

Macrozoobenthos diversity in an oxygen minimum zone off northern Namibia

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Received: 4 February 2009 / Accepted: 22 May 2009 / Published online: 12 June 2009
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Abstract A benthological survey in the Benguela upwelling area off northern Namibia (located at 17.3°S and water depth ranging between 26 and 117 m) showed the concentration of dissolved oxygen and the accumulation of organic-rich sediments to control macrozoobenthic community patterns. In contrast to highly biodiverse nearshore areas with well-structured shell deposits of the brachiopod *Discinisca tenuis* (Sowerby 1847), the benthic community in the oxygen minimum zone (OMZ) decreased strongly in species numbers. Nevertheless, a well-established community ranging from 13 to 31 species persisted. Species densities (300–3,350 ind m⁻²) and biomass (4–109 g afdw/m²) were surprisingly high for areas with near bottom oxygen concentrations from 0.06 to 0.88 ml l⁻¹. In contrast to OMZ's of other upwelling areas, where the benthic macrofauna is generally dominated by small-bodied polychaetes, off Namibia larger key organisms like the bivalve *Nuculana bicuspidata* (Gould 1845) and the snail *Nassarius vinctus* (Marrett 1877) accounted for a large proportion of the macrozoobenthos >1 mm. This is supposed to have a distinct effect on the functional properties of the sediments.

Introduction

Marine oxygen minimum zones (OMZ thereafter; <0.5 ml l⁻¹) impinge upon the continental margins at

depths of 100–1,000 m along much of the Eastern Pacific, Arabian Sea and off West Africa (Levin 2003; Cowie and Levin 2009). Studies at OMZ boundaries, where strong oxygen gradients occur over short distances can demonstrate effects of oxygen availability on the regulation of benthic communities and their influence on nutrient and carbon cycling (Levin et al. 2006). Research conducted by Gutierrez et al. (2000) and Smith et al. (2000) demonstrated the effects of low dissolved oxygen and high input of fresh organic matter on the bioturbation potential of macrofauna, to be one of the major functional processes occurring in OMZ areas. When conditions of dissolved oxygen concentrations are observed to be below 0.15 ml/l, physiological adaptation sets in (Gooday et al. 2009; Hughes et al. 2009), bioturbation may be reduced and chemosynthesis-based nutrition (via heterotrophy and symbiosis) becomes an important process (Levin 2003; Levin et al. 2009). Shelf sediments off the Namibian coast comprise extensive areas of diatomaceous mud, which supports minimal quantities of higher marine life although it contains high concentrations of organic matter and reduced sulphur (Sakko 1998). In the core of the OMZ's off Namibia, the macrofauna species diversity has been observed to be reduced, whereas higher abundances and biomasses have been observed at the edge of the OMZ (Sanders 1969). Fluctuations of environmental conditions are an inherent feature of this extreme environment, which has been in existence for more than two million years (Shannon 1985). Clearly, species that have persisted under these conditions have evolved mechanisms for coping with the inherent variability of this environment (Sakko 1998).

Whereas several macrozoobenthic investigations from intertidal waters off Southwest Africa have been published (Penrith and Kensley 1970; Kensley and Penrith 1980; McLachlan 1985; Tarr et al. 1985; Donn and Cockcroft

Communicated by U. Sommer.

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1989; Hammond and Griffiths 2006) the benthic communities in subtidal regions have been poorly studied (Sakko 1998). Sanders (1969), was one of the first researchers, who explored macrobenthic community structures (e.g. species number, abundance and diversity) off Walvis Bay impacted by the OMZ. Since then, similar research has been carried out in OMZ regions of the eastern Pacific Ocean and the Arabian Sea (Levin et al. 2000, 2002, 2009; Gallardo et al. 2004; Gooday et al. 2009; Hughes et al. 2009; Palma et al. 2005). But to date, there is still a lack of comprehensive studies, which deal with OMZ-related macrofauna distribution in shelf waters off Namibia or the Benguela upwelling area. Some grab stations at depths between 150 and 201 m, which contained macrofauna, mostly polychaetes (*Paraprionospio* sp.) were analysed by Gallardo et al. (1998). Some other megafauna species (i.e. *Diopatra* sp., Anthozoa, Decapoda, Asteroidea, and Holothuroidea) were sampled at one station in a depth of 178 m.

During research cruises conducted off Angola and Namibia in 2004 and 2008 on board of German research vessels Alexander von Humboldt and Maria S. Merian, we investigated the macrozoobenthos distribution in the upper fringe of the Namibian OMZ. The aim of this study was to describe the community patterns in this specific habitat and therewith to complement Sanders' (1969) results from the deeper areas (102–2,140 m off Walvis Bay). For the first time, the macro-infauna in this oxygen-reduced environment was compared with the highly diverse nearshore sediments. Following the oxygen gradient in bottom water from 26 to 117 m water depth, the change in diversity, abundance and biomass is shown. Our investigation focused on organisms >1 mm with a view on the assessment of functional properties. One major ecosystem-relevant function of soft bottom sediments has been defined as transport across the sediment/water interface and the exchange of matter between sediment and water (Norling et al. 2007). Bioturbation and biopumping activities of larger size classes of macrofauna contribute to an over proportional degree to these fluxes than smaller organisms.

The OMZ off Namibia differs from those beneath other upwelling regions by the close vicinity to the surface productive zone (~50 m). In this area, the supply of fresh organic matter to the sediment is not substantially reduced by water column decomposition. The vicinity to both sea surface and coast may as well affect the physical stability of the bottom water and may foster occasional intrusions of oxygenated water masses due to current or wave action. Under these conditions, we expected differences in composition, biomass and functional properties of the inhabiting macrofauna when compared with deeper and more stable OMZs in other oceanic regions.

Materials and methods

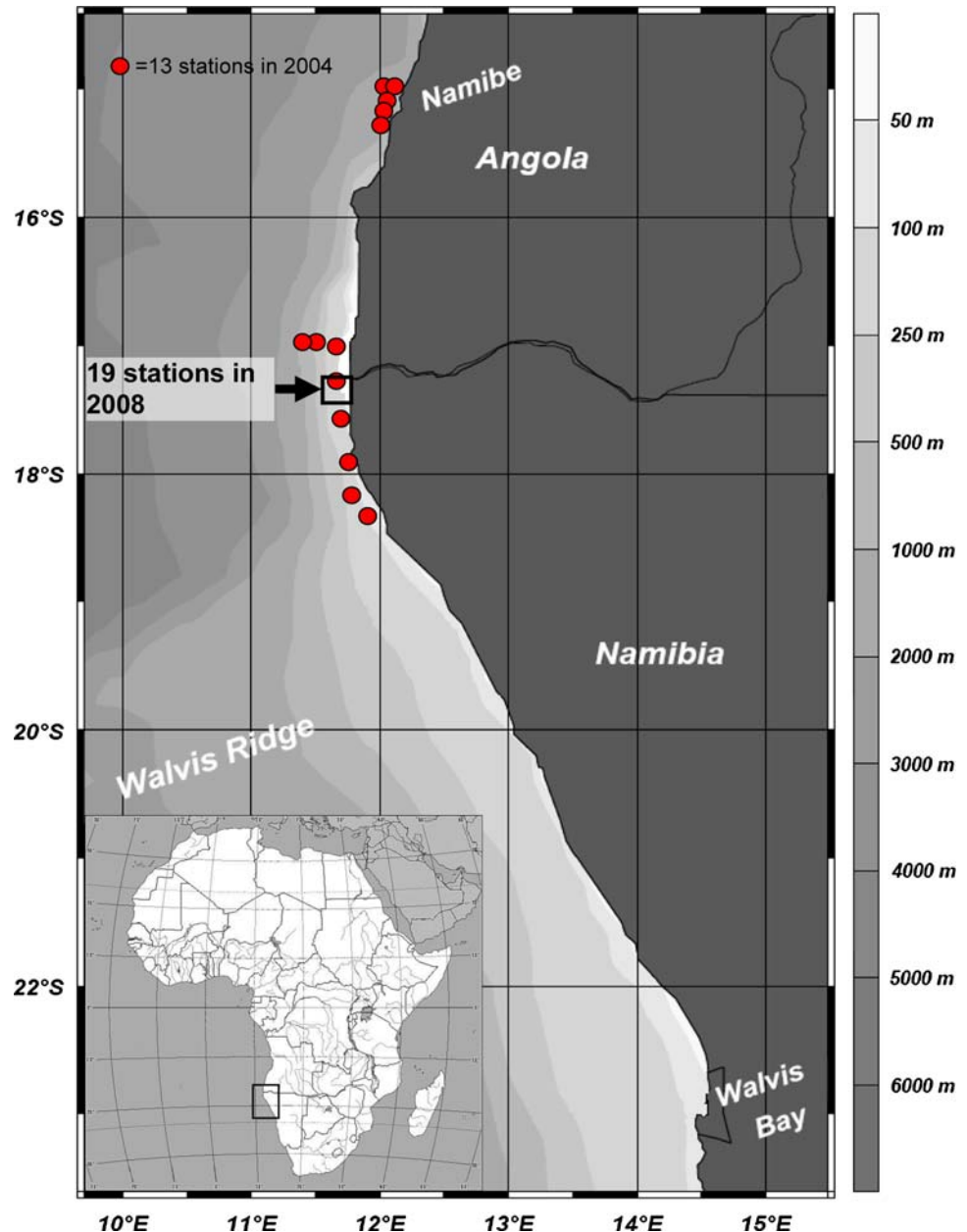
Study area

Namibia has a coastline of about 1,500 km extending in a north-south direction (Bianchi et al. 1999). The coastal waters off Namibia are part of the Benguela upwelling, one of the major upwelling systems of the world with large hypoxic and anoxic sublittoral areas, which affect many abundant species (Sakko 1998). Results from recent geological studies on the Namibian mud belt have revealed that the oxygen-reduced environment on the shelf has been sustained for millennia (West et al. 2004). Hydrological and biological patterns (i.e. pelagic fish larvae, zooplankton biomasses) of the Angola-Benguela Frontal Zone were recently described in detail by Postel et al. (2007), Mohrholz et al. (2008) and Bodungen et al. (2008). The sediments are predominantly of biogenic origin as a result of the high productivity in the upwelled waters of the Benguela system. Results presented in this study are from benthic samples and environmental data collected at 19 locations off northern Namibia. Sampling was conducted during March 2008 south of the Cunene, the border river to Angola (Fig. 1). In May 2004, a cruise along the Namibian and Angolan coast on a larger station grid was conducted. Data from this cruise were used for targeting the area studied in 2008.

Sampling

Triplicate benthic samples were taken with a 0.1 m² van Veen grab at each station. Additional dredge hauls (containing a net mesh size of 5 mm) were taken for collection of larger, mobile or rare species. All samples were sieved through a 1-mm² screen and animals were preserved on board in 4% buffered formaldehyde. Sorting procedures were conducted at the laboratory with a stereomicroscope with 10–40× magnification. All macrofauna samples were identified to the lowest taxonomic level whenever possible. The nomenclature was checked following the World Register of Marine Species (WoRMS: <http://www.marinespecies.org/index.php>). Environmental variables such as salinity, temperature, chlorophyll fluorescence and oxygen concentrations in the water column down to the sediment boundary were recorded by means of a profiling CTD-system (Seabird, USA) with attached oxygen (Seabird) and fluorescence (Dr. Haardt, Germany) sensors and a 13-bottle sampling rosette. Oxygen sensors were calibrated by immediate potentiometric Winkler titration of three samples per water-column, including the closest position to the sediment, in the ships laboratory. Chlorophyll was determined fluorometrically following JGOFS-protocols (UNESCO 1994). An additional sediment sample was taken to extract the upper surface sediment layer (≤20 mm) for analyses of

Fig. 1 Study area in waters off Southwest Africa. *Dots* indicate the sampling stations during the cruise of 2004. The *black rectangle* corresponds to the 2008 survey



median grain size (laser particle sizer Cilas 1180L), organic matter estimation by weight loss upon ignition (afdwt) and direct determination of organic carbon and nitrogen content by means of an Hekatech (Germany) elemental analyzer (Euro EA). Table 1 displays characteristic values for bottom water and sediment variables of stations sampled during this study. At the near shore shell deposits elemental and grain size analyses were not possible due to the coarseness properties of the sediments.

Statistical analyses

For each benthic sample the abundance of species was counted. Following this, the replicate data were averaged to

a total abundance per square metre at each station (no pooling).

Statistical methods were employed for the exclusion of species contributing to less than 1% to the species abundance. The initial number of 257 species had to be reduced (Legendre and Gallagher 2001) to exclude outliers species. This was done, successively by employing dominance as filter criteria and creating a final data matrix of 19 dominant species for the 19 stations (Table 2).

Multivariate analysis was conducted by superimposing the results of group averaged hierarchical clustering based on Bray-Curtis similarities of 4th-root transformed abundance data for 19 stations on non-metric multidimensional scaling (MDS) surface. By using this method, benthic

Table 1 Characteristic environmental variables in bottom water and sediment 2008

Stn-name	Depth (m)	Latitude (S)	Longitude (E)	Variables in bottom water				Variables in surface sediment		
				S (psu)	Oxy ml l ⁻¹	T (°C)	Chl <i>a</i> (µg l ⁻¹)	Org (% wt.)	C org (% wt.)	GS (µm)
BE01	106	17.268	11.603	35.7	0.31	16.2	0.93	7.13	5.9	21
BE03	64	17.268	11.687	35.7	0.51	16.6	4.18	10.21	4.9	17
BE06	31.5	17.267	11.724	35.7	0.83	17.5	41.01	4.22	1.5	48
BE09	49	17.289	11.71	35.7	0.53	16.9	8.39	8.99	3.7	20
BE11	82	17.289	11.658	35.7	0.32	16.5	1.44	12.67	5.6	15
BE12	102	17.29	11.603	35.6	0.39	16.2	0.69	7.53	3.3	21
BE14	114	17.316	11.601	35.6	0.12	16.2	1.06	8.53	3.7	18
BE16	83.5	17.316	11.659	35.7	0.24	16.4	2.02	7.57	4	18
BE17	26	17.316	11.723	35.7	1.21	17.8	23.2	–	–	–
BE18	56	17.339	11.704	35.7	0.88	17.3	6.66	9.12	3.8	18
BE20	84.5	17.339	11.659	35.7	0.33	16.5	2.17	8.55	4	18
BE23	114	17.34	11.602	35.6	0.06	16.2	0.95	5.53	3.1	25
BE26	82	17.368	11.659	35.7	0.4	16.5	0.98	11.49	4.9	17
BE29	53.4	17.368	11.704	35.7	0.67	17.2	16.3	9.24	5.1	17
BE30	29.6	17.39	11.724	35.7	1.19	17.5	12.88	–	–	–
BE33	57.7	17.39	11.704	35.7	0.6	17	6.87	7.5	4.2	18
BE39	116.8	17.39	11.602	35.6	0.06	16	0.99	7.76	3.2	28
BE41	117	17.421	11.602	35.6	0.08	15.7	0.81	6.4	2.8	24
BE42	93	17.42	11.652	35.7	0.14	16.3	0.72	12.48	5.2	15

S salinity, T temperature, Oxy oxygen, Chl chlorophyll—all in water overlying the sediment (0.5–1 m), Org organic content, C org organic carbon content, GS grainsize—all of sediment surface (10–15 mm)

assemblages could be assigned to clear clusters. A one-way analysis of variance (ANOVA) (Clarke and Corley 2006) and ANOSIM tests were conducted to assess the significance of this classification. Species responsible for classification were determined applying SIMPER exploratory analysis and visual re-examination of the modified data matrix whereupon benthic assemblages had been determined and described (PRIMER; Clarke and Warwick 1994).

Results

The environmental conditions for macrofauna were variable within the stations over the whole grid (Table 1). The oxygen bottom water concentrations varied between 0.06 and 0.83 ml l⁻¹ over muddier stations. Values exceeding 1 ml l⁻¹ were observed over the coastal bottom deposits. The onset of intense bottom water oxygen deficiency (<0.3 ml O₂ l⁻¹) was observed at approximately 80 m depth (Fig. 2). Chlorophyll concentrations in the whole water column were high with means between 5.5 and 7 µg Chl *a* l⁻¹ in surface intermediate and bottom water. These values were more than 20 times higher than in the adjacent oceanic mixed layer, providing excellent food supply for the whole

area. Organic carbon content of surface sediment (means: OM 8.5%, Corg 4% wt. of sediment dry mass) was in the lower range for the Namibian mud belt, for the centre of which values of up to 25% wt. of organic carbon are reported (Bremner 1981). The reason for this difference is rather supposed to be the higher input of mineralic matter from the near-by coast than a difference in the pelagic production regime and a resulting lower supply of organic matter.

At the deeper stations, the variability between the measured environmental variables, especially the sediment characteristics (e.g. organic content and grain size, details are provided in Table 1) was low, showing no clear direction and no significant correlation to macrofaunal densities (Spearman correlation).

Although the taxonomic determination and especially the correct nomenclature are not finally completed for all groups, we are able to present an extensive list of taxa. Especially, the final identification of some rare species will add to the knowledge of faunal biodiversity in this region. Two distinct communities, could be distinguished during the study. On the one hand, the characteristic OMZ community with very abundant gastropod and bivalve species (see later) and otherwise the shell community mainly characterised by the deposits of a brachiopod. Ninety-two

Table 2 The most abundant macrofaunal species characterising the oxygen minimum zone (OMZ) and the shell zone of the brachiopod *Discinisca tenuis*

Macrofaunal species	% Contribution to total abundance		% Contribution to total biomass	
	OMZ community	Shell community	OMZ community	Shell community
Gastropoda				
<i>Bullia skoogi</i>	1		1	
<i>Nassarius vinctus</i>	37		31	
<i>Philine aperta</i>	1			
<i>Tectonatica sagraiana</i>	2		2	
Bivalvia				
<i>Costellipitar peliferus</i>	1		2	
<i>Nuculana bicuspidata</i>	36		58	
Polychaeta				
<i>Cirratulus filiformis</i>	1			
<i>Diopatra neapolitana capensis</i>	1	1	1	6
<i>Euclymene</i> cf. <i>luderitziana</i>	1	1		2
<i>Lumbrineris</i> cf. <i>coccinea</i>	4	3	2	6
<i>Paraprionospio pinnata</i>	4			
<i>Polydora</i> cf. <i>normalis</i>	1	14		10
<i>Pseudonereis variegata</i>	1	1		1
<i>Sabellaria eupomatoides</i>	6			
Amphipoda				
<i>Maera hironellei</i>		8		5
<i>Melita zeylanica</i>		7		1
Tanaidacea				
<i>Apseudes</i> sp.		6		
Echinodermata				
<i>Ophiolepis</i> cf. <i>affinis</i>		12		19
Brachiopoda				
<i>Discinisca tenuis</i>		2		7
Total values per m ² (min/max)	309/3,349 ind	9,421/14,261 ind	4/109 g afdw	52/83 g afdw
Species number (min/max)	13/31	116/156		

Contribution percentage is the mean percentile contribution per species to the total community abundance and biomass respectively. Total values (minimum/maximum) for abundance, biomass and species number are given at the bottom of the table

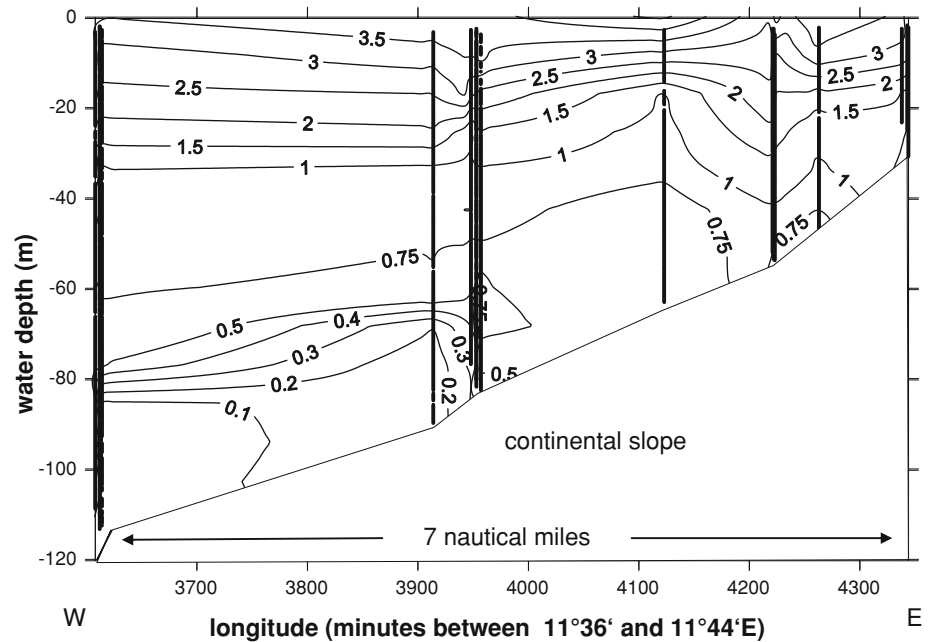
species were observed at the deeper, low oxygen stations (Fig. 3a). The most dominating groups were the polychaetes, gastropods and amphipods. Very similar relations were found at the two shallower stations (Fig. 3b). Again the polychaetes, gastropods and amphipods dominated the community. However, the overall species diversity was 2.4 times higher than in the OMZ area. Altogether 257 taxa were observed in near and offshore waters off northern Namibia.

A clear difference was observed between communities living in the OMZ and those situated nearshore in the shell deposits of the brachiopod *Discinisca tenuis* (Sowerby 1847) (Fig. 4). The first cluster is characterised by relative low species richness, relatively low abundance, high biomass and is mainly dominated by the bivalve *Nuculana*

bicuspidata (Gould 1845) and the gastropod *Nassarius vinctus* (Marrett 1877). The second cluster is distinctly more diverse (Table 2, Fig. 5) with both high abundance and biomass values.

Between 13 and 31 species (altogether 92 taxa) are forming the “OMZ-community”. Fourteen species show a high frequency and contribute most to the abundance (Table 2). The most dominant species are: *N. bicuspidata* and *N. vinctus* the polychaetes *Lumbrineris* cf. *coccinea* (Renier 1804), *Paraprionospio pinnata* (Ehlers 1901) and *Sabellaria eupomatoides* Augener 1918. The elevated abundances (300–3,350 ind m⁻²) and high biomass (up to 109 afdw g m⁻²) are quite surprising for an area where the near bottom water oxygen concentrations range between 0.06 and 0.88 ml/l (Fig. 5).

Fig. 2 Oxygen concentration (ml l^{-1}) collected at shelf stations between $17^{\circ}16'$ and $17^{\circ}25'$ (9 nm) in west-east direction. Vertical lines indicate sampling positions and oxygen profiles



The “shell community” consists of more than 210 species. Only very few are characteristic and show both high frequencies¹ and high abundances. The continuous occurrence of the brachiopod *D. tenuis* (very often dead shells) is conspicuous. The ophiuroid *Ophiolepis* cf. *affinis* is very common in this zone (Table 2). Furthermore, amphipods like *Maera hirondelei* Chevreux, 1900 and *Melita zeylanica* Stebbing, 1904 find optimal living conditions in these well-structured beds. The polychaetes *Diopatra neapolitana capensis* (Day 1960), *Lumbrineris* cf. *coccinea* (Renier 1804) and *Polydora* cf. *normalis* (Day 1957) settle on the surface or within the interstices of *Discinisca* shells with high abundances and biomasses (Table 2). The total abundances range between 9,500 and 14,200 ind. m^{-2} and the biomasses between 52 and 83 afdw g m^{-2} , respectively (Fig. 5, above 1 ml l^{-1} oxygen).

A similarity dendrogram (Fig. 6), comparing the sites on the basis of abundances of the 19 recorded dominant species, clearly demonstrates that samples from the OMZ and the shell deposits form tight groups. At the 10% similarity level of the cluster analysis, the separation of two groups of sampling stations and at 35% one single site (BE06) was clearly distinctive. Results of hierarchical cluster analysis were supplemented by the MDS ordination (not shown in this publication but available upon request). In order to confirm the significance of the categorisation, a one-way ANOVA was used. The hypothesis of significant difference ($p < 0.01$) between the groups “OMZ community” and “Shell community” could be corroborated (global $R = 1$).

¹ Data collected during as part of 2004 cruise, containing additional near shore stations are included in this assessment.

Particularly, the clustering of the biomasses (not shown in figures) demonstrates both a high level of separation (only 15% similarity) of two well-distinguished communities and the interim position of the location BE06. The 16 remaining stations group at a similarity level of ca. 80%.

The obvious differences between the communities supported by SIMPER analysis demonstrate, which species were responsible for characterising the infauna of the various stations. A complete list of species and their counts (ind m^{-1}) of the five very low oxygen stations ($< 0.15 \text{ ml l}^{-1}$) of the Namibian OMZ is presented in Table 3. The remarkable distribution of the gastropod *N. vinctus* and the bivalve *N. bicuspidata* heavily dominated the OMZ community (Fig. 7). The relative abundance of *N. vinctus* ranged between 26 and 65% and that of *N. bicuspidata* between 14 and 64%, respectively. In terms of biomass, these dominances were even more evident (Fig. 7b).

Discussion

This study was performed to increase the scarce database on macrobenthos distribution in the Namibian mud belt region. In contrast to this area, the littoral benthos off Southwestern Africa is much better investigated (McLachlan 1985; Penrith and Kensley 1970; Kensley and Penrith 1980; Tarr et al. 1985; Donn and Cockcroft 1989; Hammond and Griffiths 2006). Off Namibia, Sanders (1969) investigated some macro-infaunal community parameters on one transect from the mud belt to the deep sea. Few other studies have dealt with megafauna and the impacts of trawl fishery on benthic biodiversity in the deep sea (Atkinson and

Fig. 3 Macrozoobenthos composition in offshore waters off northern Namibia in 2008: **a** OMZ community including 16 stations with oxygen values between 0.06 and 0.88 ml l⁻¹; **b** shell community including 2 stations with values between 1.19 and 1.21 ml l⁻¹. The intermediate station BE06 was not considered. For definition of the communities the Bray-Curtis Similarity was used (Fig. 6)

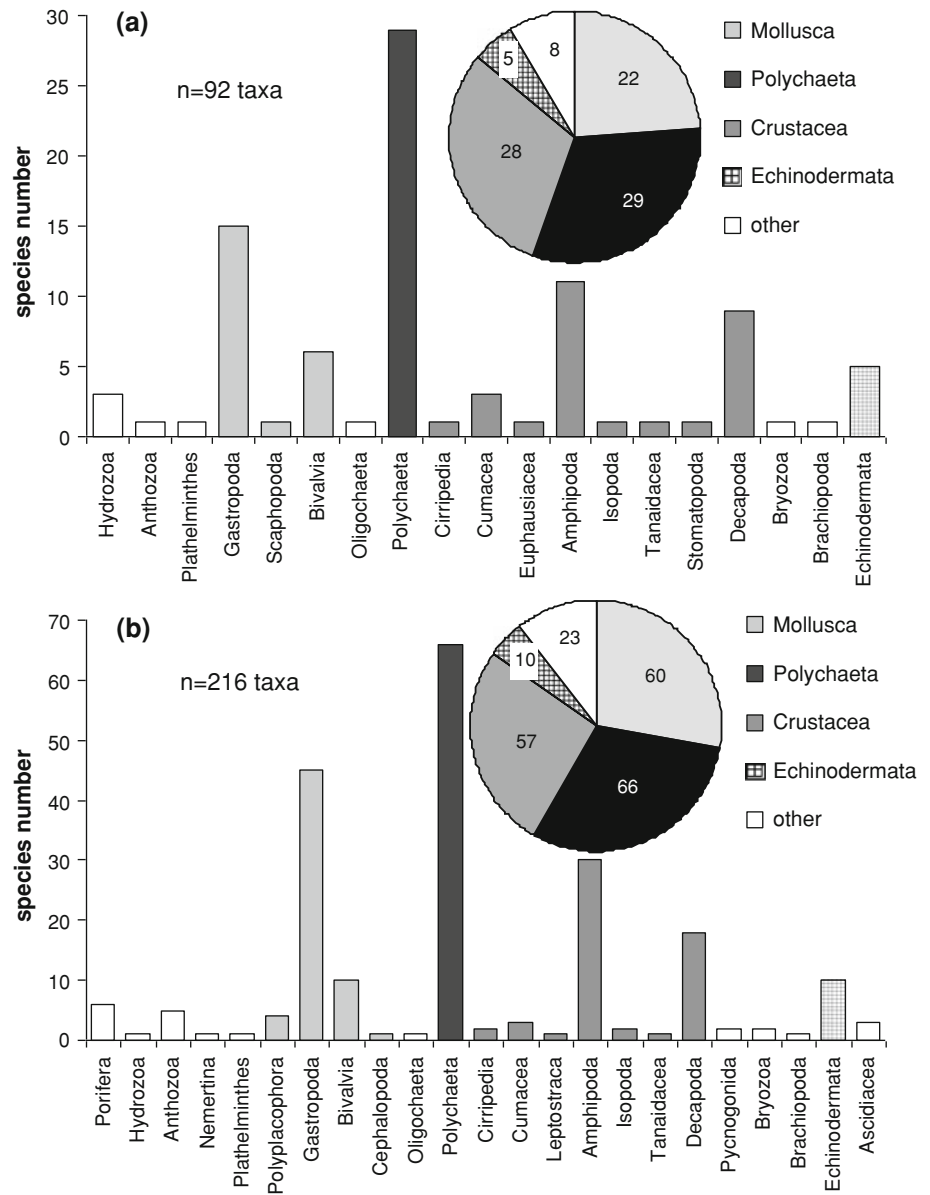


Fig. 4 Characteristic image of benthic samples of **(a)** the oxygen minimum zone with dominating *Nuculana bicuspidata* and *Nassarius vinctus* and **(b)** the near shore oxygenated zone with live and dead shells of *Discinisca tenuis*



Field 2008; Lange 2008; Ramos et al. 2008). The distribution of benthic ostracods in the Benguela upwelling system and its association with particular environmental characteristics was investigated by Dingle (1995) and Mangalo

(2004) studied some dominant molluscs in the offshore benthos. The present study examines patterns in composition, abundance and biomass of benthic macro-infaunal communities within the OMZ and the nearshore shell deposits of

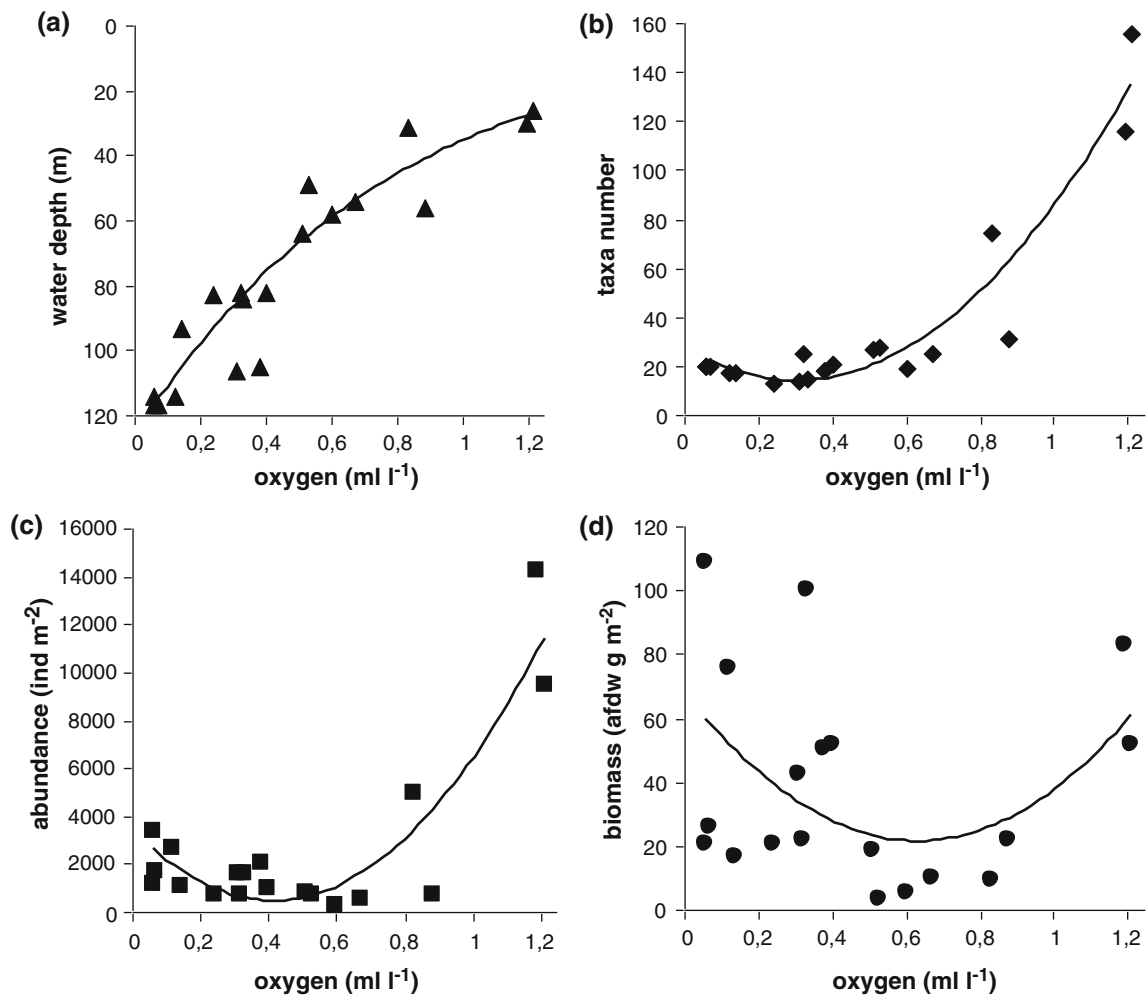


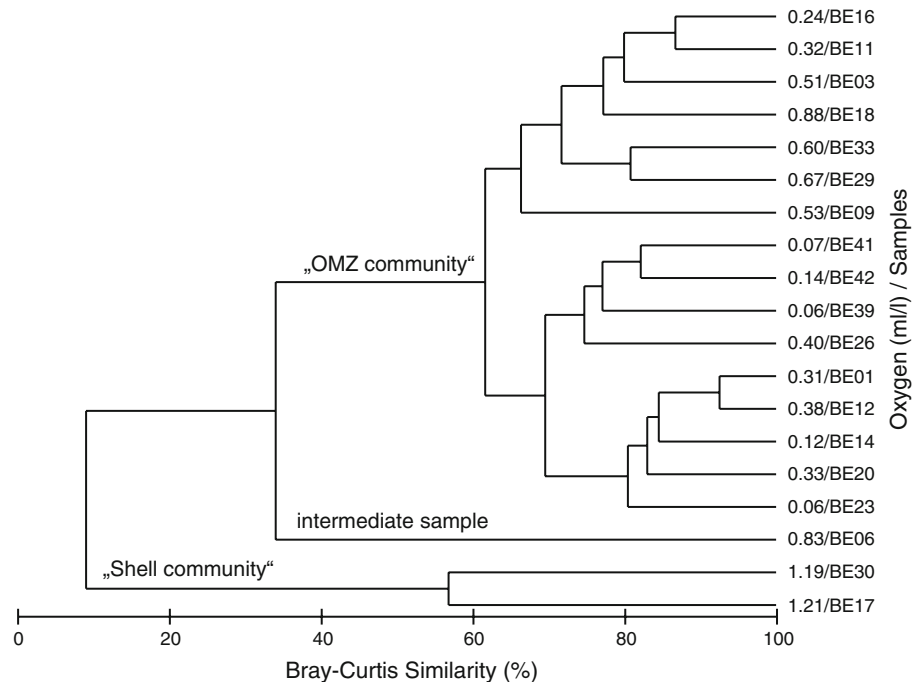
Fig. 5 Water depth and some macrozoobenthic parameters in relation to near bottom oxygen concentrations: oxygen compared to: **a** water depth, **b** macrozoobenthic species number, **c** abundance and **d** biomass. The best fitted regression is indicated by a *solid line*

the brachiopod *D. tenuis* in the northern Benguela area. The endemic disc-lamp shell *D. tenuis* occurs in large numbers and dense beds at the low water mark (and sublittoral). Clear formations can be observed by its deposits in the northern Benguela region (Hiller 1990; Sakko 1998). The associated macrobenthic fauna in these highly diverse sub-tidal waters differed extremely from the OMZ area.

As expected, few macrofaunal species were found in the hypoxic mud belt at depths between 50 and 120 m. However, a small assemblage of highly specialised animals appears to cope physically, physiologically and to some extent in their behaviour with this hostile environment where anoxia and exposure to hydrogen sulphide regularly occurs. Particularly in areas, where bottom water is not totally anoxic/sulphidic, surface-dwelling fauna consisted of an established macrofaunal community. Although existing literature often consents to the hypothesis that both diversity and biomass within the OMZ would be lower than beneath the OMZ, in the present study (similar to Gallardo

et al. 2004 from Chilean waters) this was only true for diversity. This study's macrofaunal densities are lower than those at upwelling areas of Peru and Chile (Levin et al. 2002; Gallardo et al. 2004) but are similar to those found by Palma et al. (2005) at the continental margin of Chile. Contrary to studies from OMZ's under other upwelling areas (see review by Levin 2003), where generally small-bodied polychaetes dominate, in waters off Namibia two molluscs species reach up to 90% of the abundance and biomass, respectively (Fig. 7). We have to point out that in all these studies sediments were sieved through either 300 or 500 μm meshes, whereas we used a 1 mm² mesh sieve. So, these findings may be partially biased by the use of coarser sieves, which may have resulted in the loss of soft-bodied small taxa (e.g. polychaetes) during our sieving procedure. Some of the species or genera found in the OMZ of South-west America were found in the Benguela region too. *P. pinnata*, *Cirratulus* sp. and *Lumbrineris* sp. were frequently observed in Namibian and South American upwelling areas

Fig. 6 Dendrogram showing similarity of 19 sampled stations based on the abundance of 19 dominant species recorded (Table 2). The bottom water oxygen values of the different stations are indicated



as well (Table 2). The biomass in Namibia is, however, a manifold of that in Chilean waters due to the dominance of mollusc species. Up to 109 g ash-free dry weight per m² (equates 1.4 kg wet weight and 827 g dry weight, respectively) were measured (Fig. 5d). In comparison, approximately 65 g m⁻² wet weight was published by Levin et al. (2002), Gallardo et al. (2004) and Palma et al. (2005) for the OMZ off Chile and Peru although the surface-dwelling gastropod *Astyris permodesta* (Dall 1890) is present in the Santa Barbara Basin and in a Basin off Peru as well (Bernard et al. 2000; Levin et al. 2003).

Lutjeharms and Meeuwis (1987) partitioned the Benguela system into six upwelling cells based on different surface water conditions. The central upwelling proceeds in the vicinity of Luderitz with declines to the north and south. Our investigation area was situated in the northernmost of these cells (Namib cell). The far northern region of the Namib province coincides with the area of transition between the temperate and the tropical biogeographical provinces (Sakko 1998). The front between the cool waters of the Benguela system and the warm Angolan Current waters oscillates seasonally in the vicinity of the Cunene River mouth (Shannon et al. 1987; Mohrholz et al. 2008). Since the Angola Basin is a primary source of advected oxygen-poor water (Mohrholz et al. 2008), the effects of dysoxia will be greater in the northern cells than in the southern Benguela region, which is more affected by oceanic, oxygen-rich, advected Antarctic Intermediate Water. Upwelling in the Benguela as well shows a clear seasonal cycle with a maximum for the northern Benguela region during late austral winter to spring (Shannon 1985). The

bottom water generally becomes hypoxic to anoxic during the late austral summer (sampling time of this study) to autumn when hypoxic, nutrient-rich South Atlantic central water (SACW) from the Angola Gyre is transported into the Benguela Current area, whereas more intense ventilation occurs during late winter to spring when fresher Eastern South Atlantic Central water (ESACW) is drawn onto the shelf (Mohrholz et al. 2008).

The observed hypoxic conditions during our study and the impressive colonisation of the OMZ by the dominating bivalve *N. bicuspidata* and the gastropod *N. vincetus* cannot be a short-term and local event. The long-lived species seem to be adapted to the recurrence of nearly anoxic and hypoxic conditions in this region and the sediment properties witness the continuous existence of these conditions over historical time-scales. This view is encouraged by the findings of Mangalo (2004) and our own results from the 2004 expedition. The biomass of the macrofauna community does not decline in the observed oxygen gradient (Fig. 2) between 50 and 120 m water depth (0.88–0.06 ml O₂ l⁻¹). This suggests that the *Nuculana-Nassarius*-community found within the OMZ gets at least a certain discontinuous low supply of oxygen to convert the abundant organic food to biomass. It as well needs adaptational capabilities to overcome times of extremely low oxygen concentrations. These will be related to either an increase or a decrease of bioturbation and/or pumping activities and therefore will affect the functional role of the macrofauna in this area. This community is probably rather representative for the fringes of the upwelling cells of the northern Benguela (Cunene River to Walvis Bay, 17° to 23°S) than for the

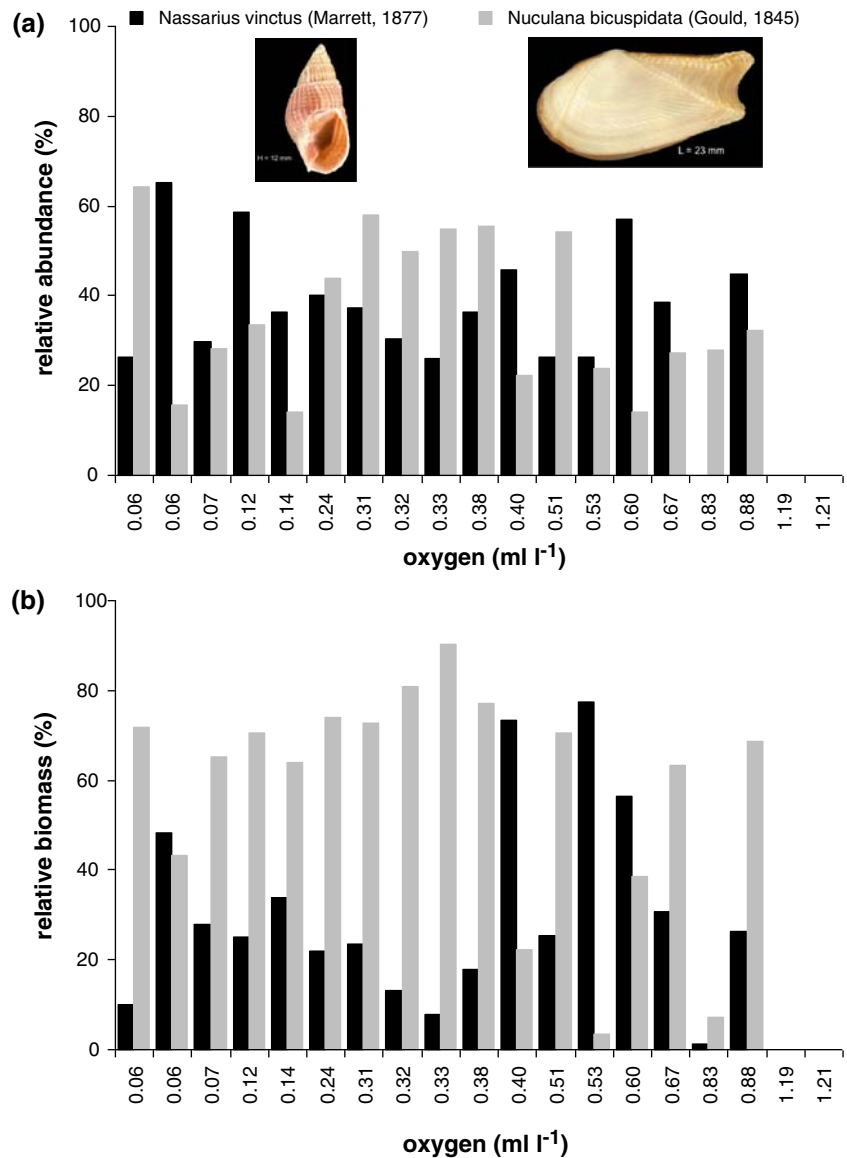
Table 3 List of species and their counts (ind m⁻¹) of the five very low oxygen stations (<0.15 ml l⁻¹) of the Namibian OMZ

Group	Taxa	BE14 0.12 ml l ⁻¹	BE23 0.06 ml l ⁻¹	BE39 0.06 ml l ⁻¹	BE41 0.08 ml l ⁻¹	BE42 0.14 ml l ⁻¹
Anthozoa	Anthozoa indet.		3			
Hydrozoa	Hydrozoa indet.	1	1		1	1
Bivalvia	<i>Costellipitar peliferus</i> (Cosel, 1995)	3	10	1	1	1
Bivalvia	<i>Nuculana bicuspidata</i> (Gould, 1845)	881	2,150	180	483	146
Gastropoda	<i>Agathotoma</i> cf. <i>merlini</i> (Dautzenberg, 1910)		3			
Gastropoda	<i>Bullia skoogi</i> (Odhner, 1923)	10	3	14	3	1
Gastropoda	<i>Mangelia</i> sp.	17				
Gastropoda	<i>Nassarius vincitus</i> (Marrett, 1877)	1,544	881	745	514	378
Gastropoda	<i>Tectonatica sagraiana</i> (d'Orbigny, 1842)	20	24	3	14	10
Gastropoda	Turridae indet.	14				
Polychaeta	Aphroditidae indet.				3	
Polychaeta	Cirratulidae/Paraonidae indet.				17	
Polychaeta	<i>Diopatra</i> cf. <i>neapolitana capensis</i> Day, 1960		1			
Polychaeta	<i>Glycinde kameruniana</i> Augner, 1918	10		7	7	7
Polychaeta	<i>Nephtys hombergii</i> Savigny Lamarck, 1818		10	7	31	14
Polychaeta	<i>Paraprionospio pinnata</i> (Ehlers, 1901)		7	78	456	231
Polychaeta	<i>Phyllamphicteis</i> sp.				3	
Polychaeta	<i>Polydora</i> sp.	3				
Polychaeta	<i>Pseudonereis variegata</i> (Grube, 1857)	10	10	10	7	10
Polychaeta	<i>Sabellaria eupomatoides</i> Augner, 1918	75	201	51	95	214
Polychaeta	Sabellidae indet.				3	
Polychaeta	<i>Sigambra robusta</i> (Ehlers, 1908)	10	17	17	61	7
Amphipoda	<i>Ampelisca spinimana</i> Chevreux, 1900		3			
Amphipoda	<i>Eriopisa epistomata</i> Griffiths, 1974			7		
Amphipoda	<i>Eriopisella epimera</i> (Griffiths, 1974)					3
Amphipoda	<i>Lembos</i> cf. <i>leptocheirus</i> Walker, 1909				3	
Amphipoda	<i>Leucothoe dentitelson</i> Chevreux, 1925					7
Amphipoda	<i>Listriella lindae</i> Griffiths, 1974		10		7	
Amphipoda	Lysianassidae indet.		3			
Amphipoda	<i>Pardia</i> sp. ?	3	3	7		3
Cumacea	Cumacea indet.					3
Cumacea	<i>Iphinoe africana</i> Zimmer, 1908	3				
Cumacea	<i>Iphinoe</i> cf. <i>brevipes</i> Hansen, 1895			1		
Decapoda	<i>Callianassa</i> sp. ?	3	3			
Decapoda	Dendrobranchiata indet.	10		7	7	3
Decapoda	<i>Diogenes</i> sp. ?	7	3		3	
Stomatopoda	Stomatopoda indet.			1		
Echinodermata	<i>Ophiura</i> sp. ?			1		
	Abundance in total (ind./m ²)	2,627	3,349	1,137	1,720	1,040

centre with severe anoxia and high hydrogen sulphide concentrations. These results concord with Bailey (1991), who observed that box core samples taken in the vicinity of Walvis Bay have frequently been devoid of infauna, confirming the semi-permanence of strong anoxia (Gallardo et al. 1998). On the ecological level further studies are necessary to clarify (1) which are the limiting

environmental conditions for the distribution of this *Nuculana-Nassarius*-community (2) Its distribution in terms of water depth and the lateral distribution towards the southern upwelling cells. (3) Its effects on sediment/water exchange especially for nitrate and oxygen, and finally (4) if the shift in benthic diversity patterns observed between the fringe and the centre of the upwelling area is similar to

Fig. 7 Relative abundance (a) and biomass (b) of two dominant macrozoobenthic species of the oxygen minimum zone at 19 stations sampled in 2008 off Namibia



results reported from the OMZ of the Eastern Pacific and the Arabian Sea (Levin 2003).

From our observations at the upper fringe of the Namibian OMZ the generalisation of Levin (2003): “In contrast to the Foraminifera, calcified invertebrates are absent or only weakly calcified where oxygen levels fall below 0.3 ml l⁻¹” cannot be supported in view of the high molluscs biomass at the extremely low oxygen concentrations. Our study rather backs Mullins et al. (1985), who under the Californian upwelling found fringes of OMZ’s to be centres of macrofauna abundance and activity. Probably, it is not the absolute environmental conditions that are determining the structure of macrofauna communities in OMZ’s margins but rather the steepness and the stability of the gradients at the fringes. In general, food availability remains a significant determinant of animal abundance and biogenic structure depth for assemblages evolving under permanent

severe hypoxia (Levin et al. 2009). However, contrary to Oman and Peruvian conditions the Benguela OMZ starts directly beneath the euphotic zone and extremely fresh material is supplied to the sediment. This promotes high oxygen reduction rates but at the same time offers the possibility for occasional oxygen replenishment by current-, tide- or even wave-induced turbulent processes. Like in many other environmental interfaces it may as well be that the transport dynamics of reactants are of primary importance for the structural and functional properties of the biology in this gradient system.

Acknowledgments We thank Dr. U. Struck (Berlin), Dr. V. Mohrholz (Rostock), U. Hehl (Rostock), M. Römer (Hamburg) and C. Berg (Rostock) for assistance during sampling at RV Maria S. Merian. We are thankful to the team of Physical Oceanography of our Institute (e.g. S. Krüger) for assistance in CTD measurements. We wish also to thank I. Glockzin and A. Hagenmeier (both Rostock) for analysis of benthic

samples in the laboratory. Provision of additional taxonomical assistance was provided by W. Massier (Swakopmund), Prof. M. Hollmann (Bochum) and M. Huber (Zürich), we are mostly grateful to their support and expertise. We would like to express our gratitude to Silvana Birchenough (Suffolk) for helping to smooth our English.

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