ABSTRACT. – Relationships between the surface features created by infaunal bioturbators and the diversity and structure of a macrobenthic community were identified at spatial scales of 30 to 100 cm for an area of shallow (10 m) subtidal sediment at Jennycliff Bay (Plymouth, UK) in May 2000. At spatial scales ≥ 80 cm, macrofaunal heterogeneity, and diversity, was greater in areas that contained many different surface features compared with areas containing few features. This observation is field evidence to substantiate suggestions that the non-destructive quantification of conspicuous surface features is a useful surrogate of macrobenthic diversity. This surrogate may be most useful in assessing large scale impacts on sediment habitats such as faunistic changes over long distances, long-term temporal changes in a particular place or assessing differences between habitats or geographical locations.

INTRODUCTION

Bioturbation has a substantial influence on the physical and chemical properties of the sediments; burrowing and/or feeding activities can have a strong influence on sediment granulometry, the penetration of oxygen, nutrient flux and the frequency of sediment disturbance (e.g. Widdicombe & Austen 1988, Rowden & Jones 1993, Nedwell & Walker 1995). As the properties of the sediment change so too does its suitability for colonisation and exploitation by secondary species. Bioturbing organisms have been shown to impact on macrobenthic communities both directly through physical interactions (e.g. predation) and indirectly through changes in the sediment environment. However, the scale of bioturbation impact is not solely a result of differences in the intensity and frequency of disturbance (Widdicombe et al. 2000). Mesocosm studies have shown that the intensity of bioturbation and the identity (or functional type) of the bioturbator responsible, act simultaneously on different elements of macrobenthic communities (Widdicombe & Austen 1999, Widdicombe et al. 2000). Further evidence for the importance of sediment complexity in the maintenance of high diversity macro-infaunal communities was provided by Thrush et al. (2001). These authors suggested that between 74 and 86% of the variance in macrobenthic diversity was explained by habitat structure. Clearly bioturbation is an important process in producing heterogeneity or complexity within the sediment habitat thus maintaining levels of diversity.
In the face of growing environmental pressures on coastal marine ecosystems the need to assess and monitor changes in marine communities is greater than ever. In particular, legislation designed to protect marine habitats and biodiversity (e.g. EC Habitats Directive 1992) has placed great demands on those responsible for the management of coastal resources. However, traditional methods of biodiversity assessment that involve the qualification of entire communities are highly labour intensive and therefore expensive (McIntyre 1983, Warwick 1993). If efficient monitoring and management is to be achieved over large areas of coastal waters, techniques need to be developed that allow rapid, cost effective assessment of community structure and diversity. Such methods do not need to deliver outputs with high levels of precision, it is sufficient that they produce information that is “fit for purpose”. A number of authors (e.g. James et al. 1995, Kendall & Widdicombe 1999) have shown that when assessing the pattern of distribution of benthic assemblages, coarser sieve meshes or identification to higher taxa produce results that differ little from those produced using a complete survey design. Others have suggested the use of surrogates, elements of the biota whose presence predicts biological properties of the whole assemblage. For example, Oslgard & Sommerfield (2000) suggested that analysis of a small subset of the polychaete fauna might be sufficient to predict the diversity of the whole assemblage. Similarly, Warwick & Light (2002) have investigated the use of molluscan death assemblages on seashores to predict the biodiversity of the adjacent offshore fauna. Other studies have shown that it is not always necessary to identify organisms to species level as the same patterns of community change may be observed for data at the family or genus level (Warwick 1988; Oslgard et al. 1997).

Even with a reduced sample processing effort, classical analysis of benthic samples remains both costly and time consuming. As remote collection of benthic sediment is destructive it must be used with great discretion in environmentally sensitive areas. If the extent of bioturbation and the identity of the bioturbators combine to influence local sediment diversity, the acquisition of information on bioturbators and their distribution might be used to predict patterns of infaunal benthic biodiversity. Although the majority of benthic organisms have some bioturbational impact, it seems intuitive that larger bodied, highly active species will have the greatest impact on sediment structure and associated communities. These larger animals often create characteristic surface features (Nash et al. 1984, Atkinson & Nash 1990, Atkinson et al. 1998, Parry 2002) from which their identity can be deduced.

To facilitate the identification and mapping of bioturbators and surface features, data may be collected from quantitative remotely operated vehicle (ROV) observations. Such data have been validated previously against those derived from direct diver observation (Parry et al. 2002) and have proved to be an accurate and effective representation of the biogenic landscape. Furthermore, spatial referencing of ROV images allows mapping of megafaunal assemblages within benthic landscapes (Parry et al. 2003).

Through the intensive study of a relatively small area of bioturbated seabed, the current study aims to establish whether a relationship exists between the identity and abundance of biologically produced surface features and the structure and diversity of infaunal macrobenthic communities. The potential of surface features as an accurate surrogate of macrobenthic community structure and diversity is discussed.

**METHODS**

**Sample area:** The field sampling was conducted between 30th-31st May 2000 at Jennycliff Bay (50°21.0'N 04°07.8'W), a sheltered bay within Plymouth Sound. This area is an extensive stretch of sandy mud (Marine Biological Association 1957) with a water depth of approximately 10 m and generally low current speeds. Jennycliff Bay supports high megafaunal densities, characterised by thalassinidean shrimp (Upogebia deltata and Callianassa subterranea), Goneplax rhomboides and several large bivalve species (Parry 2002). Patterns in macrobenthic community structure have been well studied at this site (Kendall & Widdicombe 1999).

**Characterisation of biogenic landscape:** Megafaunal assemblage data extracted from remote observations of the seabed may be considered descriptors of the biologically-mediated landscape rather than an absolute estimate of megafaunal species abundance because different burrows have a variable number of surface openings. Nevertheless, the morphology of surface features may be used to infer the identity of species responsible for burrow construction (e.g. Nickell & Atkinson 1995). The definition of megafaunal assemblage used in the present study encompassed surface dwelling megafauna and biogenic sediment features, such as burrow openings and mounds, because many soft-sediment megafaunal species bury deep in the sediment. To describe the biologically-mediated landscape, the abundance of both megafaunal individuals and surface features was used to construct matrices of Bray–Curtis similarity.

To quantify the abundance and diversity of both megabenthic and macrobenthic infauna a 3 × 3 m steel frame was deployed. This frame was subdivided into a grid of 50 × 50 cm and was fixed to the sea floor by embedding the steel legs at each corner of the frame firmly into the sediment. The area within each of the 50 × 50 cm cells was filmed using a Remotely Operated Vehicle (ROV) and the images recorded on video tape. The ROV camera was fitted with the Automated Benthic Image Scaling System (ABISS), a structured lighting array that
was used for image scaling (Pilgrim et al. 2000). Benthic Imager software (University of Plymouth, UK) (Pilgrim et al. 2000) was used to analyse the laser spot pattern and calculate camera orientation allowing accurate measurements (±5%) of features to be taken from each still image. Still images were selected and captured from the videotape such that the entire survey plot was represented to allow measurement of all biogenic surface-features observed. Features counted included burrows, tubes and all surface dwelling megafauna. The identity of species responsible for burrow construction was determined where possible using the morphological characteristics described by Marrs et al. (1996) and by direct sampling of observed features (Parry 2002).

Sampling macro-infauna: After the grid had been mapped by the ROV, 61 macrofauna samples were taken, one sample at the centre of each cell and a sample at each intersection (Fig. 1). Macrofaunal samples were taken by divers using 10 cm diameter plastic cores (0.008 m² surface area) pushed into the sediment to a depth of 30 cm. These were carefully excavated and sealed inside plastic bags. On the surface, the sample bags were opened and the water inside decanted over a 0.5 mm mesh. Each bag was filled with 10% buffered formalin and sealed. After 4 days, the samples were washed over a 0.5 mm mesh before all animals were extracted. Animals were identified under a binocular microscope to the lowest practical taxonomic level. In the case of the cirratulid polychaetes, the separation of individuals of the genera Monticellina / Tharyx, Caulerilla 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 followed Howson & Picton (1997).

Relating surface features to macrobenthic community structure: Megafauna have been defined operationally as those organisms large enough to be observed by a camera (Grassle et al. 1975), yet the absolute dimensions of an organism in an image depend upon image resolution. In the present study, all epibenthic megafaunal individuals and biotic sediment structures associated with burrowing megafauna detected in underwater images were measured using Benthic Imager (Pilgrim et al. 2000), but were only included in analyses if the diameter exceeded 10 mm.

The euclidean distance between each macrofaunal core and each megafaunal surface-feature was calculated using MATLAB software (version 5.0, The MathWorks Inc.). Around each macrofauna core biogenic features were quantified with progressively larger circles of 30, 40, 50, 60, 70, 80, 90 and 100 cm diameter. These circles are subsequently referred to as virtual quadrats. Within each of the virtual quadrats data on the identity and abundance of surface features were obtained from analysis of the video images.

Multivariate data analyses followed the methods described by Clarke (1993) using the PRIMER version 5.0 software package (Clarke & Warwick 1994). Analysis was carried out on both untransformed and Wi transformed macrofauna data, using the Bray-Curtis similarity measure, to examine different components of the community. Analysis of untransformed data is sensitive to changes in the abundance of the dominant species whilst analysis of Wi transformed data detects effects on community structure generally including changes in the abundance of the rarer species, without being unduly influenced by dominant, high abundance species.

Pair-wise Bray-Curtis similarities (untransformed data) between megafaunal surface-feature samples of the same size were calculated and similarity matrices for each of the eight sample sizes created. RELATE was used to compare each of these matrices with the equivalent matrix calculated from the infaunal abundance data. For the smallest virtual quadrat size (30 cm diameter) all macrofauna samples were used in the analysis. However, for larger quadrats an area of overlap existed when the quadrat was overlain neighbouring macrofauna samples. Consequently, for comparisons involving quadrats greater than 30 cm in diameter smaller subsets of macrofaunal samples were used to ensure sample independence.

For quadrats of 40 cm and 50 cm diameter 2 separate subsets of macrofauna cores were used (Fig. 2a), whilst for quadrats with a diameter greater than 50 cm a subset of 9 macrofauna samples (B2, B6, B10, F2, F6, F10, J2, J6 and J10) was used (Fig. 2b).

For each of the nine, non-overlapping, 1 m diameter surface-feature samples, a mean Bray-Curtis similarity value (Wi transformed data) was calculated from pair-wise analyses using all of the 5 macrofauna cores contained within the area of the surface-feature sample. To establish the extent to which the number of different types of surface-features in any given area predicted macrofaunal heterogeneity, mean Bray-Curtis similarity was plotted against surface feature diversity (number of different types of surface feature within a given area).

Relating surface feature diversity to macrobenthic diversity: Univariate measures of diversity [number of species, number of individuals, Margalef species richness (d), Shannon-Wiener diversity (H')] and Pielou’s evenness (J’) were calculated, using PRIMER, for each macrofauna sample and plotted against the diversity of the surrounding surface features. This was done for all sizes of virtual quadrat. In addition, for quadrats with a diameter of 1 m, the 5 macrobenthic samples contained within each one were pooled and the diversity of these pooled samples was compared with the diversity of the surroun-
dingsurfacefeatures.Inallcasesurfacefeaturediversitywasthenumberofdifferenttypeofsurfacefeaturewithinagivenarea.

RESULTS

Surface features observed

A total of eleven different megafaunal biotic feature types were identified from the images (Table I). Biogenic sediment features included thalassinidean mud shrimp burrow openings (*Upogebia deltaura* and *Callianassa subterranea*) and mounds (*Callianassa subterranea*), angular crab burrows (*Goneplax rhomboides*), bivalve siphons and a variety of unknown surface openings and feeding pits. Megafaunal species included the infaunal bivalves *Lutraria lutraria*, *Acanthocardia* sp. and Unknown Bivalve 1, plus ophiuroids.

Macrofauna community of study area

A total of 124 taxa were identified during this study with the community being numerically dominated by polychaetes (73), molluscs (19) and crustaceans (19). The species rich community at Jennycliff Bay was typical for sandy-mud sediments of unpolluted boreal regions of the northeast Atlantic.

Relating surface features to macrobenthic community structure

For small virtual quadrat sizes (less than 80 cm diameter), patterns of similarity generated by surface feature abundance data were different from patterns generated using the macrofauna abundance data (Table II). Significant correlations were observed when the larger virtual quadrat sizes were used. Changes in the relative abundance of the numerically dominant macrofauna (untransformed data) correlated to changes in the surface features for virtual quadrat sizes of 90 cm and 1 m, whilst macrobenthic community changes due to the rarer species (√ transformed data) were correlated to changes in the surface features for virtual quadrat sizes of 80 cm, 90 cm and 1 m (Table II). This would suggest that changes in the identity and density of surface features over these larger, spatial...
scales mimic those changes observed in both the numerically dominant and the rarer macrofaunal species.

In areas with a large number of different surface features, the macrobenthic community exhibited more small scale (<1 m) heterogeneity than in areas with a low diversity of surface features (Fig. 3). This response was only observed in transformed data and would suggest that this increased patchiness is due to changes in the identity and abundance of the rarer species.

**Relating surface feature diversity to macrobenthic diversity**

No relationship was observed between the diversity of individual macrofauna cores and the diversity of the surrounding megabenthic surface features. However, if 5 macrofauna cores, taken within each of the nine 1 m diameter surface feature quadrats, are pooled then a relationship between macrobenthic diversity and that of surface features emerges. At this scale as the diversity of surface features increases so does that of macrobenthos (Fig. 3). During sampling it was observed that one quadrat contained a very extensive *Goneplax* burrow. It was considered that the large amount of disturbance associated with this feature would have masked the effects of the other features and caused lower than expected macrobenthic diversity. This sample was therefore omitted from the analysis. The relationship between surface feature diversity and macrobenthic diversity gradually broke down as the different diversity indices used became increasingly more reliant on eveness in preference to species richness.

### Table I. – Description of the surface features observed.

<table>
<thead>
<tr>
<th>Conspicuous surface feature</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thalassinidean opening</td>
<td>Circular funnel-shaped opening leading to vertical shaft. <em>Melinna palmate</em> tubes often visible within opening.</td>
</tr>
<tr>
<td>Thalassinidean mound</td>
<td>Sediment mound that is darker than sediment surface (anoxic). Mound diameter at base approximately 8cm. Circular opening approximately 2cm diameter at the summit of mound.</td>
</tr>
<tr>
<td><em>Goneplax rhomboides</em> burrow</td>
<td>Oblique burrow opening approximately 4cm wide. Ejected sediment often visible as scree from burrow entrance.</td>
</tr>
<tr>
<td><em>Acanthocardia</em> sp.</td>
<td>Single surface opening with fused bivalve tips visible at surface. Pale viscera siphon tips that appear as two spots when contracted in response to ROV passing overhead.</td>
</tr>
<tr>
<td><em>Lutraria lutaria</em></td>
<td>Single surface opening with fused bivalve siphon tips visible at the surface. Dark viscera siphon tips.</td>
</tr>
<tr>
<td><em>Ophiura</em> sp.</td>
<td>Large brittlestar with disc diameter approximately 35mm. Arm length approximately 4 times disc diameter.</td>
</tr>
<tr>
<td>3-siphoned opening</td>
<td>Single surface opening approximately 2cm diameter containing three circular holes, each approximately 5mm.</td>
</tr>
<tr>
<td>Circular 1cm flush opening</td>
<td>Circular hole approximately 1cm diameter, flush with sediment surface.</td>
</tr>
<tr>
<td>Unknown bivalve siphon</td>
<td>Single surface opening with fused siphon tips visible at surface. Pale viscera tips that appear hourglass in shape when contracted in response to ROV passing overhead.</td>
</tr>
<tr>
<td>Paired pit</td>
<td>Single surface opening approximately 2 cm diameter containing two circular holes, each approximately 5 mm diameter.</td>
</tr>
<tr>
<td>Obscured burrow</td>
<td>Biogenic sediment structure partially obscured by <em>Laminaria</em> sp. or other detritus.</td>
</tr>
</tbody>
</table>
DISCUSSION

This study has shown that for the particular macrobenthic community observed, faunal heterogeneity, and diversity, was greater in areas that contained many different surface features compared with areas containing few features. This observation is field evidence to substantiate previous work that suggested macrofaunal diversity would be highest in areas populated by a high diversity of bioturbating species (Widdicombe et al. 2000, Widdicombe & Austen 1999). This assumption had previously been based on experimental evidence that showed different species of bioturbators, or types of bioturbation, generated characteristic associated communities of macrofauna. If such a mechanism was responsible for the relationships seen in the current study it would be expected that the strongest patterns should be visible in the identity and abundance of the rare species, as was the case. Only when macrofauna community data was analysed using moderately heavy transformation, thus reducing the impact of numerically dominant species and enhancing that of rare species, were any relationships observed.

By using a particularly fine scale of spatial resolution it could be seen that, only when analysing areas of 80 cm in diameter and larger was the diversity and community structure of surface features related to that of the infauna. The reason the relationship is only seen for the largest size of surface feature quadrats is most probably related to the scale at which the surface features occur. A single feature may be in excess of 30 cm across and consequently the smaller virtual samples contained only a few surface features. This low number of surface features per quadrat would make macrobenthic – surface feature comparisons unrealistic. It is clear that the processes involved in the creation of sediment surface features, particularly bioturbation, might be considered to set infaunal diversity at the scale of habitats rather than that of samples. This suggests the greatest value of using surface features as a surrogate for diversity would come when assessing large scale impacts on sediment habitats; faunistic changes over long distances, long-term temporal changes in a particular place or assessing differences between habitats or geographical locations.

Whilst visual mapping of the sediment surface provides an enormous amount of information on the identity and distribution of many key bioturbating species there are some species (e.g. polychaetes such as Nephtys sp., burrowing echinoids and nuculacid bivalves) which do not create conspicuous surface features. These “invisible” species have been shown to have a significant impact on the diversity and structure of macrobenthic communities (Widdicombe et al. 2000, Widdicombe & Austen 1999).

Table II. – Comparisons of surface feature community structure (untransformed data) with macrobenthic community structure (untransformed and transformed data) at a range of spatial scales using RELATE (bold values indicate significant correlations).

<table>
<thead>
<tr>
<th>Megafaunal sample diameter (cm)</th>
<th>Untransformed macrofauna</th>
<th>¥² transformed macrofauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rho value</td>
<td>P statistic</td>
<td>Rho value</td>
</tr>
<tr>
<td>30</td>
<td>-0.118</td>
<td>94.64</td>
</tr>
<tr>
<td>40</td>
<td>-0.063</td>
<td>67.71</td>
</tr>
<tr>
<td>50</td>
<td>0.060</td>
<td>24.52</td>
</tr>
<tr>
<td>60</td>
<td>-0.003</td>
<td>49.61</td>
</tr>
<tr>
<td>70</td>
<td>0.117</td>
<td>16.34</td>
</tr>
<tr>
<td>80</td>
<td>0.324</td>
<td>10.72</td>
</tr>
<tr>
<td>90</td>
<td>0.344</td>
<td>9.52</td>
</tr>
<tr>
<td>100</td>
<td>0.381</td>
<td>7.36</td>
</tr>
<tr>
<td>100</td>
<td>0.460</td>
<td>3.44</td>
</tr>
</tbody>
</table>

Fig 3. – Top, the relationship between megabenthic surface feature diversity and infaunal homogeneity [as measured by mean Bray-Curtis similarity] (± 95% confidence intervals). Bottom, relationship between surface feature diversity and the total number of macrofaunal species from 5 pooled samples (R=0.6697).
bioturbarators should be examined and the differential effects of such species on the macrofauna need to be considered when interpreting the data. Additionally, to be a truly valuable assessment tool, the relationship must be shown to exist in other geographic locations and in different soft-sediment habitats.

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