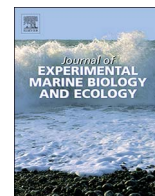




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The structure and organisation of integral marine benthic communities in relation to sieve mesh size

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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 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 at either site. Instead, they showed a dramatic stepwise change between the 250 μm and 500 μm mesh size samples, being relatively constant in the < 500 μm and > 500 μm categories, with diversity higher in the former. Higher proportions of species in the < 500 μm categories showed evidence of spatial clustering than in the > 500 μm categories. This suggests a fractal structure within but not between the < 500 μm and > 500 μm 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.

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

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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'

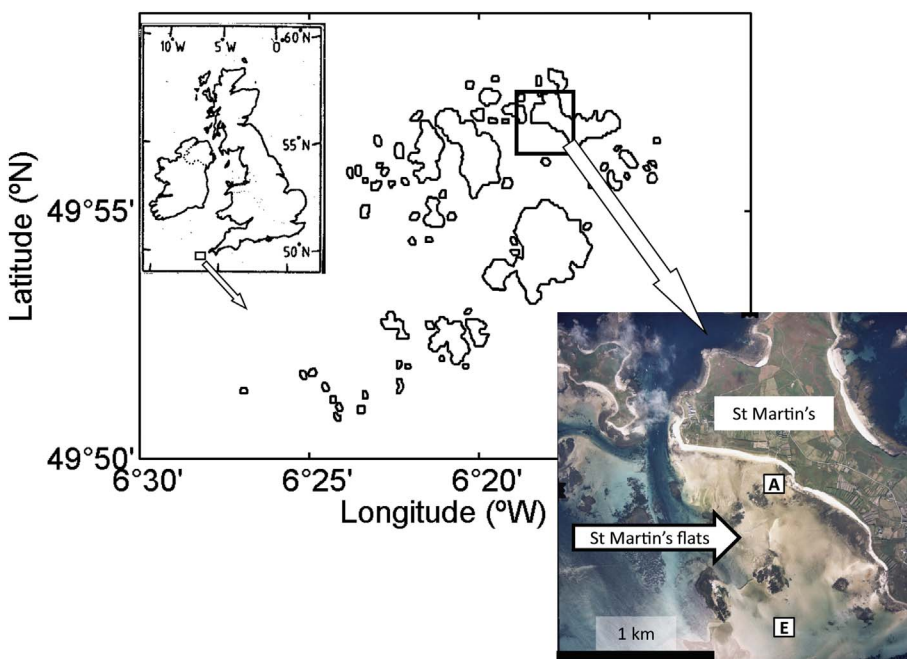


Fig. 1. Location of the Isles of Scilly, the island of St Martin's, and St Martin's flats indicating the location of the two sampling site (E = *Ensis* site, A = *Arenicola* site).

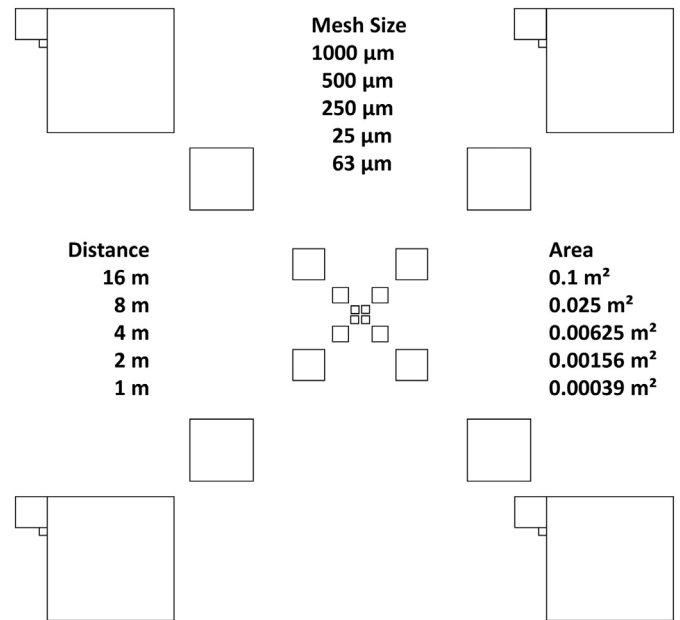


Fig. 2. Diagrammatic layout of the sampling design showing sieve mesh sizes, sample (core) sizes and sample spacing.

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

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