# Relationships between oxygen, organic matter and the diversity of bathyal macrofauna

Lisa A. Levin[a,*], John D. Gage[b]

[a] Marine Life Research Group, Scripps Institution of Oceanography, La Jolla, CA, 92093-0218, USA
[b] Scottish Association for Marine Sciences, P.O. Box 3, Oban, Argyll PA34 4AD, UK

## Abstract

The relationships of environmental factors with measures of macrobenthic community diversity were examined for the total fauna, and for polychaetes only, from 40 bathyal stations in the North Atlantic, eastern Pacific and Indian Oceans (154–3400 m). Stepwise multiple regression revealed that depth, latitude, sediment organic-carbon content and bottom-water oxygen concentration are significant factors that together explained 52–87% of the variation in macrobenthic species richness ($E[s_{100}]$), the Shannon–Wiener index ($H'$), dominance ($D$), and evenness ($J'$). Percent sand and percent clay were not significant factors. After removal of depth and latitudinal effects, oxygen and organic-carbon concentrations combined accounted for 47, 67, 52 and 32% of residual variation in macrobenthic $E(s_{100})$, $H'$, $D$, and $J'$, respectively. Organic carbon exhibited a stronger relationship than oxygen to measures of community evenness, and appeared to have more explanatory power for polychaetes than total macrobenthos. When only stations with oxygen $< 1$ ml l$^{-1}$ were considered, oxygen concentration became the dominant parameter after depth. Results suggest existence of an oxygen threshold ($< 0.45$ ml l$^{-1}$), above which oxygen effects on macrobenthic diversity are minor relative to organic matter influence, but below which oxygen becomes a critical factor. Our regression results lead us to hypothesize that for bathyal faunas, oxygen at low concentrations has more influence on species richness, while organic carbon regulates the distribution of individuals among species (community evenness).

Examination of rarefaction curves for Indo-Pacific stations reveals that total macrobenthos, polychaetes, crustaceans and molluscs all exhibit reduced species richness within oxygen minimum zones (OMZs). However, representation under conditions of hypoxia varies among taxa, with polychaetes being most tolerant. Molluscs and crustaceans often (but not always) exhibit few individuals and species in OMZs, and sometimes disappear altogether, contributing

---

* Corresponding author. Fax: 619-534-6500; e-mail: llevin@ucsd.edu.

to reduced macrobenthic diversity and elevated dominance in these settings. The linear negative relationship observed between bathyal species richness and sediment organic-carbon content (used here as a proxy for food availability) may represent the right side (more productive half) of the hump-shaped, diversity–productivity curve reported in other systems. These analyses suggest there are potentially strong influences of organic matter and oxygen on the diversity and composition of bathyal macrobenthos, especially in the Indo-Pacific Ocean. © 1998 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

Since the recognition of high macrobenthic species richness in the deep sea (Hessler and Sanders, 1967; Sanders, 1968; Sanders and Hessler, 1969), much attention has been directed towards understanding the factors that control deep-sea diversity (reviewed in Rex, 1983; Rex et al., 1997). Of particular interest has been the relationship of large-scale diversity patterns to latitude (Rex et al., 1993, 1997), water depth (Rex, 1981, 1983; Watts et al., 1992; Paterson and Lambshead, 1995; Rex et al., 1997), nutrient availability (Sanders, 1968; Watts et al., 1992; Levin et al., 1994b), oxygen (Sanders, 1969; Levin et al., 1991), hydrodynamics and related sediment properties (Etter and Grassle, 1992; Thistle et al., 1985, 1991; Gage, 1997). At smaller scales, researchers have addressed the roles of biogenic habitat heterogeneity (reviewed in Grassle and Grassle, 1994; Rice and Lambshead, 1994) and biological interactions (Dayton and Hessler, 1972; Grassle and Sanders, 1973; Huston, 1979) in maintaining local diversity.

While macrobenthic species richness in samples from deep water can be substantially greater than in shallow water (Gage and Tyler, 1991; Gage, 1996), there are a number of deep-sea settings where species richness is low and dominance is high. These include benthic environments in contact with oxygen minimum zones (OMZs) beneath upwelling regions (Sanders, 1969; Levin et al., 1997), isolated basins such as the Norwegian Sea (Dahl et al., 1976), and hydrothermal vents (Grassle et al., 1985; Grassle, 1989). In the first of these, hypoxia and organic matter enrichment are believed to act in concert to depress diversity, although the mechanisms involved are unclear.

Most of the work on global-scale diversity patterns has focused on the deep Atlantic Ocean, primarily because large data sets are available for this region (Rex et al., 1997). By omitting the Indo-Pacific, however, these studies exclude many bathyal, marginal settings where organic matter and oxygen availability are likely to exert a strong influence on diversity. In order to explore the potential effects of organic matter and oxygen availability on bathyal diversity, we have assembled data from stations in the Pacific, Indian and Atlantic oceans, both inside and outside oxygen minimum zones.

Direct assessment of organic matter influence on macrobenthic diversity has focused on both local and large scales (Rex et al., 1997). At local scales of meters or less, spatially and temporally varying organic input can affect the abundance,

composition, life histories and diversity of macrobenthos (reviewed in Gooday and Turley, 1990; Snelgrove and Butman, 1994; Grassle and Grassle, 1994; Rice and Lambshead, 1994). Patchiness in organic input is now commonly recognized to be an important source of within-habitat diversity (Smith, 1986; Grassle and Morse-Porteous, 1987; Snelgrove et al., 1992, 1996).

At much larger scales our understanding is more limited. Many terrestrial systems reveal strong control of diversity by productivity (Rosenzweig and Abramsky, 1993; Wright et al., 1993). Connell and Orians (1964) proposed that the high diversity characteristic of tropical rain forests and coral reefs is related to high productivity. Rex et al. (1993, 1997) suggest that lower diversity documented at high latitudes for bivalves, gastropods and isopods may be related to high and variable carbon flux. Watts et al. (1992) examined the relationship of diversity to satellite-based estimates of surface productivity in the Atlantic for polychaetes, gastropods, cumaceans and bivalves and found little association once depth effects were removed. However, Schaff et al. (1992) demonstrated an inverse relationship between carbon flux and macro-benthos species richness at three NW Atlantic margin sites of comparable depth. Examination of bathyal polychaete assemblages along regional organic enrichment gradients off North Carolina and on a Pacific seamount also revealed reduced diversity at the most enriched sites (Levin et al., 1994b), but on the seamount this effect was confounded by a strong negative correlation of oxygen and enrichment (Levin et al., 1991).

Current emphasis on carbon flux as an influence on benthic processes, particularly in many North Atlantic studies, should yield an abundance of regional studies in which gradients of organic input to the seabed can be related to benthic diversity. In one such study, Cosson et al. (in press) report maximal polychaete diversity beneath the most productive of three sites in the tropical northeast Atlantic. However, these results are confounded by site variation in water depth and distance from shore. From the limited available data, general, large-scale relationships between deep-sea macro-benthic diversity and food availability remain obscure.

Examination of terrestrial, aquatic and marine environments suggests a parabolic relationship between food availability and faunal diversity (Pearson and Rosenberg, 1978; Rosenzweig and Abramsky, 1993; Rosenzweig, 1995). This pattern involves increasing diversity with increasing organic nutrients up to some intermediate level, and then a decline in diversity with even greater organic inputs. In their marine examples, Rosenzweig and Abramsky (1993) use depth as a proxy for productivity or food availability. The well-documented, hump-shaped, depth–diversity relationship mentioned above could result from factors other than food input, such as range boundaries (Pineda, 1993) or disturbance (Paterson and Lambshead, 1995). Nevertheless, it may be critical to assess where along the organic nutrient gradient a particular data set falls before trying to generalize about organic-matter influence on deep-sea diversity.

Oxygen effects on benthic communities have been reviewed recently by Diaz and Rosenberg (1995). Although oxygen-related patterns are well studied in shallow water and polluted settings, there are few detailed investigations of macrobenthic diversity along deep-water oxygen gradients. Reduced diversity in the southern California

Table 1

Station locations, physical/sediment characteristics, and faunal sampling information for sites included in the analyses. Station numbers correspond to locations mapped in Fig. 1. Where cells are left blank, there were no data

| Station | Depth (m) | Latitude/ longitude | Sediment data | | | | | Faunal data | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Oxygen (ml/l) | % Organic carbon | % Sand | % Clay | Sediment and oxygen references | Sieve size (mm) | Corer area (cm²) | Sample number | Faunal references |
| 1. Hebridian Slope | 400 | 56 41'N 09 00'W | 6.21 | 0.18 | 99.7 | 0.2 | 1, 2 | 0.42 | 2500 | 3 | 17 |
| 2. Hebridian Slope | 600 | 56 43'N 09 00'W | 6.21 | 0.18 | 88.6 | 1.9 | 1, 2 | 0.42 | 2500 | 1 | 17 |
| 3. Hebridian Slope | 1000 | 56 45'N 09 11'W | 5.58 | 0.13 | 79.5 | 3.3 | 1, 2 | 0.42 | 2500 | 2 | 17 |
| 4. Hebridian Slope | 1400 | 56 38'N 09 29'W | 6.27 | 0.65 | 19.7 | 12.8 | 1, 2 | 0.42 | 2500 | 1 | 17 |
| 5. Hebridian Slope | 1600 | 56 39'N 09 23'W | 6.27 | 0.65 | 19.7 | 12.8 | 1, 2 | 0.42 | 2500 | 1 | 17 |
| 6. Hebridian Slope | 1800 | 56 37'N 09 49'W | 6.25 | 0.55 | 21.1 | 15.7 | 1, 2 | 0.42 | 2500 | 2 | 17 |
| 7. Hebridian Slope | 2000 | 57 08'N 12 09'W | 6.22 | 0.46 | 22.5 | 17.6 | 1, 2 | 0.42 | 2500 | 1 | 17 |
| 8. NC Slope (I) | 850 | 32 52'N 76 27'W | 5.82 | 1.2 | 34 | 29 | 3, 4, 5 | 0.30 | 225 | 4 | 3 |
| 9. NC Slope (II) | 850 | 34 15'N 75 44'W | 4.61 | 2.1 | 20 | 37 | 3, 4, 5 | 0.30 | 225 | 14 | 3 |
| 10. NC Slope (III) | 850 | 35 24'N 74 48'W | 5.6 | 1.7 | 31 | 26 | 3, 4, 5 | 0.30 | 225 | 11 | 3 |
| 11. Hatteras (9) | 604 | 35 28'N 74 47.6'W | 4.08 | 1.73 | 47.4 | 21.9 | 6 | 0.30 | 2500 | 9 | 18 |
| 12. Hatteras (10) | 2003 | 35 26'N 74 41'W | 4.57 | 1.24 | 45.5 | 20.9 | 6 | 0.30 | 2500 | 6 | 18 |
| 13. NC Lookout (4) | 2000 | 34 11'N 75 39'W | 5.61 | 1.97 | 19.5 | 38.8 | 6 | 0.30 | 2500 | 9 | 18 |
| 14. SC Slope (14A) | 600 | 32 32'N 77 15'W | 4.05 | 3.67 | 92.4 | 5.2 | 6 | 0.30 | 2500 | 3 | 18 |
| 15. SC Slope (14) | 805 | 32 24'N 77 01'W | 5.5 | 2.95 | 41 | 25.9 | 6 | 0.30 | 2500 | 9 | 18 |
| 16. SC Slope (15) | 1993 | 32 12'N 76 42'W | 5.89 | 1.71 | 63.2 | 17.5 | 6 | 0.30 | 2500 | 6 | 18 |
| 17. SC Slope (16) | 3008 | 31 35'N 75 11'W | 5.81 | 1.3 | 6 | 55.8 | 6 | 0.30 | 2500 | 9 | 18 |
| 18. Santa Maria Basin | 154 | 34 40'N 120 50'W | 2.7 | 0.52 | 53.3 | 5 | 7 | 0.30 | 1000 | 24 | 7 |
| 19. Santa Maria Basin | 410 | 34 40'N 121 W | 1.0 | 0.66 | 34.4 | 6.5 | 7 | 0.30 | 1000 | 24 | 7 |
| 20. Santa Maria Basin | 565 | 34 53'N 121 10'W | 0.6 | 2.55 | 4 | 31.6 | 7 | 0.30 | 1000 | 21 | 7 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 21. Santa Catalina Basin | 1130 | 32°58'N 118°22'W | 0.41 | 6.5 | | | 8, 9 | 0.42 | 1000 | 5 | 8 |
| 22. La Jolla Canyon | 310 | 32°52'N 117°17'W | 1.39 | 0.41 | | | 10 | 0.30 | 400 | 7 | 10 |
| 23. La Jolla Canyon | 500 | 32°54'N 117°20'W | 1.37 | 2.14 | | | 10 | 0.30 | 400 | 17 | 10 |
| 24. Del Mar Margin | 300 | 32°56'N 117°20'W | 1.15 | 2.55 | | | 10 | 0.30 | 1200/400 | 5/3 | 10 |
| 25. Del Mar Margin | 500 | 32°56'N 117°22'W | 0.74 | 3.53 | | | 10 | 0.30 | 1200 | 5/3 | 10 |
| 26. San Diego Trough | 1230 | 32°28'N 117°29'W | 0.71 | 2 | 3 | 44.3 | 8,11 | 0.42 | 2500 | 22 | 8 |
| 27. Fieberling Guyot | 580 | 32°28'N 127°48'W | 0.80 | 0.12 | 96.02 | 2.38 | 12 | 0.30 | 225 | 16 | 12 |
| 28. Fieberling Guyot | 635 | 32°28'N 127°49'W | 0.80 | 0.13 | 95.75 | 0.93 | 12 | 0.30 | 225 | 4 | 12 |
| 29. Volcano 7 | 750 | 13°25'N 102°28'W | 0.09 | 3.35 | 77.95 | 13.9 | 13 | 0.30 | 225 | 6 | 13 |
| 30. Volcano 7 | 800 | 13°25'N 102°28'W | 0.13 | 1.48 | 81.17 | 8.08 | 13 | 0.30 | 225 | 4 | 13 |
| 31. Volcano 7 | 1500 | 13°25'N 102°30'W | 0.81 | 0.56 | 74.9 | 6.81 | 13 | 0.30 | 225 | 7 | 13 |
| 32. Volcano 7 | 3000 | 13°25'N 102°36'W | 2.55 | 1.17 | 13.12 | 50.8 | 13 | 0.30 | 225 | 3 | 13 |
| 33. Peru Margin | 170 | 6°30'S 80°58'W | 0.35 | 1.5 | 64.5 | 9.2 | 14 | 1.0 | 1000 | 3 | 14 |
| 34. Peru Margin | 220 | 8°21'S 79°55'W | 0.20 | 3.5 | | | 14 | 1.0 | 1000 | 3 | 14 |
| 35. Oman Margin | 400 | 19°22'N 58°15'E | 0.28 | 4.99 | 23.6 | 6 | 15, 16 | 0.30 | 2500 | 4 | 19 |
| 36. Oman Margin | 675 | 19°19'N 58°15'E | 0.51 | 3.97 | 30.2 | 3.8 | 15, 16 | 0.30 | 2500 | 3 | 19 |
| 37. Oman Margin | 850 | 19°14'N 58°23'E | 0.41 | 4.01 | 25.1 | 4.5 | 15, 16 | 0.30 | 2500 | 5 | 19 |
| 38. Oman Margin | 1000 | 19°16'N 58°29'E | 0.34 | 1.93 | 47.2 | 3.3 | 15, 16 | 0.30 | 2500 | 4 | 19 |
| 39. Oman Margin | 1250 | 19°14'N 58°31'E | 0.47 | 2.67 | 36.4 | 5.1 | 15, 16 | 0.30 | 2500 | 5 | 19 |
| 40. Oman Margin | 3400 | 19°00'N 59°00'E | 1.07 | 2.71 | 20.3 | 6.4 | 15, 16 | 0.30 | 2500 | 5 | 19 |

*Note:* Often only a subsample of the core was analyzed.

References: (1) Mitchell et al. (1996)   (2) Mitchell (1997)   (3) Schaff et al. (1992)   (4) DeMaster et al. (1994)   (5) Blair (unpublished)   (6) Blake et al. (1987)   (7) Hyland et al. (1991)   (8) Jumars (1974)   (9) Smith (1983)   (10) Vetter and Dayton (1998)   (11) Thistle (1978)   (12) Levin et al. (1994a)   (13) Levin et al. (1991)   (14) D. Gutierrez (pers. comm.)   (15) Patience and Gage (1996)   (16) Gage (1995)   (17) Gage (unpublished)   (18) Blake and Grassle (1994)   (19) Levin et al. (unpublished).

borderland basins has been linked to low oxygen levels (Jumars, 1974; Jumars and Gallagher, 1982; Smith, 1983). Studies by Sanders (1969) off W. Africa, by Levin et al. (1991) in the eastern Pacific, and Levin et al. (1997) in the Arabian Sea show extreme depression of macrobenthic diversity within oxygen minimum zones. In all three oceans, the oxygen minima occur beneath upwelling regions where organic matter flux to the seabed is high. Thus, it is difficult to distinguish the actual importance of oxygen stress (as opposed to organic enrichment) in determining diversity changes associated with OMZs.

Paleoceanographic biofacies models include monotonic reduction in diversity of biogenic traces and fossils along gradients of oxygen depletion (Rhoads and Morse, 1971; Savrda and Bottjer, 1991), although there is controversy about the nature of the ichnofacies expected in hypoxic settings (Ekdale and Mason, 1988; Wheatcroft, 1989). But in such studies, oxygen levels are inferred from organic-carbon data (Berry and Wilde, 1978; Demaison and Moore, 1980), confounding effects of oxygen stress and organic loading.

In the present paper, we investigate factors that may control patterns of diversity (species richness, $H'$, dominance and evenness) in bathyal macrobenthos, with emphasis on bottom-water oxygen concentration and sediment organic-carbon content. We ask whether bathyal diversity patterns in the Atlantic and Pacific oceans are explained by similar parameters. Direct comparisons are made between cross-margin transects which do, and do not, intercept OMZs. For Indian and Pacific ocean stations, we consider whether the diversities of different major taxa (polychaetes, molluscs and crustaceans) respond in similar fashions to gradients in bottom-water oxygen and sediment organic carbon, and whether changes in diversity along these gradients are related to shifts in taxonomic representation.

## 2. Methods

### 2.1. Data sets

We have utilized macrobenthic and accompanying sediment data collected from a variety of bathyal sites in all three major oceans (Table 1, Fig. 1). Data sets were selected for inclusion in the study based on availability of information regarding bottom-water oxygen concentration, sediment organic-carbon content, particle size, and species-level macrobenthic counts. Data are included for macrobenthos sampled between 154 and 3400 m water depth. The stations for which data are available are clustered in the eastern Pacific ocean, northwest and northeast Atlantic ocean, and in the northwest Arabian sea (Fig. 1). The southern hemisphere is represented only by several stations off Peru; polar areas, fjords and seep environments are completely unrepresented. In all cases, the biological indices are based on data for taxa traditionally considered to be macrobenthic and do not include meiofaunal forms such as nematodes, ostracods, harpacticoid copepods or foraminifera that might have been present in samples. Previously unpublished data are provided from cross-slope studies on the Oman margin (Arabian Sea) (Levin and Gage, unpublished) and the Hebridian
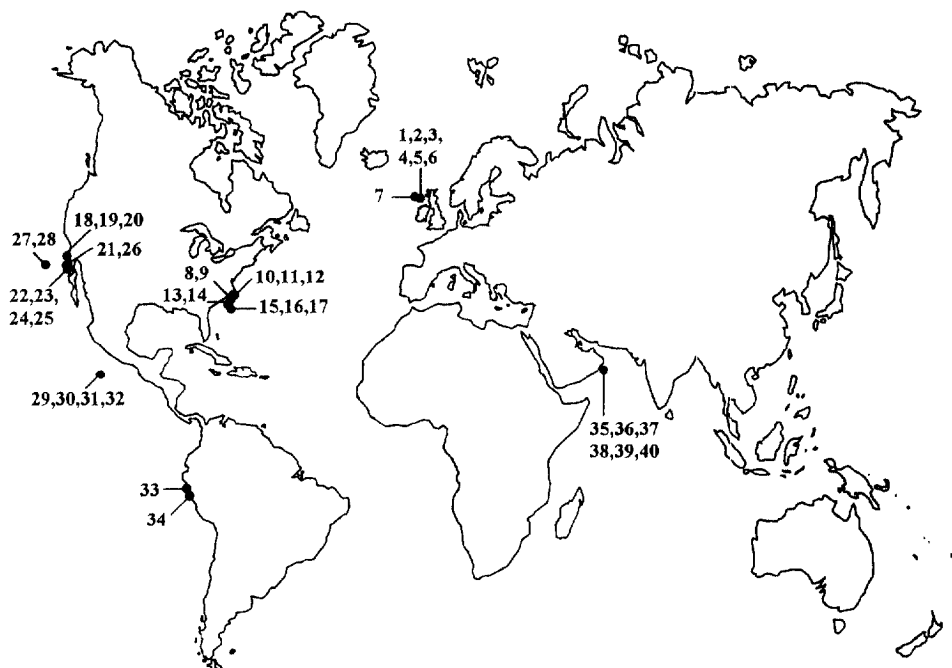
Fig. 1. Map showing locations of stations included in this study. See Table 1 for station names and site characteristics.

slope (northeast Atlantic, polychaetes, bivalves and crustaceans only) (Gage, unpublished). Additional data were obtained for the Peru margin (D. Gutierrez, pers. comm.) and the southern California margin off Del Mar and in the La Jolla Canyon (Vetter and Dayton, 1998). The Oman margin data were collected in Oct./Nov. 1994 as part of the British Arabesque program, on the R. R. S. *Discovery* cruise 211 (Gage, 1995). Macrobenthos sampling details are given in Gage (1995) and Levin et al. (1997). The Hebridian slope samples were collected on various dates from June 1976 to August 1982. Information on sample collection methods and sample treatment is given by Gage (1977, 1979). The Peru margin data were collected in 1989 by the Peruvian oceanographic agency IMARPE (D. Gutierrez, pers. comm.). Information about sieve size, core size and number of samples is given for each data set in Table 1. Variation among data sets in sampling methods and the spatial and temporal coverage of samples cannot be avoided and is undoubtedly a source of noise in the following analyses.

Those data sets generated in the early 1970s (Hebridian slope, Santa Catalina Basin and San Diego Trough) are based on animals retained on a 0.420 mm mesh screen. All other data sets were generated with a 0.300 mm mesh, except for the Peru margin, where a 1.0 mm mesh was used. We acknowledge that the larger mesh sizes may cause

macrobenthic diversity to be underestimated slightly relative to the smaller mesh size, but feel that the bias should not significantly alter our results. In the Santa Catalina Basin, macrofaunal abundances obtained from 0.300 and 0.420 mm mesh differ by only 2%, thus diversity effects are probably minor (Smith, pers. comm.).

Sediment properties and bottom-water oxygen concentrations are listed for each station in Table 1. Sediment total organic-carbon content is used as a proxy for organic matter availability, although we recognize it does not always accurately reflect carbon flux to the seabed (e.g. Smith et al., in press). In many cases, no better information about food availability to benthos was available. In a few instances, Hebridian slope sediment data were estimated based on data for nearby stations.

## 2.2. Analyses

Rarefaction estimates of species richness and rarefaction curves (Hurlbert, 1971), the Shannon–Wiener diversity index $(H')$, and Pielou's evenness index $(J')$ were computed from raw data using the "BioDiversity" program (©Natural History Museum, London/Scottish Association of Marine Sciences) for stations 1–10 and 21–40 (Table 1). When species-level identifications were available for all taxa, diversity data were generated for total macrobenthos. When species-level identifications were available only for selected groups, analyses were limited to polychaetes, molluscs and crustaceans (or a subset of these). Rarefaction estimates of the expected number of species in a 100-individual sample $[E(s_{100})]$ were used as an estimate of species richness for total macrobenthos and polychaetes at each station. Smaller sample sizes were used for the mollusca $[E(s_{50})]$ and crustaceans $[E(s_{20})]$. The Shannon–Wiener diversity index $(H')$ and Pielou's evenness $(J')$ were calculated using log base 2. Rank 1 dominance (hereafter referred to as dominance, $[D]$) was defined as the percentage of the total fauna represented by the singlemost abundant species. Diversity data for stations 11–20 were taken from the published literature (Table 1). Diversity estimates were based on pooled data using all available samples from each station (Table 1). This integration over variable space and time scales represents an added source of variation for the diversity indices, but was necessary to obtain diversity estimates based on reasonable numbers of individuals and to use published data.

Regression analyses to evaluate relationships between environmental parameters and biological diversity measures were carried out using JMP™ (SAS Institute, 1989) for the combined data set (all oceans) and separately for the Atlantic ocean and for the Indian and Pacific oceans (hereafter referred to as Indo-Pacific stations). We also analyzed a truncated Indo-Pacific data set comprised of stations for which bottom-water oxygen concentrations were below $1 \text{ ml l}^{-1}$. Simple and stepwise multiple regressions of environmental parameters (depth, latitude, bottom-water oxygen concentration, sediment organic-carbon content, percent sand and percent clay) against biological indices (species richness $[E(s_n)]$, diversity $[H']$, dominance $[D]$ or evenness $[J']$) were performed. Dominance values (percentages) were arcsine transformed to achieve normality. The stepwise regression procedure (Draper and Smith, 1981) was carried out manually, using $P \leqslant 0.10$ as the acceptance criterion for each

environmental factor. The regression explaining the greatest amount of variation with all parameter coefficients significant (or nearly significant) is presented as the best fit.

To focus on the specific influence of bottom-water oxygen and sediment organic-carbon content, additional regressions were carried out in which depth and latitude effects were removed by regression from the diversity data, as well as from the bottom-water oxygen and sediment organic-carbon data. Oxygen and organic-carbon residuals were then regressed against diversity residuals. Significance for the analyses was set at $\alpha = 0.05$. Depth was removed as a quadratic because the best fit to our data (for all indices) was a parabola (second-order polynomial). However, in the truncated, low-oxygen Indo-Pacific data ($O_2 < 1 \, ml \, l^{-1}$), depth was linearly related to diversity and was removed as a linear fit. Latitude (without a N–S distinction) was removed as a linear fit as well from all data sets. Diversity measures [$E(s_{100})$, $H'$, $D$, and $J'$] were calculated for total macrofauna and for polychaetes only.

The influence of depth, oxygen, latitude, organic matter, % sand and % clay on taxonomic composition (% polychaetes, molluscs, and crustaceans) was evaluated by simple regression for data from Indo-Pacific stations. Taxon percentages were arcsine transformed prior to analysis to achieve normality.

## 3. Results

### 3.1. Physical variables

Bottom-water oxygen concentrations were non-overlapping at the Atlantic stations (4.05–6.27 ml l$^{-1}$) and the Indo-Pacific stations (0.09–2.70 ml l$^{-1}$) (Table 1). Eight of the stations fell within well-developed OMZs (defined as regions where bottom-water oxygen concentration is $< 0.5 \, ml \, l^{-1}$). These include the summit of Volcano 7 (stations 29 and 30) and the Peru margin (stations 33 and 34) in the eastern Pacific, and the Oman margin in the Arabian Sea (stations 35–38) (Table 1). The Santa Catalina Basin also has a low bottom-water oxygen concentration (0.4 ml l$^{-1}$).

Among the stations studied, % total sediment organic carbon (TOC) ranged from 0.1 to 6.5%, sand content ranged from 3 to 99.7% and clay content ranged from 0.2 to 50.8% (Table 1). These ranges are believed to be representative of the majority of bathyal settings in the world's oceans. Coefficients of determination ($r^2$) among physical variables for the Indo Pacific and the Atlantic data alone and for the combined data are given in Table 2a and b, respectively. Significant negative correlations were observed between sediment organic-carbon content and bottom-water oxygen concentration and between % sand and % clay in all three data sets (Table 2). Latitude was positively correlated with oxygen and negatively correlated with organic carbon in the combined (Table 2b) and Atlantic data sets (Table 2a).

### 3.2. Diversity measures

The bathyal settings analyzed exhibited a broad range of values for each biological index examined. Macrobenthic species richness [$E(s_{100})$] ranged from 4.5 to 62, $H'$

Table 2

Coefficient of determination ($r^2$) for linear relationships between environmental parameters. Direction of the relationship is given in () when the regression is significant at $P \leqslant 0.05$. ***$P < 0.001$ **$P < 0.01$ *$P < 0.05$, NS = $P > 0.10$ (a) Indo-Pacific values are given above the diagonal, Atlantic values below the diagonal. $(n) = 17$ for Atlantic; $n = 17$ for Indo-Pacific regressions involving particle size; $n = 23$ for all others. (b) Data are given for the combined Atlantic and Indo-Pacific data sets. $n = 40$, except those involving % Sand or % Clay $(n = 34)$

(a)

|  | Oxygen | Organic carbon | Depth | Latitude | % Sand | % Clay |
|---|---|---|---|---|---|---|
| Oxygen | — | 0.220* (−) | 0.067 NS | 0.118 NS | 0.035 NS | 0.122 NS |
| Org. Carbon | 0.465** (−) | — | < 0.001 NS | 0.020 NS | 0.261* (−) | 0.001 NS |
| Depth | 0.076 NS | 0.018 NS | — | 0.072 NS | 0.121 NS | 0.167 NS |
| Latitude | 0.388** (+) | 0.643** (−) | 0.008 NS | — | 0.016 NS | 0.002 NS |
| % Sand | 0.030 NS | 0.001 NS | 0.368** (−) | 0.026 NS | — | 0.317* (−) |
| % Clay | 0.021 NS | 0.116 NS | 0.303* (+) | 0.422** (−) | 0.552*** (−) | — |

(b)

|  | Oxygen | Organic carbon | Depth | Latitude | % Sand | % Clay |
|---|---|---|---|---|---|---|
| Oxygen | — | 0.186* (−) | 0.113* (+) | 0.567** (+) | 0.007 NS | 0.079 NS |
| Org. Carbon |  | — | 0.014 NS | 0.194** (−) | 0.086 NS | 0.001 NS |
| Depth |  |  | — | 0.003 NS | 0.209** (−) | 0.245** (+) |
| Latitude |  |  |  | — | < 0.001 NS | 0.002 NS |
| % Sand |  |  |  |  | — | 0.403*** (−) |
| % Clay |  |  |  |  |  | — |

ranged from 1.33 to 6.39, dominance ranged from 5 to 71%, and evenness ($J'$) ranged from 0.36–0.91. Polychaete ranges were 4–47 for $E(s_{100})$, 0.8–5.5 for $H'$, 6–82% for dominance (the most abundant polychaete as a percentage of total polychaetes), and 0.36–0.91 for $J'$. Estimates of $H'$ and $J'$ were available only for Indo-Pacific stations. Estimates of species richness [$E(s_{100})$], $H'$, $D$ and $J'$ are shown as a function of depth, latitude, bottom-water oxygen concentration, and sediment organic-carbon content for total macrobenthos in Fig. 2a–d and for polychaetes in Fig. 3a–d.

## 3.3. Relationships of physical parameters to diversity: multiple regression models

Multiple regression analyses indicate that a combination of depth, latitude, sediment organic-carbon content and/or bottom-water oxygen concentration can explain 52–87% of the variation in estimates of macrobenthic species richness [$E(s_{100})$], $H'$, $D$ and $J'$ in the combined and Indo-Pacific data sets (Table 3). Percent sand and clay did not appear as significant parameters in any of the macrobenthos or polychaete models. Organic carbon and depth were significant in all regressions for these two data sets. Oxygen did not appear in the best fit models of [$E(s_{100})$], $D$ and $J'$ in the combined data set, and latitude was not significant in the $J'$ regressions. When only low-oxygen sites ( < 1 ml l$^{-1}$) in the Indo-Pacific were considered, depth and oxygen accounted for 57–85% of variation in $E(s_{100})$, $H'$, $D$, and $J'$ (Table 3). Latitude, organic carbon, % sand and % clay content were not significant factors.

Similar results were obtained for polychaete $E(s_{100})$, $H'$, $D$ and $J'$. However, latitude was rarely significant and oxygen had no explanatory power in the combined data set (Table 4).

The Atlantic data set was very small, primarily because there was only limited overlap between indices available for different stations. For total macrobenthos (NW Atlantic stations only), oxygen and organic carbon explained 88% of the variation in species richness [$E(s_{100})$], but no physical variables provided a significant regression for dominance (Table 3). For polychaetes (mainly NE Atlantic data), depth explained 77% of variation in dominance, but no factors provided a significant regression for species richness (Table 4).

### 3.3.1. Oxygen and organic-carbon influence

After removal of depth and latitude effects, bottom-water oxygen concentration and sediment organic-carbon content together accounted for 32–67% of residual variation in $E(s_{100})$, $H'$, $D$, and $J'$ for total macrobenthos in the Indo-Pacific (Table 5, Fig. 4). The two factors appear to contribute more or less equally (within a factor of two) to variation of most measures (Fig. 4). When only low-oxygen sites in the Indo-Pacific were considered, oxygen and organic carbon together accounted for 68% of residual variation in $E(s_{100})$, and 59% of residual variation in $H'$. At low oxygen sites, organic carbon alone accounted for 35% of residual variation in $D$ and 25% of residual variation in $J'$, while oxygen, surprisingly, was not a significant factor (Table 5). Oxygen and organic matter did not explain any residual variation in $E(s_{100})$ or $D$ of the combined data set, but oxygen accounted for 53% of $E(s_{100})$ variation in the Atlantic data (Table 5).

When only polychaetes were considered, organic carbon explained 16–29% of residual variation (after removal of depth and latitude effects) in $E(s_{100})$, $H'$, $D$ and $J'$ of the combined data set but none of the residual variation in the Atlantic (Table 6). In the Indo-Pacific, oxygen and organic carbon together explained 32–52% of residual variation in these four polychaete parameters, with organic carbon being the primary explanatory factor for all measures except dominance (Table 6, Fig. 5). In the low-oxygen, Indo-Pacific data, oxygen and organic matter together accounted for 61–66% of residual variation in polychaete $E(s_{100})$ and $H'$, with fairly equal contributions from
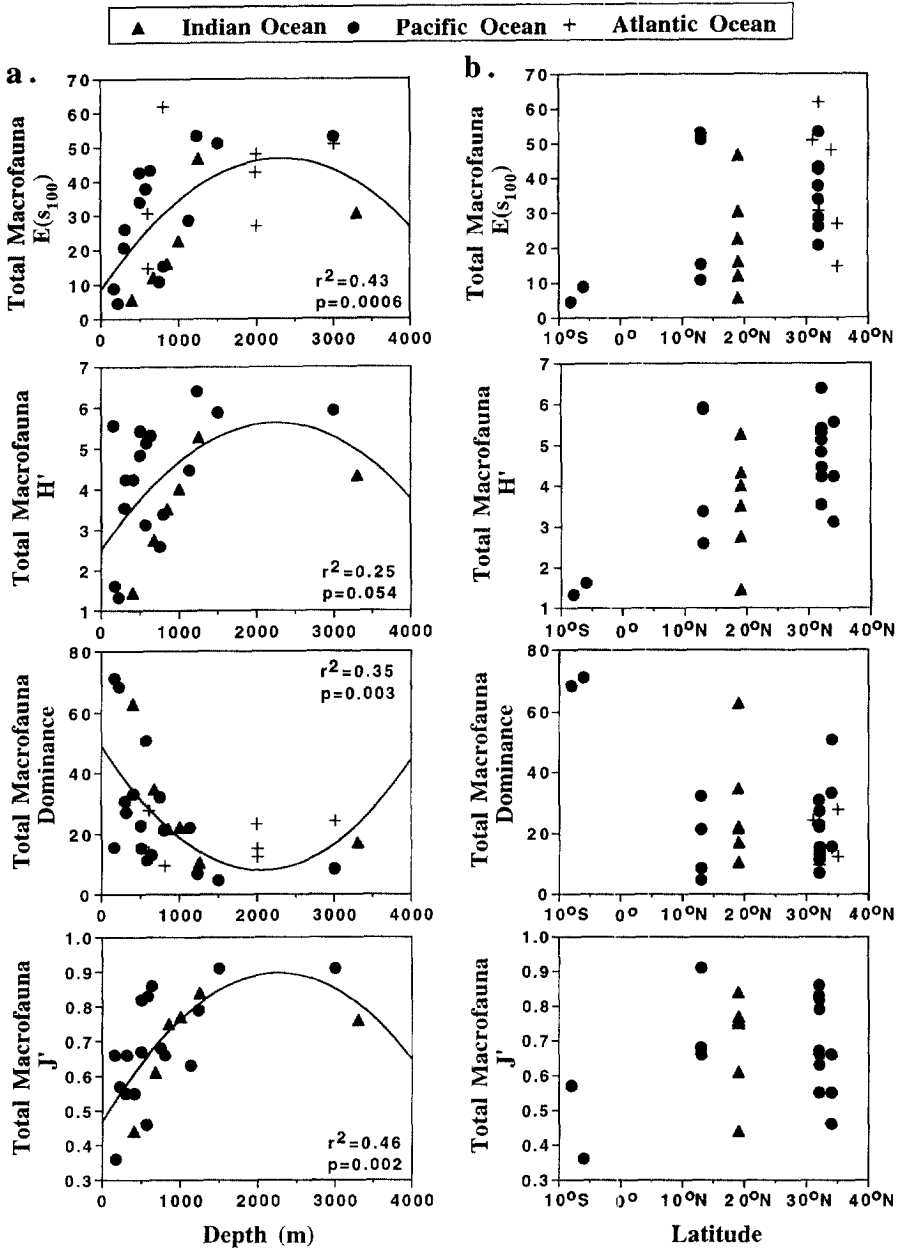
Fig. 2. Relationships of total macrofaunal diversity measures to (a) water depth, (b) latitude, (c) bottom-water oxygen concentration, and (d) sediment percent organic-carbon content. Significant regression curves and coefficients of determination ($P \leq 0.05$) are shown for analyses based on all available data combined. Regressions involving depth were fitted as a second order polynomial; all others are linear regressions. No regressions involving latitude were carried out, because across-ocean analyses were
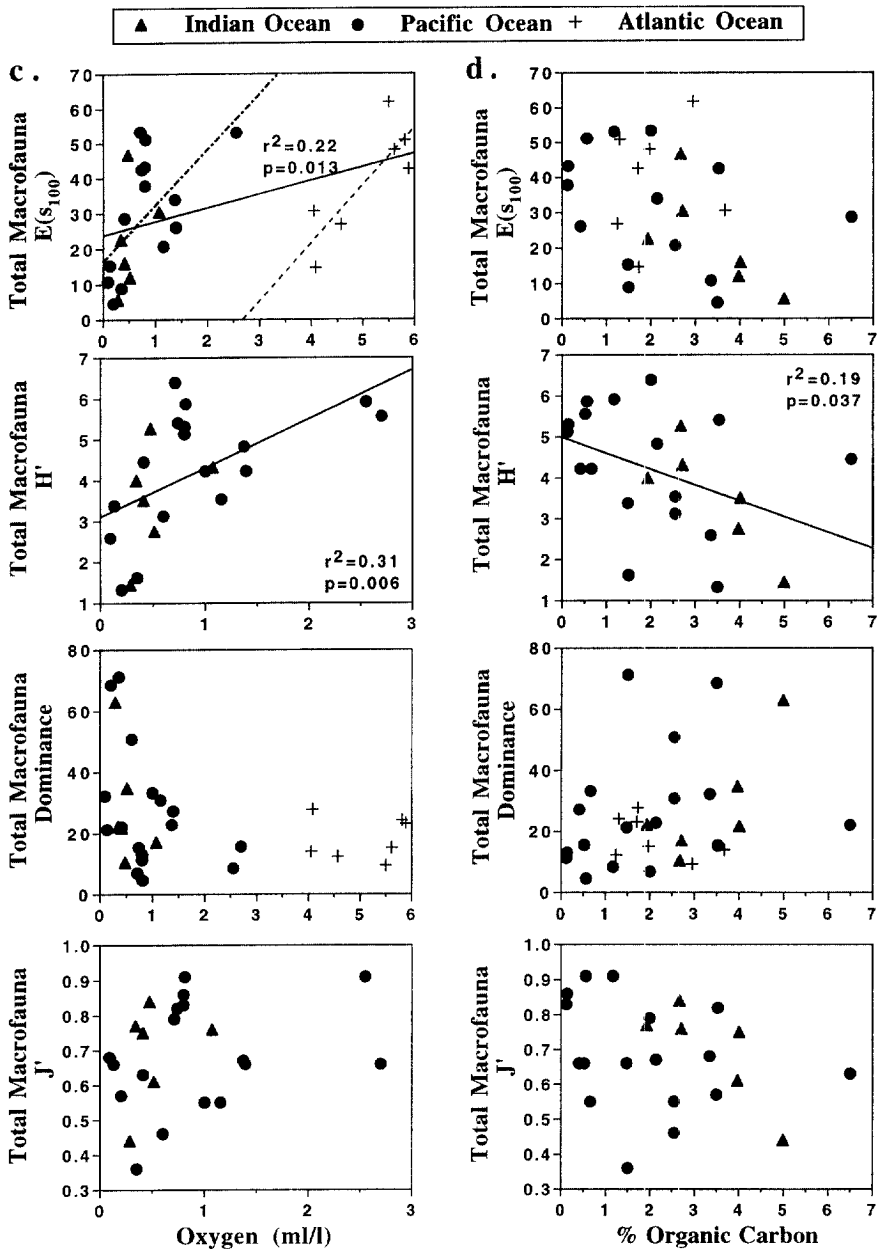
Fig. 2. (Continued)

considered inappropriate and latitudinal ranges within oceans were small. (c) also shows the linear regressions of oxygen against $E(s_{100})$ for the Indian and Pacific Ocean data combined (dashed and dotted line, $r^2 = 0.32$, $P = 0.009$) and the Atlantic data alone (dashed line, $r^2 = 0.68$; $P = 0.022$).
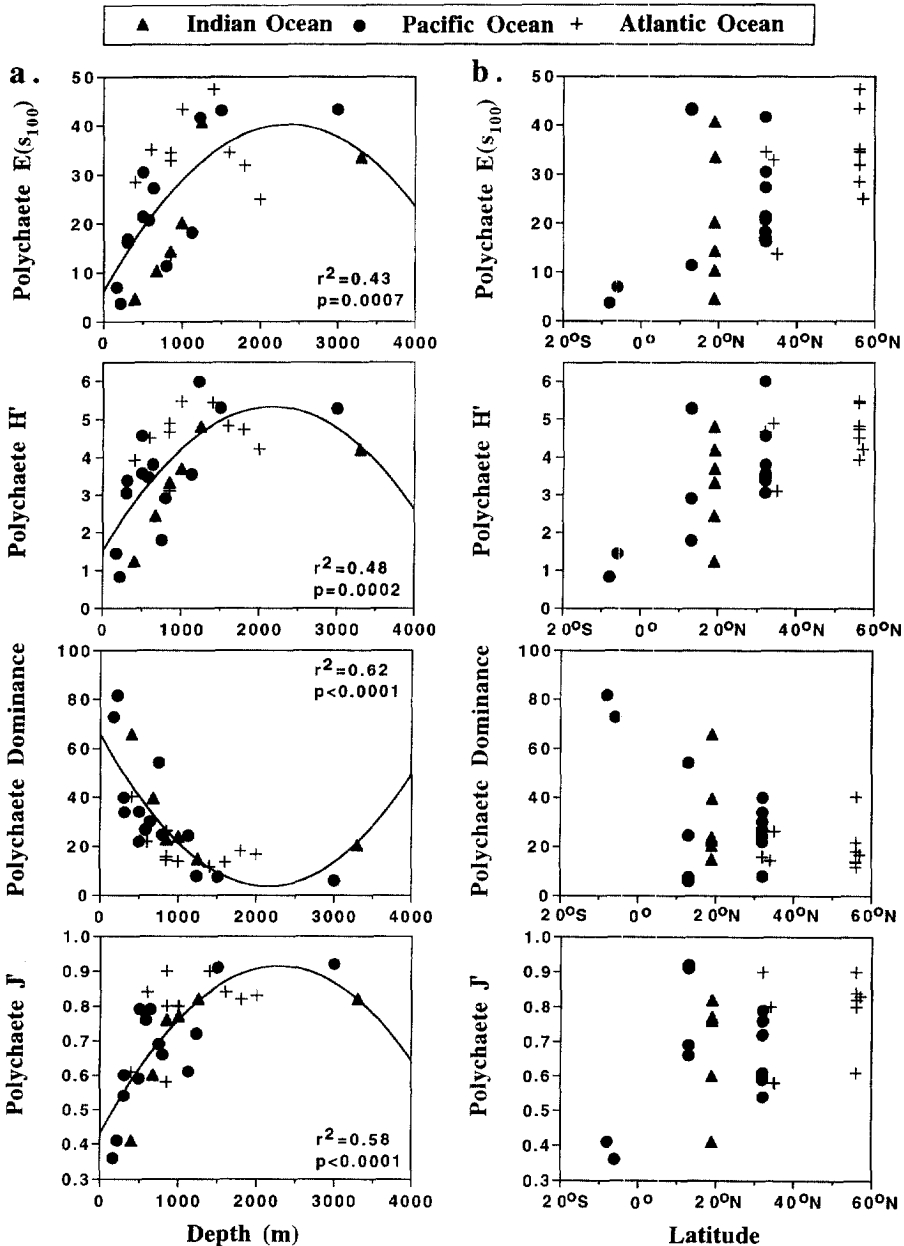
Fig. 3. Relationships of polychaete diversity measures to (a) water depth, (b) latitude, (c) bottom-water oxygen concentration and (d) sediment percent organic-carbon content. Significant regression curves and coefficients of determination ($P \leqslant 0.05$) are shown for analyses based on all available data combined. Regressions involving depth were fit as a second-order polynomial; all others are linear regressions. No regressions involving latitude were carried out, because across-ocean analyses were considered inappropriate and latitudinal ranges within oceans were insufficient.
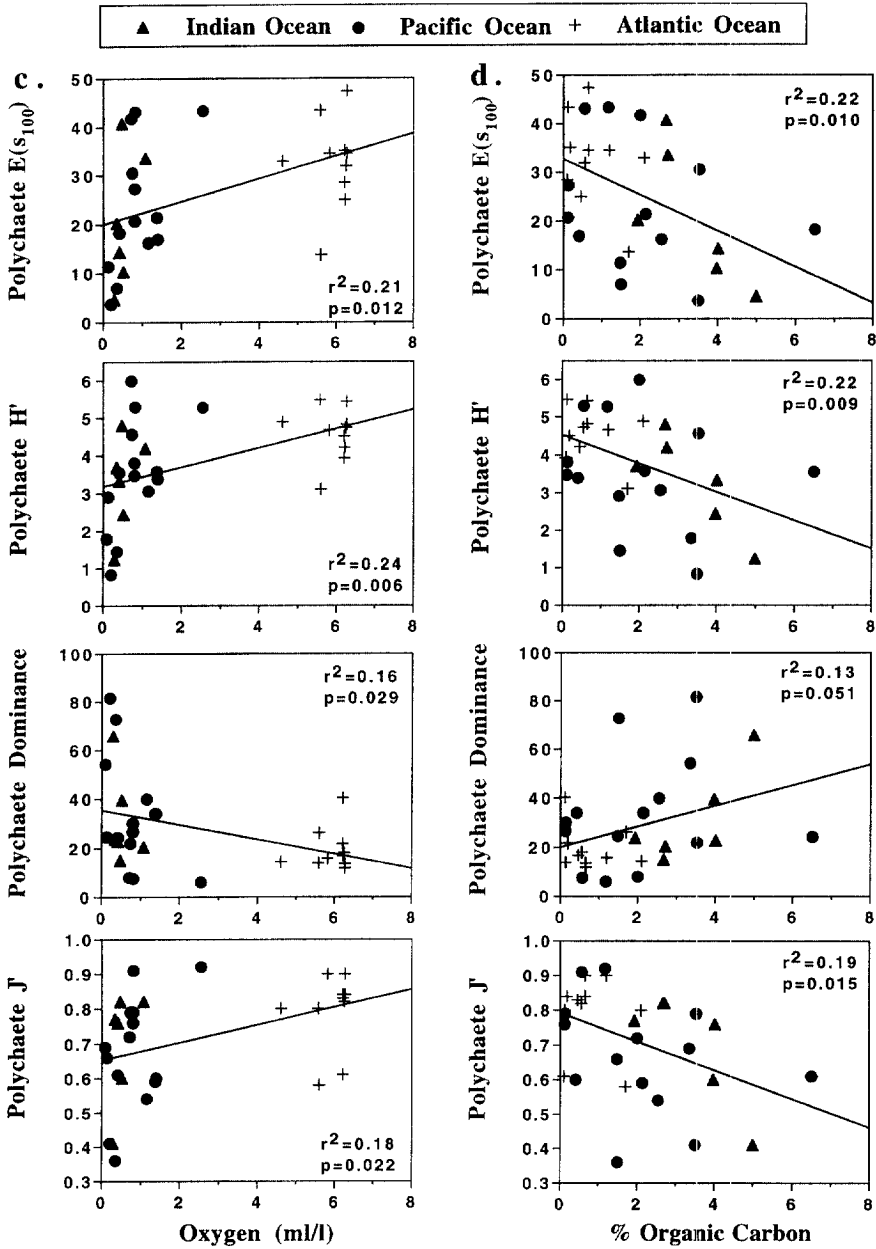
Fig. 3. (Continued)

Table 3
Best fit multiple regressions for parameters explaining total macrofaunal diversity. Factors included in the analysis were depth (incorporated in quadratic form), latitude ( = Lat.), bottom-water oxygen concentration (ml l$^{-1}$ O$_2$), % sediment organic C ( = Org. C), % sand and % clay content (all linear). See text for explanation of regression methods and diversity measures

| Total Macrofuna | Full data set (Atlantic and Indo-Pacific) | | | Indo-Pacific ocean | | |
|---|---|---|---|---|---|---|
| | Multiple regression | Parameter | Coefficient $P$ | Multiple regression | Parameter | Coefficient $P$ |
| Species richness $[E(s_{100})]$ | $R^2 = 0.526$ $P = 0.002$ $F = 6.10$ $n = 27$ | Depth Lat. Org. C | 0.010 0.046 0.101 | $R^2 = 0.768$ $P < 0.0001$ $F = 12.42$ $n = 20$ | Depth Org. C Lat. | 0.0005 0.005 0.003 |
| Dominance | $R^2 = 0.523$ $P = 0.0007$ $F = 6.85$ $n = 30$ | Depth Org. C Lat. | 0.001 0.072 0.074 | $R^2 = 0.825$ $P < 0.0001$ $F = 16.02$ $n = 23$ | Depth Org. C O$_2$ Lat. | 0.0001 0.037 0.042 0.046 |
| $H'$ | $R^2 = 0.874$ $P < 0.0001$ $F = 23.38$ $n = 23$ | Depth Lat. O$_2$ Org. C | < 0.0001 0.002 0.004 0.012 | $R^2 = 0.874$ $P < 0.0001$ $F = 23.57$ $n = 23$ | Depth Lat. O$_2$ Org. C | < 0.0001 0.0019 0.004 0.012 |
| $J'$ | $R^2 = 0.617$ $P = 0.0003$ $F = 10.18$ $n = 23$ | Depth Org. C | 0.0003 0.012 | $R^2 = 0.616$ $P = 0.0003$ $F = 10.56$ $n = 23$ | Depth Org. C | 0.0003 0.013 |

| Total Macrofauna | Low-oxygen Indo-Pacific ocean (oxygen < 1 ml/l) | | | Atlantic ocean | | |
|---|---|---|---|---|---|---|
| | Multiple regression | Parameter | Coefficient $P$ | Multiple regression | Parameter | Coefficient $P$ |
| Species richness $[E(s_{100})]$ | $R^2 = 0.854$ $P < 0.0001$ $F = 21.42$ $n = 15$ | O$_2$ Depth | 0.0001 0.002 | $R^2 = 0.883$ $P = 0.014$ $F = 15.08$ $n = 7$ | O$_2$ Org. C | 0.006 0.059 |
| Dominance | $R^2 = 0.764$ $P < 0.0001$ $F = 21.02$ $n = 16$ | Depth O$_2$ | 0.0003 0.015 | | No fit | |
| $H'$ | $R^2 = 0.840$ $P < 0.0001$ $F = 34.16$ $n = 16$ | O$_2$ Depth | 0.0002 0.0004 | | No data | |
| $J'$ | $R^2 = 0.565$ $P = 0.005$ $F = 8.45$ $n = 16$ | Depth O$_2$ | 0.014 0.059 | | No data | |

Table 4
Best fit multiple regressions for parameters explaining polychaete diversity. Factors included in the analysis were depth (incorporated in quadratic form), latitude ( = Lat.), bottom-water oxygen concentration ( = $O_2$ (in ml $l^{-1}$)), % sediment organic C ( = Org. C), % sand and % clay content (all linear). See text for explanation of regression methods and diversity measures

| Polychaetes | Full data set (Atlantic and Indo-Pacific) | | | Indo-Pacific Ocean | | |
|---|---|---|---|---|---|---|
| | Multiple regression | Parameter | Coefficient $P$ | Multiple regression | Parameter | Coefficient $P$ |
| Species richness $E(s_{100})$ | $R^2 = 0.576$ $P = 0.0001$ $F = 10.89$ $n = 28$ | Depth Org. C | 0.0006 0.021 | $R^2 = 0.721$ $P = 0.0002$ $F = 12.90$ $n = 19$ | Depth $O_2$ | 0.0007 0.020 |
| Dominance | $R^2 = 0.684$ $P < 0.0001$ $F = 18.03$ $n = 29$ | Depth Org. C | < 0.0001 0.053 | $R^2 = 0.869$ $P < 0.0001$ $F = 28.80$ $n = 20$ | Depth $O_2$ Lat. | < 0.0001 0.046 0.015 |
| $H'$ | $R^2 = 0.610$ $P < 0.0001$ $F = 13.07$ $n = 29$ | Depth Org. C | 0.0002 0.016 | $R^2 = 0.816$ $P < 0.0001$ $F = 16.62$ $n = 20$ | Depth $O_2$ Lat. | < 0.0001 0.029 0.037 |
| $J'$ | $R^2 = 0.645$ $P < 0.0001$ $F = 15.16$ $n = 29$ | Depth Org. C | < 0.0001 0.005 | $R^2 = 0.765$ $P < 0.0001$ $F = 17.39$ $n = 20$ | Depth Org. C | < 0.0001 0.012 |
| Polychaetes | Low-oxygen Indo-Pacific ocean (oxygen < 1 ml/l) | | | Atlantic ocean | | |
| | Multiple regression | Parameter | Coefficient $P$ | Multiple regression | Parameter | Coefficient $P$ |
| Species richness $E(s_{100})$ | $R^2 = 0.826$ $P < 0.0001$ $F = 26.05$ $n = 14$ | Depth $O_2$ | 0.001 0.002 | | No fit | |
| Dominance | $R^2 = 0.843$ $P < 0.0001$ $F = 32.33$ $n = 15$ | Depth $O_2$ | < 0.0001 0.010 | $R^2 = 0.767$ $P = 0.006$ $F = 11.53$ $n = 10$ | Depth | 0.006 |
| $H'$ | $R^2 = 0.861$ $P < 0.0001$ $F = 37.189$ $n = 15$ | Depth $O_2$ | 0.0001 0.0006 | | No data | |
| $J'$ | $R^2 = 0.663$ $P = 0.002$ $F = 11.289$ $n = 15$ | Depth $O_2$ | 0.005 0.046 | | No data | |

Table 5

Coefficients of determination and their significance for the linear relationships of total macrofaunal diversity measures to bottom-water oxygen concentration and sediment organic-content combined ($R^2$) and for each parameter alone ($r^2$). Effects of depth and latitude have been removed; depth as a quadratic fit (linear for low-$O_2$ Pacific data) and latitude as a linear fit. Significant regressions ($P \leqslant 0.05$) are shown in bold type

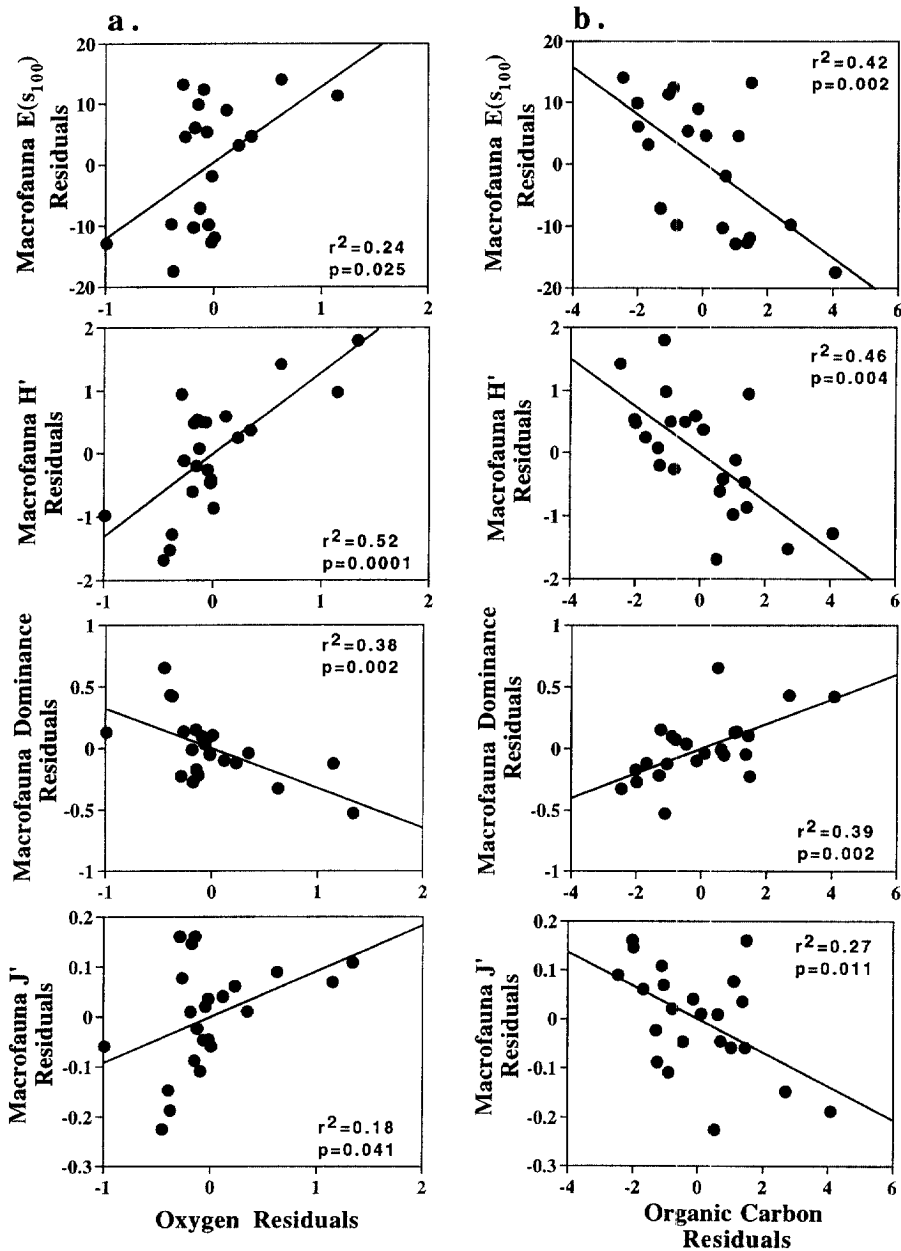| Total Macrofauna | | $E(s_{100})$ | | | Dominance | | | $H'$ | | | $J'$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $O_2$ + Org. C | $O_2$ | Org. C | $O_2$ + Org. C | $O_2$ | Org. C | $O_2$ + Org. C | $O_2$ | Org. C | $O_2$ + Org. C | $O_2$ | Org. C |
| Combined data | $R^2$ or $r^2$ | 0.101 | 0.0002 | 0.100 | 0.154 | 0.029 | 0.106 | No data | | | No data | | |
| | $F$ | 1.35 | 0.01 | 2.78 | 2.45 | 0.85 | 3.35 | | | | | | |
| | $P$ | 0.279 | 0.938 | 0.108 | 0.105 | 0.364 | 0.078 | | | | | | |
| | $n$ | 27 | 27 | 27 | 30 | 30 | 30 | | | | | | |
| Indo-pacific data | $R^2$ or $r^2$ | **0.472** | **0.236** | **0.420** | **0.519** | **0.375** | **0.383** | **0.667** | **0.518** | **0.456** | **0.316** | **0.184** | **0.270** |
| | $F$ | **8.03** | **5.88** | **13.78** | **10.81** | **12.62** | **13.02** | **20.16** | **22.58** | **17.58** | **4.63** | **4.75** | **7.78** |
| | $P$ | **0.003** | **0.025** | **0.002** | **0.001** | **0.002** | **0.002** | **0.0001** | **0.0001** | **0.0004** | **0.022** | **0.041** | **0.011** |
| | $n$ | **21** | **21** | **21** | **23** | **23** | **23** | **23** | **23** | **23** | **23** | **23** | **23** |
| Low-$O_2$ Indo-Pacific data | $R^2$ or $r^2$ | **0.678** | **0.599** | **0.486** | 0.353 | 0.186 | **0.345** | **0.588** | **0.471** | **0.476** | 0.279 | 0.192 | **0.252** |
| | $F$ | **12.60** | **19.46** | **12.32** | 3.55 | 3.20 | **7.37** | **9.27** | **12.45** | **12.72** | 2.52 | 3.32 | **4.71** |
| | $P$ | **0.001** | **0.007** | **0.004** | 0.059 | 0.095 | **0.017** | **0.003** | **0.003** | **0.003** | 0.119 | 0.090 | **0.048** |
| | $n$ | **15** | **15** | **15** | 16 | 16 | **16** | **16** | **16** | **16** | 16 | 16 | **16** |
| Atlantic data | $R^2$ or $r^2$ | 0.529 | **0.525** | 0.224 | 0.220 | 0.191 | 0.082 | No data | | | No data | | |
| | $F$ | 2.81 | **6.22** | 1.73 | 1.97 | 3.55 | 0.13 | | | | | | |
| | $P$ | 0.152 | **0.041** | 0.236 | 0.176 | 0.079 | 0.265 | | | | | | |
| | $n$ | 8 | **8** | 8 | 17 | 17 | 17 | | | | | | |

Fig. 4. Relationships for Indo-Pacific stations of macrofaunal species richness, diversity, dominance or evenness residuals to (a) bottom-water oxygen residuals and (b) organic carbon residuals, after effects of depth and latitude have been removed. Depth was removed as a quadratic fit, latitude as a linear fit. Significant regression lines and coefficients of determination are shown for $P \leqslant 0.05$.
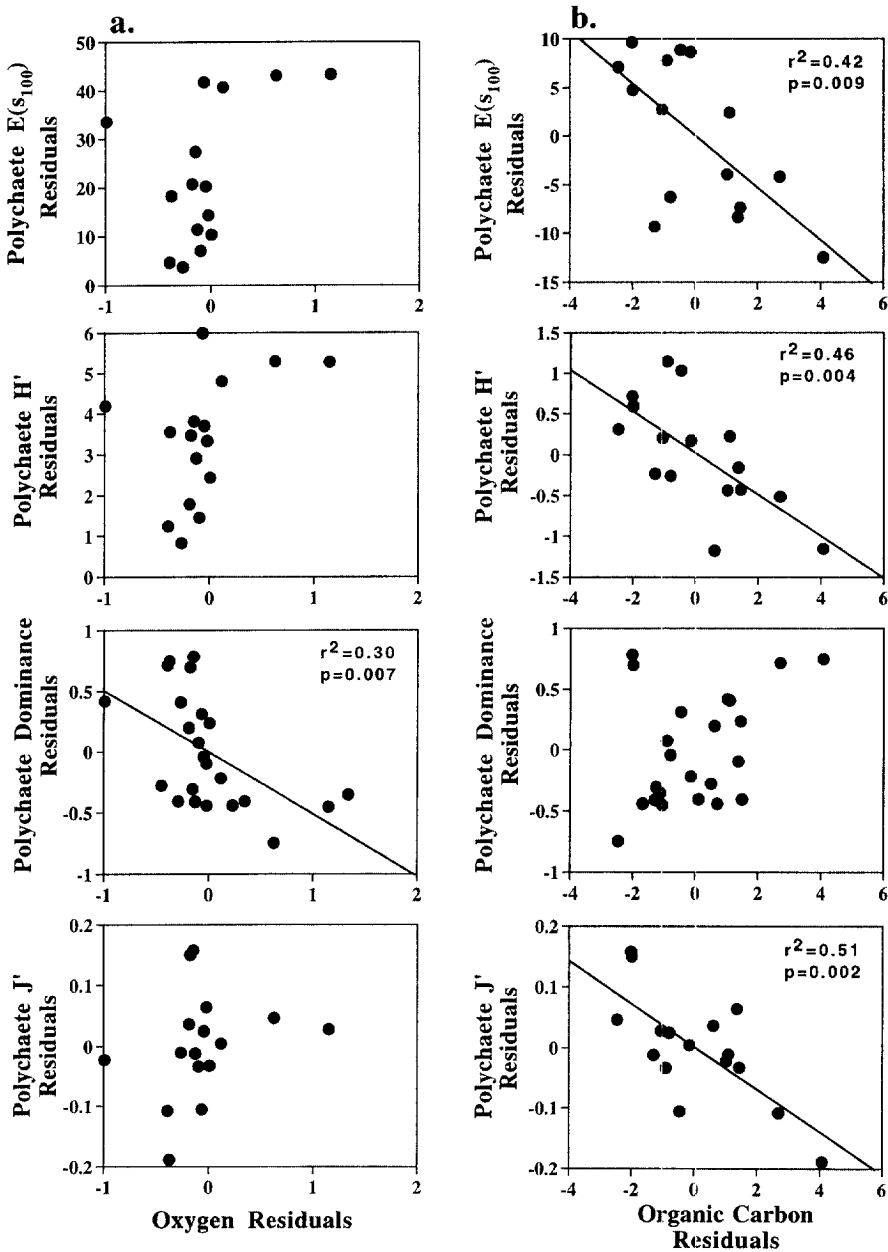
Table 6
Coefficients of determination for the linear relationships of polychaete diversity measures to bottom-water oxygen concentration and sediment organic-carbon content combined ($R^2$) and for each parameter alone ($r^2$). Effects of depth and latitude have been removed; depth as a quadratic fit (linear for low-$O_2$ Pacific data) and latitude as a linear fit. Significant regressions ($P \leqslant 0.05$) are shown in bold type

| Polychaetes | | $E(s_{100})$ | | | Dominance | | | $H'$ | | | $J'$ | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $O_2 +$ Org. C | $O_2$ | Org. C | $O_2 +$ Org. C | $O_2$ | Org. C | $O_2 +$ Org. C | $O_2$ | Org. C | $O_2 +$ Org. C | $O_2$ | Org. C |
| Combined data | $R^2$ or $r^2$ | 0.212 | 0.018 | **0.212** | 16.01 | 0.011 | **0.159** | 0.206 | 0.010 | **0.203** | **0.292** | 0.027 | **0.291** |
| | $F$ | 2.83 | 0.47 | **5.92** | 2.10 | 0.26 | **4.36** | 2.86 | 0.25 | **5.86** | **4.53** | 0.67 | **9.46** |
| | $P$ | 0.082 | 0.520 | **0.024** | 0.147 | 0.613 | **0.048** | 0.079 | 0.624 | **0.024** | **0.024** | 0.422 | **0.0053** |
| | $n$ | 24 | 24 | 24 | 25 | 25 | 25 | 25 | 25 | 25 | 26 | 26 | 26 |
| Indo-Pacific data | $R^2$ or $r^2$ | **0.420** | 0.101 | **0.419** | **0.318** | **0.295** | 0.148 | **0.458** | 0.081 | **0.457** | **0.521** | 0.062 | **0.513** |
| | $F$ | **4.34** | 1.47 | **9.38** | **4.66** | **8.79** | 3.64 | **5.49** | 1.244 | **11.76** | **7.08** | 0.93 | **14.73** |
| | $P$ | **0.038** | 0.248 | **0.009** | **0.022** | **0.007** | 0.070 | **0.019** | 0.283 | **0.004** | **0.008** | 0.351 | **0.002** |
| | $n$ | 15 | 15 | 15 | 23 | 23 | 23 | 16 | 16 | 16 | 16 | 16 | 16 |
| Low-$O_2$ Indo-Pacific data | $R^2$ or $r^2$ | **0.606** | **0.507** | **0.498** | **0.446** | 0.152 | **0.443** | **0.656** | **0.458** | **0.605** | **0.473** | 0.134 | **0.464** |
| | $F$ | **7.71** | **11.31** | **10.91** | **4.43** | 2.157 | **9.55** | **10.51** | **10.13** | **18.39** | **4.93** | 1.841 | 0.37 |
| | $P$ | **0.009** | **0.006** | **0.007** | **0.039** | 0.168 | **0.093** | **0.003** | **0.008** | **0.001** | **0.029** | 0.197 | **0.007** |
| | $n$ | 13 | 13 | 13 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 | 14 |
| Atlantic data | $R^2$ or $r^2$ | 0.175 | 0.015 | 0.052 | 0.020 | 0.010 | 0.0001 | 0.339 | .104 | 0.028 | 0.067 | 0.007 | 0.056 |
| | $F$ | 0.74 | 0.12 | 0.45 | 0.07 | 0.09 | 0.001 | 1.80 | 0.93 | 0.23 | 0.25 | 0.06 | 0.50 |
| | $P$ | 0.510 | 0.734 | 0.524 | 0.931 | 0.778 | 0.978 | 0.235 | 0.363 | 0.643 | 0.783 | 0.818 | 0.498 |
| | $n$ | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |

Fig. 5. Relationships for Indo-Pacific stations of polychaete species richness, diversity, dominance or evenness residuals to (a) bottom-water oxygen residuals or (b) organic carbon residuals after effects of depth and latitude have been removed. Significant regression lines and coefficients of determination are shown for $P \leqslant 0.05$.

each parameter (Table 6). Organic carbon alone explained 44–46% of variation in polychaete $D$ and $J'$ at the low $O_2$ sites, with no significant contribution from oxygen (Table 6).

### 3.4. Do all taxa respond similarly to oxygen and organic matter availability?

Rarefaction curves for Indian and Pacific Ocean macrofauna, polychaetes, molluscs and crustaceans indicate that stations within the eastern Pacific and Arabian Sea OMZs exhibit lower species richness (for all taxa) than other stations (Fig. 6a–d). The OMZ stations shown here (29, 30, 33–38) are characterized by oxygen $\leqslant 0.45$ ml l$^{-1}$, often high sediment organic-carbon content, water depths $\leqslant 1000$ m, and latitudes between 19°N and 6°S (Table 1). The Santa Catalina Basin (SCB) is also characterized by low oxygen and high organic carbon, but occurs at a higher latitude and deeper water depth than OMZ stations. This station is interesting because the rarefaction curve for total macrofauna falls just above the OMZ stations and overlaps the 3400 m site off Oman (Fig. 6a). The rarefaction curve presented by Smith et al. (1998) for background macrofauna in SCB sediments also falls well above those of the OMZ stations. However, not all SCB taxa respond similarly. In the SCB, polychaete diversity was comparable to that of OMZ stations (Fig. 6b), but mollusc (Fig. 6c) and crustacean diversities (Fig. 6d) were notably higher than in many OMZ and non-OMZ stations.

To contrast diversity of margin macrobenthos in the presence and absence of an OMZ, we compared polychaete diversity along two cross-slope transects, one for the well-oxygenated Hebridean slope (NW Atlantic 56°N, 400–2000 m) and one for the Oman margin, which intercepts an OMZ (NW Indian Ocean, 19°N, 400–3400 m). Both transects exhibited diversity maxima at mid-slope depths (Fig. 7a and b). Comparisons between the two margin transects indicate that, at depths between 400 and 1000 m (the OMZ range off Oman), species richness was 2–4 times lower off Oman than on the Hebridian slope. However, below these depths (e.g. 1250 m), species richness was roughly comparable in the two regions (Fig. 7a and b). These observations imply that factors other than depth or latitude can exert control over polychaete species richness. The relatively high macrofaunal species richness observed at 1250 m on the Oman margin (Fig. 6a and Fig. 7b), where measured bottom water oxygen concentrations averaged 0.47 ml l$^{-1}$, suggests that the threshold for low oxygen influence on diversity occurs below 0.5 ml l$^{-1}$.

### 3.5. Taxonomic response as a diversity influence

Do changes in diversity along gradients of increased sediment organic-carbon content or decreased bottom-water oxygen concentrations result in part from loss of major taxonomic groups? This question was examined for the Indo-Pacific stations, where bottom-water oxygen and organic-matter concentrations span a broad range (Table 1) and exhibit strong correlations with diversity (Tables 5 and 6). Plots of polychaete, mollusc, and crustacean representation (percent of total fauna) as a function of bottom-water oxygen concentration (Fig. 8a) and sediment organic-carbon
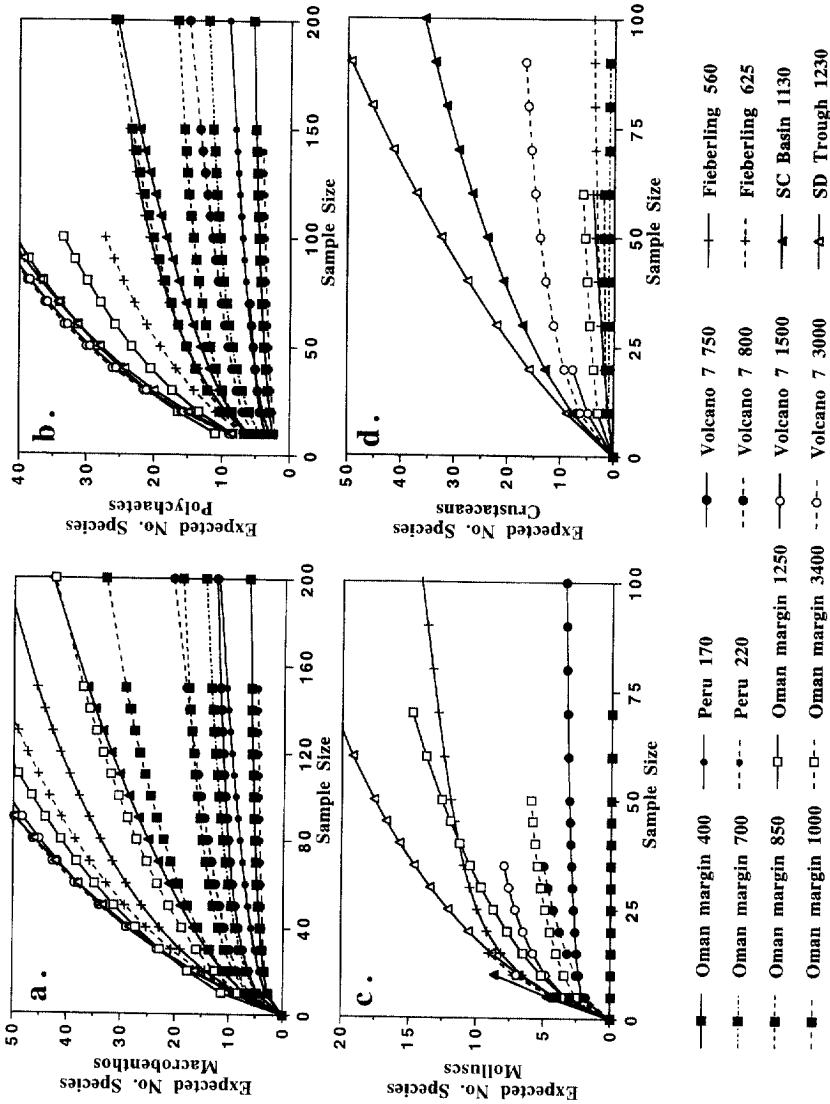
Fig. 6. Rarefaction curves for (a) total macrobenthos, (b) polychaetes, (c) molluscs, and (d) crustaceans from bathyal stations in the Indian and Pacific Oceans. Numbers after location names in the legend give the station water depth in meters. Stations with filled symbols are sites where bottom-water oxygen concentration was < 0.45 ml l$^{-1}$. No curves are shown for stations where ≤ 1 species were collected.
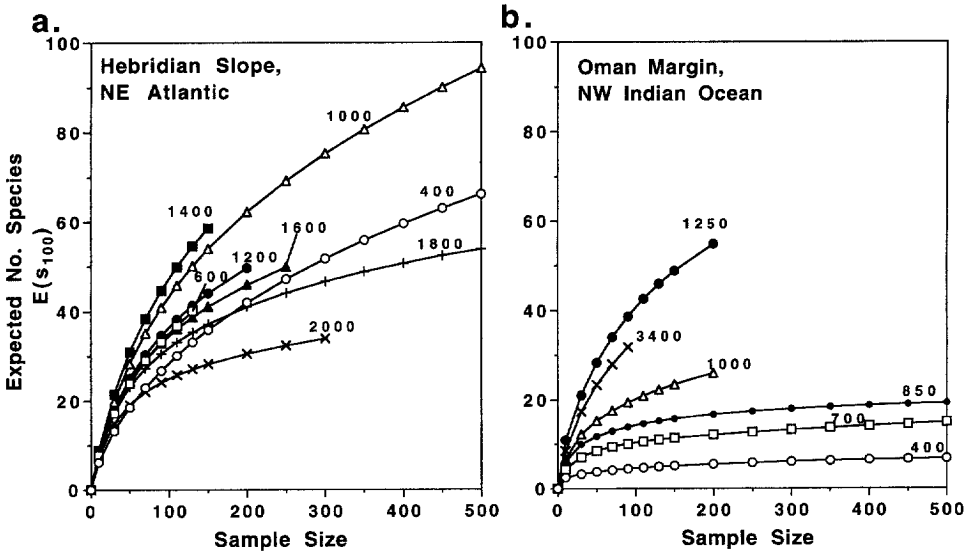
Fig. 7. Polychaete rarefaction curves for cross-slope stations from (a) the Hebridian slope in the NE Atlantic and (b) the Oman margin in the Arabian Sea. Numbers near curves indicate water depth in meters. See Table 1 for station locations and physical properties.

content (Fig. 8b) reveal that polychaetes are more tolerant of low oxygen and organic enrichment than molluscs or crustaceans. Polychaetes were well represented at most stations, although diversity was very low off Peru, on the summit of Volcano 7 and on the upper Oman margin (Fig. 6b). Molluscs were absent from the Peru and Oman margin OMZ stations; they were relatively common within the OMZ on Volcano 7, but with low diversity (mainly aplacophorans) (Fig. 6c). Crustaceans were absent from OMZ stations on Volcano 7, and on the Peru and upper Oman margins, with the exception of the amphipod *Ampelisca* sp. (Fig. 6d). The rarity of several major taxa (molluscs and crustaceans) within OMZs must contribute to the extraordinarily low species richness and evenness observed in these settings.

Despite the taxonomic patterns revealed by the rarefaction curves described above (Fig. 6), simple linear regressions of percent representation of each taxon against depth, latitude, oxygen, organic carbon, % clay and % sand yielded only a few significant (but relatively weak) relationships. Polychaete representation was negatively correlated with oxygen ($r^2 = 0.197$, $P = 0.034$) and latitude ($r^2 = 0.181$, $P = 0.043$) and positively correlated with organic-carbon content ($r^2 = 0.176$, $P = 0.047$). Mollusc representation was not correlated with any parameters, though a positive association with percent sand was nearly significant ($r^2 = 0.206, P = 0.067$). The strongest associations were observed for crustaceans; representation was positively correlated with oxygen ($r^2 = 0.365$, $P = 0.005$) and water depth ($r^2 = 0.305$, $P = 0.012$). However, when depth effects were removed from both parameters, oxygen was no longer correlated with crustacean representation.
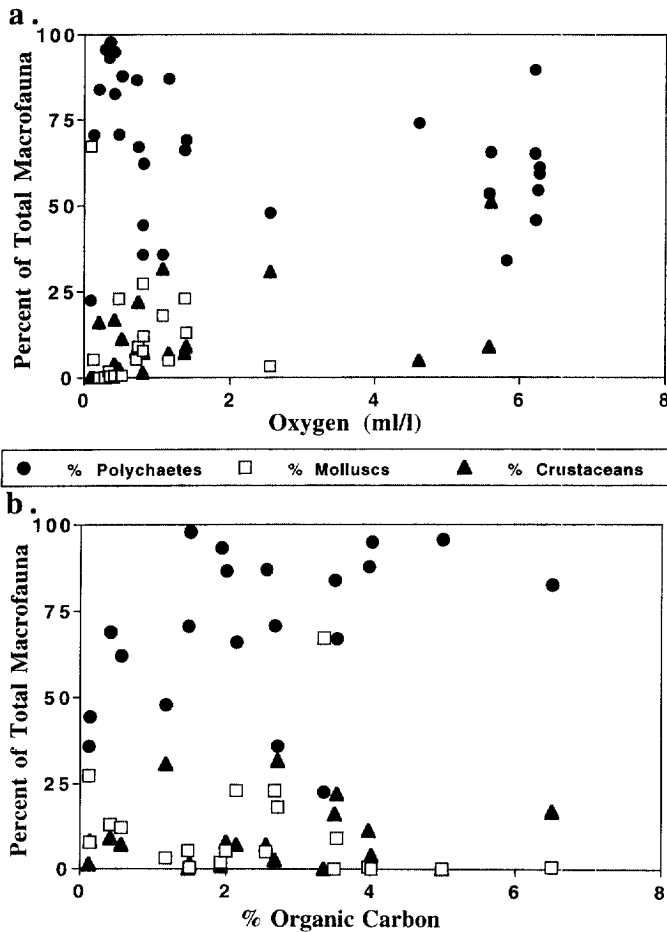
Fig. 8. Representation of polychaetes, molluscs, and crustaceans (percentage of the total macrofauna) as a function of (a) bottom-water oxygen concentration and (b) sediment organic-carbon content.

## 4. Discussion

### 4.1. Controls on species diversity

In a recent review of large-scale patterns of species diversity, Rex et al. (1997) point out that ecological, oceanographic and historical processes influence diversity on many space and time scales. This paper has examined several abiotic factors acting on relatively large space scales. Of those factors evaluated here, no single parameter appeared to be a master variable controlling species richness of bathyal macrobenthos in the world's oceans. However, depth, sediment organic-carbon content, and

bottom-water oxygen concentration all were significantly correlated with measures of macrofaunal diversity.

### 4.1.1. Depth

In the present study, depth was generally the most significant parameter, although it was not always the most important for a given diversity index (Tables 3 and 4). The observed depth – diversity relationships were parabolic (Fig. 2a and Fig. 3a), though somewhat truncated due to the limited depth range of the stations examined. Depth as a diversity influence has been tied to productivity and food supply (Rosenzweig, 1995; Rex et al., 1997), hydrodynamic regime (Paterson and Lambshead, 1995; Gage, 1996), and sediment diversity (Etter and Grassle, 1992). Beneath upwelling zones, depth is also associated with bottom-water oxygen concentration, although not linearly.

### 4.1.2. Organic carbon

Sediment organic-carbon content is viewed as a weak proxy for food availability. Organic carbon in sediments is strongly influenced by particle size (Milliman, 1994), which is often a function of hydrodynamic regime. High concentrations of organic carbon in sediments are associated with reduced pore-water oxygen content. Despite these confounding influences, organic carbon was the second most significant factor studied, in terms of its ability to explain variation in diversity (Tables 3 and 4). In some instances, organic carbon appears to exhibit a stronger relationship with the distribution of individuals among species ($D$ and $J'$), than with species diversity ($E[s_{100}]$) or $H'$). We hypothesize that this occurs because food is less likely to influence species persistence than factors affecting population size (such as population growth rate and possibly competitive abilities). We also note that organic carbon is frequently a more significant parameter for polychaete diversity measures than for total macrobenthic diversity measures, implying potentially less importance to non-polychaete taxa (Tables 5 and 6). Certain polychaetes are noted for their opportunistic response to organic enrichment in shallow waters (Pearson and Rosenberg, 1978; Levin et al., 1996). *In situ* experiments indicate that a similar polychaete-dominated response may occur in the deep sea (Grassle and Morse-Porteous, 1987; Desbruyères et al., 1980, 1985; Snelgrove et al., 1992). It is not surprising, then, to find high-density and low-diversity polychaete-dominated assemblages in organically enriched or stressed bathyal settings (Levin et al., 1991, 1994a, 1997).

The absence of an accurate measure of food availability in this study limits our ability to assess fully the influence of this food on diversity. We originally had hoped to use estimates of carbon flux to the seabed as a proxy for food availability, but information was lacking for most of the stations. Measures of sediment organic-carbon content provide no indication of carbon lability (accessibility to macrobenthic organisms). In bathyal settings, sediment organic carbon is often correlated with POC flux, but bottom-water oxygen levels may also influence sediment organic-carbon content (Emerson, 1985). In hypoxic settings, low oxygen slows organic matter degradation relative to better-oxygenated regions.

Another possible proxy for food availability in deep-sea sediments is macrofaunal abundance (R. Etter and C. Smith, pers. comm.). Smith et al. (in press) has shown a strong positive relationship between macrofaunal abundance and POC flux in the abyssal equatorial Pacific. In the present study, regression analyses of total macrofaunal and polychaete density normalized to no. $m^{-2}$ (all data sets combined) against species richness ($E[s_{100}]$), with depth and latitude effects removed, reveal a weak but significant negative linear relationship between abundance and species richness ($r^2 = 0.17$, $P = 0.035$ for macrofauna, $r^2 = 0.16$, $P = 0.034$ for polychaetes). The same type of analyses carried out for Indo-Pacific data only yielded similar negative relationships between density and species richness ($r^2 = 0.12$, $P = 0.05$ for macrofauna; $r^2 = 0.18$, $P = 0.07$ for polychaetes) that were much weaker than those observed between sediment organic carbon and species richness ($r^2 = 0.42$; $P < 0.01$ for macrofauna and polychaetes) (Fig. 4b and Fig. 5b).

### 4.1.3. Oxygen

The present analyses indicates a strong relationship between macrobenthic diversity measures and bottom-water oxygen concentrations in the Indo-Pacific and Atlantic data sets (Table 5). Its absence from most best-fit regressions in the combined data set may be related to the lack of overlap of bottom-water oxygen values at the Atlantic and Indo-Pacific stations (Table 1 and Fig. 2c). Despite differences in oxygen availability, there is considerable overlap in species richness and dominance estimates in the Atlantic, Indian and Pacific Oceans (Figs. 2 and 3). The significant positive relationship of oxygen with macrobenthic species richness in the Atlantic (Table 3 and Fig. 2c) may result from a negative association between carbon flux and bottom-water oxygen concentrations. For example, carbon flux is exceedingly high ($> 150 \, g \, C \, m^{-2} \, yr^{-1}$) off Cape Hatteras, North Carolina, (DeMaster et al., 1994) where the lowest Atlantic oxygen concentrations in this study were encountered.

Not surprisingly, oxygen exhibited a highly significant relationship with species richness and $H'$ (second only to depth) when stations with $< 1 \, ml \, l^{-1}$ $O_2$ were evaluated (Tables 3–6). These results suggest that there is an oxygen threshold (below $1 \, ml \, l^{-1}$ and probably $< 0.45 \, ml \, l^{-1}$) above which oxygen has relatively minor influence on macrobenthic species richness, but below which it is a powerful control. The same was not true for dominance and evenness, which were explained mainly by sediment organic-matter content, even at low-oxygen stations (Tables 5 and 6). We propose that tolerance to low bottom-water oxygen concentration is more likely to dictate whether a species will be present or not (and thus influence $E(s_{100})$ and $H'$), whereas food availability, as suggested above, exerts primary control on dominance and evenness.

Benthic foraminifera, like macrofauna, exhibit reduced diversity and extreme dominance in oxygen minimum zones (reviewed in Sen Gupta and Machain-Castillo, 1993). There is considerable controversy over the relative importance of nutritional conditions (organic matter flux) vs bottom-water oxygenation in determining foraminiferal microhabitats and their distribution and diversity patterns (Corliss and Emerson, 1990; Rathburn and Corliss, 1994). Jorrisen et al. (1995) present a conceptual model in which they suggest that the living depth of benthic foraminifera is

controlled by the availability of metabolizable food particles in the sediment under oligotrophic conditions, but by critical oxygen levels under eutrophic conditions. This model parallels our interpretation of how oxygen and organic matter interact in controlling macrofaunal diversity patterns. However, this scenario is complicated by the significant influence of sediment organic carbon on pore-water oxygen concentration, and the likelihood that pore-water oxygen level has a greater influence on foraminifera than on many macrofauna (which can maintain direct contact with overlying water).

In a review of effects of hypoxia on marine benthic macrofauna, Diaz and Rosenberg (1995) conclude that polychaetes are the taxon most tolerant to low oxygen, followed by bivalves, and that crustaceans are less tolerant than both of these groups. Molluscs and crustaceans, which are usually rare on the hypoxic, polychaete-dominated Peru shelf, increased greatly in abundance and diversity during the 1982–83 El Niño, when an influx of oxygenated water was observed (Tarazona et al., 1988; Arntz et al., 1991). Data from our study (Figs. 6 and 8) support the above-mentioned differences in the tolerances of major taxa to hypoxia. Exceptions exist, however, as we found selected amphipod species abundant in the core of the Peru and Oman margin OMZs, and aplacophoran molluscs abundant in the OMZ off Mexico on the summit of Volcano 7.

### 4.1.4. Latitude

Although latitude was a significant factor in the combined and Indo-Pacific multiple regressions for all macrobenthic diversity estimates except evenness (Tables 3 and 4), latitudinal analyses that extend beyond single ocean basins may be inappropriate. Latitudinal species richness gradients are well established for bivalves, isopods and gastropods in the North Atlantic, where diversity is greatest near the tropics, but latitudinal patterns vary among taxa and region in the South Atlantic (Rex et al., 1993, 1997). Evenness (Pielou's $J'$) was shown to decrease with increasing latitude for North Atlantic isopods and gastropods, although latitude explained less of the variation in $J'$ than for species richness (Rex et al., 1993). Latitude is associated with surface production and carbon flux as well as with varying historical influences over geological time (Rex et al., 1997; Wilson, 1998). In the present study of bathyal macrobenthos and polychaetes, some of the lowest species richness and $H'$ values occurred on the upper slope at low latitudes in the Indian and Pacific oceans (Fig. 2b and Fig. 3b), where OMZ's are best developed.

### 4.1.5. Particle size

Sediment % sand and % clay were uncorrelated with diversity measures for macrobenthos or polychaetes. However, positive correlations with % clay (after removal of depth effects) were observed for crustacean species richness ($E[s_{20}]$) ($r^2 = 0.548$, $P = 0.009$, $n = 11$) in the Indo-Pacific. Due to lack of appropriate sediment data, we were unable to test for influence of particle size diversity, which Etter and Grassle (1992) have shown to correlate positively with macrobenthic species richness in the western North Atlantic. They suggest that depth-related patterns of species diversity reflect the effects of silt diversity and are a consequence of changes in

sediment characteristics with depth. This remains a viable hypothesis in need of testing for the Indo-Pacific fauna.

### 4.2. Is there a hump-shaped diversity curve linked to food availability?

Diversity data for the Indo-Pacific show a linear decline with increasing organic-carbon content of sediments (from 0.1 to 6.5% TOC; Fig. 4b and Fig. 5b), rather than the hump-shaped diversity (vs productivity) curve proposed by Rosenzweig and Abramsky (1993) and Rosenzweig (1995) for plants and deep-sea sediments. If sediment organic-carbon content is related to food availability, then there may be a negative linear relationship between diversity and food in bathyal sediments. Because bathyal settings are largely associated with continental margins, they experience higher organic matter inputs than open-ocean regimes. It may be that all the bathyal settings studied experience relatively high organic matter inputs that place them on the right side of the parabolic diversity–productivity curve referred to above. Increasing levels of organic matter may lead to reduced species richness or elevated dominance by stimulating population growth rates of some species that then outcompete others under conditions of reduced pore-water oxygen concentrations. Strong responses by polychaetes appear to drive bathyal macrobenthic diversity patterns at high organic-carbon (productivity) levels. This group represents a greater fraction of the total fauna (Fig. 8) and exhibits reduced species richness and evenness (Fig. 5b) under enriched conditions. In heavily enriched settings on the Oman and Peru margins (stations 34 and 35; Table 1), two polychaete species comprised over 90% of the macrofaunal individuals present.

### 4.3. Conclusions and recommendations

Although interactive biological factors have not been considered here, no single, readily measured physico-chemical parameter associated with the benthic environment appears to explain most of the species richness of bathyal macrobenthos in the world's oceans. Our results suggest that organic-matter availability may play a major role in determining community structure (especially evenness and dominance) of macrobenthic assemblages on continental slopes. However, the use of sediment organic carbon (which may include large quantities of refractory material) as a proxy for food quantity probably has blurred the response measured. Although it is difficult to separate from organic matter availability as an influence, oxygen is shown to exhibit a strong correlation with species richness and $H'$, and to a lesser extent with $D$ and $J'$, primarily at concentrations below $1 \, \mathrm{ml\,l^{-1}}$. Comparisons of diversity patterns in polychaetes to those of total macrobenthos and other taxa suggest that the relative influence of different physico-chemical parameters varies among taxonomic groups. Sediment organic-carbon content exhibits a stronger relationship with polychaete diversity than with that of other taxa.

Both oxygen concentrations and organic fluxes in margin environments may change on relatively short (seasonal, interannual and interdecadal) time scales as a result of natural climate variation or anthropogenic activities (Tyson and Person,

1991). Though direct causal relationships were not established in this study, our results strongly suggest that temporal changes in bottom-water oxygen concentration and organic inputs to sediments may alter both the diversity and general taxonomic composition of bathyal macrobenthos. Such changes have been observed during and after El Niño conditions on the Peru shelf (Arntz et al., 1991). Thus, oxygen and organic matter almost certainly will have greater influence on short-term fluctuations in diversity than will parameters such as water depth or latitude, which vary only on geological time scales.

The scope of the present analysis was limited by the lack of bottom-water oxygen concentration data for some macrobenthic studies and by a shortage of published macrobenthos species lists and counts. Our interpretations may have been restricted most by small sample sizes and the absence of a reliable indicator of food availability to the benthos. We close by emphasizing the need for standardized measurements of physico-chemical properties of benthic environments in conjunction with macrobenthic studies, including estimates of carbon flux to the seabed and bottom-water oxygen concentration. We also encourage publication of species-level data whenever possible. With time such actions should lead to improved understanding of global-scale patterns of diversity in the deep sea.

## Acknowledgements

## References

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. Geol. Soc. Special Publications No. 58, London, pp. 131–154.

Berry, W.B.N., Wilde, P., 1978. Progressive ventilation of the oceans: an explanation for the distribution of the lower Paleozoic black shales. American Journal of Science 278, 257–275.

Blake, J.A., Hecker, B., Grassle, J.F., Brown, B., Wade, M., Boehm, P.D., Baptiste, E., Hilbig, B., Maciolek, N., Petrecca, R., Ruff, R.E., Starczak, V., Watling, L., 1987. Study of biological processes on the U.S. south Atlantic slope and rise, Phase 2. OCS Study, MMS 86-0096, Contract No. 14-12-0001-30064, 414 pp. + appendices.

Blake, J.A., Grassle, J.F., 1994. Benthic community structure on the U.S. South Atlantic slope off the Carolinas: spatial heterogeneity in a current dominated system. Deep-Sea Research 41, 835–874.

Connell, J.H., Orians, E., 1964. The ecological regulation of species diversity. American Naturalist 98, 399–414.

Corliss, B.H., Emerson, S., 1990. Distribution of rose bengal stained deep-sea benthic foraminifera from the Nova Scotian continental margin and Gulf of Maine. Deep-sea Research 37, 381–400.

Cosson, N., Sibuet, N., Paterson, G.L.J., Vangriesheim, A., (in press). Polychaete diversity at tropical Atlantic deep-sea sites environmental effects. Marine Ecology Progress Series.

Dahl, E., Laubier, L., Sibuet, M., Stromberg, J.O., 1976. Some quantitative results on benthic communities of the deep Norwegian Sea. Astarte 9, 61–79.

Dayton, P.K., Hessler, R.R., 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Research 19, 199–208.

Desbruyerès, D., Bevas, J.Y., Khripounoff, A., 1980. Un cas de colonization rapide d'un sedimenté profond. Oceanologica Acta 3, 285–291.

Desbruyères, D., Deming, J., Dinet, A., Khripounoff, A., 1985. Reactions de l'écosystème benthique profond aux perturbations: nouveaux resultats expérimentaux. In: Laubier, L., Monniot, C. (Eds.), Peuplements profonds du Golfe de Gascogne. IFREMER, Brest, pp. 121–142.

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

DeMaster, D.J., Pope, R.H., Levin, L.A., Blair, N.E., 1994. Biological mixing intensity and rates of organic carbon accumulation in North Carolina slope sediments. Deep-Sea Research 41, 735–753.

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: an Annual Review 33, 245–303.

Draper, N.R., Smith, H., 1981. Applied Regression Analysis. 2nd ed., Wiley and Sons, New York, p. 709.

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

Emerson, S.K., 1985. Organic carbon preservation in marine sediments. In: Sundquist, E.T., Broecker, W.S. (Eds.), The Carbon Cycle and Atmospheric $CO_2$: Natural Variations Archean to Present, Geophysical Monograph, vol. 32, American Geophysical Union, Washington, DC, pp. 78–88.

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.

Gage, J.D., 1977. Structure of the abyssal macrobenthic community in the Rockall Trough. In: Keegan, B.F., O'Cedigh, P., Boaden, P.J.S. (Eds.), Biology of Benthic Organisms. Pergamon, Oxford, pp. 247–260.

Gage, J.D., 1979. Macrobenthic community structure in the Rockall Trough. Ambio Special Report 6, 43–46.

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, 9 October–11 November 1994. p. 71. Scottish Association for Marine Science, P.O. Box 3, Oban, Scotland.

Gage, J.D., 1996. Why are there so many species in deep-sea sediments?. Journal of Experimental Marine Biology and Ecology 200, 257–286.

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., Tyler, P.A., 1991. Deep-Sea Biology: a Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, Cambridge, p. 504.

Gooday, A.J., Turley, C.M., 1990. Responses by benthic organisms to inputs of organic material to the ocean floor: a review. Philosophical Transactions of the Royal Society of London 331, 119–138.

Grassle, J.F., 1989. Species diversity in deep-sea communities. Trends in Ecology and Evolution 4, 12–15.

Grassle, J.F., Brown-Leger, L.S., Morse-Porteous, L., Petrecca, R., Williams, I., 1985. Deep-sea fauna of sediments in the vicinity of hydrothermal vents. Bulletin of the Biological Society of Washington 6, 443–452.

Grassle, J.F., Grassle, J.P., 1994. Notes from the abyss: the effects of a patchy supply of organic material and larvae on soft-sediment benthic communities. In: Giller, P.S., Hildrew, A.G., Raffaelli, D.G. (Eds.), The 34th Symposium of the British Ecological Society: Aquatic Ecology: Scale, Pattern and Process.. Blackwell Scientific Publications, Oxford, pp. 499–515.

Grassle, J.F., Morse-Porteous, L.S., 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-Sea Research 34A, 1911–1950.

Grassle, J.F., Sanders, H.L., 1973. Life histories and the role of disturbance. Deep-Sea Research 20, 643–659.

Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep sea. Deep-Sea Research 14, 65–78.

Hurlbert, S.M., 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52, 577–586.

Huston, M., 1979. A general hypothesis of species diversity. The American Naturalist 113, 81–101.

Hyland, J., Baptiste, E., Campbell, J., Kennedy, J., Kropp, R., Williams, S., 1991. Macroinfaunal communities of the Santa Maria Basin on the California outer continental shelf and slope. Marine Ecology Progress Series 78, 147–161.

Jorrisen, 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., 1974. Dispersion patterns and species diversity of macrobenthos in two bathyal communities. Ph.D. thesis. University of California, San Diego.

Jumars, P.A., Gallagher, E.D., 1982. Deep-sea community structure: three plays on the benthic proscenium. In: Ernst, W.G., Morin, J.G. (Eds.), The Environment of the Deep Sea. Prentice-Hall, Englewood Cliffs, NJ, pp. 218–254.

Levin, L.A., Caswell, H., Bridges, T., DiBacco, C., Cabrera, D., Plaia, G., 1996. Demographic responses of estuarine polychaetes to pollutants: life table response experiments. Ecological Applications 6, 1295–1313.

Levin, L.A., Gage, J., 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.E., Hutchinson, S. (Eds.), Responses of Marine Organisms to their Environments. Proceedings of the 30th European Marine Biology Symposium. University of Southampton, UK, pp. 1–8.

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., Leithold, E.L., Gross, T.F., Huggett, C.L., DiBacco, C., 1994a. Contrasting effects of substrate mobility on infaunal assemblages inhabiting two high-energy settings on Fieberling Guyot. Journal of Marine Research 52, 489–522.

Levin, L.A., Plaia, G.R., Huggett, C.L., 1994b. 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.

Milliman, J.D., 1994. Organic matter content in U.S. Atlantic continental slope sediments: Decoupling the grain-size factor. Deep-Sea Research 41, 797–808.

Mitchell, L., Harvey, M., Gage, J.D., Fallick, A.E., 1997. Organic carbon dynamics in shelf edge sediment off the Hebrides: a seasonal perspective. Internationale Revue der gesamten Hydrobiologie 82, 425–435.

Mitchell, L., Gage, J.D., Fallick, A.E., Stewart, A., 1996. Benthic fluxes on the Hebridean shelf edge. In: Botrell, S.H. (Ed.), Proceedings of the 4th International Symposium on the Earth's Surface, July 1996, Ilkley, U.K. International Association of Geochemistry and Cosmochemistry, University of Leeds, pp. 92–95.

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. and Gage, J.D., 1996. Sediment biogeochemical proxies at the Oman margin oxygen minimum zone. In: Botrell, S.H. (Ed.), Proceedings of the 4th International Symposium on the Earth's Surface, July 1996, Ilkley, U.K. 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 of the marine environment. Oceanography and Marine Biology Annual Review 16, 229–311.

Pineda, J., 1993. Boundary effects on the vertical ranges of deep-sea species. Deep-Sea Research 40, 2179–2192.

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

Rex, M.A., 1981. Community structure in the deep-sea benthos. Annual Review of Ecology and Systematics 12, 331–353.

Rex, M.A., 1983. Geographical 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.

Rex, M.A., Stuart, C., Etter, R.J., 1997. Large-scale patterns of species diversity in the deep-sea benthos. In: Ormond, R.J.A., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: Causes and Consequences. Cambridge University Press, Cambridge, pp. 94–121.

Rex, M.A., Stuart, C.T., Hessler, R.R., Allen, J.A., Sanders, H.L., Wilson, G.D.F., 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. Nature 365, 636–639.

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

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. Blackwell Scientific Publications, Oxford, pp. 469–497.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, p. 436.

Rosenzweig, M.L., Abramsky, H., 1993. How are diversity and productivity related?. In: Ricklef, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. 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.

Sanders, H.L., Hessler, R.R., 1969. Ecology of the deep-sea benthos. Nature 163, 1419–1424.

SAS Institute, Incorporated, 1989. JMP User's Guide, Version 2. SAS Institute, Inc. Cary, NC, 584pp.

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.

Schaff, T., Levin, L., Blair, N., DeMaster, D., Pope, R., Boehme, S., 1992. Spatial heterogeneity of benthos on the Carolina continental slope: Large (100 km)-scale variation. Marine Ecology Progress Series 88, 143–160.

Sen Gupta, B.K., Machain-Castillo, M.O., 1993. Benthic foramnfera in oxygen-poor habitats. Marine Micropaleontology 20, 183–201.

Smith, C.R., 1983. Enrichment, disturbance and deep-sea community structure: the significance of large organic falls to bathyal benthos in Santa Catalina Basin. Ph.D. thesis. University of California, San Diego.

Smith, C.R., 1986. Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep sea. Journal of Marine Research 44, 567–600.

Smith, C.R., Maybaum, H.L., Baco, A.R., Pope, R.H., Carpenter, S.D., Yager, P.L., Macko, S.D., Deming, J.W., 1998. Sediment community structure around a whole skeleton in the deep northeast pacific: macrofaunal, microbial and bioturbation effects. Deep-Sea Research II 45 (1–3), 335–364.

Smith, C.R., Berelson, W., DeMaster, D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Pope, R.H., Stephens, M., in press. Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. Deep-Sea Research II.

Snelgrove, P.V.R., Butman, C.A., 1994. Animal-sediment relationships revisited: cause versus effect. Oceanography and Marine Biology 32, 111–177.

Snelgrove, P.V.R., Grassle, J.F., Petrecca, R.F., 1992. The role of food patches in maintaining high deep-sea diversity: field experiments with hydrodynamically unbiased colonization trays. Limnology and Oceanography 37, 1543–1550.

Snelgrove, P.V.R., Grassle, J.F., Petrecca, R.F., 1996. Experimental evidence for aging food patches as a factor contributing to high deep-sea macrofaunal diversity. Limnology and Oceanography 41, 605–614.

Tarazona, J., Salzwedel, H., Arntz, W., 1988. Positive effects of "El Nino" on macrozoobenthos inhabiting hypoxic areas of the Peruvian upwelling system. Oecologia 76, 184–190.

Thistle, D., 1978. Harpacticoid dispersion patterns: implications for deep-sea diversity maintenance. Journal of Marine Research 36, 377–395.

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.

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. Geol. Soc. Special Publications No. 58, London, pp. 1–24.

Vetter, E.W., Dayton, P.K., 1998. Effects of detrital enrichment on macrofaunal communities in submarine canyons. Deep-Sea Research II 45 (1–3), 25–54.

Watts, M.C., Etter, R.J., Rex, M.A., 1992. Effects of spatial and temporal scale on the relationship of the surface pigment biomass to community structure in the deep-sea benthos. In: Rowe, G.T., Pariente, G.T. (Eds.), Deep-Sea Food Chains and the Global Carbon Cycle. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 245–254.

Wheatcroft, R.A., 1989. Dynamics of surficial trace assemblages in the deep sea. Deep-Sea Research 36, 71–91.

Wilson, G.D.F., 1998. Historical influences on deep-sea isopod diversity in the Atlantic Ocean. Deep-Sea Research II 45 (1–3), 279–302.

Wright, D.H., Currie, D.J., Maurer, B.A., 1993. Energy supply and patterns of species richness on local and regional scales. In: Ricklef, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. The University of Chicago Press, Chicago, pp. 66–74.