The critical scale of small-scale spatial variation in ecological patterns and processes in intertidal macrobenthic seagrass assemblages

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ABSTRACT

Earlier work on benthic faunal assemblages in intertidal seagrass beds has shown maximal structural variation at spatial scales <150 m. To examine more closely spatial variation of species assemblages within this range, numbers of target taxa in the beds on North Stradbroke Island, Moreton Bay, Australia, were sampled at nested spatial scales of 0.5, 5, 30 and 90 m at two localities 900 m apart. Variance components were largest at the smallest scales, that at 0.5 m comprising 55% of the total and that at 5 m 13%. Individual species were patchily dispersed and their assemblages were randomly structured at all studied spatial scales. Although assemblage composition differed significantly between the two localities, overall faunal abundance and species richness were relatively uniform across the whole study area. These seagrass beds show little turn-over of dominant species and little evidence of niche partitioning through space over scales of <1 km. In this they contrast markedly with the equivalent intertidal dwarf-eelgrass beds of Knysna in South Africa that form a high turn-over, strongly structured, deterministic system.

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1. Introduction

Spatial variation in seagrass landscapes and faunas not only has clear implications for attempts to conserve their organismal diversity (Green and Short, 2003; Larkum et al., 2006; Barnes, 2010a) but it is also of considerable general interest to attempts at understanding the ecological processes that structure assemblages of species (Fraschetti et al., 2005; Boström et al., 2006; Burrows et al., 2009). Several studies in the last decade have described spatial variation in the structure and biodiversity of the macrofaunal assemblages within seagrass beds consequent on specific environmental factors; e.g. physical variables (Blanchet et al., 2004; Yamada et al., 2007; Barnes, 2010a; Barnes and Ellwood, 2011a), eutrophication gradients (Cardoso et al., 2004), the presence of bioturbators (Berkenbusch et al., 2007) and of invasive species (Box et al., 2010). More generally Chase (2010) has argued that there is also an intrinsic pattern underlying the relationship between spatial variation and several ecological features; specifically that spatial variation in biodiversity and in stochasticity of assemblage structure are not only related causally but that both

are also ultimately driven by latitudinal trends in productivity. He suggests, for example, that high levels of β-diversity result from the increased role of stochastic structuring processes that characterize low latitude areas of high productivity. However, a straightforward relationship between latitudinal productivity and species richness or diversity seems to be much more generally a feature of terrestrial (Harrison and Grace, 2007) than of marine habitats (Witman et al., 2004, 2008; Gobin and Warwick, 2005).

The extent to which the degree of spatial variation in structuring processes and in emergent assemblage properties such as abundance and species diversity itself varies with spatial scale has also received some investigation in seagrass. First, the manner in which variation in the composition of seagrass-associated assemblages changes with local spatial scale *per se* has been studied by partitioning variance components across nested scales of <1 m to >1 km (Vanderklift and Lavery, 2000; Lavery and Vanderklift, 2002; Balata et al., 2007; Barnes and Barnes, 2011). Secondly, the nature of processes controlling assemblage structure at any given point has been investigated by Irving et al. (2007) and Van der Heide et al. (2010) who studied the importance of feedback loops and prior colonisation events, and by Barnes and Ellwood (2011b) who investigated the importance of stochastic versus deterministic processes across a series of nested scales over the same spatial range as above, <1 m to >1 km. At much larger spatial scales, Barnes (2010b) and Barnes and Ellwood (2011b) have explored the

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relationship of abundance, diversity and control of assemblage structure of dwarf-eelgrass macrofaunas with latitude.

As yet, however, there is little appreciation of what spatial scales are most critical to the small-scale ecological changes that have been shown to occur within seagrass meadows. Previous studies of the intertidal seagrass beds along the northwestern coast of North Stradbroke, one of the Moreton Bay barrier islands in Queensland, Australia, have shown marked effects of spatial scale on both ecological pattern and process in what otherwise appears to be a rather homogeneous system overwhelmingly dominated by the dwarf-eelgrass *Nanozostera muelleri capricorni*. As also appears to be the norm on shallow-water hard substrata (Fraschetti et al., 2005), macrofaunal assemblage variance in these soft sediments was greater at a scale of 1 m than at either 150 m or 2 km (Barnes and Barnes, 2011). These spatial intervals are, however, relatively coarse and the present study aimed to investigate variation in assemblage structure in more detail over the potentially critical range of 0.5–90 m to try to locate more closely the point/s at which patterns and processes change.

2. Methods

2.1. Sample collection and processing

Samples of the assemblages of smaller macrobenthic invertebrates were taken between November 2010 and January 2011 at Dunwich on North Stradbroke, a sand-dune barrier island in the relatively pristine Eastern Banks region of Moreton Bay (Dennison and Abal, 1999), and within the same intertidal *Nanozostera muelleri capricorni* bed that formed the subject of the earlier study of changes in assemblage structure with spatial scale (Barnes and Barnes, 2011). Barnes and Barnes (2011) provide a detailed description of the site; the areas sampled in this study being parts of the same fine/medium-grained siliceous sandflat with (at the time) 100% seagrass cover. A total of 216 cores, each of 54 cm^2 area and 5 cm depth, was taken over a point-to-point distance of ≈ 1 km (from 27°29.3′S; 153°24.4′E to 27°29.7′S; 153°23.9′E) in the form of two 130 m transects (one at each locality – see below) parallel to the shoreline and approximately at LWN tidal level, 20–30 m in from the landwards limit of the seagrass bed to avoid edge effects (Tanner, 2005; Warry et al., 2009). Sampling along each transect was structured in a nested design of four spatial scales. Two replicate 'localities', with their centres some 900 m apart, were selected one to the north and one to the south of the One Mile Harbour Channel ('One Mile' and 'Polka' respectively); two 'sites', with their centres 90 m apart, were then sampled at each locality; two 'stations', with their centres 30 m apart, were sampled at each site; three 'loci', with their centres 5 m apart, were sampled at each station; and nine 'cores', distributed in a regular 3×3 grid within an area of ≈ 1 m^2 and with the centres of adjacent cores 0.5 m apart, were taken at each locus (Fig. 1). The centres of each block of nine cores along the 130 m transects were therefore located at 0, 5, 10, 30, 35, 40, 90, 95, 100, 120, 125 and 130 m. A 5 cm depth was selected because most benthic macrofauna in seagrass beds is known to occur in the top few mm of sediment (e.g. 98% in the top 5 mm in the study by Klumpp and Kwak, 2005). The core size was adopted after preliminary work had indicated that nine samples of that surface area would yield an acceptable standard error < 20% of the arithmetic mean in estimation of local seagrass macrofaunal density (Elliott, 1977). As size of basic sampling unit is in itself a potential confounding variable (e.g. Parravicini et al., 2009), adopting the same sized core as used in the earlier study of spatial variability at the site (Barnes and Barnes, 2011) also ensured comparability of the smaller and larger spatial-scale results. This sampling regime collects the smaller and most numerous members
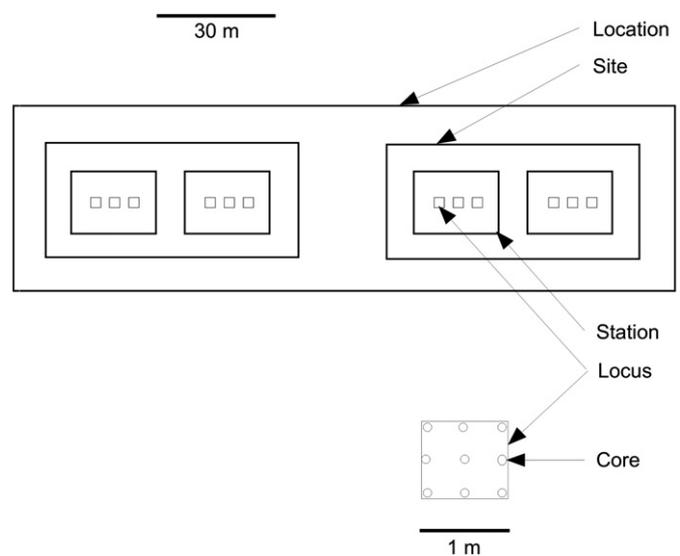

30 m

1 m

Fig. 1. Diagrammatic representation of the nested set of sampling scales within each locality, with detail of a single locus to show the arrangement of the individual cores taken within.

of the macrofauna that constitute the large majority of the biodiversity (Albano et al., 2011).

Each core sample was collected at low tide, soon after tidal ebb from the site, and was gently sieved through 710 μm mesh. All retained material (a) was placed in a large polythene bag of seawater and all seagrass was shaken vigorously to dislodge all but sessile animals and then discarded (earlier testing having shown that no detectable motile species remained within the seagrass after such treatment); (b) was then re-sieved and transported to the laboratory, where (c) it was placed in a large white tray from which the living animals were extracted by eye, extraction continuing until no further animal could be seen after a 3 min search, which preliminary trial runs had indicated was sufficient to permit the removal of all live individuals. Target members of the surface and near-surface benthic fauna were identified to species and counted. Previous work on the Dunwich seagrass macrofauna at this tidal level has shown it to be numerically dominated by gastropod molluscs, polychaete annelids, and decapod and tanaid crustaceans, these four groups comprising >90% of individuals and 70% of species (Barnes, 2010b; Barnes and Barnes, 2011). The polychaetes, however, are a 'difficult' group in that the local fauna is incompletely known (Davie and Phillips, 2008) and many of the alleged identities of common species are dubious (Wilson et al., 2002). For convenience, therefore, the present study was restricted to the other three dominant taxa, these 'target groups' representing >70% of the total individuals likely to be present. Numbers of individual members of non-target groups present in samples, however, were also recorded for assessment of total density. Generic and specific names are as per the World Register of Marine Species (WoRMS <www.marinespecies.org>) unless otherwise specified.

2.2. Statistical analyses

Faunal assemblages were compared multivariately using permutational analysis of multivariate dispersions (PERMDISP), permutational analysis of variance (PERMANOVA) including to partition the total variance into the components due to each nested sampling scale, similarity percentage analysis (SIMPER) and hierarchical clustering analysis using S17 Bray–Curtis and Euclidean

distance similarity measures, carried out via PRIMER 6 [PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research, Version 6]. PERMANOVA was conducted on similarity matrices with untransformed, square-root and fourth-root transformed versions of the data using 9999 permutations; neither similarity measure nor transformation materially affect any results and only Bray—Curtis and fourth-root transformed data are presented below. Observed patterns of species co-occurrence were compared with statistical randomisations of the original species occurrence data using ECOSIM simulations (Gotelli and Entsminger, 2010). As recommended by Fayle and Manica (2010), 30,000 random matrices were simulated for each analysis to avoid Type 1 errors. ECOSIM's randomisation algorithm maintains fixed sums for row and column totals so each matrix generated had the same number of species and samples as the original. Differences between simulated and observed co-occurrence patterns were tested using the Stone and Roberts (1990) checkerboard score (C-) index that indicates random assemblage structuring if C_{obs} is not significantly different from C_{sim}.

Univariate correlations were tested via Spearman's rank, and univariate comparisons of numbers of individuals and of species per sampling unit used one-way ANOVA (the data concerned not departing from homoscedasticity; Bartlett's test $P > 0.3$ in all cases). Departures from random of the dispersion patterns of individual species were tested by Morisita's Index of Dispersion χ^2 statistic (Morisita, 1959). Species diversity was measured as the linear Hill's (1973) $N2$ or the 'effective number of species' (Jost, 2006, 2007), and dominance by the Berger—Parker Index; Constancy Indices given are percentage frequencies of occurrence in core samples; categories of faunal rarity are *sensu* Colwell and Coddington (1994). Potential area effects on diversity and other parameters were avoided because the same total area was sampled at each sampling scale.

3. Results

The 2454 target faunal individuals collected by the core samples from the Dunwich seagrass beds comprised 77% of the total macrofaunal individuals obtained and represented a total of 42 species (indicating a total target-group species richness of 70 as estimated by the method of Chao (1984)). As expected from earlier work at the site (Barnes, 2010a; Barnes and Barnes, 2011), the fauna was sparse and numerically dominated by gastropod molluscs (30 species comprising 62% of the total faunal individuals) and particularly by rissooidean microgastropods (54% of the total fauna). Overall faunal density was 2725 ind. m^{-2}. The three most abundant target-group species were all small to minute: the <2.5 mm calopiid snail *Calopia imitata* (59% of the target-group total, and 45% of the overall total), the <5—8 mm macrophthalmid crab *Enigmaplax littoralis* (14% and 11%) and the <3.5 mm tornid snail *Pseudoliotia micans* (11% and 8%) [WoRMS treads this species as a trochoidean cyclostrematid under its original name *Cyclostrema micans*; the taxonomy here follows Ponder and de Keyzer (1998) and Healy et al. (2010)]. *Calopia*, *Enigmaplax* and *Pseudoliotia* not only dominated numbers but were the only species to have Constancy Indices ≥30. Only a further five species occurred in >10% of samples and so the large majority of target species occurred in few cores and several were rare in the sense of occurring only as singletons or doubletons at a site.

All loci had a Bray—Curtis similarity of at least 50%, those within each locality showing a similarity of 60% (Fig. 2). There was no significant difference in the multivariate dispersion of the target faunal assemblages in the two localities but their nature did differ significantly, each forming a distinct Bray—Curtis cluster (PERMANOVA: pseudo-F 13.3; $P < 0.0001$. PERMDISP: F 0.84; $P = 0.4$). Nevertheless, there were no differences between the two localities in terms of either numbers of individuals or of species per locus
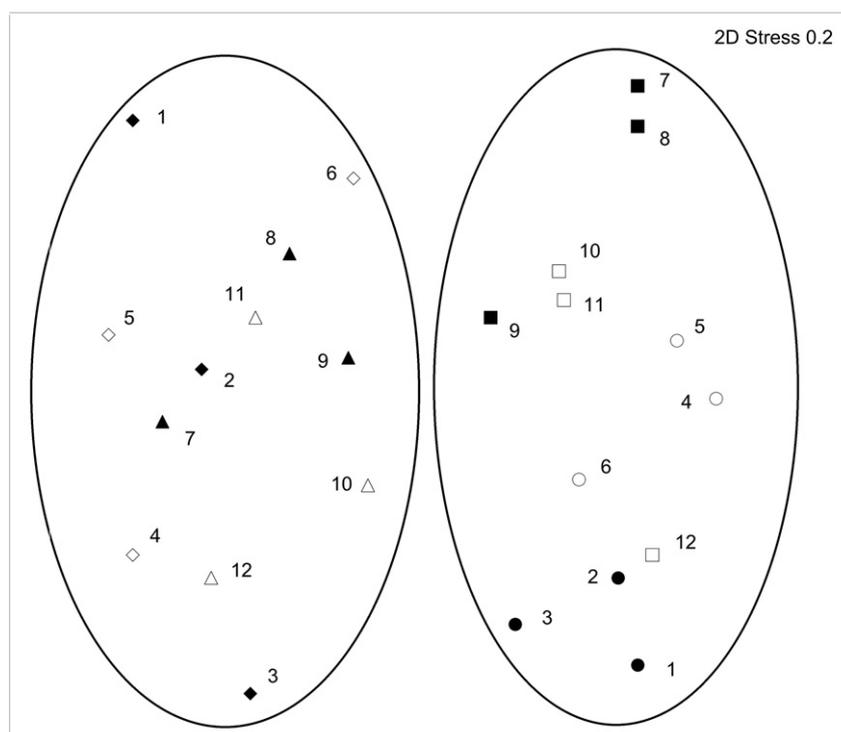
Fig. 2. Non-metric multidimensional scaling plot of the superimposed group-average S17 Bray—Curtis Similarity clusters of fourth-root transformed abundances of the assemblages of target macrofaunal taxa at the 24 loci sampled within the Dunwich intertidal seagrass bed. The two envelopes are Bray—Curtis Similarities of 60% and each encloses a single locality. Within each locality the loci are numbered in sequence along the transect, those within the same station bearing the same symbol and those within the same site bearing the same shaped symbol.

(ANOVA $F_{(1,22)}$ 1.85, $P = 0.19$; $F_{(1,22)}$ 2.43, $P = 0.13$ respectively) nor per station (ANOVA $F_{(1,6)}$ 1.06, $P = 0.34$; $F_{(1,6)}$ 2.56, $P = 0.16$ respectively). Number of individuals per locus was not uniform across the four sites (ANOVA $F_{(3,20)}$ 4.65, $P = 0.01$), however, although this was entirely consequent on only one of the six component comparisons, that between the two sites at the Polka locality (Tukey's HSD post hoc test $P = 0.02$). Species richness per locus did not differ between the four sites (ANOVA $F_{(3,20)}$ 1.40, $P = 0.28$). Coefficients of variation for groups of core samples within an individual locus averaged >0.5 for numbers of target-group individuals and >0.4 for numbers of all macrofauna. There were no significant differences in the levels of this variation between the two localities nor between that within the target groups and that within the total fauna at either locality (Tukey's HSD post hoc test $P > 0.07$).

Even though *Calopia* occurred in 92% of samples, its dispersion pattern showed marked patchiness at all spatial scales ≥30 m (station $\chi^2 > 64$, df = 26; site $\chi^2 > 177$, df = 53; location $\chi^2 > 604$, df = 107; all $P < 0.00003$), although at a spatial scale of 5 m (see Fig. 3), the pattern did not depart from random at 38% of loci ($\chi^2 < 15.5$; df = 8; $P > 0.05$). Nevertheless, its overall densities at the two localities were very similar (1209 and 1257 m^{-2}). Less abundant though far from rare species, however, did vary between the two: *Enigmaplax* numbers, for example, were significantly (2.8×) larger at Polka (Mann–Whitney $Z = 5.9$; $P < <0.0001$) (Fig. 3), whilst the apseudoidean tanaid *Longiflagrum caeruleus* and alpheoidean decapod *Alpheus edwardsii* only occurred at that locality (at densities of 67 and 53 m^{-2} respectively) and the pyramidelloidean gastropod *Donaldina anabathron* (Hedley, 1906) only occurred at One Mile (at a density of 58 m^{-2}). In contrast to *Calopia*, the dispersion of the second-most abundant animal, *Enigmaplax*, did not depart from random at 67% of loci ($\chi^2 < 15.5$; df = 8; $P > 0.05$), and at 50% of all spatial scales ≥30 m (station $\chi^2 < 39$, df = 26; site $\chi^2 < 71$, df = 53; location $\chi^2 < 130$, df = 107; all $P > 0.05$). The overall target fauna was also distributed very patchily (locus $\chi^2 > 400$; df = 23; $P < 0.00001$) (Fig. 3), as were all faunal individuals of all taxa (locus $\chi^2 > 300$; df = 23; $P < 0.00001$). There were no significant correlations between the numbers of the dominant *Calopia* and either of the two other most abundant species, nor between the total numbers of target-group individuals and those in non-target groups in the samples (Spearman r_s −0.01 to −0.07; $P > 0.3$). The relative abundance of the above species of *Enigmaplax*, *Calopia* and *Pseudoliotia*, and the occurrence of those of *Longiflagrum* and *Alpheus*, together with the abundance of the buccinoid gastropod *Nassarius burchardi*, accounted for 60% of the dissimilarity between the two localities (SIMPER). Various general ecological features of the faunal assemblages at the four sites are summarized in Tables 1 and 2.

Despite their significantly different assemblages, analysis of components of variance at the two localities produced comparable results (Table 3), slightly complicated by the need to pool the data from two spatial scales at the Polka locality because of the occurrence of an 'illogical' negative component at the scale of station (Underwood, 1997). In each case, however, the component at the smallest spatial scale of 0.5 m was, at 67–69% of the total, markedly larger than that at the next smallest scale of 5 m. The overall relationship between spatial scale and components of assemblage variance within the Dunwich beds is shown in Fig. 4, nested PERMANOVA indicating that components at and above the spatial scale of station were not significant ($P > 0.1$). *C*-score index analysis showed that assemblage organisation did not depart from random at any spatial scale between 0.5 and 900 m. This result was apparent both when a fixed number of samples were randomly selected from different scales (Table 4), thus keeping the statistical power similar, and when samples were amalgamated as scale increased, thus increasing sample size
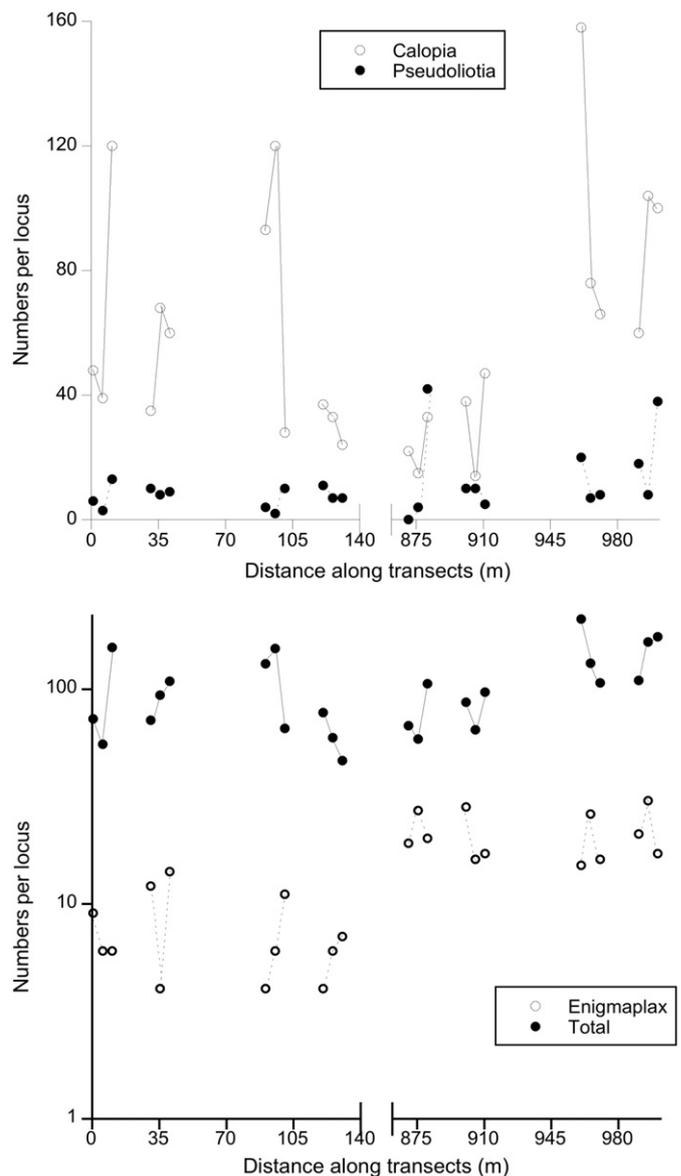

Fig. 3. Numbers of total target macrofauna and of the three most numerous species (the microgastropods *Calopia imitata* and *Pseudoliotia micans*, and crab *Enigmaplax littoralis*) present in the nine core samples at the spatial scale of locus in sequence along the two transects. Loci at the same station are joined by a line.

together with spatial scale (Table 5). The result was also consistent even when the analysis was repeated with core data pooled for each locus to reduce the variance at that smallest-scale spatial level.

Table 1
Density m^{-2} (N), species richness (S), species diversity (D) and Berger–Parker dominance (d) of the target macrofaunal taxa, and proportion of the total macrofaunal densities comprised by those target taxa (P), within the four intertidal seagrass sites at Dunwich.

Site	N	S	D	d	P
One Mile (N)	1900	22	2.13	0.67	0.72
One Mile (S)	1818	24	2.38	0.63	0.76
Polka (N)	1632	26	4.55	0.36	0.71
Polka (S)	3066	23	2.33	0.63	0.86
Overall	2104	42	2.63	0.59	0.77

Table 2
Frequencies of occurrence and rarity in the target macrofaunal taxa at the four intertidal seagrass sites at Dunwich. Percentage of species with Constancy Indices (CI) ≥ 50 and ≤ 10, mean faunal CI ($N = 54$ per site), and percentage of singleton plus doubleton species (s/d).

Site	≥ 50	≤ 10	Mean CI	s/d
One Mile (N)	9.1	63.6	14.6	54.5
One Mile (S)	4.2	58.3	14.3	45.8
Polka (N)	7.7	69.2	13.7	38.5
Polka (S)	8.7	52.2	17.8	34.8
Overall	4.8	81.0	8.5	38.1

4. Discussion

"The challenge still facing ecologists considering spatial patterns is to match these to the spatial scales of the processes causing such patterns" (Burrows et al., 2009). Within coastal marine systems, these patterns have generally been investigated at two different ranges of spatial scale, those greater and those less than 10 km, at which different ecological processes are likely to operate. Over the smaller range (<10 km, and especially <1 km) variability is likely to result from factors such as localised recruitment of juveniles (Levinton and Kelaher, 2004), aggregation of mobile consumers in areas of high food availability (Behm and Boumans, 2001), feeding or bioturbation effects of larger epibenthic nekton such as rays (Fonseca, 2011), and small-scale variation in habitat structural complexity (Matias et al., 2007) and/or component patch size (Matias et al., 2010). Further, at the smallest spatial scales, variability per unit area will also clearly be affected by the sizes of the macrofaunal species themselves (Eggleston et al., 1999) — in this study the core diameter was 20 times larger than the maximum dimension of the dominant faunal elements.

Before being in any position to relate process to pattern, however, it is first necessary to identify the specific scales at which the significant spatial variation is manifest. Such relevant investigation as has been conducted so far in respect of seagrass macrobenthic faunas has used relatively broad spatial categories, e.g. nested scales in the order of 1, 100 and 1000 m, and has found that the component of spatial variance at 1 m is always larger than that at the next largest scale (e.g. Barnes, 2010b; Barnes and Barnes, 2011; Barnes and Ellwood, 2011b); previous work at the present site having shown that it is larger at 1 m than at 150 m (Barnes and Barnes, 2011). The present study has therefore narrowed down this range considerably to a variance component maximum located at less than 5 m.

Table 3
Partitioning of variance components by nested PERMANOVA at the spatial scales of site (Si), station (St), locus (Lo) and core (Co) at two localities 900 m apart (L$_1$ and L$_2$) within the Dunwich seagrass beds.

Spatial scale	df	MS	Pseudo-F	P	UP	$\sqrt{EV}$
$Si_1(L_1)$	1	4073	1.16	0.32	3	3.2
$Si_2(L_2)$	1	6188	2.60	0.01	462	8.4
$St_1(Si_1)$	2	3514	1.55	0.16	8968	6.8
$St_2(Si_2)^a$	–	–	–	–	–	–
$Lo_1(St_1(Si_1))$	8	2265	1.37	0.05	9869	8.3
$St_2(Si_2)/Lo_2(St_2(Si_2))^a$	10	2378	1.64	0.004	9863	10.1
$Co_1(Lo_1(St_1(Si_1)))$	96	1649				40.6
$Co_2(Lo_2(St_2(Si_2)))$	96	1454				38.1
Total$_1$	107					
Total$_2$	107					

MS, mean square; UP, unique permutable units; EV, estimate of variance; the value of Co is given by the residual.
[a] The scale of station at the second locality was excluded from the final analysis, because it produced an 'illogical' negative EV in the preliminary run; data from the scales of station and locus at that locality were then pooled.
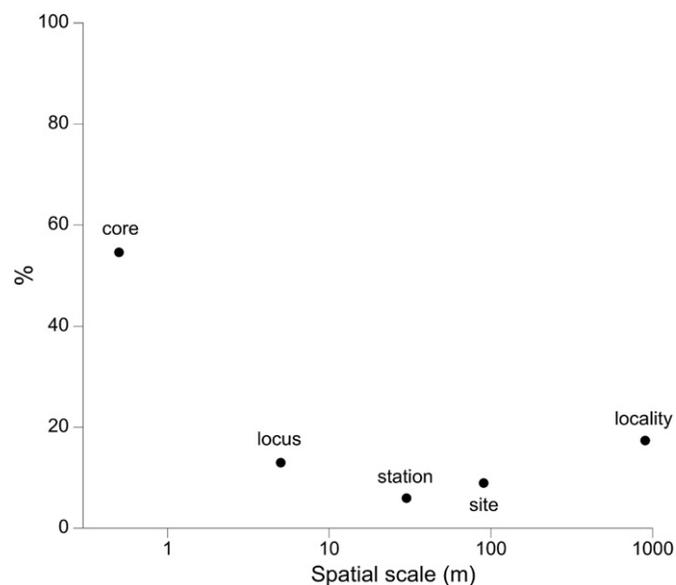

Fig. 4. Variance components as percentages of the total at various spatial scales <1 km within the Dunwich seagrass bed, showing overwhelming dominance of the component at 0.5 m. Distances along the X-axis are those between the centres of the nested sampling units stated. Components at the spatial scales of station, site and locality are not statistically significant.

The studies cited above have also investigated spatial changes in the nature of assemblage organisation over the same range of distance categories, finding in *Nanozostera noltii* beds in the North Sea and in those of *Nanozostera muelleri capricorni* at the present site that structure was random over distances of <150 m but strongly deterministic at larger scales (of 400 m at the North Sea site and 2 km in Moreton Bay) (Barnes and Ellwood, 2011b). The present study confirmed random assemblage organisation near Dunwich at small spatial scales, and showed no significant change in that organisation over the spatial scales at which variance components changed from significant to non-significant. Although the random nature of the Dunwich assemblages accords with Leigh's (1981) expectation that such a situation will prevail in low density systems, the observation that it extends over horizontal distances of up to 1 km is unexpected. Yet is very robust since not only consistent numbers of samples selected randomly from different spatial scales yielded that result, but so did increasing numbers of samples from loci to stations to sites across the two localities. This practice in itself may have been expected to lead to Type I errors and false reporting of deterministic species co-occurrence patterns (Fayle and Manica, 2010) but no such results were obtained. This suggests that the null model analyses are

Table 4
Stochasticity of assemblage structure of the species of target macrofaunal taxa at nested spatial scales of 0.5, 5, 30, 90 and 900 m within the intertidal seagrass bed at Dunwich: comparisons at each component spatial scale based on a fixed number (nine) of randomly selected core samples, comparisons at each scale being repeated ten times. Data presented are representative C-score indices derived from the observed pattern of species co-occurrence (C_{obs}) and the mean expected C-score index from randomised versions of the data (C_{sim}). No comparison produced a significant departure from randomness (see also Table 5).

Spatial scale	C_{obs}	C_{sim}	P
0.5 m	14.05	14.02	0.38
5 m	17.19	17.18	0.47
30 m	17.57	17.64	0.55
90 m	12.69	12.77	0.57
900 m	19.58	19.17	0.23

Table 5

Stochasticity of assemblage structure of species of the target macrofaunal taxa at nested spatial scales of 5, 30, 90 and 900 m, and from both localities combined, within the intertidal seagrass bed at Dunwich: comparisons of cumulative samples at increasing spatial scales. See Table 4 for symbols; in addition, '*n*' is the cumulative number of core samples in an analysis.

Spatial scale	C_{obs}	C_{sim}	n	P
5 m	10.78	10.72	9	0.23
30 m	15.32	15.34	27	0.51
90 m	17.57	17.64	54	0.55
900 m	39.58	39.17	108	0.23
Total data set	96.66	96.10	216	0.27

reflecting true randomness in species distributions at spatial scales of up to 1 km, and that these analyses are robust to the effects of sample size (Gotelli and Ulrich, 2011). In South African *Nanozostera capensis* beds, in contrast, faunal assemblages were deterministically structured at all spatial scales investigated down to 1 m (Barnes and Ellwood, 2011b). Subsequent studies at that South African site have also shown deterministic assemblage organisation there in association with the prevailing environmental gradients (Barnes and Ellwood, 2011a). At least visually, the Moreton Bay sites are much more spatially uniform and indeed the present samples were taken in such a manner as to avoid potential confounding variables such as environmental gradients of tidal height and shelter.

At spatial scales <1 km, at least insofar as represented by the target taxa, the surface and near-surface faunal assemblages of the intertidal seagrass beds near Dunwich are therefore patchily distributed, randomly organised, and most variable at spatial scales <5 m, although total abundance and species richness were relatively uniform across the whole study area. The prevalence of rare species and the low patchy density of the whole fauna will both tend to produce variable associations of species when sampled at small spatial scales. However, there is no reason yet to assume that other seagrass beds supporting much higher faunal densities will not also exhibit maximum variance at very small spatial scales. The ecologically equivalent but otherwise contrasting North Sea beds of *Nanozostera noltii*, for example, support a high density fauna (with densities some 25 times those at Dunwich) containing far fewer rare species, but components of variance there were also greatest at the smallest scale sampled (1 m) and Bray–Curtis similarity did not vary over the range 0.125–1 m (Barnes and Ellwood, 2011b). It may be relevant, however, that in these cool-temperate beds, unlike those at subtropical Dunwich, components of variance at larger spatial scales — 60 and 100 m — were also statistically significant and each contributed >25% of the total.

The non-deterministic nature of the Dunwich seagrass fauna suggests little turn-over of dominant species and provides no evidence of niche partitioning through space. In this these *Nanozostera muelleri capricorni* beds contrast markedly with the equivalent *N. capensis* beds in the marine outer basin of the Knysna estuarine bay in South Africa which form a high turn-over, strongly structured, very deterministic system (Barnes and Ellwood, 2011a). The present study did not seek to investigate the processes that might be responsible for the observed spatial scale of maximum assemblage variance, but there was no visible indication of matching habitat heterogeneity or change in its structural complexity at scales of <5 m, and it is perhaps unlikely that animals of the size of *Calopia* or *Pseudoliotia* are able to move over, to them, relatively huge distances to find and aggregate on particularly high diatom concentrations, although Coles (1979) showed that the larger rissooidean microgastropod *Hydrobia ulvae*, that also shows a patchy distribution in *Nanozostera* beds (Barnes and Ellwood, 2011b), will move into diatom-enriched areas of sediment from

over distances of several centimetres. Patterns are consonant, however, with localised input of recruits (Levinton and Kelaher, 2004; Boström et al., 2010) or heavy pressure from indiscriminate intra-sediment or epibenthic predators, as suggested earlier in respect of microgastropods at the site (Barnes, 2010b).

Spatial variation in this fauna is not just of academic interest. Seagrass systems harbour commercially important species and have effects on others in adjacent coastal seas (e.g. Vizzini, 2009). As elsewhere in the tropics and in respect of other animal groups as well (Fong, 1999; Schaffmeister et al., 2006), the mangrove-backed intertidal seagrass beds of Moreton Bay are important nursery areas for juvenile penaeid prawns (*Penaeus* and *Metapenaeus* spp.) (Masel and Smallwood, 2000; Skilleter et al., 2005), a resource of considerable local economic value (Williams, 2002; Manson et al., 2005). The small crustaceans and gastropod molluscs that occur in these beds, and generate the spatial patterns described above, are an important element in the diet of medium to large-sized juvenile penaeids (Wassenberg and Hill, 1987; O'Brien, 1994). Spatial variation in the nature of their food resources is then likely to have knock-on effects on such higher, and economically valuable, trophic levels.

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