

Spatial stability of macrobenthic seagrass biodiversity

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ABSTRACT: The magnitude and patchiness of macrobenthic biodiversity were compared across spatial scales spanning 5 orders of areal magnitude (ca. 2 m² to ca. 1.5 ha) in an intertidal seagrass bed in the warm-temperate Knysna estuarine bay, South Africa. The 75 component species and their populations were highly variably distributed across the site, abundances of the individual dominant animals being significantly patchy and composition of the macrofaunal assemblage being significantly non-uniform. Nevertheless, emergent assemblage attributes exhibited spatial constancy: values of assemblage metrics (faunal abundance, species richness, species density and species diversity) did not differ across the site or across spatial scales, and neither did the patterns of dispersion of species diversity, species richness or observed species density. Distribution of the 2 latter through space was even significantly uniform. Ecological arguments developed for temporal constancy of biodiversity seem broadly applicable to the spatial dimension at Knysna, suggesting that although apparently paradoxical, it may be the varying assemblage composition that permits this spatial stability. There is no evidence, however, that the Knysna seagrass macrobenthos is a competitively-structured assemblage with rigid niche-partitioning, a condition suggested to be necessary for temporal constancy; rather, it is more likely to be open, non-equilibrium and below carrying capacity.

KEY WORDS: Biodiversity · Patchiness · Macrobenthos · Seagrass · Spatial scales · Spatial constancy · Spatial stability

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INTRODUCTION

Attributes of assemblages of organisms are usually critically dependent on the spatial scale over which they are assessed (Wiens 1989, Turner et al. 1989, Harte et al. 2005). Indeed, the effects of spatial scale have been argued to be central to modern ecology (Levin 1992) and their understanding to form ecology's 'final frontier' (Liebhold et al. 1993, p. 303). This applies as much to small-scale patchiness as to other features (Grünbaum 2012, Dray et al. 2012), and as much to seagrass beds as to other habitats (Duffy 2006). Boström et al. (2006, p. 383), for example, concluded that stands of seagrasses are 'some of the most heterogeneous landscape structures of shallow-water marine/estuarine ecosystems in the world ...

[with] ... complex spatial configurations ... over broad (metres to kilometres) spatial scales'.

Most scale-related work on seagrass systems has been devoted to the effect of evident habitat patchiness on the distribution and abundance of the associated macrofauna (Bowden et al. 2001, Borg et al. 2010, Arponen & Boström 2012), although it is also clear that faunal patchiness across scales is commonplace even in non-fragmented seagrass meadows. For example, the spatial scale at which maximum variance in assemblage composition and structure occurs has been documented for a number of seagrass-bed components. These include epiphytes on the leaves of *Posidonia* spp. (e.g. Lavery & Vanderklift 2002, Balata et al. 2007), nektonic crustaceans and fish associated with *Posidonia* and *Zosterella*

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capricorni (McNeill & Fairweather 1993), and the benthic macrofauna of intertidal expanses of various *Zosterella* species (Barnes & Barnes 2011, Barnes & Ellwood 2011a, 2012a). Similarly to studies on faunal assemblages in other benthic marine habitats, e.g. unvegetated sediments and microalgal turfs (Olabarria & Chapman 2001), in nearly all cases it has been found that the variance component at the smallest studied spatial scale (i.e. down to ca. 1 m²) was the largest, although significant variation has been shown to occur at larger scales as well (Balata et al. 2007, Barnes & Ellwood 2011a). Moreover, it is not only the composition and structure of faunal and floral assemblages that are known to be scale dependent. Magnitudes and spatial variances of overall assemblage abundance and biodiversity have been shown to be affected by scale, albeit to date, only in non-seagrass habitats (e.g. Crawley & Harral 2001, Wang et al. 2008).

Earlier work on intertidal beds of dwarf-eelgrasses *Zosterella* spp., however, has suggested the possibility of a potentially dichotomous response of seagrass macrofaunal assemblage attributes to space. In classic fashion, absolute and relative composition of the faunal assemblages supported by *Zosterella* have been shown to vary markedly across small-scale space (i.e. linear dimensions of 0.5 to 100 m) and correspondingly the dominant species have also been demonstrated to have very patchy distributions at those scales (Barnes 2010, Barnes & Barnes 2011, Barnes & Ellwood 2011b, 2012a). Nevertheless, in marked contrast to the nature of the species populations collectively responsible for generating the attributes concerned, preliminary data on overall faunal abundance and species density of the assemblages associated with both South African *Z. capensis* and Australian *Z. capricorni* have indicated that little variation may occur in these metrics over the same spatial scales (Barnes & Barnes 2011, 2012, Barnes & Ellwood 2011b, 2012a), except in association with marked environmental gradients such as salinity (Barnes & Ellwood 2012b, Barnes 2013).

Although considerable information on the spatial variability of seagrass-associated assemblage composition is now available, including its variability across scales, data on the pattern of distribution of the emergent attributes of those assemblages are as yet very limited—too limited to permit determination of whether this apparent spatial constancy of overall form in spite of great variability of the component populations is real. The aim of the present study was therefore to ascertain in detail the extent to which emergent assemblage attributes of overall abun-

dance and biodiversity vary spatially in seagrass, and whether any effects are consistent across spatial scales from <50 m² to >1 ha. Further, this was specifically undertaken at a site at which it had previously been shown that macrobenthic faunal assemblage composition varied significantly through space (including across different spatial scales) and at which the dominant individual species showed patchy distributions (the ‘Steenbok Channel mouth’ site of Barnes & Ellwood 2011b).

MATERIALS AND METHODS

Study area

Spatial distribution of macrobenthic abundance and biodiversity was surveyed in the 5 ha intertidal seagrass bed in Kingfisher Creek Bay on the northern tip of Leisure Island in the warm-temperate Knysna estuarine bay, Garden Route National Park, Indian Ocean coast of the Western Cape, Republic of South Africa (Russell et al. 2012) (Fig. 1). This bed in the centre of Knysna’s marine outer basin is part of, and continuous with, the largest single area of seagrass (some 370 ha) in South Africa (Maree 2000, Barnes 2013). A visually uniform site was selected for study, straddling the mean low water tidal level and centred on 34° 03’ 39” S, 23° 03’ 09” E, where Cape dwarf-eelgrass, *Zosterella capensis*, was the sole seagrass species.

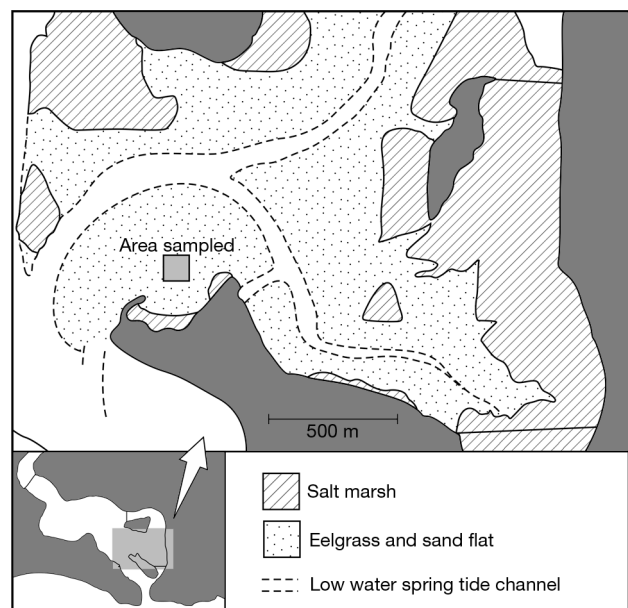


Fig. 1. The Knysna estuarine bay, Garden Route National Park, South Africa, showing the location of the sampling site

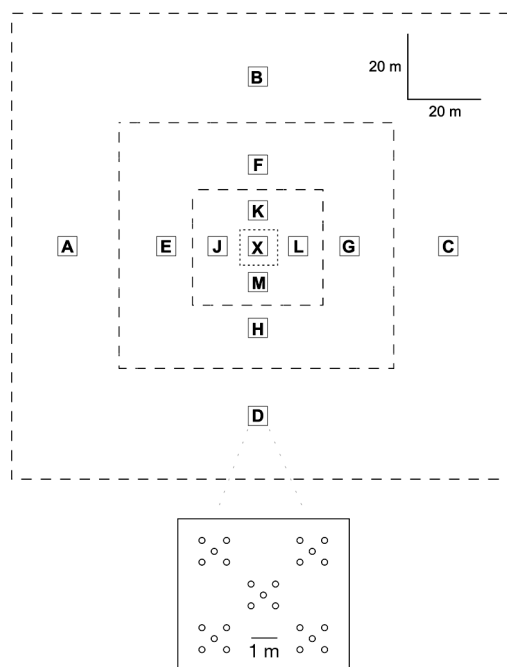


Fig. 2. Spatial layout of the 13 stations located within the sampling site, with a detail of the 5 blocks each of 5 core samples taken at each station. Line B–D is along longitude $23^{\circ} 03' 09.1''$ E, and line A–C is along latitude $34^{\circ} 03' 38.8''$ S

Protocol

Thirteen stations were established within the site over a 10 wk period during the 2013 austral summer, each sampled by 25 individual cores arranged quincuncially as 5 blocks of 5, as shown in Fig. 2. This layout was designed to achieve analysis at a series of nested exponentially-decreasing spatial scales spanning 5 orders of magnitude in area. For this purpose, the 4 stations ABCD in Fig. 2 were taken to represent an area of ca. $15\,000\text{ m}^2$, EFGH one of ca. $5\,000\text{ m}^2$ and JKLM one of ca. $1\,250\text{ m}^2$, whilst each of the 13 individual stations represents an area of ca. 50 m^2 and each of the 5 component core-blocks at each station one of ca. 2 m^2 . All stations were located in regions of dense 100% cover within a single sward of seagrass, to avoid potentially confounding variables such as percentage ground cover, patch size and proximity to edges (Irlandi 1994, Bowden et al. 2001, Tanner 2005).

Each core sample was of 54 cm^2 area and 10 cm depth, which previous studies at the site had suggested could be expected to yield an acceptable >50 animals per core block (Barnes & Ellwood 2011b). A 10 cm depth was deemed sufficient because most benthic macrofauna in seagrass beds occurs in the top few mm of sediment (e.g. 98% in the top 5 mm in

the study by Klumpp & Kwak 2005). This sampling procedure collects the smaller and most numerous members of the macrofauna that constitute the large majority of invertebrate biodiversity (Albano et al. 2011), though not the scarcer megafauna or deeply-burrowing species. All core samples were collected soon after tidal ebb from the area of shore concerned, and were gently sieved through $710\text{ }\mu\text{m}$ mesh on site. Retained material from each core (1) was placed in a large polythene bag of seawater within which all seagrass fragments were shaken vigorously to dislodge all but sessile animals and then discarded; (2) was then re-sieved and transported immediately to a local field laboratory, and (3) was there placed in a $30 \times 25\text{ cm}$ white tray in which the living fauna was located by visual examination, this continuing until no further animals could be seen during a 3 min period. Faunal individuals were identified to species and were counted. Sessile and mobile species can differentially influence spatial patterns of biodiversity (Davidson et al. 2004), and this study excluded any sessile or semi-sessile animals (e.g. *Halianthella annularis* and *Siphonaria compressa*) that had become detached from the seagrass leaves during sampling. All nomenclature is given as listed in the World Register of Marine Species (WoRMS, www.marinespecies.org; accessed May 2013).

Data analysis

Variation in composition of the macrofaunal assemblage across the site, and partitioning of its spatial variance components were assessed via PRIMER 6.1 (PrimerE: Plymouth Routines in Multivariate Ecological Research) using multivariate permutational analysis of variance (PERMANOVA) of S17 Bray-Curtis similarities with fourth-root transformed data and 999 permutations. Variability in global spatial structure and its scale dependence (sensu Cooper et al. 1997, Perry et al. 2002) was then assessed from values of various univariate assemblage metrics (Table 1) calculated for each of the 65 core-blocks using EstimateS 8.2.0 (Colwell 2011, Colwell et al. 2012). The N_2 diversity index was chosen because it does not partly duplicate species density, instead emphasising the dominance/evenness component of diversity (Magurran 2004). The Gini coefficient of inequality of species abundance was calculated using Wessa (2013), and normality was established by the Shapiro-Wilk test (Razali & Wah 2011).

Changes in magnitude of these assemblage metrics across the 3 larger spatial scales were assessed by

Table 1. Macrofaunal assemblage metrics calculated

Metric	Symbol	Notes
Abundance	N	Total number of individual animals per unit area
Observed species density	$S_{D,obs}$	Observed number of species per unit area
Estimated true species density	$S_{D,max}$	Mean of 3 disparate $S_{D,max}$ estimators: Chao-2, Michaelis-Menten mean, and Abundance-based coverage (see Colwell 2011), the latter with a set upper abundance limit of 5 individuals per sample for infrequent species
Species richness	S_R	Number of species per 50 individual animals, assessed after 100 randomization runs
Species diversity	D	Hill's (1973) N_2 (= the inverse Simpson index), yielding the linear 'effective number of species' to permit quantitative comparison (Jost 2006)

1-way ANOVA comparisons of the values from the 20 core-blocks comprising each group of 4 stations, where appropriate after $\log(x + 1)$ transformation. Local spatial dispersion in the same metrics was estimated via indices of patchiness. Several such have been proposed, of which Morisita's (1959) index of dispersion (I_d) and Lloyd's (1967) index of patchiness (I_p) have been most widely adopted (e.g. Malhado & Petreire 2004, Kristensen et al. 2006, Møller et al. 2010, Rindorf & Lewy 2012). These two, with that of Morisita in Smith-Gill's (1975) standardised format (I_m), were calculated for each assemblage metric at each spatial scale. In fact, the results showed values of Lloyd's I_p to be very closely correlated with those of Morisita's I_m for all metrics at all spatial scales (Pearson's $r > 0.8$; $p < 0.0001$) and only Morisita's I_m is reported in this study. Emergent assemblage attributes and indices dependent on relationships between means and variances (though not Morisita's I_m) may themselves be sensitive to total area and/or numbers of individuals sampled, as well as to features such as the occurrence of zero values (Hurlbert 1990, Bez 2000, Whittaker et al. 2001, Gotelli & Colwell 2001, Beukema & Dekker 2012). The locality selected was one that did not show significant spatial variation in assemblage abundance across the 13 stations (1-way ANOVA $F_{12,52} = 1.4$, $p > 0.2$), and the same fixed size and number of core samples (and therefore of total area sampled) was used to represent all spatial scales, except of necessity for the smallest of the 5 (that of ca. 2 m²). The data obtained included no zero scores for any assemblage metric assessed. To represent each of the 3 larger spatial scales, 1 of the 5 component core-blocks was randomly selected (using random numbers generated by www.random.org) from each of the 4 stations in the groups specified above, together with one from Stn X, to yield a unit analytical total of 5 core blocks; whilst for the ca.

50 m² scale all 5 core-blocks from each station comprised the same unit total. Given that the number of stations automatically provided a total of 13 replicates of all assessed patchiness indices at the ca. 50 m² spatial scale, random selection of 1 core-block per station at each of the 3 larger spatial scales was also replicated 13 times to create a balanced analysis. Unlike the other spatial scales, however, data on the ca. 2 m² scale could only be based on unit totals of 5 cores (i.e. those within a single core-block), and hence on considerably smaller samples. Further, the total number of faunal individuals obtained from each replicate at the scale of individual core sample (i.e. a minimum of 3) was deemed too small to permit realistic estimates of S_R (see Table 1 for definitions), whilst $S_{D,max}$ could only be derived from the mean of Chao-1 and Abundance-based coverage estimates. Data from the ca. 2 m² and from the 4 larger spatial scales are therefore only partly comparable, with those from the smallest scale being likely to be relatively variable (Barnes 2010, Barnes & Barnes 2011). For Morisita's I_m , 95% confidence limits for randomness lie between +0.5 and -0.5; values $> +0.5$ indicate significant patchiness, and those < -0.5 significant uniformity. As with mean values (above), variation across spatial scales in I_m was then detected using 1-way ANOVA, where appropriate after $\log(x + 1)$ transformation, followed by post-hoc Tukey HSD tests. Morisita's I_m was also used to test for departures from random of the dispersions of the individual species.

When divided by the number of sampling units, the diversity index D adopted here is also one of the indices of patchiness recommended by Payne et al. (2005). Since the number of units sampled was a constant, D provided an alternative measure of assemblage metric dispersion, independent of mean:variance relationships, and one relatively unaffected by samples with very few individuals (Payne et al. 2005).

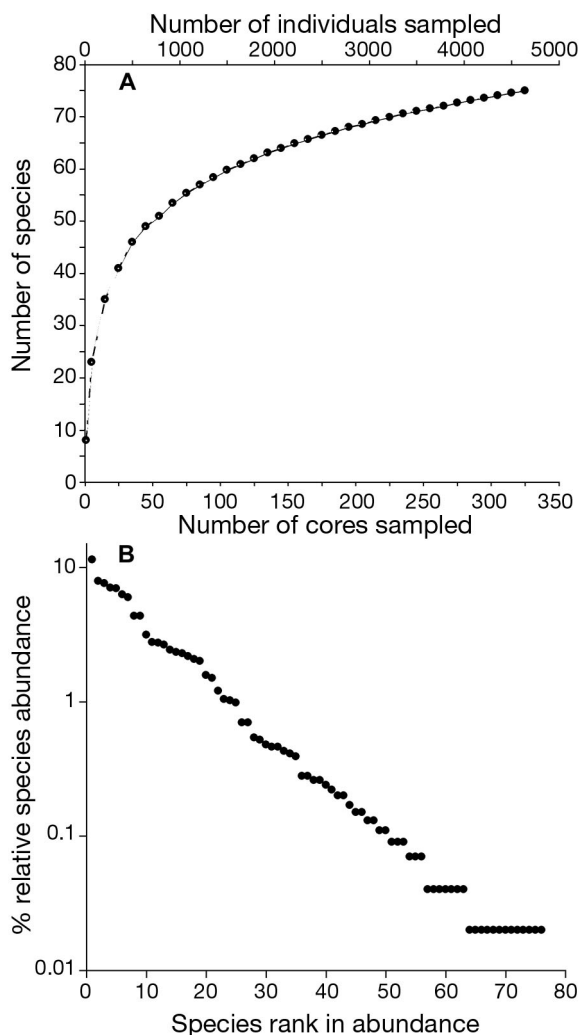


Fig. 3. Species abundance curves. (A) Mao Tau numbers of macrofaunal species in relation to cumulative number of individuals sampled, i.e. species richness, and to cumulative area sampled (as number of cores), i.e. species density. Sample accumulation order randomised 50 times. (B) Ranked species abundance curve

RESULTS

Overall, the sampled region of seagrass supported an observed total of 75 macrofaunal species (estimated true total 86) at a combined density of 2610 ind. m^{-2} . $N_2 \gamma$ species diversity was 18.9, and cumulative levels of species richness and species density were as displayed in Fig. 3A. Nine species each contributed more than 4% of faunal numbers, and together they comprised more than 60% of the total individuals (see Fig. 3B). These were the polychaetes *Prionospio sexoculata* (11.4%), *Caulleriella capensis* (7.0%) and *Simplisetia erythraensis* (7.0%), the amphipods *Melita zeylanica* (7.9%) and *Paramoera capensis*

(4.4%), the isopods *Exosphaeroma hylecoetes* (7.6%) and *Cyathura estuaria* (6.3%), and the brachyurans *Hymenosoma orbiculare* (6.0%) and *Danielita edwardsii* (4.4%). The Gini coefficient of inequality was 0.74. A Pearson correlation matrix of $\ln(x + 1)$ transformed data indicated that within this group of dominants there were only 2 positive associations (*Simplisetia* with *Caulleriella*, and *Exosphaeroma* with *Danielita*; $r > 0.33$, $p < 0.01$) together with 3 negative ones, all involving *Paramoera* (with *Simplisetia*, *Caulleriella*, and *Prionospio*; $r > -0.29$, $p < 0.02$).

As expected from the earlier study (Barnes & Ellwood 2011b), macrofaunal assemblage composition varied significantly across the site whether assessed at the level of station (PERMANOVA pseudo- $F = 3.1$, $p < 0.001$) or core-block (PERMANOVA pseudo- $F = 1.35$, $p < 0.001$). Most of this variation occurred between the individual core samples in a block, but over a third of the total variation occurred at the levels of core-block and station (Table 2). Levels of Bray-Curtis similarity between the 65 core-blocks were as low as 0.16 (mean 0.49; SE 0.002), and ranged down to 0.33 even within a single station, whilst those between the 13 stations showed a minimum of 0.37 (mean 0.64; SE 0.009). Correspondingly, 7 of the 9 most abundant species listed above occurred patchily across the 65 core-blocks (all $I_m > +0.501$, $p < 0.01$), even within a single station, although dispersions of the other two, *Cyathura* and *Hymenosoma*, did not depart from random ($I_m + 0.17$ and $+0.05$ respectively; $p > 0.2$). Assemblages in core-blocks within the same station showed greater Bray-Curtis similarity than those in comparisons across stations (means of 0.55 versus 0.49; 1-way ANOVA $F_{1,2078} = 45.5$, $p < 0.0001$) and also possessed slightly but significantly greater numbers of species in common (14.0 vs. 13.0; 1-way ANOVA $F_{1,2078} = 23.2$, $p < 0.0001$). This faunal patchiness was also reflected in the disparately-feeding taxa that were the most abundant ones in individual core-blocks. In some, these were microphagous

Table 2. Partitioning of spatial variance components across the site by nested PERMANOVA at the levels of station (S), core-block (B), and individual core sample (C) = residual. df = degrees of freedom, MS = mean square, \sqrt{EV} = estimate of variance, V = variance component as percentage of total

Spatial scale	df	MS	\sqrt{EV}	V (%)
S	12	8288	14.9	20.8
B(S)	52	2715	11.9	16.6
C(B(S))	260	2009	44.8	62.6
Total	324			

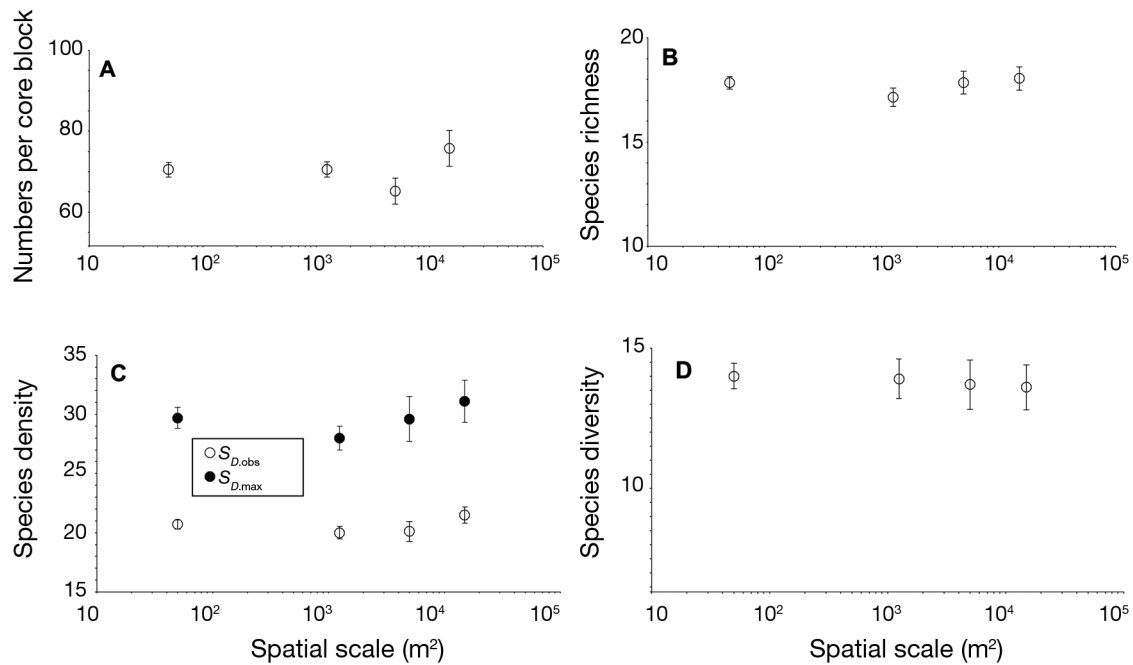


Fig. 4. Variation in mean magnitudes (\pm SE) per core-block of (A) faunal abundance, (B) species richness, (C) observed ($S_{D,obs}$) and expected ($S_{D,max}$) species density, and (D) species diversity, across the 4 larger spatial scales of ca. 15 000 m², ca. 5000 m², ca. 1250 m² (n = 20 in all 3) and ca. 50 m² (n = 65)

polychaetes (mainly in the form of palp-feeding *Caulleriella* and *Prionospio*, or more rarely the sub-surface sediment-ingesting *Euclymene*); in others, they were omnivorously-grazing amphipods (*Melita* and/or *Paramoera*) or the isopod *Exosphaeroma*. One core-block was dominated by decapod crustaceans. Such locally dominant taxa were either absent from various other core-blocks, however, or were present only as singletons.

Nevertheless, the magnitude per core-block of overall assemblage abundance, species richness, species density, and species diversity did not vary significantly across the 13 stations of the site (all 1-way ANOVA $F_{12,52} < 1.95$, $p > 0.05$; all Tukey test statistics < 4.16 , $p \geq 0.18$). Neither did any metric vary significantly across or in relation to the 3 larger spatial scales of ca. 15 000 m², ca. 5000 m² and ca. 1250 m² (assemblage abundance 1-way ANOVA $F_{2,57} = 2.38$, $p = 0.1$; other 4 metrics, 1-way ANOVA $F_{2,57} < 1.8$, $p > 0.2$; Spearman $r < 0.17$, $p > 0.22$). Granted that this was so, and also granted that the mean of the values of any metric across these scales is also the overall mean value of that metric per core-block, it follows that there will be no significant differences between the means of any metric across both those 3 larger scales and also the 2 smaller ones (ca. 50 m² and ca. 2 m²); i.e. between the mean values of any of the 5 metrics across all 5 spatial scales.

These mean values are displayed in Fig. 4. The reliability of these conclusions could not be affected by the potential occurrence of any positive spatial auto-correlation, in that its effect on ANOVA would be to increase the chances of Type 1 statistical errors (Dale & Fortin 2002), whereas no null hypotheses were in fact rejected. Overall, the 65 core-blocks supported mean metrics with small standard errors: $N = 70.5$ (SE 1.8), $S_R = 17.8$ (SE 0.3), $S_{D,obs} = 20.7$ (SE 0.4), $S_{D,max} = 29.7$ (SE 0.9) and $D = 14.0$ (SE 0.4); values of each of S_R , $S_{D,obs}$ and D not departing from normal distributions (Shapiro-Wilk $W = 0.96$ to 0.98 , $p > 0.06$) (Fig. 5). Thus, each core-block, for example, supported some 27% (SE 0.5%) of the site's total species pool. Although there was also no significant variation in any assemblage metric along the shore (all ANOVA $F_{6,58} < 1.0$, $p > 0.4$) or down it (all ANOVA $F_{6,58} < 2.1$, $p > 0.06$), there was a significant tendency for species density, though not species richness, to increase towards lower tidal levels (Spearman $r > 0.3$, $p < 0.02$), involving an overall increase in the mean observed density of 3.6 species over the 104 m from Stn D to Stn B.

Over the site as a whole (i.e. across all 65 core-blocks), the dispersion of values of N and $S_{D,max}$ per core-block bordered on significant patchiness (both $I_m = +0.500$), those of S_R and $S_{D,obs}$ were significantly uniform ($I_m = -0.519$ and -0.521 , respectively), whilst

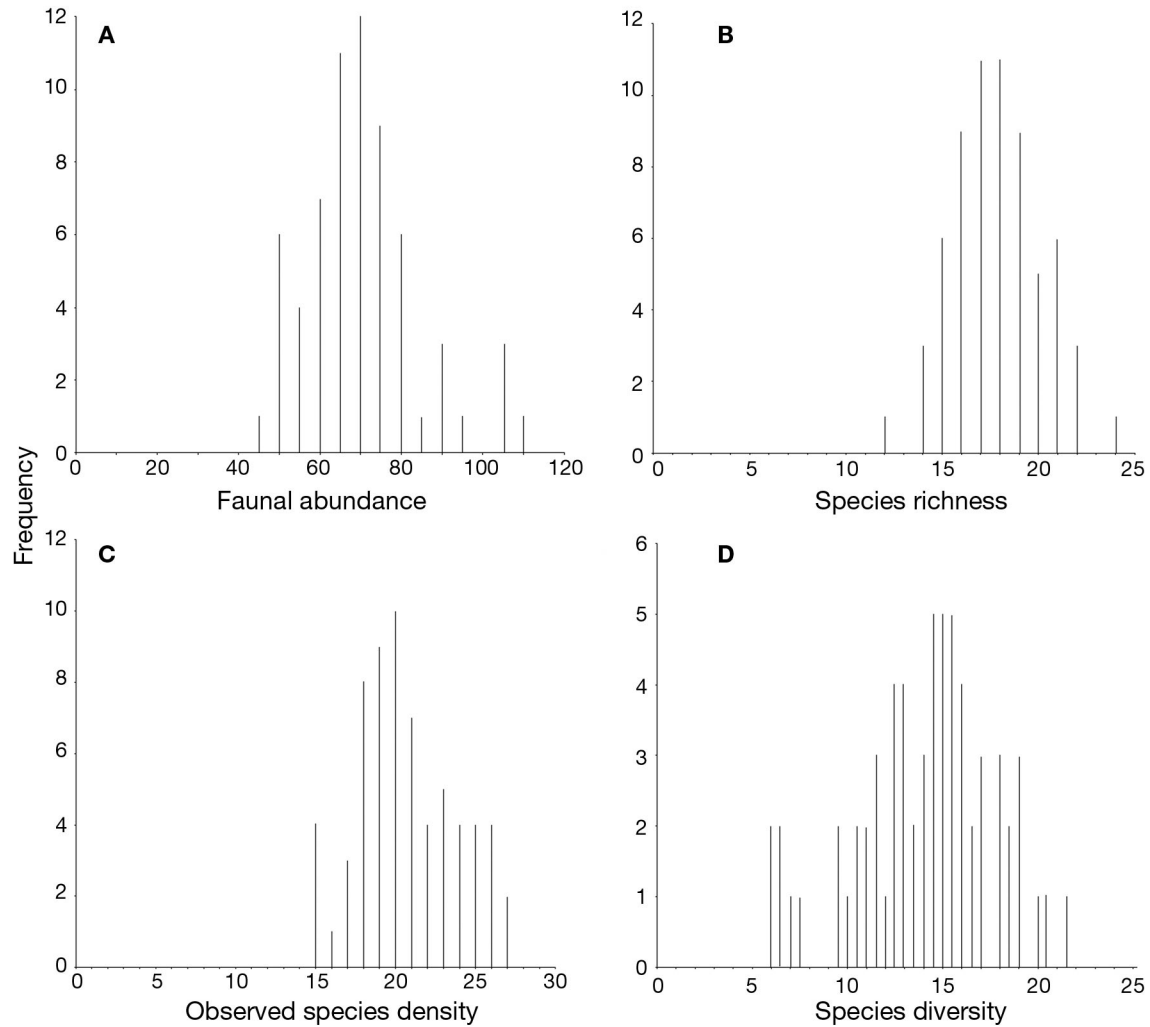


Fig. 5. Frequency distribution across the 65 core-blocks of the magnitude of (A) faunal abundance, (B) species richness, (C) observed species density, and (D) species diversity

those of D were random ($I_m = +0.01$). Values of I_m for the same 5 metrics across spatial scales are displayed in Fig. 6. Across scales, mean values of the dispersions of all metrics at all scales remained within the statistical bounds of randomness, although again those of S_R and $S_{D.obs}$ tended towards uniformity, whilst those of N and $S_{D.max}$ tended towards patchiness (Fig. 6). Excluding the strictly non-comparable data for the ca. 2 m² scale, there was no variation in I_m across spatial scales in respect of S_R , $S_{D.obs}$ and D (all ANOVA $F_{3,48} < 2.1$, $p > 0.1$), but there were significant differences in the dispersion of I_m for both N and $S_{D.max}$ (ANOVA $F_{3,48} > 3.9$, $p < 0.02$) in each case solely consequent on differences between the ca. 1250 m² scale and those at ca. 15 000 m² in the case of N (Tukey test statistic 6.11, $p < 0.001$) and those at ca. 5000 m² in the case of $S_{D.max}$ (Tukey test statistic 4.61,

$p = 0.01$). Variation at the level of the individual core sample was, however, extremely high—too high to permit realistic estimation of biodiversity metrics. Individual samples contained as few as 3 and as many as 39 individuals, with a coefficient of variation of 40%; cf. a difference factor of < 2 and a coefficient of variation of 21% at the scale of core-group. Nevertheless, dispersion about the means of the individual core samples at the ca. 2 m² scale did not differ from those between the core-blocks at the larger spatial scales except for that of $S_{D.max}$ at 1250 m² (Tukey $p = 0.001$).

The relationships between spatial dimensions and the means and dispersions of various of the assemblage metrics are summarised in Box 1. Lack of significant variation across spatial scales in D , when expressed as an index of patchiness (Payne et al.

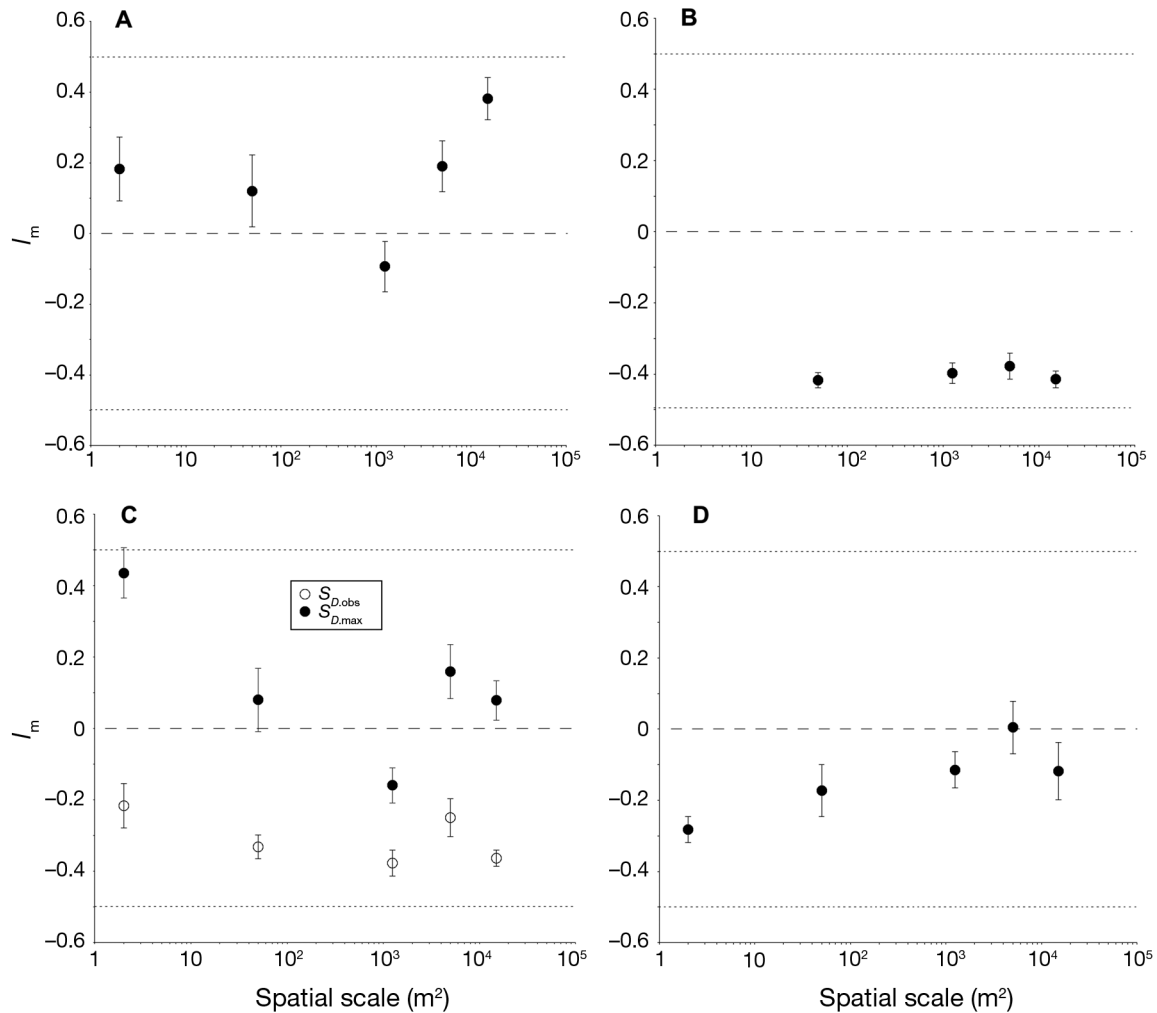


Fig. 6. Variation in standardised Morisita's index, I_m (mean \pm SE; $n = 13$), of the spatial dispersion of (A) faunal abundance, (B) species richness, (C) observed ($S_{D,obs}$) and expected ($S_{D,max}$) species density, and (D) species diversity, across the 5 scales of ca. 15000 m² to ca. 2 m². Note that the spatial scale of ca. 2 m² is represented by much smaller sized samples than those at the 4 larger scales

2005), also serves as independent evidence for spatial constancy of the dispersion of emergent assemblage properties independent of mean:variance relationships (ANOVA $F_{2,57} = 0.05$, $p = 0.95$).

DISCUSSION

Much research effort has been devoted to documenting and explaining small-scale spatial variation in aquatic abundance and biodiversity (e.g. Morrisey et al. 1992, Hewitt et al. 2005, Gallucci et al. 2009), but small-scale spatial constancy in assemblage biodiversity metrics has received almost no attention. However, its likely occurrence has not gone unno-

ticed. Downes et al. (1993), working on a river system in Victoria, Australia, found that although faunal densities (both overall and of individual species) varied substantially, species density and species richness of benthic invertebrates on stones did not change across spatial scales. Likewise, Payri et al. (2012) remarked on the lack of spatial variation in benthic algal species density around the ca. 1000 km rim of Baa Atoll in the Maldives, despite there being a large species pool.

In contrast, temporal stability of biodiversity has received detailed investigation (Pandolfi 1996, Brown et al. 2001, Clark & McLachlan 2003, Goheen et al. 2005). Analysing their long-term datasets of bird, rodent and fossil pollen biodiversity, Brown et al.

Box 1. Summary of spatial constancy in the magnitudes and dispersions of various assemblage metrics over the site as a whole and in relation to spatial scale within the site

- (1) Magnitude of (a) abundance, (b) species richness, (c) observed species density and (d) species diversity per core-block across the 13 stations
— NO SIGNIFICANT VARIATION
- (2) Variation in mean (a) abundance, (b) species richness, (c) observed species density and (d) species diversity per core-block with spatial scale or across or down the shore
— NO SIGNIFICANT DIFFERENCES
- (3) Dispersion of values of abundance per core-block across site
— BORDERLINE PATCHY
- (4) Dispersion of values of (a) species richness and (b) observed species density per core-block across site
— SIGNIFICANTLY UNIFORM
- (5) Dispersion of values of species diversity per core-block across site
— RANDOM
- (6) Variation across spatial scales in the levels of dispersion about mean (a) species richness, (b) observed species density and (c) species diversity per core-block
— NO SIGNIFICANT DIFFERENCES

(2001) concluded that number of species 'has remained remarkably constant despite large changes in composition. The results suggest that while species composition may be highly variable and change substantially in response to environmental change, species diversity is an emergent property of ecosystems that is often maintained within narrow limits' (p. 321). They also considered that, again with respect to temporal constancy, 'regulation of species richness ... within relatively narrow bounds despite substantial turnover in species composition is a frequent but not universal phenomenon' (p. 325). The present results clearly accord with this interpretation, although here within a spatial context: emergent assemblage attributes did not vary statistically through space, yet the component populations and species did. The dispersion of species richness and observed species density across the site even showed significant uniformity. The conditions that Brown et al. (2001) and Goheen et al. (2005) have posited as being necessary for such biodiversity constancy to occur, paraphrased here for the spatial dimension, were (1) relatively constant overall resource availability but spatially variable habitat conditions; (2) the presence of regional and local species pools capable of (a) providing potential re-colonists, of (b) exploiting between them all the resource spectrum and of (c) withstanding all likely local environmental

conditions; and (3) that persistent structural relationships ('assembly rules') of the type proposed by Diamond (1975) (see McGill et al. 2007) determine how resources are apportioned among the component species. They further argued that number of species can remain relatively constant because the assemblage reacts to change in its habitat through changes in its composition, not only in the relative abundance of those species present at any one location but through exchanges with the wider species pool of the metacommunity of which any area in question is part. Hubbell (1997) has also stressed how even small migration rates could stabilise assemblages. In other words, the constant biodiversity yet a fluctuating faunal assemblage is not a paradox; the latter may be necessary to attain the former. Biodiversity can provide 'biological insurance' (Loreau et al. 2003, de Mazancourt et al. 2013). Fluctuating local dynamics have also been suggested to be at least partly responsible for the persistence of seagrass itself: Yamakita et al. (2011), studying a comparable 1 km² *Zostera* + *Zosterella* seagrass system in Tokyo Bay over a period of 26 yr, considered that the asynchronous local changes that occurred in different areas of the site may have contributed to the long-term temporal stability of the bed as a whole.

In the specific context of the Kingfisher Creek Bay seagrass bed, there is no reason to expect overall carrying capacity markedly to vary spatially (i.e. condition 1 above) (although carrying capacity is unlikely to be attained, see below), and granted the size and interconnected nature of the Knysna seagrass system as a whole, there is no reason why the fauna should not be capable of rapidly dispersing to, and hence if appropriate re-colonising, any individual local areas (condition 2a). Further (re: condition 2b), the total macrobenthic faunal pool (which for the seagrass beds in Knysna's marine outer basin is some 130+ species; Barnes 2013 and unpubl. data), although being describable as largely a guild of detritus/microphytobenthos feeders (plus associated predators), is a taxonomically and ecologically disparate assemblage likely to be able to utilise a wide range of seagrass-associated resources (Duffy et al. 2003, Moore et al. 2004, Heck & Valentine 2006). No 2 of the 18 species present at the site in mean densities of >50 m⁻² could be described as being ecologically equivalent. Those most similar in ecology were probably the cirratulid *Caulleriella* and the spionid *Prionospio*, both being of the same size range and collecting food at or just above the sediment surface using a pair of elongate ciliated palps (Fauchald & Jumars 1979, Dauer et al. 1981).

Indeed, the 2 species occurred together in >90% of core-blocks (and were either jointly present or jointly absent from 59% of individual core samples). Hence they are probably the most likely candidates to be sufficiently similar in their food and habitat requirements potentially to compete interspecifically. There was, however, no evidence of such interaction and no inverse relationship between numbers of the 2 ($r = 0.11$, $p > 0.4$).

It is relevant here, as well as to the applicability of persistent assembly rules to the site (condition 3 above), that it is unlikely that the Knysna seagrass fauna is structured by competition for either food or space. Barnes & Ellwood (2011b, 2012a) found intertidal *Zosterella* assemblages in both Knysna and Moreton Bay, Queensland, to be randomly structured over spatial scales of up to 900 m except along clear habitat gradients, with no evidence of niche partitioning. There are insufficient data to permit valid comparisons of intertidal productivity of *Zosterella* species across latitudes, although the limited data tabulated by Duarte & Chiscano (1999) suggest that it may be smaller in temperate *Z. noltei* than in lower latitude *Z. capricorni*, although only by a factor of 2. On the other hand, the abundance of the benthic macrofauna of sedimentary shores is often very much greater at latitudes of 40 to 60° than it is at <40° (Ricciardi & Bourget 1999). Overall densities of the animals dominating this Kingfisher Creek Bay site, as well as those in the intertidal *Z. capricorni* meadows of southern Queensland at 27°S (Barnes & Barnes 2012), were only some 5% of those of the (equivalently-sized) species that inhabit the comparable *Z. noltei* meadows at 44 to 52°N (Blanchet et al. 2004, Barnes & Ellwood 2011a). Even in high latitudes (Moksnes et al. 2008), although much more so in lower ones (Lewis & Anderson 2012), it is top-down control (e.g. by the juvenile fish and crustaceans using the meadows as nurseries; Heck et al. 2003, Verweij et al. 2006) that is thought to limit the abundance of epifaunal and infaunal seagrass invertebrate populations. The assemblage at Knysna thus appears to comprise a suite of essentially complementary species (sensu Loreau 2000) exploiting subtly or overtly different resources at levels below carrying capacity. The precise members of the local species pool that dominate the system are also temporally as well as spatially variable in that a somewhat different suite was recorded there during the same season 2 yr earlier (Barnes & Ellwood 2011b). *Prionospio*, amphipods and brachyurans were then less abundant whilst *Simplisetia* and *Orbinia* were more so (although it is relevant to the above to note

that *Caulleriella* numbers were unchanged). Although located in the outer basin of the Knysna embayment in which salinity usually exceeds 33 (Largier et al. 2000), the site lies at the mouth of an estuary, and during the floods that occur on average once every 10 to 12 yr (Day et al. 1951) salinity there can drop temporarily to almost freshwater levels, particularly during low tide. Which species are locally dominant at any one point in space and/or time may therefore have a large stochastic element.

The ranked species abundance curve shown in Fig. 3B is clearly of the linear form characteristic of both Motomura's (1932) geometric (log) series and of Tokeshi's (1990) random-assortment models (see also Hubbell 1997), with a value of k equal to 0.1. A geometric-series curve has been taken to indicate niche apportionment through pre-emption, particularly in harsh environments (Whittaker 1965), and the assemblage's relatively high Gini coefficient is potential evidence of environmental stress (Wittebolle et al. 2009). In contrast, the Tokeshi and Hubbell models are essentially dynamic and stochastic. These would seem particularly relevant in that under them species carve out their own niches independently of others and species abundances are not mutually related, which appear apt descriptors of the Knysna seagrass assemblage both spatially and temporally. The characteristics of this seagrass site and species pool would therefore seem in some measure to conform to those postulated as necessary to achieve temporally stable levels of biodiversity. However, assembly 'rules' are by nature deterministic (Belyea & Lancaster 1999), and there is little to support the operation of strict competitively-induced niche partitioning at Knysna. Insofar as the mechanisms really are distinct (Hubbell 2001, Weiher et al. 2011), the evidence from the Knysna seagrass suggests that more open, non-equilibrium, dispersally-influenced stochastic processes can achieve the same end, provided that the overall resource spectrum remains unchanged. Indeed Loreau & de Mazancourt (2013) argue that, contrary to much received wisdom, interspecific competition has a destabilising influence on assemblages.

Whatever the processes structuring the macrofaunal assemblages at Knysna are, spatial constancy is almost certainly not just an aberrant feature of the local South African intertidal zone. The data obtained by Barnes & Barnes (2011, 2012), working on seagrass beds near Dunwich in Moreton Bay, subtropical Australia (another large and continuous seagrass system, though dominated by a different *Zosterella* species), suggest that it is likely that

exactly the same situation occurred there. Each individual Dunwich seagrass station supported the same proportion ($21.5 \pm 1.1\%$) of the observed total fauna of 160 species. The prediction of Brown et al. (2001), cited above, that the phenomenon is a frequent one may well therefore apply spatially as well. In Moreton Bay, however, the seagrass assemblages showed a ranked species abundance curve of different form (Barnes & Hamylton 2013), being of the markedly concave type seen in a number of other benthic marine invertebrate systems (Hughes 1984), including the high-latitude *Z. noltei* stand referred to above (R. S. K. Barnes unpubl. data). Whether this is because of the operation of somewhat different assembly processes at these sites (e.g. as in the population dynamics models of Hughes 1984) is not at present known.

The conclusion of this study is therefore that constancy of biodiversity yet variability of assemblage components can occur not just temporally, but that it can be manifested spatially as well. The study also supports the notion that biodiversity metrics such as species richness and species density are dependent emergent features of faunal assemblages that can be maintained within narrow limits by dynamic ecological local and metacommunity processes. To a degree the same might apply to species diversity, although Magurran & Henderson (2010) have pointed out that species diversity metrics are by their nature insensitive to change. Disturbance of those ecological processes, however, whether natural or as is increasingly the case anthropogenic—including at the Knysna site trenching for bait worms—will lead to loss of biodiversity, such as has happened at the other major Western Cape seagrass site at Langebaan on the Atlantic coast (Pillay et al. 2010). Of particular concern must be the current widespread loss or fragmentation of seagrass systems (Reed & Hovel 2006, Yeager et al. 2011) which will result in impairment of dispersal pathways, especially for species with direct development which include the amphipods and isopods, and many of the gastropods, that are such important components of benthic seagrass assemblages.

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