foraminiferal analysis**

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150  Sediment samples were taken using push-cores (8.3-cm internal diameter, surface area 54.1
151  cm$^2$) deployed from the *Shinkai* 6500 submersible. On board the *Yokosuka*, each core was
152  sliced and each sediment slice was preserved in 8% borax-buffered formalin. The study of the
153  benthic foraminiferal communities is based on an examination of the first two half-centimeter
154  levels (0-1 cm).

155  In the laboratory, the fixed sediment from the 0-0.5- and 0.5-1.0-cm layers was washed
156  separately through 300- and 150-μm screens and stained overnight on the sieve in Rose
157  Bengal solution. The <150 μm size fractions were kept and stored in borax-buffered formalin
158  for possible future analyses. The 150-300 and > 300 μm fractions of the two sediment layers
159  were sorted wet (in water) under a binocular microscope for all Rose-Bengal-stained
160  foraminifera.

161  The Rose Bengal technique is considered to be an inexpensive and easy method to recognize
162  foraminifera that were alive (or recently alive) when collected (Walton, 1952; Murray and
163  Bowser, 2000). However, especially in low-oxygen settings, the cell material may persist long
164  after death, resulting in false positives (Corliss and Emerson, 1990; Bernhard, 2000). In order
165  to minimize over-estimation in the live foraminiferal counts, strict staining criteria were
166  always applied. Specimens were considered 'alive' only when all chambers, except for the last
167  one or two, were well stained. Furthermore, doubtful specimens were compared with
168  perfectly stained specimens of the same species and non-transparent agglutinated and miliolid
169  taxa were broken to inspect their contents. Soft-shelled monothalamous taxa, which are
170  largely undescribed, were included in the data analyses. All foraminifera were identified to
171  the lowest possible taxonomic level and assigned to informal species categories for diversity
172  analyses. Species identifications followed previous studies from the Arabian Sea (e.g. Maas,
173  2000; Schumacher et al., 2007; Larkin and Gooday, 2009; Caulle et al., 2014; Taylor and
174  Gooday, 2014). A special effort was made to discriminate hormosinacean species (the
175  superfamily Hormosinacea includes genera with uniserial chambers such as *Reophax,*
176  *Hormosina, Hormosinella,* and *Nodosinella*), extending the recent taxonomic study of Taylor
177  and Gooday (2013), which was based on different material from the same sites as the present
178  study. Deep-sea hormosinacean species are often difficult to identify; many are undescribed
179  and some widely-reported 'species' represent complexes of morphologically similar species
180  (i.e. morphotypes). Hence it was necessary to assign many species within the genera
181  *Hormosina, Reophax* and the monothalamous genus *Lagenammina* to informal categories. In
182  some cases, these are the same as those illustrated by Taylor and Gooday (2013) but others

183   have not been recognised previously. Since foraminifera are extremely abundant in finer

184   sediment fractions, we confined our study to the >150-µm faction of the 0-1 cm layer.

185   For all stations, diversity indices, including species richness (S; count of number of taxa in a

186   sample), Shannon index (H' $\log_e$), and Evenness (J) were calculated using the statistical

187   software "PAST" (PAleontological STatistics; Version 2.14; Hammer et al., 2009). We use

188   the term 'entire live' to refer to all stained foraminifera, i.e. agglutinated and calcareous taxa

189   combined.

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191   **3.  Results**

192   **3.1. Foraminiferal densities**

193   The total densities of live (Rose-Bengal stained) foraminifera in the upper 1-cm layer (>150-

194   µm fraction) decreased from ~3000 ind./50 cm² at 535 m in the OMZ core to ~300 ind./50

195   cm² at 2000 m below the OMZ (Fig. 2). Foraminifera were concentrated in the 150-300 µm

196   fraction, which at most stations accounted for about three-quarters of the total density. Faunas

197   were dominated by multichambered agglutinated species, which represented between 48%

198   (2000 m) and 75% (649 m) of the assemblages, whereas calcareous species did not exceed

199   32% (535 m) of the total fauna (Fig. 2 and Table 1). The relative abundance of

200   monothalamids was lowest (2%) at 649 m and highest (30%) at 2000 m. The absolute

201   densities of multichambered agglutinated and calcareous species decreased with increasing

202   water-depth (Fig. 2). At 535 m, in the core of the OMZ, their densities were ~1870

203   (agglutinated) and ~990 ind./50cm² (calcareous), respectively, compared to ~150 ind./50 cm²

204   and ~55 ind./50 cm², at the deepest site (2000 m). Monothalamids did not show a clear trends

205   along the transect. The highest densities were found in the core (535 m; ~150 ind. /50cm²) and

206   in the lower part (1100 m; ~115 ind. /50 cm²) of the OMZ. The lowest densities (~25 ind.

207   /50cm²) were found at the 649 m site.

208

209   **3.2. Species richness, diversity and dominance of living foraminiferal faunas**

210   A total of 214 morphospecies was identified (0-1 cm layer, 150-µm size fraction), of which

211   131 were agglutinated (77 referred to the superfamily Hormosinacea), 79 were hyaline and

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212  only 4 were miliolids. Monothalamous species, the majority of which were undescribed, were
213  included in the diversity analysis.

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

229  Evenness fluctuated along the transect (Fig. 3). There was an increase from low values at 535
230  m to a peak at 800 m in the total and multichambered agglutinated components, followed by a
231  sharp decline to 1100 m with higher values again at 2000 m. For calcareous species, evenness
232  followed a similar trend down to 800 m but then increased further at 1100 m followed by
233  somewhat lower values at 2000 m. The evenness of the calcareous and agglutinated species
234  was consistently higher than that of the entire live fauna. When considering calcareous and
235  agglutinated species separately, diversity measures may be substantially different from those
236  of the entire live fauna.

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238  **3.3. Foraminiferal assemblage composition**

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

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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

273   Our analyses were confined to the uppermost (0-1 cm) sediment layer, which would normally

274   result in an under-representation of deeper-dwelling species. Foraminiferal microhabitats are

275   largely controlled by organic matter input and oxygen penetration into the sediment (Corliss

276   and Emerson, 1990; Jorissen et al., 1995). As a result, although foraminifera often occur in

277   sediment layers down to a depth of 5 cm or more where oxygen is plentiful, they are generally

278   concentrated near the sediment surface in hypoxic, organically-enriched settings. Previous

279   studies of the Arabian Sea OMZ core found most of the stained fauna in the first cm of the

280   sediment (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007; Larkin and Gooday,

281   2009). In many hypoxic settings, compression of redox profiles leads to the absence of a well-

282   defined vertical sequence of microhabitats and the presence of deep-infaunal taxa close to the

283   sediment surface. Intermediate and deep infaunal taxa were scarce on the Indian margin, and

284   have rarely been reported within the OMZ in previous Arabian Sea studies (Jannink et al.,

285   1998; Kurbjeweit et al., 2000; Mass, 2000, Schumacher et al., 2007; Larkin et al., 2009;

286   Caulle et al., 2014). In our material, *Chilostomella oolina* was the only species of this type

287   that represented >2% of the 'live' fauna, being found mainly at 800 m (Fig. 4B). Similar

288   observations were made by Schumacher et al. (2007) on the Pakistan margin, where C. *oolina*

289   was found exclusively in the 0-0.5 cm layer across the OMZ (306-738 m depth). Species of

290   the deep infaunal genus *Globobulimina* are also abundant in the first sediment cm on the

291   Pakistan margin (at 576 m; Erbacher and Nelskamp, 2006). These species occur at several cm

292   depth in the sediment in better oxygenated environments (Corliss and Emerson, 1990;

293   Kitazato, 1994; Rathburn et al., 2000). Since our study was limited to the topmost cm of the

294   sediment, it is possible that intermediate- and deep-infaunal species were missed at

295   transitional sites and below the OMZ (1100 and 2000 m). However, we think that it is

296   unlikely that analysis of deeper sediment layers would have led to substantial changes of

297   foraminiferal diversity, although density values may have slightly increased, especially at the

298   deeper sites (1100 and 2000 m). This view is supported by data in Caulle et al. (2014) from

299   sites located along an oxygen gradient on the Murray Ridge (885 to 3010 m depth), where

300   foraminiferal diversity was very similar in the 0-1 and 0-10 cm sediment layers (>150 μm

301   fraction).

302   Confining our analyses to the >150 μm size fraction introduces a second source of bias. In

303   low-oxygen settings, small-sized (63-150 μm) foraminifera are particularly abundant (e.g.

304   Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007), possibly because small

305   species have a higher tolerance to low-oxygen conditions (Caulle et al., 2014). However, the

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306 very considerable time and effort involved in sorting the dense populations present in size
307 fractions <150 µm precluded their analysis in the present study. Even so, the >150 µm size
308 fraction alone yielded abundant and diverse faunas with stained assemblages containing
309 between 279 and 3177 individuals, belonging to 214 species. Moreover, Schumacher et al.
310 (2007) and Caulle et al. (2014) demonstrated that adding the small-sized fraction (63-150 µm)
311 did not lead to a major change in bathymetric trends in foraminiferal diversity and faunal
312 composition. Although analysing the finer size fractions may add some small-sized species,
313 leading to slight changes in absolute and relative abundances, most of the species found in
314 the small size fraction occurred also in the coarser fraction. Finally, a major advantage of
315 working on the >150 µm size fraction is that it allows direct comparison with
316 paleoceanographic studies, which are mainly based on the >125 or >150 µm fractions.

317

318 **4.2. Dense high diversity assemblages in extreme hypoxic conditions**

319 On the basis of macrofaunal data from the Arabian Sea, Levin and Gage (1998) concluded
320 that species dominace is related to the organic carbon flux to the sea floor, whereas species
321 richness is mainly related to BWO concentrations. In a general sense and at a community
322 scale, our Indian margin density and diversity patterns confirm these conclusions; absolute
323 densities were higher in the core of the OMZ than at deeper sites (Fig. 2) whereas diversity
324 indices described the opposite trend ( Fig. 3). Community densities have largely been
325 discussed in previous studies carried in the Arabian Sea OMZ (e.g. Jannink et al., 1998;
326 Gooday et al., 2000; Schumacher et al., 2007; Larkin et al., 2009; Caulle et al., 2014). On the
327 Indian margin, trends in foraminiferal density across the OMZ are very similar to those
328 reported in previous studies in the Arabian Sea and are explained by the large quantities of
329 labile organic matter present in the OMZ sediments (Fig. 2). At the time of sampling
330 (September – October 2008), the Indian margin OMZ was extremely hypoxic compared to
331 previous observations in the Arabian Sea (e.g. Maas, 2000; Gooday et al., 2000; Schumacher
332 et al., 2007; Larkin and Gooday, 2009; Vandewiele et al., 2009; Koho et al., 2013; Caulle et
333 al., 2014). Oxygen concentrations in the core of the OMZ were ~0.3 µM compared to ~2 µM
334 on the Murray Ridge (Pozzato et al., 2013; Koho et al., 2013; Caulle et al., 2014) and ~4 µM
335 on the Pakistan margin (Schumacher et al., 2007; Larkin and Gooday, 2009). However, the
336 performance of oxygen sensors is continously improving, and detection limits are decreasing.

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

339    Inspite of the very low oxygen concentrations, species richness (i.e. the number of species) in
340    our samples was surprisingly high, particularly at the most severely hypoxic site (535 m; Fig.
341    3), compared to previous data from the Arabian Sea (e.g. Jannink et al., 1998; Maas, 2000;
342    Schumacher et al., 2007; Larkin and Gooday, 2009; Caulle et al., 2014). This difference may
343    be the result of our unusually careful taxonomical analysis of the samples, which took into
344    account monothalamids and the diverse hormosinaceans. These species are often difficult to
345    identify and many are undescribed (Taylor amd Gooday, 2014). A total of 77 hormosinacean
346    species was recognized, based on the number of chambers, chamber shape and size, wall
347    construction, and the shape of the apertural neck. Similar careful taxonomy was applied to a
348    sample from the core of the Oman margin OMZ (412 m depth), where BWO levels were
349    more than one order of magnitude higher than off India, although still very low (~5.5 µM
350    versus ~0.35 µM) (Gooday et al., 2000). Foraminiferal species diversity and richness there
351    were comparable to values reported in the present study (H'(log$_e$) ~ 2.8, S=64), although the
352    hormosinaceans were less diverse (Gooday et al., 2000).

353    Compared to the monothalamids and hormosinaceans, the taxonomy of calcareous
354    foraminifera in the Arabian Sea is better known and their comparison with earlier studies is
355    more straightforward. To facilitate comparisons with the data of Schumacher et al. (2007) and
356    Caulle et al. (2014) diversity metrics were recalculated for calcareous species only (Fig. 6).
357    These reveal that faunal diversity within (535 to 1100 m depth) and below (2000 m) the
358    Indian margin OMZ is still higher than in other parts of the Arabian Sea. The high diversity in
359    the core of the OMZ (Fig. 6), where oxygen concentrations were almost zero (~0.3 µM; at
360    535 m) at the time of sampling, is particularly striking (Fig. 5). The presence at the 535-m site
361    of a species that we assign to *Hoeglundina* cf. *elegans* is also very surprising (Fig. 4 B).
362    Based on a fossil record from the Murray Ridge (Northern Arabian Sea) spanning the last
363    120,000 years, den Dulk et al. (1998) concluded that *H. elegans* can tolerate mild hypoxia but
364    not the severely hypoxic conditions found in the core of the OMZ. The occurrence of a
365    morphologically similar species in the OMZ core on the Indian margin could be explained by
366    the hydrodynamic setting of this region. At 535 m, sharp-crested ripples (crests up to 10 – 12
367    cm high) were observed (Hunter et al., 2011; observations of U. Witte reported in Taylor and
368    Gooday, 2014), indicating rapid water movements. A current speed of 15 cm/s was recorded
369    here during the *Yokosuka* cruise (observations of H. Nomaki, reported in Taylor and Gooday,

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370  2014). Intermittent strong currents could lead to short periodic increases of BWO allowing
371  low-oxygen-sensitive species such as *H.* cf. *elegans* to colonise the area, where they can
372  apparently persist during the severely hypoxic periods. This hypothesis is supported by the
373  occurrence at 535 m of numerous dead thyasirid bivalves and gastropods (between 150-300
374  μm in size), which usually do not inhabit such severely oxygen depleted environments (Levin,
375  2003b). Thyasirids have been reported in the lower part of the OMZ on the Pakistan margin,
376  where BWO varies between ~ 4.5 and 9 μM (Oliver and Levin, 2006; Levin et al., 2009).
377  *Hoeglundina elegans* is a commonly reported deep-sea species that is distributed across a
378  wide bathymetric and geographical range in all oceans (Murray, 1991). Most records are from
379  bathyal (<3000 m) or even sublittoral (e.g., 140 m; Fontanier et al., 2002) depths, but
380  morphologically identical specimens also occur at > 4000 m in the eastern equatorial Pacific
381  (Gooday, unpublished data). The species found in the OMZ core on the Indian margin appears
382  identical to typical examples of *H. elegans* in terms of test morphology. Nevertheless, we
383  refer to it as *H.* cf. *elegans* because its occurrrence in a severely hypoxic setting is
384  unexpected, and for consistency with Enge et al. (2014). Whether it is genetically coherent
385  with *H. elegans* from oxic environments in other oceans remains to be determined.

386  Another factor that could explain the high diversity of stained foraminifera in the OMZ core
387  off India is the post-mortem preservation of the cell material. In this severely hypoxic
388  environment the cytoplasm could persist for months or longer (Corliss and Emerson, 1990;
389  Bernhard, 2000). Although, as explained above, strict staining criteria were applied, it might
390  still be difficult to confidently discriminate between individuals that had been dead for some
391  time and those that were alive when collected. More reliable assays, such as the Cell Tracker
392  Green (CTG) technique (e.g. Bernhard, 2000; Bernhard et al., 2006), could give a better
393  estimate of the "living" fauna. Alternatively, the temporal persistence of species that are not
394  known for their tolerance of low-oxygen conditions could be explained by a shift to anaerobic
395  types of metabolism. Many foraminiferal species can accumulate intracellular nitrates in low-
396  oxygen settings (Piña-Ochoa et al., 2010), and some are able to respire these nitrates
397  (Risgaard-Petersen et al., 20xx). Unfortunately, no measurement of nitrate concentrations and
398  denitrification rates are available for the dominant species of the Indian Margin OMZ.
399  Another possibility is that these foraminifera can lower their metabolism (i.e., become
400  dormant) during the most adverse periods. Geslin et al. (2011) showed that most benthic
401  foraminiferal species have low oxygen respiration rates per unit of cytoplasmic volume,

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

404

405     **4.3. The tolerance of agglutinated foraminifera to low-oxygen conditions**

406     Agglutinant foraminiferal species are often considered to be less tolerant of low-oxygen
407     conditions than calcareous foraminifera (Moodley et al., 1997; Gooday et al., 2000, 2001,
408     2009; Neira et al., 2001). However, this is not the case everywhere. In the Black Sea, soft-
409     shelled monothalamids were more abundant than calcareous foraminifera in samples taken
410     across the transition from hypoxic to sulphidic conditions (depth range 120-240 m) (Sergeeva
411     et al., 2012). On the Indian margin, agglutinated species are the dominant component (up to
412     76% at 649 m) of foraminiferal assemblages. They include soft-shelled monothalamids, but
413     the majority belong to genera such as *Reophax* and *Hormosinella* together with species of the
414     single-chambered genus *Lagenammina* (Fig. 4B and Table 1). On the Indian margin, where
415     oxygen concentrations during the *Yukosuka* cruise were extremely low in the OMZ core, these
416     multi-chambered uniserial agglutinants are more abundant  than calcareous foraminifera.

417     Previous studies have observed differences in foraminiferal composition related to sediment
418     characteristics (e.g. Kaminski, 1985). The hydrodynamic context of the Indian margin, and
419     particularly of sites in the OMZ core (535 to 800 m), influences sediment grain size. At the
420     535 m site, the sand fraction represents 44% of the sediment compared to 9.6% at 800 m
421     (Levin et al., 2013). Therefore, it is possible that the dominance of hormosinacean species at
422     the OMZ sites is partly a consequence of the relatively coarse sediment. However,
423     hormosinaceans, together with *Lagenammina,* are common in many fine-grained, deep-sea
424     settings (e.g. Gooday et al., 2010b). In the Arabian Sea, similar proportions of *Reophax* and
425     *Lagenammina* species have been reported in and below the OMZ on the Murray Ridge
426     (Caulle et al., 2014) and the Oman margin (Gooday et al., 2000), and in the core of OMZ on
427     the Pakistan margin (Larkin and Gooday, 2009) (Fig. 6). The general abundance of
428     hormosinacean species associated with the Arabian Sea OMZ suggests that it cannot be
429     attributed to sediment grain size alone. In fact, these observations reinforce our conclusion
430     that some hormosinaceans can tolerate strong oxygen depletion (Caulle et al., 2014).

431     Nevertheless, a tolerance to hypoxia does not fully explain why hormosinacean and
432     *Lagenammina* species are so common in our samples. One possible explanation is that it is
433     related to the quality of the available organic matter. Many agglutinated foraminifera seem to

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434    be less dependent on fresh food inputs than calcareous taxa, feeding instead on more

435    refractory material (e.g. Gooday, 2003; Gooday et al., 2008; Koho, 2008; Koho et al., 2008;

436    Phipps et al., 2012; Caulle et al., 2014). Another possible factor is that enhanced organic

437    matter recycling and associated $CO_2$ release into the pore waters depresses pH within OMZs

438    (Gooday et al., 2010a), making the secretion of a carbonate test more energetically

439    demanding. Seawater pH is reduced to below 7.1 on the Oman margin between 391 and 1265

440    m (Milliman et al., 1999). Taylor and Gooday (2014) observed that some globigerinacean

441    shells incorporated in the tests of stained *Reophax* and *Lagenammina* specimens at our 535

442    and 800 m sites were partly corroded, and traces of dissolution were evident in our material as

443    well. It is clear, however, that different hormosinacean and *Lagenammina* species display

444    different degrees of tolerance to hypoxia on the Indian margin. For instance, *Reophax* spp. 7

445    and 10 were mainly found in the core (535 - 800 m depth) (Fig. 4A and Table 1), and appear

446    to be particularly well adapted to oxygen-poor conditions. It is possible that they have a

447    facultative anaerobe metabolism. It has been demonstrated that some foraminiferal species

448    may use nitrate as a second source of electron acceptor for respiration (denitrification)

449    (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010). In fact, Piña-Ochoa et al. (2010)

450    showed that some agglutinated foraminifera collect nitrate, although only four *Reophax*

451    specimens (3 *Reophax micaceus* from the Bay of Biscay and 1 *Reophax* sp. from the Perù

452    OMZ) were measured and no nitrate pool were detected. It can be suggested that

453    hormosinacean species from the Arabian Sea OMZ are able to denitrify to thrive under this

454    severe environment. However, further investigations are needed before any firm conclusions

455    can be made on this topic.

456    Unlike Reophax spp. 7 and 10, *Reophax* aff. *scorpiurus, Reophax* spp. 31 and 5 were

457    confined to the deepest site (2000 m) (Fig. 4A and Table 1). Indeed, these species are

458    abundant and diverse in many deep-sea environments, including fully oxic abyssal plains

459    (e.g., Gooday et al., 2010b).

460

461    **4.4. Distribution of species across the OMZ**

462    There is a succession of both calcareous and agglutinated foraminiferal species along the

463    OMZ transect (Fig. 4 and Table 1). Sites in the core (535 and 649 m) have rather similar

464    assemblages and are dominated (> 2%) by *Reophax* spp. 7 and 10 and *Ammodiscus* sp. 1

465    (agglutinated), and *Cassidulina* sp. 1, *Bolivina* aff. *dilatata, Praeglobobulimina* sp. 1,

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466    *Hoeglundina* cf. *elegans* and *Ehrenbergina trigona* (calcareous) (Fig. 4 and Table 1). Most of

467    these species are restricted to these two sites where oxygen concentrations were extremely

468    low at the time of sampling (BWO ~0.2 and 0.3 μM). The calcareous species, except for *H.*

469    cf. *elegans* (see above), are typical of organically-enriched environments with low oxygen

470    concentrations (Bernhard and Gupta, 2003). Many of them (*Hoeglundina* cf. *elegans* as well

471    as *Uvigerina peregrina, Cassidulina* sp. 1 and *Praeglobobulimina* sp. 1) demonstrated a large

472    and rapid (~ 4 days) carbon uptake in tracer experiments on the Indian margin using labelled

473    phytodetritus (Enge et al., 2014). *Uvigerina* ex gr. *semiornata* exhibited a similar response in

474    experiments conducted on the Pakistan margin in 2003 (Larkin et al., 2014). The ability of

475    these species to feed rapidly on organic matter under extremely low oxygen concentrations

476    may lead to the development of large population densities.

477    The lower boundaries of OMZs are often characterised by enhanced biogeochemical activity

478    (Paulmier and Ruiz-Pino, 2009) and elevated faunal abundance in both the benthic and

479    pelagic communities (e.g. Sanders and Hessler, 1969; Mullins et al., 1985; Ward et al., 1989;

480    Levin et al., 1991; Wishner et al., 1995; Levin, 2003) On the Pakistan margin an edge effect

481    of this kind was evident among foraminiferal populations at around 750 m depth (Gooday et

482    al., 2009) and might therefore be expected at our 800 m site (BWO ~2.2 μM). Hence it is

483    rather surprisingly that faunal density are minimal here (~320 ind/50cm²; Fig. 2). If

484    foraminifera do exhibit an edge effect on the Indian margin it must be at some depth between

485    800 m and the next deepest site at 1100 m.

486    The assemblage at 800 m comprises a mixture of calcareous species typical of the OMZ core

487    (e.g. *Bolivina* aff. *dilatata, Cassidulina* sp. 1) and those that are more widely distributed (e.g.

488    *Cancris auriculus, Chilostomella oolina*), together with *Reophax* spp. 7 and 10 and

489    *Lagenammina* sp. 1 (Fig. 4 and Table 1). Apparently, the oxygen concentration here is still

490    low enough to allow species adapted to the core of the OMZ to remain competitive, but also

491    high enough to allow taxa such as *Cancris auriculus* and *Chilostomella oolina* to colonise the

492    site, resulting in maximum diversity. *Cancris auriculus* is also found in the OMZ (BWO ~ 5

493    μM) on the Pakistan margin (Larkin and Gooday, 2009) A different foraminiferal assemblage

494    is observed in the lower part of the OMZ (1100 m; BWO ~15 μM), where *Reophax horridus,*

495    *Reophax spiculifera, Reophax* sp. 10, *Chilostomella oolina, Hoeglundina* cf. *elegans,*

496    *Globocassidulina subglobosa* and *Bulimina aculeata* (Fig. 4 and Table 1) are all abundant.

497    Most of these species are widely distributed in the bathyal deep sea and, except for *H.* cf.

498    *elegans,* they are not found in the OMZ core. An inability to tolerate very low oxygen

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499 concentrations, perhaps combined with strong competition from better adapted species,

500 probably precludes their penetration into this harsh environment. It thus appears that there is a

501 critical oxygen threshold between ~2 µM and ~15 µM (i.e. 800 and 1100 m depth) for benthic

502 foraminifera on our Indian margin transect. Due to the sample site spacing, it is difficult to

503 specify a more precise value.

504 Changes in the composition of foraminiferal assemblages are also observed in other areas of

505 the Arabian Sea. On the Pakistan margin, Schumacher et al. (2007) found transitional

506 assemblages, mainly composed of *Bolivina* aff. *dilatata, Praeglobobulimina* sp. 1, *Uvigerina*

507 *peregrina* and *Chilostomella oolina,* between ~600 and ~800 m (BWO 4.7 - 5.8 µM), a depth

508 range spanning the lower part of the OMZ core and the upper part of the 'lower transition

509 zone' (Gooday et al., 2009). On the Murray Ridge, this change occurs at 1172 – 1306 m

510 (BWO ~5.0 - 13.8 µM) where the widely distributed species (e.g., *Globocassidulina*

511 *subglobosa, Ehrenbergina trigona, Fursenkoina* spp.) occur together with species typical of

512 the OMZ core that may have more restricted distributions (e.g. *Ammodiscus* sp. 1) (Caulle et

513 al., 2014). These studies are consistent with the existence of a transitional assemblage where

514 the BWO starts to increase, either at the base of the OMZ core, or around the lower boundary

515 of the OMZ.

516

517 **4.5. BWO, deposit and flux of organic matter, benthic foraminiferal faunas: comparison**

518 **of study sites**

519 Compared to previous studies in the Arabian Sea (e.g. Maas, 2000; Gooday et al., 2000;

520 Schumacher et al., 2007; Vandewiele et al., 2009; Larkin and Gooday, 2009; Koho et al.,

521 2013; Caulle et al., 2014), the OMZ of the Indian margin appears to be more severely

522 depleted in oxygen, in view of possible bias due to instrumental development. In fact,

523 conditions here were virtually anoxic, at least during the sampling period. On the other hand,

524 the similar values for surface sediment organic matter quantity and quality (THAA content)

525 between study areas suggests an absence of major regional differences in these parameters

526 (Fig. 5; Vandewiele et al., 2009; Koho et al., 2013; Cowie et al., 2014). This is surprising in

527 view of the concentrations of sea-surface chlorophyll a, mirroring primary production, which

528 are much lower on the Indian margin compared to the rest of the Arabian Sea (Fig. 1B). The

529 comparably high Corg values of the superficial sediments here (in contrast to the low surface

530 water PP) could be partly explained by the lower oxygen concentrations on the Indian Margin

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531 (Fig. 5) coupled to local hydrodynamics (seasonal development of a belt of intense oxygen

532 depletion linked to northward surface currents) leading to a better preservation of organic

533 matter (Cowie et al., 2014). This would imply that the availability of labile organic carbon on

534 the Indian margin is only partly determined by the sea-surface primary productivity. Instead,

535 severe mid-water hypoxia leading to limited organic matter degradation during transit through

536 the water column may play an important role in the presence of abundant high quality OM on

537 the sea floor. However, it has to be kept in mind that there are many indicators of OM quality

538 (e.g. THAA, concentration of single amino-acid, enzymatically hydrolysable amino acids)

539 and their interpretations are often problematic. It is not clear how these indices describe the

540 bio-availability of the organic components. Nevertheless, we think that our data suggest that

541 on the Indian margin, BWO as well as hydrodynamics represent a more important control on

542 benthic foraminiferal abundance and species composiion than sea-surface primary production.

543 The same foraminiferal species are found on the Indian margin and at previously studied sites

544 in the Arabian Sea (Fig. 7). *Praeglobobulimina* sp. 1 is restricted to extremely low oxygen

545 concentrations (<10 μM), mainly corresponding to the core of the OMZ on the Indian margin,

546 the Murray ridge and the Pakistan margin, while *Cassidulina* sp. 1 and *Bolivina* aff. *dilatata*

547 are generally found at oxygen concentrations <10 μM (Fig. 7). This highlights the strong

548 adaptation of these indicator species to hypoxic environments. *Praeglobobulimina* sp. 1 and

549 *B.* aff. *dilatata* have not been reported in other oceanic basins, including the OMZ in the East

550 Pacific or the well-studied upwelling area off North-West Africa. This raises the issue of

551 whether some species inhabiting OMZs are endemic to particular regions. It has been

552 suggested that severely stressed environments, notably by extreme hypoxia, may induce rapid

553 morphological and genetic changes (Verhallen, 1987) as well as promoting allopatric

554 speciation though the creation of barriers to gene flow (Rogers, 2000). The visually

555 conspicuous spider crab *Encephaloides armstrongii* is an example of a species that appears to

556 be restricted to the OMZ in the northern Arabian Sea and Bay of Bengal (Creasey et al.,

557 1997). However, the question of endemism within OMZ settings needs to be explored through

558 a combination of molecular genetics and morphological analysis.

559 *Ehrenbergina trigona* and *Chilostomella oolina* appear in a BWO interval from ~ 0 to ~ 22

560 μM (Fig. 7). It appears that many Arabian Sea foraminiferal species are living in a specific

561 range of BWO concentrations, defining ecological niches for the different species. The fact

562 that the same species occur on the Indian margin, the Pakistan margin and the Murray ridge,

563 in the same BWO interval, but probably with very different export production (based on

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

566

567 **4.6. Implications in paleoceanography**

568 Our results suggest that BWO may play the major role in regulating benthic foraminiferal
569 assemblages in the Arabian Sea. This conclusion could have important implications for the
570 reconstruction OMZ variability in the Arabian Sea over geological time scales. Foraminiferal
571 marker species typical of the OMZ (*Praeglobobulimina* sp. 1, *Cassidulina* sp. 1, *Bolivina* aff.
572 *dilatata, Ehrenbergina trigona*) should provide critical and reliable information about past
573 BWO, making it possible to quantitatively reconstruct past changes in intensity and extension
574 of the OMZ. On the other hand, some species, such as *Bulimina aculeata* and *Hoeglundina* cf.
575 *elegans,* are both found in the OMZ and below (Fig. 7). It seems that the ecological
576 preferences of these two species differ from site to site. This could suggest a high adaptability
577 of these two species to several environmental conditions (BWO and organic carbon). It could
578 also be the result of the presence of cryptic species, with a very similar morphology.
579 However, due to their wide ecological range, *Bulimina aculeata* and *Hoeglundina* cf. *elegans*
580 cannot be used as tracers of past-oxygen concentrations. Additionally, absolute foraminiferal
581 diversity indices have to be interpreted very carefully in paleoreconstructions from the
582 Arabian Sea, as our results show that low BWO does not always synonym of low
583 foraminiferal diversity.

584

585 **5. Conclusions**

586 This study focused on the response of living (Rose Bengal stained) benthic foraminifera to the
587 combination of low organic-matter fluxes and extremely low oxygen concentrations on the
588 poorly studied Indian margin. A transect through the OMZ yielded a dense and relatively
589 diverse live assemblage in the extreme hypoxic conditions prevailing at 535 m in the OMZ
590 core and a much sparser but more diverse assemblage in well-oxygenated waters at 2000 m
591 depth, below the OMZ. The unexpectedly high diversity in the OMZ core, which contradicts
592 the commonly accepted paradigm of low oxygen areas being characterized by low diversity
593 faunas, may reflect the adaptation of the predominantly agglutinated species present here to
594 these extreme conditions. However, this high diversity in the OMZ, may also result from

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595 periods of higher oxygenation mediated by the activity of bottom currents in this region. The

596 presence of *Hoeglundina* cf. *elegans* and dead thyasariid bivalves support the hypothesis of

597 strong intermittent oxygen fluctuations. Moreover, extremely low oxygen concentrations may

598 enhance the preservation of cellular material after the death of the organism, increasing the

599 apparent diversity of the Rose Bengal stained assemblage.

600 The high abundances of *Reophax* and *Lagenammina* species suggest that these agglutinated

601 foraminifera species are more tolerant to low-oxygen settings than previously thought.

602 Although their ecology is not well understood, their presence may be related to the quality

603 and quantity of the organic matter within the OMZ. However, foraminiferal assemblages

604 (both agglutinated and calcareous taxa) change along the oxygen transect. An assemblage

605 comprising species tolerant of severe hypoxia in the core of the OMZ is suceeded by a

606 transitional assemblage in the lower part of the OMZ, and finally a fauna composed of more

607 widely distributed species below the OMZ. We suggest that this faunal succession is mainly

608 controlled by the bottom-water oxygen concentrations. There appears to be an oxygen

609 threshold between 2 and 15 μM that separates foraminifera typical of the hypoxic core, which

610 probably have a restricted (endemic) distribution, from more cosmopolitan species that are

611 less tolerant of hypoxia and characterise the deeper sites.

612 A comparison of benthic foraminiferal assemblages from the Indian margin with those

613 reported in previous studies from other parts of the Arabian Sea suggests that similar species

614 are common at sites with the same bottom-water oxygenation but subject to different organic-

615 matter flux regimes. Thus bottom-water oxygen levels may exert the main control on species

616 distributions in this region. This would enhance the utility of foraminiferal species as reliable

617 tools to reconstruct past OMZ variability in the Arabian Sea.

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926

**A**

Ocean Data View

**B**
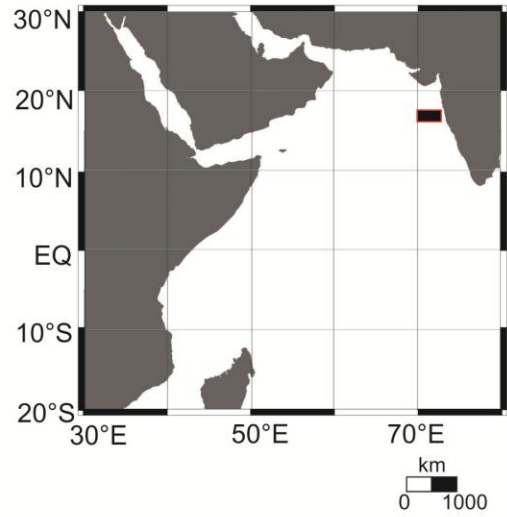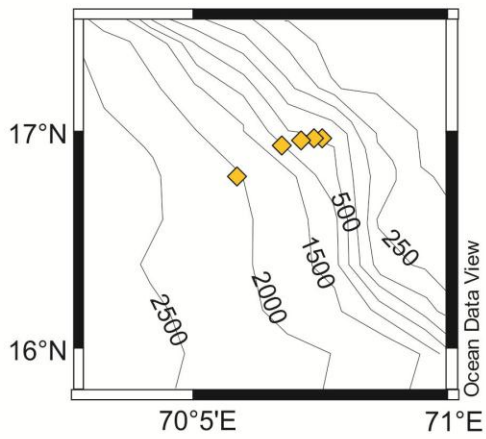
Sea-surface Chlorophyll a (mg/m3)
Winter monsoon (Dec-Jan 2008)
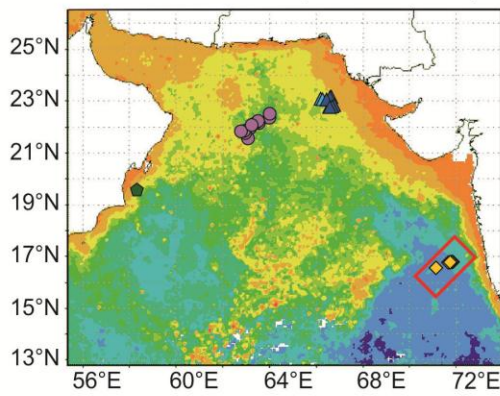
Sea-surface Chlorophyll a (mg/m3)
Inter-monsoon (Apr-Jun 2008)
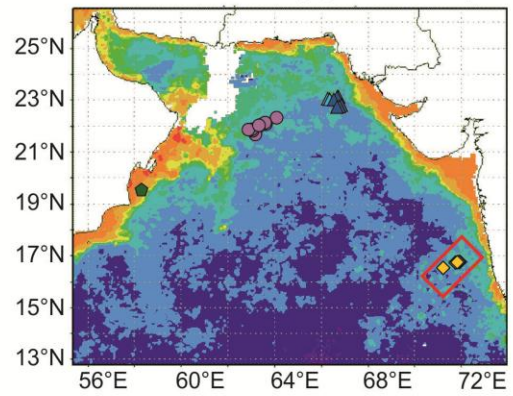
Sea-surface Chlorophyll a (mg/m3)
Inter-monsoon (Sep-Dec 2008)
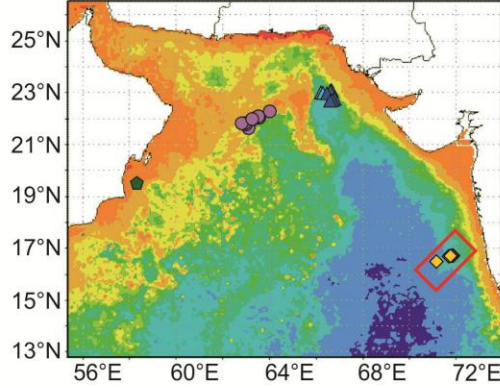
Sea-surface Chlorophyll a (mg/m3)
Summer monsoon (Jun-Sep 2008)

Chla (mg/m3)

0.08  0.1  0.2  0.3  0.4  0.5  0.6  0.7  1  2.5  10  30
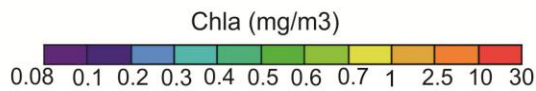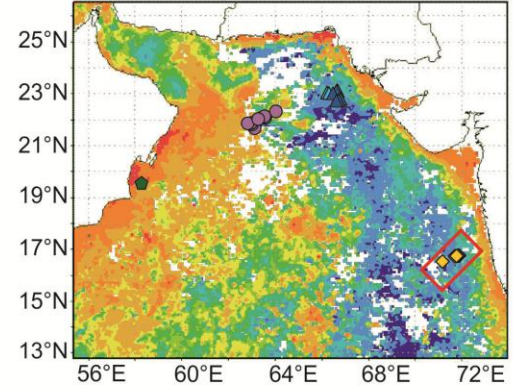
◆ **Indian margin (September-October 2008)**
● Murray Ridge (January 2009)
△ Pakistan margin (March - May 2003)
▲ Pakistan margin (September - October 2003)
⬟ Oman margin (October - November 1994)

928 **Fig. 1.** (A) Study area and station location. (B) Sea-surface chlorophyll a concentration (mg/m
929 [3]) during the monsoonal cycle in 2008 at our study sites and previous studies of live benthic
930 foraminfera from the Arabian Sea (Gooday et al., 2000; Schumacher et al., 2007; Caulle et al.,
931 2014); http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/

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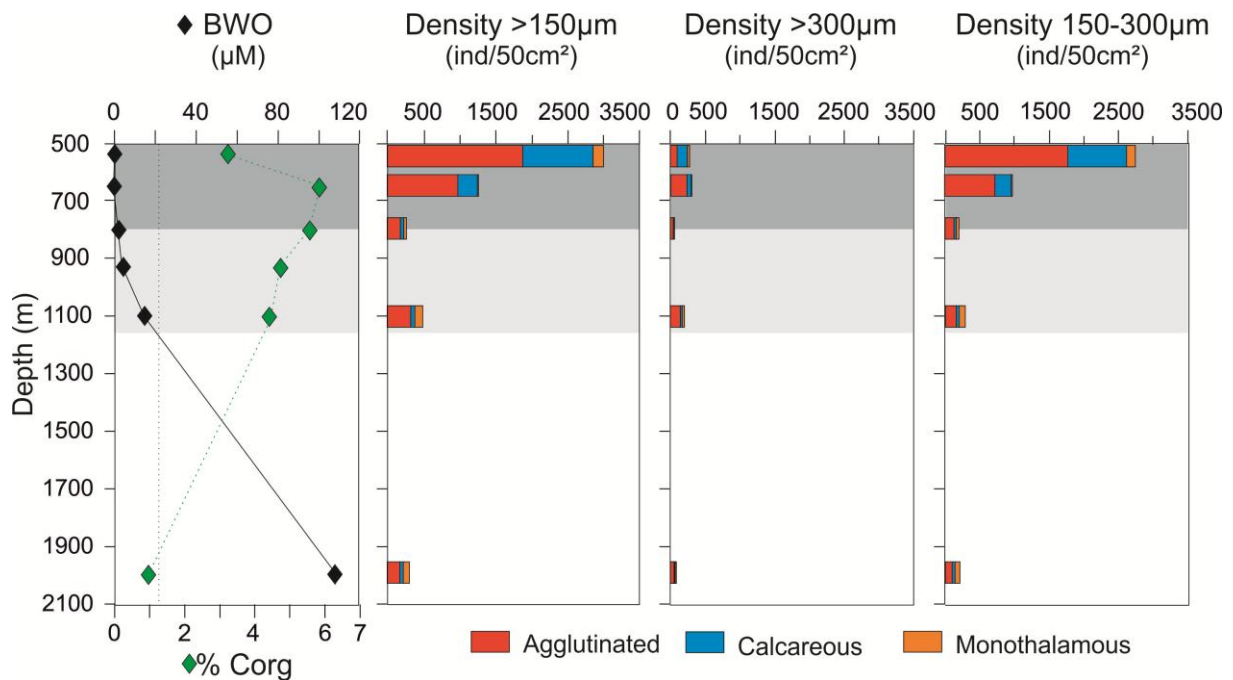


934

935 **Fig. 2.** Total stained foraminiferal abundances (ind/50cm²) in the 150-300 μm, >300 μm and
936 >150 μm (i.e. 150-300 and >300 μm combined) fractions of the first cm (0-1 cm layer) along
937 the sampling transect. The BWO concentration (μM) and Corg content (wt. %) are from
938 Hunter et al. (2012) and Cowie et al. (2014). The vertical dashed line corresponds to the 22
939 μM limits defining an OMZ according to Levin et al. (2003). The dark grey shadow
940 represents the core of the OMZ (<2 μM; Paulmier and Ruiz-Pino, 2009) and the light grey
941 shadow the lower part of the OMZ (2-22 μM; Levin, 2003).

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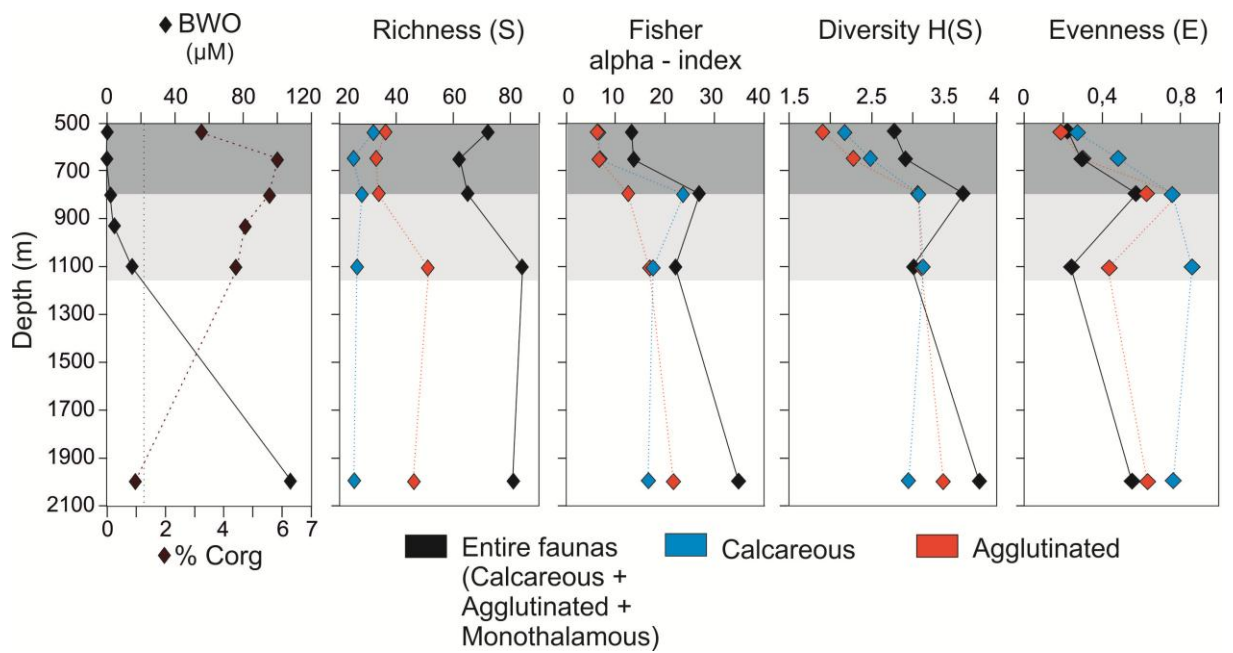
**Fig. 3.** Stained foraminiferal diversity indices (in the >150µm fraction) along the sampling transect. The Corg content (wt. %) is from Hunter et al. (2012) and Cowie et al. (2014). The dashed line corresponds to the 22 µM limit defining an OMZ according to Levin et al. (2003). The dark grey shadow 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).

% of agglutinated species

A

Legend:

- *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

952

32

% of calcareous species

**B**

**Legend:**
- B. aff. *dilatata*
- *Cassidulina* sp. 1
- *Hoeglundina* cf. *elegans*
- *Praeglobobulimina* sp.
- *U. peregrina* type *parva*
- *E. trigona*
- *C.oolina*
- *B. aculeata*
- 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.
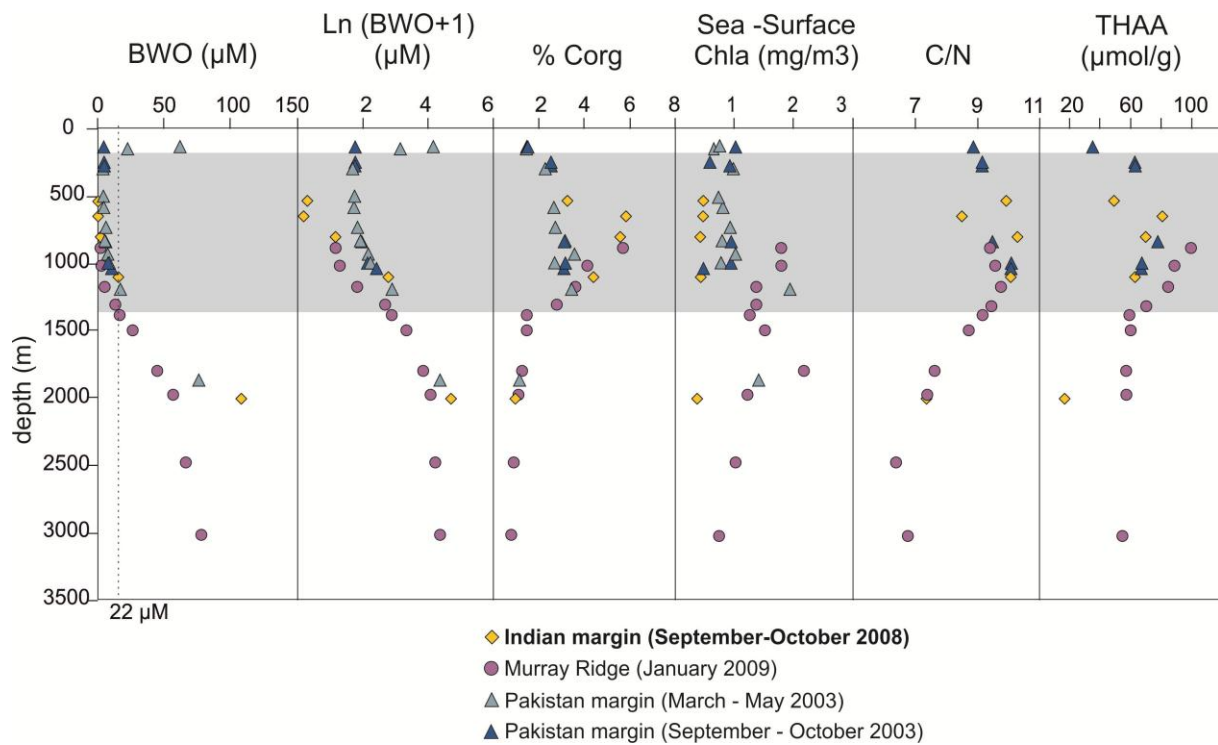
**Fig. 5.** Regional comparison of the environmental parameters on the Indian and Pakistan margins and the Murray ridge. The Corg content, C/N, THAA concentration and DI data are from Hunter et al. (2012) and Cowie et al. (2014) for the Indian margin; from Vandewiele et al. (2009) for the Pakistan margin; 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.
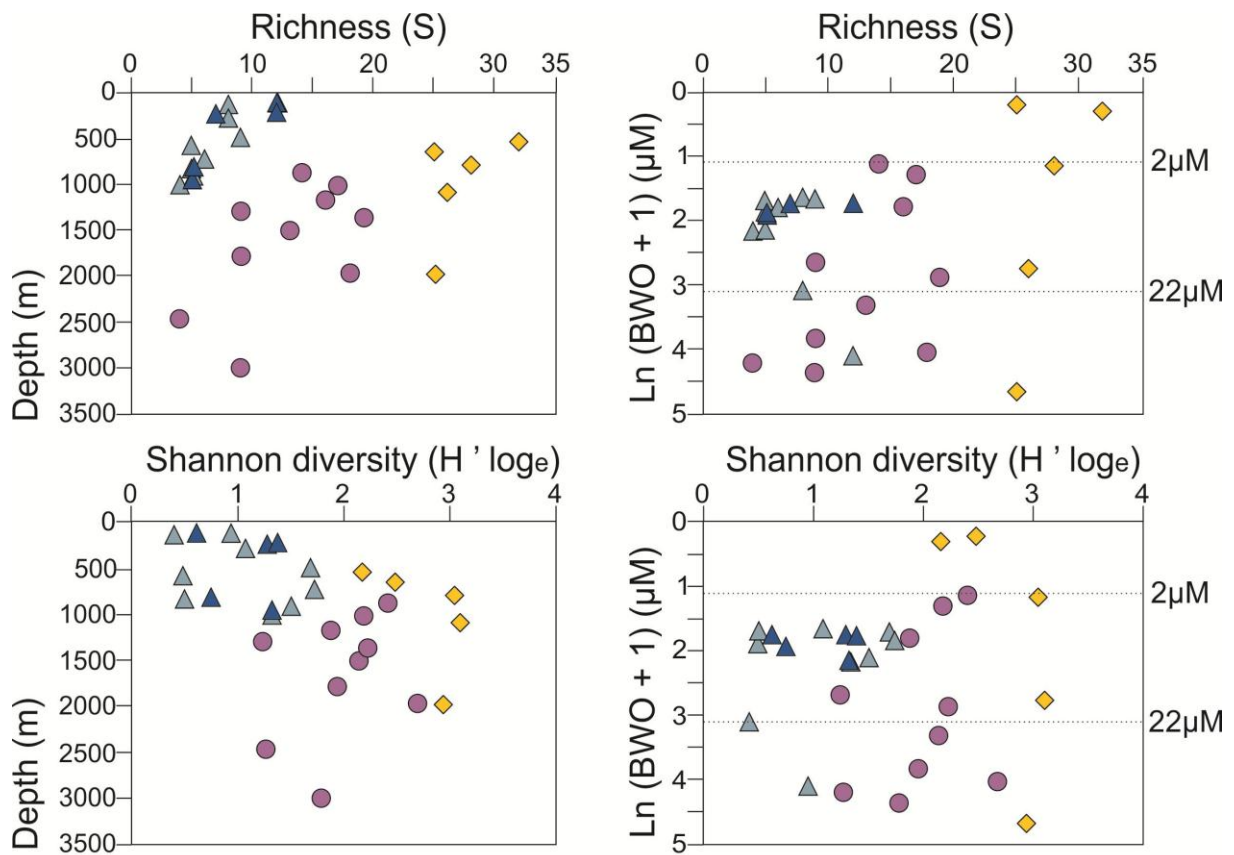
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**Fig. 6.** Species richness and Shannon index (calculated for the calcareous fauna only) vs. depth (m) and Ln (BWO+1) for the Indian margin, the Pakistan margin and the Murray ridge. Because some values were <1, the BWO was expressed using the natural 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).

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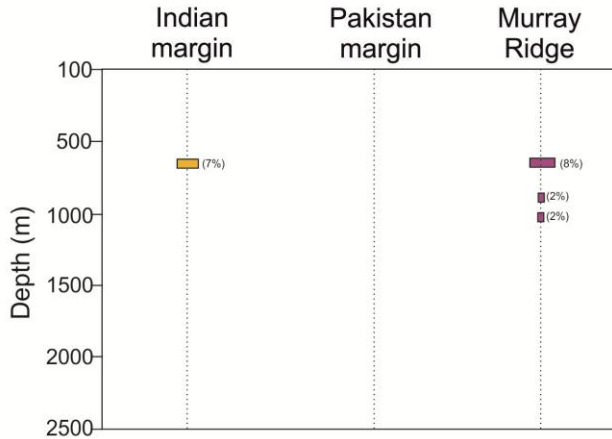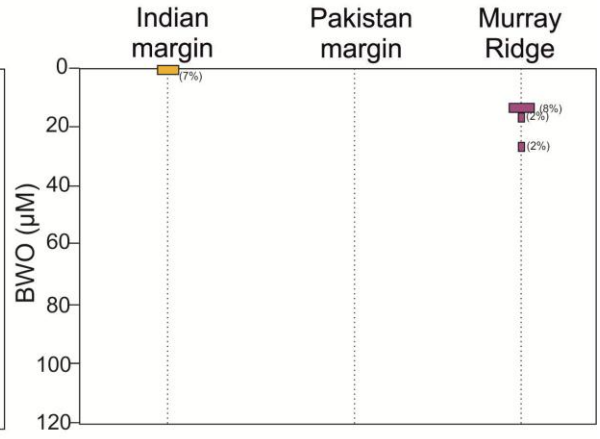
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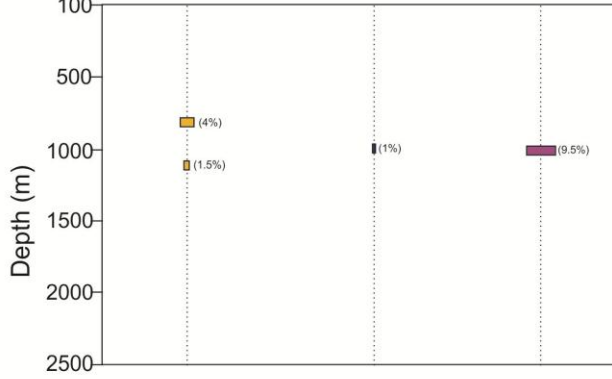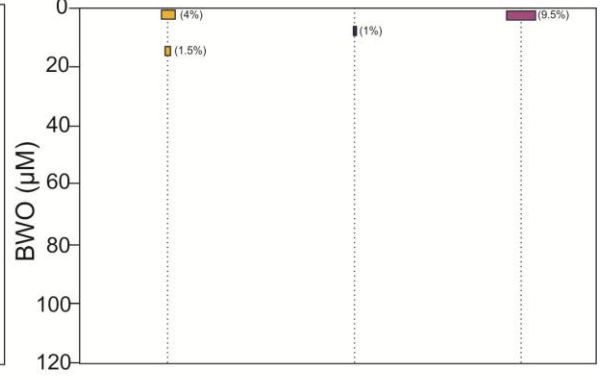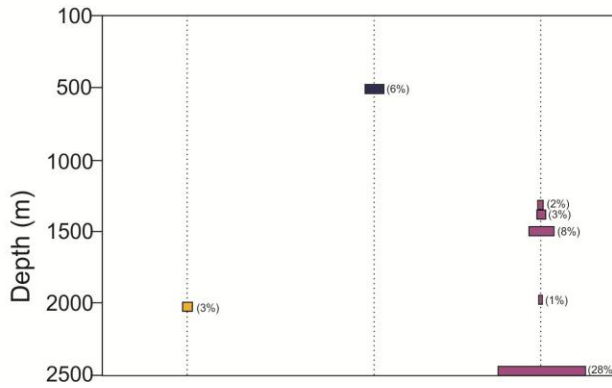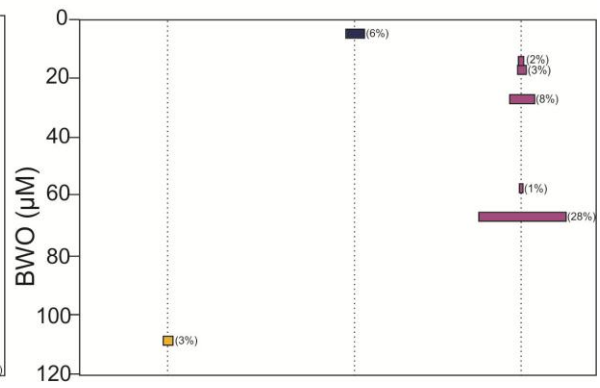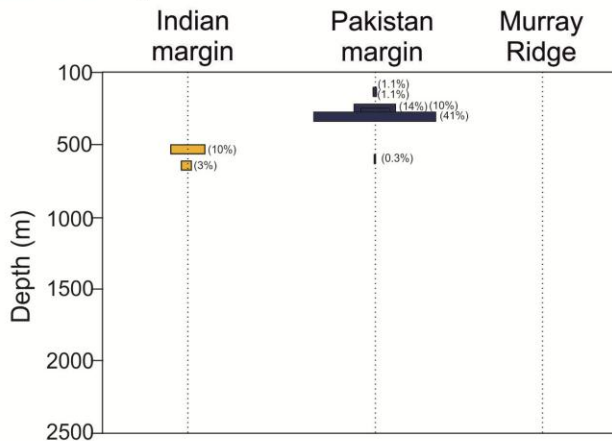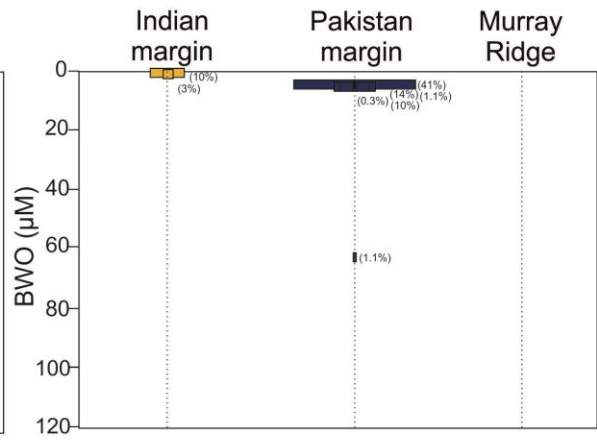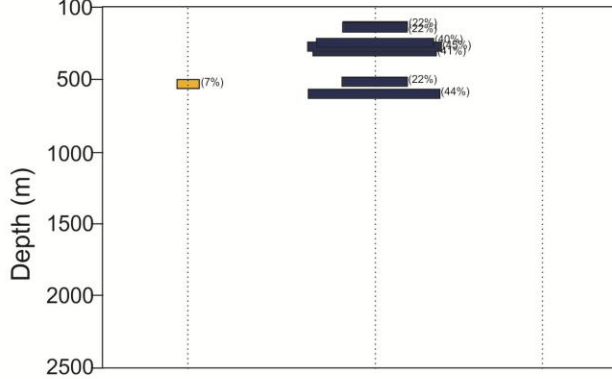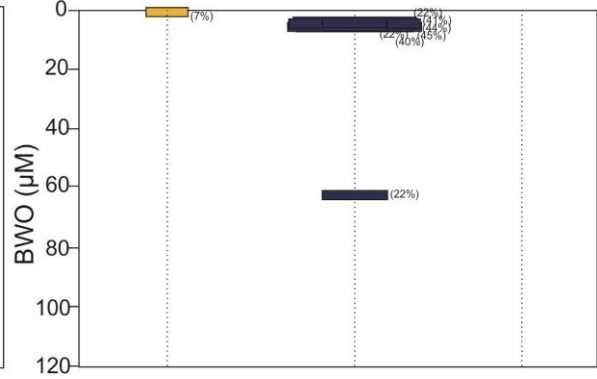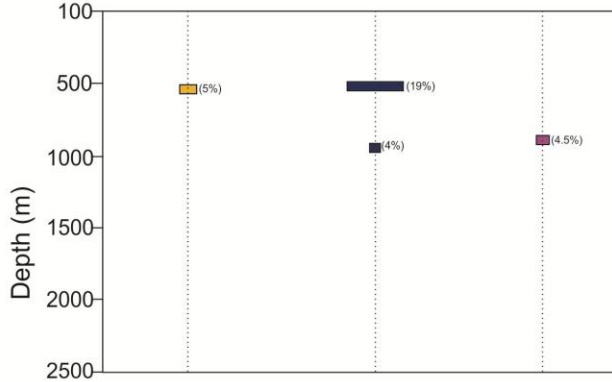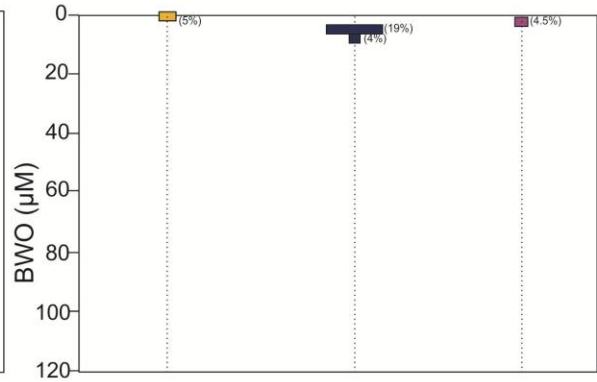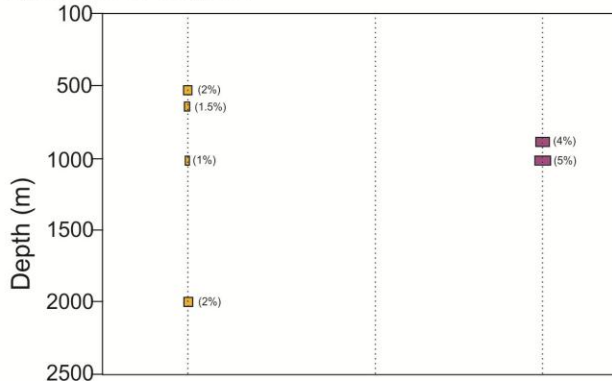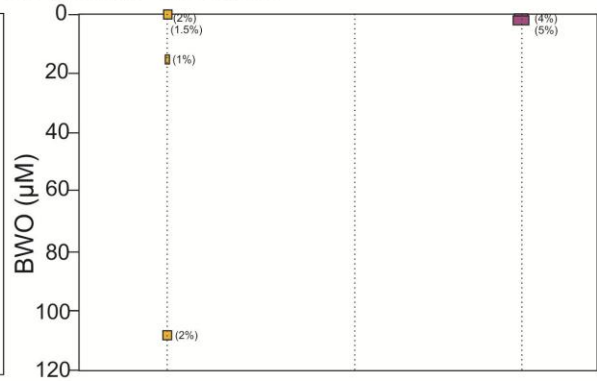
978 **Fig. 7.** Comparison of species occurrences vs. depth (left panel) and BWO (μM; right panel)
979 for three regions in the Arabian Sea. *Cassidulina* sp. 1 (from the Indian margin) and
980 *Cassidulina laevigata* (Schumacher et al., 2007) was grouped into *Cassidulina* sp.. Percentage
981 species occurrences are indicated in brackets.

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| 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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1003 **Table 1.** Top 10 ranked species at each site. The number to the right of each name indicate

1004 counts of specimens with the relative abundances (%) in brackets.

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