

Comparative study of the structure of some tropical and temperate marine soft-bottom macrobenthic communities

R. M. Warwick¹ and Ruswahyuni^{1, 2}

¹ Natural Environment Research Council, Institute for Marine Environmental Research; Prospect Place, The Hoe, Plymouth PL1 3DH, Devon, England

² Department of Fisheries, Universitas Diponegoro; Jl. Hayam Wuruk 4A, Semarang, Jawa Tengah, Indonesia

Abstract

Macrobenthic sampling of a transect of six stations on the North coast of Central Java in October 1985 revealed three distinct communities which can be regarded as parallels of those from north temperate waters: (i) An *Amphioplus* (*Lymanella*) *laevis*/*Lovenia* sp. community parallel with the *Amphiura chiajei*/*Brissopsis lyrifera* community. (ii) A *Tellinides timorensis* community parallel with *Tellina* spp. communities. (iii) A *Laciolina philippinarum* community parallel with *Macoma* spp. communities. A strict comparison of the structure of the first two of these communities with their counterparts in England shows that within-habitat diversity is similar in both regions. Diversity at two shallower subtidal stations is higher than at two deeper stations: this is attributed to the effects of natural, low-level, physical disturbance which maintains the communities in a sub-climax stage. Total abundance and biomass of the macrobenthic fauna was lower at the Javanese stations than in their temperate counterparts.

Introduction

Most studies on marine benthic macrofaunal communities have been conducted in north temperate regions, and theory relating to community structure is based largely on these studies. By contrast, tropical macrobenthos is poorly known and comparisons with temperate regions are conflicting and frequently anecdotal, particularly with respect to species diversity and the occurrence of parallel bottom communities in the sense of Thorson (1957). Such comparisons are not only of academic interest, but the structure of benthic communities is now frequently used in pollution-effects monitoring programmes, so that it is important to establish baselines for tropical regions.

The classic paper of Sanders (1968) analysed data which showed that within-habitat marine benthic diversity

for soft-bottoms was higher in the tropics than in boreal regions. Nurtured by a great deal of anecdotal information, and perhaps the expectation of parallels with terrestrial communities, coral reefs etc., this idea is now entrenched in the textbooks of marine ecology (e.g. Gray, 1981). The debate now centres on the processes leading to high tropical diversity. Pianka (1966) recognised six more or less distinct hypotheses explaining latitudinal diversity gradients: the time theory, the theory of spatial heterogeneity, the competition hypothesis, the predation hypothesis, the theory of climatic stability and the productivity hypothesis. Various combinations of these hypotheses have also been invoked, e.g. the stability-time hypothesis (Sanders, 1968) and the general hypothesis of species diversity (Huston, 1979).

In the specific case of soft-bottom marine benthos, conflicting evidence and papers questioning the validity of Sanders' empirical data have largely been ignored. Thorson (1952, 1957) reviewed a number of comprehensive faunistic papers which showed that the increases in numbers of species towards the tropics is very pronounced in the epifaunas of hard-bottoms, but that the number of infaunal species of soft-bottoms was roughly the same in arctic, temperate and tropical seas. Fischer (1960) also showed that the diversity gradient for molluscs along the east and west coasts of the USA and Canada was more pronounced for gastropods (mainly epifaunal) than for lamellibranchs (which include many infaunal species). Gradients over broad geographic areas relate to evolutionary constraints on diversity, whereas diversity at a given sampling station also involves mechanisms operating over shorter ecological timescales. Sanders' (1968) study made comparisons among single stations, using four main criteria to ensure comparability of data from different water depths and geographical regions [however, Abele and Walters (1979 a, b) regard all these criteria as unfulfilled in Sanders' study]. They are:

(1) The sampling and sample-processing techniques must be the same for all the samples. It is relevant to the

present study that all Sanders' tropical samples (the RH series) were collected with a Higgins meiobenthic sled, whilst all the temperate shallow-water or estuarine samples were taken with an anchor dredge or by hand-coring. Differences in the sampling characteristics of these devices are intuitively obvious, and have been formally compared by Gage (1975).

(2) The comparison should be based on equal sample sizes. Sanders recognised this problem and his rarefaction technique was specifically designed to overcome it. Although his technique tends to slightly overestimate species richness (Hurlbert, 1971; Fager, 1972; Simberloff, 1972), this is perhaps the least contentious aspect of his comparative study.

(3) The communities should be taxonomically homogeneous. Sanders used only the polychaete-bivalve fraction of the fauna in his analysis, assuming that it was representative of total species diversity. Abele and Walters have shown that the total and relative contribution of these two taxa was highly variable in Sanders' samples, in those cases where this could be ascertained. Unfortunately the raw data for his eleven tropical samples have not been published and are unavailable, so that the comparability of tropical and temperate samples in this respect is uncertain.

(4) The samples should come from the same habitat. Abele and Walters have demonstrated that, in Sanders study, variation in sediment characteristics significantly affected species richness. Under this criterion we would further add that the communities being compared should be at a similar successional stage relative to the influences of natural or anthropogenic disturbances, since this will also clearly influence the diversity profile.

Despite these damning criticisms, the published evidence for higher within-habitat diversity of soft-bottom benthos still rests with Sanders' study. In this paper we have attempted to compare tropical and temperate communities on a much more limited scale than Sanders, but paying attention to strict compliance with the four criteria listed above. Standardisation of sampling and processing procedure can only be achieved by attention to the smallest details of methodology: sampling device, sieve mesh-size, exact method of sieving and taxonomic rigour applied to the analysis. Taxonomic homogeneity can be satisfied by analysis of the entire fauna rather than selected taxa. Equality of sample size is, however, surprisingly difficult to achieve. To the benthic ecologist this is usually quoted as the area of sea-bottom sampled, but diversity calculations depend on equality in numbers of individuals, and equal areas inevitably yield different numbers. Methods of plotting relative species-abundance which are independent of sample size are therefore commonly used, or diversity indices are calculated after reducing the numbers of individuals to the same value by various techniques, of which Sanders' rarefaction seems the most appropriate (Caswell, 1976). Strict comparability of habitats is also difficult to achieve, as no two samples are likely to come from exactly the same water depth or

from granulometrically identical sediments. These variables can be standardised as much as possible, but it is difficult to know the level of similarity which is biologically acceptable. The animals themselves are perhaps the best judges of this, and comparisons between the same parallel communities, in the sense of Thorson (1957), in different geographic regions would be the ideal. The applicability of the parallel community concept to the tropics is, however, still under debate. Some authors (e.g. Longhurst, 1958, in West Africa) have been able to recognise parallels with temperate communities, while others (e.g. Thorson, 1966, in the Gulf of Thailand) have not. The successional stage of a community relative to disturbances of various kinds is difficult to assess, although Warwick (1986) and Warwick *et al.* (1987) describe a possible method.

Materials and methods

New data on the structure of some tropical communities in Indonesia have been obtained for comparison with studies which had already been completed in England and for which the data were already available in either published or manuscript form. One of us (RMW) has had personal involvement at all stages of the sampling and sample-processing in both regions, thus assuring uniformity in the smallest technical details.

A transect of six stations was sampled in October 1985 in Mlonggo Bay ($6^{\circ}31.5'S$; $110^{\circ}40.3'W$), on the North coast of Central Java close to the University of Diponegoro's marine field station at Jepara (Fig. 1). Two stations were intertidal, Station 1 consisting of fine ripple-marked sand at mid-tide level (MTL) on open unvegetated coast, and Station 2 within about 200 m of Station 1 but on smooth, slightly siltier sand near mangroves, again at MTL. The remaining four stations were subtidal, at depths of 5, 10, 20 and 30 m.

The subtidal stations were sampled following the methods of Buchanan and Warwick (1974), in order to enable a comparison with their data on a sublittoral mud community off the coast of Northumberland, England. Ten 0.1 m^2 replicate van Veen grab samples were taken at each station, with the boat at anchor. These were emptied into a large plastic container and then transferred to a series of plastic buckets. The intertidal samples were collected by pushing a 0.06 m^2 -square metal box core into the sediment and excavating the sediment within it, using a spade, to a depth of 25 cm, again transferring the samples to plastic buckets. Seventeen such cores were taken at each station, totalling an area of 1 m^2 . The samples were spaced in a pseudo-random fashion over an area approximately $100 \text{ m} \times 25 \text{ m}$, parallel with the shore line, in order that the data would be strictly comparable with similar macrofaunal data from the Exmouth region, England, which were available in manuscript form at the Institute for Marine Environmental Research, Plymouth. The only difference in sampling procedure was that at Exmouth ten 0.1 m^2 replicate cores had been taken.

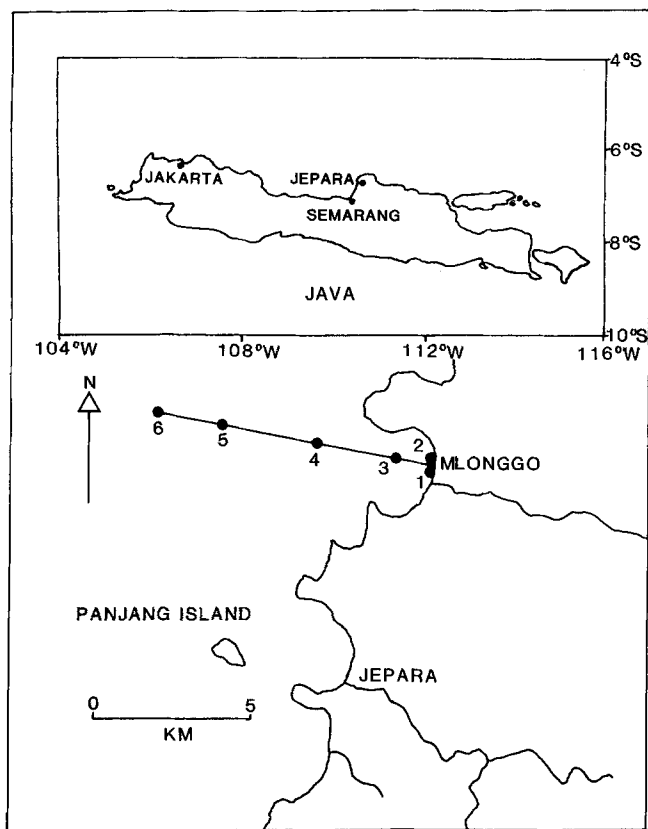


Fig. 1. Locations of Javanese sampling stations. 1, 2: Intertidal stations; 3, 4, 5, 6: subtidal stations at 5, 10, 20 and 30 m, respectively

All samples were returned to the laboratory at Jepara, where they were sieved by gently "puddling" through 0.5 mm square-meshed sieves. The samples were back-washed into pots of 10% formalin, stained with Rose Bengale, and a few days later washed on a fine sieve (63 μm) with tap water and emptied into large, shallow, white trays from which the fauna was picked out from the sieve debris. The macrobenthos was stored in tubes of 10% formalin. It was sorted into species or putative species and each species was counted and weighed on return to England. The biomass of each species was determined as blotted wet weight. Bivalves, gastropods and echinoderms were not generally decalcified. (These procedures were necessary because the material will be required for subsequent taxonomic work.) To enable comparisons with other studies, corrections for calcium carbonate content have been made using data for common English species available in Plymouth, i.e., *Tellina tenuis* for bivalves, *Thais lapillus* for gastropods, *Echinocardium cordatum* for echinoids and *Ophiura texturata* for ophiuroids, by determining wet weight prior to and after decalcification with formic acid. The exception to this was the common gastropod *Cerithidea cingulata*, the numerical and biomass dominant at Intertidal Station 2, which had to be decalcified in order to determine the ratio of living to dead shells. Dry weight is taken as one quarter of wet weight.

Sediment samples were analysed following Buchanan (1984), using dry sieve analysis for the sand fraction and pipette analysis for the silt/clay fraction.

To compare the similarity between the Javanese stations in terms of species composition, classification and ordination techniques followed the recommendations of Field *et al.* (1982). The similarity matrix was established using double square-root-transformed species-abundance data and the Bray-Curtis measure of similarity. The classification used group-average sorting, and the ordination technique used was multidimensional scaling (MDS). To compare diversity profiles both in terms of numbers and biomass between the Javanese sites, and with the English sites, *k*-dominance curves (Lamshead *et al.*, 1983) have been employed. Comparison of *k*-dominance curves for numbers and biomass has also been used to assess the successional stage of the Javanese and English communities, to see whether they are subjected to any form of disturbance (Warwick, 1986; Warwick *et al.*, 1987).

Results

Sediment analysis

The intertidal stations consisted of well-sorted fine sand, both with a median particle diameter around 150 μm , but Station 2 had a higher silt/clay (< 63 μm) content (7.2%) than Station 1 (4%). This was a surprisingly small difference in view of the appearance of the two beaches: at Station 2, fine flocculent material was apparent on the surface of the sediment, but this was not evidenced by a large silt/clay content in the depth-integrated (surface to 15 cm) sediment core. The sediment at the three most offshore stations (10, 20 and 30 m) consisted of well-sorted fine silt with a median particle diameter around 12 μm , with 99% silt/clay. At the 5 m station, the sediment was very poorly sorted and consisted of a mixture of about 60% sand, with a median particle diameter similar to that of the intertidal sediments, and 40% fine silt similar to that of the deeper stations, with very few particles of intermediate size. This therefore appears to be a mixture of intertidal and offshore sediments, and calculation of the median particle diameter would be meaningless. Further details of the sediment analyses are given by Ruswahyuni (1986).

Faunal composition of the Javanese stations

Since this is a relatively unknown fauna, many of the species could not be positively identified. We have therefore refrained from providing tables of the raw data on numbers and biomass, which are, however, available in an unpublished M.Sc. thesis lodged at the library of the University of Newcastle upon Tyne (Ruswahyuni, 1986). This thesis also contains an inventory of photographs and drawings of most species.

Three communities have been recognised which have direct parallels with communities from north temperate waters. The offshore mud community is characterised by the brittle star *Amphioplus (Lymanella) laevis*. *Amphioplus* spp. communities are considered to be the tropical equivalents of *Amphiura* spp. communities of boreal regions (Longhurst, 1958). The occurrence of the irregular echinoid *Lovenia* sp. at the 30 m station suggests close parallels with the *Amphiura chiajei/Brissopsis lyrifera* community from northern Europe. The Intertidal Sand Station 1 is characterised by the presence of the bivalve *Tellinides timorensis*. The genus *Tellinides* has very close morphological similarity to *Tellina*, and this community can be regarded as a parallel of the *Tellina tenuis* community from northern Europe. The slightly siltier Sand Station 2 is characterised by the bivalve *Laciolina philippinarum* which is closely similar to *Macoma* spp., and this community can be regarded as a parallel of the *M. balthica* community from northern Europe. The 5 m offshore station with mixed silt and sand sediment had species of both *Amphioplus* and *Tellinides* present, and can be regarded as transitional between the intertidal sand and offshore mud communities.

The presence of these first-order characterising species is not sufficient for us formally to designate these three communities as isocommunities of *Macoma*, *Tellina* and *Amphiura* communities in the sense of Thorson (1957): more taxonomic rigour will need to be directed towards the second- and third-order species present before this is possible. However, the presence of these first-order species is sufficient to establish the communities as ecologically similar for the purposes of comparing community structure with their temperate counterparts, which is the main aim of this paper.

Classification and ordination

The dendrogram (Fig. 2A) shows a major dichotomy between the intertidal (1 and 2) and sublittoral (3–6) stations. The two deepest stations (20 and 30 m, Stations 5 and 6 on the dendrogram) are linked at the highest level of similarity, the 10 m station (4) is linked to this group at the next highest level and the 5 m station (3) at the next. MDS ordination (Fig. 2B) essentially confirms this pattern, except that the 5 m station (Station 3) is not so closely linked to the other sublittoral stations and is dissimilar both to the intertidal and offshore groups.

Community structure

Because of differences in sample size (total numbers of individuals) we have not quoted diversity, species richness or evenness indices. Plotting relative species-abundances in the form of *k*-dominance curves has the added advantage that biomass as well as numbers units can be used in comparisons. The *k*-dominance curves for species abun-

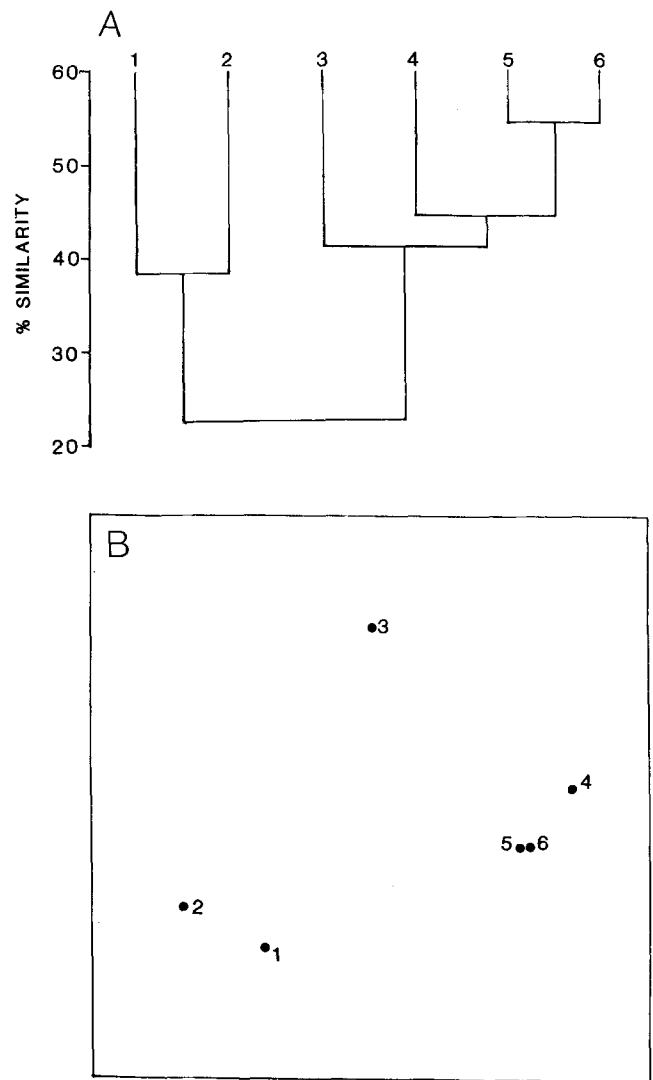


Fig. 2. Results of classification (A) and multidimensional scaling ordination (B) of Javanese stations. Station notation as in Fig. 1

dance (Fig. 3a) indicate that the 5 and 10 m sublittoral stations (numbered 3 and 4 on Fig. 3) have a higher diversity than the other stations, but that the intertidal and offshore stations cannot be clearly separated as the lines cross. Essentially, these diversity profiles can be divided into three pairs of very similar stations in which the curves closely coincide: Intertidal Stations 1 and 2, and sublittoral stations at 5 and 10 m, and 20 and 30 m (Stations 3 and 4, 5 and 6, respectively). The *k*-dominance curves for species biomass (Fig. 3b) show a rather similar pattern to those for abundance. Biomass diversity at the 5 and 10 m stations (3 and 4 on Fig. 3) is higher than for the intertidal or offshore stations. However, only the 5 and 10 m stations are closely similar, whereas Intertidal Station 2 shows much higher biomass dominance by the first few top-ranked species than Intertidal Station 1, and the 30 m station (6 in Fig. 3) shows higher dominance than the 20 m station (5).

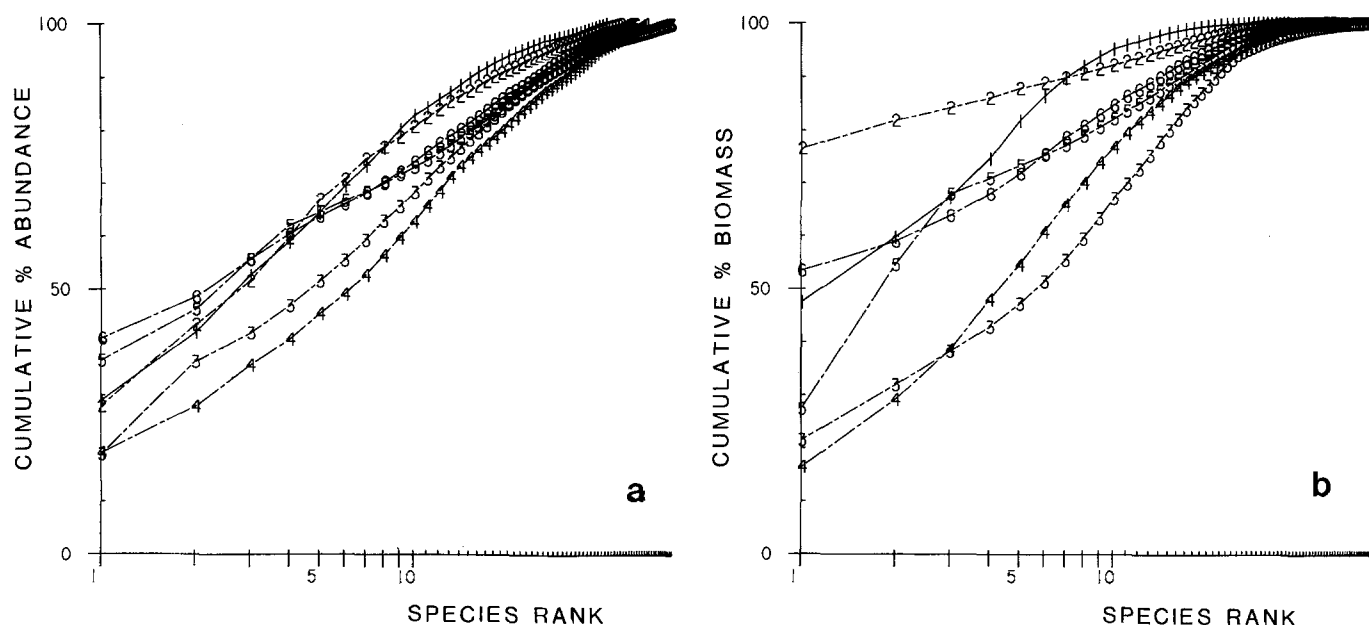


Fig. 3. k -dominance curves for (a) species abundance and (b) species biomass for the six Javanese stations. Station notation as in Fig. 1

A comparison of the k -dominance curves for abundance and biomass (Fig. 4) for each station shows that the two intertidal stations and the 30 m station are in what can be regarded as the climax state (Warwick *et al.*, 1987), with the biomass curve entirely above the abundance curve, indicating dominance of the biomass by large (long-lived?) species. On the other hand the 5, 10 and 20 m stations have plots which indicate that the community is in an intermediate successional stage, with the abundance and biomass curves crossing. We do not believe that these three stations represent a moderately polluted state, since there are no obvious sources of pollution nearby, and in any case it is unlikely that any such source would influence the middle of the transect but not its ends. We therefore assume that the disturbance is natural. Divers working at these three stations (for the purpose of collecting a parallel series of core samples for meiofaunal analysis) noted that the water column above the bottom contained an extremely dense silt suspension, so that there was not a well-defined sediment/water interface. The physical disturbance resulting from resuspension of fine sediment due to tidal and wave action is therefore the most likely factor maintaining the communities in a sub-climax stage.

The three offshore stations (10, 20 and 30 m) have the same community and sediment type as the offshore muds off the coast of Northumberland, England (Buchanan and Warwick, 1974). These latter authors provide data on species abundances and biomass for an 80 m depth station, which we have used for comparison with the Javanese community. The Northumberland community is in a mature, unpolluted state with the k -dominance curve for species biomass entirely above the abundance curve (Warwick, 1986). Using strict criteria, the only comparable Javanese station is the 30 m one, since the indications are

that the 10 and 20 m stations are in an intermediate successional stage. However, we have also included the 20 m station (Station 5) in our comparison in view of its close similarity to the 30 m station (6) in species composition (Fig. 2) and diversity profile, at least for abundances (Fig. 3a). Comparison of the abundance curves (Fig. 5a) shows that the Javanese and Northumberland curves are rather close together and cross one another. The Javanese curves show a higher dominance for the commoner species than Northumberland, but less dominance for the rarer species. Comparison of species-biomass curves (Fig. 5b) reveals a similar pattern. The 30 m Javanese curve crosses the Northumberland curve in a similar configuration to the abundance curves, and the Javanese 20 m curve is very close to the Northumberland one, crossing it twice.

We have compared the Intertidal Station 1 community with data from an intertidal sand-flat near Exmouth, England, characterised by the bivalve *Tellina tenuis*. Although this sand-flat is in the mouth of the Exe estuary, the salinity of the overlying water at this tide level (MTL) is never reduced below 31‰ at any time of the year. Comparison of the k -dominance curves for abundance and biomass show the mature climax configuration, with the biomass curve entirely above the abundance curve (not illustrated, but compare continuous lines in Fig. 6a and b). The sand at Exmouth was rather coarser than its Javanese counterpart (median diameter 300 μm as opposed to 150 μm), but was otherwise similar in having a ripple-marked surface, in retaining a permanent water-table, in its thixotropic character, and in the greyish colouration of the deeper layers but without any obvious smell of H_2S . The k -dominance curves for both abundance and biomass (Fig. 6a and b, respectively) for the two locations are close together and cross each other. Both for abundance and biomass, dominance of the commoner

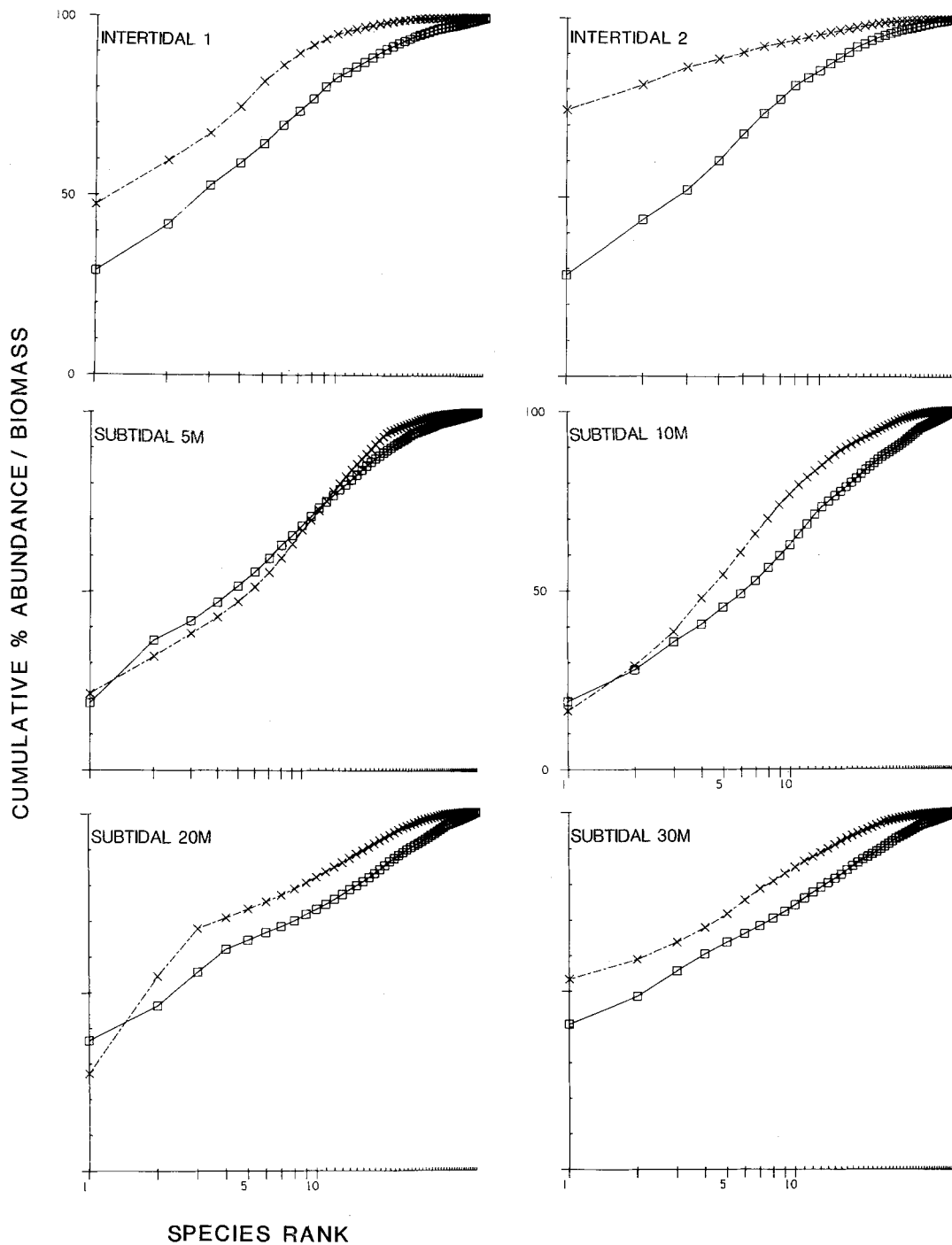


Fig. 4. Comparison of k -dominance curves for species abundance (squares and continuous lines) and species biomass (crosses and dashed lines) at the six Javanese stations

species is higher and of the rarer species lower at the Javanese site than the English site.

No data for an intertidal *Macoma* spp. community from a sediment of similar grain composition were available for comparison with the Javanese Intertidal Station 2. Neither could we locate any such communities in the vicinity of Plymouth to obtain any original data, as we could only find *Macoma* spp. communities in much siltier sediments. We have also been unable to find data or field

situations comparable with the Javanese mixed community station at 5 m depth.

Finally, we have made a comparison of the total abundance and biomass of macrobenthic animals (Table 1). The Javanese Intertidal Station 1 has lower total abundance and biomass than its counterpart in England. Also, all the offshore Javanese stations have lower abundance and biomass than the Northumberland station. These are also appreciably lower than values for other

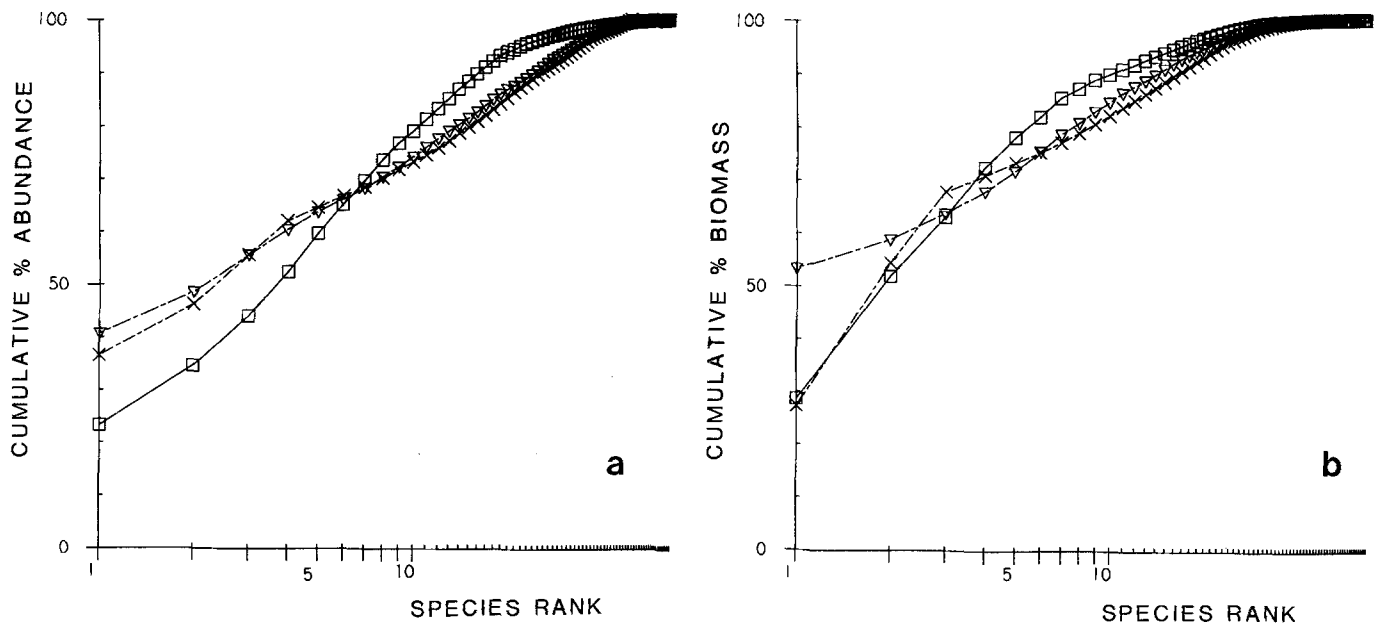


Fig. 5. Comparison of k -dominance curves for (a) species abundance and (b) species biomass at the Northumberland station (squares and continuous line) with the Javanese 20 m (crosses) and 30 m (triangles) stations (dashed lines)

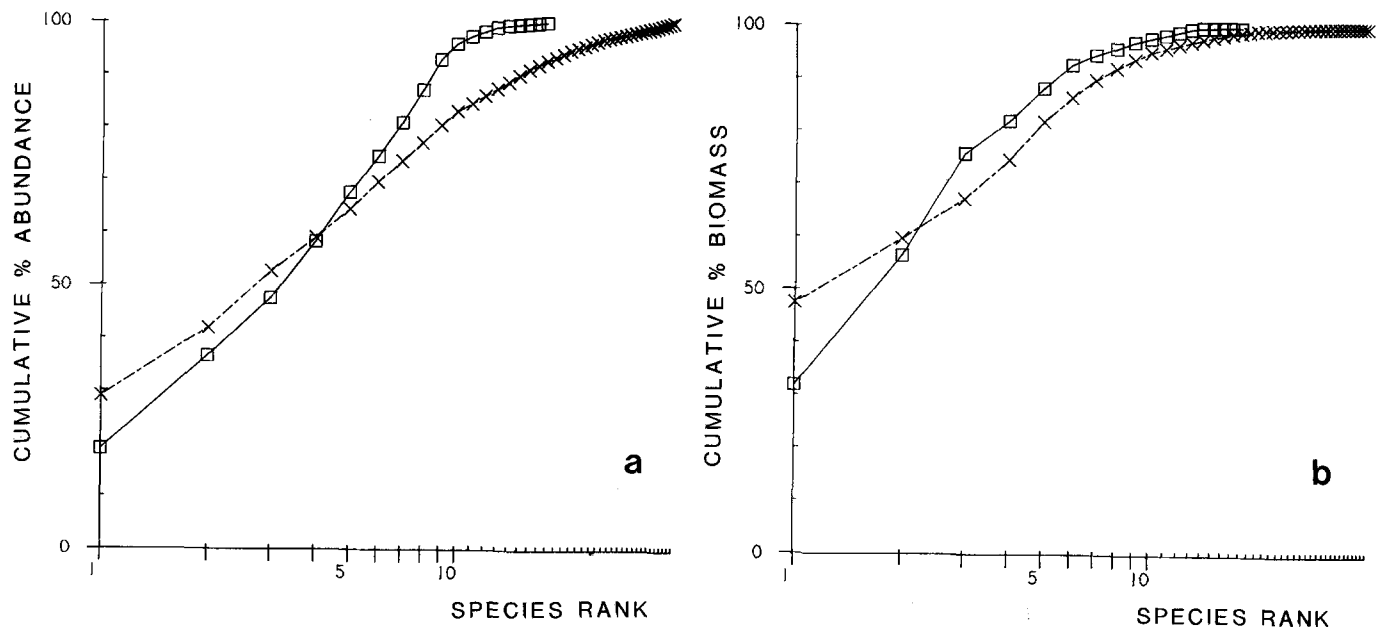


Fig. 6. Comparison of k -dominance curves for (a) species abundance and (b) species biomass at Exmouth (squares and continuous line) and Javanese Station 1 (crosses and dashed line) intertidal sands

shallow sublittoral communities which we know have been sampled and processed by identical methods: a *Venus* sp. community (Warwick *et al.*, 1978) and an *Abra* sp. community (Warwick and George, 1980), both off the coast of South Wales, UK.

Discussion

This study has shown that the macrobenthic communities of the North Java coast can be characterised as parallel

communities to those from temperate waters, and we have recognised three such parallels. In the two community types where we feel that strict comparisons are justified, we have been unable to detect any unequivocal differences in diversity between the tropical and temperate situation.

Criticism can even be levelled at these two comparisons, since in the case of the sublittoral mud communities the water depths were different, and in the case of the intertidal sand community the grain size was different. However, there is no evidence that, in shelf communities,

Table 1. Comparison of total numbers ($N\ m^{-2}$) and biomass (B , mg dry wt m^{-2}) between Javanese and UK stations

Station	N	B
Intertidal		
Java Station 1	463	1 563
Exmouth sandflat	694	4 215
Subtidal		
Java 5 m	739	383
10 m	330	703
20 m	360	1 814
30 m	422	1 058
Northumberland 80 m	1 065	4 522
S. Wales (<i>Venus</i> community 13.5 m)	4 231	55 493
(<i>Abra</i> community 14 m)	2 284	11 105

diversity increases with water depth. Indeed, the reverse is true for our Javanese study. We are satisfied that in both instances we have considered stable climax communities. The inshore sublittoral Javanese stations were in a sub-climax state, which we assume to result from natural physical disturbance, and the higher diversity of these communities can be accounted for in terms of the intermediate disturbance hypothesis (Connell, 1978) and the general theory of species diversity proposed by Huston (1979). Neither can we find any evidence in the literature to suggest that a change in grain size from 150 to 300 μm in the case of the intertidal sand communities would be sufficient to influence the diversity profiles of macrobenthos significantly.

Many more comparisons of this nature will need to be made before any generality can be achieved, but they certainly weaken the evidence for higher within-habitat diversity in tropical soft-bottom communities. Equally strict comparisons also need to be made between hard-bottom epifaunal communities from habitats of similar physical complexity along latitudinal gradients before any firm conclusions can be established regarding differences between these and soft-bottom communities in respect to latitudinal gradients of diversity. For the epifauna, however, the evidence of Golikov and Scarlato (1973) suggests that, within similar habitats, the distribution of biomass among species is similar at all latitudes (p. 221 and Fig. 1 of Golikov and Scarlato, 1973). At the present time, theorization and speculation on causal mechanisms are misplaced in view of the paucity of adequate empirical data of a strictly comparative nature. If, however, within-habitat diversity of epifaunal communities should indeed prove to show stronger latitudinal gradients than infaunal communities, any global theory of species diversity should be able to account for this difference and it would be useful in resolving arguments for or against the various theories.

The lower abundance and biomass of benthic macrofauna from the Javanese sites compared with their temperate counterparts prompts speculation. Possibly, less of the primary production by phytoplankton reaches the bottom in the tropics because production is more or less

continuous and in phase with the zooplankton grazers. On the other hand, in temperate regions primary production is highly seasonal and much of the spring bloom settles to the bottom before the zooplankton population has built up sufficiently to graze it. A very subjective comparison of commercial fish-landings at Jepara and Plymouth fish markets certainly indicates a much higher ratio of pelagic to demersal biomass at Jepara. This supports the view that more of the primary production in the Jepara region is cycled through the planktonic system, and less reaches the benthos. Petersen and Curtis (1980) made more objective comparisons of energy flow through the major components of tropical (Phangnga Bay, Thailand), temperate (North Sea) and subarctic (Disko Bugt, W. Greenland) shelf ecosystems, and came to essentially similar conclusions.

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