The structure and organisation of integral marine benthic communities in relation to sieve mesh size

P.J. Somerfield1,\*, S.L. Dashfield1, R.M. Warwick1,2

1 Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, UK

2 Centre for Fish and Fisheries Research, School of Veterinary and Life Sciences, Murdoch University, South Street, Perth, Western Australia 6150, Australia

\* Corresponding author.

Email address: pjso@pml.ac.uk

Telephone +44 1752 633100

ABSTRACT

Few studies consider meiofauna and macrofauna at the same time, even though both form parts of wider ecological networks, and fewer consider interactions between sample size, body size and spatial clustering. It has been suggested that the elements of the structure of the physical environment have fractal properties. 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 and, as we move up the size spectrum, species composition should change in a regular and gradual fashion. This study examines the degree to which infaunal assemblage structure varies with mesh size, sample size and sample dispersion within two different areas of homogeneous intertidal sediment, a muddy sand and a coarse sand, in the Isles of Scilly, UK. In each area samples were extracted using a standard range of 5 mesh sizes (63, 125, 250, 500, 1000 m), 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 at either site. Instead, they showed a dramatic stepwise change between the 250 m and 500 m mesh size samples, being relatively constant in the <500 m and >500 m categories, with diversity higher in the former. Higher proportions of species in the <500 m categories showed evidence of spatial clustering than in the >500 m categories. This suggests a fractal structure within but not between the <500 m and >500 m body size categories, which apparently is not driven by differences in sediment structure. The biology of marine metazoan benthos does not scale continuously across the full range of taxa and body size as has been recently suggested, but may do so for individual taxa and restricted size ranges.

Key words: Body size; Fractal; Diversity; Sampling methods; Meiobenthos; Macrobenthos

Highlights

* Sample sizes and distances among samples were scaled to sieve mesh for sampling two sites.
* Some aspects of community organisation had fractal-like properties, others did not.
* Major changes in community organisation at a size of 0.5 mm were found at each site.
* The macrofauna-meiofauna boundary is better described using traits than by sieve apertures alone.

1. Introduction

It is widely recognised that marine benthic communities may be discriminated into different ecological units of increasing size, from microbenthos through the meiobenthos and macrobenthos to megabenthos, and each requires its own methods for sampling and for the processing of samples (Eleftheriou, 2013). The vast majority of studies of marine benthic communities, however, focus on only one component. These differently-sized and ecologically distinct units nevertheless form parts of an integrated and interactive system, and by studying integral communities it may be possible to improve our understanding of the mechanisms that determine patterns in biodiversity.

Many aspects of marine species’ biology vary with body size including range size, diet, life history, population density and distribution, as well as the diversity of species, to the extent that body size may be seen as a ‘master’ trait (White, et al., 2007; Webb et al., 2009). Many of these relationships may be statistically modelled using empirical power functions, implying that the systems are complex with self-similar or fractal properties (Brown et al. 2002 and references therein). It may also be that the environment also has physical and temporal fractal structure (Bell et al. 1993 and references therein), so that if habitat complexity is a key determinant of species diversity all organisms at any particular size should perceive the environment as being equally complex and should, therefore, be equally diverse. Community composition should also change smoothly and gradually along the size spectrum. A linear increase, on log scales, in the number of macrobenthic species per hundred individuals with body weight in marine assemblages suggests that species are distributed according to clustered spatial processes that may also be related to body size by a power function (Warwick and Clarke 1996).

Warwick et al. (2006) described a study intended to test various fractal predictions by sampling the metazoan assemblage of an intertidal sand flat, using a self-similar sampling design in which sample sizes and distances among samples scaled with the sieve mesh used to extract the fauna across a range of meshes from 63 µm to 1000 µm. They showed that aspects of species diversity, species composition and species dispersion varied smoothly with increasing mesh size across parts of the size spectrum, but showed dramatic changes between samples sieved on 250 and 500 µm meshes, suggesting fractal structure within parts of the size spectrum but not over all of it. The present study builds on that work by adding a complete set of samples, from another part of the same sand flat where the sediment has different properties, in order to examine the generality of the findings relevant to the following fractal predictions:

1. That species diversity is the same for all size-classes of animals.

2. That 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

Samples were collected on St Martin’s flats, Isles of Scilly (Fig. 1). The islands are a granite archipelago situated 40 km south-west of the English mainland. The large semi-exposed sandflat is located on the south of the island of St Martin’s and has a patchy distribution of coarse and fine sands with a variable, but very low, silt/clay content and a permanent water table. Over most of the sandflat there is no visual evidence of reducing conditions (such as a blackening of the sediment) in the upper 15 cm, except in small areas that have the highest silt/clay content. Davies (1990) described the area as follows: “St Martin's Flats is the largest continuous area of sand in the Isles of Scilly. Tidal currents vary over the area resulting in different degrees of sediment sorting which in turn leads to different infaunal communities.” The macrofaunal communities of the sandflat were described by Warwick and Somerfield (2015).

Two areas were selected for sampling: 1) An “*Ensis*” site (49°57′33.78″N 6°17′34.1″W) of smooth, waterlogged sand at ELWST with evidence of live *Ensis* and large numbers of empty *Ensis* shells on sediment surface, and 2) An “*Arenicola*” site (49°57′58.6″N 6°17′ 35.3″W), of finer sand with some blackening close to the surface, between MTL and HWNT and characterised by abundant *Arenicola* holes and casts on the sediment surface (Fig. 1).

Core samples for faunal analysis were collected using a range of different corers from the *Ensis* site in April 2001, and from the *Arenicola* site in September, over periods of low spring tides. All cores were taken to a depth of 20 cm. At each site the four largest samples (0.1 m2) were taken from points on the corners of a square 16 m apart and the fauna was sieved through a 1 mm mesh sieve (Fig. 2). 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 m2 (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 relevant site and sieve mesh size only. Animals were extracted from the sediment and processed using standard methods appropriate to their size (Eleftheriou and Moore 2013; Somerfield and Warwick 2013). All animals in all samples were identified to species or putative species and counted. Two cores were taken for sediment analysis at each site. Sediment was dried and sieved through the same sizes of sieves as those used to extract the fauna.

2.2. Data analysis

Univariate indices derived from the data were the number of species (S), abundance (N), Hurlbert's ES(n), the expected number of species present in an increasingly rarefied sample of n individuals (here 50) selected at random (without replacement) from a finite collection of N individuals and S species, and average taxonomic distinctness (Δ+), the average path length between species (in this case through a taxonomic hierarchy assembled using the taxa matching function on the World Register of Marine Species, http://www.marinespecies.org/aphia.php?p=match). The latter two indices have been shown to be sample-size independent. For Δ+ a funnel plot was constructed to demonstrate the expected distribution of samples under a null hypothesis of random assembly from the species pool (Clarke and Warwick, 1998) conditional on more frequently occurring species occurring more frequently (Somerfield et al., 2008).

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; Warwick et al., 2008) in which the percentage cumulative abundances of species are plotted against species abundance rank, the latter on a log scale.

Non-metric multidimensional scaling (nMDS) based on fourth-root transformed species abundance data and the Bray–Curtis similarity measure between samples was used to visualise relationships among samples (Clarke et al., 2014). To visualise the nature of contributions to inter-sample similarity by species contributing ≥ 2 % of any one sample, hierarchical agglomerative clustering with Type 3 similarity profiles was used to determine groups of species varying coherently across samples (Somerfield and Clarke 2013) and their variation was visualised using a shade plot (Clarke et al. 2014).

For all samples, and for the samples in each size category, an Index of Dispersion (D = variance/mean) was calculated for each species and significance tests used to determine species for which D > 1 (Clarke et al. 2006). (Note that fractal dimension is also traditionally designated as D, with which this index of dispersion should not be confused).

All statistical analyses were conducted using PRIMER v7 (Clarke et al., 2014; Clarke and Gorley, 2015).

3. Results

As expected, the sediments differed between sites (Fig. 3). At the *Ensis* site the sediment was coarse with the majority of the sediment retained on the 500 µm and 1 mm meshes, while at the *Arenicola* site the sediment was made up of smaller particles, the majority of the sediment being retained on the 250 and 500 µm meshes. 19235 individuals belonging to 444 species or putative species were identified in samples from the *Ensis* site, while 42548 individuals in 293 species were identified from the *Arenicola* site. Although the sites were sampled in different seasons there is no evidence that the proportion of larval forms differed between sites, so the intersite differences are considered to be primarily the result of differences in sediment type, as intended.

Despite the strong sample-effort dependency of S and N and differences in sample size scaling with the sieve meshes, it is nevertheless clear there were more species in the samples sieved on mesh sizes ≤ 250 µm compared to samples sieved on meshes ≥ 500 µm at both sites (Fig. 4). There were more species ≤ 250 µm at the *Ensis* site than the *Arenicola* site, and more individuals at the *Arenicola* site than the *Ensis* site. While differences in S and N between 500 and 1000 µm samples were clear at the *Ensis* site, they were less so at the *Arenicola* site. ES(50) shows a fractal pattern at the *Ensis* site, with samples ≤ 250 µm similar to each other and clearly different from samples ≥ 500 µm, which also have similar values of ES(50) to each other. At the *Arenicola* site samples ≥ 500 µm have similar ES(50) values to each other and to equivalent samples from the *Ensis* site. Samples ≤ 250 µm are highly variable in terms of ES(50) and the fractal pattern observed at the *Ensis* site is less clear. Nevertheless, ES(50) for samples ≤ 250 µm tends to be higher than for samples ≥ 500 µm. Average taxonomic distinctness (Δ+) increases with mesh size across all mesh sizes at the *Ensis* site according to a power function (Δ+ = 93.653.area0.01, R² = 0.78) but only up to 500 µm at the *Arenicola* site (Δ+ = 96.472.area0.02, R² = 0.70), decreasing in the largest samples.

Differences in numbers of species and individuals reflect differences in relative abundance and dominance, which are visualised in k-dominance plots (Fig. 5). Again it may be seen that there are clear differences in dominance and diversity at the *Ensis* site (and fractal structure) with samples ≤ 250 µm similar to each other and clearly different from samples ≥ 500 µm. At the *Arenicola* site the differences are less clear, with 250 and 125 µm samples similar to each other and clearly different from samples ≥ 500 µm, but the 63 µm samples, while similar in terms of diversity to samples ≤ 250 µm, are relatively less even (more highly dominated).

Ordination by nMDS based on transformed abundances shows relationships among samples derived from similarity in (transformed) species composition (Fig. 6). While the low stress (0.05) indicates that the final plot is an excellent representation of the underlying similarities, the Shepard diagram shows that the similarities generally fall into two groups. Larger similarities (to the left of the plot – note reversed scale) reflect differences among samples from adjacent meshes within sites, whereas the smaller similarities tend to reflect differences between sites as well as differences between samples ≤ 250 µm and samples ≥ 500 µm between and within sites. Among samples ≤ 250 µm and samples ≥ 500 µm, within sites changes in community structure are smooth and small between adjacent mesh sizes with the exception of changes between 250 µm and 500 µm samples. Samples ≤ 250 µm within sites tend to be similar to each other, and different from samples ≥ 500 µm. Sites are different from each other, and the changes from one mesh to another in one site mirror changes in the other.

Looking at the numerical composition of samples at the level of classes (Fig. 7), samples ≤ 250 µm at the *Ensis* site are dominated by copepods and nematodes (Chromadorea and Enoplea) with small contributions from a range of other groups including gastrotrichs, arachnids (halacarid mites) and anthozoans (*Halammohydra* spp.). Among nematodes the relative importance of enoplids increases with mesh size, as does the contribution from polychaetes. The composition of samples from the *Arenicola* site in the same range differs substantially, in that they are highly dominated by nematodes, copepods are less dominant and fewer other groups contribute. As at the *Ensis* site, the contribution from polychaetes and the relative importance of enoplids among nematodes increase with mesh size. At both sites samples ≥ 500 µm are dominated by polychaetes but otherwise they differ substantially in composition. The other major contributing group at the *Arenicola* site is malacostracans (primarily amphipods) along with some molluscs (gastropods and bivalves) and enoplid nematodes in the 500 µm samples. The second-most important contribution in 1000 µm samples from the *Ensis* site is from bivalves but the samples also contain substantial numbers from a range of groups including nematodes. There is a major contribution by nematodes in the 500 µm samples along with smaller contributions from a range of groups including phoronids.

Selecting only the 51 species that contribute at least 2 % of the abundance in any site/size combination, clustering with Type 3 Simprof identifies a number of coherent groups of species (Fig. 8). These show that different species are dominant at different sites, and in samples ≤ 250 µm and samples ≥ 500 µm within each site. At the *Ensis* site species that are more abundant in 250 µm samples differ from those tending to be more abundant in smaller samples. There are no dominant species in common in samples ≥ 500 µm from the two sites, and few among samples ≤ 250 µm. It is also clear that within each site many species are found both in samples ≤ 250 µm and also ≥ 500 µm.

Using D, the average mean/variance ratio across site/mesh combinations, as a clustering measure there are major differences among groups of samples. Species in samples ≤ 250 µm from the *Arenicola* site have more spatially clustered (patchy) distributions than species in other site/mesh combinations (Fig. 9), the degree of species’ patchiness in samples ≤ 250 µm from the *Ensis* site is similar to that among species in samples ≥ 500 µm from the *Arenicola* site, and the species in samples ≥ 500 µm from the *Ensis* site are the least patchy. The median value of D across all samples is 1.9 (Table 1), while within site/mesh combinations it is 1.0 in groups of samples ≥ 500 µm. In samples ≤ 250 µm from the *Ensis* site it ranges between 1.3 and 1.9, while for the *Arenicola* site it is approximately 3 for 63 and 125 µm samples but 6 for the 250 µm samples. Maximum values (indicating the cluster size of the most clustered species) are also variable. For all samples it is 310. Across site/mesh combinations values from the *Ensis* site are much lower than the equivalent values from the *Arenicola* site. Results of permutations tests to determine whether values of D differ significantly from 1 show that overall 50.4 % of species are clustered (Table 1). The proportion of species with poisson distributions (D = 1) at the *Ensis* site is generally well above 50 %, while at the *Arenicola* site most species are clustered in samples ≤ 250 µm but not in samples ≥ 500 µm.

Funnel plots (Fig. 10) are constructed in such a way that if the appropriate null hypothesis is true the majority of points plotting the values of Δ+ against S will fall inside the limits of the funnel which is derived from simulations (Clarke and Warwick, 1998). Here the null hypothesis is that species within samples are a random (taxonomically determined) subset of all of the species recorded, though the frequencies of occurrence vary among species so frequently-occurring species are selected more often in the random selections used to determine the funnels (Somerfield et al., 2008). Samples from the smallest (63 µm) samples tend to fall below the funnel (Fig,. 10), along with some samples of 125 or 250 µm, indicating that the species in them are more closely related than a random subset from the total species pool. The species in the majority of samples ≥ 250 µm are representative, in terms of their taxonomic spread, of the overall species pool.

In this study sample size scales with sieve mesh (as well as with distance between samples) so it is possible that many of the observed results reflect differences in sampling effort rather than differences in the ecology of the species being sampled. A graph of log2 S against log2 N (Fig. 11) indicates that there is evidence of power relationship(s) between the two. The overall relationship is log2 S = 2.9684(log2 N)0.45 (R² = 0.62), but two things are apparent from the plot. First, it is clear that the overall relationship is not well fitted as the relationship among samples ≤ 250 µm from the *Ensis* site differs, with higher S for a given N but a similar slope. If these samples are omitted the relationship for the rest of the samples is log2 S = 2.9831(log2 N)0.40 (R² = 0.91), while the relationship for the ≤ 250 µm samples from the *Ensis* site alone is log2 S = 7.4649(log2 N)0.40 (R² = 0.91). The second is that the overall relationships are largely (but not entirely) driven by differences between groups of samples of different sizes, and it is not at all clear that there is much of a relationship within many of the site/mesh groups.

4. Discussion

4.1. Is species diversity the same for all size-classes of animals?

As the number of species observed (S) is sample-size dependentt, simply sieving a single sample through a series of meshes of different sizes would not be an appropriate way to addresswhether species diversity is the same for different size-classes. Larger organisms would be relatively less adequately sampled than smaller ones, and any chosen area of sample would be most appropriate for only part of the sampled size-spectrum. The issue is addressed here by scaling the sizes of samples with the mesh sizes used to extract them. Had the number of species in samples from each site/mesh group of samples been the same, it could have been concluded that species diversity, if appropriately sampled, is the same across size classes and therefore has fractal (self-similar) properties. From the results it is clear that, in general, this is not the case. There are clear differences in S among site/mesh groups of samples. Similar issues are pertinent to N, and ES(n) is intended to correct for this. It was for this reason that Warwick et al. (2006) applied this measure to their analysis of the *Ensis* samples, concluding that over ranges of meshes (63 – 250 and 500 – 1000 µm) there was evidence of fractal self-similarity in species diversity. Extending the analysis to samples from a contrasting site nearby indicates, however, that the relationship is fragile. While ES(50) differs between, and varies rather less within, samples over the same ranges, the similarities and differences are less stark.

4.2. Is community structure, in terms of the distribution of numbers of individuals among species, the same for all size-classes of animals?

The k-dominance plots indicate clear differences among mesh groups of samples within sites, so community structure is not the same for all sampled size classes of animals. At the *Ensis* site, as noted previously (Warwick et al., 2006), the profiles clearly separate samples ≤ 250 µm and samples > 250 µm. For samples from the *Arenicola* site profiles for the 125 and 250 µm groups are very similar, but the profiles for the samples > 250 µm do not overlap and the profile for the 63 µm occupies an intermediate position. Thus the pattern in the dominance structure across ranges of meshes at the *Ensis* site is not clearly repeated at the *Arenicola* site.

4.3. Does species composition change in a regular fashion across the faunal size-spectrum?

The species composition of assemblages clearly does not change in a regular fashion across the faunal size-spectrum, as multivariate analyses show that there are major shifts in composition between the 250 and 500 µm samples at both sites. Among dominant species at each site there are some that span this division, but the general picture from the multivariate analyses, as well as from the examination of composition in terms of higher taxa, is one of relatively small changes among samples 63 – 250 µm and 500 – 1000 µm compared to the relatively large shifts in composition at the 250 – 500 µm boundary.

4.4. Are clustering patterns scaled to animal size?

Species in samples ≤ 250 µm within sites have a similar distribution of the index of dispersion D, which differs from that for organisms in samples > 250 µm. Patchily distributed species are more prevalent in the 63 – 250 µm samples and the highest levels of clustering, at each site, are found in the 250 µm samples. There are clear differences in the clustering structure between sites, however, with more patchily-distributed species at the *Arenicola* site. At the *Ensis* site the majority of species are not patchily distributed, while this is only true for species in the 500 – 1000 µm mesh range at the *Arenicola* site. Thus it is true that clustering patterns differ among samples of different sizes, but it cannot be concluded that size and clustering are linked by a simple scaling relationship.

4.5. Separating meiofauna from macrofauna

In an integral and interlinked benthic assemblage, are there distinct meiofaunal and macrofaunal assemblages, and if so which animals constitute the meiofauna, and which constitute the macrofauna? Building on decades of research (Higgins and Thiel 1988; Giere, 2009) many definitions of meiofauna use mesh size as a discriminator. For example, Somerfield and Warwick (2013) define the size boundaries of meiofauna based on the standardised mesh apertures of sieves with 500 μm (or 1000 μm) as upper and 63 μm (or 42 μm) as lower limits, saying that all fauna passing through the coarser mesh and retained on the finer one may be considered to be meiofauna. The present study, showing repeated and consistent differences between the fauna in samples retained on 63 – 250 and 500 – 1000 µm meshes, may be added to the body of evidence that these components of the fauna are genuinely different and demand separate attention. There is a problem, however, with such a mesh-based definition. Few meiofaunal researchers go to the trouble of passing samples through a coarser mesh, instead relying on a combination of sample (or more generally, sampler) size and expert opinion or expertise. Thus it is common to take ‘meiofauna’ samples using a small corer, extract the fauna using an appropriate (smaller) mesh such as a 63 µm one, and to identify all of the sampled organisms, perhaps focusing on taxa associated with a meiofaunal mode of life such as nematodes and copepods. It seems unlikely that, if a pre-screening through a coarser mesh were employed, this would alter our view of the importance of the meiofauna in such studies. A related problem is the treatment of organisms from groups traditionally regarded as meiofauna in macrofaunal studies. In the latter, which make up the majority of marine benthic studies, samples are simply sieved on a 500 µm or 1000 µm mesh and the retained organisms are identified. Meiofaunal taxa such as nematodes are generally regarded as taxonomically ‘difficult’ or not ‘really’ macrofauna because most nematodes are meiofaunal, and as a consequence they are, at best, lumped together as ‘nematodes’ or, frequently, ignored or removed from the data prior to analysis. Indeed, so prevalent is this practice that the removal of nematodes from macrofaunal datasets has been embedded in data manipulation rules for implementing European policy, such as assessing the ecological status of transitional and coastal waters for the EU Water Framework Directive (see e.g. Phillips et al, 2014; Prior et al. 2004). This is despite the fact that nematodes in macrofaunal samples (even if only identified to phylum) may be important contributors to benthic production in organically polluted situations (Warwick and Clarke, 1993). In 500 µm samples from the *Ensis* site there were on average > 84 individuals belonging to > 9 species, and even in the 1000 µm samples there were on average > 2 individuals from > 1 species of nematode, which may not sound much but it should be borne in mind that these samples only contained an average of 14 species and 59 individuals. At the *Arenicola* site there were on average 6 individuals from > 3 species in 500 µm samples but none in the 1000 µm samples. As samples sieved on different meshes were separate samples, the extent to which specimens in the ≤ 250 µm samples would have been excluded by pre-screening through a 500 µm mesh is unknown. The finding that the overlap in size distributions between 0.5 and 1.0 mm varies with conditions is likely to be general, as Shiriyama and Horikohsi (1989) showed that the organisms in this size rrange tended to be predominantly from meiofaunal taxa in the deep sea, and from macrofaunal taxa at shallower depths. To exclude individuals and species simply because they are of an inconvenient size seems problematic.

An alternative approach is to use a more ecological definition, recognising that the meiofauna form a discrete ecological unit linking micro- and macrobenthos (Giere 2009). It was the recognition of this unit that led Mare (1942) to coin the term ‘meiobenthos’ in the first place, and it should be remembered that the sieve mesh used by her to define the group (100 µm) differs from those used to define the group today. The existence of the unit in sands has long been recognised (Remane 1933; Nicholls 1935). Above and beyond size (or sieve meshes) the combination of traits shared by meiobenthic taxa and discriminating them from macrobenthic taxa, including direct development, adult dispersal, semelparous reproduction with short generation times, feeding by discriminate use of particles with selection on the basis of quality, and asymptotic adult body size (Warwick 1984, 2017) are well known and often repeated. As large nematodes, for example, retain these traits even though they are at the larger end of the meiobenthic spectrum it makes little sense to exclude them. Similarly, it has long been recognised that smaller individuals from ‘macrobenthic’ taxa, especially juveniles, may at times be an important component of the fauna in the meiobenthic size range. These so-called ‘temporary meiofauna’ contribute to the overall ecology of the system, so to ignore them also makes little sense if the aim is to understand how the system functions.

4.6. Representative sampling

Another feature of meiofauna which is also often repeated is their high diversity, both in terms of species and phyla (Giere 2009). Although the scaling of samples in this study is intended to ameliorate the effects of the sampling-effort dependency of S and N, it only partially does so. It is instructive to look at a diversity measure that is sampling-effort independent, at least to the extent that there is no mechanistic relationship between its values and those of S or N, namely the average taxonomic breadth of samples, Δ+. At both sites there is a linear increasing trend in Δ+ with increasing mesh size (Fig. 4), although the relationship breaks down for the largest samples at the *Arenicola* site. Thus as sample size (and mesh size) increases the species in those samples become less closely related to each other. This might reflect a tendency among higher taxa for there to be fewer larger species, or a tendency for larger sample volumes to capture more individuals from sparsely distributed higher taxa, or both. Given that species selections for simulations were conditioned on the frequency of occurrence of species in constructing the funnel plot (Fig. 10) but the mean value of Δ+ remains independent of M (the numbers of species selected for each simulation), the former seems more likely. Either way, it is important to note that the smallest samples, representing the typical small cores sieved on a 63 µm mesh collected in many meiobenthic studies, do not collect the taxonomic breadth of the whole meiofaunal (or integral meiofaunal and macrofaunal) assemblage. For meiobenthic studies a larger sample size (perhaps collecting a number of small cores and pooling them) makes sense, especially if the aim of the study is to understand relationships among species either in terms of their taxonomic composition or in terms of their functional roles (Somerfield et al. 2008). An alternative, and perhaps preferential, approach would be to collect larger sample volumes and to extract the meiofauna using larger meshes such as 125 or 250 µm. While there is potentially a great deal of effort involved doing either, the additional effort could potentially be ameliorated by judicious and appropriate subsampling during analysis (Somerfield and Warwick 2013). While scientists are often driven to standardise methods to allow comparability among datasets and studies, perhaps more thought needs to be given to the purpose of a study before deciding on details of the methods to be employed. Thus we agree with Bachelet (1990), who said that “the mesh selected for a particular task should be chosen with a clear idea of the study aims. It is thus suggested that a 1·0 mm mesh is sufficient only for biomass estimates or bionomics studies, whereas sieves with 0·1–0·2 mm mesh openings should be used in studies involving population dynamics of macrofauna, to provide an adequate estimate of abundances of individuals in small size classes.” While the focus of his work was on macrofaunal species, on the basis of the results presented here the conclusions are just as relevant to meiofaunal investigations.

4.7. Macroecological relationships and patterns among individual samples

Continuing the theme of appropriateness of samples, a recent debate in the literature about whether meio- and macrobenthos are discrete entities with distinct ecological attributes (Bett 2013, 2014; Warwick 2014) used data from the *Ensis* site discussed here to show, at that site at least, that the two components of the fauna are ecologically distinct entities. The debate, however, hinged on simple size-based mathematical simulations and whether these could reproduce biomass spectra similar to those reported for integral assemblages (e.g. Schwinghamer 1981) with a trough separating meiofaunal and macrofaunal groups at an equivalent spherical diameter of about 500 µm. The debate also included discussion of species abundance spectra, in which numbers of species (or proportions of species) with maximum size within x2 geometric size classes are plotted against those size classes, often as mixed lognormal distribution curves (Warwick 1984). These curves show a trough at the same position, equating to a body mass of 45 µg, and have been shown to be highly conserved. It should also be noted that biomass spectra are more variable (Yamanaka et al. 2012). The fact that both types of spectra show troughs in similar places is strong evidence for the meiofauna-macrofauna dichotomy but they are very different and convey very different information. In his simulations, however, Bett (2013) linked the two to show that either could be artefactual based on the same set of simulations. He did so by using the relationship Si = Ni0.5, where Si is the number of species in x2 geometric size class i, and Ni is the number of individuals in that class. This relationship was originally derived from extensive studies of abundance, diversity and body-size of terrestrial arthropods (Siemann et al., 1996, 1999) but has been shown to hold for some groups of marine molluscs (Fa and Fa 2002; McClain 2004). The data collected for this study are not appropriate for the construction of either type of spectrum, or to examine the relationship Si = Ni0.5directly, as biomass (either of individuals or of species) was not recorded, and because all individuals in samples were included regardless of their maximum size. Looking at the relationships between log2 S and log2 N (Fig. 11), however, it is notable that the exponents (0.45 for all samples, 0.4 for all samples with *Ensis* samples ≤ 250 µm omitted and 0.4 for those samples separately), while not 0.5, are not very different. More importantly, the relationship is driven mainly by differences among groups of samples rather than differences among individual samples. Recalculating it for pooled site/mesh samples it becomes log2 S = 2.55.(log2 N)0.58, R² = 0.82, but it should be remembered that samples from the *Ensis* site have relatively high S for a given N. Removing these, the relationship becomes log2 S = 3.88.(log2 N)0.49, R² = 0.99, a remarkably good agreement with the relationship of Siemann et al. (1999) which, they explained, could be generated by a general rule of resource division together with similar minimum population sizes among species.

Exploring the generality of this relationship, and other macroecological relationships such as the Cross Community Scaling Relationship (CSSR), the Global Size-Density Relationship (GDSR), the size spectrum (also called the Individual Size Distribution, ISD), the Local Size-Density Relationship (LDSR) or relationships between body mass and abundance such as are predicted from metabolic theory (Brown et al. 2004, White et al. 2007), are worthy goals which may be addressed by examining integral marine benthic communities, including meiofauna. This would help to put meiobenthic research where it should be, an important discipline within broader integral benthic ecological studies. Each, however, requires more than the fitting of a statistical model to existing data, or indeed to modelled data. Also required are a clear understanding of the underlying ecological models being explored, a clear route to discriminating among competing models, and data of the right type(s) collected at the appropriate scales.

5. Conclusions

There is no single perfect fractal relationship underlying species distributions in marine benthic communities, although some aspects of community structure may have fractal-like structure over limited domains. The composition of the benthic fauna is very different at the two sites sampled for this study, but at both sites there are major differences in the diversity and organisation of the benthic fauna between samples sieved on meshes ≤ 250 µm and larger samples sieved on meshes ≥ 500 µm, corresponding to the traditional division between meiobenthos and macrobenthos. In the coarse clean sand at the *Ensis* site large nematodes from several species contributed a significant proportion of the abundance in samples sieved on the 500 µm mesh, so a meiobenthic definition incorporating traits is preferred to one focusing purely on sieve mesh apertures. The prevalence of power-law relationships is a symptom of a complex system, and it is time for meiofaunal ecology to embrace and explore this complexity using appropriate methods, moving beyond simple descriptions of which taxa occur where.

Acknowledgements

The original fieldwork and some of the analysis was supported by the UK Department for Food and Rural Affairs (Defra) under contracts AE1137 and CDEP 84/5/29. We also acknowledge past financial support from the UK Natural Environment Research Council (NERC) through core strategic research funding to Plymouth Marine Laboratory. Aspects of the work were supported by NERC and Defra through the Marine Ecosystems Research Programme (grant number NE/L003279/1). We acknowledge all those who helped with faunal identifications, in particular J.M. Gee who identified the copepods and without whose skills and dedication this study would not have been possible.

References

Bachelet, G., 1990. The choice of a sieving mesh size in the quantitative assessment of marine macrobenthos: a necessary compromise between aims and constraints. Mar. Environ. Res. 30, 21–35.

Bell, G., Lechowicz, M.J., Appenzeller, A., Chandler, M., Deblois, E., Jackson, L., Mackenzie, B., Presiosi, R., Schallenberg, M., Tinker, N., 1993. The spatial structure of the physical environment. Oecologia 96, 114–121.

Bett, B.J., 2013. Characteristic benthic size spectra: potential sampling artefacts. Mar. Ecol. Progr. Ser. 487, 1–6.

Bett, B.J., 2014. Macroecology and meiobenthos: reply to Warwick (2014). Mar. Ecol. Progr. Ser. 505, 299–302.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Towards a metabolic theory of ecology. Ecology 85, 1771–1789.

Brown, J.H., Gupta, V.K., Li, B.-L., Milne, B.T., Restrepo, C., West, G.B., 2002. The fractal nature of nature: power laws, ecological complexity and biodiversity. Phil. Trans. R. Soc. Lond. B 357, 619–626.

Clarke, K.R., Chapman, M.G., Somerfield, P.J., Needham, H.R., 2006. Dispersion-based weighting of species counts in assemblage analyses. Mar. Ecol. Progr. Ser. 320, 11–27.

Clarke, K.R., Gorley, R.N., 2015. PRIMER v7: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Gorley, R.N., Somerfield, P.J., Warwick, R.M., 2014. Change in marine communities: an approach to statistical analysis and interpretation, 3rd edn. PRIMER-E, Plymouth.

Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35, 523–531.

Davies, J., 1990. Benthic marine ecosystems of Great Britain: a review of current knowledge. Western Channel and the Bristol Channel and approaches (MNCR coastal sectors 8 and 9). CSD Report, No. 1173. Nature Conservancy Council, Peterborough.

Eleftheriou, A., (ed) 2013. Methods for the study of Marine Benthos. 4th Edn. John Wiley and Sons, Chichester.

Eleftheriou,A., Moore, D.C., 2013. Macrofauna Techniques. Chapter 5 in: Eleftheriou, A. (ed) Methods for the study of Marine Benthos, 4th Edn. John Wiley and Sons, Chichester. pp 175–252.

Fa, D.A., Fa, J.E., 2002. Species diversity, abundance and body size in rocky shore Mollusca: a twist on Siemann, Tilman and Haarstad’s parabola? J. Molluscan Stud. 68, 95–100.

Giere, O., 2009. Meiobenthology: the microscopic motile fauna of aquatic sediments. 2nd edn. Springer-Verlag, Berlin.

Higgins, R.P., Thiel, H. (eds), 1988. Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, DC.

Lambshead, P.J.D., Platt, H.M., Shaw, K.M., 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. J. Nat. Hist. 17, 859–874.

Mare, M.F., 1942. A study of a marine benthic community with special reference to the micro-organisms. J. Mar. Biol. Ass. U.K. 25, 517–554.

McClain, C.R., 2004. Connecting species richness, abundance and body size in deep-sea gastropods. Global Ecol. Biogeogr. 13, 327–334.

Nicholls, A.G., 1935. Copepods from the interstitial fauna of a sandy beach. J. Mar. Biol. Ass. U.K. 20, 379–405.

Phillips, G.R., Anwar, A., Brooks, L., Martina, L.J., Miles, A.C., Prior, A., 2014. Infaunal Quality Index: Water Framework Directive classification scheme for marine benthic invertebrates. Report SC080016. Environment Agency, Bristol.

Prior, A., Miles, A.C., Sparrow, A.J., Price, N., 2004. Development of a classification scheme for the marine benthic invertebrate component, Water Framework Directive. Phases I & II – Transitional and coastal waters. R&D Interim Technical Report E1-116, E1-132. Environment Agency, Bristol.

Remane, A., 1933. Verteilung und Organisation der benthonischen Mikrofauna der Keiler Bucht. Wiss. Meeresunters. 21, 161–221.

Schwinghamer, P., 1981. Characteristic size distributions of integral benthic communities. Can. J. Fish. Aquat. Sci. 38, 1255–1263.

Shiriyama, Y., Horikoshi, M., 1989. Comparison of the benthic size structure between sublittoral, upper-slope and deep-sea areas of the western Pacific. Int. Revue ges. Hydrobiol. 74, 1–13.

Siemann, E., Tilman, D., Haarstad, J., 1996. Insect species diversity, abundance and body size relationships. Nature 380, 704–706.

Siemann, E., Tilman, D., Haarstad, J., 1999. Abundance, diversity and body size: patterns from a grassland arthropod community. J. Anim. Ecol. 68, 824–835.

Somerfield, P.J., Clarke, K.R., 2013. Inverse analysis in non-parametric multivariate analyses: distinguishing groups of associated species which covary coherently across samples. J. Exp. Mar. Biol. Ecol. 449, 261–273.

Somerfield, P.J., Clarke, K.R., Warwick, R.M., Dulvy, N.K., 2008. Average functional distinctness as a measure of composition in assemblages. ICES J. Mar. Sci. 65, 1462–1468.

Somerfield, P.J., Warwick, R.M., 2013. Meiofauna Techniques. Chapter 6 in: Eleftheriou, A. (ed) Methods for the study of Marine Benthos, 4th Edn. Wiley-Blackwell Ltd, Oxford. pp 253–284

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

Warwick, R.M., 2014. Meiobenthos and macrobenthos are discrete entities and not artefacts of sampling a size continuum: comment on Bett (2013). Mar. Ecol. Progr. Ser. 505, 295–298.

Warwick, R.M., 2017. **The contrasting histories of marine and freshwater meiobenthic research – a result of differing life histories and adaptive strategies?** J. Exp. Mar. Biol. Ecol. (this volume).

Warwick, R.M., Clarke, K.R., 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. Mar. Ecol. Progr. Ser. 92, 221–231.

Warwick, R.M., Clarke, K.R., 1996. Relationships between body size, species abundance and diversity in marine benthic assemblages: facts or artifacts? J. Exp. Mar. Biol. Ecol. 202, 63–71.

Warwick, R.M., Clarke, K.R., Somerfield, P.J., 2008. K-dominance curves. In: Jørgensen, S.E., Fath, B.D. (eds), Encyclopedia of Ecology. Elsevier, Oxford. pp 2055–2057.

Warwick, R.M., Dashfield, S.L., Somerfield, P.J., 2006. The integral structure of a benthic infaunal assemblage. J. Exp. Mar. Biol. Ecol. 330, 12–18.

Warwick, R.M., Somerfield, P.J., 2015. Assessing the conservation status of marine habitats: thoughts from a sandflat on the Isles of Scilly. J. Sea Res. 98, 109–119.

White, E.P., Morgan Ernest, S.K., Kerkhoff, A.J., Enquist, B.J., 2007. Relationships between body size and abundance in ecology. Trends Ecol. Evol. 22, 323–330.

Webb, T.J., Tyler, E.H.M., Somerfield, P.J., 2009. Life history mediates large-scale population ecology in marine benthic taxa. Mar. Ecol. Progr. Ser. 396, 293–306.

Yamanaka, Y., White, P.L.C., Spencer, M., Raffaelli, D., 2012. Patterns and processes in abundance-body size relationships for marine benthic invertebrates. J. Anim. Ecol. 81, 463–471.

FIGURE LEGENDS

Figure 1. Location of the Isles of Scilly, the island of St Martin’s, and St Martin’s flats indicating the location of the two sampling site (E = *Ensis* site, A = *Arenicola* site).

Figure 2. Diagrammatic layout of the sampling design showing sieve mesh sizes, sample (core) sizes and sample spacing.

Figure 3. Cumulative proportional mass of sediment particles retained on meshes with increasing aperture from samples taken from the two sites.

Figure 4. Box whisker plots of univariate indices for each site/mesh group of samples. The whiskers delineate the range, the box delineates first and third quartiles, and the horizontal line within the box is the median. S = number of species; N = number of individuals; ES(50) = Hurlbert’s expected number of species for 50 individuals; Delta+ = average taxonomic distinctness, Δ+.

Figure 5. k-dominance plots from samples pooled within site/mesh combinations from each site.

Fig. 6. Results on non-metric multidimensional scaling derived from Bray-Curtis similarities among samples calculated using fourth-root transformed abundances, showing the Shepard plot (upper panel) and the final ordination plot (lower panel, stress = 0.05).

Figure 7. Proportional contribution of higher taxa (generally Classes) to the total abundance across pooled site/mesh samples.

Figure 8. Shade plot indicating proportional abundances of dominant species (defined as those contributing ≥ 2 % of any one site/mesh combination) across site/mesh combinations (scale is the square root of the proportions, so 10 = 100 %). Dashed lines in the variables cluster dendrogram indicate groups of species for which a Type 3 Simprof test (9999 permutations, p = 0.01) fails to reject a hypothesis of no coherence among species.

Figure 9. Cumulative frequency plot (‘sample distribution function’) for dispersion indices (D) calculated over all species in each site/mesh combination, and average D calculated for all site/mesh combinations (ALL). D scale (x-axis) is plotted logarithmically, and the y-axis (numbers of species with dispersion less than the specified D value) is plotted as a percentage of the total number of species in each combination.

Figure 10. Funnel plot derived using average taxonomic distinctness (Δ+) and frequency-based selection of species for simulations, overlaid with values calculated from samples.

Figure 11. Graph of number of species (S) against abundance (N) for all samples. Note log2 scales.