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## Habitat heterogeneity and its relationship to biodiversity in oxygen minimum zones

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**Abstract.** Oxygen minimum zones (OMZs) are major oceanographic features, particularly in the eastern Pacific Ocean and the Arabian Sea. Where OMZs intercept continental margins, sources of seafloor habitat heterogeneity include bottom-water oxygen and sulphide gradients, substrate characteristics, bacterial mats, and variations in sediment organic matter content and pH. On some margins (e.g. Peru), hard grounds represent a distinct subhabitat colonized by encrusting faunas. However, heterogeneity within OMZs is created mainly by strong seafloor oxygen gradients, reinforced by changes in sediment characteristics and organic carbon content. For the Pakistan Margin, combining these parameters revealed clear environmental differences between the OMZ core and the upper and lower boundary regions. In all Pacific and Arabian Sea OMZs examined, alpha and beta diversity and macrofaunal assemblage composition were related closely to oxygen, particularly in the OMZ core where very low oxygen levels were the main drivers of community structure and composition. However, detailed sampling across the lower boundary of the Pakistan Margin OMZ suggests that other factors, notably organic matter quantity and quality and sediment characteristics, come into play as oxygen concentrations begin to rise. Off Oman, faunal composition was more homogenous in the OMZ core than at sites above and below this zone. The influence of OMZs on diversity at larger spatial scales is difficult to assess. Hypoxia is associated with a reduction in species richness, but there is also evidence for endemism in OMZs 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.

**Keywords:** continental margin, OMZ, hypoxia, alpha diversity, beta diversity, regional diversity

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## 1. The Problem

Oxygen minimum zones (OMZs), defined as layers of the water column where dissolved oxygen (DO) concentrations fall below  $0.5 \text{ ml L}^{-1}$  ( $<22 \text{ } \mu\text{M}$ ), are important hydrographic features in 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 and Levin, 2004; Paulmier and Ruiz, 2008). They persist over geological time scales and result from a combination of factors, including high surface productivity and limited water-column ventilation resulting from stratification and isolation of older, oxygen-depleted water masses. The upper boundaries of Pacific OMZs may move up and down in response to decadal El Nino events (Arntz et al., 2006; Hormazábal et al., 2006; Sellanes et al., 2007), or seasonal productivity cycles, for example, in the Arabian Sea (Brand and Griffiths, 2009; Pantoja and Ruiz, 2008), 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 (da Sousa et al., 1996; Pantoja and Ruiz, 2008). Other parameters also vary across OMZs. In particular, organic-matter concentrations, which are typically inversely linked to oxygen, are often high (Levin and 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 typically very soft and unconsolidated in the core regions of OMZs. Variations in these parameters create gradients on the seafloor, rather than spatially distinct habitats. More discrete, visually obvious source of heterogeneity are created by extensive bacterial mats, authigenic phosphorites (Veeh et al., 1973; Froelich et al., 1988), and the accumulated skeletal parts and carcasses of marine organisms (Milessi et al., 2005; Billett et al., 2006).

Where these mid-water features impinge on the seafloor on the outer shelf, upper slope and oceanic seamounts, they have a strong effect on the abundance, diversity, and composition of benthic faunas (Levin 2003). Benthic communities in the core regions of OMZs typically exhibit depressed levels of diversity and species richness and high dominance by a few tolerant species (Levin 2003). The lower parts of OMZs (lower transition zone), however, are often regions of intense biological activity characterized by huge abundances of a few species belonging to taxa such as ophiuroids or spider crabs (Levin 2003; Gooday et al., 2009). 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, 2005). Thus, although

OMZs exhibit sharply depressed diversity, fine-scale faunal zonation in response to strong seafloor gradients may increase species richness. It is also possible that they act as barriers that enhance diversity over evolutionary time by promoting genetic differentiation. In this paper, we explore the sources of heterogeneity within OMZs and their influence on biodiversity. Specifically, we ask: 1) how can habitat heterogeneity within OMZs be defined, 2) how does it influence alpha and beta diversity within particular OMZs and 3) how does it influence regional (gamma) diversity on continental margins?

## **2. Sources of heterogeneity and mechanisms linking them to biodiversity**

### *2.1. Oxygen and sulphide*

Levin (2003, Fig. 2 therein) compiled oxygen profiles across different OMZs. Although the thickness of these features, and the location of their upper and lower boundaries, varies across margins, the general pattern is consistent. Water-column DO usually falls rapidly across the upper boundary, the depth of which may vary seasonally, and rise more-or-less gradually (depending on local conditions) 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. As mentioned above, sulphide is not usually a major stress factor in OMZs. Where present, however, it inhibits aerobic respiration and can also react with trace amounts of oxygen to form hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), leading to cell damage (Bernhard and Bowser, 2008).

Reduced bottom-water DO limits oxygen penetration of the sediment and thereby 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 attributes 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 has been observed in spionid, dorvilleid, and lumbrinerid, nereid, terebellid and onuphid polychaetes inhabiting OMZs (Lamont & Gage, 2000; Levin et al., submitted, unpublished data). Nematodes in the genus *Glochinema* are covered with hairs that appear adapted to oxygen uptake in the OMZ (Neira et al., 2005). Enhanced numbers and size of ctenidia have been also observed in a new *Leptochiton* species (Mollusca, Polyplacophora) inhabiting bone-covered sediments within the OMZ off northern Chile (Schwabe and Sellanes, submitted). Some hypoxia-tolerant foraminiferal species have flattened test morphologies 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. Because community biomass size diversity is lower, OMZ communities encompass fewer size classes than those found on well-oxygenated margins (Quiroga et al., 2005).

Physiological adaptations to hypoxia include the widespread presence of haemoglobin in taxa that normally lack this respiratory pigment (Levin, 2003), and the storage by some foraminifera of nitrate that is respired to dinitrogen gas when oxygen is scarce (Risgaard-Petersen et al. 2006; Høglund et al., 2008). Nitrate storage has been recognised in 27 foraminiferal species, many of them associated with OMZs (Høglund, 2008). The cytoplasm of some species living in sulphidic/hypoxic settings contains numerous peroxisomes. These organelles are believed to break down  $H_2O_2$ , eliminating this harmful chemical and releasing oxygen (Bernhard and Bowser, 2008). The presence of endosymbionts and sequestered chloroplasts constitutes another adaptation to hypoxic/sulphidic conditions in foraminifera (Bernhard et al., 2000; Bernhard, 2003) and metazoans (Giere and Krieger, 2001). Six species of endosymbionts are present in the oligochaete *Olavius crassitunicatus* from the Peru Margin (Blazjak et al., 2005). Enzymatic adaptations for anaerobic metabolism, involving lactate and pyruvate oxidoreductase, have been reported for polychaetes from OMZ sediments off Central Chile (González and Quiñones, 2000). Of nine species analyzed, only those with two or more pyruvate oxidoreductases were able to occupy sites with permanent bottom-water oxygen deficiency.

## 2.2. Organic matter (OM)

Low DO exerts a powerful influence on the degradation of organic matter. 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% 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 (summarized by Cowie and Levin, 2009; Cowie et al., 2009). Much of the OM in the sediment was degraded. Concentrations varied by a factor of 3 across the margin. However, although there was a general enhancement of OM across the OMZ, there were also variations that were unrelated to oxygen. In particular, OM content was maximal within the lower transition zone rather than in the OMZ core, where DO was lowest. On the other hand, the proportion of degraded material was lower in the OMZ core than at depths above and below the core. The factors causing these variations in OM content and quality are unclear, but 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 phytosterols.

### *2.3 Low pH*

High amounts of OM and elevated respiration rates within OMZs are likely to lead to acidic conditions where oxygen depletion is most intense and create a pH gradient across the zone. Relatively few pH measurements have been made in OMZs. Low values ( $< 7.5$ ) are associated with low oxygen ( $< 0.2 \text{ ml L}^{-1}$ ) waters at depths of 60-1200 m on the Mexican Margin (Fernandez-Alamo and Färber Lorda, 2006), and at 800 m off southern California (Levin and Tanner, 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 to 7.8 (C. Tanner, K. Oguri, personal comm.).

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; Mojtahid 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 (Ramirez-Llodra and Olabarria, 2005; Levin et al., 1997). This suggests that some organisms with calcareous hard-parts have adapted to persistent, slightly acidic conditions.

### *2.4. Substratum characteristics*

Sediment types are often heterogeneous across OMZs (Levin et al., 2002). The upper boundary regions are typically characterised by coarse substrates. Sediments in OMZ cores are unconsolidated with a high water content, easily resuspended and penetrated as well as being usually rich in OM with a substantial phytodetritus component (Pfannkuche et al. 2000). Extensive areas of seafloor off Goa are covered in large ripples, presumably created by current activity, despite being overlain by severely oxygen-depleted water. The nature of the sediment poses life-style challenges to benthic organisms. 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). Some nematodes have specialized external morphologies and ornamentation. Species of the genus *Glochinema* living in OMZs have rather large bodies with spiny ornamentation that increases their surface area (Neira et al., 2001, 2005). In addition to long somatic setae that may enhance oxygen uptake, the presence of various rows of long ambulatory setae probably aid balance and locomotion on soft sediment. Ambulatory setae are a unique taxonomic characteristic of Epsilonematidae, a family most associated with phytal and coarse sandy sediments. With a specific gravity close to that of water, it is unlikely that any nematode has balance problem. Another example is *Desmotersia levinae*, recently described from the Peru Margin OMZ core where it occupies mostly subsurface sediments (Neira and Decraemer, 2009). In this species, the surface area of the slender body is increased by a dense hairy, spiny ornamentation that may contribute to better motility and balance, and avoid the animal sinking deep in slurry-like sediments.

Authigenic phosphorites provide hard substrates for attached organisms around the upper and lower boundaries of the Peru Margin OMZ. Among these are 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 and Glenn, 1997). These attached faunas are concentrated in the upper and lower parts of the Peru Margin OMZ, an example of an edge effect. A similar phosphorite habitat (including also abundant whale bones) and fauna is present within the OMZ core off Concepción at 240 m depth (J. Sellanes, personal observation). A new species of polyplacophoran (*Lepidozonia balaenophila* Schwabe and Sellanes 2004) was described from this site and the fauna also included an unknown species of actiniaria, solitary scelactinians, an asteroid (*Poraniposis echinaster*), a squat lobster (*Cervimunida jhoni*), a mantis shrimp (*Pterygosquilla armata*), a pandalid shrimp (*Heterocarpus reedi*) and four species of fish.

### 2.5. Biogenic structures and activities

On a small spatial scale, biogenic structures may create substantial habitat heterogeneity within OMZs. Such structures include polychaete tubes, the mud ‘houses’ of ampeliscid amphipods, and tree-like tests of the foraminiferan *Pelosina*. Polychaete tubes are known to provide a substrate for attached foraminifera (e.g. Langer and Bagi, 1994; Mackensen et al., 2006). Although we are not aware of any reports of such associations from an OMZ setting, the dense concentrations of polychaete tubes within some OMZs suggests that they are likely. Associations between protists of different sizes may be fairly common. At 1000-m depth within the Pakistan Margin OMZ, tree-like

*Pelosina* tests provide a substrate for the gromiid *Gromia pyriformis* and the foraminiferan *Bathysiphon* sp. (Gooday and Bowser, 2006). Large, mobile animals, including the vast numbers of spider crabs observed in the lower OMZ off Oman (Bett, 1995), represent another potential substrate for attached organisms.

Bacterial mats often provide a localised, 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 and Nelskam, 2006). The overall abundances of stained benthic foraminifera were much lower, however, within the mat.

Animal traces (*lebenspurren*) 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 seafloor was more or less devoid of traces at 300, 400 and 700 m, but characterised 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 and fewer but larger burrows, biogenic depressions and locomotory traces at 1250 m (Murty et al., 2009). Similarly, sediment mixing by bioturbation is dependant on the extent to which burrowing macrofauna are eliminated by oxygen depletion (Cowie and Levin, 2009; Levin et al., 2009).

## 2.6. Carcasses

Large numbers of dead jellyfish were photographed on the seafloor within and below the Oman Margin OMZ (300-3300 m water depth) in December 2002 (Billett et al., 2006). At depths within the OMZ (<1000 m), the jellyfish appeared undecomposed and many were observed rolling downslope along the seafloor. 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 seafloor off Pakistan (Murty et al., 2009). 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, pers. comm.) and large numbers of swimming crabs (*Charybdis smithii*) were found dead on the abyssal seafloor in the northern Arabian Sea (Christiansen and Boetius, 2000). If they occurred within the OMZ, these animal remains could influence biodiversity 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.

### *2.6. Regional setting*

Proximity to major rivers may lead to increased habitat heterogeneity. The upper continental slope off N. California receives copious amounts of wood from the Eel R., which frequently sends flood deposits across the shelf onto the slope. Some of this material may fuel the methane seeps that occur at ~500 m. Large amounts of wood have also been observed on the Costa Rica seafloor within the OMZ (Levin, unpubl.). Bottom topography is also important. Rao and Veerayya (2002) 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.

## **3. Methods**

### *3.1. Data sources.*

The data analysed were derived from published and unpublished sources. They originated from the Chilean and Mexican Margins (eastern Pacific), the Oman, Pakistan and Indian Margins (Arabian Sea), and the eastern side of the Bay of Bengal (Table 1)..

### *3.2. Statistical methods*

#### *3.2.1. 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.



### 3.2.2. 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 symbology. The Berger–Parker ( $n_{\max}/N$ ) and 'Rank 1 dominance' ( $100*n_{\max}/N$ ) 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):  $\beta_c = (A_s + D_s) / 2$ , where  $A_s$  is the number of arriving species (i.e. their apparent minimum depth of occurrence) and  $D_s$  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 from the maximum depth sampled and arrivals doubled to compensate.

### 3.2.3. 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).

### 3.2.4. 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).

## 4. Observations and results

### 4.1. Defining HH within OMZs.

Visually obvious habitat heterogeneity within OMZs is created by phosphatic hardgrounds, whale bones and other hard substrates. HH arising from gradients in bottom-water DO and other parameters is more subjective. Cowie and Levin (2009) and Gooday et al. (2009) partitioned the Pakistan Margin OMZ into the following regions, based mainly on DO and the presence or otherwise of sediment laminations: 1) seasonally hypoxic zone (140-250 m;  $O_2$  fluctuating from 0.11 to 2.05 mL

L<sup>-1</sup>; laminations appearing at 250 m); 2) OMZ core (250-750 m; O<sub>2</sub> = 0.10-0.14 mL L<sup>-1</sup>; fully laminated sediments); 3) OMZ transition zone (750-1000 m; O<sub>2</sub> = 0.12-0.17 mL L<sup>-1</sup>; partially laminated sediments); 4) OMZ boundary (1000-1300 m; O<sub>2</sub> = 0.15-0.50 mL L<sup>-1</sup>) and 5) a region beneath the OMZ (1300 – 1850 m; O<sub>2</sub> >0.50 mL L<sup>-1</sup>). Despite important faunal differences between OMZs, similar subjective schemes may be applicable on other margins.

An extensive dataset of other sediment parameters (Corg, TN, δ<sup>13</sup>C, δ<sup>15</sup>N, silt/clay content) is available across the Pakistan Margin OMZ, between 140 and 1850 m depth (Fig. 1). Plots of individual parameters against water depth show that 1) the shallowest and deepest sites are distinct from those clustered within the OMZ and 2) 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 Principal Components Analysis, 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 enrichment, tend to reinforce the environmental contrasts created by strong oxygen gradients within OMZs.

#### 4.2. The influence of HH on diversity and assemblage composition within OMZs

##### 4.2.1. Alpha diversity

The best alpha diversity dataset is for macrofauna. 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) (Figs 2a,b). These trends in diversity with depth are similar to those observed in the Rockall Trough (Fig. 2e) (Paterson and 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 core of the intense Chilean OMZ near Antofagasta, diversity is strongly depressed (Fig. 2c; Palma et al., 2005). The relationships between oxygen and macrofaunal diversity on the Bay of Bengal, Pakistan and Oman Margins (Figs 2 d-f) 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<sub>2</sub> = 0.12-0.14 mL L<sup>-1</sup> = 5-6 μM), increases rapidly between 800 and 900 m, and reaches maximal values at 1000 m (Fig. 2g). The 700 to 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 ~1000 m (Fig. 2f).

There are strong correlations between alpha diversity and 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. 3a,b). Substantial variations also occur in sediment OM content and granulometry in this region. Simple (non-parametric) correlations generally yield significant results between these parameters, all of which are related to depth, and diversity measures. However, when one of the parameters is isolated through partial partial correlation analysis, i.e. the linkage to depth is removed, 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. Across the lower transition zone off Pakistan, Spearman's rank correlation likewise yields significant correlations of species richness with both depth and DO (Figs 3c,d), as well as between DO and all other diversity parameters (Table 3). There are also significant correlations 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 R1D and  $\delta^{13}\text{C}$  (intermonsoon), R1D and total N and  $\text{C}_{\text{org}}$  (late-to-postmonsoon), and between  $H'$  ( $\log_2$ ) and bottom-water DO (late-to-postmonsoon).

The diversity of hard-shelled foraminifera ( $>63\text{-}\mu\text{m}$  fraction in unreplicated. samples) was low in the Pakistan OMZ core ( $\text{O}_2 < 0.12 \text{ mL L}^{-1}$ ), as well as above and below the OMZ ( $\text{O}_2 > 0.5 \text{ mL L}^{-1}$ ), and maximal at intermediate DO values ( $\text{O}_2 = 0.2\text{-}0.5 \text{ mL L}^{-1}$ ) (Schumacher et al., 2007). Replicated macrofaunal foraminiferal data ( $>300 \mu\text{m}$  fraction) reveal consistently higher diversity during the intermonsoon than during the monsoon at 140 m (seasonally hypoxic) off Pakistan, with dominance showing a slight drop. 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 140m than at 300 m during the monsoon (hypoxic), but more comparable or even higher during the intermonsoon (oxic). These different trends, summarised in a plot of diversity versus dominance (Fig. 4), suggest that diversity and dominance are related to differences in DO concentrations.

The invertebrate megafauna are typically more strongly impacted by hypoxia than the macrofauna or meiofauna. 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. 5). This ‘edge effect’ 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 megafaunal diversity along the Antofagasta transect is broadly similar to trends off Concepción and Chiloé, where the OMZ is weak or absent (Fig. 5).

#### 4.2.2. Beta diversity

An extensive suite of data for macrofaunal beta diversity (i.e. species turnover expressed as a cumulative percentage) is summarised in Fig. 6. On margins without an OMZ (Figs 6a,e), or with only a weakly developed OMZ (Fig. 6b), turnover is more or less uniform down to a depth of 1,200-1,800 m, below which there is little change in species composition down to a maximum depth of 2,000-3,000 m. On margins with an OMZ (Fig. 6c,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 700-1100 m off Pakistan (Fig. 6g). Cumulative species turnover is low between 720 and 850 m, but increased below 850 m, most steeply between ~920-980 m as DO rose from ~0.14 mL L<sup>-1</sup> to 0.16 mL L<sup>-1</sup>. This pattern is mirrored in the change in assemblage composition on the Pakistan Margin, as represented in plots of MDSx versus depth and oxygen (Fig. 7). In samples taken along the axis of the Gulf of California (Mexico), between 740 and 2250 m, the rate of polychaete species turnover was lower above ~1300 m (DO <~0.8 mL L<sup>-1</sup>), than it was at greater depths (data not shown).

The relationship between foraminiferal species turnover and oxygen across the Pakistan Margin was highly significant ( $p < 0.001$ ). 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. 8. 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 ( $O_2 \sim 0.13 \text{ mL L}^{-1}$ ) for foraminifera. Macrofaunal beta diversity is very high across the lower transition zone.

#### 4.2.3. 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. Off Pakistan an MDS plot revealed significant correlations between foraminiferal species composition and both DO ( $r_s = 0.658$ ,  $p = 0.05$ ) and depth ( $r_s = -0.936$ ,  $p < 0.001$ ) (Fig. 9). TWINSPLAN 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, 512 and 598-m sites from the 738-1000-m sites (Fig. 10). 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 macrofaunal 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. 11). A TWINSPLAN tabulation shows that most of the common species occur at both sites. Thus, changes in the abundance of the common species are mainly responsible for the observed shifts in diversity and dominance (Fig. 12.). 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.

#### 4.3. Faunal homogeneity

Based on replicated box core samples from the Oman Margin, Levin et al. (2000) concluded that macrofaunal heterogeneity was greater at 1250 and 3400 m sites, situated respectively near the lower boundary and below the OMZ, than within the central part of the OMZ. Our analysis of within-site similarity (Bray-Curtis,  $\log x+1$  transformed data) of the same macrofaunal data confirms that faunal composition is more homogeneous at the OMZ sites (particularly 400 and 850 m) than at either 1250 m (where similarity is minimal) or 3300 m (Fig. 13).

#### 4.4. Influence of OMZs on regional-scale diversity

Although some faunal commonalities exist between OMZs, there is no general consistency in the dominant species of foraminifera (Bernhard and Sen Gupta, 1999) and metazoans (Levin 2003) inhabiting OMZs. Among the species mentioned by Levin (2003) as possibly endemic to particular OMZs are two polychaetes, a mytilid bivalve and a tunicate (off Oman), an oligochaete (Peru/Chile Margin), an aplacophoran (Volcano 7, equatorial Pacific) and a meiofaunal polychaete and a gastrotrich (Santa Barbara Basin). The spider crab *Encephaloides armstrongi* is known only from the Bay of Bengal, the Oman Margin, and the Gulf of Oman and probably confined to the northern Indian Ocean (Creasey et al., 1997a). At shallower depths, the hypoxia tolerant fauna include spionids, onuphids and cossurids (Levin et al. submitted – SCOR ms). The two dominant 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, whereas cosmopolitan species typify the lower part of the OMZ and deeper regions (Schumacher et al., 2007). Despite their relative proximity, there are a number of 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; cirratulid mudballs were common at 820-900 m off Oman while a different species occurred at 1850 m off Pakistan. Although quantitative data on endemism are rare, there is some evidence that levels may be enhanced in OMZs compared with seeps and normal slope areas. In a study of seep and non-seep margin sediments at 500 and 800 m in the NE PACific (Levin et al., this volume), 17% and 25% of macrofaunal species were confined to the OMZ at 800 m off Oregon and California respectively. These proportions are substantially higher than those in seep-related habitats (14- 40% off Oregon; 8-22% off California) (Levin et al., this volume).

The influence of OMZs on regional-scale diversity is poorly understood, and we know almost nothing about connectivity between different OMZs, or between hypoxic and oxic margins. On the Oregon Margin, where seeps occur within an OMZ, only 32-35% of macrofaunal species occur at seep and non-seep sites. On the Oregon and Californian Margins, SIMPER analyses revealed a higher degree of similarity between samples from the OMZ (54-57%) than between seep samples from clam bed or bacterial mat sediments in a seep (32-37%) (Levin et al., this volume). However, there was more dissimilarity between seep and OMZ habitats off Oregon (90-91%) than between seep and normal seafloor habitats off California (82-89%). This suggests that 1) the NE Pacific OMZ encompasses less HH, and consequently has lower biodiversity, than seeps in the same area and 2) OMZ assemblages are distinctly different from those inhabiting seeps and normal slope areas on the

same margin. Thus, although hypoxia leads to a reduction in species richness, many of the species found in OMZs do not occur in other continental margin settings. On balance, we therefore consider it likely that OMZs enhance regional diversity.

## 5. Discussion

### 5.1. *Different size/taxonomic groups show different patterns*

The composition of eukaryotic communities inhabiting OMZ settings exhibits several general tendencies (Levin 2003). First, organisms belonging to smaller size classes, namely the meiofauna and to a lesser extent the macrofauna, dominate faunas in OMZ cores. Among other things, this probably reflects the higher surface area to volume ratio of small animals (Veit-Köhler et al., 2008). Megafaunal animals (and protists) are generally absent (Murty et al., 2009), except for demersal fishes that can swim in and out of oxygen-depleted bottom water masses. Second, 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; Veit-Köhler et al., 2008). Third, animals with calcareous hard parts, for example, echinoderms, are usually absent (although a few gastropod species persist in OMZ cores). However, among the protists, 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 have a stronger negative impact on the regional biodiversity of larger animals than on smaller animals and protists, particularly polychaetes, nematodes, and foraminifera (Fig. 7). However, the diversity of even the tolerant taxa is severely reduced in hypoxic settings.

### 5.2. *Oxygen and organic matter as controls on biodiversity*

The depression of species richness and 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, 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., 2008). At a site on the central Chilean shelf off Concepción,

macrofaunal diversity increased during El Niño (oxygenated) events compared to ‘normal’ years, when the site lay within the OMZ (Sellanes et al., 2006). Similar changes in macrofaunal species richness were observed on the shelf off central Peru (Gutiérrez et al., 2008).

However, the diversity of OMZ communities is influenced by OM as well as by DO. Levin and Gage (1998) emphasised the influence of DO on species richness and of OM on evenness and dominance measures; i.e. they suggested that OM controls the abundance of species while DO controls the number of species that can occur in a particular area. 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 (R1D) were related to 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, evenness and dominance 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 between taxa and size classes, and will be higher in the case of megafauna than, for example, foraminifera (Fig. 8). In the lower parts of OMZs, however, as DO start 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 to keep in mind is that the relationships between environmental and community parameters including diversity are hump-shaped and therefore not really suitable for linear correlation analysis. The non-linear nature of these relationships are clearly evident in species-abundance-biomass (SAB) curves along gradients of organic enrichment, compiled by Pearson and 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 (e.g., Fig. 5).



### *5.2. Influence of biotic interactions and biotic substrates 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 seafloor heterogeneity, which they create either directly or indirectly by focusing OM (Grassle and Morse-Porteous, 1987; Thiel et al., 1988; Snelgrove and Smith, 2002). These features originate from the activities megafaunal animals and protists which are rare or absent in OMZ cores where DO is lowest. Off Pakistan, tracks and burrows were seen at 140 m site, shallow depressions at 900 and 1000 m, and numerous closely-spaced burrows and mounds at 1100 m (Murty et al., 2009). However, the sediment surface at 300, 400 and 700 m was generally devoid of traces and biogenic structures, apart from arborescent tests of the agglutinated foraminiferan *Pelosina* at 400 and 700 m. 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 (Fig. 13), 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, as suggested by Phleger and 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 characterised by dense aggregations of animals such as ophiuroids, crustaceans or polychaetes that are developed beneath the ore 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

### *5.3. 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). According to Rogers (2000), these kinds of fluctuations would have led to repeated up- and down-slope movements of species and increased possibilities for population fragmentation and speciation events. 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) 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. These were based on the morphological evolution of populations of the foraminiferan *Bulimina* in relation to periods of severe hypoxia/anoxia represented by sapropel layers of Upper Pliocene age 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.

#### 5.4. Future prospects

Evidence from the palaeo-record that OMZs have waxed and waned as a result of climatic fluctuations in the geological past raises the prospect that similar changes may occur in the future (Helly and Levin, 2004). During the last 50 years, the vertical extent of mid-water oxygen minimum zones 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 being 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 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, is most pronounced in this ocean (Stramma et al., 2008).

## **6. 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 Arabian Sea and eastern Pacific margins. 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 elucidation.

2) Much remains to be learnt 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, either 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. An inventory 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 would help to determine whether endemic species are common in OMZ settings, and also whether cryptic speciation is prevalent.

4) Although OMZs are remarkably stable over ecological timescales, particularly when compared with seasonally hypoxic coastal settings, they have undergone repeated expansions and contractions over geological time. It has been suggested these fluctuations have led to speciation, but this idea 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 influences biodiversity in OMZs. Evidence from other settings suggests that the effect will be a negative one. However, more data on pH are needed in order to assess whether this rarely-measured parameter is a significant driver of diversity trends within OMZs.

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## Figure captions

Fig. 1. Trends in environmental parameters with depth across the Pakistan Margin OMZ. (a) – (f) Parameters plotted as normalised transforms (i.e. standard deviation units). Note that arrows indicate increasing values. (g) – (h) Principal Components Analysis of normalised environmental data shown in a-f. PCA1 encompasses 71% of the variation in these data.

Fig. 2. Alpha diversity ( $H' \log_e$ , solid 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) eastern Indian Margin (Bay of Bengal), e) Rockall Trough (data from Paterson and Lamshead, 1995), f) western Indian Margin, g) Pakistan Margin (data from Hughes et al. (2009) and Levin et al. (2009)), h) Oman Margin (data from Levin et al., 2009). The Rockall Trough has been included as an example of a typical normally-oxygenated margin. The bottom-water oxygen concentrations are shown as a dotted line. For the Indian Margin, oxygen values are taken from de Sousa et al. (1996, Fig. 2), modified by data from RV *Yokosuka* cruise YK08/11.

Fig. 3. Species richness versus depth and oxygen for the upper boundary of the OMZ in the Bay of Bengal (a,b) and the lower boundary of the OMZ on the Pakistan Margin (c,d). Pakistan Margin data are from Levin et al. (2009), All the trends are statistically significant.

Fig. 4. Foraminifera (rose-Bengal-stained, >300- $\mu\text{m}$  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 and Gooday (2009).

Fig. 5. Diversity of invertebrate megafauna across Pakistan Margin (data from Murty et al., 2009) and along three transects off Chile: Antofagasta (strong OMZ), Concepción (weak OMZ) and Chiloé (no OMZ).

Fig. 6. 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) eastern Indian Margin (Bay of Bengal), e) Rockall Trough (data from Paterson and Lamshead, 1995), f) western Indian Margin, g) Pakistan Margin (data from Hughes et al. (2009) and Levin et al. (2009)), h) Oman Margin (data from Levin et al., 2009). The Rockall Trough has been included as an example of a typical normally-oxygenated margin. Bottom-water oxygen concentrations are indicated by a dotted line. For Indian Margin, oxygen values are taken from de Sousa et al. (1996, Fig. 2), modified by data from RV *Yokosuka* cruise YK08/11.

Fig. 7. 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 transformations. Based on data from Levin et al. (2009).

Fig. 8. Beta diversity (cumulative species turnover as a percentage) for megafauna, macrofauna, and foraminifera (rose-Bengal-stained, hard-shelled, >63- $\mu\text{m}$  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, 950 m for foraminifera, macrofauna and megafauna respectively) of the inflection points where turnover begins to increase.

Fig. 9. Multidimensional scaling ordination of foraminifera (rose-Bengal-stained, hard-shelled, >63- $\mu\text{m}$  fraction) across the Pakistan Margin. Symbol size within plot proportional to oxygen concentration. Labels are water depths. Relationships between x and y axes and water depth and oxygen are also indicated. Based on data from Schumacher et al. (2007).

Fig. 10. Grouping of foraminiferal assemblages (hard-shelled species, >63- $\mu\text{m}$  fraction) across the Pakistan Margin, based on TWINSPAN analysis. Numbers are water depths of sampling sites. Based on data from Schumacher et al. (2007).

Fig. 11. Multidimensional scaling ordination of foraminiferal assemblages (rose-Bengal-stained, >300- $\mu\text{m}$  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 and Gooday (2009).

Fig. 12. TWINSPAN analysis tabulation of foraminifera (rose-Bengal-stained, >300- $\mu\text{m}$  fraction) from 140 and 300 m (monsoon and intermonsoon seasons) on the Pakistan Margin. Species abundance reduced to -, 1, 2, 3 scale on a log basis. Rank of site and species 'splits' is indicated by the number of vertical or horizontal lines. Data from Larkin and Gooday (2009).

Fig. 13. Macrofaunal assemblage heterogeneity on the Oman Margin. a) Two-dimensional MDS Multidimensional scaling ordination of polychaete assemblages from six water depths, adapted from Levin et al. (2000). b) Average within-site (i.e with depth) Bray-Curtis similarity of  $\log(x+1)$  transformed assemblage data,

Table 1. Data analysed

<b>Area</b>	<b>Faunal data</b>	<b>Environmental data</b>	<b>Reference</b>
Chilean Margin:			
- Antofagusta	Macrofauna, Megafauna	O <sub>2</sub> , %TOC, CPE, grain size	Palma et al. (2005)
- Concepcion	Macrofauna, Megafauna	O <sub>2</sub> , %TOC, CPE, grain size	Palma et al. (2005)
- Chiloe	Macrofauna, Megafauna	O <sub>2</sub> , %TOC, CPE, grain size	Palma et al. (2005)
Gulf of California	Polychaetes	O <sub>2</sub> , %OM, grain size	Mendez (2006, 2007)
Oman Margin	Macrofauna	O <sub>2</sub> , %TOC, CPE, grain size, C:N, Hydrogen index	Levin et al. (2000)
Pakistan Margin	Macrofauna, Foraminifera	O <sub>2</sub> , %TOC, pigments, grain size, C:N, $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$	Levin et al. (2009), Hughes et al. (2009), Schumacher et al. (2008)
Indian Margin	Macrofauna		
Bay of Bengal	Macrofauna	O <sub>2</sub> , %OM, grain size	
Rockall Trough	Polychaetes	O <sub>2</sub>	Paterson & Lamshead (1995)

Table 2. Simple (non-parametric) correlations and partial correlations (i.e. with linkage to depth removed) between these 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.

	<b>Depth</b>	<b>S</b>	<b>d</b>	<b>Brill</b>	<b>Fisher</b>	<b>ES101</b>	<b>H'2</b>	<b>J'</b>	<b>1-I'</b>	<b>R1D</b>
<b>Simple (non-parametric) correlations</b>										
<b>Depth</b>	-	-0.767**	-0.837**	-0.847**	-0.851**	-0.804**	-0.847**	-0.807**	-0.809**	ns
<b>Sand or Mud content (a)</b>	0.532*	0.605**	0.546*	0.479*	0.554*	0.546*	0.479*	ns	ns	ns
<b>Particle size</b>	ns	0.486*	ns	ns	ns	ns	ns	ns	ns	ns
<b>Organic matter</b>	0.709**	-0.770**	-0.682**	-0.653**	-0.681**	-0.739**	-0.653**	-0.614**	-0.607**	ns
<b>Dissolved oxygen</b>	-0.768**	0.587**	0.674**	0.623**	0.689**	0.642**	0.623**	0.495*	0.525*	ns
<b>Partial correlations</b>										
<b>Sand or Mud content (b)</b>		ns	ns	ns	ns	ns	ns	ns	ns	ns
<b>Particle size</b>		ns	ns	ns	ns	ns	ns	ns	ns	ns
<b>Organic matter</b>		ns	ns	ns	ns	ns	ns	ns	ns	ns
<b>Dissolved oxygen</b>		0.528*	0.573*	0.526*	0.564*	0.596*	0.530*	ns	ns	ns

[(a) identical values of opposite sign; (b) identical values; \* p<0.05, \*\* p<0.01]

Table 3. The significance (p as %) and sense (+,-) of Spearman's rank correlations between depth, oxygen concentration, macrofaunal abundance, diversity, community composition and species turnover and sedimentary environmental factors across the lower boundary of the Pakistan Margin OMZ (data from Levin et al., in press).

	Depth, Oxygen Abundance	S <sup>a</sup>	J <sup>b</sup>	D <sub>Mg</sub> <sup>c</sup>	HB <sup>d</sup> , α, H <sub>2</sub> <sup>f</sup> , D <sup>g</sup>	S <sup>(59)</sup> , RID <sup>i</sup>	MDSx <sup>j</sup> , TO <sup>k</sup>
<b>Depth (+), Oxygen (+)</b>	0.1 ns	0.1	0.5	0.1	0.1	0.1	0.1
<b>δ<sup>13</sup>C (+), DI<sup>l</sup> (+)</b>	0.1 ns	0.1	0.1	0.1	0.1	0.1	0.1
<b>THAA<sup>m</sup> (-)</b>	0.1	5	0.1	5	0.1	0.1	0.2
<b>AA-N<sup>n</sup> (-)</b>	0.1 ns	0.1	ns	0.1	0.5	1	0.1
<b>δ<sup>15</sup>N (+)</b>	ns	5	1	ns	2	5	ns
<b>Silt and Clay (-)</b>	2	ns	ns	2	ns	5	5
<b>Total N (+)</b>	ns	0.1	5	ns	ns	ns	ns
<b>BALA+GABA<sup>o</sup> (+)</b>	ns	5	ns	ns	ns	ns	ns
<b>Organic C (+), Chlorins<sup>p</sup> (-)</b>	ns	0.1	ns	ns	ns	ns	ns
<b>C:N ratio or Bacterial C</b>	ns	ns	ns	ns	ns	ns	ns

<sup>a</sup> total species; <sup>b</sup> Pielou's evenness; <sup>c</sup> Margalef's index; <sup>d</sup> Brillouin index; <sup>e</sup> Fisher's index; <sup>f</sup> Shannon index (log<sub>2</sub>); <sup>g</sup> Simpson's index (1-λ' form); <sup>h</sup> Rarefied species richness (n=59); <sup>i</sup> Rank 1 dominance (inverse form); <sup>j</sup> Multidimensional scaling x-ordinate (no transformation, sqrt, double sqrt, log (x+1) and presence / absence transformations); <sup>k</sup> Species turnover (cumulative form); <sup>l</sup> amino acid base degradation index; <sup>m</sup> total amino acid yield, carbon normalised; <sup>n</sup> total N in amino acids; <sup>o</sup> β-alanine and η-amino butyric acid; <sup>p</sup> chlorophyll and pheopigments.

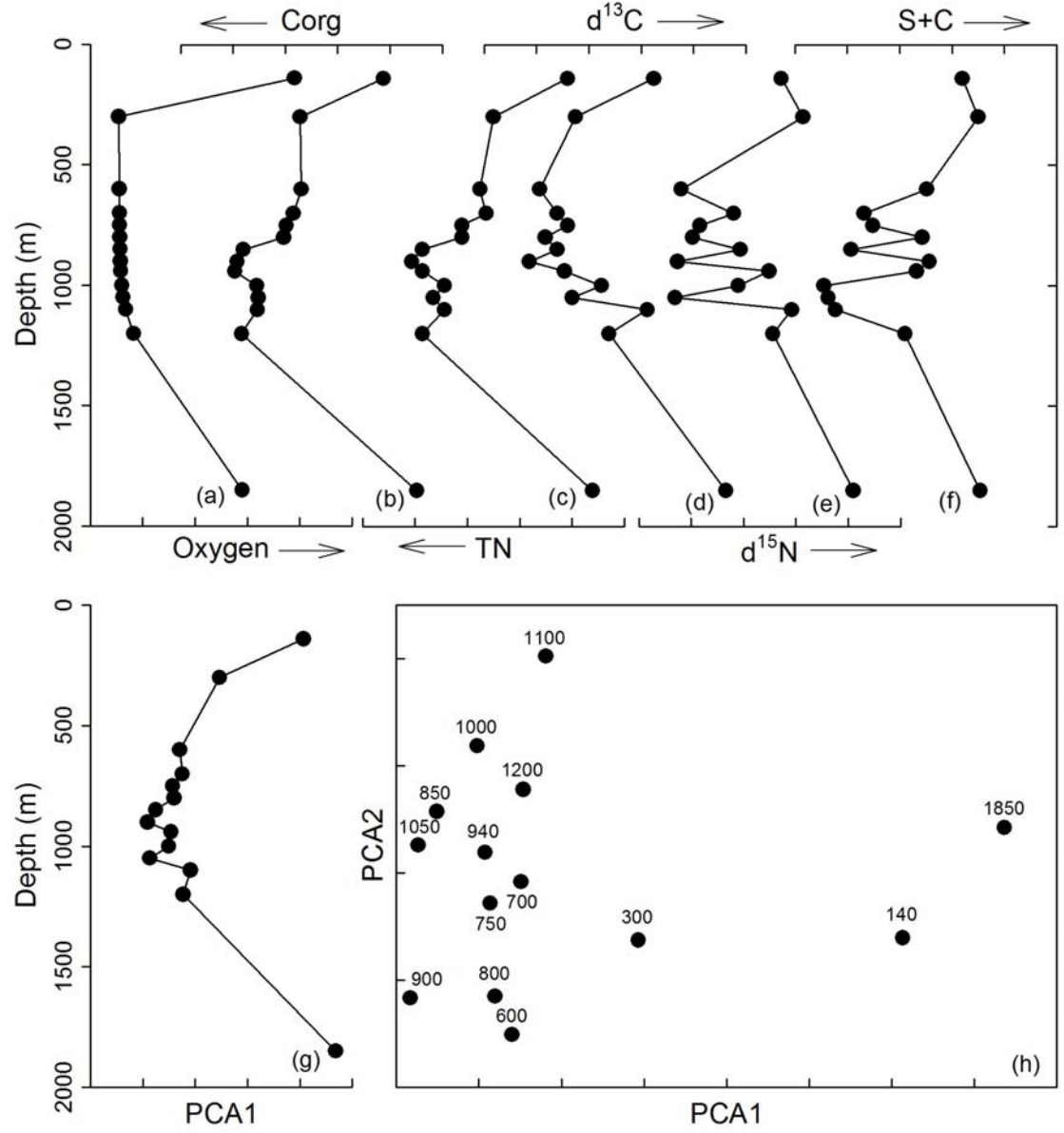


Figure 1



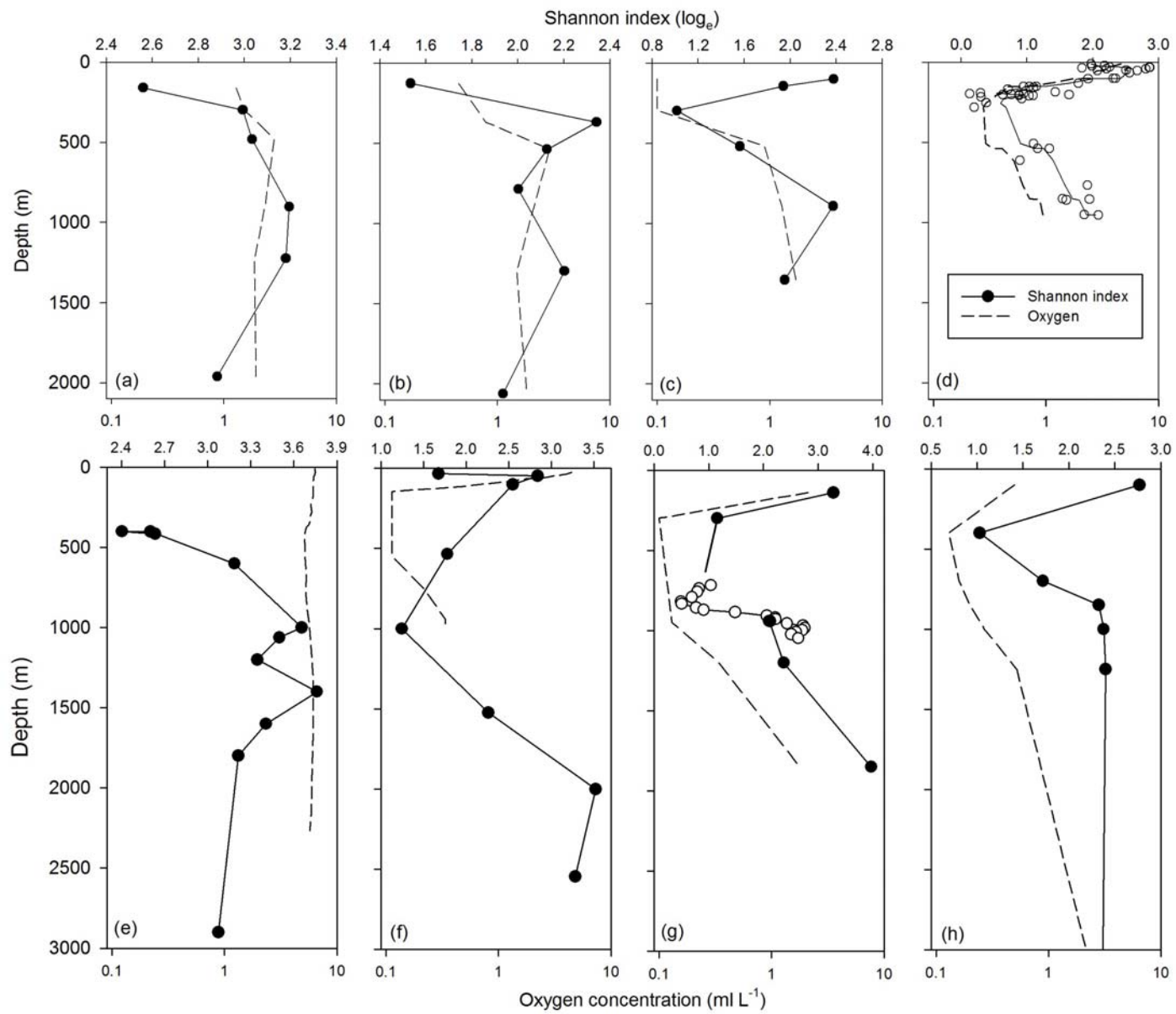


Figure 2

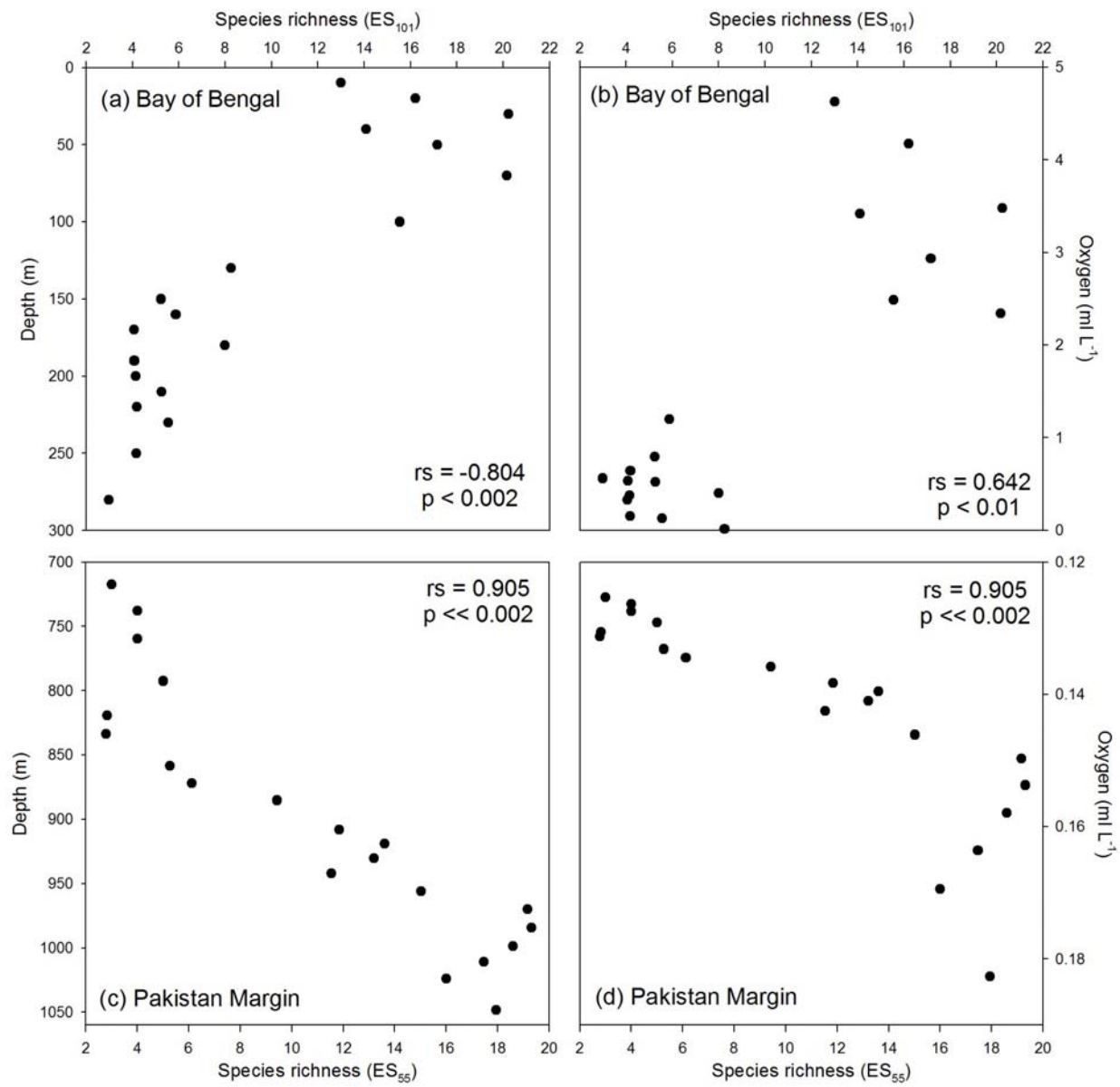


Figure 3

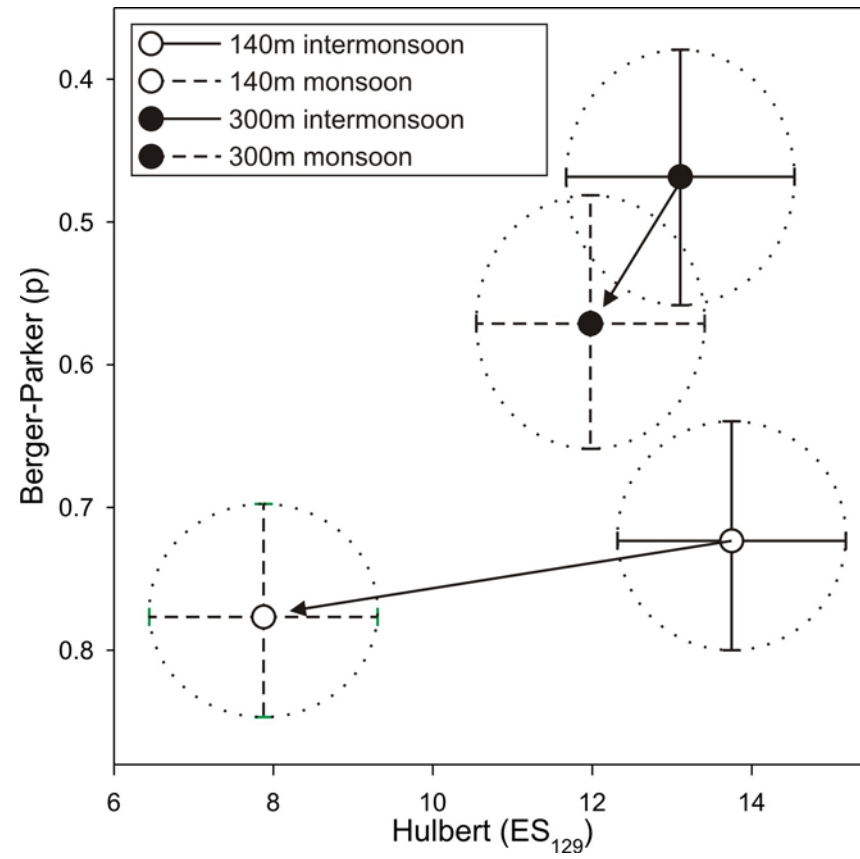


Figure 4

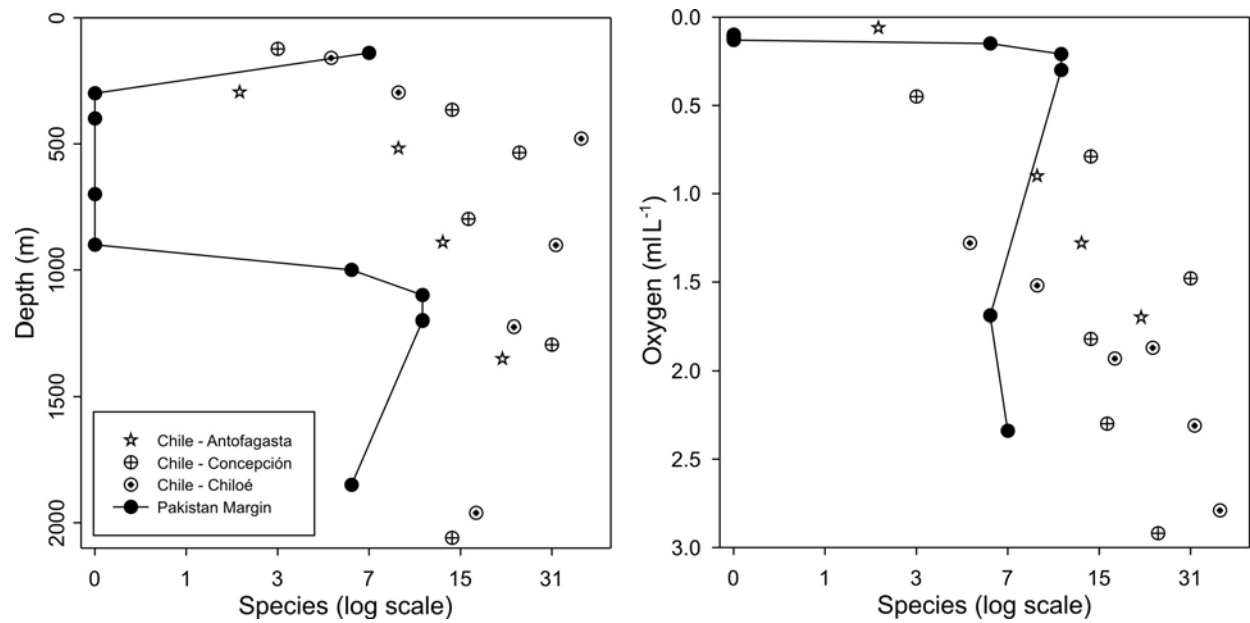


Figure 5

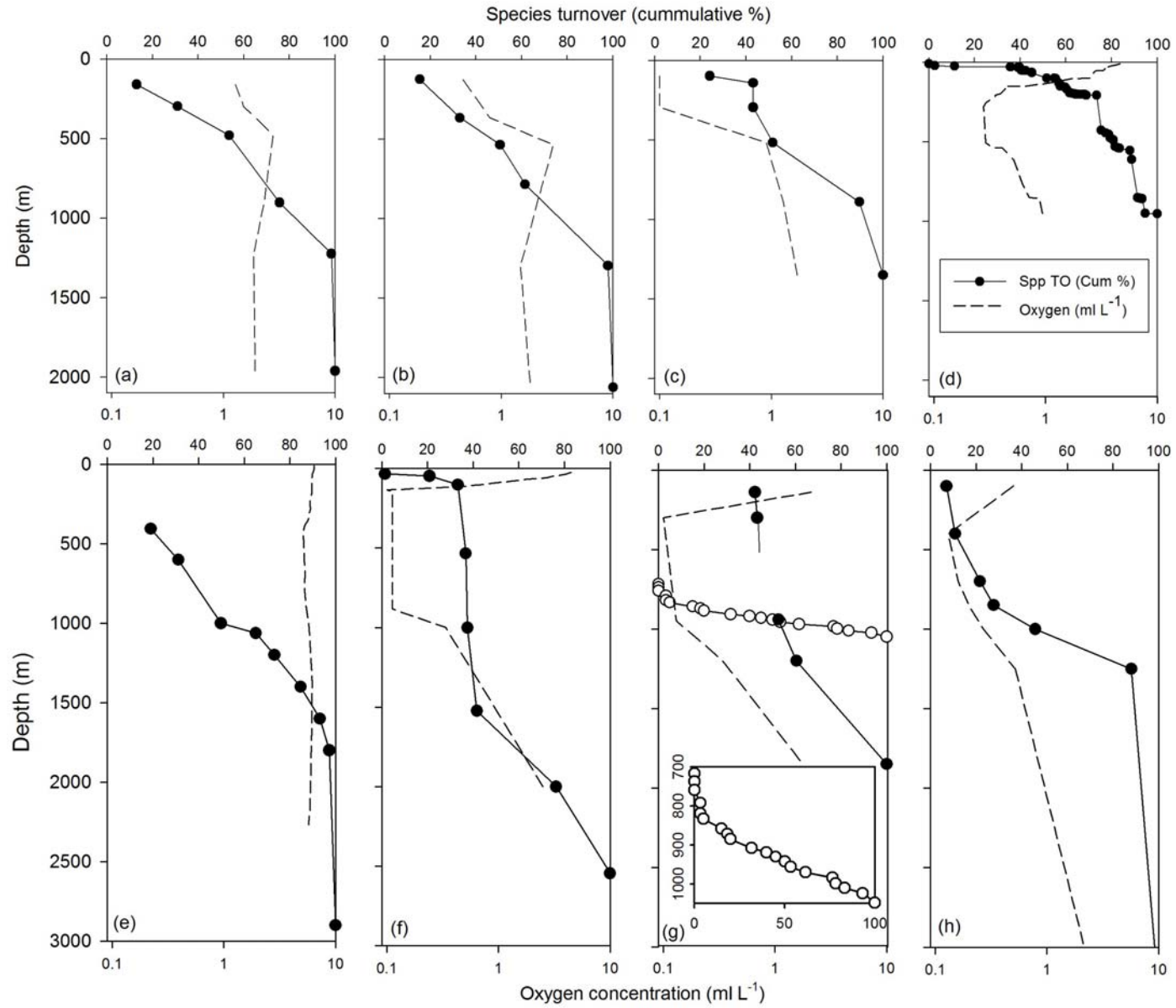


Figure 6

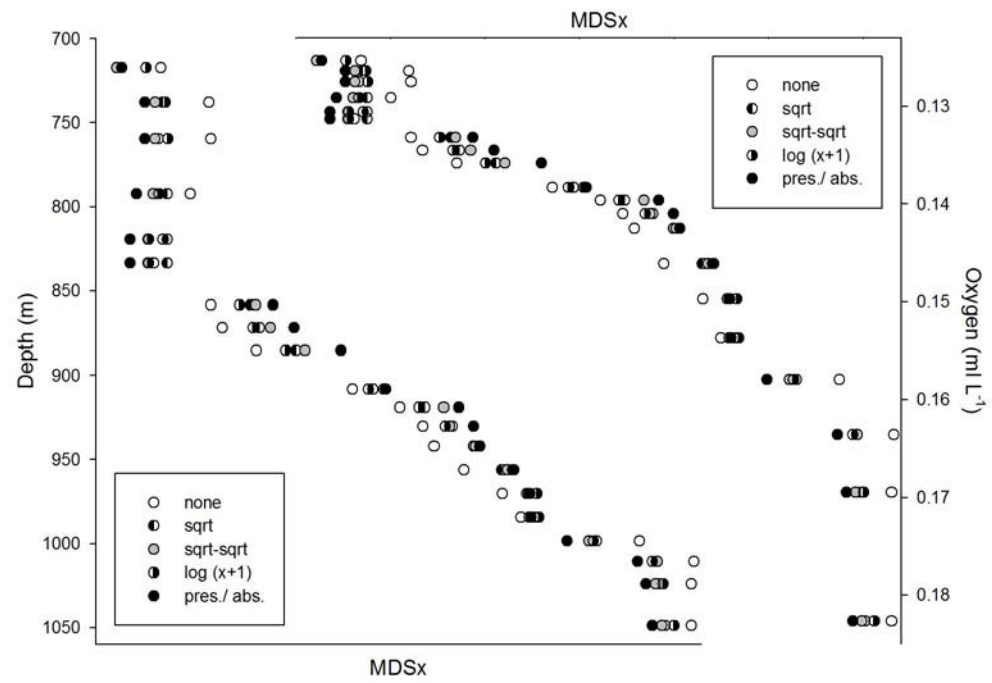


Figure 7

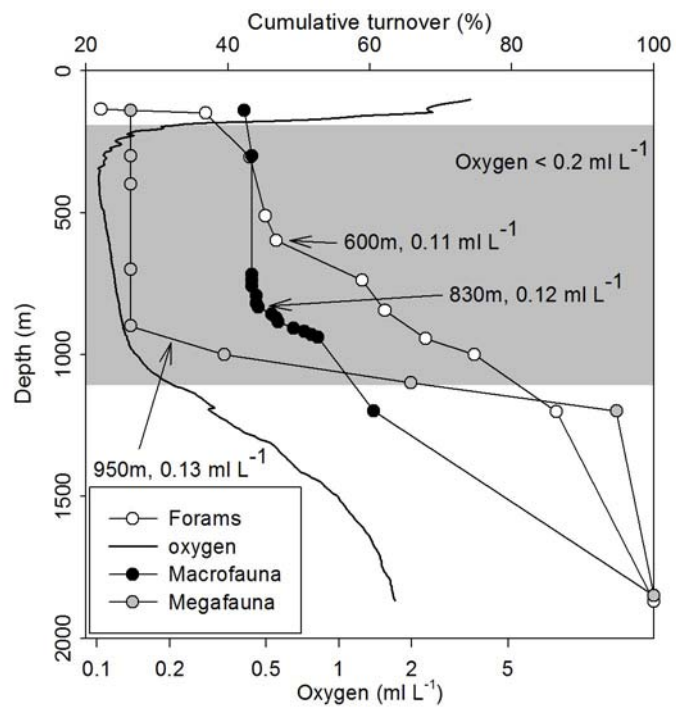


Figure 8

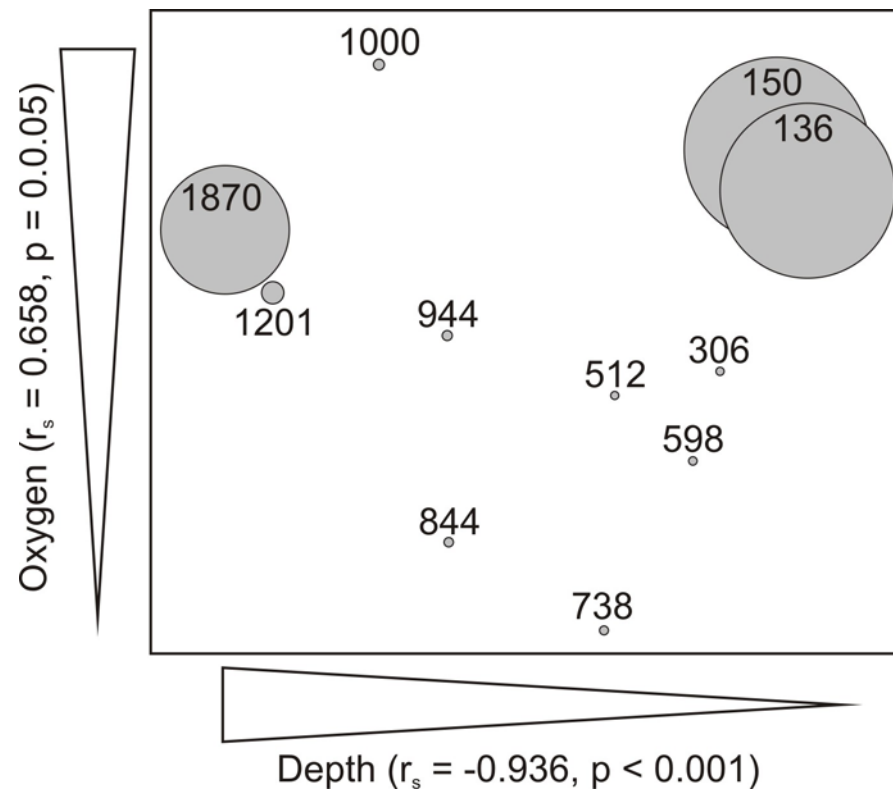


Figure 9



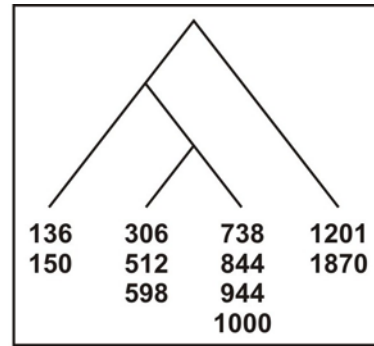


Figure 10

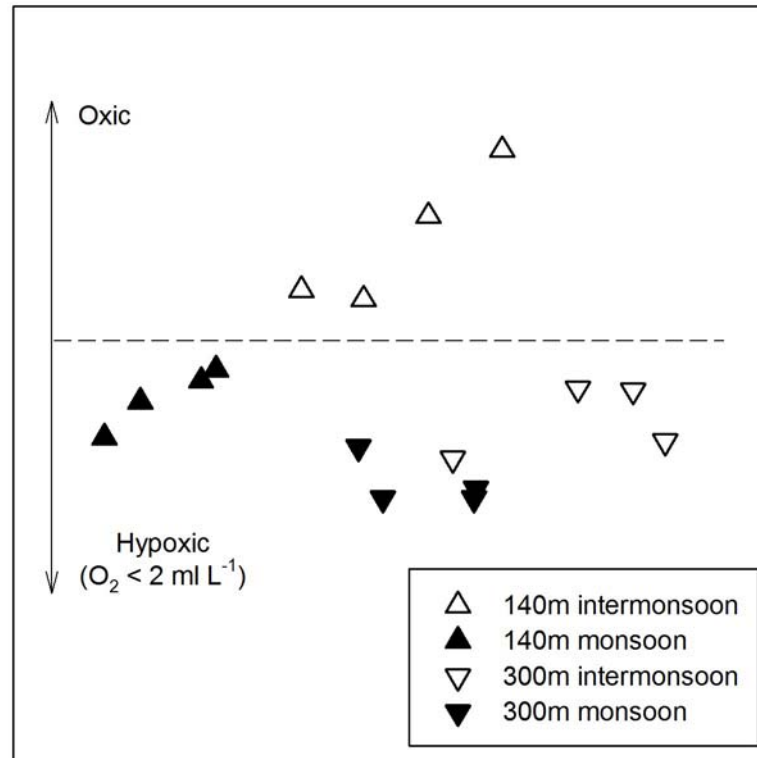


Figure 11

Species	Depth					3			1				1			
	Season	I	M	M	M	M	I	I	I	I	I	I	M	M	M	M
<i>Bathysiphon</i> sp. 2	1	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-
Allogromiid sp. 3	-	1	-	-	-	-	1	1	-	-	-	-	-	-	-	-
<i>Reophax dentaliniformis</i>	2	2	2	2	2	2	2	2	-	-	-	-	-	-	-	-
<i>Reophax</i> sp. 2	1	2	1	1	1	2	1	1	-	-	-	-	-	-	-	-
<i>Veloroninoides crassimargo</i>	1	1	1	1	2	1	1	-	-	-	-	-	-	-	-	-
Saccamminid sp. 3	1	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-
<i>Veloroninoides wiesneri</i>	1	1	1	1	1	1	-	1	-	-	-	-	-	-	-	-
Allogromiid sp. 2	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Ammodiscus cf. cretaceus</i>	2	2	1	1	1	2	1	2	1	1	-	1	1	-	-	-
<i>Bathysiphon</i> sp. 1	-	1	1	1	2	1	2	2	-	1	1	1	-	-	-	-
Saccamminid sp. 1	-	-	1	-	-	1	1	1	-	1	1	-	1	-	-	-
<i>Globobulimina cf. G. pyrula</i>	2	2	2	2	2	2	2	2	1	1	2	1	-	1	1	2
<i>Cassidulina laevigata</i>	1	-	1	1	2	1	-	1	-	1	1	-	-	1	-	-
<i>Bolivina aff. dilatata</i>	2	2	2	1	2	1	1	1	1	1	1	-	2	2	2	2
<i>Uvigerina ex. gr. semiornata</i>	3	3	3	3	3	2	3	2	2	3	3	3	3	3	3	3
<i>Saidovina amygdalaeformis</i>	-	1	-	-	-	-	-	-	-	-	-	-	1	1	-	2
<i>Hyperammia</i> sp. 1	1	-	-	-	-	1	1	-	1	1	-	1	1	1	1	1
<i>Cancris auriculus</i>	-	1	1	1	1	1	1	2	1	2	2	2	2	2	2	2
<i>Cibicides</i> sp. 1	1	1	-	-	-	-	-	-	2	1	1	1	-	-	-	1
<i>Lagenammia arenulata</i>	-	-	-	-	-	-	-	-	1	-	-	1	1	1	-	-
<i>Reophax bilocularis</i>	-	-	-	-	-	-	1	-	1	1	1	1	1	1	1	1
<i>Reophax</i> sp.1	-	-	-	-	-	-	-	-	-	1	1	1	-	1	-	1
Allogromiid sp. 1	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	-
<i>Laevidentalina aphelis</i>	-	-	-	-	-	-	-	-	1	1	-	-	1	-	-	1
<i>Lenticulina aff. iota</i>	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-
Psammosphaerid sp. 1	-	-	-	-	-	-	-	-	-	1	1	1	-	-	1	-
<i>Pelosina</i> sp. 1	-	-	-	-	-	-	-	-	1	1	1	1	1	-	-	1
<i>Amphicoryna aff. scalaris</i>	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-

Figure 12

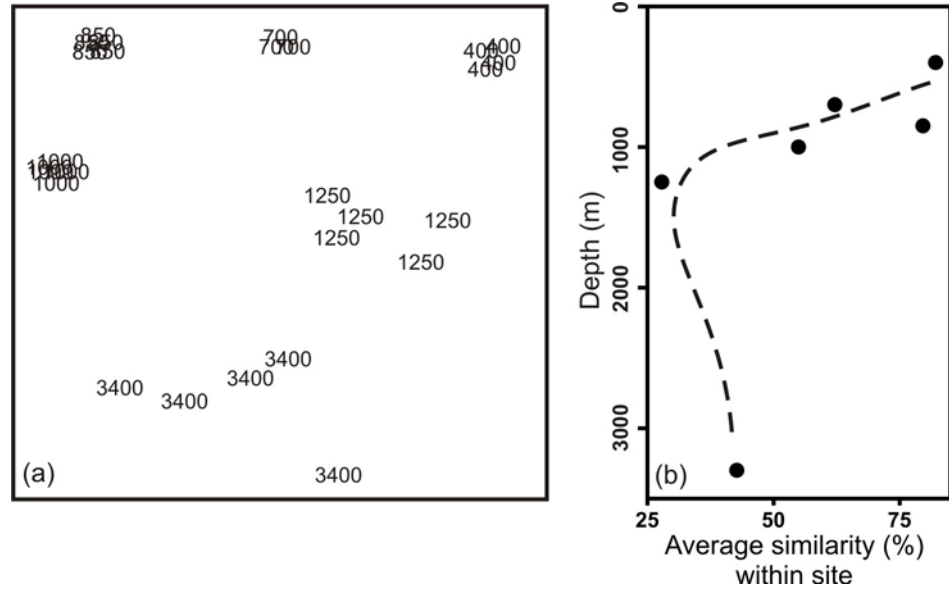


Figure 13