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**Are Arctic soft-sediment macrobenthic communities impoverished?**

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**Abstract** Samples of the macrobenthic fauna of soft sediments were collected from around Svalbard during the 1991 Arctic EPOS cruise of RV *Polarstern*. Although faunal variability could be related to sediment granulometry and depth, all stations to the south and east of the Archipelago lay within the broadly defined central Barents Sea community. In this community,  $\alpha$ -diversity was variable and sampled between 77 and 337 m showed no clear relationship to depth. Diversity in the area close to the polar front was notably high, rarefaction predicting that  $43 \pm 5.5$  species might occur in a sample of 201 individuals. *k*-Dominance plots suggested that muddy sand communities around Svalbard were no less diverse than similar assemblages in the North Sea.

**Introduction**

It is generally accepted that high-latitude communities are less diverse than those closer to the equator. While such latitudinal gradients have been identified in almost all communities that have been investigated on land and in the sea (Rohde 1992), it is not clear if such a pattern of variation exists in the soft sediment macrobenthos of shelf waters (Clarke 1992). Thorson (1957) claimed that there were approximately the same number of species in the soft sediments of tropical and polar regions and this conclusion was supported by Richardson and Hedgepeth (1977). However, Sanders (1968) asserted that he could detect a clear latitudinal diver-

sity gradient off the eastern coast of North America. Unfortunately, the original data on which these conclusions are based are unsuitable for re-evaluation in view of the lack of consistency in the sampling methods that were used to collect them (Abele and Walters 1979a, 1979b; Warwick and Ruswahyuni 1987; Clarke 1992). As a result, Warwick and Ruswahyuni (1987) advocated the collection of a new, fully comparable data set and began the process by contrasting data from the North Sea and Java. Plymouth Marine Laboratory (PML) has undertaken to further the comparison by collecting such information whenever suitable opportunities arise.

During 1990, as part of this PML study, a data set was collected from a fjord on the west coast of Spitsbergen (Kendall and Aschan 1993). The diversity of the assemblages encountered did not differ significantly from those inhabiting similar substrata at similar depths in Java (7°S) or the North Sea (55°N). This observation appeared to support the argument that maintains that high-latitude assemblages are not impoverished. However, as sampling was only from a single fjord on the warmer coast of Spitsbergen, some concern was raised concerning how representative the results were of the Arctic in general. This emphasised the need to replicate sample sites longitudinally in any latitudinal diversity study. A chance to carry out such replication within the waters around Svalbard in the western Barents Sea came with the Arctic EPOS cruise of RV *Polarstern*.

**Materials and methods**

Samples were taken at the positions shown in Fig. 1; details of their depths and sediments are provided in Table 1. It was originally intended to sample only muddy sites at depths shallower than 200 m in order to conform with the study of latitudinal diversity in soft sediments begun by Warwick and Ruswahyuni (1987) and continued by Kendall and Aschan (1993). In practice, this did not prove possible, and only stations 117 (sandy mud) and 136 (muddy sand)

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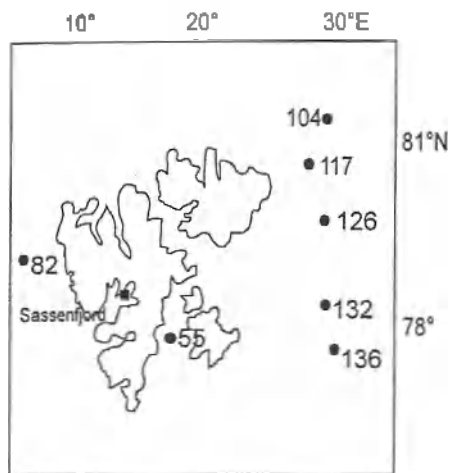


Fig. 1 Map of sites sampled during the Arctic EPOS cruise and referred to in this study. The Sassenfjord site of Kendall and Aschan (1993) is also indicated

Table 1 The number of replicates from each station analysed, their depths and their principal sedimentological characteristics (H. Grobe, personal communication)

Station	# Replicates	Depth	% Sand	TOC %
55	4	122	68.5	1.75
82	4	337	75	1.75
104	1	236	71.2	0.63
117	4	197	23.3	0.89
126	2	339	11.3	1.3
132	2	77	74.2	0.48
136	5	143	60.1	0.81

were suitable to extend the comparison. For the purposes of this paper the fauna of two samples from each of two adjacent shallow muddy sand stations (50 and 55) in Storfjord have been combined and referred to as station 55. The depth given in Table 1 is the mean for these two sites. Elsewhere, shallow sediments (< 200 m) were either stony or of coarse sand. Where samples were obtained from such sites or from deeper muddy stations their faunas are considered in this paper.

Benthic sediment samples of 0.1 m<sup>2</sup> were sub-sampled from a 0.25 m<sup>2</sup> box-corer. Material retained on a 0.5-mm round mesh screen was fixed in borax-buffered 8% formalin before being returned to the laboratory for transfer to 70% alcohol, the extraction of the macrofauna and its identification to putative species. An unavoidably long delay in the shipment of the samples extended the period of fixation to 7 months. In that time, the shells of many of the smallest bivalves and gastropods dissolved and hence they could not be identified. Full species lists will not be presented in this paper but are available on application to the author.

Biomass estimates for each species present were made on some samples from the Barents Sea transect on the basis of blotted wet weights. Molluscs and echinoderms were decalcified in 5% formic acid before weighing. Data on standing crop biomass are considered further by Piepenburg et al. (1995).

Analyses of the data were performed using the PRIMER package (Clarke 1993). All data were double square-root-transformed before setting up a similarity matrix based on the Bray Curtis similarity measure. Ordination was performed using non-metric multidimensional scaling (MDS) while classification used group average sorting. Diversity is only considered at the scale of single samples ( $\alpha$ -diversity) as no adequate protocols exist for sampling either regional ( $\gamma$ -

diversity or between-habitat ( $\beta$ -) diversity. A range of  $\alpha$ -diversity measures was calculated;  $k$ -dominance curves (Lambhead et al. 1983) permit comparison with the results of Warwick and Ruswabyuni (1987) and Kendall and Aschan (1993) while the Shannon diversity index  $H'$  (using  $\log_e$ ) has been widely used. Differences between  $k$ -dominance curves were tested for significance using the DOMSIG procedure of Clarke (1990). Species richness was compared using Hurlbert (1971) modification of Sanders (1968) rarefaction method. This method calculates the expected number of species ( $S_n$ ) in a sample of  $n$  individuals selected at random (and without replacement) from a larger collection.

## Results

The number of replicate samples and the more important sediment parameters (H. Grobe, personal communication) from each station at which the fauna has been determined are given in Table 1.

### Species assemblages

In the MDS plot (Fig. 2), samples from a single station always cluster together more closely than samples from different stations. The single sample from station 104 clusters closely to station 136 while the replicates from stations 126 and 117 appear similar. When the MDS was replotted and station numbers replaced by symbols whose size is proportional to either the depth of the site or the percentage of sand in the sediment found there (Fig. 2), it becomes apparent that the distribution of the fauna is related to both variables, which are probably not independent of each other. The uppermost stations on the plot (132 and 55) are comparatively shallow while the muddiest stations are located to its lower right-hand side. Although the samples were taken over 8° of latitude, its influence could not be detected. Classification (Fig. 3) suggests that there are three major groupings within the fauna, representing the sandy stations (104, 132, 136), the muddy stations (55, 117, 126) and station 82 which, although sandy, had a clearly separate fauna.

At the muddy sites a layer of fine mud overlies a stiff clay to a depth of between 20 and 80 mm. Most animals were concentrated in this upper layer, only *Maldane sarsi* and *Asychis biceps* penetrating significantly into the clay. Typical species were the polychaetes *Lumbrineris magnidentata*, *Leitoscoloplos cf. mammosus* and *Chaetozone setosa* and the bivalve *Yoldiella frigida*. Damage during processing prevented many cirratulids from being identified to species. *Chaetozone* was the clear dominant among those which could be determined, but others were also present, particularly species of *Tharyx* and, at station 55, *Cauleriella*. *Spiochaetopterus typicus* was typical of all the muddy sediments and its characteristic and persistent tubes made up a significant proportion of the sediment fabric. However, these tubes act as a barrier to formalin and,

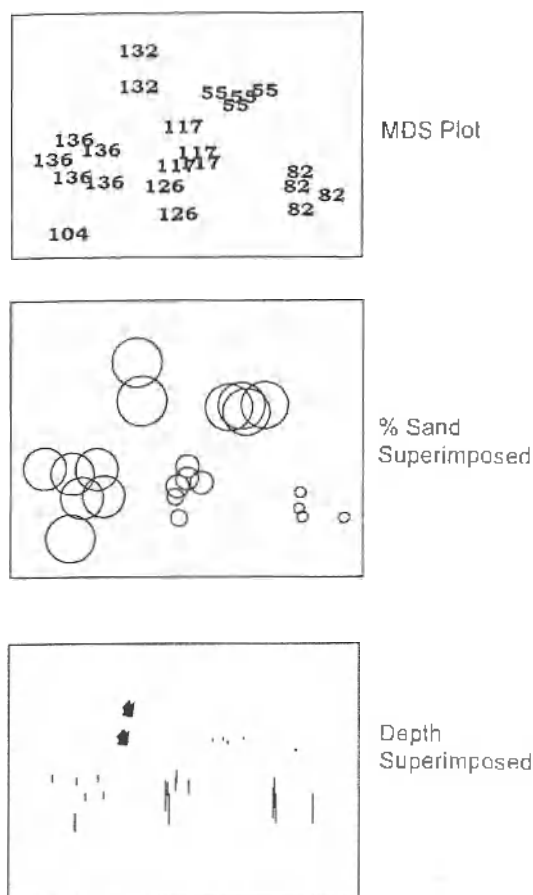


Fig. 2a MDS plot on which each replicate sample is plotted separately, numbers refer to station number; b replot of a in which circles proportional to the percentage of sand in the sediment replace station numbers; c replot of a in which vertical lines proportional to the station depth replace station numbers. Arrows indicate the position of the samples from the shallowest site

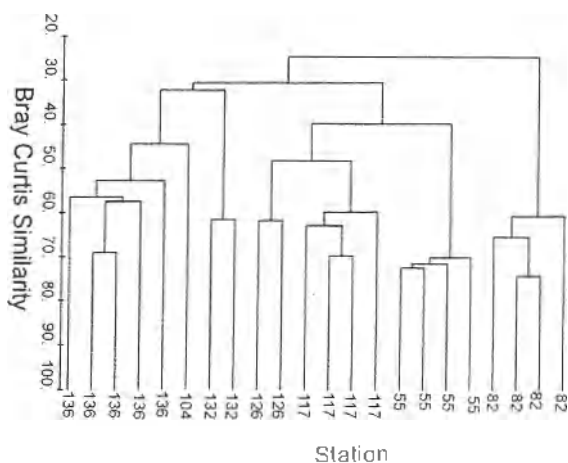


Fig. 3 Dendrogram showing similarity between samples within and between stations

as a result of individuals decomposing, it was not always possible to separate empty tubes from those that had contained living animals. Consequently *Spiochaetopterus typicus* was probably under-represented in counts and estimates of biomass.

*Maldane* and *Asychis* dominated the biomass of most muddy stations. In some instances other species made larger contributions, but they were represented by small numbers of large-bodied individuals and hence it would be difficult to extrapolate their biomass to a larger area. In this category *Ctenodiscus crispatus*, *Tridonta montagui* and *Nephtys ciliata* were typical.

Of the sandier sites, the single sample that was processed from station 104 had a fauna similar to that from station 136, 100 m shallower and more than 4° further to the south. Station 132, the shallowest sampled (77 m), was clearly different to the other sandy Stations. Stations 104 and 136 had faunas dominated by polychaetes and which overlapped in species composition with the more muddy sites. However, there were significant differences in patterns of abundance. In particular, the cumacean *Leucon acutirostris* was much more common at sandier sites, as were the small sabellid polychaete *Chone* sp. and the spionid *Spiophanes kroyeri*. However, *Leitoscoloplos* cf. *mammosus*, *Lumbrineris magnidentata* and the cirratulid species were far less frequent. In the coarser sediment of station 132 there was a further reduction in the abundance of deposit-feeding polychaetes (including *Spiophanes*); bivalves, however, were abundant. Numerically, *Dacrydium vitreum* dominated at this site but there were also substantial numbers of *Yoldiella* and *Nucula pernula*. Biomass was dominated by larger, but less numerous, bivalve species: *Hiatella arctica*, *Tridonta montagui*, *Musculus niger* and *Mya truncata*.

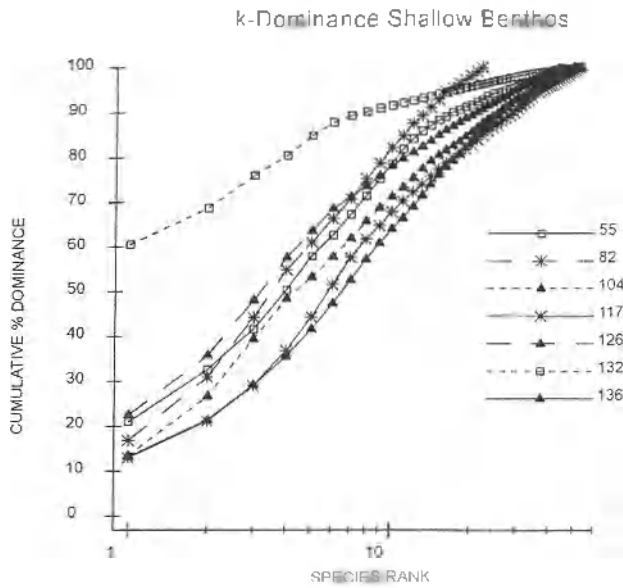
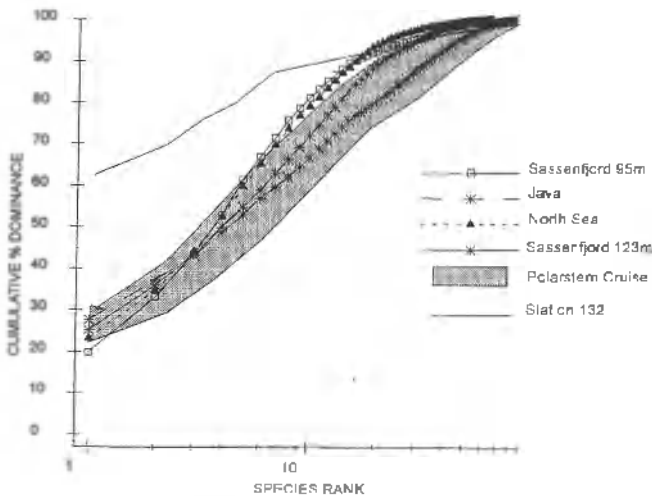
#### Community structure

At any single station both the number of species and the number of individuals per sample were unusually variable (Table 2), reflecting local patchiness in the composition of the sediment and/or the distance drifted by the ship between sampling points. Both the number of species and the number of individuals were lowest at the deepest station (82) and highest at the shallowest (132), but there was no trend at the intermediate stations.

Three measures of diversity have been considered. Hurlbert rarefactions were performed on the raw data and on the basis of these, estimates of the number of species that would be expected in a sample of 201 individuals (ES(201)) have been calculated and hence any effect of sample size discounted. To consider species alone, however, ignores the distribution of individuals between them and hence  $k$ -dominance curves and the Shannon diversity statistic  $H'$  have also been calculated. Figure 4 presents  $k$ -dominance curves based

**Table 2.** The maximum and minimum values of community measures based on 0.1 m<sup>2</sup> samples from each station

Station no.	55	82	104	117	126	132	136
No. individuals	343-405	78-194	289	293-835	719-888	1910-2490	191-295
No. species	42-48	16-26	50	52-55	53-63	52-70	40-54
ES(201)	34.3-40.8	NA	42.7	35.2-45.2	34.4-42.1	22.6-25.3	33.6-47.5
Shannon diversity H'	2.87-3.16	2.17-2.65	3.11	2.99-3.27	2.85-3.14	1.71-1.75	2.86-3.39

**Fig. 4** *k*-Dominance plots, based on averaged data, for all shallow benthic stations sampled during Arctic epos**Fig. 5** The diversity of mud or muddy sand sites shallower than 200 m in the Arctic. North Sea and Java. Shaded areas represent the maximum and minimum diversity in each area. Javanese data are represented by a single curve (central line)

on mean data from each sampling station. In such representations the lower a curve is, the higher the diversity of the sample it represents. In Fig. 4, only station 132 stands out as being of different diversity to the other sites. Formal testing of the difference between the curves, using the DOMSIG procedure, is only possible using sites with four or more replicates; it cannot be performed on data from this station. DOMSIG, however, does suggest that station 55 was more diverse (at 5% level of significance) than station 82 but less so than 136; station 136 was also more diverse than either stations 82 or 117. Using the Shannon index  $H'$ , stations 82 and 132 appeared less diverse than the others but station 136 did not stand out above the other stations. Similar conclusions were reached using rarefaction, although there were not sufficient animals present for a value of ES(201) to be calculated at station 82. In the evaluation of these results, it should be remembered that because of the dissolution in formalin of some small molluscs and the difficulty of identifying damaged cirratulid polychaetes, the estimates of diversity presented here may be lower than is actually the case.

#### Latitudinal comparisons

In making latitudinal comparisons, only those mud and muddy sand stations shallower than 200 m have been considered. Mean values for predictions of ES(201) (Table 2) at stations 55, 117 and 136 were higher than those for physically similar sites to the west of Spitsbergen, in the central North Sea and Java. The latter 2 data sets are those analysed by Warwick and Ruswahyuni (1987) but as there is no replication for the North Sea set, data from 30 muddy sand stations sampled in the same area in 1989 (Kendall; unpublished data) are also considered. Stations 117 and 136 were more diverse than sites in west Spitsbergen or Java but did not differ from the 1989 North Sea sites.

Figure 5 presents *k*-dominance curves for the sites from the central North Sea (1989 data) and Java and compares them with an undisturbed muddy sand site at 123-m depth from the west of Spitsbergen sampled in 1990 (Kendall and Aschan 1993) and stations 55, 117 and 136 sampled during the Arctic epos cruise. For convenience, only the most and least diverse site in each area have been plotted and the area between them

**Table 3** A comparison of the expected number of species for a sample of 201 individuals from stations sampled around Svalbard (this study; Kendall and Aschan 1993) and at lower latitudes (Warwick and Ruswahyuni 1987; Kendall, unpublished data)

	Java	North Sea (Warwick)	North Sea (Kendall)	W.Spitsbergen 123 m	Station no. 55	Station no. 117	Station no. 136
ES(201)	33.2 ± 1.9	34.6	43.6 ± 2.6	32.9 ± 1.4	36.8 ± 2.9	40.5 ± 4.5	43 ± 5.5

shaded. The range of Svalbard data has been overlaid by the range from the North Sea and, as Fig. 5 shows, the two almost completely overlap. Data from Java lie within the same range. When the curves for individual stations were examined using DOMSIG there were few significant differences; station 136 was more diverse than any other location studied except station 117 and the 123-m Sassenfjord site (sampled in 1990); station 55 was more diverse than the Java site.

### Discussion

Strömberg (1989) pointed out that although the macrofauna of the Barents Sea was described by Zenkevitch (1963), he presented very little data from northern Svalbard waters. While this is true, there is a description of a "middle Barents Sea community", which occurs on silt, sandy silt and silty sand at depths of 100–350 m. Among the dominant species that were said to characterise this assemblage were *Tridonta montagui*, *Spiochaetopterus typicus*, *Myriochele oculata* and *Ophiocantha bidentata*, all of which were clearly evident in the samples taken during the Arctic EPOS cruise. Although some of the species that were characteristic of the various faunal groups detected during Arctic EPOS were not recorded by Zenkevitch (1963), these tended to be of small body size and hence might have been overlooked if samples had been processed using a mesh of more than 0.5 mm. Zenkevitch considered that this assemblage could be subdivided into ten variants on the basis of the relative abundance of the component species. This observation accords well with the separation of muddy sand and sandy mud assemblages in the classification and ordination plots presented above. SIMPER analysis (Clarke 1993) suggested that these species groupings have a fundamentally similar fauna but that patterns of dominance differed as a response to sediment. The fauna of station 132 might be considered as an extreme form of Zenkevitch's central Barents Sea community. The fact that such extremes can be accommodated with a well-defined community type points out the difficulties to be encountered in determining regional patterns of diversity. For this reason, in the discussion that follows no attempt will be made to examine data collected during Arctic epos in the context of  $\beta$ -diversity; only variability in  $\alpha$ -diversity will be considered.

Sufficient evidence exists in the literature to indicate the existence of broad-scale patterns of species richness in Arctic shelf waters, although there is substantial geographical variability in the quantity and quality of information available. The seas to the north of Russia have been the object of a considerable research effort over many years (Zenkevitch 1963); extensive species lists exist and, although the quantitative basis of their collection is not always explicit, distinct patterns in diversity have been identified. However, in a review of the continental shelf benthos of the North American Arctic, Carey (1991) stated that the quantity and taxonomic composition of the benthos in this area had not been adequately described. Summarising the literature on the Arctic macrobenthos up to the early 1970s, Curtis (1975) acknowledged that diversity was variable and stated that the largest number of species is found in areas of mixing between cold polar and warmer non-polar water. In such areas, there is usually some enhancement of primary production. This linkage is a recurring theme of the Arctic benthic literature and, more recently, Carey (1991) and Grebmeier (1993) have also documented such a relationship. While the enhancement of species richness may simply be the result of animals from different biogeographic areas mixing, such observations also accord well with the predictions of Huston (1979) that species numbers should be highest under conditions of high population growth rates (such as are normally associated with high productivity) and a low incidence of disturbance. Diversity tends to be lowest in shallower coastal areas, influenced by the outflow of large rivers during the summer months (Curtis 1975; Wacasey et al. 1977). Such areas of lowered salinity might have only half the number of species found in sub-Arctic seas. Kendall and Aschan (1993) found that localised disturbance influenced the diversity of an Arctic benthic faunal community. In this case, sedimentation from a glacial stream during the summer disturbed the assemblage occupying shallow sites, reducing diversity and leading to domination by large numbers of individuals of a small body size. In other shallow areas the grounding of ice will result in scouring (Dayton et al. 1970) and hence influence local patterns of diversity. However, the sites sampled during Arctic EPOS were sufficiently deep and far enough offshore to be thought to be unaffected by such physical disturbances.

The western Barents Sea was one of the areas that Curtis (1975) picked out as having a particularly high

Sassenfjord, productivity is less than in adjacent open sea areas, as a result of high loads of suspended inorganic material from the adjacent glaciers that interfere with primary productivity (Weslawski 1993). Hence, a direct measurement of productivity itself might be a more efficient predictor of local benthic diversity than simple indications of mixing. This is not available for the Storfjord (station 50/55) where samples were collected from a pool of cold bottom water little influenced by the Atlantic. There was no evidence of high loads of suspended solids, although the area is fjordic; its fauna was similar to that of Sassenfjord (Kendall and Aschan 1993) but macrobenthic diversity was higher and did not differ significantly from that of the Barents Sea sites. The level of diversity at this site and station 117, another site where the influence of Atlantic water was less strong, can only be recorded rather than explained.

At physically similar sites sampled around Svalbard, rarefaction suggested that the number of species that might be expected in a sample of 201 individuals might vary about a level lower than that found further towards the equator. The evidence presented here suggests that there is little difference between the diversity of sites around Spitsbergen and physically similar sites sampled in the same way off the coast of northeast England (55°N) and Java (7°S). However, this apparent similarity is only of limited value when making broad latitudinal comparisons. To consolidate the impression that the variability of diversity within the Arctic overlaps considerably with that at lower latitudes, more information is required from other Arctic areas. Unfortunately, there are few studies with which a valid comparison can be made. An exception is data from shallow muddy sand and sandy mud sites in the Davis Strait (Stewart et al. 1985). When analysed using the same techniques as were employed in the examination of the Spitsbergen samples, rarefaction indicated about 35 species for 201 individuals. This

separate consideration.

Clarke (1992) pointed out that previous studies, which treated the Arctic and Antarctic together as being essentially similar areas with cold seas and an impoverished fauna, failed to appreciate the biogeographic implications of the greater age and longer isolation of the latter. In view of the differences in the geological history of the polar regions it is unrealistic to expect gradients of diversity to be symmetrical in the two hemispheres. It is clear that some (but not all) phyla in the Southern Ocean appear particularly species rich with high degrees of endemism suggesting speciation to have occurred after isolation. As an example, many species of the polychaete fauna are unique to the Southern Ocean (Knox 1977). In the Arctic however (Bilyard and Carey 1980; Kendall 1994), polychaete endemism is low as the fauna may still be recovering from recent glaciation. Despite this difference in the biogeographic origins of the fauna at both poles it remains that, just as in the Arctic, the shelf fauna of shallow sediments, a more complex situation obtains in the deep sea. Rex et al. (1993) demonstrated a decline in the species richness of gastropods, isopods and bivalves towards high latitudes in the northern hemisphere. There was less evidence for a similar pattern to the south although strong inter-regional patterns were reported. Brey et al. (1994) were unable to find a latitudinal cline in the diversity of benthos samples taken from the deep sea in the southern hemisphere by the use of an Agassiz trawl. They found that the diversity of species in the Weddell Sea was in the upper range of values for similar tropical locations.

The variation between such studies serves to demonstrate the need to examine all the components of the benthic fauna separately if an understanding of latitudinal variability in its species richness is to be reached. While some taxa clearly show a latitudinal gradient in species richness (e.g. Sanders 1968; Rex et al. 1993),

others do not necessarily comply. The annelids dominate in the majority of benthic soft sediments but little attention had been accorded to their latitudinal variability. To partially rectify this situation, Dauvin et al. (1995) combined some of the data presented in this paper with information from comparable sites in the English Channel and were unable to demonstrate any latitudinal gradient in annelid diversity between 48°N and 81°N. If the annelids do not respond to latitude then the majority of soft sediment assemblages will not show a latitudinal diversity gradient. It is evident that in further studies a considerable effort must be made to address annelid diversity and to attempt to elucidate the physiological and ecological differences between those taxa that conform to latitudinal gradients and those that do not. If differences between taxa in their response to latitude can be shown to exist, this might go some way to explaining the different latitudinal patterns of diversity on hard substrata and in soft sediments. Any further studies must consider longitudinal variation at all latitudes, but particularly in the tropics where extreme variability in species richness has long been appreciated (Valentine and Moores 1974).

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