

# Polychaete diversity at tropical Atlantic deep-sea sites: environmental effects

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**ABSTRACT:** This study assesses how differences in nutrient flux and bottom currents affect the diversity and trophic structure of deep-sea polychaete communities from the tropical northeast Atlantic at 20° to 21° N latitude. Faunal assemblages were studied from 3 sets of USNEL box cores (0.25 m<sup>2</sup>) taken at depths of 1700, 3100 and 4600 m. In terms of primary productivity, the cores were taken beneath water which is eutrophic, mesotrophic and oligotrophic, respectively. Total polychaete abundance, abundance of dominant species, and faunal similarity and diversity were compared among the 3 sites. Polychaete abundance decreased with increasing depth. Community structure reflected environmental characteristics as well as the influence of coastal upwelling. Polychaete diversity showed a parabolic distribution, with depth peaking at about 2000 m. Species richness observed at the eutrophic site was generally higher than observed at other deep-sea regions of comparable depth at temperate latitudes. This points to regional variation in processes contributing to diversity patterns of deep fauna. We suggest that the diversity pattern observed results from non-equilibrium interactions between production and disturbance in the form of current energy and bioturbation. Diversity patterns observed in the EUMELI sites seem best explained by the intermediate productivity theory. The rate of production encountered at the eutrophic site may overcome much of the impact of physical and biological disturbances, favouring a diverse species assemblage.

**KEY WORDS:** Deep sea · Tropical Atlantic · Diversity · Polychaete community · Environmental conditions

## INTRODUCTION

The deep-sea environment is now considered among the most diverse on the planet (Blake et al. 1985, Grassle & Maciolek 1992, Lamshead 1993, Blake & Grassle 1994, Gage 1996). Many studies during the last 30 yr, stimulated by the debate on deep-sea faunal diversity and its comparison to other marine and terrestrial environments, have contributed to a better understanding of processes maintaining deep-sea diversity and have provided evidence of geographical variations in bathymetric diversity patterns (Rex 1983, Grassle & Morse-Porteous 1987b, Thistle et al. 1991, Lamshead et al. 1995, Paterson & Lamshead 1995). Studies of different regions have provided evidence of new parameters likely to maintain high faunal diver-

sity, such as predators indiscriminately cropping infauna (Dayton & Hessler 1971), interspecific competition (Rex 1983, Etter & Rex 1990), physical disturbance and patch dynamics with biological interactions (Jumars & Eckman 1983, Grassle & Morse-Porteous 1987), or sediment diversity (Etter & Grassle 1992). Several studies have investigated patterns of macrofaunal diversity with depth, showing a parabolic distribution with a peak at intermediate depths. Rex (1973, 1976) found that the diversity of gastropod molluscs increased from the shelf down the slope, but decreased with increasing distance out onto the abyssal plain. On the basis of similar patterns for polychaetes, cumaceans and bivalves, Rex (1981, 1983) pointed out that there was a general 'parabolic' species richness curve with depth for macrofaunal taxa in the Atlantic Ocean. Maciolek et al. (1987) and Etter & Grassle (1992) and later Paterson & Lamshead (1995) found

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similar patterns with total macrofauna and polychaetes.

The present study of 3 deep tropical regions with contrasting physical and trophic conditions was investigated as part of the EUMELI-JGOFS programme in the northeast Atlantic. It presents an opportunity to test for a bathymetric diversity gradient and to discuss potential processes which may maintain such a pattern. This study centres on polychaete assemblages which are the dominant taxon (Cosson et al. 1997). We focus on potential links between polychaete community structure and contrasting nutrient and physical regimes, particularly bottom currents, at this tropical latitude and examine our findings in the context of current deep-sea biodiversity theories.

## MATERIAL AND METHODS

**Study area.** The EUMELI-JGOFS programme centred on 3 sites in the tropical northeast Atlantic, off Mauritania (Fig. 1), sampled over 5 cruises between 1989 and 1992. These sites are subjected to contrasting trophic conditions resulting from different primary productivities in the euphotic layer (Table 1). The objectives of the benthic research focused on inter-related studies of the physical characteristics of the bottom nepheloid layer, chemistry of the surface of the sediments, structure of the benthic communities and flux of particulate matter to the water-sediment inter-

Table 1. Environmental data at the 3 EUMELI sites

	Eutrophic (1700 m)	Mesotrophic (3100 m)	Oligotrophic (4600 m)
Primary productivity <sup>a</sup> ( $\text{g C m}^{-2} \text{yr}^{-2}$ )	650	350	120
Calculated organic flux <sup>b</sup> ( $\text{g C m}^{-2} \text{yr}^{-2}$ )	6	1.8	0.36
Sedimentation rate <sup>c</sup> ( $\text{cm } 10^3 \text{yr}^{-1}$ )	4.4	1.5	0.5
Organic content sediment <sup>d</sup> (%)	2	0.39	0.29
Near-bottom mean current speed <sup>e</sup> ( $\text{cm s}^{-1}$ )	20	5	3

Data from <sup>a</sup>Morel et al. (1996), <sup>b</sup>Rabouille et al. (1993), <sup>c</sup>Auffret et al. (1992), <sup>d</sup>Khrpounoff & Crassous (unpubl. data), <sup>e</sup>this study

face (Sibuet et al. 1993). The topographical characteristics of the 3 sites were described by Auffret et al. (1992). CTD and nephelometry vertical profiles were obtained to describe the nepheloid structure during the EUMELI 2 cruise (Vangriesheim et al. 1993).

The oligotrophic site (O) was located on the Cape Verde abyssal plain (21° N, 31° W) at 4580 to 4647 m depth. The surface sediments were whitish, nanofossil oozes, deposited at a rate of  $0.5 \text{ cm } 10^3 \text{yr}^{-1}$ . No bottom nepheloid layer appears on the profiles (Vangriesheim et al. 1993).

The mesotrophic site (M) was located on the Cape Verde Terrace (19° N, 21° W) at 3095 to 3128 m depth. The nephelometry profiles displayed a slight bottom nepheloid layer 30 m thick. The surface sediments were greyish, marly, nanofossil oozes deposited at a rate of  $1.5 \text{ cm } 10^3 \text{yr}^{-1}$ .

The eutrophic site (E) was located at 1590 to 2041 m depth off Cap Blanc (21° N, 18° W). Over this area, the bottom nepheloid layer was strong and thick (>100 m).

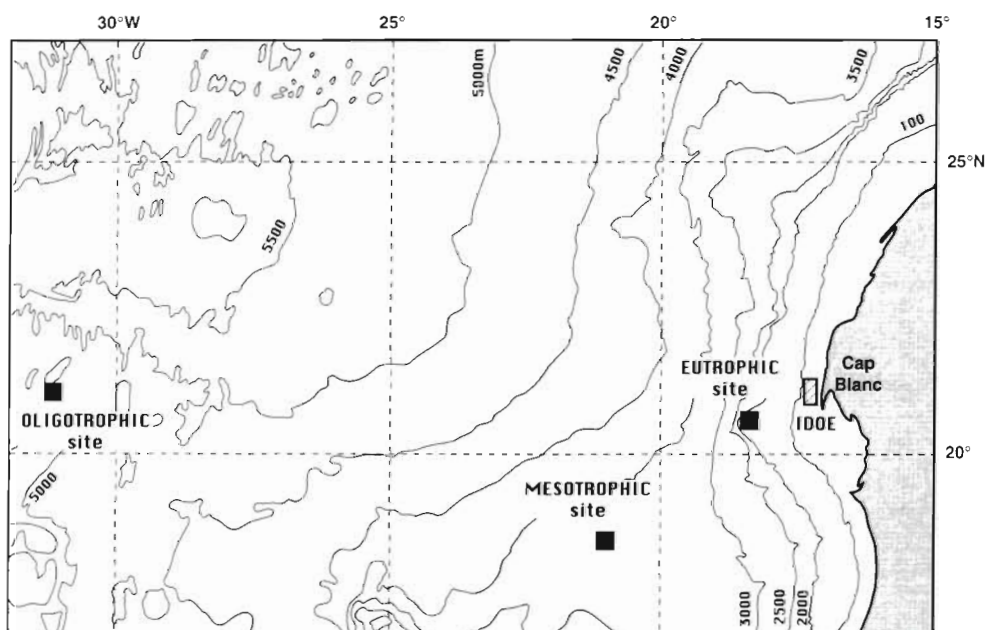


Fig. 1 Locations of the 3 EUMELI sampled sites, eutrophic (E), mesotrophic (M) and oligotrophic (O), in the tropical northeast Atlantic Ocean. The shallow IDOE station (Coastal Upwelling Ecosystem Analyses) from Nichols & Rowe (1977) is also shown. Depth contours in metres

There were also strong intermediate nepheloid layers at different depths and of varying thicknesses. The surface sediments consisted of greenish, marly, siliceous foraminifer and nanofossil oozes deposited at a rate of  $4.4 \text{ cm } 10^3 \text{ yr}^{-1}$ .

Several time-series of near-bottom currents have been obtained at the 3 sites. Those at Site E lasted only 2 d 3 h in July 1989, while those at Sites M and O lasted, respectively, 257 and 243 d from September 1991 to May 1992.

**Faunal sampling.** Faunal assemblages of polychaetes were studied from 14 box core samples, 5 at Site O, 5 at Site M and 4 at Site E, taken with an USNEL  $0.25 \text{ m}^2$  box corer. Once on board, the entire bioturbated sediment layer, which contains almost all the living organisms, was removed and preserved in 10% buffered formalin. This upper sediment layer is easily distinguished from the deeper anoxic and compact sediment. The bioturbated layer represented a thickness of about 3, 5 and 10 cm at stations O, M and E, respectively, which also reflects the variation of sedimentation rate between sites (Auffret et al. 1992). In the laboratory, the fauna was sieved through a  $250 \text{ }\mu\text{m}$  mesh, and taxa were sorted from the total sample by the team in charge of sorting. Each polychaete specimen was then identified to family and classified at least to genus and, if possible, lower. Taxonomic keys used in this study were diverse, ranging from Fauvel (1923, 1927), Fauchald (1977), George & Hartmann-Schröder (1987), to numerous papers on family and species keys. Individuals were classified into trophic groups according to the scheme proposed by Fauchald & Jumars (1979) but were modified as follows: carnivore/predator/omnivore species were considered as a single group (predators), sub-surface deposit feeders (SSD) included all burrowing motile and sessile species, and the surface-deposit-feeding group (SD) included the surface deposit feeders. Juveniles, without developed and distinct taxonomic characters, were excluded from the analysis.

**Analytical methods.** The structure of the polychaete community was analysed by a variety of methods. We calculated rarefaction curves of the expected number of species,  $E(S_n)$ , from polychaete assemblages using Hurlbert's (1971) method. Rarefaction is sensitive to rare species, an important component of deep-sea assemblages (Grassle & Maciolek 1992), and has the advantage of being robust to sample size differences. Species diversity within each trophic category was also calculated by using Hurlbert's method and compared a common number of  $n = 10$  individuals, because of the very low total abundance at the oligotrophic site. Other density and diversity data obtained near the coast in the same geographic area (Nichols & Rowe 1977) were also analysed, and subsequently all samples were compared using the Shannon-Wiener diversity index

( $H'$ , using  $\log_e$ ). Empirical rank-frequency diagrams are also presented to describe the species distribution within the community at each site (Frontier 1985, 1991). This method reveals the degree of evenness of species distribution by examining the shape of curves obtained. Comparison of faunal composition was assessed using the NNESS (Gallagher 1996) version of Grassle & Smith's (1976) normalised expected species shared.

## RESULTS

### Near bottom currents

At the 3 sites, the current is dominated by semi-diurnal (period of  $\sim 12 \text{ h}$ ), diurnal (24 h) and inertial oscillations (33.5 h at E and O, about 38 h at M). These oscillations affect the speed as well as the direction of the current. Histograms of the current speed values are shown in Fig. 2. Current velocities of between 22 and  $23 \text{ cm s}^{-1}$  were most frequent at Site E, between 5 and  $6 \text{ cm s}^{-1}$  at Site M, and at the rotor threshold at Site O, meaning that speeds were usually very low. Although the time series obtained at Site E were much shorter compared with those obtained at Sites M and O, it is clear that current speeds are much higher at this lower slope site. Mean speeds were 20, 5 and  $3 \text{ cm s}^{-1}$ , respectively, at Sites E, M and O.

Over longer time scales, the residual current (obtained after removing the tidal and inertial oscillations) also fluctuates (Khripounoff et al. in press). This probably has no direct consequence for the macrofauna, but may have indirect effects by influencing water mass transport and thus food supply.

### Patterns of abundance

The relationship between polychaete density and depth was analysed for all 14 box core samples, along with 5 van Veen grab samples from depths shallower than 500 m off Mauritania from Nichols & Rowe (1977). Fig. 3 shows that polychaete abundance declined linearly from shallow depths to the abyssal plain. In terms of total macrofauna, polychaetes accounted for 53% of the total number of individuals at E, 61% at M and 60% at O.

### Faunal composition

We collected a total of 3847 polychaetes from the 3 sites: 2086 at E, 1572 at M and 189 at O. A total of 131 species were identified representing 38 families. Total

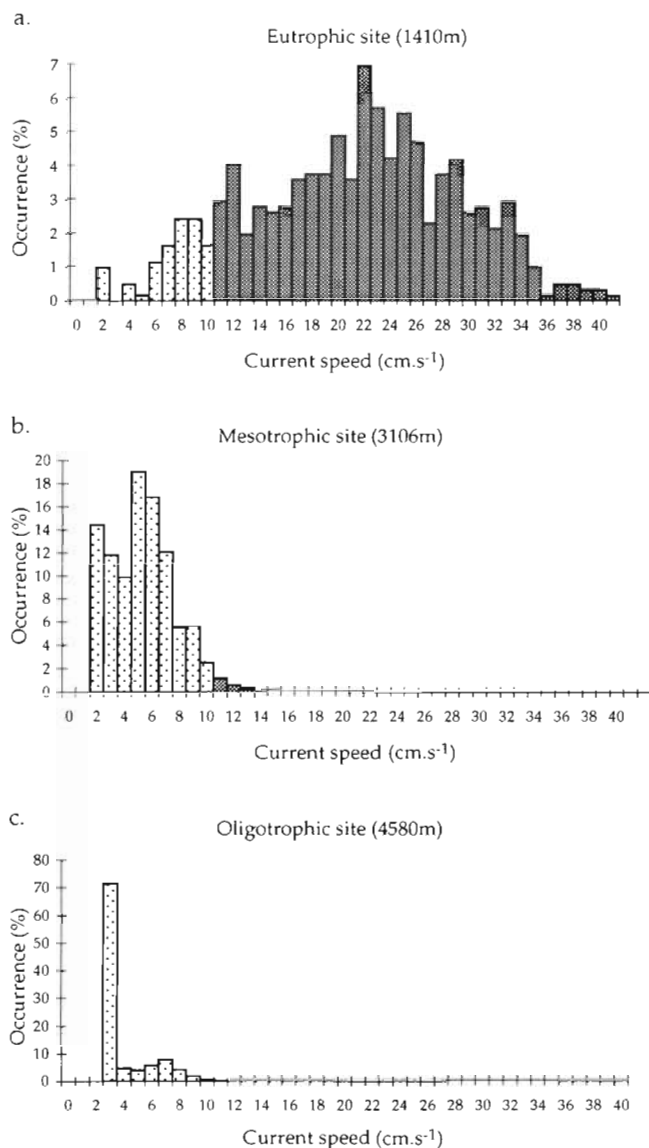


Fig. 2. Current speed histograms for the (a) eutrophic, (b) mesotrophic and (c) oligotrophic sites. For the eutrophic site measurements lasted only 2 d and 3 h, while for the mesotrophic and oligotrophic sites measurements lasted, respectively, 257 and 243 d. Velocities in excess of  $10 \text{ cm s}^{-1}$  (in dark grey) are capable of resuspending flocculent sediment

number of species was 124 at E, 80 at M and 39 at O. Table 2 indicates that 15 families represented 90, 91 and 96% of the total polychaete community at E, M and O, respectively. The Spionidae, Cirratulidae, Paraonidae and Syllidae were well-represented at all 3 deep-sea sites. Smith & Hessler (1987) considered species from the first 3 families to be opportunists. An analysis of the numbers of species in each family showed that the families Sigalionidae at Site M and Scalibregmidae at Site O accounted respectively for

6.4 and 8.2% of the polychaete community, but were represented by only 1 species (*Sthenelais* sp. at M and *Asclerocheilus* sp. 754 at O). Familial composition showed that the Cirratulidae and Spionidae were the dominant families at the deepest site. Trends along the bathymetric transect showed an increase in the rate of Cirratulidae from 1590 to 3128 m depth. No other families showed consistent trends. Species composition of the polychaete community is presented in Table 3. Among the dominant species, 4 were common at both O and M: 3 belonged to the Cirratulidae genera of *Tharyx*, *Chaetozone* and *Aphelochaeta* with the latter being dominant at O and M, and the fourth was a spionid. Three of these species were also found in lower proportion in the polychaete community at E; the exception was *Tharyx* sp. 424. At Site E the dominant species was *Magelona* sp.

Group-average clustering of NNESS (new normalized expected species shared) similarities indicated 3 major clusters (Fig. 4). The 3 sites segregate out clearly into 3 separate clusters at the 50% level of similarity. Intrasample similarity decreased with increasing depth. Within each cluster, level of sample similarity was variable. Faunal composition of the samples at Site E was very similar (95 to 97%). Samples from Sites M and O showed a greater variability in species composition (respectively 76 and 68%). This was particularly unexpected at Site O, where the diversity was lowest. NNESS analysis shows that the pattern of diversity is not, therefore, the result of an overlap of 2 polychaete assemblages. The different clusters observed along the bathymetric gradient (Fig. 4) reflect biotic and abiotic factors specific to each site. Site M was characterised by a relatively high density of Sigalionidae, which were completely absent at Sites E and O. The presence of these carnivorous polychaetes may be linked to the abundant population of xenophyophores observed at this site and which is estimated at  $3 \text{ ind. m}^{-2}$  (Sibuet et al. 1993). Fauchald & Jumars (1979) reported that deep-water Sigalionidae may feed mainly on protozoa (like foraminiferans). Changes in dominance (Table 3) support the idea that bathymetric zonation was probably induced by environmental conditions occurring at this lower slope site. Auffret et al. (1992) described Site E as a gently sloping sedimentary spur with a remarkably smooth topography, perhaps explaining the high similarity between different samples taken as far apart as 10 km within this site. Site O is subjected to gravitational reworking, which creates diverse sedimentary facies given the low sedimentation rate (Auffret pers. comm., Table 4). This model of environmental heterogeneity favours colonization by different species pools associated with the patches that the different substrata create.

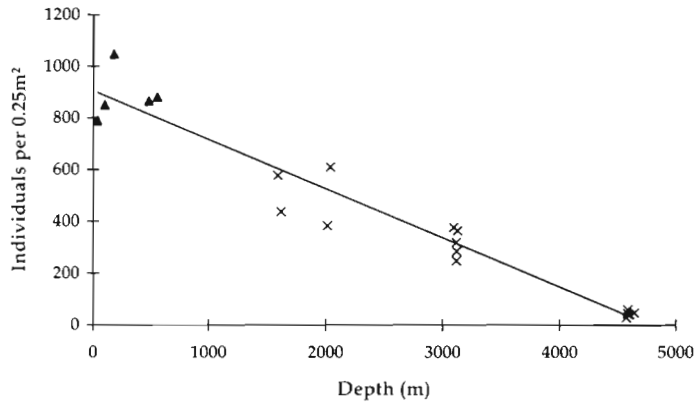


Fig. 3. Polychaete abundance versus depth. Bathymetric trend shows a significant linear decline with depth:  $y = -0.189x + 904.98$ ,  $r^2 = 0.9384$ ,  $F = 45.76$ ,  $p < 0.001$ ,  $n = 19$ . (▲) Data from Nichols & Rowe (1977), van Veen samples adjusted to give abundance per  $0.25 \text{ m}^2$ ; (x) Eumeli sites E, M, and O from this study

### Species diversity of polychaete community

In both the deep-sea and coastal environments, obtaining an accurate estimate of the number of species present at local scales is problematic. The method used here takes into account the low spatio-temporal heterogeneity of macrofauna at a local scale which exists in the deep-sea compared to coastal zones. Therefore, for each station we first determined the sampling efficiency for all taxa. For polychaetes, significant mean density can be achieved with only 2 box cores, i.e.  $0.5 \text{ m}^2$  (Cosson et al. 1997). Thus the sampling effort carried out with 5 samples at Site O, 5 at Site M and 4 at Site E during the deep-sea EUMELI programme allowed a significant estimation

of the faunal density. Secondly, species accumulation curves indicated that 96% of species were collected at E with 2 boxcores and at both M and O with 3 boxcores. This suggests that polychaete assemblages were adequately sampled by 4 boxcores from each site.

Sample species diversity ( $\alpha$  diversity), measured using Hurlbert's rarefaction (1971), showed clear differences between the sites (Fig. 5a): diversity curves show a marked and progressive decrease between the eutrophic, mesotrophic and oligotrophic sites. Curves from Site O are detailed in Fig. 5b, highlighting the low species diversity and abundance at this site.

EUMELI data were complemented by data ( $H'$ ) obtained by Nichols & Rowe (1977) with a smaller sampler (van Veen grab) within the same geographic zone in shallower waters and utilising a  $420 \mu\text{m}$  mesh. During the systematic study of those organisms retained on a  $250 \mu\text{m}$  mesh, it was ascertained that many were juveniles and so were not considered in this study. On a larger mesh size the proportion of juveniles retained is lower. According to Coleman et al. (1997), moving from a smaller to a larger mesh is likely to reduce the number of individuals rather than the number of species. Hessler & Jumars (1974) suggested that for upper bathyal sites a  $420 \mu\text{m}$  sieve mesh was appropriate, while a lower mesh size, i.e.  $297 \mu\text{m}$ , was needed to capture the equivalent faunal elements in abyssal sites. This, they argued, was because macrofaunal individuals decreased in size with depth. It is possible that the smaller sample area of the van Veen grab may result in a lower diversity. However, given the high abundance observed by Nichols & Rowe (1977), we

Table 2. Dominant polychaete families and their contribution to the polychaete community (%p) and to the total macrofauna (%m) recorded from the 3 EUMELI sites. S: number of species

Eutrophic site (1700 m)				Mesotrophic site (3100 m)				Oligotrophic site (4600 m)			
	%p	S	%m		%p	S	%m		%p	S	%m
Spionidae	17.7	13	6.4	Cirratulidae	26.4	8	17.7	Cirratulidae	25.0	3	15.5
Paraonidae	14.4	9	5.2	Spionidae	18.5	10	12.4	Spionidae	19.1	4	11.8
Syllidae	8.8	8	3.2	Sigalionidae	6.4	1	4.3	Scalibregmidae	8.2	1	5.1
Cirratulidae	7.2	8	2.6	Paraonidae	6.1	6	4.1	Syllidae	6.9	2	4.3
Capitellidae	5.9	5	2.1	Syllidae	6.0	4	4.1	Ampharetidae	6.6	2	4.1
Dorvilleidae	5.8	8	2.1	Capitellidae	5.5	4	3.7	Sabellidae	6.0	1	3.7
Ampharetidae	5.6	7	2.0	Lumbrinereidae	4.8	4	3.2	Paraonidae	5.7	1	3.5
Ophelidae	5.0	2	1.8	Sabellidae	3.2	3	2.1	Goniadiidae	5.3	1	3.3
Magelonidae	4.9	2	1.8	Ampharetidae	2.8	4	1.9	Ophelidae	3.8	1	2.4
Nephtyidae	4.9	2	1.8	Ophelidae	2.8	1	1.9	Nereidae	2.4	1	1.5
Terebellidae	3.0	4	1.1	Flabelligeridae	2.6	1	1.7	Dorvilleidae	2.4	1	1.5
Lumbrinereidae	2.5	4	0.9	Phyllodocidae	2.5	2	1.7	Glyceridae	2	1	1.2
Scalibregmidae	2.3	3	0.8	Nereidae	1.7	1	1.2	Flabelligeridae	1.8	1	1.1
Owenidae	1.9	3	0.7	Maldanidae	1.5	2	1.0	Nephtyidae	1.4	1	0.9



Table 3. Dominant polychaete species and their contribution to the polychaete community (%p), and to the total macrofauna (%m) recorded from the 3 EUMELI sites

Eutrophic site (1700 m)				Mesotrophic site (3100 m)				Oligotrophic site (4600 m)			
Species		%p	%m	Species		%p	%m	Species		%p	%m
<i>Magelona</i>	sp. 415	4.6	1.8	<i>Aphelocheata</i>	sp. 55	11.2	7.5	<i>Aphelocheata</i>	sp. 55	8.9	5.8
<i>Aricidea</i>	<i>longobranchiata</i>	3.9	1.5	<i>Sthenelais</i>	sp.	6.4	4.3	<i>Tharyx</i>	sp. 424	8.6	5.7
<i>Nephtys</i>	<i>sphaerocirrata</i>	3.9	1.5	<i>Prionospio</i>	sp. 13	5.3	3.6	<i>Asclerocheilus</i>	sp. 754	8.2	5.1
<i>Paraonnella</i>	sp.	3.8	1.5	<i>Chaetozone</i>	sp. 753	4.6	3.1	<i>Chaetozone</i>	sp. 755	6.5	4.3
<i>Dorvillea</i>	<i>rudolphi</i>	3.4	1.3	<i>Prionospio</i>	sp. 752	4.3	2.9	<i>Prionospio</i>	sp. 752	6.3	4.2
<i>Prionospio</i>	sp. 612	3.2	1.2	<i>Tharyx</i>	sp. 424	3.7	2.4	<i>Fabriciella</i>	<i>filamentosa</i>	5.5	3.6
<i>Trachytirypa</i>	sp.	3.1	1.2	<i>Capitella</i>	sp. 422	3.4	2.3	<i>Ancidea</i>	sp. 752	5.5	3.6
<i>Prionospio</i>	sp. 13	3.1	1.2	<i>Aphelocheata</i>	sp. 766	3.2	2.2	<i>Goniada</i>	sp. 52	5.1	3.3
<i>Exogone</i>	sp. 427	3.0	1.2	<i>Prionospio</i>	<i>pausipinnulata</i>	3.1	2.1	<i>Prionospio</i>	sp. 612	4.5	2.9
<i>Prionospio</i>	sp. 732	2.7	1.0	<i>Lumbrineris</i>	<i>aberrans</i>	2.6	1.7	<i>Prionospio</i>	cf. <i>fauchaldi</i>	4.0	2.6
<i>Prionospio</i>	<i>pausipinnulata</i>	2.6	1.0	<i>Trachytirypa</i>	sp.	2.4	1.6	<i>Ophelia</i>	<i>profunda</i>	3.8	2.5
<i>Chaetozone</i>	sp. 755	2.6	1.0	<i>Exogone</i>	sp. 759	2.4	1.6	<i>Flabelligella</i>	sp. 742	3.6	2.3
<i>Ampharete</i>	sp. 419	2.4	0.9	<i>Exogone</i>	sp. 1	2.2	1.5	<i>Exogone</i>	sp. 427	3.0	2.0
<i>Exogone</i>	sp. 759	2.4	0.9	<i>Flabelligella</i>	<i>affinis</i>	2.2	1.5	<i>Amphicteis</i>	cf. <i>gunneri</i>	2.4	1.6
<i>Aricidea</i>	sp. 751	2.3	0.9	<i>Aricidea</i>	<i>longobranchiata</i>	2.0	1.4	<i>Ceratocephale</i>	sp. 28	2.4	1.5
<i>Aphelocheata</i>	sp. 55	1.9	0.7	<i>Prionospio</i>	sp. 612	1.8	1.2	<i>Prionospio</i>	sp. 13	2.3	1.5
<i>Ophelia</i>	<i>profunda</i>	1.9	0.7	<i>Tharyx</i>	sp. 423	1.8	1.2	<i>Ampharete</i>	sp. 419	2.2	1.5
<i>Notomastus</i>	<i>aberrans</i>	1.9	0.7	<i>Ceratocephale</i>	sp. 28	1.7	1.2	<i>Exogone</i>	sp. 759	2.2	1.5
<i>Capitella</i>	sp. 422	1.8	0.7	<i>Asclerocheilus</i>	sp. 754	1.7	1.1	Unidentified	Glyceridae	2.0	1.3
<i>Asclerocheilus</i>	sp. 754	1.8	0.7	<i>Pseudomystides</i>	sp. 655	1.6	1.0	<i>Amage</i>	sp.	1.7	1.1
<i>Owenia</i>	sp.	1.6	0.6	<i>Laonice</i>	sp.	1.5	1.0	<i>Protodurvillea</i>	<i>minuta</i>	1.7	1.1
<i>Cossura</i>	sp.	1.2	0.5	<i>Fabriciella</i>	<i>filamentosa</i>	1.5	1.0	<i>Flabelligella</i>	<i>affinis</i>	1.7	1.1
<i>Scolelepis</i>	sp.	1.2	0.5	<i>Aphelocheata</i>	sp. 13	1.3	0.9	<i>Nephtys</i>	cf. <i>sphaerocirrata</i>	1.5	1.0
<i>Ampharete</i>	sp.	1.1	0.4	<i>Euchone</i>	sp. 43	1.3	0.9	<i>Prionospio</i>	sp.	1.4	0.9
<i>Spiophanes</i>	sp.	1.1	0.4	<i>Exogone</i>	sp. 427	1.3	0.8	<i>Sphaerosyllis</i>	sp.	1.4	0.9

would expect this to be reflected in the diversity analysis. It is not clear whether sample diversity would necessarily have risen were sample area increased.

Therefore, a diversity comparison was made between the 4 sites, calculating diversity using Shannon's

index to homogenise the total data pool (Fig. 6, see caption for equation and associated *F*-value). The resulting pattern shows a parabolic distribution from the coast to the abyssal plain with the maximum diversity occurring at about 2000 m depth.

We conducted a trophic analysis on those groups with sufficient abundance: SD and SSD feeders and carnivores/predators. SD was the most abundant trophic group (about 60% at the 3 sites), followed by the predators at approximately 25% at the E and M sites (Table 4). Analysis of species diversity of each trophic group at each site showed a similar trend, with the highest diversity found for the SD feeders and the lowest for the SSD feeders or burrowers (Fig. 7a, b, c). A comparison between sites showed a decrease of species richness with depth for all 3 trophic categories, but which was more accentuated for the SSD feeders, which were absent at Site O (Fig. 7d, see caption for equations and associated *F*-values).

Frontier & Pichod-Viale (1991) commented that the shape of the rank-frequency curves, as shown in Fig. 8, gives precise information on the distribution of individuals among species. At the eutrophic and mesotrophic sites, curves are convex and extended, confirming a high species diversity with a relatively even distribution of the species. At the oligotrophic site, the curve indicates a lower species diversity but a high evenness.

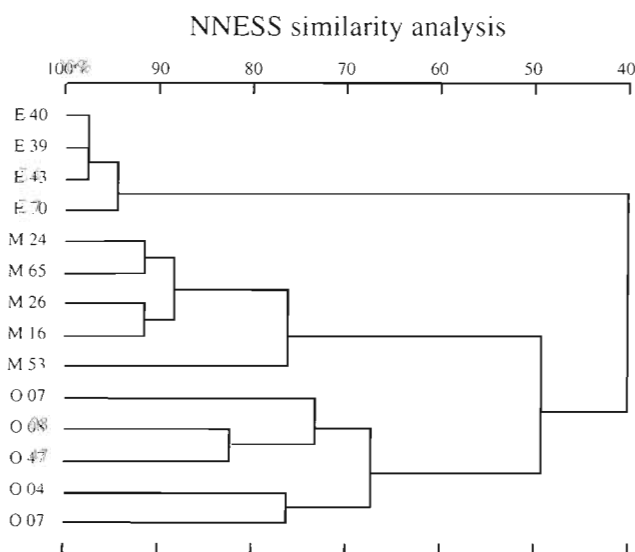


Fig. 4. New normalized expected species shared (NNESS) analysis of polychaete species composition of EUMELI box cores from 3 sites, E, M and O

Table 4. Trophic structure of the polychaete community at the 3 EUMELI sites

	Oligotrophic	Mesotrophic	Eutrophic
Surface deposit feeders (%)	68.8	60	56.1
Sub-surface deposit feeders (%)	16.6	10	18.8
Predators (%)	14.6	28.6	24.6
Filter feeders (%)	–	1.4	0.5

## DISCUSSION

### Polychaete abundance

The decrease in the abundance of polychaetes, the major macrofaunal taxon, among the 3 sites followed not only the bathymetric gradient as shown by Pater-son et al. (1994), but also reflected variation in the

trophic resource. Indeed the near-bottom organic carbon flux calculated from a model that accounts for the diagenetic reactions and transport processes (Rabouille et al. 1993) was  $6 \text{ g C m}^{-2} \text{ yr}^{-1}$  at Site E,  $1.8 \text{ g C m}^{-2} \text{ yr}^{-1}$  at Site M and  $0.36 \text{ g C m}^{-2} \text{ yr}^{-1}$  at Site O (Table 4). At Sites O and M, these calculated values are very close to those of the actual flux (Khrpounoff unpubl.). At Site E, we estimate that the calculated flux may be slightly lower than the actual flux reaching the sediment surface because of resuspension by currents. A positive linear relationship was observed between these values of organic carbon flux and the density of the total macrofauna (Cosson et al. 1997). Polychaete mean density seems to follow this general pattern. Nevertheless, the ratio of polychaete density between 2 stations and the ratio of calculated flux between the

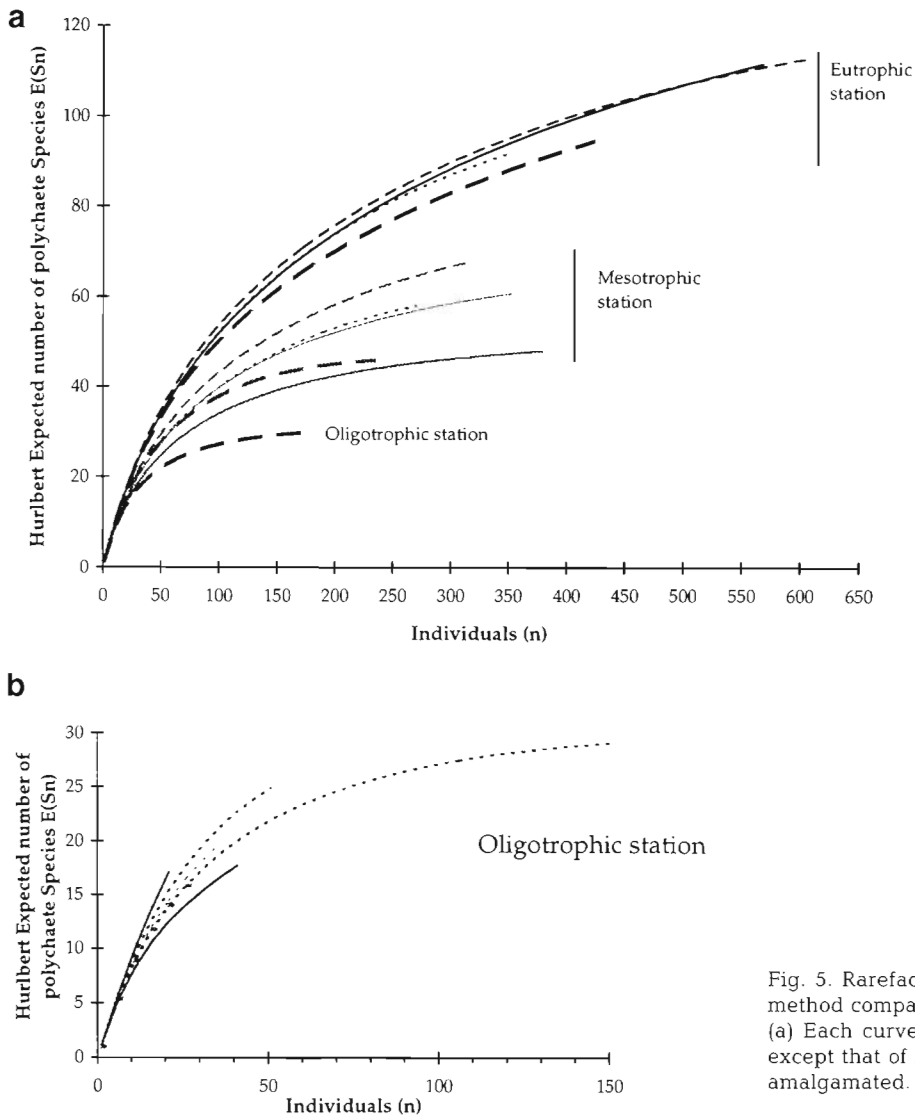


Fig. 5. Rarefaction curves plotted using Hurlbert's method comparing diversity at the 3 EUMELI sites. (a) Each curve is obtained from a single box core except that of Site O for which the 4 samples were amalgamated. (b) Individual diversity curves from box cores from site O

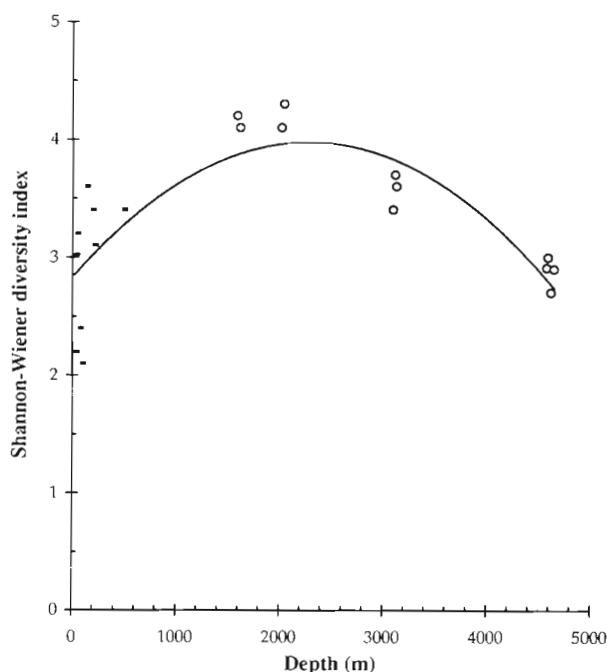


Fig. 6. Comparison of species richness using Shannon-Wiener's index from the coast to abyssal depths ( $y = -2 \times 10^{-7}x^2 + 0.001x + 2.83$ ,  $r^2 = 0.65$ ,  $F = 46.18$ ,  $p < 0.001$ ,  $n = 23$ ). (■) Data from Nichols & Rowe (1977); (○) data from this study

same stations were, respectively, 7.6 and 5 between M and O and 1.6 and 3.3 between E and M, showing that polychaetes respond to an increased food supply with increased abundance, as suggested by Sibuet (1987) and Sibuet et al. (1989). At Site O, the benthos appeared to be indicative of an abyssal plain lying beneath oligotrophic surface waters. By contrast, the high abundance noted for Site E appeared to be related to the upwelling system (Sibuet et al. 1993). The upwelling and the relatively high organic carbon flux were probably responsible for the higher abundances noted at E and M compared with sites at similar depths in Rockall Trough (Paterson 1993, Rice & Lamshead 1994) and the western Atlantic (Blake & Grassle 1994).

### Faunal diversity related to environmental factors

#### Trophic diversity

Of the 3 trophic groups analysed, only the predator group showed a trend similar to the overall species diversity pattern. Dayton & Hessler (1971) and more recently Rex (1983) suggested that predation may be important in maintaining diversity. It could be argued that the increased productivity from upwelling activity

at Sites E and M provided the opportunity for a greater range of species including predators to co-exist. Predators may contribute to community organization by reducing competition, resulting in the coexistence of species requiring the same trophic resource.

The rapid decline with depth in burrowing species may be linked to a decrease in productivity and the amount of material being bioturbated into the sediment. The higher overall organic carbon flux and organic carbon in the sediments at Site E may provide a greater opportunity for sub-surface foraging. However, at Site O there is very little sub-surface organic carbon (Georg Wolff pers. comm.), with only 29% in the first millimeters (Table 1). The opportunity to forage beneath the sediment is, therefore, limited, and this is reflected in vertical distribution of the fauna, which is restricted to the top 0 to 1 cm layer (G.L.J.P. pers. obs.). Burrowing species may well be unable to survive, while the limited resources have a lesser impact on the SD feeders.

#### Species diversity patterns

The observed polychaete diversity pattern as shown by the Shannon-Wiener index in this tropical zone (Fig. 6) supports findings that diversity patterns in the sea are complex and that they follow a parabolic trend with depth (Rex 1983, Etter & Grassle 1992, Paterson & Lamshead 1995). Comparison with other studies indicates that there is geographic variation in the depth at which the maximum species diversity occurs. For the Gay Head Bermuda transect, the highest diversity occurred between 2000 and 3000 m (Rex 1983), for a transect on the Hebridean slope it was near 1600 m (Paterson & Lamshead 1995), while for our samples in the tropical Atlantic, the diversity peak occurred between 1700 and 2000 m depth (Fig. 6). This points to regional differences in what might be a basic diversity pattern.

We also observed a parabolic relation between the surface productivity estimate and species diversity (Fig. 9, see caption for equation and associated  $F$ -value). Surface productivity could be crudely related to faunal production, which suggests that production has an important influence on polychaete diversity. The important contingent of species of medium abundance observed at the eutrophic and mesotrophic sites indicated, according to Frontier's (1985) suggestion, a mature biological system with a complex food web favouring high trophic levels. We suggest that decreasing species diversity, from highest values at 1700 m depth to lesser values at 4600 m depth, corresponds to a decrease in the structural complexity of the ecosystem.



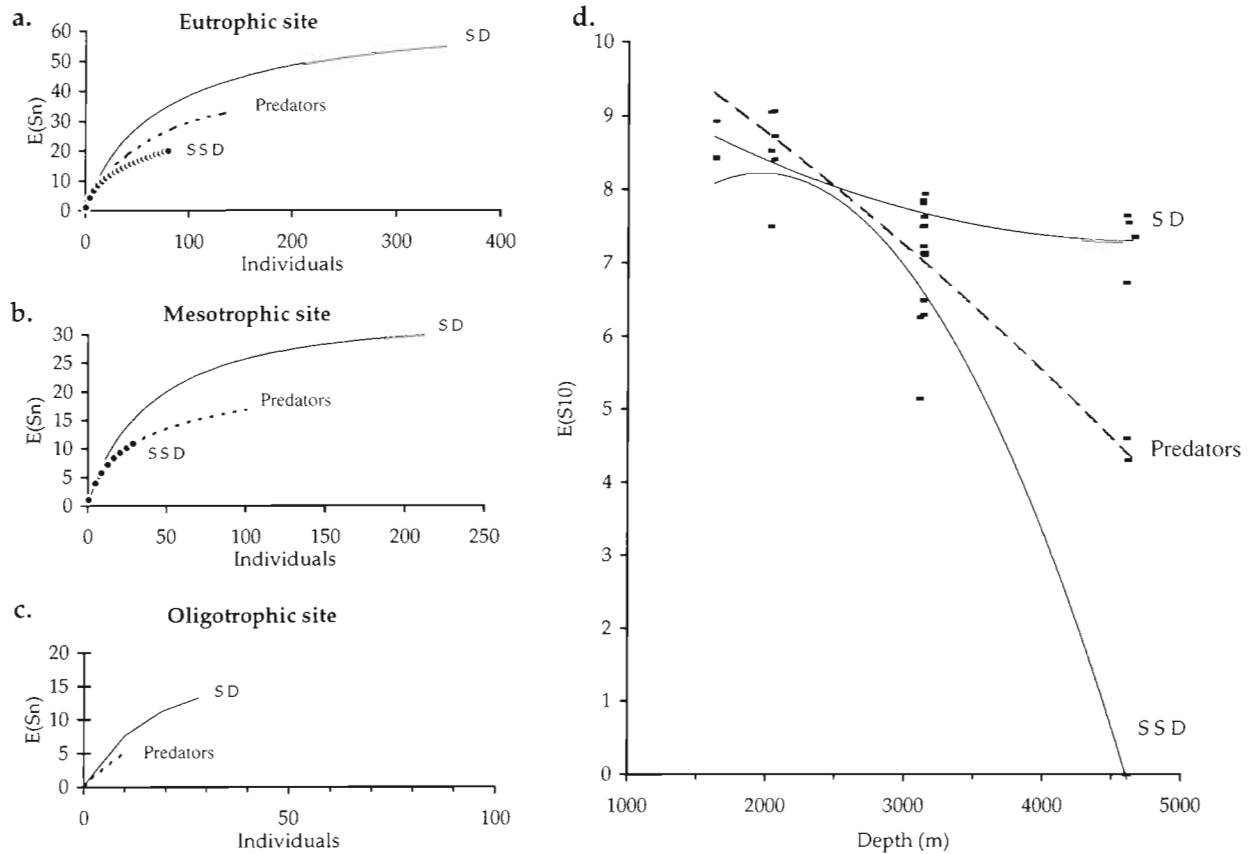


Fig. 7. Rarefaction curves comparing trophic diversity at (a) eutrophic, (b) mesotrophic and (c) oligotrophic sites. (d) Comparison of species diversity of trophic groups, standardised to the expected number of species in a subsample of 10 individuals [ $E(S_{10})$ ]. Trophic groups were assigned as predators, surface deposit feeders (SD) and sub-surface deposit feeders (SSD). (Predators:  $y = -0.0017x + 12.14$ ,  $r^2 = 0.9242$ ,  $F = 27.18$ ,  $p < 0.01$ ,  $n = 10$ ; SD:  $y = -0.0004x + 9.17$ ,  $r^2 = 0.644$ ,  $F = 26.52$ ,  $p < 0.05$ ,  $n = 11$ ; SSD:  $y = 10^{-6}x^2 + 0.046x + 3.6782$ ,  $r^2 = 0.94$ ,  $F = 27.56$ ,  $p < 0.01$ ,  $n = 8$ )

#### Comparison of observed diversity pattern with predictions from existing theories

Two major physico-chemical bathymetric gradients are present within the EUMELI region. The first is an obvious decline in current energy with depth, which is accompanied by a decline in the frequency of current speeds in excess of  $10 \text{ cm s}^{-1}$ , the minimum speed considered necessary to mobilise flocculent sediment (Rhoads & Young 1970) (Fig. 2). At Site E current speeds were most frequently in excess of  $10 \text{ cm s}^{-1}$ , with a mean velocity of  $23 \text{ cm s}^{-1}$ , but at M and O speeds rarely exceed this value. The second obvious gradient is a decline in productivity with increasing distance from coastal upwelling; this decline is reflected in the estimates of organic carbon flux into the sediment (Rabouille et al. 1993). At Site E, the esti-

mated flux,  $6 \text{ mg C m}^{-2} \text{ yr}^{-1}$ , is nearly 20 times that estimated from Site O,  $0.36 \text{ mg C m}^{-2} \text{ yr}^{-1}$ .

There are 3 main theories whose predictions can be tested with our data: the intermediate disturbance theory (Connell 1978), intermediate productivity theory

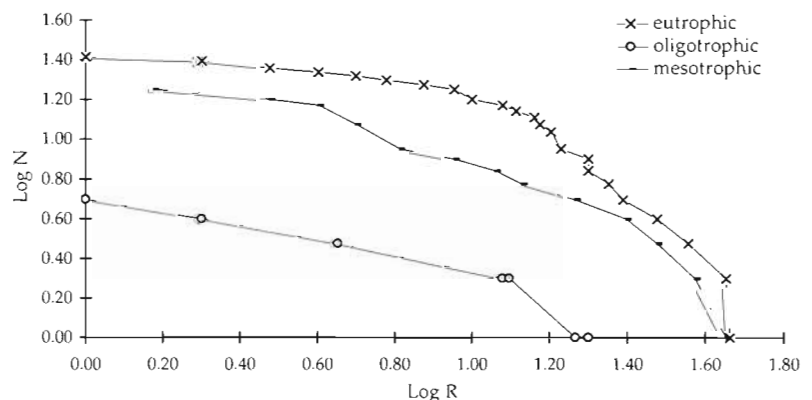


Fig. 8. Rank-frequency distribution of polychaete assemblages at the 3 EUMELI sites. R: rank of species; N: no. of individuals

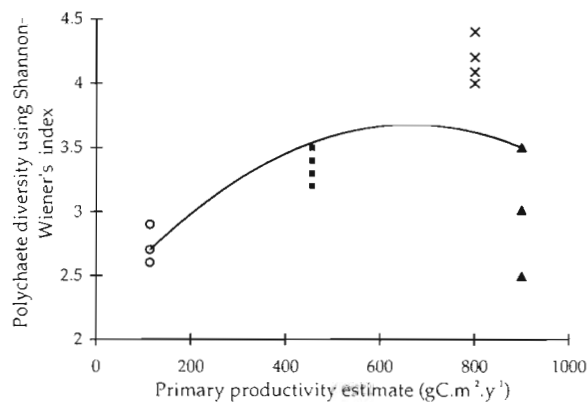


Fig. 9. Relationship between polychaete diversity estimated using  $H'$   $\log_2$  and surface primary productivity estimates ( $\text{g C m}^{-2} \text{ yr}^{-1}$ ). Equation regression:  $y = -5 \times 10^{-6}x^2 + 0.0049x + 2.5109$ ,  $r^2 = 0.598$ ,  $F = 27.583$ ,  $p < 0.01$ ,  $n = 16$ . (x) Eutrophic site; (■) mesotrophic site; (○) oligotrophic site; (▲) data from Nichols & Rowe (1977)

(Grimes 1973, 1979) and the dynamic equilibrium theory, which looks at the relationship between the frequency of disturbance and rates of competitive displacement or productivity (Huston 1979, 1994). It should be noted that predictions from these theories are not necessarily mutually exclusive.

#### Intermediate disturbance

The theory predicts that, along a gradient of increasing disturbance, diversity will be highest at some intermediate level. Fig. 10 shows how diversity varies with current speed, appearing to show agreement with predictions from the theory. However, mean velocities at M were below the minimum disturbance threshold and the frequency of speeds in excess of  $10 \text{ cm s}^{-1}$  was approximately 5%. Paterson & Lamshead (1995) used the frequency of currents in excess of  $15 \text{ cm s}^{-1}$  as their threshold for disturbance following findings of McCave (1984). If these more conservative figures are used then there is little difference in disturbance regime between M and O. The results of the similarity analysis provide circumstantial evidence that the intermediate disturbance theory is not applicable. At Site E there was high intersample similarity, indicating little patchiness in the faunal composition at the scale of the sampler. Also, bottom photographs suggest that the site is physically homogeneous at the macroscale. This implies that the area is impacted by large-scale disturbance. Paterson & Lamshead (1995) and Thistle et al. (1985, 1991) found that polychaete diversity was low in regions of high physical disturbance.

Certainly in Rockall, at sites where the frequency of high speed currents was comparable with EUMELI sites, diversity was lower than found at Site E. Finally, the composition of the fauna suggests that disturbance is not necessarily the only structuring agent. In Rockall, Paterson & Lamshead (1995) noted that opportunist species, particularly those belonging to the family Spionidae, were most abundant, even dominant, in sites where there was a high frequency of high speed currents. Within Site E, such opportunists were not particularly dominant, and the percentage occurrence of the first 5 families was fairly similar (Table 2). We suggest that the impact of disturbance from currents is mitigated by other factors. The most obvious candidate is the relatively high levels of organic matter deposited within Site E.

#### Intermediate productivity theory

Grimes (1973, 1979) proposed this theory to describe patterns of diversity in terrestrial plant communities. However, this theory can be applied to any productivity gradient. Predictions from the theory suggest that within the EUMELI region diversity would increase from the area of coastal upwelling, reaching a peak at some intermediate level, before declining with increasing depth. The theory suggests that intermediate levels of productivity would allow species to co-exist longer and thus reduce competitive displacement. Certainly, the diversity gradient in this tropical region appears to follow these predictions. We speculate that the enhanced productivity at E overcomes the influence of physical and biological disturbance. Neverthe-

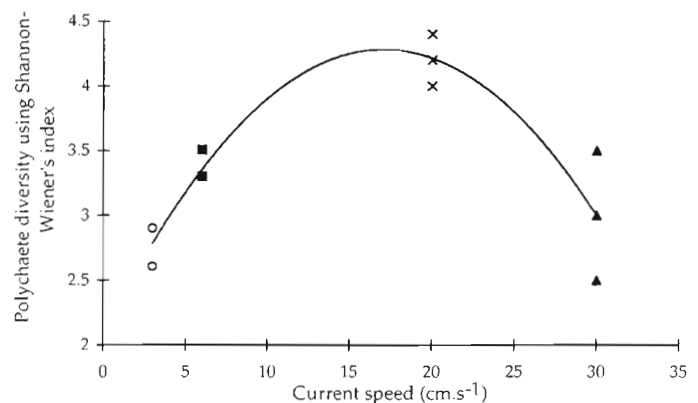


Fig. 10. Relationship between polychaete diversity estimated using  $H'$   $\log_2$  and the rate of the mean speeds of current. Regression equation:  $y = -0.0076x^2 + 0.259x + 2.0783$ ,  $r^2 = 0.8322$ ,  $F = 48.597$ ,  $p < 0.001$ ,  $n = 10$ . (x) Eutrophic site; (■) mesotrophic site; (○) oligotrophic site; (▲) data from Nichols & Rowe (1977) and current data from Thiel (1978)

less, disturbance is a factor in the community structure of the upper sites. We therefore decided to test predictions from the third theory in relation to our data.

### Dynamic equilibrium theory

Given the interaction of productivity and disturbance at our sites, particularly Site E, Huston's theory (1994) should provide a useful conceptual framework for investigating how diversity might be affected by these 2 factors (Fig. 11). The dynamic equilibrium theory predicts that diversity will be highest when rates of competitive displacement are intermediate to low and when the frequency of disturbance is similarly intermediate to low. Productivity can be used as a surrogate for rates of competitive displacement (Huston 1994). Comparing these predictions to our results suggests that Site E, the most diverse, should exhibit intermediate to low rates of productivity and disturbance. However, disturbance frequency was appreciably higher than intermediate for our gradient and, similarly, estimates of productivity were at the intermediate levels for this region (Fig. 11). Applying our results to the 'diversity hill' of the model would mean redrawing the diversity contours or re-scaling the axes. Our results illustrate some of the problems in applying the dynamic equilibrium theory, the main drawback being in defining the axes. What constitutes high and low for a set of circumstances? In particular, are such values necessarily the full range likely to be encountered? Similarly, the diversity hill is a representative rather than a definitive scale, so the contours in Huston's diagrams serve as a guide. Even if quadrats within the graphed area are used instead, we are still unable to reconcile the predictions with our results.

This study, nevertheless, is consistent with the view that the interaction between productivity and the frequency of disturbance is complex. Polychaete communities would appear to have a high diversity in areas where there is an intermediate level of productivity coupled with moderate to frequent widespread disturbance. Also, data and observations from our sites may suggest that there is a mismatch between sample size and the scale at which processes are operating. The lack of total agreement with the 3 models above suggests that a more detailed experimental programme is needed along a bathymetric gradient.

### CONCLUSION

The polychaete diversity pattern observed here results from interactions of both physical and biological processes characteristic of the deep tropical region.

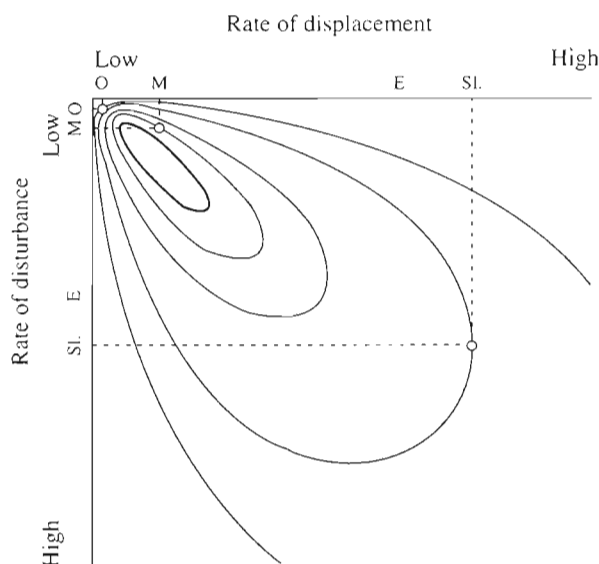


Fig. 11. Comparison of the diversity pattern observed and that predicted by the dynamic equilibrium theory from Huston (1979, 1994). Curves indicate diversity values. The values of both the rates of disturbance and displacement are suggested for the oligotrophic (O), mesotrophic (M), and eutrophic (E) sites and at an upper slope (Sl.) site. The dynamic equilibrium theory adequately predicts diversity for 3 of the sites (O, M, Sl.), but not for Site E, which presents the highest diversity. According to the Huston graphic the highest diversity (thick contour) should correspond to the situation exhibiting intermediate to low rates of productivity and disturbance. But at the Site E, the disturbance and the estimate of productivity are clearly higher than this

Polychaete species richness was markedly higher than at comparable deep areas, and declined after reaching a peak at about 2000 m depth. At the bathyal site (1700 to 2000 m depth), which was characterised by a steady-state regime, high diversity appeared to be maintained by relatively high physical disturbance combined with high productivity. The low diversity observed at the abyssal site is explained by poor food resources coupled with low environmental disturbance resulting in low growth rates and low rates of competitive displacement. This study confirms Paterson & Lambhead's (1995) suggestion that processes which create diversity patterns are different and likely to be locality-specific, and possibly taxon specific. Rex & Waren (1982) and more recently Etter & Caswell (1995) reported that disturbance conditions occurring above 2000 m, like those at Site E, may impose a physical constraint on the biota, favouring species with non-planktotrophic larval development modes. An innovative approach taking into account life cycle characteristics of the community would certainly improve our knowledge of the role of biodiversity in deep ecosystem functioning.

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