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Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea

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Abstract

Investigations of macrobenthos were carried out within and beneath the oxygen minimum zone (OMZ, $< 0.5\,\mathrm{ml\,l^{-1}}$) during Fall 1994 on the Oman margin, NW Arabian Sea. Six stations (400, 700, 850, 1000, 1250 and 3400 m) were characterized with respect to macrofaunal abundance, biomass, body size, taxonomic composition, diversity and lifestyles, and the relation of these parameters to environmental conditions. The OMZ (400–1000 m) was dominated by a dense (5818–19,183 ind $\mathrm{m^{-2}}$), soft-bodied assemblage consisting largely (86–99%) of surface-feeding polychaetes. Spionids and cirratulids dominated at the 400- and 700-m stations, paraonids and ampharetids at the 850- and 1000-m stations. Molluscs and most crustaceans were common only below the OMZ ($\geqslant 1250$ m); a species of the amphipod *Ampelisca* was abundant within the OMZ, however. Both density and biomass were elevated within the OMZ relative to stations below but body size did not differ significantly among stations. The lower OMZ boundary ($0.5\,\mathrm{ml\,l^{-1}}$) was not a zone of enhanced macrofaunal standing stock, as originally hypothesized. However, abundance maxima at 700–850 m may reflect an oxygen threshold (0.15–$0.20\,\mathrm{ml\,l^{-1}}$) above which macrofauna take advantage of organically enriched sediments. Incidence of burrowing and subsurface-deposit feeding increased below the OMZ. Species richness ($E[S_{100}]$), diversity (H') and evenness (J') were lower and dominance (R1D) was higher within than beneath the OMZ. Within-station (between-boxcore) faunal heterogeneity increased markedly below the OMZ. Surface sediment pigment concentrations and oxygen together explained 96–99% of the variance in measures of $E[S_{100}]$, H' and J' across the transect;

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grain size and % TOC did not yield significant regressions. Pigments, assumed to reflect food availability and possibly oxygen effects on organic matter preservation, were negatively correlated with species richness and evenness, and positively correlated with dominance. The reverse was true for water depth. Macrobenthic patterns of calcification and lifestyle within the Oman margin OMZ (0.13–0.3 ml l^{-1}) match the dysaerobic biofacies of paleo-environmental reconstruction models.

1. Introduction

Large areas of the world oceans experience a combination of high productivity induced by upwelling and limited mixing that leads to development of midwater oxygen minimum zones (OMZs) (Kamykowski and Zentara, 1990). These result in part from oxygen depletion through biological oxygen demand. OMZs, defined as regions where O_2 is < 0.5 ml l^{-1}, are best developed in the eastern Pacific Ocean (Wyrtki, 1966), the Arabian Sea (Wyrtki, 1973), and off West Africa (Bailey, 1991). Low midwater oxygen concentrations often lead to reduced consumer utilization of primary production and, as a result, much sinking organic matter reaches the seabed relatively undegraded (Wishner et al., 1990,1995).

Where OMZs intercept the continental margin or seamounts, strong gradients are formed in both bottom-water oxygen concentration and organic-matter input (Sanders, 1969; Levin et al., 1991; this study). These gradients influence the biogeochemical properties of sediments and the composition and distributions of meio-, macro- and megafauna (Sanders, 1969; Rosenberg et al., 1983; Thompson et al., 1985; Mullins et al., 1985; Tyson and Pearson, 1991; Wishner et al., 1990,1995; Arntz et al., 1991; Levin et al., 1991,1994,1997). Because oxygen and organic matter tend to vary inversely as one crosses upper or lower boundaries of OMZs, it has been difficult to distinguish their individual effects on benthic communities. Levin and Gage (1998) have demonstrated that both parameters strongly influence the diversity of bathyal macrobenthos after effects of depth and latitude have been removed.

Other abiotic properties known to affect macrobenthic community structure can change along continental margins. Among these are water depth (Rex, 1983), particle size and particle-size diversity (Etter and Grassle, 1992), and hydrodynamic forcing (Thistle et al., 1985,1991; Gage et al., 1995; Gage, 1997). Studies of OMZ benthos can provide valuable insight into the relative importance of these different features in the presence of oxygen and organic-matter gradients.

Investigations of modern OMZ faunas may aid prediction of future change in marine assemblages and reconstruction of paleoceanographic conditions. Current trends in climate linked to global warming and increased anthropogenic alteration of nutrient input to the coastal zone may lead to intensification and spread of low-oxygen environments in the world ocean, as is occurring in the Baltic and Black Seas. Community patterns associated with hypoxia in deep water vary somewhat from

those in shallow water (Tyson and Pearson, 1991; Diaz and Rosenberg, 1995). Knowledge of these differences will enhance our predictive capabilities. Oxygen-related marine biofacies models for macrofauna are used to infer ancient oxygen and productivity regimes from sedimentary strata. These models are based on degree of lamination, the presence of calcified micro- and macrobenthic body fossils, and on the number, diversity and lifestyle represented by ichno (trace) fossils (Savrda and Bottjer, 1991). Development of these models have relied mainly on analyses of contemporary assemblages in low-oxygen basins and on continental margins, primarily in the Pacific (Rhoads and Morse, 1971; Savrda et al., 1984; Mullins et al., 1985; Thompson et al., 1985; Rhoads et al., 1991). Information about OMZ faunas in different regions of the world will help to evaluate the generality of low-oxygen biofacies models, and aid in reconstruction of historical OMZ variability (e.g., Anderson and Gardner, 1989).

In recent years considerable attention has been directed towards the physical, chemical and biological dynamics of the Arabian Sea in the northern Indian Ocean. Because of high primary production this region is thought to be important at the global scale in carbon fluxes between the ocean and the atmosphere (Owens et al., 1991), as well as in nitrogen cycling (Law and Owens, 1990; Mantoura et al., 1993; Altabet et al., 1995). Strong seasonal winds force intense upwelling during June–September (SW Monsoon) and November–February (NE Monsoon). In addition, wind-induced deep mixing causes high productivity and intense downward particle flux in the NW Arabian Sea (Banse and McLain, 1986; Nair et al., 1989; Haake et al., 1993). Sinking of particulate production leads to nearly complete depletion of oxygen and formation of a persistent midwater OMZ between 50 and 1000 m in the NW Arabian Sea. Where this OMZ impinges on the continental margin off Oman, oxygen concentrations at the bottom are above zero, but very low (Burkill, 1998; this study). Sediments beneath the OMZ on the Oman margin exhibit exceptionally high organic-matter content due to three related factors: the presence of intermediate saline waters from nearby marginal seas, the OMZ, and the presence of high primary productivity correlated with seasonal upwelling (Lallier-Verges et al., 1993).

The present paper examines changes in the structure of macrobenthic assemblages along a transect on the Oman margin that extends from the core of the OMZ at 400 m, across the lower OMZ boundary ($\sim$1000–1250 m) to the base of the continental margin at 3400 m. Macrobenthic community attributes are correlated with physical properties in an effort to understand potential factors influencing faunal characteristics. In particular, we sought to test the following hypotheses, (i) The OMZ macrobenthos exhibits distinct patterns of abundance, taxonomic composition, species richness, dominance, and lifestyle relative to better oxygenated sites below; (ii) Diversity within the OMZ is a product of habitat homogeneity and phyletic tolerance to physical conditions; (iii) Oxygen and organic matter supersede particle size and water depth as correlates of community structure; and (iv) The lower OMZ boundary is a zone of enhanced macrofaunal abundance and biomass. We also examine the Oman margin macrofaunal assemblages in relation to existing low-oxygen biofacies models.

2. Methods

2.1. Field sampling

Macrofauna were examined from 0.25 m^2 boxcores collected along the Oman Margin, NW Arabian Sea (roughly 19°21′N, 48°15′E) during October and November 1994 on R.R.S *Discovery* Cruise 211 (Fig. 1). This cruise was one of a suite of four cruises constituting the 1994 Indian Ocean Campaign of the UK Natural

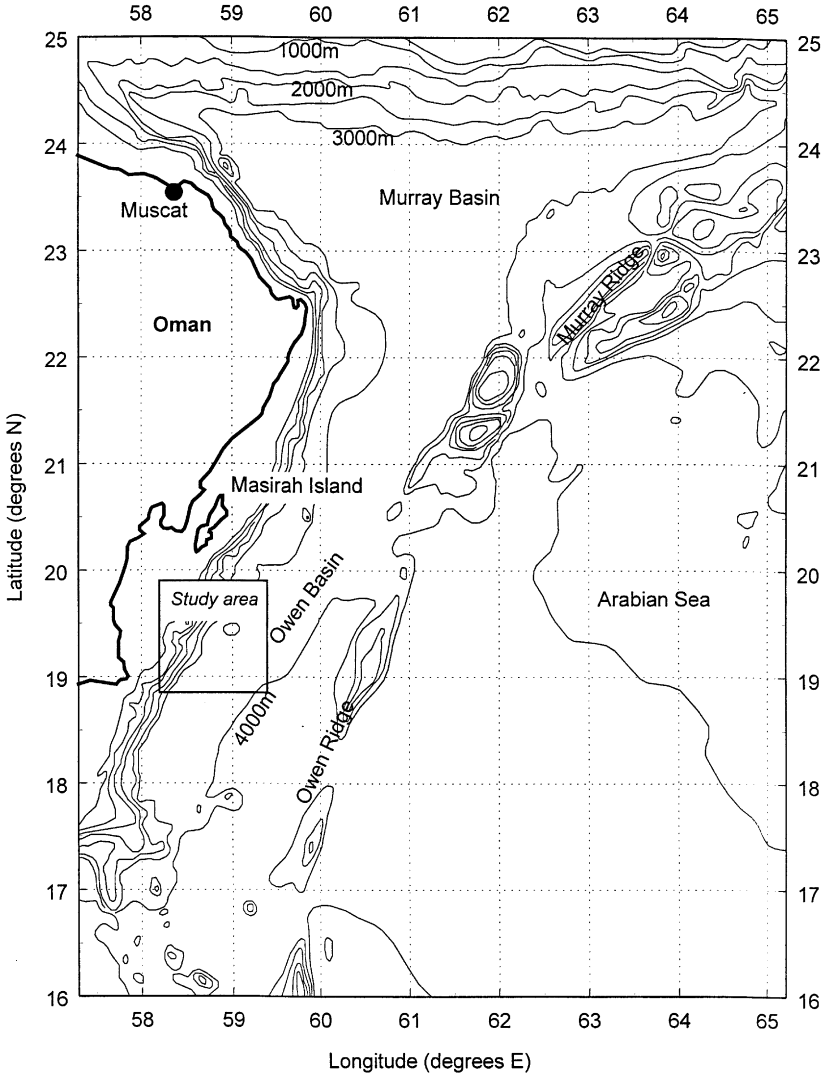

Fig. 1. Location of sampling sites during *Discovery* Cruise 211 on the Oman margin.

Environment Research Council. Data are presented for boxcores taken from six stations at approximately 400, 700, 850, 1000, 1250 and 3400 m water depth (Table 1). Positional coordinates for each boxcore (see Gage, 1995) were plotted using a GPS navigation system. Each boxcore contained ten 9.6×9.6 cm subcores (each 92.2 cm^2). A total of 27 boxcores were examined for this study; including 3–5 boxcores per station and 2–4 subcores per boxcore (Table 1). Half of these were extruded and sectioned vertically into 0–2, 2–5, 5–10 and 10–20 cm sections. In vertically sectioned cores the top 2 cm were preserved unsieved and other sediments were sieved through a 300-μm mesh screen prior to preservation in 8% buffered formalin and seawater. The other half of the subcores were sampled unsectioned to 20 cm and preserved in 8% formalin for a few days prior to transfer to 90% alcohol with 2% ethylene glycol.

Table 1
Macrobenthos sample information. Samples were taken between 9 October and 11 November, 1994

Depth (m)	Station/ sample no.	Water depth	No. subcores examined	Latitude °N	Longitude °E
400	12698/1	401	4	19 21.78	58 15.49
	12695/4	406	4	19 21.92	58 15.49
	12695/7	414	4	19 21.83	58 15.42
	12690/3	418	4	19 22.00	58 15.46
700	12685/1	674	2	19 18.95	58 15.53
	12685/8	690	2	19 18.66	58 15.64
	12685/6	700	2	19 18.88	58 15.46
850	12711/2	840	3	19 14.21	58 23.11
	12713/1	850	3	19 14.35	58 23.16
	12713/5	854	3	19 14.14	58 23.01
	12713/4	862	3	19 14.16	58 23.13
	12715/1	874	3	19 13.60	58 22.97
1000	12722/4	963	2	19 16.28	58 29.25
	12718/4	982	2	19 16.87	58 29.81
	12718/2	992	2	19 16.62	58 29.77
	12722/1	992	2	19 16.09	58 29.68
	12716/2	996	2	19 17.05	58 30.08
1250	12725/6	1244	2	19 14.31	58 31.32
	12725/2	1265	2	19 14.03	58 31.29
	12723/2	1285	2	19 14.02	58 31.42
	12723/4	1291	3	19 14.25	58 31.55
	12725/4	1310	2	19 13.91	58 31.63
3400	12687/4	3360	2	18 59.84	59 00.96
	12687/1	3372	2	18 59.51	59 00.76
	12671/4	3392	2	19 00.29	59 00.22
	12687/9	3392	2	18 59.77	59 00.49
	12730/1	3400	2	19 00.72	58 59.41

Samples for sediment grain size, carbonate, organic carbon, pigment and hydrocarbon analyses were collected by multiple corer, with core barrels 5.7 cm inside diameter. Sediments in cores were sectioned vertically in a cold room (set at ambient bottom temperatures for each station) at various intervals and then frozen at -57°C. Only data for surface sediments (0–0.5 or 0–1 cm) are reported here.

2.2. Laboratory and statistical analyses

Methods for most sediment analyses are provided in Patience and Gage (1996) and are recounted briefly here. Organic carbon analyses were carried out on the upper 5 cm of freeze-dried multicore sediments using a LECO CHN-900 analyzer. Inorganic C was removed by treatment with 20% HCl to measure organic carbon. Percentage $CaCO_3$ was calculated stoichiometrically by subtracting organic from total carbon. Grain size was measured on wet multicore samples (0–1 cm) using a Coulter LS100 laser particle size analyzer. Prior to analysis, sediments were dissociated with sodium hexametaphosphate and sonicated. Pigments (0–0.5 cm) were extracted from multicore sediments in acetone, sonicated ($3\times$ for 1 min each), centrifuged and decanted, with the entire procedure repeated twice. Analysis of pigments was by high performance liquid chromatography. Rock Eval pyrolysis, which provides information on the nature of resistant organic matter, was carried out using the methods of Espitalie et al. (1984) to yield a Hydrogen Index, expressed as mg hydrocarbon per g total organic carbon.

Bottom-water oxygen data, generated on our cruise from multicore top water and Nisken samples using Winkler titrations, appeared to be faulty, possibly due to contamination or bad reagents. We used instead oxygen data (Burkill, 1998) collected during the two "Arabesque" cruises immediately before and after ours (*Discovery* cruise 210 in August/September 1994 and *Discovery* cruise 212 in November/December 1994). We used oxygen measurements taken only from casts located along our benthic transect, from a station located in about 750 m water depth out to 3400 m. Values were obtained from CTD downcasts by either Winkler titration of water bottle samples, or from a Neil Brown Mk3B non-pulsed membrane Beckmann oxygen sensor calibrated against Winkler samples. We note that the Arabesque stations used here were located over the same spur feature (see Figs. 3 and 4 in Gage, 1995) that was sampled during *Discovery* 211, and were within 1 km of the nearest benthic station sampled on *Discovery* 211.

The oxygen values from below 200 m depth, when plotted against depth from the two Arabesque cruises, one in the monsoon, and the other during the inter-monsoon period, were very similar. There was no evidence of significant monsoon-driven temporal variability in oxygen occurring at depth on the margin. We feel therefore that the range in values observed will encompass any variability present during *Discovery* cruise 211. We fitted a power curve to a depth-truncated section of the merged data, from 248 to 1509 m depth ($n = 48$, $r^2 = 0.91$) (Smith et al., 2000) and determined predicted oxygen values at 400, 700, 850, 1000 and 1250 m (Table 2). The bottom-water oxygen value for the deepest station, (3400 m = JGOFS Stn. A1) (Table 2) is the mean of three measurements from the Arabesque data (Burkill, 1998).

Table 2
Physical characteristics of stations examined on the Oman margin during October-November, 1994.

Water depth (m)	400	700	850	1000	1250	3400
Bottom-water temperature (°C)	13.3	10.8	9.6	8.6	6.7	1.7
Bottom-water oxygen (ml l^{-1})	0.13	0.16	0.20	0.27	0.52	2.99
% TOC (0–0.5 cm)	4.99	4.03	4.01	1.93	2.67	2.72
(S.E.)	(0.44)	(0.34)	(0.16)	(0.16)	(0.07)	(0.12)
$n = 3$						
C : N (0–0.5 cm)	8.52	9.04	8.89	8.71	7.82	9.42
(S.E.)	(0.20)	(0.17)	(0.63)	(0.45)	(0.39)	(0.05)
$n = 3$						
Surface pigment 0–0.5 cm (μg/g)	770	242	167	113	68	185
(S.E.)		(49)	(39)	(17)	(26)	(101)
n	1	3	3	3	3	3
Hydrogen index (0–0.5 cm)	490	517	441	403	423	366
(mg hydrocarbon/gTOC) (SE)	(12.5)	(55.2)	(0)	(21.3)	(11.7)	(5.5)
n	2	3	2	3	3	2
% Sand (0–1 cm)	22.3	24.5	37.6	34.1	56.8	21.3
Mean grain size (μm)	42.2	46.4	66.6	92.2	79.0	42.8
Median grain size (μm)	28.7	34.3	47.1	71.7	42.1	26.5
(all $n = 1$)						
% $CaCO_3$ (0–0.5 cm)	55.1	56.7	60.5	62.0	66.1	39.48
(SE) $n = 3$	(2.5)	(0.4)	(1.7)	(2.0)	(1.0)	(3.29)

All macrofaunal samples were resieved in the laboratory through a 300-μm mesh screen and sorted under a stereo binocular microscope at 12–25 × magnification. Specimens were identified to the lowest taxon possible (usually genus) and then further sorted into nominal species. Wet biomass of formalin-preserved animals (all specimens and fragments) was measured for annelids and for total macrofauna using an analytical balance. Taxa retained on the 300-μm screen that traditionally are considered to be meiofauna (nematodes, copepods, ostracods and foraminifera) were not included in counts, biomass measurements or subsequent analyses. Sorted macrofaunal specimens, and some unsorted subcores from the boxcores listed in Table 1 have been deposited in collections of the Natural History Museum of Los Angeles County.

Summary statistics (abundance, biomass, body size, and lifestyle parameters) for each of the 6 depth stations were determined by first averaging subcore values within a boxcore and then by using boxcore means as replicates ($n = 3$–5) to calculate a station mean and standard error. Differences among stations in sediment and biological parameters were tested by one-way ANOVA. Where significance was established by ANOVA; an a posteriori Student's t-test was performed to separate station means. Statistical tests, including one-way ANOVA, simple and multiple

least-squares regression, were carried out using JMP software for the Macintosh on log-transformed data.

Multivariate analyses of macrofaunal communities were conducted using Primer and Biodiversity Pro software. Cluster analysis was performed using Bray-Curtis similarity indices run on untransformed boxcore data. Non-metric multidimensional scaling (MDS) and analysis of relative dispersion (MVDISP) were carried out on untransformed polychaete species counts (Clarke and Warwick, 1994). The relative index of multivariate dispersion examines rank dissimilarity among replicate boxcores (i.e., heterogeneity within a station), where a value of 1 is the average dispersion among stations. Because this analysis limits the number of species in the data set to 125, and requires equal sample sizes to make accurate comparisons across stations, we analyzed polychaete (rather than macrofaunal) data. Analyses were carried out on seven sets of three randomly selected cores at each station (three being the minimum number of cores collected at any one station), and averaged these to obtain relative dispersion values for each station.

Species richness was assessed based on rarefaction curves (Sanders, 1968) using the formula in Hurlbert (1971). Rarefaction curves, expected species number, and other diversity indices (H', $J' \log_2$) were calculated for pooled data from each station using the BioDiversity Program (McAleece et al., 1997). Dominance was determined to be the percent of the total represented by the most abundant species in each station (R1D) (Berger and Parker, 1970).

Feeding and dwelling-mode categories were assigned to annelid species based on information in Fauchald and Jumars (1979), Gaston (1987), and from the authors' personal observations made during shipboard processing and laboratory sorting. Annelid feeding modes were categorized as surface feeders (suspension and surface-deposit), subsurface-deposit feeders, and omnivores (including carnivores and herbivores). Dwelling habits were categorized as tube builders, burrowers and epifauna.

3. Results

3.1. Oman margin physical characteristics

Estimates of bottom-water oxygen concentration are summarized in Table 2 for depths near those sampled for macrofauna. Values were lowest at 400 m (0.13 ml l^{-1}), increased gradually to 0.27 ml l^{-1} at 1000 m, began to rise more sharply at 1250 m (0.52 ml l^{-1}), near the OMZ base, and were highest at 3400 m (2.99 ml l^{-1}) (Table 2).

Surface-sediment organic carbon concentrations were highest (between 4 and 5%) at the 400-, 700- and 850-m stations, lowest at the 1000-m station (1.6%) and intermediate at the 1250-m (2.7%) and 3400-m (2.5%) stations ($F_{5,17} = 22.4$, $P < 0.0001$) (Table 2). The highest and lowest TOC values occurred within the OMZ, indicating lack of correlation between TOC and dissolved bottom-water oxygen concentration. Surface-sediment pigment concentrations ranged from a low of 68 at 1250 m to a high of 770 μg g^{-1} at 400 m, but low samples sizes and between-core variability was such that significant differences were not observed among

stations. C : N ratios, which ranged from 7.8 to 9.4, also did not differ significantly among stations. However, hydrogen index values indicate that the organic matter at the 400- and 700-m stations was better preserved than at 3400 m ($F_{5,14} = 3.80$, $P = 0.034$) (Table 2). Mean particle size in the top cm was lowest at the 400- and 3400-m stations, and greatest at the 1000-m station. Calcium carbonate content of sediments ranged from 55 to 66% at the five uppermost stations but was only 40% at the 3400-m station.

3.2. Macrobenthic abundance, biomass and body size

Macrofaunal densities were highest in the middle of the OMZ, between 700–850 m (16,383–19,183 ind m^{-2}), intermediate at 400 and 1000 m (12,362 and 5818 ind m^{-2}, respectively), and lowest at the 1250- and 3400-m stations (2485–3190 ind m^{-2}) ($F_{5,21} = 54.66$, $P < 0.0001$; Fig. 2A). Biomass maxima were observed at 700 m (59.7 g m^{-2}) and 1000 m (43.5 g m^{-2}) ($F_{5,21} = 4.89$; $P = 0.004$, Fig. 2B), but a posteriori tests revealed significant differences only between the two deepest stations and the 700-m station.

Macrofaunal body size, estimated as g wet wt $individual^{-1}$, was variable and did not differ significantly at any of the stations ($F_{5,21} = 2.61$, $P = 0.055$). Average individual body size was positively correlated with biomass ($r^2 = 0.25$, $P < 0.008$, $n = 27$) but not with density ($P = 0.686$). The large biomass value for the 1000-m station was heavily influenced by the presence of a few sizable ophiuroids, while the high value at 700 m reflected generally larger overall size for the soft-bodied infauna.

Annelids were considered separately, as they represent a more homogeneous group for which biomass is less influenced by hard skeletal or shell components. Annelid biomass was greatest at the 700-m station (53.2 g m^{-2}), intermediate at the 850-m

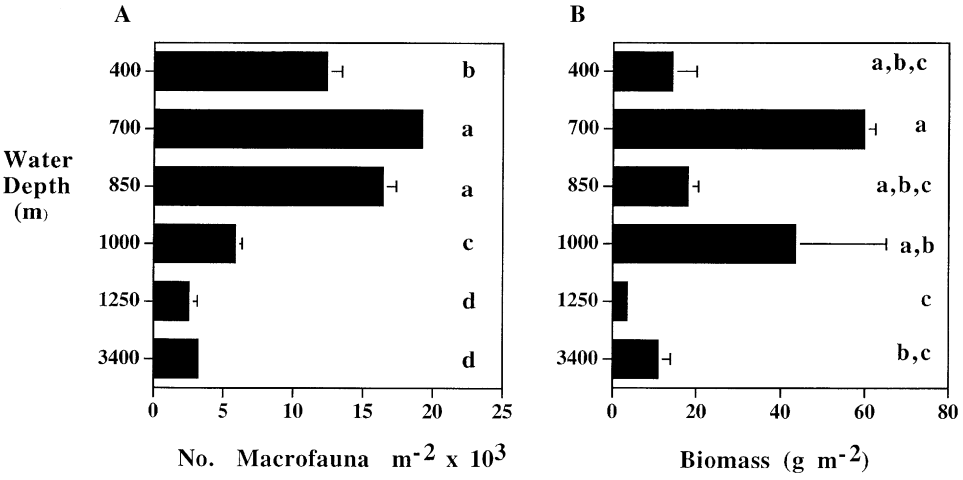

Fig. 2. Mean density (A) and biomass (B) + 1 SE for macrofauna (> 300 μm) sampled at six water depths on the Oman margin.

station (18.4 g m^{-2}) and lower, but indistinguishable at the remaining stations (4.0–8.9 g m^{-2}) ($F_{5,21} = 160.72$, $P < 0.0001$). The biomass maximum exhibited by total macrofauna at 1000 m was not evident among annelids. Annelid body size was highest at 700 m (3.2 mg ind^{-1}) and at 3400 m (3.5 mg ind^{-1}) ($F_{5,21} = 5.79$, $P = 0.002$). However, the 700-m values were significantly higher only than those at 400 m (0.8 mg ind^{-1}), and the 3400-m values were higher than the 400-, 850- and 1000-m stations (0.8–1.2 mg ind^{-1}).

3.3. Macrobenthic taxonomic composition

The uppermost four stations (400–1000 m) were dominated by polychaetes, which formed 90–96% of the total macrofauna at stations within the OMZ (Fig. 3A). The percentage of polychaetes was lower at 1250 m (71%) and nearly half that at 3400 m (37%); these percentages were significantly reduced relative to the upper four stations (ANOVA, $F_{5,21} = 95.5$ $P < 0.0001$). Polychaetes accounted for 88.8% of the individuals collected in this study; molluscs and crustaceans accounted for only 3.4 and 5.7% of the individuals, respectively. Molluscs were absent or rare ($\leqslant 0.5\%$ of the macrofauna) at stations between 400 and 850 m. Their representation increased from 1000 (1.9%) to a maximum at the 1250-m (23%) and 3400-m (18%) stations (Fig. 3A).

Crustaceans within the OMZ (400–1000 m) were limited primarily to an unknown amphipod species of *Ampelisca* (except for 2 tanaid and 1 gammarid amphipod specimens). *Ampelisca* sp. was completely absent at 400 m, accounted for 9.2 and 3.9% of macrofauna at the 700- and 850-m stations, respectively, and only 0.1% at 1000 m. Amphipods, tanaids and cumaceans were present at the 1250-m station (together 2.7% of macrofauna). At 3400 m, amphipods, tanaids and isopods together formed 31% of the total macrofauna. Other commonly occurring taxa along the transect included nemerteans, ophiuroids, anthozoans and a priapulid (Table 3). The priapulid was among the most common species (10.9% of total) at 3400 m.

Although polychaetes were consistently dominant within the OMZ from 400 to 1000 m, family representation varied among stations (Fig. 3B). Spionidae and Cirratulidae accounted for most of the polychaetes at the 400- and 700-m stations, while Ampharetidae and Paraonidae were prevalent at the 850- and 1000-m stations (Fig. 3B). Spionids comprised 66 and 69% of the total polychaetes at 400 and 700 m, respectively, but only 10–20% at the remaining stations. *Prionospio (Minuspio)* sp. A was the only spionid present and the numerically dominant taxon (66% of total macrofauna) at 400 m. *Prionospio (M.)* sp. A and *Paraprionospio* sp. A were the only spionids present at 700. A second abundant *Prionospio (M)* species appeared at 850 and 1000 m. Ampharetid, paraonid, and cirratulid polychaetes were 62% of the total polychaetes at 850 m and 71% at 1000 m (Fig. 3B). Polychaete families contributing $> 5\%$ of total macrofauna at 1250 m were the Spionidae, Syllidae, Cirratulidae, and Chrysopetalidae. At 3400 m only the Spionidae, Paraonidae and Cossuridae contributed $> 5\%$ of the total macrofauna.

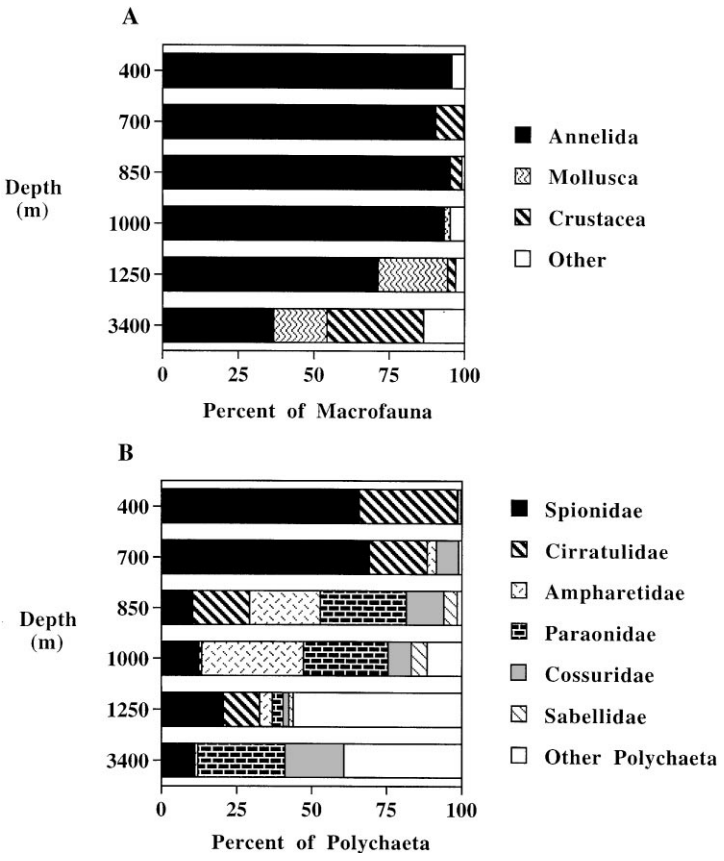

Fig. 3. Taxonomic composition of macrofauna (A) and family composition of Polychaeta (B) all (>300 μm), sampled at six water depths during 1994 on the Oman margin.

Similarity of species composition between stations varied with depth and position within or below the OMZ, although no depth station shared $\geqslant 50\%$ of species with any other station. Most stations shared 10–13 species with the adjacent station, but this fraction represented a decreasing proportion of the total species pool with increasing depth (Table 3). The 700-, 850- and 1000-m stations shared 21, 34, and 19% of total species with the station above, respectively, compared to 13 and 19% for the 1250- and 3400-m stations (Table 3).

A number of large taxa appeared in some boxcores that were not readily quantifiable from the small number of subcores examined in each boxcore. Notable among these were numerous *Amygdalum politum*, a mytilid mussel common at 400 m, and a large aggregation of a symbiont-bearing species in the bivalve family Lucinidae, occupying highly sulfidic sediments in cores between 975 and 1000 m (Gage, 1995). Both mollusc species contained red blood pigments assumed to be haemoglobin (G. Oliver, pers. comm).

Table 3
Mean no. of individuals (and SE) per 92 cm^2 subcore at each depth station on the Oman margin. *n* refers to the number of 0.25 m^2 boxcores examined

Species	400 m Mean (S.E.) ($n = 4$)	700 m Mean (S.E.) ($n = 3$)	850 m Mean (S.E.) ($n = 5$)	1000 m Mean (S.E.) ($n = 5$)	1250 m Mean (S.E.) ($n = 5$)	3400 m Mean (S.E.) ($n = 5$)
POLYCHAETA						
Amphinomidae						
Chloeia sp.A					0.07 (0.07)	
Capitellidae						
Capitellidae sp.A					0.53 (0.28)	
Maldanidae						
Axiothella sp.A					0.10 (0.10)	
Maldanidae sp.B						0.10 (0.10)
Maldanidae sp.C						0.10 (0.10)
Maldanidae sp.D					0.10 (0.10)	
Maldanidae sp.E					0.10 (0.10)	
Maldanidae sp.F				0.10 (0.10)		
Maldanidae (unid.)					0.07 (0.07)	
Cossuridae						
Cossura sp.A		10.00 (1.16)	12.80 (1.56)	5.60 (2.13)		
Cossura sp.B					0.17 (0.11)	
Cossura sp.C						2.10 (0.37)
Cossura sp.D		1.83 (0.83)	5.60 (1.27)			
Cossura sp.E	1.31 (0.28)					
Cossura sp.F					0.20 (0.20)	
Dorvilleidae						
Ophryotrocha sp.A				4.40 (3.79)		
Westheideia sp.A			0.13 (0.08)		0.17 (0.11)	
Dorvilleidae sp.A						
Dorvilleidae sp.B					0.50 (0.50)	
Lumbrineridae						
Lumbrinerides sp.A					0.73 (0.11)	
Ninoe sp.A			0.93 (0.16)	0.70 (0.20)		
Lumbrineridae (unid.)				0.20 (0.12)		

Oenonidae				
Oenonidae sp.A				0.10 (0.10)
Oenonidae (unid.)			0.07 (0.07)	
Onuphidae				
Onuphis sp.A	0.07 (0.07)			
Fauveliopsidae				
Fauveliopsis sp.A			0.20 (0.20)	
Flabelligeridae				
Diplocirrus sp.A			0.10 (0.10)	0.50 (0.00)
Opheliidae				
Armandia sp.A		0.10 (0.10)		0.30 (0.20)
Ophelina sp.A		0.20 (0.20)		
Polyopthalmus sp.A				0.10 (0.10)
Paraonidae				
Aricidea (*Acmira*) sp.A				0.10 (0.10)
Aricidea (*Acmira*) sp.B				0.20 (0.20)
Aricidea (*Acmira*) sp.C			0.27 (0.19)	
Aricidea (*Acmira*) sp.D				1.00 (0.35)
Aricidea (*Acmira*) sp.E	0.07 (0.07)	0.30 (0.20)		
Aricidea (*Allia*) ?*quadrilobata*	0.80 (0.49)	2.90 (0.49)		
Aricidea (*Allia*) sp.A	34.93 (4.96)	7.40 (1.30)		
Cirrophorus branchiatus		0.10 (0.10)	0.30 (0.20)	
Levinsenia sp.A	3.07 (0.53)	0.80 (0.80)		
Levinsenia sp.B				0.90 (0.56)
Levinsenia sp.C		3.70 (0.77)	0.07 (0.07)	0.50 (0.22)
Paradoneis nr. eliasoni	3.47 (0.40)	4.00 (0.47)	0.10 (0.10)	
Paraonis sp.C		0.10 (0.10)		
Paraonidae sp.A				0.30 (0.12)
Paraonidae sp.B		0.60 (0.37)		
Paraonidae sp.C		0.20 (0.12)		
Paraonidae sp.D				0.10 (0.10)
Paraonidae (unid.)	0.13 (0.13)	0.10 (0.10)		
Aphroditidae				
Aphroditidae sp.A			0.10 (0.10)	

Table 3 (*continued*)

Species	400 m Mean (S.E.) ($n = 4$)	700 m Mean (S.E.) ($n = 3$)	850 m Mean (S.E.) ($n = 5$)	1000 m Mean (S.E.) ($n = 5$)	1250 m Mean (S.E.) ($n = 5$)	3400 m Mean (S.E.) ($n = 5$)
Chrysopetalidae						
Dysponetus sp.A					1.47 (0.74)	
Glyceridae						
Glyceridae sp.A					0.10 (0.10)	
Goniadidae						
Goniadidae sp.A					0.07 (0.07)	
Hesionidae						
Hesionidae sp.A				0.10 (0.10)		0.10 (0.10)
Hesionidae sp.B						0.10 (0.10)
Hesionidae sp.C						0.40 (0.19)
Hesionidae sp.D.						0.20 (0.20)
Hesionidae sp.F					0.20 (0.20)	
Hesionidae sp.G					0.27 (0.11)	
Hesionidae sp.H					0.10 (0.10)	
Nephtyidae						0.10 (0.10)
Nephtyidae sp.A						
Nereididae						
Nereididae (unid.)				0.40 (0.10)		
Pholoedidae						
Pholoe sp.A						0.10 (0.10)
Phyllodocidae						
Eteone sp.A						0.10 (0.10)
Mystides sp.A			1.13 (0.44)	0.10 (0.10)		
Phyllodocidae (unid.)					0.17 (0.11)	
Pilargidae						
Sigambra sp.A		0.17 (0.17)				
Pilargidae sp.A					0.07 (0.07)	
Sphaerodoridae						
Sphaerephesia sp.A	0.19 (0.06)				0.63 (0.24)	
Sphaerephesia sp.B				1.70 (0.85)		
Sphaeradoropsis sp.A						0.50 (0.32)

Syllidae						
Eusyllinae sp.C					0.30 (0.30)	
Exogininae sp.A					0.07 (1.54)	
Exogininae sp.C						0.10 (0.10)
Syllinae sp.A					0.10 (0.10)	
Syllidae sp.A					0.10 (0.10)	0.10 (0.10)
Syllidae sp.B		0.17 (0.17)				
Syllidae (unid.)					0.40 (0.40)	
Sabellidae						
Chone sp.A		0.83 (0.17)	5.73 (0.88)	3.80 (1.18)	0.30 (0.12)	
Euchone sp.A		0.17 (0.17)				
Jasmineira sp.A		0.17 (0.17)	0.80 (0.20)			
Sabellidae (unid.)			0.13 (0.08)			
Serpulidae						
Serpulidae sp.A		0.17 (0.17)				
Acrocirridae						
Acrocirridae sp.A						0.10 (0.10)
Cirratulidae						
Aphelochaeta sp.A	31.25 (4.82)	17.17 (5.43)			0.53 (0.16)	
Aphelochaeta sp.B	0.63 (0.63)	0.17 (0.17)				
Aphelochaeta sp.C			0.47 (0.29)			
Aphelochaeta sp.D	0.13 (0.13)	2.50 (0.87)			0.50 (0.22)	
Aphelochaeta sp.E		0.17 (0.17)			0.50 (0.16)	
Aphelochaeta sp.F					0.30 (0.20)	
Aphelochaeta sp.G				0.10 (0.10)		
Monticellina sp.A			19.47 (1.36)		0.20 (0.12)	
Monticellina sp.B		4.67 (1.48)	7.73 (1.87)		0.10 (0.10)	
Monticellina sp.C		5.17 (3.56)	0.13 (0.13)	0.70 (0.34)		
Tharyx sp.A	3.56 (1.13)					
Cirratulidae sp.A					0.10 (0.10)	
Cirratulidae sp.B		0.17 (0.17)				
Cirratulidae (juv.)		0.67 (0.67)				
Cirratulidae (unid.)				0.10 (0.10)	0.20 (0.20)	
Spionidae						
Paraprionospio sp.A		45.17 (3.59)	0.73 (0.24)	0.70 (0.26)		
Prionospio (*Minuspio*) sp.A	71.63 (5.33)	64.83 (16.89)				

Table 3 (*continued*)

Species	400 m Mean (S.E.) ($n = 4$)	700 m Mean (S.E.) ($n = 3$)	850 m Mean (S.E.) ($n = 5$)	1000 m Mean (S.E.) ($n = 5$)	1250 m Mean (S.E.) ($n = 5$)	3400 m Mean (S.E.) ($n = 5$)
Prionospio (*Minuspio*) sp.B			14.67 (1.18)			
Prionospio (*Minuspio*) sp.C				6.60 (1.15)	0.57 (0.25)	
Prionospio (*Minuspio*) sp.D						0.10 (0.10)
Prionospio (*Prionospio*) sp.A					0.20 (0.12)	
Prionospio ?*plumosa*				0.50 (0.50)		
Prionospio (unid.)					0.07 (0.07)	0.50 (0.16)
Spiophanes sp.A					2.73 (0.91)	
Spiophanes sp.B						0.30 (0.12)
Spiophanes sp.C				0.90 (0.37)	0.30 (0.12)	
Spiophanes (unid.)				0.20 (0.12)		
Spionidae sp.A						0.20 (0.20)
Spionidae sp.C						0.10 (0.10)
Spionidae (unk.)					0.10 (0.10)	
Sternaspidae						
Sternaspis sp.A						0.30 (0.12)
Ampharetidae						
Eclysippe sp.B	0.19 (0.12)	1.67 (1.20)	22.60 (1.72)	8.50 (1.31)		
Lysippe sp.A		3.17 (0.33)	12.07 (0.64)	15.60 (5.85)		
Melinna sp.A					0.10 (0.10)	
Ampharetinae sp.A				0.70 (0.26)		
Ampharetinae sp.B					0.70 (0.58)	
Ampharetidae sp.B					0.10 (0.10)	
Ampharetidae (unid.)						0.10 (0.10)
Pectinariidae						
Pectinaria (*P.*) sp.A						0.10 (0.10)
Terebellidae						
Terebellidae sp.A					0.40 (0.19)	
Unk. sp.D						0.20 (0.20)
Unk. sp.E						0.20 (0.12)

Unk. sp.F						0.10 (0.10)
Unk. sp.G						0.10 (0.10)
Unk. sp.H					0.20 (0.20)	
Unk. sp.I					0.20 (0.20)	
Unk. sp.J					0.10 (0.10)	
Unk. sp.K					0.07 (0.07)	
Unk. sp.L					0.07 (0.07)	
Unk. sp.M)						0.10 (0.10)
Unk. sp.N				0.10 (0.10)		
Unk. sp.O				0.20 (0.20)		
Unk. (14)					0.10 (0.10)	
Unidentified polychaete				0.20 (0.12)	0.13 (0.13)	
OLIGOCHAETA						
Oligochaeta sp.A			0.13 (0.13)			
NEMERTEA						
Nemertea (unid.)	5.00 (1.82)	0.33 (0.33)	1.33 (0.28)	0.50 (0.16)	0.30 (0.20)	0.90 (0.10)
MISC. VERMIFORMS						
Vermes B						0.20 (0.12)
Vermes (unid.)			0.07 (0.07)	0.10 (0.10)		
MOLLUSCA						
APLACOPHORA						
Prochaetodermatidae						
Rhabdoderma sp.A			0.27 (0.19)	0.10 (0.10)		2.90 (0.97)
Spathoderma sp.A					0.07 (0.07)	
Scutopidae						
Psilodens sp.A					0.10 (0.10)	
Chaetodermomorpha sp.A					0.10 (0.10)	
BIVALVIA						
Lucinidae						
Lucinoma sp.A				0.30 (0.20)		
Lucinidae (juv)					0.20 (0.20)	
Kelliellidae						
Kelliella sp.A					0.20 (0.20)	
Thyasiridae						
Thyasira sp.C					0.63 (0.32)	0.10 (0.10)
Thyasira sp.L						0.20 (0.20)

Table 3 (*continued*)

Species	400 m Mean (S.E.) ($n = 4$)	700 m Mean (S.E.) ($n = 3$)	850 m Mean (S.E.) ($n = 5$)	1000 m Mean (S.E.) ($n = 5$)	1250 m Mean (S.E.) ($n = 5$)	3400 m Mean (S.E.) ($n = 5$)
Thyasira (*Mendicula*) sp.F					2.37 (1.13)	0.20 (0.20)
Thyasira (*Mendicula*) sp.G						0.70 (0.34)
Thyasira (unid.)				0.20 (0.20)		
Nuculidae						
Nucula sp.A						0.30 (0.20)
Nucula (unid.)						0.10 (0.10)
Nuculanidae						
Ledella sp.A						0.10 (0.10)
Nuculoma sp.A						1.80 (0.66)
Yoldiella sp.K					0.10 (0.10)	
Nuculanidae sp.A			0.13 (0.08)			
Propeamussiidae						
Propeamussium sp.A					0.07 (0.07)	
Mytilidae						
Amygdalum politum	0.06 (0.06)					
Protobranchia sp.A					0.17 (0.11)	0.30 (0.12)
Protobranchia sp.B						0.50 (0.32)
Protobranchia (unid.)					0.10 (0.10)	0.10 (0.10)
Septibranchia sp.A						0.10 (0.10)
Bivalvia sp.D				0.20 (0.12)		
Bivalvia sp.E				0.10 (0.10)		
Bivalvia (unid.)		0.33 (0.33)	0.20 (0.13)	0.20 (0.20)	0.73 (0.37)	0.60 (0.25)
GASTROPODA						
Eulimidae						
Eulima sp.A					0.27 (0.19)	
Pyramidellidae						
?*Pyramidella* sp.A		0.17 (0.17)				
Gastropoda sp.B				0.10 (0.10)	0.13 (0.13)	
Gastropoda sp.C					0.07 (0.07)	
Gastropoda sp.F0.30 (0.20)					0.30 (0.20)	
Gastropoda sp.G0.10 (0.10)					0.10 (0.10)	
Gastropoda (unid.)			0.07 (0.07)		0.10 (0.10)	0.20 (0.12)

SCAPHOPODA					
Gadilidae					
Cadulus sp.A	0.33 (0.33)				
Scaphopoda sp.A					0.20 (0.12)
Scaphopoda (unid.)				0.10 (0.10)	
CRUSTACEA					
Decapoda (unid.)		0.07 (0.07)			
Cumacea					
Cumacea sp.A				0.10 (0.10)	
Tanaidacea					
Tanaidacea sp.A					4.50 (3.27)
Tanaidacea sp.B					0.50 (0.39)
Tanaidacea sp.C				0.33 (0.14)	
Tanaidacea (unid.)		0.13 (0.08)			
Amphipoda					
Ampeliscidae					
Ampelisca sp.A	16.33 (7.38)	6.73 (1.68)	0.40 (0.19)		
Gammaridea sp.A			0.10 (0.10)		
Gammaridea sp.B				0.27 (0.11)	0.30 (0.30)
Gammaridea sp.C			0.20 (0.20)		0.10 (0.10)
Isopoda					
Asellota					
Macrostylidae					
Macrostylus sp.A					3.20 (0.52)
Isopoda sp.A					0.40 (0.29)
Crustacea (unid.)					0.10 (0.10)
COELENTERATA					
Anthozoa (unid.)	0.33 (0.17)		0.40 (0.40)		0.10 (0.10)
Hydrozoa (unid.)			0.20 (0.20)	0.10 (0.10)	
(unid.)			0.10 (0.10)		
ECHINODERMATA					
Ophiuroidea (unid.)			0.80 (0.34)	0.53 (0.16)	0.10 (0.10)

3.4. Multivariate community analyses

Community composition, examined through similarity analyses, was distinct at each of the six stations sampled. The 400- and 700-m stations and the 850- and 1000-m stations were most similar to one another (Fig. 6). Within each depth station, cores were most homogeneous at depths $\leqslant 850$ m. Markedly increased within-station (between-core) heterogeneity occurred below the OMZ, at the 1250- and 3400-m stations (Fig. 6). Comparable results were obtained for polychaetes. A multidimensional scaling plot revealed different polychaete community composition among sites, and increased within-station heterogeneity among cores beneath the OMZ (Fig. 7). This heterogeneity is quantified by the multivariate index of dispersion (Fig. 7).

3.5. Macrobenthic diversity and dominance

Macrobenthic species richness was normalized to the number of individuals sampled by rarefaction. Rarefaction richness for pooled samples was lowest at 400 m ($E[S_{100}] = 5.07$), and increased with depth to 1200 m ($E[S_{100}] = 33.6$), then declined at 3400 m ($E[S_{100}] = 28.7$) (Fig. 4, Table 4). At 400 m, a collection of 1823 individuals yielded only 11 species, but at 700 m, 1061 individuals yielded 28 species (Table 4). Species richness per unit area (calculated as the mean number of species per 92 cm^2 subcore) was significantly lower at 400 m (5.1 spp. $core^{-1}$) than at all stations except the 700-m station (11.5 spp. $core^{-1}$) ($F_{5,26} = 12.46$, $P < 0.0001$). Species richness per core did not differ significantly among the other stations (14.9–17.6 spp. $core^{-1}$) (Table 4).

The Shannon index, H', and Pielou's evenness measure, J', also reflected increasing diversity and evenness with depth to 1250 m and a decline in these indices at the deep station (Table 4). Dominance patterns were the inverse of species richness patterns shown by rarefaction and the Shannon index (Table 4). Dominance at the two shallowest stations was extremely high. *Prionospio* (*M.*) sp. A, the most abundant species at 400 and 700 m, formed 66 and 37% of the total macrofauna at these two stations, respectively. The top-ranked species at the other stations were a paraonid polychaete, *Aricidea (Allia)* sp.A at 850 m (21.3% of total fauna), an ampharetid polychaete, *Eclyssipe* sp. B at 1000 m (22.3%), an exogonid syllid polychaete at 1250 m (10.8%), and a tanaid (15.3%) at 3400 m.

Most of the patterns described above are a reflection of the polychaete assemblage. Diversity of molluscs and crustaceans, the two other main groups of the macrobenthic community (Table 3), was very low on the Oman margin. Maximum mollusc richness among stations occurred at 1250 m, where 14 species were found among the 69 molluscan specimens collected. These consisted of 5 bivalve, 7 gastropod, 1 aplacophoran and 1 scaphopod species. Maximum crustacean richness was at 3400 m, although only 7 species (3 amphipods, 1 isopod, 2 tanaids and 1 unidentified individual) were present among the 91 crustacean individuals in the samples examined (Table 3).

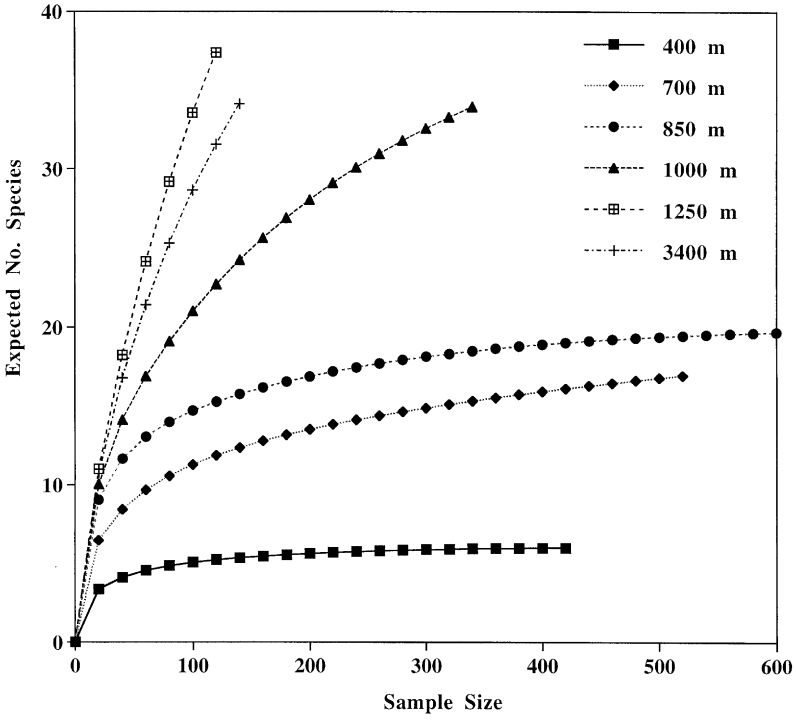

Fig. 4. Rarefaction curves for macrofauna (> 300 μm) sampled at six water depths during 1994 on the Oman margin.

Table 4
Diversity measures for macrofauna (⩾ 300 μm) on the Oman margin. Boxcore data were pooled at each station, unless noted otherwise.

	Station depth (m)					
	400	700	850	1000	1250	3400
Total no. individuals examined	1823	1061	1691	264	300	294
Total no. species	11	28	32	33	78	57
*No. species per subcore (92 cm^2)	5.1(0.1)[a]	11.5 (2.1)[a,b]	16.8 (1.0)[b]	17.6 (1.0)[b]	15.6 (2.3)[b]	14.9 (1.2)[b]
$E[S_{100}]$	5.07	11.3	14.7	21.0	33.6	28.7
H' ($\log_2$)	1.45	2.74	3.53	4.07	5.43	4.88
J' ($\log_2$)	0.44	0.59	0.72	0.71	0.85	0.81
R1D (%)	65.8	39.6	22.8	23.8	14.9	20.4

Note: * indicates mean and (SE) calculated for boxcores at each station. Stations sharing the same letter have values not significantly different from one another (ANOVA, a posteriori student's *t*-test).

3.6. Faunal lifestyles

We have focused our evaluation of faunal lifestyles on annelids (polychaetes and oligochaetes), which accounted for 90% of the 5433 specimens examined in this study. All of the annelids collected at 400 m and 95% of those from 700 m are surface-deposit feeding taxa. The frequency of surface-deposit feeding among annelids was high within the OMZ to 1000 m (86–99%), but dropped markedly at the 1250- (44%) and the 3400-m station (53%). Below 850 m there was an increased proportion of subsurface-feeding and omnivorous taxa (Fig. 5A). The greatest representation of carnivory was at 1250 m (49%). The greatest proportion of subsurface-deposit feeders occurred at 3400 m (38%) (Fig. 5A).

Dwelling-mode patterns also differed among annelids within and below the OMZ (Fig. 5B). At stations between 400 and 1000 m, $\geqslant 50\%$ of the macrofaunal individuals were tube or mudball builders. Among these were spionids, ampharetids, sabellids, and mudball-constructing cirratulids (Levin and Edesa, 1997). At 1250 and 3400 m, the majority of annelid species were burrowing forms 68 and 73%, respectively. Epifaunal annelids were quite rare ($\leqslant 1\%$) at all sites.

3.7. Environmental correlates of community structure

Of seven environmental variables examined, only oxygen exhibited significant ($P < 0.05$) linear correlations with macrofaunal density and no significant relationships with biomass were observed (Table 5). Percentage TOC was negatively correlated with body size ($r^2 = 0.73$, $P = 0.031$) (Table 5). Measures of diversity and

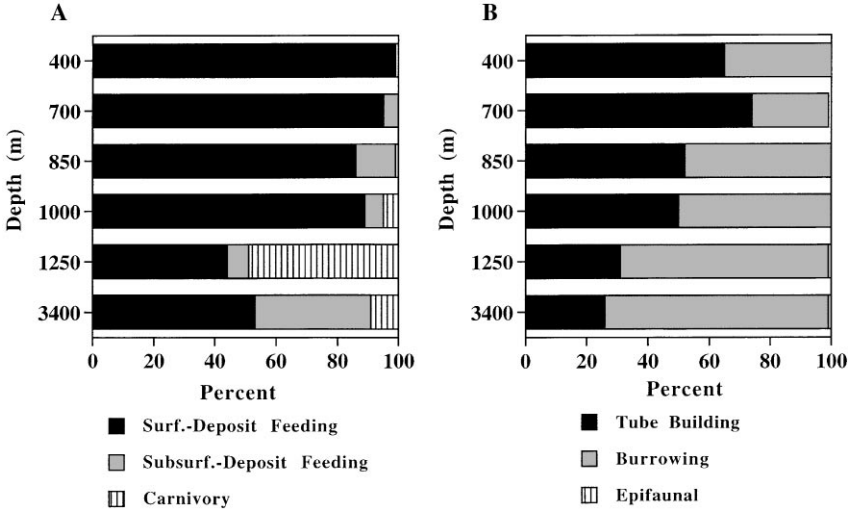

Fig. 5. Feeding modes (A) and Lifestyles (B) for Polychaeta (> 300 μm) at six water depths on the Oman margin. Surface-deposit feeding includes taxa which may also filter feed.

Table 5
Simple linear regressions analyzed for seven environmental variables against measures of macrofaunal community structure at 6 stations on the Oman margin

	Density	Biomass	Body size	$E[S_{100}]$	H'	J'	Dominance
Depth	$r^2 = 0.56$ $P = 0.087$	NS	NS	$r^2 = 0.70$ $P = 0.038$	$r^2 = 0.67$ $P = 0.048$	$r^2 = 0.66$ $P = 0.048$	$r^2 = 0.55$ $P = 0.093$
Oxygen	$r^2 = 0.68$ $P = 0.045$	NS	NS	NS	NS	NS	NS
%TOC	NS	NS	$r^2 = 0.72$ $P = 0.032$	NS	NS	NS	NS
Grain size	NS	NS	NS	NS	NS	NS	NS
Pigments	NS	NS	NS	$r^2 = 0.83$ $P = 0.011$	$r^2 = 0.87$ $P = 0.007$	$r^2 = 0.84$ $P = 0.011$	$r^2 = 0.88$ $P = 0.006$
C : N	NS	NS	NS	NS	NS	NS	NS
Hydrogen index	$r^2 = 0.59$ $P = 0.074$	NS	NS	$r^2 = 0.60$ $P = 0.071$	$r^2 = 0.55$ $P = 0.089$	$r^2 = 0.56$ $P = 0.088$	$r^2 = 0.52$ $P = 0.104$

Note: Environmental parameters were water depth (m), bottom-water oxygen concentration (ml l^{-1}), percent total organic carbon 0–0.5 cm, mean grain size (μm) 0–1 cm, total sediment pigment concentration (μg g^{-1}) 0–0.5 cm, C : N ratio 0–0.5 cm, and Hydrogen Index 0–0.5 cm. $n = 6$ (1 value per station) for all regressions. All data were log-transformed prior to analysis. Coefficient of variation is shown where $P \leqslant 0.10$. NS = Not significant.

dominance were significantly linearly correlated with water depth and surface pigment concentration (Table 5). Rarefaction species richness, H' and J' were negatively correlated with pigments, which accounted for 83, 97 and 84% of the variance in these indices, respectively (Fig. 8). Dominance was positively correlated with pigment concentration ($r^2 = 0.88$, $P = 0.006$). Water depth was positively correlated with $E[S_{100}]$, H' and J', accounting for 66–70% of variance in simple linear regressions (Table 5). Water depth and pigment concentrations were not significantly correlated with one another ($r^2 = 0.30$, $P = 0.260$), although water depth and bottom-water oxygen were ($r^2 = 0.93$, $P = 0.002$).

Oxygen-diversity relationships appeared parabolic within the 400–3400 m depth range examined. Increasing oxygen (from 400 m) led to increasing diversity up to 0.52 ml l^{-1}, but diversity declined again at the deep station (3.0 ml l^{-1}). When fit with a second-order quadratic, oxygen explained 88-96% of variation in $E[S_{100}]$, H', J', and R1D. When only stations with $\leqslant 0.5$ ml l^{-1} O_2 were considered (400–1250 m), linear regressions of bottom-water oxygen accounted for 88 ($P = 0.019$), 80 ($P = 0.040$), 77 ($P = 0.049$), and 82% ($P = 0.034$) of the variance in $E[S_{100}]$, H', J', and R1D, respectively.

Multiple linear regressions were carried out for those community indices for which more than one environmental variable was correlated by linear regression at $P \leqslant 0.10$. Oxygen was also included as this variable was highly significant within the OMZ (see above). Nearly all of the variance (97–99%) in $E[S_{100}]$, H' and J' could be

Table 6
Multiple linear regressions of environmental data against indices of diversity for macrofauna ($\geqslant$ 300 μm) at 6 depths on the Oman margin

Diversity index	R^2	P	$F_{2,5}$	Environmental parameter	Probability (P)
P					
$E[S_{100}]$	0.999	< 0.0001	5657.5	Pigment conc. Oxygen	< 0.0001 ($-$) < 0.0001 ($+$)
	0.993	0.0006	206.3	Pigment conc. Water depth	0.002 ($-$) 0.004 ($+$)
H'	0.990	0.0010	147.5	Pigment conc. Oxygen	0.0011 ($-$) 0.0090 ($+$)
	0.998	0.0001	763.0	Pigment conc. Water depth	0.0002 ($-$) 0.0008 ($+$)
J'	0.964	0.0068	40.1	Pigment conc. Oxygen	0.0070 ($+$) 0.0467 ($-$)
	0.974	0.0042	55.8	Pigment conc. Water depth	0.0094 ($+$) 0.0283 ($-$)
R1 dominance	No significant multiple regressions				

$+$ or $-$ indicates direction of effect.

explained by a combination of surface sediment pigment concentration and oxygen, or a combination of surface pigment and water depth, with surface pigment always being the more significant of the two variables (Table 6). When surface pigments, water depth and oxygen were regressed together against $E[S_{100}]$, only pigments and oxygen exhibited significant coefficients.

4. Discussion

4.1. Attributes of OMZ macrofauna

The Oman margin OMZ is considered here to encompass the 400- through 1000-m stations, with the 1250-m station just outside the lower boundary. Macrofauna present within the Oman margin OMZ were mainly soft-bodied polychaete species, with spionids and cirratulids prevalent in the upper portion, and paraonids and ampharetids in the lower portion (Fig. 3). Of the non-polychaete taxa, only nemerteans and ampeliscid amphipods were common within the OMZ (Table 3). Macrofaunal composition data from other fine-grained OMZ and deep-water, low-oxygen systems (e.g., Southern California borderland basins, Scandinavian fjords) suggest that polychaetes, particularly spionids, are the predominant taxon when oxygen values fall between 0.1 and 0.5 ml l^{-1} (Rhoads and Morse, 1971; Thompson

et al., 1985; Arntz et al., 1991; Harper et al., 1991; Levin et al., 1991; Diaz and Rosenberg, 1995; Levin and Gage, 1998). However, at oxygen levels $< 0.1\ ml\ l^{-1}$, other taxa may be more common than polychaetes in OMZs. On Volcano 7 in the eastern Pacific (750 m, $0.08\ ml\ l^{-1}$), macrofaunal communities were dominated by an aplacophoran (47%), with polychaetes only of secondary importance (33%) (Levin et al., 1991). At 300 m, in a partially laminated basin off Peru ($O_2 \sim 0.02\ ml\ l^{-1}$), gutless tubificid oligochaetes attained densities of $\sim 12{,}000\ m^{-2}$, nemerteans were common, but only a few rare polychaete species were present (Levin, unpublished data). The absence of capitellids from all of the OMZ settings described above is notable. *Capitella* spp. are abundant in enriched regions of the eastern Pacific shelf and uppermost slope (e.g., Vetter, 1996; Vetter and Dayton, 1998), but may not tolerate the very low oxygen levels characteristic of the OMZ.

The absence of infaunal crustaceans, except for ampeliscid amphipods, appears to be a general characteristic of OMZ faunas, among both macrofauna (Levin and Gage, 1998) and meiofauna (Levin et al., 1991). Ampeliscid amphipods were a dominant component of macrofaunal assemblages in the OMZ off Peru (e.g., 36% of macrofauna at 565 m, $0.26\ ml\ l^{-1}$, Levin et al., unpublished data) and were common at the 700- and 850-m stations off Oman as well (Table 3). Harper et al. (1991) reported that ampeliscids became a community dominant on the Texas shelf several months preceding severe hypoxic events, and suggested they were responding to elevated food inputs. Ampeliscid amphipods may possess physiological mechanisms that enhance oxygen uptake and perhaps sulfide tolerance. However, they do not appear to be present in slope settings with oxygen levels $< 0.15\ ml\ l^{-1}$. Polychaetes exhibit morphological adaptations to low oxygen, in the form of elongate, filamentous branchiae (Lamont and Gage, 2000).

Molluscs were rare and echinoderms were absent within the Oman margin OMZ except at 1000 m (Table 3). Large ophiuroids were abundant at 1000 m ($\sim 87\ m^{-2}$). Generally, echinoderms are thought to be rare in OMZs because calcareous shells and skeletons are difficult to maintain under low-pH, low-oxygen conditions (Rhoads and Morse, 1971; Rhoads et al., 1991). However, Thompson et al. (1985) noted abundant calcareous taxa within the central California OMZ at O_2 levels $\geqslant 0.3\ ml\ l^{-1}$. At the 1000-m station, where bivalves and echinoderms begin to appear, bottom-water oxygen concentrations were $\sim 0.3\ ml\ l^{-1}$ (Table 2).

Macrofaunal densities within the Oman margin OMZ were significantly higher than below (Fig. 2A). We observed no distinct patterns of biomass or average body size associated with the OMZ. The oxygen levels associated with the OMZ sites studied during Fall 1994 ($0.13–0.27\ ml\ l^{-1}$) were apparently not sufficiently low to substantially suppress macrofaunal densities, as was suggested to occur within OMZs on Volcano 7 off Mexico (Levin et al., 1991) and off West Africa (Sanders, 1969). Instead, high organic matter availability within the OMZ may actually enhance densities in some parts of the OMZ. However, the significantly lower macrofaunal density at 400 m, relative to the 700- and 850-m stations (Fig. 2A), may reflect effects of lower oxygen or sulfide stress. Lower Eh and pH were observed in surface sediments at 400 than at 850 m (Meadows et al., 2000).

4.2. Diversity patterns, causes and control

Macrofaunal diversity patterns (Fig. 4, Table 4) suggest that whatever is controlling diversity is not constant within the OMZ. The 400-m community is exceedingly species poor, with extraordinarily high dominance for a slope assemblage. Values of $E[S_{100}]$, H' and J' at the 400-m station are lower than those reported for macrobenthos from the eastern Pacific (Levin et al., 1991) and NW Africa OMZs (Sanders, 1969) and lower than recorded in hypoxic shallow shelf environments off Peru (Arntz et al., 1991) and Louisiana (Rabalais et al., 1995). Comparably low diversity and evenness can be found on the upper slope off Peru at depths of 200–300 m (Gutierrez, unpubl. data; Levin, unpubl. data) and in intertidal salt marshes (Levin et al., 1998). Highest diversity values were observed off Oman at 1250 m, just below the OMZ, but fell again at 3400 m (Fig. 4). This finding is consistent with mid-slope diversity maxima reported from other environments (Rex, 1983; Paterson and Lambshead, 1995; Cosson et al., 1997).

The Arabian Sea sample set reveals two diversity trends: poor representation of non-polychaete taxa within the OMZ (Fig. 3A), and increased heterogeneity between boxcores below the OMZ (Figs. 6 and 7). We hypothesize that several factors are responsible. Physical controls, associated with uniformly high organic inputs and low oxygen, may create a highly stressed, homogeneous seabed environment at each OMZ station, whereas biological interactions may become more significant below the OMZ. The increased incidence of burrowing taxa and large megafaunal species below the OMZ generates more and larger biogenic sediment structures (Smith et al., 2000), which will in turn promote spatial variation in species distributions on the scale of meters or less (Jumars and Eckman, 1982). Biogenic structures and megafauna are

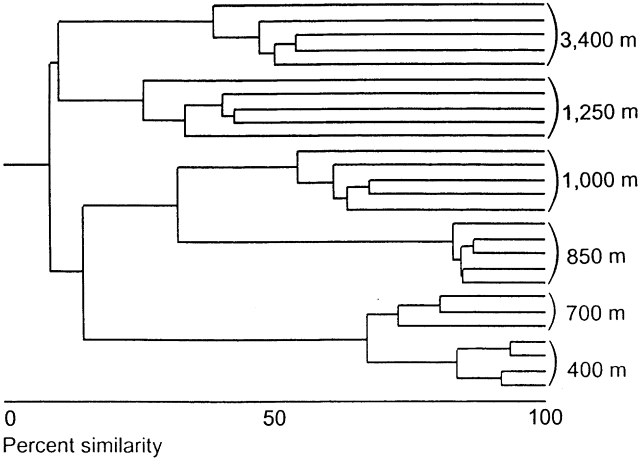

Fig. 6. Cluster analysis based on Bray–Curtis similarity indices. Data are for macrofaunal assemblages in boxcores collected on the Oman margin. Stations between 400 and 1000 m are within the oxygen-minimum zone.

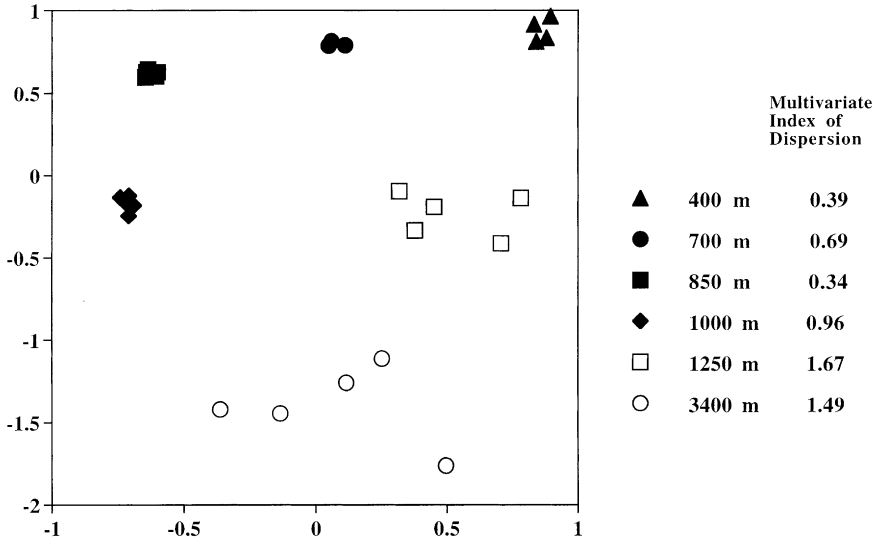

Fig. 7. Two-dimensional MDS plots of polychaete assemblages from six water depths on the Oman margin. Stress = 0.11. The global multivariate index of dispersion reflects relative within-station variability among cores.

often associated with increased patchiness of organic-matter supply, which can promote spatial heterogeneity of macrofaunal assemblages (Rice and Lambshead, 1994).

Sample separation probably does not explain changes in within-station heterogeneity. Maximum spatial separation between cores at each station was 0.41 km at 400 m, 0.59 km at 700 m, 1.41 km at 850 m, 1.88 km at 1000 m, 0.86 km at 1250 m and 3.0 km at 3400 m. Lower macrofaunal densities at 1250 and 3400 m may have contributed to elevated between-core heterogeneity below the OMZ.

4.3. Environmental influences on OMZ community structure

Stations sampled along the Oman margin varied considerably in water depth, oxygen, temperature and sediment properties (Table 2, Meadows et al., 2000). Surface-sediment pigments, bottom-water oxygen concentration, and water depth appeared to be highly correlated with measures of community diversity, but these environmental factors were only marginal predictors of macrofaunal standing stock (Tables 5 and 6). Analysis of a larger bathyal data set by Levin and Gage (1998), encompassing OMZ samples from several places, suggested a strong negative relationship between bottom-water oxygen concentration and species richness, with sediment TOC more strongly correlated with evenness indices. On the Oman margin, much of the variance in species richness, evenness and dominance could be explained by pigment concentrations (Fig. 8). High pigment concentrations were associated with species-poor, high-dominance assemblages. The pigments encountered in

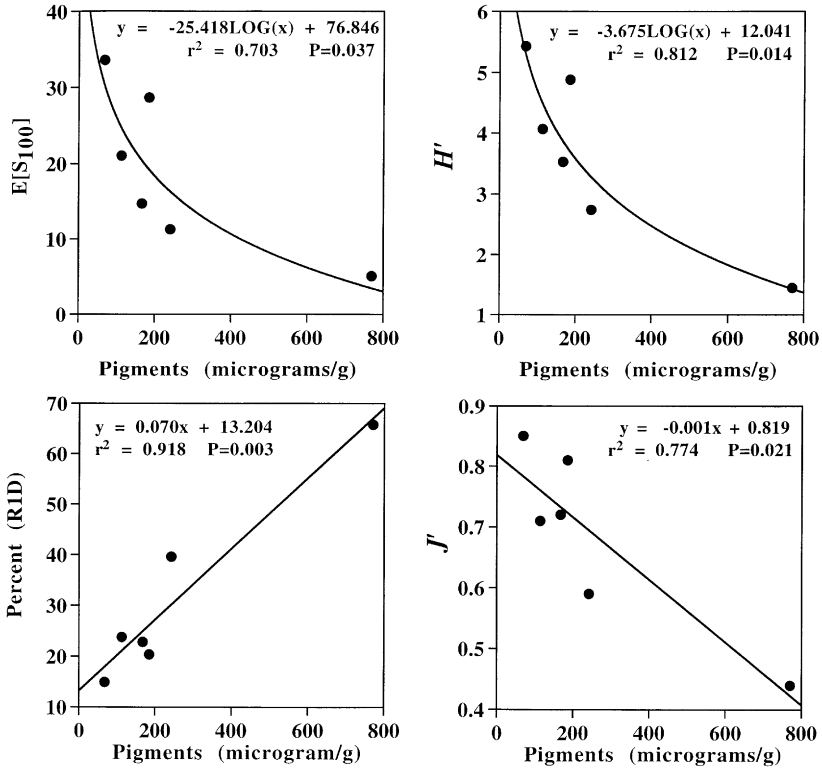

Fig. 8. Regressions of diversity measures against surface pigment concentration for six depth stations on the Oman margin. The best fit for each diversity index is shown: for species richness and H' this is a log line, and for R1D and J', a simple linear fit.

the Oman margin sediments included a variety of chlorophyll degradation products (phaeophorbide and phaeophytin compounds), (R. Goercke, A. Shankle, pers. comm). We assume that these phaeopigment concentrations primarily reflect organic matter fluxes and food availability. However, pigment preservation within the OMZ also may be influenced by other factors including currents (Pederson et al., 1992), oxygen exposure (Harnett et al., 1998), porewater oxygen concentration (Demaison and Moore, 1980), or resuspension and porewater advection (Reimers, 1998), factors which may themselves affect diversity. In past analyses of diversity, water depth has been considered a proxy for organic input; surface productivity reaching the seabed generally declines with depth (Rex, 1976). However, in our study, water depth and pigment concentrations were not significantly correlated, largely due to variable hydrodynamic regimes.

A strong role for organic matter in determining macrofaunal diversity is well documented in shallow-water systems, particularly those subject to anthropogenic enrichment (Pearson and Rosenberg, 1978,1987; Weston, 1990; Rosenberg, 1995). At the high levels occurring in the Arabian Sea, food probably will exert greater influence

on population growth rates (and population size), than on species presence or absence, although ultimately productivity must affect species richness. Where species are sufficiently tolerant of low-oxygen to take advantage of enriched food conditions within the OMZ, high dominance is likely. Certain spionid and cirratulid polychaetes appear to be hypoxia-tolerant, enrichment-specialists at the 400- and 700-m stations off Oman.

Models of productivity/diversity interactions generally predict a parabolic (unimodal) relationship, with added food availability increasing diversity at low levels but decreasing diversity at high levels (Grimes, 1973; Rosenzweig and Abramsky, 1993; Huston, 1994). The Oman margin stations experience relatively high organic deposition compared to other deep-sea settings. The Oman stations appear to fall on the right half of the food-diversity parabola, where diversity decreases with increasing organic inputs.

Deep-water benthic foraminiferal assemblages are believed to be structured largely by oxygen and organic matter availability (Jorrisen et al., 1995; Kaminski et al., 1995; Loubere, 1996; DeStigter, 1996; Gooday and Rathburn, 1999). Studies which have examined the interplay of oxygen and food in determining population and community dynamics of foraminifera suggest that oxygen becomes important only at low values, probably below $0.3\,ml\,l^{-1}$ (Anderson and Gardner, 1989; Bernhard et al., 1997; Kaminski et al., 1995), but above these levels, carbon supply takes precedence (Rathburn and Corliss, 1994; Jorrisen et al., 1995). It appears that bathyal macrofaunal community structure within OMZs also is regulated largely by oxygen and organic-matter availability. Oxygen is correlated with taxonomic composition and species richness in OMZs at concentrations $\leqslant 0.4\,ml\,l^{-1}$, but organic matter influences the distribution of individuals among species over a broad range of bottom-water oxygen concentrations. On the Oman margin, community-level responses to different conditions at the 400- and 3400-m stations were similar for metazoan macrofauna and foraminifera (Gooday et al., 2000).

4.4. OMZ boundary effects

Enhancement of biological standing stocks and biogeochemical activity have been proposed to occur at the upper and lower boundaries of OMZs, both in the benthos (Sanders, 1969; Mullins et al., 1985; Thompson et al., 1985; Levin et al., 1991; Wishner et al., 1995) and water column (Ward et al., 1989; Lipschultz et al., 1990; Karl and Knauer, 1984; Wishner et al., 1995). The present study on the Oman margin did not examine the upper OMZ boundary, but the lower OMZ boundary ($\sim 0.5\,ml\,l^{-1}$) was near the 1250-m station. Abundance and biomass data exhibited no enhancement at this boundary (Fig. 2). Such an effect would have been expected if the boundary represented an oxygen threshold above which opportunistic species could take advantage of unutilized organic matter within sediments (Levin et al., 1991). If such a threshold were to exist, it is more likely to occur around 700 m ($\sim 0.15\,ml\,l^{-1}$), where macrofaunal abundance and biomass maxima were observed (Fig. 2). Almost certainly, the position of an effective OMZ boundary or interface will vary with the taxon or process under consideration.

Table 7
Summary of oxygen-related biofacies models for marine strata (based on Savrda and Bottjer, 1987,1991; Rhoads et al., 1991; Eckdale and Mason, 1988)

ZONE OXYGEN ($ml\,l^{-1}$)	Anaerobic 0.0	Quasi-anaerobic 0.0–0.1	Exaerobic 0.1–0.2/episodic hypoxia	Dysaerobic-lower 0.1–0.3	Dysaerobic-upper 0.3–1.0	Aerobic > 1.0
METAZOANS	None	Meiofauna (nematodes), sedentary macrofauna (polychaetes)	Taxa with chemosymbionts	Low diversity	Moderate diversity	Diverse
			Tolerant opportunitists	Soft-bodied	Poorly to well calcified	Large organisms Well calcified
				Burrowers	Tube dwellers + burrowers	All dwelling modes
		All low diversity	Low diversity	Low diversity	Moderate diversity	High diversity
			Shelled forms, epibenthic			
			Most meiofauna	Most meiofauna	All meiofauna	All meiofauna
PROTOZOANS	Anaerobic microbes	Foraminifera, low diversity	Chemosynthetic mats	Low-diversity foraminifera	All forms	All forms

BIOGENIC STRUCTURES/ TRACE FOSSILS	None	Microscopic burrows	Limited macroscopic burrows	Abundant, small/Low diversity Deposit-feeding structures or tubes	Abundant, diverse/Large dwelling structures	Abundant, diverse/Large structures
PENETRATION INTO SEDIMENTS	None	Shallow	Limited, shallow	Shallow/Variable	Variable	Deep
BODY FOSSILS	None	Microfossils (e.g., foram tests) allochthonous vertebrate remains	Shelly, monospecific	Rare	Common	Abundant
BIOTURBATION	None	Microbioturbation	Minimal	Low	Increasing	Intense
RPD	None	Shallow RPD (mm)	RPD at sediment surface	Shallow RPD	Shallow–Moderate	Deep RPD
LAMINATION	Physically laminated	Physically laminated	Physically laminated	Minimal lamination	No lamination	No lamination

4.5. Oxygen-related biofacies models

Low-oxygen biofacies models, based on body and trace fossils of invertebrates and foraminifera, have been applied to examination of OMZ variability off California (Anderson and Gardner, 1989), evaluation of petroleum source rocks (Tyson, 1987), reconstruction of basin hydrography (Byers, 1977; Seilacher, 1982), and oxygenation event regimes associated with shale formation (Wignal and Hallam, 1991; Oschmann, 1991). Parameters examined in these models include sedimentary fabric and degree of lamination, the diversity, size, and vertical distribution of dwelling and feeding traces, and degree of calcification of invertebrates. In general, use of ichnofossils allows greater resolution at very low oxygen concentrations than does the use of body fossils (Savrda and Bottjer, 1991).

Key features of the low-oxygen biofacies models are reviewed by Rhoads et al. (1991) and Savrda and Bottjer (1991) and are summarized in Table 7. Although there is general agreement that a number of distinct zones occur between oxygen concentrations of 0–0.3 ml l^{-1} there is disagreement about where cutoffs occur for the development of different assemblage types. The Oman margin OMZ at the time we sampled can be considered by current definitions to be a dysaerobic zone. The dysaerobic zone was defined initially as having oxygen concentrations of 0.3–1 ml l^{-1} by Rhoads and Morse (1971), 0.1–0.5 ml l^{-1} (lower dysaerobic) by Savrda et al. (1984), and 0.1–0.3 ml l^{-1} by Thompson et al. (1985). Within this zone, biofacies models predict marked decreases in organism and burrow size, density, abundance and diversity with declining oxygen (Rhoads et al., 1991).

Macrofaunal assemblages of the upper Oman margin (400–700 m) are consistent with existing dysaerobic-zone biofacies models (Table 7) in being mainly soft-bodied and small, with few calcified forms. The presence of the thin-shelled mussel *Amygdalum politum* at 400 m reveals clearly that calcified taxa can persist at oxygen levels <0.15 ml l^{-1}. Diversity of macrofaunal species and thus biogenic structures are low at the uppermost two sites, with tube building dominant (Fig. 5B). Diversity of macrofaunal dwelling habits increases downslope, with burrowers best represented below the OMZ (Fig. 5B). The Oman margin observations support the suggestion by Wheatcroft (1989) that shallow tube-dwelling forms (domichnia ichnofacies) should dominate at low oxygen levels, rather than the subsurface burrows (fodinichnia facies) proposed by Eckdale and Mason (1988,1989). However, metazoan macrofauna living under quasi-anaerobic conditions on the Peru margin (0.02 ml l^{-1}) were mainly burrowing oligochaetes, with no tube builders present (Levin et al., unpubl.). In sandy sediments of Volcano 7, at $\sim$0.08 ml l^{-1}, a sparse fauna exhibited a broad mix of burrowing, epibenthic and tube-building lifestyles (Levin et al., 1991). Thus, it appears impossible to formulate generalizations about the dwelling habits of low-oxygen macrofauna. We speculate that even under dysaerobic conditions, organic inputs and energy regime will affect the structure of macrofaunal communities and their traces, thereby confounding detection of community response to low oxygen. Future generations of low-oxygen biofacies models will need to integrate the effects of a range of environmental parameters.

5. Conclusions

1. The Oman margin OMZ between 400 and 1000 m supports dense, soft-bodied, low-diversity macrofaunal assemblages heavily dominated by spionid, cirratulid, ampharetid and paraonid polychaetes. The upper (400–700 m) and lower portions of the OMZ (850–1000 m) exhibit distinct taxonomic and diversity patterns. Fewer than half the species were shared among adjacent stations.
2. Macrofaunal densities were generally higher, and diversity was lower within the OMZ (400–1000 m) than below (1250 m, 3400 m).
3. Lower macrofaunal diversity within the OMZ appears related to intolerance to low oxygen among many major taxa, and to extreme spatial homogeneity of assemblages within stations. Significantly greater within-station (between boxcore) heterogeneity of samples was encountered beneath the OMZ.
4. The lower OMZ boundary (0.5 ml l^{-1}) is not a zone of enhanced faunal standing stock, as originally hypothesized. However, maxima in abundance, biomass and annelid body size encountered at 700 m (0.16 ml l^{-1}) may reflect a threshold release from oxygen stress in enriched sediments.
5. Sediment pigment and dissolved oxygen concentrations (as well as pigments and water depth) explained 88–96% of the variance in macrofaunal species richness and evenness. Pigment concentrations were negatively correlated with species richness and evenness, and positively correlated with dominance. Grain size, TOC and C : N exhibited little relation to macrofaunal community structure. A downslope trend of increasing oxygen availability and decreasing organic matter availability is thought to be the major influence on macrofaunal zonation within the OMZ.
6. Macrofaunal assemblages and life habits within the Oman margin match the dysaerobic biofacies of models used in paleo environmental reconstruction. Oman margin observations suggest that dense, surface-feeding, tube-building assemblages and weakly calcified bivalves occur in organic-rich sediments where O_2 levels are between 0.1 and 0.3 ml l^{-1}.

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References

Altabet, M.A., Francois, R., Murray, D.W., Prell, W.L., 1995. Climate-related variations in denitrification in the Arabian Sea from sediment $^{15}N/^{14}N$ ratios. Nature 373, 506–509.

Anderson, R.Y., Garner, J.V., 1989. Variability of the late pleistocene-early holocene oxygen minimum zone off Northern California. In: Peterson, D.H. (Ed.), Aspects of Climate Variability in the Pacific and the Western Americas. Geophysical Monograph 55. American Geophysical Union, pp. 75–84.

Arntz, W.E., Tarazona, J., Gallardo, V., Flores, L., Salzwedel, H., 1991. Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58, London, pp. 131–154.

Bailey, G.W., 1991. Organic carbon flux and development of oxygen deficiency on the modern Benguela continental shelf south of 22°S, spatial and temporal variability. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58, London, pp. 171–183.

Banse, K., McClain, C.R., 1986. Winter blooms of phytoplankton in the Arabian Sea as observed by the Coastal Zone Color Scanner. Marine Ecology Progress Series 34, 201–211.

Berger, W.H., Parker, F.L., 1970. Diversity of planktonic Foraminifera in deep-sea sediments. Science 168, 1345–1347.

Bernhard, J.M., Sen Gupta, B.K., Borne, P.F., 1997. Benthic foraminiferal proxy to estimate dysoxic bottom-water concentrations, Santa Barbara Basin, US Pacific continental margin. Journal of Foraminiferal Research 27, 301–310.

Burkill, P., 1998. Arabesque Data Set, CD Rom Electronic Publication. British Oceanographic Data Centre. Birkenhead, UK.

Byers, C.W., 1977. Biofacies patterns in euxinic basins, a general model. In: Cook, H.E., Enos, P. (Eds.), Deep-water Carbonate Environment. Society of Economic Paleontologists and Mineralogists Special Publication No. 25, pp. 5–17.

Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities, an Approach to Statistical Analysis and Interpretation. Natural Environmental Research Council, UK, 144pp.

Cosson, N., Sibuet, M., Galeron, J., 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. Deep-Sea Research 44, 247–269.

DeStigter, H.C., 1996. Recent and fossil benthic foraminifera in the Adriatic Sea, distribution patterns in relation to organic carbon flux and oxygen concentration at the seabed. Geologica Ultraiectina. Mededelingen van de Faculteit Aardwetenschappen Universiteit Utrecht No. 44, 254pp.

Demaison, G.J., Moore, G.T., 1980. Anoxic environments and oil source bed genesis. American Association of Petroleum Geologists Bulletin 64, 1179–1209.

Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia, A review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology Annual Review 33, 245–303.

Ekdale, A.A., Mason, T.R., 1988. Characteristic trace-fossil associations in oxygen-poor sedimentary environments. Geology 16, 720–723.

Ekdale, A.A., Mason, T.R., 1989. Commentary and reply on "Characteristic trace-fossil associations in oxygen-poor sedimentary environments". Geology 17, 674–676.
Espitalie, J., Deroo, G., Marquis, F., 1984. La pyrolyse Rock-Eval et ses applications. Revue de l'Institut Francais du Petrole 40, 563–784.
Etter, R.J., Grassle, J.F., 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature 360, 576–578.
Fauchald, K., Jumars, P., 1979. The diet of worms, A study of polychaete feeding guilds. Oceanography Marine Biology Annual Review 17, 194–284.
Gage, J.D., 1995. Benthic community and fluxes in relation to the oxygen minimum zone in the Arabian Sea, Cruise Report, R.R.S. *Discovery* cruise 211/94, 9th October–11th November 1994. Scottish Association for Marine Science, Oban, Scotland, 71pp.
Gage, J.D., 1997. High benthic species diversity in deep-sea sediments, the importance of hydrodynamics. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity, Patterns and Processes. Cambridge University Press, Cambridge, pp. 148–177.
Gage, J.D., Lamont, P.A., Tyler, P.A., 1995. Macrobenthic communities at contrasting sites off Portugal, Preliminary results. 1. Introduction and diversity comparisons. Internationale Revue der gesamten Hydrobiologie 80, 235–250.
Gaston, G.R., 1987. Benthic Polychaeta of the Middle Atlantic Bight: feeding and distribution. Marine Ecology Progress Series 36, 70–73.
Gooday, A.J., Rathburn, A.E., 1999. Temporal variability in deep-sea benthic foraminifera: a review. In: van der Zwaan, G.J., Gradstein, F. (Eds.), Earth Sciences Review 46, 187–212.
Gooday, A.J., Bernhard, J.M., Levin, L.A., Suhr, S.B., 2000. Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas. Deep-Sea Research II 47, 25–54.
Grimes, J.P., 1973. Control of species diversity in herbaceous vegetation. Journal of Environmental Management 1, 141–167.
Haake, B., Ittekkot, V., Rixen, T., Ramaswamy, V., Nair, R.R., Curry, W.B., 1993. Seasonality and interannual variability of particle fluxes to the deep Arabian Sea. Deep-Sea Research 40, 1323–1344.
Harnett, H.E., Kell, R.G., Hedges, J.I., Devol, A.H., 1998. Influence of oxygen exposure time on organic carbon preservation in continental margin sediments. Nature 391, 572–574.
Harper Jr., D.E., McKinney, L.D., Nance, J.M., Salzer, R.R., 1991. Recovery responses of two benthic assemblages following an acute hypoxic event on the Texas continental shelf, northwestern Gulf of Mexico. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58, London, pp. 49–64.
Hurlbert, S.M., 1971. The non-concept of species diversity, A critique and alternative parameters. Ecology 52, 577–586.
Huston, M., 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, 681pp.
Jorissen, F.J., de Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. Marine Micropaleontology 26, 3–15.
Jumars, P.A., Eckman, J.A., 1982. Spatial structure within deep-sea benthic communities. In: Rowe, G.T. (Ed.), The Sea, Vol. 8. Wiley–Interscience, New York, pp. 399–451.
Kaminski, M.A., Boersma, A., Tyszka, J., Holbourn, A.E., 1995. Response of deep-water agglutinated foraminifera to dysoxic conditions in the California Borderland basins. In: Kaminski, M.A., Geroch, S., Gasinski, M.A. (Eds.), Proceedings of the Fourth International Workshop on Agglutinated Foraminifera. Krakow Poland. September 12–19, 1993. Grzybowski Foundation Special Publication No. 3, pp. 131–140.
Kamykowski, D., Zentara, S.J., 1990. Hypoxia in the world ocean as recorded in the historical data set. Deep-Sea Research 37, 1861–1874.
Karl, D.M., Knauer, G.A., 1984. Vertical distribution, transport and exchange of carbon in the northeast Pacific Ocean. Evidence for multiple zones of biological activity. Deep-Sea Research 31, 221–243.
Lallier-Verges, E., Bertrand, P., Desprairies, A., 1993. Organic matter composition and sulfate reduction intensity in Oman margin sediments. Marine Geology 112, 57–69.

Lamont, P.A., Gage, J.D., 2000. Morphological responses of macrobenthic polychaetes to low oxygen on the Oman continental slope, NW Arabian Sea. Deep-Sea Research II 47, 9–24.

Law, C.S., Owens, N.J.P., 1990. Significant flux of atmospheric nitrous oxide from the northwestern Indian Ocean. Nature 346, 826–828.

Levin, L.A., Edesa, S., 1997. The ecology of cirratulid mudballs on the Oman Margin. Marine Biology 128, 671–678.

Levin, L.A., Gage, J.D., 1998. Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. Deep-Sea Research 45, 129–163.

Levin L.A., Gage, J.D., Lamont, P., Cammidge, L., Martin, C., Patience, A., Crooks, J., 1997. Infaunal community structure in a low-oxygen, organic rich habitat on the Oman continental slope, NW Arabian Sea. In: Hawkins, L., Hutchinson, S. (Eds.), Responses of Marine Organisms to their Environments. Proceedings of the 30th European Marine Biology Symposium, University of Southampton, pp. 223–230.

Levin, L.A., Huggett, C.L., Wishner, K.F., 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. Journal of Marine Research 49, 763–800.

Levin, L.A., Plaia, G.R., Huggett, C.L., 1994. The influence of natural organic enhancement on life histories and community structure of bathyal polychaetes. In: Young, C.M., Eckelbarger, K.J. (Eds.), Reproduction, Larval Biology, and Recruitment of the Deep-sea Benthos. Columbia University Press, New York, pp. 261–283.

Levin, L.A., Talley, T.S., Hewitt, J., 1998. Macrobenthos of *Spartina foliosa* (Pacific Cordgrass) salt marshes in southern California, Community structure and comparison to a Pacific mudflat and a *Spartina alterniflora* (Atlantic Smooth Cordgrass) marsh. Estuaries 21, 129–144.

Lipschultz, F., Wofsy, S.C., Ward, B.B., Codispoti, L.A., Friedrich, G., Elkins, J.W., 1990. Bacterial transformations of inorganic nitrogen in the oxygen-deficient waters of the Eastern Tropical South Pacific Ocean. Deep-Sea Research 37, 1413–1541.

Loubere, P., 1996. The surface ocean productivity and bottom water oxygen signals in deep water benthic foraminiferal assemblages. Marine Micropaleonotology 28, 247–261.

Mantoura, R.F.C., Law, C.S., Owens, N.J.P., Burkill, P.H., Woodward, E.M.S., Howland, R.J.M., Lewellyn, C.A., 1993. Nitrogen biogeochemical cycling in the northwestern Indian Ocean. Deep-Sea Research 40, 651–672.

McAleece, N., Lambshead, P.J.D., Paterson, G.L.J., Gage, J.D., 1997. BioDiversity Professional, copyright Natural History Museum, London and Scottish Association for Marine Sciences,Oban. [Beta version].

Meadows, A., Meadows, P.S., West, F.J.C., Murray, J.M.H., 2000. Bioturbation, geochemistry and geotechnics affected by the oxygen minimum zone on the Oman continental slope and abyssal plain, Arabian Sea. Deep-Sea Research II 47, 259–280.

Mullins, H.T., Thompson, J.B., McDougall, K., Vercoutere, T.L., 1985. Oxygen-minimum zone edge effects, evidence from the central California coastal upwelling system. Geology 13, 491–494.

Nair, R.R., Ittekkot, V., Manganini, S.J., Ramaswamy, V., Hake, B., Degens, E.T., Desai, B.N., Honjho, S., 1989. Increased particle flux to the deep ocean related to monsoons. Nature 338, 749–751.

Oschmann, W., 1991. Distribution, dynamics and palaeoecology of Kimmeridgian (Upper Jurassic) shelf anoxia in western Europe. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society, Tulsa, Oklahoma, pp. 381–395.

Owens, N.P., Law, C.S., Mantoura, R.F.C., Burkill, P.H., Lewellyn, C.A., 1991. Methane flux to the atmosphere from the Arabian Sea. Nature 354, 293–296.

Paterson, G.L.J., Lambshead, P.J.D., 1995. Bathymetric patterns of polychaete diversity in the Rockall Trough, northeast Atlantic. Deep-Sea Research 42, 1199–1214.

Patience, A.J., Gage, J.D., 1996. Sediment biogeochemical proxies at the Oman margin oxygen minimum zone. In: Botrell, S.H. (Ed.), Proceedings of the Fourth International Symposium on the Earth's Surface, July 1996, Ilkley, UK. International Association of Geochemistry and Cosmochemistry, University of Leeds, pp. 105–108.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution in the marine environment. Oceanography Marine Biology Annual Revue 16, 229–311.

Pearson, T.H., Rosenberg, R., 1987. Feast and famine, Structuring factors in marine benthic communities. In: Gee, J.H.R., Giller, P.S. (Eds.), Organization of Communities, Past and Present. Blackwell Scientific Publishers, Boston, pp. 373–395.

Pederson, T.F., Shimmield, G.B., Price, N.B., 1992. Lack of enhanced preservation of organic matter in sediments under the oxygen minimum on the Oman margin. Geochimica et Cosmochimica Acta 56, 545–551.

Rabalais, N.N., Smith, L.E., Harper, D.E., Justic, D., 1995. Effects of bottom water hypoxia on the benthic communities of the southeastern Louisiana continental shelf. OCS Study MMS 94-0054. US Dept. of the Interior. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, Louisiana, 105pp.

Rathburn, A.W., Corliss, B.H., 1994. The ecology of deep-sea benthic foraminifera from the Sulu Sea. Paleoceanography 9, 87–150.

Reimers, C., 1998. Feedbacks from the sea floor. Nature 391, 536–537.

Rex, M.A., 1976. Biological accomodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity. Deep-Sea Research 23, 975–987.

Rex, M.A., 1983. Geographic patterns of species diversity in the deep-sea benthos. In: Rowe, G.T. (Ed.), The Sea, Vol. 8. Wiley–Interscience, New York, pp. 453–472.

Rhoads, D.C., Morse, J.W., 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. Lethaia 4, 413–428.

Rhoads, D.C., Mulsow, S.G., Gutschick, R., Baldwin, C.T., Stolz, J.F., 1991. The dysaerobic zone revisited, A magnetic facies? In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society, Tulsa, Oklahoma. pp. 187–199.

Rice, A.L., Lambshead, P.J.D., 1994. Patch dynamics in the deep-sea benthos: the role of a heterogeneous supply of organic matter. In: Giller, P.S., Hildrew, A.G., Raffaelli, D.G. (Eds.), Aquatic Ecology: Scale, Pattern and Process. Blackwell Scientific Publications, Oxford, pp. 469–498.

Rosenberg, R., Arntz, W.E., Chuman de Flores, E., Flores, L.A., Carbajal, G., Finger, G., Tarazona, J., 1983. Benthos biomass and oxygen deficiency in the upwelling system off Peru. Journal of Marine Research 41, 263–279.

Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. Netherlands Journal of Sea Research 34, 303–317.

Rosenzweig, M.L., Abramsky, H., 1993. How are diversity and productivity related? In: Ricklerf, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives., 1993. The University of Chicago Press, Chicago, pp. 53–65.

Sanders, H.L., 1968. Marine benthic diversity: a comparative study. American Naturalist 102, 243–282.

Sanders, H.L., 1969. Benthic marine diversity and the stability-time hypothesis. Brookhaven Symposia on Biology 22, 71–81.

Savrda, C.E., Bottjer, D.J., Gorsline, D., 1984. Development of a comprehensive oxygen-deficient marine biofacies model, evidence from Santa Monica, San Pedro, and Santa Barbara Basins, California Continental Borderland. American Association of Petroleum Geologists Bulletin 68, 1179–1192.

Savrda, C.E., Bottjer, D.J., 1987. Trace fossils as indicators of bottom-water redox conditions in ancient marine environments. In: Bottjer, D.J. (Ed.), New Concepts in the Use of Biogenic Sedimentary Structures for Paleoenvironmental Interpretation. Society of Economic Paleontologists and Mineralogists, Pacific Section, Volume and Guidebook Vol. 52, pp. 3–26.

Savrda, C.E., Bottjer, D.J., 1991. Oxygen-related biofacies in marine strata, An overview and update. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. The Geological Society of London, London, pp. 201–219.

Seilacher, A., 1982. Posidonia shales (Toarcian, S. Germany) – Stagnant basin model revalidated. In: Gallitelli, E.M. (Ed.), Paleontology, Essential of Earth History. STEM Mucchi, Modena, pp. 25–55.

Smith, C.R., Levin, L.A., Hoover, D.J., McMurtry, G., Gage, J.D., 2000. Variations in bioturbation across the oxygen minimum zone in the northwest Arabian Sea. Deep-Sea Research II 47, 227–257.

Thistle, D., Ertman, S.C., Fauchald, K., 1991. The fauna of the HEBBLE site, Patterns in the standing stock and sediment-dynamic effects. Marine Geology 99, 413–422.

Thistle, D., Yingst, J.Y., Fauchald, K., 1985. A deep-sea benthic community exposed to strong bottom currents on the Scotian Rise. Marine Geology 66, 91–112.

Thompson, J.B., Mullins, H.T., Newton, C.R., Vercoutere, T., 1985. Alternative biofacies model for dysaerobic communities. Lethaia 18, 167–179.

Tyson, R.V., 1987. The genesis and palynofascies characteristics of marine petroloeum source rocks. In: Brooks, J., Fleet, A.J. (Eds.), Marine Petrolem Source Rocks. Geological Society Special Publication No. 26, London, pp. 47–67.

Tyson, R.V., Pearson, T.H., 1991. Modern and ancient continental shelf anoxia: an overview. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58, London, pp. 1–24.

Vetter, E.W., 1996. Enrichment experiments and infaunal population cycles on a Southern California sand plain: response of the leptostracan Nebalia daytoni and other infauna. Marine Ecology Progress Series 137, 83–93.

Vetter, E.W., Dayton, P.K., 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. Deep-Sea Research 45, 25–54.

Ward, B.B., Glover, H.E., Lipschultz, F., 1989. Chemoautotrophic activity and nitrification in the oxygen minimum zone off Peru. Deep-Sea Research 36, 1031–1051.

Weston, D.P., 1990. Quantitative examination of macrobenthic community changes along an organic enrichment gradient. Marine Ecology Progress Series 61, 233–244.

Wheatcroft, R.A., 1989. Comment and Reply on "Characteristic trace-fossil associations in oxygen-poor sedimentary environments". Geology 17, 674.

Wignall, P.B., Hallam, A., 1991. Biofacies stratigraphic distribution and depositional models of British onshore Jurassic black shales. In: Tyson, R.V., Pearson, T.H. (Eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society, Tulsa, Oklahoma, pp. 291–310.

Wishner, K., Levin, L.A., Gowing, M., Mullineaux, L., 1990. Involvement of the oxygen minimum in benthic zonation on a deep seamount. Nature 346, 57–59.

Wishner, K.F., Ashjian, C.J., Gelfman, C., Gowing, M., Kann, L., Levin, L.A., Mullineaux, L., Saltzman, J., 1995. Pelagic and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone. Deep-Sea Research 42, 93–115.

Wyrtki, K., 1966. Oceanography of the eastern Pacific Ocean. Oceanography Marine Biology Annual Review 4, 33–68.

Wyrtki, K., 1973. Physical oceanography of the Indian Ocean. In: Zeitzschel, B. (Ed.), The Biology of the Indian Ocean. Springer, Berlin, pp. 18–36.