



Live (Rose Bengal stained) foraminiferal faunas from the northern Arabian Sea: faunal succession within and below the OMZ

C. Caille¹, K. A. Koho^{2,3}, M. Mojtahid¹, G. J. Reichart^{2,3}, and F. J. Jorissen¹

¹Laboratory of Recent and Fossil Bio-Indicators, CNRS UMR6112 LPG-BIAF, Angers University, 2 Bd Lavoisier, 49045 Angers Cedex 01, France

²Utrecht University, Faculty of Geosciences, Department of Earth Sciences, Budapestlaan 4, 3584 CD Utrecht, the Netherlands

³Royal Netherlands Institute for Sea Research (Royal NIOZ), Landsdiep 4, 1797 SZ 't Horntje (Texel), the Netherlands

Correspondence to: C. Caille (clemence.caille@univ-angers.fr)

Received: 19 August 2013 – Published in Biogeosciences Discuss.: 23 September 2013

Revised: 7 January 2014 – Accepted: 16 January 2014 – Published: 26 February 2014

Abstract. Live (Rose Bengal stained) benthic foraminifera from the Murray Ridge, within and below the northern Arabian Sea oxygen minimum zone (OMZ), were studied in order to determine the relationship between faunal composition, bottom water oxygenation (BWO), pore water chemistry and organic matter (organic carbon and phytopigment) distribution. A series of multicores were recovered from a ten-station oxygen (BWO: 2–78 μM) and bathymetric (885–3010 m depth) transect during the winter monsoon in January 2009. Foraminifera were investigated from three different size fractions (63–125 μm , 125–150 μm and > 150 μm). The larger foraminifera (> 125 μm) were strongly dominated by agglutinated species (e.g. *Reophax* spp.). In contrast, in the 63–125 μm fraction, calcareous taxa were more abundant, especially in the core of the OMZ. On the basis of a principal components analysis, three foraminiferal groups were identified and correlated to the environmental parameters by canonical correspondence analysis. The faunas from the shallowest stations, in the core of the OMZ (BWO: 2 μM), were composed of “low oxygen” species, typical of the Arabian Sea OMZ (e.g. *Rotaliatinopsis semiinvoluta*, *Praeglobobulimina* sp., *Bulimina exilis*, *Uvigerina peregrina* type *parva*). These taxa are adapted to the very low BWO conditions and to high phytodetritus supplies. The transitional group, typical for the lower part of the OMZ (BWO: 5–16 μM), is composed of species that are tolerant as well to low-oxygen concentrations, but may be less critical with respect to organic supplies (e.g. *Globocassidulina subglobosa*, *Ehrenbergina trigona*). Below the OMZ (BWO: 26–78 μM), where food availability

is more limited and becomes increasingly restricted to surficial sediments, cosmopolitan calcareous taxa were present, such as *Bulimina aculeata*, *Melonis barleeanus*, *Uvigerina peregrina* and *Epistominella exigua*. Miliolids were uniquely observed in this last zone, reflecting the higher BWO and/or lower organic input. At these deeper sites, the faunas exhibit a clear succession of superficial, intermediate and deep infaunal microhabitats, which can be linked to the deeper oxygen and nitrate penetration into the sediment.

1 Introduction

Oxygen minimum zones (OMZs) are present at intermediate water depth (250–1500 m) along the continental margin of the eastern Pacific, off southwest and northwest Africa, in the Bay of Bengal and in the northern Indian Ocean (Arabian Sea). OMZs are defined as areas where the oxygen concentration in the water column is < 22 μM (Levin, 2003; Helly and Levin, 2004). Mostly, they are also areas of high primary productivity where low-oxygen concentrations develop naturally and have persisted over geological timescales (Reichart et al., 1998) due to enhanced organic matter degradation. Where the OMZs intersect with the continental margin, the ocean floor is exposed to low-oxygen levels. Despite very low oxygen concentrations, protozoan and metazoan assemblages thrive in these environments (e.g. Jannink et al., 1998; Levin et al., 2000; Levin, 2003; Schumacher et al., 2007). These low-oxygen tolerant benthic assemblages can

attain high densities, but typically have a low diversity (e.g. den Dulk et al., 1998; Jannink et al., 1998; Schumacher et al., 2007). The poor ventilation also impacts biogeochemical processes in the water column and within the sediment. This results in enhanced sequestration of organic material in the sediment. Consequently, OMZs are considered as important organic carbon sinks (e.g. Cowie, 2005; van der Weijden et al., 1999; Koho et al., 2013). In this context, OMZs are key areas for understanding hypoxic–anoxic events and their impact on the benthic ecosystem. A good knowledge of the ecology and life cycle adaptations of the benthic fauna living in these low-oxygen areas is essential.

The Arabian Sea is one of the most intense OMZs in the world, with oxygen concentrations $< 2 \mu\text{M}$ in its core (Paulmier and Ruiz-Pino, 2009). The intensity of the Arabian Sea OMZ is closely related to the Indian monsoon system (Wyrtki, 1973). The SW (June–September) and NE (December–March) monsoons lead to intense seasonal changes of surface hydrography and vertical particle flux to the deep sea (Nair et al., 1989; Haake et al., 1993; Rixen et al., 1996). During the summer (SW) monsoon (June to September), an intense coastal upwelling develops off the coast of Somalia, Oman and southwestern part of India. This upwelling triggers high biological productivity in the photic zone (e.g. Ryther and Menzel, 1965; Caron and Dennett, 1999; Rixen et al., 2000), leading to high export of organic carbon to intermediate water depths, where it is intensely recycled and remineralized. A second high biological productivity event occurs during the winter (NE) monsoon (e.g. Caron and Dennett, 1999; Rixen et al., 2000), when nutrient availability increases due to convective mixing of the sea surface water (Banse and McClain, 1986; Madhupratap et al., 1996). The strength of the Arabian Sea OMZ is not only due to high biological productivity but is also related to the semi-enclosed nature of the northern Arabian Sea (Wyrtki, 1973; Shetye et al., 1994), in combination with the renewal of intermediate waters by relatively oxygen-poor intermediate water masses from the south and west (Swallow, 1984; Olson et al., 1993). Low-oxygen conditions in the Arabian Sea are also influenced by the lateral advection of high-salinity waters from the Persian Gulf and the Red Sea, which contribute to the stratification of the OMZ waters by preventing the vertical mixing of surface waters with the low-oxygenated deeper waters (Indian Ocean Central Water) (Schulz et al., 1996; Reichert et al., 1998).

To date, only a few studies have dealt with living (Rose Bengal stained) benthic foraminiferal faunas from the Arabian Sea OMZ. These studies have mostly focused on the Pakistan (Jannink et al., 1998; Maas, 2000; Erbacher and Nelskamp, 2006; Schumacher et al., 2007; Larkin and Gooday, 2009) and Oman margins (Stubbings, 1939; Hermelin and Shimmield, 1990; Naidu and Malmgren, 1995; Gooday et al., 2000). In addition, Kurbjeweit et al. (2000) and Heinz and Hemleben (2003, 2006) compared the foraminiferal distribution during different periods of the monsoonal cycle in

the central, eastern and western parts of the Arabian Sea. Most of these studies described a general zonation of benthic foraminiferal faunas across the OMZ. However, since geochemical measurements were generally not included in these studies, no clear, specific correlations could be established with the controlling environmental parameters. Nevertheless, foraminiferal abundances and distributions have been suggested to be controlled by organic matter supply and oxygen content. Since oxygen and organic matter content are often inversely correlated, their interpretation is difficult.

Here, we explore for the first time the distribution and abundance of living benthic foraminiferal faunas from the Murray Ridge, northern Arabian Sea. Foraminiferal data were correlated with geochemical data obtained at the same stations described in the studies of Kraal et al. (2013) and Koho et al. (2013) in order to examine the influence of environmental parameters on foraminiferal distribution along the study transect. Kraal et al. (2013) examined pore water geochemistry (oxygen and nitrate pore water profiles); whereas Koho et al. (2013) described bottom water oxygenation, phytopigments concentration (chlorophyll *a*) and organic carbon content. Our study gives new insights into foraminiferal ecology of the Arabian Sea. Our specific aims are to (i) describe the live benthic foraminiferal faunal (Rose Bengal stained) distribution on the Murray Ridge, and (ii) identify the main environmental parameters that control the benthic foraminiferal faunas along the study transect. Our results also provide new elements which may be useful for a future calibration of benthic foraminiferal assemblages as paleoenvironmental proxies in the Arabian Sea. A thorough understanding of the relationships between recent environmental parameters and benthic foraminiferal assemblages is essential for the interpretation of paleoceanographic data.

2 Material and methods

2.1 Study area

During the interdisciplinary PASOM cruise (Process study on the Arabian Sea Oxygen Minimum Zone) in January 2009, a ten-station transect was sampled along the Murray Ridge, northern Arabian Sea (Fig. 1), along a strong oxygen gradient. The Murray Ridge is a seamount with its top culminating in the core of the OMZ, and offers an ideal natural laboratory for investigation of biological processes along BWO and organic carbon gradients. The PASOM cruise was designed to cover a transect through the OMZ (885–3010 m), specifically targeting the transition zone from low-oxygen to more oxic conditions below the OMZ. All sediment samples were retrieved with a multicorer, allowing the recovery of undisturbed surface sediment samples. The multicorer was equipped with eight cores measuring 6.6 cm in diameter and four cores measuring 10 cm in diameter. All cores collected for foraminiferal (\varnothing 6.6 cm) and geochemical analyses (\varnothing 6.6

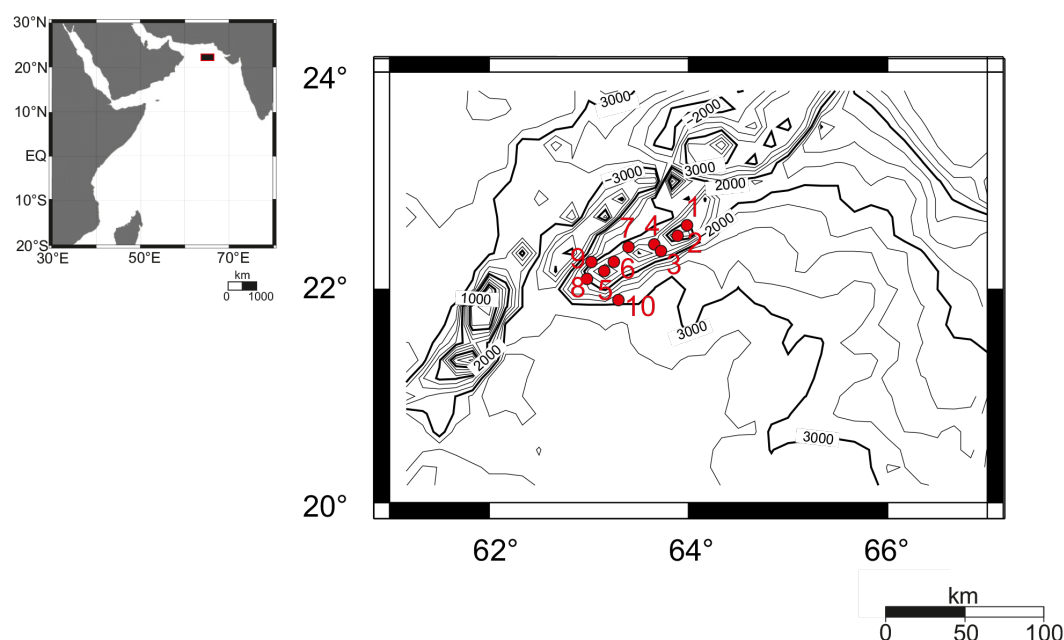


Fig. 1. Study area and station locations on the Murray Ridge, northern Arabian Sea. The black area on the regional map corresponds to the study area.

and 10 cm) were retrieved from the same multicore cast. Most cores were sliced at 0.5 cm resolution down to 2 cm sediment depth, at 1 cm intervals between 2 and 6 cm and then every 2 cm intervals down to 10 cm. Only the cores used for pore water extraction and organic carbon (OC) analyses were sliced differently: 0.5 cm intervals in the top 2, 1 cm intervals down to 6 and 2 cm intervals down to 10 cm.

2.2 Foraminiferal analyses

On board, samples were stained in Rose Bengal (Walton, 1952) in 95 % ethanol solution (1 g L^{-1}). They were gently shaken for several minutes and further stored in the Rose Bengal solution. In the laboratory, sediment samples were wet sieved into > 150 , 125–150 and 63–125 μm fractions. To obtain a good staining, the samples were treated again with Rose Bengal for a minimum of 48 h. All well-stained foraminifera were picked wet (50 % ethanol – 50 % water) from $> 150 \mu\text{m}$ and 125–150 μm fractions from all levels until 10 cm depth under a binocular microscope. Foraminifera from the small-size fraction (63–125 μm) were only investigated from the first centimetre of the sediment (0–0.5 and 0.5–1 cm) due to the extremely time-consuming character of the analysis.

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

Green (CTG), which is more reliable (e.g. Bernhard, 2000; Bernhard et al., 2006), in order to keep our results comparable with previous studies on living benthic foraminifera from the Arabian Sea, mostly based on Rose Bengal (e.g. Jannink et al., 1998; Mass, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009). In order to minimize the chance of bias in our counts of living foraminifera, very strict staining criteria were always applied. Specimens were considered living only when all chambers except the last one(s) were well stained. Furthermore, doubtful specimens were compared with perfectly stained specimens of the same species and non-transparent agglutinated and miliolid taxa were broken to inspect their contents. Fragments of branching and tubular foraminifera (e.g. *Hyperammina*, *Rhizammina*) were not included in the data analyses because of their easily breakable tests, which makes it very difficult to quantify them correctly. Foraminiferal taxonomy was based on commonly used taxonomic reference works (e.g. Loeblich and Tappan, 1988; Jones, 1994) and on some taxonomic studies with emphasis on the Arabian Sea and other low-oxygen areas (e.g. Mass, 2000; Schumacher et al., 2007; Larkin and Gooday, 2009); see taxonomic appendix in the Supplement for more details.

For all stations, diversity indices, including species richness (S : count of number of taxa in a sample), Shannon index ($H(S)$), and evenness (J) were calculated using the free statistical software PAST (PALEontological STATistics; Version 2.14; Hammer et al., 2001).

To better constrain the relationship between species variability and environmental conditions, principal component analysis (PCA) and canonical correspondence analysis

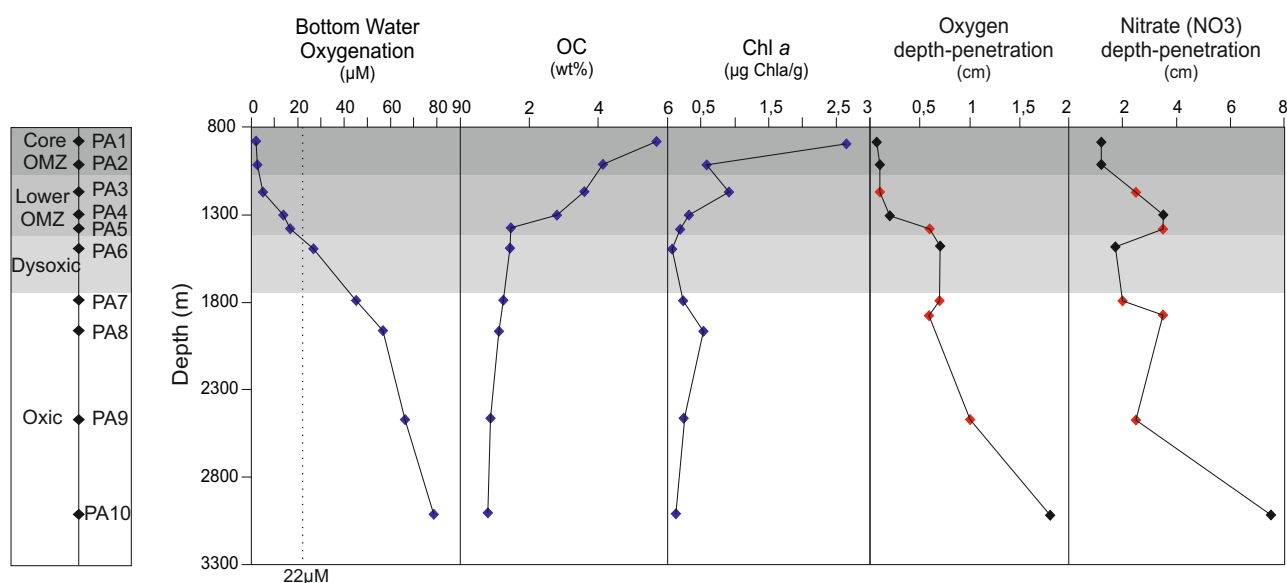


Fig. 2. Environmental parameters: bottom water oxygenation, organic carbon (OC; 0–1 cm), chlorophyll *a* (Chl *a*, 0–1 cm), oxygen and nitrate penetration depths. In red: the results from this study; in blue: the results published in Koho et al. (2013); in black: the results published in Kraal et al. (2013). The dashed line at 22 µM corresponds to the definition of the OMZ according to Levin et al. (2003).

(CCA) were conducted using Statistica 8 software. The PCA was run on species that contributed > 2 % to the total abundance of the entire database. Two PCA analyses were carried out; the first one investigating the entire core (down to 10 cm, > 125 µm fraction), and the second one investigate the top 1 cm of the sediment (0–1 cm, > 63 µm fraction). The CCA was applied for investigating environmental parameters (OC, BWO, Chl *a*, oxygen and nitrate penetration depth) and for foraminiferal species groups derived from PCA analysis.

2.3 Dissolved oxygen and nitrate

In short, dissolved O₂ concentrations in the water column and on the seafloor measured with an oxygen sensor (Sea-Bird SBE43, accuracy 2 % (Sea-Bird Electronics Inc., 2011)) that was built into the framework of a conductivity, temperature and depth (CTD) profiler (all data published in Koho et al. (2013); see Fig. 2 for details).

The pore water oxygen concentration was determined immediately following core recovery in a temperature-controlled laboratory setup at in situ temperature (some data published in Kraal et al., 2013; see Fig. 2 for details). All measurements were done with Unisense oxygen microelectrodes (OXO100 or OXO50). The microelectrodes were two-point calibrated at 100 % O₂ saturated seawater (bubbled with oxygen) and in a solution containing sodium ascorbate (0.1 M) to obtain the 0 % reading.

The details of pore water extraction for nitrate analyses are outlined in Kraal et al. (2013). In short, sediment slicing was carried out in a N₂-purged glove box in a temperature-controlled laboratory set at in situ temperature (some data are published in Kraal et al., 2013; see Fig. 2 for details). Sediment samples were transferred to 50 ml plastic centrifuge tubes under N₂ atmosphere and centrifuged for 20 min at 4500 rpm outside the glove box. The centrifuge tubes were then transferred back into the glove box where the supernatant pore water was filtered over 0.45 µm Teflon filters and frozen (−20 °C) until the analyses. Pore water nitrate concentrations were measured by an autoanalyser at the Royal Netherlands Institute for Sea Research (NIOZ) in Den Burg, the Netherlands.

2.4 Organic carbon and phytopigment analyses

The details of organic carbon analyses are outlined in Koho et al. (2013) (all data published in Koho et al., 2013; see Fig. 2 for details). In short, the sediment from which the pore waters were extracted was further used for solid phase analyses and frozen at −20 °C until analyses. In the laboratory, sediment was weighed, freeze-dried and decalcified by reacting twice with 1 mol L^{−1} HCl (4 and 12 h). After two subsequent rinses with ultrapure water, the decalcified samples were freeze-dried and organic C and N were measured with a CNS analyser (Fisons Instruments NA 1500).

The phytopigments were extracted from a different core than the one used for the organic carbon analyses. However, the core came from the same multicore cast. The details of phytopigment analyses are outlined in Koho et al. (2013).

In short, the samples were stored at -80°C until analysed and freeze-dried prior to pigment extraction in 10 ml of acetone : water (90 : 10). The full pigment composition was obtained through application of high-performance liquid chromatography (HPLC) equipped with a C_{18} reverse phase column at the Royal Netherlands Institute for Sea Research (NIOZ – Yerseke). The calibration was based on working standards prepared from commercially available compounds (DHI, Denmark). The pigment concentrations are reported as $\mu\text{g g}^{-1}$ of sediment.

3 Results

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

3.1 Environmental parameters

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

Organic carbon (OC) and chlorophyll *a* (Chl *a*) contents, for the top first centimetre, progressively changed along the study transect (Fig. 2; Koho et al., 2013). The highest concentrations ($\text{OC} = 5.7\text{ wt \%}$; $\text{Chl } a = 2.6\mu\text{g g}^{-1}$) were observed in the core of the OMZ (885 m and 1013 m). In the dysoxic (1495 m) and oxic zones (1791 to 3010 m), organic carbon and Chl *a* values were lower, $< 2\text{ wt \%}$ and $< 0.5\mu\text{g g}^{-1}$, respectively (Fig. 2). Minimum concentrations ($\text{OC} = 0.82\text{ wt \%}$; $\text{Chl } a = 0.1\mu\text{g g}^{-1}$) were found at the deepest site (3010 m). Generally, the organic carbon and Chl *a* concentrations decreased with increasing water depth and BWO.

The oxygen penetration depth into the sediment increased along the transect and was strongly related to the BWO content ($R^2 = 0.89$; $p = 4.7 \cdot 10^{-4}$) (Fig. 2). At the shallowest site (885 m, $\text{BWO} \sim 2\mu\text{M}$) within the OMZ, oxygen penetration was about 0.1 cm, whereas at the deepest site (3010 m, $\text{BWO} \sim 78.3\mu\text{M}$), oxygen was available until 1.8 cm depth.

The nitrate penetration depth showed a weaker, but still significant, correlation with the BWO content ($R^2 = 0.64$; $p = 0.046$), increasing from the 1.2 cm at 885 m (OMZ site) to 7.5 cm at 3010 m (oxic site).

3.2 Foraminiferal assemblages of the 0–10 cm interval ($> 125\mu\text{m}$ fraction)

3.2.1 Total abundance

Live foraminiferal (Rose Bengal stained) abundances for the whole cores (down to 10 cm) were investigated in three different size fractions: $125\text{--}150\mu\text{m}$, $> 150\mu\text{m}$ and $> 125\mu\text{m}$ (Fig. 3a), the $> 125\mu\text{m}$ fraction being the sum of the first two. All size fractions showed a similar distribution of foraminiferal absolute abundance, and no clear trend was seen along the transect (Fig. 3a).

In the $> 125\mu\text{m}$ fraction, total live foraminiferal abundance varied from ~ 90 to $\sim 970\text{ ind/50 cm}^2$, the two extremes being observed in the two sites from the core of the OMZ (at 1013 and 885 m, respectively). The lower OMZ stations (1172, 1306 and 1379 m) displayed values from 215 ind/50 cm^2 to 450 ind/50 cm^2 , the dysoxic site (1495 m) contained $\sim 970\text{ ind/50 cm}^2$, whereas the oxic sites (1791 to 3010 m) had densities varying from $\sim 400\text{ ind/50 cm}^2$ to $\sim 870\text{ ind/50 cm}^2$ (Fig. 3a).

Agglutinated foraminifera were dominant at all stations, always constituting more than half of the total assemblage (Fig. 3a). In the lower part of the OMZ (stations at 1172, 1306 and 1379 m), they attained $\sim 70\%$ on average. Abundance of hyaline taxa varied along the transect without a clear pattern. Miliolids were only present at the oxic sites (1791 to 3010 m depth), always constituting less than 14 % of total standing stocks.

3.2.2 Diversity and dominance

A total of 191 taxa have been identified, of which 71 are agglutinated, 99 are hyaline and 21 are miliolids. Species richness differed considerably between the OMZ stations (core and lower part) and the dysoxic sites (1495 m) (Fig. 3a). The lowest number of species (17) was observed at 1013 m depth, in the core of the OMZ. At the dysoxic site (1495 m), a maximum of 68 species was recorded. At the oxic sites (1791 to 3010 m), species richness was more constant, with about 50 species at all stations (Fig. 3a). The species richness followed generally that of the total abundance, suggesting that the number of foraminifera found was largely determined by the sample size. In addition, in general higher species richness coincided with a higher Shannon index and a lower evenness (Fig. 3a). Species were also distributed fairly evenly at all sites, evenness varying from 0.4 to 0.6 (Fig. 3a).

Shannon diversity ($H(S)$) was minimal in the core of the OMZ (2.3 to 2.5). It was higher at the dysoxic and oxic sites, where values around 3.0 were observed. Maximal diversity

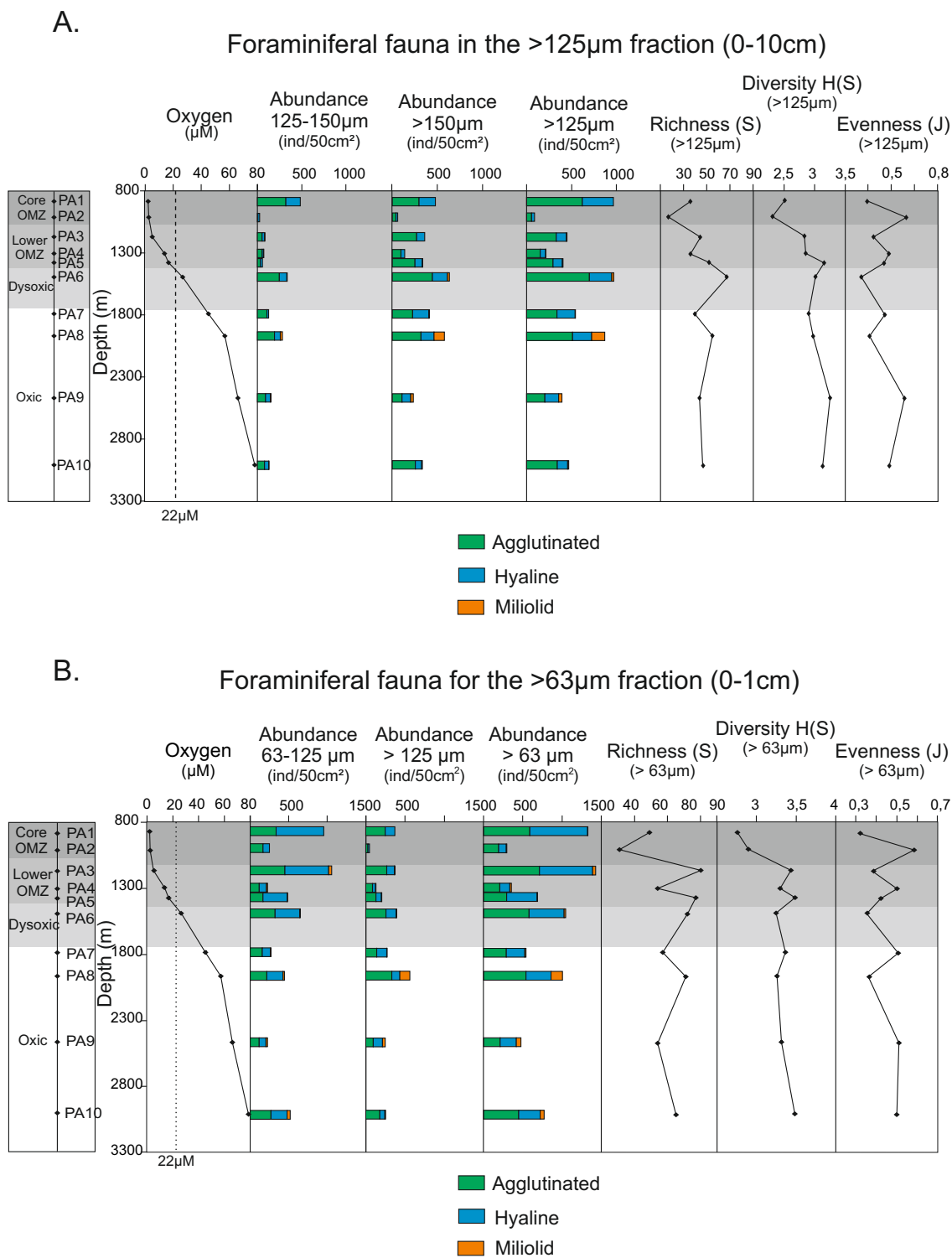


Fig. 3. (A) Live (Rose Bengal stained) foraminiferal abundances (ind/50 cm²) in the 125–150 μ m, > 150 μ m and > 125 μ m fraction for the entire core (0–10 cm) and foraminiferal biodiversity indices (in the > 125 μ m fraction) along the sampling transect. The dashed line at 22 μ M corresponds to the definition of the OMZ according to Levin et al. (2003). (B) Live foraminiferal abundances (ind/50 cm²) in the 63–125 μ m, > 125 μ m, > 63 μ m fractions for the first cm (0–1 cm) of the sediment and foraminiferal biodiversity indices (in the > 63 μ m fraction) along the sampling transect. The dashed line at 22 μ M corresponds to the definition of the OMZ according to Levin et al. (2003).

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

3.2.3 Distribution patterns of individual species

Foraminiferal species distribution displayed important changes along the transect (Fig. 4), although some agglutinated species, such as *Reophax agglutinans*, *Reophax micaceus* and *Lagenammina difflugiformis*, were found at most of the stations.

In the core of the OMZ, where oxygen and nitrate penetration were very shallow (~ 0.1 cm and ~ 1.3 cm, respectively), a faunal density maximum was concentrated in the upper 1.5 cm (Fig. 4). Nevertheless, at both sites, living foraminifera were found down to 3–4 cm. The fauna of both stations was dominated by the agglutinated species *Reophax agglutinans*, *Lagenammina difflugiformis*, *Ammodiscus* sp., *Cribrostomoides* cf. *jeffreysii*, *Verneuilinulla propinqua*, *Reophax dentaliniformis* and *Hormosina guttifer* and the hyaline species *Uvigerina peregrina* type *parva*, *Rotaliatinopsis seminvoluta*, *Praeglobobulimina* sp., *Fursenkoina mexicana*, *Bulimina exilis*, *Chilostomella oolina*, *Gyroidina soldanii* and *Fursenkoina* sp.

In the lower part of the OMZ (1172 to 1379 m), maximum densities were consistently observed in the first cm of the sediment, but small numbers of stained specimens were present down to 6–8 cm depth (Fig. 4). Here, the oxygen and nitrate penetration depth increased to 0.6 cm and 3.5 cm depth, respectively. The faunas of this zone were dominated by the agglutinated species *Reophax* cf. *spiculifer*, *Reophax agglutinans*, *Lagenammina difflugiformis* and *Verneuilinulla propinqua* and the hyaline species *Bulimina* cf. *mexicana*, *Ehrenbergina trigona*, *Melonis barleeanus*, and *Uvigerina peregrina*. The infaunal taxa were dominated by agglutinated taxa, among which several *Reophax* species, whereas only some scarce individuals of the hyaline taxa *Chilostomella oolina* and *Fursenkoina* sp., were found deeper in the sediment (3–4 cm).

At the dysoxic (1495 m) and oxic (1791 to 3010 m) stations, live foraminifera were found down to 10 cm depth (Fig. 4), although maximum densities were recorded in the oxygenated first two centimetres of the sediment (Fig. 4). *Lagenammina difflugiformis*, *Reophax agglutinans*, *Bulimina aculeata* and *Uvigerina peregrina* dominated the fauna. Both *B. aculeata* and *U. peregrina* showed two in-sediment maxima here: in the first half centimetre, which was well oxygenated, and at 3–5 cm depth, below the oxygen and nitrate penetration depth. At the oxic sites (1791 to 3010 m), miliolid taxa appeared (Fig. 4). Among these, *Pyrgo murrhina* was most frequent and was found at the 1970 and 2470 m sites (Fig. 4). Other species, with maxima close to the sediment surface, included *Uvigerina peregrina*, *Lagenammina difflugiformis*, *Bulimina aculeata*, and *Reophax agglutinans*. Also, the density of intermediate and deep infaunal species increased at these sites. *Melonis barleeanus* was

found down to 3–4 cm (1791 to 2470 m) and *Fursenkoina* sp. was found in small numbers at the 1791 to 2470 m sites, down to the 6–8 cm level. Furthermore, *Reophax* species were found down to 10 cm depth regardless of the absence of oxygen and nitrate in the sediment. Other species were found at 3010 m compared to the other oxic sites (1791 to 2470 m). At 3010 m, faunas were dominated by agglutinated species, such as *Hormosina guttifer*, *Reophax agglutinans* and *Lagenammina difflugiformis*, and by the hyaline *Oridorsalis umbonatus*.

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

3.3.1 Total foraminiferal abundance and diversity

The 63–125 μ m fraction was examined in the topmost 1 cm only (Fig. 3b). In this first centimetre, all investigated size fractions (63–125 μ m, > 125 μ m) show a similar pattern, and no clear trend is seen along the transect (Fig. 3b).

On average, foraminiferal abundances in the > 63 μ m fraction of the 0–1 cm level (Fig. 3b) were at least twice as high as the densities in the > 125 μ m fraction. The abundance of small (63–125 μ m) foraminifera was particularly high in the core and lower part of the OMZ and at the dysoxic station (1495 m) where this fraction accounted for 62–84 % of the total foraminiferal abundance (Fig. 5). At the oxic stations (1791 to 3010 m), foraminifera of the 63–125 μ m fraction and > 125 μ m fraction were more even; the 63–125 μ m fraction contributed 44–49 % to the total assemblage. At 3010 m, the 63–125 μ m was dominant again, accounting for ~ 67 % of the total fauna (Fig. 5).

In general, the 63–125 μ m fraction was dominated by calcareous taxa (~ 30 –65 %). Consequently, in the > 63 μ m fraction, the relative abundance of calcareous taxa was higher than in the > 125 μ m fraction (Fig. 3b).

Similarly to > 125 μ m fraction (top 10 cm), Shannon diversity of the > 63 μ m fraction (top 1 cm) was relatively low (2.8) in the core of the OMZ (885 and 1013 m), but increased to 3.3 to 3.5 at deeper sites (1172, 1306 and 1379 m) (Fig. 3b). Species richness had a similar trend to Shannon diversity (Fig. 3b). Evenness values did not show a very clear trend, although low evenness values were generally found where high values of species richness and diversity were recorded. In general, all diversity indices were systematically higher when the 63–125 μ m size class was included (Fig. 3b).

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

Small hyaline species, such as *Bolivina seminuda* and *Nuttallides pusillus*, were common in the core of the OMZ (885–1013 m) (Fig. 5). In addition, small individuals of *Uvigerina peregrina* type *parva* were abundant. The agglutinated species *Trochammina* sp. 1, *Veleroninoides wiesneri*

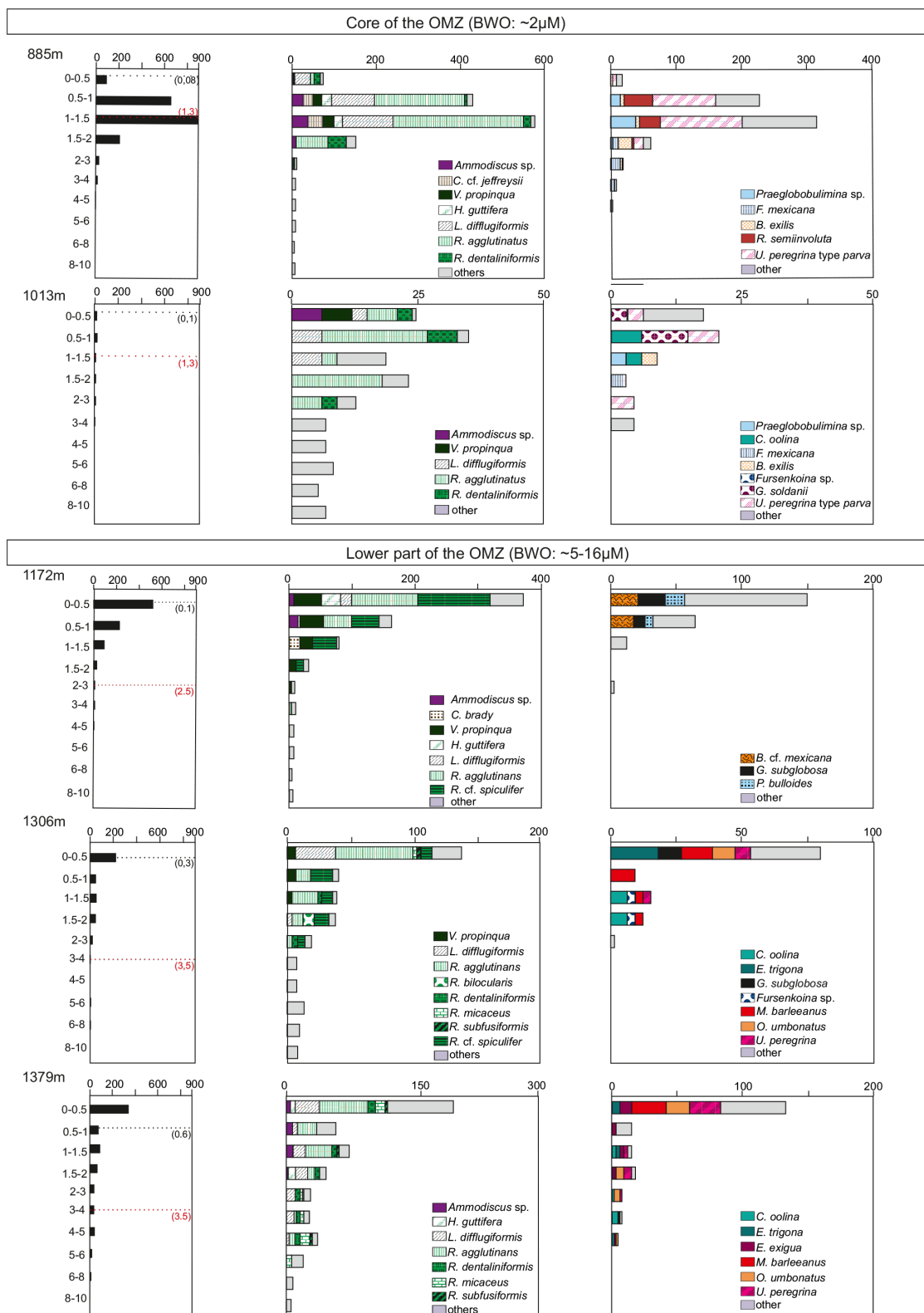


Fig. 4. Vertical densities ($\text{ind}/50\text{ cm}^3$) and abundances ($\text{ind}/50\text{ cm}^3$) of the dominant live foraminiferal species ($> 5\%$ for each station) in the $> 125\text{ }\mu\text{m}$ fraction. The first panel of each row represents the total foraminiferal densities. The black dotted line refers to the oxygen penetration (cm) into the sediment, and the red dotted line to the nitrate penetration depth (cm). The second panel of each row represents the vertical distribution of the dominant agglutinated taxa. The third panel of each row represents the vertical distribution of the dominant hyaline and miliolid taxa. Note the different horizontal scales between the third and second panels and between stations.

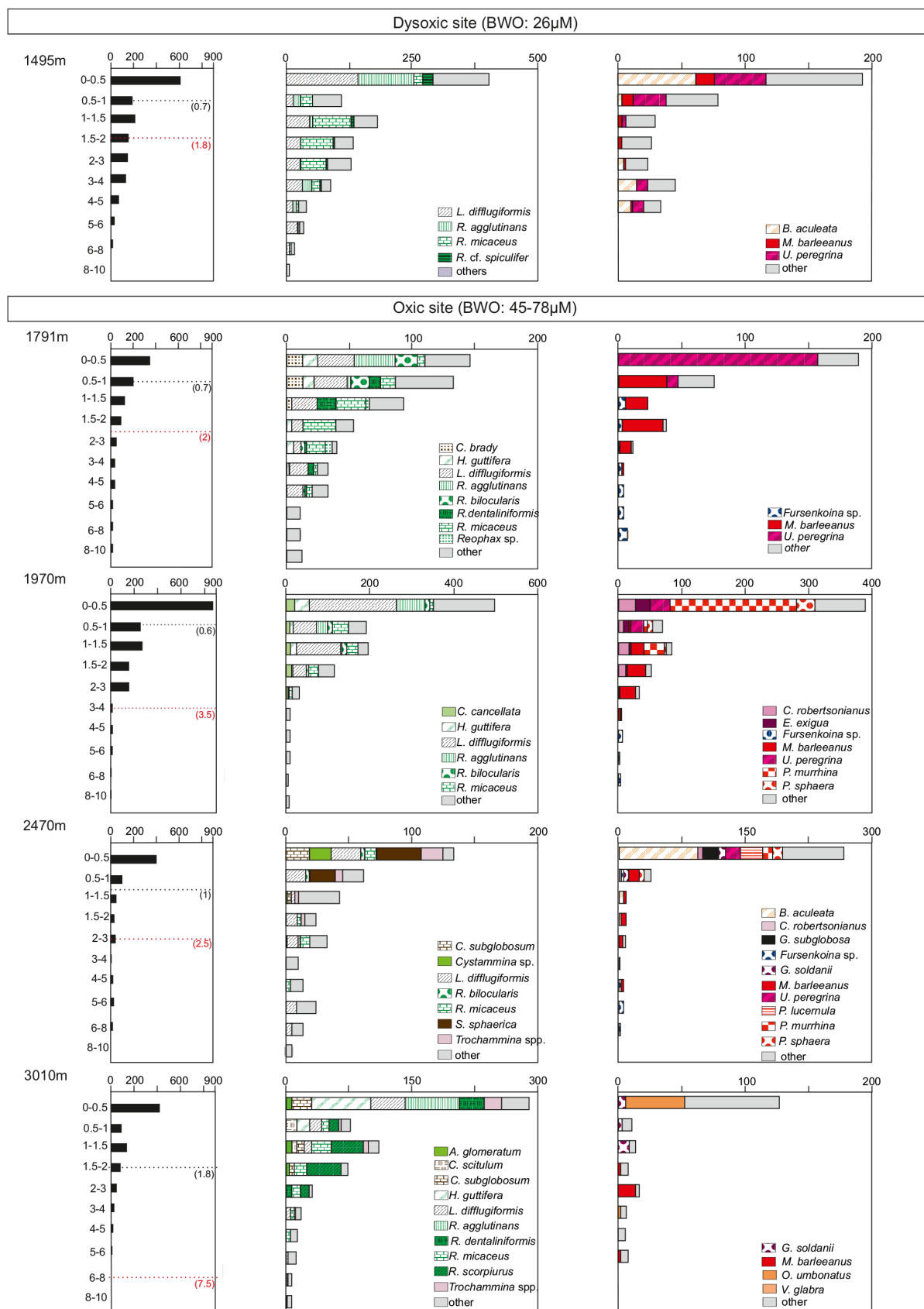


Fig. 4. Continued.

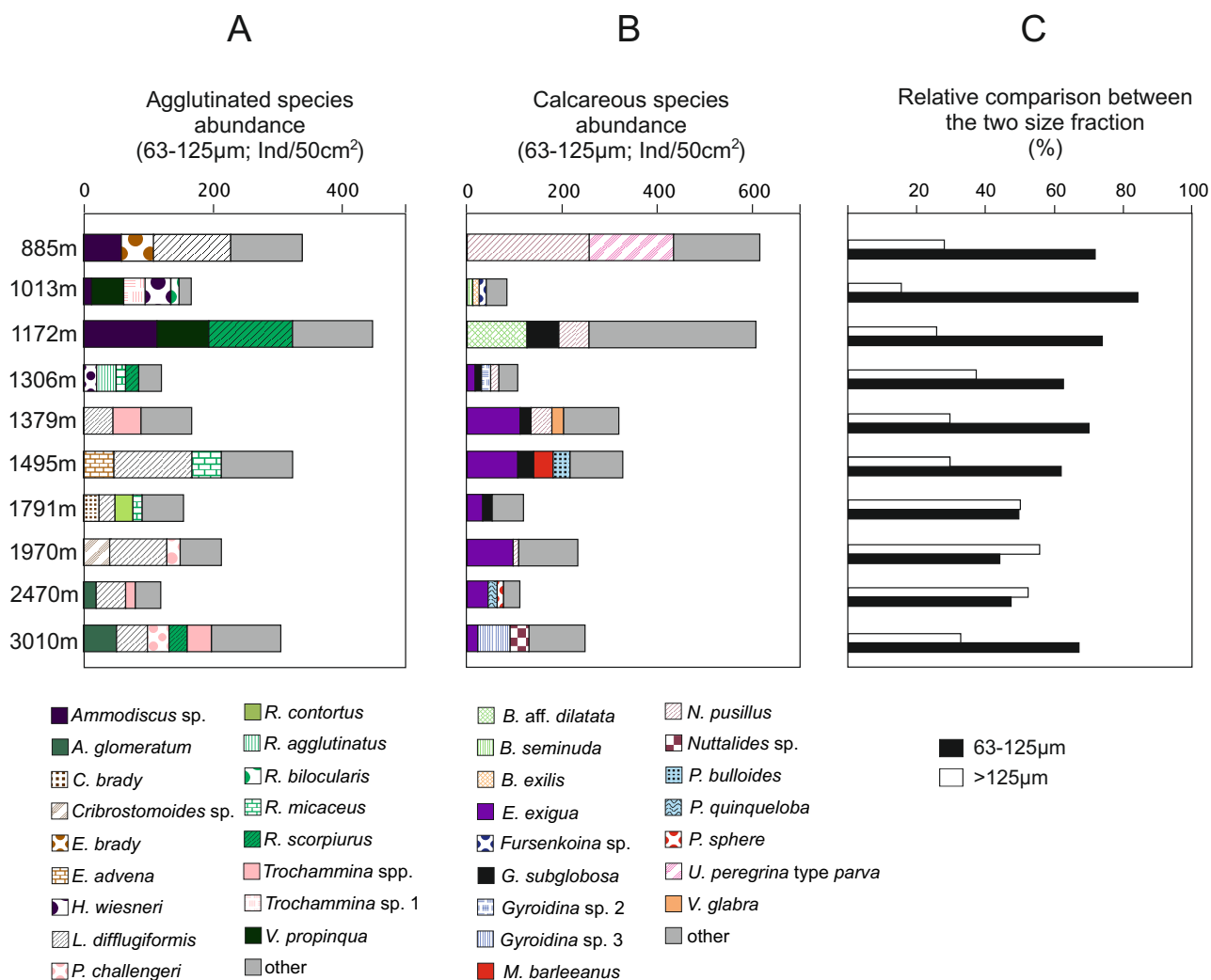


Fig. 5. (A) Species composition and abundance (ind/50 cm³) in the 63–125 µm fraction for the upper centimetre of the sediment for agglutinated species (> 5 %). (B) Species composition and abundance (ind/50 cm³) in the 63–125 µm fraction for the upper centimetre of the sediment for calcareous species (> 5 %). (C) Relative contribution of the two size fractions (63–125 µm and > 125 µm) to the foraminiferal faunas in the 0–1 cm level.

and *Reophax bilocularis* were also abundant in the 63–125 µm fraction. As in the larger size classes, many OMZ taxa were either restricted to these sites, or occurred only in very low abundances at deeper sites.

In the lower part of the OMZ, small hyaline species: *Gyroidina* sp. 2, *Bolivina* aff. *B. dilatata*, *Bolivina* sp. 1, *Nuttallides pusillus*, *Gavelinopsis translucens* and *Epistominella exigua* were abundant. In addition, as in the > 125 µm fraction, *Reophax* species were common at these sites (Fig. 5).

The foraminiferal assemblages at the dysoxic site (1495 m) and in the oxic zone (1791 to 3010 m) revealed high abundances of *Epistominella exigua*, *Globocassidulina subglobosa*, *Nuttallides* sp. 1, *Uvigerina peregrina*, *Melonis barleeanus*, *Pullenia* spp., *Reophax* spp. and *Cribr stomoides* spp. (Fig. 5). Of these taxa, only *Nuttallides* sp. 1 was largely restricted to the 63–125 µm fraction; other

taxa were also found in abundance in the > 125 µm fraction. At the deepest and best ventilated sites (1970 and 2470 m depth), *Pyrgo murrhina*, *Pyrgoella sphaera* and *Pyrgo lucernula* were the best represented miliolid taxa (Fig. 5).

3.4 Foraminiferal assemblages and relation to environmental parameters: statistical analysis (PCA and CCA)

Our principal component analysis (PCA) was based on the relative abundances of the dominant species (> 2 %) in the > 125 µm (0–10 cm) size fraction (Fig. 6a). Axis 1 explains ~ 30 % and axis 2–16 % of the total variance. Three faunal groups were clearly identified in the PCA analysis (Fig. 6a). Group 1 was characterized by species living in the core and lower part of the OMZ (Figs. 4 and 6). Group 2 mainly

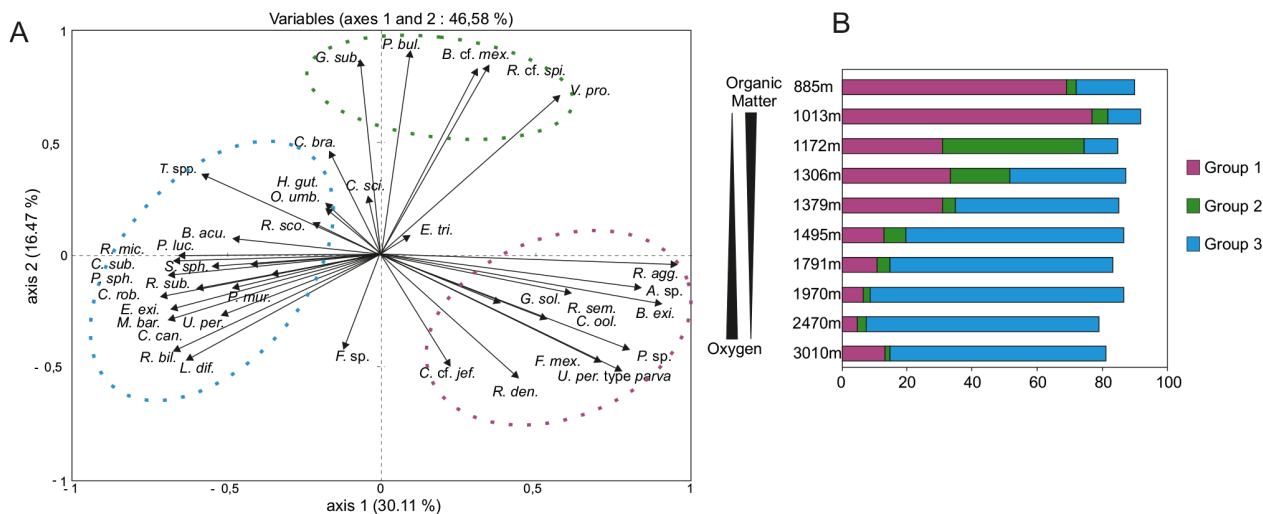


Fig. 6. (a) PCA plot based on the relative abundances of the dominant species (> 2 % in at least one station) for the entire core (0–10 cm) in the > 125 µm size fraction. (b) Plot of the percentages of the three defined groups at the various sites.

Abbreviations: Group 1: *Ammodiscus* sp. (*A. sp.*), *Bulimina exilis* (*B. exi.*), *Chilostomella oolina* (*C. ool.*), *Cribrostomoides cf. jeffreysii* (*C. cf. jef.*), *Fursenkoina Mexicana* (*F. mex.*), *Gyroidina soldanii* (*G. sol.*), *Praeglobobuliminasp.* (*P. sp.*), *Reophax agglutinans* (*R. agg.*), *Reophax dentaliniformis* (*R. den.*), *Rotaliatinopsis semiinvoluta* (*R. sem.*), *Uvigerina peregrina type parva* (*U. per. type parva*). Group 2: *Bulimina cf. mexicana* (*B. cf. mex.*), *Cribrostomoides brady* (*C. bra.*), *Cribrostomoides scitulum* (*C. sci.*), *Ehrenbergina trigona* (*E. tri.*), *Globocassidulina subglobosa* (*G. sub.*), *Pullenia bulloides* (*P. bul.*), *Reophax cf. spiculifer* (*R. cf. spi.*), *Verneuilinella propinqua* (*V. pro.*). Group 3: *Bulimina aculeata* (*B. acu.*), *Cibidoides robertsonianus* (*C. rob.*), *Cribrostomoides subglobosus* (*C. sub.*), *Cyclammina cancellata* (*C. can.*), *Epistominella exigua* (*E. exi.*), *Hormosina guttifera* (*H. gut.*), *Lagenammina difflugiformis* (*L. dif.*), *Melonis barleeanus* (*M. bar.*), *Oridorsalis umbonatus* (*O. umb.*), *Pyrgo lucernula* (*P. luc.*), *Pyrgo murrhina* (*P. mur.*), *Pyrgoella sphaera* (*P. sph.*), *Reophax bilocularis* (*R. bil.*), *Reophax micaceus* (*R. mic.*), *Reophax scorpiurus* (*R. sco.*), *Reophax subfusiformis* (*R. sub.*), *Saccamina sphaerica* (*S. sph.*), *Trochammina* spp. (*T. spp.*), *Uvigerina peregrina* (*U. per.*).

Table 1. Canonical correspondence analysis factor with the three groups defined by PCA and environmental components. The abbreviation OC refers to organic carbon, Chl *a* to chlorophyll *a* concentration, BWO to bottom water oxygenation.

	Axis 1	Axis 2	Axis 3	Axis 4
Group 1	−0.863	−0.370	0.161	−0.297
Group 2	−0.423	0.827	0.349	0.124
Group 3	−0.909	−0.079	−0.343	0.179
Depth (m)	−0.935	−0.112	0.304	0.068
BWO (µM)	−0.940	−0.152	0.122	0.165
Chl <i>a</i> (µg g ^{−1})	−0.775	−0.380	0.245	0.375
OC (wt %)	−0.930	−0.240	0.240	0.143
Oxygen	−0.907	−0.192	0.301	−0.064
penetration depth (cm)				
Nitrate	−0.656	−0.008	0.521	−0.158
penetration depth (cm)				

consisted of species present in the lower part of the OMZ and in the dysoxic zone (Fig. 6a). Finally, group 3 contained species dominating the faunas at the deeper, oxic sites. A second PCA analysis was performed on the basis of the relative

abundance data of dominant species in the > 63 µm fraction (0–1 cm). As in the PCA presented above, three very similar groups were obtained (see Appendix C in Supplement), with only few changes in species composition (e.g. *Nuttallides pusillus*, *Bolivina* spp.) compared to the first PCA. Due to the similarity of the two PCA analyses, only the PCA based on the > 125 µm size will be discussed further. We assume this one is more robust as it is based on the complete cores with foraminifera analysed down to 10 cm depth in sediment. Moreover, most paleoceanographic studies are based on the > 125 µm fraction.

We consider that species groups 1, 2 and 3 each contain a number of taxa with rather similar ecological requirements, which therefore can be lumped together. Subsequently, CCA was performed on the geochemical data (depth, BWO, OC, oxygen and nitrate penetration depth) and on the cumulative percentages of these three species groups (Fig. 7 and Table 1). CCA axis 1 explains 72.91 % of the variance and axis 2 12.92 % of the total variance. As could be expected, groups 1 and 3 were strongly correlated with the measured environmental parameters and plot on opposite sides of axis 1 (Table 1). Group 1 was associated with high Chl *a* concentration and the organic carbon content whereas group 3 was linked to high oxygen concentration (BWO and oxygen penetration

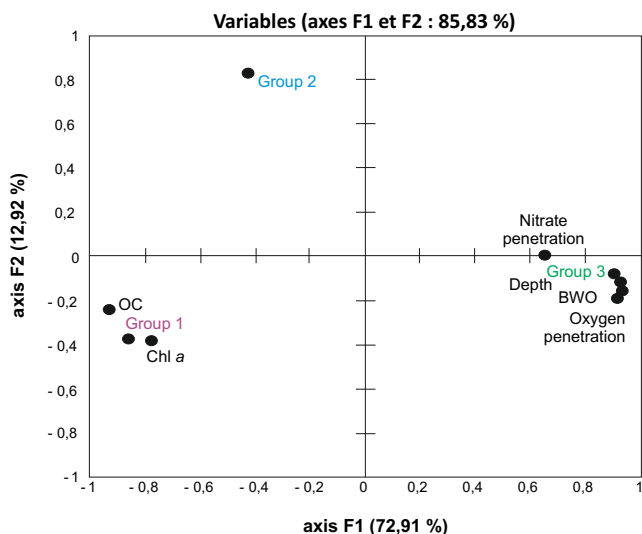


Fig. 7. CCA of the groups defined by PCA with the environmental parameters: bottom water oxygenation (BWO), chlorophyll *a* concentration (Chl *a*), amount of the organic carbon (OC), oxygen and nitrate penetration depth (cm) into the sediment.

depth). Inversely, the bathymetrically intermediate group 2 did not show significant correlations with any of the environmental parameters (Fig. 7), and plots on the positive side of axis 2 (Table 1), which does not display significant correlations with the measured environmental parameters (Table 1 and Fig. 7).

4 Discussion

4.1 Live benthic foraminiferal (Rose Bengal stained) abundances

Although food availability is generally considered as the main ecological parameter controlling the foraminiferal distribution and abundance at continental margin settings (e.g. Jorissen et al., 1995, 2007; Koho, 2008), the standing stocks of foraminifera on the Murray Ridge, sampled during the winter monsoon (January 2009), which is a period of high biological productivity (e.g. Caron and Dennett, 1999; Rixen et al., 2000), did not demonstrate a clear link with the organic carbon content, Chl *a*, or any other measured environmental parameter, such as BWO or water depth (Figs. 2 and 3). This observation is in contrast with previous studies on the Arabian Sea OMZ, where a decrease in foraminiferal abundance with water depth was observed (Jannink et al., 1998; Schumacher et al., 2007; Fig. 7). Since these earlier studies presented very few environmental parameters, a direct comparison of foraminiferal abundances can only be made on the basis of water depth and/or bottom water oxygen concentration, but not on the basis of the quality and quantity of sedimentary organic carbon, which are supposed to be the

predominant controlling parameters. Due to the high seasonality of the Arabian Sea monsoonal system, many important environmental parameters (BWO, organic matter quality and quantity, oxygen and nitrate penetration depth) may show important seasonal variability. Consequently, it is highly reductive to base a comparison of the living benthic (Rose Bengal stained) foraminiferal abundances between sites on water depth and/or water column oxygen concentration.

The study of Schumacher et al. (2007) was performed on the continental margin off Pakistan during the spring intermonsoon (March–April 2003) from 136 m to 1870 m depth. When comparing sites with similar water depths, higher faunal densities are found in our study (Fig. 7). The opposite could be expected, since sea surface Chl *a* content and BWO were higher at the continental margin sites off Pakistan in March–April 2003 (Fig. 7; Schumacher et al., 2007) than at our sites in January 2009 ($\sim 1\text{--}2.5\text{ mg m}^{-3}$ vs. $0.7\text{--}1\text{ mg m}^{-3}$ at our sites (data from http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month). The study of Jannink et al. (1998) investigated two transects (from 500 to 2000 m depth) from the Pakistan margin (fall intermonsoon, October 1992), which showed a large (4-fold) difference in foraminiferal abundance (Fig. 7) with much higher foraminiferal standing stocks on transect II. The authors tentatively explained this difference being due to a three-week time lag between the two samplings. Short-term variation of primary production and export production could have led to much higher phytodetritus supplies to the seafloor prior to the sampling of transect II. Our foraminiferal abundances, representing the productive conditions of the winter monsoon (January 2009), were fairly similar to those described by Jannink et al. (1998) for their poorer transect I (Fig. 7). Kurbjewit et al. (2000) compared six sites (from 1916 to 4425 m) across the Arabian Sea during the fall intermonsoon (September/October 1995). Only two sites are comparable with our stations (~ 1916 and ~ 3100 m), where similar foraminiferal abundances were observed (Fig. 7).

If the finer-size fraction (63–125 μm , first cm only) is included in the comparison, foraminiferal standing stocks increase considerably (Fig. 3b). Small-sized foraminifera accounted for up to 72 % of the total assemblage at the OMZ sites, whereas at most deeper sites they only accounted for about 50 % (Fig. 5). Similar observations have been made for the Pakistan margin of the Arabian Sea OMZ (Jannink et al., 1998; Larkin and Gooday, 2009). The dominance of small-size foraminifera may be a consequence of the intermittent character of major phytodetritus falls, which mainly concern the shallower sites, likely favouring more opportunistic small-sized taxa (e.g. Fontanier et al., 2005). However, their dominance could also be indicative of a larger tolerance to extreme low-oxygen conditions. Bradshaw (1961) and Geslin et al. (2011) demonstrated a linear relationship between test size and oxygen respiration rates, suggesting that smaller (63–125 μm) foraminiferal species could be relatively advantaged by strongly oxygen-depleted waters.

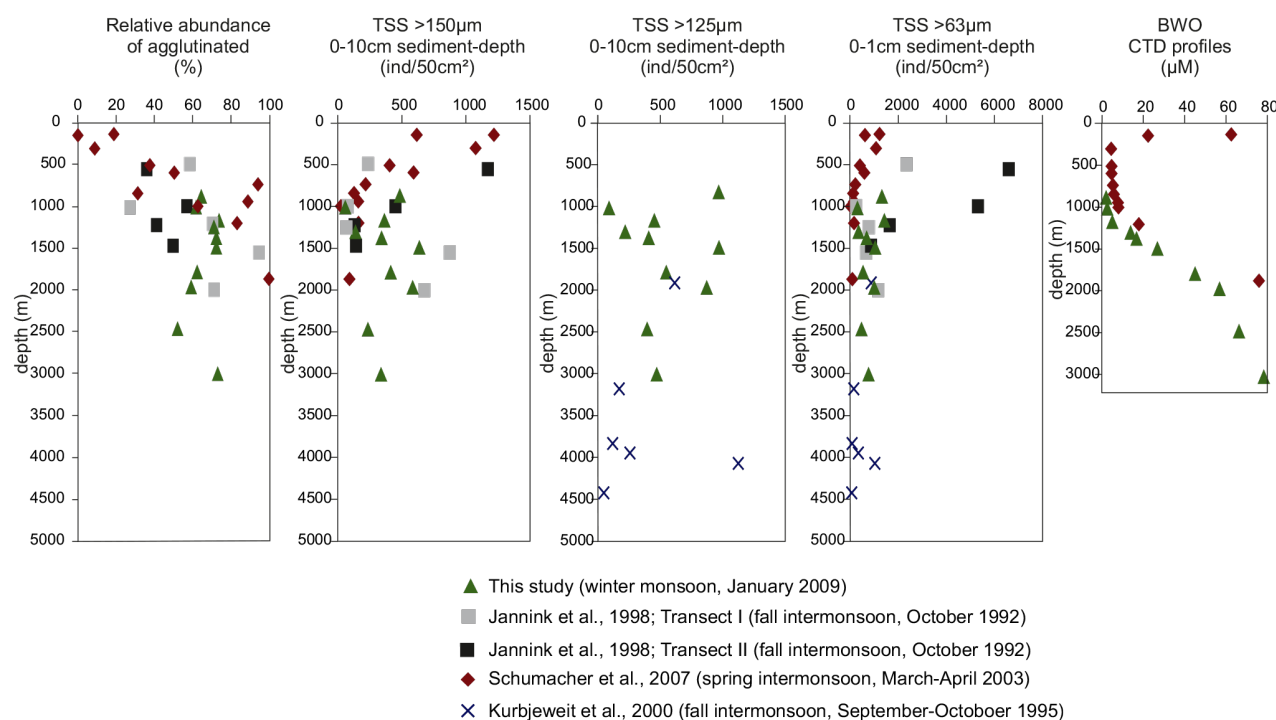


Fig. 8. Comparison of relative abundance of agglutinated faunas, foraminiferal abundances (ind/50 cm²) and BWO between our data and previous studies on the Arabian Sea (Jannink et al., 1998; Kurbjeweit et al., 2000; Schumacher et al., 2007). Note the scale difference.

4.2 Foraminiferal diversity

Unlike foraminiferal abundances, diversity parameters showed clear trends along the studied transect (Fig. 3). Within the OMZ, diversity is lower than at deeper, more ventilated sites, which is in agreement with previous studies in the area (Jannink et al., 1998; Schumacher et al., 2007; Gooday et al., 2009) and in the Peruvian OMZ (e.g. Cardich et al., 2012; Mallon et al., 2012).

Diversity minima are often linked to highly variable and/or stressful environmental conditions (intermediate disturbance hypothesis; e.g. Wilkinson, 1999). The lower diversity of foraminiferal faunas in the OMZ is very likely the result of the disappearance of species sensitive to very low oxygen concentrations. Although most benthic foraminifera are supposed to be insensitive to low BWO down to at least 50 µM ($\sim 1 \text{ mL L}^{-1}$) (Jorissen et al., 2007), the very low concentrations in the core of the OMZ are probably beyond the tolerance levels of many species and favour the development of specialized species assemblages highly tolerant to very low BWO. This is coherent with the hypothesis of Levin and Gage (1998) who suggest that species richness is mainly controlled by low oxygen. Additionally, low diversity indices in the central and lower part of the OMZ may be reinforced by important (and highly intermittent) organic matter supplies, which would favour the dominant opportunistic taxa at the expense of less frequent K-selected taxa.

4.3 Dominance of agglutinated species along the study transect

The ecological preferences of agglutinated foraminifera are still not well understood. Previous studies on agglutinated foraminifera have suggested that in general, agglutinated foraminifera are less tolerant to low-oxygen conditions than calcareous foraminifera (Moodley et al., 1997; Gooday et al., 2000, 2001, 2009; Neira et al., 2001). However, the strong dominance of agglutinated species at all stations of our BWO gradient suggests the contrary; they appear to be just as tolerant of strongly oxygen-depleted conditions as calcareous taxa.

The high proportion of agglutinated species (between 52 and 72 %) along the whole transect seems independent of the BWO or the organic carbon content (Fig. 8). Some agglutinated taxa (mainly *Reophax* spp. and *Lagenammina difflugiformis*) are present at all stations. Earlier studies on the Arabian Sea confirm this strong dominance of agglutinated foraminifera at sites deeper than 1200 m (e.g. Kurbjeweit et al., 2000; Schumacher et al., 2007). For instance, Kurbjeweit et al. (2000) described a dominance of agglutinated species at their deepest sites (1916 to 4425 m), coinciding with our deepest stations (1970 to 3010 m), and also Schumacher et al. (2007) recorded very high proportions of agglutinated taxa at their deepest sites (738 to 1870 m; Fig. 8).

It is interesting to note that from 200 to about 1000 m depths, the data of Jannink et al. (1998), and especially of Schumacher et al. (2007), show a clear increase in the percentage of agglutinated taxa. Only below 1000 m do agglutinated species become dominant, and no further trend is visible. This confirms earlier suggestions that calcareous taxa are strongly favoured by abundant supplies of fresh phytodetritus, whereas agglutinated species are less dependent on fresh food input (e.g. Koho, 2008; Phipps, 2012a). In the case of the Arabian Sea, it would also suggest that below 1200 m depth, the amount of labile organic matter arriving at the seafloor decreases substantially. This is confirmed by the Chl *a* data along our transect (Koho et al., 2013).

4.4 What controls species succession along the study transect? Oxygen versus food quantity and quality

We identified three faunal groups by PCA analysis (Fig. 6). These three groups are very distinct in their faunal composition, and present a clear succession along the oxygen and depth transect. Species from group 1 are mainly concentrated in the OMZ and more particularly in the core of the OMZ. This group is strongly correlated with Chl *a* and organic carbon content (Fig. 7 and Table 1). On the contrary, group 3 is present at deeper sites where the BWO and the oxygen penetration depth are higher and where fresh phytodetritus is probably scarce (low Chl *a* values, Fig. 2). An interesting question is what are the ecological requirements of the species of group 2 (Figs. 6 and 7), which are mainly found at 1172 m and 1379 m at the lower boundary of the OMZ. In the canonical correspondence analysis, no correlations have been found between group 2 and the geochemical data. It appears that this group represents a transitional community able to flourish where intermediate conditions are not optimal for taxa of the other two groups, neither for OMZ taxa nor for “oxic” taxa.

In the following three paragraphs, we will discuss the ecology of the dominant taxa of each of these three groups in detail.

4.4.1 OMZ taxa: high food quality availability vs. low-oxygen condition

The OMZ taxa are mainly composed of hyaline species, which were exclusively found in the core of the OMZ (*Bulimina exilis*, *Uvigerina peregrina* type *parva*, *Rotaliatinopsis semiinvoluta*, *Praeglobobulimina* sp. and *Fursenkoina* sp.) (Fig. 6). However, also some agglutinated species belong to this group (*Reophax agglutinans*, *Reophax dentaliniformis*, *Cribr stomoides* cf. *jeffreysii* and *Ammodiscus* sp.). Most of these OMZ taxa were found in the two first cm of the sediment, with a density maximum in the 0.5–1.5 cm interval, roughly corresponding to the depth of maximum nitrate penetration (Fig. 4). However, the very similar composition of the three upper half cm samples, with an absence of exclu-

sively infaunal taxa, suggests that the surface minimum could be an artefact due to the very soupy nature of the superficial sediment, which made it impossible to sample the first half centimetre very precisely.

Among the agglutinated taxa, only two species are restricted to the OMZ: *Ammodiscus* sp. and *Cribr stomoides* cf. *jeffreysii* (Fig. 4). *Cribr stomoides* cf. *jeffreysii* has also been described by Maas (2000) and Schumacher et al. (2007) in the core of the OMZ. The presence of *Ammodiscus* sp. in the OMZ is consistent with previous observations from the Arabian Sea (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007), which characterized this taxon as highly tolerant to low-oxygen conditions and feeding on fresh organic matter. *Ammodiscus* sp. was described as *A. cretaceous* from 233 to 902 m water depth by Maas (2000).

Reophax agglutinans was present along the whole depth transect, but in the PCA analysis was merged with the OMZ taxa. At the OMZ sites, *R. agglutinans* was living in the two first cm of the sediment, partly below the limit of nitrate penetration. Very similar observations were made for *Reophax dentaliniformis*. The fact that these taxa appear along the whole depth transect suggests that they are less dependent on the availability of labile organic matter than other species characterizing the core of the OMZ.

Generally, calcareous taxa presented a much clearer bathymetrical species succession than agglutinated ones (Fig. 4) and therefore appear to be more sensitive to the ecological parameters changing along the depth transect (e.g. BWO and organic matter quantity and quality). Our observations suggest that some of the hyaline species are very tolerant to low oxygen conditions. *Bulimina exilis* is one of the most common species encountered in the core of the OMZ from the northeastern Arabian Sea (Jannink et al., 1998; Schumacher et al., 2007; Larkin and Gooday, 2009). Previous studies demonstrated that this taxon thrives under conditions of high input of relatively fresh phytodetritus (Caralp, 1989; Jannink et al., 1998) and is able to survive in very oxygen-restricted environments (e.g. Jannink et al., 1998; Mass, 2000). *Bulimina exilis* is also a common species of high productivity and/or low-oxygen environments in the OMZ of SW Africa (Schmiedl et al., 1997) and off Cape Blanc (Morigi et al., 2001). In a record of the Younger Drias off northwest Africa, Filipsson et al. (2011) interpret high percentages of *B. exilis* as indicative of low dissolved oxygen concentration of the bottom water in combination with high labile organic matter input. The intermediate to deep infaunal microhabitat (Fig. 4) of *B. exilis* corroborates its strong tolerance of low-oxygen concentrations (Jorissen et al., 1998).

Another common species of this group is *Rotaliatinopsis semiinvoluta*, which occurs only at the 885 and 1172 m stations. Our data confirm previous findings of *R. semiinvoluta* in the Arabian Sea (Jannink et al., 1998) and suggest that this species is an endemic species in the OMZ of the Arabian Sea, adapted to live under very low oxygen conditions, and favoured by a strong and intermittent flux of fresh organic

matter. In a paleoceanographic study of the Arabian Sea, den Dulk et al. (1998) suggested that *R. semiinvoluta* may rapidly respond to changes in BWO, occurring at the base of the OMZ where it could thrive seasonally. *Praeglobobulimina* sp. is also only present at the 885 and 1013 m sites. This taxon is similar to the one described by den Dulk et al. (2000), Maas (2000) and Schumacher et al. (2007). Likewise, in these studies, *Praeglobobulimina* sp. is restricted to the core of the OMZ. It appears therefore that it is adapted to the very low oxygen conditions and may need relatively fresh organic matter.

Uvigerina peregrina inhabits a wide range of continental slope environments, including relatively low oxygen settings (e.g. Jannink et al., 1998; Maas, 2000; Schumacher et al., 2007) but also relatively well-ventilated sites (e.g. Fontanier et al., 2005; Koho, 2008; Mojtahid et al., 2010). It abounds in regions with relatively highly organic matter content (e.g. Lutze and Colbourn, 1984; Hermelin and Shimmield, 1990; Schmiedl and Mackensen, 1997) but also in areas with more moderate organic matter enrichment (e.g. Fontanier et al., 2005; Mojtahid et al., 2010). It has been described previously as a dominant faunal element in the Arabian Sea OMZ (e.g. Hermelin and Shimmield, 1990; Jannink et al., 1998; Gooday et al., 2000; Schumacher et al., 2007). In this study, we observed two different morphotypes of *U. peregrina* (Fig. 9). Specimens found in the core of the OMZ are somewhat smaller, smoother and have weakly developed lower costae. They correspond to *U. peregrina* forma *parva* of Lutze (1986) (Fig. 9, 3–4). At deeper sites, specimens have larger and higher costae and become more spinose (Fig. 9, 1–2). These specimens present morphotypes ranging from typical *U. peregrina* (*U. peregrina* s.s.) to *U. auberiana* (d'Orbigny, 1839) (fully spinose specimens). A similar morphological variation in *U. peregrina* has been noted in the eastern Atlantic (e.g. Lutze, 1986; Schönfeld, 2006; Koho, 2008; Gooday and Jorissen, 2012). *Uvigerina peregrina* forma *parva* and *U. peregrina* s.s. do not occur together. *Uvigerina peregrina* forma *parva* is only present in the core of the OMZ where BWO is very low and where food availability is probably much higher, whereas *U. peregrina* s.s. occurs from 1306 to 2407 m (Fig. 4). Because most of the deeper sites show a continuous variability from *U. peregrina* s.s. to *U. auberiana*, these two taxa have been counted together (as *U. peregrina*). They appear to be indicative of slightly higher BWO and somewhat less abundant organic matter supplies.

The presence of these species of this group in almost anoxic conditions at the sediment–water interface and within the superficial sediment could be related to an eventual facultative anaerobic metabolism. It is possible that in the absence of oxygen, these taxa are able to shift to nitrate reduction. It has been demonstrated recently that many foraminiferal species accumulate intracellular nitrate in low-oxygen settings (Piña-Ochoa et al., 2009). However, until now, nitrate respiration has only been shown for a limited number of

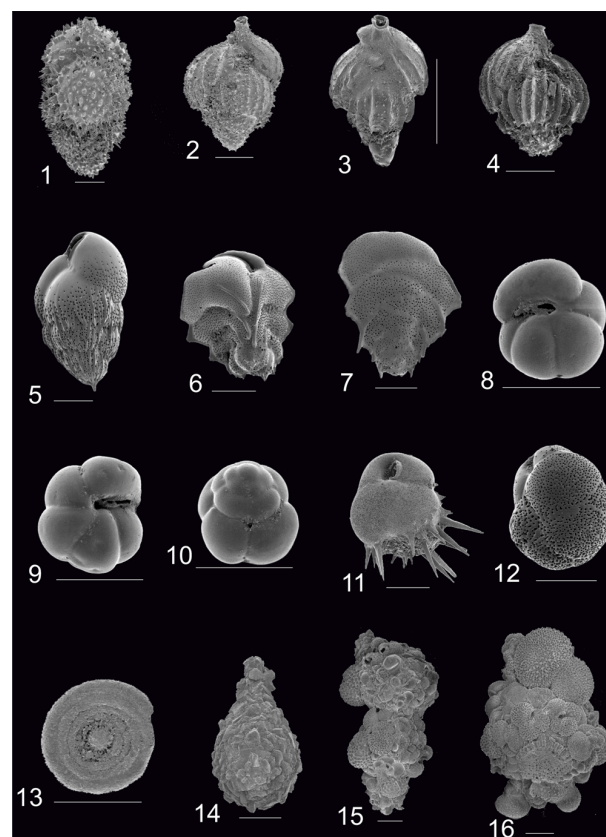


Fig. 9. SEM pictures of the main foraminiferal taxa. Scale bar = 100 μ m.

- 1: *Uvigerina auberiana* d'Orbigny, 1839, PA8 (1–1.5 cm), > 150 μ m. Regrouped with *Uvigerina peregrina* s.s. under *U. peregrina*.
- 2: *Uvigerina peregrina* s.s. Cushman, 1923, PA8 (1–1.5 cm), > 150 μ m.
- 3–4: *Uvigerina peregrina* type *parva* Lutze, 1986, PA1 (1–1.5 cm), 3: 63–125 μ m, 4: > 150 μ m.
- 5: *Praeglobobulimina* sp., PA1 (1–1.5 cm), > 150 μ m.
- 6–7: *Ehrenbergina trigona* Goës, 1896, PA4 (0–0.5 cm), > 150 μ m.
- 8–10: *Rotaliatinopsis semiinvoluta* (Germeaad, 1946), PA1 (1–1.5 cm), 63–125 μ m.
- 11: *Bulimina aculeata* d'Orbigny, 1826, PA8 (1–1.5 cm), > 150 μ m.
- 12: *Globocassidulina subglobosa* (Brady, 1881), PA3 (0–0.5 cm), > 150 μ m.
- 13: *Ammodiscus* sp., PA2 (0–0.5 cm), > 150 μ m.
- 14: *Lagenammina difflugiformis* (Brady, 1879), PA8 (0–0.5 cm), > 150 μ m.
- 15–16: *Reophax agglutinans* Cushman, 1913, PA8 (0–0.5 cm), > 150 μ m.

taxa (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010; Koho et al., 2011). Unfortunately, to date, no measurements of denitrification rates have been performed for the dominant species of the Arabian Sea OMZ. Therefore, the possibility

of an anaerobic metabolism of some of the dominant OMZ taxa remains speculative.

4.4.2 Lower OMZ: transitional assemblages between the OMZ core and oxic conditions

Conspicuous faunal elements of the lower OMZ (1172–1379 m) are *Bulimina* cf. *mexicana*, *Pullenia bulloides* (both at 1172 m), *Reophax* cf. *spiculifer*, *Verneuilinulla propinqua*, *Globocassidulina subglobosa* (all three at 1172 and 1306 m) and *Ehrenbergina trigona* (1306 and 1379 m). Highest abundances of these taxa were found in the first cm of the sediment, although living (Rose Bengal stained) foraminiferal were present in fair numbers down to 2 to 5 cm depth. This maximum microhabitat depth roughly corresponded to the maximum depth of nitrate penetration (2.5 to 3.5 cm).

Most of these species have been described in the literature as tolerant to relatively low oxygen conditions (e.g. den Dulk et al., 1998, 2000; Jannink et al., 1998; Schumacher et al., 2007). *Globocassidulina subglobosa* is a major species in the lower part of the OMZ, although it is also found in small numbers at deeper sites. *Globocassidulina subglobosa* is known to have a cosmopolitan character; it is found in the Atlantic Ocean (Gofas, 1978; Weston, 1982; Murray et al., 1986), in the central Pacific (Gofas, 1978) and in the Indian Ocean (Lagoe, 1977; Corliss, 1983b; Peterson, 1984). Its presence in the small fraction at our deepest sites can be explained by its opportunistic behaviour: rapid colonization of episodic fresh phytodetritus (Jorissen et al., 2007 and references therein). The environmental preferences of *Ehrenbergina trigona* are poorly known. Its presence in the lower part of the OMZ is consistent with the observations of Hermelin and Shimmield (1990), who found this species at mid bathyal depths (770, 955 and 1048 m) within and below the core of the OMZ. These authors suggested that *E. trigona* could be an endemic species to the Arabian Sea OMZ environment. However, *E. trigona* has been reported from a variety of oceans, including the Pacific Ocean (Jones, 1994), the Atlantic Ocean (Lohmann, 1978; Mackensen et al., 1995) and the southeast Indian Ocean (Corliss, 1979). In the Arabian Sea, this species can be used as an indicator species for the lower part of the OMZ, which could make it a useful proxy for the past variability of the base of the OMZ.

Little is known about ecological preferences of agglutinated species in this group (*Reophax* cf. *spiculifer*, *Verneuilinulla propinqua*). On the basis of our data, it appears that these species are tolerant to relatively low oxygen conditions, still with elevated levels of organic supplies.

In the canonical correspondence analyses, group 2, representing the lower OMZ taxa, does not correlate with the environmental parameters (e.g. BWO, OC, Chl *a*). The main question is what precise environmental parameters favour this assemblage. In many aspects, the lower OMZ is characterized by transitional conditions: increasing BWO and decreased organic matter quantity and quality (Figs. 2, 6 and 7).

It is interesting to note that group 2 is mainly composed of cosmopolitan species, whereas group 1 contains some specialized taxa of the core of the OMZ, which may be endemic in the Indian Ocean (e.g. *Rotaliatinopsis semiinvoluta*, *Praeglobobulimina* sp., *Ammodiscus* sp.). This suggests that the cosmopolitan taxa of group 2 could adapt to the moderately oxygen-poor and food-enriched conditions found at the lower part of the OMZ, but not to the far, more extreme conditions reigning in the core of the OMZ, where some endemic species have evolved a higher tolerance to these adverse conditions, leading to a clear competitive advantage over the species of group 2.

4.4.3 Below the OMZ: higher bottom water oxygenation vs. lower organic matter quantity and quality

A diverse foraminiferal assemblage, including miliolids, hyaline and agglutinated species (Fig. 6), were found at all deeper sites, with BWO > 26 μM $\mu\text{mol L}^{-1}$. At these sites, organic matter availability was lower, as indicated by the lower Chl *a* and organic carbon contents (Fig. 2).

At these sites (1495 to 3010 m), highest foraminiferal abundances were found in the first cm of the sediment, although substantial numbers of living foraminifera were present until 8 to 10 cm depth, much deeper than maximal oxygen and nitrate penetration. Only at the deepest site (3010 m), living foraminifera became very scarce below 3 cm, well above the nitrate penetration depth.

The third group defined by the PCA analysis was mainly dominated by agglutinated species such as *Lagenammmina difflugiformis*, *Reophax micaceus*, *Hormosina guttifera*, *Reophax subfusiformis* and *Trochammina* spp. A high proportion of agglutinated species in deeper waters is usually attributed to increasingly oligotrophic conditions, resulting from diminished organic matter quantity and quality (e.g. Ohga and Kitazato, 1997; Schmiedl et al., 1997; Kurbjeweit et al., 2000; Koho, 2008; Phipps et al., 2012). In the sediment, the distribution of agglutinated taxa did not seem to be controlled by geochemical limits (Fig. 4). Also, their vertical distribution in the sediment appeared to be independent of oxygen and nitrate penetration depth (Fig. 4). Phipps (2012) suggested that most agglutinated taxa have lower trophic requirements than calcareous taxa, which would enable them to live in deeper, more food-limited sediment layers. This is corroborated by our data. Additionally, some authors suggested that agglutinated species would prefer living deeper in the sediment to avoid competition with calcareous species (e.g. Buzas et al., 1989; Van der Zwaan et al., 1999; Gooday, 2003; Phipps, 2012).

The assemblage of group 3 also contained some hyaline taxa, the most common ones being *Bulimina aculeata*, *Oridorsalis umbonatus*, *Melonis barleeanus*, *Epistominella exigua* and *Uvigerina peregrina*. The presence of *Bulimina aculeata* below the OMZ is consistent with previous studies

of the Arabian Sea (e.g. Zobel, 1973; Jannink et al., 1998). *Oridorsalis umbonatus* has been observed in various well-oxygenated environments. Mackensen et al. (1995) related this species to environments with low food supply. Also, the conspicuous occurrence of the intermediate infaunal taxon *Melonis barleeanus* suggests a relative dominance of less labile organic matter (Caralp, 1989; Koho et al., 2013). Moreover, *M. barleeanus* appears in fairly high numbers in intermediate infaunal microhabitats at all stations from 1379 to 3010 m depth. Its microhabitat depth mimics the oxygen penetration depth, and gradually deepens from 0 to 1 cm at 1379 m, 0.5–1 to 3 cm at 1791 and 1970 m, and 2 to 3 cm at 3010 m depth. The occurrence of *M. barleeanus* partly below the oxygen penetration depth and above the nitrate penetration depth is consistent with numerous previous studies (e.g. Corliss, 1979; Jorissen et al., 1995, 1998; Koho, 2008; Mojtahid et al., 2010). It appears that this species is able to thrive in absence of oxygen as long as nitrate is present in the pore water. The presence of intermediate and deep infaunal taxa in anoxic sediments could be explained by a facultative anaerobic metabolism of the concerned species (e.g. Risgaard-Petersen et al., 2006).

Contrary to *Melonis barleeanus*, the presence of *Epistominella exigua* suggests episodic fresh phytodetritus reaching the seafloor (Gooday et al., 1996). *Epistominella exigua* is mainly present in the 63–125 μm size fraction (Fig. 5). The organic matter data suggest only small amounts of fresh organic matter (Chl *a* contents are very low, $\leq 0.5 \mu\text{g g}^{-1}$). However, the organic matter measurements represent a snapshot in time (during sampling) and do not exclude intermittent supplies of fresh phytodetritus at other periods of the year. Although our samples have been retrieved during the eutrophic winter monsoon (in January), maximum productivity and subsequent phytodetritus pulses would be expected during the SW or summer (and early fall) monsoon. The available numbers of *E. exigua* may represent a background population, which could respond by massive reproduction and growth to phytodetritus deposits.

In our data set, miliolids (*Pyrgo murrhina*, *Pyrgoella sphaera*, *Pyrgo lucernula*) were absent from the core and lower part of the OMZ, and are exclusively found in fair numbers below the OMZ. Similar observations have been made in other Arabian Sea studies (e.g. Jannink et al., 1998; den Dulk et al., 2000; Schumacher et al., 2007). In general, miliolids are rare or absent in oxygen-deficient environments (e.g. Mullineaux and Lohmann, 1981; Nolet and Corliss, 1990; Jorissen et al., 1995) strongly suggested that they are more sensitive to oxygen stress than other species. In a study of two piston cores collected from 920 and 1470 m, Den Dulk et al. (2000) suggested that a high abundance of miliolids could reflect periods of periodically increased BWO. Furthermore, Den Dulk et al. (2000) speculated that the percentage of miliolids could be a robust proxy for reconstructing past changes in bottom and pore water oxygenation. However, miliolid tests, which are composed of high magnesium

calcite, are more sensitive to alkalinity and pH changes of the bottom water. Acidic bottom waters, such as those present in the OMZ, potentially could result in the loss of their shells from the fossil record.

5 Conclusions

Live foraminiferal faunas (Rose Bengal stained) from the northern Arabian Sea OMZ were studied in order to determine the links between foraminiferal community and environmental parameters (e.g. BWO, Chl *a*, OC, oxygen and nitrate penetration depth).

On a transect from the core of the OMZ to 3000 m water depth on the Murray Ridge, foraminiferal abundances neither show a clear bathymetrical gradient nor a correlation with any of the measured environmental parameters. The standing stocks appear to reflect a complex response to environmental parameters. Their comparison between different studies is strongly hampered by the fact that they may show a strong temporal variability, in response to intermittent phytodetritus fluxes. Conversely, diversity indices increase towards greater water depth (and increasing BWO), with lower diversity in the core of the OMZ and higher diversity below the OMZ. Only few species are well adapted to the extreme low BWO of the OMZ core, resulting in a lower diversity.

By means of statistical analyses (principal component and canonical correspondence analyses), we identified a succession of three well-separated foraminiferal assemblages along the bathymetrical transect. Evidently, these faunal groups show a strong correlation with the measured environmental parameters. These three groups, typical for the core of the OMZ, the lower OMZ and the zone below the OMZ, provide a framework for the reconstruction of past variability of the Arabian Sea OMZ:

1. Species inhabiting the core of the OMZ (e.g. *Rotaliatinopsis semiinvoluta*, *Bulimina exilis*) are indicative of high organic matter quality and quantity. In addition, they are adapted to very low oxygen conditions. It is probable that the diversity minimum, observed in the core of the OMZ, is due to the fact that bottom oxygen concentration ($\sim 2 \mu\text{M}$) is beyond the tolerance limits of most species found at deeper sites.
2. Species found in the lower part of the OMZ inhabit a transitional niche, with slightly higher oxygen concentration, less abundant organic supplies, and of a lower quality. Some species, which are largely restricted to this zone (*Ehrenbergina trigona*, *Globocassidulina subglobosa*), are precious markers for fluctuations of the bathymetrical position of the lower OMZ through time.
3. The group of species found at the “oxic” sites (BWO: 16–78 μM) is composed of cosmopolitan taxa, which

are less competitive under lower oxygen concentrations. Miliolids, which are restricted to this zone, appear to be excellent markers of oxygen concentrations $> 16 \mu\text{M}$.

Supplementary material related to this article is available online at <http://www.biogeosciences.net/11/1155/2014/bg-11-1155-2014-supplement.zip>.

Acknowledgements. Ship time on R/V *Pelagia* was provided by the PASOM project financed by the Netherlands Organization for Scientific Research (NWO; grant number 817.01.015). We are very grateful to the SCIAM laboratory for the foraminiferal SEM images. The second author acknowledges NWO-ALW (Earth and Life sciences council) for funding (grant number 820.01.011 to G. J. van der Zwaan).

Edited by: H. Kitazato



The publication of this article is financed by CNRS-INSU.

References

- Banase, K.: Seasonality of phytoplankton chlorophyll in the central and northern Arabian Sea, *Deep-Sea Res.*, 34, 713–723, 1987.
- Banase, K. and McClain, C. R.: Winter blooms of phytoplankton in the Arabian Sea as observed by the Coastal Zone Colour Scanner, *Mar. Ecol. Prog. Ser.* 34, 201–211, 1986.
- Barranguet, C., Kromkamp, J., and Peene, J.: Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos, *Mar. Ecol. Prog. Ser.*, 173, 117–126, 1998.
- Bernhard, J. M.: Postmortem Vital Staining in Benthic Foraminifera; Duration and Importance in Population and Distributional Studies, *J. Foraminif. Res.*, 18, 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, 2000.
- Bernhard, J. M. and Sen Gupta, B.: Foraminifera of oxygen-depleted environments, in: *Modern Foraminifera*, edited by: Sen Gupta, B., Kluwer Academic, Dordrecht, 200–216, 1999.
- 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*, 24, PA4210, doi:10.1029/2006PA001290, 2006.
- Berger W. H.: Planktonic foraminifera: Selective solution and lysocline, *Mar. Geol.*, 8, 111–138, 1970.
- Bradshaw, J. S.: Laboratory experiments on the ecology of foraminifera, *Contribution from the Cushman Foundation for Foraminiferal Research*, 12, 87–106, 1961.
- Burkill, P. H., Mantoura, R. F. C., and Owens, N. J. P.: Biogeochemical cycling in the northwestern Indian Ocean: a brief overview, *Deep-Sea Res. II*, 40, 643–649, 1993.
- Buzas, M. A., Collins, L. S., Richardson, S. L. and Severin, K. P.: Experiments on predation, substrate preference, and colonization of benthic foraminifera at the shelfbreak off the Ft. Pierce Inlet, Florida, *Journal of Foraminiferal Research*, 19, 146–152, 1989.
- Caralp, M. H.: Abundance of *Bulimina exilis* and *Melonis barleeanum*: relationship to the quality of organic matter, *Geo-Mar. Lett.*, 9, 37–43, 1989.
- Cardich, J., Morales, M., Quipuzcoa, L., Sifeddine, A., and Gutierrez, D.: Benthic foraminiferal communities and microhabitat selection on the continental shelf off central Peru, A.V. Altenbach et al. (eds), in: *Anoxia: Evidence for Eukaryote survival and paleontological Strategies, Cellular Origin, Life in Extreme Habitats and Astrobiology* 21, 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 Res. II*, 46, 1665–1690, 1999.
- Corliss, B. H.: Distribution of Holocene deep-sea benthonic foraminifera in the southwest Indian Ocean, *Deep-Sea Res.*, 30, 95–117, 1983b.
- Corliss, B. H.: Recent deep-sea benthonic foraminiferal distributions in the southeast Indian Ocean: inferred bottom-water routes and ecological implications, *Mar. Geol.*, 31, 115–138, 1979.
- Corliss, B. H. and Emmerson, S.: Distribution of Rose Bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine, *Deep-Sea Res.*, 37, 381–400, 1990.
- Cowie, G.: The biogeochemistry of Arabian Sea surficial sediments: A review of recent studies, *Progress in Oceanography*, 65, 260–289, 2005.
- 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, *Mar. Micropaleontol.*, 35, 43–66, 1998.
- Den Dulk, M., Reichart, G., van Heyst, S., Zachariasse, W., and Van der Zwaan, G.: Benthic foraminifera as proxies of organic matter flux and bottom water oxygenation? A case history from the northern Arabian Sea, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 161, 337–359, 2000.
- 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, 751–775, 2006.
- Filipsson, H. L., Romero, O. E., Stuut, J.-B. W., and Donner, B.: Relationships between primary productivity and bottom-water oxygenation off northwest Africa during the last deglaciation, *J. Quat. Sci.*, 26, 448–456, 2011.
- Fontanier, C., Jorissen, F. J., Chaillou, G., Anschutz, P., Grémare, A., and Griveaud, C.: Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay: Faunal response to focusing of refractory organic matter, *Deep-Sea Res. Pt. I*, 52, 1189–1227, 2005.

- Geslin, E., Risgaard-Petersen, N., Lombard, F., Metzger, E., Langellet, D., and Jorissen, F.: Oxygen respiration rates of benthic foraminifera as measured with oxygen microsensors, *J. Experim. Mar. Biol. Ecol.*, 396, 108–114, 2011.
- Gofas, S.: Une approche du paléoenvironnement océanique: les foraminifères benthiques calcaires traceurs de la circulation abyssale, Ph.D. thesis, University of Western Brittany, France, 1978.
- Gooday, A. J.: Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes, *Deep-Sea Res. I*, 43, 1395–1421, 1996.
- Gooday, A. J.: Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: a review of environmental influences on faunal characteristic, *Adv. Mar. Biol.*, 46, 1–90, 2003.
- Gooday, A. J. and Jorissen, F. J.: Benthic Foraminiferal Biogeography: Controls on Global Distribution Patterns in Deep-Water Settings, *Ann. Rev. of Mar. Sci.*, 4, 237–262, 2012.
- 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 Res. Pt. II*, 47, 25–54, 2000.
- Gooday, A. J., Kitazato, H., Hori, S., and Toyofuku, T.: Monothalamous Soft-Shellled Foraminifera at an Abyssal Site in the North Pacific: A Preliminary Report, *J. Oceanogr.*, 57, 377–384, 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 Res. Pt. II*, 56, 488–502, 2009.
- 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 Res.*, 40, 1323–1344, 1993.
- Hammer, Ø., Harper, D., and Ryan, P. D.: PAST: Palaeontological statistics software package for education and data analysis, *Palaeontol. Electr.*, 4, 1–9, 2001.
- Heinz, P. and Hemleben, C.: Regional and seasonal variations of recent benthic deep-sea foraminifera in the Arabian Sea, *Deep-Sea Res. Pt. I*, 50, 435–447, 2003.
- Heinz, P. and Hemleben, C.: Foraminiferal response to the North-east Monsoon in the western and southern Arabian Sea, *Marine Micropaleontology*, 58, 103–113, 2006.
- Helly, J. J. and Levin, L. A.: Global distribution of naturally occurring marine hypoxia on continental margins, *Deep-Sea Res. Pt. I*, 51, 1159–1168, 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, *Mar. Geol.*, 91, 1–29, 1990.
- 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, 1483–1513, 1998.
- Jones, R. W.: The Challenger Foraminifera, Oxford University Press, Oxford, New-York, Tokyo, 149 pp., 1994.
- Jorissen, F. J., de Stigter, H. C., and Widmark, J. G. V.: A conceptual model explaining benthic foraminiferal microhabitats, *Mar. Micropaleontol.*, 26, 3–15, 1995.
- Jorissen, F. J., Wittling, I., Peyrouquet, J. P., Rabouille, C., and Relexans, J. C.: Live benthic foraminiferal faunas off Cape Blanc, NW-Africa: Community structure and microhabitats, *Deep-Sea Res. Pt. I*, 45, 2157–2188, 1998.
- Jorissen, F. J., Fontanier, C., and Thomas, E.: Chapter Seven Paleooceanographical Proxies Based on Deep-Sea Benthic Foraminiferal Assemblage Characteristics, in *Developments in Marine Geology*, Volume 1, edited by Claude Hillaire-Marcel and Anne De Vernal, Elsevier, 263–325, available from: <http://www.sciencedirect.com/science/article/pii/S1572548007010123> (last accessed: 14 August 2013), 2007.
- Koho, K. A.: The dynamic balance between food abundance and habitat instability: benthic foraminifera of Portuguese margin canyons. PhD thesis, University of Utrecht, 2008.
- 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.
- 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, 1131–1141, doi:10.5194/bg-10-1131-2013, 2013.
- Kraal, P., Slomp, C. P., Reed, D. C., Reichart, G.-J., and Poulton, S. W.: Sedimentary phosphorus and iron cycling in and below the oxygen minimum zone of the northern Arabian Sea, *Biogeosciences*, 9, 3829–3880, 2013, <http://www.biogeosciences.net/9/3829/2013/>.
- 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 Res. Pt. II*, 47, 2913–2955, 2000.
- Lagoe, M. L.: Recent benthic foraminifera from the Central Arctic Ocean, *J. Foraminif. Res.*, 7, 106–129, 1977.
- 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, 403–421, 2009.
- Levin, L.: Oxygen minimum zone benthos: adaptation and community response to hypoxia, *Oceanogr. Mar. Biol.*, 41, 1–45, 2003.
- Levin, L. A. and Gage, J. D.: Relationships between oxygen, organic matter and the diversity of bathyal macrofauna, *Deep-Sea Res.*, 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 Res. Pt. II*, 47, 189–226, 2000.
- Loeblich, Jr., A. R. and Tappan, H.: Foraminiferal Genera and their classification, Van Nostrand Reinhold Company, New York, 970 pp., 1988.
- Lohmann, G. P.: Abyssal benthonic foraminifera as hydrographic indicators in the western South Atlantic Ocean, *J. Foraminif. Res.*, 8, 6–34, 1978.

- Lutze, G. J.: *Uvigerina* species of the eastern North Atlantic, in: Atlantic-European Oligocene to Recent *Uvigerina*, edited by: Van der Zwaan, G. J., Jorissen, F. J., Verhaken, P. J. J. M., and von Daniels, C. H., Utrecht Micropaleontological Bulletins, the Netherlands, 35, 21–46, 1986.
- Lutze, G. F. and Coulbourn, W. T.: Recent benthic foraminifera from the continental margin of northwest Africa: Community structure and distribution, *Mar. Micropaleontol.*, 8, 361–401, 1984.
- Maas, M.: Verbreitung lebendgefärbter benthischer Foraminiferen in einer intensivierten Sauerstoffminimumzone, Indo-Pakistanischer Kontinentalrand, nördliches Arabisches Meer (Distribution of Rose Bengal stained benthic foraminifera within an intensified oxygen minimum zone, Indo-Pakistan Continental Margin, Northwest Arabian Sea), *Meyniana*, 52, 101–128, 2000.
- Mackensen, A., Schmiedl, G., Harloff, J., and Giese, M.: Deep-sea foraminifera in the Southern Atlantic Ocean: ecology and assemblage generation, *Micropaleontology*, 41, 342–358, 1995.
- Madhupratap, M., Prasanna Kumar, S., Bhattachiri, P. M. A., Dileep Kumar, M., Raghukumar, S., Nair, K. K. C., and Ramaiah, N.: Mechanisms of the biological response to winter cooling in the northeastern Arabian Sea, *Nature*, 483, 549–552, 1996.
- Mallon, J., Glock, N., and Schönfeld, J.: The response of benthic foraminifera to low-oxygen conditions of the Peruvian oxygen minimum zone, A.V. Altenbach et al. (eds), in: Anoxia: Evidence for eukaryote survival and paleontological strategies, *Cellular Origin, Life in Extreme Habitats and Astrobiology* 21, 305–321, 2012.
- Middelburg, J. J. and Levin, L. A.: Coastal hypoxia and sediment biogeochemistry, *Biogeosciences*, 6, 1273–1293, doi:10.5194/bg-6-1273-2009, 2009.
- Mojtahid, M., Jorissen, F., Lansard, B., Fontanier, C., Bombled, B., and Rabouille, C.: Spatial distribution of live benthic foraminifera in the Rhône prodelta: Faunal response to a continental–marine organic matter gradient, *Mar. Micropaleontol.*, 70, 177–200, 2009.
- Mojtahid, M., Griveaud, C., Fontanier, C., Anschutz, P., and Jorissen, F. J.: Live benthic foraminiferal faunas along a bathymetrical transect (140–4800 m) in the Bay of Biscay (NE Atlantic), *Revue de Micropaléontologie*, 53, 139–162, 2010.
- 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), *Mar. Ecol. Prog. Ser.*, 158, 151–163, 1997.
- Morigi, C., Jorissen, F. J., Gervais, A., Guichard, S., and Borsetti, A. M.: Benthic foraminiferal faunas in surface sediments off NW Africa: Relationship with the organic flux to the ocean floor, *J. Foraminif. Res.*, 31, 350–368, 2001.
- Mullineaux, L. S. and Lohmann, G. P.: Late Quaternary Stagnations and recirculation of the eastern Mediterranean: Changes in the deep water recorded by fossil benthic foraminifera, *J. Foraminif. Res.*, 11, 20–39, 1981.
- Murray, J. W., Weston, J. F., Haddon, C. A., and Powell, A. D. J.: Miocene to recent bottom water masses of the north-east Atlantic: An analysis of benthic foraminifera, in: North Atlantic Palaeoceanography, edited by: Summerhayes, C. P. and Shackleton, N. J., special Publication of the Geological Society, London, 21, 219–230, 1986.
- 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, 49–55, 1995.
- Nair, R. R., Ittekkot, V., Manganini, S. J., Ramaswamy, V., Haake, B., Degens, E. T., Desai, B. N., and Honjo, S.: Increased particle flux to the deep ocean related to monsoons, *Nature*, 338, 749–751, 1989.
- 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 Res. Pt. I*, 48, 2453–2472, 2001.
- Nolet, G. J. and Corliss, B. H.: Benthic foraminiferal evidence for reduced deep-water circulation during sapropel deposition in the eastern Mediterranean, *Mar. Geol.*, 94, 109–130, 1990.
- Ohga, T. and Kitazato, H.: Seasonal changes in bathyal foraminiferal populations in response to the flux of organic matter (Sagami Bay, Japan), *Terra Nova*, 9, 33–37, 1997.
- Olson, D. B., Hitchcock, G. L., Fine, R. A., and Warren, B. A.: Maintenance of the low-oxygen layer in the central Arabian Sea, *Deep-Sea Res. II*, 40, 673–685, 1993.
- Paulmier, A. and Ruiz-Pino, D.: Oxygen minimum zones (OMZs) in the modern ocean, *Prog. Oceanogr.*, 80, 113–128, 2009.
- Peterson, L. C.: Recent abyssal benthic foraminiferal biofacies of the eastern Equatorial Indian Ocean, *Mar. Micropaleontol.*, 8, 479–519, 1984.
- Phipps, M. D.: Les foraminifères benthiques de la marge portugaise: Impact des apports organiques sur la densité, la biodiversité et la composition des faunes, Ph.D. thesis, University of Angers, France, 2012.
- 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), *J. Foraminif. Res.*, 42, 66–81, 2012.
- Piña-Ochoa, E., Høglund, 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, *Proc. Natl. Acad. Sci.*, 107, 1148–1153, 2009.
- Piña-Ochoa, E., Høglund, 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, *Proc. Natl. Acad. Sci. USA*, 107, 1148–1153, 2010.
- Rao, R. R., Molinari, R. L., and Festa, J. F.: Evolution of the climatological near-surface thermal structure of the tropical Indian Ocean. 1. Description of mean monthly mixed layer depth, and sea-surface temperature, surface current, and surface meteorological fields, *J. Geophys. Res.*, 94, 10801–10815, 1989.
- Reichart, G. J., den Dulk, M., Visser, H. J., van der Weijden, C. H., and Zachariasse, W. J.: A 225 kyr record of dust supply, paleoproductivity and the oxygen minimum zone from the Murray Ridge (northern Arabian Sea), *Palaeogeography, Palaeoclimatology, Palaeoecology*, 134, 149–169, 1997.
- Reichart, G. J., Lourens, L. J., and Zachariasse, W. J.: Temporal variability in the northern Arabian Sea oxygen minimum zone (OMZ) during the last 225 000 years, *Paleoceanography*, 13, 607–621, 1998.

- Risgaard-Petersen, N., Langezaal, A. M., Ingvarsdén, 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, 93–96, 2006.
- 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, *J. Geophys. Res.*, 101, 28569–28582, 1996.
- Rixen, T., Ittekkot, V., Haake-Gaye, B., and Schäfer, P.: The influence of the SW monsoon on the deep-sea organic carbon cycle in the Holocene, *Deep-Sea Res. II*, 47, 2629–2651, 2000.
- Ryther, J. H. and Menzel, D. W.: On the production, composition and distribution of organic matter in the western Arabian Sea, *Deep-Sea Res.*, 12, 199–209, 1965.
- Schiebel, R.: Rezente benthische Foraminiferen in Sedimenten des Schelfes und oberen Kontinentalhanges im Golf von Guinea (Westafrika) (Recent benthic foraminifera in sediments of the shelf and upper continental slope from the Gulf of Guinea (West Africa)), *Berichte- Reports Geologisches und Paläontologisches Institut des Universität Kiel*, vol. 59, 1–179, 1992.
- Schmiedl, G.: Rekonstruktion des spätquartären Tiefenwasserzirkulation und Produktivität im östlichen Südatlantik anhand benthischer Foraminiferen (Late Quaternary benthic foraminiferal assemblages from the eastern South Atlantic Ocean: reconstruction of deep water circulation and productivity changes), *Berichte zur Polarforschung*, 160, 1–207, 1995.
- Schmiedl, G. and Leuschner, D. C.: Oxygenation changes in the deep western Arabian Sea during the last 190,000 years: Productivity versus deepwater circulation, *Paleoceanography*, 20, PA2008, doi:10.1029/2004PA001044, 2005.
- Schmiedl, G. and Mackensen, A.: Late Quaternary paleoproductivity and deep water circulation in the eastern South Atlantic Ocean: Evidence from benthic foraminifera, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 130, 43–80, 1997.
- Schmiedl, G., Mackensen, A., and Müller, P. J.: Recent benthic foraminifera from the eastern South Atlantic Ocean: dependence on food supply and water masses, *Marine Micropaleontology*, 32, 249–287, 1997.
- Schönfeld, J.: Taxonomy and Distribution of the *Uvigerina Peregriana* Plexus in the Tropical to Northeastern Atlantic, *J. Foraminif. Res.*, 36, 355–367, 2006.
- Schulz, H., Von Rad, U., and Von Stackelberg, U.: Laminated sediments from the Oxygen-Minimum Zone of the Northeastern Arabian Sea, in: A. E. S. Kemp (ed.), *Paleoclimatology and Paleoceanography from laminated sediments*, Geol. Soc. (London) Spec. Publ. 116, 185–207, 1996.
- 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), *Mar. Micropaleontol.*, 62, 45–73, 2007.
- Shetye, S. R., Gouveia, A. D., and Shenoi, S. S. C.: Circulation and water masses of the Arabian Sea, in: *Biogeochemistry of the Arabian Sea*, Indian Academy of Sciences, edited by: Lal, D., Bangalore, 9–25, 560 080 India, 1994.
- Stubbings, H. C.: The marine deposits of the Arabian Sea. An investigation into their distribution and biology, *Scientific Reports of the John Murray Expedition 1933–1934*, 3, 31–158, 1939.
- Swallow, J. C.: Some aspects of the physical oceanography of the Indian Ocean, *Deep-Sea Res.*, 31, 639–650, 1984.
- Timm, S.: Rezente Tiefsee-Benthosforaminiferen aus Oberflächensedimenten des Golfes von Guinea (Westafrika) – Taxonomie, Verbreitung, Ökologie und Korngrößenfraktion, *Berichte – Reports, Geologisches und Paläontologisches Institut des Universität Kiel*, 59, 1–192, 1992.
- Van der Weijden, C. H., Reichert, G. J., and Visser, H. J.: Enhanced preservation of organic matter in sediments deposited within the oxygen minimum zone in the northeastern Arabian Sea, *Deep-Sea Res.*, 46, 807–830, 1999.
- Van der Zwaan, G. J., Jorissen, F. J., Verhallen, P. J. J. M. and von Daniels, C. H.: *Uvigerina* from the Eastern Atlantic, North Sea Basin, Paratethys and Mediterranean, in: *Atlantic-European Oligocene to Recent Uvigerina*, edited by: Van der Zwaan, G. J., Jorissen, F. J., Verhallen, P. J. J. M., and von Daniels, C. H., *Utrecht Micropaleontological Bulletins*, 35, 7–19, 1986.
- Walton, W. R.: Techniques for recognition of living foraminifera, *Contribution Cushman Foundation of Foraminiferal Research*, 3, 56–60, 1952.
- Weston, J. F.: Distribution and ecology of Recent Deep Sea benthic foraminifera in the Northeast Atlantic Ocean, Ph.D thesis, University of Exeter, England, 1982.
- Wilkinson, D. M.: The Disturbing History of Intermediate Disturbance, *Oikos*, 84, 145–7, 1999.
- Wyrki, K.: Physical oceanography of the Indian Ocean, in: *The Biology of the Indian Ocean*, edited by: Zeitschel, B., Springer, Berlin, 18–36, 1973.
- Zobel, B.: Biostratigraphische Untersuchungen an Sedimenten des indisch-pakistanischen Kontinentalrandes (Arabisches Meer), *“Meteor” Forsch.-Ergebnisse C*, 9–73, 1973.