



SPECIAL TOPIC

Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones

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Abstract

Oxygen minimum zones (OMZs; midwater regions with O_2 concentrations $<0.5 \text{ ml l}^{-1}$) are mid-water features that intercept continental margins at bathyal depths (100–1000 m). They are particularly well developed in the Eastern Pacific Ocean, the Arabian Sea and the Bay of Bengal. Based on analyses of data from these regions, we consider (i) how benthic habitat heterogeneity is manifested within OMZs, (ii) which aspects of this heterogeneity exert the greatest influence on alpha and beta diversity within particular OMZs and (iii) how heterogeneity associated with OMZs influences regional (gamma) diversity on continental margins. Sources of sea-floor habitat heterogeneity within OMZs include bottom-water oxygen and sulphide gradients, substratum characteristics, bacterial mats, and variations in the organic matter content of the sediment and pH. On some margins, hard grounds, formed of phosphorites, carbonates or biotic substrata, represent distinct subhabitats colonized by encrusting faunas. Most of the heterogeneity associated with OMZs, however, is created by strong sea-floor oxygen gradients, reinforced by changes in sediment characteristics and organic matter content. For the Pakistan margin, combining these parameters revealed clear environmental and faunal differences between the OMZ core and the upper and lower boundary regions. In all Pacific and Arabian Sea OMZs examined, oxygen appears to be the master driver of alpha and beta diversity in all benthic faunal groups for which data exist, as well as macrofaunal assemblage composition, particularly in the OMZ core. However, other factors, notably organic matter quantity and quality and sediment characteristics, come into play as oxygen concentrations begin to rise. The influence of OMZs on meiofaunal, macrofaunal and megafaunal regional (gamma) diversity is difficult to assess. Hypoxia is associated with a reduction in species richness in all benthic faunal groups, but there is also evidence for endemism in OMZ settings. We conclude that, on balance, OMZs probably enhance regional diversity, particularly in taxa such as Foraminifera, which are more tolerant of hypoxia than others. Over evolutionary timescales, they may promote speciation by creating strong gradients in selective pressures and barriers to gene flow.

Problem

Oxygen minimum zones (OMZs), defined as layers of the water column where dissolved oxygen (DO) concentrations fall below 0.5 ml l^{-1} ($<22 \mu\text{M}$), are important hydrographic features on the eastern margins of ocean basins, notably the Pacific and to a lesser extent off SW Africa, as well as in the northern Indian Ocean (Helly & Levin 2004; Paulmier & Ruiz-Pino 2009; Zettler *et al.* 2009). They persist over geological time scales and result from a combination of factors, including high surface productivity and limited water-column ventilation caused by stratification and isolation of older, oxygen-depleted water masses. The upper boundaries of OMZs may move up and down in response to decadal El Niño events (Arntz *et al.* 2006; Hormazábal *et al.* 2006; Sellanes & Neira 2006; Sellanes *et al.* 2007), or seasonal monsoonal cycles (Paulmier & Ruiz-Pino 2008; Brand & Griffiths 2009), exposing benthic communities in these boundary regions to strongly fluctuating bottom-water DO. In the central and eastern Arabian Sea, there is evidence for substantial seasonal variations in DO in the upper 1000 m of the water column (de Sousa *et al.* 1996; Paulmier & Ruiz-Pino 2008). Other parameters also vary across OMZs. In particular, organic matter concentrations, which typically are linked inversely to oxygen, are often high (Levin & Gage 1998). Hydrogen sulphide may be present within OMZ sediments but more often is removed by the formation of iron sulphides. The sediments themselves are often very soft and unconsolidated in the core regions of OMZs as a result of high water content. Variations in these parameters create gradients on the sea floor, rather than spatially distinct habitats. More discrete, visually obvious sources of heterogeneity are created by bacterial mats, authigenic phosphorites (Veeh *et al.* 1973; Gallardo 1977; Froelich *et al.* 1988; Schmaljohann *et al.* 2001), and the accumulated skeletal parts and carcasses of marine organisms (Milessi *et al.* 2005; Billett *et al.* 2006).

Where mid-water OMZs impinge on the seafloor on the outer shelf, upper slope and oceanic seamounts, they strongly influence the abundance, diversity, and composition of benthic faunas (Levin 2003). Benthic communities in the core regions of OMZs typically exhibit depressed diversity and species richness and high levels of dominance by a few tolerant species (Levin & Gage 1998). However, the lower parts of OMZs (lower transition zone) are often regions of intense biological activity characterized by huge abundances of a few species belonging to taxa such as ophiuroids and spider crabs (Levin 2003; Gooday *et al.* 2009) (Fig. 1D,E). These so-called 'edge effects' (Mullins *et al.* 1985; Thompson *et al.* 1985) are believed to reflect a release from oxygen limitation combined with an abundance of food (Wishner *et al.*

1990; Levin *et al.* 1991; Levin 2003). Within lower transition zones, differential tolerances to hypoxia (Gooday *et al.* 2009) lead to shifts in assemblage composition across short vertical distances (Wishner *et al.* 1990, 1995; Levin 2002; Levin *et al.* 2010). Thus, although OMZs exhibit sharply depressed diversity, fine-scale faunal zonation in response to strong seafloor gradients may increase species richness by enhancing species turnover (beta diversity). It is also possible that OMZs act as barriers that enhance diversity over evolutionary time by promoting genetic differentiation (Rogers 2000).

Diversity is a key aspect of benthic community structure on continental margins and may be linked to a number of ecosystem functions (Danovaro *et al.* 2008). It has several distinct components, namely richness (number of species), evenness (distribution of individuals among species), and dominance (contribution of the most abundant species). In addition, diversity can be considered on multiple spatial scales. We define alpha diversity as the number of species at a single sampling station, and beta diversity as the turnover of species across stations. At a larger scale, gamma diversity is the regional species richness, obtained by combining species lists across stations. In this paper, we first explore the varied sources of environmental and substratum heterogeneity within OMZs and then consider their influence on biodiversity. We combine re-analyses of published data for the Arabian Sea and eastern Pacific and new data for the Bay of Bengal to address the following questions: (i) how is habitat heterogeneity manifested within OMZs, (ii) which aspects of heterogeneity exert the greatest influence on alpha and beta diversity within particular OMZs and (iii) how does OMZ-associated heterogeneity influence regional (gamma) diversity on continental margins?

Sources of heterogeneity and mechanisms linking them to biodiversity

Oxygen and sulphide

A compilation of oxygen profiles across different OMZs reveals that, although the thickness of these features, and the depths of their upper and lower boundaries, vary across margins, the general pattern is consistent (Levin 2003). Water-column DO usually falls rapidly across the upper boundary, the depth of which may vary seasonally, and rises more or less gradually across the more stable lower boundary. Between these two transitional regions lies the OMZ core, where DO remains depressed. Oxygen profiles are generally stable over time. Sulphide is not usually a major stress factor in OMZs. Where present, however, sulphide inhibits aerobic respiration and can also react with trace amounts of oxygen to form

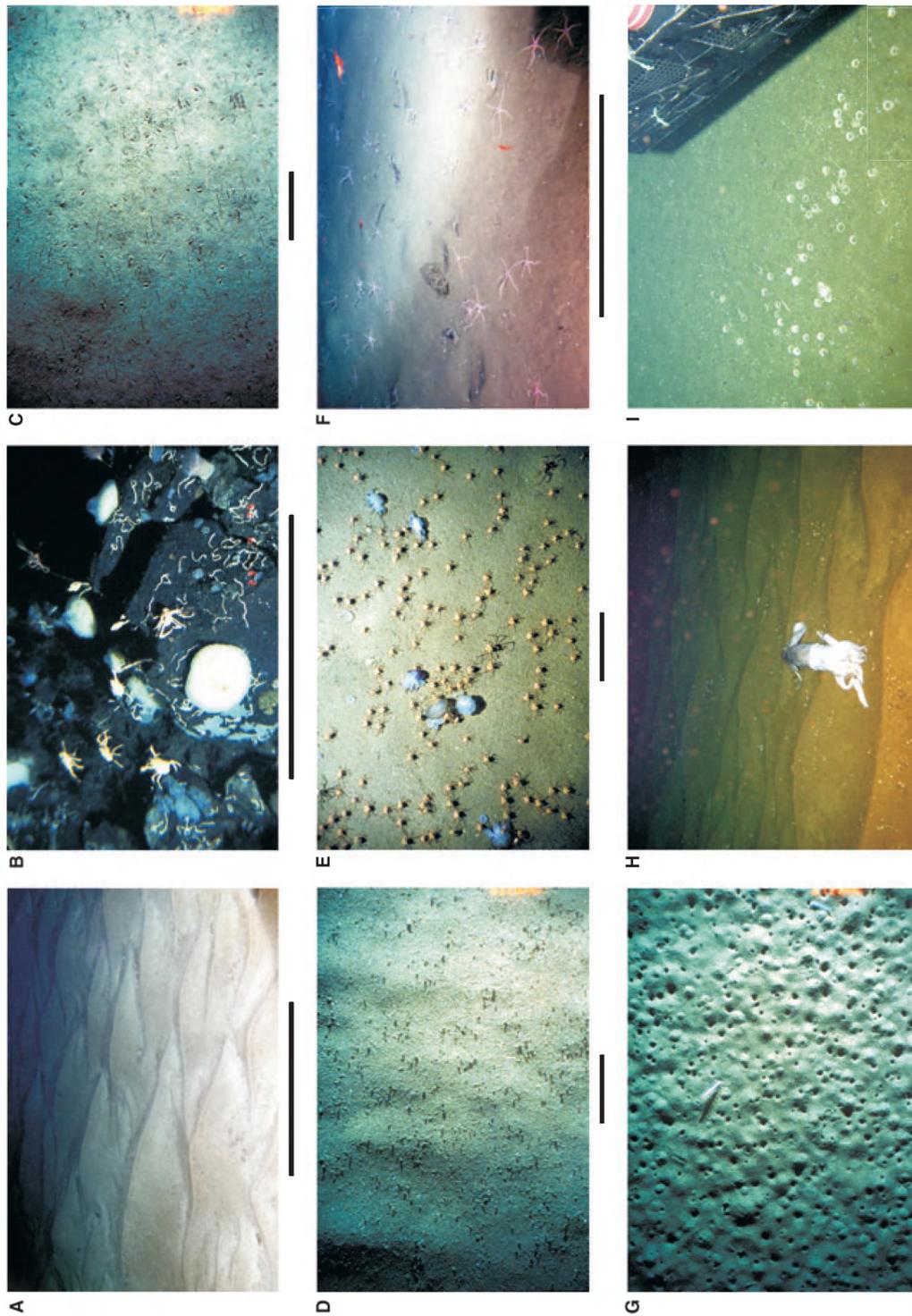


Fig. 1. Sea floor photographs showing habitat heterogeneity associated with oxygen minimum zones. (A) Ripple marks at 500 m depth in the core of the Indian margin OMZ; image courtesy of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) and the National Institute of Oceanography (NIO, India). (B) Dense populations of galatheid crabs, sponges and serpulid polychaetes on rocky substratum close to the summit of the Volcano 7 seamount, which penetrates the OMZ in the eastern Pacific. (C) Sea floor with large numbers of polychaete worm burrows, some with emerging worms (probably *Linopherus* sp.), ~900 m depth on Pakistan margin. (D) Sea floor with large numbers of the arborescent foraminiferan *Pelosiina*, ~780 m depth on Pakistan margin. (E) Sea floor with large numbers of spider crabs (*Encephaloides armstrongi*) and jellyfish carcasses at ~1000 m depth on Oman margin. (F) Abundant ophiuroids at ~850 m depth on the Indian margin; image courtesy of JAMSTEC and NIO. (G) Sea floor with numerous closely spaced small burrow openings and mounds, ~1100 m depth on Pakistan margin. (H) Squid carcass lying on rippled sea floor, ~550 m depth on the Indian margin; image courtesy of JAMSTEC and NIO. (I) Fish vertebrae on the Indian margin, ~760 m; image courtesy of JAMSTEC and NIO. The scale bars indicates a length of approximately 50 cm near the centre of each image. The images are arranged in the order in which they are mentioned in the text.

hydrogen peroxide (H₂O₂), leading to cell damage (Bernhard & Bowser 2008).

Reduced bottom-water DO limits oxygen penetration into the sediment, and hence the living space available to benthic organisms, compared to well-oxidized sediments. Morphological and physiological adaptations link oxygen (and sulphide) gradients to biodiversity. The fact that many species lack these adaptations leads to depressed diversity within OMZ cores. Morphological adaptations have been observed in many OMZ invertebrates and generally involve an increase in gill surface area, as in some crustaceans and polychaetes (reviewed in Levin 2003). Elongation and proliferation of branchiae have been observed in spionid, dorvilleid, lumbrinerid, nereid, terebellid and onuphid polychaetes inhabiting OMZs (Lamont & Gage 2000; Levin *et al.* 2009, 2010; unpublished data). A new *Leptochiton* species (Mollusca, Polyp-lacophora) inhabiting bone-covered sediments within the OMZ off northern Chile exhibits enhanced numbers and size of ctenidia (Schwabe & Sellanes in press). Nematodes in the genus *Glochinema* are covered with hairs and long setae, enhancing body surface area for a more efficient oxygen uptake in the OMZ (Neira *et al.* 2001a, 2005). Some hypoxia-tolerant foraminiferal species have flattened tests that increase their surface/volume ratio, thereby enhancing oxygen uptake. Reduced body size, which also leads to an increase in the surface/volume ratio, is a typical feature of some OMZ metazoan macrofauna. Macrofaunal community biomass size diversity may be lowered within OMZs (Quiroga *et al.* 2005) through the preferential loss of large species/size classes. A similar effect is also known for macrofaunal communities subject to organic enrichment, although this reflects a dominance by small opportunistic species with a high turnover rate, able to exploit a rich food supply (*e.g.* Warwick 1986).

Organic matter (OM)

Low DO exerts a powerful influence on the degradation of organic matter. In general, there is a negative relationship between bottom-water DO and measures of sediment organic-matter content on margins with OMZs (Levin & Gage 1998), although the relationship is by no means straightforward (Cowie 2005; Cowie *et al.* 1999; Middelburg & Levin 2009). Limited light combined with oxygen depletion slows the microbial decomposition of sinking OM, resulting in the accumulation of undegraded, labile OM. It is common to find sediments containing >4% (up to 20.5%) of organic carbon in OMZs, contributing a different but concurrent source of heterogeneity. The most detailed information about variations in OM quality (composition) and quantity across an OMZ is from the

Pakistan margin (Cowie *et al.* 1999, 2009). Here, much of the OM in the sediment was degraded and concentrations varied by a factor of three. However, although there was a general enhancement of OM across the OMZ, there were also variations that were unrelated to oxygen. In particular, the proportion of degraded material was lower in the OMZ core than at depths above and below the core, reaching maximal values within the lower transition zone (Woulds *et al.* 2007; Vandewiele *et al.* 2009). The factors causing these variations in OM content and quality are unclear, but are probably related to differences in the activities of benthic communities. On the Oman margin, Smallwood *et al.* (1999) reported that large animals (spider crabs and ophiuroids) altered the biochemistry of labile OM, leading to the depletion of phyosterols.

Low pH

High amounts of OM and elevated respiration rates within OMZs create acidic conditions where oxygen depletion is most intense. Relatively few pH measurements have been made in OMZs. Low values (<7.5) are associated with low oxygen (<0.2 ml l⁻¹) waters at depths of 60–1200 m on the Mexican margin (Fernández-Alamo & Färber-Lorda 2006), and at 800 m off southern California (Levin L. and Tanner C., unpublished). Values <7.0 were measured in OMZ core sediments off Peru (Neira and Sellanes unpublished). Off Costa Rica and India, the lowest oxygen values corresponded to pH values of 7.7–7.8 (C. Tanner and L. Levin, K. Oguri, personal communication).

The impact of low pH on marine animals is poorly understood (Fabry *et al.* 2008). Recent experiments suggest that it can lead to mortality in nematodes and harpacticoid copepods (Thistle *et al.* 2005; Fleeger *et al.* 2006). The scarcity in OMZ cores of organisms with calcareous hard-parts may be linked to this factor (Thompson *et al.* 1985). Echinoderms and other taxa that secrete highly soluble high-Mg calcite are particularly susceptible to lowered pH. The disappearance of calcareous Foraminifera in some heavily polluted coastal areas is probably related to the corrosive effects of acidic porewaters (Green *et al.* 1993; Mojtabid *et al.* 2008). Nevertheless, calcareous Foraminifera are typically abundant in OMZ cores (Gooday *et al.* 2000), and a few gastropod and thin-shelled bivalve species persist in these regions (Levin *et al.* 1997; Ramirez-Llodra & Olabarria 2005). This suggests that some organisms with calcareous hard-parts have adapted to persistent slightly acidic conditions (Wood *et al.* 2008).

Substratum characteristics

Within OMZs, sediment types are often heterogeneous (Levin *et al.* 2002). The upper boundary regions are typi-

cally characterized by coarse substrata. Sediments in the core regions of OMZ are unconsolidated with a high water content, easily resuspended and usually rich in OM with a substantial phytodetritus component (Pfanckuche *et al.* 2000; Neira *et al.* 2001b). Extensive areas of sea floor off Goa and Pakistan are covered in large ripples (Fig. 1A), presumably created by current activity, despite being overlain by severely oxygen-depleted water (B.J. Bett, L.A. Levin, A.J. Gooday unpublished observations). Rippled foraminiferal sands are found on the summits of seamounts protruding into the OMZ (Levin *et al.* 1991) and rippled muds occur in the Chilean margin (Sellanes *et al.* 2010).

The nature of the sediment confronts benthic organisms with life-style challenges. Mechanisms to cope with very soft, fluid, unstable sediments include morphological adaptations and the construction of mud dwellings that provide stability (reviewed in Levin 2003). As mentioned above, some nematodes have specialized external morphologies and ornamentation. In addition to long somatic setae that may enhance surface area, species of *Glochinema* have long sensory setae and various rows of long ambulatory setae (Gourbault & Decraemer 1996) that possibly aid mobility in the soupy muds of OMZs (Neira *et al.* 2001a, 2005). Another example is *Desmotersia levinae*, recently described from the Peru margin OMZ core where it occupies mostly subsurface sediments (Neira & Decraemer 2009); the slender body of this species is covered by a dense, hairy setation.

Hard substrata within OMZs are typically formed of authigenic phosphorite, carbonate or volcanic material such as basalt (Fig. 1B; Sellanes *et al.* 2009, Fig. 1B therein). Phosphorites are often associated with areas of upwelling and high surface productivity (Kolodny 1981). Off Peru, they provide hard substrata for attached organisms, including at least 10 species of Foraminifera, which are probably deposit feeders, as well as a variety of suspension-feeding metazoans including serpulid worms, bryozoans, chitons, brachiopods, psolid holothurians and gastropods (Resig & Glenn 1997). These attached faunas are concentrated in the upper and lower parts of the OMZ, an example of an edge effect. A similar phosphorite habitat (including also abundant whale bones) and associated fauna is developed at 240 m depth within the Chilean OMZ core off Concepción (J. Sellanes, personal observation). Further north, off Antofagasta, authigenic crusts devoid of obvious megafauna and animal traces, occur in the OMZ core where $DO = 0.06 \text{ ml l}^{-1}$ (Sellanes *et al.* 2009). A new species of polyplacophoran, *Lepidozona balaenophila*, was described from this site (Schwabe & Sellanes 2004) and the fauna also included an unknown species of actiniarian, solitary scleractinians, an asteroid (*Poraniposis echinaster*), decapods (*Cervimunida jhoni*,

Pterygosquilla armata, *Heterocarpus reedi*) and four species of fish (J. Sellanes, personal observation).

Where methane seepage occurs, anaerobic methane oxidizers precipitate calcium carbonate (Aloisi *et al.* 2002). Massive carbonate platforms and chemohermes may form inside oxygen minimum zones along much of the eastern Pacific, e.g. off Oregon, California, Costa Rica and Chile (Bohrmann *et al.* 1998; Stakes *et al.* 1999; Han *et al.* 2004; Bahr *et al.* 2007). The carbonate rocks may be colonized by seep-endemic fauna (mainly provannid gastropods, limpets, cnidarians in the OMZ) and a diversity of more widespread annelids (L. Levin, unpublished data). Basalt substrates and manganese crusts on seamounts that protrude into OMZs are covered by strongly zoned polychaetes, sponges, crustaceans and echinoderms (Wishner *et al.* 1990, 1995) (Fig. 1B).

Biogenic structures and activities

On a small spatial scale, substantial habitat heterogeneity may be created within OMZs by biogenic structures that provide fauna with hard surfaces for attachment and elevation into higher flow conditions. Such structures include polychaete tubes, cirratulid mudballs, the mud 'houses' of ampeliscid amphipods, and the tree-like tests of the foraminiferan *Pelosina*. Polychaete tubes are known to provide a substratum for attached Foraminifera (e.g. Langer & Bagi 1994; Mackensen *et al.* 2006). Cigar-shaped mudballs made by the cirratulid polychaete *Monticellina* sp. at 840–875 m off Oman support four species of polychaete, nemerteans, nematodes and arborescent and calcareous Foraminifera (Levin & Edesa 1997). Associations between protists of different sizes may also be fairly common. Tree-like *Pelosina* tests occur across the Pakistan margin of the Arabian Sea (Fig. 1D). At 1000 m depth, they provide a substratum for the gromiid *Gromia pyriformis* and the foraminiferan *Bathysiphon* sp. (Gooday & Bowser 2005). Large, mobile animals, including vast numbers of spider crabs off Oman (Bett 1995) (Fig. 1E) and ophiuroids on the Pakistan and other margins (Fig. 1F), as well as very abundant bivalves and gastropods at an OMZ site on the Namibian margin (Zettler *et al.* 2009), also represent potential substrates for attached organisms. Crabs belonging to an undescribed species that is abundant at methane seeps at the base of the OMZ off Peru (~600 m) carry large tunicates on their carapaces (observed from tapes provided by R. Jahnke, Skidaway Institute, USA). *Calypptogena* spp. inhabiting seep sediments within the Costa Rica OMZ support a diversity of sabellid and capitellid polychaetes on parts of their shells that protrude above the sediment-water interface.

Bacterial mats often provide a localized, firmer, less toxic and geochemically distinct substratum within OMZs. On the Pakistan margin, a *Beggiatoa/Thioploca* mat yielded two foraminiferan species not present in adjacent sediments, as well as higher abundances of three other species and slightly higher diversity values compared to a core taken outside the mat (Erbacher & Nelskamp 2006). However, the overall abundances of stained benthic Foraminifera were much lower within the mat.

Animal traces (*lebensspuren*) and surficial bioturbation (Cullen, 1973) create small-scale sediment heterogeneity, the intensity and nature of which may change across relatively short distances within an OMZ. However, these features largely disappear in the core regions, where large animals are absent. Off Pakistan, the sea floor was more or less devoid of traces at 300, 400 and 700 m, but characterized by burrows, locomotory and grazing traces at 140 m, shallow depressions at 900 and 1000 m, numerous small, closely spaced burrow openings and mounds at 1100 m (Fig. 1G), and fewer but larger burrows, biogenic depressions and locomotory traces at 1250 m (Murty *et al.* 2009). Similarly, sediment mixing by bioturbation is dependent on the extent to which burrowing macrofauna are eliminated by oxygen depletion (Smith *et al.* 2000; Cowie & Levin 2009; Levin *et al.* 2009).

Carcasses

Accumulations of dead jellyfish were photographed on the sea floor off Oman (300–3300 m water depth) in December 2002 (Billett *et al.* 2006). At depths within the OMZ (<1000 m), the jellyfish appeared to be intact and many were observed rolling downslope (Fig. 1E). Aggregations occurred within canyons and dense concentrations of decomposing 'jelly detritus' were seen on the continental rise. Dead jellyfish, fish and decapods have been photographed on the sea floor off Pakistan (Murty *et al.* 2009), and squid and large fish vertebrae were present on the Indian margin (Fig. 1H, I). There have been similar observations of salps and pyrosomes at 400 m at the base of a vertical slide in the core of the OMZ off Costa Rica (G. Rouse, personal communication) and off the Ivory Coast (West Africa) (Labrato & Jones, 2009). Large numbers of swimming crabs (*Charybdis smithii*) were found dead on the abyssal sea floor in the northern Arabian Sea (Christiansen & Boetius 2000). If they occurred within the OMZ, these animal remains could influence biodiversity by further depressing DO in the sediment and thereby eliminating meiofaunal and macrofaunal species, or by providing food for scavengers such as amphipods. They could also be exploited by opportunistic species, for example, the fauna attached to whale bones in the OMZ off Chile.

Regional setting

Proximity to major rivers may lead to increased habitat heterogeneity. The upper continental slope off northern California receives copious amounts of wood from the Eel River, which frequently sends flood deposits across the shelf onto the slope (Syvitski *et al.* 1996). Some of this material may fuel the methane seeps that occur at ~500 m (Levin *et al.* 2010). Large amounts of wood have also been observed within the OMZ off Costa Rica (Levin, unpublished data). Bottom topography is also important. Rao & Veerayya (2000) report enhanced levels of organic carbon associated with coarse-grained, biogenic sediments on topographic highs on the Indian margin. The Oman margin is traversed by numerous submarine canyons, which generate substantial heterogeneity, as they do on non-OMZ margins.

Methods

Data sources

The data originated from the Chilean and Mexican margins (eastern Pacific), the Oman, Pakistan and Indian margins (Arabian Sea), and the western side of the Bay of Bengal and are derived mainly from sources that are either published or submitted (Table 1). Sellanes *et al.* (2010) review results from the Chilean margin. The Bay of Bengal dataset will be submitted in the near future (Raman *et al.*, in preparation).

Statistical methods

Data transformations

For the purposes of presentation, and to better meet the various assumptions of subsequent statistical analyses, the primary data were usually subject to transformation (*e.g.* see Sokal & Rohlf 1995). Normalization (*i.e.* conversion to zero mean and unit variance) was employed for presentation purposes (Fig. 2) and in the joint analysis of environmental variables (principal components analysis, Fig. 2; partial correlation analysis, Table 2). Where percentage or proportion data were subject to further statistical analysis they were first arcsin-transformed (Berger–Parker data, Fig. 5). A range of transformations was applied to species abundance data prior to multivariate analysis (Fig. 8). However, unless stated otherwise, all results presented were based on a $\log(x + 1)$ transformation.

Diversity measures

A range of alpha diversity measures was calculated using the PRIMER 5 software package (Clarke & Warwick 1994); see Magurran (2004) for formulations and symbol-

Table 1. Data analysed.

Area	Faunal data	Environmental data	Reference
Chilean margin			
Antofagasta	Macrofauna, Megafauna	O ₂ , %TOC, CPE, grain size	Palma <i>et al.</i> (2005), Quiroga <i>et al.</i> (2009)
Concepcion	Macrofauna, Megafauna	O ₂ , %TOC, CPE, grain size	Gallardo <i>et al.</i> (2004), Palma <i>et al.</i> (2005), Quiroga <i>et al.</i> (2009)
Chiloe	Macrofauna, Megafauna	O ₂ , %TOC, CPE, grain size	Palma <i>et al.</i> (2005), Quiroga <i>et al.</i> (2009)
Gulf of California	Polychaetes	O ₂ , %OM, grain size	Méndez (2006); Méndez (2007)
Oman margin	Macrofauna	O ₂ , %TOC, CPE, grain size, C:N, Hydrogen index	Levin <i>et al.</i> (2000)
Pakistan margin	Megafauna, Macrofauna, Foraminifera	O ₂ , %TOC, pigments, grain size, C:N, δ ¹³ C, δ ¹⁵ N	Schumacher <i>et al.</i> (2007), Hughes <i>et al.</i> (2009), Levin <i>et al.</i> (2009), Larkin & Gooday (2009), Murty <i>et al.</i> (2009)
Indian margin	Macrofauna	O ₂ , %OM, grain size	Ingole <i>et al.</i> 2010
Bay of Bengal	Macrofauna		Raman <i>et al.</i> (unpublished)
Rockall trough	Polychaetes	O ₂	Paterson & Lambshead (1995)

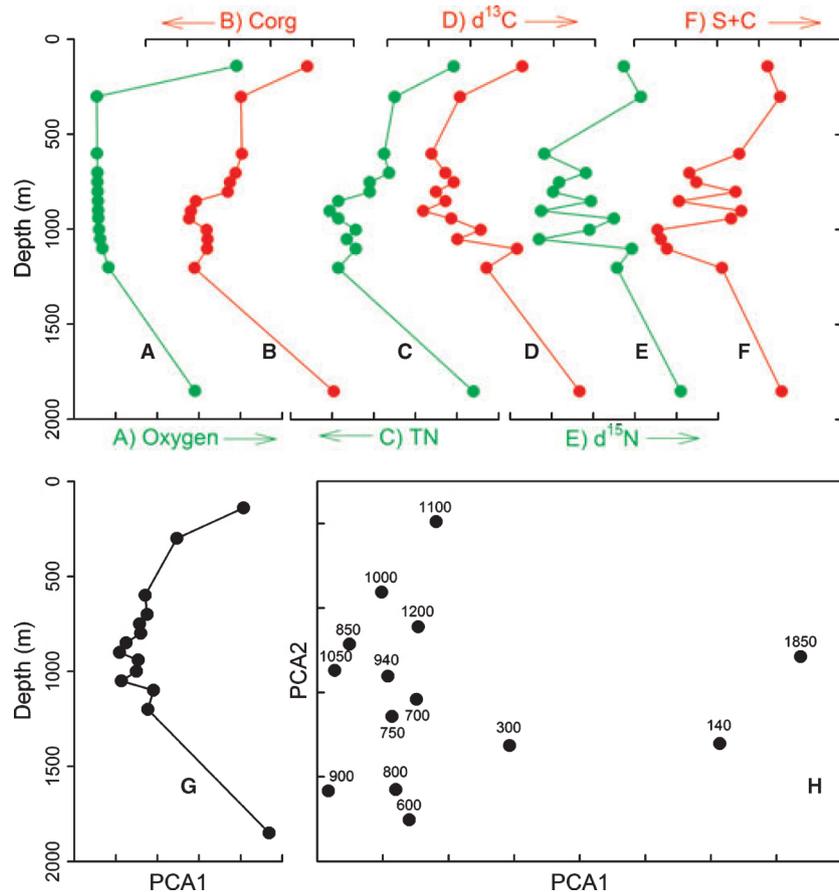


Fig. 2. Trends in environmental parameters with depth across the Pakistan margin OMZ. (A–F) Because the values of the various parameters are numerically very different, they are plotted on a common scale having zero mean and a standard deviation of 1. Each point therefore represents the original value minus the mean and divided by the standard deviation. (G–H) Principal components analysis of the normalized environmental data shown in A–F. PCA1 encompasses 71% of the variation in these data. C_{org} = organic carbon; δ¹³C = stable carbon isotope ratio; S + C = % sand + clay; TN = total nitrogen; δ¹⁵N = stable nitrogen isotope ratio.

ogy. The Berger–Parker (n_{max}/N) and ‘Rank 1 dominance’ ($100 \cdot n_{max}/N$) indices were also calculated by spreadsheet operation. Beta diversity was assessed on the basis of species turnover with depth and presented on a cumulative percentage scale (Fig. 7). The beta diversity measure used here is effectively that of Cody (1975): $\beta_c =$

$(As + Ds)/2$, where As is the number of arriving species (*i.e.* their apparent minimum depth of occurrence) and Ds is the number of departing species (*i.e.* their apparent maximum depth of occurrence). Arrivals are discounted from the minimum depth sampled and departures doubled to compensate; similarly, departures are discounted

Table 2. Simple (non-parametric) correlations and partial correlations (*i.e.* with depth and other variables held constant statistically) between environmental parameters and macrofaunal diversity measures for the Bay of Bengal (eastern Indian margin). Note that with partial correlation analysis, only oxygen exhibits significant correlations with various diversity measures (n.s. not significant; * $P < 0.05$; ** $P < 0.01$).

	Depth	S ^a	D _{Mg} ^b	HB ^c	α^d	S ₍₁₀₁₎ ^e	H' ₂ ^f	J' ^g	D ^h	R1D ⁱ
Simple (non-parametric) correlations										
Depth	–	–0.767**	–0.837**	–0.847**	–0.851**	–0.804**	–0.847**	–0.807**	–0.809**	n.s.
Sand/Mud ^d	0.532*	0.605**	0.546*	0.479*	0.554*	0.546*	0.479*	n.s.	n.s.	n.s.
Particle size	n.s.	0.486*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Organic matter	–0.709**	–0.770**	–0.682**	–0.653**	–0.681**	–0.739**	–0.653**	–0.614**	–0.607**	n.s.
Dissolved oxygen	–0.768**	0.587**	0.674**	0.623**	0.689**	0.642**	0.623**	0.495*	0.525*	n.s.
Partial correlations										
Sand/Mud ^k	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Particle size	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Organic matter	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Dissolved oxygen	–	0.528*	0.573*	0.526*	0.564*	0.596*	0.530*	n.s.	n.s.	n.s.

^aTotal species. ^bMargalef's index. ^cBrillouin index. ^dFisher's index. ^eRarefied species richness ($n = 101$). ^fShannon index (\log_2). ^gPielou's evenness.

^hSimpson's index ($1-\lambda'$ form). ⁱRank 1 dominance. ^jIdentical values of opposite sign. ^kIdentical values.

from the maximum depth sampled and arrivals doubled to compensate.

Univariate statistics

Non-parametric correlations (Spearman's Rank; Siegel & Castellan 1998) were carried out using the MINITAB 15 (Minitab Inc.) statistical software package. Partial correlation analysis (Sokal & Rohlf 1995) was carried out using the SPSS 17 (SPSS Inc., Chicago, USA) software package. Confidence intervals (Fig. 5) were calculated based on the t -distribution, as described in Sokal & Rohlf (1995).

Multivariate statistics

Principal components analysis (PCA; Fig. 2) and non-metric multi-dimensional scaling (MDS; Fig. 10) ordinations were carried out using PRIMER 5. Two-way indicator species analysis (TWINSPAN; Fig. 11) was performed with the PC-ORD 4 (MjM Software) software package using an approximately logarithmic scale of cut levels for species abundance. For general details of all three multivariate methods, see Jongman *et al.* (1995).

Observations and Results

Defining Habitat Heterogeneity within OMZs

Visually obvious habitat heterogeneity (hereafter HH) within OMZs is created by phosphatic hardgrounds, whale bones and other hard substrata. HH arising from gradients in bottom-water DO and other parameters is more subjective. Cowie & Levin (2009) and Gooday *et al.* (2009) partitioned the Pakistan margin OMZ into regions, based mainly on DO and the presence or otherwise of sediment laminations: (i) seasonally hypoxic

zone (140–250 m; O₂ fluctuating from 0.11 to 2.05 ml l⁻¹; fully formed laminations appearing at 250 m); (ii) OMZ core (250–750 m; O₂ = 0.10–0.14 ml l⁻¹; fully laminated sediments); (iii) OMZ transition zone (750–1000 m; O₂ = 0.12–0.17 ml l⁻¹; partially laminated sediments); (iv) OMZ boundary (1000–1300 m; O₂ = 0.15–0.50 ml l⁻¹) and (v) a region beneath the OMZ (1300–1850 m; O₂ > 0.50 ml l⁻¹). Similar subjective schemes may be applicable on other margins, but there are also important differences. Lamination is relatively rare in most OMZs, and the formation of laminae (or their disruption) may be controlled by the interaction of DO and organic matter rather than by DO alone. For example, no laminae were present at DO concentrations of 0.09–0.13 ml l⁻¹ on the summit of Volcano 7 (Levin *et al.* 1991) or on the Oman margin (Smith *et al.* 2000), where OM concentrations were high, whereas they were strongly developed at these oxygen concentrations on the Pakistan margin (Hughes *et al.* 2009; Levin *et al.* 2009).

An extensive dataset of sediment parameters (Corg, TN, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, silt/clay content) is available across the Pakistan margin OMZ (Fig. 2). Plots of individual parameters against water depth show that (i) the shallowest (140 m) and deepest (1850 m) sites are distinct from those clustered within the OMZ and (ii) the 300-m site in the core of the OMZ usually yields values that are intermediate between the 140-m site and the cluster of sites between 700 and 1250 m. When the parameters are combined using PCA, a plot of PCA axis 1 values (representing 71% of the variance of the dataset) with depth reveals this pattern clearly. These analyses suggest that sediment parameters, particularly those associated with organic matter, tend to reinforce the environmental

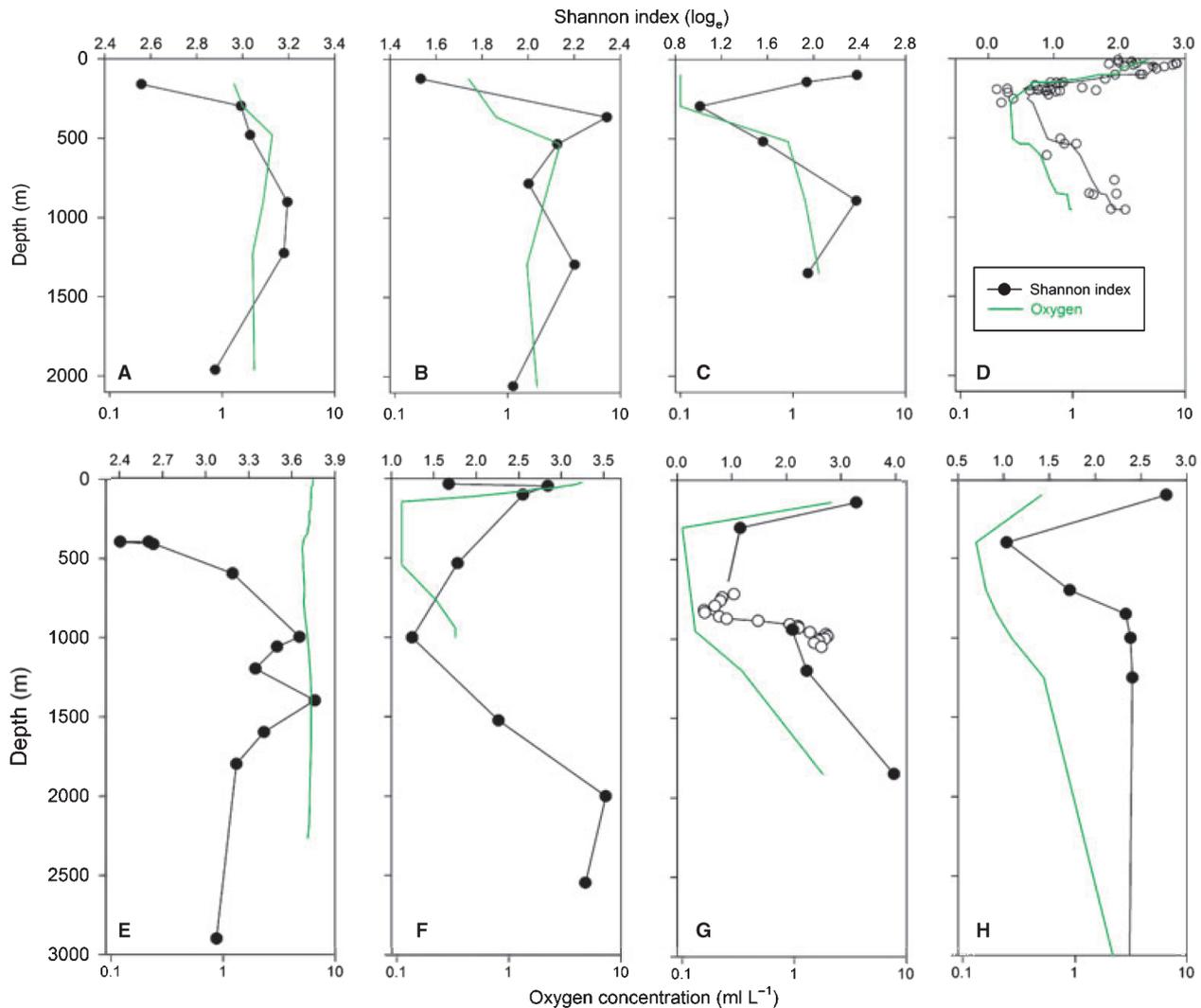


Fig. 3. Alpha diversity ($H' \log_e$, solid black line) versus depth for transects (A) off Chiloé (no OMZ), (B) off Concepción (weak OMZ), (C) off Antofagasta (strong OMZ) (all on the Chilean margin), (D) Bay of Bengal (eastern Indian margin), (E) Rockall Trough (no OMZ; data from Paterson & Lamshead 1995), (F) western Indian margin, (G) Pakistan margin (solid symbols = data from Hughes *et al.* 2009; open symbols = data from Levin *et al.* 2009), (H) Oman margin (data from Levin *et al.* 2000). The Rockall Trough has been included as an example of a typical normally oxygenated margin. Bottom-water oxygen concentrations are shown as a coloured line. For the western Indian margin (F), oxygen values are taken from de Sousa *et al.* (1996, Fig. 2), modified by data from RV *Yokosuka* cruise YK08/11.

contrasts created by strong oxygen gradients within OMZs.

The influence of HH on diversity and assemblage composition within OMZs

Alpha diversity

The best alpha diversity dataset is for macrofauna. Levin & Gage (1998) demonstrated depressed diversity within Indo-Pacific OMZs. Their analysis indicated that DO and OM contributed roughly equally to measures of ES_{100} , H' , D and J' for Indopacific macrobenthos, together

accounting for 32–67% of variation after removing effects of latitude and depth. Here we highlight specific datasets that reveal between-margin differences in faunal responses to oxygen gradients.

On the Chilean margin, diversity (H') is relatively high on the upper slope where the OMZ is either weakly developed (Concepción) or absent (off Chiloé) (Fig. 3A,B). These trends in diversity with depth are similar to those observed in the Rockall Trough (Fig. 3E) (Paterson & Lamshead 1995). In both cases, diversity peaks at mid-slope depths, a typical pattern on well-oxygenated margins. However, where oxygen levels are lowest in the

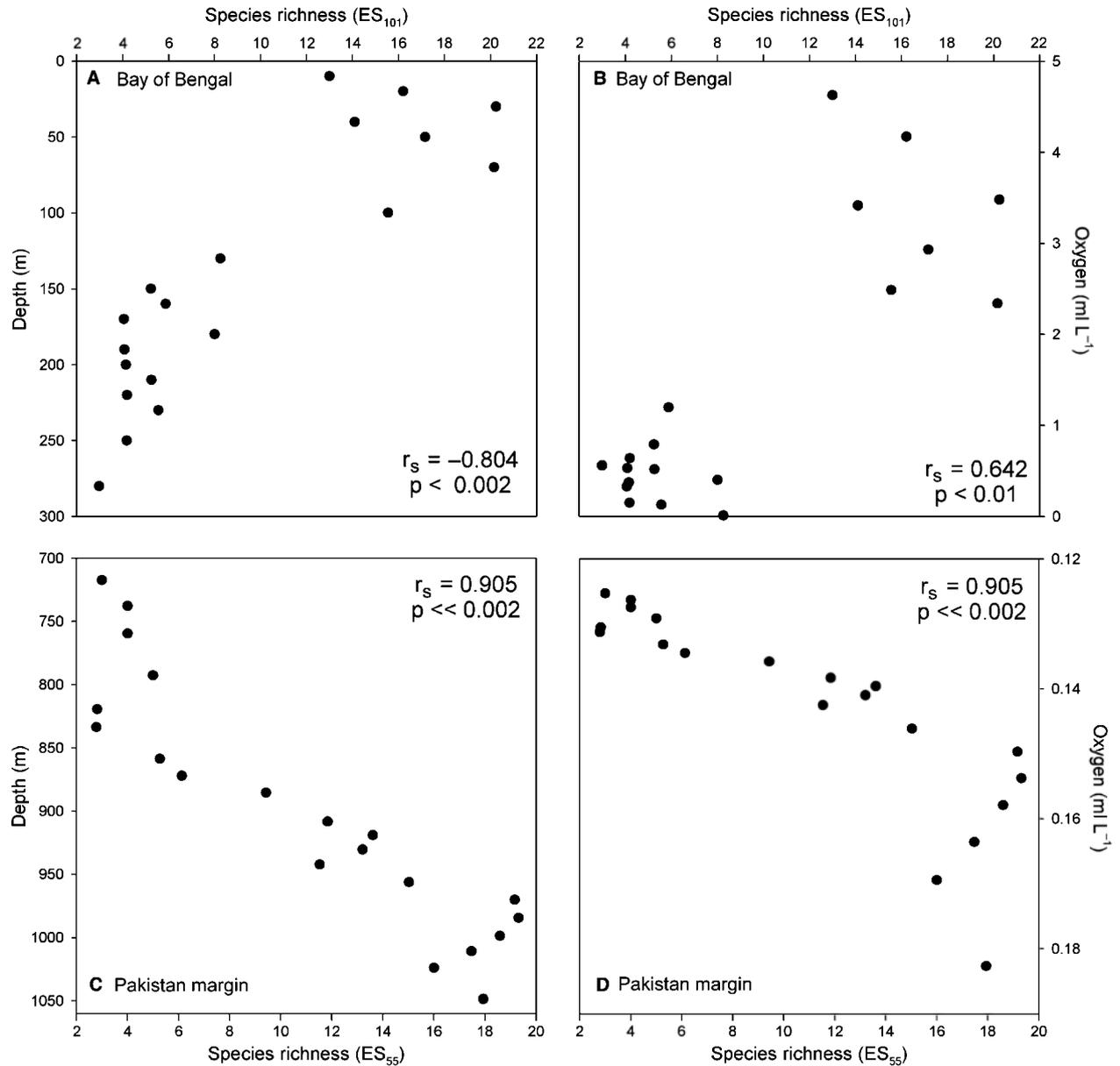


Fig. 4. Species richness *versus* depth and oxygen for the upper boundary of the OMZ in the Bay of Bengal (A,B) (data from Raman unpublished) and the lower boundary of the OMZ on the Pakistan margin (C, D) (data from Levin *et al.* 2009). All the trends are statistically significant.

core of the intense Chilean OMZ near Antofagasta, diversity is strongly depressed (Fig. 3C; Palma *et al.* 2005). The relationships between oxygen and macrofaunal diversity on the Bay of Bengal, Indian, Pakistan and Oman margins (Fig. 3D,F–H) are similar to those seen off Antofagasta. A particularly detailed profile of macrofaunal diversity in relation to DO is available for the lower transition zone (700–1050 m) off Pakistan (Levin *et al.* 2009). Species richness and diversity is minimal between 700 and 850 m ($O_2 = 0.12$ – 0.14 ml l⁻¹), increases rapidly between 800 and 900 m, and reaches maximal values at 1000 m

(Fig. 3G). The 700–850-m assemblage is overwhelmingly dominated by the polychaete *Linopherus* sp. Off the western coast of India, however, macrofaunal diversity is most strongly depressed at 500 and 1000 m (Fig. 3F herein; Ingole *et al.*, submitted).

Alpha diversity is strongly correlated with water depth and bottom-water DO. Across the upper boundary of the Bay of Bengal OMZ (10–300 m depth) there is a significant relationship between water depth and rarefied macrofaunal species richness ($P < 0.002$), and between DO and species richness ($P < 0.01$) (Fig. 4A,B). Substan-

Table 3. The significance of Spearman's rank correlations between depth, oxygen concentration, macrofaunal abundance, diversity (S , J , D_{mg} , HB , α , H' , D , $S_{(59)}$, $R1D$), community composition (MDSx) and species turnover (TO) and (left-hand column) sedimentary environmental factors across the lower boundary of the Pakistan margin OMZ. The + and – symbols in the left-hand column indicate whether the correlations are positive or negative. For example, the upper row of figures shows that depth is positively correlated with oxygen (and vice versa) and both these parameters are significantly and positively correlated with diversity, community composition and species turnover, but not with abundance. Data from Levin *et al.* (2009).

	Depth, Oxygen	Abundance	S^a	$J^{b,c}$	D_{Mg}^c	HB^d , α^e , H'_2^f , D^g	$S_{(59)}^h$, $R1D^i$	MDSx ^j , TO ^k
Depth (+), Oxygen (+)	0.001	n.s.	0.001	0.005	0.001	0.001	0.001	0.001
$\delta^{13}C$ (+), Dl^l (+)	0.001	n.s.	0.001	0.001	0.001	0.001	0.001	0.001
THAA ^m (–)	0.001	0.05	0.001	0.05	0.001	0.001	0.002	0.001
AA-N ⁿ (–)	0.001	n.s.	0.001	n.s.	0.001	0.005	0.01	0.001
$\delta^{15}N$ (+)	n.s.	0.05	0.01	n.s.	0.02	0.05	n.s.	n.s.
Silt and clay (–)	0.02	n.s.	n.s.	0.02	n.s.	0.05	0.05	0.05
Total N (+)	n.s.	0.001	0.05	n.s.	n.s.	n.s.	n.s.	n.s.
BALA+GABA ^o (+)	n.s.	0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Organic C (+), Chlorins ^p (–)	n.s.	0.001	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
C:N ratio or Bacterial C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

^aTotal species. ^bPielou's evenness. ^cMargalef's index. ^dBrillouin index. ^eFisher's index. ^fShannon index (\log_2). ^gSimpson's index ($1-\lambda'$ form). ^hRarefied species richness ($n = 59$). ⁱRank 1 dominance (inverse form). ^jMultidimensional scaling x-ordinate (no transformation, sqrt, double sqrt, $\log(x + 1)$ and presence/absence transformations). ^kSpecies turnover (cumulative form). ^lAmino acid base degradation index. ^mTotal amino acid yield, carbon normalised. ⁿTotal N in amino acids. ^o β -alanine and η -amino butyric acid. ^pChlorophyll and phaeopigments.

tial variations also occur in sediment OM content and granulometry in this region. Simple (non-parametric) correlations between these depth-related parameters and diversity measures are significant. However, when one of the parameters is isolated through partial correlation analysis, only oxygen exhibits a significant correlation with various diversity measures (Table 2). Thus, despite the existence of these important sources of sediment heterogeneity, the strongest correlation between diversity and an environmental parameter is with oxygen. This suggests that the oxygen gradient is the main source of habitat heterogeneity influencing macrofaunal diversity within the Bay of Bengal OMZ (~130–600 m). Across the lower transition zone off Pakistan, Spearman's rank assessment likewise yields significant positive correlations of species richness with both depth and DO (Fig. 4C,D), as well as between DO and all other diversity parameters (Table 3). There are also significant correlations (both positive and negative) between diversity and measures of OM quality (usually $P < 0.001$) and the silt/clay fraction (usually $P < 0.05$), but not between diversity and total organic carbon or nitrogen. These correlations are based on combined data for the intermonsoon (March–May 2003) and late-to-postmonsoon (August–October 2003) periods. Levin *et al.* (2009), Appendix 4 therein analysed data from these two periods separately and found significant ($P < 0.05$) correlations between dominance (R1D) and $\delta^{13}C$ (intermonsoon), R1D and total N and C_{org} (late-to-postmonsoon), and between H' (\log_2) and bottom-water DO (late-to-postmonsoon). A link between

species (taxon) richness and DO also exists on the slope (Sanders 1969) and shelf (Zettler *et al.* 2009) off Namibia (SE Atlantic).

The diversity of hard-shelled Foraminifera (> 63- μm fraction in unreplicated samples) was low in the Pakistan OMZ core ($O_2 < 0.12 \text{ ml l}^{-1}$), as well as above and below the OMZ ($O_2 > 0.5 \text{ ml l}^{-1}$), and maximal at intermediate DO values ($O_2 = 0.2\text{--}0.5 \text{ ml l}^{-1}$) (Schumacher *et al.* 2007). Replicated foraminiferal data (> 300 μm fraction) from a 140-m site off Pakistan revealed consistently higher diversity during the intermonsoon season, when the site was above the OMZ, than during the monsoon season, when surface productivity was higher and the site was within the OMZ (Larkin & Gooday 2009). Dominance showed a slight drop over the same period. A similar but more muted seasonal response is evident at the permanently hypoxic 300-m site. Comparing the two sites, diversity is consistently lower at 140 m than at 300 m during the monsoon (hypoxic), but more comparable or even higher during the intermonsoon (oxic). These different trends, summarized in a plot of diversity *versus* dominance (Fig. 5), suggest that diversity and dominance are related to differences in DO concentrations.

The invertebrate megafauna are typically more strongly impacted by hypoxia than are the macrofauna or meiofauna (Gooday *et al.* 2009). Off Pakistan, diversity is zero (*i.e.* megafauna are absent) where DO is lowest, but there is a rapid recovery of diversity at slightly higher oxygen levels across the lower transition zone (Fig. 6). This 'edge effect'

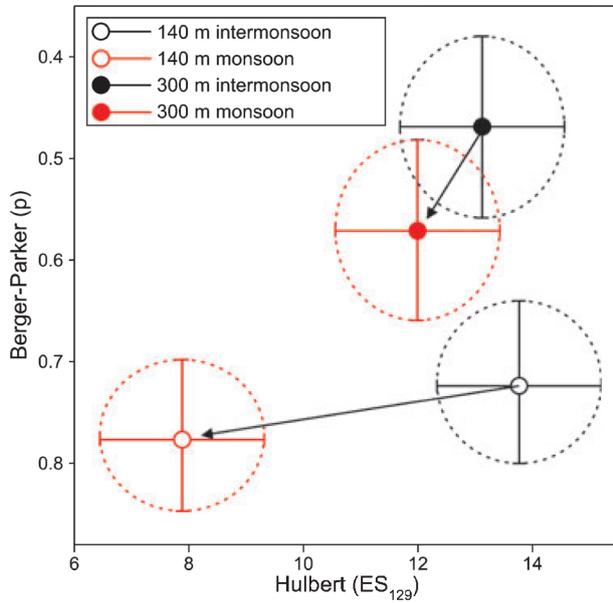


Fig. 5. Foraminifera (Rose-Bengal-stained, >300- μm fraction) from 140 and 300 m (monsoon and intermonsoon seasons) on the Pakistan margin. Joint plot of Berger-Parker Index (Rank 1 dominance) and rarefied species richness (Hulbert), showing 95% confidence limits. Data from Larkin & Gooday (2009).

reflects a release from oxygen stress combined with a rich food supply (Levin 2003; Murty *et al.* 2009). Off Antofagasta, where DO concentrations fall to levels comparable to those off Pakistan, megafauna (mainly one gastropod species) are still present in the OMZ core and there is no indication of an edge effect. In fact, the trend in megafauna-

al diversity along the Antofagasta transect is broadly similar to trends off Concepción and Chiloé, where the OMZ is weak or absent (Fig. 6). However, it should be noted that megafauna may be influenced by oxygen at concentrations > 0.5 ml l^{-1} , particularly in coastal waters (*e.g.* Middelburg & Levin 2009). Fodrie *et al.* (2009) noted a 10% depression of megafaunal evenness at 2000 m on the Aleutian margin ($\text{DO} = 1.11 \text{ ml l}^{-1}$), compared to deeper, better oxygenated sites.

Beta diversity

An extensive suite of data for macrofaunal beta diversity (*i.e.* species turnover expressed as a cumulative percentage) is summarized in Fig. 7. On margins without an OMZ (Figs 7A,E), or with only a weakly developed OMZ (Fig. 7B), turnover is more or less uniform down to 1200–1800 m depth, below which there is little change in species composition down to the maximum depth sampled (2000–3000 m). On margins with an OMZ (Fig. 7C,D,F–H), species turnover is rapid above the OMZ, consistently depressed within the OMZ, then increases again as DO levels begin to rise across the lower boundary. The lower boundary pattern is illustrated clearly by the detailed macrofaunal dataset from 700 to 1100 m off Pakistan (Fig. 7G). Species turnover is low between 720 and 850 m, but increases below 850 m, most steeply between ~920–980 m as DO rises from ~0.14 to 0.16 ml l^{-1} . This pattern is mirrored by the change in assemblage composition on the Pakistan margin, as represented in plots of MDSx *versus* depth and oxygen (Fig. 8). In samples taken along the axis of the Gulf of California (Mexico), where a pronounced OMZ is

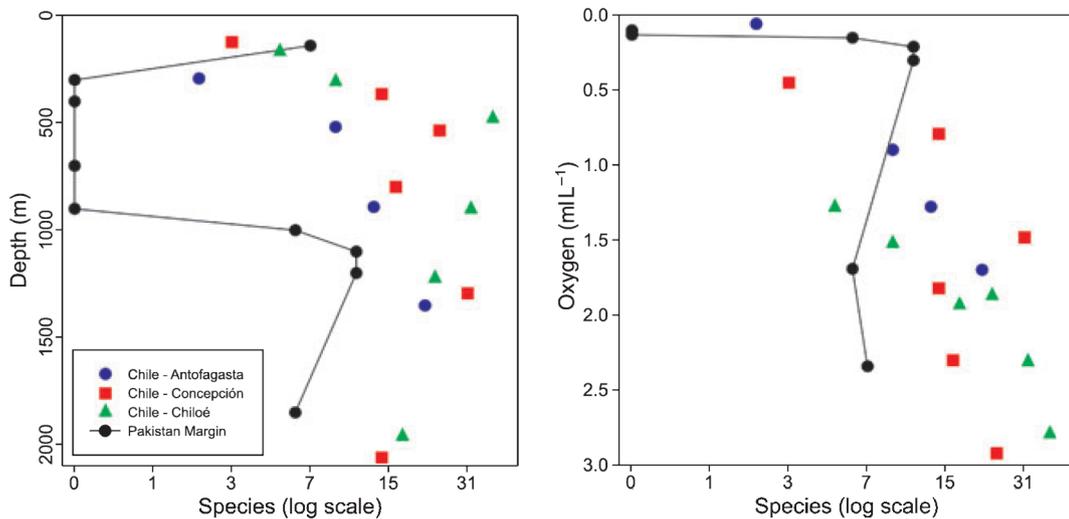


Fig. 6. Diversity of invertebrate megafauna across the Pakistan margin (data from Murty *et al.* 2009) and along three transects off Chile: Antofagasta (strong OMZ), Concepción (weak OMZ) and Chiloé (no OMZ) (data from Quiroga *et al.* 2009).

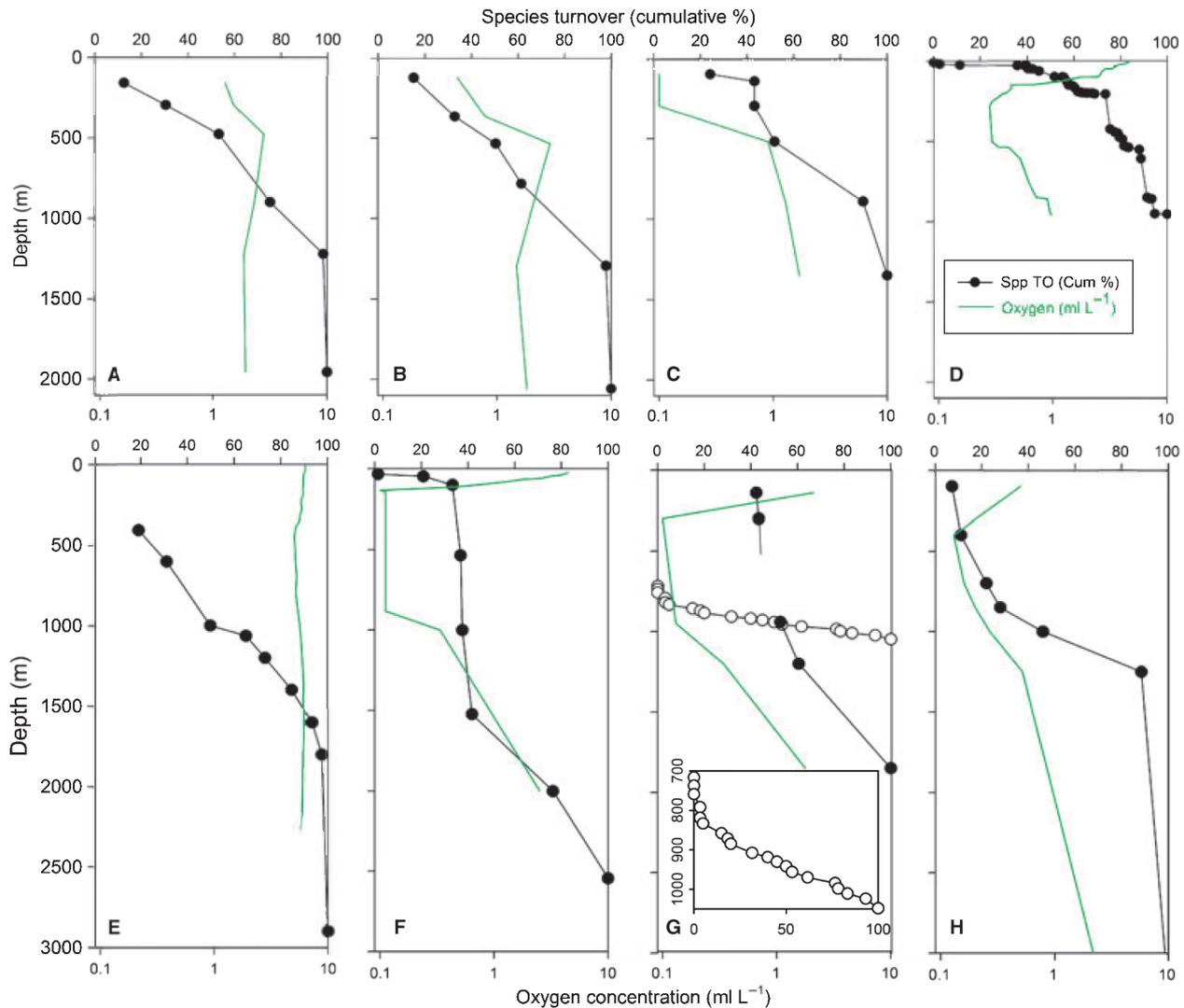


Fig. 7. Beta diversity (solid line, cumulative species turnover as a percentage) plotted against water depth along transects (A) off Chiloé (no OMZ), (B) off Concepción (36° N, weak OMZ), (C) off Antofagasta (23° N, strong OMZ) (all from Chilean margin), (D) Bay of Bengal (eastern Indian margin), (E) Rockall Trough (no OMZ; data from Paterson & Lambshead 1995), (F) western Indian margin, (G) Pakistan margin (solid symbols = data from Hughes *et al.* 2009; open symbols = data from Levin *et al.* 2009), (H) Oman margin (data from Levin *et al.* 2000). The Rockall Trough has been included as an example of a typical normally oxygenated margin. Bottom-water oxygen concentrations are indicated by a coloured line. For the western Indian margin (F), oxygen values are taken from Da Sousa *et al.* (1996), modified by data from RV *Yokosuka* cruise YK08/11.

present, the rate of polychaete species turnover between 740 and 2250 m was lower above ~1300 m ($DO < \sim 0.8 \text{ ml l}^{-1}$) than it was at greater depths (based on analysis of data from Méndez 2006, not shown).

The rate of change in foraminiferal species turnover across the Pakistan margin shows a clear correspondence with DO (Fig. 8). Beta diversity was high across the upper OMZ boundary (136, 150 m), depressed in the core (306–598 m), and then higher across the lower part of the OMZ (598–944 m) before declining again below the OMZ

(1201–1870 m). These trends are compared with those of the macrofauna and megafauna across the same margin in Fig. 9. Both size classes were more or less absent in the OMZ core and the turnover therefore zero. Turnover begins to increase again at 830 m ($O_2 \sim 0.12 \text{ ml l}^{-1}$) for macrofauna and 950 m ($O_2 \sim 0.13 \text{ ml l}^{-1}$) for megafauna, in both cases deeper than the inflection point of 600 m ($O_2 \sim 0.11 \text{ ml l}^{-1}$) for Foraminifera. Macrofaunal beta diversity is very high across the lower transition zone; the first 150-m band (750–850 m) of this intensively sampled

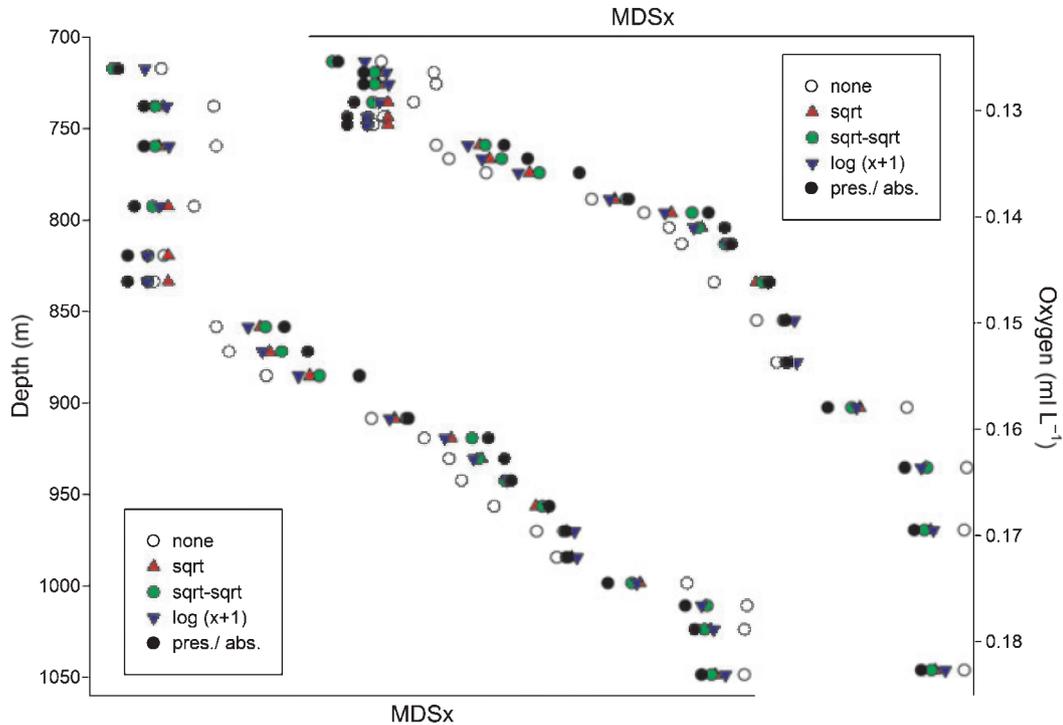


Fig. 8. Multidimensional scaling ordination x-ordinate versus depth and oxygen across the Pakistan margin lower transition zone for a range of data transformations. Note that trends are very similar, regardless of data transformation. Based on data from Levin *et al.* (2009).

region accounts for only 9.5% of species turnover, compared with 73% in the next 150 m (850–1000 m), reducing to 17.6% in the final 100 m (1000–1100 m).

Assemblage composition in relation to habitat characteristics

MDS ordinations reveal significant correlations between species composition and DO. On the Chilean margin off Concepción, there were significant differences in macrofaunal composition between sites at 124 m ($O_2 = 0.45 \text{ ml l}^{-1}$) and 365 m ($O_2 = 0.79 \text{ ml l}^{-1}$) within the OMZ, and deeper sites below the OMZ (Palma *et al.* 2005). Gallardo *et al.* (2004) report distinct macrofaunal assemblages at 122, 206, 365 and 840 m in the same area. Polychaete families showed zonal changes within and beneath the OMZ on the Peru (Levin *et al.* 2002), Oman (Levin *et al.* 2000) and Pakistan margins (Levin *et al.* 2009), with molluscs, crustaceans and echinoderms typically common within the lower OMZ or below it.

An MDS plot revealed significant correlations off Pakistan between foraminiferal species composition and both DO ($r_s = 0.658$, $P = 0.05$) and depth ($r_s = -0.936$, $P < 0.001$) (Fig. 10). TWINSpan analysis based on species occurrences weighted according to abundance, showed a primary split between the two deepest (1201, 1870 m) and the shallower (136–1000 m) sites, a second-

order split between the two shallowest sites (136, 150 m) and those of intermediate depth (306–1000 m), and a third-order split separating the 306-m, 512-m and 598-m sites from the 738–1000-m sites (Fig. 11A). These divisions reflect groups of species that are present only, or mainly, at the two deepest sites (1201, 1870 m), the two shallowest sites (136, 150 m), and intermediate sites (306–1000 m). Another group of species spans these three zones. It appears, therefore, that strong oxygen gradients on the Pakistan margin modify underlying depth-related patterns of foraminiferal species distributions.

An MDS ordination of foraminiferal data from 140 m (seasonally hypoxic) and 300 m (permanently hypoxic) off Pakistan distinguishes the two sites as well as oxic (140 m, intermonsoon) from hypoxic assemblages (Fig. 12). A TWINSpan analysis shows that most of the common species (*e.g.* *Globobulimina cf. Globobulimina pyrula*, *Uvigerina ex. gr. semiornata*, *Cancris auriculus*) occur at both sites. Thus, changes in the abundance of the common species are mainly responsible for the observed shifts in diversity and dominance (Figs 5 and 11B). We conclude that the heterogeneity created by changes in DO concentrations (and a modest depth difference) at these two contrasting sites off Pakistan do not lead to any substantial increase in biodiversity.

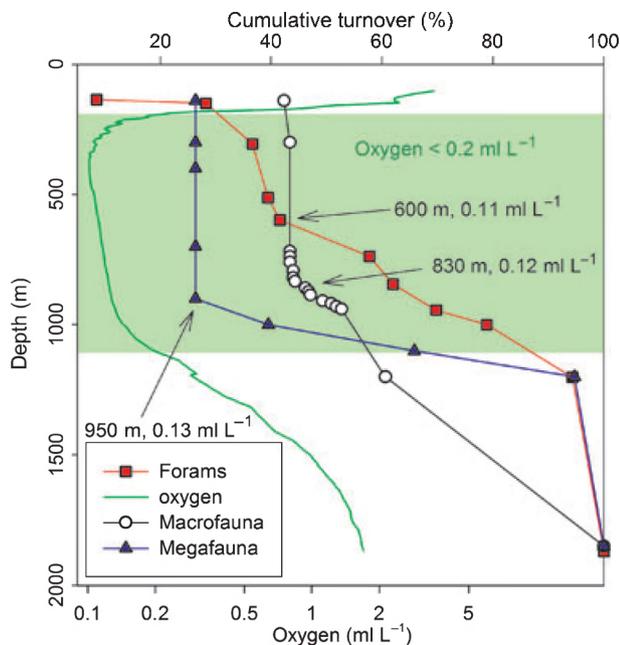


Fig. 9. Beta diversity (cumulative species turnover as a percentage) for megafauna, macrofauna, and Foraminifera (Rose-Bengal-stained, hard-shelled, > 63- μ m fraction) across the Pakistan margin. The oxygen profile is also shown. Foraminiferal data from Schumacher *et al.* (2007), macrofaunal data from Hughes *et al.* (2009) and Levin *et al.* (2009), megafaunal data from Murty *et al.* (2009). Note the increasing depths (600, 830 and 950 m for Foraminifera, macrofauna and megafauna, respectively) of the inflection points where turnover begins to increase through the lower boundary of the OMZ.

Discussion

Influence of OMZs on regional-scale diversity

Recent molecular studies of the foraminiferan *Virgulinitella fragilis* demonstrate that genetically very similar but disjunct populations may live in widely separated hypoxic localities (Tsuchiya *et al.* 2008). In general, however, OMZs do not yield a consistent suite of dominant foraminiferal (Bernhard & Sen Gupta 1999) or metazoan (Levin 2003) species. Among the species mentioned by Levin (2003) as possibly endemic to particular OMZs are two polychaetes, a mytilid bivalve and a tunicaten (off Oman), an oligochaete (Peru/Chile margin), an aplacophoran (Volcano 7, equatorial Pacific) and a meio-faunal polychaete and a gastrotrich (Santa Barbara Basin). Sellanes *et al.* (2010) list two nematode, one oligochaete, four polychaete and three mollusc species that appear to be confined to the OMZ core along the SE Pacific margin. The spider crab *Encephaloides armstrongi* is known only from the Bay of Bengal, the Oman margin, and the Gulf of Oman and is probably confined to the northern Indian Ocean (Creasey *et al.* 1997). The two dominant

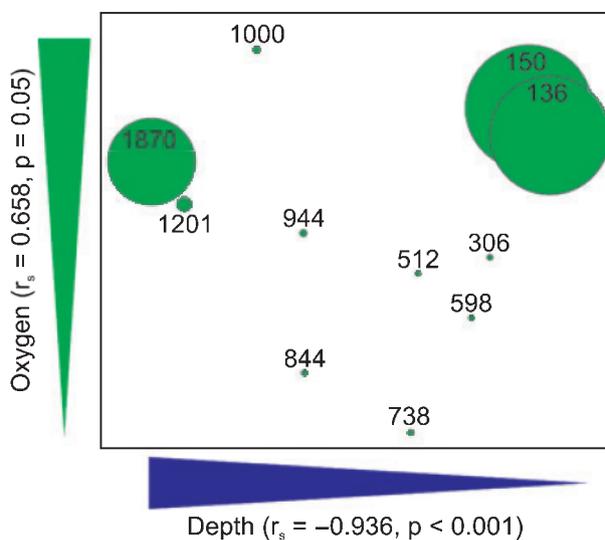


Fig. 10. Multidimensional scaling ordination of Foraminifera (Rose-Bengal-stained, hard-shelled, > 63- μ m fraction) across the Pakistan margin. Symbol size within plot proportional to oxygen concentration. Labels are water depths. Relationships between x- and y-ordinates and water depth and oxygen are also indicated. Based on data from Schumacher *et al.* (2007).

foraminiferal species in the core of the Pakistan margin OMZ (*Uvigerina* ex gr. *U. semiornata* and *Bolivina* aff. *B. dilatata*) are believed to be endemic to the Arabian Sea, whereas cosmopolitan species typify the lower part of the OMZ and deeper regions (Schumacher *et al.* 2007). Despite their relative proximity, there are some faunal differences between opposite sides of the Arabian Sea (Gooday *et al.* 2009). For example, the polychaete *Linopherus* was a dominant species in the lower transition zone off Pakistan but absent off Oman (Levin & Edessa 1997); cirratulid mudballs were common at 820–900 m off Oman, while a different species occurred at 1850 m off Pakistan (L. Levin unpublished).

The degree, if any, to which OMZs enhance regional diversity is difficult to establish. In a study of seep and non-seep sediments at depths of 800 m (within OMZ) and 500 m (above OMZ) on the Oregon and Californian margins, Levin *et al.* (2010) found that only four species were confined to an OMZ setting, suggesting that their contribution to regional diversity is minimal in this area. However, the NE Pacific oxygen minimum zone is relatively weak, with core DO concentrations of 0.2–0.3 ml l⁻¹. More intense OMZs will probably be associated with a higher degree of endemism. Thus, although hypoxia depresses diversity within OMZs, it is possible that OMZs enhance diversity at a regional scale. Sellanes *et al.* (2010) reached a similar conclusion based on a review of datasets from the Chilean margin.

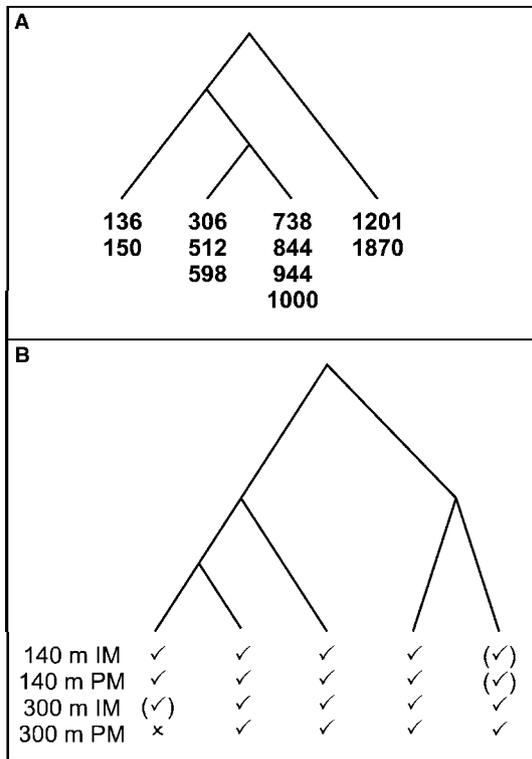


Fig. 11. TWINSpan analyses of foraminiferal assemblages on the Pakistan margin. (A) Site groupings; numbers indicate water depths of sampling sites (hard-shelled species, > 63- μ m fraction, Rose-Bengal stained; data from Schumacher *et al.* 2007). (B) Species groupings [✓] present, [(✓)] represented, [x] absent in intermonsoon (IM) and post-monsoon (PM) samples at two water depths (140 and 300 m) (> 300- μ m fraction, Rose-Bengal stained; data from Larkin & Gooday 2009).

Different size/taxonomic groups show different diversity patterns

Eukaryotic communities inhabiting OMZ settings exhibit several general characteristics (Levin 2003). First, organisms belonging to smaller size classes, namely the meiofauna and to a lesser extent the macrofauna, dominate faunas in OMZ cores. This probably reflects the higher surface area to volume ratio of small benthic animals (Veit-Köhler *et al.* 2009), aided in some nematodes by the development of long spines and setae (Neira *et al.* 2001a, 2005; Neira & Decraemer 2009). Additional physiological adaptations include the widespread presence of haemoglobin in taxa that normally lack this pigment (Levin 2003), the presence of endosymbionts and sequestered chloroplasts in Foraminifera (Bernhard *et al.* 2000; Bernhard 2003) and metazoans (Giere & Krieger 2001; Blazejak *et al.* 2005) and enzymatic adaptations for anaerobic metabolism, involving lactate and pyruvate oxidoreductase, in polychaetes

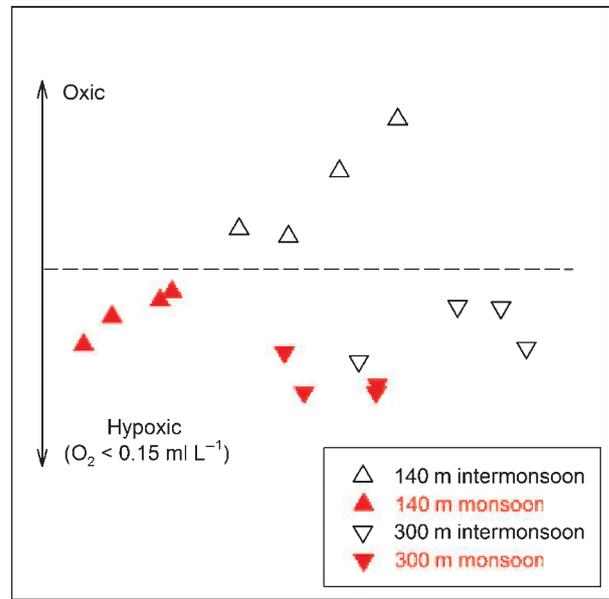


Fig. 12. Multidimensional scaling ordination of foraminiferal assemblages (Rose-Bengal-stained, > 300- μ m fraction) from 140 and 300 m (monsoon and intermonsoon seasons) on the Pakistan margin, using full species abundance data for site-season comparisons of species composition. Data from Larkin & Gooday (2009).

(González & Quiñones 2000). Some Foraminifera store and respire nitrate (Risgaard-Petersen *et al.* 2006; Høglund 2008; Høglund *et al.* 2008), and possibly use intracellular peroxisomes to break down H_2O_2 , releasing oxygen (Bernhard & Bowser 2008). Secondly, certain taxonomic groups are more tolerant of hypoxia than others. Polychaetes are generally the most tolerant macrofaunal taxon (Levin *et al.* 1997), while nematodes and Foraminifera are the most tolerant meiofaunal taxa (Gooday *et al.* 2000; Neira *et al.* 2001b; Veit-Köhler *et al.* 2009). Thirdly, animals with calcareous hard parts, for example echinoderms, are usually absent (although a few gastropod species persist in OMZs). Among the protists, however, Foraminifera with calcareous tests are often abundant where DO is lowest. These different degrees of tolerance to oxygen depletion are well illustrated on the Pakistan margin, where maximum abundances for benthopelagic megafauna, invertebrate megabenthos, metazoan macrofauna, and Foraminifera (the metazoan meiofauna was not analysed) are located progressively closer to the OMZ core, with only Foraminifera persisting across the OMZ (Gooday *et al.* 2009). One implication of these contrasting patterns is that OMZs will tend to enhance the regional diversity of smaller organisms, such as polychaetes, nematodes and Foraminifera, to a greater extent than that of the megafauna (Fig. 9).

Oxygen and organic matter as controls on biodiversity

The depression of diversity on margins impacted by an OMZ is often attributed to the deleterious effects of hypoxia. Support for this idea comes from the decrease in macrofaunal species richness along the Chilean margin from Chiloé (42° S, no OMZ, 26–43 species) to Concepción (36° S, weak OMZ, 14–31 species) to Antofagasta (22° S, strong OMZ, 4–15 species) (Palma *et al.* 2005). A similar decline in meiofaunal diversity at the higher taxon level is observed among metazoan meiofauna (Veit-Köhler *et al.* 2009). At a site on the central Chilean shelf off Concepción, macrofaunal diversity increased during El Niño (oxygenated) events compared to La Niña years, when the site lay within the OMZ (Sellanes *et al.* 2007). Similar changes in macrofaunal species richness were observed on the shelf off central Peru (Gutiérrez *et al.* 2008).

The diversity of OMZ communities, however, is influenced by OM as well as by DO. Levin & Gage (1998) emphasized the influence of DO on species richness and of OM on evenness and dominance measures, *i.e.* they suggested that DO controls the number of species that occur in a particular area, whereas OM controls the abundance of the hypoxia-tolerant species. Based on high-resolution sampling across the lower boundary zone of the Pakistan margin OMZ, Levin *et al.* (2009) came to a rather different conclusion, namely that species richness was related most closely to measures of sediment OM content and quality while diversity (H') and dominance (RID) were related to both DO and OM content. Levin *et al.* analysed intermonsoon and post-monsoon samples separately. We combined these samples to increase the power of the test and found significant positive correlations (all $P < 0.001$) between DO and a suite of diversity, species richness, and evenness parameters, as well as MDSx with all possible transformations (Table 3). There were also significant correlations between these parameters and various measures of OM quality (P usually < 0.001) and sediment granulometry ($P < 0.05$), although not with C_{org} . These results suggest that, in addition to DO, OM quality and, to a lesser extent, sediment granulometry influence macrofaunal diversity.

It seems clear that oxygen is the overriding factor controlling biodiversity in the core regions of OMZs where DO is lowest. As noted above, the concentration at which DO becomes a dominant factor will vary among taxa and size classes, and will be higher in the case of megafauna than, for example, Foraminifera (Fig. 9). However, in the lower parts of OMZs, as DO starts to rise and the stress caused by hypoxia diminishes, a variety of other environmental factors will begin to exert an influence on diversity and create habitat heterogeneity. Among these, OM

amounts and quality are particularly important, together with sediment granulometry. When examining correlations, an important caveat is that the relationships between environmental and community parameters including diversity may be hump-shaped (Levin *et al.* 2001) and therefore not detected by linear correlation analysis. The non-linear nature of these relationships is clearly evident in species-abundance-biomass (SAB) curves along gradients of organic enrichment, compiled by Pearson & Rosenberg (1978; Fig. 1 therein). These also show different community responses in different settings, a degree of variation that is likely to apply in OMZs as well (*e.g.* Fig. 6).

Influence of biotic interactions and biogenic substrata on diversity

Biotic interactions, or the lack of them, may influence diversity within OMZs. Animal tracks, pits, mounds, burrows, dwelling structures and other biogenic constructions are an important source of sea floor heterogeneity, which they create either directly or indirectly by focusing OM (Grassle & Morse-Porteous 1987; Thiel *et al.* 1989; Snelgrove & Smith 2002). The megafaunal animals and protists that create these features are rare or absent in OMZ cores where DO is lowest. On the Pakistan margin, tracks and burrows were seen at 140 m, shallow depressions at 900 and 1000 m, and numerous closely spaced burrows and mounds at 1100 m (Fig. 1G) (Murty *et al.* 2009). However, the sediment surface at 300, 400 and 700 m (Fig. 1F,H) was generally devoid of traces and biogenic structures, apart from arborescent tests of the agglutinated foraminiferan *Pelosina* at 400 and 700 m (Fig. 1D). Consistent with a reduction in surface structure associated with hypoxia, Levin *et al.* (2000) reported greater macrofaunal homogeneity in replicate samples from within the Oman margin OMZ compared to samples from below the OMZ, prompting the conclusion that hypoxia 'may impose habitat homogeneity, contributing to spatially uniform assemblages of low species richness.' The absence or scarcity of larger predators where hypoxia is severe may serve to further depress diversity and increase the dominance of a few species through competitive exclusion, as suggested by Phleger & Soutar (1973) for Foraminifera in eastern Pacific basins. Carcasses preserved in OMZ cores could attract scavengers, leading to a slight increase in species richness. However, these animals are likely to be only temporary residents.

Biological interactions probably become more important as DO levels rise, particularly in the narrow zones characterized by dense aggregations of animals such as ophiuroids, crustaceans or polychaetes beneath the core regions of many OMZs (Mullins *et al.* 1985; Bett 1995;

Levin 2003; Gooday *et al.* 2009). Animal activity in these zones may enhance sediment heterogeneity and predation will probably intensify trophic complexity.

Evolutionary processes creating diversity in OMZs

Oxygen minimum zones have the potential to promote speciation in a number of ways. Over geological time scales, OMZs have expanded and contracted in response to changes in surface productivity linked to climatic cycles, notably during the Pleistocene (Den Dulk *et al.* 1998). High-resolution sediment records from the Pakistan margin reveal the presence of bioturbated sediments corresponding to the early Holocene (7–10.5 ka), the Younger Dryas (11.7–13 ka), Heinrich event 1 (15–17 ka) and Heinrich event 2 (22.5–25 ka). These suggest that the OMZ was very weakly developed during late Pleistocene and early Holocene periods of reduced surface productivity (Von Rad *et al.* 1999). Rogers (2000) suggested that such fluctuations would lead to repeated up- and down-slope movements of species and increased possibilities for population fragmentation and speciation. OMZs may also have caused the isolation of populations, either in oxygenated refugia or, in the case of hypoxia-tolerant species, within the OMZs themselves, again leading to speciation. Significant genetic differentiation has been reported between populations of the spider crab *Encephaloides armstrongi* (Creasey *et al.* 1997) (Fig. 1E) and the squat lobster *Munidopsis scobina* (Creasey *et al.* 2000) on the Oman margin. Based on these and other results, Rogers (2000) concluded that strong gradients in DO and other physical parameters across OMZ boundaries can result in the isolation and genetic differentiation of populations, sometimes compounded by different sex- and size-related responses to hypoxia. These ideas are consistent with the observations of enhanced genetic diversity among molluscs on the mid-slope regions of continental margins (Etter *et al.* 2005). Similar hypotheses, with particular reference to mesopelagic fish, were formulated by White (1987).

Verhallen (1987) also developed ideas about the evolutionary effects of deep-sea hypoxia based on morphological changes over time in populations of the foraminiferan *Bulimina* in relation to periods of severe hypoxia/anoxia, represented by Upper Pliocene sapropel layers in the Mediterranean. He noted that rapid morphological changes ('speciation') coincided with periods of sapropel formation and suggested that rapid genetic change may occur where populations are severely stressed by extreme hypoxia. One possible outcome of fluctuating OMZs is the accumulated enhancement of diversity at bathyal depths. Most margins examined exhibit a mid-slope diversity maximum (Rex 1983, and other references).

Contributions of the OMZ to this diversity pattern remain to be demonstrated but are possible even in oceans without a strong modern-day OMZ.

Future prospects

Evidence from the palaeo-record that oxygen minimum zones have waxed and waned as a result of climatic fluctuations in the geological past raises the prospect of similar changes occurring in the future (Helly & Levin 2004). During the last 50 years, the vertical extent of mid-water OMZs has increased in the eastern tropical Atlantic and equatorial Pacific at the same time as DO has declined (Stramma *et al.* 2008). These trends are particularly apparent in the Atlantic where the vertical expansion amounts to 85% since the 1960s. Off southern California, DO has declined since 1984 over at least the upper 500 m of the water column, with the strongest relative decrease observed at 300 m (Bograd *et al.* 2008). These trends may be linked to climatic changes, in particular global warming leading to a rise in ocean temperature, thereby enhancing upper-ocean stratification, reducing mixing, and decreasing the solubility of oxygen in seawater.

The effect of an increase in the extent and intensity of OMZs on regional and global benthic biodiversity on continental margins is difficult to assess, but the overall impact will probably be negative. OMZs are more weakly developed in the Atlantic than in the Pacific and Indian Oceans, and hence the scope for their intensification, and the resulting likely decrease in biodiversity, could be most pronounced in this ocean (Stramma *et al.* 2008).

Gaps in Knowledge and Hypotheses for the Future

1 Our knowledge of cross-margin trends in diversity and faunal composition in OMZ settings has grown steadily during the last two decades, particularly on the Arabian Sea and eastern Pacific Ocean. This continuing research effort is revealing that, although OMZ communities share many environmental and faunal characteristics, they also exhibit features that are peculiar to each margin. The factors underlying these differences are often unclear and require clarification.

2 Much remains to be learned about biological interactions within OMZs, and particularly their effects on diversity. For example, the dense swarms of large animals (*e.g.* ophiuroids, spider crabs) that occur in narrow bands within the lower transition zones may impact the smaller organisms living in the sediment, through predation, sediment disturbance or alteration of the sediment chemistry. Little is known about the nature of these possible interactions, how they may influence diversity, and how they vary across OMZs.

3 The contribution of OMZs to regional diversity is largely unknown. This reflects the lack of detailed knowledge of the species composition of OMZ assemblages. Inventories of metazoan and foraminiferan species present in different OMZs would help to alleviate this gap. There is some evidence for endemism among foraminiferal and macrofaunal species. Molecular studies of similar morphospecies from different margins may cast some light on whether endemic species are common in OMZ settings, and also whether cryptic speciation is prevalent.

4 Although OMZ core regions are remarkably stable over ecological timescales, particularly when compared with seasonally hypoxic coastal settings, they have undergone repeated expansions and contractions over geological time. The idea that these fluctuations have led to speciation has never been tested. The most recent weakening of the Pakistan margin OMZ occurred in the early Holocene. This relatively recent event possibly had an impact on modern assemblages. Again, molecular approaches may yield some insights into these questions.

5 We know very little about how pH interacts with other environmental factors to influence biodiversity in OMZs. Evidence from other settings suggests that the effect will be a negative one. However, more data on pH are needed to assess whether this rarely measured parameter is a significant driver of diversity trends within OMZs.

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