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Small scale patterns in the structure of macrofaunal assemblages of shallow soft sediments

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Abstract

The spatial scale of local patterns in the fauna of two contrasting shallow water sediment assemblages has been investigated using hierarchical sampling. Replicate samples were taken at separations of 50 cm, 5 m, 50 m and 500 m. No significant differences between samples could be detected on any of these scales in a fine sand assemblage. However, in a heavily bioturbated sandy mud, samples separated by more than 50 m were significantly different from each other. This separation was largely a result of changes in the pattern of dominance among the most abundant species, particularly annelids. In a complimentary set of analyses, animals were regrouped either by higher taxa or by body size. The numerically important annelids and crustaceans showed a pattern of spatial similarity close to the full data set, but that shown by molluscs was clearly distinct. Large bodied animals were also independent of the main pattern while smaller species conformed to it. In the case of the latter, separation of sites at the 50 m scale could be related to patterns of species richness as well as dominance.

Keywords: Benthos; Scale; Spatial pattern; Survey methods

1. Introduction

Benthic ecological studies of soft sediments are carried out for many reasons, from faunal description to the detection and assessment of the impact of pollution. In most cases, they are costly, as although sampling might be relatively inexpensive, the costs of analysis can be high. In view of this expense, every effort must be made to ensure that their design is such that the sampling design employed provides the most cost efficient solution to the question being posed. The broad acceptance of multivariate data analysis

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has provided the impetus for a number of authors to suggest ways in which costs can be reduced. Standard benthic data sets contain a vast amount of information and much of this can be considered redundant in the context of pattern description (Clarke and Warwick, 1988). A number of ways have been suggested by which some of this unneeded information can be dispensed with, without significantly affecting the biological interpretation of the faunal pattern. These include the use of larger sieve meshes (James et al., 1995) and hence having a smaller number of animals to identify or changing the taxonomic resolution with which animals are identified (Warwick, 1988; James et al., 1995; Somerfield and Clarke, 1995). Although others have examined the effects of changing the size of the sampling device or optimising the number of replicate samples (Bros and Cowel, 1987; Veijola et al., 1996) less attention has been focussed in community studies on the spatial layout of the sampling stations and separation of replicates within them. While a substantial literature exists on the spatial scales at which individual species are distributed (for example, Angel and Angel, 1967; Gage and Geekie, 1973; Thrush, 1991) the conclusions are not necessarily appropriate for the design of community studies.

Although studies have been performed on the spatial distribution of single species (see above), or small groups of species, comparatively few have addressed spatial variability of whole faunal assemblages. This is surprising, as such studies are vital for the formulation of monitoring and management strategies. Those who have done so have concentrated on the univariate analysis of either diversity or of the abundance of taxonomic groups (Morrisey et al., 1992). This paper will address the need for information on the spatial variability of benthic assemblages. In the deep ocean, Jumars (1975) examined the hypothesis that species diversity was independent of location and sample size, but concluded that processes operating at the scale of a single large macrofaunal individual might be of greater importance. On the other hand, Morrisey et al. (1992) employed a hierarchical spatial sampling programme to acquire data on the benthic fauna of shallow soft sediments in Botany Bay, Australia. They analysed information on eight major taxa as well as community properties such as the total individuals and total number of species to describe significant local variation at scales from 10 m to 3.5 km.

An appreciation of spatial scaling is central to the design of any ecological study (Weins, 1989), but in the past the distribution of sampling stations, the size of sampler employed and the number of replicates taken have often been based on tradition and the experience of the scientist doing the planning (Andrew and Mapstone, 1987). However, when an investigation is planned to elucidate the relationship between process and faunal response it is vital that the spatial extent of the sampling matches that of the process in question. The most clearly conspicuous features of a study too small in scale may mask the effects of an over-riding process operating over a greater area; conversely, in a broad scale survey the causes of local variation will not be apparent. In planning, it is vital to appreciate both the scale at which the environment changes and that at which biological properties within it are distributed.

The relationship between the distribution of different grades of sediment and that of the benthic fauna has long been appreciated (Jones, 1951; Gray, 1974). Sediments are relatively easy to map, particularly with the aid of acoustic or visual imaging (Magorrian

et al., 1995; Ruhmor, 1995), and sampling is often stratified on that basis. However, we know little of the characteristics of faunal variability within patches of apparently similar sediment. Before remote imaging can be used with confidence to map or predict the conservation value of the seafloor fauna, it is vital to obtain information on the scale of faunistic variability within such patches. In this study, we have used a hierarchical sampling design to investigate the spatial variability in two areas of subtidal sediment which have previously been regarded as homogeneous.

In single species studies the size of the sample has a clear effect on the way in which its pattern of distribution is perceived (Andrew and Mapstone, 1987, and references therein). In general, sample sizes smaller than the scale at which a species is aggregated will give more variable estimates of density than those which are larger than it. In community studies, variation in abundance and distribution of many species combine in the description of multivariate pattern. Here too, the size of the sampler must play a role in determining the description of variability. Some species will be sampled consistently and will contribute to a pattern, others will be sampled badly and little consistency will be detected in their pattern of distribution. Although the relationship between body size and abundance is not simple (Blackburn and Gaston, 1997), larger bodied animals tend to be less abundant than smaller ones. Some small species will also be intrinsically rare but, in general, it is reasonable to assume that animals of larger size, relative to the dimensions of the sampler, will contribute little to conventional, abundance-based, analysis. In this study, we have attempted to investigate the role of animals of different body sizes in determining the pattern within the assemblages investigated.

2. Methods

2.1. Sampling

Samples were taken from Jennycliff Bay and Cawsand Bay in Plymouth Sound, Devon, United Kingdom (50°20′N, 4°10′W) during July/August 1995. Each area was sampled within a week and there was a 2-week interval between the sampling periods.

The sites sampled in Jennycliff Bay were in an area that the Marine Biological Association (1957) describes as "a fairly extensive stretch of sandy mud". All samples came from depths of 10–12 m. The site in Cawsand Bay was at a similar depth and on a bottom of fine sand (Gibbs, 1969). The choice of these two locations was based on their difference in sediment type and on the extent of relatively homogeneous sediment at each.

Samples were taken using a hierarchical design based on nested equilateral triangles of side length 50 cm, 5 m, 50 m and 500 m. The 50 m triangles were labelled A, B and C. To minimise sampling effort, sampling at the 5 m scale was only carried out in triangle A and samples at the 50 cm scale were only taken in a single 5 m triangle at A (Fig. 1). In a single 5 m corner of triangle A, triangles of 50 cm side were set out at the apices and three contiguous cores taken at the corner of each (27 samples). These were used to test for effects at the 5 m scale. Effects at 50 m were assessed separately for triangles A, B and C by comparing the samples taken within each of the three 5 m

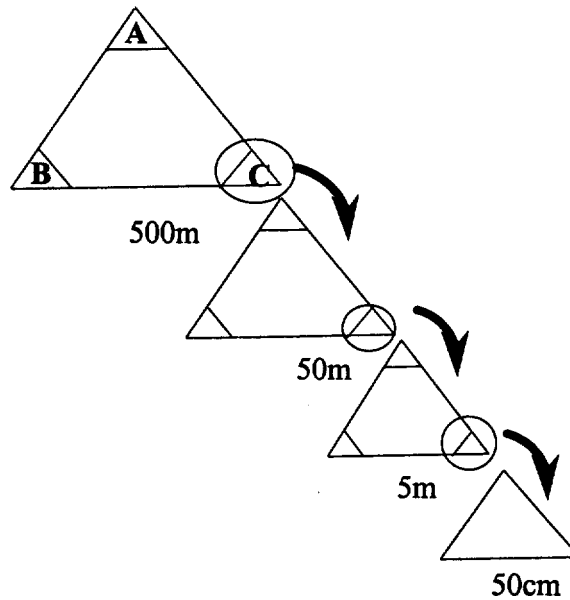

Fig. 1. Schematic representation of the hierarchical sampling scheme employed. Samples were taken in the corners of triangles nested at 500 m, 50 m (all locations), 5 m and 50 cm (Triangle A only).

triangles at their corners. In samples B and C, as there was no replication below the 5 m scale, there are fewer data on which to base similarity estimates. Effects at 500 m were estimated by considering only the samples taken at the corners of triangles A, B and C.

Core samples were taken by divers using 10 cm diameter plastic tubes (0.008 m^2 surface area) pushed into the sediment to a depth of 30 cm. These were then carefully excavated and sealed inside plastic bags. On the surface, the samples were sieved over a 0.5 mm mesh and the residue transferred to 10% buffered formalin. In the laboratory the sample was washed in water and transferred to 70% alcohol before all animals were extracted under a binocular microscope and identified to the lowest practical taxonomic level. In the case of the cirratulid polychaetes, the separation of individuals of the genera *Monticellina/Tharyx*, *Caulerialla* and *Chaetozone* was normally possible, however when damaged the individual species of *Monticellina/Tharyx* could not be reliably separated and hence have been combined in all data analyses. Wherever possible, species nomenclature has followed Howson (1987).

2.2. Data analysis

The data were analysed to examine the statistical significance of changes in community structure at the various spatial scales investigated. Considerably more data were collected in the A triangles than in Bs or Cs. Only replicates at the full separation (of 50 cm, 5 m, 50 m or 500 m) were considered in analysis and hence no single analysis used the complete data set.

The data were analysed untransformed and treated by $\sqrt{}$, $\sqrt{\sqrt{}}$ or presence/absence to evaluate the relative importance of dominance and species richness. As the strength of the transformation is increased the influence of the dominant species declines. While the MDS configuration of untransformed analyses is dominated by the commonest species, in presence/absence transformed analyses all species have the same influence. Two-way nested ANOSIM (Clarke and Green, 1988) was used to test for significant differences between the fauna at the various distances of separation. To visualise these analyses the data have been subjected to non-metric multidimensional scaling (MDS). All multivariate analyses and α-diversity calculations were performed using the PRIMER package (Clarke, 1993). For ease of comparison of the assemblages that we studied with those investigated by others, univariate measures of community structure have been calculated using the PRIMER package. Species accumulation curves were generated using the BiodiversityPro package (Natural History Museum/Scottish Marine Biological Association).

To investigate the species responsible for the patterns shown by ordination, further analyses were carried out on subsets of the full data matrix defined by major taxa and body size. The similarity of the whole data set to each of these subsets (untransformed and $\sqrt{}$, $\sqrt{\sqrt{}}$ and presence/absence transformed) was compared using second stage MDS (Somerfield and Clarke, 1995; Olsgard et al., 1997). This procedure generates a correlation between each pair of similarity matrices to produce a derived similarity matrix that is itself subject to ordination. The resulting plot gives an objective comparison between the matrices.

For consideration of the effects of body size all species were allocated to one of three classes based on a combination of geometric weight classes (Warwick, 1984). The allocation was based on the blotted wet weight of the largest individual encountered converted to dry weight using published conversion factors (Kendall et al., 1997). Species of geometric weight classes 10–14 were classed as small, animals between 15 and 19 were classed as mid-sized and the remaining animals classed as being large.

3. Results

3.1. Jennycliff Bay

The divers reported that the sandy mud (median grain size 4ϕ) of Jennycliff Bay is heavily bioturbated by the activities of the burrowing thalassinids *Upogebia deltura* and *Callianassa subterranea*. This was subsequently confirmed by ROV observations that also showed large specimens of *Mya truncata* to be common. None of these animals was taken by coring. Samples taken from the surface layer had a fauna numerically dominated by surface deposit feeding cirratulid polychaetes, principally *Chaetozone gibber* (Woodham and Chambers, 1994) and the ampharetid polychaete *Mellina elizabethae*. At slightly greater sediment depths were found moderate numbers of the infaunal maldanids *Euclymene oerstedi* and *Praxilella affinis*, exogonid syllid polychaetes and the caprellid *Pariambus typicus* were occasionally very common.

Table 1
Comparative data on the diversity of Cawsand Bay and Jennycliff Bay. All estimates are for 0.008 m^2 cores

	Number of species mean±95% CI	Number of individuals mean±95% CI	Shannon H'_e mean±95% CI
Cawsand Bay	21.45±1.1	78.82±6.31	2.36±0.06
Jennycliff Bay	31±1.43	196±16.15	2.59±0.08

3.2. Cawsand Bay

Numerically dominant in the fine sand (median grain size 3.4ϕ) samples from Cawsand Bay was the polychaete *Magalona filiformis*, although *Scoloplos armiger*, *Chaetozone gibber* (Woodham and Chambers, 1994) and *Mellina elizabethae* were well represented in all samples. The echinoderms *Amphiura brachiata* and *Amphiura filiformis* and lophophores of *Phoronis mulleri* were far more common than in the muddier sediments of Jennycliff Bay. Divers reported no visual evidence of bioturbation, but commented that the sediment surface was strongly rippled.

3.3. Assemblage structure

Samples from the community at Cawsand contained both fewer species and fewer individuals than those from Jennycliff Bay. Shannon diversity tended to be lower at Cawsand (Table 1). Species accumulation curves (Fig. 2) show that the number of species taken at Jennycliff is substantially larger than that from Cawsand. The mean Bray Curtis similarity between the two areas is 46% ($\sqrt{\sqrt{}}$ transformed data) or 51% based on species presence or absence. A total of 125 taxa were recorded, of these 54 were allocated to geometric size classes 10–14, 56 to classes 15–19 and only 15 to larger classes; of the total, 54 taxa were annelid and 34 were crustacean.

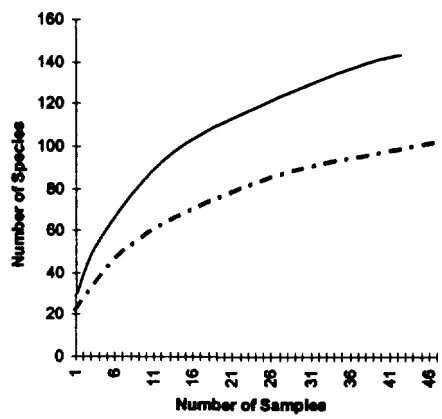

Fig. 2. Species accumulation plot for Jennycliff (———) and Cawsand Bay (- - -).

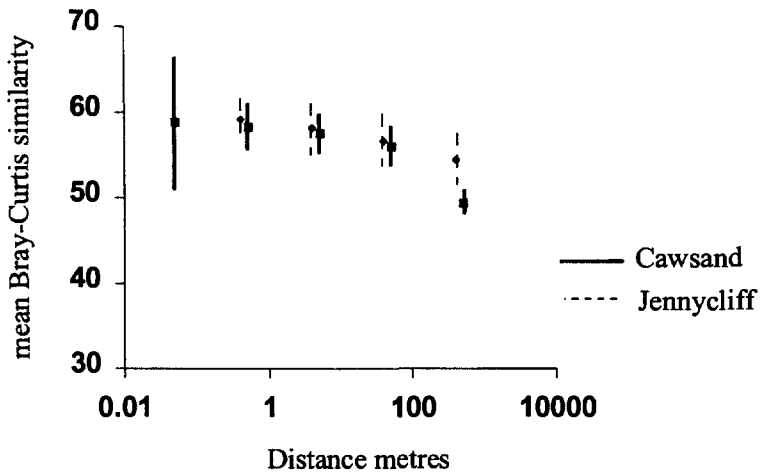

Fig. 3. Plot of the mean Bray Curtis similarity (untransformed data) against distance (±95% CI) for Cawsand Bay (———) and Jennycliff Bay (- - -).

3.4. Spatial variability

In Fig. 3 all possible combinations of sites have been considered in a plot of Bray Curtis similarity against the distance between samples. This generalised comparison is included as a demonstration of a broad pattern and should be considered alongside the ordination of the data in Fig. 4. The broad trend at both sites is for the mean similarity at separations of less than 50 m to be more or less consistent. The apparent homogeneity is extended to 500 m at Jennycliff, but a slight declining trend to 500 m is apparent at Cawsand. In this plot, the large number of comparisons tends to mask the true extent of between-sample variability.

A comparison of the fauna at different orders of spatial separation using one-way

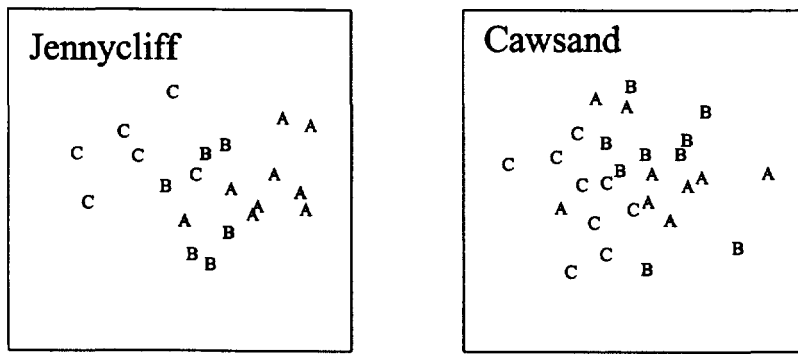

Fig. 4. MDS plot of $\sqrt{\sqrt{}}$ transformed community data for Jennycliff (stress 0.19) and Cawsand (stress 0.24). In these plots only the three samples (5 m separation) at the corners of each of the three 50 m triangles (A,B,C) has been represented.

Table 2
Significance of the sample statistic (Global R) for groups of samples separated by distances of 5, 50 and 500 m. Missing samples prevent full analysis of triangles B and C

Differences between samples separated by:	5 m (50 cm as reps)	50 m (5 m as reps)			500 m (50 m as reps)
Triangles used in analysis:	A1 only $n=8$	A only $n=26$	B only $n=9$	C only $n=9$	A B C $n=27$
Jennycliff untransformed	48.6	37.9	NA	NA	0.7
Jennycliff $\sqrt{\sqrt{}}$ transformed	27.9	18.2	NA	NA	1.4
Cawsand untransformed	53.2	31.9	45.7	14.6	11.3
Cawsand $\sqrt{\sqrt{}}$ transformed	53.6	68.9	63.9	57.5	33

ANOSIM showed different results at Cawsand and Jennycliff (Table 2). At the former, there was a tendency for the significance of the Global R value to approach 5% significance as the distance between sampling areas increased, but this was never achieved. The fauna must be regarded as being homogeneous over the whole 500 m triangle. At Jennycliff, below 50 m the samples could be treated as being from a homogeneous assemblage, but there was a significant difference between samples taken 500 m apart. This difference was detectable in both untransformed and $\sqrt{\sqrt{}}$ transformed data sets, suggesting that both species composition and patterns of dominance shifted over 500 m. Pairwise tests showed that triangles A, B and C all differed significantly from each other. Similarity percentage analysis suggested that these differences were primarily due to patterns in the distribution of the caprellid amphipod *Pariambus typicus* and changes in the relative abundance of the cirratulid polychaetes *Chaetozone gibber* and *Monticellina dorsobranchialis*.

The comparison between Jennycliff and Cawsand is presented in Fig. 4 as MDS plots of $\sqrt{\sqrt{}}$ transformed data. The representation of the Jennycliff data might be regarded as adequate (stress 0.19), but that for Cawsand (stress 0.24) is far less satisfactory. Other data transformations were applied and their effects are considered below.

3.5. Effects of body size and taxonomic grouping

In an attempt to evaluate the role of the major taxa and that of individuals of different body sizes on the separation of the three 50 m triangles at Jennycliff, the raw data were split to give separate listings for large- (15 taxa), mid- (56 taxa) and small-bodied animals (48 taxa). Within these groupings the variance:mean ratio was calculated for each species and its significance tested using χ^2. The proportion of species with an aggregated distribution increased as body size decreased (large 33%, mid 38%, small 46%). The data were also divided into major taxonomic groupings: annelids (60 taxa), molluscs (18 taxa) and crustacea (40 taxa). Obviously, the same animals appear in both the taxonomic and the body-size listings.

Each class of data has been subjected to a range of transformations. Rather than present large numbers of separate MDS plots for comparison, the second-stage MDS procedure has been adopted. Fig. 5 is the output plot from this analysis where similarity matrices with a similar configuration are plotted close to each other.

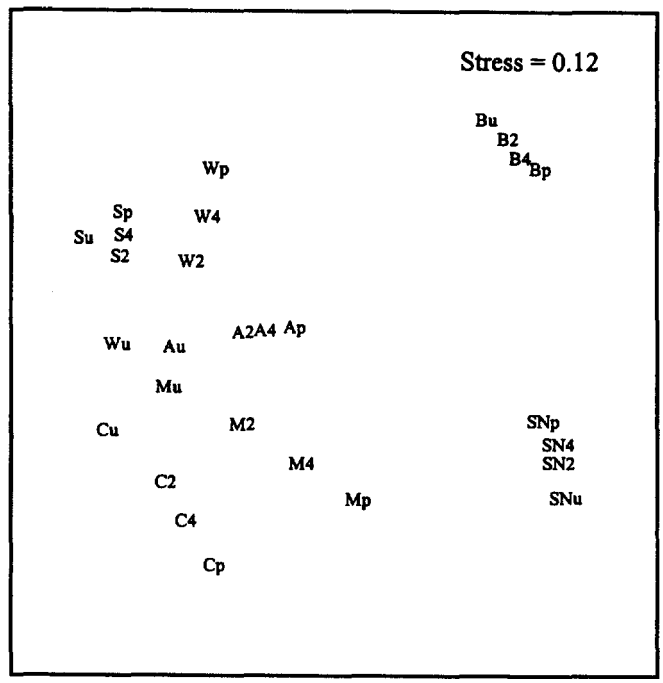

Fig. 5. Second-stage MDS plot of Jennycliff data showing the similarity between similarity matrices computed for animals of different body sizes. Legend: A, all species; W, annelids; C, crustaceans; SN, molluscs; B, large body size; M, mid body size; S, small body size. Suffix letters relate to the transformation applied; u, untransformed; 2, square-root transformed; 4, double square root transformed; p, presence/absence transformed.

The similarity matrix for the untransformed whole data set is most closely mirrored by the untransformed matrices for polychaetes and animals of mid-body size, suggesting that these groups strongly influence the separation of triangles A, B and C at Jennycliff. The untransformed matrix for crustacea is also similar to that for the whole, untransformed data set. On the other hand, large-bodied animals and molluscs showed a pattern of distribution far removed from the whole assemblage pattern. In the remaining cases, the matrices for untransformed data lie closely together, but as the severity of transformation increases, the similarity among the matrices of a particular faunal group decreases and they are distributed along radii away from the plot centre. Not only does the similarity within a group decrease as the transformation becomes more severe, but the difference between the various faunal groups is accentuated. The configuration on the plot of the various transformations for small-bodied animals does not follow a radial arrangement, as the matrix for untransformed data does not lie towards the centre of the plot. It appears that the pattern of faunal distribution which has been detected at the 50–500 m scale is influenced more by shifts in the pattern of dominance of the most common mid-body-sized animals, principally annelids and crustaceans, than by substantial changes in the species composition.

As was noted above the importance of mid-bodied animals and annelids is supported by SIMPER analysis on both untransformed and $\sqrt{\sqrt{}}$ transformed data. These analyses suggest that many of the differences between triangles A, B and C can be related to variation in the patterns of abundance of the mid-sized polychaetes *Monticellina dorsobranchialis*, *Chaetozone gibber* and *Melinna palmata*, the small syllid polychaete *Exogone hebes* and the mid-sized caprellid *Pariambus typicus*. Discrimination between 50 m triangles based on presence/absence data tended to reflect the distribution of crustacea, particularly *Ampelisca typica*, *A. brevicornis* and *Eudorella truncatuala*, although the annelids *Notomastus latericus* and *Praxilella affinis* also made significant contributions.

4. Discussion

This study was intended to quantify the scale at which community heterogeneity could be detected in apparently homogeneous environments. It was based on two contrasting areas, a sandy mud, the surface of which was heavily bioturbated, and a very fine sand. In the former, we were able to show spatial heterogeneity on the scale of 50–500 m; the latter appeared to be faunally homogeneous. Without a prior knowledge of this scale, we considered it unrealistic to collect physical data simultaneously with the biological samples for possible use in explanation of any pattern we discovered. Nevertheless, we can raise two hypotheses to explain the differences between the two areas. It is possible that at the 50–500 m separation there were small but consistent differences in abiotic sediment variables sufficient to influence patterns of species dominance. Unfortunately, it was impractical to take sub-samples from our small cores and the process of diver-sampling itself disturbs surface sediment at the scale of the 5 m triangles. We cannot address the hypothesis of small-scale sedimentological variability.

An alternative hypothesis relates the broad-scale distribution of the infauna to patterns of bioturbation caused by larger-bodied species not collected by our sampling programme. The divers who collected the cores reported that the muddy sand of Cawsand Bay was not bioturbated, while in Jennycliff Bay the seafloor was covered by mounds of sediment ejected from the burrows of thalassinid shrimps. In the fine sand, the fauna is apparently structured by physical processes with few biological interactions, while the converse is true in the muddy areas. Our small cores, deployed to a strict pattern, prevented us from quantifying the shrimps, but box core samples of 0.1 m^2 taken on other occasions contained as many as three to four individuals of *Upogebia deltura* and/or *Callianassa subterranea*. The latter may expel 1–2 cm^3 of sediment from the burrow system every hour (Stamhuis et al., 1997) creating localised patches of unstable sediment, smothering animals with low mobility and inhibiting larval settlement and/or recruitment (Posey et al., 1991; Lindsay et al., 1996). This would in turn lead to faunal gradients on the scale of centimetres running away from individual mounds. It is unlikely that these small-scale changes would be apparent in a standard grab or core sample but, at that scale of sampling, differences between the fauna associated with different densities of shrimps might be evident. Unfortunately, we cannot use our data to map the thalassinids; neither the spatial scale of our sampling nor the size of our sampler

was sufficiently large. However, ROV observations, made 1 year after this diving survey, show that the distribution and abundance of thalassinids within the area of our 500 m triangle does vary. It is hoped that in the near future the relationship between the smaller infauna and those of larger body size can be investigated closely.

Every species reacts to spatial and temporal variation in the environment at its own unique scale. This is most probably some function not only of body size, but also of feeding mode and mobility (Milne, 1992; Hewitt et al., 1996). The latter demonstrated, for example, that a moderately mobile infaunal bivalve displayed patchiness on a spatial scale greater than a similar but less mobile species. They also showed evidence that the distribution of juveniles was at a significantly smaller scale than that of the adults and suggested that the relationship between body size and scale of patchiness is consistent. They were unable to show, however, any differences in the scale at which these bivalves were distributed in different sediments and interpreted this as biological processes dominating over physical processes in setting the patch characteristics of a particular species. Other workers have also shown patchiness at scales of around 10 m for other bivalves (McArdle and Blackwell, 1989) and between 5 and 30 m for a range of intertidal polychaetes and molluscs (Thrush et al., 1989). Patchiness on yet smaller scales has been described in sub-sampled box cores taken from deep water (Jumars, 1975; Volckaert, 1987). Morrisey et al. (1992), in their study of the distribution of major taxa in offshore sediments, showed significant spatial variation at scales from 10 m to 3.5 km. The existence of such patterns indicates that, within these taxa, species are showing some similarity of response to the environment. If this is so, the identification and description of patchiness would be even clearer if, rather than using a univariate approach, species identities were conserved and a multivariate analytical approach applied.

We have shown that while in the fine sand of Cawsand Bay there was apparent homogeneity of the fauna at all scales from 50 cm to 500 m this was not true for the muddier sediment of Jennycliff. At the latter, homogeneity was apparent at separations of up to 50 m, but at 500 m samples seemed to come from different assemblages. This suggests that there are fundamental differences in the way that fauna and environment interact. Analysis indicates that the interactions are subtle and are most clearly demonstrated by changes in the patterns of dominance, particularly among mid-sized animals. In the second-stage MDS plot, untransformed data matrices for annelids and crustaceans showed a configuration similar to that of the whole data matrix and it can be assumed that spatial patterns of dominance within both groups are broadly similar. This is not the case for the molluscs, in which the pattern of similarity differed sharply to that among the other major taxa. Separate MDS analysis of the molluscan data failed to show any separation of the three triangles. This might suggest that the molluscs in Jennycliff Bay have a distinctive response to their environment. It is more probable that we are describing an artefact of sampling. This group of 18 taxa was made up of species that were seldom numerically important, rarely occurring at an abundance of greater than 10 individuals in a sample. It remains likely that the molluscs have been under-sampled and even if they do respond to the environment in the same way as other groups, we were not collecting enough individuals to demonstrate this. Similarly, when large body-sized animals (geometric weight class 19 +) are considered the similarity between their

spatial distribution and that of the whole assemblage was poor. More than 60% of these species appeared to be randomly distributed. It is most probable that individual samples were too small to collect sufficient individuals to describe a clear spatial pattern. Smaller-bodied animals conformed to the overall spatial pattern of similarity but, unlike other groups in our analysis, they did not shift from the plot centre as the severity of data transformation increased. In this case, both patterns of dominance and patterns of species distribution conformed to the pattern of the whole, untransformed data matrix. It appears that, in our study, smaller-bodied animals show clear species distribution patterns on the 500 m scale, while such a pattern was not evident as body size increased. Our data give a clear indication of the size-scaled interaction between body size, abundance and sample dimension.

The sensitivity of multivariate techniques to changes in community composition at small spatial scales is clearly an advantage. However, in the context of monitoring and environmental management this can lead to difficulties in survey design and interpretation. It is clear that these methods can detect changes in community composition in relatively small areas that might otherwise be treated as homogeneous. The patterns detected are the result of species responding in similar ways to biotic and abiotic constraints. On balance, the factors operating at the broader scale are most likely to be physical while those operating on a smaller scale are likely to be biological. In the case of Jennycliff Bay, we have suggested above that small-scale patterns of disturbance resulting from the activities of thalassinid shrimps might be responsible for the patterns we have detected in the largely annelid infauna. We were not able to quantify thalassinid distribution and so could not speculate on the factors setting their pattern. We have advanced slightly, but not too far. As Milne (1992) noted, ecological patterns are regulated by dynamics occurring simultaneously at several spatial or temporal scales. Sampling with a small core only told us about the spatial distribution of a small proportion of the animals living within our study area. This was appropriate for our purpose, but if we had intended to interpret the mechanism underlying the pattern, we would have required a broader scale programme and a different sampling design. We might also have needed to sample on more than one occasion as we can reasonably assume that the composition of a faunal assemblage is largely shaped by events in the past. We do not know if our results would have been similar had we sampled in winter or late spring when the number of animals in infaunal assemblages tends to be at its lowest (Buchanan and Moore, 1977). Furthermore, Rowden and Jones (1993) showed that, in the winter, sediment processing by thalassinids slows and the bioturbation of the sediment that they cause is greatly reduced.

The existence of faunal homogeneity on a small scale nested within a larger scale of variability carries with it substantial implications for the design of monitoring studies. While some sites such as Cawsand Bay appear to be homogeneous at distances of up to and possibly beyond 500 m, others show patchiness at a smaller scale. Disturbingly, we have shown that in Jennycliff Bay this was between 50 and 500 m. The area which benthic biologists treat data as coming from the same station varies from place to place and from ship to ship. Until the use of the Global Positioning System became commonplace, a station worked by a big ship on the open sea would probably cover a larger area than one sampled by an inshore vessel, but in both cases replicate samples

would generally fall within a 500 m diameter circle. Morrisey et al. (1992) suggested that temporal monitoring at a single station would be confounded by local spatial variability in the fauna. Buchanan (1993) responded to this by stating that in studies such as his own, navigational errors were such that samples were not closely grouped but spread over a wide area. Precise position fixing has given us the ability to return to an exact sampling position and to group replicates closely together. This may not be desirable. Just as Morrisey et al. (1992) showed that univariate measures were patchy on a comparatively small spatial scale, we have shown similar variability in the context of community analysis. The conclusions that these authors drew do not change; if replicate samples are grouped too closely together there is a danger of confounding the objective of the sampling programme. For this reason, as well as for those of sampling disturbance (Skilleter, 1996), over-concentration of replicates at a particular sampling station must be avoided.

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References

Andrew, N.L., Mapstone, B.D., 1987. Sampling and the description of spatial pattern in Marine Ecology. Oceanogr. Mar. Biol. Annu. Rev. 25, 39–90.

Angel, H.H., Angel, M.V., 1967. Distribution pattern analysis in a marine benthic community. Helgol. Meeresunters. 15, 445–454.

Blackburn, T.M., Gaston, K.J., 1997. A critical assessment of the form of the interspecific relationship between abundance and body size in animals. J. Anim. Ecol. 66, 233–249.

Bros, W.E., Cowel, B.C., 1987. A technique for optimizing sample size (replication). J. Exp. Mar. Biol. Ecol. 114, 63–71.

Buchanan, J.B., 1993. Evidence of benthic pelagic coupling at a station off the Northumberland coast. J. Exp. Mar. Biol. Ecol. 172, 1–10.

Buchanan, J.B., Moore, J.J., 1977. Long term studies at a benthic station off the coast of Northumberland. Hydrobiologia 142, 121–128.

Clarke, K.R., 1993. Non parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a biological effects study. Mar. Ecol. Prog. Ser. 46, 213–226.

Clarke, K.R., Warwick, R.M., 1988. Quantifying structural redundancy in ecological communities. Oecologia 113, 278–289.

Gage, J., Geekie, A.D., 1973. Community structure of the benthos in Scottish sea lochs. Mar. Biol. 19, 41–53.

Gibbs, P.R., 1969. A quantitative study of the polychaete fauna of certain fine deposits in Plymouth Sound. J. Mar. Biol. Assoc. UK 49, 311–326.

Gray, J.S., 1974. Animal sediment relationships. Oceanogr. Mar. Biol. Annu. Rev. 12, 223–261.

Hewitt, J.E., Thrush, S.F., Cummings, V.J., Pridmore, R.D., 1996. Matching patterns with processes; predicting the effects of size and mobility on the spatial distribution of the bivalves *Macoma liliana* and *Austrovenus stutchburyi*. Mar. Ecol. Prog. Ser. 135, 57–67.

Howson, C.M. (Ed.), Directory of the British Marine Flora and Fauna. A Coded Checklist of the Marine Flora and Fauna of the British Isles and its Surrounding Seas, Marine Conservation Society, Ross on Wye.

James, R.J., Lincon Smith, M.P., Fairweather, P.G., 1995. Sieve mesh size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. Mar. Ecol. Prog. Ser. 118, 187–198.

Jones, N.S., 1951. Marine bottom communities. Biol. Rev. 25, 283–313.

Jumars, P., 1975. Deep sea diversity; does it have a characteristic scale? J. Mar. Res. 32, 217–246.

Kendall, M.A., Warwick, R.M., Somerfield, P.J., 1997. Species size distributions in Arctic benthic communities. Polar Biol. 17, 389–392.

Lindsay, S.M., Wethey, D.S., Woodin, S.A., 1996. Modelling interactions of browsing predation, infaunal activity and recruitment in marine soft-sediment habitats. Am. Nat. 148, 684–699.

Marine Biological Association, 1957. Plymouth Marine Fauna.

McArdle, B.H., Blackwell, R.G., 1989. Measurement of density variability in the bivalve *Chione stutchburyi* using spatial autocorrelation. Mar. Ecol. Prog. Ser. 52, 245–252.

Milne, B.T., 1992. Spatial aggregation and neutral models in fractal landscapes. Am. Nat. 39, 32–57.

Morrisey, D.J., Howitt, L., Underwood, A.J., Stark, J.S., 1992. Spatial variation in soft-sediment benthos. Mar. Ecol. Prog. Ser. 81, 197–204.

Magorrian, B.H., Service, M., Clarke, W., 1995. An acoustic bottom classification survey of Strangford Lough, Northern Ireland. J. Mar. Biol. Assoc. UK 75, 987–992.

Olsgard, F., Somerfield, P.J., Carr, M.R., 1997. Relationships between taxonomic resolution and data transformations in analyses of a macrobenthic community along an established pollution gradient. Mar. Ecol. Prog. Ser. 149, 173–181.

Posey, M.H., Dumbauld, B.R., Armstrong, D.A., 1991. Effects of a burrowing mud shrimp on abundances of macro-infauna. J. Exp. Mar. Biol. Ecol. 148, 283–294.

Rowden, A.A., Jones, M.B., 1993. Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidea). J. Exp. Mar. Biol. Ecol. 173, 265–272.

Ruhmor, H., 1995. Monitoring the marine environment with imaging methods. Scientia Marina 59 (Suppl. 1), 129–138.

Skilleter, G.A., 1996. An experimental test of artifacts from repeated sampling in soft sediments. J. Exp. Mar. Biol. Ecol. 205, 137–148.

Somerfield, P.J., Clarke, K.R., 1995. Taxonomic levels in marine community studies revisited. Mar. Ecol. Prog. Ser. 127, 113–119.

Stamhuis, E.J., Schreurs, C.E., Videler, J.J., 1997. Burrow architecture and turbatory activity of the Thalassanid shrimp *Callianassa subterranea* from the central North Sea. Mar. Ecol. Prog. Ser. 151, 155–163.

Thrush, S.F., Hewitt, J.E., Pridmore, R.D., 1989. Patterns in the spatial arrangement of polychaetes and bivalves in intertidal sandflats. Mar. Biol. 102, 529–536.

Thrush, S.F., 1991. Spatial patterns in soft bottom communities. Trends Ecol. Evol. 6, 75–79.

Veijola, H., Merilaeinen, J.J., Marttila, V., 1996. Sample size in the monitoring of benthic macrofauna in the profundal of lakes: evaluation of the precision of estimates. in: Simola, H., Viljanen, M., Slepukhina, T., Murthy, R. (Eds.), Proceedings of the First International Lake Ladoga symposium, St Petersburg, Russia, 22–26 November 1993, Ecological Problems of Lake Ladoga, pp. 301–315.

Volckaert, F., 1987. Spatial pattern of soft bottom polychaeta of Nova Scotia, Canada. Mar. Biol. 93, 627–639.

Warwick, R.M., 1984. Species size distributions in marine benthic communities. Oecologia 61, 32–41.

Warwick, R.M., 1988. The level of taxonomic discrimination required to detect pollution effects on marine benthos communities. Mar. Pollut. Bull. 19, 259–268.

Weins, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385–397.

Woodham, A., Chambers, S., 1994. A new species of Chaetozone (Polychaeta Cirratulidae) from Europe with a re-description of Caulerialla zetlandica (McIntosh). In: Dauvin, J.C., Laubier, L., Reish, D.J., (Eds), Actes de la 4ème Conference International de Polychètes. Mem. Mus. Hist. Nat., Paris, 162, pp. 307–316.