

Biomass of the invertebrate megabenthos from 500 to 4100 m in the northeast Atlantic Ocean

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Abstract

Data are presented on the biomass of the invertebrate megafauna at 22 stations on the continental slope in the Porcupine Seabight (PSB) (northeast Atlantic Ocean). Samples were collected between 1980 and 1982. Several units of biomass are used, all of which illustrate a decrease by a factor of about 30 from 500 to 4100 m. Log-normal curves were fitted to the data, the gradients of which were very similar for all biomass units and similar to the value for a transect down the continental slope in the western Atlantic. Biomass levels in the PSB are compared with those from other deep-sea environments. Some published values are more than ten times higher than the values reported here, while others are less than a tenth. The reasons for these differences and trends are discussed in terms of food supply. Sampling variability was examined at two stations, but by chance one (at 1300 m) appeared to encompass a sharp faunal discontinuity of the dominant fauna and the other (at 4000 m) contained very small numbers of large animals. For these reasons, sample variability was high at the repeat stations. Suspension-feeders and crustaceans dominated the biomass at upper-slope depths, while echinoderms were dominant on the middle and lower slope. As a result of this phyletic change, there was a small but insignificant decrease in mean body weight with increasing depth. Within phyla there was also a small but insignificant decrease with depth. If large species are excluded from the biomass/depth regression, the gradient changes considerably, demonstrating the increasing importance of small species at greater depths. The size distribution of megafaunal biomass was examined at several stations. This indicated that the megafauna form a functional group distinct from the macrofauna, just as the macrofauna are distinct from the meiofauna.

Introduction

The most important current problems in deep-sea biology undoubtedly relate to rates of processes. However, all rate measurements must be perceived in the context of the abundance of the organisms to which they apply, so that biomass estimates are an essential prerequisite for an understanding of the energetics of any biological community.

In the study of deep-sea benthic communities many estimates of the biomass of the smaller and more abundant elements have been made since these are amenable to quantitative collection by corers and grabs; however, few data are available on the biomass of the larger and more sparsely distributed organisms (Haedrich and Rowe, 1977; Haedrich *et al.*, 1980; Sibuet and Lawrence, 1981; Ohta, 1983; Smith and Hamilton, 1983; Sibuet *et al.*, 1984). In these studies the megafauna has often appeared to form a significant proportion of the total benthic biomass (e.g. Smith and Hamilton, 1983; Sibuet *et al.*, 1984). However, most estimates have been expressed in terms of wet weight, a measure difficult to interpret when comparing samples dominated by organisms with very different body compositions. It has been suggested that numerical abundance is as satisfactory a unit of biomass as any other (Rowe and Menzel, 1971) but, although this may be valid when comparing samples collected in identical ways, a slight reduction in the lower size limit captured or the inclusion of more infaunal organisms may lead to substantial increases in the numerical abundance, but to only a small increase in biomass.

This paper describes the trend of biomass of the megabenthic invertebrates expressed in terms of wet, dry and ash-free dry weight, along a transect in the Porcupine Seabight (PSB) to the southwest of Ireland. Comparisons are made with other sections of the PSB benthic fauna (Pfannkuche, 1985) and with biomass estimates from other bathyal and abyssal regions. The size structure of the megafauna has also been examined, as has been done for smaller organisms in shallow water (Schwinghamer, 1981).

The megafauna has been variously defined as those organisms visible in photographs of the seafloor (e.g. Rice *et al.*, 1982) or those caught by trawls and sledges (e.g. Haedrich *et al.*, 1980). In this study, such organisms are defined as those captured by the Institute of Oceanographic Sciences (IOS) epibenthic sledge (4.5 mm mesh size).

Materials and methods

Study area

The PSB is a horseshoe-shaped embayment in the continental slope about 200 km southwest of Ireland (Fig. 1). The physiography of the area has been outlined by Billett and Hansen (1982) and further details not previously available are given here. The sediments along the transect are a coccolith-foram marl with a carbonate content of 45 to 67% dry weight (R.F.C. Mantoura *et al.*, in preparation). The coarsest sediments are found at the top of the slope (median $\Phi=4.4$, at 510 m), but become finer with increasing depth (Md $\Phi=7.4$, at 960 m). From 1 500 to 4 100 m, Md Φ is in the range 8.0 to 8.6. The distribution of species of benthic hard-shelled multilocular Foraminifera can be used as an indication of sediment transport, and results obtained in this way have indicated that from 500 to 3 000 m there is negligible downslope transport. Samples taken at 3 600 and 4 100 m, however, contained species typical of upper and middle slope depths, indicating downslope sediment transport, possibly from the canyons or from the steep sides of the Goban Spur to the east (Weston, 1985 and personal communication). Sediments in the PSB are oxidised over at least the top 9 cm, as indicated by the colour. Sharp colour changes are found at 10 cm at mid-slope depths, but changes are gradual at the top and bottom of the slope. The organic carbon content of the sediment shows no distinct trend with water depth and differs little from 0.5% dry weight, as estimated by CHN analyses after HCl digestion of carbonate (J. Taylor, Scottish Marine Biological Association, personal communication). Throughout the PSB, near-bed currents are tidal, and very rarely exceed 15 cm s^{-1} (20 min average) 1 m above the bottom (Lampitt, 1985 and unpublished data).

Sample collection and treatment

From 1980 to 1982, samples of the benthic megafauna were collected at 22 stations (34 hauls) in the PSB using the IOS epibenthic sledge (Aldred *et al.*, 1976; Rice *et al.*, 1982) at depths between 525 and 4 080 m (Fig. 1).

At depths of about 1 300 and about 4 000 m, pairs of transponders were deployed 2 km apart so that the sledge could be fished with greater geographical precision than elsewhere (shallow and deep repeat stations). This was to facilitate an examination of spatial variability of the megafauna on a scale of only a few hundred metres and to indicate the degree of confidence which could be given to single samples within other areas of the PSB. At these lo-

calities the sledge was fished in such a way that during its time on the sea bed the position of the ship was known relative to the two transponders. The sledge tracks were calculated assuming the warp to be in a straight line behind the ship, and it was found that at the shallow station they were all within a circle of 2 km diameter and at the deep site all within a circle of 11 km diameter. The fishing depths at these transponder localities, transmitted by the sledge monitor during fishing, varied from 1 275 to 1 333 m and from 4 030 to 4 080 m, respectively. Ten sledge runs were accomplished at the shallow station and four at the deep station.

At most stations, a single 4.5 mm stretched mesh net, with mouth opening of 2.3 m, was used. At the shallow repeat-stations three smaller nets, two with 4.5 mm stretch mesh and one with 1.0 mm mesh, were used simultaneously; but the samples from only the two outer coarse nets, giving a total collecting width of 1.6 m, were used for biomass determination.

An odometer wheel measured the distance the sledge travelled on the sea bed. Although there is evidence of some slippage of the odometer wheel, very good correlation has been found between the abundance of animals photographed by the sledge camera and abundance of animals collected simultaneously by the net (Rice *et al.*, 1982). This may be because the slippage is compensated by sledge inefficiency due to either a bow-wave effect or occasional lifting of the bottom bar off the sea bed. Depending on the expected catch size, the length of tow was determined so that the area sampled varied between 600 and 3 400 m^2 , calculated from the odometer reading and the mouth widths of the nets.

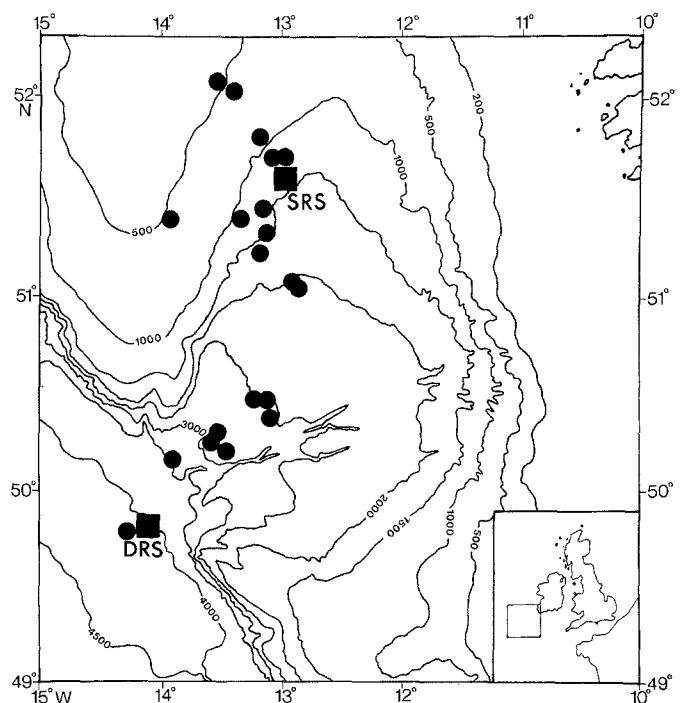


Fig. 1. Sampling sites in the Porcupine Seabight. Shallow (SRS) and deep (DRS) repeat stations are indicated by squares

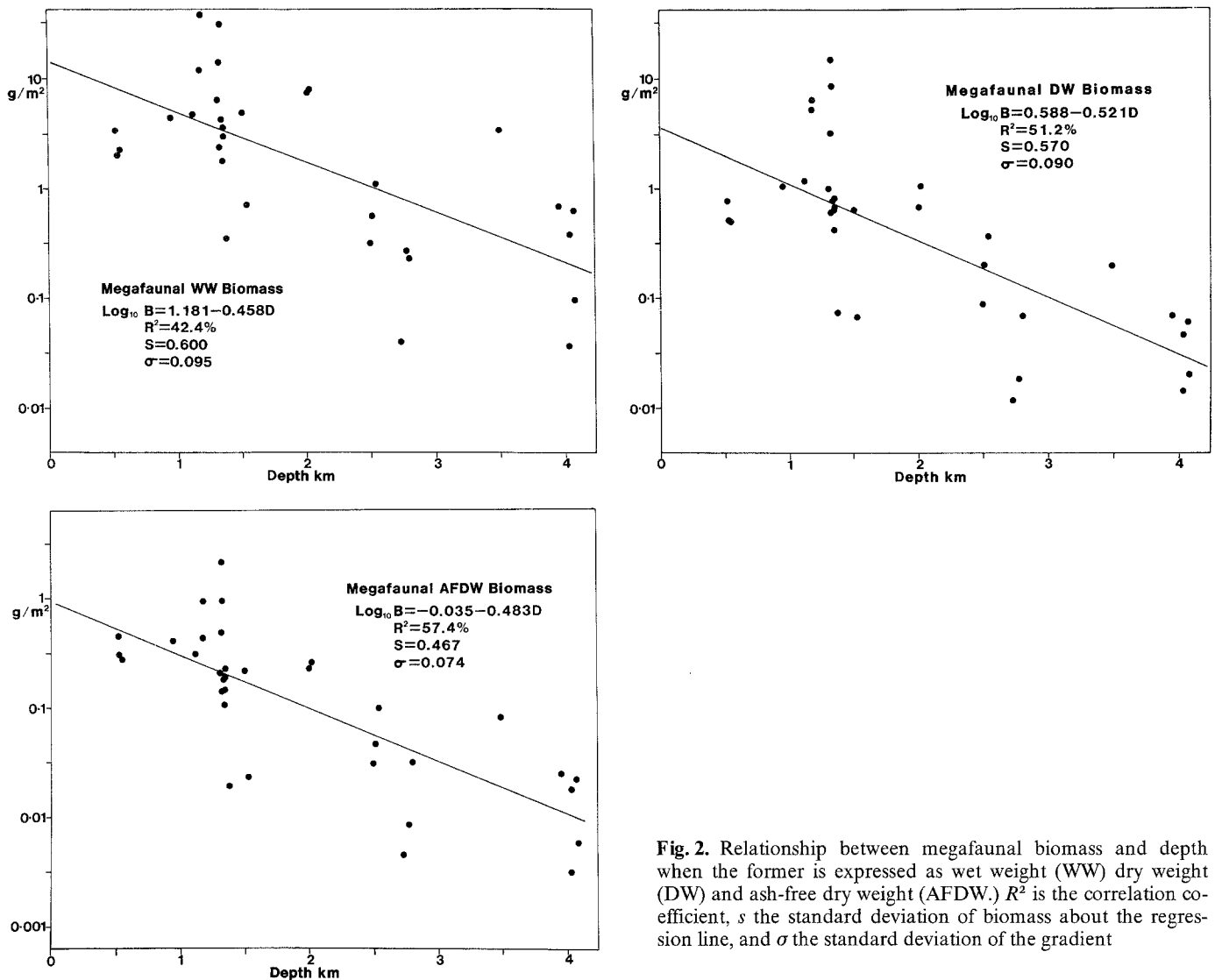


Fig. 2. Relationship between megafaunal biomass and depth when the former is expressed as wet weight (WW) dry weight (DW) and ash-free dry weight (AFDW.) R^2 is the correlation coefficient, s the standard deviation of biomass about the regression line, and σ the standard deviation of the gradient

Samples were frozen soon after collection and subsequently sorted to the species level wherever possible. Specimens were counted and blotted dry prior to wet weighing. (The coelomic fluid of holothurians and echinoids was removed prior to wet-weighing.) From 13 hauls, all the specimens were then dried in a vacuum oven at 60°C for up to 14 h. Subsamples of the dried material were then analysed for ash content (500°C for 4 h). A conversion table was then produced giving the proportion of water and ash in each species or genus. For the remaining hauls, these conversion tables were used to derive dry and ash-free dry-weight values. The sledge is not thought to collect fish efficiently and these were therefore excluded from the data set.

Results

Total megafaunal biomass and depth

The relationship between biomass and depth for all 34 sledge hauls in the PSB is shown in Fig. 2, expressed as wet

weight (WW), dry weight (DW) and ash-free dry weight (AFDW). In all three cases there is a significant negative relationship between biomass and depth ($P < 0.001$). The gradient of the regression is influenced little by the biomass unit, with values of 0.46 ± 0.09 for wet weight, 0.52 ± 0.09 for dry weight and 0.48 ± 0.07 for ash-free dry weight. However, the correlation coefficient R^2 improves from 42.4% for WW, to 51.2% for DW and 57.4% for AFDW. The standard deviation of biomass from the regression improves from 0.60 for WW to 0.57 for DW and 0.47 for AFDW.

Composition of megafauna and depth

For the purposes of this paper the megafauna may be divided into three groups: the crustaceans, echinoderms, and "other phyla", the last being dominated in terms of biomass by sessile suspension-feeders. The three groups were affected to different degrees by increasing depth (Figs. 3 and 4), with crustacean biomass and abundance declining very much more quickly with depth than values for the

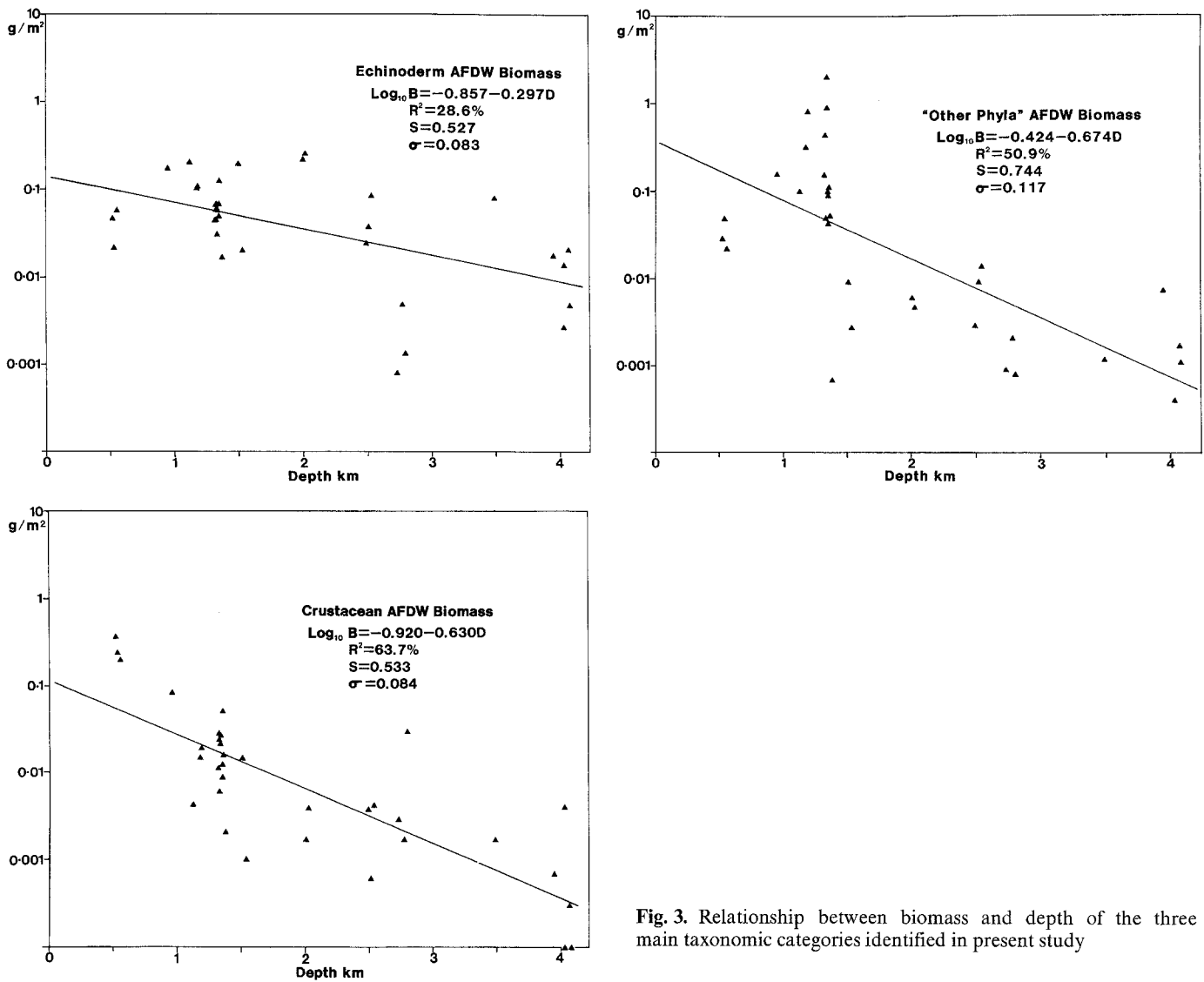


Fig. 3. Relationship between biomass and depth of the three main taxonomic categories identified in present study

echinoderms. "Other phyla" fell between these two extremes. The effect of these differences was to cause a shift in relative importance of the groups. In general, the crustaceans (mainly decapods) were dominant only at depths shallower than 1 000 m. Suspension-feeders were also important here, but reached very substantial levels (about 95% of total biomass) between 1 100 and 1 400 m depth (see "Small-scale distribution" section), while the echinoderms were important at all depths, but particularly at the deeper levels.

Total megafaunal abundance and depth

The relationship between numerical abundance and depth is shown in Fig. 4. The scatter of the points about the line is somewhat less than in the regression of AFDW biomass on depth ($s = 0.34$ and 0.47 , respectively). Abundance declined less rapidly than biomass, with a gradient of 0.35 ± 0.05 as opposed to 0.48 ± 0.07 for AFDW biomass, indicating that the mean body weight declined with increasing depth.

Body weight and depth

This has been examined both by considering mean body (AFDW) weight of all specimens in each sample and in each of the three main categories, and by partitioning the total biomass into small and large species. There was a small and insignificant decline in the mean body weight of all megafauna with increasing depth ($P > 0.05$). This decline was also evident in each of the three main categories¹, but was significant at the 5% level only for "other phyla". The effect of depth on body weight is shown more clearly by examining the separate contribution that small and

¹ If mean body AFDW (g) = W and depth (km) = D :

For all megafauna $\log_{10} W = -0.28 - 0.14 D$

($R^2 = 15.9\%$ $s = 0.35$ $\sigma = 0.056$)

For crustaceans $\log_{10} W = -0.56 - 0.023 D$

($R^2 = 0.3\%$ $s = 0.46$ $\sigma = 0.073$)

For echinoderms $\log_{10} W = -0.48 - 0.090 D$

($R^2 = 3.4\%$ $s = 0.53$ $\sigma = 0.085$)

For "other phyla" $\log_{10} W = -0.31 - 0.23 D$

($R^2 = 29.8\%$ $s = 0.40$ $\sigma = 0.063$)

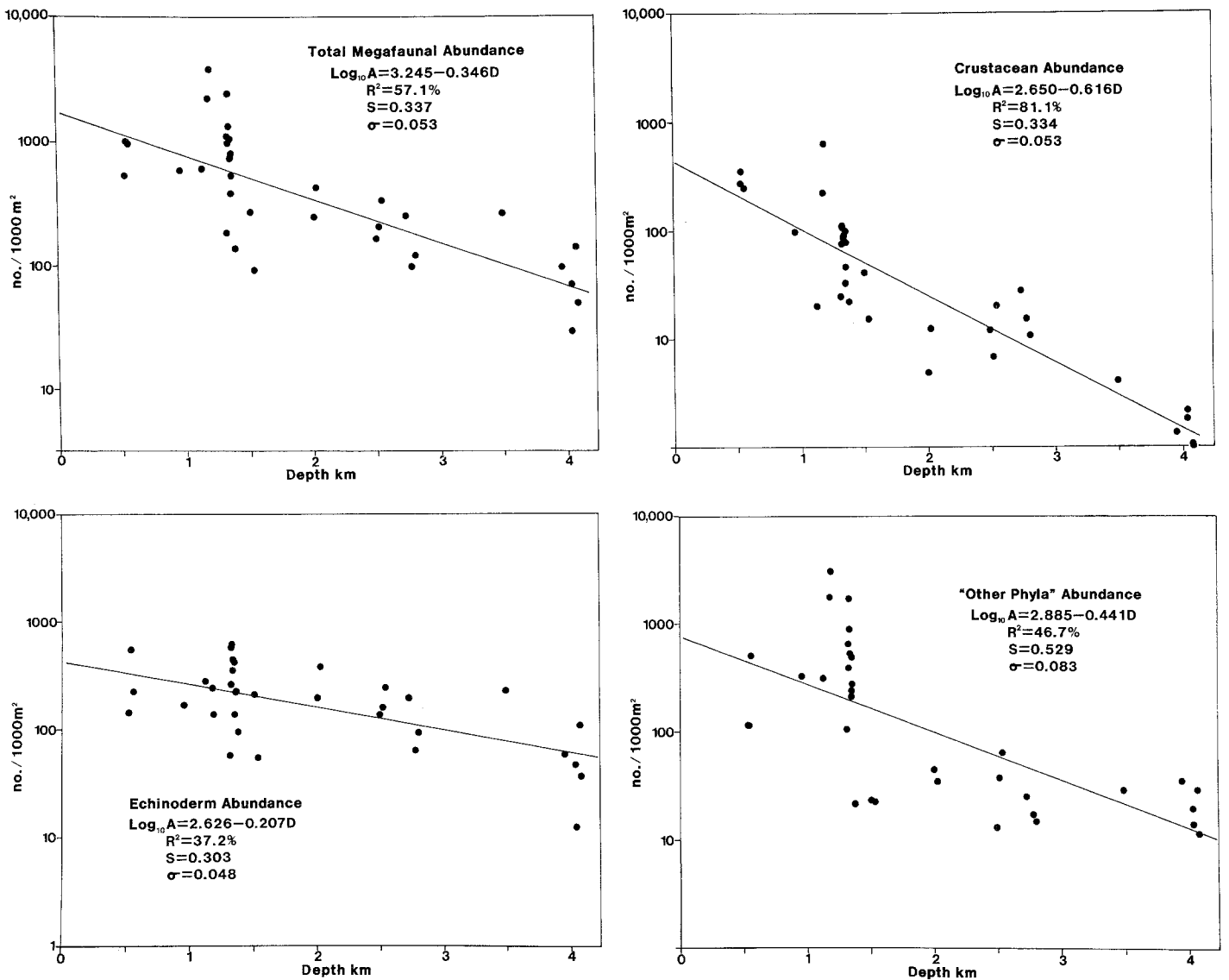


Fig. 4. Relationship between abundance and depth of all megafaunal specimens and of each of the three main taxonomic categories

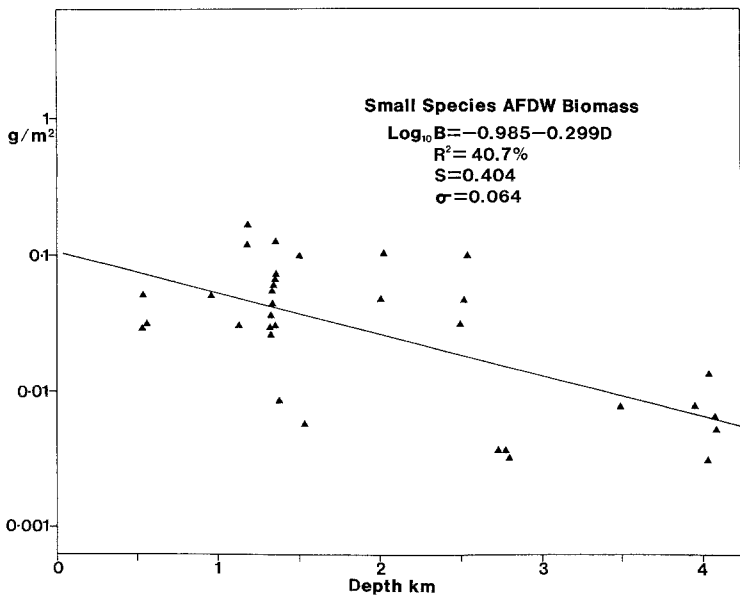


Fig. 5. Relationship between ash-free dry weight biomass and depth for species with a mean ash-free dry weight of less than 1 g (small species)

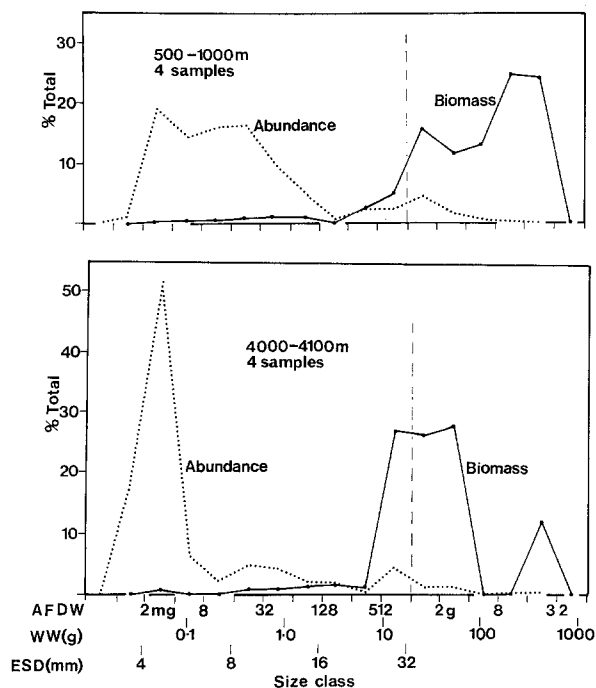


Fig. 6. Distribution of megafaunal biomass (ash-free dry wt: AFDW) and abundance of specimens collected in the four shallowest and four deepest hauls. Values expressed as percentage of total biomass and abundance. Dashed line is at 1.0 g mean AFDW and represents the boundary between “small” and “large” species (see “Results – Body weight and depth”). Specimens were allocated to a particular size-category on the basis of the mean weight of that species in the haul. For comparison with size-classes previously published, wet weight (WW) classes (Haedrich *et al.*, 1980) have been calculated using the conversion factor derived in this paper of 17.5 g WW per g AFDW. This factor has also been used to calculate equivalent spherical diameter (ESD) (Schwinghamer, 1981) assuming a specific gravity of wet specimens of 1

large species make to the total biomass. Small species may be arbitrarily defined as those with a mean body weight less than 1 g AFDW. The biomass/depth plot for small species (Fig. 5) has a much shallower gradient than that for all species (0.30 ± 0.06 vs 0.48 ± 0.07). Dominance of the megafauna by large species at shallow depths by a factor of 10 was reversed at the base of the slope, where small species became more important.

The decrease in mean body weight was almost entirely due to changes in species composition. At the shallower stations, biomass was dominated by the crab *Geryon tridens* and the sponge *Pheronema carpenleri*, two large organisms with weights in the size range 16 to 32 g and 4 to 8 g (AFDW), respectively, while at the bottom of the slope (about 4 000 m) echinoderms in the size range 0.5 to 4 g AFDW were dominant. This difference is reflected in plots of biomass in species mean-weight classes. Examples of two such plots are shown in Fig. 6, where four samples from each end of the transect have been amalgamated. In samples from the top of the slope 11% of the biomass was accounted for by small species (sum of values in size classes less than 1 g), whereas at the base of the slope the value was 34%, demonstrating the increase in importance of

small species with increased depth. As might be expected, small species were numerically dominant in both cases, providing 93 and 98% of the specimens at the top and bottom of the slope, respectively. The deep samples showed a greater numerical bias towards the smaller size categories than those at the top of the slope, with more than half the specimens having a mean species weight < 4 mg. Species less than 2 mg were not adequately represented in our samples since they would readily pass through the net. If the weight classes in these graphs had been expressed in terms of specimen weight instead of species weight, the curves would have been smoother but the general picture would be unchanged.

Small-scale distribution

The shallow repeat site at about 1 300 m seemed to differ from most other areas in the PSB in having very sharp faunal discontinuities. A twenty-fold range in total AFDW biomass occurred amongst the samples from this site, largely due to the varying abundance of the suspension-feeding hexactinellid sponge *Pheronema carpenleri*. This is a large species which reached a density of 475 per 1 000 m² and a biomass of about 2 g m⁻² (AFDW) in a sample from 1 293 m. For convenience, the data are presented as a biomass/depth plot (Fig. 7), but from phototranssect data (Rice and Thurston, in preparation) it is apparent that the ten hauls covered only the lower boundary of the *P. carpenleri* range. Shallower than 1 283 m, this sponge continued to increase in importance and the apparent decrease in biomass from 1 293 to 1 286 m is due to patchiness. Between 1 300 and 1 330 m, biomass and density levels of suspension-feeders were much lower than at 1 280 to 1 300 m, and tended to be dominated by the sponge *Thenaea* sp. and species of Madreporaria. Several species, such as a pectinid bivalve, polychaetes and a small ophiuroid (*Ophiactis abyssicola*) which would not normally be captured by the sledge, are commensal with *P. carpenleri* and they therefore contributed significantly to megafaunal numerical abundance, as defined here, at stations with *P. carpenleri*. Their contribution to megafaunal biomass was, however, insignificant. One might expect the biomass of other megafaunal species to follow the variations in biomass of such a dominant species as *P. carpenleri* but, apart from the sponge commensals, none of the megafauna appeared to show any evidence of co-variance. Variances in the biomass estimates for the suspension-feeders are thus considerably higher (71% of log mean biomass) than the value for fauna which are not suspension-feeders (16%). The graphs of biomass and abundance of the three groups (Figs. 3 and 4) further serve to indicate that the environmental factors apparently influencing the suspension-feeders had no effect on the crustaceans or echinoderms.

The deep repeat-site did not appear to encompass any sharp faunal discontinuities. The megafauna in this region was sparse and the small numbers caught lead to larger errors in the estimate of the population mean than would be

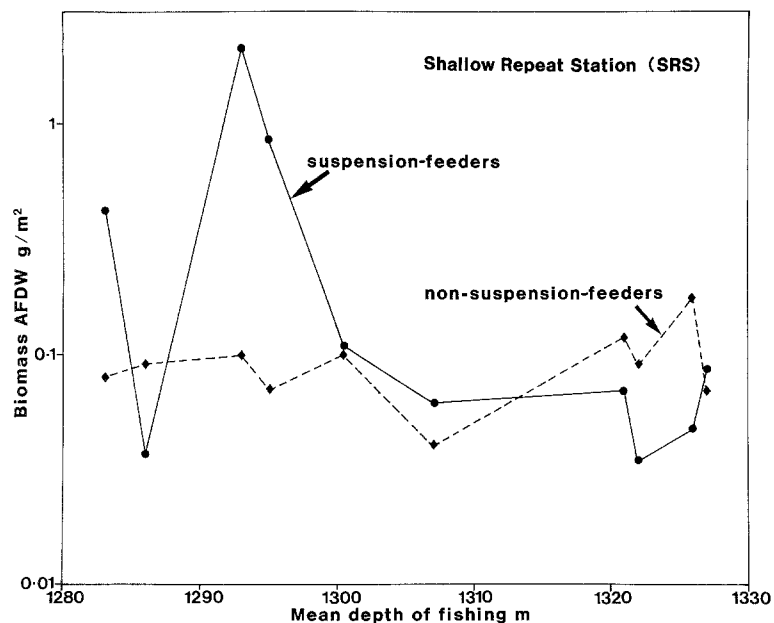


Fig. 7. Biomass of sessile suspension-feeders and non-suspension-feeders at the shallow repeat station

obtained at mid-slope depths. AFDW biomass at this site was $12.6 \pm 9.5 \text{ mg m}^{-2}$ and total megafaunal abundance 73 ± 49 per 1000 m^2 .

Discussion

Spatial variability

The object of establishing shallow and deep repeat-stations on the transect line was to estimate confidence intervals for biomass measurements which could then be applied, albeit cautiously, to other parts of the transect where only single samples were available. Although the standard deviation of log AFDW biomass of the shallow repeat site (0.415) is close to that for the biomass-depth regression at all stations (0.467), comparison of this site with the other depths where two or more samples were taken (500, 2 000, 2 500 m: Fig. 2) suggests that the repeat-site is particularly variable. A closer inspection of the data presented here (Fig. 7) and phototransect data (Rice and Thurston, in preparation) gives a very strong indication that this area encompasses a sharp faunal discontinuity with respect to the dominant fauna (*viz.* *Phoronema carpenteri*). If this is the case, the objective of establishing a repeat-site here may not be achieved, as the site may no longer be considered a single environment.

Such a sharp discontinuity (ten-fold drop in biomass over 12 m vertical distance) has not been reported previously for the megafauna, but although the data contribute little to the debate on the causes of bathymetric zonation (Carney *et al.*, 1983 and references therein), they do show that such zones may have very sharp margins. They also show that a boundary in the distribution of one species may not be associated with any change in the rest of the benthos. Differences in the degree of motility of the fauna or their trophic position have been put forward to explain

differences in the degree of zonation (Rex, 1977; Haedrich *et al.*, 1980). Although both factors may affect faunal distributions at the shallow repeat site, species of lower trophic level such as sponges might be expected to be less heavily zoned than the rest of the megafauna (Rex, 1977). Furthermore, some sessile suspension-feeders have very wide depth ranges (Belyaev, 1972; *in:* Carney *et al.*, 1983). It is perhaps significant that this particular boundary coincides with the lower boundary of the oxygen minimum layer of the Mediterranean outflow ($200 \mu\text{M O}_2$). A zone of rapid faunal change has also been found at the lower boundary of the Pacific oxygen minimum between 400 and 700 m ($22 \mu\text{M O}_2$) (Pearcy *et al.*, 1982).

At the deep transponder site, the standard deviation of the log AFDW biomass is again similar to that of the regression line at 0.402 and much of this is due to the very low numbers of large species. At both shallow and deep transponder sites, exclusion of large species ($> 1 \text{ g AFDW}$ species mean weight) from the biomass calculation lowers the standard deviation (*viz.* 0.212 and 0.268, respectively).

The standard deviation of the regression of biomass of small species on depth (Fig. 5) is 0.404, a value considerably higher than the standard deviations of small-species biomass at either repeat site. This implies that departures from the regression line reflect departures from a semilog relationship rather than an artefact of sampling.

Comparison of biomass units

The only previous deep-sea biomass transect which was expressed in more than one unit of biomass was that of Rowe and Menzel (1971) on the macrofauna of the deep Gulf of Mexico. They concluded that any one of the units WW, DW and organic carbon was a satisfactory index of biomass. The gradient of the biomass-depth regressions differed little (0.54, 0.57 and 0.52, respectively) and even nu-

merical abundance was considered a reasonable biomass estimate. One might expect that the unit used for megafaunal biomass might be more critical than that for the macrofauna because of greater differences in body composition between phyla. Comparing areas dominated by such different fauna as decapod crustaceans, sponges, asteroids and holothurians, for instance, would therefore demand a more biologically meaningful unit of biomass such as AFDW (present study), calorific value, organic carbon or nitrogen.

However, the results presented here show that whichever unit is used, essentially the same relationship of biomass with depth is evident. The gradients do not differ significantly, although there is a distinct reduction in error about the regression when expressing biomass as DW as opposed to WW, and a further improvement when AFDW is used. In fact, using AFDW as opposed to WW reduces the standard deviation of biomass about the regression by 36%.

Because the three gradients are so similar, useful single conversion factors may be derived from the regression. At any depth, the wet weight is about 5 times the dry weight, which in turn is about 3.5 times the ash-free dry weight. This compares with the macrofauna of the Gulf of Mexico where the wet weight was 9.1 times the dry weight (Rowe and Menzel, 1971).

A separate, but related, issue is the trend of body composition of the various faunal groups down the slope. Changes in water or ash content might be expected, but no significant trends were found for crustaceans, holothurians, asteroids, echinoids or ophiuroids. Mean values for all the collected specimens are presented in Table 1.

Geographic variation in megafaunal biomass

Previous quantitative studies of the deep-sea megafaunal biomass have not been made using sampling gear of known catching efficiency and, at least for invertebrates, those estimates should be considered as minima. The IOS epibenthic sledge, however, provides abundance estimates of the megafauna which correspond very closely with estimates based on phototranssects (Rice *et al.*, 1982). Variations in megafaunal abundance between areas may be large in comparison with differences resulting from the method of capture. It is important, therefore, to compare

the values presented here with the very few values obtained in other areas of the deep sea.

The most extensive previous study was made on the continental slope and rise off southern New England (western Atlantic) (Haedrich *et al.*, 1980). These samples were taken primarily to study faunal zonation, biomass estimates being expressed as mean values for each of eight zones which were identified on the basis of faunal composition. The authors did not express their results in terms of biomass per unit area, presumably because of doubts about fishing efficiency (Haedrich *et al.*, 1975). However, we have calculated biomass values based on raw catch-data supplied by R. L. Haedrich and on the published information on fishing behaviour of their trawls (Haedrich *et al.*, 1980). The regression of wet weight megafaunal biomass including fish (B in g m^{-2}) on depth (D in km) for all 105 of their stations was $\log_{10} B = 0.0693 - 0.31 D$. In their samples Haedrich *et al.* (1980) found that fish contributed about 40% to the biomass at the top of the slope, and 60 to 70% below 2 500 m (in the PSB the fish contribute about 20% at the top of the slope and 65% at the base: N. R. Merrett, personal communication). By comparing the regression derived in the present study with that for the data of Haedrich *et al.* (1980) (all stations) and reducing their total biomass values by the above values to remove the fish contribution, the PSB appears to support an invertebrate biomass about 18 times higher at 500 m (8.95 vs 0.49 g m^{-2}) and 10 times higher at 4 000 m (0.22 vs 0.022 g m^{-2}) than the slope off southern New England. It should be pointed out, however, that after a comparison of megafaunal abundance measured by both trawl and photography, Haedrich *et al.* (1975) concluded that the trawl underestimated abundance by "an order of magnitude or more".

Megafaunal biomass has also been estimated on the Demerara Abyssal Plain (Sibuet *et al.*, 1984, their Station B). Fish contributed about 20% to the megafaunal wet weight biomass, and the invertebrate dry weight biomass of 4.5 mg m^{-2} was less than half the value for the PSB regression of 11.7 mg m^{-2} (extrapolated to the same depth of 4 800 m). At a similar depth, but at a site subject to particulate input from the Amazon, the invertebrate megafaunal biomass was 37 mg m^{-2} , a value double the PSB value (extrapolated to 4 440 m).

In the Bay of Biscay at 2 100 m, the megafaunal biomass was found to be 156 cal m^{-2} (Khrpounoff *et al.*, 1980). Using a value of 4.5 cal mg^{-1} AFDW (Wissing *et al.*, 1973, for benthic invertebrates) this is equivalent to a biomass of $35 \text{ mg AFDW m}^{-2}$. It is not clear if this includes fish, but it compares with a value of 85 mg m^{-2} derived from the regression for the PSB for invertebrate megafauna at that depth.

By comparison with other deep oceans, the invertebrate megabenthos of the Atlantic is relatively well sampled. In the Pacific, no quantitative data appear to have been published for the oligotrophic central gyres although data are available on fish biomass (Pearcy *et al.*, 1982, and references therein). At 1 300 m in the Santa Catalina Basin,

Table 1. Body composition of invertebrate megabenthos. Values are means for all specimens collected

	% water	% ash	% organic
Crustacea	71.89	11.28	16.83
Echinodermata	86.13	9.71	4.16
Holothurioidea	93.58	3.64	2.78
Asteroidea	63.84	27.11	9.05
Echinoidea	73.86	19.94	6.20
Ophiuroidea	48.10	43.23	8.67

Smith and Hamilton (1983) reported a megafaunal biomass (WW) of 68 g m^{-2} . Ninety-nine per cent of this comprised one species of ophiuroid and the total was eighteen times higher than the value from the PSB regression. If converted to AFDW using Table 1, the Santa Catalina Basin supports a megafaunal biomass 25 times larger than the PSB.

Ohta (1983) determined the megafaunal biomass in Suruga Bay off Japan using a photographic technique. The wet weight of total megafaunal biomass increased from 2 g m^{-2} at shallow depths ($< 90 \text{ m}$) to about 50 g m^{-2} at $1\,000 \text{ m}$, followed by a decline to about 0.8 g m^{-2} at $2\,800 \text{ m}$, the greatest depth sampled. In the upper middle slope subzone (400 to 700 m), about 10 g m^{-2} were found. Fish contribute about 25% to the total here, leaving an invertebrate biomass of 7.5 g m^{-2} . This is very close to the value of 9.0 g m^{-2} for the PSB at 500 m . In the deeper trough-floor subzone ($2\,000$ to $2\,830 \text{ m}$), however, with only three stations, the invertebrate megafaunal biomass was 0.20 g m^{-2} , a value six times lower than the PSB value of 1.2 g m^{-2} at $2\,400 \text{ m}$.

Thus, the megafaunal biomass of the PSB seems to be very similar to that in the Bay of Biscay, in the Demerara Abyssal Plain and at the top of the slope off Japan, but about 18 times lower than that in the Santa Catalina Basin and may be considerably higher than that off southern New England.

A major question posed by these findings is what is the reason for these variations in biomass. It is well established that regional variations in the biomass of both the meio- and macrofauna are closely linked to the nutrient supply (Rowe, 1971; Hessler and Jumars, 1974; Thiel, 1979; Carey, 1981; Pfannkuche *et al.*, 1983), and this has been taken to indicate food limitation as the factor controlling faunal biomass in the deep sea, as opposed to factors such as predation or space. If explanations for global variability of biomass are to be obtained, biomass trends over relatively short horizontal distances should also be examined. In the present study the gradient of the wet-weight biomass/depth regression (0.458 ± 0.095) is very similar to that off Southern New England (0.315 ± 0.057) (Haedrich *et al.*, 1980).

Except in areas where horizontal transport is indicated (Carey, 1981; Smith and Hamilton, 1983), nutrient supply may be taken as the carbon flux measured by sediment traps. This is directly related to surface primary productivity and inversely related to water depth (Suess, 1980) so that for depths greater than 50 m , the percentage of primary production Y reaching a particular depth X (m) is given by $Y = 701 X^{-0.782}$ (Parsons *et al.*, 1984, p. 226). Vertical changes in material flux are not yet available for the PSB, but using this regression the flux at $4\,000 \text{ m}$ would be expected to be 34% of that at $1\,000 \text{ m}$, while the megafaunal biomass (AFDW) at $4\,000 \text{ m}$ is only 3.6% of that at $1\,000 \text{ m}$. If, on the other hand, only the small megafaunal species are considered (Fig. 5), the biomass at $4\,000 \text{ m}$ is 13% of that at $1\,000 \text{ m}$, a value closer to the estimated difference in food supply. No data are available on the

macrofaunal biomass for the PSB, but it appears that the metazoan meiofauna biomass in the Seabight (Pfannkuche, 1985) is influenced even less by depth than is that of the small megafauna. The meiofauna (42 to $1\,000 \mu\text{m}$) had biomass levels about twice that of the megafauna on the upper slope, but nearly 40 times greater at the bottom of the transect. The gradient of the regression was -0.00898 , and biomass at $4\,000 \text{ m}$ was about 70% that at $1\,000 \text{ m}$, while the estimated food input is only 34%. Although the error of this estimate of meiofaunal biomass is small, it should be pointed out that the trend may not continue out into the abyssal plain. Rutgers van der Loeff and Lavaleye (1984) measured meiofaunal and macrofaunal biomass on the Porcupine Abyssal Plain about 450 km from the mouth of the PSB at depths of $4\,000$ to $4\,800 \text{ m}$. The biomass of the meiofauna (50 to $1\,000 \mu\text{m}$) is about 100 times lower than at the base of the slope in the PSB, and equivalent to the megafaunal biomass in the PSB at $4\,000 \text{ m}$. These authors also found that the macrofauna ($> 1 \text{ mm}$) had biomass values about four times higher than the meiofauna.

In contrast to the PSB, in the area south of New England there was little difference in the biomass/depth gradient between the megafauna and smaller organisms (in this case the macrofauna). In this area, the gradient of macrofauna biomass on depth was found to be 0.39 (Rowe *et al.*, 1982), while that for the megafauna was 0.315 (derived by us from Haedrich *et al.*, 1980). The organic carbon flux south of New England, measured using sediment traps (Rowe and Gardner, 1979), was very close to or even slightly higher than the estimated values for the PSB, yet the megafaunal biomass (Haedrich *et al.*, 1980) may be much less than in the PSB. In the Demerara Abyssal Plain, Sibuet *et al.* (1984) compared two sites at similar depths, one of which (Station A) is supplied with particulate material from the River Amazon. Sediment trap data showed that the organic carbon flux at Station B, which was not subject to Amazon input, was 65% of that at Station A, while the invertebrate megafaunal biomass was 12% of that at A. The biomass of the meio- and macrofauna at Station B were, respectively, 38 and 50% of those at Station A, and the conclusion was drawn that the megafauna are more sensitive to food supply than smaller size groups (Sibuet *et al.*, 1984). It seems that an explanation of biomass variations based simply on food limitation cannot be applied to the megabenthos as has been done for smaller size groups (Rowe, 1971; Thiel, 1979; Carey, 1981; Pfannkuche *et al.*, 1983).

Before discussing the reasons for this apparent sensitivity of the megafauna to reduced food supply, it is worth estimating the proportion of the total food input utilised by them. This may be done using data on the *in situ* metabolic rates of two megafaunal species; the ophiuroid *Ophiophthalmus normani* and the holothurian *Scotoplanes globosa* at $1\,300 \text{ m}$ in the eastern Pacific Ocean (Smith, 1983). Both species are of similar body dry weight, and for specimens of 0.5 g dry weight, a value not significantly different from the mean body weight in the PSB, their weight-specific respiration rates were 70 and $72 \mu\text{l O}_2 \text{ g}^{-1} \text{ dry wt}$

h^{-1} , respectively. A value of $71 \mu\text{l O}_2 \text{g}^{-1} \text{dry wt h}^{-1}$ is equivalent to a food demand of $0.78 \text{ mg C g}^{-1} \text{dry wt d}^{-1}$ assuming an RQ of 0.85 (Parsons *et al.*, 1984 p. 132). Using this value and the PSB biomass/depth regression (Fig. 2: DW) we can calculate a daily respiratory demand of the megafauna of 0.91 mg C m^{-2} at 1 000 m and $0.025 \text{ mg C m}^{-2}$ at 4 000 m. If the nutrient supply rates based on the primary productivity value of $200 \text{ mg C m}^{-2} \text{d}^{-1}$ (Koblentz-Mishke *et al.*, 1970) are applied to the vertical flux regression of Suess (1980), the food supply would be $6.32 \text{ mg C m}^{-2} \text{d}^{-1}$ at 1 000 m and $2.14 \text{ mg C m}^{-2} \text{d}^{-1}$ at 4 000 m. The megafauna would therefore require 14 to 1.0%, respectively, of the food input for metabolic purposes.

The estimated reduction of the proportion of food input used with increasing depth is compatible with food limitation as the factor controlling megafaunal biomass only if other factors change. Firstly, the ratio of production to biomass may increase with decreasing food supply. Intuitively this seems unlikely, but for the moment it cannot be discounted since data on growth rates in the deep sea are both rare and contradictory (e.g. Turekian *et al.*, 1975; Zezina, 1975). An alternative possibility is that with decreasing food supply the megafauna occupy a position further along the food chain, so that greater accumulated losses between each trophic level make less food available. For the asteroids and maybe other taxa, the reverse trend is apparent, for although carnivores are common at shallow depths, with increasing depth they become much less common and omnivores dominate (Carey, 1972). Another alternative and more attractive hypothesis concerns the quality of the food supply. Although the majority of the food supplied to the benthos is probably in the form of fast-sinking aggregates of phytodetritus (Deuser *et al.*, 1981; Honjo, 1982; Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, in press), qualitative changes in the material during its descent may render it indigestible to the megafauna. If the percentage of the food input utilized by the megafauna, small as it is, represents the maximum percentage they are able to assimilate, a small change in the overall flux and composition may represent a substantial change in their available food supply. The remaining food is presumably used by other faunal groups, since the percentage of organic carbon preserved in sediments does not increase with water depth.

The size/depth relationship

The two methods of examining body size in this paper both suggest that small species gain in importance with increasing depth. The mean body weight (AFDW) shows a small and insignificant decline with increasing depth in a similar fashion to that reported for the decapods and echinoderms (WW) in the western Atlantic, although fish appeared to be bigger deeper (Polloni *et al.*, 1979, but see Pearcy *et al.*, 1982). Mean body weight is not, however, a very useful parameter since it is influenced greatly by the large numbers of small organisms which make a negligible contribution to the total biomass and it is therefore very sensitive to the

sampling technique employed. (Polloni *et al.* used two types of trawl which may have different sampling capabilities.) Haedrich *et al.* (1980) gave data on the size distribution of the same specimens as those used by Polloni *et al.* They expressed the results as abundance in each of six size-categories, the lower five of which are shown in Fig. 6 for comparison with our data. In contrast to the data of Haedrich *et al.*, samples between 500 and 1 000 m in the PSB are dominated numerically by species in the wet weight size-range 0.1 to 1.0 g. We feel that this may not be a real difference, but may reflect the difference between the sampling capabilities of the trawls used by Haedrich *et al.* (37 mm mesh size) and that of the IOS sledge (4.5 mm mesh size) to capture species with equivalent spherical diameter of 5.8 to 12.4 mm (*sensu* Schwinghamer, 1981). Another point of apparent difference between the western Atlantic and the PSB is that at mid-slope depths, but not elsewhere, Haedrich *et al.* collected some very large organisms in the size range 1 to 100 kg. They suggested that this indicates a requirement to forage further than at shallower depths because of the reduced food supply, but the absence of these large organisms at greater depths is less easy to explain. Our data are not directly comparable with those of Haedrich *et al.*, since several of the distinctive features of the size spectra from the western Atlantic, including the one just mentioned, are due to fish (Haedrich, personal communication) a group specifically excluded by us.

Megafauna have traditionally been thought of as large macrofauna. If this is the case, most of the biomass would be in the small size-categories, and removing large species from the biomass/depth regression would have little effect on that regression. In fact, it actually reduced the gradient of the regression significantly (Figs. 2 and 5). Fig. 6 shows a sharp cut-off at the lower size-limit which is at a much larger size than that determined by the mesh size of the net. [In the samples from about 4 000 m, species of mean weight (AFDW) greater than about 300 mg are responsible for 90% of the biomass, while the net would probably retain all specimens greater than 2 mg (equivalent spherical diameter ~ 4 mm)]. Thus, the relative rarity in our samples of species in this size range seems to be a true reflection of the epifaunal community and not simply a sampling artifact.

We suggest that the megafauna are a distinct epifaunal functional group as has been proposed for the micro-, meio- and macrofauna (Schwinghamer, 1981; Warwick, 1984). It seems likely that when biomass size-spectra are available for both the macro- and megafauna at one site, there will still be a trough between these categories. However, the problems of obtaining such macrofaunal size-spectra are considerable, since the larger macrofaunal organisms are both too sparse to be sampled adequately by small numbers of box core or grab hauls, and live too far beneath the sediment surface to be sampled with trawls, sledges or cameras. Indeed, because of the small numbers of large macrofauna in box cores, they have often been disregarded in studies of the infauna (e.g. Gage, 1977).

Table 2. Biomass of different faunal groups relative to that of the meiofauna at the same site. The meiofaunal biomass is taken as unity. Sites are arranged in order of probable decreasing food supply. Note that two of the megafaunal values are relative to macrofaunal biomass since no meiofaunal data were available. Dashes indicate no data

Nanobiota	Metazoan meiofauna	Macrofauna	Invertebrate megafauna	Location	Source
17.6	1	144	–	Intertidal, high-organic silt/sand	(5)
7.5	1	37.2	–	Intertidal, low-organic sand	(5)
–	1	24	–	Martha's Vineyard, shelf	(10)
–	1	45	0.80	500 m W. Atlantic Ocean	(10, 4)
–	1	6.0	–	100 m N. E. Atlantic Ocean, neritic zone	(2)
–	1 ^a	0.30	–	800 m N. W. Africa	(3)
–	–	1	8.5	1 300 m Santa Catalina Basin, East Pacific Ocean	(7)
–	1	2.9	1.2	4 440 m Amazon Cone	(6)
–	1 ^a	–	0.58	500 m N. E. Atlantic Ocean, Porcupine Seabight	(1)
–	1	1.6	0.70 ^b	2 100 m N. E. Atlantic Ocean, Bay of Biscay	(2)
–	1	2.3	0.42	4 840 m Demerara Abyssal Plain	(6)
–	1 ^a	0.13	–	3 000 m N. W. Africa	(3)
–	1	3.9	–	N. E. Atlantic Ocean, 4 000–4 800 m	(9)
–	1 ^a	–	0.24	4 000 m, N. E. Atlantic Ocean, Porcupine Seabight	(1)
–	–	1	0.019	4 000 m W. Atlantic Ocean	(4)
–	1	0.95	–	5 100 m Vema Fault, W. Equatorial Atlantic	(2)
4.1	1	0.16	–	5 800 m Central North Pacific Ocean	(8)

Source	Biomass unit
(1)	Pfannkuche (1985) and present study
(2)	Khripounoff <i>et al.</i> (1980)
(3)	Pfannkuche <i>et al.</i> (1983) [assuming wet wt of meiofauna = 4 × dry wt: Warwick (1984)]
(4)	Rowe <i>et al.</i> (1982); Haedrich <i>et al.</i> (1980)
(5)	Schwinghamer (1981)
(6)	Sibuet <i>et al.</i> (1984)
(7)	Smith and Hamilton (1983)
(8)	Snider <i>et al.</i> (1984)
(9)	Rutgers van der Loeff and Lavaleye (1984)
(10)	Wigley and McIntyre (1964)

^a Meiofaunal biomass values given in Pfannkuche *et al.* (1983) and Pfannkuche (1985) are very much higher than other published values. The reason is not clear, but if they reflect a methodological difference, the derived ratio may not be strictly comparable with those derived from other published values

^b It is not clear whether the megafauna biomass value quoted in Khripounoff *et al.* (1980) includes fish

A number of studies have indicated increasing importance of small organisms within the meio- and macrofauna with increasing depth (Thiel, 1975, and references therein). The data of Sibuet *et al.* (1984) and the present study suggest that this can be extended to include the megafauna.

Contribution of megafauna to total biomass

Criteria for distinguishing between different faunal groups and methods of measuring biomass vary between authors, but a general comparison of biomass distribution is possible since regional variations are so large. In Table 2, data from several sources are presented on the biomass of particular size-categories relative to that of the meiofauna. They are arranged in order of probable decrease in food input, and demonstrate how great is the shift in biomass. Although the exact sequencing may be disputed, the general shift towards smaller-sized classes with decreasing food input is clear. It seems that the megafauna dominate

the fauna in terms of biomass only when the food input is high, as in the Santa Catalina Basin or the Amazon Cone where advective transport is substantial, and become relatively less important with decreasing food supply. This is not to say, however, that they are not key elements in shaping the structure of deep-sea food webs; it is almost certain that the activities of the deposit-feeding megafauna influence the meiofauna and macrofauna both by ingesting these smaller animals and as a result of their physical disturbance of the sedimentary environment.

Conclusion

The data presented here indicate that the logarithmic decline in biomass with depth found on the western side of the Atlantic Ocean is not restricted to that particular area. Whichever unit of biomass is used, the gradients of the regressions from the northeast Atlantic reported in this study and those previously obtained in the west are so similar as

to suggest some fundamentally similar control of biomass, even though the absolute values on the west may be much less than those found in this study. From a comparison of these and other sites, it seems that the megafauna is more sensitive to changes in the food input than are the smaller size classes. The contribution of the megafauna to the total benthic biomass therefore decreases with reduced food supply and so also with increasing depth. The biomass of small species of megafauna (< 1 g AFDW) did not decline as rapidly with increasing depth as total megafauna, and thus they became a more important component of the megafauna at greater depths. There is, however, no statistically significant decline in mean body weight with increasing depth.

The vast majority of the epifaunal biomass retained by the sledge net used in this investigation was made up of species with mean ash-free dry weights greater than 300 mg, and these may form a functional group as has been proposed for the micro-, meio- and macrofauna.

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