



## Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds

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### Abstract

Much recent work on patch-occupancy dynamics has been concentrated in terrestrial ecosystems, with few examples evident from soft-sediment marine habitats. Seagrass landscapes have recently been recognised to be potentially ideal marine models for the study of such ecological concepts. Infaunal macroinvertebrate assemblages of two patch sizes of the seagrass *Zostera marina* were compared: small (< 15 m diameter) and large (> 30 m diameter), using an unreplicated random block design. Further comparison was made between infaunal assemblage composition at the edge and centre of each patch. Univariate statistical analysis of data indicated significantly greater total numbers of taxa in samples from large patches than in small. Multivariate analyses indicated significant differences in assemblage composition due to both patch size and in-patch location, and revealed that differences were due to small changes in the relative abundances of many taxa. Possible mechanisms underlying the observed variations of assemblage composition with patch size and in-patch location are discussed. Although the present results support some of the theories relating to the control of infaunal assemblage composition, explanations are not applicable across all taxonomic groups. At the scale of the present study, seagrass patch size and edge-effects appear to be less significant than 'regional' factors, which relate to relatively small variation in environmental parameters, for the structuring of infaunal macroinvertebrate assemblages. © 2001 Published by Elsevier Science B.V.

**Keywords:** In-patch location; Edge effects; Macroinvertebrate assemblage; Patch size; Seagrass; Species–area relationship; *Zostera marina*

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## 1. Introduction

Concepts of patch-occupancy dynamics and the relationships between habitat heterogeneity, disturbance and observed levels of biodiversity have received recent attention in both terrestrial and marine ecology (e.g. Shaffer, 1994; Hanski, 1994; Robbins and Bell, 1994). The patch-dynamics approach seeks to understand observed distributions of organisms by viewing the environment, at all scales, as a mosaic of heterogeneous units between which organisms, larvae or propagules can migrate and within which community interactions occur (see Pickett and White, 1985; Kolasa and Pickett, 1991). In parallel with the development of patch-dynamics theory, there has been an increasing focus on the study of ecological processes at the landscape scale of reference as opposed to single point or regional/biogeographic scales (e.g. Hanski, 1994; Forman, 1995; Bell et al., 1995; Irlandi et al., 1995). In this context, a landscape is defined as being a heterogeneous area composed of a set of interacting ecosystems that are repeated in similar form throughout (Forman, 1995). Such studies are of particular relevance in assessing the effects of habitat fragmentation through natural or anthropogenic disturbance and, thus, in the planning of conservation strategies and environmental impact assessments (Pickett and Thompson, 1978; McNeill and Fairweather, 1993; Thrush et al., 1997a).

To date, most work related to the processes of patch-occupancy dynamics in marine habitats has been conducted at small scales for hard-substrate sessile assemblages (e.g. Sousa, 1984; Keough, 1984; Farrell, 1989; Underwood and Skilleter, 1996). However, with increasing anthropogenic impacts in coastal marine environments and the concomitant awareness of the requirement for effective assessment of effects on ecosystems at landscape scales and above (Underwood, 1996; Thrush et al., 1997a), there is a need for information relating to the ecological effects of habitat patch size at this scale, particularly for soft sediment environments. In this context, it has been suggested that seagrass landscapes represent potentially ideal marine models for the study of the ecological concepts of patch-dynamics and habitat-fragmentation (Robbins and Bell, 1994).

It is well-documented that in relation to surrounding unvegetated soft sediment habitats, seagrass beds are areas of high productivity and high biodiversity (Stoner, 1980; Bostrom and Bonsdorf, 1997). The leaves and root-rhizome system of seagrass create habitats of relatively high structural complexity, which by contrast to bare sediments, provide many spatial niches for a variety of fauna (Heck and Wetstone, 1977; Knowles and Bell, 1998) and are believed to afford shelter from predation (Orth et al., 1984). By reducing the effects of current and wave-action at the sea-bed, seagrass beds also encourage the deposition of fine/organic sediments and, thus, alter the particle-size structure of the substrata on which they grow (Fonseca et al., 1983) and the availability of food for benthic fauna (Castel et al., 1989). The increased productivity, habitat modification and generation of spatial refugia in otherwise unvegetated areas make it likely that seagrass beds are important in maintaining the biodiversity of shallow, sub-littoral ecosystems in which they occur.

More than 50 species of seagrass have been recorded globally of which one, *Zostera marina* L. is by far the most abundant and widespread in northern temperate waters (den

Hartog, 1970). This species typically grows as monospecific stands ('beds' or 'meadows') with clearly defined boundaries in areas of otherwise bare soft substrate. Thus, by comparison with other marine and terrestrial landscapes, which may include a number of structural species and considerable heterogeneity within habitat patches, beds of *Z. marina* represent a relatively simple system in which individual patches may be viewed as distinct and homogeneous habitat "islands". Studies of faunal assemblages in seagrass beds to date have largely concentrated on comparisons with the assemblages in adjacent, unvegetated sediments (e.g. Edgar et al., 1994) and the role of habitat complexity afforded by structural attributes of the seagrass in influencing assemblage composition (e.g. Heck and Wetstone, 1977). While it has been consistently demonstrated that seagrass beds contain greater faunal diversity and abundance than surrounding bare sediments, and that there are correlations between increased faunal abundance and diversity and some measures of seagrass structural complexity (e.g. Webster et al., 1998), these phenomena have not been related to the potentially confounding effects of patch size. In terrestrial landscapes, habitat area per se has been shown to influence the number of taxa present (e.g. Simberloff, 1976); larger areas supporting greater numbers of species. If the same relationship applies in seagrass habitats, it has implications, at one scale, for the interpretation of studies on the effects of seagrass structural complexity (Attrill et al., 2000) and, at a larger scale, for assessment of the implications of habitat fragmentation (e.g. Frost et al., 1999).

Thus, the present study aims to address the effect of patch size and edge effects on infaunal macroinvertebrate assemblage composition of seagrass beds. Such effects are well-documented in terrestrial landscape ecology (Yahner, 1988; Forman, 1995) and previous studies have presumed that they also occur in *Z. marina* seagrass landscapes (Webster et al., 1998; Frost et al. 1999). However, they have not as yet been demonstrated experimentally.

## 2. Materials and methods

### 2.1. The study site

The seagrass beds studied are situated in the Isles of Scilly (45 km off the southwest peninsula of England; 49°57'N, 06°19'W), a small archipelago of low-lying, granite islands and reefs enclosing areas of shallow, mixed substrate habitats surrounded by deeper continental shelf waters (Fig. 1a). Seagrass beds within the Isles of Scilly are found on clean sand substrates at depths down to approximately 10 m below chart datum (CD; the level of the lowest astronomical tide). In order to minimise the effects of natural variables other than patch size and in-patch location, the patches used in this study were selected, as far as possible, to have consistent depth (chart datum), shoot density and sediment characteristics.

### 2.2. Experimental design

Initial observations revealed that seagrass beds exhibit two basic forms, discrete small patches and large reticulate patches. Such differences in bed form have been linked to

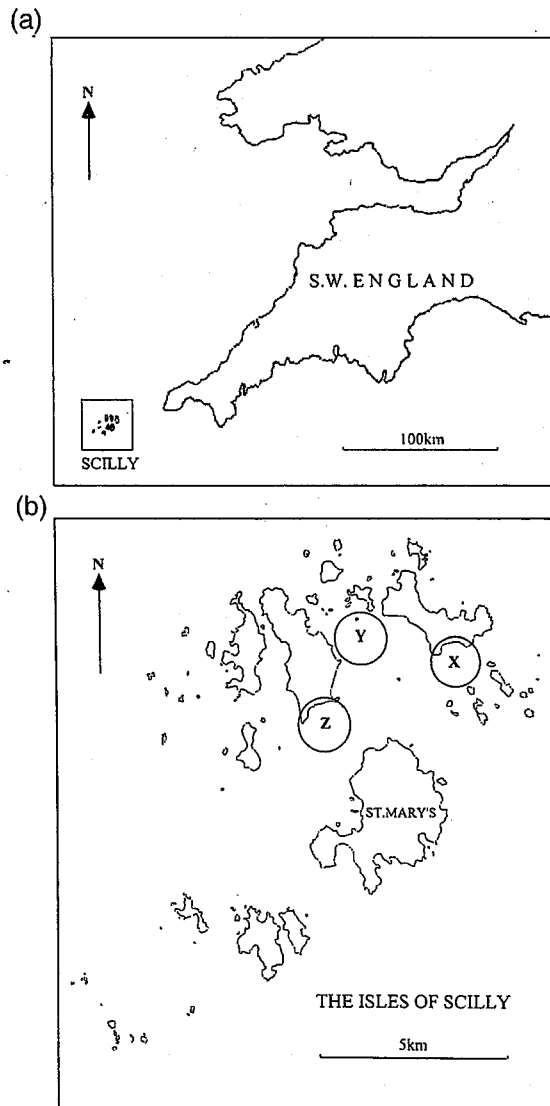


Fig. 1. (a) The location of the Isles of Scilly study site off the coast of England. (b) The location of the blocks (X, Y, Z) in each of which one large and one small *Z. marina* patch were sampled for associated macroinvertebrate infauna.

the influence of bottom currents and wave action (Fonseca et al., 1983; Irlandi et al., 1995). Therefore, a blocked strategy was adopted to enable some estimation to be made of the effects of environmental variability across the area (Fig. 1b). In particular, the degree of exposure to wave action resulting from the prevailing southwest winds and variations in the strength of tidally induced currents. Limitations of sample collecting and processing time, together with a lack of suitably sized patches within each block and

at the required depth, resulted in an unreplicated random blocks design, with three replicates of each patch size across blocks but no replication of patch size within blocks. Without such replication the inability to measure variability among samples of the same factor within blocks means that there is no logically valid test for the main effects under investigation unless it is assumed that there are no interactions between them (Underwood, 1997). This assumption is unlikely to be correct in practice, as the recognised heterogeneity of the area was the reason for blocking in the first place. However, consideration of possible interactions and their effects upon the outcome of tests for the main effects of patch size and in-patch location suggested that such interactions, if actually present but assumed to be zero in the analysis, would result in increased probability of Type II errors in testing for main effects. That is, main treatment effects would be masked by interaction effects. Thus, although the design adopted is evidently not optimal, it appears unlikely that the resulting analysis will detect a significant effect where none exists and any significant result should indicate that a genuine effect is present. The concomitant increased likelihood of failure to reject the null hypothesis when false, however, and the inability to assess how the effects of patch size or in-patch location vary spatially within blocks, remain problems with this sampling design which necessitate caution in the interpretation of, and limit the validity of, generalisations made from its results (see Underwood, 1997, pp. 386–389, and references therein, for a detailed critique of completely randomised and unreplicated random blocks experiments in relation to analysis of variance).

Following measurement of patch sizes during initial observations, a 'small' patch was defined as being < 15 m on its longest dimension and a 'large' patch as being > 30 m (i.e. twice as large) on its shortest dimension of continuous coverage. This definition overcame measurement problems associated with the discontinuous nature of large patches. Within each patch 'centre' and 'edge' ( $\leq 1$  m from boundary) locations were established by measurement across the smallest dimension of the patch from the most clearly defined boundary.

### 2.3. Sample collection

Sampling was conducted over a 7-day period in September 1998 on low water spring tides by wading and snorkelling. At each randomly defined sampling location a 10-cm diameter wire template was dropped haphazardly from above the water surface. A quadrat ( $0.0625 \text{ m}^2$ ) was placed over the template and the number of seagrass shoots within it counted. Shoots within the 10-cm diameter template were then gathered into a collecting tube and cut off at their base. With the template still in place, a 10-cm diameter PVC corer (to 15 cm depth) was used to take an infauna sample. By the nature of this sampling technique, epibenthic fauna (though not epiphytic fauna) were included in the infauna samples. Four replicate cores were taken at each sampling location (3 blocks  $\times$  2 patch sizes  $\times$  2 in-patch positions  $\times$  4 replicates = 48 samples). A sediment core (3 cm diameter, 5 cm depth) was taken adjacent to each fauna core for granulometric and organic content analysis. Fauna samples were sieved (0.5 mm mesh) on site and preserved in 10% formalin in seawater for laboratory sorting and identification. Sediment cores were frozen within four hours of sampling to allow later determination of

organic content. Depth and time were recorded for each station, with depth measurements subsequently adjusted to chart datum by relating the time of measurement to data recorded from the electronic tide gauge at St. Mary's. Sampling depth at the study site varied between 0.25 m below and 0.38 m above CD. However, such a small range of depths is considered to be of little ecological significance with respect to seagrass assemblages (Webster et al., 1998).

#### 2.4. Laboratory analysis

In the laboratory, each fauna sample was washed on a 0.5-mm sieve to remove formalin. Organisms were picked from the sediments by hand and preserved in 70% alcohol prior to being identified to species level, wherever possible, using low power microscopy. *Zostera* root–rhizome material was removed from the fauna sample, the rhizomes and roots separated and dried to constant weight in a desiccating oven (100°C) for dry weight measurement. Separate measurements of the two major elements of the root–rhizome matrix were taken in order to calculate a putative index of below-ground structural complexity (i.e. ratio of rhizome dry-weight to root dry-weight). The frozen sediment cores were each divided into three sub-samples for granulometric analysis, organic content analysis and contingency use. Granulometric analysis was performed by means of the low-angle laser light scatter (LALLS) technique (Malvern Master-sizer), samples having first been sieved to remove and weigh the  $\geq 2$  mm fraction. Total organic content of the sediment was evaluated by the standard combustion technique. Samples were first dried to constant weight in a desiccating oven (100°C) prior to combustion in a muffle furnace for 4 h at 500°C. Percentage organic matter content was calculated from the weight-change following combustion.

#### 2.5. Data analysis

Data were analysed by both univariate and multivariate statistical techniques. ANOVA tests (Minitab Version 10.5) were performed on sediment variables (mean grain size, percentage  $< 63$   $\mu\text{m}$ , sorting, organic content), seagrass parameters (shoot density, root–rhizome biomass, ratio of root:rhizome biomass) and macroinvertebrate community indices (abundance, number of taxa and Shannon–Weiner diversity— $H' \log_e$ ) using a restricted, fully orthogonal factorial model in which patch size and in-patch location are fixed factors and block is treated as a random factor. All data were tested using Cochran's *C*-test and square-root or log (natural) transformed where necessary to correct for departures from homoscedasticity. For all ANOVA analyses, significance was determined at the  $\alpha = 0.05$  level in order to optimize Type I/Type II error rates (Underwood, 1994, 1997). Linear regression analyses were performed to examine the significance of associations between environmental factors (identified by ANOVA analysis as being of significance) and infaunal abundance, number of taxa and Shannon–Weiner diversity. However, before any statistical analysis, logarithmic (natural) transformations were completed on data where necessary to ensure conformance to an approximate normal distribution. To ensure that the required statistical assumptions (normally distributed residuals, homoscedastic variances) were met, diagnostic tests

(Shapiro–Wilk  $W$ ) were applied to all regression residuals (d'Agostino, 1986). Homoscedastic residual variances were confirmed by examining plots of the standardised residuals for evidence of characteristic patterns of increasing or decreasing variance, as recommended by Draper and Smith (1981).

Multivariate analysis was undertaken by utilising the PRIMER (Plymouth Routines in Multivariate Ecological Research) package (Clarke and Warwick, 1994). Using a ranked similarity matrix based on Bray–Curtis similarity measures of double square root transformed infauna data, an ordination plot was produced by non-metric multi-dimensional scaling (MDS). Formal significance tests for differences between patch size groups and in-patch location groups across blocks were performed using two-way ANOSIM (Clarke and Green, 1988) and the taxa contributing to any dissimilarities observed were investigated by the similarities percentages procedure SIMPER (Clarke, 1993). The relationship between assemblage structure and environmental variables was examined using the BIOENV procedure with the sediment and seagrass variables indicated above (variables were checked for co-correlation using Spearman's Rank Correlation).

### 3. Results

#### 3.1. Univariate analysis

ANOVA revealed no significant differences in sediment characteristics by block, patch size or in-patch location for mean particle size, sorting coefficient or organic content (Table 1). However, there was a significant difference ( $P < 0.05$ ) detected in the fine fraction content of the sediment (percentage  $< 63 \mu\text{m}$ ) for patch size, with

Table 1

Summary of ANOVA results on environmental data from *Z. marina* beds in the Isles of Scilly. The model takes block, patch size and in-patch location as main factors. Block is treated as a random factor. Significant results are marked: \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

#### (a) Sediment parameters

Source	df	Mean grain size		Sorting		Percent $< 63 \mu\text{m}$		Organic content	
		F	P	F	P	F	P	F	P
Block	2	2.24	0.309	5.43	0.155	17.74	0.053	0.67	0.598
Size	1	1.95	0.297	0.07	0.816	21.46	0.044*	1.52	0.343
Location	2	3.69	0.124	2.97	0.162	1.14	0.405	0.99	0.446

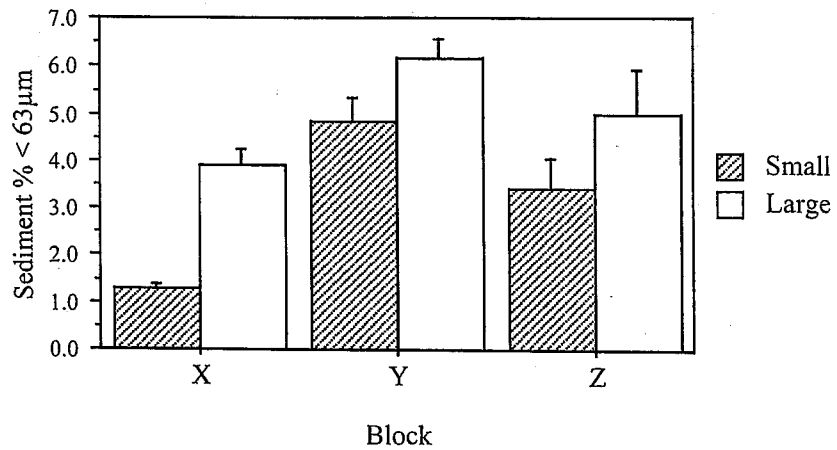
#### (b) Seagrass parameters

Source	df	Shoot density		Root–rhizome biomass		Root:rhizome index	
		F	P	F	P	F	P
Block	2	0.01	0.987	13.83	0.067	0.02	0.831
Size	1	0.77	0.473	4.68	0.163	0.01	0.933
Location	2	21.61	0.007**	0.84	0.496	1.12	0.410

sediments from larger patches having a higher percentage of fines than those from small patches (Fig. 2a).

Seagrass shoot density ranged from 112 to 188 shoots  $m^{-2}$ . Whilst variations were not found to be great by block or patch size, significant differences were apparent by in-patch location ( $P < 0.01$ ), with shoot density greater at the centre of patches than at the edge locations (Fig. 2b). No statistically significant differences were detected between block, patch size or in-patch location for any of the below-ground seagrass parameters.

a)



b)

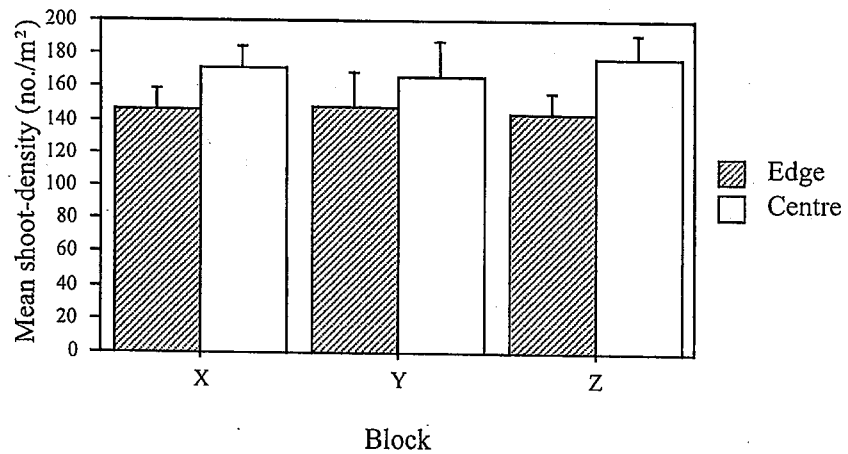


Fig. 2. (a) Mean sediment percent < 63  $\mu m$  in relation to patch size. (b) Mean *Zostera* shoot density in relation to in-patch location (error bars 1 S.E.,  $n = 8$ ) for each regional block of the experiment (X, Y, Z).



A total of 4531 individuals representing 89 taxa from eight phyla were identified in the samples. Mean macroinvertebrate abundance ranged from 7194 to 26706 individuals  $m^{-2}$ . Differences between blocks in number of taxa, total abundance and diversity were significant ( $P < 0.01$ ) (Table 2), with all three variables increasing in the order X, Y, Z. (Fig. 3a). Whilst a significant effect ( $P < 0.01$ ) of patch size on total number of macroinvertebrate taxa was apparent, large patches having more taxa than small patches

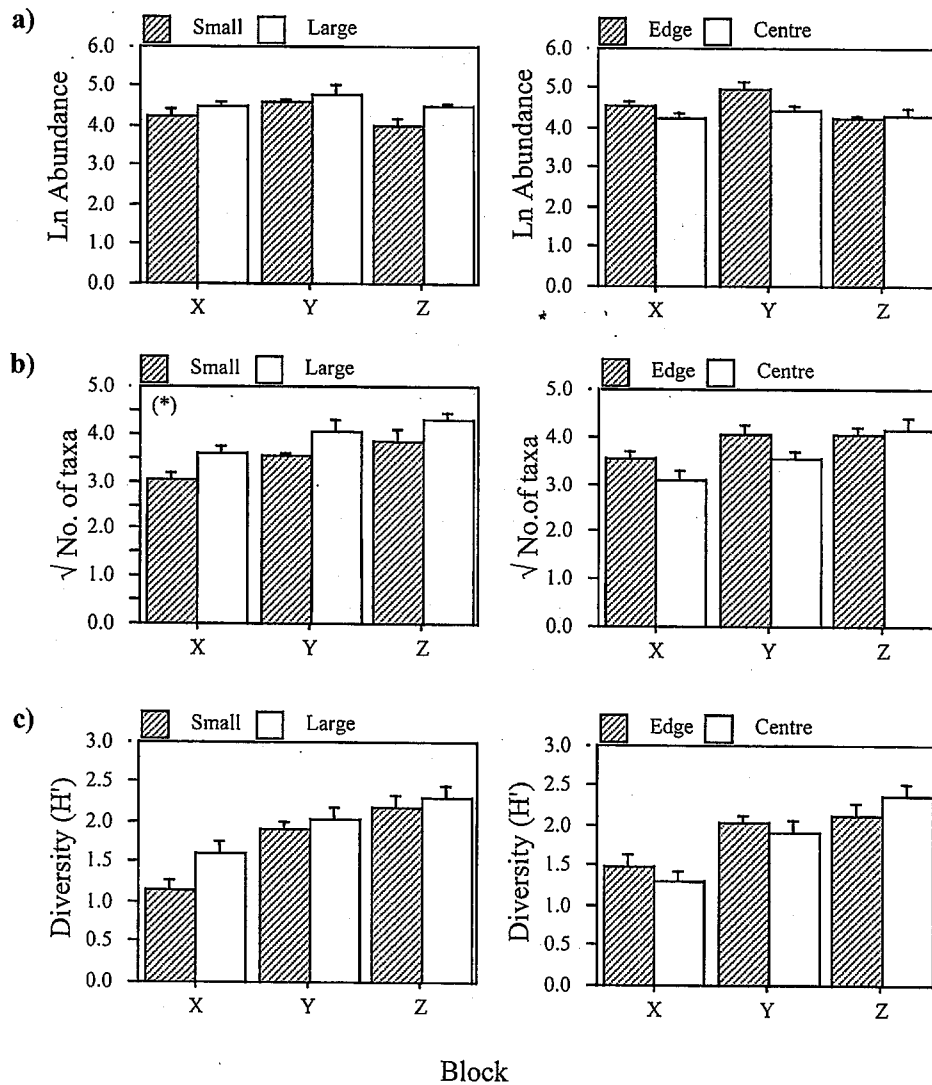


Fig. 3. Total macroinvertebrate infauna in *Z. marina* patches: (a) abundance (ln transformed), (b) number of taxa (square-root transformed), (c) Shannon–Weiner diversity ( $H' \log_e$ ). Mean values (error bars 1 S.E.,  $n = 8$ ) for small and large patches and edge and centre in-patch locations are shown in each regional block of the experiment (X, Y, Z).

Table 2

Summary of ANOVA results on infaunal macroinvertebrate data from *Z. marina* beds in the Isles of Scilly. The model takes block, patch size and in-patch location as main factors and block is treated as a random factor. Significant results are marked: \*,  $P < 0.05$ , \*\*,  $P < 0.01$ .

Source	df	Number of taxa		Number of individuals		Diversity ( $H' \log_e$ )	
		F	P	F	P	F	P
Block	2	12.58	< 0.001**	6.08	0.005**	21.31	< 0.001**
Size	1	188.23	0.005**	11.72	0.076	4.24	0.176
Location	2	2.49	0.255	2.11	0.284	0.03	0.881

(Fig. 3b), no significant effect of patch size was found on measures of abundance or diversity. In-patch location showed no significant effect on any of the univariate fauna variables measured.

Linear regressions of macro-infaunal abundance, number of taxa and diversity against the significant environmental variables revealed significant relationships between all parameters and percentage fines (Table 3, Fig. 4). Although the amount of variation explained by any single factor was generally low. No significant relationships were apparent with shoot density (Table 3).

### 3.2. Multivariate analysis

The MDS ordination of taxon abundance data reveals the most obvious clustering of samples to be by block, i.e. Block Y samples are situated towards the right-hand side of the plot, Block X to the top left and Block Z to the bottom left. Within each block grouping there is a degree of further clustering by both patch size and in-patch location (Fig. 5). Formal two-way crossed ANOSIM tests on the Bray–Curtis similarity data confirm these apparent separations, showing significant effects of block, patch size and in-patch location ( $P < 0.001$  in all cases) on assemblage composition. The high global  $R$  values for the effects of block ( $R = 0.755$ ) suggest that this factor has a greater influence on assemblage composition than either patch size ( $R = 0.350$ ) or in-patch location ( $R = 0.234$ ).

Table 3

Results of linear regression of significant environmental variables (percent < 63  $\mu\text{m}$ , shoot density) with univariate assemblage parameters. All significant regressions had homoscedastic residuals and significant Shapiro–Wilk (SW) statistics ( $n = 48$ ).

Parameters	$R^2$	F	P	SW
Percent < 63 $\mu\text{m}$ versus log abundance	0.1944	11.10	0.0017	0.9697
Percent < 63 $\mu\text{m}$ versus number of taxa	0.2240	13.28	< 0.0001	0.9548
Percent < 63 $\mu\text{m}$ versus $H'e$	0.2024	11.68	< 0.0001	0.9775
Shoot density versus log abundance	0.0038	0.18	0.6758	–
Shoot density versus number of taxa	0.0179	0.84	0.3649	–
Shoot density versus $H'e$	0.0092	0.43	0.5167	–

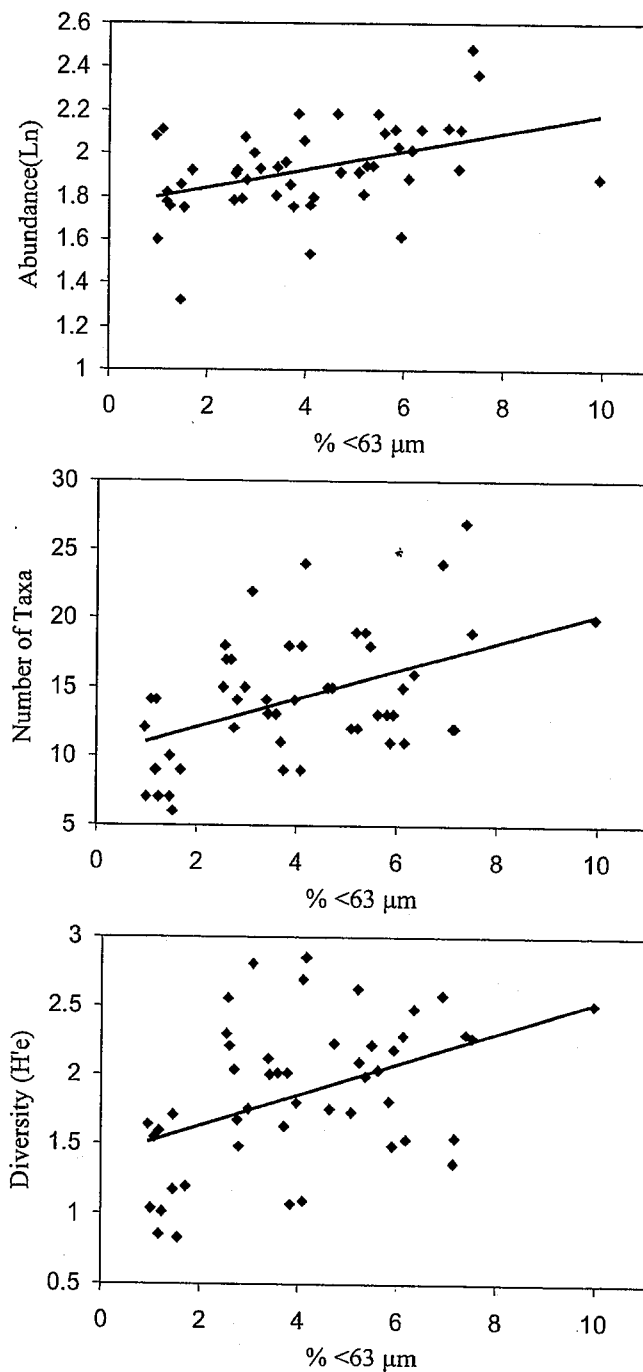


Fig. 4. Scattergrams representing the relationship between sediment percentage < 63 μm and univariate assemblage parameters, together with fitted regression lines (see Table 3 for regression details).

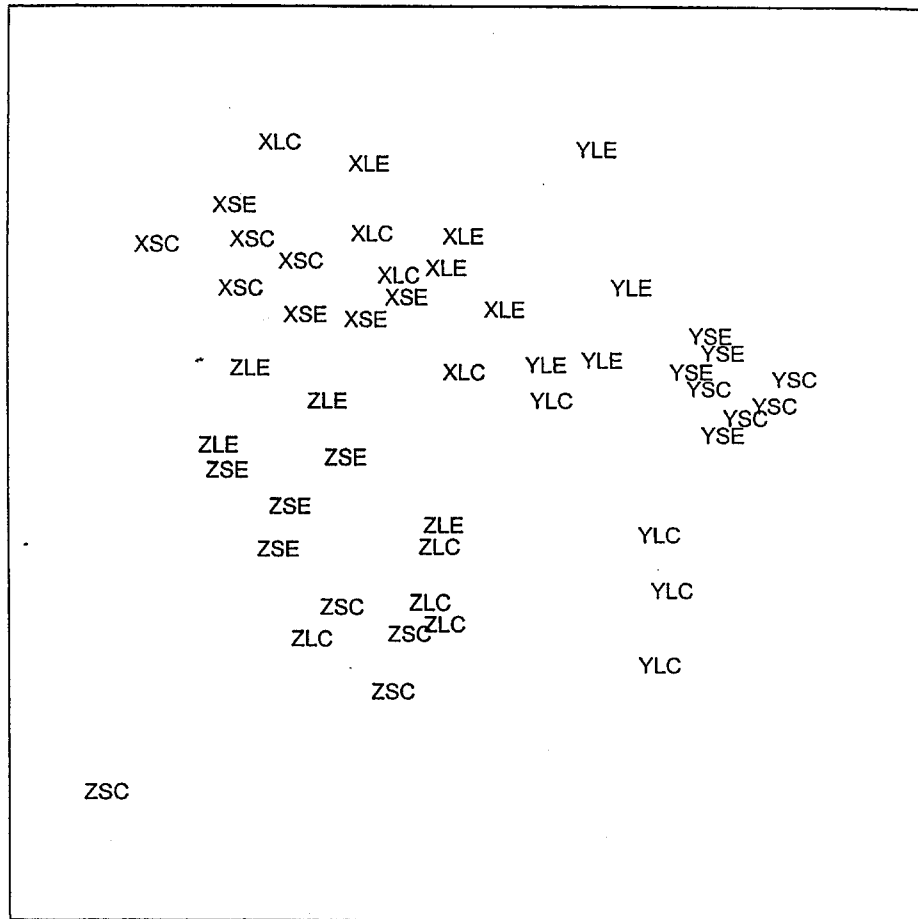


Fig. 5. MDS ordination of infaunal macroinvertebrate data from patches of *Z. marina* in the Isles of Scilly. Samples (four replicates) are identified by: block (X, Y, Z); patch size (S = small, L = large); in-patch location (E = edge, C = centre) (Bray–Curtis similarity on  $\sqrt{\sqrt{}}$  transformed data) (stress = 0.17). Symbol positions are based on Bray–Curtis similarities of double square-root transformed data and the distance between samples is proportional to their relative similarity. Axes have no units.

SIMPER revealed that the average dissimilarity between patch size groups was 58.70%, with no single species having a particularly large contributory influence. The maximum contributions to dissimilarity were from the spionid polychaete *Spio filicornis* (Muller) (4.95%) and the tanaiid crustacean *Apeudes latrellei* (Milne–Edwards) (4.82%) but 14 species were responsible for 50% of the total dissimilarity, indicating that the observed differences are due to a broad change in assemblage makeup rather than the influence of one or a few significant species (Table 4a). The average dissimilarity between in-patch location groups was 57.84%, with again no single species having a particularly large influence on the dissimilarity observed. A similar suite of 14 species was responsible for half of the observed dissimilarity (Table 4b). The SIMPER analyses

Table 4

The taxa contributing most (50% cut-off) to the dissimilarity between the infaunal macroinvertebrate assemblages of (a) large and small patches of *Z. marina*; (b) edge and centre locations within patches of *Z. marina* (SIMPER double square-root transformed data)

(a) Patch size				
Taxa	Average abundance (ind core <sup>-1</sup> )		Contribution (%)	Cumulative (%)
	Large	Small		
<i>Spio filicornis</i>	31.33	19.29	4.95	4.95
<i>Apseudes latrellei</i>	10.42	9.88	4.82	9.77
<i>Aora gracilis</i>	4.88	1.25	3.94	13.71
<i>Notomastus latericeus</i>	5.29	1.46	3.87	17.58
Oligochaeta	2.46	6.38	3.76	21.34
Nematoda	8.13	12.29	3.59	24.93
Ostracoda	3.96	2.21	3.50	28.43
<i>Dexamine spinosa</i>	1.58	0.25	3.41	31.84
<i>Capitella</i> sp.	2.21	4.96	3.35	35.18
<i>Microdeutopus stationis</i>	2.79	0.50	3.13	38.32
<i>Phyllococe maculata</i>	1.33	1.42	3.13	41.44
Actinidae sp.	0.67	3.17	2.94	44.38
<i>Urothoe poseidonis</i>	1.33	0.50	2.53	46.92
<i>Melita obtusata</i>	1.04	0.46	2.51	49.43

(b) In-patch location				
Taxa	Average abundance (ind core <sup>-1</sup> )		Contribution (%)	Cumulative (%)
	Edge	Centre		
<i>Spio filicornis</i>	34.08	16.54	5.36	5.36
<i>Apseudes latrellei</i>	15.13	5.17	5.08	10.44
Oligochaeta	4.29	4.54	3.84	14.28
Nematoda	12.04	8.38	3.75	18.03
<i>Notomastus latericeus</i>	4.04	2.71	3.57	21.60
<i>Aora gracilis</i>	2.67	3.46	3.56	25.16
Ostracoda	1.75	4.42	3.54	28.70
<i>Capitella</i> sp.	4.71	2.46	3.41	32.11
<i>Phyllococe maculata</i>	1.46	1.29	3.17	35.23
Actinidae sp.	2.00	1.83	3.03	38.31
<i>Microdeutopus stationis</i>	1.08	2.21	3.00	41.32
<i>Dexamine spinosa</i>	0.92	0.92	2.79	44.10
<i>Urothoe poseidonis</i>	0.79	1.04	2.67	46.77
<i>Heteromastus filiformis</i>	0.29	2.25	2.47	49.25

indicate how the relative abundance of these taxa change with both patch size and in-patch location. For example, Oligochaeta, Nematoda and the polychaete *Capitella* sp. are in greater abundance in small patches than in large; whereas the majority of the other taxa are either more abundant in large patches or show similar abundances in both patch sizes. Similarly, the polychaetes *Spio filicornis*, *Notomastus latericeus* (M. Sars), *Capitella* sp., and Nematoda in addition to the tanaid *Apseudes latreilli* are in higher

abundance at the edge of patches than at the centre; whereas the amphipods *Aora gracilis* (Bate), *Microdeutopus stationis* (Della Valle) and *Urothoe poseidonis* Reibisch, together with Ostracoda, are more abundant at the centres of patches than at the edges.

The single environmental variable which best explained the patterns of assemblage composition was sediment sorting (BIOENV:  $\rho_w = 0.329$ ), followed by mean grain size ( $\rho_w = 0.281$ ), and sediment organic content ( $\rho_w = 0.097$ ). None of the seagrass parameters correlated positively with assemblage composition, the highest correlation being a combination of mean grain size, sediment sorting, and percent fine fraction (BIOENV:  $\rho_w = 0.361$ ).

#### 4. Discussion

The most significant differences in infaunal assemblage parameters in this study were those between the regional blocks of the experiment and the strongest correlates of these patterns were sediment characteristics. Thus, although the experimental blocks were in relatively close proximity to one-another and the ranges of depth and *Zostera* shoot-densities sampled were carefully controlled, sediment variation across the study area apparently exerts a greater influence on infaunal assemblages than either patch size or in-patch location. Such variation is likely to be related to differences in the degree of exposure to wave action and tidally induced currents. Despite these larger scale 'regional' variations, however, significant differences in the macroinvertebrate assemblages were associated with the effects of both habitat patch size and within-patch location: samples from the larger areas of seagrass contained more taxa than those from smaller areas and assemblage composition differed between edge and centre locations within a patch. These data, therefore, support the presence of both a species–area relationship and edge effects.

Although the species–area relationship is one of the most broadly consistent generalisations in ecology, it is still essentially an observed phenomenon and the precise mechanisms that cause it are debatable. Indeed, its validity as a paradigm has been questioned both generally (e.g. Connor and McCoy, 1979) and specifically in marine systems (Anderson, 1998). Three principle mechanisms have been proposed to account for a species–area relationship (Huston, 1994; Rosenzweig, 1996): equilibrium between immigration and extinction; increase of environmental heterogeneity with increasing area; and the possibility that the effect is an artefact of sampling, a phenomenon persistent in many seagrass studies (Attrill et al., 2000). This latter possibility is expressed in the "random placement hypothesis" (Arrhenius, 1921; Coleman, 1981) which proposes that equal areas sampled, regardless of the size of patch available, should result, on average, in the same number of species being found and, thus, that observed species–area relationships are merely a consequence of greater sampled area in larger patches. McGuinness (1984) has argued that in all species–area investigations the random placement hypothesis should be treated as the null hypothesis to be tested and rejected before more complex hypotheses are considered. As the sampling effort and, thus, the area sampled, in this study was the same for all patches and as no correlation was evident between assemblage parameters and any measures of seagrass root–rhizome

biomass (which might imply variation in the area sampled at the scale of the individual plant rather than that of the whole patch), it seems unlikely that the random placement hypothesis is applicable. Similarly, the lack of significant correlations of assemblage parameters with any of the measures related to environmental complexity within patches (shoot-density, root:rhizome ratio, sediment sorting), suggests that the experiment has successfully controlled for such effects of habitat heterogeneity. Significant correlations of all three univariate assemblage measures with sediment fines (percent < 63  $\mu\text{m}$ ), and the greater percentage of fine sediments in large patches suggest a possible confounding factor in ascribing the observed effect to a species–area relationship. However, the accumulation of fine sediments in seagrass beds is a consequence of reduced levels of physical disturbance within patches due to the physical damping effect of seagrass itself (Fonseca et al., 1983) and is, inevitably, a covariate of patch size. Thus, although the proportion of fine sediments may have an influence on infaunal assemblage composition, any effect is inseparable from that of area alone.

The greater number of taxa recorded in large patches is, therefore, primarily an expression of the first explanation for the species–area relationship; a balance between immigration and extinction rates within individual patches, in which patch area per se influences assemblage composition. Purely physical considerations make it intuitively logical that immigration via dispersive larvae will be greater in larger patches, but unless the probability of population extinction is also lower in larger patches greater numbers of species per unit area sampled would not be expected. The theoretical arguments underlying the assumption of lower extinction rates in larger habitat patches are based on the premise that larger patches support larger populations and that such populations are less likely to suffer local extinction through competitive exclusion or stochastic events such as disturbance or failure of recruitment (Shaffer, 1981; Gilpin and Soulé, 1986; Shaffer, 1994). Relating this to the present study, two main factors are generally postulated as being structuring mechanisms within seagrass beds which are likely to affect rates of extinction and which may, thus, be causative factors in the observed distributions of infauna: physical disturbance and predation.

It is well-documented that seagrass patch edges experience greater environmental disturbance from water movement and wave-action and consequently that smaller patches with high edge to area ratios are subject to greater overall disturbance than large patches (Fonseca et al., 1983; Irlandi et al., 1995). In light of this, it is likely that fundamental life-history attributes of different taxa, such as their colonising and competitive abilities, are significant in the observed distributions between patch sizes. Keough (1984) suggests that, if competitive ability entails a trade-off against dispersive ability, interactions in small patches, with frequent disturbance, will be mostly among poor competitors with wide dispersal and rapid colonisation ('r' strategists, see Pianka, 1974). In large patches, by contrast, where disturbance is less frequent, more 'K' type species, with limited dispersal and good competitive abilities are likely to be present. In marine benthic habitats, the established pattern of assemblage change with increasing disturbance is for the number of species present to decrease and for the total number of individuals to increase as some species become locally extinct allowing the populations of opportunistic 'r' type species to expand (e.g. Warwick and Clarke, 1994). In the present study, univariate analyses indicated that there were significantly more taxa in

larger patches, supporting the predicted response to reduced disturbance. Total abundance, by contrast, did not differ significantly between patch sizes in univariate analyses. Multivariate analysis, however, revealed that the species which contribute the most to the significant difference observed in assemblage composition between the in-patch locations generally have a higher abundance at the edge than at the centre of the seagrass bed. Of these, *Capitella* sp., *S. filicornis* and nematodes in particular, are known to be opportunistic taxa characteristic of disturbed habitats (Grassle and Grassle, 1974; Warwick et al., 1990; Aller and Stupakoff, 1996) and were found in highest abundance at patch edges, as predicted by the theoretical arguments above. The ecology of other taxa found in higher abundance at patch edges, such as the tanaid crustacean *A. latrellei*, is less well-documented but an explanation of their distributions based on life-history traits and physical disturbance regimes may also be appropriate.

There is, however, an alternative explanation for the observation of higher abundance of these species at patch edges which should be considered. It is possible that some of these species may be primarily inhabitants of the unvegetated sediments adjacent to the seagrass patch and, thus, exhibit a concomitant decrease in abundance with an increase in factors such as the structural aspects of the seagrass which change relative to distance from the edge of the seagrass bed. In the present study, no samples were taken outside the seagrass patches due to logistical constraints. However, grab sample data from a recent survey of unvegetated substrates close to seagrass beds in the X and Y blocks suggest that many of the infaunal taxa which were abundant in the seagrass patches are also common in bare sediments (AMBIOS, 1998). In particular, the species noted above, which were found to be important in discriminating between edge and centre patch locations, were also amongst the most numerous taxa recorded from adjacent sediments (AMBIOS, 1998). Similar patterns have been observed in other seagrass studies. Edgar and Robertson (1992), in Australian *Amphibolis* beds, found no significant difference in the abundance of two common polychaetes between various densities of seagrass, including bare sediment, whilst Bostrom and Bonsdorf (1997), in the Baltic Sea, reported that annelid infaunal assemblages in seagrass beds and adjacent bare sediments were dominated by the same species. From these examples and the results of the present study, it would appear that for many infaunal macroinvertebrates seagrass patches may not represent habitat 'islands' in any precise sense and that the abundance of some species may in fact decrease within patches as compared to bare sediments. This runs counter to the general observations in the literature that total macroinvertebrate abundance is significantly higher in seagrass than bare sediments (e.g. Orth, 1977; Stoner, 1980; Edgar et al., 1994). However, such studies frequently include epiphytic as well as infaunal taxa and the argument for increased macrofaunal abundance in seagrass habitats may rest largely on the additional occurrence of species directly associated with the above-ground component of seagrass. In the present study, those taxa which did show an increase in abundance at centre locations included amphipods which generally adopt an epibenthic mode of life (Hayward and Ryland, 1995), an observation which might well be related to the differences in shoot density detected between centre and edge locations and the concomitant reduction of disturbance due to wave-action. A suitable direction for more detailed experimental work would be to concentrate on the distribution and relative abundance of different taxonomic/functional groups across the boundary be-



tween seagrass beds and adjacent sediments. Such work is needed in order to determine whether the edge effects observed here are indeed due to a within-patch disturbance gradient or are a consequence of inhibitory effects of seagrass root–rhizome on species which populate bare sediment. Adjacent habitats other than bare sediment should also be considered as the proximity of seagrass patches to other habitat types may have a significant effect on infaunal distributions and abundances. If a significant proportion of infaunal taxa are not restricted to seagrass habitats, direct recruitment from neighbouring areas of fucoid or kelp habitat, for example, may occur. In conjunction with reproduction and recruitment data the results of such studies might help to clarify whether seagrass beds act as net sources or sinks (Pulliam, 1988; Pulliam and Danielson, 1991) of fauna and resources in relation to surrounding habitats. This information in turn would have implications for the management of inshore areas (including seagrass beds), in particular the need to focus attention on mosaics of habitats rather than habitat in isolation.

In contrast to the gradients of physical disturbance across seagrass beds, which are well-understood, relative levels of predation inside and outside seagrass beds have not proved easy to assess. It is generally suggested, however, that patch edges and smaller patches experience greater predation pressure than patch centres and larger patches. These arguments are based on the premise that the physical complexity of seagrass shoots and root–rhizome afford refugia from predation and it has been postulated that concomitant decreases in predation pressure are important in structuring infaunal assemblages within seagrass beds (Orth, 1977; Reise, 1978; Heck and Thoman, 1981; Castel et al., 1989). Most published work relating to the effects of predation in structuring seagrass assemblages has concentrated on epiphytic fauna rather than infauna (Orth et al., 1984) and it might be anticipated that any predation effects will be less pronounced for infaunal assemblages as their environment alters less abruptly with the transition from seagrass bed to bare sediment than does that of epifaunal species. Nonetheless, it might reasonably be predicted, from existing studies, that infauna at patch-edge locations and in small patches experience greater predation pressures than those at patch-centre locations and in large patches. In the context of this study, therefore, increased predation might be expected to result in significantly higher overall faunal abundance at patch-centre locations and in large patches.

That such effects are not apparent from the ANOVA analysis of the present study suggests that if predation is operating differentially inside and outside patches, its effects on infaunal assemblage structure are too weak to be detected by our experiment or may be masked by the influence of other factors such as the effects of physical disturbance discussed above. Edge samples were taken within approximately 1 m of the patch edge and, thus, if a transitional gradient of abundance was present on a scale significantly smaller than this it would not have been detected. However, multivariate analysis revealed an in-patch location effect, in particular an increase in the abundance of annelid worms at patch edges. As discussed above, this response is in accord with the predicted assemblage response to elevated levels of physical disturbance but as the predicted response to higher levels of predation is the reverse of this pattern, greater predation pressure at patch edges might be expected to negate, partially or wholly, any effect of disturbance. There is, therefore, no evidence from our data for the predicted effects of

predation. This suggests some alternative possibilities. Firstly, that predation pressures are constant from bare sediment to seagrass habitats and annelid distribution is dependent on alternative factors. Secondly, that patterns of predation pressure differ for different components of the infauna and thirdly, that predation may possibly be greater within seagrass beds than in adjacent sediments.

Most previous studies have concluded that predator efficiency is reduced in seagrass beds due to the shelter afforded by structural complexity of the habitat, whether above or below the sediment interface (Orth et al., 1984; Castel et al., 1989; Irlandi et al., 1995). However, there are exceptions to this. Edgar and Robertson (1992) concluded from predator exclusion experiments that predation was not significant in explaining increased abundance of macroinvertebrates in seagrass beds. Webb and Parsons (1991) also found that the abundance of sediment-dwelling copepods in seagrass beds and bare sediments was unaffected by epibenthic predators. In the present study it was noted that fish (*Pomatoschistus minutus* (Pallas), *Gobiusculus flavescens* (Fabricus), *Crenilabros melops* (L.) and *Syngnathidae* sp.), crabs (*Carcinus maenas* (L.)), or both, were numerous in all but one (small patch in Block X) of the seagrass patches sampled, whereas these predatory species were not seen on open substrates. It was particularly noted for the Y block patches that the sites disturbed by sampling were immediately foraged by numerous *C. maenas*. Again, no firm conclusions can be drawn from these observations but they suggest that predation pressures might be at least as significant for infaunal species within seagrass beds as in open sediments. In this respect considerations of scale are relevant. Although published predation-based explanations of higher macroinvertebrate abundance in seagrass beds are based on the provision of physical refugia from predation (e.g. Mattila, 1995), it seems probable that the predator species themselves may also gain a refuge from their own predators (larger fish, gulls, cormorants and seals in this instance) in seagrass beds. Consequently, abundances of epibenthic predators within seagrass patches might logically be expected to be higher than on open sediments. Thus, the same factors that are proposed to reduce predation pressures on macroinvertebrate infauna within seagrass beds could also, when applied at the next trophic level, effectively increase predation pressures on infauna. In light of this, it might be reasonable to hypothesise that the observed increase in number of taxa in larger seagrass patches is brought about in part by predator-mediated coexistence (e.g. Wootton, 1992), rather than by a reduction of predator efficiency within the seagrass beds. If this were indeed the case, we would predict significantly higher numbers of active epibenthic predators to be found within seagrass patches than on bare sediment and for the numbers of taxa in seagrass beds to decrease over time if such predators are experimentally excluded.

The question of scale may also have more general importance in relation to the effect of patch size. Although the species–area relationship and related edge-effects remain a paradigm in terrestrial ecology and have been demonstrated experimentally (Simberloff, 1976) and observationally (Riebsell, 1982), studies of marine assemblages have provided contradictory and inconclusive evidence for its existence (e.g. Schoener and Schoener, 1981; Keough, 1984; Tsuchiya and Nishihira, 1985; Svane and Ompe, 1993). More recently, Anderson (1998) has investigated the influence of habitat area on assemblage structure in marine fouling communities and concluded that the species–area

relationship does not always hold for these assemblages due to spatial, temporal and successional stochasticity of both physical and biological processes. Similarly, Svane and Setyobudiandi (1996), working with the associated macroinvertebrate assemblages of mussel bed patches, found that evidence for a species–area relationship was inconsistent and suggested that inherent variability amongst samples at the smallest scale of sampling (replicate cores at individual in-patch locations) concealed patterns found at higher spatial levels.

The present study is less rigorous in terms of spatial and temporal replication than either of the examples above, but the pattern of greater species number in larger patches appears to be more pronounced. In light of work by Morrissey et al. (1992) and others, on the patchiness of distribution of organisms at all scales, it is worth noting that both Anderson (1998) and Svane and Setyobudiandi (1996) were working at somewhat smaller scales than the present study (maximum patch size 0.016 and  $\sim 15 \text{ m}^2$ , respectively, as compared to  $> 500 \text{ m}^2$  here) and at considerably smaller scales (orders of magnitude) than the terrestrial examples noted above. As the effects of stochastic variability become relatively more pronounced at smaller scales of reference (Anderson and Underwood, 1994; Shaffer, 1994; McCann et al., 1998), it may be that the species–area relationship and the mechanisms postulated for its existence are indeed phenomena which operate in marine ecosystems but that their effects are masked by environmental ‘noise’ at progressively smaller scales and only become discernible at larger, landscape, regional or biogeographic scales. Experimental testing of such scale dependency of species–area effects, employing fully replicated, nested sampling designs (e.g. Morrissey et al., 1992; Thrush et al., 1997b) covering a wide range of measurement scales and in a variety of habitat types, would be an useful direction for further work and might have implications for the design of marine conservation areas (see McNeill and Fairweather, 1993; Thrush et al., 1997a).

Perhaps the clearest point to emerge from this study, however, is that although patch size and edge effects do, indeed, appear to exert influences on infaunal assemblage structure, apparently minor regional variations in physical environmental parameters (Table 5) are shown to be more significant in all analyses. Furthermore, all combinations of the measured physical variables in this study leave some 60% of infaunal assemblage variability unexplained, suggesting either that other factors are influencing variation in assemblage structure across the study area, or that there is a high degree of stochastic variability associated with these assemblages. A recent extensive study of seagrass infauna in New Zealand (Turner et al., 1999) similarly identified that about 75% of all

Table 5  
Mean ( $\pm 1$  S.E.) values of physical environmental parameters measured in each experimental block of *Z. marina* beds in the Isles of Scilly

Parameter	Block X	Block Y	Block Z
Depth (m)	0.022 $\pm$ 0.045	0.180 $\pm$ 0.024	0.275 $\pm$ 0.026
Mean sediment particle size ( $\phi$ )	1.749 $\pm$ 0.047	1.289 $\pm$ 0.177	2.199 $\pm$ 0.026
Sediment sorting	0.767 $\pm$ 0.031	1.484 $\pm$ 0.077	0.740 $\pm$ 0.033
Sediment $< 63 \mu\text{m}$ (%)	2.593 $\pm$ 0.375	5.503 $\pm$ 0.351	4.184 $\pm$ 0.580
Organic carbon (%)	1.374 $\pm$ 0.079	2.158 $\pm$ 0.250	1.830 $\pm$ 0.130

variability in benthic assemblage composition remained unexplained despite a more comprehensive range of environmental variables being included in the analyses than was possible here. Such results suggest that the effects of any species–area relationship in small or medium scale benthic community studies may be inconsequential in comparison to the influence of physical environmental variability and stochastic events.

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