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The integral structure of a benthic infaunal assemblage

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Abstract

It has been suggested that the scaling relationships of many features of the physical environment and biological traits are fractal-like, but for the marine benthic infauna certain aspects of the environment clearly are not. These include temporal features such as the cycles of annual climate, primary production and tides, and also some spatial features such as sediment granulometry and the size of the primary producers that constitute the food supply. We explicitly addressed these issues by determining the degree to which infaunal assemblage structure (diversity, species composition, spatial pattern) varies with mesh size, sample size and sample dispersion within an apparently homogeneous area of coarse intertidal sand in the Isles of Scilly, UK. Samples were extracted using a standard range of 5 mesh sizes (63, 125, 250, 500, 1000 μm), with the sample areas and distances between samples scaled to the mesh size. All metazoans were identified to species level. Diversity and species composition did not show a gradual and even degree of change over the size range. Instead, they showed a dramatic stepwise change between the 250 and 500 μm mesh size samples, being relatively constant in the <500 and >500 μm categories, with diversity higher in the former. Higher proportions of species in the <500 μm categories had values of an index of dispersion significantly different to 1 than among species in the >500 μm categories. This suggests a fractal structure within but not between the <500 and >500 μm body size categories. The implications of this for rapid diversity assessment by extrapolation between size classes are discussed. Although the interplay between 3 and 2 dimensional processes in what is a essentially a 2-D study may account for some of the observations, comparative studies suggest that these patterns do not simply correspond to the physical scaling of habitat complexity, and they must therefore relate to some more universal scaling relationships that are not fractal-like. We suggest that the important relationships are those between body size and various biological characteristics such as feeding behaviour, reproductive mode and life history as they are affected by the spatial and temporal structure of the environment.
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1. Introduction

Almost all studies of the diversity and community structure of benthic metazoan assemblages concern only one size component, either the macrobenthos or meiobenthos, and in meiofaunal studies very few (if any) of the taxa are identified to species level. However, these assemblages constitute an interactive system involving all the species, and our understanding of the mechanisms that determine biodiversity might be improved by the analysis of such integral communities.

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Attempts have been made to describe the influence of body size on diet, life history, population density and species diversity by fitting empirical power functions, implying that the organisation of the system is self-similar or fractal-like (Brown et al., 2002 and references therein). It has also been suggested that the spatial and temporal structure of the physical environment is fractal (Bell et al., 1993 and references therein), and if habitat complexity largely determines species diversity this leads to the prediction (for a single perfect fractal) that all organisms, regardless of size, will perceive the environment as equally complex and should have equivalent diversity. Also, as we move up the size spectrum from the smallest to largest organisms, the species composition should change in a regular and gradual fashion. If a fractal relationship between body size and diversity exists, then this would provide a means of extrapolating between scales and predicting overall diversity from, say, the diversity of the larger macrobenthos. This would be a valuable practical tool for the rapid assessment of biodiversity. It may also be the case that the dispersion patterns of benthic animals are related to body size by a power function. Warwick and Clarke (1996) noted, for the macrobenthos only, that there was a linear increase in the log of the number of species per 100 individuals with increasing log body weight. They suggested that a plausible explanation for this is that species are distributed according to clustered spatial processes, with patch sizes scaled to organism size. Such a relationship was suggested for both macrozoobenthos and microphytobenthos by Azovsky et al. (2000). The spatial variability of some individual sessile marine species has also been shown to be fractal (Erlandsson et al., 2005 and references therein). However, self-similarity at all scales (a perfect fractal) may be unrealistic for ecological systems, and self-similarity may be confined to a finite domain or domains (Brown et al., 2002).

The present study was therefore designed to test the following fractal predictions with respect to the metazoan assemblage of an intertidal sandflat:

1. That species diversity is the same for all size-classes of animals.
2. That the community structure, in terms of the distribution of numbers of individuals among species, is the same for all size-classes of animals.
3. That species composition changes in a regular fashion across the faunal size-spectrum.
4. That clustering patterns are scaled to animal size.

2. Materials and methods

2.1. Field sampling

The study site was an area of uniform clean coarse sand (median diameter 575 μm, 0.1% silt/clay) with a permanent water table, at extreme low water of spring tides on St Martin's Flats, Isles of Scilly, UK (Fig. 1). Core samples were collected in April 2001 with the four largest samples (0.1 m^2) arranged on the corners of a square 16 m apart and the fauna was sieved through a 1 mm mesh sieve. Smaller samples sieved through 500, 250, 125 and 63 μm meshes were collected at sequentially halved distances apart using sequentially halved linear dimensions of corer, so that the 63 μm-sieved samples were 1 m apart with a core area of 0.0039 m^2 (Fig. 2). The 63 and 250 μm samples were also replicated at the largest (16 m) distance. Hereafter the sample groupings are designated by the sieve mesh size only. Animals were extracted from the sediment and processed using standard methods appropriate to their size (Holme and McIntyre, 1984). All animals in all samples were identified to species or putative species and counted.

2.2. Data analysis

Since diversity indices based on species richness and evenness are all inter-correlated, only two indices have been calculated for each sample, Shannon diversity H' (which the most commonly used index but is sample-size dependent) and Hurlbert's $E(S_n)$, the expected number of species present in an increasingly rarefied sample of n individuals selected at random (without replacement) from a finite collection of N individuals and S species (which has been shown to be independent of sample size). In the present study, $E(S_n)$ was calculated at $n=50$. Diversity profiles (distribution of numbers of individuals among species) averaged over all replicates for each size category were visualised as k-dominance curves (Lambshead et al., 1983) in which the percentage cumulative abundances of species are plotted against species abundance rank, the latter on a log scale. Multivariate analysis of all samples was by non-metric multidimensional scaling (MDS) based on standardised root transformed species abundance data and the Bray–Curtis similarity measure between samples. For the samples in each size category the Index of Dispersion (D=variance/mean) was calculated for each species. (Note that fractal dimension is also traditionally designated as D, with which this index of dispersion should not be confused).

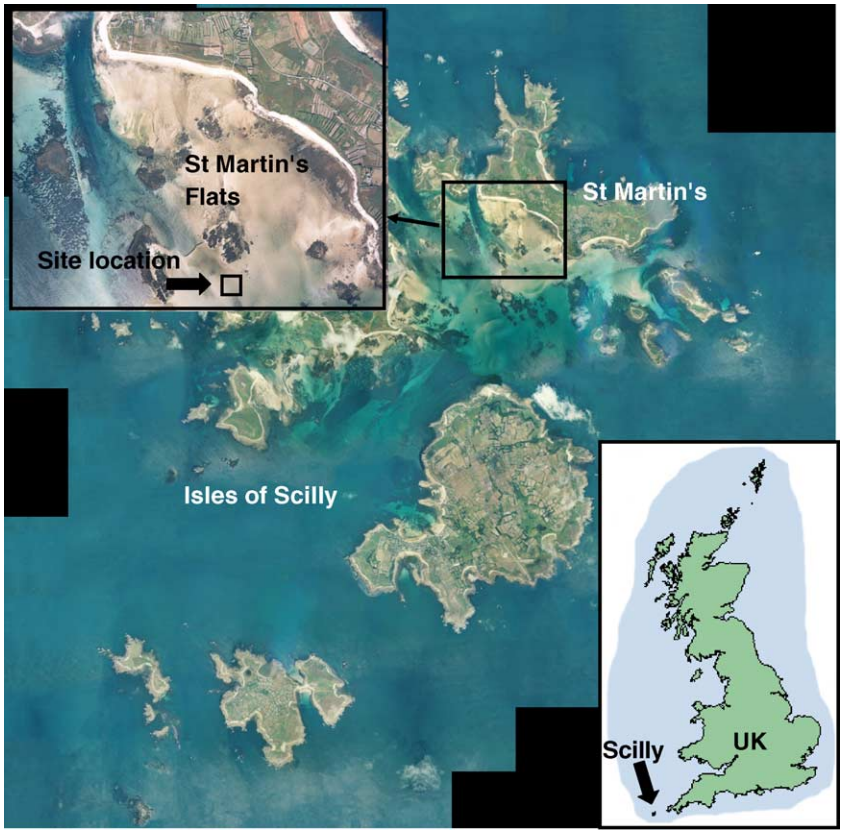

Fig. 1. Map of the UK showing location of Isles of Scilly, with aerial photographs showing the location of the sampling site. Photographs courtesy of English Nature.

Species were given a value of 1 (=Poisson) unless shown to differ significantly by an exact permutation test (Clarke et al., in press). Cumulative clustering was then plotted against species ranked in the order of decreasing values of *D*.

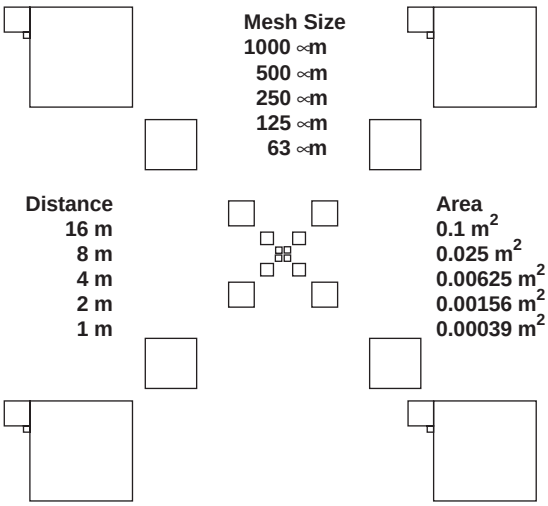

Fig. 2. Diagrammatic layout of sampling design showing sample size, sample spacing and sieve mesh sizes.

3. Results

Altogether 464 species were found in the study, the dominant taxa being nematodes (207 spp.) and harpacticoid copepods (75 spp.). Because the spatial clustering of the 63 and 250 μm samples (1 and 4 m apart, respectively) replicated at the largest 16 m distance did not differ substantially with distance (see below), all samples in these size categories have been combined for statistical analysis. Thus there are 8 samples in each of these size categories, and 4 in the other categories.

Species diversity was constant across the 63–125–250 μm size categories, with a stepwise reduction to the 500 and 1000 μm categories, which also had equivalent values (Fig. 3). Thus, species diversity was not constant across the entire size spectrum, but was constant across two separate size ranges traditionally characterised as "meiofauna" and "macrofauna". Similarly, the diversity profiles visualised as *k*-dominance curves were

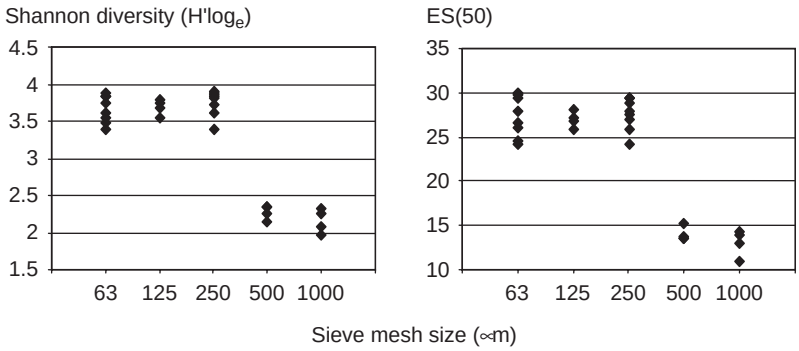

Fig. 3. Diversity indices calculated for all samples of each mesh size.

remarkably constant within these same two size groupings, but markedly different between them (Fig. 4), with the 63–125–250 μm curves much less elevated (higher diversity) than the 500 and 1000 μm curves.

Clustering patterns within each of the size categories were not the same, but rather they fall into groups (Fig. 5). Spatial separation of replicates appeared to have little or no effect, with the 63 μm curves based on 1 and 16 m spacings, and the 250 μm curves based on 4 and 16 m spacing being almost identical. The degree of clustering did not relate sequentially to the size categories, with the 125 and 250 μm samples having the greatest degree of clustering, followed in decreasing order by the 63, 500 and 1000 μm samples. It should be noted that these curves are formulated to focus on the degree of clustering among the few most clustered species. Among species within each size category (from 63 to 1000 μm) the proportions showing significant (non-Poisson) spatial clustering were 21%, 25%, 28%, 11% and 3%. Thus the dichotomy between meiofaunal and macrofaunal organisms is maintained to some extent, as although the proportion of species in the 250 μm samples with non-random spatial distribution is higher than other meiofaunal groups, the proportion in the macrofaunal groups is smaller than in all meiofaunal size categories.

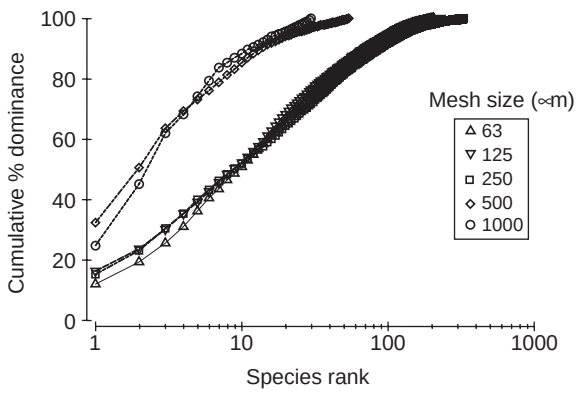

Fig. 4. *k*-dominace curves averaged over all replicates for each mesh size.

MDS plots for the entire dataset showed two very tight clusters corresponding with the same to size groupings (Fig. 6), indicating a dramatic change in species composition between these two groupings but relative consistency of composition within groups. Analysis of each of these two clusters separately showed clear groupings of the 63, 125 and 250 μm samples with similar spacing between each, i.e. a gradual and regular change in community composition across this size range. The average Bray–Curtis dissimilarity between the 63 and 125 μm samples was 49.0% and between the 125 and 250 μm samples 50.4%. The 500 and 1000 μm samples also showed a clear separation into two groups, but because of the arbitrary scaling of MDS plots the magnitude of this change compared with that of the meiofaunal size groups cannot be compared visually. However, the average Bray–Curtis dissimilarity between the 500 and 1000 μm groups was 62.0%, slightly higher than between the meiofaunal groups. The biggest difference in average similarity was, as expected, between the 250 and 500 μm groups, at 78.6%.

4. Discussion

The above results show unequivocally that the relationship between body size and community structure/composition does not conform to a single perfect fractal across the entire metazoan size-spectrum, but that within two restricted domains, 63–125–250 and 500–1000 μm, it does. These size groupings conform to what have been traditionally regarded as meiofauna and macrofauna, respectively (i.e. organisms retained on a 0.5 mm aperture mesh are regarded as macrofauna, and

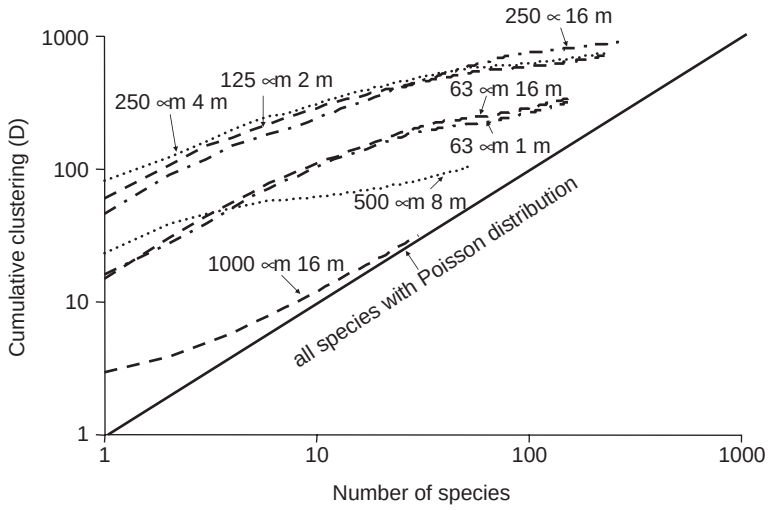

Fig. 5. Cumulative clustering of species in each mesh size/distance combination.

those passing though a 0.5 mm mesh but retained on a 63 μm mesh are regarded as meiofauna). The constancy of species diversity and dominance profiles within these two domains is remarkable, as is the regular sequential change in community composition, at least for the meiofaunal domain. If spatial clustering scaled with body-size across the whole size spectrum the cumulative curves would have been the same, which is clearly not the case. However, the proportion of species with significantly non-random ($D \neq 1$) spatial distributions among meiofaunal samples ranged from 21% to 28%, and was much smaller among species within the >500 μm body size category, supporting the sharp dichotomy observed in other measures. Clearly, mechanisms that determine clustering patterns are related to those that determine diversity profiles and species composition, but the degree to which they operate differs. It should be remembered that the design of this study focuses on factors which scale with mesh-size; mesh aperture and core diameter changing by a factor of 2 between size categories. All samples, however, were taken to a standard depth of 20 cm. Thus the volumes of the samples scale with area, differing by a factor of 4 between categories. Infaunal species inhabit a 3-

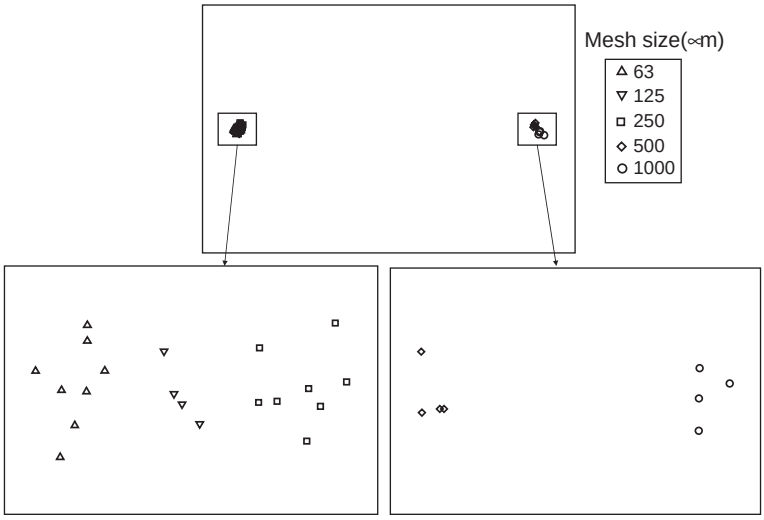

Fig. 6. MDS plots based on standardised √ transformed species abundance data and the Bray–Curtis similarity measure. Top: all samples (stress = 0.01). Left: the 63,125 and 250 μm cluster analysed separately (stress = 0.08). Right: the 500 and 1000 μm cluster analysed separately (stress = 0.01).

dimensional world bounded by the sediment-water interface above and a range of boundaries (ranging from chemical, e.g. limiting oxygen or sulphide concentrations, to physical, e.g. bedrock) below. It may be that spatial-clustering : body-size relationships scale with volume, but the surface area below which that volume is distributed scales non-linearly, increasing with the square of the linear dimension until lower-boundary constraints come into play, and then with the cube of the linear dimension thereafter. If true, this could, conceivably, account for elements of the patterns observed here. For the smallest organisms (63 μm samples) the vertical component of spatial distribution would be driving observed differences in clustering, while samples for the >500 μm categories should possibly have been larger (with an area 8 times or more larger than that collected), in which case they would also have contained a greater diversity of species. The interplay between vertical and horizontal distributions and spatial patterns of organisms is worthy of further research.

In searching for explanations for the meiofauna/macrofauna dichotomy it is constructive to compare the present data with that from other habitat types where environmental constraints differ. Rather few studies have attempted to enumerate species abundances across the whole meiofauna–macrofauna size-spectrum. Several studies of marine shallow water sediment-dwelling benthos from temperate latitudes have shown a bimodal species size distribution, with many meiofaunal and many macrofaunal species, but few of intermediate size (Warwick, 1984; Warwick et al., 1986; Warwick and Joint, 1987; Kendall et al., 1997). An intuitive explanation for this follows Schwinghamer's (1981) explanation for the ataxonomic benthic biomass spectrum concerning the constraint on body size of sediment granulometry. Shwinghamer found a biomass trough at exactly the same body size as the species body size trough (between 0.5 and 1 mm equivalent spherical diameter) and argued that this size defines the upper limit of the interstitial meiofauna and is the region of a shift from interstitial to burrowing lifestyles, with a class of intermediate-sized animals capable of neither. However, this explanation does not bear critical examination, since the bimodal species body size distribution is apparent in thixotropic muddy sediments where the interstitial mode is not possible (Warwick, 1984), and also in sediment-free algal habitats where such sedimentary constraints do not exist (Gee and Warwick, 1994). Also, in fresh water sediments, evidence suggests that the meiofauna/macrofauna dichotomy does not exist. Strayer (1986) found that in the sediments of Mirror Lake, New Hampshire, USA, both the biomass spectrum and the species size distribution were unimodal, in marked contrast to the marine situation. Physical sedimentary constraints are clearly the same in the freshwater and marine situations, but the reproductive characteristics of the species involved are very different. Most shallow water temperate marine macrobenthos have planktonic larvae, whereas many species in the freshwater benthos are the larval stages of flying insects. The conservative nature of the species body size spectrum in marine habitats therefore adds credence to the suggestion that it results from evolutionary adaptations to the spatial and temporal structure of the marine environment which will affect the regional species pool, rather than ecological constraints imposed by the physical nature of particular habitats.

The meiobenthos are considered to be the first metazoans to evolve in the Middle Precambrian, with the Plathelminthes (including Gnathostomulida) and 'Aschelminthes' (Nematoda, Gastrotricha, Kinorhyncha) being considered the most primitive forms (Boaden, 1989). These all have reproductive adaptations associated with small size: direct benthic development, dispersal as adults, short generation times (<1 y), semelparity, and reaching an asymptotic body size after which growth stops and reproduction commences. It is probable that this early meiofauna had the full range of trophic specialisations before the major macrobenthic groups (Annelida, Arthropoda, Mollusca, Echinodermata) appeared. They were, and are, motile forms seeking food particles in a highly discriminate manner. Macrofaunal species have an alternative set of size related life history and feeding traits: planktonic larval development and dispersal, long generation times (>1 y), iteroparity (usually), and continuing growth between successive spawnings. They may be either sedentary or motile, and feed more unselectively on particles of food. Warwick (1984) suggested that the bimodal pattern of species size distribution is apparent because there is a particular size at which meiofaunal life history and feeding traits can be optimised, and another for macrofauna traits, compromises either being non-viable or disadvantageous. Warwick (1989) went on to suggest the reason why it should have been necessary for larger animals to have evolved a planktonic larva was to avoid competition with and predation by the permanent meiobenthos, which constitute a highly efficient consumer unit. Eggs produced by macrobenthic species, and consequently the larvae hatching from them, fall exactly in the same size range as the adult meiobenthos, and settle out of the plankton to the bottom at a size

corresponding to the position of the trough in the bimodal species body size distribution. It had already been suggested that the planktotrophic larval phase in macrobenthos is principally a migration for feeding and safety (with dispersal as an inevitable secondary biproduct), and that "Life-history theories for marine animals cannot ignore a strong historical component stretching back to the origin of the metazoa" (Strathmann, 1985).

Although the scaling relationships of many environmental features may be fractal-like, for the marine benthic infauna certain aspects of the environment are clearly not. These include temporal environmental features such as the cycles of annual climate, primary production and tides, and also some spatial features such as sediment granulometry and the size of the primary producers that constitute the food supply. Also, although some scaling relationships between body size and biological traits such as respiration rate or lifespan may be described by simple power functions across the whole size spectrum, others such as life history patterns cannot. These environmental features and biological traits may, however, be fractal-like over limited domains. We therefore suggest that species with internally coherent sets of meiofaunal or macrofaunal traits that have developed over evolutionary time constitute distinct but coherent ecological units whose community structure and composition may be governed by different fractal domains of the marine environment. In practical terms this implies that prediction of diversity from one domain to another, i.e. between macrobenthos and meiobenthos, may not be a straightforward option, but on the other hand the mesh size used for assessment of diversity for either of these size components may not be as important a variable as is often thought.

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